On the associations between *Haplosyllis* (Polychaeta, Syllidae) and gorgonians (Cnidaria, Octocorallaria), with the description of a new species

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The present paper includes a morphological, ecological and biological updating of the three gorgonian associated spe cies of *Haplosyllis* (Polychaeta, Syllidae) known to date: *H. chamaeleon* (symbiont with *Paramuricea clavata* in the Mediterranean), *H. anthogorgicola* (symbiont with *Anthogorgia bocki* in the Japanese seas) and ***H. villogorgicola***, a new species living symbiotically with *Villogorgia bebrycoides* which is only known from Tenerife (Canary Islands, Eastern Central Atlantic). The new species is described on the basis of ecological, morphological, morphometric and statistical analysis of relevant characteristics. Each host colony harboured about 15 pale-yellowish worms, whose cryptic colouration mimicked that of the host. They occurred either on the host branches or partly hidden inside cav ities formed by the fusion of two branches. The new species is characterized by the presence of simple chaetae with clearly bidentate tips all along the body, the presence of gland pore aggregates distributed in two lateral rows and two ventral patches on each palp and the absence of ciliary tufts on the pharyngeal papillae. ***H. villogorgicola* sp. nov.** is closely related to *H. chamaeleon*. Thus, it is compared with two populations of this species collected in the north-west and south-west Mediterranean. Stolons of *H. chamaeleon* are re-described as tetracerous and a peculiar posterior end regeneration process occurring in adult worms during the stolon formation is described. *H. anthogorgicola* is also re-described, with particular emphasis on its appendage and chaetal arrangements. The main features of the three associations are discussed in light of the current knowledge on symbiotic polychaetes, par ticularly cnidarian-associated syllids

ADDITIONAL KEYWORDS: adaptation – Annelida – ecology – gorgonian – Polychaeta – reproduction – symbiosis – taxonomy.

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INTRODUCTION

An evolutionary tendency towards the establishment of close associations with other marine organisms, mainly benthic invertebrates, is a rather common phenomenon among polychaetous annelids (Martin & Britayev, 1998). In addition to the benefits (often mutual) that may be derived from symbiotic partner ships, this mode of life usually conveys a high degree of specificity, to the extent that at least one of the involved partners can no longer be considered a free-living organism. Symbiotic relationships often give rise to the evolution of specialized features involving, for instance, morphological, behavioural, physiological or reproductive adaptations. This tendency is particularly remarkable among polychaetes, whose associa tions are often surprisingly complex (Martin & Britayev, 1998). Modern descriptions of symbiotic rela tionships should therefore approach the problem from many different points of view in order to better char acterize the complexity – as well as to define the singularity – of a given association.

The Syllidae is a large polychaete family with more than 800 species worldwide (according to Glasby *et al*., 2000), with about 30 of them being known as symbionts. Syllids are particularly frequent and abundant in sponges, either as endobionts (Pearse, 1932; West-inga & Hoetjes, 1981; Pascual, Núñez & San Martín, 1996) or symbionts (Reiswig, 1973; Magnino & Gaino, 1998; López *et al*., 2001). They also occur in associa tion with ascidians, crustaceans, echinoderms and cnidarians (Martin & Britayev, 1998; López *et al*., 2001).

Several syllid species belonging to different genera (viz. *Alcyonosyllis*, *Autolytus*, *Bollandia*, *Brania*, *Syllis*, *Proceraea*, *Procerastea*) are known from cnidarian hosts (Allen, 1915, 1921; Caullery, 1925; Spooner, Wilson & Trebble, 1957; Pettibone, 1963; Gardiner, 1976; Wright & Woodwick, 1977; Alós, 1989; Hartmann-Schröder, 1991, 1992; Glasby, 1994; López, San Martín & Jiménez, 1996; Britayev, San Martín & Sheiko, 1998; Britayev & San Martín, 2001; Glasby & Watson, 2001). Four of them belong to the genus *Haplosyllis*: *H. spongicola* from *Versluisya ramosa* (Hickson, 1940), *H. anthogorgicola* from *Anthogorgia bocki* (Utinomi, 1956), *H. chamaeleon* from *Paramuri cea clavata* (Laubier, 1960, 1968; López *et al*., 1996) and *H. bisetosa* from unidentified alcyonaceans (Hartmann-Schröder, 1960; Glasby & Watson, 2001). Of these, only the fi rst three are associated with gor gonian hosts. However, it seems difficult to accept that *H. spongicola* Grube, originally described as a sponge-associated Mediterranean species, occurs also associ-ated to a gorgonian in the Indian Ocean. Moreover, recent studies point out that *H. spongicola* is, in fact, a species complex (D. Martin, personal observations). Thus, the report of this species on *V. ramosa* needs a further study to be confirmed.

