RELATIONSHIP BETWEEN SPONGES AND A TAXON OF OBLIGATORY INQUILINES: THE SILIQUARIID MOLLUSCS

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Some coenogastropod molluscs are adapted to living embedded in a matrix of sediment, coral or sponge tissue. In the latter case the siliquariid molluscs are obligatory inhabitants of the sponge hosts. Siliquariidae is a small family with three extant genera with circum-tropical and temperate distribution. Information on their association with Porifera is so far limited to 15 records. The present study analyses 35 sponge species hosting siliquariids from the Mediterranean Sea, E. Atlantic, New Zealand, Philippines and New Caledonia, living in a water depth between 10-440 m. A close species-specific association was not found, although only a restricted number of sponge families host siliquariid molluscs. From these data it is apparent that siliquariids prefer hosts with a compact and rigid sponge skeletal structure, produced by a radial organisation and/or high spicule density. Commensal siliquariids show different growth rates. When their larvae settle on the sponge surface larval shells (protoconchs) are partially overgrown by the host sponge. As soon as the mollusc begins development it opens a slit along its entire length, hence commencing close interactions with the sponge. The mollusc is able to modify the shape of the longitudinal slit, adapting it to the sponge aquiferous system by transforming the slit into a series of contiguous holes that communicate with the sponge's excurrent canals. Based on the trend that there is a successively decreasing diameter of these canals, it seems evident that the siliquariid conveys self-drained water into the sponge incurrent canal system. This behaviour was studied using x-ray photography and casts obtained from resin injections into the aquiferous system. It is clear that the mollusc obtains most benefit from this association, achieving: protection against predators, defence from sediment clogging, and increased feeding efficiency. Minor benefits are obtained by the sponge host: increased water inflow with an energy saving, and a secondary source of food from the mollusc's expelled water. The sponge does not seem to be negatively affected by the siliquariid presence and is able to maintain, through its plasticity, its original skeletal structure. This form of strict and integrated association between filter-feeders may well be interpreted as commensalism and probably as facultative mutualism. ☐ *Porifera, siliquariid molluscs, association, commensalism, symbiosis, adaptations, behaviour.*

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Symbiotic associations between sponges and other organisms involve a diversity of taxa, from bacteria to large crustaceans (see review by Sarà et al., 1998), whereas other associations, less integrated or intimate, involve other sponge dwellers which, according to cases, may be regarded as commensals or inquilines. Most studies on these latter associations (e.g. Pearse, 1932; Pansini, 1970; Bacescu, 1971; Rützler, 1975; Koukouras, 1996) have examined the descriptive aspects of the association whereas only a few have focused on the interaction between host and commensal (Forbes, 1966; Connes et al., 1971; Uriz et al., 1992).

Concerning molluscan commensals, natural suspension feeders such as bivalves are most frequently associated with sponges (e.g. *Chlamys varia* in *Halichondria panicea* (Forester, 1979), *Hyatella artica* in *Geodia cydonium* (Santucci, 1922), *Ostrea permollis* in *Stelletta grubii* (Forbes, 1966)), whereas associations between sponges and gastropods are rare and restricted only to sessile gastropods with a filter feeding strategy that requires important shell adaptations (Seilacher & Gunji, 1993; Savazzi, 1996). The shells of gastropods living embedded in sponges do not exhibit a fixed geometrical constraint but a 'heteromorph' growth pattern (Morton, 1951, 1955; Gould, 1966; Savazzi, 1996; Schiaparelli

et al., 1998), as seen in several Vermiculariinae and in all slit-bearing Siliquariidae (genera *Tenagodus* and *Pyxipoma*).

The obligatory association of these molluscs with sponges is supported by the absence of any scar on the shells from attachment to a substrate (Deshayes, 1864; Savazzi, 1996). Slit-bearing Siliquariidae represent a separate unit from other uncoiled gastropods (as Vermetidae, Vermiculariinae and *Stephopoma*, the third siliquariid genus), due to the presence of the shell's longitudinal slit that drains the incoming water-flow from the shell aperture. In the adult mollusc the slit is only partially open and functional, with partial closure due to secondary carbonate deposition. During its growth the living mollusc shifts its position along the shell aligning the mantle cavity opening with the functional apertures of the slit. As for most ciliary feeders the water incurrent flow is produced by means of cilia on numerous filamentous gills; these gills also retain food particles (Morton, 1951).

According to Bieler (1992, 1996) three genera are presently included in the family Siliquariidae: *Pyxipoma* Mörch, 1861, with a short longitudinal slit and a smooth shell; *Tenagodus* Guettard, 1770, with a longer slit and either a smooth or a spiny shell; and *Stephopoma* Mörch, 1861, which is devoid of slit and shows a vermetid-like ecology. Siliquariid molluscs have a wide range of shell coiling patterns with whorls developing either on a single or on several planes. In addition, some *Tenagodus* species are able to produce a series of transversal cracks in their smooth shells, thus allowing adjustment to the curvature of shell coils (Savazzi, 1996). This capacity to modify adult shell shape is unique amongst molluscs (Savazzi, 1996).

