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Inter-population variability and character description in the sponge-associated *Haplosyllis spongicola* complex (Polychaeta: Syllidae)

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Key words: Polychaeta, Syllidae, species-complex, adult morphology, stolon morphology, morphometry

Abstract

Haplosyllis spongicola is probably the most representative symbiotic syllid harboured by sponges and has been widely reported from tropical, subtropical and temperate seas. Its external morphology seems to be very well adapted for its life-style, with all chaetae being simple and having two small teeth and a large main fang. However, the species has been the subject of a long-lasting taxonomic controversy, which gave rise to more than 15 synonymies, with hundreds of records worldwide. The present paper is based on the study of more than 28 populations obtained from around the world. These populations have been carefully analysed using different approaches (morphometry, morphology and biology). As a consequence, the existence of a pseudo-sibling species-complex within the so-called cosmopolitan *H. spongicola* has been revealed. The most relevant characters (as well as their variability) that will allow a future identification of the species involved in the complex are fully described, illustrated and analysed.

Introduction

There is growing evidence that many marine species with large distribution ranges (the so-called cosmopolitan species) are more subdivided than originally thought (Hilbish, 1996). Two main complementary research directions may address this question. The reinterpretation of the target species is based on accurate morphological studies and the separation of morphologically indistinguishable species using complementary approaches, such as life-history or genetics. Although generic, these statements directly concern the systematics of the polychaetous annelids.

The polychaetes substantially contribute to the biodiversity of benthic communities. There are more than 80 currently recognized families (Fauchald & Rouse, 1997), which include more than 10 000 species (many of them being considered to have a cosmopolitan distribution). The lack of consistent morphological information, however, is still a major source of uncertainty in current polychaete classifications (Fauchald & Rouse, 1997). Recent accurate morphological studies repeatedly showed that species formerly considered as cosmopolitan should be divided into several valid species. These cryptic species, which are known as "pseudo-sibling species-complexes" (Mayr & Ashlock, 1991), include taxa that may be readily distinguished morphologically once the appropriate characters are recognised. A striking example was reported by Pettibone (1993), who divided the 'cosmopolitan' scaleworm *Harmothoe lunulata* into 21 species belonging to 3 different genera (*Malmgreniella*, *Paragattiana*, and *Wilsoniella*).

On the other hand, the cryptic species that are impossible to distinguish based on the morphological characters of adult specimens are known as "sibling species-complexes" (Mayr & Ashlock, 1991). They result from divergence in some features (habitat, life-history, genetics) without divergence in morpho-

logy. Although sibling species appear to be common among marine invertebrates, a comprehensive review of sibling species in the sea had not been undertaken until Knowlton (1993) reported about 90 different examples, 19 of them being polychaetes. Although the broad habitat and geographic distribution information characterizing many polychaetes still requires re-evaluation in this context, several attempts have been made (but see also Knowlton, 1993, and references therein) using life-history traits (Smith, 1958; Grassle & Grassle, 1976; Wilson, 1984; Fong & Garthwaite, 1994; Bastrop et al., 1995), karyotypes (Grassle et al., 1987; Robotti et al., 1991), protein electrophoresis (Robotti, 1978; Abbiati & Maltagliata, 1996), and genetics (Cadman & Nelson-Smith, 1990; Wu et al., 1991; Lenaers & Bhaud, 1992; Manchenko & Radashevsky, 1993, 1994; Röhner et al., 1997; Jollivet et al., 1998; Pernet, 1999).

The present study addresses the need to clarify the status of *Haplosyllis spongicola* (Grube, 1855). This species is probably the most representative symbiotic syllid harboured by sponges (Martin & Britayev, 1998). Its external morphology is relatively simple, with all chaetae being simple and having two small teeth on its large main fang and seems to be very well adapted to its life style. However, *H. spongicola* has been the subject of a long-lasting taxonomic controversy, which has given rise to more than 15 synonymies, together with hundreds of reports from tropical, subtropical and temperate seas (Licher, 2000).

In this paper, several *H. spongicola* populations from around the world have been carefully studied using different approaches (morphology, morphometry and biology) to assess whether *H. spongicola* is a real cosmopolitan species or a complex of pseudo-sibling or sibling species. The most relevant characters allowing a future identification of the species involved in the complex have been fully described, illustrated and analysed, as well as their inter-population variability.

Table 1. List of known synonymies within the *Haplosyllis spongicola* species-complex (extracted from Licher, 2000)

Species code	Synonymized species names	Citations
1	*Syllis (Haplosyllis) djiboutiensis* Gravier 1900	4
	Syllis djiboutiensis	1
	Haplosyllis djiboutiensis	8
2	*Haplosyllis gula* Treadwell, 1924	1
3	*Syllis hamata* Claparède, 1868	11
	Haplosyllis hamata	5
	Syllis (Haplosyllis) hamata	5
	Haplosyllis (Syllis) hamata	1
4	*Syllis spongicola* Grube, 1855	45
	Haplosyllis spongicola	166
	Syllis (Haplosyllis) spongicola	72
5	*Syllis spongicola spongicola* Cognetti, 1957	5
6	*Haplosyllis spongicola brevicirra* Rioja, 1941	2
	Syllis (Haplosyllis) spongicola brevicirra	1
7	*Syllis spongicola tentaculata* Marion, 1878	6
	Haplosyllis spongicola tentaculata	4
	Haplosyllis tentaculata Rho & Lee, 1987	1
8	*Syllis setubalensis* Mcintosh, 1885	2
	Syllis (Haplosyllis) spongicola setubalensis	1
9	*Syllis aurantiaca* Eisig, 1881	4
10	*Syllis oligochaeta* Bobretzky, 1870	1
11	*Haplosyllis oligochaeta pontica*	1
12	*Syllis streptocephala* Grube, 1857	5
13	*Syllis uncinigera* Grube, 1878a	3
14	*Syllis violaceo-flava* Grube, 1878a	2
15	*Haplosyllis madeirensis* Czerniavsky, 1881	1
	TOTAL NUMBER OF CITATIONS =	358

Materials and methods

As mentioned above, Licher (2000) recently summarized about 15 synonymies of *Haplosyllis spongicola* (Table 1), with a commonly accepted cosmopolitan distribution being one of the most surprising features of the complex (Fig. 1). Based on 28 different populations collected all around the world (Table 2), the present study describes the existing character variability within the complex. It should be pointed out, however, that it has not been possible to study all populations using all the different approaches, because of the differences in availablility of specimens, their state of preservation and the stage of their life-cycle when collected.

For light microscope observations (LM), the specimens were placed on slides in a solution of glycerine and distilled water. LM micrographs were made with a ZEISS Axioplan stereomicroscope equipped with the SPOT hardware and software (SP100 KAF1400 digital camera, software version 2.1.) from DIAGNOSTIC INSTRUMENTS INC.

For scanning electron microscope observations (SEM), the specimens were washed three times in distilled water (30 min each), run through a series of increasing ethanol concentrations, and stored in 70% ethanol until required. Immediately prior to viewing in a HITACHI S.570 scanning electron microscope (Laboratorio de Microscopía Electrónica of the Institut de Ciències del Mar of Barcelona, CSIC), they were run through a series of increasing ethanol concentra-

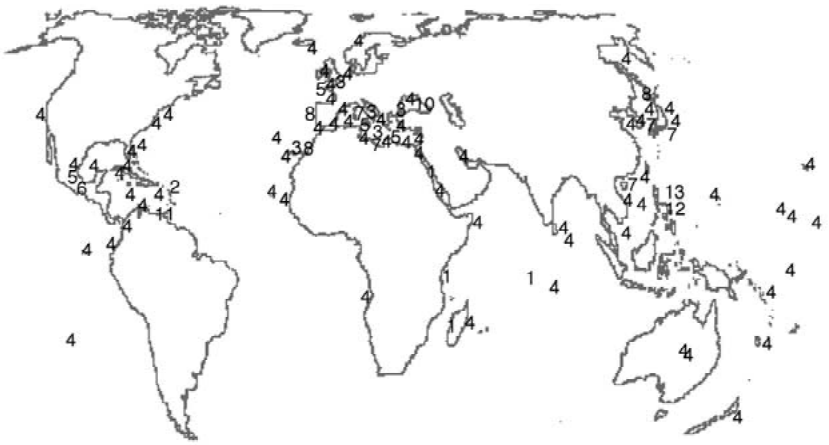

Figure 1. Geographical distribution of the known reports of species included in the *Haplosyllis spongicola* complex; the numbers correspond to the species codes indicated in Table 1.

tions ending with 100%, 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. The studied populations are deposited in the personal collections of the authors, except for the populations obtained as loans from the National Museum of Natural History of the Smithsonian Institution (USNM) and the Australian Museum of Sydney (AMS) (Table 2).

