New observations on scleractinian corals from Indonesia: 2. Sipunculan-associated species belonging to the genera *Heterocyathus* and *Heteropsammia*

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Three Indonesian species of *Heterocyathus* and two of *Heteropsammia* are briefly diagnosed. Remarks are given on their synonymy, phenotypic variation, and ecology. All five species are found on soft substrata in the proximity of coral reefs and live in association with a sipunculan worm. This interspecific assocation is discussed with regard to whether it is mutualistic or parasitic.

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Introduction

Corals of the Indo-Pacific scleractinian genera *Heterocyathus* Milne Edwards & Haime, 1848, and *Heteropsammia* Milne Edwards & Haime, 1848, live unattached on soft substrata in association with a sipunculan worm in the proximity of coral reefs. The worm, previously known as *Aspidosiphon jukesi* Baird, 1873 (Rice, 1976; Saiz Salinas, 1986), a junior subjective synonym of *A. muelleri* Diesing, 1851 (Cutler & Cutler, 1989), maintains the coral in an upright position and is even able to move it around (Feustel, 1966; Goreau & Yonge, 1968; Yonge, 1975). Despite their remarkable superficial resemblance in morphology and life history, the two coral genera are classified in separate families, and even in different suborders (Wells, 1956): *Heterocyathus* in the family Caryophylliidae (suborder Caryophylliina) and *Heteropsammia* in the family Dendrophylliidae (suborder Dendrophylliina). Their similarity in sipunculan-scleractinan association is a striking example of convergent co-evolution.

The coral larvae usually settle on gastropod shells that are already occupied by the worm (Feustel, 1966: fig. 5). Bore holes indicate that many of the shells become available after the mollusks are killed by predatory snails. Because there are sufficient empty shells (Feustel, 1966: fig. 6), there is no reason whatsoever to assume that the worm itself bores through the shell (as suggested by the erroneous translation by Yonge, 1975). Occasionally, corals on scaphopod shells can be found (Fowler, 1890: 414; Felix, 1913: 332, pl. 27 fig. 9; Eguchi, 1968: pl. C4 fig. 1, pl. C27 figs. 12-14).

The hosting corals may be infested by boring organisms as well, such as sponges, date mussels and polychaete worms (Schindewolf, 1958; Arnoud & Thomassin, 1976). The sipunculan worm may have to share its cavity with small bivalves, copepods and ascothoracican crustaceans (Bouvier, 1895; Bourne, 1906; Cutler, 1965; Rice, 1976; Grygier, 1981, 1985, 1991; Zibrowius & Grygier, 1985), whereas epibiontic polychaetes and barnacles may be found on the coral surface (Schindewolf, 1958; Zann, 1980).

Specimens of *Heterocyathus* and *Heteropsammia* can be observed in assemblages with other free-living corals, such as *Trachyphyllia geoffroyi* (Audouin, 1826), *Cynarina lacrymalis* (Milne Edwards & Haime, 1848), and some species of Fungiidae (Salvat, 1964; Goreau & Yonge, 1968; Guérin-Ancey, 1970; Scheer, 1971; Pichon, 1974; Gill & Coates, 1977; Fisk, 1983; Best & Hoeksema, 1987; Best et al., 1989; Chardy et al., 1988; Nishihira & Poung-In, 1989). In Indonesia, mixed assemblages of *Heterocyathus* and *Heteropsammia* were most frequently found in congregations with several *Fungia (Cycloseris)* species, for example in Teluk Slawi, a sheltered bay at Komodo (Best et al., 1989; Hoeksema & Moka, 1989), and around the offshore patch reefs of SW Sulawesi (Hoeksema, 1990). They were observed in large aggregations on soft substrata below the reef slopes, at depths varying between 15 and 40 m. The brown colour of living animals is due to the presence of zooxanthellae (see also Yonge, 1975). They are therefore considered reef-associated or hermatypic (Goreau & Yonge, 1968), whereas they also can be sampled at greater depths, e.g. 50-100 m (Zou et al., 1988). Schuhmacher & Zibrowius (1985: table 1) classify *Heteropsammia michelini* Milne Edwards & Haime, 1848 (= *H. cochlea* Spengler, 1781) as both zooxanthellate and non-zooxanthellate, but also as ahermatypic, i.e. not occurring on reefs.

Identification of the Indonesian representatives of *Heterocyathus* and *Heteropsammia* used to be problematic because many nominal species have been described, including fossil ones, whereas no taxonomic revision is available. By using original descriptions, illustrations and type specimens (those available to us are mentioned specifically in the text), nominal species are referred to in preliminary synonymies of the Indonesian species, or otherwise mentioned separately in the discussions on the genera.

This is the third systematic paper dealing with Indonesian free-living reef corals. Material was collected during the Siboga Expedition (1899-1900), Danish Expedition to the Kei Islands (1922), Snellius Expedition (1929-1930), Alpha Helix Expedition (1975), Rumphius IV Expedition (1980), Snellius-II Expedition (1984), and the Buginesia Project in SW Sulawesi (1984-1986). The two previous publications concern some Faviina (Best & Hoeksema, 1987) and Fungiidae (Hoeksema, 1989).

Key to Indonesian species of *Heterocyathus* and *Heteropsammia*

1. Corallum wall with distinct costae; original substratum (shell) frequently clearly visible .... **(*Heterocyathus*) 2.**
- Costae consisting of indistinct, wavy, granulate rows; original substratum usually overgrown by the coral .... **(*Heteropsammia*) 4.**
2. Calicular centre usually white; corallum either flat or high (columnar) .... 3.
- Calicular centre (and occasionally other parts of corallum) black or dark brown; corallum compact and columnar .... ***Heterocyathus sulcatus***
3. Septa of lower order cycles more exsert than others and distinctly radiating outside the periphery of the corallum wall .... ***Heterocyathus alternatus***

- Adjacent septa more or less equal in size and densely packed .... ***Heterocyathus aequicostatus***
4. Adult corallum with a single calice, which is either round or elliptical, or having an 8-shaped outline .... ***Heteropsammia cochlea***
- Adult corallum with at least two distinct calices .. ***Heteropsammia eupsammides***

Taxonomic account

Suborder **Caryophylliina** Vaughan & Wells, 1947
Family **Caryophylliidae** Gray, 1847
Subfamily **Caryophylliinae** Gray, 1847

Heterocyathus Milne Edwards & Haime, 1848

Type species: *Heterocyathus aequicostatus* Milne Edwards & Haime, 1848, by subsequent designation (Milne Edwards & Haime, 1850).

Heterocyathus Milne Edwards & Haime, 1848a: 323-324; 1850: xv; 1851a: 25; 1857: 51; Duncan, 1884: 24; Gardiner, 1904: 104; Harrison, 1911: 1021-1026; Folkeson, 1919: 6-8; Faustino, 1927: 83; Sakakura, 1935: 182-183; Yabe & Eguchi, 1942: 127; Vaughan & Wells, 1943: 207; Wells, 1956: F424; Eguchi, 1968: C36; Cheng, 1971: 2; Ditlev, 1980: 82; Boshoff, 1981: 37; Scheer & Pillai, 1983: 157; Zibrowius & Grygier, 1985: 121; Wells, 1986: 31; Chevalier & Beauvais, 1987: 741, fig. 515.III.2.

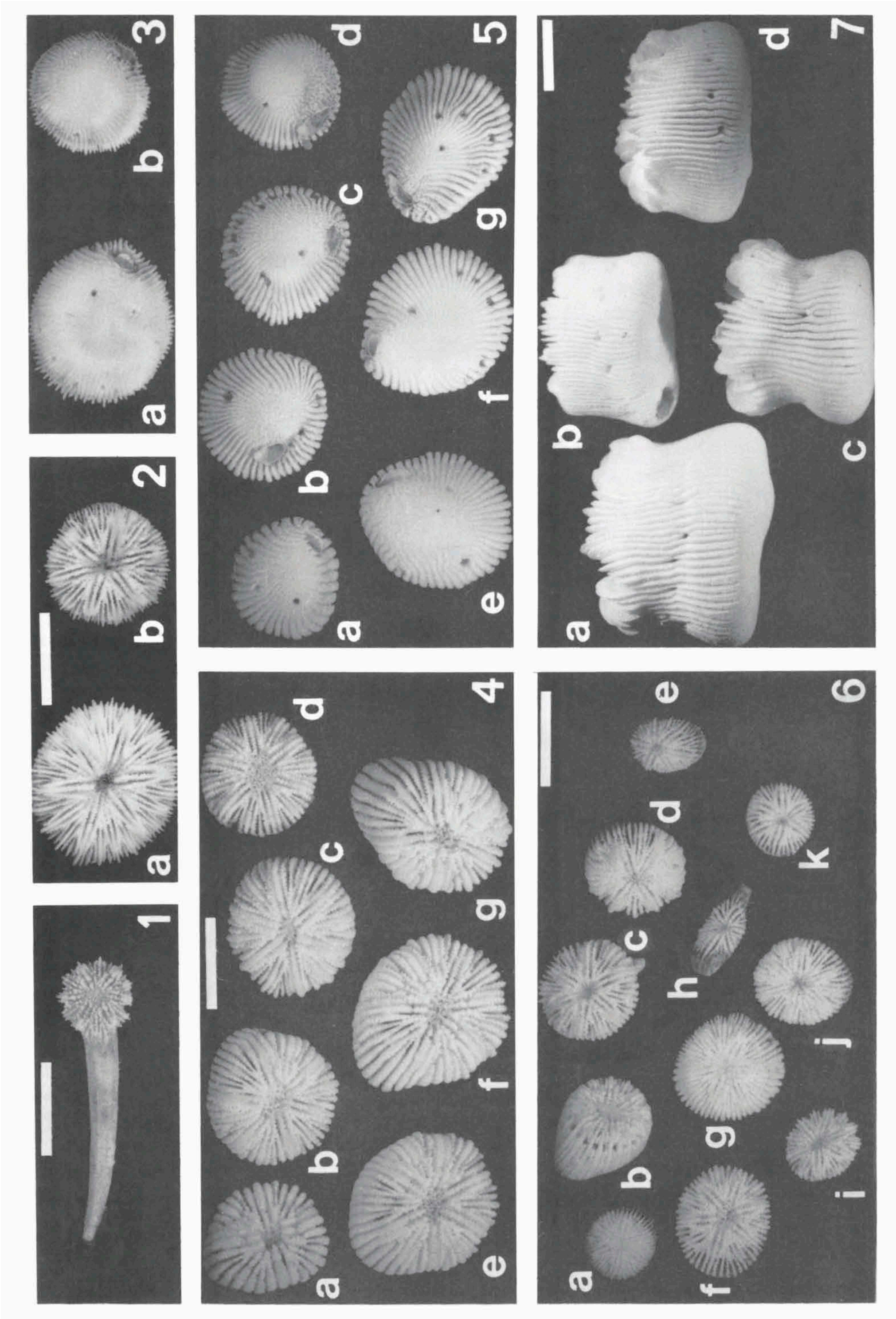
Stephanoseris Milne Edwards & Haime, 1851a: 127; 1851b: 116-117; 1860: 56-57; Duncan, 1884: 153; Vaughan, 1905: 415-416; Wells, 1986: 61. (Type species *Heterocyathus roussaeanus* Milne Edwards & Haime, 1848, by monotypy).

