

A taxonomic revision of the genus *Haplosyllis* Langerhans, 1887 (Polychaeta: Syllidae: Syllinae)

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Abstract

The genus *Haplosyllis* Langerhans, 1887 is revised based on available types and newly collected specimens. 19 species are considered as valid, five as incertae sedis and four are referred to nomina dubia. *Trypanoseta* (Imajima, 1966) is synonymised with *Haplosyllis*, as the presence of trepan is considered a non-robust taxonomic feature, affecting *H. ohma* **new comb.** (Imajima & Hartman, 1964) and *H. granulosa* **new comb.** (Lattig, San Martín & Martín, 2007). *Haplosyllis streptocephala* (Grube, 1857) is a new combination and two species are considered to belong to *Alcyonosyllis* Glasby & Watson, 2001: *A. bisetosa* **new comb.** (Hartmann-Schröder, 1960) and *A. gorgoniacola* **new comb.** (Sun & Yang, 2004). All valid species are described and figured except those described during the last decade, which only includes diagnoses and chaetae illustrations. A dichotomous key to all valid species of *Haplosyllis* is provided.

Key words: *Haplosyllis*, Syllidae, taxonomy, revision, identification key

Introduction

The genus *Haplosyllis* Langerhans, 1887 (Polychaeta, Syllidae, Syllinae) has an unresolved taxonomy; it is characterized by the articulated cirri, palps fused only at bases and the simple bidentate chaetae. The genus is relatively small, includes 19 species, 5 incertae sedis and 4 nomina dubia (present study). Together with *Alcyonosyllis* Glasby & Watson, 2001, *Haplosyllides* Augener, 1924 *Parahaplosyllis* Hartmann-Schröder, 1990, constitute the only syllid taxa lacking compound chaetae, while some species of *Trypanosyllis* Claparède, 1864 and *Syllis* Lamarck, 1818 may also have simple chaetae in some parapodia along the body.

Members of *Haplosyllis* reproduce by schizogamy (stolonization), in which only the posterior end is transformed into an epitokous sexual stage (Garwood 1991; Franke 1999). There are two kinds of stolons in *Haplosyllis*: acephalous stolons, which bear a pair of parapodial ocular spots on each segment, and stolons with a well-developed head, often with large eyes and cephalic appendages (Martin *et al.* 2003; San Martín 2003).

The species of *Haplosyllis* are usually found inside sponges (Cognetti 1957; Magnino & Gaino 1998; Martin & Britayev 1998; López *et al.* 2001; Martin *et al.* 2003), but have also been reported in association with gorgonians (Utinomi 1956; López *et al.* 1996; Martin *et al.* 2002), and other polychaetes (Treadwell 1909), as well as from a variety of substrates, such as coarse sand, detritic and muddy bottoms, intertidal algae, calcareous concretions and *Posidonia oceanica* meadows (Laubier 1966; Campoy 1982; Martin 1987; Núñez *et al.* 1992; Paola *et al.* 2006; Lattig *et al.* 2007). The sparse ecological data suggest interesting relationships with their hosts, being ectoparasites in the case of polychaetes (Treadwell 1909), kleptoparasitic to mutualistic in the case of gorgonians (Martin *et al.* 2002), or mutualists in the case of sponges (Martin & Britayev 1998; Magnino & Gaino 1998; Sardá *et al.* 2002; Martin *et al.* 2003).

Taxonomic history. The type species, *H. spongicola* was first described from the Adriatic Sea (Grube, 1855). Since then, a few more species were reported with simple and currently inaccurate descriptions (e.g. *H. uncinigera* (Grube, 1878), *H. violaceoflava* (Grube, 1878) and *H. djiboutiensis* Gravier, 1900). In the early 1950s and 1980s, the description of species such as *H. anthogorgicola* Utinomy, 1956; *H. depressa chamaeleon* Laubier, 1960; *H. trifalcata* Day, 1960, and *H. agelas* Uebelacker, 1982, showed the existence of marked differences in the arrangement of both chaetae and cirri, indicating that *Haplosyllis* was not as simple as initially thought. During the last decade the use of Scanning Electron Microscopy (SEM) has allowed the description of several new species with detailed accounts of the

chaetal morphology. Among them, *H. basticola* Sardá, Ávila & Paul, 2002; *H. villogorgicola* Martin, Núñez, Riera & Gil, 2002; *H. lobo* Paola, San Martín, & Martin, 2006; *H. carmenbritoae* Lattig, San Martín & Martin, 2007 and *H. granulosa* (Lattig, San Martín & Martin, 2007).

The assignation of species to *Haplosyllis* has been traditionally based on the presence of simple bifid chaetae (being always similar in appearance), and the cirri length (described as short or long). The absence of studies on the variability of these characters has caused long taxonomic histories, involving a high number of subspecies (for details, see Lattig *et al.* 2007), and synonymies (Augener 1913; Fauvel 1919; 1923; Imajima 1966; Licher 1999; Wehe & Fiege 2002). In the revision of genus *Typosyllis*, Licher (1999) included a review of *Haplosyllis*, recognising 12 valid species, and considering *Haplosyllis spongicola* as a cosmopolitan species, with more than 350 citations and 15 synonymies (i.e. most subspecies or species described before the 1940s). Conversely, Martin *et al.* (2003) reported a high morphological variability for most relevant characters, and suggested that *H. spongicola* was a species-complex, whose components may be distinguished with proper observations, and then formally described. This idea has been supported by the progressive increase of new described species, and will be further confirmed with the continuity of the *Haplosyllis* revision, which will include about 15 new species from Indonesia (in press), Australia, the Red Sea and the Caribbean Sea (papers in preparation).

The present study has two specific aims, to define the variability of the most important taxonomic characters, particularly the chaetal morphology and the cirri length pattern, and to clarify the taxonomic position of all currently known species and subspecies within the genus *Haplosyllis*. The oldest and poorly known taxa here considered as valid species, are described, figured, and discussed; for species with accurate descriptions, only a diagnosis is given. A key for all *Haplosyllis* species is also provided. Several species initially considered as belonging to *Haplosyllis* are transferred to different genera (i.e. *Alcyonosyllis* and *Trypanosyllis*).

Material and methods

All morphological observations were mainly based on types and in few cases additional material have been used. The loans of *H. cratericola* and *H. gorgoniicola* were not allowed by the relevant museums, while the type materials of *H. chamaeleon*, *H. violaceoflava*, *H. spongicola brevicirra* and *H. hamata* were impossible to locate or are lost.

Drawings were made to scale with a *camera lucida* attached to a compound microscope. Microphotographs were taken with a ProgRes C10 plus digital camera (Jenoptics, Jena) attached to a Zeiss Stemi 2000-C compound microscope. The hand drawings and digital microphotographs of chaetae and aciculae were digitized with “CorelDraw version10” software. When allowed, selected specimens were prepared for SEM following the standard procedure. Digital SEM images were captured with the Windows PRINTERFACE system using a HITACHI S-3500N microscope at the “Servei de Microscopia Electrònica” of the “Institut de Ciències del Mar” of Barcelona (ICM, CSIC).

The hosts and habitat descriptions were based on literature. The geographical distribution only includes that of the examined material as well as the published records for which the species identity was confirmed.

Abbreviations of institutions and museums

CEAB (Centre d'Estudis Avançats de Blanes, Spain), CSIC (Consejo Superior de Investigaciones Científicas, Spain), ICM (Institut de Ciències del Mar, Barcelona, Spain), IOCAS (Institute of Oceanology, Chinese Academy of Sciences, China), LACM (Los Angeles County Museum of Natural History, U.S.A), MNCN (Museo Nacional de Ciencias Naturales, Madrid, Spain), MNHN (Muséum National d'Histoire Naturelle, Paris, France), BMNH (British Museum of Natural History, London, UK), NPW (Muzeum Przyrodnicze, Wrocław, Poland), NSMT (National Science Museum, Tokyo, Japan), SAM (South African Museum, Cape Town, South Africa), SMBL (Seto Marine Biological Laboratory, Japan), SMF (Senckenberg Museum, Frankfurt am Main, Germany), USNM (United States National Museum, Smithsonian Institution, U.S.A), YPM (Peabody Museum of Natural History, Yale University, U.S.A), ZISP (Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia), ZMB (Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany), ZMH (Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Germany), ZMUC (Zoologisk Museum, University of Copenhagen, Denmark).

Character descriptions

Body size. Body length varies from small (less than 1 mm long) to very long (60 mm long), with 8 to 126 segments. Large worms are more often considered as specialized predators while small ones are usually reported as symbionts (Martin *et al.* 2003). Body width (measured just before the first proventricular segment, excluding parapodia) ranges from 0.3

mm to about 2 mm wide. Typically, the body is wider at the proventricle region, then, become abruptly thinner towards the posterior end (e.g. *H. spongicola*) or gradually thinner (e.g. *H. chamaeleon*).

Body shape, colour, pigmentation and epidermal glands. Like most syllids, members of *Haplosyllis* are dorsally arched and ventrally flat; Most species are white-cream or yellow-pale in colour, and do not have colour marks. Some displays different colouring, mimicking that of their hosts (e.g. *H. basticola*). Dorsal anterior pigmentation occurs in a few species (e.g. the dark brown pigmentation in palps, prostomium and anterior segments of *H. uncinigera*). Most species have round dorsal and ventral granules (usually corresponding to glandular structures). When granules are abundant, the species may have a granulose aspect (e.g. *H. granulosa*, see Lattig *et al.* 2007, Fig. 5A–B). When granules are small, the species do not have such a granulose aspect (e.g. *H. basticola*), or granules may be absent.

Body regions. Members of *Haplosyllis* do not have clear body divisions, but four generic regions are here considered to facilitate the identification of specimens: **anterior region** (from palps till the beginning of proventricle, including the prostomium); **proventricle region**, here considered as a transition region, not used for chaetae identification; **midbody region** (from the end of proventricle to the posterior 4–10 segments); **posterior-most region** (last segments, often with chaetae clearly smaller than the previous ones). Chaetal descriptions are usually based on anterior and midbody regions.

Palps are similar in all species, long, broadly triangular, fused at their bases, and clearly divergent all along their length, typically longer than prostomium. The prostomium has two basic shapes (modified from Martin *et al.* 2003); oval, common in small individuals, with width/length ratio close to 1 (e.g. Fig. 8A), or subpentagonal, wider than long (e.g. Figs 5A, 22A, 23A). The prostomium tends to be wider in specimens with broader bodies. The prostomium always has two pair of eyes and three antennae; the central antenna longer than the lateral ones. The peristomium, usually is smaller than subsequent segments, typically has two pairs of tentacular cirri, the dorsal one longer than the ventral cirrus. Lengths of antennae and tentacular cirri are always reported as number of articles.

Sensory organs. The sensory organs may occur in different body structures, and usually they are only visible under SEM. The nuchal organs, consist of two dorsal, densely ciliated grooves between the prostomium and peristomium (e.g. Lattig *et al.* 2007, Figs 2H, 6A, 6C), like in most Syllidae (San Martín 2005). Palps may have sensory organs, either on the lateral sides, as two or more rows of cilia (e.g. *H. basticola*, Fig. 7B–D), or on the ventral side, also as groups of cilia (Lattig *et al.* 2007, Fig. 4A). The pharyngeal papillae typically

have groups of cilia on ventral side (Fig. 14C). When pharynx is everted, is possible to observe a dense ring of cilia surrounding the crown of papillae (Fig. 17C). A variation of these sensory organs, both in the case of nuchal organs and palps, are pore holes and plates only observed in *H. carmenbritoae* (Martin *et al.* 2003, Fig. 6D; Lattig *et al.* 2007, Fig. 4C–D).

Dorsal cirri. Cirri length is measured as number of articles. Most *Haplosyllis* species have similar proportions for the first five dorsal cirri: first cirri are the longest; second, third and fourth are shorter, gradually increasing in size (with the second one shortest, third and fourth intermediate), and fifth short (Figs 6A, 13A). However, *H. spongiphila* (which has a doubtful taxonomic position within the genus), has a different pattern, with all cirri extremely long.

Anterior cirri are usually long; at the proventricular region cirri may become abruptly shorter (Figs 5A, 8A), or gradually decrease in length toward posterior end (Figs 6A, 12A), being of similar size (Fig. 6A) or alternating long and short (e.g. *H. chamaeleon*, see López *et al.* 1996, fig. 2A). Alternation in length is difficult to observe in many species, thus, it has not been considered as a relevant taxonomic character.

At midbody region, dorsal cirri may be long, intermediate or short (measured with respect to the longest cirri). Long ones are much longer than body width (e.g. *H. chamaeleon*). Intermediate cirri reach $\frac{1}{2}$ or up to $\frac{3}{4}$ parts of body width (Fig. 12A). Short cirri are much shorter than $\frac{1}{2}$ of body width (Fig. 5A).

Ventral cirri. Ventral cirri are typically digitiform, similar in all species. Anterior cirri are similar in length or longer than parapodial lobes (Figs 12B, 13C, 14D), while midbody cirri gradually decreases in size toward the posterior end, usually are shorter than parapodial lobes (Figs 12C, 13D, 14E).

Proventricle and pharynx. The proventricle is considered short when extends through 3–4 segments, long when Extends through 3–4 segments (Martin *et al.* 2003). The number of muscular cell rows is difficult to count, but apparently maintain a similar range within populations.

The pharynx is usually orange, with long anterior tooth, surrounded by a ring of cilia and 9–12 soft papillae. Pharynx width is measured in relation to proventricle width, being markedly thinner (e.g. *H. carmenbritoae*, see Lattig *et al.* 2007, fig. 3A), similar (Figs 5A, 8A), or often reaching the proventricle as a funnel (Fig. 13A). The papillae number varies from 9 to 12, which appear to be a constant, but this information is not available for many

species. Some species have a trepan with about 10 small triangular teeth (Fig. 17A–B) (for more details see remarks on *H. spongicola*).

Chaetae. Martin *et al.* (2003) defined the terms allowing the description and comparisons between typical *Haplosyllis* chaetae (see fig. 11 of mentioned paper). The length of main fang (LMF) must be compared with the chaetal width (SW); LMF may be similar or shorter (Fig. 1A), or considerably longer (Fig. 1B) than SW.

The region between the base of proximal apical tooth and the beginning of upper side (US) of main fang (MF) is called the mid-joining point between teeth (MJP). The MJP is **straight** when the base of proximal tooth is clearly separated from US of MF, being long, or relatively short (Fig. 2A); **diagonal** when the slope of MJP is not clearly distinguishable from that of US of MF (Fig. 2B), and **curved** when MJP is so short that the base of proximal tooth directly joins US of MF (Fig. 2C).

US of MF may be smooth (Fig. 7F) or may have denticles with variations in size, varying between and within species. Denticles may be small and numerous (Fig. 18A); long, reaching the base of proximal tooth (Fig. 2C), or one long and several short (e.g. *H. granulosa*, see Lattig *et al.* 2007, fig. 6F). Although its presence may be perceived under a light microscope, the serration on the US of MF may be better described using SEM.