The relationships between the populations under study based on morphometric measurements were assessed by a Principal Component Analysis (PCA), which was carried out on normalized data using the PRIMER 5.2.2 (©PRIMER-2000) routines (Clarke & Gorley, 2001).

Results

After a detailed study of the 28 populations listed in Table 2, several characters emerge as relevant to the inter-population variability both in adults and the reproductive stolons. In the former, the following characters have been analysed: adult body size, shape of prostomium and palps, position of antennae, presence of sensory organs in palps, type of nuchal organs, length of appendages (antennae, tentacular cirri, dorsal and anal cirri), shape of pharynx, proventriculum and acicula, and chaetal arrangement and profile. In the stolons, in spite of size differences, the main distinguishing variability occurs in the presence or absence of a well-developed head and the corresponding cephalic organs and the presence of parapodial eye-spots. Among the studied characters, those being easily measurable under light microscopy have been used to analyse the inter-population morphometric relationships (body length, width, and number of chaetigers; extension of proventriculum; number of chaetae in anterior, middle and posterior regions).

Adult size

Initially, the studied populations reveal marked differences in adult size, either in length or in number of segments (Table 3). We are certain that most specimens are adults, as they often are mature and show traces of the stolon formation process. However, the range of variability between the largest specimens (Mediterranean, about 2 cm in length average, but up to 4 cm in some complete specimens or even 6 cm in an incomplete, stolonizing specimen) and the smallest specimens (Indian Ocean: at most 0.3 cm) is strikingly evident when placed side by side (Fig. 2). Moreover, these size differences are always connected with density differences inside the host, the bigger specimens often living a solitary existence inside the host, while the smallest often occurs in large numbers (hundreds or thousands of specimens) inside a single host-sponge specimen (López et al., 2001).

Anterior-most region

The shape of the prostomium is highly variable among the different populations. Three main forms may be distinguished, the first two (i.e. round oval and subpentagonal) have a similar width to length ratio (Fig.

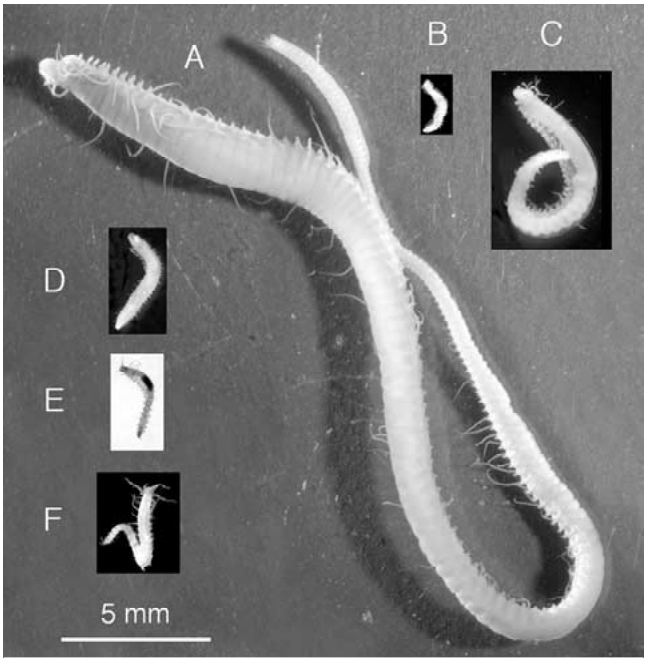

Figure 2. Range of size variability within the *Haplosyllis spongicola* complex. (A) Cape of Creus. (B) Corsica. (C) Blanes. (D) Arabian Gulf. (E) Australia (morphotype-1). (F) Barbados.

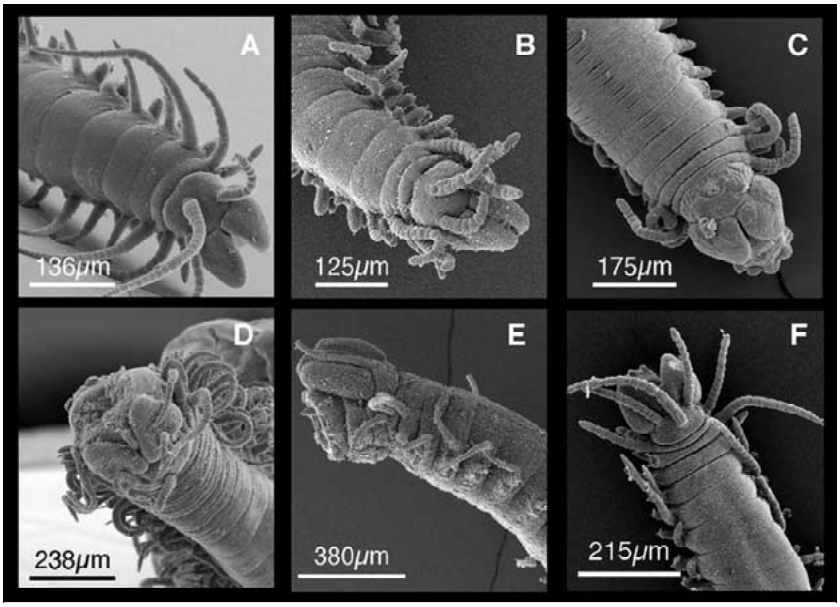

Figure 3. Examples of prostomium shape, palps vs. prostomium length and position of antennae within the *Haplosyllis spongicola* complex. (A) Belize (morphotype-1). (B) Papua New Guinea. (C) Tanzania. (D) Mediterranean (Blanes). (E) Bahamas. (F) Australia (morphotype-1).

Table 2. Summary of the available information on the geographical location of the studied populations of the *Haplosyllis spongicola* complex

MEDITERRANEAN	
-	Cape of Creus, Catalonian coast, NW Mediterranean Sea, C. Alós coll.
-	Punta Santa Anna, Blanes, Catalonian coast, NW Mediterranean Sea, D. Martin, coll.
-	Arenys de Mar, Catalonian coast, NW Mediterranean Sea, D. Martin, coll.
-	Corsica Island, E. Dutrieux coll.
ATLANTIC OCEAN	
-	Tenerife, Canary Islands, J. Núñez coll.
-	Belize, morphotype 1 27-12-99, 15m. E. Ballesteros coll.
-	Belize, morphotype 2 31-12-99, 11m. E. Ballesteros coll.
-	Belize, morphotype 3. E. Ballesteros coll.
-	Great Bahama Bank, South Exuma Cays, off Lee Stocking Island, M. Maldonado coll.
-	Barbados, off Holetown, 13° 11.3 ′ N, 59° 38.5′ W. H. Reiswig coll.
-	Discovery Bay, Jamaica, 15-aug-1969, USNM num. 41087.
-	Sea Horse Key, Florida, USA, 7-nov-1960, USNM 30026.
-	Pajaros Island, Puerto Rico. USNM 51687.
PACIFIC OCEAN	
-	Bahia Falsa, La Paz, California, pen. of Mexico, 30-sept-1971, USNM 48910.
-	Easter Island, in tide pool between Hanga Roa and Hanga Piko, 15-febr-1969, USNM 49520.
-	Papua New Guinea. G. Magnino coll.
-	Sydney, Australia. Morphotype 1. AMS W26384.
-	Sydney, Australia. Morphotype 2. AMS W26379.
SOUTH CHINA SEA	
-	Nhatrang Bay, Tam Island, SE coast of Vietnam, 3–7m, 7-11-85, T.A. Britayev coll.
-	The seaport of Nhatrang city, Tam Island, SE coast of Vietnam, 04-04-89, T.A. Britayev coll.
-	Cambodia, Kampong Son Bay, 20m, 12-11-99. B. Tursch and Y. Kantor coll.
-	Taiwan, Lungstung Bay, 4-7-99. V. Radashevsky coll.
INDIAN OCEAN	
-	Pulo Melila, Banjak Is. West of Sumatra, 2° 15 ′ N 97° 25 ′ E, TE VEGA st. 98, nov. 1963, Kohn coll. USNM 45365.
-	Off Asaluyeh, Arabian Gulf, Iran, 52° 34′ E 27° 29′ N. E. Dutrieux coll.
-	Mwamba Kuni reef bank, Bayamoyo, Zanzibar Channel, Tanzania. G. Magnino coll.
RED SEA	
-	Hurgada, coast of Egypt. G. Magnino coll.
-	Great Bitter Lake, N. Ben Eliahu coll.
-	Kafiah, Sinai Peninsula, N. Ben Eliahu coll.

