A new type of symbiosis: *Heterocyathus japonicus* (Cnidaria: Scleractinia) living on *Fissidentalium vernedei* (Mollusca: Scaphopoda)

H. Zibrowius

Helmut Zibrowius, Centre d'Oceanologie de Marseille, Station Marine d'Endoume, Rue Batterie des Lions, 13007 Marseille, France, e-mail: hzibrowi@com.univ-mrs.fr.

After introductory remarks on the solitary coral genera *Heterocyathus* and *Heteropsammia*, commonly known to be symbiotic with a sipunculan inhabiting a gastropod shell, *Heterocyathus japonicus* is redescribed in detail. It occurs from Taiwan to northern Honshu, Japan. It is the first of these symbiotic corals to be found in association with an alternative partner, living specimens of the large scaphopod *Fissidentalium vernedei*. The coral always occupies the apical end of the shell, the part that protrudes from the sediment. It is thus preserved from being buried and is maintained in an upright position (the same advantages it also gets when its partner is a sipunculan). On live *F. vernedei*, *H. japonicus* incrusts a manganese rich black mineral coating that characterizes the exposed, apical part of the shell. It is speculated about which factors may cause coral larvae to associate with the partner (sipunculan squatting a shell, scaphopod in its own shell).

Introduction

The solitary Indo-Pacific scleractinian genera *Heterocyathus* Milne Edwards & Haime, 1848 (Caryophylliidae) and *Heteropsammia* Milne Edwards & Haime, 1848 (Dendrophylliidae) are known for their convergent symbiotic way of life. Typically, the larva settles on a gastropod shell (more rarely a scaphopod shell, a free tube of the serpulid polychaete *Ditrupa*, or possibly some other hollow structure) that is already inhabited by a sipunculan. The coral then tends to spread over the substrate and the sclerenchyme of the base may incrust the entire shell, leaving only a small orifice for the locomotion and feeding needs of the sipunculan.

The protecting shell with the attached coral is dragged on the sediment surface by the foraging sipunculan. When turned over accidentally, the sipunculan returns the shell to the upright position. The coral is thus preserved from being buried in the sediment.

When the sipunculan grows, the squat shell may prove too small for it, but unlike hermit crabs inhabiting simple shells, the sipunculan does not need to move to a larger lodging. The coral overgrowing the shell can provide the necessary squat extension by growing around the protuding worm and adding a sclerenchyme continuation to the shell. The sipunculan may also contribute by dissolving the shell, now overgrown by the coral, and thus enlarge space inside.

This is, summarized, the current information on *Heterocyathus* and *Heteropsammia* that can be found in the literature (selected references: Bouvier, 1895; Feustel, 1965;

Yonge, 1975; Rice, 1976; Gill & Coates, 1977; Schindewolf, 1959; Hoeksema & Best, 1991).

The representatives of the dendrophylliid genus *Heteropsammia* are morphologically quite homogenous. They occur throughout the tropical Indo-West Pacific, in about the same area where coral reefs exist. Caryophylliid corals symbiotic with a shell-squatting sipunculan are morphologically very diversified, but as a whole have traditionally been referred to the genus *Heterocyathus*. Their large diversity may raise the question if these forms should really be referred to only one genus, but resolving this problem is not within the scope of this paper. *Heterocyathus* (herein in the conventional wide sense) is more widely distributed than *Heteropsammia*. Representatives occur throughout the Indo-West Pacific, from South Africa (Natal) to northern Japan, the Fiji Islands and New South Wales. The Hawaiian Islands and New Zealand appear to be outside the range, but *Heterocyathus* has also been reported from the eastern Pacific (Gulf of California and further south along the Mexican coast).

Within both *Heteropsammia* and *Heterocyathus*, various and often extensive synonymies have been proposed in the literature (most recently again by Hoeksema & Best, 1991), but an exhaustive critical revision of all forms has still to be done.

Because of their remarkable way of life and wide distribution, essentially in shallow tropical waters, *Heterocyathus* and *Heteropsammia* traditionally had much attention. Nonetheless, the abundant literature dealing with both genera does not preclude that new aspects of their biology can still be discovered.

The main object of this paper is to present a new type of association (figs 1-11), wherein *Heterocyathus japonicus* (Verrill, 1866) is symbiotic with the large scaphopod *Fissidentalium vernedei* (Sowerby, 1860). Previously, this species of *Heterocyathus* sensu lato had recognizably been reported as the partner in a coral-sipunculan association of the classical type.

Since the coral in question, in spite of illustrations and brief characterizations in the literature, had been confused and synonymized with congeneric forms, it is here redescribed in detail. Likewise, information is provided separately on the scaphopod partner of the association.

Each partner (coral, scaphopod) will first be considered from the taxonomic and biogeographic points of view before their symbiotic association is analysed.

List of abbreviations: scientific institutions housing material studied herein:

AMNH   = American Museum of Natural History, New York, U.S.A.
CAS   = California Academy of Sciences, San Francisco, U.S.A.
MNHN   = Muséum National d'Histoire Naturelle, Paris, France.
MOM   = Musée Océanographique, Monaco, France.
NHMW   = Naturhistorisches Museum, Wien, Austria.
NMNH   = National Museum of Natural History, Smithsonian Institution, Washing-
          ton D.C., U.S.A.
NSYSU   = Institute of Marine Biology, National Sun Yat-Sen University, Kohsiung,
          Taiwan.
SAM   = South Australian Museum, Adelaide, Australia.
SMF   = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.M., Ger-
          many.

TUS   = Tôhoku University, Institute of Geology and Paleontology, Sendai, Japan.
YPM   = Yale Peabody Museum, New Haven, U.S.A.

Part 1. The coral partner

Heterocyathus japonicus (Verrill, 1866)

Stephanoseris japonica Verrill, 1866: 47-48 [material examined]; Vaughan, 1905: 416.
Heteropsammia; Ikeda, 1922: 278, fig. 2-5.
Stephanoseris carthausi; Satô, 1930a: 23, pl. 3, fig. 13-14; Satô, 1930b: 324 [same as 1930a].
Heterocyathus japonicus; Satô, 1937a: 164, pl. 4, fig. 18; Satô, 1937b: 1857, fig. 9 [same as 1937a]; Satô,
    1939: 413 [same as 1930a, b; 1937a, b]; Yabe & Eguchi, 1942: 127-128, pl. 11, fig. 6a-b [material
    examined]; Mori, 1964: 313, pl. 46, fig. 4; Eguchi, 1968: C37, pl. C4, fig. 1, pl. C27, fig. 12-14.
[?] *Heterocyathus japonicus*; Yabe & Eguchi, 1941: 102 [name only]; Eguchi, 1970: 33 [name only]; Jiang
    et al., 1983: 918 [name only].
Heterocyathus sp.; Mori, 1964: 314, pl. 46, fig. 5.
Heterocyathus mai Cheng, 1971: 3 [in part: specimen on *Marginella bernardi*], pl. 1, fig. 2.
[unidentified]; Springsteen & Leobrera, 1986: pl. 82, fig. 6 ; Gordon, 1990: 19 [photographic plate].

Not *Stephanoseris lamellosa* Verrill, 1865: 149; Verrill, 1866: 46-47, pl. 2, fig. 4, 4a [material examined];
    Vaughan, 1905: 416.
Not *Heterocyathus japonicus*; Marenzeller, 1888: 17-20 [material examined].

