

New symbiotic associations involving Syllidae (Annelida: Polychaeta), with taxonomic and biological remarks on *Pionosyllis magnifica* and *Syllis* cf. *armillaris*

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Several new symbiotic associations involving Syllidae (Annelida: Polychaeta) are reported. The number of known host sponge species infested by *Haplosyllis spongicola* is updated to 36, with seven hosts being reported for the first time (i.e. *Aplysina corrugata*, *Aplysina* sp., *Cliona* sp., *Cliona viridis*, *Phorbas tenacior*, one sponge from Iran, one sponge from Cambodia). Two infestation patterns (a few worms per host cm³ in temperate waters and 10s or 100s in tropical waters) are identified. The taxonomic and ecological characteristics of the species are discussed. Five associations occurring between four syllid worms and decapod crustaceans are fully reported for the first time. *Syllis* cf. *armillaris*, *S. ferrani* and *S. pontxioi* occurred inside gastropod shells occupied by hermit crabs as well as *Pionosyllis magnifica*, which was also found inside the branchial chambers of the giant crab *Paralithodes camtschatica*. The description of *Pionosyllis magnifica* is emended on the basis of the new specimens found, while some taxonomic remarks on *Syllis* cf. *armillaris* are given. In addition, further evidence of sexual (*P. magnifica*) and asexual (*S. cf. armillaris*) reproduction in symbiotic syllids is provided.

INTRODUCTION

The Syllidae are a very large and diverse polychaete family. Syllids are found in many different habitats, including the surfaces and inner channels and cavities of other marine invertebrates. About 28 species have been reported in association with cnidarians, crustaceans, echinoderms and ascidians but they are particularly frequent and abundant in sponges (Martin & Britayev, 1998).

Sponges are one of the most common host group (including about 16% of the host species) for parasitic polychaetes (Martin & Britayev, 1998), where they often exceed the density of other inhabitants (Dauer, 1974; Tabachnikov, personal communication). Probably the most representative syllid harboured by sponges is the cosmopolitan species *Haplosyllis spongicola* (Grube). It is a typical example of a polyxenus relationship among symbiotic polychaetes, with 22 different host sponge species reported to date (Martin & Britayev, 1998). In this paper, the number of host sponge species harbouring *H. spongicola* is updated to 35, on the basis of both newly collected material, museum collections and bibliographical sources. Moreover, we discuss the 'cosmopolitan' character of the species based on the infestation characteristics of the sponge–worm associations.

There were a very few known symbiotic relationships between syllid worms and decapod crustaceans. The first reported association was that between *Syllis cornuta* Rahtke and an unidentified hermit crab (Fauvel, 1923). It was not until 1982 that other associations between a syllid (i.e. *Eusyllis blomstardi*) and several species of pagurids

were reported (Hoberg et al., 1982). Recently, some other associations involving *Pionosyllis magnifica* Moore and *Syllis* cf. *armillaris* (Müller) were also reported (Martin & Britayev, 1998). In this paper, the details of these associations are described and discussed. Moreover, the morphological description of *P. magnifica* is emended in the light of new specimens found during the present study, while some taxonomic remarks on *Syllis* cf. *armillaris* are given. In addition, further evidences of sexual (*P. magnifica*) and asexual (*S. cf. armillaris*) reproduction in symbiotic syllids are provided. Additionally, some new associations involving the species *Syllis ferrani* Alós & San Martín and *Syllis pontxioi* San Martín & López are reported for the first time.

MATERIALS AND METHODS

The study was based on preserved specimens, which are deposited within the author's personal collections (except for those specimens where the corresponding museum and catalogue number are indicated in the 'Examined material' section). For scanning electron microscope (SEM) observations, the preserved worms were washed three times in distilled water (30 min each), run through a series of ethanol concentrations, and stored in 70% ethanol until observation. Immediately prior to viewing in a Hitachi S.570 SEM (Laboratorio de Microscopía Electrónica of the Institut de Ciències del Mar of Barcelona, C.S.I.C.), they were run through a series of ethanol concentrations ending with 100% alcohol, critical-point dried, attached to a stub, and coated with gold. All

images were captured and stored in digital format using the Printerface System hardware and software.

When possible, infestation intensities were estimated after extracting the worms from each host (i.e. decapod hosts, referred to as worms per host) or from a piece of known volume (i.e. sponge hosts, referred to as worms per cm³ of host). Worm extractions and counting were made under a Zeiss Stemi 2000-c stereomicroscope. Light microscope observations and line drawings were made with a Leitz Diaplan stereomicroscope equipped with interference contrast optics (Nomarsky) and linked to a *camera lucida*. Light microscope micrographs were made with a Zeiss Axioplan stereomicroscope equipped with the SPOT hardware and software (SPI00 KAF1400 digital camera and software version 2.1.) from Diagnostic Instruments Inc.

RESULTS

Family SYLLIDAE Grube, 1850

Subfamily Syllinae Grube, 1850

Genus *Haplosyllis* Langerhans, 1879

Haplosyllis spongicola (Grübe, 1855) (Table 1)

Haplosyllis spongicola—Licher (2000), pp. 344–346.

Material examined

More than 100 specimens from *Aplysina corrugata*, *A. fistularis* and *Aplysina* sp., collected on July 1981 by H. M. Reiswig, 15–20 m depth; 115 specimens from *A. bathyphila*, collected in 1998 by M. Maldonado, 40–115 m depth; 210 specimens from *Haliclona* sp., collected on 7 December 1985 by T.A. Britayev, 3–4 m depth; 68 specimens from *Aaptos* cf. *aaptos*, collected on 4 April 1989 by T.A. Britayev, 2.5 m depth; 360 specimens from an unidentified pink sponge collected in October 1998 by E. Dutrieux, 14–15 m depth; 95 specimens from *Cliona* sp., National Museum of Natural History, Smithsonian Institution, USNM 51687; three specimens from *C. viridis* in gamma (massive) growth stage, collected in early summer, 1999 by D. Martin, 9 m depth; three specimens from *Phorbas tenacior*, collected in late spring, 1999 by D. Martin, 6 m depth; 10 specimens from unidentified white sponge collected on 12 November 1999 by Dr B. Tursch and Dr Y. Kantor, 20 m depth.

All known geographical locations and infestation intensities for the currently known host sponge species are summarized in Table 1.