Little is known about the biology, ecology and geographical distribution of these obligate sponge dwellers because most reports in the literature concern descriptions of empty shells or shell fragments (Bieler & Hadfield, 1990). Virtually nothing is known about their reproduction, larval longevity and dispersal capacity. In addition, siliquariids are rather rare and live mainly at considerable depths. For these reasons, their associations with host sponges have never been extensively studied: only Morton (1955) remarked on the association between the mollusc slit and the sponge aquiferous system, and Savazzi (1996) hypothesised the existence of a

unidirectional water outflow from the mollusc into the sponge aquiferous system.

This study aims to clarify the different aspects of the sponge-siliquariid association, notwithstanding the lack of access we have to living material available for study. More specific topics involving the functional morphology of siliquariid molluscs are treated in a separate paper (Schiaparelli et al., in preparation).

MATERIALS AND METHODS

To date only 35 sponge specimens associated with siliquariid molluscs were studied, collected from the W Mediterranean, E Atlantic and the Pacific area including Philippines, Japan, New Caledonia and N New Zealand. Most of this material was collected by the Muséum National d'Histoire Naturelle, Paris from several deep-water expeditions, and kindly trusted us for study. Several small lots of specimens were also obtained from other sources (Museo di Zoologia of Bologna and private collections). Most of the studied material comes from relatively deep waters (10-550m depth).

All the massive sponge specimens with siliquariids embedded in their bodies were carefully studied in toto. X-ray photographs of some *Penares* and *Spongosorites* specimens were made using health diagnostic X-ray facilities, to ascertain the distribution and alignment of molluscs within the sponge body. Casts of the water flow routes were made by injecting a setting resin into both the shell's main aperture and the sponge's oscule in alcohol preserved specimens and, after the compound had set, by dissolving the sponge body by soaking it in HCl (Bavestrello et al., 1988). Much better results would have been obtained through *in situ* application of resin into living specimens, but this has not yet been possible due to the restricted material available to us.

Sub-samples of the two associated organisms were then separated for species identification. Spicules were prepared by dissolving pieces of sponge in nitric acid in a vial, then dehydrated and mounted either on slides with Eukitt resin or directly on stubs. The skeletal arrangement was studied by hand cut (tangential and transversal) sponge sections.

The abundant siliquariid material available, allowed us to leave specimens intact to study in toto and to dissect and prepare the main diagnostic parts for ultramicroscopy (protoconchs,

TABLE 1. Literature of sponges associated with siliquarid molluscs. References refer to papers reporting whole animals, not just empty shells.