Psammoseris Milne Edwards & Haime, 1851a: 127; 1851b: 116; 1860: 55-56; Tenison-Woods, 1879: 8-10; Duncan, 1884: 152; Gardiner, 1905: 933; Vaughan, 1905: 417; Vaughan & Wells, 1943: 238; Wells, 1956: F436; Veron, 1986: 610; Wells, 1986: 54. (Type species *Heterocyathus hemisphaerica* Gray, 1849, by monotypy; in original genus description cited as "*Heterocyathus hemisphericus* Gray, 1850").

Spongiocyathus Folkeson, 1919: 11; Wells, 1986: 60. (Type species *Spongiocyathus typicus* Folkeson, 1919, by monotypy.).

Diagnosis.— Corals free-living. Costae at lateral sides are distinct and either equal or unequal in thickness. At aboral side costae transform into a cluster of more or less evenly distributed granulations. Lower part of each corallum shows a relatively large worm opening (occasionally two) and several small pores. Original substratum (usually a gastropod or scaphopod shell) either visible from the outside or completely overgrown by coral.

Remarks.— A discussion on the synonymy of *Heterocyathus* with regard to *Stephanoseris* and *Psammoseris* was given by Folkeson (1919). In addition, he established the genus *Spongiocyathus*, which according to him shows a striking resemblance to *Heterocyathus* except for the septa of the former, which appear to have a "marked spongious consistence". Since it is not unusual for coral species to show either solid or porous septa, we do not consider this an important distinguishing character. For an illustration of this, see e.g. Veron's (1986: 610) illustration of the coral he identified as *Psammoseris hemispherica*. In the literature, *Spongiocyathus* has not been mentioned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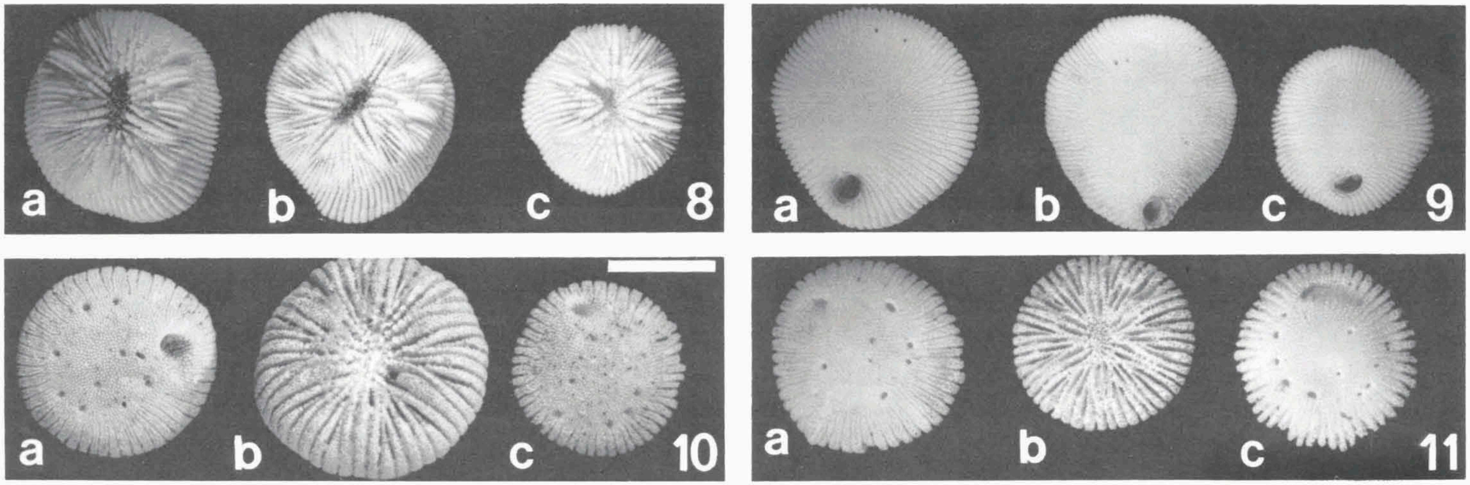


Figs. 1-11. *Heterocyathus equicostatus* (scale bars: 0.5 cm). Fig. 1. Small coral on scaphopod shell; Kei Is. (RMNH 18245). Figs. 2-3. Small, column-shaped specimens; SW Sulawesi, Langkai I., 30 m deep (RMNH 18232). Figs. 4-5. Slightly larger specimens; SW Sulawesi, Barang Caddi, 27 m deep (RMNH 18228); pores at aboral side or higher. Fig. 6. Small specimens from SW Sulawesi, Lankai I.; RMNH 18233); (h) original substratum still visible. Figs. 7-8. Large, columnar corals from Komodo I., Slawi Bay (RMNH 18234); pores above aboral side. Figs. 10-11. Round, flat corals from NW Java (RMNH 18220, 18223); pores at aboral side.

further, except by Vaughan & Wells (1943) and Wells (1956, 1986), who placed it in the synonymy of *Psammoseris*, a genus they erroneously classified with the Dendrophylliidae. Perhaps they did this because several authors considered this genus and *Stephanoseris* to be related to the dendrophylliid genus *Heteropsammia* (Moseley, 1881; Von Marenzeller, 1888; Vaughan, 1905; Folkeson, 1919). According to Vaughan & Wells (1943) a difference between *Psammoseris* and *Heteropsammia* is the lack of lateral perforations in the former. However, the specimens originally classified in *Psammoseris* are flat, which may explain why the perforations (or pores) from the sipunculan tube may be seen at the lower side of the corallum (figs. 10-11), instead of from a lateral view (fig. 7).

In the present study, we distinguish three Indonesian *Heterocyathus* species, which are all monostomatous, i.e. *H. aequicostatus* Milne Edwards & Haime, 1848; *H. alternatus* Verrill, 1865; and *H. sulcatus* (Verrill, 1866). Additional Recent *Heterocyathus* species that occur outside Indonesia are not known to us.

Stephanoseris exarata is a name cited by Fowler (1890: 418), which, together with some unpublished names, was given by Brüggemann to specimens in The Natural History Museum [the former British Museum (Natural History)]. It therefore has to be considered a *nomen nudum*.

Heterocyathus aequicostatus Milne Edwards & Haime, 1848 (figs. 1-11)

Heterocyathus aequicostatus Milne Edwards & Haime, 1848a: 324, pl. 10 fig. 8 (locality unknown); 1857: 51; Alcock, 1893: 141; Bouvier, 1895: 10; Gardiner, 1904: 105-112, 125 (partim), pl. 3 figs. 1-11, 22-32, 39-43; 1905: 955; Bourne, 1905: 193-194, 213-226, pl. 3, pl. 4 figs. 12-21; Harrison & Poole, 1909a: 898-899, pl. 85 figs. 1a-f; 1909b: 913; Harrison, 1911: 1026, pl. 58 fig. 12; Folkeson, 1919: 8-10 (partim), pl. 1 figs. 8-9; Faustino, 1927: 83-87, pl. 8 figs. 1-7; Yabe & Eguchi, 1932b: 443; Sakakura, 1935: 185-186, pl. 5 figs. 10-11; Gardiner & Waugh, 1938: 186-187; Umbgrove, 1938: 265; Eguchi, 1941a: 417; Yabe & Eguchi, 1941a: 213, figs. 6a-b; 1941b: 270, figs. 3-4; 1942: 127; Vaughan & Wells, 1943: pl. 41 fig. 17; Umbgrove, 1946: 88; 1950: 643; Durham & Barnard, 1952: 87-88, pl. 11 figs. 49a-d; Schindewolf, 1958: pl. 2 fig. 6; Eguchi, 1968: C36-C37, pl. C28 fig. 1, pl. C29 figs. 8-9; Pichon, 1974: fig. 6; Ditlev, 1980: 82-83, fig. 360; Wijsman-Best, Faure & Pichon, 1980: 620; Boshoff, 1981: 37; Scheer & Pillai, 1983: 158, pl. 36 fig. 9; Wells, 1984: 310, fig. 4.1; Zibrowius & Grygier, 1985: 121; Pillai, 1986: 188; Veron, 1986: 558-559 (partim); Hu, 1988: 146, 147, pl. 3 figs. 9, 12-13, 16-17; Nishihira, 1988: 221; Nishihira & Poung-In, 1989: fig. 2.

Heterocyathus roussaeanus Milne Edwards & Haime, 1848a: 324-325, pl. 10 figs. 9-9a ("Habite Zanzibar"); Vaughan & Wells, 1943: pl. 41 figs. 16-16a; Schindewolf, 1958: pl. 2 figs. 1-5, pl. 3 figs. 7-9, pl. 6 fig. 8, pl. 7 fig. 7; Feustel, 1966: fig. 2.