Species have bidentate chaetae, but they may also be unidentate (Figs 9A, 21B). Bidentate chaetae have been here grouped into three categories according to the appearance of the apical teeth: 1) both teeth may be similar in size or the distal tooth slightly smaller than the proximal one (Figs 4B, 6F, 12H, 23H); 2) the proximal tooth may be considerably shorter than the distal one, most common in the smaller midbody chaetae of each parapodium (Figs 12I, 23G); or 3) the proximal tooth is very long, with pointed tip, and the distal tooth much smaller and slender, difficult to observe or appearing to be unidentate (Fig. 9C).

Anterior and midbody chaetae may be all similar (Figs 6D, 6F, 8B, 8F, 8D, 13E, 13G–H), the anterior ones much thinner, with a small MF (Figs 12D, 23E), or midbody chaetae different in shape from anterior ones (Figs 18A–B, 20C, 20E), often similar but with midbody chaetae unidentate (Fig. 21A–B). The anterior chaetae (first 6–9 chaetigers) are usually shorter; from proventricular region chaetae became progressively longer. The midbody parapodia may have all chaetae similar in shape (e.g. *H. granulosa*, *H. loboii*, *H. spongicola*, *H. ohma*), or 1–2 longer chaetae clearly different from the smallest one with respect to the shape of apical teeth and MJP (Figs 12G–H, 23G–H).

Aciculae. Four acicular shapes have been previously defined for the last segments of midbody region of the *Haplosyllis* species (see Fig. 10A–D in Martin *et al.* 2003). Two of

them were too similar, and only three are used in this review. Aciculae may have a curved, upwards directed tip (Fig. 3A–B), an almost 90° bent tip (Fig. 3C), or a straight tip (Fig. 3D). The number of aciculae per parapodia may vary from only one (e.g. *H. basticola*), to two or more (e.g. *H. uncinigera* and *H. cratericola*). Posterior aciculae are usually larger and have better well defined shapes than the anterior ones, and this is extremely useful in the identification of species.

Systematics

Genus *Haplosyllis* Langerhans, 1879

Haplosyllis Langerhans, 1879: 527.

Trypanosyllis (*Trypanoseta*) Imajima and Hartman, 1964: 129.

Geminosyllis Imajima, 1966: 233.—Kudenov & Harris, 1995: 71, fig. 1.26.—Lattig *et al.* 2007: 561–562.

Trypanoseta Aguado *et al.* 2008: 544

Type species. *Syllis spongicola* Grube, 1855

Diagnosis. Body cylindrical, reaching large size, from 0.1 mm to 60 mm length. Prostomium with four eyes, sometimes with anterior ocular spots. Three long antennae. Palps robust, triangular, fused at bases. Two pairs of tentacular cirri. Antennae, dorsal cirri and tentacular cirri distinctly moniliform, some species with posterior cirri apparently smooth (but corresponding to a single small article). Ventral cirri digitiform, gradually decreasing in size from anterior to posterior end. Pharynx with one tooth surrounded by 9–12 soft papillae. Trepan, if present, with approximately ten teeth. Chaetae all simple, variable in number, 1–3 or up to 12 per parapodia. Capillary chaetae absent. Schizogamic reproduction by means of a single sexual stolon for each parental individual (scissiparity).

Remarks. *Haplosyllis* was initially defined as having a single pharyngeal tooth (see Lattig *et al.* 2007) and the presence of an additional pharyngeal trepan was the main character to distinguish *Haplosyllis* from *Trypanoseta* (Imajima 1966). The dissection and SEM observations of many specimens of *H. spongicola* (sensu Lattig *et al.* 2007) revealed in many cases the presence of a trepan (Fig. 17A–C). As *H. spongicola* is the type species of

Haplosyllis, the diagnosis of the genus must be modified, and *Trypanoseta* is no longer considered valid. Besides, Aguado *et al.* (2007) showed a clear phylogenetic difference between *Haplosyllis* and *Trypanoseta* based on molecular data. These authors used two specimens of *H. spongicola* from the Mediterranean, and other two identified as *Haplosyllis* sp. and *T. ohma*. However, the former were from Australia (where the presence of *Haplosyllis spongicola* is doubtful), while the latter species was recorded from St. Juan (Washington, U.S.A.), a location distant from Japan, the Type Locality of *T. ohma*. Taking into account our observations on the morphology of the respective type species, we suggest that the results of Aguado *et al.* (2007) better reflect the large genetic differences that may occur within *Haplosyllis* rather than supporting *Trypanoseta* as a distinct genus. More species need to be analysed genetically in order to obtain reliable results for this genus, both to define intra-generic differences and to define its phylogenetic position within the Syllidae.

Key to the *Haplosyllis* species

- 1 Anterior chaetae clearly different from midbody chaetae; some with an incision on MF, unidentate or pseudocompound 2
- Anterior chaetae similar to midbody chaetae, often small, with short MF..... 5
- 2 Small worms, 2–3 mm long. Chaetae from first 6 chaetigers, with an incision on MF (Fig. 5C) *H. anthogorgicola*
- Medium to long worms, 6–20 mm long (rarely 4–6 mm). Anterior chaetae without such incision 3
- 3 Anterior chaetae with clear traces of fusion between blade and shaft; midbody chaetae completely simple, without such traces (Figs 19C, 20C–D) *H. spongiphila*
- All chaetae simple, without such traces of fusion; some with anterior unidentate chaetae, or with small denticles on MF (Figs 18A–C, 21A) 4
- 4 Anterior chaetae bidentate. Midbody chaetae unidentate. Denticles on MF absent (Fig. 21A–B) ... *H. streptocephala*
- All chaetae bidentate. Anterior ones with small denticles on MF, usually eroded in midbody chaetae (Fig. 18A–D) *H. spongicola*
- 5 Midbody parapodia with 2–3 chaetae differing in size and shape. Smallest chaeta with short proximal tooth; largest chaeta with MJP long and straight (Fig. 23E, G, H)..... 6
- Midbody parapodia with chaetae all similar (Figs 10B, 22F)..... 7

6 Pharynx extending 10–11 segments. Largest chaetae of each midbody parapodium with short, almost invisible distal tooth (Fig. 23A, H). 4–6 posterior aciculae	<i>H. uncinigera</i>
-Pharynx extending 4–6 segments. Largest chaetae of each midbody parapodium with apical teeth similarly in size, or distal one slightly shorter but clearly visible (Fig. 12H). 1–2 posterior aciculae.....	<i>H. djiboutiensis</i>
7 Midbody chaetae with proximal tooth long, with pointed tip; distal tooth absent or very short, thin (Fig. 9B–C)	8
-Midbody chaetae with apical teeth of similar length, sometimes proximal tooth slightly shorter	9
8 Anterior and midbody chaetae unidentate, or with a very small distal tooth; more hooked and clearly bidentate when posterior-most. Body yellow to violet “in vivo”, with dark violet dorsal marks	<i>H. chamaeleon</i>
-All chaetae bidentate, distal tooth small, often difficult to see. Body uniformly yellowish, without marks.....	<i>H. villogorgicola</i>
9 Chaetae with MJP short and curved. Denticles of US of MF absent (Figs 4B, 7F, 10B)	10
-Chaetae with MJP diagonal (Fig. 2C) or straight (only in largest chaetae) (Figs 8D, 13H, 16E). Spines of US of MF present or absent	13
10 Body fragile, slender, small, 1–5 mm long, less than 0.5 mm wide	11
-Body robust, long, 10–30 mm long, about 1 mm wide	12
11 All dorsal cirri slender. Chaetae broad, with short apical teeth, distal tooth shorter than distal one (Figs 6A, 7F)	<i>H. basticola</i>
-Tentacular cirri and first dorsal cirri slender; dorsal cirri often very broad. Chaetae slender, apical teeth long, similar in size (Fig. 10B)	<i>H. crassicirrata</i>
12 MF resembling a third tooth (Fig. 22E–F); 3–6 chaetae per parapodia	<i>H. trifalcata</i>
-MF very short, but not resembling a third tooth (Fig. 4A–C); 1–2 chaetae per parapodia	<i>H. agelas</i>
13 MJP diagonal. Denticles on US long, reaching apical teeth (Fig. 2C)	<i>H. loboi</i>
-MJP long and straight. Denticles on US never reaching apical teeth	14
14 Pharynx half as thin as proventricle	<i>H. carmenbritoeae</i>
-Pharynx broad, similar to proventricle width or slightly thinner	15
15 Pharynx short, extending 3–4 segments, broader in the middle, reaching the proventricle as a funnel (Fig. 13A)	<i>H. gula</i>

-All pharynx similarly wide, extending 4–18 segments (Fig. 8A)	16
16 Mid-sized worms, 4–10 mm long, less than 1 mm wide. All dorsal cirri short	17
-Long, robust worms, 25–44 mm long, 1–3 mm wide	18
17 Parapodia with 1–2 chaetae, spines on US of MF absent or very short	<i>H. cephalata</i>
-Parapodia with 2–7 chaetae, long spines on US of MF	<i>H. granulosa</i>
18 Parapodia with 14–20 chaetae, 8–13 aciculae. Trepan absent	<i>H. cratericola</i>
-Parapodia with 5–8 chaetae, 3 aciculae. Trepan may be present	<i>H. ohma</i>

***Haplosyllis agelas* Uebelacker, 1982 (Fig. 4A–E)**

Haplosyllis agelas Uebelacker, 1982: 857–860, fig. 1–9.—Licher, 1999: 280.

Material examined. Bahamas. Holotype USNM 62008; 4 paratypes USNM 62009; 3 paratypes ZMH-P 16467. Grand Bahama Island, from sponge *Agelas dispar*, 20 m, November 1975.

Description. Body robust, subcylindrical, strongly arched dorsally, flattened ventrally. Length 10–20 mm for 88–117 chaetigers, width 0.6–1 mm, excluding parapodia. Preserved specimens yellow-pale. Dorsal pigmentation and epidermal granules absent. Prostomium subpentagonal, wider than long, with two pairs of small red eyes in trapezoidal arrangement. Median antenna inserted on median part of prostomium, with 19 articles; lateral antennae inserted on anterior margin of prostomium, with 12 articles. Palps twice as long as prostomium, broadly triangular, fused at their bases, but separated all along their length; sensory organs of palps not seen. Single pair of dorso-lateral ciliated nuchal organs between peristomium and prostomium. Pharynx orange, 0.6 mm long, 2.7 mm wide, extending about eight segments. Anteriorly with large tooth and crown of 10 soft papillae. Pharyngeal ciliary ring not seen. Proventricle cylindrical, dark-brown, 1.1 mm long, 2.8 mm wide, extending about nine segments, with 46 muscular cell-rows. Peristomium well defined, shorter than subsequent ones. Dorsal tentacular cirri longer than ventral ones, with 14 and 7 articles respectively. Dorsal cirri broad, similar to antennae and tentacular cirri; first cirri longer than remaining ones (14–20 articles); second short (6–10 articles), third and fourth slightly longer (9–13 and 8–18 articles, respectively), fifth short (6–8 articles). Midbody cirri of similar size (5–10 articles), gradually decreasing to posterior end; longest cirri do not exceed ½ of body width. Posterior dorsal cirri short (2–6 articles). Ventral cirri digitiform, anterior most longer

than median and posterior ones. Chaetae bidentate, all similar, but anterior ones smaller (Fig. 4A–C). LMF shorter than SW; MJP curved and short; US without denticles; apical teeth similar in length, with wide angle. One or two chaetae per parapodia, sometimes with one or two chaetae non-protruding from parapodial lobe. Usually two stout aciculae per parapodium, one straight and the other slightly curved, with rounded tip upwards directed (Fig. 4D–E). Pygidium with two long anal cirri, 10 articles.

Reproduction. Uebelacker (1982) observed two specimens with coelomic oocytes beginning in chaetigers 31 and 33.

Host. Found only in association with the demosponge *Agelas dispar* Duchassaing & Michelotti, 1864.

Distribution. Bahamas, Grand Bahama Island.

Remarks. Uebelacker (1982) mentioned a slight variation in chaetal morphology due to the presence or absence of additional apical teeth. According to our observations, there is only one type of chaetae all along the body, and the observed variation probably represents broken chaetae.

***Haplosyllis anthogorgicola* Utinomi, 1956**

(Fig. 5A–H)

Haplosyllis anthogorgicola Utinomi, 1956: 247–249, fig. 2.—Imajima & Hartman, 1964: 119–120.—Imajima, 1966: 220.—Licher, 1999: 280.—Martin *et al.* 2002: 470–473, figs 11–13.

Material examined. Southern Japan. 27 Syntypes, SMBL 161, Seto, Wakayana, Honsyū, coll. H. Utinomi.

Diagnosis. Anterior dorsal cirri long, after proventricle short, with 1–6 articles (Fig. 5A). Anterior chaetae with MF deeply incised near its apex and deep fold opposite to MF (Fig. 5C); chaetae from chaetigers 6–7 with less pronounced incision (Fig. 5E); midbody chaetae without such incision (Fig. 5G). One acicula per parapodium, anterior and medium aciculae with slightly curved tip upwards directed, posterior acicula broad, with a 90° bent tip (Fig. 5D, F, H).

Reproduction. Unknown. **Host.** The gorgonian *Anthogorgia bocki*. Details on the association in Martin *et al.* (2002). **Distribution.** Southern Japan.

***Haplosyllis basticola* Sardá, Ávila & Paul, 2002**

(Figs 6A–G, 7A–F)

Haplosyllis basticola Sardá, Ávila & Paul, 2002: 168–171, fig. 1–2.

Examined material. Micronesia. Island of Guam, 20 Paratypes MNCN 16.01/8439.

Description. Small, fragile body, length 1–4 mm, for 8–25 segments, width 0.15–0.22 mm, excluding parapodia (Figs 6A, 7A), widest at proventricle level. Preserved specimens brown-purple, similar to the host sponge. Dorsal pigmentation absent. Small dorsal granules in all body. Prostomium oval to subpentagonal, wider than long, with two pairs of small red eyes in trapezoidal arrangement. Median antenna inserted on medium of prostomium, with 9–17 articles; lateral antennae inserted on anterior margin of prostomium, with 6–10 articles. Palps twice as long as prostomium, broadly triangular, separated all along their length but in close contact at the base, with sensory organs as two ventral upper-lateral rows of cilia and a few more disperse cilia (Fig. 7B–D). Nuchal organs not seen. Pharynx orange, extending about 4 segments, anteriorly with triangular tooth, crown of 9–10 soft papillae and an inner ring of cilia. Cilia of papillae not seen. Proventricle brownish, cylindrical, 0.3–0.45 mm long, extending 2–3 segments, width 0.16–0.27 mm, with 23–30 muscular cell-rows (Fig. 6A). Peristomium well defined, shorter than subsequent ones. Dorsal tentacular cirri longer than ventral ones (6–13 and 2–5 articles, respectively). Dorsal cirri slender, similar to antennae and tentacular cirri. Anterior dorsal cirri with well defined variation in length: first cirri longer than remaining ones (10–15 articles); second smaller (2–5 articles), third and fourth slightly longer than second (3–7 and 4–10 articles, respectively), fifth smaller (2–4 articles). After proventricle, cirri short, similar in length (2–5 articles), gradually decreasing to posterior segments, with 2–3 articles or non-articulated (Fig. 6B). Ventral cirri digitiform, shorter than parapodial lobes (Fig. 6C). Chaetae bidentate, all similar, broad, but anterior ones smaller. LMF similar to SW; MJP curved, short; US of MF without denticles; apical teeth similar in length, distal one slightly shorter, narrow angle between teeth (Figs 6D, F, 7E–F). One chaeta per anterior parapodia, one on midbody parapodia (sometimes second one inside parapodium,

difficult to see), and two or three on most posterior segments. One stout acicula on all chaetigers, with slightly curved tip, upwards directed (Fig. 6E, G).

