

Antiquity of the scleractinian-sipunculan symbiosis

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Extant corals symbiotic with sipunculans, i.e., the caryophylliid *Heterocyathus* and the dendrophylliid *Heteropsammia*, develop corallum modifications (in comparison with ‘ordinary’ representatives of these families) that seem to meet the needs of the coral’s worm partner. We distinguish two types of corallum modifications, designated the monoporous and the polyporous types. In the adult monoporous type, the shell inhabited by the sipunculan is usually overgrown only in part by the coral base. There are two orifices: the main one and a smaller pore in the upper part of the corallum. In the polyporous type the shell inhabited by the sipunculan is entirely overgrown and the coral produces a spiralled sipunculan housing. In addition to the main orifice there are several pores in the lower part of the corallum. *Heterocyathus priscus* sp. n. from the Early Cretaceous (Albian) of France is the oldest example of symbiosis, in which the monoporous-type corallum was modified in the same way as in extant monoporous *Heterocyathus*. We speculate that the monoporous type was ancestral, as only this type is known to occur among Cretaceous corals. Morphological similarities between *Heteropsammia* and certain species of *Heterocyathus*, such as the Pourtalès plan of septal arrangement and skeleton porosity, may point to a close phylogenetic relationship.

Key words: Scleractinia, Sipuncula, Caryophylliina, symbiosis.

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Introduction

Among extant Scleractinia representatives of two genera are well known for their symbiotic relationships with sipunculan worms, i.e., *Heterocyathus*, traditionally assigned to the suborder Caryophylliina, and *Heteropsammia*, recognized as a member of the

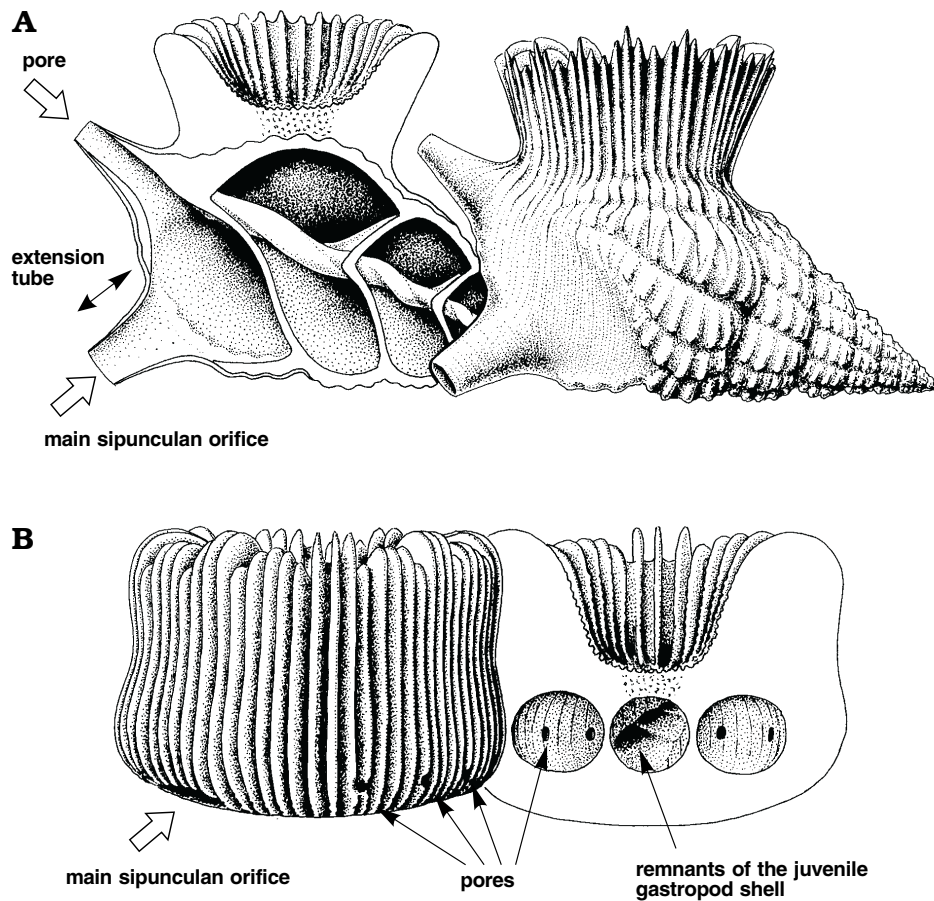


Fig. 1. Basic types of scleractinian-sipunculan partnership buildups (lateral and section views). **A.** Monoporous type with pore situated away from the lower extension tube. **B.** Polyporous type with several pores connecting the sipunculan's coral-built housing space with the outside world.

suborder Dendrophylliina. According to commonly accepted interpretation, the coral larva settles on a small shell, generally a gastropod, that is already inhabited by a sipunculan. The developing coral then spreads over the shell, always leaving open an orifice for the worm's needs. The coral may grow beyond the shell, providing complementary dwelling space for the equally growing worm partner by enveloping its protruding part.

Remarkably, when the shell is still visible and only partly or thinly overgrown by the spreading coral base (overgrowth occurring in the apertural area of the shell), an additional smaller hole (pore) may be observed in the upper part of the corallum. This pore is situated away from the lower tubular extension that bears the orifice used by the sipunculan for locomotion and feeding (**monoporous type**, Fig. 1A). By contrast, in partnerships where the original sipunculan housing is entirely covered by a thick layer of coral skeleton, no such upper pore occurs. However, one to several pores may then be observed in the lower part, connecting the sipunculan extended coral-built spiralled

housing space with the outside world, in addition to the main orifice (**polyporous type**, Fig. 1B).

In the Recent, *Heterocyathus* and *Heteropsammia* are exclusively known from the Indo-Pacific. Because of their special way of life, these corals have received wide attention and have frequently been described as partners in an elaborate symbiosis (selected references: Bouvier 1895; Cutler & Cutler 1989; Goreau & Yonge 1968; Feustel 1965; Hoeksema & Best 1991; Rice 1976; Gill & Coates 1977; Sáiz Salinas 1986; Schindewolf 1959; Yonge 1975; Zibrowius 1998).

Fossil corals similar to the Recent forms and inferred to have lived in symbiosis with unpreserved sipunculans, have occasionally been reported from the Tertiary and from the Cretaceous. Tertiary records include Europe in addition to the Indo-Pacific, whereas the Cretaceous records are from Europe, North America, and Antarctica.

In the Recent and in the Tertiary a wide morphological spectrum of these partnerships is observed, the two extreme expressions in the corallum being the monoporous type and the polyporous type, as characterized above. By contrast, the currently known Cretaceous partnerships are more uniform, all without pores in the lower part of the corallum, but often with an upper pore away from the sipunculan orifice i.e., monoporous type. Accordingly, the monoporous type probably represent an evolutionary older stage of the scleractinian-sipunculan symbiosis.

The oldest known case (Albian of eastern France) of inferred scleractinian-sipunculan symbiosis was briefly presented in a preliminary note (Löser & Stolarski 1997). Here we describe this example of the remarkably ancient association in detail.

Symbiosis is understood herein in the literal sense of living together. Unless it is specified, this does not necessarily imply a benefit for one or the other associated organism.

Material

The Cretaceous material (Middle Albian, *Hoplites dentatus* Zone) herein described as a new species comprises about 140 specimens. These were extracted from the marls of the former quarry of Le Gaty (Géraudot, Aube Département, eastern France, ca. 48°19'N, 4°19'E; Lambert coordinates X: 748.00, Y: 67.40) by Bruno Dubus and communicated by Claude Colleté, members of Association Géologique Auboise. The marls have been interpreted as relatively deep water deposits (100–200 m) and contain a rich fauna including solitary corals, molluscs, decapod crustaceans, serpulid polychaetes, echinoderms and fishes (Michelin 1838; Colleté *et al.* 1982; Löser & Stolarski 1997). General information on the former Le Gaty quarry and the related industry was provided by Touch (1982). The site is now submerged during a part of the year in the artificial Lake Seine.