Sponge Species	Mollusc Species	Locality	Depth	Reference
Erylus amorphus Burton, 1926	unidentified Siliquariid	South Africa	-	Burton, 1926
Erylus burtoni Lévi & Lévi, 1983	unidentified Siliquariid	New Caledonia	425-430m	Lévi & Lévi, 1983b
Erylus carteri Sollas, 1888	unidentified Siliquariid	Gulf of Manaar	-	Lévi & Lévi, 1983b
Erylus geodioides Burton & Rao, 1932	unidentified Siliquariid	Mergui Archipelago	119m	Burton & Rao, 1932
Erylus nigra Bergquist, 1968	unidentified Siliquariid	New Zealand	129m	Bergquist, 1978
Erylus proximus Dendy, 1916	unidentified Siliquariid	Cargados	55m	Dendy, 1916
Penares schulzei (Dendy, 1905)	unidentified Siliquariid	New Caledonia, Ceylon	182-430m	Dendy, 1905
Penares sp.	*Pyxipoma weldii* (Tennison Woods, 1876)	New Zealand	-	Morton & Miller, 1968
Racodiscula sceptrellifera (Carter, 1881)	*Tenagodus cumingii* (Mörch, 1861)	Indian Ocean	27-55m	Annandale, 1911
Racodiscula sceptrellifera (Carter, 1881)	*Tenagodus trochlearis* Mörch, 1861	Indian Ocean	-	Annandale, 1911
Siliquariaspongia japonica Hoshino, 1981	*Tenagodus cumingii* Mörch, 1861	Japan	Intertidal	Hoshino, 1981
Spongosorites topsenti Dendy, 1905	*Tenagodus muricatus* (Born 1778)	Indian Ocean	55-69m	Annandale, 1911
Spongosorites ruetzleri (Van Soest & Stentoft, 1988)	unidentified Siliquariid	Barbados	108-153m	Van Soest & Stentoft, 1988
Spongosorites siliquaria Van Soest & Stentoft, 1988	unidentified Siliquariid	Barbados, Jamaica	108-170m	Van Soest & Stentoft, 1988
Unidentified (?) sponge	*Tenagodus modestus* Dall, 1881	Bermuda	-	Dall, 1881
Unidentified (?) sponge	*Tenagodus obtusus* (Schumacher, 1817)	South Africa	-	Barnard, 1963
Unidentified sponge	*Pyxipoma lacteus* Lamarck, 1818	Indian Ocean	-	Morch, 1860
Unidentified sponge	*Pyxipoma weldii* (Tennison Woods, 1876)	New Zealand	-	Morton, 1951
Unidentified sponge	*Tenagodus anguinus* (L., 1758)	Philippines	2-3m	Savazzi, 1996
Unidentified sponge	*Tenagodus armatus* Kuroda et al., 1971	Japan	50-100m	Kuroda et al., 1971
Unidentified sponge	*Tenagodus bernardi* Morch 1860	? Senegal	-	Gould, 1966
Unidentified sponge	*Tenagodus chuni* Thiele, 1925	South Africa	40-155m	Barnard, 1963
Unidentified sponge	*Tenagodus cumingii* Morch, 1860	Philippines	-	Morch, 1860
Unidentified sponge	*Tenagodus cumingii* Morch, 1860	Western Pacific	10-100m	Kuroda et al., 1971
Unidentified sponge	*Tenagodus obtusus* (Schumacher, 1817)	Mediterranean	-	Philippi, 1836
Unidentified sponge	*Tenagodus squamatus* Blainville, 1827	Bermuda	549-732m	Gould, 1966
Unidentified sponge	*Tenagodus squamatus* Blainville, 1827	Bermuda	732m	Abbott, 1974
Unidentified sponge	*Tenagodus wilmanae* Tomlin, 1918	South Africa	150m	Kenseley, 1973
Unidentified sponge	*Tenagodus wilmanae* Tomlin, 1918	South Africa	-	Barnard, 1963

opercula and radulae). A Philips 515 microscope was used for SEM observations.

RESULTS

Twenty nine records of sponges associated with siliquariids have been recorded in the literature (Table 1), but the identification of both partners was complete only in five cases. Nevertheless, from these data, 13 sponge species in total, belonging to 6 genera and 5 families (Ancorinidae, Coppatiidae, Geodiidae, Halichondriidae, Theonellidae) have been identified (Table 1). By comparison, in the present study, preliminary identifications of 35 sponge specimens associated with siliquariids differentiated 19 sponge species belonging to the same 5 families cited above (Table 2), in addition to a fragment of an unidentified horny 'keratose' sponge. Siliquariids studied belonged to 6 species of the genus *Tenagodus* and to a single species of *Pyxipoma* (Table 2). The taxonomic part of the study, including the description of several new species of both sponges and siliquariids, will be the object of future papers.

Geographic and bathymetric distributions of material showed that 5 specimens were from temperate and 30 from tropical regions, and 34 specimens out of 35 were collected at more than 50m depth (Table 2). A similar trend is shown in literature, with 11 temperate and 18 tropical records and 12 specimens out of 17, with known depths of collection, coming from waters deeper than 50m (Table 1).

In all cases but one the sponge specimens hosted a variable number of molluscs belonging to a single species. The exception is a sponge specimen from New Caledonia, collected around 230m depth, and tentatively attributed to the genus *Epipolasis*, that hosted two species of spiny *Tenagodus* that were also recorded in association with other sponge species, indicating that their association is facultative. Some siliquariids may be associated with as many as six different sponge species, as the case of the two spiny *Tenagodus* (*Tenagodus* sp.5 and *T.* cf. *anguinus*) (Table 2).

Different specimens of *Holoxea furtiva* Topsent from distant localities hosted slightly different siliquariid species. Two Mediterranean specimens from Sardinia and Tunisia were associated with *Tenagodus obtusus*, whereas a specimen from Cabo Verde hosted *T. senegalensis*. Different specimens of the same sponge species collected in the same area (e.g.

Spongosorites cf. *solomonensis*, *Spongosorites* sp.3 and *Topsentia* sp.1) may host different siliquariid species (Table 2).