Reproduction. Both, male and female reproductive bodies have 11–12 chaetigers with a well-distinguishable head and two small antennae (Sardá *et al.* 2002).

Host. Strict endosymbiont of the large sponge *Ianthella basta* (Pallas, 1766).

Distribution. Guam, Micronesia.

Remarks. The original species description is here complemented by the description of the ciliated sensory organs on palps, and by presence of 1–3 chaetae from midbody parapodia, instead of only one (Sardá *et al.* 2002).

***Haplosyllis carmenbritoae* Lattig, San Martín & Martin, 2007**

Haplosyllis carmenbritoae Lattig, San Martín & Martin, 2007: 557–561, fig. 3–4.

Examined material. Canary Islands. Holotype MNCM 16.01/10645; 6 Paratypes MNCM 16.01/10646. Eastern coast of Tenerife, January, 1982.

Diagnosis. Body up to 3 mm long for 20–25 segments. After proventricle dorsal cirri slightly alternating with long (10–15 articles) and short (5–11 articles). Two chaetae per parapodia, longest one with straight and long MJP; long spines on US of MF. Pharynx much slender than proventricle.

Reproduction. Unknown.

Host. Collected from a *Dendrophyllia ramea* assemblage, but probably not in association with the coral.

Distribution. E Atlantic, Canary Islands.

Remarks. *Haplosyllis carmenbritoae* closely resembles *H. djiboutiensis* from the Red Sea by the body shape. However, *H. djiboutiensis* has short dorsal cirri that do not exceed body width, and lack long denticles on US of MF, characteristic of *H. carmenbritoae*.

***Haplosyllis cephalata* Verrill, 1900**

(Fig. 8A–G)

Haplosyllis cephalata Verrill, 1900: 613–614.—Licher, 1999: 280.

Examined material. Bermudas, Caribbean Sea. 4 syntypes YPM 22543; 6 syntypes YPM 22544; 3 Syntypes YPM 23002. Additional material: 3 specimens YPM 23003, same locality of syntypes.

Description. Syntypes complete, slide preparations in poor conditions. Length 3.5–6 mm, for 25–30 chaetigers, width 0.38–0.5 mm (excluding parapodia) (Fig. 8A). Preserved specimens yellow pale. Dorsal granules not seen. Prostomium oval, similar in width and length, with two pairs of small red eyes in trapezoidal arrangement. Median and lateral antennae inserted on middle and anterior margin of prostomium, respectively, with 6–7 articles; most median antennae broken. Palps twice as long as prostomium, broadly triangular, fused at their bases, but separated all along their length. Cilia of palps and nuchal organs not seen. Pharynx orange, extending 6–7 segments, width similar to proventricle, anteriorly, with large tooth (Fig. 8A); papillae and inner ring of cilia not seen. Proventricle dark-brown, cylindrical, about 0.7 mm long and 0.2 mm width, extending 4–6 segments, with 42–52 muscular cell-rows. Peristomium well defined, shorter than subsequent ones. Dorsal tentacular cirri long (7 articles), tentacular ventral cirri broken. Dorsal cirri slender, similar to antennae and tentacular cirri. First dorsal cirri long (14 articles), second, third and fourth intermediate (5–7 articles); remaining cirri always small (1–4 articles) (Fig. 8A). Ventral cirri digitiform. Chaetae bidentate, all similar, but anterior ones smaller (Fig. 8B, D, F). LMF similar than SW; MJP straight and short; denticles on US not seen; apical teeth similar in length. One or two chaetae per parapodia. Two aciculae of equal size per anterior and most posterior parapodia, one straight, the other with curved tip upwards directed (Fig. 8C, G); single acicula on midbody parapodia, broad, with curved tip (Fig. 8E). Pygidium lacking.

Reproduction. Unknown.

Host. Found inside unidentified sponges (Verrill, 1900).

Distribution. Caribbean Sea, Bermudas

Remarks. The syntypes of *Haplosyllis cephalata* are on a permanent microslide, affecting the body shape and details of chaetal and acicular morphology. However, the species can be well identified by the marked differences in cirri length of anterior cirri (relatively long) and midbody ones (significantly shorter), as well as by the presence of stout curved acicula. The body seems to be stout, the proventricle is long and the presence of dorsal granules was not evident.

***Haplosyllis chamaeleon* (Laubier, 1960)**

(Fig. 9A–C)

Haplosyllis depressa chameleon Laubier, 1960: 75, figs 1–2.—Alós, 1989: 359, figs 71–72.—Baratech & San Martín, 1987: 45, figs 8–9.

Haplosyllis chamaeleon.—López *et al.* 1996: 108–110, fig. 2.—Licher, 1999: 280; Martin *et al.* 2002: 461, 464–470, figs 5B–G, 6–10.—San Martín, 2003: 320–323, fig. 177–178.

Type material. *Haplosyllis depressa chamaeleon* from Banyuls-sur-Mer (W Mediterranean), coll. Yves Bouligand. Probably lost.

Examined material. NW Mediterranean Sea. 4 specimens MNCN 16.01/7834, Cape of Creus, from *Paramuricea clavata*, coll. C. Alós. Atlantic Ocean. 3 specimens MNCN 16.01/11362, Ria de Arousa, Pontevedra, Spain, from *Paramuricea grayii*, 30 m. coll. Álvaro "Boris" Altuna.

Diagnosis. Dark-violet marks across the dorsum, persistent in preserved specimens. All dorsal cirri long, longest ones, twice as long as body width; midbody dorsal cirri alternating with short (13–20 articles) and long (26–32 articles). Three to five hooked chaetae per parapodia, anterior and midbody unidentate (Fig. 9A) or with very small, hair-like distal tooth (Fig. 9B), more hooked and clearly bidentate in posterior parapodia (Fig. 9C); LMF shorter than SW.

Host. Strict ectosymbiont of the gorgonians *Paramuricea clavata* (Risso, 1826) and *P. grayii* (Johnson, 1861). Details on the association with *P. clavata* in Laubier (1960) and Martin *et al.* (2002).

Reproduction. *H. chamaeleon* reproduces by cephalous stolons (more details in Martin *et al.* 2002).

Distribution. W Mediterranean Sea and E Atlantic Ocean.

Remarks. Originally described as a subspecies of *Haplosyllis depressa* (*H. depressa chamaeleon*) from Banyuls-sur-Mer (NW Mediterranean); the species was erected as a new valid one by López *et al.* (1996) based on specimens living on the same host gorgonian from Chafarinas Islands, SW Mediterranean Spain (35°11'08"N 2°25'14"W).

The specimens found in the Atlantic coasts of the NE Iberian Peninsula extends the geographical range of *H. chamaeleon*, which can no longer be regarded as Mediterranean endemic species. Similarly, the species was considered as a typical example of monoxenous symbiotic association (Martin & Britayev, 1998; Martin *et al.* 2002), but the Atlantic specimens were associated with a different host gorgonian, *Paramuricea grayii*. Therefore,

this is the first record both for the presence of the species in the Atlantic and for its association with *P. grayii*.

***Haplosyllis crassicirrata* Aguado, San Martín & Nishi, 2006**

(Fig. 10A–C)

Haplosyllis crassicirrata Aguado, San Martín & Nishi, 2006: 10, fig. 1–2.

Examined material. Japan. Holotype MNCN 16.01/10135; 2 Paratypes MNCN 16.01/10136. Yoshio, Boso Peninsula, 35°08'10"N 140°18'16"E.

Diagnosis. Body fragile, up to 2.1 mm long for 16 chaetigers. Yellow-pale, with orange marks. Dorsal tentacular cirri and first dorsal cirri long and slender (11–15 and 20–27 articles, respectively); subsequent cirri similar to body width (up to 6 articles), some considerable broader and thick. Two chaetae per parapodia, all similar; MJP short and curved (Fig. 10A–C).

Host. Unknown. Types collected intertidally on a rocky shore.

Reproduction. Unknown.

Distribution. Boso Peninsula, Japan.

Remarks. Our observations on the type material confirm the similar chaetal morphology for all body regions. The original description was based on two small specimens, possibly juveniles, characterized by broad dorsal cirri. However, among a large collection of Australian specimens, some had broad cirri as the type specimens, while others had both broad and normal cirri, similar to the first dorsal cirri of the holotype. These specimens will be described in a subsequent paper.

***Haplosyllis cratericola* Buzhinskaja, 1990**

(Fig. 11A–F)

Syllis (*Haplosyllis*) *cratericola* Buzhinskaja, 1990: 25–27, fig. 4.

Haplosyllis cratericola.—Licher, 1999: 280.

Type material. Russia. Kurile Archipelago, Yankichi Island, Kratemaia Bay. Holotype ZISP 1/47543. coll. Kamenev. Expedition Institute Biology of Sea, from muddy-gravels, 5 m, August 1985. (Observed by Dr. Gagaev, invertebrate curator of ZISP).

Description. Holotype broken in two pieces; anterior part broad, length 16 mm, width 3 mm, for 32 chaetigers; medium body fragment width 28 mm, for 28 chaetigers (Fig. 11A, C). Yellow-pale. Prostomium subpentagonal, wider than long, with two pairs of small eyes in trapezoidal arrangement. Antennae long and slender, median antenna on medium of prostomium, with 40 articles; lateral antennae on anterior margin of prostomium, about 27 articles. Palps long, broadly triangular, divergent all along their length. Cilia on palps and nuchal organs not seen. Pharynx extending about 10 segments, anteriorly with large sharp tooth and crown of 10 soft papillae; cilia on papillae not seen. Proventricle long, extending about 11 segments. Peristomium well defined, shorter than subsequent ones. Dorsal and ventral tentacular cirri very long (40 and 22 articles, respectively). Dorsal cirri slender, similar to antennae and tentacular cirri; anterior cirri long (about 50 articles), midbody cirri shorter (30–35 articles). Ventral cirri digitiform, not longer than parapodial lobes (Fig. 11B). Chaetae all bidentate (Fig. 11D–E); from midbody parapodia onwards: LMF shorter than SW; MJP straight and long; MF broad; denticles on US of MF absent; apical teeth equal in length. Up to 20 chaetae on anterior parapodia; up to 14 on midbody. Aciculae straight, broad, with rounded tips (Fig. 11F), 12–13 and 8–10 on anterior and posterior parapodia, respectively.

Host. Unknown.

Reproduction. Unknown.

Distribution. Russia, Kurile Archipelago.

Remarks. Licher (1999) incorrectly named *Haplosyllis cratericola* as described by Buzhinskaja in 1980, but it was originally described by Buzhinskaja in 1990. *H. cratericola* resembles *Haplosyllis ohma* n. comb. (see relevant section) with regard to dorsal cirri length, chaetal shape and biogeographical distribution but differs in that *H. cratericola* has almost double the number of chaetae per parapodia and the pharynx seems to lack the trepan. As the presence/absence of trepan has been shown to be a non-robust character in *Haplosyllis* and that our observations are based on the holotype only, we have decided to consider the species as valid. However, a more detailed study of the chaetal variability and pharynx morphology should be carried out. The present description is based on the original description as well as photographs and observations of the holotype by Dr. Sergey Gagaev (ZIR).

***Haplosyllis djiboutiensis* Gravier, 1900**

(Fig. 12 A–J)

Syllis (Haplosyllis) djiboutiensis Gravier, 1900: 147–149, pl. 9, fig. 3.

? *Syllis (Haplosyllis) djiboutiensis*.—Fauvel, 1919: 353.

Examined material. Djubal ("Gubal", Saudi Arabia), Red Sea. Polytype MNHN 48.

Description. Polytype with anterior and posterior ends in poor conditions, body slender, length 8 mm, for 38 chaetigers, width 0.35 mm (excluding parapodia) (Fig. 12A), yellow-pale. Prostomium subpentagonal, wider than long, with two pairs of small red eyes in trapezoidal arrangement. Median (22 articles) and lateral (14 articles) antennae on medium and anterior margin of prostomium, respectively. Palps long, broadly triangular, fused at their bases, divergent all along their length. Cilia on palps and nuchal organs not seen. Pharynx orange, extending about five segments, anteriorly with large anterior tooth; ring of cilia and papillae cilia not seen. Proventricle cylindrical, dark-brown, length 0.45 mm, extending four segments, width 0.28 mm, with 36 muscular cell-rows (Fig. 12A). Peristomium similar in length to first chaetiger. Dorsal tentacular cirri longer than ventral ones (13–15 and 7–11 articles, respectively). Dorsal cirri slender, similar to antennae and tentacular cirri. First dorsal cirri longer than remaining ones (23 articles), second short (12 articles), third and fourth intermediate, longer than second (15 and 19 articles, respectively), fifth short (10 articles), sixth intermediate (15 articles). After proventricle, cirri alternating with long (7–9 articles) and short (4–5 articles); longest cirri do not exceed body width. Cirri broken at posterior end. Ventral cirri digitiform, anterior cirri longer than parapodial lobe, gradually shorter to posterior end (Fig. 12B–C). Chaetae all bidentate, anterior ones smaller, with short MF (Fig. 12D–E). Usually two chaetae on each midbody parapodia, different in size and shape; in largest chaeta LMF similar than SW; MJP straight and long; US of MF with denticles; distal tooth slightly shorter than posterior one (Fig. 12H), apparently very small when MF is in backward position (Fig. 12G). In smaller chaeta MJP short; proximal tooth smaller than distal one (Fig. 12I). Aciculae stout, with curved tip, upwards directed (Fig. 12F, G, J), two on each parapodia. Pygidium broken.

Host. There is no information on habitat and depth range for the types. However, Gravier (1900) originally described a sponge spicule as long aciculae, which suggest this species is associated with a sponge.

Reproduction. Unknown.

Distribution. Red Sea. Probably also in Madagascar, Fauvel (1919), but this record should be confirmed with examination of material.

Remarks. *Haplosyllis uncinigera* and *H. djiboutiensis* were considered as synonymous due their similarity of their chaetae (Augener 1913). In the original drawing of *H. djiboutiensis*, chaetae appear to be as unidentate, very similar to ones of *H. uncinigera*. According to our observations, in the largest chaeta of *H. djiboutiensis*, the distal tooth is slightly smaller than proximal one, but usually, both teeth are clearly seen (except when main fang in in backward position, appearing to be unidentate), each parapodium has two aciculae, pharynx extends through 4–5 segments and the dorsum has a granulose aspect. In *H. uncinigera*, chaetae also have a unidentate appearance, but the angle between teeth is narrow and distal tooth very small, thin, making it difficult to observe, each parapodium has four to six aciculae, pharynx extends through 10 segments, and the dorsum do not has such granulose aspect. It is difficult to distinguish both species due the unidentate appearance of chaetae, and detailed examination of the distal tooth is required. *H. djiboutiensis* is similar to *H. granulosa* and *H. carmenbrittoae* but can be easily distinguished (see remarks of each species).