From an evolutionary point of view, the polychaetes have developed progressive adaptations to the symbi otic mode of life (Martin & Britayev, 1998). Particularly among syllids, the chaetae tended to change from the typically articulated type of most free-living forms to simplified, hooked forms, some of them showing remarkable coincidence in shape and, although not demonstrated, probably in functionality, too. Their bodies tended to acquire camouflage colourings, either by being able to alter the colour pattern to more closely resemble that of their different hosts in polyxenous species (e.g. *Alcyonosyllis phili* in Glasby & Watson, 2001) or by simply matching exactly the host colour in monoxenous species (e.g. *Haplosyllis chamaeleon* in Laubier, 1960, 1968). A less evident but highly functional adaptation is the

symbionts' tendency to develop specific behaviours such as short-distance host recognition (e.g. *Haplosyllis chamaeleon* in Laubier, 1960). Finally, they may induce their host to react by building abnormal structures, either thought to be a defence from (e.g. in the case of parasitic asso ciations) or a protection for (e.g. in the case of com mensal or mutualistic associations) the symbiont.

The specimens here described as ***Haplosyllis villogorgicola* sp. nov.** were harboured by the gorgon ian *Villogorgia bebrycoides* (Koch) from Tenerife (Canary Islands, Eastern Central Atlantic). However, they closely resembled *H. chamaeleon*, which lives in association with the Mediterranean gorgonian *Paramuricea clavata* (Risso). In addition to classical morphological characters, the erection of *H. villogorgicola* as a new species is supported by eco-logical and morphometric features, as well as by statistical comparisons with two Western Mediterranean populations of *H. chamaeleon* (from the Cape of Creus and the Chafarinas Archipelago). *Haplosyllis chamaeleon* is re-described based on the resulting new information, which includes stolon morphology and the adult pattern of regeneration after the stolon release. The third gorgonian-associated *Haplosyllis* species known to date, *H. anthogorgicola*, is also re-described. In this case, the new information includes the append age and chaetal arrangements, the sensory organs and the specific characteristics of its association with *Anthogorgia bocki* Aurivillius. Some adaptive trends shown by symbiotic polychaetes, mainly cnidarian-associated syllids, are also discussed in connection with the associations here described.

MATERIAL AND METHODS

The specimens of the new species were collected in Punta Guadamojete (Radazul, south-eastern coast of Tenerife, Canary Islands) (Fig. 1), in February and October 1997. Three colonies of the host *Villogorgia bebrycoides* were obtained, each one harbouring about 15 symbiotic syllids. Scuba divers collected the colo nies by hand at depths of 82 and 84 m. After collection, each colony was kept in cooled seawater (10 ∞C) for several hours in order to describe host and symbiont colour patterns and symbiont behaviour. Samples were then gently anaesthetized with MgCl. The syllids and other accompanying fauna were separated from the colonies and fixed with a 10% buffered formalin/ seawater solution for 48 h. They were then washed three times in distilled water and transferred to 70% ethanol. The specimens of *Haplosyllis chamaeleon* belonged to the personal collections of Carmen Alós (Cape of Creus population), Eduardo López and Guill ermo San Martín (Chafarinas Islands population). The specimens of *Haplosyllis anthogorgicola* belong to the collections of the Seto Marine Biological Labora tory (SMBL), Japan.

For light microscope observations, some specimens were placed on slides with glycerine gel. Line draw ings were made with a Leica DMLB compound micro scope equipped with interference contrast optics (Nomarski) and linked to a *camera lucida*. Light microscope micrographs were made with a Zeiss Axioplan compound microscope equipped with SPOT hardware and software (SP100 KAF1400 digital cam era and software version 2.1. by Diagnostic Instru ments Inc.).