Material.— **a)** *Heteropsammia japonicus* **in association with gastropod shell-inhabiting sipunculan:**
YPM 767, 1 specimen glued on slide, part of Verrill's (1866) syntype series of *Stephanoseris japonica*;
labeled "type" (incorrectly mentioned as holotype by Hoeksema & Best, 1991: 227); herein designated
as lectotype of *S. japonica*; Japan, S Kyushu, Kagoshima, 36 m, coll. W. Stimpson, North Pacific Explor-
ing Expedition 1853-1856; YPM 4573, sublots a and b, respectively 5 and 6 specimens, Tokyo Bay, coll.
E.S. Morse, date unknown, received 1878-1879; labeled *Stephanoseris japonica* [not part of Verrill's 1866
syntype series]; TUS 53670, 3 specimens overgrowing small elongate gastropod shells, Japan, NE
Honshu, Sôyû-maru stat. 83, 2.xi.1926, 40°35'30"N, 141°38'00"E, 55 m; labeled *Heterocyathus nipponica*
[= unpublished MS name] but mentioned and illustrated under *H. japonicus* by Yabe & Eguchi (1942:
pl. 11, fig. 6a-b); TUS 53669, 2 specimens, one low, damaged but rather complete and partly covering
bulbous gastropod shell, the other very incomplete on shell fragment, Japan, N Honshu, Mutsu Bay,
Moura-shima, 22 m, viii.1932, labeled *Heterocyathus nipponica* [= unpublished MS name] but men-
tioned by Yabe & Eguchi (1942) under *H. japonicus*.
b) *Heteropsammia japonicus* **in association with scaphopod shell-inhabiting sipunculan:** NMNH
83020 (coral collection), 15 mostly incomplete specimens on 14 shells of *Dentalium octangulatum* Dono-
van, 1804, origin unknown, W Pacific, received from B.L. Burch [originally from Charles Snell, shell
dealer at Trinidad, California]; NMNH 88397 (coral collection), 15 mostly incomplete specimens on
14 shells of *Dentalium octangulatum*, Korea, Pusan Harbour, dredgings, 1950s, from Charles Snell, as
above [lot examined as photocopy].
c) *Heteropsammia japonicus* **in association with** *Fissidentalium vernedei*: AMNH 236899 (mollusc
collection), 1 specimen on shell (empty) of *Fissidentalium vernedei*, Japan, 1971; from Ray Summers
collection; CAS 17669 (coral collection), 1 specimen on shell (with soft parts) of *Fissidentalium
vernedei*, off Zhejiang, Taiwan Strait, 27°30'N, 121°30'E, 80-100 m, trawled, Franz B. Steiner, 17.vi.1971;
CAS 15969 (mollusc collection), 4 specimens on shells (3 still containing scaphopod soft parts, 1
empty) of *Fissidentalium vernedei*, and 1 detached specimen (from all evidence from same type of
scaphopod substrate), East China Sea, N of Taiwan, 26-27°N, 121-122°E, 73-110 m, trawled, Franz B.
Steiner, 15.x.1972 [while navigating as a radio officer, F.B.S. collected shells or bought them from local
fishermen; these specimens may thus have been purchased from Taiwanese trawlers]; NMNH 78649
(coral collection), 3 specimens on shells (empty) of *Fissidentalium vernedei*, and 1 specimen on broken

off apical end of shell, already identified as *H. japonicus* on *F. vernedei*, received from J.W. Wells [additional information from labels is confused, possibly material sent to J.W.W. at different dates: sent by Howard E. Evans to J.W.W. on 7.i.1976; received from H.E.E. on 4.ii.1971; another label mentions Cheng (presumably Y.-M. Cheng, author in 1971 of paper on *Heterocyathus* from Taiwan), but also "locality and collector are questionable"]; NMNH 93907 (coral collection), 1 specimen on shell (empty) of *Fissidentalium vernedei*, "landed in Taiwan by trawlers", from Tom Burch collection, originally from Chuck [Charles] & Barbara Snell [shell dealers at Trinidad, California]; NMNH 93908 (coral collection), 1 specimen on shell (empty) of *Fissidentalium vernedei*, bought by S.D. Cairns in 1975 at Miami, Florida [shop had many shells bearing the coral]; NMNH 706904 (mollusc collection), 2 specimens on shells (empty) of *Fissidentalium vernedei*, received in 1971 from Nell Murbarger, West Coast Curio Co., California [comments by N.M.: In a shipment of 300 *Dentalium vernedei* received from Kaosiung, Taiwan, nearly 15% of the total had this coral growth on the smaller end; in nearly 50 years of importing shells from the Orient I had never encountered this occurrence before]; SAM D18743 (mollusc collection), 1 specimen on shell (empty) of *Fissidentalium vernedei*, Japan, from Sylvia Lewis collection, originally purchased from Mrs. Cox; NSYSU Mol-Sca-1, 1 specimen (incomplete, partly removed) on shell (empty) of *Fissidentalium vernedei*, obtained by Y.-M. Chiu in 1990 at Dali fishing harbour, NE Taiwan, collected by shrimp trawler operating close to shore at a depth of not more than 100 m (usually within 30 m depth).

d) Other species, for comparison: YPM 765, 3 specimens, and YPM 766, 2 specimens, Verrill's (1866) syntype series of *Stephanoseris lamellosa* (one syntype illustrated herein: figs 15-16); Japan, Ryu-Kyu Islands, 14 m, coll. W. Stimpson, North Pacific Exploring Expedition 1853-1856; NHMW 8185, 5 specimens on a single gastropod shell (*Pleurotoma altocarinata* Sowerby; figs 12-14), Japan, donated by crownprince Rudolf, mentioned by Marenzeller (1888) under *Heterocyathus japonicus*.

Description.— Symbiotic with either a shell inhabiting sipunculan (figs 17, 19, 20, 22-23, 25, 26) or with *Fissidentalium vernedei* (figs 1-11), the coral incrusts a shell substrate. The upper part of the corallum is cylindrical, commonly around 7-8 mm in diameter (rarely attaining 10 mm) and 5-6 mm height. The lower part spreads widely over the shell. Depending on the size and shape of the shell and the age of the coral, its base may cover an area much larger than that of the calice (figs 1-11, 19, 20). The apical end of the shell of a live *F. vernedei* may thus be incrusted on all sides (fig. 49) and along several centimetres (maximum extension observed 41 mm). Small and short gastropod shells can be totally covered by a thick layer of sclerenchyme to the extent that the shape of the shell is hardly recognizable (fig. 22).

The costae as the outer peripheral extensions of the septa are of the same number (generally 48). They are all well developed, subequal, extend all along the upper cylindrical part of the corallum and continue over the incrusting base. Typically, whitish (at least less pigmented) costae (C1, C2, C3) regularly alternate with greyish to brownish costae (C4) (figs 19, 32, 33, 50). Exceptionally, all costae are uniformly brownish (figs 10, 47) or all are only slightly pigmented to whitish (figs 3, 39). On the other hand, in eroded specimens the pigmentation may fade. On the upper cylindrical part the costae are closely packed, with deep and narrow intercostal furrows sepa-

Figs 1-11: *Fissidentalium vernedei* bearing *Heterocyathus japonicus* (about natural size), plate illustrating state of preservation of museum specimens (upper part of coral often damaged); proportions coral - shell; angle of coral orientation; extension of black mineral coating on apical part of shell; extension of incrusting coral base. Fig. 1: AMNH 236899 (length 115 mm). Fig. 2: CAS 15969 (length 96 mm). Fig. 3: CAS 17669 (length 108 mm). Figs 4-6: NMNH 78649 (length 107 mm, 107 mm, 112 mm). Fig. 7: NMNH 93907 (length 92 mm). Fig. 8: NMNH 93908 (length 111 mm). Figs 9-10: NMNH 706904 (length 105 mm, 110 mm). Fig. 11: SAM (length 99 mm).

rating them. Near the undamaged calicular edge, the whitish costae are generally narrower than the pigmented ones (figs 23, 26, 33, 38). In smaller specimens costae may be less compact than a first view would suggest: being essentially crests broadened by abundant laterally projecting spiny granules, hence the impression of proportionally narrow and deep intercostal spaces. In other specimens they are more massive. The free edge of the costae is slightly granular (not bearing a line of sharp granules) to rather smooth. On the spreading base the costae increase in width, become less regular, sometimes divide and, as the sclerenchyme thins peripherally, may continue as lines of granules. Given their crowded laterally projecting spiny granules that reduce the intercostal space, the costae somewhat resemble those of certain turbinoliids, such as illustrated by Cairns (1997: pl. 2h) for *Thrypticotrochus multilobatus* Cairns, 1989.