Specimens of *Haplosyllis* have been reported from different localities nearby the area of distribution of *H. djiboutiensis* as “*H. spongicola*”, such as the Red Sea (Amoureux 1983; Hartmann-Schröder 1960), Madagascar (Fauvel 1919) or the Suez Canal (Fauvel 1927). In light of our results, these records must be regarded as doubtful unless material from these localities can be examined.

***Haplosyllis granulosa* (Lattig, Martín & San Martín, 2007) new comb.**

Geminosyllis granulosa Lattig, Martín & San Martín, 2007: 561, figs 5–6.

Haplosyllis spongicola.—San Martín, 2003: 324, fig. 179B (in part)

Syllis spongicola spongicola.—Cognetti, 1955: 1–3, fig. 1a.—Cognetti, 1957: 10–14, fig. 2a.—Cognetti, 1961: 294.

Examined material. W Mediterranean, Nerja (Spain). Holotype MNCN 16.01/10606; 155 Paratypes MNCN 16.01/10607.

Diagnosis. Body slender, length 5–10 mm for 28 to 52 chaetigers. Dorsal surface granulose. Trepan with 10 small teeth. First dorsal cirri long (18–30 articles), midbody dorsal

cirri less than ½ body width. Chaetae all bidentate, 2–7 chaetae on each parapodium, MJP straight; US of MF with long denticles.

Host. Unknown. Found in calcareous concretions of *Mesophyllum lichenoides* and *Lithophyllum expansum*, 3–25 m, and among rhizomes of *Posidonia*, 2–20 m (Lattig *et al.* 2007).

Reproduction. *Haplosyllis granulosa* reproduces by acephalous stolons with one pair of blackish ocular spots per parapodia. One paratype was observed early during the formation of the stolon, with the reproductive body still attached to the adult. The specimen had 54 segments, the last 14 forming the stolon.

Distribution. W Mediterranean Sea.

Remarks. The species resembles *H. djiboutiensis* in number of segments occupied by both pharynx and proventricle, the granulose aspect, length pattern of dorsal cirri and in chaetal shape. They can be distinguished from each other by the chaetal morphology (all similar in *H. granulosa* while both chaetae of each parapodium are different in *H. djiboutiensis*). It would be interesting to obtain more specimens of *H. djiboutiensis* in order to document the morphological variability of their chaetae.

***Haplosyllis gula* Treadwell, 1924**

(Figs 13 A–I, 14 A–H)

Haplosyllis gula Treadwell, 1924: 11–12, pl. II, fig. 19–23.—Hartman, 1956: 251.

Examined material. Barbados, Caribbean Sea. 11 types USNM 20327, attached to polychaete hosts (3 to an unidentified glycerid, 8 to a unidentified eunicid) and 3 non-attached; 2 prepared for SEM). Collected by the Barbados-Antigua Expedition of 1918.

Description. Body translucent, slender, fragile, small. Length 2.5–3.8 mm, for 26–31 segments, width 0.23–0.27 mm, excluding parapodia. Anterior end wide, with noticeable broad pharynx, becoming gradually thinner from midbody to posterior end (Figs 13A, 14A). Preserved specimens yellow-pale. Prostomium subpentagonal, wider than long, difficult to observe due to broad pharynx; two pairs of small red eyes in trapezoidal arrangement. Median antenna with 17–27 articles, inserted on medium of prostomium; lateral antennae with 8–11 articles, inserted on anterior margin of prostomium. Palps long, broadly triangular, fused at their bases, separated all along their length; with cilia on ventral side. Pharynx reddish-brown,

broad (0.14 – 0.26 mm wide), short, about 0.3 mm long, reaching to proventricle as funnel, extending about three segments; anteriorly, with small tooth, crown of 11–12 soft papillae, and an inner ring of short, numerous cilia (Fig. 14B–C). Papillae with cilia on ventral base and upper side. Proventricle cylindrical, dark-brown, 0.31– 0.42 mm long, extending 3–4 segments, about 0.2 mm wide, with 23–27 muscular cell-rows (Fig. 13A). Peristomium well defined, shorter than subsequent ones. Dorsal tentacular cirri (8–18 articles) longer than ventral ones. Dorsal cirri slender, slightly shorter at the tip, similar to antennae and tentacular cirri (Fig. 13A– B). First cirri long (19–29 articles), second small (7–13 articles), third and fourth slightly longer than second (12–14 and 21–26 articles, respectively), fifth small (6–11 articles) and sixth long (16–18 articles) (Fig. 13A). Subsequent cirri long, some exceed body width, gradually decreasing to posterior end, alternating with short (5–7 articles) and long (15–19 articles). Posterior cirri small (1–7 articles) (Fig. 13B). Ventral cirri triangular, anterior ones similar or longer than parapodial lobes (Figs 13C, 14D); posterior cirri very short (Figs 13D, 14E). Chaetae bidentate, all similar, US of MF with small denticles (only visible under SEM). Anterior chaeta smaller, with MJP straight and long (Figs 13E, 14F). Two chaetae per midbody parapodia, with LMF similar than SW; apical teeth long, distal one slightly smaller than proximal tooth; longer chaeta with MJP point straight and long (Figs 13H, 14G), short and slightly curved in smaller chaeta (Figs 13G, 14H). Aciculae stout, with curved tip 90° bent; two on anterior parapodia, one on midbody parapodia (Fig. 13F, I).

Reproduction. Unknown.

Host. Unknown. Probably a facultative parasite of other polychaetes. Types found attached to unidentified glycerid and eunicid polychaetes.

Distribution. Barbados, Caribbean Sea.

Remarks. *Haplosyllis gula* was described by Treadwell (1924). Since then, the species has only been mentioned in Hartman's (1956) catalogue. According to our observations, the type material is in excellent condition, except some specimens having broken antennae. The shape of prostomium is difficult to distinguish due the presence of its noticeably broad, dark-red pharynx. These unusual characteristics together with the long, triangular anterior ventral cirri, make it easy to recognise.

Most specimens of the type series were firmly attached to the branchiae or dorsal cirri of other polychaetes. The broad pharynx of *H. gula* seems to be an adaptation to an ectoparasitic mode of life. The number of ectoparasitic polychaetes reported to remain firmly attached to their respective host is very few. In addition, like *H. gula* and with a few

exceptions, they are only known from their original descriptions, which are often based on a single or a very few specimens (Martin & Britayev 1998).

In addition to *Haplosyllis gula*, two specimens of *Haplosyllis* reported as *H. cephalata* by Treadwell (1909), were found attached to parapodial cirrus of an unknown eunicid host. No specific modifications were reported, but only the basal section of the host cirrus retained its form inside the pharynx of the parasite, and the distal part was apparently disintegrated and digested inside the parasite's gut. These two specimens were not described and it is not mentioned if were deposited or not in a collection. Taken into account the geographical proximity and the similar habits and host, we suggest that they may correspond to *H. gula* instead of *H. cephalata*. Two more syllids have been reported as sucking ectoparasites: *Haplosyllides aberrans* (Fauvel, 1939) found inside the ventral brood pouch of the shrimp *Platycaris latirostris* Holthuis, 1952, attached to a pleopod of the host (Martin *et al.* 2008) and *Parasitosyllis claparede*, was attached to an unidentified polychaete with the help of a highly modified pharynx (Potts 1913), but also the polynoid *Thormora johnstoni* (Kinberg, 1855), which lives in the burrows of the palolo worm, *Palola viridis* Gray, 1847, was similarly attached to the caudal part of the host (Hauenschild *et al.* 1968).

***Haplosyllis lobo* Paola, San Martín & Martin, 2006**

Haplosyllis lobo Paola, San Martín & Martin, 2006: 347.352, fig. 1–4.

Examined material. Argentina, La Plata. One paratype MNCN 16.01/9034. Expedition G–II 12, 38°05'3''S 57°22'W, coarse sand, coll. "Lobo" Orensanz col., 1975.

Diagnosis. Robust body, up to 7.8 mm long. Trepan with 5–8 small, triangular teeth. Chaetae with long denticles on US of MF, reaching base of proximal tooth; MJP diagonal (Fig. 2C). Aciculae straight.

Reproduction . Unknown.

Host: The specimens were found in coarse sandy sediments, but the presence of sponge spicules on some worms suggested a possible association with a host sponge (Paola *et al.* 2006).

Distribution. SW Atlantic Ocean, La Plata, Argentina.

Remarks. The long and numerous spines on US of MF of *Haplosyllis lobo* are similar to the serration of *Trypanoseta* sp. recently described by Aguado *et al.* (2008). *H. lobo* is the unique species of *Haplosyllis* recorded from the SW Atlantic.

***Haplosyllis ohma* (Imajima & Hartman, 1964) new comb.**

(Figs 15A–D, 16A–F)

Trypanosyllis (*Trypanoseta*) *ohma* Imajima & Hartman, 1964: 129–130, pl. 31, fig. a–d. *Geminosyllis ohma*.—Imajima, 1966: 233–235, fig 43, a–g.—Kudenov & Harris, 1995: 71, fig. 1.26.

Examined material. Northern Japan, Shirikishinai. Holotype LACM–AHF Poly 0857, littoral zone. Paratype NSMT 18772, 120 m. coll. M. Imajima, June 1959.

Description. Body subcylindrical, variable in size. Holotype length 25 mm, for 65 segments, width 1.2 mm; paratype robust, length 32 mm, for 82 chaetigers, width 2 mm (Fig. 15A, C). Preserved specimens yellow-pale. Prostomium subpentagonal, with two pairs of small red eyes in trapezoidal arrangement. Median antenna (30 articles) inserted on median part of prostomium, between posterior eyes. Lateral antennae (25 articles) inserted on anterior margin of prostomium. Palps long, broadly triangular, fused at their bases, separated all along their length. Cilia on palps and nuchal organs not seen. Pharynx cylindrical, extending about 12 segments; anteriorly with triangular tooth, surrounded by crown of 10 soft papillae; trepan with 10 triangular teeth (Figs 15B, D); cilia on papillae not seen. Proventricle cylindrical, extending about 12 segments, obscured by body robustness. Peristomium well defined, shorter than subsequent ones. Dorsal tentacular cirri longer than ventral one, with 30 and 12 articles, respectively. Antennae, tentacular cirri and dorsal cirri similar, slender. Anterior dorsal cirri long, first cirri longer than remaining ones (31–36 articles), second short (16–18 articles), third, fourth and fifth slightly longer (24–29 articles), sixth long (32 articles); subsequent cirri long, with 28–35 articles, gradually decreasing to posterior end. Ventral cirri digitiform, not longer than parapodial lobe. All chaetae bidentate, anterior ones smaller, with short spines on US of MF (Fig. 16A–B). Midbody chaetae broad, with MJP straight, long; LMF shorter than SW; apical teeth long, well separated (Fig. 16C–E). Four to six chaetae per anterior parapodia, five to eight on midbody chaetigers. Aciculae enlarged, with rounded tip (Fig. 16F), three or more per parapodia. Pygidium not seen.

Reproduction. Unknown

Host. Unknown

Distribution. Northern Japan; Russia (Kurile Islands); Southern California, USA (?).

Remarks. The holotype was much shorter than the paratype, but also the depth from which collected (shallow vs. 120 m, respectively) and pharynx morphology (triangular, small teeth vs. terminal soft lobules, respectively) were different (Fig. 15B, D). This material (a holotype with chitinized trepan and a paratype with soft lobules) are the types on which the description of *Trypanoseta* as new genus was based. Thus, either they really belong to different species or this population has exactly the same variability in the pharyngeal anterior end as the Mediterranean *Haplosyllis* (i.e. *H. spongicola* and *H. granulosa*). Accepting the second as the valid hypothesis may confirm the synonymy between *Trypanoseta* and *Haplosyllis*.

The chaetal morphology of the paratype resembles *H. cratericola*, which also seems to lack pharyngeal trepan (but has twice the number of chaetae and aciculae present per parapodia). Additional material from the type locality needs to be examined in order to clarify the status of these types.

The record of the species in Southern California, USA (Kudenov & Harris 1995), which consist only of small sexually immature individuals, must be regarded as tentative until additional material is available or the existing material re-examined.

***Haplosyllis spongicola* (Grube, 1855)**

(Figs 17A–C, 18A–D)

Syllis spongicola Grube, 1855: 104–105.—Marion & Bobretzky, 1875: 24–25, fig. 7

Syllis setubalensis McIntosh, 1885: 195–196, pl. 30, fig. 5; pl. 33, fig. 6; pl. 15a fig. 16–17.

Syllis spongicola tentaculata.—Marion, 1879: 19–20, fig. 4 a–c.—Cognetti, 1955: 1–3, fig. 1b.—Cognetti, 1957: 10–14, fig. 2b.—Cognetti, 1961: 294.

? *Syllis spongicola tentaculata*.—Imajima, 1966: 221–222, fig. 38 i–n.

? *Haplosyllis spongicola*.—Sun, 1996: 20–21, fig. 3.

Haplosyllis spongicola.—Amoureux, 1977: 398.—Campoy, 1982: 363–365, in part.—Hartmann-Schröder, 1981: 27, fig. 3–4.—San Martín, 2003: 323–325, fig. 179 a, c, d y 180, in part.—Lattig *et al.* 2007: 554–556, figs 1–2.

Geminosyllis sp. 1 Lattig *et al.* 2007: 564–566, figs 7–8.

Non: *Haplosyllis spongicola*.—Fauvel, 1923: 257–258, fig. 95.—Imajima, 1966: 220–221 fig. 38, a–h.

Non: *Syllis spongicola spongicola*.—Cognetti, 1955: 1–3, Fig. 1a.—Cognetti, 1957: 10–14, fig. 2a.—Cognetti, 1961: 294.

Examined material. Lesina, Adriatic Sea, Mediterranean. Syntype MPW 399. Coast of Portugal, Holotype of *Syllis setubalensis* BMNH, 850 m.

Additional material: Portugal, personal collection of Joao Gil (CEAB–CSIC): SEPLAT 6: sta. 15 (1) 65 m; sta. 21 (1) 70 m; sta. 22 (4) 52 m; sta. 25 (1) 61 m; sta. 54 (3) 58 m; sta. 55 (1) 64 m; sta. 89 (1) 490 m. SEPLAT 7: sta.96 (1) 112 m; sta. 105 (1) 27.5m; sta. 149 (2) 113 m; sta. 175 (5) 202 m; sta. 179 (1) 120 m; sta. 212 (1) 147 m; sta. 220 (2) 28 m; sta. 223 (1) 38 m; sta. 231 (1) 32 m; sta. 289 (1) 338 m. Las Águilas, Murcia, Spain, 28 m (2).

South of Ireland. 20 specimens MNHN, 40 specimens MNHN. Continental slope, 850–1000 m, Expedition Thalassa 1973.

W Mediterranean: 2 specimens MNCN 16.01/10591, Rhizomes of *Posidonia oceanica*, 5 m, October 1989; 2 specimens MNCN 16.01/10588, on *Eunicella singularis*, 9 m, August 1984; 6 specimens MNCN 16.01/10592, on algae *Udotea petiolata*, 12 m, April 1985; 2 specimens MNCN 16.01/10594, on *Paramuricea clavata*, 23 m, April 1983; 1 specimen 16.01/10593, 1 specimen 16.01/10587 on *Paramuricea clavata*, 15 m, August 1984. Cabo de Creus, coll. Carmen Alós.