3A–C, F), while the third is clearly wider than long (Fig. 3D–E). The relationships between prostomium and palp lengths may also vary, the palps being longer (Fig. 3D–F) or similar in length (or slightly shorter) (Fig. 3A–C) in comparison to the prostomium, independent of the prostomial shape. The antennae may be located near the anterior margin of the prostomium (usually directed upwards) (Fig. 3E) or attached to the middle of the prostomium (Fig. 3A–D, F).

Like most polychaetes, *Haplosyllis* specimens bear different types of sensory organs in the anterior region. Their morphology and distribution (often only visible under SEM) show also a marked variability, particularly the nuchal organs, palps and pharyngeal papillae. The most frequent type of nuchal organ is a pair of variably developed ciliated regions, which are located laterally between prostomium and peristomium (Fig. 4B–D). However, some populations show either pore-hole or papillate areas (Fig. 4A, E). Although some populations may have smooth palps (i.e., without visible sensory organs), most of them have different combinations of sensory organs, which are typically located ventrallly on palps (often two pairs below each palp) (Fig. 5) or laterally (often distributed in two longitudinal rows) (Fig. 6). Like nuchal organs, the typical external morphology of these sens-

Table 3. Summary of the morphometric measurements obtained from the different populations of the *Haplosyllis spongicola* complex. *n* = number of measured specimens; avg = average; std = standard deviation; ant = anterior chaetigers; mid = mid-body chaetigers; post = posterior chaetigers

Locality		Body			Proventriculum						Number of chaetae		
		length	width	chaetiger	chaetiger			length	width	ratio	ant	mid	post
		(mm)	(mm)	numb.	begin	end	numb.	(μm)	(μm)	w/l			
Cape of Creus	avg	16.50	0.90	66.20	10.90	19.00	7.90	2164.3	617.4	0.29	2.20	2.10	2.00
$n = 10$	std	11.60	0.50	23.80	2.40	2.70	1.60	1353.7	412.6	0.03	0.40	0.30	0.00
Arenys	avg	8.52	0.63	60.10	7.80	16.65	9.80	1351.2	357.6	0.27	2.00	2.00	2.00
$n = 20$	std	3.91	0.16	17.48	1.06	2.42	2.22	467.1	134.4	0.05	0.00	0.00	0.00
Corsica Is.	avg	2.28	0.35	36.25	4.00	9.25	6.25	460	155	0.35	2.00	2.00	2.00
$n = 4$	std	0.72	0.03	4.04	0.82	1.50	0.96	67.9	17.4	0.02	0.00	0.00	0.00
Arabian Gulf	avg	3.61	0.45	34.84	4.95	10.28	6.34	737	237.7	0.33	1.84	1.89	2.12
$n = 11$	std	1.08	0.08	5.08	0.64	0.76	0.85	153.5	47.4	0.02	0.71	0.68	0.33
Sinai	avg	3.30	0.34	31.25	5.44	11.50	6.94	700.4	195.8	0.29	1.75	1.25	2.00
$n = 8$	std	1.00	0.07	5.63	1.12	1.42	1.02	183.4	51.1	0.04	0.47	0.47	0.00
Great Bitter L.	avg	3.71	0.30	37.89	4.86	9.56	5.65	555.9	162	0.31	1.36	1.42	1.24
$n = 17$	std	1.29	0.06	9.56	0.35	1.25	1.21	134.8	34.8	0.06	0.50	0.51	0.44
U.S.A.	avg	4.34	0.40	38.70	6.00	12.00	7.00	893.1	213.5	0.26	2.16	2.16	1.70
$n = 13$	std	0.89	0.05	6.32	0.58	1.16	1.00	210.9	35.4	0.06	0.38	0.38	0.49
Puerto Rico	avg	6.99	0.33	33.16	6.08	8.85	3.62	730	217	0.31	1.00	1.00	1.00
$n = 12$	std	1.36	0.05	5.17	0.87	0.69	0.51	94.7	31	0.05	0.00	0.00	0.00
Jamaica	avg	2.42	0.29	24.78	3.06	6.50	4.34	328.9	173.9	0.54	2.12	2.00	1.89
$n = 18$	std	0.69	0.07	3.92	0.94	0.99	0.60	111.1	60.2	0.03	0.33	0.00	0.33
Bahamas	avg	4.50	0.34	32.07	4.75	8.57	4.57	666.6	193.3	0.31	1.00	1.00	1.00
$n = 16$	std	1.05	0.08	4.66	0.94	1.29	0.69	191.7	43.2	0.04	0.00	0.00	0.00
Easter Is.	avg	4.53	0.42	36.80	4.60	10.00	6.40	710	230	0.33	2.60	2.60	2.40
$n = 5$	std	0.55	0.03	3.50	0.55	0.71	0.55	53.4	35.4	0.03	0.55	0.55	0.55
Mexico	avg	8.55	0.48	40.67	7.50	10.00	3.50	873.4	297.5	0.35	1.34	1.67	1.67
$n = 6$	std	0.71	0.07	2.43	0.55	0.64	0.55	212.1	65.5	0.05	0.52	0.52	0.52
Sumatra	avg	2.57	0.31	26.12	4.00	7.78	4.56	404.5	160	0.42	2.12	2.34	1.78
$n = 9$	std	1.19	0.12	9.38	1.23	1.99	0.89	152.1	48.5	0.06	0.34	0.50	0.45
Taiwan	avg	1.79	0.21	21.44	4.94	8.57	4.63	322.4	112.7	0.36	2.00	2.57	3.00
$n = 16$	std	0.45	0.04	6.00	0.69	0.92	0.54	50.8	16.9	0.05	0.00	0.52	0.64
Vietnam	avg	2.59	0.31	28.35	5.00	9.65	9.25	507	159.3	0.32	1.00	1.10	2.00
$n = 20$	std	1.06	0.10	8.77	1.42	2.80	16.75	221.6	71.4	0.07	0.00	0.31	0.00
Australia	avg	3.00	0.27	20.00	5.40	8.40	3.00	403	163.2	0.42	1.00	1.40	1.00
$n = 5$	std	0.29	0.08	3.00	0.90	0.90	0.00	97.5	35.1	0.05	0.00	0.55	0.00
Papua	avg	2.39	0.34	20.00	3.60	7.60	4.00	393.2	174.2	0.45	1.00	1.00	1.00
$n = 5$	std	0.34	0.08	3.00	0.90	0.90	0.00	85.1	37.6	0.03	0.00	0.00	0.00

ory organs is a complex combination of ciliary tufts (Figs 5A and 6A–B). However, some populations have glandular pore holes distributed in patches (ventrally, Fig. 5D–E) or located inside cavities (laterally, Fig. 6C–D). Only two different types of papillae have been observed on the distal pharyngeal end: smooth or ciliated ones. The latter have variably developed tuft or row of cilia from the tip towards the outer edge (Fig. 7).

Appendages

One of the most conspicuous characters within the different populations is the length of the antennae (central and lateral), tentacular cirri (dorsal and ventral), dorsal cirri and anal cirri (in terms of number of articles, in order to avoid possible errors induced by different responses to the fixation process). The length appears to be highly specific within a certain population. Sev-

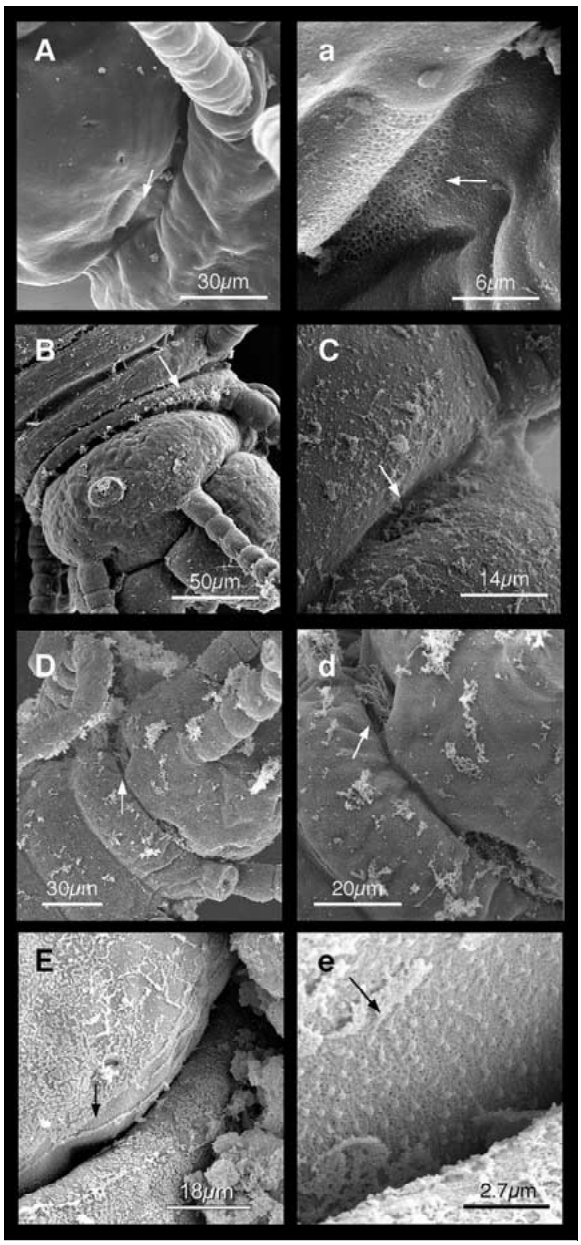

Figure 4. Types of nuchal organs in the *Haplosyllis spongicola* complex. (A) a. Pore hole plates (Canary Is.): (A) General view; a. Detail. (B) Ciliary tufts. (Arabian Gulf). (C) Ciliary tufts (Barbados). (D) d. Ciliary tufts (Australia, morphotype-1): (D) General view; d. Detail. (E) Papillate areas (Belize, morphotype-3). The arrows indicate the location of the nuchal organs.