Heterocyathus cochlea; Gray, 1849: 77, pl. 2 figs. 1-2a; 1850: 410.

Heterocyathus hemisphaerica Gray, 1849: 77, pl. 2 figs. 3-4 ("Hab. Chinese Seas"); 1850: 410. **Syn. nov.**

Psammoseris hemispherica; Milne Edwards & Haime, 1851a: 127; 1851b: 116; 1860: 56; Veron, 1986: 610.

Stephanoseris rousseaui; Milne Edwards & Haime, 1851a: 127; 1851b: 117; 1860: 57.

Stephanoseris lamellosa Verrill, 1865: 149 ("Loo Choo Islands" = Ryukyu Is., Japan); 1866: 46-47, pl. 2 figs. 4-4a; Vaughan, 1905: 416. **Syn. nov.**

Stephanoseris japonica Verrill, 1866: 47-48 ("Kagosima, Japan"); Vaughan, 1905: 416. **Syn. nov.**

Heterocyathus philippinensis Semper, 1872: 254 (partim), pl. 20 figs. 13-14 ["Pandanon (Westküste von Bohol)", Philippines]; Eguchi, 1941a: 414.

Heterocyathus philippensis; Semper, 1881: (partim) figs. 87a-a' (wrong spelling).

Heterocyathus japonicus; Von Marenzeller, 1888: 17; Yabe & Eguchi, 1942: 127-128, pl. 11 figs. 6a-b; Eguchi, 1968: C37, pl. C4 fig. 1, pl. C27 figs. 12-14.

Heterocyathus lamellosus; Von Marenzeller, 1888: 19.

Heterocyathus oblongatus Rehberg, 1892: 9, pl. 2 figs. 1-2 ("Aus dem südchinesischen Meere", "8° 29' N.").

Heterocyathus wood-masoni Alcock, 1893: 141-142, pl. 5 figs. 4-4a ("Andaman Sea").

Stephanoceris rousseaui; Bouvier, 1895: 10 (wrong spelling).

Psammoseris rousseaui; Gardiner, 1905: 934, pl. 93 fig. 27.

Stephanoseris carthausi Felix, 1913: 332-333, pl. 27 figs. 9-9b (Pliocene, "Padas malang", Java, Indonesia); 1915: 36; Makiyama, 1926: 5-9; Sakakura, 1935: 189. **Syn. nov.**

Heterocyathus elberti Felix, 1913: 363-364, pl. 27 figs. 1-1c ("Rangoen bei Sondé. Unter(?)pliocäner Mergel", Java, Indonesia); 1915: 38-40, pl. 2 fig. 5; 1920: 29-30; Gerth, 1921: 395-396, pl. 57 fig. 12; Makiyama, 1926: 10-12; Umbgrove, 1926: 30-31; Hayasaka, 1931: 68-69; 1932: 7; Gerth, 1952: pl. 6 fig. 12; Cheng, 1971: 3-4, pl. 2 figs. 5-7. **Syn. nov.**

Spongiocyathus typicus Folkeson, 1919: 11, pl. 1 figs. 12-15 ("42-45 miles W.S.W. off Cape Jaubert", NW Australia). **Syn. nov.**

Heterocyathus sandalinus Gerth, 1921: 397, pl. 57 figs. 3-5 (Miocene, "Tji Boerial" and "Kali Tjemoro", Java, Indonesia); 1952: pl. 6 figs. 4-5. **Syn. nov.**

Heterocyathus rembangensis Gerth, 1921: 397, pl. 57 figs. 6-7 (Miocene, "Ngampel", Java, Indonesia); 1952: pl. 6 figs. 6-7.

Heterocyathus rousseaui; Gerth, 1921: 398, pl. 55 fig. 4, pl. 57 fig. 13; 1952: pl. 6 figs. 10-11; Umbgrove, 1926: 30; 1929: 58.

Heterocyathus cf. *rousseaui*; Gerth, 1925: 26.

Heterocyathus aequicostatus elberti; Sakakura, 1935: 186-187, pl. 5 figs. 1-5.

Heterocyathus aequicostatus delicatus Sakakura, 1935: 189, pl. 5 figs. 12-16.

Heterocyathus (Stephanoseris) carthausi; Sakakura, 1935: 189-190.

Heterocyathus woodmasoni; Van Soest, 1979: 111.

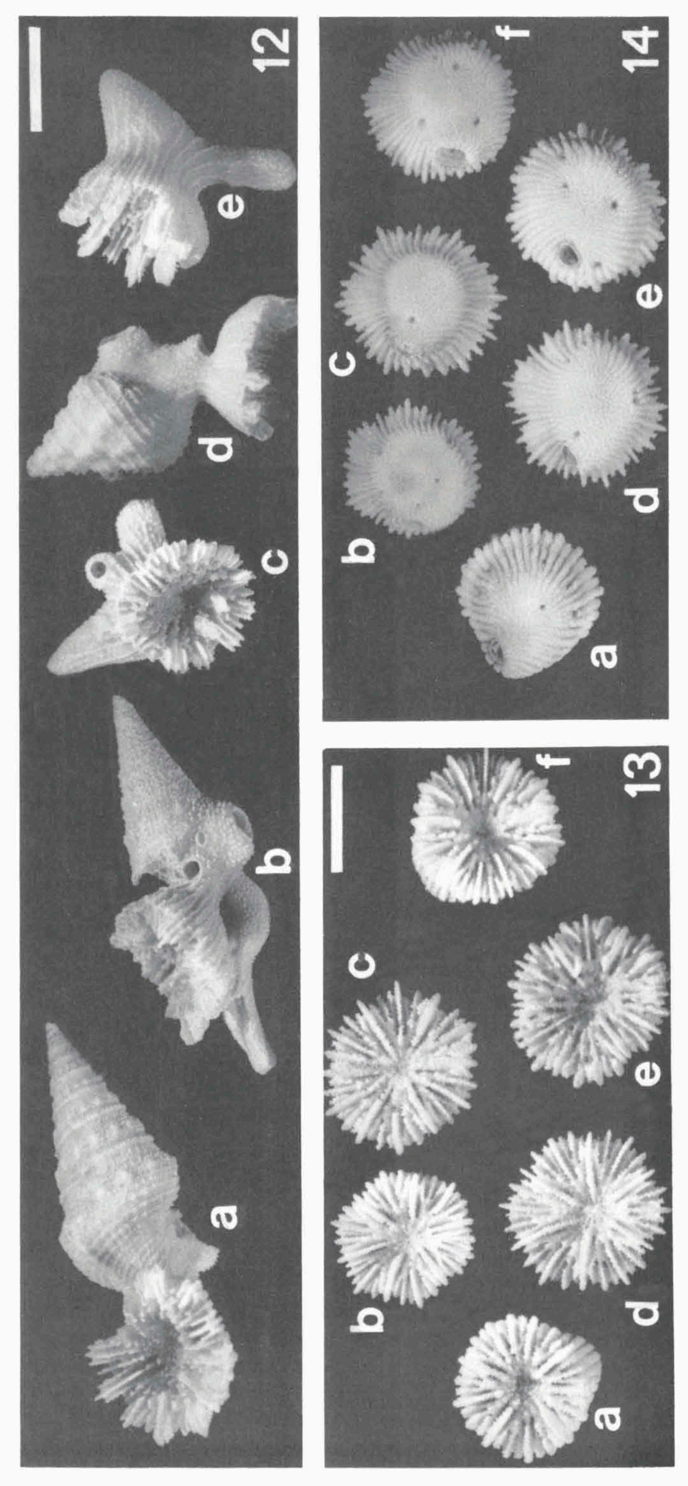
Heterocyathus elongatus Hu, 1987: 39-40, pl. 1 figs. 17-18 (Plio-Pleistocene, "Maansham Mudstone, Tantzu village, Nanwan bay, Hengchun peninsula, southern Taiwan"). **Syn. nov.**

Type material.— *Stephanoseris lamellosa* Verrill, 1865: 5 syntypes (YPM 765-766) Ryukyu Is., Japan; *Stephanoseris japonica* Verrill, 1866: holotype (YPM 767) Kagosima, Japan; *Heterocyathus wood-masoni* Alcock, 1893: 10 syntypes (ZMA 1270-1271) Andaman Sea.