E Atlantic, Cantabric Sea: 8 specimens MNCN 16.01/10550, 114–116 m, 43°40'59''N 7°04'35''O. 3 specimens MNCN 16.01/10553, 146 m, 43°40'27''N 5°13.36'0. Expedition Fauna Ibérica, June 1991.

Diagnosis. Body robust, variable in size, up to 60 mm long, for 35–110 chaetigers. Dorsal cirri long, whip-shaped. Chaetae all bidentate, anterior ones broad, US of MF with small denticles (Fig. 18A, C). Midbody chaetae variable, depending on size of specimens: in small worms (about 0.5 mm long), MJP straight and long; LMF similar than SW (Fig. 18D). In longer worms (> 1 cm long), MJP short and curved; LMF longer than SW (Fig. 18B).

Host. Found in association with different sponge species (López *et al.* 2001), but more likely a specialized predator than a true sponge symbiont (Martin & Britayev, 1998).

Distribution. Mediterranean and European Atlantic waters. Also reported from the Indo-Pacific (Imajima 1966; Lee & Rho 1994; Sun 1996), but this material need to be rechecked. Recorded from 5 to 1000 m.

Remarks. Observing the pharynx under SEM, we have found a variety of anterior margins ranging from those with smooth, to those with well defined trepans, either with small apparently eroded teeth (Fig. 17A), or with blunt, to triangular teeth (Fig. 17B). Sometimes, pharyngeal margins are impossible to distinguish due the presence of a densely ciliated ring (Fig. 17C). When present, teeth may occupy the whole pharyngeal margin or only a semicircle (usually opposite to the long anterior tooth).

Haplosyllis spongicola show different chaetal morphologies in anterior and midbody chaetae, as well as in small and large worms (Fig. 18 A–D). Small worms (about 5 mm in length) have small denticles on US of MF, and LMF is similar to SW in all chaetae; long specimens (i.e. more than 10 mm length) have a long LMF. These variations may reflect the existence of an allometric variability. The same occurs with the shape of cirri, which may vary from long, broad to very long whip-shaped. Typically, the largest worms have more whip-shaped cirri.

Haplosyllis spongicola has a variable ecological signal. Its bathymetric range is very wide (from shallow to very deep waters), and has been collected in different types of hard substrata, in association with gorgonian fields, algal mats, calcareous algae crusts or *Posidonia* meadows. Although it has been reported from inside sponges, the worm are found solitary or in low numbers and the sponges seem not to be hosts but a source of food. Contrary to other *Haplosyllis* species, which are strict endosymbionts found in large quantities inside their sponge hosts (Martin & Britayev 1998).

The specimens reported as *Geminosyllis* sp. 1 in Lattig *et al.* (2007) fits within the morphological variability of *H. spongicola* and, thus, are here considered as the same species. Similarly, the examination of the holotype of *H. setubalensis* and additional material from Portugal (30–330 m) and the Thalassa 1973 expedition (Atlantic coast of France, 1000 m) allowed us to confirm the synonymy of this species with *H. spongicola*, as previously reported by Licher (1999).

***Haplosyllis spongiphila* (Verrill, 1885)**

(Figs 19A–F, 20A–E)

Syllis spongiphila Verrill, 1885: 435–436.—Horst, 1922:196.—Hartman, 1944: 435, pl. 24, fig. 10.—Pettibone, 1963: 114, fig. 31 a–h.

?*Syllis spongiphila*.—Imajima, 1966: 250–251, fig. 49 a–k.

Haplosyllis spongiphila.—Licher, 1999: 283, fig. 10D.

Examined material: NW Atlantic, U.S.A. >100 cotypes USNM 9864. Massachusetts, Martha's Vineyard, 127–580 m, 4 September 1880.

Description. Body robust, length 1–2 cm for 60–80 chaetigers, about 0.8 mm width (excluding parapodia) (Fig. 20A). Frequently, posterior segments in poor condition. Preserved specimens yellow-pale. Prostomium subpentagonal, wider than long, with two pairs of small red eyes in trapezoidal arrangement. Median antennae inserted on medium of prostomium, with 43–55 articles; lateral antennae inserted on anterior margin, with 21–31 articles. Palps long, broadly triangular, fused at their bases, divergent all along their length. Sensory organs on palps and nuchal organs not seen. Pharynx orange, very long, extending 14–21 segments; with large anterior tooth surrounded by crown of about 10 papillae; ring of cilia not seen. Proventricle cylindrical, dark-brown, shorter than pharynx, extending 7–13 segments, with 56–69 muscular cell-rows. Peristomium shorter than subsequent ones. Dorsal tentacular cirri very long, with 28–45 articles, ventral cirri smaller. Dorsal cirri similar to antennae and tentacular cirri, very long, slender, whip-shaped. First cirri long (41–50 articles), second and third slightly shorter (24–30 and 38–48 articles respectively); fourth very long (50–72 articles), fifth short (27–35 articles), sixth long (48–59 articles). Subsequent cirri exceed body width, slightly alternate with long (46–61 articles) and short (18–42 articles), but difficult to observe. Posterior cirri usually broken. Anterior ventral cirri digitiform, broad, longer than parapodial lobes (Fig. 19A), midbody ventral cirri, slender, slightly longer than parapodial lobe (Fig. 19B). Chaetae all bidentate, anterior ones, with blade partially fused to shaft (Figs 19C–D, 20B–C). Midbody chaetae completely simple, with narrow mark of fusion between blade and shaft (Figs 19E, 20D–E); LMF shorter than SW, but progressively longer from anterior to posterior chaetae; numerous short spines on US of MF; a long denticle on posterior chaetae; MJP long, relatively straight; apical tooth equal in length, well separated. Four to six chaetae on anterior parapodia; two or three at midbody. Aciculae straight and broad, two or three per parapodia (Fig. 19F). Pygidium broken.

Reproduction. Unknown

Host. It has been reported as common and often abundant among sponges and hydroids (Hartman 1944), but without references to the specificity of the association.

Distribution. NW Atlantic, Massachusetts. Caribbean Sea.

Remarks. *Haplosyllis spongiphila* was first considered as a *Syllis*, but the original chaetal description was inaccurate. The chaetae were reported as having blades partially fused

to shafts, resembling *H. anthogorgicola* (Pettibone 1963), as compound and pseudocompound (Imajima 1966) and more recently, as simple, and therefore must belong to *Haplosyllis* (Licher 1999). Our observations confirm that midbody chaetae are simple, but the anterior ones are similar to pseudocompound chaetae, showing clear traces of the fusion of blade and shaft. However, this has been previously reported for other *Haplosyllis* species (e.g. *H. anthogorgicola* and *H. lobo*). Thus, we agree with Licher (1999) in that the species must be considered as belonging to *Haplosyllis*.

Haplosyllis spongiphila is currently considered a cosmopolitan species occurring in the Caribbean (Perkins & Savage 1975; Verrill 1885), NW Atlantic (Hartman 1944; Pettibone 1963) and Japanese (Imajima 1966) waters. However, the specimens from Japan were reported as having well defined compound chaetae, suggesting that the Indo-Pacific populations could be a different species, not belonging to *Haplosyllis*.

***Haplosyllis streptocephala* (Grube, 1857) new comb.**

(Fig. 21 A–B)

Syllis streptocephala Grube, 1857: 1871–182.—Horst, 1922: 196.—Perkins & Savage, 1975: 31.

Examined material. St. Croix, Caribbean Sea. Holotype ZMUC Pol-922.

Description. Body robust, length 2 cm, for 133 chaetigers, width 1 mm (excluding parapodia). Orange brown. Prostomium subpentagonal, wider than long, with two pairs of small eyes in trapezoidal arrangement, difficult to see by pigment loss. Median and lateral antenna similar in size (17–19 articles), inserted on medium and anterior margin of prostomium, respectively. Palps twice as long as prostomium length, broadly triangular, fused at their bases, separated all along their length. Sensory organs of palps and nuchal organs not seen. Palps and prostomium much thinner than tentacular segment and subsequent chaetigers. Pharynx long, extending about 11 segments, obscured by body robustness; anterior tooth and papillae not seen. Proventricle cylindrical, dark-brown, extending 11 segments, with about 90 muscular cell-rows. Peristomium very short. Dorsal tentacular cirri long (17–21 articles), ventral ones broken. Dorsal cirri, tentacular cirri and antennae similar, whip-shaped. First dorsal cirri longer than remaining ones (28 articles), second short (14 articles), third and fourth slightly longer (20 and 24 articles, respectively), fifth short (15 articles), sixth slightly longer (19 articles); subsequent cirri do not exceed body width, with 13–21 articles, gradually

decreasing to posterior end (9–13 articles). Ventral cirri digitiform, not longer than parapodial lobes. Anterior chaetae bidentate, with apical teeth equal in size; two or three chaetae per parapodia (Fig. 21A). Midbody chaetae broad, unidentate, but similar in shape to anterior ones (Fig. 21B); all chaeta with MJP long and straight; LMF shorter or similar than SW; US of MF without denticles. Three to five chaetae per parapodia. Pygidium broken.

Reproduction. Unknown

Host. The presence of spicules in the body of the holotype suggests a possible association with sponges.

Distribution. Caribbean Sea.

Remarks: *Haplosyllis streptocephala* was first described within the genus *Syllis*, but its chaetal shape agrees with *Haplosyllis*. Their chaetae are highly characteristic, broad and totally unidentate from medium body to posterior end. Both palps and prostomium are much thinner than the rest of the body, which distinguishes it from other *Haplosyllis* species. As the description is based only on the holotype, it is not possible to assess whether this is a species-specific characteristic (or a peculiarity of that particular specimen), as well as to provide ecological and reproduction data.

***Haplosyllis trifalcata* (Day, 1960)**

(Fig. 22 A–L)

Syllis trifalcata.—Day, 1960: 308, fig. 6g–i.

Syllis (Haplosyllis) trifalcata.—Day, 1967: 241, fig. 12 j–l.

Haplosyllis trifalcata.—Licher, 1999: 284.

Examined material. South Africa. Holotype SAM A–20932, False Bay, 34°12'4''S 18°43'5''E, 42 m.

Description. Holotype robust, length 1.3 cm for 89 segments. The specimen was in poor conditions, ventrally opened at anterior end. Preserved specimen Yellow-pale. Dorsal granules abundant on posterior segments, scarce from medium body to anterior end. Prostomium subpentagonal, wider than long, with two pairs of small red eyes in trapezoidal arrangement. Antennae broad, short; median antenna slightly longer (14 articles) than lateral ones (10 articles), inserted on medium and anterior margin of prostomium, respectively. Palps broad ventrally bent behind proventricle (Fig. 22A). Cilia on palps and nuchal organs not

seen. Pharynx orange, length 1.1 mm, extending 8–9 segments, width 0.2 mm; anteriorly, with large tooth; papillae not seen. Proventricle dark-brown, length 0.28 mm, extending 5–6 segments, width 0.93 mm, with 35 muscular cell-rows. Peristomium well defined, shorter than subsequent ones. Dorsal tentacular cirri longer than ventral ones (12 and 9 articles, respectively). Dorsal cirri similar to antennae and tentacular cirri, long and broad. Dorsal anterior cirri similar in length: first with 13 articles, second with 11 articles, third broken, fourth with 13 and fifth with 10; midbody dorsal cirri not as broad as anterior ones, with 7–13 articles, gradually shorter to posterior end; posterior cirri short (1–4 articles). Ventral cirri digitiform, anterior ones longer than midbody and posterior ones (Fig. 22 B, C, D). Chaetae most frequently bidentate, three to six per parapodia, similar all along body; apical teeth long and wide; MJP very short, curved; MF very close to apical teeth, giving a tridentate appearance; LMF shorter than SW, without spines on its US (Fig. 22 E–G). In posterior-most chaetigers, one chaeta with three apical teeth, MF apparently lacking, with a transversal incision below the tridentate cusp (Fig. 22H); one simple bifid chaeta on posterior-most parapodia (Fig. 22I). Anteriorly, two small aciculae, one with straight rounded tip, other with slightly curved upwards directed tips (Fig. 22J). One orange, broad, with curved tip downwards directed tip at midbody (Fig. 22K), and one with slightly curved tip on the most posterior segments (Fig. 22L). Pygidium with two long anal cirri (12–13 articles).

Reproduction. Unknown.

Host. Unknown.

Remarks. *Haplosyllis trifalcata* was originally described as having 3–6 simple chaetae on each parapodium, all them similar, with three claw-like teeth; this apparently tridentate chaetae is the most frequent type in the holotype (Fig. 22E–G). However, there is an additional chaeta on the most posterior parapodia, showing a transversal incision below the tridentate cusp (Fig. 22H). This lead us to postulate that the origin of these tridentate chaetae may result from the fusion of blade and shaft, as suggested for other *Haplosyllis* species (see remarks on *H. spongiphila*). By homology the presence of the incision supports that the third “tooth” is an upwards-directed MF instead of an additional apical teeth.

The holotype was ventrally dissected, affecting its original shape and making it difficult to determine its proportions.

***Haplosyllis uncinigera* Grube, 1878**

(Fig. 23 A–J)

Syllis uncinigera.—Grube, 1878: 113–114.

Haplosyllis hainanensis.—Sun, 1996: 19–20, fig. 2 a–f.—Sun and Yang, 2004: 317–318, figs 185 a–h. New synonymy

? *Haplosyllis djiboutiensis*.—Augener, 1913: 213

Examined material. Philippines, Bohol: Holotype ZMB F.1977, coll. Grube. Syntypes of *Haplosyllis hainanensis*. South China Sea, Haianan Islands. Yezhu Island: 1 specimen SMF 10856, among Serpulidae, March 1992; 1 specimen SMF 10855, among dead corals, March 1992; 3 specimens SMF 10857, among corals and crinoids, 6–11 m, November 1990. Xincun Island: 2 specimens SMF 10858, among corals, 1–3 m, March 1992.