Our study of the Cretaceous association has been complemented by comparison with Recent material of *Heterocyathus* and *Heteropsammia* originating from French expeditions in the Indo-Pacific and additional series stored in various museums.

A selection of Albian and Recent corals have been examined with the scanning electron microscope (SEM), cut and used for preparation of thin and polished sections and casts.

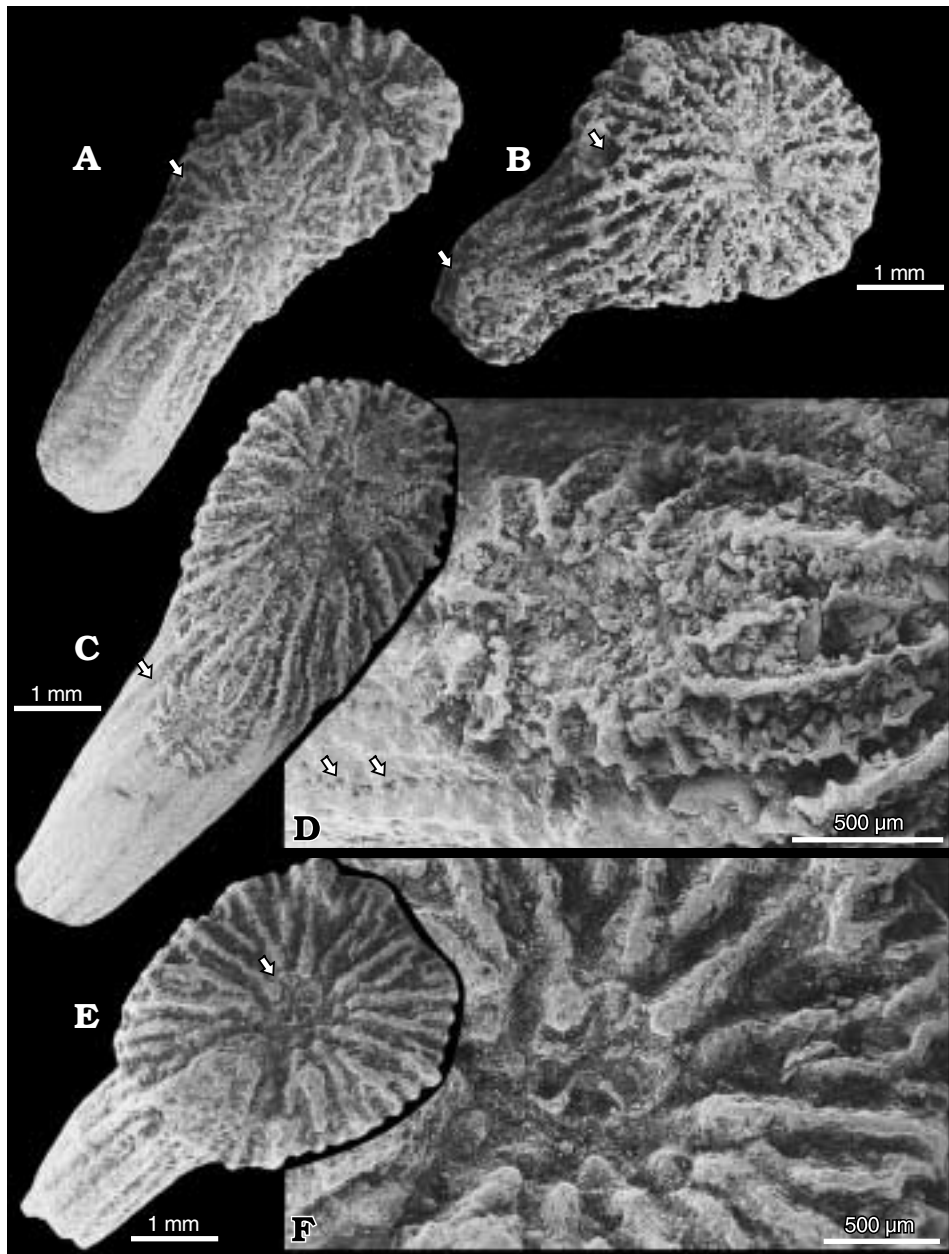


Fig. 3. *Heterocyathus priscus* sp. n. **A.** Juvenile (arrow) attached to adult that overgrows an elongated substrate; MNHN-P/R11005. **B.** Twelve-septate juvenile attached near base of adult (arrow); septal granulations; pore near the calicular edge (arrow); Holotype MNHN-P/R11004. **C, D.** Juvenile (arrow on C) (**D** – enlargement), with three incomplete septal cycles, attached to the adult; desmocyte attachment scars (arrows) along shallow costal grooves MNHN-P/R11006. **E, F.** Six-septate skeleton (**F** – enlargement) on adult calice (arrow); MNHN-P/R11007. All from Cretaceous (Middle Albian), Le Gaty quarry, Aube department, France.

Material. — Exclusively from the type locality. 140 specimens varying in size (Fig. 2) and state of preservation.

Diagnosis. — Small (GCD up to 5.5 mm), monoporous *Heterocyathus*. Four cycles of septa. Septal axial borders with multiple lobes mostly indistinguishable from the papillose columella.

Adult corallum. — The corallum is attached, solitary, low, patellate to sub-cylindrical, the general shape dependent on substrate configuration. The calices of adults are sub-circular to slightly elliptical (GCD/LCD ranges from ca. 1 to 1.5, average 1.2). Greater and lesser calicular diameters are up to 5.5 mm and 4.4 mm, respectively (Fig. 2). The larger calicular axis corresponds to the main axis of the substrate.

Various types of substrate are encrusted that occasionally can still be observed without sectioning: most commonly shells of various gastropods (Fig. 5D), rarely scaphopod shells (Fig. 5C), and other non-identified tubular structures, possibly including serpulid polychaete tubes. Occasionally, the same substrate may bear two corals, a juvenile sitting on a larger one (Fig. 3B, C).

Depending on the size of the substrate the shape of the adult corallum varies considerably. Small gastropod shells and possibly other substrates are completely overgrown (the most common case, e.g., Fig. 5G, H) whereas parts of larger shells remain uncovered (Fig. 5C, D).

Usually, a coral-built, tube-like extension is developed at the aperture of the encrusted shell or tube substrate (Fig. 3A–C, E, 5E, H). It extends the substrate lumen and is open at the end (orifice diameter ca. 1 mm). The inner wall of this tubular extension shows a fine transverse annulation (Fig. 4B). In many cases a pore (about half the size of the orifice) occurs within the corallum. Generally it is situated close to the calicular edge, well above the orifice, and approximately at the same side (Fig. 3B, 4E, 5F–H; monoporous type as defined herein). This is the common situation when the substrate is an entirely covered gastropod shell. Alternatively and more rarely, a pore can be observed at the opposite end, at the apex of the shell (Fig. 4C) or, in the case of a tubular substrate (Fig. 5C), open at the two ends. Sections reveal that the orifice and the pore are connected within the corallum (Fig. 5F, H).

The septa are thin, spaced out and hexamerally arranged in four cycles, typically 48 in number ($S_1-2 > S_3 > S_4$). Septa S_1 are slightly more exsert than septa of the other cycles (Fig. 4C). Septa S_4 fuse with their common S_3 forming deltoid groups (Figs. 3E, 4A, E). Septal faces are covered with small spinose granulations. Multiple lobes are developed on the axial edge of all septa and those on S_1-3 contribute to the formation of the papillose columella (Fig. 4E, F). The fossa is usually shallow.