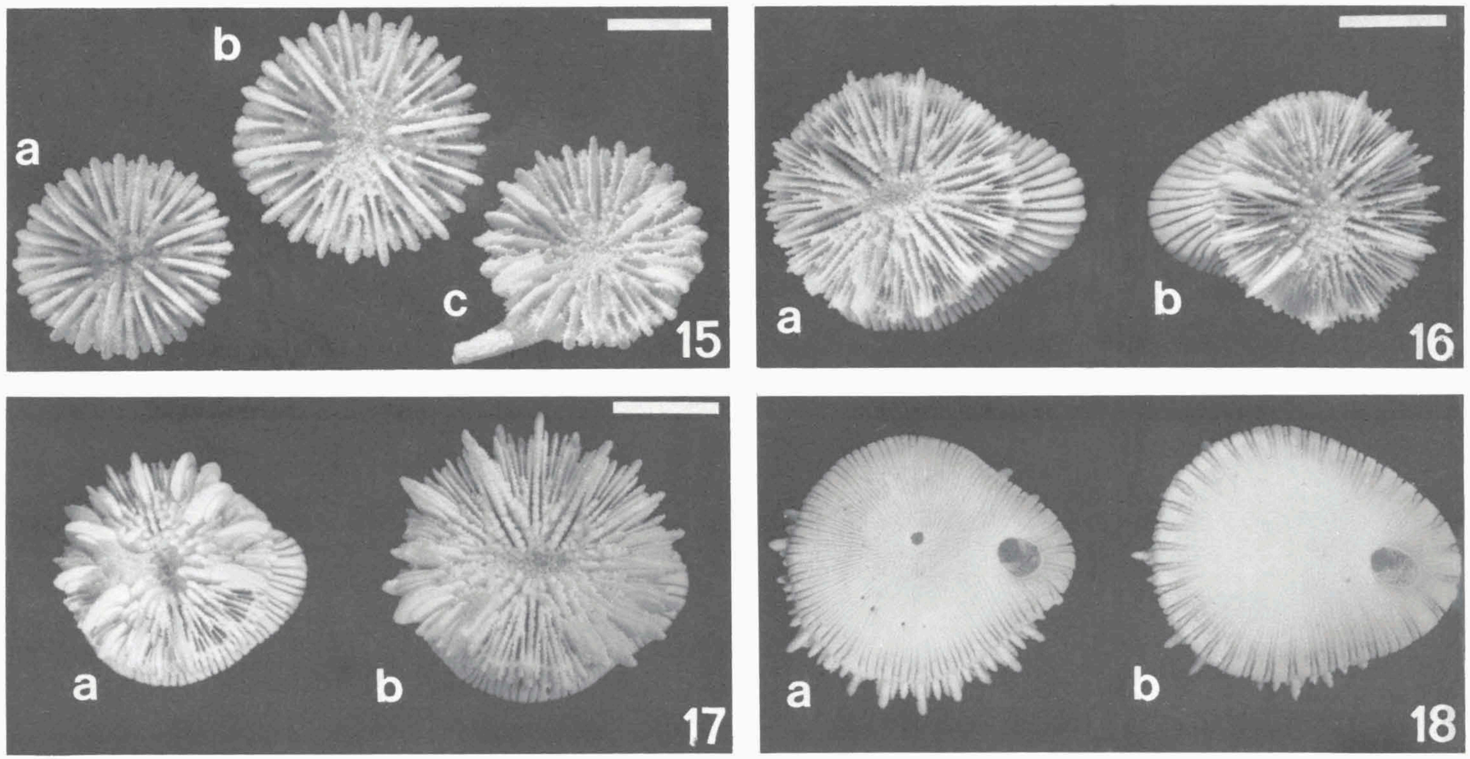
Material from Indonesia.— S Sumatra: 1 (RMNH 18218), 9 (RMNH 18219); Tujuh Is. (SE Sumatra): 1 (ZMA 5625); W Java: 13 (RMNH 18220), 1 (RMNH 18221), 8 (RMNH 18222), 5 (RMNH 18223); Lombok: 31 (ZMA 1264); 7 (ZMA 5516); N Sulawesi: 4 (ZMA 1266); SW Sulawesi: 24 (RMNH 18224), 26 (RMNH 18225), 1 (RMNH 18226), 7 (RMNH 18227), 10 (RMNH 18228), 4 (RMNH 18229), 4 (RMNH 18230), 6 (RMNH 18231), 2 (RMNH 18232), 19 (RMNH 18233); Buton (SE Sulawesi): 1 (ZMA 1263); Komodo: 9 (RMNH 18234); Sumbawa: 5 (ZMA 1262), 2 (ZMA 1267); Ambon: 18 (RMNH 18235), 79 (RMNH 18236); Banda: 3 (RMNH 18237), 2 (RMNH 18238), 3 (RMNH 18239), 36 (RMNH 18240), 2 (RMNH 18241); Kei Islands: 3 (RMNH 18242), 1 (RMNH 18243), 1 (RMNH 18244), 1 (RMNH 18245), 7 (RMNH 18246), 3 (RMNH 18247); Waigeu (W Irian Jaya): 1 (ZMA 1269).

Diagnosis.— Corallum usually compact in shape, without any visible trace of original substratum; it can also be found encrusting on a relatively large gastropod or scaphopod shell, which protrudes from the lower side. Costae and septa distinct; they may be unequal in size. Septa not distinctly protruding laterally. Coralla either flat with a round, symmetrical outline, having the sipunculan worm opening and pores at the aboral side (figs. 10-11), or higher (columnar) with an asymmetrical outline due to the extending worm opening (figs. 8-9), and with pores at the surrounding sides (figs. 7). Pali usually densely packed and occasionally indistinct. Central part of calice is white; either shallow (in flat corals) or relatively deep (in column-shaped specimens).

Remarks.— Due to its variability in shape, the species has been given many names and has been classified in four genera. The five syntypes of *Stephanoseris lamellosa* and the holotype of *S. japonica* are all attached to a relatively large substra-



Figs. 12-14. *Heterocyathus alternatus* (scale bars: 0.5 cm). Fig. 12. Original substrata clearly visible (a-b, d) or already overgrown (c, e); SE Sumatra, Lampung Bay (RMNH 18259). Figs. 13-14. Small, flat specimens from SW Sulawesi, Samalona I., ca. 25 m deep (RMNH 18284); worm pores at the aboral side.



Figs. 15-18. *Heterocyathus alternatus* (scale bars: 0.5 cm). Fig. 15. Large, flat specimens from NW Java (RMNH 18271); (c) worm tube sticking out of corallum. Fig. 16-18. High, columnar corals; NW Java (RMNH 18272); orientation of calice and position of worm opening vary with regard to each other (compare figs. 17 and 18).

tum; neither of them is star-shaped or black-centred and therefore they all belong to *Heterocyathus equicostatus*. The ten syntypes of *H. woodmasoni* that are in the Amsterdam museum (ZMA 1270-1271) are remarkably flat, but fit well within the phenotypic range of *H. aequicostatus*.

In the Spermonde Archipelago, SW Sulawesi, *H. aequicostatus* was found to co-occur with the two other *Heterocyathus* species and *Heteropsammia cochlea* on the sandy bottom below the slopes (25-40 m deep) of reefs more than 5 km offshore. All specimens collected at this locality are relatively small (usually less than 0.5 cm in diameter). At Komodo, *H. aequicostatus* could be found on muddy slopes (> 15 m deep) near the coast in assemblages that also contained the two *Heteropsammia* species. Specimens of all species are relatively large here; those of *H. aequicostatus* are usually about 1 cm in diameter.

Heterocyathus alternatus Verrill, 1865
(figs. 12-18)

Heterocyathus alternata Verrill, 1865: 149 ("Gaspar straits" = Selat Gelasa, between the islands Bangka and Belitung, Sumatra, Indonesia); 1866: 41-42, pl. 2 figs. 6-6a.
Heterocyathus philippinensis Semper, 1872: 254 (partim), pl. 20fig. 12 ["Pandanon (Westküste von Bohol]", Philippines); Moseley, 1881: 144-145; Alcock, 1893: 141.
Heterocyathus parasiticus Semper, 1872: 255, pl. 20 figs. 17a-c ("Canal von Lapinig bei Bohol", "Cabulan bei Bohol", "aus dem chinesischen Meer" and "2 fossile Exemplare aus dem Thonsandstein von Minanga am rechten Ufer des Catalangan und Ilarön in der Provinz La Nueva Isabela auf Luzon", Philippines); 1881: fig. 87c; Gerth, 1921: 396-397, pl. 57 figs. 1-2; Eguchi, 1941a: 414; Gerth, 1952: pl. 6 figs. 1-3, 13. **Syn. nov.**
Heterocyathus philippensis; Semper, 1881: (partim) fig. 87b (wrong spelling).
Heterocyathus aequicostatus; Gardiner, 1904: 105-112, 125 (partim), pl. 3 figs. 12-21, 33-38; Scheer & Pillai, 1974: 61, pl. 28 figs. 3-4.
Heterocyathus heterocostatus Harrison, 1911: 1026-1027, pl. 57 fig. 6, pl. 58 fig. 14 ("Karachi", Pakistan); Gardiner & Waugh, 1938: 187. **Syn. nov.**
Heterocyathus alternatus; Harrison, 1911: pl. 58 fig. 13; Folkeson, 1919: 10-11, pl. 1 figs. 10-11.
Heterocyathus aequicostatus parasiticus; Sakakura, 1935: 187-189, pl. 5 figs. 6-9.
Heterocyathus mai Cheng, 1971: 2-3, pl. 1 figs. 2-9, pl. 2 figs. 1-4, 10 ("Recent; Anping, Tainan, Taiwan, China"); Hu, 1988: 150, pl. 3 figs. 1-8, 10-11, 18. **Syn. nov.**

Type material.— *Heterocyathus alternata* Verrill, 1865: holotype (YPM 6828) E Sumatra, Indonesia; *Heterocyathus heterocostatus* Harrison, 1911: 9 syntypes (BMNH 1950.1.9.1031-1048) Karachi, Pakistan).
Additional material from **Indonesia**.— S Sumatra: 8 (RMNH 18248), 60 (RMNH 18249), 114 (RMNH 18250), 1 (RMNH 18251), 5 (RMNH 18252), 9 (RMNH 18253), 4 (RMNH 18254), 24 (RMNH 18255), 6 (RMNH 18256), 1 (RMNH 18257), 11 (RMNH 18258), 32 (RMNH 18259), ± 500 (RMNH 18260), ± 750 (RMNH 18261); W Java: 5 (RMNH 18262), 4 (RMNH 18263), 3 (RMNH 18264), 8 (RMNH 18265), 37 (RMNH 18266), 1 (RMNH 18267), 15 (RMNH 18268), 3 (RMNH 18269), 4 (RMNH 18270), 54 (RMNH 18271), 10 (RMNH 18272), 14 (RMNH 18273), 2 (RMNH 18274), 21 (RMNH 18275), 58 (RMNH 18276), 36 (RMNH 18277), 12 (RMNH 18278), 22 (RMNH 18279), 24 (RMNH 18280), 122 (RMNH 18281); Lombok: 1 (ZMA 1264); N Sulawesi: 12 (ZMA 1266); SW Sulawesi: 4 (RMNH 18282), 5 (RMNH 18283), 8 (RMNH 18284), 5 (RMNH 18285), 3 (RMNH 18286), 45 (RMNH 18287); Taka Bone Rate: 6 (ZMA 1265); Ambon: 7 (RMNH 18288); Banda: 3 (RMNH 18289); Kei Islands: 3 (RMNH 18290), 2 (RMNH 18291), 3 (RMNH 18292), 3 (RMNH 18293), 23 (RMNH 18294).