Description. (In parenthesis counts of *H. hainanensis*). Holotype complete, length 3.2 cm, for 115 segments, width 1 mm (Fig. 23A). The body was fragile and flat due preservation conditions, and probably by many times observed at microscope. Syntypes of *H. hainanensis* in better conditions but most chaetae eroded at the tips; long and robust, length 2–3.2 cm for 55–125 segments, width 1–1.4 mm. Few dorsal granules on most posterior segments, almost absent at midbody and anterior regions. Palps, prostomium and first anterior segments often dark-brown pigmented. Prostomium subpentagonal, with two pairs of small eyes in trapezoidal arrangement (difficult to see on holotype). Antennae all similar in length, median with 24 (20) articles and lateral with 23–24 (16) articles inserted on medium and anterior margin of prostomium, respectively. Palps long, broadly triangular, fused at their bases, clearly divergent all along their length. Sensory organs of palps and nuchal organs not seen. Pharynx orange, long, extending 18 (14–15) segments; anteriorly, with large tooth (Fig. 23A) and terminal crown of 10 soft papillae. Proventricle cylindrical, length 4 mm, extends for 10–11 chaetigers, width 0.8 mm, dark-brown, with muscular cell-rows obscured by body robustness. Peristomium well defined, shorter than subsequent ones. Dorsal tentacular cirri longer than ventral ones, with 26 (14–22) and 13 (9) articles respectively. Dorsal cirri whip-shaped, similar to antennae and tentacular cirri. Anterior cirri long, longest one slightly exceed body width; first dorsal cirri long, with 36 (24–27) articles, second short, 20 (17–19) articles, third and fourth long, 30 (21–27) and 40 (27–29) articles, respectively, fifth broken, (> 25 (15–22) articles). Midbody cirri long, slightly alternating with long, for 29–33 (18–27) articles, and short, for 16–23 (12–22) articles, become shorter on posterior-most parapodia, with 3–8 (11–22) articles (Fig. 23D). Ventral cirri digitiform, anterior cirri equal in length to parapodial lobes (Fig. 23B), midbody cirri shorter (Fig. 23C). All chaetae bidentate, anterior

ones much smaller (Fig. 23E); midbody parapodia with 2–3 chaetae; smallest one with short thin proximal tooth (Fig. 23G); largest chaetae with distal tooth much smaller than proximal one, angle between teeth narrow, giving unidentate appearance; MJP long, straight; LMF similar to SW (Fig. 23H). Aciculae of two types, one straight, other with curved upwards directed tips (Figs 23F, I–J); four to six aciculae per parapodia. Pygidium with two long anal cirri with about 13 articles.

Reproduction. Unknown.

Host. Unknown. The South China specimens were found from 1 to 11 m among serpulids, dead corals and crinoids, but no specific associations were reported.

Distribution. Philippines; South China Sea; probably Australia (Augener 1913).

Remarks. *Haplosyllis uncinigera* was synonymized to *H. spongicola* (Licher 1999). However, its long body, the number of segments occupied by the pharynx and proventricle and, especially the chaetal shape and its geographical distribution, suggests it is a valid species.

Haplosyllis hainanensis, from South China Sea, is here considered as a synonymy of *H. uncinigera*. The South China specimens have up to three chaetae on each parapodium (most of them with broken or eroded tips); depending on the position in which chaetae is being observed, the two larger ones appear to be as unidentate; when chaetae is in lateral position, it is possible to observe the short distal tooth. Additionally, some specimens of *H. hainanensis* were brown pigmented on the anterior region.

The Australian specimens reported by Augener (1913) as *Haplosyllis djiboutiensis*, probably belong to *H. uncinigera*, due the chaetal shape and geographical distribution. *H. djiboutiensis* is here considered a valid species, differing from *H. uncinigera* in terms of chaetal shape, and the length of pharynx and proventricle (see remarks of *H. djiboutiensis*).

***Haplosyllis villogorgicola* Martin, Núñez, Riera & Gil, 2002**

Haplosyllis villogorgicola Martin, Núñez, Riera & Gil, 2002: 457–461, figs 2–4, 5A, 6.

Examined material. Canary Islands. 6 Paratypes MNCN 16.01/7833. Punta Guadamonte, Radazul, southeastern coast of Tenerife, 28°24'N 16°19'W.

Diagnosis. Body slender, fragile, length 4–13 mm, up to 80 chaetigers. Dorsal cirri long, some longer than body width. Midbody cirri alternating with short (13–22 articles) and

long (14–44 articles). Chaetae with distal tooth smaller than proximal one, very thin. Three to five chaetae per parapodia.

Reproduction. Unknown.

Host. Specific ectosymbiont of the gorgonian *Villogorgia vebricoides* (Koch, 1887) (Martin et al. 2002).

Remarks. The species is illustrated, described and compared with the closely related *H. chamaeleon* in Martin et al. (2002).

Haplosyllis Incertae sedis

Haplosyllis aurantiaca (Eisig, 1881)

Syllis aurantiaca Eisig, 1881: 270–277.

Type material. Naples, Mediterranean Sea.

Remarks. Licher (1999) considered *Syllis aurantiaca* as a synonymy of *Haplosyllis spongicola*. The type material is probably lost, and the original description does not contain illustrations of chaetae and cirri, being impossible to confirm either the synonymy or the validity of the species.

Haplosyllis hamata (Claparède, 1868)

Syllis hamata Claparède, 1868: 505–507, pl.15, fig.2.

Type material. Naples, Mediterranean Sea.

Remarks. The type material appears to be lost and the original description does not allow its correct characterization and comparison with other valid species of the genus. Being Mediterranean, and the slender body, short cirri, the presence of dorsal granules and the length of proventricle and pharynx, suggest that it may probably synonymy of *Haplosyllis granulosa*. However, this synonymy cannot be confirmed.

Haplosyllis oligochaeta (Bobretzky, 1870)

Syllis oligochaeta Bobretzky, 1870: 229–230, figs 51–52

Type material. Black Sea.

Remarks. The species was considered as a synonymy of *Haplosyllis spongicola* (Licher 1999). There is a single report, the description it not accurate enough as required to characterize the species, and the type material is not available.

Haplosyllis violaceo-flava (Grube, 1878)

Syllis violaceo-flava Grube, 1878: 115–116 T. VII, fig. 3.

Type material. Philippines, Bohol.

Remarks. Licher (1999) considered *Haplosyllis violaceoflava* as a synonymy of *Haplosyllis spongicola*. It has not been possible to assess the validity of the species, as the type material is probably lost. The chaetae were not well described in the original description, as being simple bifid chaetae apparently very similar to those of *H. uncinigera*. Additionally, the dark spots on the anterior segments, which were mentioned by Grube (1878), are also present in some specimens of *H. uncinigera*.

Haplosyllis spongicola brevicirra Rioja, 1941

Haplosyllis spongicola brevicirra Rioja, 1941: 695–696, figs 5–6.

Type material. Acapulco, México.

Remarks. *Haplosyllis spongicola brevicirra* differs from *H. spongicola* in terms of cirri (shorter) and chaetal shape (Rioja 1941). The types were non available and the original description is too brief, so impossible to decide whether it can be a synonymy of a valid *Haplosyllis* species or a new one.

Nomina dubia

***Haplosyllis maderensis* Czerniavsky, 1881**

Haplosyllis maderensis Czerniavsky, 1881: 393

Remarks. The species only appears in an identification key in Czerniavsky (1881), without having a formal description (Licher 1999).

***Haplosyllis oligochaeta massiliensis* Czerniavsky, 1881**

Syllis oligochaeta forma *massiliensis* Czerniavsky, 1881: 393

Remarks. *H. oligochaeta maderensis* only appears in an identification key in Czerniavsky (1881), without having a formal description (Licher 1999).

***Haplosyllis oligochaeta pontica* Czerniavsky, 1881**

Haplosyllis oligochaeta pontica Czerniavsky, 1881: 394

Type material. Sevastopol, Black Sea.

Remarks. The single citation of the species does not contain an accurate description and the type material appears to be lost.

***Haplosyllis palpata* Verrill, 1900**

Haplosyllis palpata Verrill, 1900: 614; Licher 1999.

Type material. Bermudas, Caribbean Sea. 1 Syntype (?) YPM 23002.

Remarks. It has not been possible to check the validity of *Haplosyllis palpata* because: 1) the YPM could not confirm that the specimen marked on the microslide really

corresponds to a syntype of the species, as it was mixed with specimens clearly belonging to *H. cephalata*; 2) the specimen is a juvenile, with most anterior cirri broken and the chaetae in a position that makes difficult accurate observations; 3) the original description lacks illustrations and does not provide enough information to characterize the species; 4) there is no other registered material.

Taxa that do not belong to *Haplosyllis*

***Alcyonosyllis bisetosa* (Hartmann-Schröder, 1960) new comb.**

Haplosyllis bisetosa Hartmann-Schröder, 1960: 85–86, fig. 51–53.—Amoureux et al. 1978.—Licher, 1999: 280.

Examined material. Djubal ("Gubal", Saudi Arabia), Red Sea. Holotype ZMH P–14745; 1 Paratype ZMH P–14746. November 1957.

Remarks. Hartman-Schröder (1960) described the species as having cirri and antennae with few articles or totally smooth. This was later confirmed based on specimens collected at Sinai (Amoureux et al. 1978). Our observations confirm that the chaetae have a long and straight MJP, and minute MF, resembling those of *Alcyonosyllis phili* Glasby and Watson, 2001. The species is here considered as belonging to *Alcyonosyllis*, however, the type material is in poor condition, especially the cirri.

***Alcyonosyllis gorgoniacola* (Sun & Yang, 2004) new comb.**

Haplosyllis gorgoniacolo Sun & Yang, 2004: 314, figs 182–183.

Type material. Xisha Island, South China Sea, deposited at IOCAS.

Remarks. The originally described smooth non-articulated, dorsally bent cirri, alternating wide and thin, the hooked simple chaetae with a small subterminal tooth and its association to unidentified orange gorgonians, agrees with *Alcyonosyllis* (Glasby & Watson 2001). In addition, the species name was first spelled as “*gorgoniacolo*” (Sun & Yang 2004), the correct spelling must be “*gorgoniacola*”.

Alcyonosyllis xeniaecola (Hartmann-Schröder, 1993)

Haplosyllis xeniaecola (Hartmann-Schröder, 1993): 305–310, figs 1–8.—Licher, 1999: 384.

Type material. Indonesia, Molukken Islands. Holotype ZMF 4433.

Remarks. Glasby & Watson (2001) correctly transferred the species to *Alcyonosyllis*.

Trypanosyllis depressa (Augener, 1913)

Haplosyllis depressa Augener, 1913: 217–217, figs 29–30.—Licher, 1999: 280.

Trypanosyllis (Trypanobia) depressa.—Imajima, 1966: 242, fig. 46.

Type material: SW Australia. Syntype ZMH V–7946

Remarks. The species was transferred to *Trypanosyllis (Trypanobia)* Imajima & Hartman, 1964 (Imajima 1966). Later, it was referred to *Haplosyllis* (Licher 1999). However, its flat body and the absence of a subterminal tooth lead us to consider that the species certainly belong to *Trypanosyllis*.

Trypanosyllis dollfusi (Fauvel, 1933) new comb.

Syllis (Haplosyllis) depressa var. *dollfusi*.—Fauvel, 1933: 50–52, fig. 4.

Haplosyllis dollfusi.—Licher, 1999: 280

Type material. Not known.

Remarks. Fauvel (1933) described this subspecies based on Red Sea specimens. As mentioned above, the main species was transferred to *Trypanosyllis* by Imajima (1966). Licher (1999) raised *H. depressa* var. *dollfusi* to the range of species status within genus *Haplosyllis*. As López et al. (1996) mentioned, this subspecies is more similar to *Trypanosyllis depressa*, than to any species of *Haplosyllis*. Therefore, we consider it as belonging to *Trypanosyllis*.

Acknowledgements

We would like to thank Kristian Fauchald and Linda Ward (USNM), the late Miguel Villena and Javier I. Sánchez (MNCN), Angelika Brandt (ZMH), Eric Lazo-Wasem (YPM), Tarik Meziane (MNHN), Dieter Fiege (SMF), Minoru Imajima (NSMT), Leslie Harris (LACM-AHF), Emma Sherlock (BMNH), Jolanta Jurkowska (NPW), Danny Eibye-Jacobsen and Kristine J.K. Sørensen (ZMUC), Elizabeth Hoenson (SAM) and Birger Neuhaus (ZMB), for the loans of type material and other collection information. The SEM images were possible by the careful work of Jose Manuel Fortuño from the SEM Service of the ICMB-CSIC. A special thank to Guillermo San Martín (UAM) for reading the manuscript and his valuable comments. We are also very grateful to Sergey Gagaev (ZISP) for the observations, information and photographs of *Haplosyllis cratericola*. We want to thank Maria V. Plyuscheva and Daniel Von Schiller (CEAB-CSIC) who kindly translated some Russian and German descriptions. We also extend our gratitude to all those that helped with the study of *Haplosyllis hainanensis*: Dieter Fiege for providing advice and literature and Jin Zhou and Yanli Lei (IOCAS) for helping with literature, Russian translations and search of the type material. Special thanks to Joao Gil (CEAB-CSIC), for his kind advice on taxonomic problems, for having all literature that we were unable to find, and for the loan of the Portuguese material, and to Kristian Fauchald, for his helpful taxonomic guidance. We also thank Florencio Aguirrezabalaga and Alvaro Altuna (INSUB) for the loan of specimens of *H. chamaeleon* from Galicia. We are also grateful to Maite Aguado (UAM), who kindly shared her annotations and observations of *H. uncinigera*, to Irene Malonda (UAM) for the loan of her *Haplosyllis* specimens, to Maria Ana Tovar-Hernández (UNAM, México) for helping us with literature, to Elvira Morote (ICMB-CSIC) and Marc Rius (UB, Barcelona) who kindly carried the holotype of *H. trifalcata* from the SAM to Spain and returned it, allowing us to examine this material. Finally, we would like to thank the two reviewers and Pat Hutchings (Australian Museum) who proposed important modifications for the manuscript.

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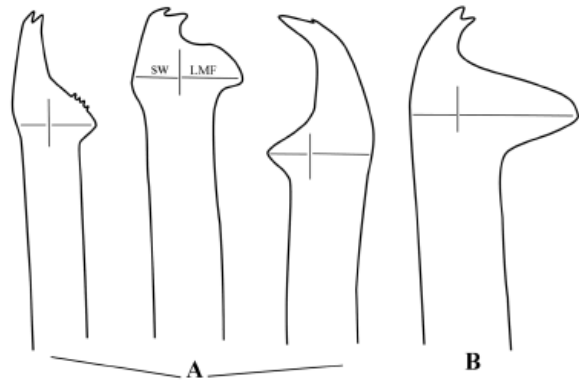


FIGURE 1. Comparison between length of main fang (LMF) and chaetal width (SW). A—LMF is similar or shorter than SW, B—LMF is longer than SW.

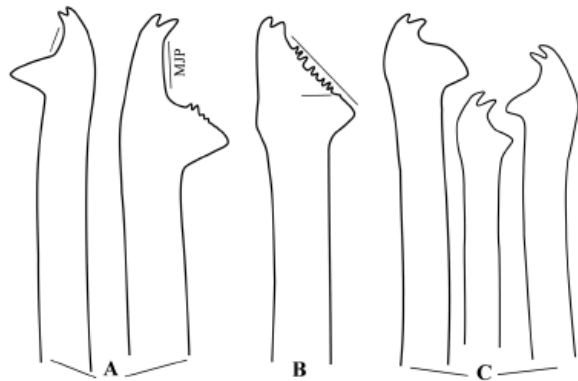


FIGURE 2. Different chaetal shapes according to MJP. A—straight, relatively short (left), or long (right), B—diagonal, C—curved and short. Lines are: A, B, distance between base of proximal tooth and beginning of MF; B, beginning of MF (small), slope of MJP and MF (long).