eral characteristics may be analysed in order to define the length. The overall length of all appendages may vary from very long to short cirri along the body (Fig. 8A). The relationships between the anterior and posterior appendages may range from specimens having a marked length difference (the anterior-most much longer than the mid-body and posterior-most ones, Fig. 8B) to specimens showing a gradual decrease in length along the body (Fig. 8A,C). At mid-body, the dorsal cirri may show variably marked alternation in length, with either all cirri being similar in length, the long cirri only slightly longer than the short ones, or the long cirri much longer than the short ones (e.g. twice or three times longer) (Fig. 8A–C). An extreme case occurs in populations in which the dorsal cirri on middle and posterior regions are reduced to a single, often very small article (Fig. 8A–B). Finally, there is also a marked variability in the length of the anal cirri (Fig. 9).

Internal structures

The presence or absence of a pseudo-trepan in *H. spongicola* has been reported for the Mediterranean populations. According to San Martín (1984), specimens from the same population may either have a well-developed or slightly marked pseudo-trepan, or this structure may be absent. The NW Mediterranean specimens have a clearly chitinized pharyngeal border showing the same previously reported variability. Within this population, the shape of the pharyngeal border seems to be related to the worm size. The smallest specimens have well-defined pseudo-trepans, which seem to be eroded in large specimens. Although other populations around the world may show chitinized pharyngeal borders (e.g. Corsica, Arabian Gulf), in the studied populations, the presence of a pseudo-trepan seems to be restricted to the NW Mediterranean specimens.

The proventriculum may be either sub-rectangular (clearly longer than wide) or ovoid (slightly longer than wide, with more or less rounded sides). The width/length ratio clearly reflects this inter-population variability, ranging from 0.25 to 0.53. Independently, the proventriculum may be short (extending through 3–4 chaetigers) or long (extending from 6 to 9–10 chaetigers). Moreover, the position of the proventriculum in the body (starting chaetiger and number of occupied chaetigers) also differs among populations (Table 3).

In the last body segments, which have a single acicula per parapodium, the studied populations showed four different acicular shapes. Some specimens have an acicula with an oblique end and a pointed tip clearly directed upwards (Fig. 10A) or a 90 degrees-bent end with rounded tip (Fig. 10B).

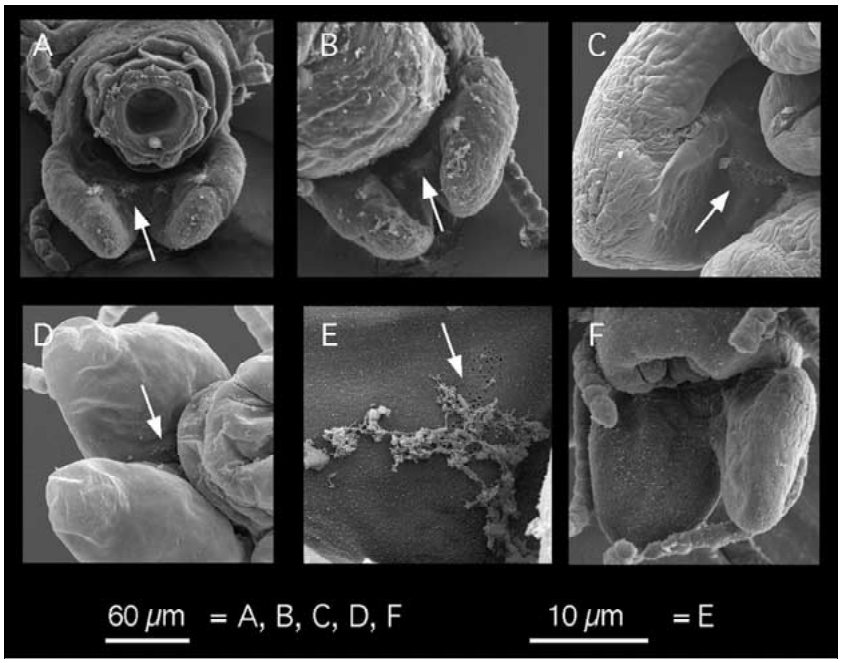

Figure 5. Examples of ventral sensory organs of palps in the *Haplosyllis spongicola* complex. Paired ciliary tufts: Arabian Gulf (A), Corsica (B) and Cape of Creus (C). Pore holes: Canary Islands (D, E). Smooth: Barbados (F).

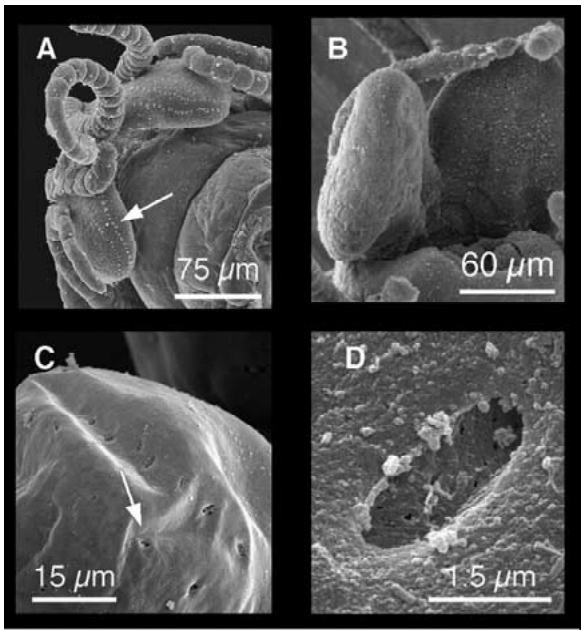

Figure 6. Examples of lateral sensory organs on palps in the *Haplosyllis spongicola* complex. (A) Paired rows of ciliated tufts (Papua New Guinea). (B) Smooth laterals (Belize, morphotype-1). (C, D) Paired rows of pore hole cavities (Canary Islands).

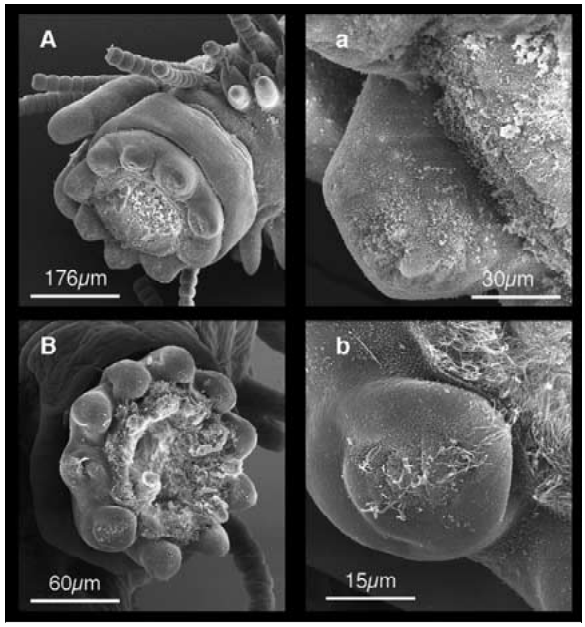

Figure 7. Examples of pharyngeal papillae from the *Haplosyllis spongicola* complex. (A) a. Smooth papillae (Canary Islands): (A) General view; a. Detail. (B) b. Ciliated papillae (Cape of Creus): (B) General view; b. Detail.