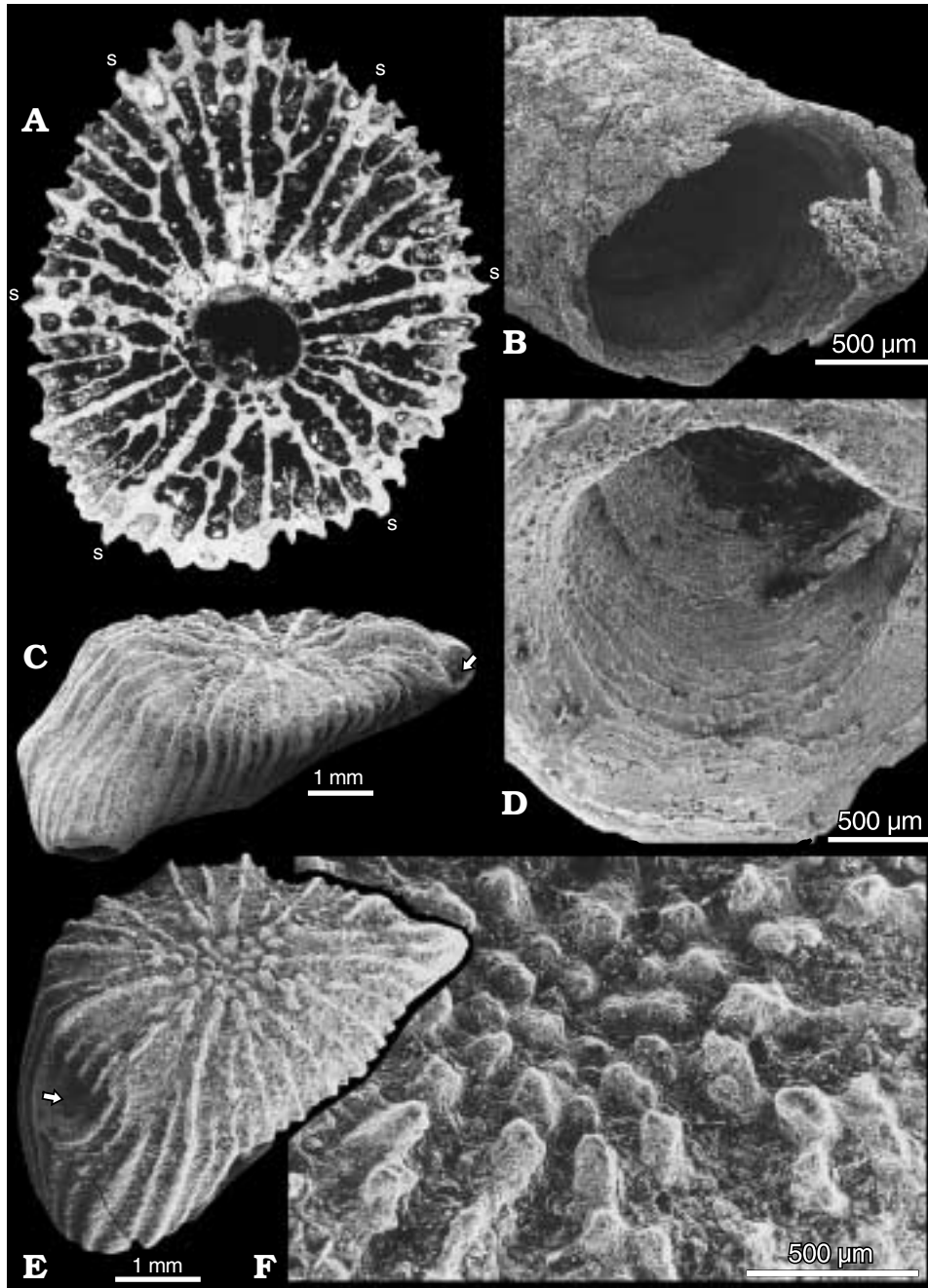
Costae with granular ornamentation are developed on the entire corallum, their thickness decreasing from lower to higher cycles. At the aboral side the costae are less distinct and converge towards the protruding substrate and the tube-like prolongation. Small, slightly irregularly-shaped pits (ca. 40 μ m in diameter) can be seen along intercostal grooves on well-preserved specimens (Fig. 3C, D).

Only occasionally septa are interconnected in the distal part by sclerenchymal (?epithecal) deposits. The wall tends to be more solidly developed towards the lower part of the corallum (Figs. 3B, 4A, C).

The skeleton is recrystallized (calcitic). The only possible traces of the original microstructural organization are distinct, narrow and elongated zones observed occasionally inside the septum (Fig. 4A). Most likely, these zones mirror the former mid-septal zone of calcification centers that underwent a diagenesis different from that of the zone of lateral fibers (compare Stolarski 1990: pl. 8: 1; Gautret *et al.* 2000)

Early stages. — A minute six-septate stage that is attached to the calice center of an adult (Fig. 3E, F) could represent the initial stage of *H. priscus*. It might be interpreted as well as having been formed after strong regression of the 'parent' polyp. Since its diameter (ca. 0.6 mm) equals that of the prototheca of the co-occurring *Trochocyathus conulus* Phillips, 1829 (see Löser & Stolarski 1997), it may instead represent the initial stage of this other species that settled on the dead *H. priscus*

Fig. 4. **A–C, E, F.** *Heterocyathus priscus* sp. n. **A.** Transverse section of calice with four cycles of septa (S_1 asterisked). Septa S_4 connected with adjacent S_3 form deltoid groups. In centre, part of the gastropod shell, substrate for the coral; ZPAL H.XX/1. **B.** Transversely annulated inner surface of the sipunculan extension tube; MNHN-P/R11008. **C.** Specimen with the second orifice (arrow) located on the opposite side than the



main sipunculid entrance, an oblique view; MNHN-P/R11009. **D.** *Heterocyathus mai* Cheng, 1971. Transversely annulated inner surface of the sipunculan extension tube; MNHN-BIM /1. **E, F.** *Heterocyathus priscus* sp. n. Oblique view of specimen with well preserved septal lobes, columellar papillae (**F** – enlargement), and pore (arrow); MNHN-P/R11010. **A–C, E, F.** Cretaceous (Middle Albian), Le Gaty quarry, Aube department, France. **D.** Recent, Philippines, MUSORSTOM-3, Stat. 139, 11°52.9'N, 122°14.7'E, 240–267 m.