Diagnosis.— Corallum not compact in shape, but with loosely arranged, distinctly exsert septa that give the calice a star-shaped appearance. Corals may overgrow original substratum, or be found encrusting a larger gastropod shell that protrudes from its lower side. Costae and septa distinct; septa distinctly varying in size, whereas costae may be either equal or unequal in size. Coralla either flat with symmetrical outline and sipunculan worm opening and pores at the aboral side (figs. 13-14), or higher (columnar) with an asymmetrical outline due to the extending worm opening and with pores at aboral side or at surrounding sides (figs. 17-18). Central part of calice white and either shallow (in flat corals) or relatively deep (in column-shaped specimens). Pali are usually densely packed.

Remarks.— A great majority of the *Heterocyathus* specimens that were found encrusting on large gastropod shells belongs to this species. The variable shape of this species, represented by corals encrusting on a shell (e.g. some syntypes of *H. heterocostatus*) and by others that have completely overgrown the substratum (e.g. the holotype of *H. alternata*), has contributed to the confusion about the identity of this species. The star-like appearance is clear in both growth forms, but is most pronounced in specimens that have failed to overgrow the substratum.

In SW Sulawesi (Spermonde Archipelago) small specimens without a visible shell were found in assemblages with small individuals of *H. aequicostatus*, *H. alternatus* and *Heteropsammia cochlea*. In these assemblages, the outline of *H. alternatus* individuals was a very distinctive character.

Heterocyathus sulcatus (Verrill, 1866)
(figs. 19-23)

Stephanoseris sulcata Verrill, 1866: 48 ("Ceylon" = Sri Lanka); Vaughan, 1905: 416.

Psammoseris cyclicioides Tenison-Woods, 1879 (partim): 10-11, pl. 1 figs. 1-5 ("Princess Charlotte's Bay", NE Australia). **Syn. nov.**

Heterocythus sulcatus; Von Marenzeller, 1888: 19.

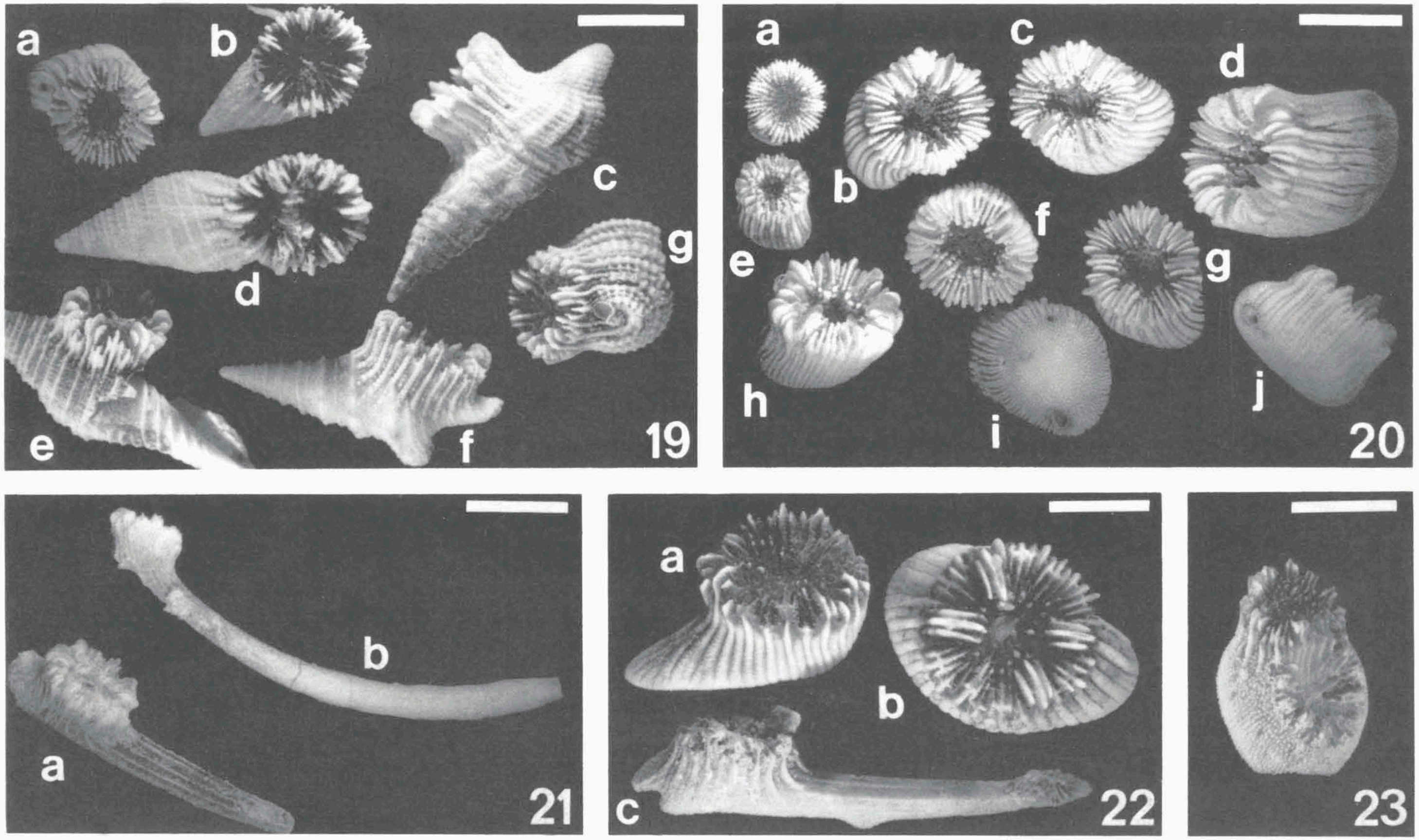
Heterocyathus pulchellus Rehberg, 1892: 8-9, pl. 1 figs. 7a-b ("Zwei Exemplare von der Westküste Australiens"). **Syn. nov.**

Heterocyathus aequicostatus; Folkeson, 1919: 8-10 (partim), pl. 1 figs. 4-7.

Type material.— *Stephanoseris sulcata* Verrill, 1866: holotype (YPM 764) Sri Lanka; *Psammoseris cyclicioides* Tenison-Woods, 1879: lectotype and 6 paralectotypes (MM), 25 paralectotypes (AM G7017), Princess Charlotte's Bay, NE Australia.

Material from **Indonesia**.— S Sumatra: 5 (RMNH 18075), 1 (RMNH 18076); W Java: 7 (RMNH 18077), 2 (RMNH 18078), 2 (RMNH 18079), 1 (RMNH 18080), 1 (RMNH 18081), 5 (RMNH 18082), 3 (RMNH 18083), 2 (RMNH 18084), 39 (RMNH 18085), 62 (RMNH 18086), 34 (RMNH 18087); Madura: 1 (ZMA 1268); Lombok: 14 (ZMA 5531); N Sulawesi: 14 (ZMA 1266); SW Sulawesi: 105 (RMNH 18088), 61 (RMNH 18089), 36 (RMNH 18090), 11 (RMNH 18091), 1 (RMNH 18092), 4 (RMNH 18093), 2 (RMNH 18094), 26 (RMNH 18095), 12 (RMNH 18096); Taka Bone Rate: 6 (RMNH 18097), 2 (ZMA 1265); Ambon: 2 (RMNH 18098), 3 (RMNH 18099), 5 (RMNH 18100), 47 (RMNH 18207); Banda: 7 (RMNH 18208), 18 (RMNH 18209), 76 (RMNH 18210); Kei Islands: 16 (RMNH 18211), 1 (RMNH 18212), 1 (RMNH 18213), 1 (RMNH 18214), 2 (RMNH 18215), 2 (RMNH 18216), 1 (RMNH 18217); Irian Jaya: 13 (USNM 80023).

Diagnosis.— Corallum either compact in shape, without any visible trace of the original substratum, or encrusting on a larger gastropod or scaphopod shell, which protrudes from its lower side. Costae and septa are prominent and may be either equal or unequal in size. They may be dark brown and white, in an alterting pattern.



Figs. 19-23. *Heterocyathus sulcatus* (scale bars: 0.5 cm). Fig. 19. Corals in various stages of overgrowing gastropod shells; NW Java (RMNH 18085). Fig. 20. Column-shaped corals with small shell inside; SW Sulawesi, Samalona I., 25 m deep (RMNH 18089). Fig. 21. Specimens on scaphopod shells; same data (RMNH 18088). Fig. 22. Large corals from Ambon (RMNH 18207); (a-b) large shells completely overgrown; (c) two corals on a scaphopod shell. Fig. 23. A specimen on a *Heteropsammia* corallum; Ambon (RMNH 18098).

Septa usually not very exsert laterally and therefore do not give the calice a star-shaped outline. Coralla not flat but usually columnar with extending sipunculan worm opening at aboral side, and pores surrounding the coral just above base (fig. 20). Central part of calice dark brown or black, and relatively deep. Pali are usually densely packed.

Remarks.— Despite the broken condition of the holotype of *Stephanoseris sulcata*, which was already noted by Verrill (1866), the characteristic colour of its calicular centre can still be distinguished. Many of the syntypes of *Psammoseris cyclicioides* also show a distinctly black centre (e.g. Tenison-Woods, 1879: pl. 1 fig. 3). Since four syntypes (AM G7017 belong to another species, *Heteropsammia cochlea*, a lectotype is herein designated for *P. cyclicioides*, which is the specimen resembling most one of the syntypes illustrated by Tenison-Woods (1879: pl. 1 fig. 2). Together with six paralectotypes also identified as *H. sulcatus*, it is kept in the Macleay Museum (Sydney). Besides the four misidentified specimens mentioned above, there are 25 additional paralectotypes of *P. cyclicioides* in the Australian Museum (AM G7017), which all belong to *H. sulcatus*. In contrast to other authors, Rehberg (1892) was very specific about the characteristic dark centre of specimens belonging to this species, which he described as *Heterocyathus pulchellus*. The illustrations of the two syntypes of this species are also very clear; these corals were originally deposited in the Godeffroy Museum (Hamburg), and are probably lost (see Hoeksema, 1989: 221).