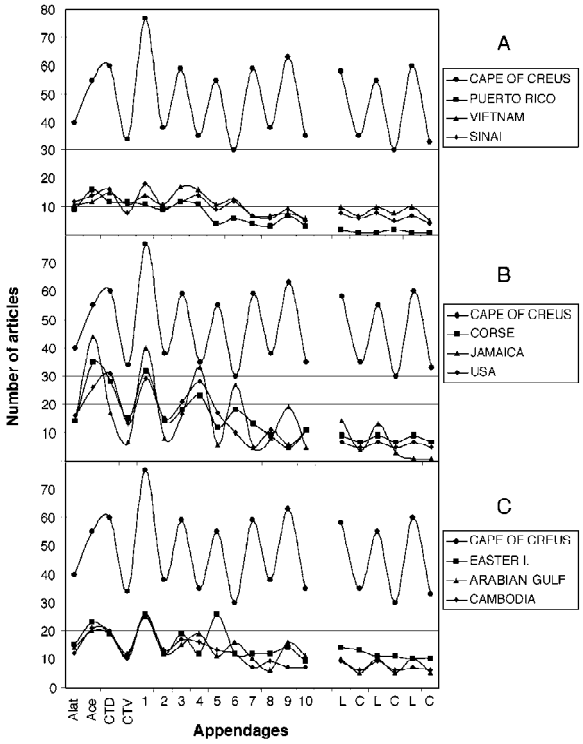

Figure 8. Examples of different patterns of alternation in length of the appendages in the *Haplosyllis spongicola* complex, compared with the NW Mediterranean population from Cape of Creus (i.e. with the longest cirri and the most marked alternation). (A) Short appendages with non-marked alternation. (B) Anterior-most cirri much longer than the posterior-most, with marked alternation. (C) Anterior-most cirri slightly longer than the posterior-most, with non-marked alternation. Alat: lateral antennae; Ace: central antennae; CTD: dorsal tentacular cirri; CTV: ventral tentacular cirri; 1 to 10: fins 10 dorsal cirri; L: posterior-most long dorsal cirri; C: posterior-most short dorsal cirri.

However, the most common aciculum has a curved end, with a tip more or less directed downwards (Fig. 10C). Finally, the less frequent shape was that of the aciculum having a straight tip (Fig. 10D).

Chaetal morphology

The chaetae of *H. spongicola* have always been figured as simple chaetae having two small teeth on its main fang, often based on LM observations (Fig. 10E–H). The results of our research within the worldwide complex have shown differences between chaetal arrangement and profile (Fig. 11A). Although the variability here reported is mainly based on SEM observations, some characteristics are also visible under light microscopy. *H. spongicola* typically shows two chaetae per parapodium. However, some populations consistently show only one, while others have three or more (Table 3). When more than one chaeta per parapodium is present they may have the same or different profiles, and may be similarly sized or with one chaeta larger than the other(s). In the latter case, the characters appearing to be species-specific often occur in larger chaetae, while smaller chaetae show less inter-population differences. However, it should be pointed out that species-specific chaetal characteristics often occur in anteriormost or posteriormost body regions (except for the presence/absence of unidentate chaetae), while mid-body chaetae may be eroded and their characters difficult to distinguish.

Several comparisons between measurements of the (large) chaetae may be made (Fig. 11B). The base of the main fang may be either longer or similar in length to the distance between the main fang upper insertion point and the mid-joining point between teeth. The main fang may either be shorter, similar in length or longer than the chaetal width. The upper side of the main fang may be clearly longer than the lower side or both sides may be similar in length.

There are usually two teeth at the tip of the chaeta. In this case, the two teeth may be similar in size or the distal tooth may be clearly smaller (Fig. 12). The angle between the teeth may be either narrow (Figs 12D and 14A,E) or wide (Figs 12A and 14B–D). However, some populations have clearly unidentate chaetae (Figs 10F and 12E), while others have extra teeth in some chaetae (three or even four) in either the anterior or posterior parts of body (Fig. 13A–F).

Although the main fang may have a smooth or slightly ridged upper side (as figured for the 'typical' *H. spongicola* chaetae), many populations have different types of denticles on this side (Fig. 14). There is variability (seen in lateral view) in the number of denticles present which may be a few (often 6 or less) or many (more than 10), and in the shape of the denticles which may show either a slight increase in size from the tip of the main fang to its base or may be small near the tip and much larger near the base). In frontal view, the denticles may be seen to be distributed in a single longitudinal row from the tip to the base of the main fang or they may form a series of transverse rows, having more denticles when closer to the base of the main fang. Distinguishing between chaetae having a nearly circular or a flattened elliptical main fang (in cross section) is possible either in an upper or frontal view of the chaetae. Usually, this last distinction is related to the shape of the cross section

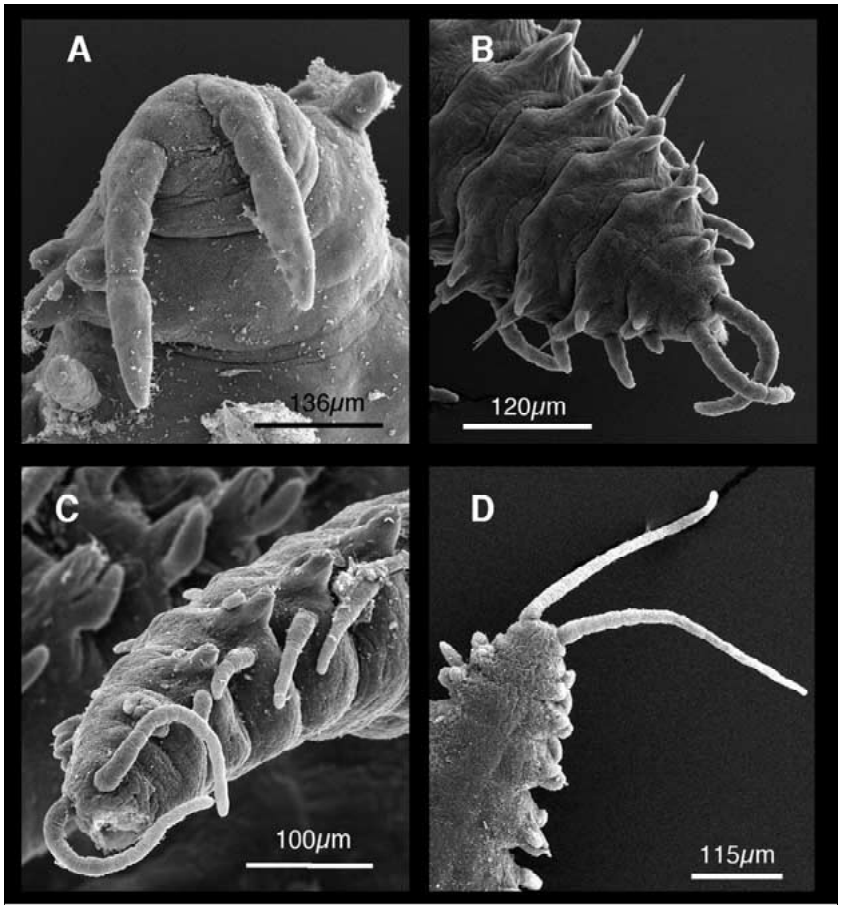

Figure 9. Examples of anal cirri in the *Haplosyllis spongicola* complex. Short: (A) Barbados. (B) Taiwan. Long: (C) Cambodia. (D) Florida.

for the whole chaetae and may be observed in frontal view (Fig. 14).

It is clear that the orientation of the chaetae during the SEM observations is critical either to allow proper comparisons or to observe all relevant features.

Stolon morphology

Although still not well-defined, the shape of the stolons has often been considered as a powerful tool to assess the taxonomy of syllids, even at subfamily level (Estapé & San Martín, 1991; Garwood, 1991). The typical stolon reported for *H. spongicola* is acephalous and bears a pair of parapodial ocular spots on each segment. Although it is not easy to find these stolons in benthic samples, the presence of parapodial ocular spots may be observed early during the stolon formation process, with the reproductive segments still attached to the adult body (Fig. 15). Among the studied specimens, the presence of ocular spots has been observed in the Mediterranean Sea and the Arabian Gulf (Fig. 15A,B, respectively). Even whilst still attached to the parents, the stolons of these two populations greatly differ in size and number of segments. As expected, they are larger in the largest Mediterranean specimens (about 0.6 cm in length and having more than 30 segments with ocular spots; Fig. 15A) and shorter in the small Arabian Gulf specimens (about 0.2 cm in length and having about 10 segments with ocular spots; Fig. 15B).