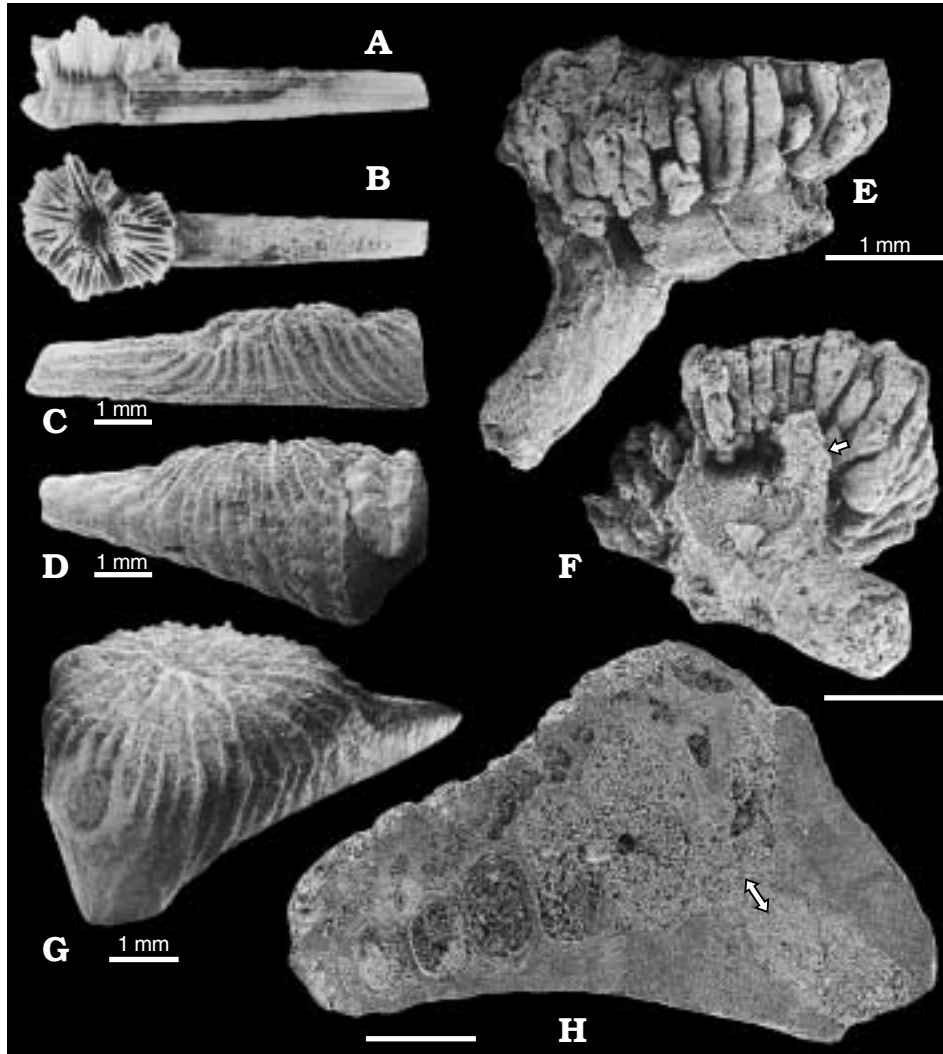


Fig. 5. **A, B.** *Heterocyathus mai* Cheng, 1971, Recent, Philippines, MUSORSTOM-3, Stat. 139, 11°52.9'N, 122°14.7'E, 240-267 m. Specimen (MNHN-BIM /2) encrusting scaphopod shell (sipunculan removed); lateral (A) and distal (B) views. **C–H.** *Heterocyathus priscus* sp. n., Cretaceous (Middle Albian), Le Gaty quarry, Aube department, France. **C.** Specimen encrusting scaphopod shell; MNHN-P/R11011. **D.** Specimen encrusting elongate gastropod shell; MNHN-P/R11012. **E, F.** Natural sediment cast obtained from specimen MNHN-P/R11013 by dissolving skeleton in acetic acid; visible are: infillings of gastropod shell (on E), of sipunculan extension tube between sipunculan orifice and pore (arrow). **G, H.** Specimen envelopping gastropod shell, with pore (G); MNHN-P/R11014. **H.** Polished and etched section in plane of orifice and pore, showing connecting canal, now filled with sediment (arrows). Scale bar 1 mm.

corallum. Another small individual (ca. 0.9 mm in diameter) settled on a larger one, is more likely to be the initial stage of the *H. priscus* skeleton (Fig. 3B). It has twelve normally arranged septa, a solid wall, and a circular outline. The granular type of septal ornamentation is the same as in the large specimen to which it is attached and it is only slightly smaller (by 0.1 mm) than a specimen that clearly represents *H. priscus* with well expanded costae (Fig. 3C, D).

No juveniles standing alone on a substrate are available (Fig. 2). Those observed incrust larger coralla and start to have a marked expansion of the radial elements outside the wall. Intriguingly, septa of such associated juvenile and adult specimens are occasionally connected (Fig. 3A, C, D). This can be explained by budding or by aggregation of genetically close specimens (compare aggregated colonies of *Siderastrea* and *Manicina* described by Duerden 1904 and Boschma 1929, respectively). Since adults of *H. priscus* invariably have only one large calice we assume that those small specimens actually are independent juveniles that occasionally fused because of genetic proximity.

Remarks. — Contrary to what had been said in the preliminary note (Löser & Stolarski 1997), the wall of *H. priscus* is not synapticulothecate of the type found in dendrophylliids i.e., a porous wall formed of irregularly arranged synapticalae (bars between neighboring septa resulting from fusion of grains of the septal faces). The general aspect of the theca is more caryophylliid-like, with a solid (non-porous) wall, and with strong narrow costae (no nodules as in the Cretaceous dendrophylliid *Wadeopsammia nodosa*). Septal connections observed in some specimens that may resemble synapticalae or dissepiments are skeletal (?epithecal) sheets (Fig. 3B) similar to those occurring in, for example, extant *Trochocyathus* (compare Roniewicz & Stolarski 1999: fig. 12E).

H. priscus resembles the coral identified in Darrell & Taylor (1993) as *Deltocyathus? complanatus* Squires, 1958 from the Santonian or Campanian Santa Marta Formation of James Ross Island, Antarctica (see also section entitled Fossil record of scleractinian-sipunculian associations). However, *H. priscus* differs from the Antarctic fossil in having narrower costae, and a smaller number of septa in the adult stage (full 4 septal cycles in *H. priscus* versus 5 septal cycles, the 5th being incomplete, in '*D.? complanatus*').

Recent equivalents

We examined a large number of specimens very similar and at least closely related to *Heterocyathus mai* Cheng, 1971 found in moderately deep water in the Philippines (many stations of cruises MUSORSTOM-1,-2,-3 in 1976, 1980, 1985, especially off Luzon, depth ca. 180 m). The form in question has a calice diameter of about 10 mm or slightly more, a light, in part brownish skeleton, 48 thin, widely-spaced septa arranged in a distinct Pourtalès plan, very exsert groups of S₁ and adjacent S₄ septa, the axial edge of septa being denticulate to lobate, and the central area filled with a more or less spongy not prominent columella. Most specimens were found on proportionally large shells which they do not fully incorporate and were involved in a partnership with sipunculans of the monoporous type.

Below we describe various stages of shell colonisation that can be compared with stages of shell colonisation in the Albian *Heterocyathus priscus*:

(1) Coral sitting on a still entire gastropod shell and having not yet spread to the edge of the shell aperture.

(2) Coral as in case 1 but shell having a hole in its more proximal part (away from the aperture), the hole being surrounded and narrowed into a low chimney-like structure by coral tissue. The hole itself may result from the incidental breakage of the shell or from the former predatory attack on gastropod (Fig. 6H, I; compare Fig. 4C).

(3) Coral sitting near the gastropod shell aperture that is surrounded and narrowed by coral tissue, one part of the aperture already being pinched off and forming a distinct pore. In cases where the gastropod shell aperture extends into a siphon, the pore is almost invariably located at the end of the siphon (Fig. 6F, J).