Considering the five families of sponges that host these siliquariids, three types of skeletal patterns were distinguished: a radial structure in Ancorinidae, Coppatiidae and Geodiidae; a disordered structure in Halichondriidae, and the usual articulated, solid 'lithistid' structure in Theonellidae. Analyzing the distribution of siliquariids belonging to the genus *Tenagodus*, which has species with either smooth or spiny shells, we found a remarkable correlation with the sponge skeletal architecture. 1) Smooth *Tenagodus* species were always associated with sponges that had radial structure (Table 2). These molluscs were completely embedded in the sponge body with only the shell apertures protruding from the sponge surface (Fig. 1A). X-ray photographs showed that the direction of shell growth is straight, determined largely by the radial pattern of the sponge skeleton (Fig. 1B). According to the position of the shell apertures, which are almost flush with the sponge surface, it may be inferred that the growth rate of the associated organisms is nearly the same. This behaviour was observed only in small and medium sized siliquariid species with smooth shells. 2) Conversely, spiny *Tenagodus* species were always associated with sponges having disorderly arranged skeletons (Table 2). In these cases the molluscs were not completely embedded in the sponge body because part of the shell laid on the sponge surface (Fig. 1C). X-ray photographs showed that spiny siliquariids shorten as much as possible the ray of curvature of their first coils, and that a precise direction of shell growth cannot be defined (Fig. 1D). Shell uncoiling is more accentuated towards the sponge surface. The mollusc growth rate certainly exceeded that of the sponge when the shell develops on the host surface. The same behaviour was observed in large size smooth *Tenagodus* specimens (Fig. 2B), which, instead of laying on the sponge surface, raise the terminal part of their shells (Schiaparelli et al., in prep.).

Siliquariids associated with Theonellidae were completely entrapped among desmas. Here they are so constrained by the rigid skeletal structure that they are unable to transversally crack their shells, varying their shape as described by Savazzi (1996), and consequently obliged to grow very irregularly.
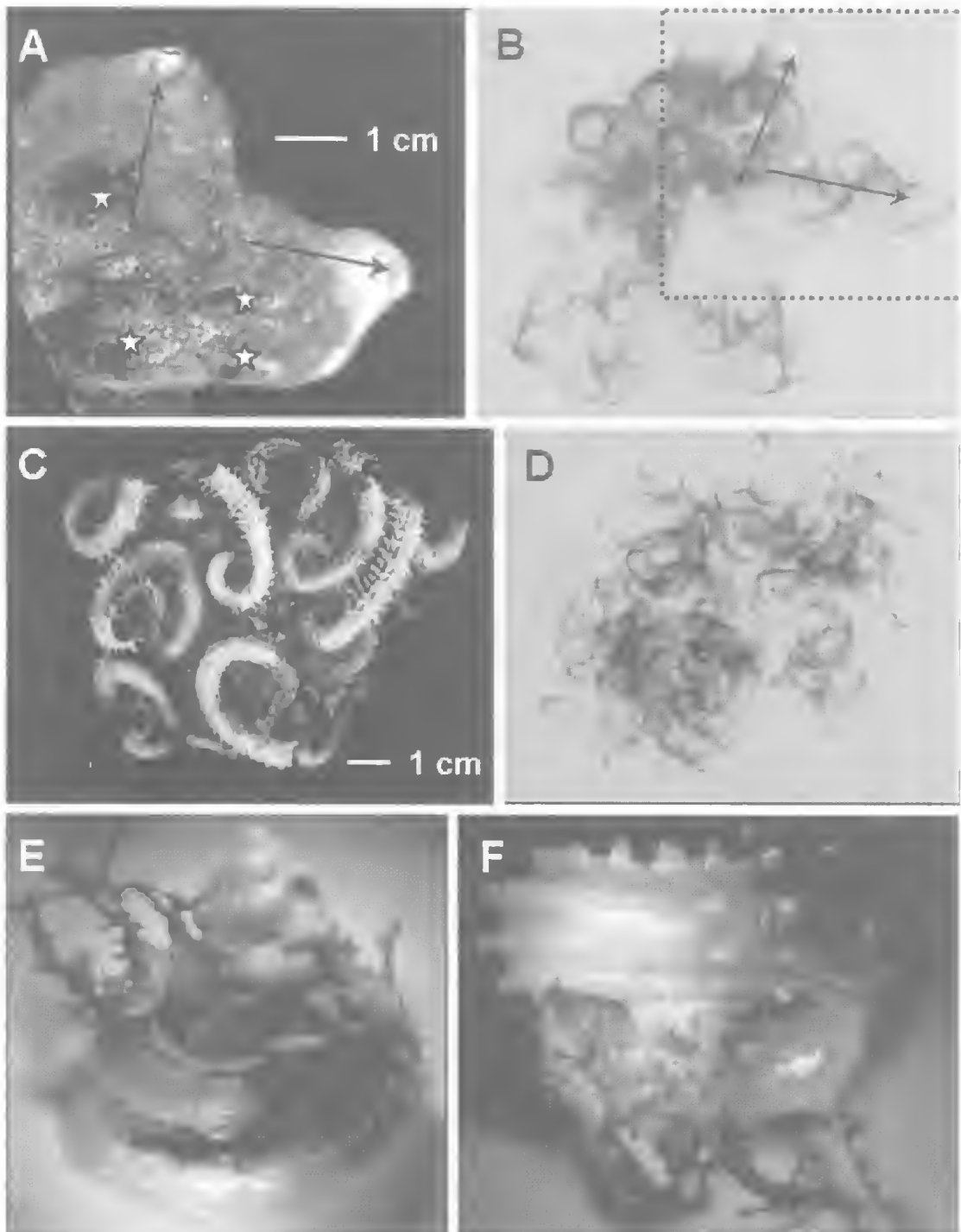
Siliquariid protoconchs (larval shells which