Some of the small tropical populations within the complex, such as those in Barbados and Australia (morphotype-1) show different stolon morphologies (Fig. 16). The stolons do not have parapodial ocular spots and have a well-developed head. Two pairs of well-developed reddish eyes are present on the prostomium, the anterior pair being larger than the posterior one, which has a crystalline-like structure visible by transparency under a light microscope. Adult specimens are small and the stolons correspondingly small

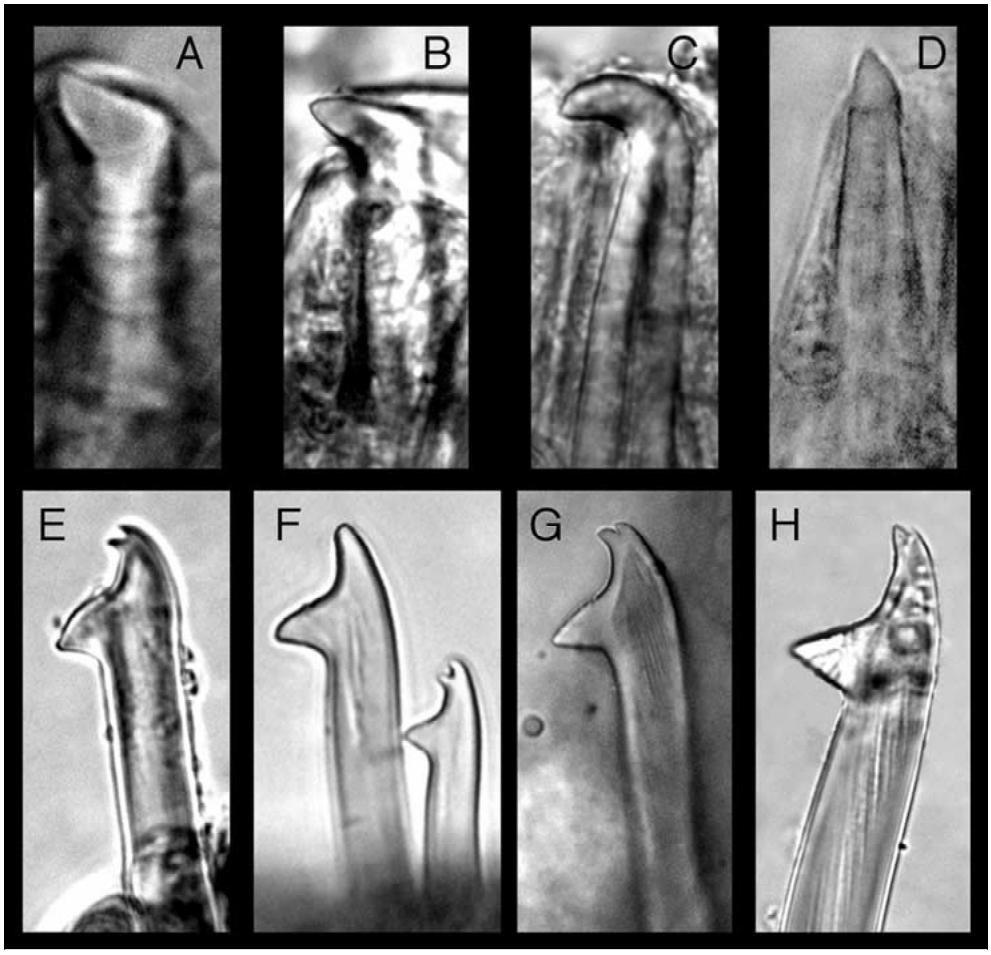

Figure 10. Light microscope images of the four types of acicular tips (A, B, C, D) and the corresponding chaetae (E, F, G, H) in the *Haplosyllis spongicola* complex. (A, E) Barbados. (B, F) Arabian Gulf. (C, G) Cape of Creus. (D, H) Belize (morphotype-2).

(less than 0.1 cm long and about 0.2 cm long in the Barbados and Australian populations, respectively, for about 10 chaetigers). These stolons also have cephalic appendages: one digitiform pair in the Australian population and one semi-spherical pair in the Barbados population. The exact nature of these appendages could not be assessed. However, the digitiform appendages are more or less distinctly ringed and bear tufts of cilia at the joints (like the adult antennae and cirri) and thus are more probably antennae, while the semi-spherical ones are smooth and thus are tentatively considered as palps.

An additional characteristic of these populations is that in all cases, male and female adults with stolons occur inside the host sponge (as well as all possible developmental stages from young juveniles with 3 or 4 segments), while only detached female stolons occur inside the host. No detached male stolons have been found inside the host sponge, in either the Caribbean or the Australian populations.

Morphometric analysis

The PCA analysis based on morphometric measurements (which are summarized in Table 3) is highly discriminative (Fig. 17). The different populations are distributed along the first axis (52.9% of variance explained) according to size-related variables (body length, proventriculum length or number of chaetigers), with the largest specimens having the most negative values. The second axis (18.5% of variance explained) is mainly correlated with the number of chaetae. The populations having consistently one chaetae per parapodium show the most negative values, the specimens with mainly (or typically) two

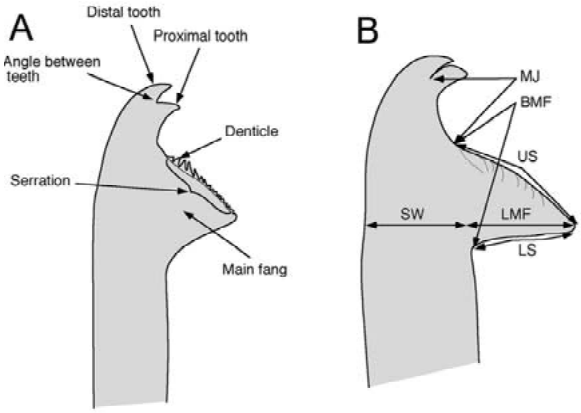

Figure 11. Scheme of typical chaeta of the *Haplosyllis spongicola* complex. (A) Terminology used to describe the chaetal morphology. (B) Definition of the measures used to compare the chaetal profile. MJ: mid-joining point between teeth. BMF: basis of the main fang. SW: chaetal width. LMF: length of the main fang. US: upper side of the main fang. LS: lower side of the main fang.

chaetae per parapodium show intermediate values, and the most positive values of the axis corresponded to those populations having two or more chaetae per parapodium. Although the resulting spatial distribution along the two axes give rise to a clear isolation of the different populations, some trends may be specifically pointed out.

Some detected associations may be correlated with the biogeographical vicinity of the involved populations. For instance, the specimens from the Sinai Peninsula and the Arabian Gulf occupy nearly the same position as those from the Great Bitter Lake (Israel), while the populations from Papua-New Guinea and Australia are also located very close to one another. On the other hand, the largest specimens occur in the two Ibero-Mediterranean populations (i.e. Cape of Creus and Arenys). However, the range of variability is higher than those observed among the other populations, to the extent that some of the specimens are located closer to the position of the remaining populations. Accordingly, there are some fine morphological characters suggesting that two different species are involved, particularly in the shape of the appendages and the chaetal profile (see Fig. 12A–B). Moreover, there is a marked discontinuity between the position of these two populations and the specimens from Corsica, which clearly belong to a different morphotype (e.g. they were small and had unidentate chaetae in the mid-body region) (Fig. 12E).

Like the Iberian and Corsica populations, the different Caribbean populations occupy two extreme positions: the specimens from Florida and Jamaica on one side and those from Puerto Rico and Bahamas on the other. The same situation is observed for the two Pacific populations (i.e. Mexico and Easter Island) and for the Asian populations (Taiwan, Sumatra and Vietnam). In all cases, the morphology of these populations will certainly help in the future definition of their taxonomic status.

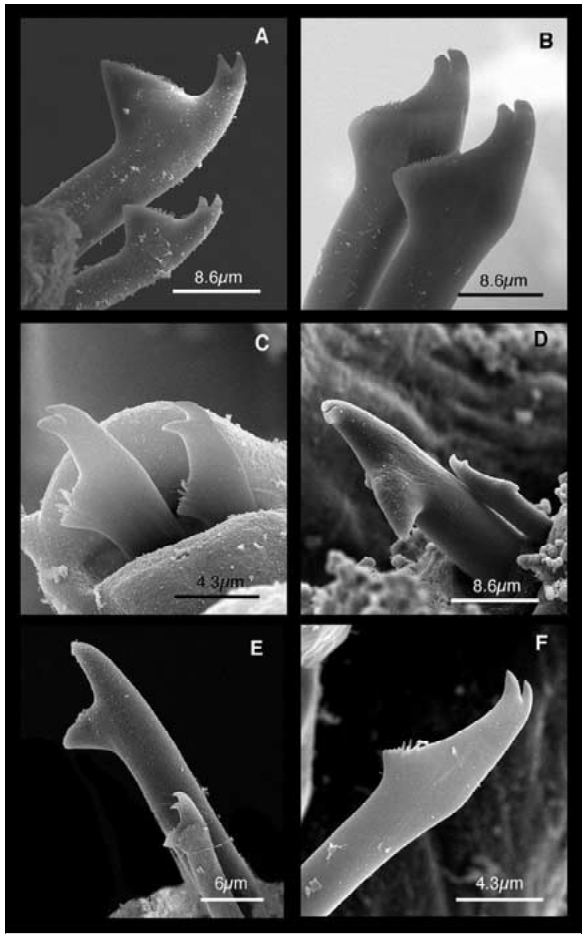

Figure 12. Variability of the shape of chaetae on the same parapodium, angle between teeth and shape of the distal tooth in the *Haplosyllis spongicola* complex. (A) Blanes. (B) Cape of Creus. (C) Canary Island, (D) Bahamas. (E) Corsica. (F) Florida.