Ecology

Haplosyllis spongicola inhabited the host aquiferous system when the channels are large enough to harbour the worms. However, they could also inhabit the tissues of the sponge, often inside cavities surrounded by thick protective layers generated by the host sponge in response to the presence of the worms (Martin & Britayev, 1998). Among the studied associations, the first location was common for tropical hosts, which harboured small sized (often less than 0.5 cm in length) worms. The second location occurred in temperate hosts, which harboured much longer (reaching up to 5 cm in length) worms. In agreement with the above differences in location and worm's size, two infestation patterns were observed: (i) 10s or 100s of individuals per

host cm³ in tropical hosts; and (ii) less than one worm per host cm³ in the Mediterranean (i.e. temperate) sponges (Table 1).

The species has been previously reported from detritic and muddy bottoms, 'maërl', intertidal algae, photophilic and sciaphilic algae on infralittoral hard bottoms, organogenic calcareous concretions (such as encrusting algae and corals) and *Posidonia oceanica* meadows (foliar and rhizome strata). The species has been also mentioned in association with colonies of other organisms, such as hydroids (López et al., 1996), *Microcosmus* sp. and *Phyllochaetopterus socialis* (Campoy, 1982), and vermetid reefs (Amoureux & Gantès, 1976; Baratech & San Martín, 1987; Ben-Eliahu, 1977; Campoy, 1982; Núñez et al., 1992) or associated to organogenic calcareous concretions (Laubier, 1966; López et al., 1996; Martin, 1987; Núñez et al., 1992).

World distribution

Cosmopolitan in warm (tropical and subtropical) waters. Occasionally reported from temperate boreal waters.

Pionosyllis magnifica Moore, 1906

Figures 1–3

Pionosyllis magnifica—Moore (1906), page 223, pl. 10, figures 9–11; Annenkova (1938) page 152; Uschakov (1950) page 176, figure 13; Hartman (1968), page 447; Kudenov & Harris (1995), page 54, figure 1.19.

Eusyllis magnifica—Pettibone (1954), page 261; Banse & Hobson (1974), page 56, figure 14f.

Material examined

Bering Sea, 5752.05'–5756.04'N 17040.05'–17040.00'W, r/v Adler, cruise no. 18, station 150, 50 m depth, September 1973; two specimens collected by Victor N. Goriachev on *Paralithodes camtschatica*. Southern coast of Kamchatka peninsula, point Lopatka, 6–8 m depth, August 1985; one specimen collected by Andrey A. Adrianov in a gastropod shell occupied by *Pagurus* sp..

Emended description

Body long, thick, up to 28 mm long, 0.85 mm wide without parapodia, for 73 setigers. Colour white to yellowish (in alcohol) with brownish ventral spots or bodies at the base of posterior parapodia (Figure 3B). Prostomium subpentagonal, wider than long, with four eyes in trapezoidal to rectangular arrangement; median antenna originating between the anterior pair of eyes, longer than the length of prostomium and palps together; lateral antennae originating slightly in front of the anterior eyes, shorter than median antenna (Figure 1A). Palps wide, fused dorsally at their bases.

Two pairs of tentacular cirri, dorsal ones similar in length to median antenna and ventral ones shorter (Figure 1A). Parapodia with distinct anterior and posterior lobes; dorsal cirri spindle-shaped, relatively short, similar in length to half of body width, but slightly longer on anterior segments; ventral cirri thick, shorter than parapodial lobes, thick and rounded in anterior parapodia to conical in mid-body and posterior parapodia (Figures 1B & 2A). Anterior parapodia bearing about 30 compound setae, with distally spinose shafts, relatively long bidentate

Table 1. List of host sponge species harbouring *Haplosyllis spongicola*, with the geographical location of the association, known infestation intensities (Int., worms host cm⁻³) and references