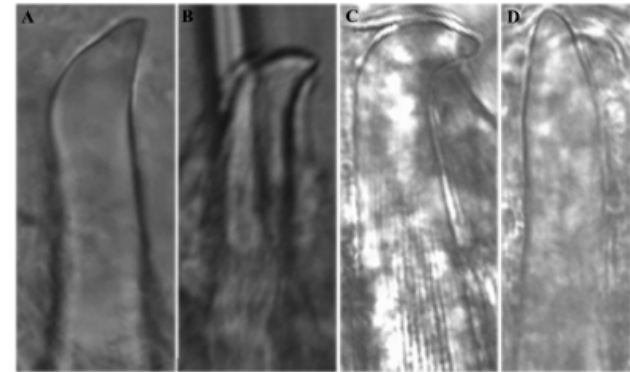


FIGURE 3. Acicular shapes. A–B—aciculae with curved tips upwards directed, C— acicula with curved tips 90° bent, D—straight acicula.

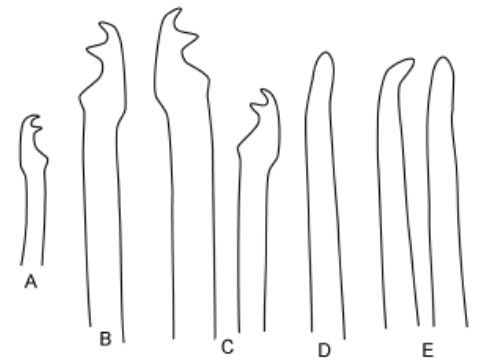


FIGURE 4. *Haplosyllis agelas*. A— anterior chaeta, B—midbody chaeta, C—posterior chaetae; D—midbody acicula; E—posterior body aciculae. Scale bar 20 μ m.

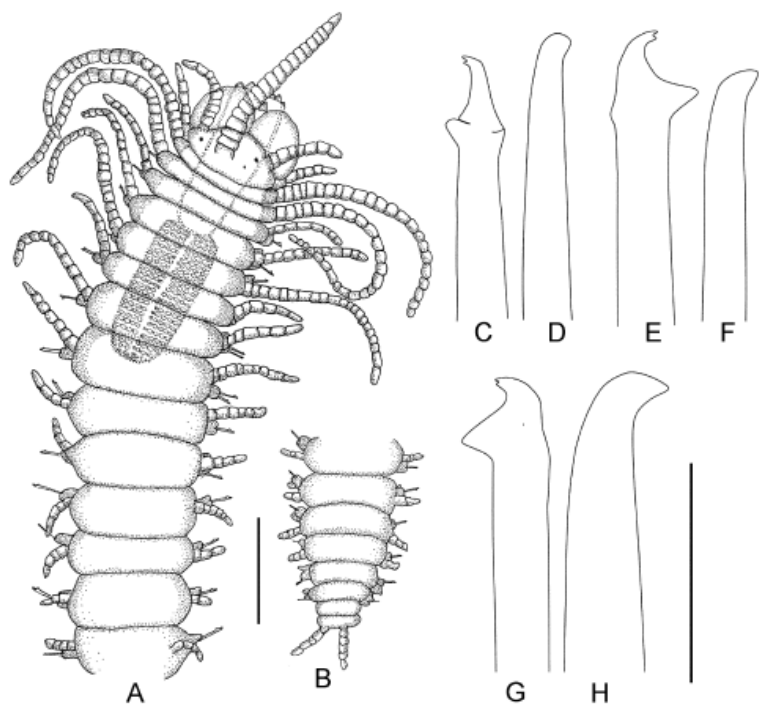


FIGURE 5. *Haplosyllis anthogorgicola*. A— anterior end, dorsal view; B—posterior end, dorsal view; C— anterior chaeta; D— anterior acicula; E— midbody chaeta; F— midbody acicula; G— posterior chaeta; H— posterior acicula. Scale bars: A–B = 200 μm ; C–H = 20 μm .

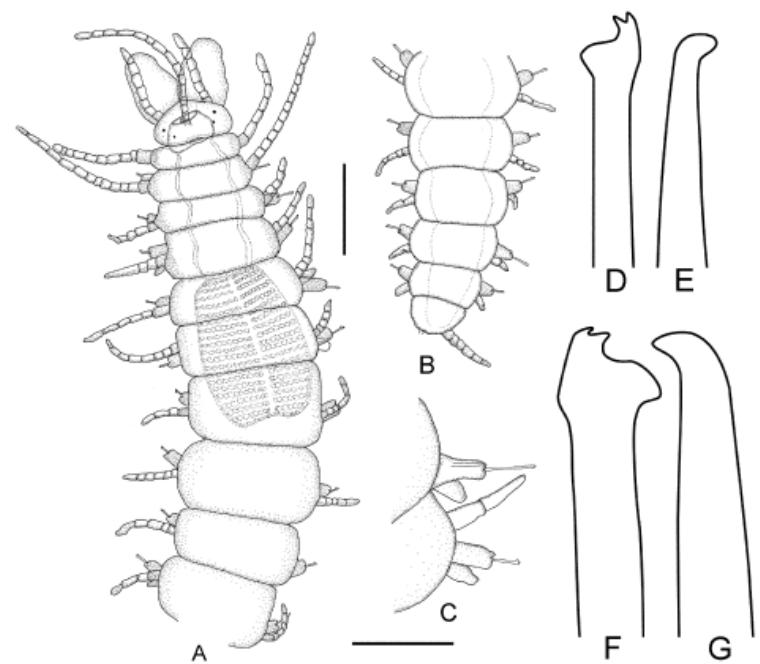


FIGURE 6. *Haplosyllis basicola*. A— anterior end, dorsal view; B—posterior end, dorsal view; C— anterior parapodia, chaetigers 4 and 5; D— anterior chaeta; E— anterior acicula; F— midbody chaeta; G— midbody acicula. Scale bars: A–B = 200 μm ; C = 97 μm ; D–G = 20 μm .

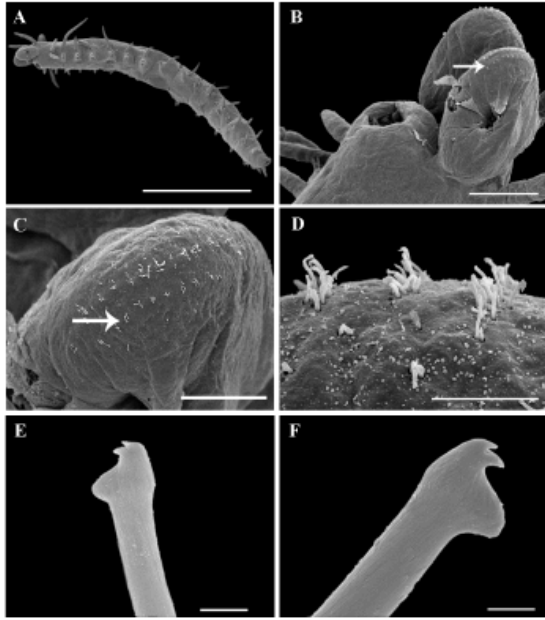


FIGURE 7. SEM micrographs of *Haplosyllis basticola*. A—whole body, lateral view; B— anterior end, ventral view showing palps with rows of cilia; C—upper-ventral side of palps with rows of cilia (indicated by arrow); D—detail of cilia; E— anterior chaeta; F—posterior chaeta. Arrow of B indicates position of ciliated sensory organs of palps. Scale bars: A–B = 250 μ m; C = 10 μ m; D–F = 2.5 μ m.

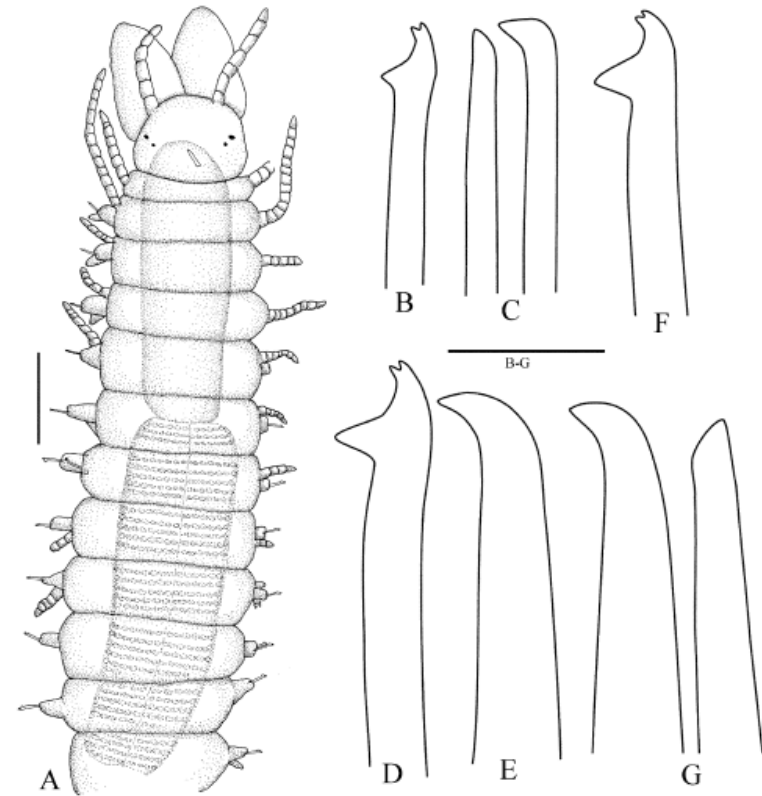


FIGURE 8. *Haplosyllis cephalata*. A— anterior dorsal view; B— anterior chaeta; C— anterior aciculae; D— midbody chaeta; E— midbody acicula; F— posterior most chaeta; G— posterior most acicula. Scale bars: A = 200 μ m; B–G = 20 μ m.

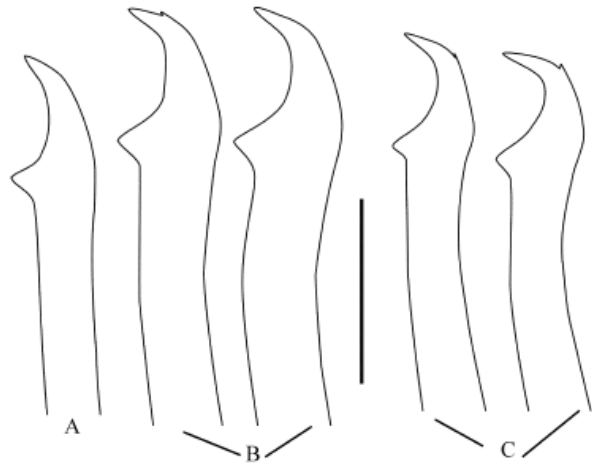


FIGURE 9. *Haplosyllis chamaeleon*. A— anterior chaeta; B—midbody chaetae; C—posterior chaetae. Scale bar 20 μ m.

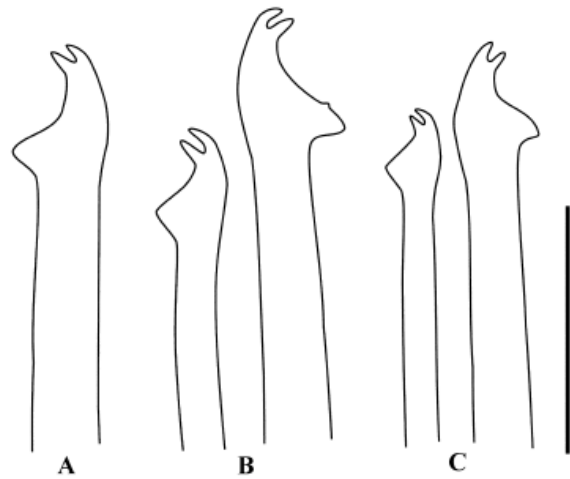


FIGURE 10. Holotype of *Haplosyllis crassicirrata*. A— anterior chaeta; B—midbody chaetae; C—posterior chaetae. Scale bar 10 μ m.

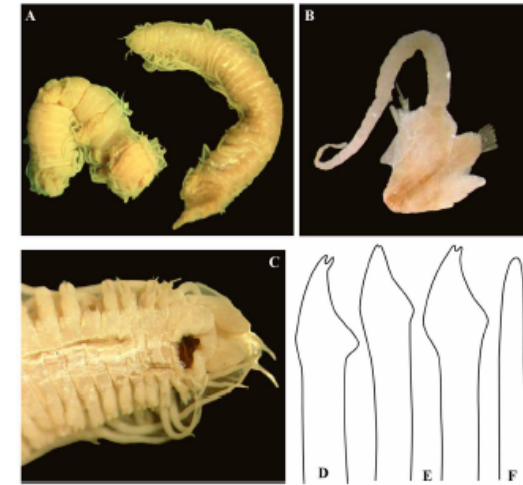


FIGURE 11. *Haplosyllis cratericola*. A—two fragments of holotype; B—parapodium; C— anterior end, ventral view; D— anterior chaeta; E—midbody chaetae; F—acicula. A and B are photographs by Dr. Sergey Gagaev (Zoological Institute of Russia), C edited from a photograph, D and E redrawn from Buzhinskaja (1990). No scales available.

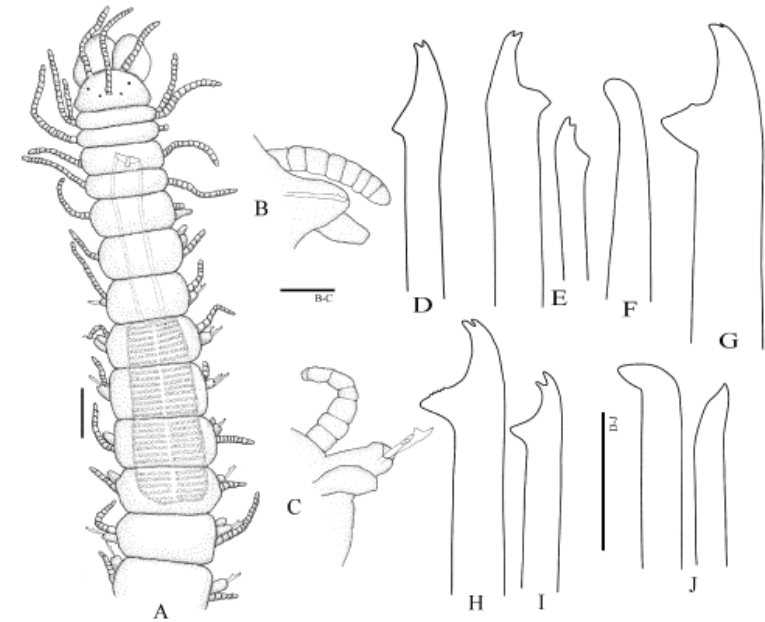


FIGURE 12. Polytype of *Haplosyllis djiboutiensis*. A— anterior end, dorsal view; B— anterior parapodium; C— midbody parapodium; D— chaeta from chaetiger two; E— chaetae from chaetiger five; F— anterior acicula; G— largest chaeta, midbody, main fang in backward position; H— largest chaeta, midbody; I— shortest chaeta, midbody; J— aciculae, midbody. Scale bars: A = 200 μ m; B–C = 50 μ m; D–J = 20 μ m.