FIG. 1. Associations between siliquariids and sponges. A, Specimen of *Penares intermedia* (Dendy, 1905): the shell apertures are indicated by arrows, whereas the oscules are marked by stars. B, X-ray photograph of the same specimen of *P. intermedia* showing the associated siliquariids (*Tenagodus* sp. 4): the arrows mark the axes of two coiled shells. C, Specimen of *Spongosorites* sp.1 associated with *Tenagodus* cf. *anguinus*. D, X-ray photograph of *Spongosorites* sp.1. E-F, Two aspects of an aquiferous system cast of a *Topsentia* sp.1 specimen associated with *Tenagodus* cf. *anguinus*.

TABLE 2. List of sponge species associated with siliquarid molluscs. Different shades of grey refer to the sponge skeletal structure and to the external morphology of the shells.

Specimen	Sponge Family	Sponge Species	Mollusc Species	Locality	Depth
SI 23/30	Theonellidae	*Discodermia cf. laevidiscus* Carter, 1880	*Tenagodus* sp. 4	Philippines	92-97m
SI 13/31	Geodiidae	*Erylus* sp. nov.	*Tenagodus* sp. 4	New Caledonia	234-242m
SI 25	Geodiidae	*Erylus* sp. nov.	*Tenagodus* sp. 4	Philippines	92-97m
SI 33	Geodiidae	*Erylus nigra* Bergquist, 1968	*Tenagodus* sp. 4	New Caledonia	415m
SI 5	Geodiidae	*Geodia cf. parasitica* Bowerbank, 1873	*Tenagodus senegalensis*	Senegal	-
SI 4	Coppatiidae	*Holoxea furtiva* Topsent, 1892	*Tenagodus obtusus*	Italy	-
SI 1/2	Coppatiidae	*Holoxea furtiva* Topsent, 1892	*Tenagodus obtusus*	Tunisia	9, 32m
SI 3	Coppatiidae	*Holoxea furtiva* Topsent, 1892	*Tenagodus senegalensis*	Cabo Verde	55-60m
SI 97	Coppatiidae	*Jaspis* sp.	*Tenagodus ponderosus*	(?) Australia	-
SI 12/34	Ancorinidae	*Penares intermedia* (Dendy, 1905)	*Tenagodus* sp. 4	New Caledonia	430m
SI 19/26	Ancorinidae	*Penares* sp. nov.	*Tenagodus* sp. 4	New Caledonia	270-300m
SI 20	Ancorinidae	*Penares* sp. 1	*Tenagodus* sp. 4	Philippines	92-97m
SI 35	Ancorinidae	*Penares* sp. 2	*Pyxipoma weldii*	New Zealand	-
SI 8	Halichondriidae	(?) *Epipolasis* sp.	*Tenagodus cf. anguinus* + *Tenagodus* sp. 3	New Caledonia	234-242m
SI 15	Halichondriidae	*Spongosorites cf. salomonensis* Dendy, 1921	*Tenagodus cf. anguinus*	New Caledonia	243m
SI 32	Halichondriidae	*Spongosorites cf. salomonensis* Dendy, 1921	*Tenagodus* sp. 6	New Caledonia	440m
SI 7	Halichondriidae	*Spongosorites* sp. nov.	*Tenagodus* sp. 3	New Caledonia	242m
SI 16	Halichondriidae	*Spongosorites* sp. nov.	*Tenagodus* sp. 3	New Caledonia	300m
SI 9	Halichondriidae	*Spongosorites* sp. 1	*Tenagodus cf. anguinus*	New Caledonia	270-300m
SI 17	Halichondriidae	*Spongosorites* sp. 1	*Tenagodus cf. anguinus*	New Caledonia	260m
SI 27	Halichondriidae	*Spongosorites* sp. 1	*Tenagodus cf. anguinus*	New Caledonia	237-550m
SI 18	Halichondriidae	*Spongosorites* sp. 2	*Tenagodus* sp. nov. 2	New Caledonia	397-439m
SI 24	Halichondriidae	*Spongosorites* sp. 3	*Tenagodus cf. anguinus*	Philippines	92-97m
SI 29	Halichondriidae	*Spongosorites* sp. 3	*Tenagodus* sp. 5	Philippines	183-187m
SI 11	Halichondriidae	*Topsentia* sp. nov.	*Tenagodus* sp. 3	New Caledonia	233m
SI 14	Halichondriidae	*Topsentia* sp. 1	*Tenagodus* sp. nov. 1	Philippines	186-187m
SI 21	Halichondriidae	*Topsentia* sp. 1	*Tenagodus cf. anguinus*	Philippines	92-97m
SI 22	Halichondriidae	*Topsentia* sp. 1	*Tenagodus cf. anguinus*	Philippines	92-97m
SI 28	Halichondriidae	*Topsentia* sp. 2	*Tenagodus cf. anguinus*	New Caledonia	410-440m
SI 6	?	fragment of a horny sponge, dark violet	*Tenagodus maoria*	New Zealand	-