Host sponge	Geographical location	Int	References
<i>Aaptos</i> cf. <i>aaptos</i>	The seaport of Nhatrang city, Tam Island, south-east coast, Vietnam, south China Sea	83	present study
<i>Adocia neens</i>	Florida, Gulf of Mexico, Atlantic Ocean	—	(Dauer, 1974)
<i>Aplysina aerophoba</i>	Canary Islands, Atlantic Ocean	—	(Núñez et al., 1992)
<i>A. bathyphila</i>	2346'N 7505'W, off the south-east side of Lee Stocking Island, South Exuma Cays, Great Bahama Bank	35	(Maldonado & Young, 1998b)
<i>Aplysina cauliformis</i>	1311.3'N 5938.5'W, off Holetown, Barbados	—	(Tsurumi & Reischwig, 1997)
<i>A. corrugata</i>	off Holetown, Barbados	232	present study
<i>A. fistularis</i>	off Holetown, Barbados	142	present study
	off Lee Stocking Island, South Exuma Cays, Great Bahama Bank	—	(Maldonado & Young, 1998a)
<i>Aplysina</i> sp.	off Holetown, Barbados	136	present study
<i>Anomohianthella lamella</i>	Papua New Guinea	177	
<i>Axinella verrucosa</i>	Palamós, Catalonia, north-west Mediterranean Sea	0.05	(Uriz, 1978)
<i>Clatrina coriacea</i>	Gulf of Naples, south Italy, north-west Mediterranean Sea	—	(Cognetti, 1957)
<i>Cliona viridis</i>	Els Caials, Cadaqués, Catalonia, north-west Mediterranean Sea	0.02	present study
<i>Cliona</i> sp.	Pajaros Island, Puerto Rico	37	present study
<i>Dysidea fragilis</i>	Canary Islands, Atlantic Ocean	—	(Núñez et al., 1992)
<i>Fasciospongia cavernosa</i>	Ras-Milan, Gulf of Suez, south-west coast of Sinai, Red Sea	—	(Amoureux et al., 1980)
<i>Gellioides digitalis</i>	1.5 km south Lucaya, Grand Bahama Island, 15–17 m depth	—	(Uebelacker, 1978)
<i>Geodia gibberos</i>	Florida, Gulf of Mexico, Atlantic Ocean	—	(Dauer, 1974)
<i>Haliclona</i> sp.	Nhatrang Bay, Tam Island, south-east coast Vietnam, south China Sea	70	present study
<i>Halichondria agglomerans</i>	off Blanes, Catalonia, north-west Mediterranean Sea	—	(Uriz, 1978)
<i>H. panicea</i>	Temara Lagoon, Moroccan coast near Rabat	—	(Amoureux & Gantès, 1976)
<i>Halichondria</i> sp.	off Plymouth, English Channel	—	(Spooner et al., 1957)
<i>Ircinia campana</i>	Florida, Gulf of Mexico, Atlantic Ocean	—	(Dauer, 1974)
<i>I. fasciculata</i>	Cape of Creus, Catalonia, north-west Mediterranean Sea	—	(Alós et al., 1982)
<i>I. felix</i>	off Lee Stocking Island, South Exuma Cays, Great Bahama Bank	20–50	(Maldonado & Young, 1998a)
<i>I. ramosa</i>	Florida, Gulf of Mexico, Atlantic Ocean	—	(Dauer, 1974)
<i>Ircinia</i> ssp.	Canary Islands, Atlantic Ocean	—	(Núñez et al., 1992)
<i>Liosina paradoxa</i> ^a	Mwamba Kuni reef bank, Bayamoyo, Zanzibar Channel, Tanzania (Indian Ocean)	56–240	(Magnino & Gaino, 1998)
<i>Neofibularia nolitangere</i>	coral reefs, Caribbean Sea, Florida and Bahamas	—	(Humann, 1992)
<i>Petrosia ficiiformis</i>	Cape of Creus, Catalanian coast, north-west Mediterranean Sea	—	(Alós et al., 1982)
<i>Phorbas tenacior</i>	Punta Santa Anna, Blanes, Catalonia, north-west Mediterranean Sea	0.2	present study
<i>Reniera rosea</i>	Gulf of Naples, south Italy, north-west Mediterranean Sea	—	(Cognetti, 1957)
<i>Rhizaxinella pyrifera</i>	off Blanes, Catalanian coast, north-west Mediterranean Sea	0.09	(Uriz, 1978)
<i>Speciospongia vesparia</i>	Florida, Gulf of Mexico, Atlantic Ocean	—	(Dauer, 1974)
<i>Theonella swinhoei</i>	Mwamba Kuni reef bank, Bayamoyo, Zanzibar Channel, Tanzania (Indian Ocean)	68	(Magnino & Gaino, 1998; Magnino et al., 1999)
	Hurgada, coast of Egypt, Red Sea	—	(Magnino et al., 1999)
<i>Verongula reischwigi</i>	Discovery Bay, north coast of Jamaica	50–100	(Reischwig, 1973)
<i>Xytophene sigmatum</i>	Florida, Gulf of Mexico, Atlantic Ocean	—	(Dauer, 1974)
Yellow sponge	Gulf of Mexico	21000 ^b	(Bacescu, 1971)
Sponge	South and East Seas, Korea	—	(Lee & Rho, 1994)
White sponge	Kampan Song Bay, Cambodia	12	present study
Pink sponge	2729'N 5234'E, off Asaluyeh, Iranian coast, Persian Gulf	52	present study
Thick sponges	Les Albères, French coast, north-west Mediterranean Sea	—	(Laubier, 1966)

^a, mentioned as '*Phorospongia* (*Chondropsis*) sp. (Magnino & Gaino, in press)' in Martin & Britayev (1998); ^b, number of worms found inside a single host of unknown volume.

blades, with both teeth distinctly separated and similar in length, and short straight marginal spines (Figures 1D & 2B); the number of setae decreasing backward. Each posterior parapodia bearing about 22 compound setae, with short, triangular, bidentate blades, with proximal

tooth somewhat longer and bigger than distal tooth (Figure 1E). The blades showed slight antero–posterior and dorso–ventral gradation in length, having 26–32 m on anterior parapodia and about 20 m on posterior ones (Figure 1D,E). Simple setae not seen. Each anterior

parapodia with four aciculae (Figure 1C), decreasing to two on posterior ones (Figure 1F). The aciculae are slender, with rounded, irregular tips. All specimens with thin supporting acicula in the base of cirrophores and several thin, small capillary natatory setae (Figures 1G & 2A,C). Each segment with numerous ventral tufts of cilia (Figure 2A,D&E) and surrounded by one transverse ciliary ring interrupted by parapodia (Figure 2A,D).

Pharynx short, extending about 4–7 segments, with an anterior large tooth, and a crown of about ten papillae (Figure 3A). Proventriculum similar in length to pharynx extending from setiger 8 to 15 in specimen from giant crab, and from setiger 9 to 16 in specimen from hermit crab, barrel-shaped, with about 40 rows of muscular cells.

Remarks

Pionosyllis magnifica is a relatively unknown species. Kudenov & Harris (1995) reported the species as known only from the North American Pacific coast. However, they included the specimens found by Annenkova (1938) within the synonymies. These worms were collected at the Japan Sea and, thus, closer to the occidental coast of the Pacific Ocean where our specimens were found. *Pionosyllis magnifica* was originally drawn in the first description of the species, this iconography being repeated by Hartman (1968) and, after reviewing the holotype, also by Kudenov & Harris (1995). Now new drawings and SEM micrographs based on our specimens are provided, which show several slight differences with the original description. The specimens examined have a smooth pharyngeal tooth, which is not surrounded by small denticles. The median antenna is inserted between the anterior pair of eyes, while it was previously described as inserted in front of them and at the same level as the lateral antennae. In addition, they had segmental pairs of brownish bodies, which have never been previously reported. The shape of the pharyngeal end fully justifies the original inclusion of the species in *Pionosyllis*, instead of *Eusyllis* (Banse & Hobson, 1974; Pettibone, 1954). On the other hand, the position of the antennae is not enough to define our worms as a new species while the presence of segmental brownish bodies has no taxonomic relevance. After dissecting and studying them under SEM, numerous long cilia on their inner surface were observed. This allows us to assume that could be nephridia modified to function as gonoducts in our specimens, which were all reproductive females.

Ecology

The commensal specimens from Bering Sea were found inside the branchial chambers of the giant crab *Paralithodes camtschatica* living on a sandy bottom. The commensal specimen from Lopatka Point was sheltered inside the apex (i.e. upper teleoconch whorls) of a gastropod shell occupied by *Pagurus* sp.. All the studied specimens are ovigerous females bearing coelomic oocytes. The oocyte diameter varied from 91–121 µm (the Bering Sea) to 240–290 µm (Lopatka point). The presence of notopodial setae indicates transformation to the epitokous stage.