The calice is subcircular to slightly elliptical, with the larger calicular axis generally aligned with the main axis of the shell substrate. All specimens examined have the calice more or less damaged, especially having septal edges broken off. The following account of the calicular structures thus combines observations from the whole series. Inside the calice, all radial elements and the columella generally have a brownish pigmentation. The fossa is shallow. The central columellar area is spongy to papillose, with many crowded thin elements towards which merge the larger but generally narrow more peripheral paliform lobes (figs 18, 27, 33).

The septa are thin, delicate, spaced out (not crowded) and hexamerally arranged in four cycles, typically 48 in number, the whole arranged in a Pourtalès plan and resulting in a "star-like" pattern with deltoid groups (figs 18, 21, 35). Exceptionally a few additional septa occur in halfsystems adjacent to the greater calicular axis. A specimen from Sôyû-maru stat. 83 thus has 54 septa and costae (figs 22-24; specimen previously illustrated by Yabe & Eguchi, 1942).

The peripheral part of S3 (least exsert septa cycle) are enclosed into small deltoid groups (S4 converging towards S3). S2 may be enclosed into larger deltoid groups (S3 converging towards S2 near the columella, but often this junction is incorporated into the columella and S2 are independent like S1).

S1 and S2 are similar in being highly exsert and forming distinct lancets together with the adjacent S4 (figs 17, 22-23, 26), but lancets including S2 are slightly lower. S3 are much lower than septa of all other cycles. All septa are high rounded plates with a

Figs 12-14: *Heterocyathus japonicus* sensu Marenzeller, 1888, NHMW 8185, Japan. Fig. 12: gastropod shell bearing 5 corallites (total length 45 mm). Fig. 13: corallite on siphonal canal (calice 10.8 mm). Fig. 14: corallite on central part of shell (calice 10.7 m).

Figs 15-16: *Heterocyathus lamellosus*, syntype of *Stephanoseris lamellosa* Verrill, 1865, YPM 765, Ryukyu Islands, incrusting gastropod shell, side view also showing secondary orifice, and calicular view (calice 5.9 mm).

Figs 17-24: *Heterocyathus japonicus*. Figs 17-18: syntype of *Stephanoseris japonica* Verrill, 1866, YPM 767, Kagoshima, incrusting gastropod shell, side view and calicular view (calice 6.8 mm). Figs 19-21: YPM 4573b, Tokyo Bay, E.S. Morse. Fig. 19: specimen totally covering gastropod shell, with main orifice on a tubular extension and distinct secondary orifice (calice 6.3 mm). Figs 20-21: side view and calicular view of specimen incrusting elongate gastropod shell (calice 6.6 mm). Figs 22-24: TUS 53670, from Sôyû-maru stat. 83, incrusting gastropod shells; 3 views of specimen 1, illustrated by Yabe & Eguchi (1942) (calice 7.4 mm).
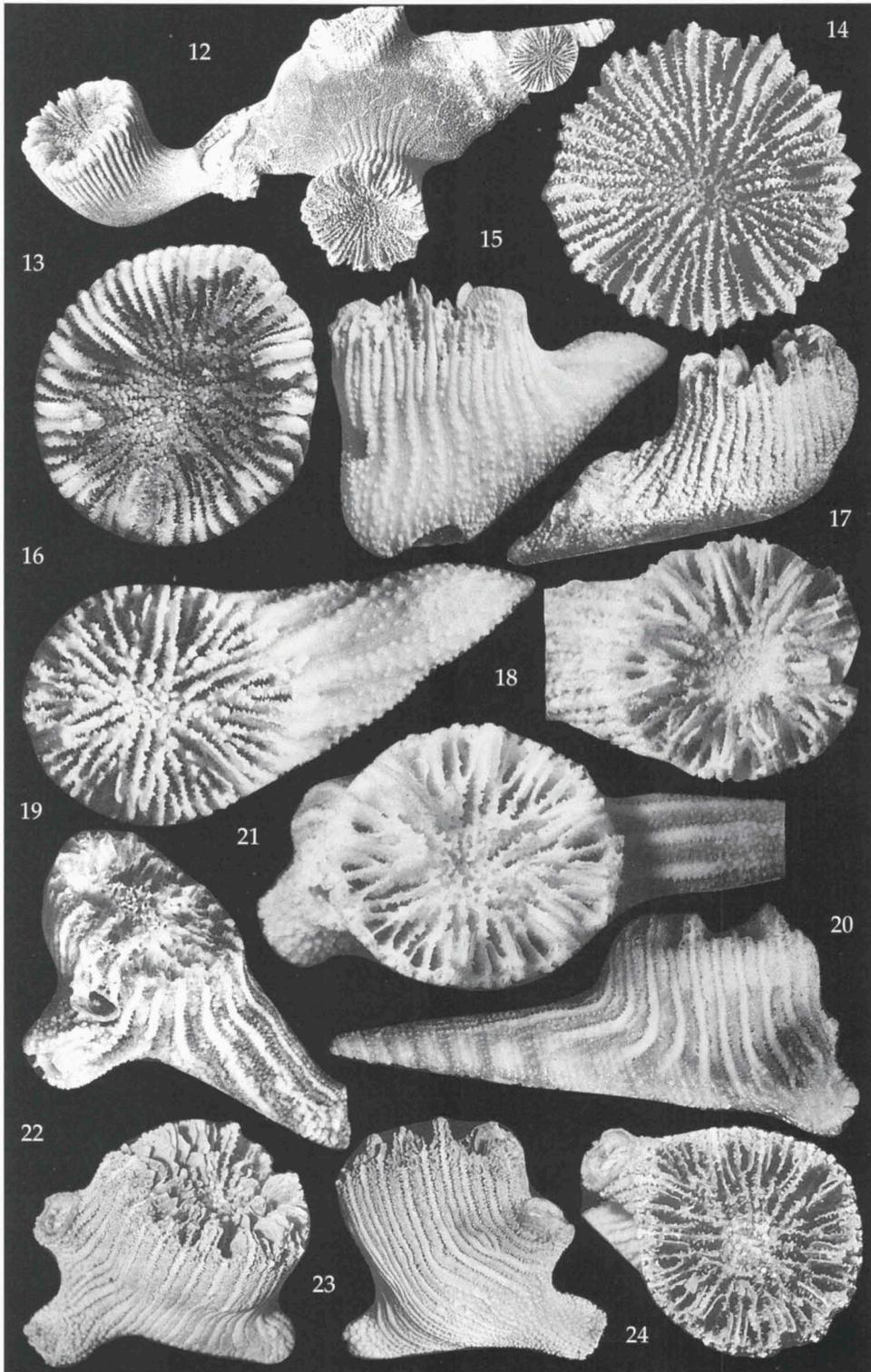
steep axial edge. S4 flanking S1 may be as wide as S2; otherwise width (and height) decreases S1>S2>S4>S3.

The lower axial edge of S1 and S2 bears 1-3 or more, slender paliform lobes, the more axial one merging indistinguishably into the columella (figs 17, 22, 27, 33). The paliform lobe at about the junction with the converging S4 may be larger than the paliform lobes of S1 and S2 (fig. 22).

Septal faces bear slender pointed granules higher than septal thickness (figs 21, 36). Similar granules occur on the paliform lobes. The overall impression of space (fig. 35) between the septa varies with the specimens, depending on the thickness of the septa and the height of the granules.

The corallum is relatively porous (figs 18, 31, 36, 37, 50) but to a lesser extent than in Dendrophylliidae. Pores penetrate the septa, the wall in the intercostal furrows, and even the costae near the calicular edge.

When incrusting a gastropod shell, the coral may partly close the shell orifice with sclerenchymatous accretions, the original shell orifice being generally larger than needed by the sipunculan. In an advanced stage there may even be two orifices, a lower and larger one used by the extruded sipunculan for locomotion and foraging, and a smaller one, generally connected with or developed from the siphonal canal of the gastropod shell (figs 19, 21, 22-24, 26). Of uncertain function, the second orifice is generally turned upward (away from the sediment). Each orifice may be placed at the end of a short tubular extension made of coral sclerenchyme.