Sponges with radial skeletal growth	Sponges with disordered skeletons	Siliquariids with smooth shells	Siliquariids with spiny shells

are separated by a boundary (concave septum) from the adult shells, called teloconchs), have been observed on the surface of several sponge specimens. According to characteristics of their coils (number and size), they belong both to planctotrophic and lecitotrophic species (Schetelma, 1978). Planctotrophic larvae have been observed in *Tenagodus senegalensis* to settle preferentially near the mollusc slit, where they probably find the most suitable water-movement conditions. Recruits are covered by the host sponge and develop in the remaining space between the adult siliquariids.

The functional associations between sponges and associated molluscs were also ascertained by the study of casts. Resin injected into the oscule of a specimen of *Topsentia* sp.1 containing *Tenagodus* cf. *anguinus* came out from the main aperture of the shell and vice versa (Fig. 1F). Casts show that the water pushed by the mollusc ciliary movement seeps through the slit (Fig. 1E) and enters the sponge aquiferous system. There is a reciprocal morphological adaptation of the two associated organisms because the sponge moulds its aquiferous system on the continuous slit aperture and then the mollusc divides this simple slit into a series of holes (Fig. 2AD). Spicule tracts correspond to the carbonate pillars separating the holes (Fig. 2CD). The wide aquiferous system canals (0.6mm diameter) conveying water from the mollusc into the sponge, fit perfectly with the slit holes (Fig. 1E). Thereafter these canals divide either dichotomously or by emitting transverse branches (Fig. 1F). Their size decreases continuously up to a minimum detectable diameter of 0.1mm.

Casts, however, are interpreted as single moments of a continuous growth process which involves both the partners in the association. Particularly important is the shifting of the living mollusc, as far as it grows, towards the shell opening, which causes the moulding of a new part of a functional slit. The growth process also determines a rapid closure by carbonate deposition of the non-functional slit apertures behind the mollusc body: holes in *Tenagodus* (Fig. 2E) and a continuous slit in *Pyxipoma* (Fig. 2F). It was also observed that whenever an open part of the slit accidentally lost its sponge covering it was immediately closed by the mollusc.

DISCUSSION

A siliquariid mollusc living within a sponge has three primary needs: 1) to be at least partially covered by the sponge in order to get support and protection; 2) to have the water-outflow drained through the sponge body; and 3) to maintain the shell opening free for the water-inflow, laying on the sponge surface or variously raised. Such requirements may be fulfilled only by sponges with peculiar characteristics, as demonstrated by the restricted number of sponge taxa currently known to host siliquariids. Some of these characteristics may be tentatively identified as: a massive growth form, assuring an adequate volume to host the molluscs; and a solid structure, generally bound to a high spicule content, contributing to maintain a constant space ratio between the associated organisms, in order to guarantee a plain water outflow. A soft, elastic sponge which continually moves is probably less adapted to maintain a steady association – involving the aquiferous system - with a host dwelling in a rigid shell. The host molluscs, however, display a remarkable adaptive capacity to different situations as demonstrated by the fact that two species of siliquariids were found associated with six different sponge species. As a rule each siliquariid species colonises a single species of sponge (with the exception of the New Caledonian sponge mentioned above), with the number of successful mollusc recruits related to sponge size. Siliquariid recruitment is either through lecithotrophic larvae, which develop *in situ*, or planktotrophic larvae that are released into deep, relatively still waters, and probably do not disperse over large areas. Several factors may favour the recruitment of young siliquariids in this association. One of these is the combined pumping activity of the sponge and associated molluscs, that produces a water current from the surroundings towards the sponge surface which may attract the swimming larvae.

According to our observations it seems probable that the association between sponges and siliquariids is not species specific. This hypothesis is supported by the behaviour of *Holoxea furtiva*, a sponge with a wide geographic distribution that hosts two siliquariid species in geographically distant localities. Similarly, different specimens of the same sponge species in the same geographic locality host different siliquariids (e.g. *Spongosorites* cf. *salomonensis*, *Spongosorites* sp. 3 and *Topsentia* sp. 1), also support this contention.