For scanning electron microscope (SEM) observa-tions, the worms were washed three times in distilled water (30 min each), run through a series of in creasing ethanol concentrations, and stored in

70% ethanol until observation. Immediately prior to view ing in a Hitachi S.570 scanning electron microscope (Laboratori de Microscopia Electrònica of the Institut de Ciències del Mar de Barcelona, CSIC), they were run through a series of increasing ethanol concentrations ending with 100%, critical point dried, attached to a stub, and coated with gold. All images were captured and stored in digital format using Printerface System hardware and software (GW Electronics, & K.E. Development Ltd). Parametric two-way analysis of variance (ANOVA) was used to test differences in dorsal cirri arrangement (of the first ten chaetigers) and length (as number of articles) in the three studied populations (measured on a minimum of five adult specimens for each population). The ANOVA was performed using the origin of the populations and the cirri position along the body as factors. Data were log-transformed in order to meet the assumptions of normality and homoscedasticity (Zar, 1984). Multiple comparisons between populations and cirri positions were carried out by Tukey HSD test. Cross-correlation analyses were used to examine the strength of the association (given by Pearson correlation coefficient, *r*) between the patterns of dorsal cirri arrangement in the three studied populations. The coupling between two pat terns may involve a position lag, which is estimated as the lag required to obtain maximal Pearson's correlation index in the cross-correlation analysis. The lag is the position displacement in the relation of the cirri length of one population versus another one. All analyses were carried out using the SYSTAT 5 (vers. 5.2.1, copyright SYSTAT Inc., 1990–92) statistical package.

The holotype and paratypes of the new species are deposited in the Museo de Ciencias of Santa Cruz de Tenerife (TFMC). Several paratypes will also be deposited in the Museo Nacional de Ciencias Naturales of Madrid (MNCNM), in the SEM collection of the Institut de Ciències del Mar of Barcelona (SEMI CMB) and in the collection of the Departamento de Biología Animal (Zoología) of the University of La Laguna (DZUL). The alcohol-preserved specimens of the two studied populations of *H. chamaeleon* are deposited in the MNCNM, while those observed by SEM are also deposited in the SEMICMB collection. All specimens of *H. anthogorgicola* are deposited in the Seto Marine Biological Laboratory (SMBL), Japan.

RESULTS

FAMILY SYLLIDAE GRUBE, 1850
SUBFAMILY SYLLINAE GRUBE, 1850
GENUS *HAPLOSYLLIS* LANGERHANS, 1879

HAPLOSYLLIS VILLOGORGICOLA SP. NOV.

(FIGS 2–4, 5A, 6)

Material examined. Holotype: Punta Guadamojete (Radazul, south eastern coast of Tenerife, Canary Islands, 28∞24¢ N; 16∞19¢ W), inhabiting colonies of *Villogorgia bebrycoides*, collected February 1997 at 84 m by A. Sotillo (TFMCBMAN/000215). Paratypes, 11 (TFMCBMAN/ 000216), six

(MNCN16.01/7833), two (*canari*-1 and *canari*-2, SEMICMB) and 11 (DZUL) specimens: same data as for holotype. One (*canari*-2 SEMICMB), ten (TFMCBMAN/000217) and six (DZUL) specimens: same data as for holotype but collected October 1997 at 82 m.

Etymology: The name refers to the specific name of the host, *Villogorgia bebrycoides*: *Villogorgicola* means 'harboured by *Villogorgia*'.

Description: Body long, tapering posteriorly. Dorsum convex, without traces of pigment marks. Colour pale yellowish *in vivo*, light brownish to whitish in pre served specimens. Adult specimens measuring up to 13.25 mm long and 0.72 mm wide (anterior region, without parapodia), for up to 79 chaetigers (Table 1 and Figs 2A, 3A,B).

Prostomium oval, about twice as wide as long (Figs 2A, 3C) with two pairs of eyes in trapezoidal arrangement, and a pair of anterior eyespots located behind the insertion of the lateral antennae (Fig. 2A). Palps broad, divergent, fused in proximal third but clearly separated in the distal two-thirds (Fig. 3C,D), with two row-like glandular regions formed by gland pore aggregates below each palp, one large central, the other located at the basis of the fused region (Fig. 3D,F). Median antenna inserted in the middle of prostomium, posterior to the lateral ones, twice as long as the lateral ones and slightly thinner than dorsal cirri, up to 0.92 mm long for 30 articles; lateral antennae inserted near anterior margin of prostomium, similar in length to the prostomium and palps together (up to 0.66 mm) for 16 articles (Figs 2A, 3C). Prostomium with three dorsal ciliary regions located just at the basis of each antenna (Fig. 3C,E). Nuchal organs consisting of two dorso-lateral ciliary regions located at the junction between the prostomium and the peristomium (Fig. 3E). Peristomium similar in length to the first chaetiger (half as long as the remaining segments), bearing two dorso-lateral ciliary regions at the basis of the dorsal tentacular cirri and several small mid-dorsal ciliary tufts (Fig. 3C,E). Dorsal tentacular cirri about three times longer than ventral cirri, measuring up to 1.83 mm for up to 47 articles; ventral tentacular cirri similar in length to lateral antennae, up to 0.71 mm for 15 articles (Table 1, Figs 2A, 3B).