In the Spermonde Archipelago (SW Sulawesi), this species was common in assemblages with *H. aequicostatus*, *H. alternatus*, and *Heteropsammia cochlea*, where it cannot always be easily recognized since the characteristic dark colour of the calice may be hidden by soft tissue.

One of the specimens from Ambon was found on a *Heteropsammia* corallum (fig. 23); it was presumably already dead and still occupied by the sipunculan worm when the *Heterocyathus* larva settled on it. This might indicate that the presence of the worm and not necessarily the availability of a particular substratum is a condition for the planula to settle.

Suborder **Dendrophylliina** Vaughan & Wells, 1947
Family **Dendrophylliidae** Gray, 1847

Heteropsammia Milne Edwards & Haime, 1848

Type species: *Heteropsammia michelinii* Milne Edwards & Haime, 1848 [= *Heteropsammia cochlea* (Spengler, 1781)], by monotypy.

Heteropsammia Milne Edwards & Haime, 1848b: 89; 1850: lii; 1860: 105-106; Semper, 1872: 264; Duncan, 1884: 176; Tenison-Woods, 1878: 339; Van der Horst, 1922: 26; Faustino, 1927: 235; Gardiner & Waugh, 1939: 241; Yabe & Eguchi, 1942: 142; Vaughan & Wells, 1943: 240-241; Wells, 1956: F436; Schindewolf, 1958: 28-33; Scheer & Pillai, 1974: 65; Veron & Pichon, 1979: 416; Boshoff, 1981: 42; Zibrowius & Grygier, 1985: 129; Wells, 1986: 32; Chevalier & Beauvais, 1987: 691, 693.

Wadeopsammia Wells, 1933: 227-228; Vaughan & Wells, 1943: 235-236; Wells, 1956: F433; 1986: 68. (Type species *Trochosmilia nodosa* Wade, 1926, by original designation). Syn. nov.

Heteropsammina ; Ditlev, 1980: 86 (wrong spelling).

Diagnosis.— Corals free-living. Wall granulated with indistinct, narrow and wavy costae. Lower part of corallum shows a relatively large worm opening (sometimes two) and several small pores. Original substratum usually completely overgrown and invisible from the outside (exception in Veron & Pichon, 1979: fig. 727).

Remarks.— The genus is considered similar to *Wadeopsammia* (Wells, 1933), which is only represented by its type species, *W. nodosa* (Wade, 1926). The holotype of this Upper Cretaceous North American species (USNM I 32703) was found in Tennessee, whereas the only other available specimen was found in Texas (USNM I 75183; Wells, 1933: pl. 15 figs. 23-25). The main distinctive character of this genus is the turbinate shape of its representatives. However, both specimens of the type species are small (calice diameter up to 7 mm), and since juvenile *Heteropsammia* corals may also be turbinate (if up to 3-4 mm wide), the difference between the two genera is too small to keep them separate. The species is still considered distinct from others and should therefore be classified as *Heteropsammia nodosa* (**comb. nov.**).

In the present study, two Indonesian *Heteropsammia* species are distinguished, i.e. *H. cochlea* (Spengler, 1781), the adults of which have a single calice, and *H. eupsammides* (Gray, 1849), the adults of which have at least two calices. In earlier studies (e.g. Veron & Pichon, 1979) the two were considered conspecific because alleged intermediate forms were available. During the present study, however, many relatively large corals were found without any sign of a potential fission of the calice; therefore these are considered adults of the monostomatous *H. cochlea*. Specimens that have been recognized as intermediate forms may be corals of the polystomatous *H. eupsammides* that were collected halfway in the process of calice division. At Komodo Island, specimens of both species were found co-occurring, with no distinct intermediate forms. However, the distinction between the two species will remain difficult since immature specimens cannot be separated based on skeleton morphology. Additional Recent *Heteropsammia* species that occur outside Indonesia are not known to us.

Heteropsammia elliptica Tenison-Woods, 1878 (p. 339-340, pl. 6 figs. 3a-b; "Port Jackson", Australia) has been described and illustrated as a fixed coral species without an indication of a mutualistic relationship with a sipunculid worm; therefore, by definition, it should not belong to the genus. No type specimen (probably only a holotype) could be found in any of the Australian museums where Tenison-Woods most likely could have deposited the material (i.e., AM, MM, QM). Very little is known about *Heteropsammia pisum* Alcock, 1902 (p. 110-111); no illustrations are given and type material is untraceable (see Van Soest, 1979).

Heteropsammia analoga is a name cited by Fowler (1890: 418), which, together with some unpublished names, was given by Brüggemann to specimens in The Natural History Museum [the former British Museum (Natural History)]. It therefore has to be considered a nomen nudum. *H. nipponica* and *H. ovalis* var. *japonica* are mentioned by Yabe & Eguchi (1932b: 443, 444) as a new species and a new variety, respectively. Only the latter was described later (Yabe & Eguchi, 1942), leaving the former as a nomen nudum.

Heteropsammia cochlea (Spengler, 1781)
(figs. 24-28)

Madrepora cochlea Spengler, 1781: 240-248, figs. A-D ("Tranquebar", SE India); Gmelin, 1791: 3763.

Heteropsammia michelinii Milne Edwards & Haime 1848b: 89-90 ["Habite Wanpoa (Chine)"]; 1860: 106; Semper, 1872: 264-265, pl. 20 figs. 5-6; Tenison-Woods, 1880: 293-300, pl. 15 figs. 4-8; Faustino, 1927: 235-236, pl. 76 figs. 1-6; Yabe & Eguchi, 1932a: 21-23, pl. 3 figs. 1-5; Eguchi, 1941a: 417; Yabe & Eguchi, 1942: 143-143.

Heteropsammia cochlea; Milne Edwards & Haime, 1851a: 135; 1860: 106; Bouvier, 1895: 10, fig. 3, pl. 1 fig. 4; Van der Horst, 1922: 66-67; 1926: 51; Faustino, 1927: 236-238, pl. 76 fig. 7-8; Gardiner & Waugh, 1939: 242; Eguchi, 1941b: 419; Yabe & Eguchi, 1942: 143; Umbgrove, 1950: 648; Schindewolf, 1958: pl. 1, pl. 3 figs. 1-5, pls 4-5, pl. 6 figs. 1-7, pl. 7 figs. 1-6, pl. 8; Feustel, 1966: fig. 2; Cheng, 1971: 4, pl. 2 figs. 8-9; Veron & Pichon, 1979: 416-420 (partim); Zibrowius & Grygier, 1985: 129, figs. 43-44; Veron, 1986: 576-577 (partim); Nishihira, 1988: 227; Veron & Marsh, 1988: 123; Nishihira & Poung-In, 1989: fig. 2; Veron & Hodgson, 1989: 279.

Not *Heterocyathus cochlea*; Gray, 1849: 77; 1850: 410 [= *Heterocyathus aequicostatus* Milne Edwards & Haime, 1848].

Heteropsammia michelini; Milne Edwards & Haime, 1857: pl. E2 figs. 3a-b; Tenison-Woods, 1878: 339; Moseley, 1881: 196; Semper, 1881: fig. 86; Bouvier, 1895: 10; Bourne, 1905: 213, 226-231, pl. 4 figs. 22-25; Harrison & Poole, 1909a: 906-907; 1909b: 916; Van der Horst, 1922: 66, pl. 8 fig. 7; Hayasaka, 1931: 68; 1932: 7; Gardiner & Waugh, 1939: 241; Eguchi, 1941a: 415-416; Yabe & Eguchi, 1941a: 215, figs. 7-8; Vaughan & Wells, 1943: pl. 50 figs. 6-6a; Boschma, 1959: 273; Pichon, 1974: fig. 6 (partim); Scheer & Pillai, 1974: 65-66, pl. 32 figs. 1-2 (partim).

Heteropsammia rotundata Semper, 1872: 265-266, pl. 20 figs. 10a-b ("Pandanon 25 faden Tiefe (Westküste von Bohol)", Philippines); Alcock, 1893: 145.

Heteropsammia ovalis Semper, 1872: 266, pl. 20 figs. 11a-b ("Thonsandstein bei Maasin am ufer des Agusan (Mindanao)", Philippines); Felix, 1920: 28-29, pl. 128 figs. 1-1c; Makiyama, 1926: 3-5; Faustino, 1927: 238-239, pl. 76 figs. 9-10; Eguchi, 1941a: 414, 415.

Psammoseris cyclicioides Tenison-Woods, 1879 (partim): 10-11.

Heteropsammia aphrodes Alcock, 1893: 145-146, pl. 5 figs. 9-9a ("Indian Seas", "off Ganjam Coast"); Harrison, 1911: 1036; Boshoff, 1981: 42-43.

Heteropsammia cf. *ovalis*; Gerth, 1921: 430, pl. 57 figs. 8-9; Eguchi, 1941b: 418, 420; Gerth, 1952: pl. 6 figs. 8-9.

Heteropsammia aff. *cochlea*; Hayasaka, 1931: 69-70.

Heteropsammia ovalis var. *formosensis* Yabe & Eguchi, 1932a: 23-25, pl. 3 figs. 6-13 (Pliocene, "West of Shogunyama, Byôritsu-gai" and "510 m. south-east of Jôtsûshôwan, Tsûshô-shô", both "Byôritsu-gun, Shinckiku-shû, Taiwan. Byôritsu Beds"); Eguchi, 1941b: 419; Yabe & Eguchi, 1942: 143.