Characterization of three specimens from Sôyû-maru stat. 83.— (TUS 53670): Specimen 1 (figs 22-24; calice 6.9 × 7.4 mm) fully incrusts a gastropod shell of which no part can be seen any longer. The lower orifice is at the end of a short tubular sclerenchymatous structure, the other orifice is strongly turned upward, its edge forming a slightly compressed funnel. Between the main orifice and the sclerenchyme-covered shell apex the incrusting coral base measures 9.9 mm. The apex is pierced by a pore much smaller than the two orifices at the other end. The pore probably corresponds to a shell damage and the presence of the sipunculan prevented it from being totally closed. Specimen 2 (fig. 25; calice 7.5 × 8.2 mm) sits on a gastropod shell (16.7 mm) that is not totally covered by sclerenchyme, still free at the "lower" side near and along part of the shell orifice. There is only one sipunculan orifice, delimited by sclerenchyme within the shell orifice. The siphonal canal is not yet transformed, still open, but already invested by a thin layer of sclerenchyme. Specimen 3 (figs 26-27;

Figs 25-27: *Heterocyathus japonicus*, continued, TUS 53670, from Sôyû-maru stat. 83, incrusting gastropod shells. Fig. 25: side view of specimen 2 (calice 8.2 mm). Fig. 26-27: side view and calicular view of specimen 3 (calice 7.6 mm).

Figs 28-32: *Heterocyathus japonicus* on *Dentalium octangulatum*, NMNH 83020, in various position on shell. Figs 28-30: shell (length 21, 27, 25 mm) bearing coral next or near distal orifice. Fig. 31: coral (calice 6 mm) at distal orifice. Fig. 32: coral at apical end leaving apical shell orifice open (calice 5.3 mm).

Figs 33-37: *Heterocyathus japonicus* on *Fissidentalium vernedei*. Figs 33-34: CAS 15969, oblique side view and calicular view (calice 10.2 mm; same as figs 2, 38). Fig. 35: NMNH 706904, calicular view also showing upward turned apical orifice (calice 11.2 mm; same as figs 10, 47). Figs 36-37: NMNH 93908, calicular and oblique side view (calice 7.5 mm, same as figs 8, 40, 46).
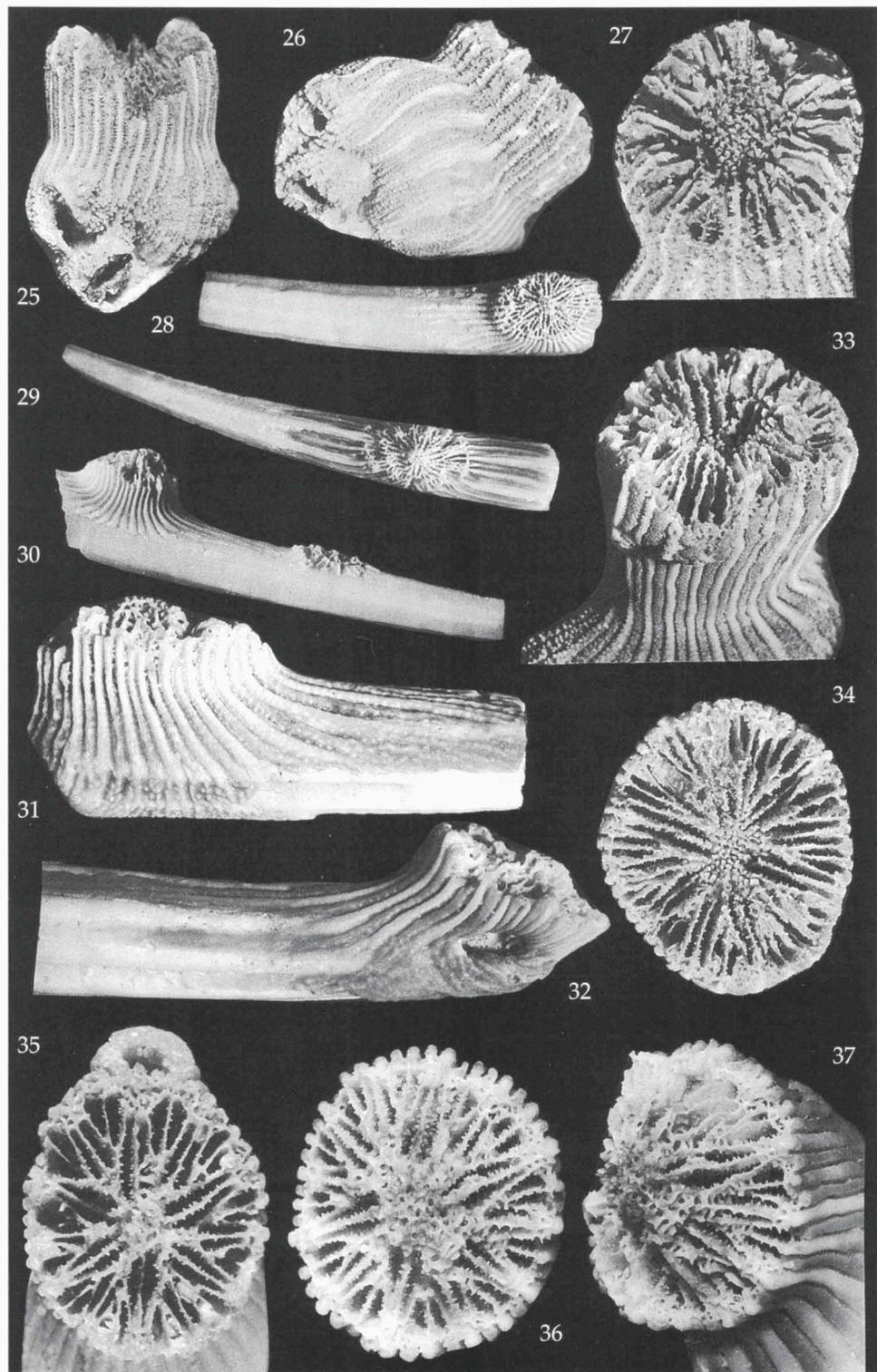
calice 6.7 × 7.6 mm) sits on a gastropod shell (12.4 mm) completely covered by sclerenchyme, but the layer is still very thin along part of the shell orifice. The main sipunculan orifice is protruding as a short sclerenchyme tube out of the shell orifice. The upper orifice is well delimited by sclerenchyme within the siphonal canal. At least in specimens 2 and 3 the lower sclerenchyme delimited sipunculan orifice contains an inner wall sheathing of tiny black sand grains compacted together by the sipunculan. Whether such a coating is a constant feature should be analyzed on a larger series of freshly obtained material.

Type locality and type material.— The description of *Stephanoseris japonica* Verrill, 1866, was based on several specimens (number not indicated) from Kagoshima, depth 36 m (southern Kyushu, Japan, coll. W. Stimpson, North Pacific Exploring Expedition 1853-1856). Only one of the syntypes could be found (YPM 767): the one characterized by Verrill as bearing a young coral on the basal extension. This specimen (figs 17-18) is here selected as the lectotype of *S. japonica*. Hoeksema & Best (1991: 227) were mistaken in presenting it as the holotype. The specimen incrusts an elongate gastropod shell.

Discussion.— Vaughan (1905) was aware of a certain porosity of the septa and theca in Verrill's types of *Stephanoseris japonica* and *S. lamellosa*. He even viewed this detail (together with the deltoid septal arrangement) as a typical eupsammiid (i.e., dendrophylliid) feature and suggested that classification in a distinct genus of that family could be justified. Yabe & Eguchi (1942) and Eguchi (1968) also insisted on porosity in *Heterocyathus japonicus*.