Pionosyllis magnifica has been previously reported from mud, pebble-mud and shelly-sand bottoms, intertidal to 150 m depth (Hartman, 1968; Kudenov & Harris, 1995). There are no mentions of the species in association with other benthic organisms.

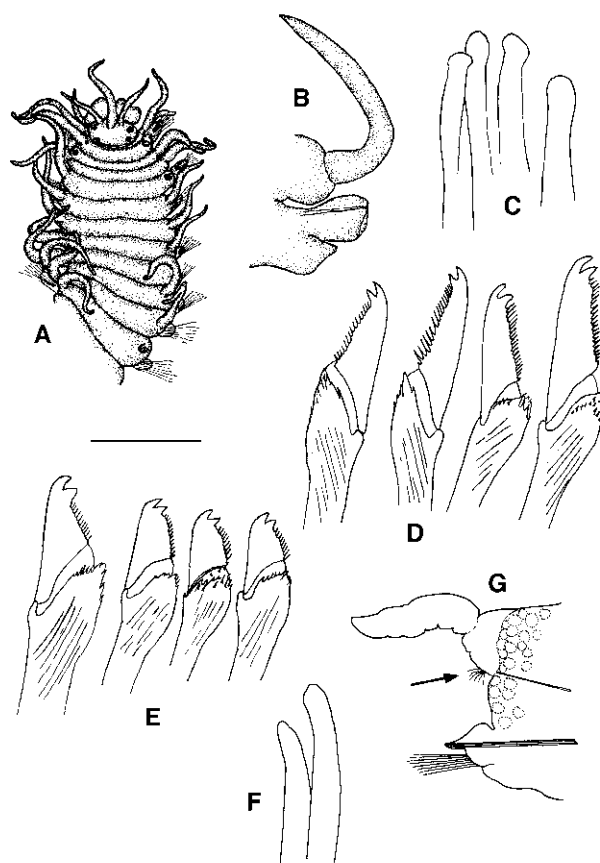


Figure 1. *Pionosyllis magnifica*. A, Anterior end in dorsal view; B, posterior parapodium, setae not drawn; C, aciculae from an anterior parapodium; D, compound setae from an anterior parapodium; E, compound setae from a posterior parapodium; F, aciculae from a posterior parapodium; G, parapodium from mid body with noto- and neurosetae; the arrow indicates the position of notosetae. Scale bars: A, 0.7 mm; B, 0.12 mm; C–F, 20 µm; G, 0.52 mm.

World distribution

North Pacific: southern coast of Kamchatka, Japan Sea, Bering Sea, coast of North America.

Syllis cf. *armillaris* (Müller, 1776)

Figures 4&5

Typosyllis armillaris.—Licher (2000), pp. 189–196, figure 84.

Typosyllis aciculata orientalis—Imajima & Hartman (1964), page 130, pl. 31 figures e–f, pl. 32 figures a–t.

Material examined

Pacific Ocean, Sala-Y-Gomez submerged ridge, 2540'–2537'S 8525–8526'W, 26 April 1987, r/v Shtokman, cruise no. 18, station 1923, 162–190 m depth, 20 specimens; station 1993, 230–280 m depth, one specimen Indian Ocean, sea mount 'Error', 1019.7'–1016.25'N 5607.3'W, September 1988, r/v Vitiaz II, cruise no. 17, station 2573, one juvenile and five adult specimens from *Paguristes* sp.

Description

Body long and slender, without colour marks. 2.1–14.5 mm long and 0.14–0.29 mm wide (at proventriculum level without parapodia), 38–124 setigers. Prostomium