Dorsal cirri alternating short (slightly longer than body width) and long (two to three times longer than the former) all along the body (Table 1), except for the first ten chaetigers, where the sequence was: 1 long, 2 short, 3 intermediate, 4 long, 5 short, 6 long, 7 short, 8 short, 9 long, 10 short (Fig. 2A). First cirrus longer than lateral antennae, dorsal tentacular cirrus and the remaining long dorsal cirri; second cirrus shorter than central antenna, ventral tentacular cirrus and the remaining short dorsal cirri (Table 1, Fig. 6). Ventral cirri shorter than parapodial lobes (Figs 2K, 3B, 4A,B), except at the posterior region (Fig. 4C). Pre-chaetal lobe round and broad, similar in length to the post-chaetal lobe. Post-chaetal lobe conical with rounded tip (Figs 2K, 4A–C).

Three to five thick hooked simple chaetae per parapodium (Figs 2J, 4D–J, 5A), with a triangular swelling near the tip, typical of the genus. All chaetae with bidentate tips (distal tooth more or less difficult to see, depending on the position of the chaetae) and very similar in shape all along the body (Fig. 2C). Anterior-most parapodia with three to four chaetae (Fig. 2C–E), markedly less hooked than those in the mid-body (bearing three to five chaetae) (Fig. 2F) and posterior-most parapodia (three

chaetae) (Fig. 2G,J). Anterior and mid-body parapodia with three to five distally enlarged acicula (Fig. 2H,I), which become thicker in mid-body region. Posterior parapodia with a single, distally enlarged, thick aciculum. Pre-pygidial region with seven to eight incompletely developed cha etigers having short dorsal cirri with only two to three articles (Fig. 2B). Pygidium squared (Fig. 2B), with two long anal cirri measuring up to 0.73 mm for 27 articles. Anal cirri lost in most specimens.

Pharynx broad, similar in length to the proventriculum (Table 1), extending for about four segments (Fig. 2A). Anterior end of the pharynx provided with a small, pyriform dorsal tooth, a crown of ten soft smooth papillae, and an inner ciliary ring just at the basis of the papillae (Fig. 3C,D). Proventriculum cylin drical, extending throughout four to six chaetigers, with about 34 muscular cell-rows.

Morphometric analysis: The characters measured for ***H. villogorgicola* sp. nov.** were not significantly different to those of the two Mediterranean populations of *H. chamaeleon* (see Table 1), except for the length of the first ten dorsal cirri (Fig. 6). Although the length pattern was the same in the three populations (cross correlation analysis, lag = 0, $r > 0.98$, $P < 0.05$), the number of articles of those cirri varied significantly depending on both their position and the population (two-way ANOVA, $F > 29{,}1$, $P << 0.001$). The results of the *posthoc* test for the length of the cirri are summarized in Table 2. The test revealed that the observed differences were caused by ***H. villogorgicola* sp. nov.**, which differed significantly from the two *H. chamaeleon* populations (Tukey HSD, $P = 0.00002$).

Ecology: In the Canary Islands, *Villogorgia bebrycoides* colonizes hard bottoms with corals, the axes of other gorgonians, rocks, shell-masses and, less frequently, unstable detritic bottoms. It is particularly common in the orange coral, *Dendrophyllia ramea* (Linné), assemblage (Arístegui *et al*., 1987). The specimens of ***Haplosyllis villogorgicola* sp. nov.** were only found on the largest host colonies (14 cm to 17 cm high), while small colonies (about 5 cm high) never harboured the symbionts. The gorgonian *Paramuricea grayi* (Johnson) also occurs in the same assemblages as the infested colonies of *V. bebrycoides*. However, no specimens of *Haplosyllis* were found on these colonies.

Living worms are pale yellowish and their colour exactly mimics that of the host colonies (Fig. 5H). The syllids may be found on the host branches among the polyps, but they are more common partly hidden (about one-quarter of the total length) inside cavities formed by the fusion of two branches (Fig. 5I). These cavities are gall-like structures, whose formation in the host is probably induced by the presence of the symbiont.

Accompanying fauna: The colonies of *V. bebrycoides* harboured an abundant associated epifauna, including both mobile and sedentary species. Contrary to ***H. villogorgicola* sp. nov.**, however, there are ubiquitous epifaunal species often found on many different hard bottoms. Among them are the bivalve *Pteria hirundo* (Linné), the syllids *Grubeosyllis limbata* (Cla-parède) and *Eusyllis lamelligera* Marion & Bobretzki, the amphipod *Caprella aequilibra* Say and several harpacticoid copepods.