Discussion

The variability observed within the sponge-associated *Haplosyllis* species-complex is so wide that it may be stated that virtually all studied morphotypes show enough taxonomically robust differences to be formally described as different species. As a consequence,

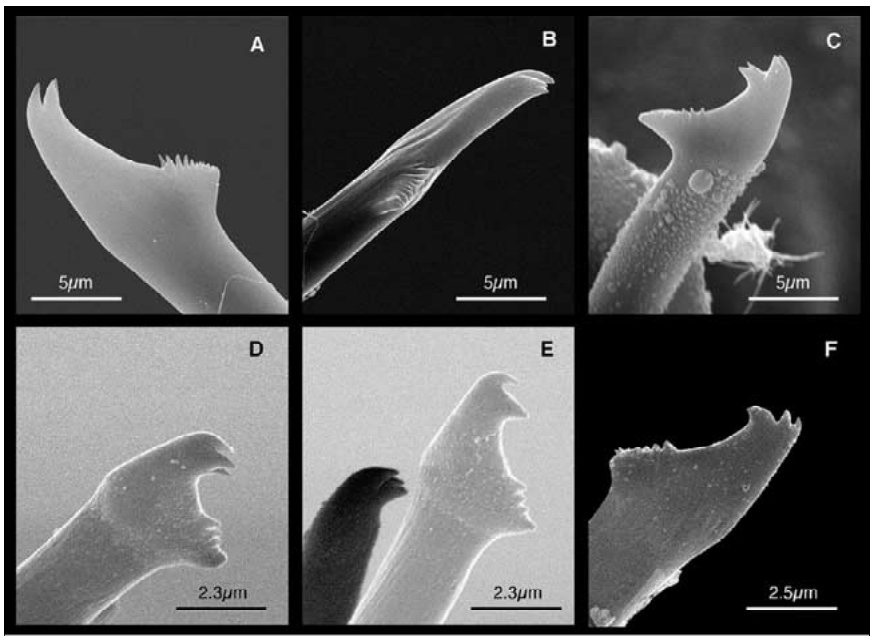

Figure 13. Examples of populations of the *Haplosyllis spongicola* complex with spare tooth in some chaetae. (A–C) Mexico (A–B: anterior-most, C: posterior-most). (D–F) Taiwan (D: anterior-most, E–F: posterior-most).

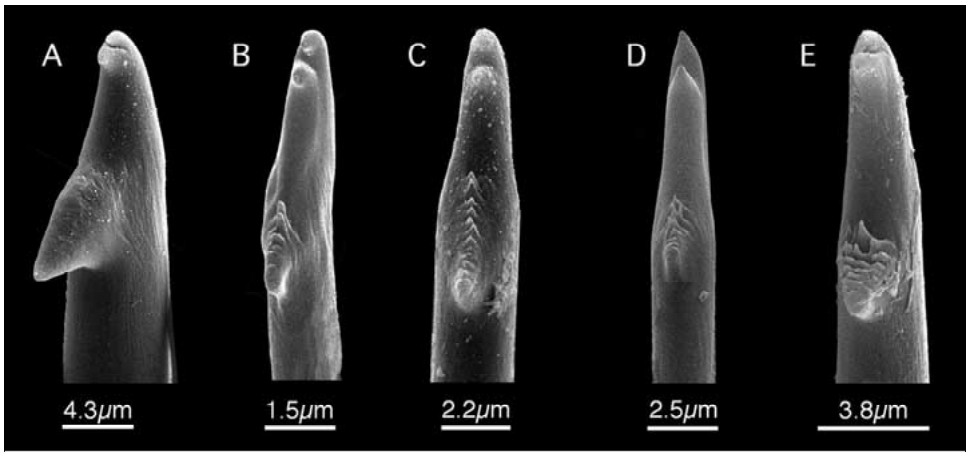

Figure 14. Chaetae in frontal view, showing details of the different types of serration on the main fang present in the *Haplosyllis spongicola* complex. (A) Bahamas. (B) Australia. (C) Blanes. (D) Mexico. (E) Belize.

the so-called *Haplosyllis spongicola* must be considered as a pseudo-sibling species-complex. Some of the studied populations clearly belong to previously unknown taxa, which merit being described as new species. However, we have started an extensive examination of type specimens for as many as possible of the known synonymized species, in order to clarify its taxonomic validity and to re-describe them (when required) in the light of new characters reported here.

One of the consequences of the reported differences is that mention of the different species or subspecies, which are currently being considered as synonymies of *H. spongicola*, in geographical locations other than the original one, must be viewed with care. For instance, the presence of *H. spongicola spongicola* or *H. spongicola tentaculata* (either as subspecies or species), originally described from the Atlantic and the Mediterranean coasts of Europe and later reported from Japan or Korea (Cognetti, 1957, 1961; Imajima,

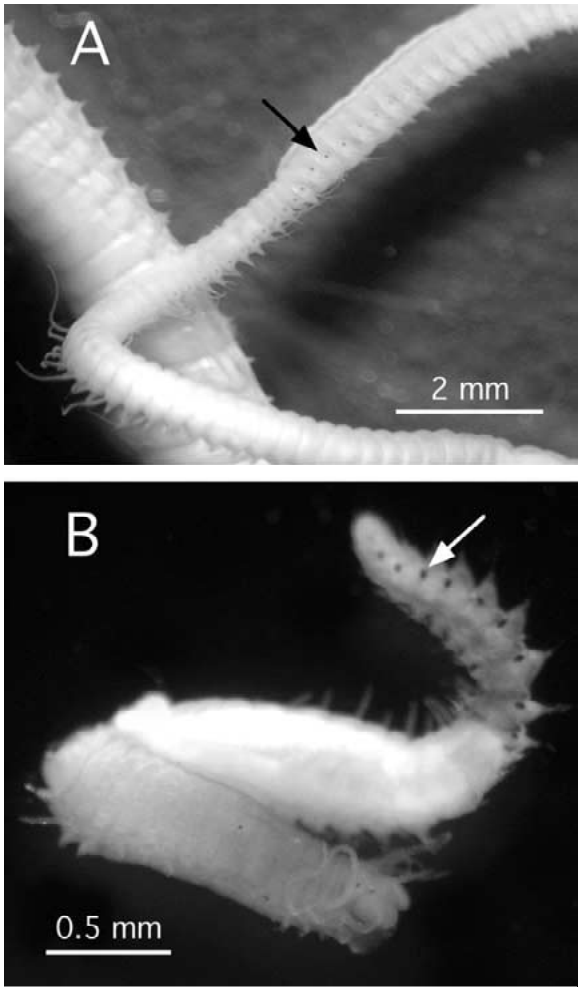

Figure 15. Examples of stolons of the *Haplosyllis spongicola* complex with acephalous stolons and parapodial eye-spots. (A) Cape of Creus. (B) Arabian Gulf. The arrows indicate the position of the ocular spots.

1966; Campoy, 1982; San Martín, 1984; Lee & Rho, 1994). Similarly, the mention of one species of the complex from a given area does not mean that all specimens found in the same area will necessary be conspecific. A clear example of the marked sympatry occurring within the complex may be the finding of 6 or even 7 different morphotypes in the Caribbean basin or the three found in the western Mediterranean. As the type locality of the original description of *H. spongicola*, the Mediterranean populations deserve special attention. According to the corresponding descriptions, the western Mediterranean morphotypes may correspond to the previously described species *H. spongicola* (Grube, 1855), *H. tentaculata* (Marion, 1878) and *H. hamata* (Claparède, 1868). Together with the examination of type specimens, the authors are currently working on the formal re-description of these three species, as a first step in the process of solving the species complex taxonomy.

Some trends on the possible grouping of species at a level higher than species have already been pointed out by means of the multivariate analysis of morphometric data. Certainly, the morphometric variables estimated in the present study are only part of the whole set of measurements that may be estimated within syllids (e.g. the length and width of the pharynx and most of the chaetal characters described in this study, which may be measured, have not been included). However, the characters used in our study have a clear advantage: they are easily measurable using light microscopy. Moreover, used as a part of a multivariate analysis, they were able to show clear trends in the inter-population relationships, which may be a complementary tool for the formal, more descriptive, taxonomic approach. As a consequence, together with the formal descriptions (or re-descriptions) of the morphotypes involved in the complex, a cladistic analysis of the phylogenetic relationships within the complex is also being carried out by the authors. These two approaches will provide a framework to define the new sponge-associated species of "*Haplosyllis spongicola*" that will certainly be discovered in the future.