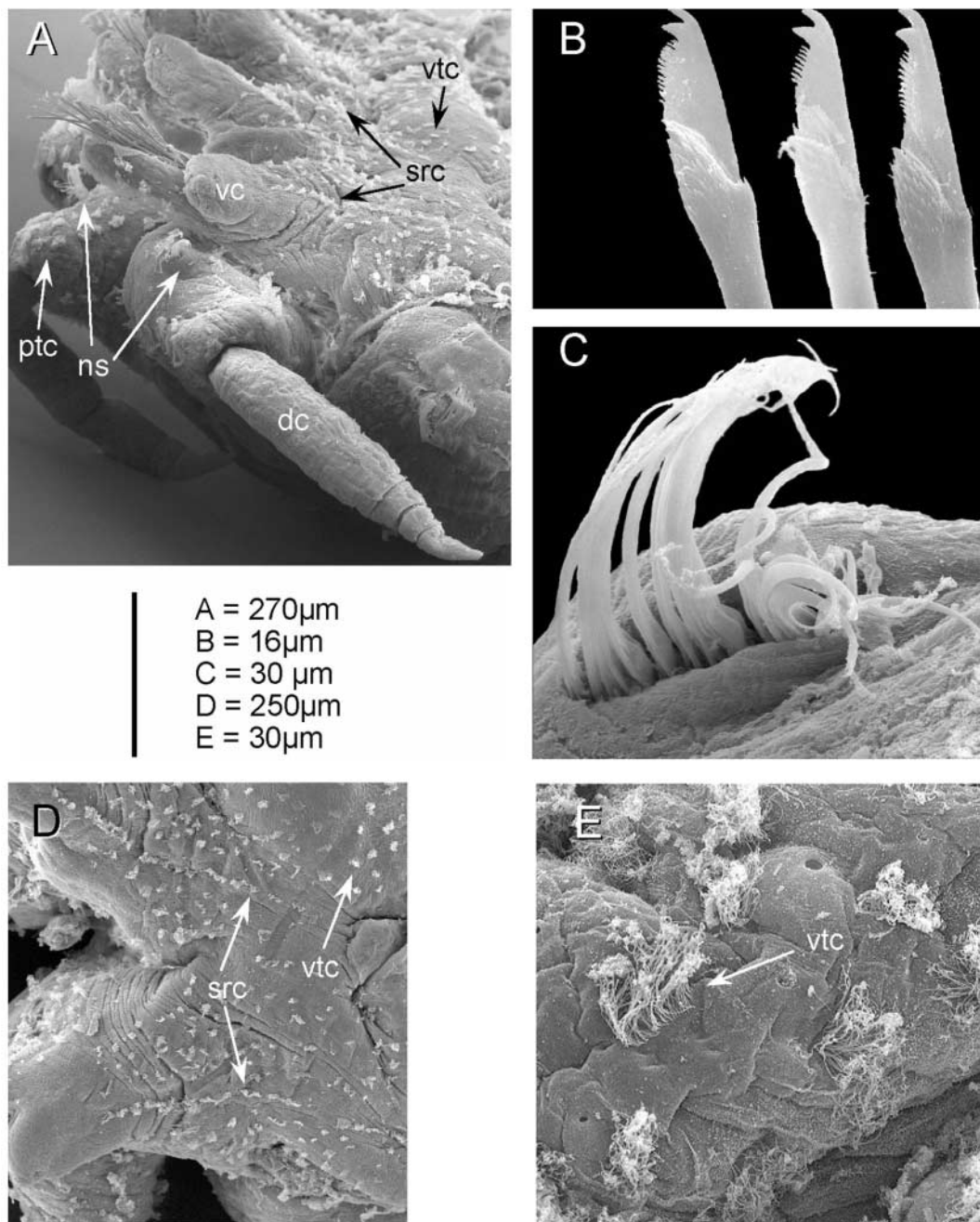


Figure 2. SEM micrographs of *Pionosyllis magnifica*. A, Mid-body segments in ventral view; B, compound setae from mid-body region; C, notosetae from mid body; D, ventral surface of mid region under higher magnification; E, detail of the ventral tufts of cilia. dc, dorsal cirrus; ns, natatory setae; ptc, parapodial tufts of cilia; src, segmental rings of cilia; vtc, ventral tufts of cilia.

oval, wider than long. Eyes not seen (perhaps an artefact of fixing). Palps broad and triangular. Median antenna originating from middle of prostomium, with a well-developed ceratophore and 16 articles. Lateral antennae originating from near the anterior margin, with 11–12 articles.

Two pairs of tentacular cirri, the dorsal one (20–25 articles) 1.5 times longer than the ventral one (13–14 articles), both having well-developed cirrophores. Dorsal cirri spindle-shaped, showing a slight alternation in length, with 12 (long) and 8–9 (short) articles at mid-body region (Figure 4A,B), and also a slight antero–posterior gradation in length (up to 17 articles in anterior setigers and shorter in the posterior ones). Ventral cirri shorter than parapodial lobe. Up to 18 articulated setae per parapodial lobe in the anterior parapodia, the blades being long and finely

serrated, bearing a subdistal tooth smaller than the distal one but clearly developed and slight dorso–ventral gradation in blade length (dorsal 41.5 μ m, ventral 31.7 μ m) (Figure 4C). Up to five setae per parapodium in median and posterior parapodia, bearing only three at the posterior most ones; blades short, stout and triangular with a very small subdistal tooth, sometimes difficult to distinguish from serration, without clear dorso–ventral gradation (blade length from 20.5 to 26.5 μ m) (Figure 4E). Two to four aciculae per parapodium in the anterior segments; 1–2 with straight tip, the others with rounded tips (Figure 2D). One or two aciculae per parapodium in median and posterior segments, one with straight and blunt tip, the other with oblique and subdistally enlarged tip (Figure 4F). The latter is the single type in the last 20 setigers.

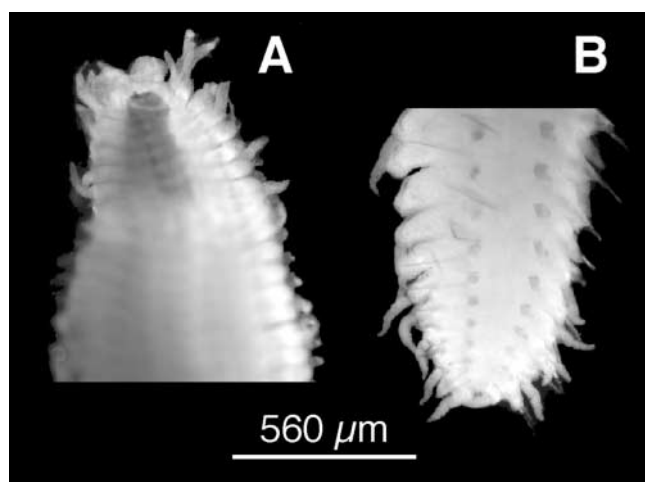


Figure 3. *Pionosyllis magnifica*. A, Anterior end in ventral view; B, posterior end in ventral view.

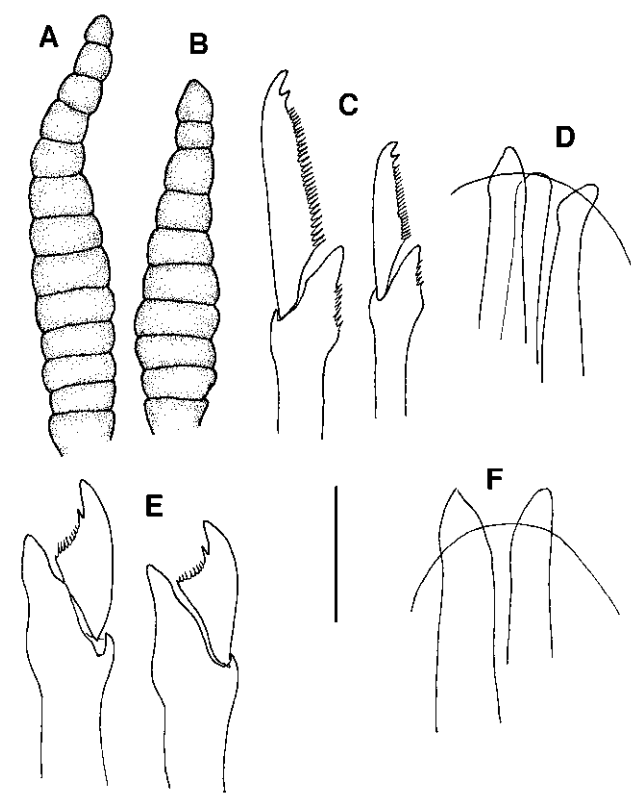


Figure 4. *Syllis* cf. *armillaris*. A, Dorsal cirrus of setiger 64; B, dorsal cirrus of setiger 67; C, compound setae from an anterior parapodium (setiger 6); D, aciculae from an anterior parapodium (setiger 6); E, compound setae from a posterior parapodium (setiger 70); F, aciculae from a posterior parapodium (setiger 70). Scale bars: A–B, 1 mm; C–F, 20 μ m.