Only one of Verrill's (1866) syntypes (now lectotype; figs 17-18) of *Stephanoseris japonica* could be found (YPM 767). It is easily identified as a specimen specially mentioned by Verrill for bearing a secondary small corallite on the spreading base. It is a small specimen, still glued to a slide and not adequately cleaned. It fully incrusts an elongate gastropod shell, is about 5 mm high and has a calice 6.2 × 6.8 mm in diameter. The 48 widely spaced septa are arranged in a "star-pattern"; the central columella zone is rather dense. The prominent costae are granular, continued, and similar in development; C1, C2, C3 are slightly lighter in colour and slightly more narrow.

Verrill's characterization of the costae partly contradicts what can be observed on the lectotype (above). According to Verrill, the costae are alternately larger and smaller; C1, C2, C3 quite prominent, thickened towards the base, evenly dentate, or strong-

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Figs 38-50: *Heterocyathus japonicus* on *Fissidentalium vernedei*, continued. Fig. 38: CAS 15969, side view with apical shell orifice (calice 10.2 mm; same as figs 2, 33-34). Fig. 39: CAS 17669, side view with apical shell orifice (calice 7.2 mm; same as fig. 3). Fig. 40: NMNH 93908, side view with apical shell orifice (calice 7.5 mm; same as figs 8, 36, 37). Fig. 41: AMNH 236899, side view with apical shell orifice (calice 7.4 mm; same as fig. 1). Fig. 42, NMNH 78649, side view with apical shell orifice (calice 7.0 mm; same as fig. 4). Fig. 43: NMNH 78649, side view with apical shell orifice (calice 7.9 mm). Fig. 44: CAS 15969, side view with apical shell orifice (calice 8.0 mm). Fig. 45: NMNH 93907, side view with apical shell orifice (calice 7.5 mm; same as fig. 7). Fig. 46: NMNH 93908, detail of coral base incrusting black mineral coating (same as figs 8, 36, 37, 40). Fig. 47: NMNH 706904: uniformly brown specimen spreading over black mineral coating (calice 7.0 mm, same as fig. 10). Figs 48-50: NMNH 706904, side view and lower view showing black mineral crust underlying spreading coral base, and side view showing apical shell orifice to the right and small hole in coral base corresponding to unidentified overgrown organism to the left (calice 7.3 mm; same as fig. 9).
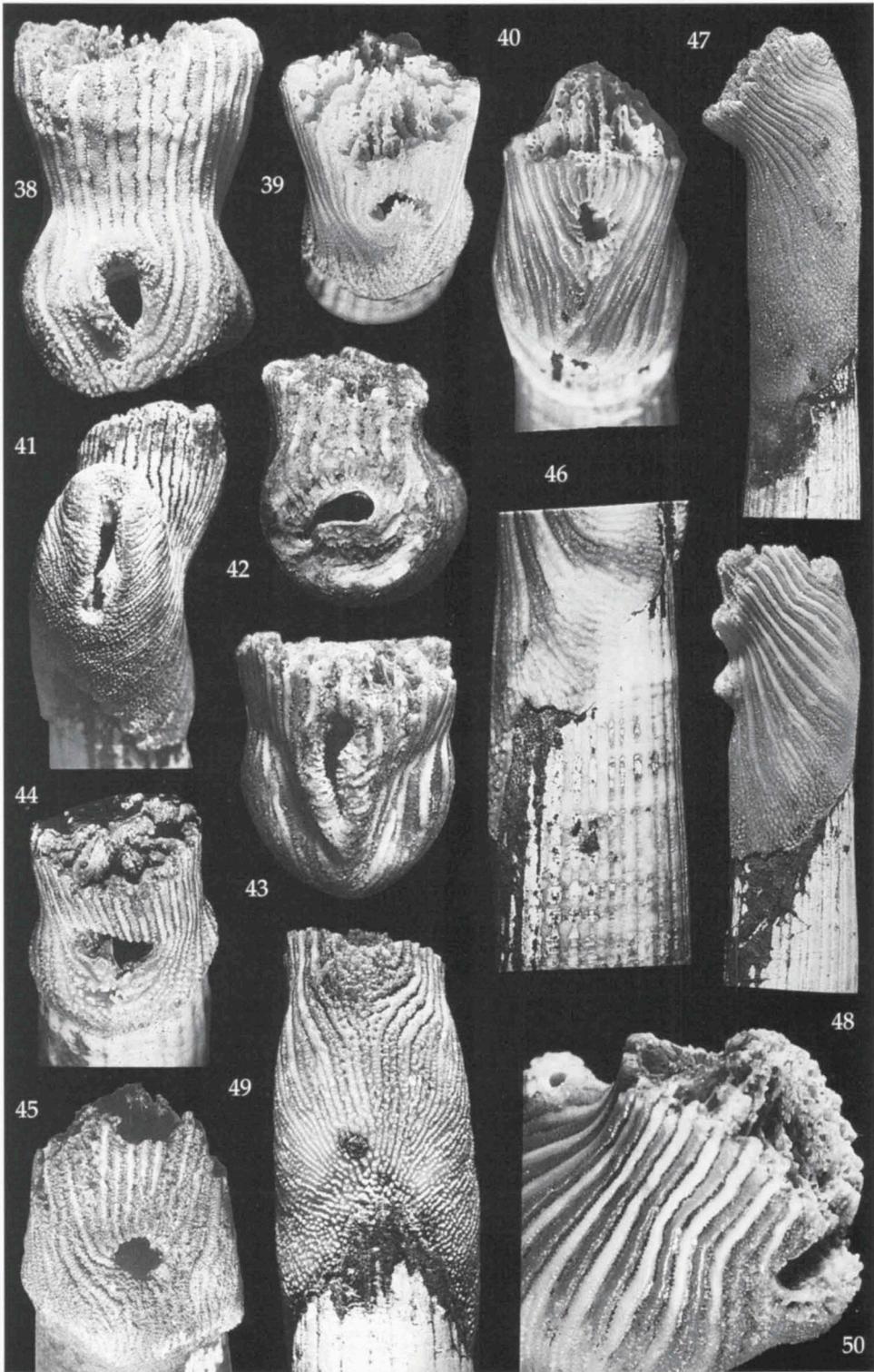
ly granulate along their whole length; granules or teeth often in two or three rows towards the base, where the costae are thickened; C4 much less developed, little prominent, with the edges covered by strong, sharp granulations.

One may deduce that Verrill's type series had not been homogenous. As for the remaining lectotype (YPM 767), it seems that the calicular and costal structures are of the same type as observed in the series of specimens from various other origins (Taiwan to northern Honshu; see material section) and which also comprises larger specimens. These all have "turbinoliid-like" costae (high, wide, separated by narrow deep furrows) and widely spaced, perforate, thin septa arranged in deltoid groups (Pourtalès plan), thereby producing a distinct "star-pattern".

The synonymy list above for *H. japonicus* is based on the analysis of descriptions and illustrations and on reexamination of specimens. In the literature on sipunculans from Japan, this coral had first been identified as *Heteropsammia* by Ikeda (1922). Satô (1930a, 1930b, 1937a, 1937b, 1939) reported it as *Stephanoseris carthausi* before changing his identification to *Heterocyathus japonicus*, a name that remained in use in the coral literature.

Stephanoseris carthausi Felix, 1913, was described on the basis of a single specimen from the Pliocene of Java, attached to an elongate tubular substrate (not a gastropod shell). This form may be more similar to *Heterocyathus mai* Cheng, 1971, a recent species from Taiwan. Its costae differ from those in *H. japonicus*: according to Felix, C1 to C3 are equal and covered by pointed granules; C4 are poorly developed, being simple lines of pointed granules.

Yabe & Eguchi (1942) and Eguchi (1968) considered *H. japonicus* and *H. lamellosus* to be identical, but these authors were not aware that *H. lamellosus* was the older name by one year , which would give it priority in case of synonymy. The first cursory and the second more detailed and illustrated description of *Heterocyathus lamellosus* (originally *Stephanoseris*; Verrill, 1865, 1866) were based on specimens (number not indicated) from the Ryu-Kyu Islands, southern Japan. Five syntypes are deposited at the Yale Peabody Museum (no. 765, 766; one illustrated herein: figs 15-16). They partly or fully incrust small gastropod shells of different shape, are about 5 mm high and have a calice about 6 mm in greater diameter. According to Verrill (1866), this species resembles *H. japonicus*, but is distinguished by the costae, the C4 being thinner and not continuous to the base (fig. 15). Examination of the syntype series now confirmed Verrill's description of the costae. Accordingly, because of the difference of the costae, Verrill's two species are herein kept separate.