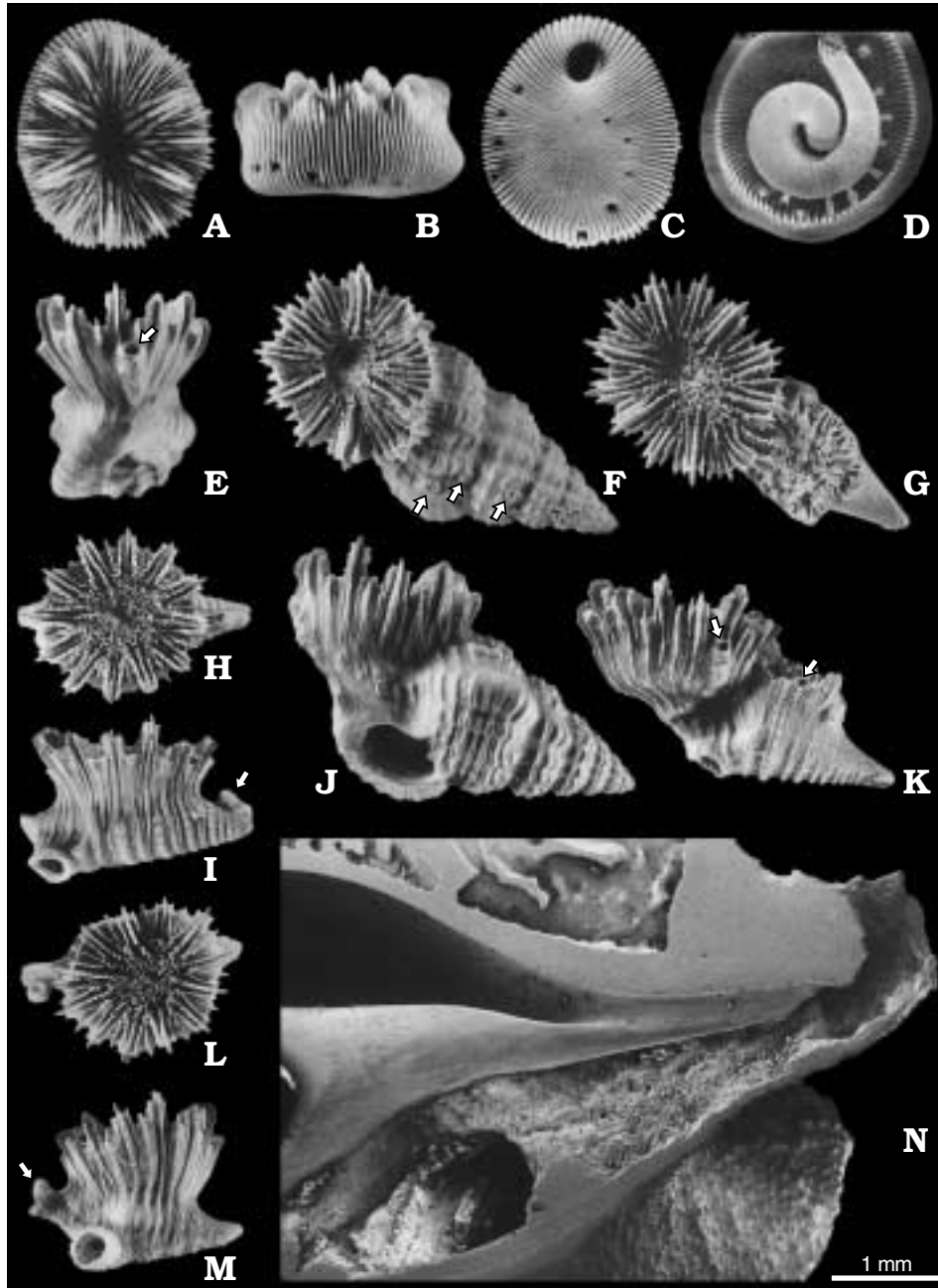


Fig. 6. **A–D.** *Heterocyathus aequicostatus* Milne-Edwards & Haime, 1848. ZPAL H.XX/49 in distal (**A**), lateral (**B**), and proximal (**C**) views; an example of a species that entirely overgrows the substrate (poly-porous type). **D.** Plastic infilling of the coiled sipunculan cavity (corallum dissolved) with several lateral canals opening as pores on the proximal or lateral corallum surfaces. Recent, New Caledonia, Stat. 1138, 19°26.5'S, 163°46.5'E, 42 m. **E–N.** *Heterocyathus mai* Cheng, 1971, Recent, Philippines, MUSORSTOM-2, Stat. 66, 14°00.6'N, 120°20.3'E, 192–209 m. **E, F, J.** MNHN-BIM /3 attached to adapical region of gastro- →

(4) Coral as in case 3, but aperture extended into a distinct tube-like structure and a pore at top of a more marked higher chimney-like structure migrating upward along the coral (Fig. 6L–N; compare Figs. 4E, 5F–H).

(5) More than one coral settled on the same gastropod shell. In matters of the upper pore, cases 1 and 3 can be combined: the coral next to the natural shell aperture having formed a pore whereas the more distant coral did not and remained unmodified. However, in this case two corals representing different generations settled next to the natural aperture (one after the death of the other), both may have developed an upper pore (Fig. 6G, K; compare Fig. 3A–C).

(6) Coral sitting at one end of an elongate scaphopod shell (or other elongate tubular structure) with an aperture at each end. As long as one end is still open, no deviated upper pore is formed by the coral settled at the opposite end (Fig. 5A, B; compare Fig. 5C).

Discussion

Arguments for an Albian scleractinian-sipunculan association

Several attributes of *Heterocyathus priscus* provide evidence that it lived together with a sipunculan worm. These characteristic features are found in Recent scleractinian-sipunculan partnerships involving various *Heterocyathus* and *Heteropsammia* species and are listed below:

(1) Recent *Heterocyathus* and *Heteropsammia* species encrust free, small shell or tube substrates and live on soft bottoms. It is widely acknowledged that the coral and sipunculan partners benefit from the cohabitation. The coral is dragged over the sediment surface as the sipunculan probes and feeds in the sediment (e.g., Bouvier 1894; Feustel 1965; Goreau & Yonge 1968; Yonge 1975; Gill & Coates 1977; Fisk 1981, 1983; Hoeksema & Best 1991).

(2) These Recent corals are solitary and encrust a shell or tube substrate except for an orifice that is kept open. Keeping an orifice open even when the whole shell is thickly encrusted by the coral is of vital importance for the sipunculan housed in the shell, as recognized by Bouvier (1894). There is no example of a shell that has its aperture entirely sealed. In cases where the sipunculan dies the aperture could, in principle, be sealed, but the coral, deprived of its symbiont, is condemned too, as has been shown experimentally by Fisk (1981). Significantly, in the particular case of *Heterocyathus japonicus* settled on the hind end of a live *Fissidentalium vermedei* shell, a vital orifice for the scaphopod has also to be kept open (Zibrowius 1998).

(3) Recent *Heterocyathus* and *Heteropsammia* are able to produce a tube-like extension of the original substrate. The symbiotic relationship starts when a coral larva

pod shell. Shell aperture slightly narrowed by the coral (no sipunculan extension-tube); upper pore (arrow on E) migrated upward, at end of chimney-like structure an extension of shell siphon. Three juveniles (arrows on F) attached to gastropod shell. G, K. MNHN-BIM/4, two corals representing different generations settled next to the natural aperture (one after the death of the other); both developed an upper pore (arrows on K). H, I. MNHN-BIM/2 with orifice on short extension tube from shell aperture and chimney-like pore formed from a hole near shell apex (arrow on L). L–N. MNHN-BIM/5 with orifice on tubular extension and pore on chimney-like structure originating from siphon. N. Shell cut in siphon plane, sipunculan orifice in the narrowed shell aperture and pinched off pore at the siphon end.

settles on a suitable substrate already inhabited by a sipunculan. Since the sipunculan also grows, the shell may become too small to shelter it, but unlike hermit crabs, the worm does not need to move to a larger housing. On the contrary, the coral can provide the necessary protection by growing around the protruding worm to form a sclerenchyme extension in continuation of the shell. This can happen in two ways. Either the extension built by the coral is a simple tube-like prolongation that points away from the shell (i.e., monoporous type, as in some *Heterocyathus* but not *Heteropsammia* species; Fig. 1A), or the resulting prolongation is coiled in a spiral and is totally incorporated into the corallum which tends to be sub-cylindrical in its upper part and to have a more or less bulging ridge around its base (i.e., polyporous type as in some *Heterocyathus* and all *Heteropsammia* species; Fig. 1B¹). The Albian coral represents the monoporous type.