Pharynx long, extending through 14 setigers. Tooth not seen (although expected to be near anterior end of pharynx). Proventriculum long, cylindrical, extending through 8–10 setigers, with 42 rows of muscle cells.

Remarks

Syllis cf. *armillaris* was first described from Arctic waters (Greenland), although it is currently considered cosmopolitan (Licher, 2000; Uebelacker, 1984). Our material differs slightly from re-description of the species by Licher (2000). The posterior setal blades in our specimens

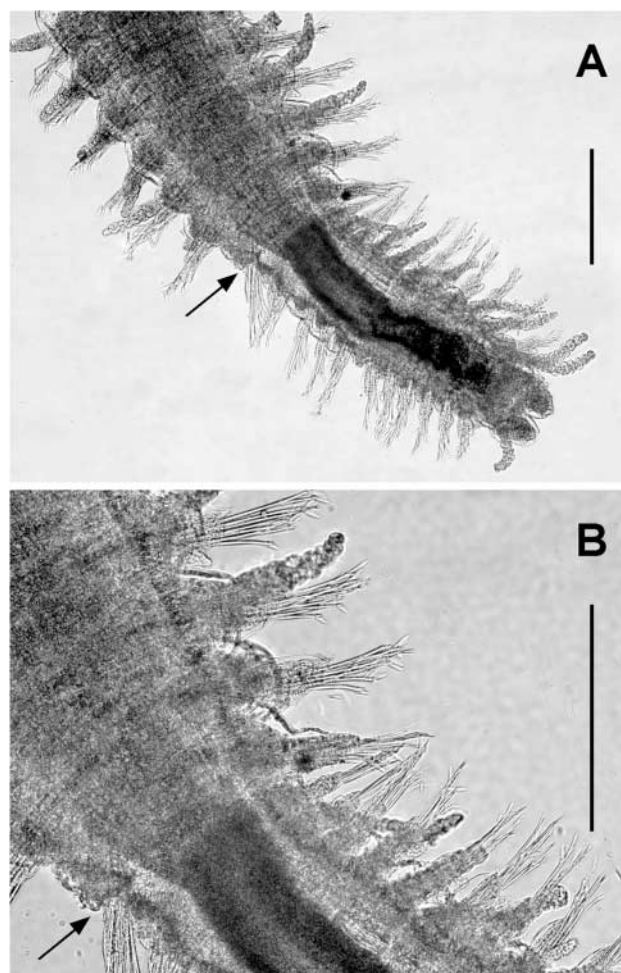


Figure 5. *Syllis* cf. *armillaris*. A, Specimen regenerating anterior end; B, detail of the border between old and new segments. The arrows indicate the exact location of the border.

are shorter and proportionally stouter. Furthermore, they do not show any dorso–ventral gradation in length, contrary to Licher's description, and the shape of dorsal cirri is more definitely spindle-shaped in our specimens. Finally, their pharynx is longer, extending through 14 instead of 9 setigers. However, Uebelacker (1984), mentioned a slight dorso–ventral gradation in blade length, as well as a range of pharynx length extending from setigers 4 to 13. Although a review of the different morphologies of the populations of the species reported around the world is out of the scope of the present paper, we suggest that they could support the existence of a sibling species-complex, perhaps with overlapping geographical distribution. As a consequence, we decided to fully describe our specimens to allow a future assessment of the geographical range of an eventual new species described within the frame of a new study on this complex.

Ecology

The commensal specimens were found in upper teleoconch whorls of the shells occupied by *Paragiopagurus boletifer* De Saint-Laurent, 1972 and *Paguristes* sp., and under the base of actinian polyp attached to the upper surface of shells. The usual number of worms per one host ranged from 1 to 3. Up to ten worms were found in only one case, four of them having regenerated anterior ends

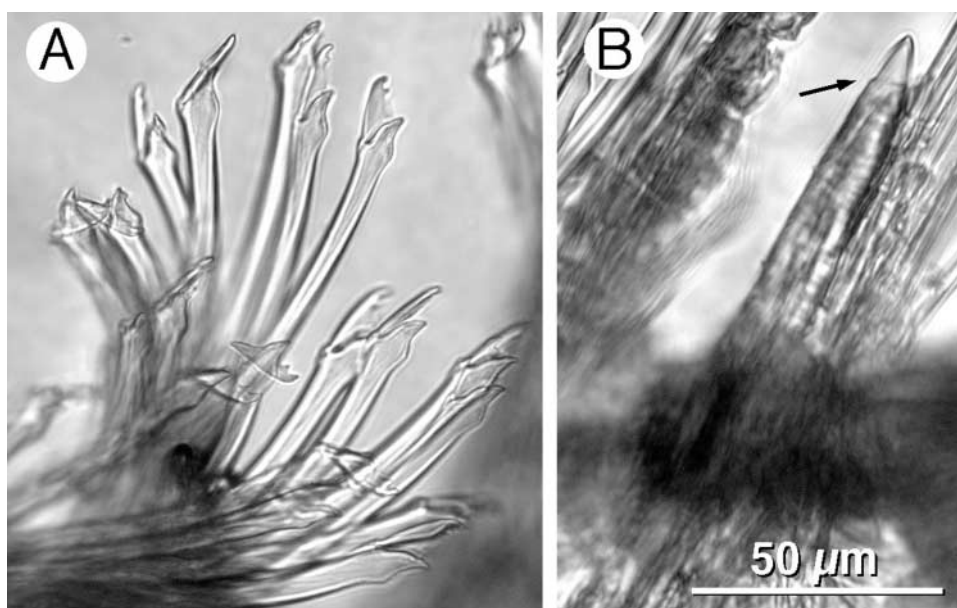


Figure 6. *Syllis pontxioi*. A, Setae from a posterior parapodium; B, acicula from posterior parapodium; the arrow indicates the position of the acicula.

(Figure 5A). These worms showed a distinct border between old and new segments, well-defined by the posterior edge of proventriculum and the small size of segments in the regenerated anterior part (Figure 5A,B). The number of regenerated setigers was invariably equal to 11, indirectly supporting asexual reproduction.