From present knowledge the association between sponges and siliquariids seems to be relatively frequent in the tropics and in deeper waters – where the latter taxon is more abundant –
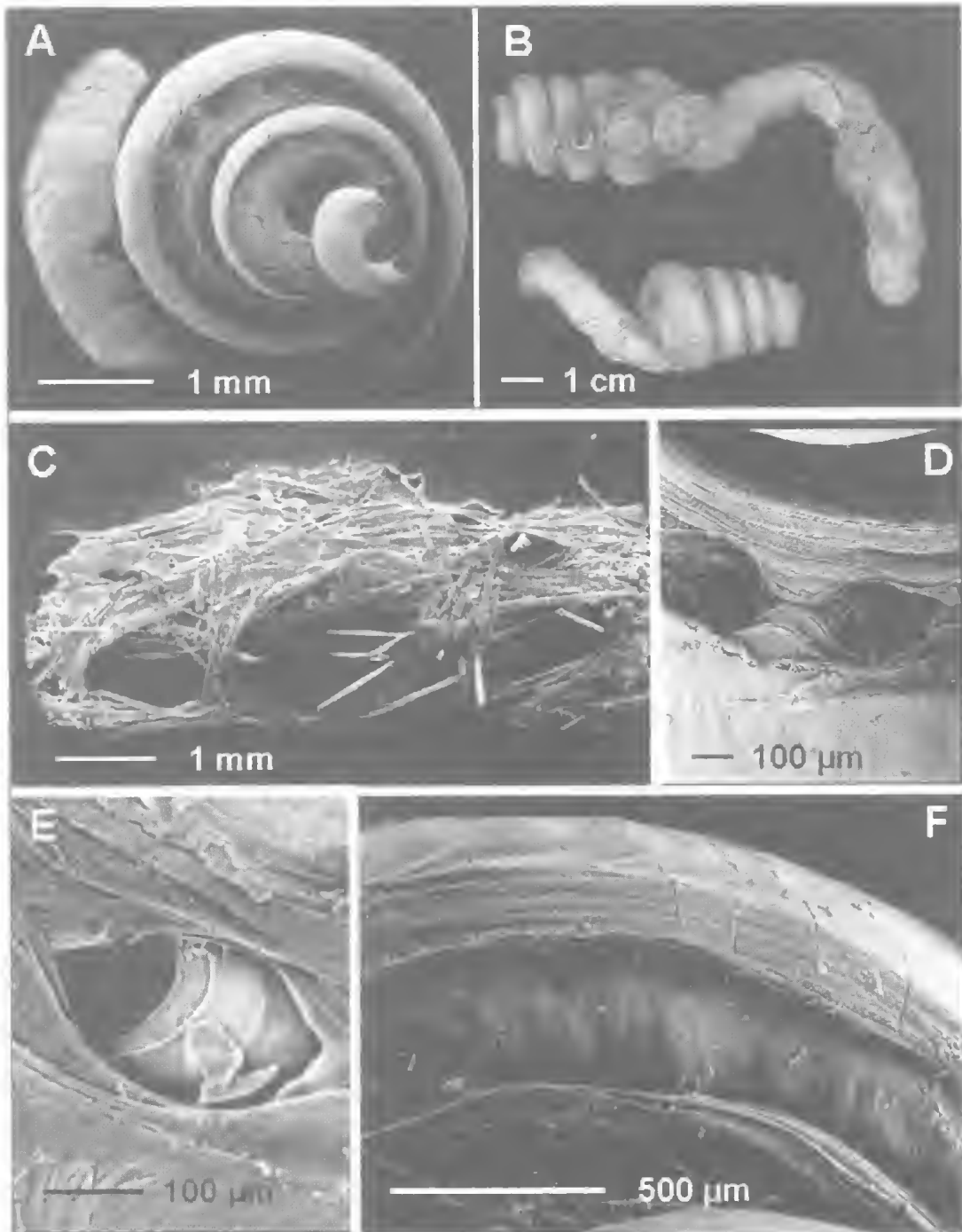
FIG. 2. Associations between siliquariids and sponges. A, Specimen of *Tenagodus* with a slit divided into holes. B, Large, smooth specimens of *Tenagodus senegalensis* with a continuous slit and the terminal part of the shell uncoiled. C, Portion of a *Jaspis* sp. specimen overgrowing a siliquariid slit. D, Formation of holes in the slit of a *Tenagodus* specimen by carbonate denticulation. E, Closure of a slit hole in a *Tenagodus* specimen by a carbonate lunula during the molluscan growth. F, Continuous slit closed in a specimen of *Pyxipoma weldii*.

but these conclusions are based on restricted samples, and future surveys of the shallow-water areas might alter this presumed distribution pattern.