The observed differences in size, sensory organs and reproductive bodies would certainly be related to the ecology and behaviour of the different species. However, behavioural and ecological studies (e.g. to assess the complexities of the host-symbiont relationships) will require both field and laboratory experimental studies and, thus, are beyond the scope of the present study. Nevertheless, we are confident that they will be the source of highly interesting information in the near future. For instance, the recently described species *Haplosyllis basticola* Sardá et al., 2002 from Guam, which clearly belonged to the complex (Sardá et al., 2002), had a similar adult morphology and exactly the same type of stolon as the Australian (morphotype-1) population. Curiously enough, both populations have been found living inside host sponges belonging to the same family (i.e. Ianthellidae). Like the adult morphology, the few known life history data support the existence of different taxa within the complex. However, in this case, the differences are so marked that we suggest that they may indicate differences at a taxonomic level higher than species.

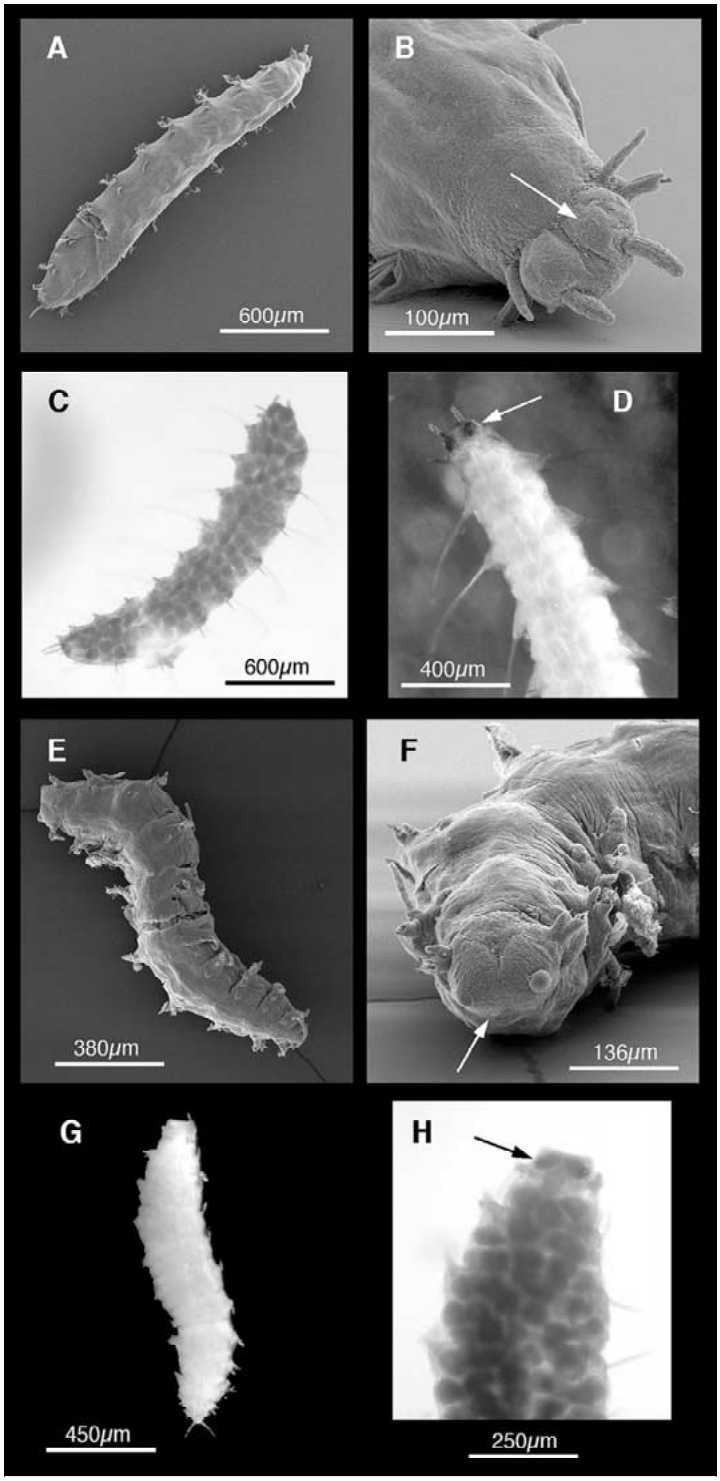

Figure 16. Examples of stolons of the *Haplosyllis spongicola* complex with well-developed head. (A) Whole view of a female stolon (SEM). (B) Detail of the head (SEM). (C) Whole view of a female stolon (LM). (D) Detail of the anterior end (LM). (E) Whole view of a female stolon (SEM). (F) Detail of the head (SEM). (G) Whole view of a female stolon (LM). (H) Detail of the anterior end (LM). (A–D) Australia (morphotype-1). (E–H) Barbados. The arrows indicate the position of eyes.

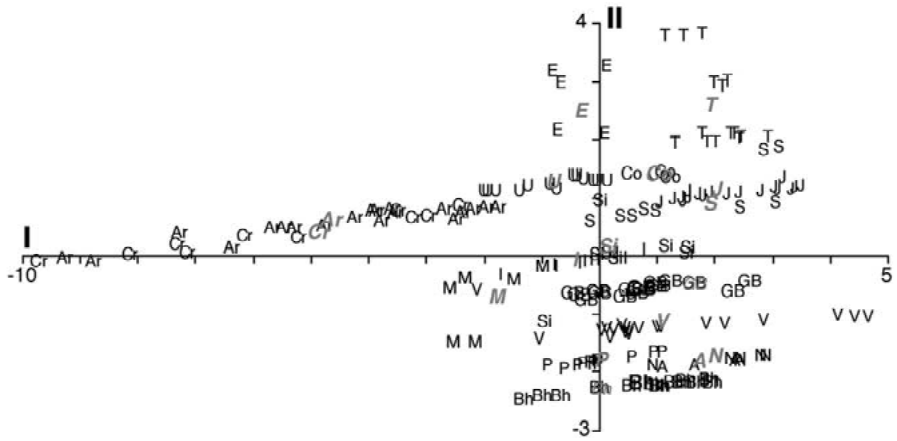

Figure 17. Results of the PCA analysis performed on the morphometric parameters measured on the studied populations of the *Haplosyllis spongicola* species complex. U = U.S.A. (Florida); S = Sumatra; P = Puerto Rico; M = Mexico; J = Jamaica; I = Iran (Arabian Gulf); E = Easter Island; Co = Corsica Island; Cr = Cape of Creus; A = Australia; N = Papua / New Guinea; Ar = Arenys; Si = Sinai Peninsula; GB = Great Bitter Lake; Bh = Bahamas; T = Taiwan; V = Vietnam (from *Haliclona*); Grey labels indicate the relative position of the mean population values. Number of specimens measured per population as in Table 3.

A particularly interesting feature, from an ecological point of view, is the presence of female stolons (or, even better, the absence of male stolons) inside the host sponges in some of the Australian and Caribbean populations. This allowed us to suggest that female stolons are not able to leave the host, while male stolons can be released and are responsible for fertilization of females from different host specimens. A similar strategy has been reported for the sponge symbiont syllid *Haplosyllides floridana* Augener, 1924. This species was first described as *H. floridanus* on the basis of a planktonic, free-swimming male stolon, while the non-reproductive specimens were described as *Syllis* (*Haplosyllis) aberrans* Fauvel, 1939 Both species were later synonymized under *Haplosyllis floridana* (Uebelacker, 1982) and the present status was established by San Martín et al. (1997). The presence of both male and female stolons inside the host sponge in *Haplosyllis basticola* (Sardá et al., 2002) may either indicate a different reproductive strategy or a delayed phase of the life cycle for this species. Male and female stolons left the host during sample treatment in the laboratory as did also the non-reproductive adults and juveniles. However, no conclusion may be inferred on the release of stolons in natural conditions. We suggest that the observed behavior is more likely an escape strategy related to the stress caused when collected and kept in the laboratory (i.e. like coral 'bleaching'). Similar escape behaviour has been reported for other symbiotic polychaetes like *Histriobdella homari* (see Martin & Britayev, 1998).

Relative to biodiversity, a rough estimate may assume the number of polychaete species to be increased by an order of magnitude, if more potential species-complexes are analysed in depth. However, what is probably more important is that so many of the complexes discovered to date include species that often are 'typical', abundant, accessible, economically important, or used to assess the state of health of benthic communities. Consequently, to know whether the same nominal species found in different areas are really the same species or just similar organisms with significantly different biological and/or ecological features emerges as a matter of high relevance.

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