Judging from the literature (descriptions and illustrations), occasional examination of specimens in museum collections, and the study of several lots of the Yabe & Eguchi collection (TUS), the genus *Heterocyathus* is represented in Japanese waters by more than one species. This paper focuses on *H. japonicus* and it is beyond its scope to identify and revise the other species. All that can be said here is that other *Heterocyathus* from Japan have generally, conventionally, and at least in part mistakenly, been referred to *H. aequicostatus* Milne Edwards & Haime, 1848. Originally described on the basis of one specimen from an unknown locality and subsequently considered as of wide Indo-Pacific distribution, *H. aequicostatus* has widely become a catch-all species; see for example the excessive synonymy proposed by Hoeksema & Best (1991), which also includes the clearly distinct *H. japonicus*. It cannot be decided here

if the name *H. aequicostatus* is correctly applied to another species from Japan that is recognizable in the descriptions and illustrations by Yabe & Eguchi (1942: 127, pl. 121, figs 4-5) and Nishihira (1989: 221, fig.).

Without having seen it, Yabe & Eguchi (1942) and Eguchi (1968) referred *H. japonicus* sensu Marenzeller (1888) to *H. aequicostatus*, believing that it differed from Verrill's *H. japonicus*. Re-examination of Marenzeller's material (figs 12-14) now confirmed that it belongs to a distinctive species, probably not even of *Heterocyathus* (sensu lato) as provisionally accepted herein. The five corals on a single gastropod shell show a remarkable variation and may not have been alive at the same time. Given the rather large size of the shell and the unmodified (but damaged) shell orifice, one may question if the shell was inhabited by a hermit crab rather than by a sipunculan. Between the incrusting coral bases, the shell is covered by a black mineral crust similar to that found on *Fissidentalium vernedei* (see Part 2). As in the case of the scaphopod and by the same method of analysis, the crust was revealed to be rich in manganese.

H. aequicostatus sensu Eguchi (1968: C36-C37, pl. C28, fig. 1, pl. C29, figs 8-9) from Sagami Bay is a caryophylliid attached to a larger non-mobile substrate and not symbiotic with a sipunculan.

Two orifices in *H. japonicus* and other species.— When incrusting a gastropod shell occupied by a sipunculan, *H. japonicus* may show a feature that also occurs in various other species of *Heterocyathus* (sensu lato), but which up to now has had caught little attention. Frequently there is an upper smaller second orifice near or within the former (now partly closed) shell aperture, in addition to the downward directed main orifice that is the one used by the sipunculan for locomotion and feeding purposes. Such a well defined second orifice can be seen in the lectotype of *Stephanoseris japonica* (on the other side than illustrated by fig. 17). A second orifice is present also in specimens from Sôyû-maru stat. 83 (figs 22-24, 26). Likewise, it characterizes the specimen illustrated by Ikeda (1922, figs 2, 4), and possibly the one illustrated by Satô (1930, pl. 3, fig. 14). Ikeda hypothesized a function of the upper second orifice in controlling water pressure inside the shell related with the movements of the sipunculan.

A similar second orifice (fig. 15) exists in four out of five syntypes of *H. lamellosus* (Verrill, 1865).

The same type of second orifice characterizes *Heterocyathus mai* Cheng, 1971, from Taiwan, and has inconclusively been commented by that author. A form similar to *H. mai*, collected in great number off Luzon in the Philippines during cruise MUSORSTOM 3 in 1985 (depth ca. 180 m; not included by Cairns & Zibrowius, 1997) also generally produces a second orifice.

A second orifice can further be seen on Indonesian specimens (similar to the Taiwan and Philippines forms) illustrated by Hoeksema & Best (1991: fig. 12b-c; not commented in the text) and referred by these authors to *H. alternatus* Verrill, 1865.

The sipunculan partner of *H. japonicus*. — In the more recent literature, the sipunculan partner living with the various species of *Heterocyathus* and *Heteropsammia* is commonly presented as a single species belonging to the genus *Aspidosiphon* Diesing, 1851. For some time it had been known best under the self-explanatory name *Aspidosiphon corallicola* Sluiter, 1902, before the older name *A. jukesii* Bairds, 1873, was

reintroduced. Regardless, more and even older names had been given to the (sometimes misinterpreted) sipunculan partner, resulting in an abundant synonymy (Rice & Stephen, 1970; Rice, 1976; Sáiz Salinas, 1986). Cutler & Cutler (1989) considered the coral-associated Indo-Pacific *Aspidosiphon* identical with *A. muelleri* Diesing, 1851, a species originally known from the Mediterranean (type locality: Palermo) where it is not associated with a coral. The coral genera *Heterocyathus* and *Heteropsammia* would thus have as a partner a worldwide species, which elsewhere has an 'ordinary' lifestyle. This point of view surely deserves to be verified by other sipunculan taxonomists, especially using new techniques for discerning subtle differences.

The Japanese literature on the sipunculan partner of *H. japonicus* (as *Stephanoseris carthausi* or *Heterocyathus japonicus*, see synonymy list) strangely contrasts with the elsewhere reported uniformity of the coral symbiont (a single species of *Aspidosiphon*). The sipunculan associated with *H. japonicus* had first been presented by Ikeda (1922) as a new species of *Phascolion* (Sagami Sea, central E Honshu, 73 m). Full description as *Phascolion ikedai* was given by Satô (1930a, 1930b) (N Honshu: Mutsu Bay, 54 m), followed by an additional record (Satô, 1937a, 1937b; NE Honshu: Onagawa Bay, 34 m). All these records were reiterated by Satô (1939). All later accounts of *P. ikedai* (Stephen & Edmonds, 1971; Murina, 1977; Cutler & Cutler, 1981, 1985; Cutler et al., 1984) are based on Satô's work. These later authors considered *P. ikedai* as of uncertain status, Satô's description needing verification on the basis of topotypic material (type material missing).

The *H. japonicus - P. ikedai* association can be more complex. Ikeda (1922) and Satô (1930a) found a syllid polychaete to be the third partner, living together with the sipunculan as a subtenant in the coral overgrown shell. The syllid remained undescribed.

In this context (subtenant of the sipunculan) it may be worth mentioning a similar complex association reported by Knudsen (1944) from Sunda Strait and Java Sea: a sipunculan, a small bivalve (*Jousseaumiella*) and a syllid, all living together inside a gastropod shell, but which in this case did not bear a coral. When questioned about the material presumed to be preserved at the Copenhagen zoological museum, D. Eibye-Jacobsen (in litt., 1998) stated that the polychaete partner, as illustrated by Knudsen, does not look like a syllid, and that it could not be found in the collection.

Distribution of *H. japonicus*.— Based on information obtained from the Japanese coral and sipunculan literature and presuming that material mentioned by Yabe & Eguchi (1942) and Eguchi (1968) from many stations was homogeneous (only two lots reexamined here), it is concluded that *H. japonicus* exists all along Japan, from Tsushima strait and SE Shikoku to the northern end of Honshu. It is noteworthy that there are confirmed records from Mutsu Bay (material examined here, TUS) and from near Cape Shiriya (specimens illustrated by Miura, 1964). At ca. 40°30'N these are the highest latitude records of *Heterocyathus*, far beyond any coral reef area. The species also occurs in Taiwanese waters where available information is less precise.