The relationship between the shell morphology (smooth or spiny) and the sponge skeletal architecture (radial or disordered) is particularly strong. Of possible hypotheses to explain why smooth siliquariids are associated with radially structured sponges, and spiny ones with disorderly arranged skeletons, the most consistent seems to be that the choanosomal space is so reduced due to high spicule density, and the physical constraints so strict due to the presence of radial spicule tracts, that only smooth shells can adapt to the radial structure. Smooth siliquariids, in fact, which have transversally cracked shells, may adapt their shells to extremely confined spaces by changing the curvature of their coils. However, when smooth *Tenagodus* specimens are tightly entrapped into an articulated 'lithistid' desma reticulation (e.g. *Discodermia*), they are unable to modify their shell shape and must change their normal growth habit becoming uncoiled (Schiaparelli et al., in prep.). Spiny siliquariids, on the contrary, which very rarely show shell cracks, cannot modify their shape in order to adapt to very hard sponges and are associated with disorderly arranged skeletal structures (such as those found in Halichondriidae), where the available space inside the skeleton is certainly wider. Since the main factor that forces all siliquariids to live permanently within sponges is the demand for protection against predators (Vermej, 1987), the production of spines by these molluscs may be interpreted as a reaction against an inadequate protection from the host sponge. The fact that the last coils of spiny species lay uncovered on the sponge surface is due to the mechanical protection offered by the spines against muricid molluscs which, according to the shape of perforations (Carriker & Jockelson, 1968), seem to be the most common siliquariid predators. Smooth species, on the contrary, are much more vulnerable, as demonstrated by the high number of unsuccessful muricid holes (in the uncovered shell portions) and by the attitude to close, by means of a calcareous lamina, every portion of their slit accidentally left uncovered by the host sponge.

The prompt responses shown by siliquariids to new situations, together with the ability to shift their position along the shell during growth, determine a continuous and complex variation of the slit morphology (Schiaparelli et al., in prep.). Casts show that close relationships are established with the sponge aquiferous system to obtain an effective drain of water pumped by the mollusc. Water entering the shell aperture is pushed by ciliary beating through the slit towards the sponge canals, thus obtaining an obligate flow direction. The sponge does not try to clog the slit but, on the contrary, seems to mould its skeletal structure on it. The mollusc, on the other hand, is able to modify the slit shape by forming holes that correspond exactly to the sponge canals. The dichotomous branching and ever-decreasing diameter of canals, even if negligible as an absolute figure given its variation between specimens (Bavestrello et al., 1988), are typical of the sponge incurrent system (Bavestrello et al., 1990, 1995). Therefore the sponge receives from each associated siliquariid a continuous water flow.

CONCLUSIONS

Associations between sponges and siliquariids are examined in terms of benefits and disadvantages for either partner. A sponge associated with siliquariids may obtain two major benefits: 1) a considerable energy-saving for the pumping activity, due to the water flow pushed by the mollusc; 2) an additional food supply coming from the fine edible particles that a gastropod ctenidium is unable to hold. The presence of shells, on the contrary, could be an obstacle to the formation of the normal skeletal frame, but the sponge plasticity seems to easily overcome this constraint.

Siliquariids may obtain a greater amount of benefits from their association with sponges: 1) an effective defence from predators, which is certainly mechanical and possibly chemical (in the latter case, however, the mollusc should have developed a form of resistance to the sponge bioactive products, with the assumption that the association between both partners has a significant evolutionary history); 2) in terms of space the sponge primarily offers the mollusc a steady platform of support, even on unstable, detritic bottoms, and secondly a raised position, less disturbed by the sediment, which may confer trophic advantages to the filter-feeder; and 3) the sponge pumping activity, determining a continuous water flow towards the sponge surface, certainly brings food particles that the siliquariid can consume and, possibly, even attracts molluscan larvae.

Theoretically, the main potential disadvantage for a siliquariid associated with a sponge is the risk of being killed by the host growth overwhelming its shell apertures. However, even if some sponges, under special conditions, are able to increase their growth rates several-fold (Ayling, 1983), such cases of overwhelming by the host would probably occur very rarely, because the growth of the terminal part of the shell, bearing the aperture, is probably very rapid, especially in spiny species.

Finally, siliquariid molluscs have developed such basic structural adaptations to live in association with sponges (see also Schiaparelli et al., in prep.), that the obligatory nature of their relationship is a logical and predictable consequence. On the contrary, sponges may or may not react negatively to the 'invasion' or colonisation of their body by siliquariids, but they are surely getting remarkable benefits in terms of food, and are obviously free to live without associated siliquariids. The association, therefore, may be viewed as a form of commensalism and probably even of facultative (for the sponges at least) mutualism.

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