Syllis cf. *armillaris* has been previously reported from muddy detritic bottoms, calcareous encrusting algae, intertidal rocks, rhizomes of *Cymodocea nodosa* and *Posidonia oceanica* meadows and photophilous and sciaphilous algae on infralittoral hard bottoms. The species has been also mentioned in association with hydroids (López et al., 1996), sponges (Alós, 1988; Amoureux et al., 1980), colonies of the ascidiacean *Microcosmus* sp. (Campoy, 1982), vermetid reefs (Ben-Eliahu, 1977; Campoy, 1982) and *Sabellaria* reefs (Gruet, 1972).

World distribution

Cosmopolitan.

Syllis pontxioi San Martín & López, 2000

Figure 6

Typosyllis gerlachi—non Hartmann-Schröder, 1960—Campoy (1982): 410–411, plate 45; Parapar et al. (1996): 59.

Syllis pontxioi—San Martín & López (2000), pp. 429–430, figure 3.

Material examined

Indian Ocean, sea mount 'Error', 1019.7'–1016.25'N 5607.3'W, September 1988, r/v Vitiaz II, cruise no. 17, station 2573, one juvenile and one broken specimen from *Clibanarius* sp., one juvenile and five adult specimens from *Paguristes* sp.

Remarks

According to Licher (2000), the worms reported (erroneously) as *Syllis truncata cryptica* Ben-Eliahu in the Iberian

Peninsula since Campoy (1982) corresponded, in fact, to *Syllis gerlachi* Hartmann-Schröder, 1960 while those reported as *Syllis* (or *Typosyllis*) *gerlachi* must belong to a different species. These worms have been recently re-described as a new species, *S. pontxioi* (San Martín & López, 2000). *Syllis pontxioi* is characterized by its very short antennae, tentacular cirri and dorsal cirri (which, in addition, are very slender) and its thick and bidentate ventral simple setae. However, the most characteristic features for this species are the mid-body and posterior falciger blades, which are very short and with enlarged proximal tooth, and its stout posterior aciculae, whose tips are provided with hollow and convex edge. The specimens found living commensally with hermit crabs perfectly fitted with the description of *S. pontxioi*, particularly in the last two characteristics (Figure 6A,B).

Ecology

The commensal specimen was found inside the apex of gastropod shells occupied by the hermit crabs *Paguristes* sp. and *Clibanarius* sp.. *Syllis pontxioi* has been previously reported from *Amphioxus* sands, muddy sands and muddy gravels (between 11 and 200 m depth). The species has been also reported as sponge endobiont (Alós et al., 1982).

World distribution

Northern coast of Spain (Basque Country, Asturias, Galicia). Western Mediterranean. Indian Ocean.

Syllis ferrani Alós & San Martín 1987

Syllis ferrani—Alós & San Martín (1987), pp. 37–42, figures 2–5.

Typosyllis ferrani—Licher (2000), 221–223, figure 93.

Material examined

Mediterranean Sea off Cartagena, Medits 97 cruise, trawl 34; one complete specimen collected on May 1997

by Pere Abelló from a shell occupied by *Pagurus excavatus*, 81 m depth.

Remarks

The single specimen found perfectly matched with the original description of the species.

Ecology

The commensal specimen was found inside a gastropod shell occupied by the hermit crab *Pagurus excavatus*. *Syllis ferrani* has been previously reported from precoralligenous aggregates of calcareous algae and rhizome stratum of *Posidonia oceanica* meadows from 8 to 33 m depth and in association with sponges (López et al., 1996).

World distribution

Western Mediterranean Sea, Cape of Creus (Catalonian coast of the Iberian Peninsula) and Chafarinas Islands (Alboran Sea).

DISCUSSION

Up to 33 species of syllids have been reported as living in close association with other marine invertebrates, representing about 9% of the total known symbiotic polychaetes (Martin & Britayev, 1998). Twenty-three species have commensal habits, while 11 have been considered as parasites. The former are associated with sponges, cnidarians, sipunculids, echinoderms (i.e. asteroids, ophiuroids, holothuroids), bryozoans and decapods. The latter are mainly parasites of sponges, but some species parasitize cnidarians, polychaetes, nemerteans and tunicates.

With a few exceptions, symbiotic syllids showed only slight adaptations to their particular mode of life. Among the few known (see Martin & Britayev, 1998 and references therein), there are: (i) life-cycle adaptations, such as the presence of isolated heterosexual pairs on the same host individual in *Amblyosyllis cincinnata* (commensal); (ii) reproductive adaptations, such as the ichneumon-like life-cycle (i.e. direct oviposition inside living host hydrothecae, with subsequent feeding of juveniles on polyp tissues) in *Proceraea* sp. (parasite); (iii) behavioural adaptations, such as host recognition in *Haplosyllis chamaeleon* (parasite); (iv) colour mimicry in *H. chamaeleon*, *Branchiosyllis oculata* (parasite) and *Branchiosyllis exilis* (commensal); (v) specialized attachment structures such as hooked setae in the symbiotic species of the genera *Haplosyllides*, *Haplosyllis*, *Trypanosyllis*, *Bollandia*, *Procerastea* and *Branchiosyllis*.

The external morphology of *H. spongicola* is very well adapted to its life style and appears to be relatively simple, with all setae being simple and having two small teeth on its large main fang. However, there are a very few data on the relationships between *H. spongicola* and its host sponges (Martin & Britayev, 1998). Grazing of *H. spongicola* on individuals of the Mediterranean host *Cliona viridis* that had already attained its largest growth stage (i.e. gamma or massive stage, according to Rosell & Uriz, 1991) was observed (D. Martin, personal observation). In that case, for instance, one sponge specimen measuring about 62 cm³ harboured only one large worm (about 3 cm in length), located directly inside the sponge tissues. However, the presence of this worm (probably temporal) apparently did not disturb the normal growth of the

sponge. The situation was similar to that found in *Phorbas tenacior*, *Axinella verucosa* and *Rhizaxinella pyrifera*, always harbouring less than one worm per host cm³ (Table 1). The last two species, however, react to the presence of the worms by producing a thick protective layer around them (Uriz, 1978).