H. japonicus appears to be typical of soft bottoms at shelf depths, generally at less than 100 m.

Part 2. The scaphopod partner

Fissidentalium vernedei (Sowerby, 1860)

Dentalium vernedei Sowerby, 1860: 101-102, pl. 223, fig. 3; Pilsbry, 1897: 80-81, pl. 3, fig. 35, 43; Hirase & Taki, 1955: pl. 127, fig. 1.
Fissidentalium (*Fissidentalium*) *vernedei*; Habe & Kosuge, 1964: 3.
Fissidentalium (*Pictodentalium*) *vernedei*; Habe, 1964: 16-17, pl. 1, fig. 9, pl. 4, fig. 30-31; Habe, 1977: 332, pl. 68, fig. 9; pl. 72, fig. 1; Habe, 1981: 226; Springsteen & Leobrera, 1986: 286, pl. 82, fig. 6.
Pictodentalium vernedei: Kira, 1975: 117, pl. 41, fig. 13.
[unidentified]: Gordon, 1990: 19 [photographic plate].

Material.— **a) Specimens not bearing a symbiotic coral**: MNHN: 1 specimen in old collection, origin not indicated. - 1 specimen, China, Jousseaume, 1921. - 3 specimens, China, Denis, 1945; MOM: 1 specimen, Japan (no details); SMF: 2 specimens, Taiwan, received from shell dealer Jens Hemmen; NMNH 203105, 273072, 343371, 609212, 613944 and 1 unnumbered lot: altogether 13 specimens labeled as from Japan, Okinawa and China [examined as photocopies].
b) Specimens bearing symbiotic *Heterocyathus japonicus*: See Part 1, material section (samples marked by an asterisk *).

Diagnosis.— Large stout tusk shell (figs 1-11), yellowish in ground colour with light brownish ring pattern, only slightly curved in older stages, with about 40-50 rounded longitudinal ribs. Apical orifice circular towards the concave side, forming a slit towards ventral side. The literature reports large shells about 130-150 mm long, 13-15 mm in aperture diameter, 3.4-5.3 mm in apex diameter.

Remarks.— This large East Asian tusk shell has frequently been illustrated, especially in the Japanese mollusc literature. A good description is given by Habe (1964). Additional references to those listed above are found in Habe (1964; 1981).

The apical end of the shell is commonly incrusted by a black mineral deposit. This is not part of the natural colour pattern and generally is not mentioned in the descriptions.

Distribution.— In the older malacological literature the distribution of F. vernedei is imprecisely given as China and Japan. The more recent Japanese literature (for example Habe, 1964; 1981) is more detailed concerning Japan: Kyushu, Shikoku, Honshu (north to Sagami Bay or to Boso Peninsula; or south of central Honshu). According to Habe (1964), the species is locally common in Japan, on muddy and sandy bottoms. Depth indications in the Japanese literature commonly are 20-100 m (Habe & Kosuge, 1964; Habe, 1977) whereas 20-1000 m (Habe, 1964) undoubtedly is a printing error. Material studied here of the association with the coral H. japonicus shows that the species occurs further south, at least in Taiwanese waters. The indication Palawan (southern Philippines) in Springsteen & Leobrera's (1986) shell book needs confirmation.

Biology.— Foraging for the tiny infauna (foraminiferans, etc.), scaphopods typically live head downwards and the greater part of the tubular shell buried in the sediment, keeping only the apical part outside. The inflow of water through the apical shell orifice permits oxygen uptake, the outflow feces evacuation and spawning.

Fissidentalium vernedei conforms to this common life style. It is obliquely buried in the sediment, the concavity of the shell turned upwards and having up to one third of

the shell length (measured along the concave side) projecting out of the sediment.

The extension to which the apical part is kept above the sediment-water interface is indicated by a black mineral incrustation of mainly manganese oxides up to ca. 0.1 mm thick (figs 1-11, 46-49; see below). Given the oblique position of the curved shell in the sediment, the black zone is wider along the concave upper than along the convex lower side. The limit between the blackened and the naturally coloured zones is a straight line that runs obliquely across the shell (in side view) and which in the life position of the scaphopod corresponds to the horizontal sediment-water interface. The black deposit on the emerged apex of *F. vernedei* has nothing to do with the black coating that can be found on shells buried in reduced sediments and where the dark colour is due to the formation of iron sulphide.

Mineral coating of the shell apex.— The chemical composition of the black crust was analyzed with a scanning electron microscope (Philipps 515) equipped for analysis by energy dispersion (EDAX PV 9900) (Marseille, Saint-Jerome university campus; technician: Christian Dominici; 17.12.1993). Tiny fragments of black crust were removed from five specimens of *F. vernedei* (bearing *H. japonicus*): AMNH 236899, NMNH 78649, NMNH 93907, NSYSU Mol-Sca-1, SAM D18743). 3 or 4 analyses were run per specimen, on different crust particles. Significant high peaks were obtained for Mn, followed by Fe (commonly 5 times less).

As for the origin of the black crust on *F. vernedei* (whether bearing a coral or not), it is presumed that it is caused by some bacterial action. Currents are modified around the apical part of the shell that projects out of the sediment; the apex orifice canalizes water inflow and outflow; in addition, the surrounding zone is exposed to defecation through the same orifice. These various factors may all be of benefit to a bacterial population on the shell.

In this context it may be mentioned that the black coating of the shell apex (and presumably a similar causing agent) is not unique to *F. vernedei*. A cursory search in the collection of MNHN revealed similarly positioned black coating in the following deep-water species (see Scarabino, 1995):

- *Antalis sedecimcostatum* (Boissevain, 1906), Philippines, cruise MUSORSTOM-3, CP106, 2.vi.1985, 13°47.0'N 120°30.3'E, 640-668 m.

- *Compressidentalium compressiusculum* (Boissevain, 1906), Philippines, cruise MUSORSTOM-2, CP50, 27.xi.1980, 13°36.7'N 120°33.7'E, 810-820 m; cruise ESTASE, CP6, 5.xii.1984, 4°38.0'N 119°49.0'E, 2570 m.

- *Fissidentalium magnificum* (E.A.Smith, 1896), Philippines, cruise MUSORSTOM-1, CP47, 25.iii.1976, 13°40.7'N 120°30.0'E, 685-757 m.

- *Fissidentalium shoplandi* (Jousseaume, 1897), Philippines, cruise MUSORSTOM-2, CP39, 25.xi.1980, 13°02.8'N 122°37.1'E, 1030-1190 m; CP82, 2.xii.1980, 13°46.1'N 120°28.4'E, 550 m.

- *Stenodentalium rhabdotum* (Pilsbry, 1905), cruise MUSORSTOM-3, CP106, 2.vi.1985, 13°47.0'N 120°30.3'E, 640-668 m.

Part 3. The newly discovered coral-scaphopod association of
Heterocyathus japonicus and *Fissidentalium vernedei*

Descriptive notes.— *Heterocyathus japonicus* is remarkable by being the first of the commonly sipunculan associated solitary corals found to live with, alternatively, another very different partner. For the coral this other association has the same vital function of maintaining it above the sediment surface.

In this newly discerned association with *F. vernedei*, *H. japonicus* is attached to the apical end of the tubular shell. Its widely spreading base incrusts the shell on all sides (fig. 46), thereby surrounding the apical orifice and covering part of the blackened area. There is only one coral per shell and the apical shell orifice is never overgrown (figs 38-45): the orifice is maintained functional in the interest of the coral. Were it sealed off by the coral, the scaphopod would die. However, the sclerenchyme deposit of the coral base that strengthens the shell apex generally modifies the apical orifice. Surrounded by sclerenchyme, the orifice (figs 38-45, 50) varies considerably in shape (from nearly circular to more or less elongate or crescent-shaped, regular to irregular), size (e.g. 1×1.5 to 1×4 mm), and its main axis orientation (vertical, horizontal or intermediate positions).

The coral's orientation is roughly in the plane of the shell's curve (with slight individual deviations; figs 1-11). It is thus maintained by the deeply anchored scaphopod in the highest possible position, pointing up and away from the sediment. From common knowledge on scaphopod behaviour the following can be deduced: When accidentally overthrown, the *F. vernedei* is able to re-enter the sediment and re-anchor itself. Thus, perturbations with respect to the upright position are only temporary for *H. japonicus*, which benefits from a quasi-stable position above the sediment. There is a clear analogy with the coral's classical symbiosis with the sipunculan. The scaphopod may also have an advantage from bearing the coral epibiont: given the strengthening overgrowth of the protruding shell end by the coral, which may be less tasty and whose nematocysts may have a deterrent effect, a potential predator may be less tempted to attack the tusk shell.