(4) These Recent corals have the same type of annulation on the inner wall of the coral-built extension as found in the Albian coral (Fig. 4B, D), most likely related to accretion phases of the epitheca.

(5) A pore located above and away from the orifice, as frequently observed in the Albian coral (Figs. 3B, 4C, E, 5F, G), also occurs in various (not all) Recent species of *Heterocyathus* (but not *Heteropsammia*).

According to the original description by Cheng (1971), all specimens of a large series of *Heterocyathus mai* from Taiwan invariably had an orifice and an upper pore, briefly commented on by the author. Various specimens illustrated by Cheng (1971: figs. 1: 2–9, 2: 1–4, 10) are in the right position to exhibit this situation clearly.

A pore as in *H. mai* also characterises a closely related form from the Philippines

Observations on this form are presented above in the Recent equivalents section and are discussed below under Formation and function of the pores. Hoeksema & Best (1991) illustrated a series of five specimens from Sumatra, identified as *Heterocyathus alternatus*. At least two of them (their fig. 12b, c) are shown in a position that reveals the upper pore, but which was not commented on by the authors. Darrell & Taylor (1993: p. 193, fig. 3.13) mentioned a similar situation for *Heterocyathus sulcatus* from the South China Sea ('two small subcircular holes'; in fact an earlier stage, the two holes not yet being widely separated; see Formation and function of the pores). Zibrowius (1998: p. 331, figs. 19, 22–24, 25–26) attracted attention to the pore ('upper smaller second orifice') that can be observed in *Heterocyathus japonicus* from Japan. It was also found in the re-examined lectotype and recognized in the specimen illustrated by Ikeda (1922: figs. 2, 4), and possibly the one illustrated by Satô (1930: pl. 3, fig. 14). Likewise, that type of pore was found to exist in four out of five syntypes of *H. lamellosus* from Japan, Ryu-Kyu Islands (Zibrowius 1998: p. 331, fig. 15).

Altogether, *Heterocyathus* partnerships of the monoporous type are known from a wide geographical area: Japan, the Philippines, Indonesia, and the north-western Australian shelf (we also refer here to unpublished observations not discussed in detail).

¹ An analogy to the coral-built extensions of the sipunculid tube are shell-like structures produced by some deep-sea anemones (e.g., *Stylobates aenus* Dall, 1903) and hydroids (e.g., *Janaria mirabilis* Stechow, 1921) to accommodate hermit crabs (see Dunn *et al.* 1980 and Cairns & Barnard 1984, respectively). Also some bryozoans symbiotic with hermit crabs construct tubular extensions of the gastropod shell inhabited by the crab (see Taylor 1991, 1994).

The upper pore as characterised above is typical of partnerships where the coral-built extension is tubular and points away. When the coral-built extension is coiled in a spiral and is entirely incorporated into the corallum, pores in variable number (from one to many) generally occur on the lower side of the corallum and/or low on the lateral side (polyporous type). This situation is also known from some Tertiary fossils but not from any Cretaceous one.

Although there is a very high likelihood that the Albian coral had a sipunculan symbiont, it would be extremely difficult to exclude that the symbiont belonged to a different biological group. For example, Vermeij (1987: pp. 240–255) listed a wide diversity of animals ('conchicoles') that can inhabit empty mollusc shells.

Formation and function of the pores

Concerning the formation and function of the upper pore in the Albian partnership we have the same questions that have been posed previously by various authors who have investigated Recent scleractinian-sipunculan partnerships. Since no experimental work has yet been done concerning formation and function of the upper pore (monoporous type) and the series of pores (polyporous type) all proposed explanations are speculative.

Ideas concerning pore formation seem to cover only the polyporous type: (1) the series of pores are 'perforated' by the sipunculan using 'minute asperities which beset the proboscis' (Tenison-Woods 1880: p. 298); (2) formed by the coral when growing around extensions of the sipunculan (Jousseume in Bouvier 1895); interestingly, sipunculan appendices implied by that author do not exist (Cutler 1994); (3) pinched off from the orifice during growth (Sluiter 1902); or (4) bored into the corallum by some other organism (Schindewolf 1959; chemical dissolution has been excluded by Jousseume in Bouvier (1895) and by Schindewolf (1959)).

The main theory regarding pore function refers to water circulation within the sipunculan living quarters and was put forward for both the upper pore (monoporous type: Ikeda 1922) and the series of pores (polyporous type: Feustel 1965). Another idea was that sipunculan defecates through pores close to the orifice (in the polyporous type; Semper 1880; Sluiter 1902). It has also been argued that the pores may house some still unknown boring organism (Schindewolf 1959), or that the coral could release special charges of nematocysts from these pores in order to protect the sipunculan partner (firing a broadside! – polyporous type; Bourne 1905: p. 230).

Adopting the hypothesis of the upper pore or the series of pores being related to water circulation (presumably effluent exits), and referring to a large series of Recent specimens from the Philippines closely related to *H. mai* (above, under Recent equivalents), we infer how the pores in the corallum are formed.

Analysing various situations, we speculate that a pinched off part of the aperture or a hole surrounded by coral tissue and canalising water exchange tends to be transformed into a chimney-like structure if there is no other larger opening still free of coral cover. The transformation of such corallum-surrounded openings extended into a chimney is a matter of balance between the coral tissues' tendency to spread and the deviating water flow produced by the sipunculan.

Fossil record of scleractinian-sipunculan associations

Fossil corals inferred to have lived in symbiosis with a sipunculan have been reported from the Tertiary and the Cretaceous of widely distant areas.

Tertiary fossils of *Heterocyathus* and *Heteropsammia* are well documented from Japan, Taiwan, the Philippines and Indonesia, i. e., where both genera still occur nowadays (Semper 1872; Felix 1903, 1913; Gerth 1921, 1923, 1925, 1933, 1952; Makiyama 1926; Umbgrove, 1926, 1929, 1938, 1946, 1950; Yabe & Eguchi 1932, 1942; Sakakura 1935; Hu 1987, 1988). Some of these fossils are ascribed to species that are known also from the Recent, others to yet exclusively fossil nominate species (*Stephanoseris carthausi* Felix, 1913; *Heterocyathus elberti* Felix, 1913; *Heterocyathus elongatus* Hu, 1987; *Heterocyathus rembangensis* Gerth, 1922; *Heterocyathus sandalinus* Gerth, 1922; *Heteropsammia ovalis* Semper, 1872).

Given that during the Tertiary, up to the Miocene, various now exclusively Indo-Pacific coral genera were present in the Mediterranean – European area (Chevalier 1961), *Heterocyathus* and *Heteropsammia*, now exclusively Indo-Pacific, might be expected there too as Tethyan relicts. Indeed, there are two reported occurrences of *Heteropsammia* (none of *Heterocyathus*) in the European Tertiary (De Angelis 1894, Bouvier 1895). A closer look, however, reveals that they are not true *Heteropsammia* and one is *Heterocyathus*. We use this opportunity to analyse in more detail these erroneous *Heteropsammia* records, hoping that they will no longer uncritically be transmitted in the literature (they had still been referred to by Gill & Coates 1977; Darrell & Taylor 1993).