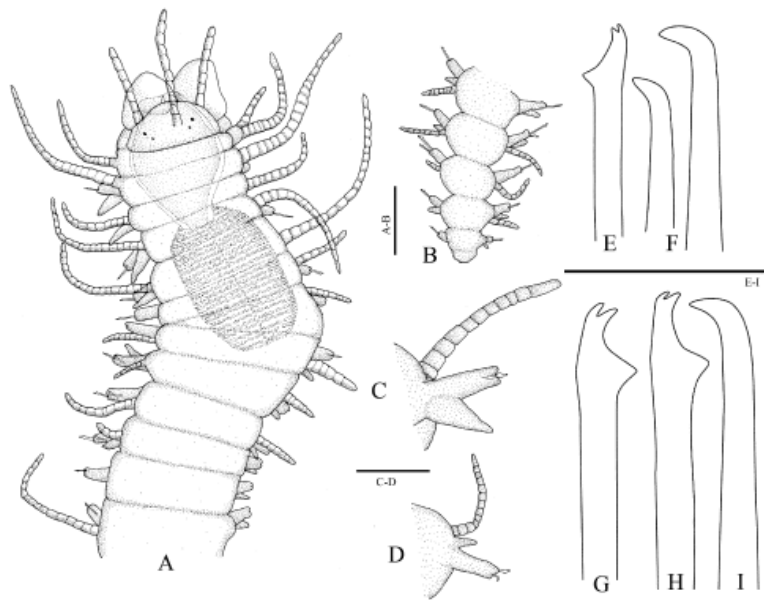


FIGURE 13. *Haplopyllis gula*. A—anterior end, dorsal view; B—posterior end, dorsal view; C—anterior parapodium; D—posterior parapodium; E—anterior chaeta; F—anterior aciculae; G—shortest chaeta, midbody; H—largest chaeta, midbody; I—posterior acicula. Scale bars: A–B = 200 μ m; C–D = 100 μ m; E–I = 20 μ m.

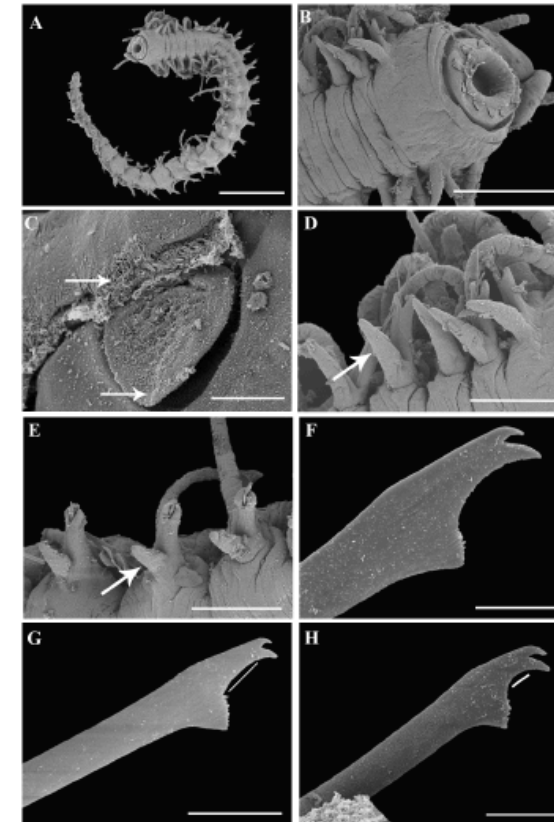


FIGURE 14. SEM micrographs of *Haplopyllis gula*. A—whole body, ventral view; B—anterior end, ventral view; C—ciliated sensory organs, pharyngeal papillae; D—anterior parapodia; E—midbody parapodia; F—anterior chaeta; G—largest chaeta, midbody parapodium; H—smaller chaeta, midbody parapodium. Arrows in C indicating cilia of pharyngeal papillae, in D and E pointing ventral cirri. Bars in G and H indicate MJP. Scale bars: A = 500 μ m; B = 200 μ m; D–E = 100 μ m; C, G = 10 μ m, F, H = 5 μ m.



FIGURE 15. *Haplosyllis ohma*. Holotype: A—whole body, dorsal view; B— anterior end showing trepan; Paratype: C— medium body, ventral view; D— anterior end showing trepan. Scale bars: A = 2 mm; B = 0.4 mm; C–D = 1 mm.

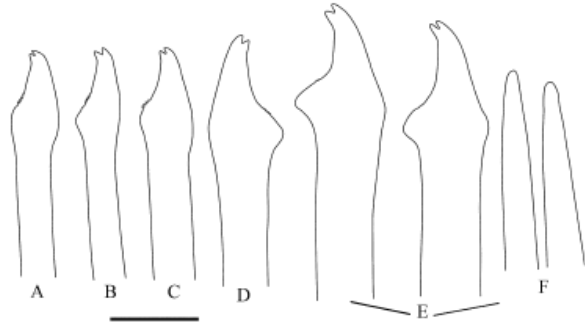


FIGURE 16. *Haplosyllis ohma*. Chaetae from holotype: A—second chaetiger; B—fourth chaetiger; C—midbody chaetiger; D—posterior chaetae. Paratype: E—midbody chaetae; F—midbody aciculae. Scale bar 20 μ m

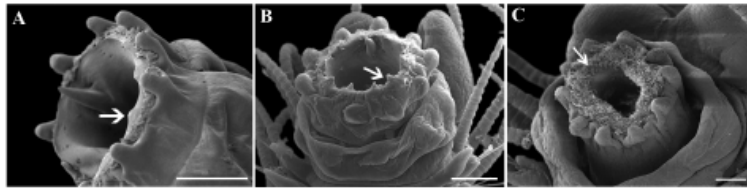


FIGURE 17. SEM micrographs of the pharynx of *Haplosyllis spongicola*. A—trepan with small teeth arranged in semicircle around pharyngeal tooth; B—complete trepan, small and triangular teeth; C—pharynx covered by a dense ring of cilia, not visible if trepan is present. Arrows pointing to trepan tooth in A and B, the cilia in C. Scale bars: A = 300 μ m; B–C = 100 μ m.

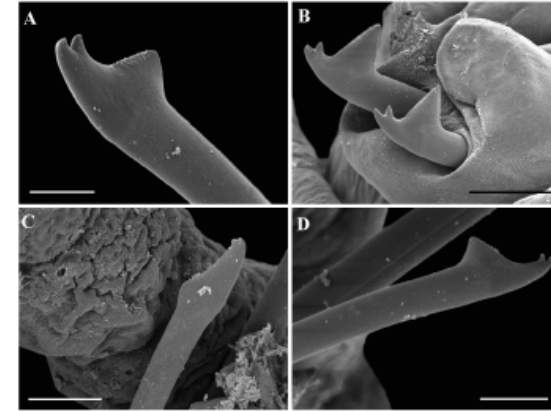


FIGURE 18. *Haplosyllis spongicola*. Long specimen, 1.4 cm long: A—third chaetiger; B—midbody chaeta. Small specimen, 5 mm long: C—third chaetiger; D—midbody chaetae. Scale bars: A, C, D = 10 μ m; B = 30 μ m.

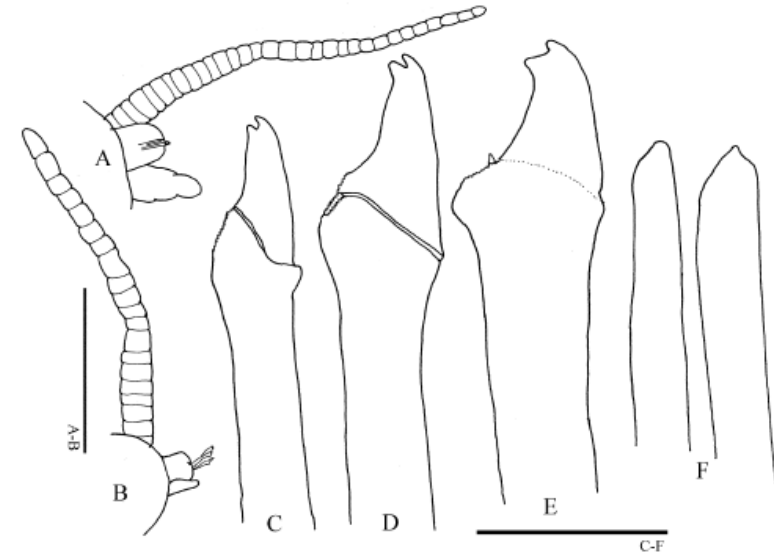


FIGURE 19. A cotype of *Haplosyllis spongiphila*. A— anterior parapodium; B—midbody parapodium; C— anterior chaetae, fourth chaetiger; D— anterior chaetae, sixth chaetiger; E—midbody chaeta; F—midbody aciculae. Scale bars: A–B = 100 μ m; C–F = 20 μ m.

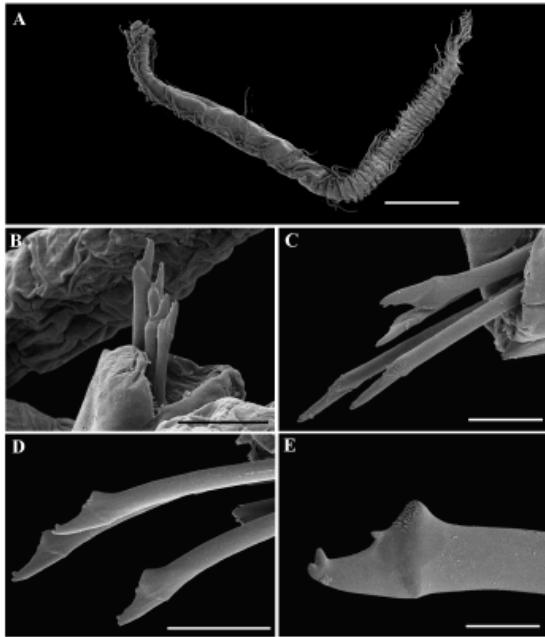


FIGURE 20. SEM micrographs of *Haplosyllis spongiphila*. A— anterior end, ventral view; B— anterior parapodium, second chaetiger; C— chaetae from chaetiger 10; D— midbody chaetae, chaetiger 27; E— midbody chaetae, chaetiger 55. Scale bars: A = 3 mm; B, D = 30 μ m; C = 20 μ m; E = 10 μ m.

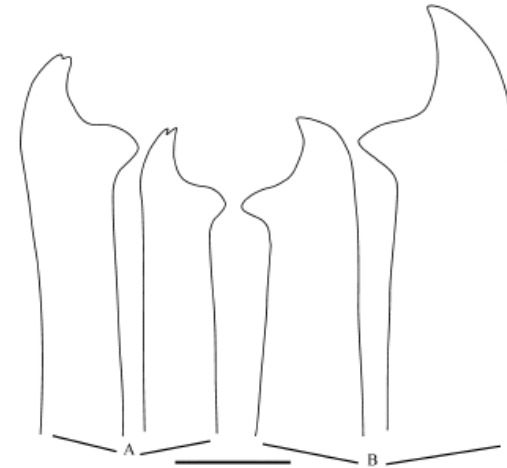


FIGURE 21. Holotype of *Haplosyllis streptocephala*. A— bidentate chaetae, anterior chaetiger; B— unidentate chaetae, midbody. Scale bar: 20 μ m.

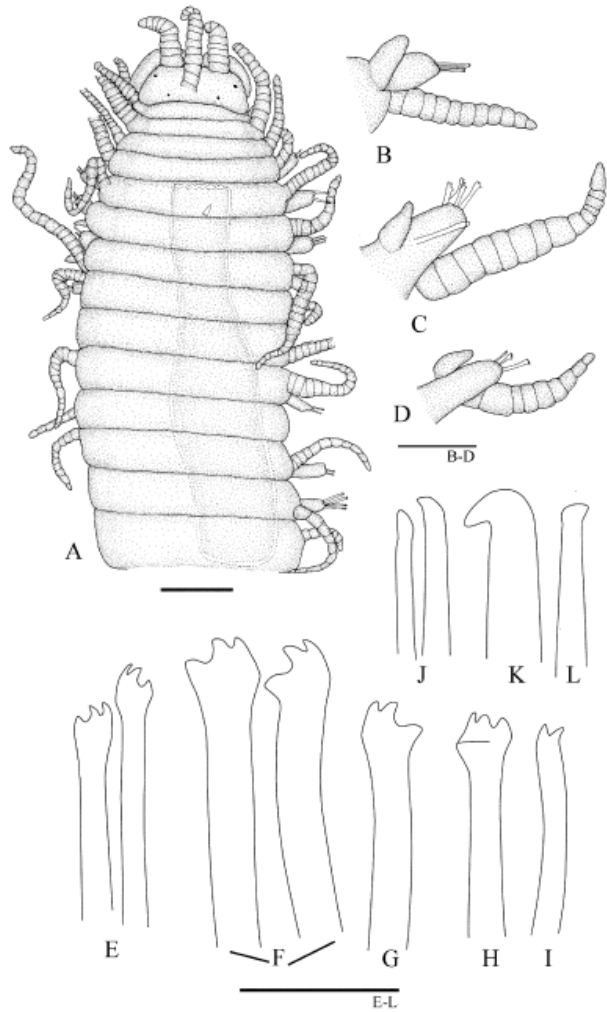


FIGURE 22. Holotype of *Haplosyllis trifalcata*. A— anterior end, dorsal view; B— anterior parapodium; C— midbody parapodium; D— posterior most parapodium; E, F, G— anterior, midbody and posterior bidentate chaetae, respectively; H— tridentate chaeta, posterior parapodia; I— simple chaeta, posterior most parapodia; J, K, L— anterior, midbody and posterior aciculae, respectively. Scale bars: A = 200 μ m; B–D = 100 μ m; E–L = 20 μ m.

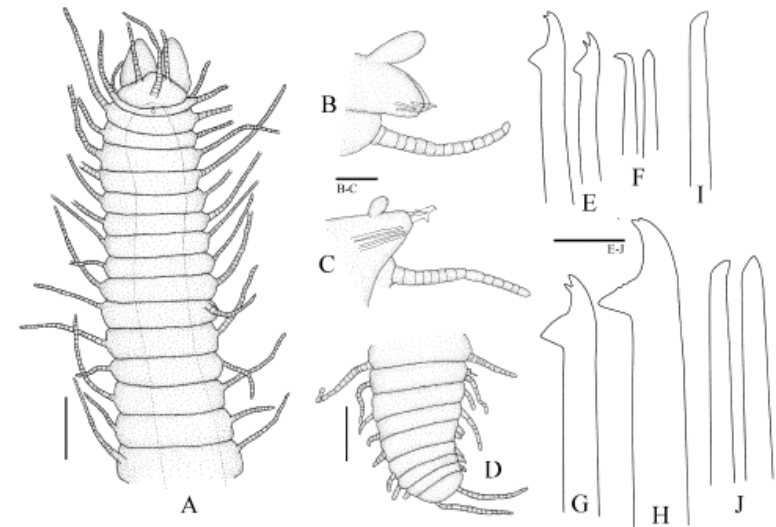


FIGURE 23. *Haplosyllis uncinigera*. A— anterior end, dorsal view; B— anterior parapodium; C— midbody parapodium; D— posterior end, dorsal view; E— anterior chaetae; F— anterior aciculae; G— smaller chaeta, midbody; H— largest chaetae, mid-body; I— posterior most acicula; J— aciculae, midbody. Scale bars: A = 500 μ m; D = 200 μ m; B–C = 100 μ m; E–J = 20 μ m.