Since in the available specimens the incrusting base of *H. japonicus* on *F. vernedei* is generally somewhat damaged peripherally (where it is thinner), one easily can see that the coral base spreads over a continuous black crust (figs 46-49). Settling on and subsequently covering that mineral crust is within the normal abilities of *H. japonicus*.

All complete or nearly complete coral-bearing shells studied herein are adults: total length 89-115 mm, distal diameter 11.4-15.5 mm, apical diameter 5.1-7.1 mm (because of the incrustation by the coral the apical shell diameter data are extrapolated rather than precisely measured). No information was available on the minimum size of younger shells required for successful colonization by the coral. The explanation may be that all specimens presenting the symbiosis have come into the possession of museums via shell dealers and collectors, and that bigger shells are more appreciated and fetch a better price than small ones, an equation known to local fishermen. It can also be assumed that their gear (fish and shrimp trawls) more efficiently collected larger tusk shells than small ones. Illustrations of the symbiosis in popular shell books (Springsteen & Leobrera, 1986; Gordon, 1990) also show only big shells.

Distribution of the association.— The sparse and approximate collecting data for the association indicate Taiwan and the East China Sea as the area of origin (see Part 1, material section: samples marked by an asterisk *). Complementary evidence was obtained from Jens Hemmen, shell dealer at Wiesbaden, Germany (in litt., 1990), who is familiar with *F. vernedei* bearing a solitary coral. In previous years such specimens had regularly been imported from Taiwan to be sold to private shell collectors. Enterprising Taiwanese fishermen are the suppliers by selling *F. vernedei* (as well any other larger shells) obtained during commercial trawling for fish and shrimps in upper

shelf depths. This explains that occasionally large lots of the scaphopod bearing the coral are for sale.

Additional evidence of the symbiosis is found in books for shell amateurs. In a book produced for a Manila shell dealer (Springsteen & Leobrera, 1986: pl. 82, fig. 6) one shell bearing *H. japonicus* is illustrated; it is said to come from Palawan, southern Philippines. This geographical indication may be not fully reliable. In Philippine waters the association should rather be expected in the northern area facing Taiwan. Although many species range from Japan through the Philippines to Indonesia, this indicated southern occurrence needs verification.

In another shell book with splendid colour plates (Gordon, 1990: 19) a large lot of *F. vernedei* bearing *H. japonicus* is illustrated. This apparently shows a box full of neatly arranged specimens in a shell shop (New York City), as acknowledged in general terms on the back flap. The illustration is not captioned and scaphopods are only summarily mentioned in the book.

The indication "Japan" found with some specimens should not be trusted blindly since it may be an extrapolation by shell dealers or collectors: *F. vernedei* is particularly well documented from Japan. Since both partners, tusk shell and coral, are known from Japan, independently (see Part 1. The coral partner; Part 2. The scaphopod partner), it could be expected that the association also occurs there, but this has yet to be demonstrated. Should it really occur in Japanese waters, it would at least be strange that this spectacular association did not catch the attention of Japanese mollusc and coral workers.

Although *F. vernedei* had been described as early as 1860 and repeatedly mentioned in the 19th century literature (as a species from China and Japan), no specimen bearing *H. japonicus* has yet been found in the older museum collections. An enquiry sent out in 1990-1991 to institutions world-wide caused many replies. But the few positive ones concerned specimens that had been received starting with the 1970s, with donated private shell collections.

Discussion.— Different arguments can be proposed for considering the epibiosis of *H. japonicus* on *F. vernedei* as the expression of a special symbiosis. A few specimens of the association are preserved in museum collections with still the scaphopod animal occupying its shell, and not a squatting sipunculan. In addition, the coral is always found in a precise position with respect to the shell apex, the shell curve and the black mineral-coated area.

The case of *H. japonicus* settled on the much smaller *Dentalium octangulatum* (USNM 83020, USNM 88397, see Part 1, material section) generally appears different. Here, the coral has settled in various positions (figs 28-32), from next to the distal shell orifice to next to the apical orifice, with occasionally two corals on the same substrate (fig. 30). A similar case is illustrated by Eguchi (1968: pl. C4, fig. 1; pl. C27, fig. 12-14): two specimens of *H. japonicus* alive and distant on an elongate substrate (probably *D. octangulatum*), one near the apex, one near the other end. This appears contrary to typical scaphopod feeding habits, i.e., the tusk shell living partly buried in the sediment. Accordingly it is concluded that these shells were already sipunculan squats and had thus been maintained at the sediment surface by the new inhabitant. It is unusual that *H. japonicus* is found incrusting the apical end of the shell and leaving the apical orifice open (Fig. 32). This may indicate that *H. japonicus* may also asso-

ciate in exceptional cases with live *D. octangulatum*. Unfortunately the two lots examined of *D. octangulatum*bearing *H. japonicus* (which can be traced back to the same shell dealer) have been preserved dry and 'cleaned' (inhabitant removed).

It may be worth exploring similarities between the new *H. japonicus-F. vernedei* symbiosis and the symbiosis briefly mentioned by Wakefield Pagels & Fautin (1994): an actinian living on a deep-water scaphopod in the NE Pacific (off California, 4100 m). The latter case appears to have analogies in the NE Atlantic (Gulf of Biscay): the MNHN possesses several lots of the big deep-water scaphopod *Fissidentalium exuberans* (Locard, 1897) (det. B. Metivier) having an actinian attached to the shell (cruise BIOGAS-6, 1974, CP10, 47°29.6'N 9°04.5'W, 2878 m; CP11, 47°30'N 9°07.4'W, 3056 m; DS75, 47°28.1'N 9°07.8'W, 3250 m).

One may speculate about the factors that make *H. japonicus* larvae settle on shells: sipunculan squat shells and shells of a live scaphopod. Would the larvae settle indifferently on either substrate when both types are available side by side, or would the larvae be selective? If there were chemical attraction, it would at least be unexpected that the same causing agent were released by one and the other potential partner, unless it were some widespread product of elementary metabolism. In the case of the live scaphopod used as a substrate and partner, the water circulation through the apical shell orifice might cause some attraction since the coral always settles next to it, possibly when the scaphopod already is of an advanced size. And perhaps some pumping action of the sipunculan housed in its squat shell (it needs circulation for oxygen uptake and elimination of metabolites) is detectible next to the shell. It does not seem that settlement happens indifferently on whatever small inert substrates lying on the sediment surface (a consideration that pertains all species of *Heterocyathus* and *Heteropsammia*). Were this the case, then the coral should also be found on larger and thereby stable enough dead shells, like the Mediterranean and N Atlantic *Caryophyllia smithii* Stokes & Broderip, 1828, which commonly occurs on dead shell substrates dispersed on sedimentary shelf bottoms (Zibrowius, 1980).

In areas where *Heterocyathus* and *Heteropsammia* species are easily obtainable by diving from shallow water, they should be a subject to ample experiments in order to find an answer to these biological questions. Another aspect would be to separate the corals from the usual sipunculan partner and glue them to various kind of hard substrate protected from sedimentation burial. Would the corals compete successfully with incrusting organisms? Would they develop morphological modifications?

ly replied to my inquiry ('wanted') circulated in the early 1990s.

Samples of the association and corals essential for comparison were kindly loaned by: the Institute of Marine Biology, National Sun Yat-Sen University (Kohsiung), the Department of Geology and Paleontology, Tôhoku University (Sendai), the South Australian Museum (Adelaide), the California Academy of Science (San Francisco), the Smithsonian Institution (Washington, D.C.), the American Museum of Natural History (New York), the Yale Peabody Museum (New Haven), the Naturhistorisches Museum (Wien). Scaphopods were also examined at the Muséum National d'Histoire Naturelle (Paris), the Musée Océanographique (Monaco), the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt a. M.).

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