In tropical seas, *H. spongicola* occurred inside the canals of the aquiferous system of their host, who did not show abnormal morphological structures in reaction to the presence of the worms. In addition, infestations by 10s or 100s of worms are typical in these hosts (Table 1). The coral reef *Cliona* sp. from Puerto Rico harboured a few more than 600 worms in a piece of about 16.5 cm³. The extremely numerous, small-sized tropical worms were continuously grazing and removing the host biomass without apparently causing a decrease in the host growth rate or in the sexual and asexual reproductive activities (Reiswig, 1973; Tsurumi & Reiswig, 1997). The host sponges *Ircinia felix* and *Aplysina fistularis* were able to survive and even grow when experimentally transplanted to more than 100 m depth (i.e. much deeper than their normal bathymetric distribution). The transplanted sponges lose their zooxanthellae and bacterial symbionts, while their respective polychaete populations were not stressed (Maldonado & Young, 1998a). *Haplosyllis spongicola* seems to be typically present in tropical aplysiniid sponges, reaching high densities even in the small-sized *Aplysina bathyphila* (Table 1), the single stalked species of the family Verongiidae, which inhabits vertical walls submitted to strong currents (Maldonado & Young, 1998b).

The differences between temperate and tropical populations of *H. spongicola* reported in this paper (i.e. worm's size, location on hosts, host reactions, infestation intensity) cast severe doubts on the cosmopolitanism of the species. The species have been the subject of a long-lasting taxonomic controversy, recently summarized by Licher (2000), who listed more than 15 synonymized specific names, together with more than 350 of worldwide citations of the species, either as *Syllis spongicola*, *Syllis (Haplosyllis) spongicola* or *Haplosyllis spongicola*. In light of our results, however, we agree with Campoy (1982), who first suggested the possible (and still unexplored) relationships between the presence of the species inside many different hosts and the existence of different morphotypes. A detailed analysis of more than 30 populations around the world is currently being carried out to assess the validity of all previously synonymized specific names, as well as to determine if a sibling or pseudosibling species-complex is being hidden under the name of *H. spongicola* (D. Martin & T.A. Britayev, unpublished data).

From an ecological point of view (and supporting the possible existence of a sibling species-complex) the behaviour of both temperate and tropical *Haplosyllis spongicola* populations appears to be different. We suggest that the temperate worms could behave as sponge predators. To assess if they are species-specific or generalist predators would be an interesting subject of a future experimental approach. As predators, the worms could either be able to move from one prey to another (feeding on different sponges) or to live sometimes inside their preys (providing they offer enough room to harbour the worms). Most reports of *H. spongicola* as free-living or associated to other

benthic invertebrates correspond to temperate locations. However, these reports should be viewed with caution, as the presence of sponges in the original samples may never be discarded. In fact, sponges may be avoided during the sorting process, without any further mention of this manipulation, or omitted in faunistic and/or taxonomic reports dealing with polychaetes. Thus, as already mentioned by Campoy (1982), the relationships of *H. spongicola* with the sponges may not be evident to the final reader (e.g. a polychaete taxonomist or ecologist).

Conversely, the tropical worms seemed to be strict sponge endosymbionts, living always inside the host and probably behaving as parasites. In fact, the term 'good' parasite (sensu Ricklefs, 1990) could apply to these worms, as all phases of their life-cycle occurred inside the host, often during the whole year and without disturbing the normal growth and reproductive cycle of the sponges (Tsurumi & Reiswig, 1997; D. Martin, personal observations). The exact nature of the host/symbiont relationships as well as the host specificity of the different morphotypes that could be involved in the species-complex will be assessed as a part of the same study mentioned above (D. Martin & T.A. Britayev, unpublished data).

The associations between syllids and decapod crustaceans are apparently much less frequent than those between syllids and sponges (Martin & Britayev, 1998). They have been scarcely reported and are poorly known. They have been incidentally mentioned in faunistic papers (e.g. Fauvel, 1923). Only one paper includes relevant ecological information on the association between a syllid, *Eusyllis blomstardi* and their pagurid hosts (Hoberg et al., 1982). This species has been found in the Pacific coast of North America in a white parchment tube adhering and conforming to the upper interior surface of the whorl of the host shell. This location is similar to our observations on *Pionosyllis magnifica*, which also occurs in the branchial cavity of giant crabs. These peculiar locations suggest a high degree of specificity in their relationships with the hosts. In fact, the presence of possible host crabs may not be discarded for the previous records of the species (Moore, 1906; Pettibone, 1954). Consequently, they may either reflect the real existence of free-living populations, or a complex life cycle including both free-living and symbiotic stage or, also, they might result from loss of host during sampling. Thus, we suggest that *P. magnifica* could be tentatively considered as a facultative or temporary symbiont, while the exact nature of the association (i.e. parasitic, commensalistic or mutualistic) is still undefined.

Like *P. magnifica*, *Syllis* cf. *armillaris*, *S. ferrani* and *S. pontxioi* did not show any specific morphological adaptation to the symbiotic mode of life, while these three species have been reported either as free-living or as incidentally associated to colonial or reef-building invertebrates. Like most species of the Superfamily Nereididae, the syllids are considered to be free-living predators (Fauchald & Jumars, 1979), often erroneously (Giangrande et al., 2000). Thus, in absence of morphological adaptations, further research should also be addressed to define the exact nature of these associations. Particularly to assess the possible existence of behavioural adaptations, like those developed by the well-known hermit crab commensal *Neanthes fucata* (Cram & Evans, 1980; Gilpin-

Brown, 1969; Goerke, 1971). The present data do not allow us to affirm whether the hermit crab associated syllids should be considered as commensal (i.e. feeding on the host food) or parasitic (e.g. feeding on the hermit crab eggs) symbionts or as merely inquilines.

Asexual reproduction has been also considered as an adaptation to the symbiotic mode of life, allowing the symbionts to reach high densities after colonization of a rare suitable substrate (i.e. the host) by a single larva (Martin & Britayev, 1998). This may be supported indirectly by the higher intensities of infestation among hosts sheltering symbiotic polychaetes showing traces of asexual reproduction (Tzetlin & Britayev, 1985). True asexual reproduction by architomy appears to be rare in syllids (Franke, 1999), the two only previously known species being *S. gracilis* and the parasitic *Procerastea halleziana*. The regeneration of the anterior end in some specimens of *S. cf. armillaris* in our samples, as well as the invariable number of regenerated setigers, clearly supports the capacity of reproduction by architomy in this species. Additionally, the finding of asexually reproductive specimens of *S. cf. armillaris* supports its close phylogenetic relationships with *S. gracilis*. Both species also have short fusiform dorsal cirri in mid-body, similar compound setae and sexual reproduction by pentacerous stolons (Etapé & San Martín, 1991).

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