De Angelis (1894: p. 192, pl. 1: 8, 9) described an Oligocene coral from northern Italy as *Heteropsammia antiqua*, justifying its generic attribution by the typically dendrophylliid septal arrangement and the wall structure that are in fact features not exclusive to *Heteropsammia*. De Angelis' illustrations and photographs of the holotype (kindly shown by S. Barta-Calmus to H.Z.) indicate that the coral in question is not a *Heteropsammia*, but a *Balanophyllia*. Its shape (slightly compressed and irregular, elongate turbinata) precludes symbiotic relationship with a sipunculan. Note that the case of De Angelis' species is remarkably similar to that of the Recent *Heteropsammia elliptica* Tenison Woods, 1878, from New South Wales: strangely, this was first referred to *Heteropsammia*, but subsequently recognized by the same author as a *Balanophyllia* (see Tenison Woods 1878, 1880).

Bouvier's record (1895: pp. 11, 15, pl. 1: 23) from the Miocene (Burdigalian) of [Saint-Paul-les-] Dax, southwestern France is also problematical. He mentioned three fossil specimens (seen by him at the Paris museum) which were juveniles and not suitable for detailed description. His illustration shows a solitary coral similar to certain Recent Indo-Pacific *Heterocyathus* (not *Heteropsammia*) with strong unequal costae that overgrow an elongate gastropod shell, a distinct orifice having been kept open. Unfortunately, Bouvier's fossils could not be retrieved in 1994 at the Paris museum.

Records from the Cretaceous are sparse but cover a wide stratigraphic and geographic range. *Wadeopsammia nodosa* (Wade, 1926), from the Upper Cretaceous (Maastrichtian) of North America, shows a small opening to a cavity that may indeed have sheltered a sipunculan (detailed description in Wells 1933, considered as a dendrophylliid). Although a gastropod shell may be the original substrate of the coral,

this has still to be demonstrated, no specimen of *Wadeopsammia* having been sectioned. Only two specimens are known, one from Tennessee, and one from Texas (Wade 1926; Wells 1933). *Wadeopsammia* has been considered a junior synonym of *Heteropsammia* by Hoeksema & Best (1991), who advocated extensive synonymising throughout their paper. Gill & Coates (1977) considered this coral as the 'probably oldest known representative of the 'towed' mode of life'.

Even older is the inferred scleractinian-sipunculan association reported by Darrell & Taylor (1993) from the Santonian or Campanian Santa Marta Formation of James Ross Island, Antarctica. This association involves a coral that encrusts either small gastropod shells or straight, agglutinated (?) tubes. The provisional identification (by B.R. Rosen) as *Deltocyathus? complanatus* Squires, 1958, is not convincing, the Antarctic fossils showing distinct *Heterocyathus* features whereas Squires' (1958) New Zealand species is described and illustrated as being unattached. Reinvestigation of the Antarctic specimens by us proved that one of them (shown in basal view by Darrell & Taylor 1993: fig. 8) has an upper pore thus fits well into characteristics of monoporous *Heterocyathus*.

Noetling (1885: p. 10, pl. 1: 5, 5a) reported Cenomanian corals from Baltic glacier erratics (probably former East Prussia) as of uncertain generic attribution (*Anthozoorum* gen. inc.). The corals encrust elongate gastropod shells and produce a tubular extension. These distinct *Heterocyathus* features passed unnoticed until Löser & Stolarski (1997) inferred its symbiosis with a sipunculan.

The best known fossil examples of scleractinians interpreted as hosts for sipunculans are solitary dendrophylliids or caryophylliids. The paleontological literature reports two cases of colonial scleractinians as putative associates of sipunculans (discussed below).

Symbianguia vaughani (Weisbord, 1971), see also detailed description in Wells (1973), from the Miocene of Florida and referred to the family Rhizangiidae, encrusts small gastropod shells, preserving but a small orifice, as do the solitary *Heterocyathus* and *Heteropsammia*, for the needs of their symbiont. By analogy, Wells concluded that *S. vaughani* lived associated with a sipunculan. Indeed, the size of the encrusted elongate narrow shells and the size of the narrow orifice suggests a sipunculan as the partner whereas the inferred partner of the colonial *Septastrea marylandica* (Conrad, 1841) on larger shells, from the Florida Pliocene, was a hermit crab (Darrell & Taylor 1989).

Porites convivatoris Foster, 1986 (family Poritidae), from the Upper Miocene and Lower Pliocene of the Dominican Republic (Antilles), has been described on the basis of many small ellipsoidal colonies, all containing a calcareous tube that extends down the long axis of the colony. A sipunculan symbiont had been inferred (Foster 1986) simply because of the coral surrounding an inner tube. Counterarguments are that a sipunculan partner would have had its housing orifice well above the sediment surface (in fact in the centre of the end of the elongate colony) and that on one side of the dragged colony polyps would have been in direct contact with the sediment.

Historical and systematic context

The first more detailed descriptions of solitary and as we know now, sipunculan associated solitary scleractinians are those by Milne Edwards & Haime in the middle of the

19th century. These authors, who had a deep impact on coral taxonomy, ascribed such corals to the genera *Heterocyathus* Milne Edwards & Haime, 1848, *Heteropsammia* Milne Edwards & Haime, 1848, *Psammoseris* Milne Edwards & Haime, 1851 and *Stephanoseris* Milne Edwards & Haime, 1851 (the latter two variously synonymised with the former by later authors).

Since *Heteropsammia* is a typical dendrophylliid (= eupsammiid *sensu* Milne Edwards & Haime) with a porous skeleton and distinct Pourtalès plan of septal arrangement, whereas *Heterocyathus* with its non-porous skeleton was considered as a caryophylliid (= turbinoliid *sensu* Milne Edwards & Haime), subsequently studied corals associated with sipunculans have been referred to one or the other genus, simply on the basis of being a dendrophylliid or not.

Representatives of *Heteropsammia* are homogenous in terms of skeletal architecture. They occur throughout the Indo-West Pacific, but not in the eastern Pacific. Their geographic area largely coincides with that of tropical coral reefs. They live from very shallow water (a few meters only) to depths, depending on local circumstances, down to some 50 to 100 m. The literature comprises some 8 nominate Recent and one nominate fossil (Tertiary) species of what we now recognize as true *Heteropsammia*. Various and often extensive synonymies have been proposed, most recently by Hoeksema & Best (1991). An exhaustive revision is still needed.

The situation of *Heterocyathus* is more complicated. Corals conventionally referred to this genus (being not dendrophylliids) are strikingly diverse in terms of skeletal architecture. The type species is *Heterocyathus aequicostatus* Milne Edwards & Haime, 1848 (subsequent designation by Milne Edwards & Haime 1850). Its holotype (Milne Edwards & Haime 1848: p. 324, pl. 10: 8) is an adult characterised by having totally incorporated a shell substrate and having a series of pores in the lower part of the lateral side (polyporous type of the scleractinian–sipunculan association as distinguished and illustrated herein, Figs. 1B, 6A–D). Forms similar to the holotype specimen are widely distributed in the Indo-Pacific, but records under the name *H. aequicostatus* do not always conform to this type of organisation because of frequent confusion with other species. Other forms commonly referred to *Heterocyathus* are markedly different not only in the sipunculan housing (exposed gastropod shell), but also, in septal and costal ornamentation, septal projections, and strong expression of the Pourtalès plan (various forms illustrated by Cheng 1971; Hoeksema & Best 1991; Zibrowius 1998; Cairns 1998, 1999). These forms may correspond to the monoporous type of the scleractinian–sipunculan association as distinguished herein. A further example of such *Heterocyathus sensu lato* is the form from the Philippines closely related to Cheng's *H. mai* illustrated herein (Figs. 4D, 5A, B, 6E–N) and used for comparison with the Albian *Heterocyathus priscus*.