Heteropsammia cochlea var. *alta* Yabe & Eguchi, 1932a: 25-27, pl. 3 figs. 14-19 (Pliocene, "400 m. south-east of Jôtsushowan, Tsusho-sho, Byôritsu-gun" and "950 m. southwest of Taikwa, Koriu-sho, Chikunan-gun", both "Shinckiku-shû, Taiwan. Byôritsu Beds"); 1942: 143.

Heteropsammia ovalis var. *japonica* Yabe & Eguchi, 1932b: 443 (nom. nud.); Eguchi, 1941b: 419 (nom. nud.); Yabe & Eguchi, 1942: 143, 157-158, pl. 7 figs. 21a-b ("Plio-Pleistocene, Ryukyu limestone of Kikai-zima, Kagosima-ken", Japan).

Heteropsammia michelimi; Eguchi, 1941a: 414 (wrong spelling).

Heteropsammia moretonensis Wells, 1964: 118, 120, pl. 3 figs. 1-7 (Pearl Channel, Moreton Bay, Queensland, Australia).

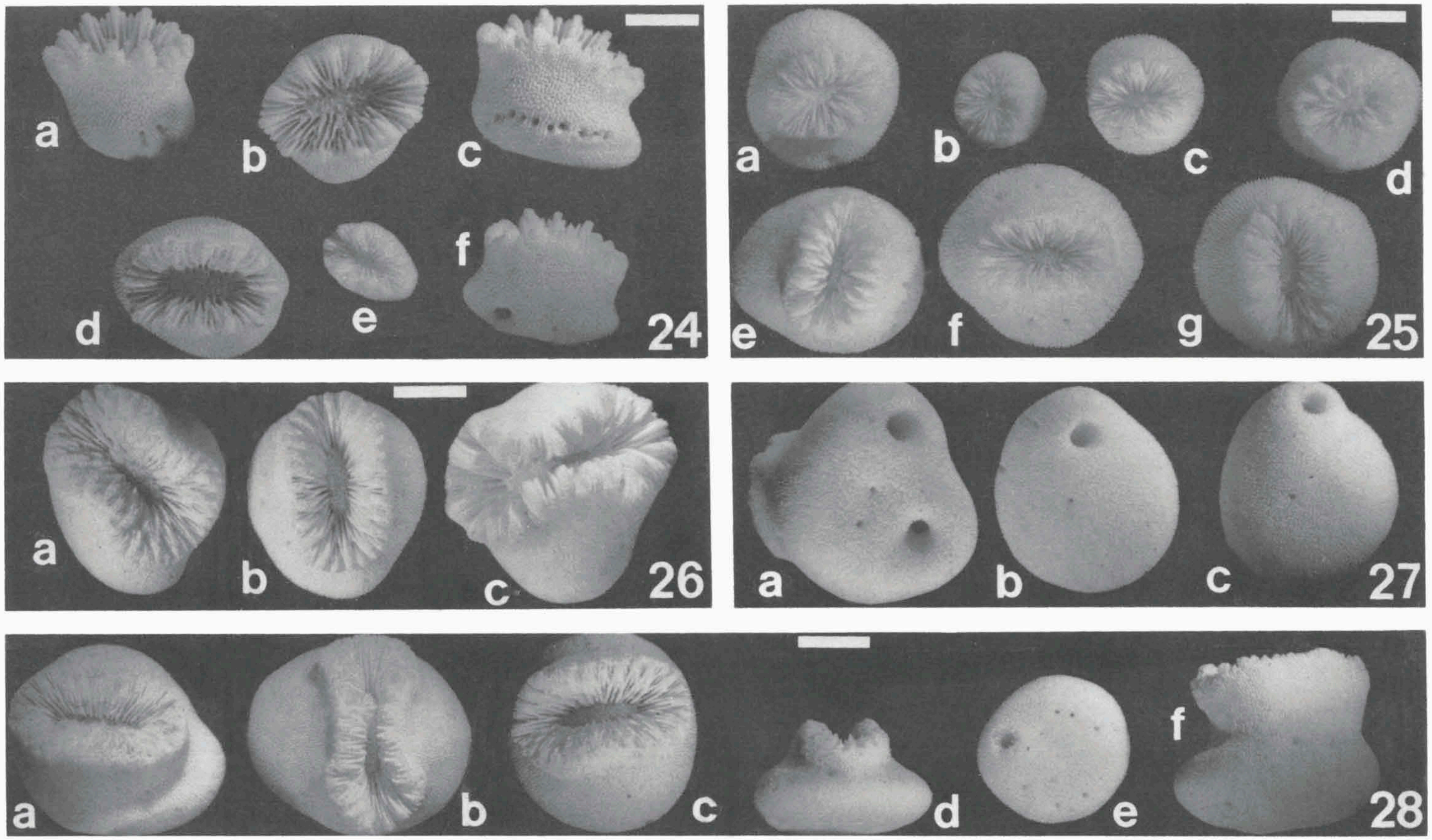
Heteropsammia cf. *cochlea*; Wijsman-Best, Faure & Pichon, 1980: 621.

Heteropsammia michelini var. *formosus* Hu, 1987: 45, pl. 1 figs. 6, 12-13 (Plio-Pleistocene, "Maansham Mudstone, Tantzu village, Nanwan bay, Hengchun peninsula, southern Taiwan").

Heteropsammia ovalis var. *formosa*; Hu, 1988: 144, 146, pl. 3 figs. 14, 19-28 (= var. *formosensis* Yabe & Eguchi, 1932).

Type material.— *Heteropsammia michelinii* Milne Edwards & Haime, 1848: holotype (MNHN 1080) Wanpoa, China; *Psammoseris cyclicioides* Tenison-Woods, 1879: 4 paralectotypes (AM G7017), Princess Charlotte's Bay, NE Australia; *Heteropsammia moretonensis* Wells, 1964: holo- and paratype (USNM 68382-68383) Moreton Bay, Australia.

Material from Indonesia.— S Sumatra: 10 (RMNH 18195), 5 (RMNH 18204); W Java: 9 (RMNH 18192), 3 (RMNH 18193), 137 (RMNH 18194), 1 (RMNH 18202), 2 (RMNH 18206); E Java: 3 (ZMA



Figs. 24-28. *Heteropsammia cochlea* (scale bars: 0.5 cm). Fig. 24. Small corals showing a narrow base and sipunculan pores around the sides; SW Sulawesi, ca. 10 km offshore, 27 m deep (RMNH 18176). Fig. 25. Small corals showing a wide, flat base; same area, ca. 30 km offshore, 30 m deep (RMNH 18173). Figs. 26-27. Corals from Komodo Island, Slawi Bay (RMNH 18199); (a) two worm openings. Fig. 28. From same sample; note pores at aboral side.

1286), 1 (ZMA 1303); Lombok: 5 (RMNH 9633), ± 250 (ZMA 618), 22 (ZMA 1276), 8 (ZMA 5458); E Kalimantan: 2 (ZMA 1280); Paternoster Is. (Kep. Tengah): 4 (ZMA 616), 10 (ZMA 1293), 1 (ZMA 1294); N Sulawesi: 10 (RMNH 9632), 32 (ZMA 613), 3 (ZMA 615), 6 (ZMA 1279), 1 (ZMA 1296), 3 (ZMA 1299), 2 (ZMA 1301); SW Sulawesi: 101 (RMNH 18168), 22 (RMNH 18169), 112 (RMNH 18170), 22 (RMNH 18171), 18 (RMNH 18172), 37 (RMNH 18173), 3 (RMNH 18174), 35 (RMNH 18175), 65 (RMNH 18176), 26 (RMNH 18177), 1 (RMNH 18178), 110 (RMNH 18179), 1 (ZMA 1295); Buton (SE Sulawesi): 7 (ZMA 1291); Taka Bone Rate: 1 (RMNH 18197), 5 (RMNH 18198), 3 (ZMA 1284); Komodo: 29 (RMNH 18199), 5 (RMNH 18200); Sumbawa: ± 100 (ZMA 617), 1 (ZMA 1278), 1 (ZMA 1285), 7 (ZMA 1288), 1 (ZMA 1292), 2 (ZMA 1298); Ambon: 1 (RMNH 18098); 16 (RMNH 18180), 1 (RMNH 18181), 9 (RMNH 18182), 29 (RMNH 18183), 1 (ZMA 5480); Obi Major: 2 (ZMA 1277), 1 (ZMA 1297); Banda: 8 (RMNH 18184), 17 (RMNH 18185), 5 (RMNH 18186), 51 (RMNH 18187), 144 (RMNH 18188), 2 (ZMA 1281), 3 (ZMA 1300); Kei Is.: 1 (RMNH 18189), 60 (RMNH 18190), 1 (RMNH 18191), 3 (RMNH 18203), 3 (RMNH 18205); W Timor: 1 (RMNH 18196), 1 (ZMA 1275); Irian Jaya: 8 (USNM 80022), 4 (ZMA 612), 1 (ZMA 1282), 1 (ZMA 1283), 1 (ZMA 1302).

Diagnosis.— Corallum wall granulated. It has a single centre (the coral is 'monocentric', or 'monostomatous'), which may be narrow at the middle section of oval corals.