Heterocyathus sensu lato occurs today throughout the Indo-Pacific: from the Red Sea and South Africa (Natal) to northern Japan, the Fiji Islands and New South Wales and even the eastern Pacific (Gulf of California and further south along the Mexican coast), but the Hawaiian Islands and New Zealand seem to be outside its range. Approximately 16 nominate species have been described from the Recent fauna (some originally referred to the genera *Stephanoseris* and *Psammoseris*) and 5 nominate species were based on Tertiary fossils. Various and often broad synonymies have been

proposed in the literature, most recently again by Hoeksema & Best (1991), whereas Zibrowius (1998) and Cairns (1999) argued against some of these synonymies.

The marked diversity of *Heterocyathus* sensu lato raises the question as to whether separation into different genera would be justifiable. Our distinction herein of the monoporous and polyporous types may provide guidelines for such a revision. Resolving this problem should be the purpose of another paper. Pending such a revision, the fossil coral from the Albian is here included under *Heterocyathus* in the conventionally broad sense.

Evolutionary notes

In common understanding symbiotic relationships between solitary corals and sipunculans developed independently in caryophylliids and dendrophylliids and thus are an example of convergent coevolution (Hoeksema & Best 1991). The data discussed herein suggest that scleractinian-sipunculan partnerships appeared not earlier than the Cretaceous (considering Albian *Heterocyathus priscus* the oldest member of the symbiotic caryophylliids, and Maastrichtian *Wadeopsammia* as the oldest symbiotic dendrophylliid). Though the scleractinian record goes back at least to the Middle Triassic and sipunculans possibly existed as early as the Palaeozoic (trace fossils; Cutler 1994), no Triassic or Jurassic scleractinians are thought to have been involved in partnerships with sipunculans. One may thus speculate that some general biological or environmental prerequisites of the scleractinian-sipunculan partnerships were not fulfilled until the Cretaceous.

Plausible prerequisites could be: (1) presence of empty shells available to corals and sipunculans for settlement; (2) no rejection reaction (avoidance or defense) between the two organisms; (3) behaviour of both partners (feeding, reproduction, etc.) not detrimental to one another; (4) ability of the coral to produce extrathecal skeleton that could overgrow the substrate and subsequently produce an extension of the sipunculan chamber; (5) small-sized corallum that would not interfere with easy transport of the symbiotic buildup.

Condition 1 seems to be fulfilled throughout the Mesozoic, at least in some environments. Conditions 2 and 3 cannot be tested in the fossil record. Condition 4, implying the presence of an edge-zone, i. e., extrathecal skeletogenous tissue, would have been the main influence on the shape of the symbiotic buildup. Non-epithecate corals able to overgrow a substrate most probably appeared late in the Jurassic, i.e., rhipidogyrids producing rather large and massive coralla similar to modern eusmiliines, and caryophylliids having small coralla (Roniewicz & Stolarski 1999). Solitary dendrophylliids that are also able to overgrow the substrate appeared in the Late Cretaceous, possibly as descendants of caryophylliids (Wells 1956). Fulfilling condition 5, small-sized caryophylliids and dendrophylliids able to overgrow the substrate were 'pre-adapted' to enter a symbiotic relationship. Benefits for the scleractinian and the sipunculan of the initial relationship further enhanced development of the partnership.

In environments with a high sedimentation rate it may be critical for coral larvae to find a suitable substrate and to avoid being buried during growth (compare Fisk 1983: p. 293). Gastropod shells inhabited by sipunculans and thus kept at the sediment surface are substrates relatively safe from burial. Sipunculans in a shelter that would 'grow' thanks to coral's own growth do not need to move over to a larger shell as her-

mit crabs inhabiting simple shells have to do². The degree of dependence between the two organisms may vary in function of the abundance of sipunculan predators and the rate of sedimentation. Given that no experimental studies have been done, one can only speculate that the sipunculan housed in a shell exerts some attraction for the coral larva. Finding juvenile *Heterocyathus* attached to adults of the same species, both in the Recent and fossil record, could be an argument for supporting this hypothesis. But even then the possibility of gregarious behavior of the planula (i.e., attraction to the conspecific adult) or a shortage of suitable substrates could not be ruled out.

Occurrence of the monoporous type of partnership starting in the Cretaceous and of the polyporous type starting in the Tertiary suggests that the former represents the evolutionarily earlier, less complex state of the symbiosis.

In fact, in the polyporous type of partnership the sipunculan is protected constantly during all its life, as suggested by the presence of a small, often juvenile gastropod shell incorporated at the beginning of the spiralled sipunculan chamber. Conversely, in the monoporous type, the shell is often of larger size and it is difficult to visualize that it was inhabited by the sipunculan from the worm's earliest stage. This would suggest that the sipunculan had settled in a shell only at a more advanced stage after a period of free life, or had moved over from a smaller shelter. A different sipunculan colonisation behavior is suggested by Taylor's observation (1991: pp. 491–492). He found that in analogous bryozoan pagurid hermit crab symbioses, a sipunculan can cohabit with the crustacean within the chamber of the bryozoan-encrusted gastropod shell. In such a case, a large shell size should not prevent a juvenile sipunculan from colonising the shell, given that another larger mobile partner already occupies it. Applied to the scleractinian-sipunculan symbiosis this, however, is a theoretical situation that needs to be tested in nature.

The monoporous type, with the straight extension pointing away from the shell, results when larger shells are outgrown and the coral provides the extension for a sipunculan that tends to keep straight. Conversely, the polyporous type results when small shells are outgrown by the sipunculan at an early stage and the sipunculan maintains coiling. If this statement is not an excessive generalisation, it would suggest that the monoporous and the polyporous types depend on different sipunculan behaviour. Is behavior of the sipunculan conditioned by the size of inhabited shell? Do different species of sipunculans behave differently? In early times authors occasionally distinguished different sipunculan partners depending on the genus of the coral partner, i.e., *Heterocyathus* or *Heteropsammia* (Deshayes 1863; Bouvier 1895; see introductory historical notes in Sáiz Salinas 1986). Later, it was generally assumed that only one sipunculan species was involved with the two genera (e.g., Sluiter 1902; Sáiz Salinas 1986; Cutler 1994). A large field remains open for experimentation with these associations.

Although suggestions of convergent coevolution of the *Heterocyathus*- and *Heteropsammia*-sipunculan partnerships prevail in modern literature, the remarkable morphological similarity concerning the polyporous type may not only reflect similar modifications in response to a similar stimulus (e.g., Rice 1976). In fact, the main char-

² It is commonly assumed that in analogous bryozoan-hermit crab symbioses (see footnote on p. 12), the constantly growing bryozoan colony eliminates the need for the hermit crab to change shells. However, as pointed out by Taylor (1994: p. 184) this has never been proven in natural populations and shell exchanges do occur in hermit crabs symbiotic with bryozoans living in aquarium tanks.

acters making the dendrophylliid and caryophylliid partnerships so similar are those which are prerequisite for the symbiosis (encrusting ability, size). On the other hand, characters like the Pourtalès plan of septal arrangement and the porous skeleton are common to all *Heteropsammia* and certain species of *Heterocyathus* sensu lato (e.g., *H. hemisphericus* Gray, 1849, as indicated by Cairns 1998; to a lesser degree *Heterocyathus japonicus* Verrill, 1866, as mentioned by Zibrowius 1998). This may even point to phylogenetic relationships and suggest that symbioses with sipunculans evolved only once in scleractinians.

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