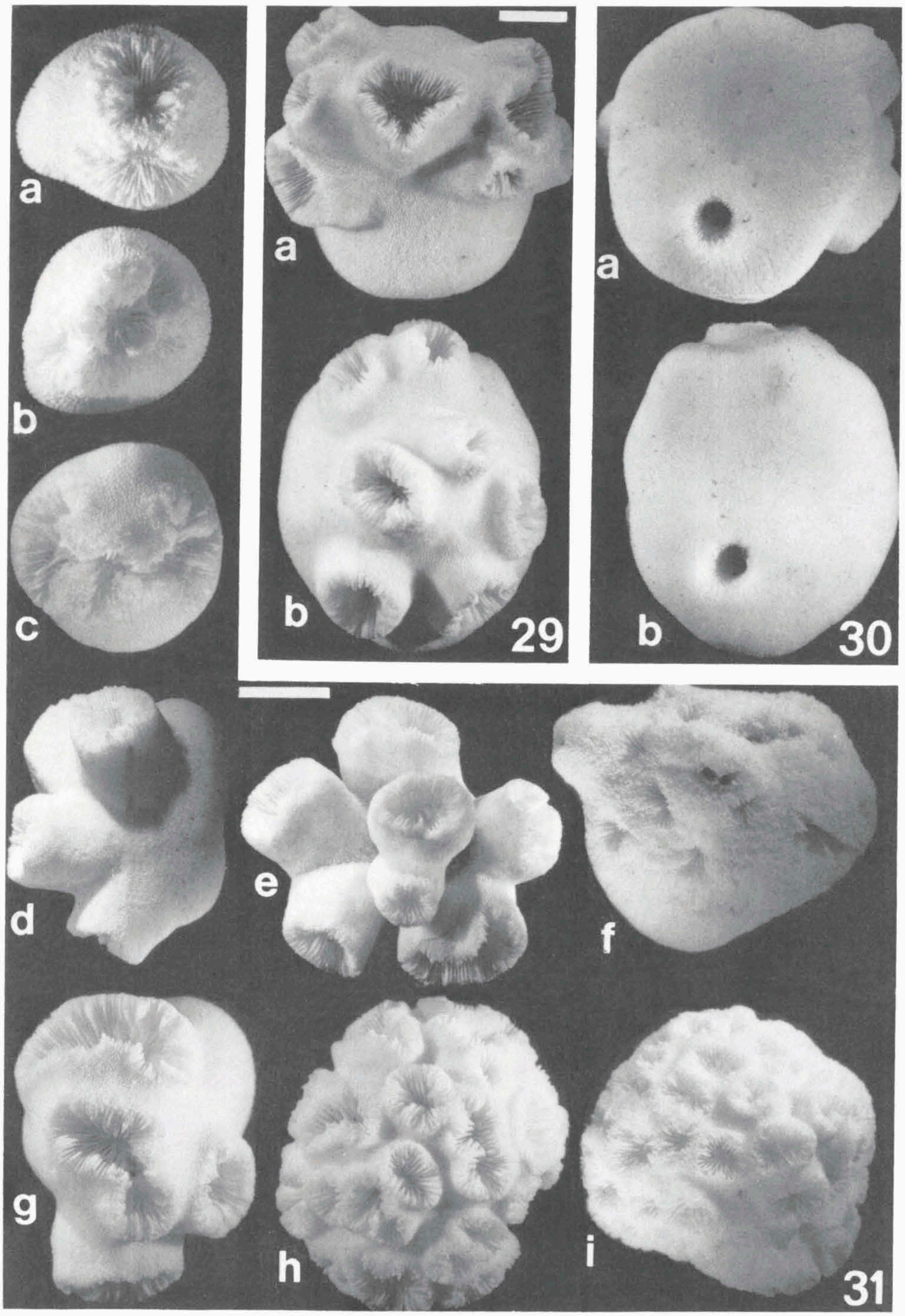
Remarks.— The species is quite variable in shape and size: the calice is either round or oval in outline, the base is narrow or expanded in relation to the oral side. In some populations (e.g. those of SW Sulawesi) the maximum corallum diameter is limited to ca. 0.5 cm, whereas in others (e.g. Komodo) many specimens of 1.0-1.5 cm diameter can be found.

In the Spermonde Archipelago, specimens collected 5-15 km offshore SW Sulawesi have coralla that are laterally flattened and that have a narrow, wedge-shaped base (fig. 24), similar to those of the holo- and paratype of *H. moretonensis*. In contrast, corals sampled 40 km offshore, at the outer rim of the shelf, where fine *Halimeda* sediment is a common substratum (Hoeksema, 1990), show a wide base that is nearly flat at the lower side (fig. 25), like in the holotype of *H. michelinii*. A flat base may help the corals to prevent sinking into the soft substratum.

Zou et al. (1988) considered *H. cochlea* and *H. michelini* distinct species, based on the size and distribution of granulations on the corallum surface. A similar observation was made by Van der Horst (1922). Unfortunately, these authors do not indicate how these parameters are related to the size of the coralla. Since they mention a correlation between the size of the granulations and the roughness of the surrounding sediment, this difference may indicate nothing more than ecophenotypic variation within a single species.

Heteropsammia eupsammides (Gray, 1849) comb. nov. (figs. 29-31)

Heterocyathus eupsammides Gray, 1849: 77, pl. 2 figs. 5-7 (" Hab. Chinese Seas"); 1850: 410-411.
Heteropsammia geminata Verrill, 1870: 370-371, fig. 1 ("Burmah"); Alcock, 1893: 145; Van der Horst, 1922: 67; Faustino, 1927: 239-240, pl. 76 figs. 11-13. **Syn. nov.**
Heteropsammia multilobata Moseley, 1881: 196-197, pl. 12 figs. 1-3 ("Off Samboangan, Mindanao Island, Philippine Islands"); Fowler, 1890: 412-416, pl. 28 figs. 5-9. **Syn. nov.**
Heteropsammia michelini; Van der Horst, 1926: 51, pl. 3 figs. 14-20; Pichon, 1974: fig. 6 (partim); Scheer & Pillai, 1974: 65-66, pl. 32 figs. 1-2 (partim).
Heteropsammia cochlea; Veron & Pichon, 1979: 416-420 (partim).
Heteropsammina michelini; Ditlev, 1980: 86, figs. 113, 376 (wrong spelling).



Figs. 29-31. *Heteropsammia eupsammides* (scale bars: 0.5 cm). Figs. 29-30. Two corals from Halmahera (RMNH 18166); note pores at lower side. Fig. 31. Corals from Komodo I., Slawi Bay (RMNH 18167); (a-c) small corals with several calices; (d-e) large corals with funnel-shaped calices; (f) coral probably containing a parasite is formed like a gall with shallow calices; (h-i) many calices (up to 40).

Type material.— *Heteropsammia geminata* Verrill, 1870: 9 syntypes (YPM 3866), 3 syntypes (USNM 38353), Burma.
Material from **Indonesia**.— E Kalimantan: 5 (ZMA 614); Komodo: 34 (RMNH 18167); W Halmahera: 2 (RMNH 18166); Banda: 1 (ZMA 5454).

Diagnosis.— Corallum wall granulated. Adults with at least two more or less distinct calices by intrastomadaeal budding (i.e., they are 'polycentric' or 'polystomatous').

Remarks.— Coralla are relatively large: specimens with a corallum diameter of 2.5 cm have been found (figs. 29-30). The number of mouths is quite variable, up to about 40 (fig. 31). In some of the animals the calices are inconspicuously small and shallow, whereas in others they protrude upward like chimney funnels (fig. 31).

Six *H. geminata* syntypes, including the specimen illustrated by Verrill (1870: fig. 1), show two distinct calices (five in YPM 3866 and one in USNM 38353). Four syntypes show a nearly divided calice (three in YPM 3866 and one in USNM 38353) and two show a clearly undivided one (YPM 3866, USNM 38353). Whether the latter two belong to *H. eupsammides* or *H. cochlea* is impossible to determine because juvenile specimens of the two species are much alike.

The specimens found at Komodo were found on a fine, muddy substratum. The large number of mouths may help to prevent smothering during excessive sedimentation.

Discussion: mutualism or parasitism?

The association between the free-living corals and the sipunculan worm is well documented but is still not completely understood (e.g. Valenciennes, 1854; Macdonald, 1862; Tenison-Woods, 1880; Semper, 1881; Bouvier, 1894a, 1894b, 1895; Sluiter, 1902; Bourne, 1905; Gerth, 1921, 1952; Schindewolf, 1958; Feustel, 1966; Yonge, 1975; Rice, 1976; Zann, 1980; Kühlmann, 1984; Schuhmacher, 1988). The names previously most in use for the sipunculan living inside both *Heterocyathus* and *Heteropsammia* corals were *Aspidosiphon jukesi* Baird, 1873, and *A. corallicola* Sluiter, 1902, both subjective junior synonyms of *A. muelleri* Diesing, 1851. This species has a very wide geographical range and is not necessarily living inside shells (Cutler & Cutler, 1989).

The hypothesis that the initial presence of a worm is required for the settlement of a sipunculan-associated coral (Feustel, 1966) is supported by the present, first published observation of a *Heterocyathus* coral on a dead *Heteropsammia* corallum, which was presumably still occupied by a living worm (fig. 23). In addition, this shows that the substratum of the coral does not need to be of molluscan origin. It also indicates that corals of the two genera may live in association with the same sipunculid species, and that there are not necessarily more sipunculan species involved as assumed by Schindewolf (1958) and Yonge (1975).

Since the coral selects a substratum already occupied by the worm, the sipunculan in its borrowed shell initially acts as host, whereas in a later stage of the symbiosis the worm appears to play the role of commensal because it lives inside the coral. Therefore, it was originally thought that the worm acted as parasite of the coral (e.g. Semper, 1881). However, the coral benefits from the worm's ability to pull it over the bottom, which is particularly important if the coral accidently becomes overturned (Hickson, 1924; Feustel, 1966; Goreau & Yonge, 1968; Yonge, 1975). If a sipunculan settles in a small shell, then the coral helps it to adjust the hole in accordance to its growth. By overgrowing the shell, the coral supplies the sipunculan with a stronger shelter against possible predators (Kühlmann, 1984), similar to a Silurian tabulate coral that overgrew the shell of its gastropod host (Kase, 1986) and a Pliocene scleractinian that encrusted gastropod shells occupied by hermit crabs (Darrell & Taylor, 1989). With these aspects taken into consideration, the association between the two organisms is clearly mutualistic. As long as the shell is not overgrown, the growing coral increases the weight of the shell without giving the worm complete protection. The weight of the coral skeleton probably hinders the worm's mobility and in that circumstance the coral appears to act as a parasite.

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