HAPLOSYLLIS CHAMAELEON **(LAUBIER, 1960)**

(FIGS 5B–G, 6–10)

Haplosyllis depressa chamaeleon (Laubier, 1960): 75, figs 1,2; (Alós, 1988): 359, figs 71,72; (Baratech & San Martín, 1987): 45, figs 8,9. *Haplosyllis chamaeleon* (López *et al*., 1996): 108, fig. 2.

Material examined: Cape of Creus (Catalonian coast of the NW Mediterranean Sea, between 42∞14¢ and 42∞22¢ N and 3∞12¢-3∞22¢ W) collected from *Paramuri cea clavata* around 30 m by C. Alós, three (*creus*-1, *creu*s-2 and *creus*-3, SEMICMB) and 11 (MNCN 16.01/ 7834) specimens. Chafarinas Islands (Alboran Sea, SW Mediterranean Sea, 35∞11¢08¢ N, 2∞25¢11¢ W) col lected from *Paramuricea clavata* at 23 m by G. San Martín and E. López, three (*chafa*-1 *chafa*-2 and *chafa*-3, SEMICMB) and 12 (MNCN 16.01/7835) specimens.

Description: Length up to 13.25 mm, width 0.78 mm (anterior region, without parapodia), up to 104 chaetigers (Table 1, Fig. 7A,B). Body long and slender, very fragile, fragmented in most specimens. Colour *in vivo* varying from yellow to violet, with dark violet marks of variable shape and size across the dorsum. Pre served specimens pale orange, with the dorsal violet marks still present and more marked in the stolons (Fig. 5D,F).

Prostomium oval, about twice as wide as long (Fig. 7C); two pairs of eyes in trapezoidal arrangement and a pair of anterior eyespots. Palps broad, fused in proximal half but clearly distinguishable one from another, with two lateral rows of small ciliary tufts (Fig. 7C,F), one large mid-ventral ciliary tuft below each palp and a large band of cilia extending from mid-palp to mid-palp at the basis of the fused region (Fig. 7D,F). Median antenna inserted in the middle of prostomium, twice as long as the lateral ones and slightly thinner than the dorsal cirri, with up to 28 articles; lateral antennae inserted near anterior mar gin of prostomium, about 1.5 times longer than prostomium and palps together, with up to 16 articles (Table 1, Fig. 7C,D). Three dorsal ciliary regions located on the prostomium, just at the base of each antenna (Fig. 7E). Nuchal organs consisting on two dorso-lateral ciliary regions located at the junction between the prostomium and the peristomium (Fig. 7E). Peristomium similar in length to the first chaetiger (half as long as the remaining segments), surrounded by a median ciliary ring (Fig. 7E), wider dorsally than ventrally. Dorsal tentacular cirri about three times longer than ventral cirri, having up to 30 articles; ventral tentacular cirri similar in length to lateral antennae, having ten articles (Fig. 7D). Dorsal cirri alternating short (slightly longer than body width, with 12–15 articles) and long (two to three times longer than the former, with 29–32 articles, except the second which was four times longer and had 60–70 articles); ventral cirri similar in length to parapodial lobe (Figs 7B, 8A,B). All dorsal cirri similar in length on the posterior-most segments, having 10– 12 articles (Fig. 8C). Pre-pygidial chaetigers (four to five) with short dorsal cirri of about three articles. After releasing the stolon, they are followed by several achaetigerous segments (10–13) with simple digitiform cirri or with only traces of their presence when closer to the pygidium (Fig. 10C). Three to five hooked simple chaetae per parapodium (Figs 8D,F, 9A,C,E, 5B,C), with a triangular swelling near the tip. All chaetae unidentate or with a very small, hair-like distal tooth in anterior and mid-body parapodia (Figs 8E,G–I, 9B,D) and more hooked and clearly

bidentate in posteriorparapodia (Figs 8J, 9E,F). Pygidium squared, with two long anal cirri provided with 30 articles of variable length (Fig. 10C). Pharynx short and broad, the distal end provided with a small, pyriform dorsal tooth, a crown of nine to ten soft papillae having a central ciliary band, and an inner ciliary ring just at the basis of the papillae (Fig. 7F). Proventriculum cylindrical, extending throughout 6.5 chaetigers, with about 28 muscular cell-rows.

Stolon formation: A few individuals from the Cape of Creus population showed traces of stolon formation, while this process occurred in virtually all adults from the Chafarinas Islands. Simultaneously to the modifications giving rise to the stolon formation, two small ventro-lateral protuberances appeared in the last adult segment (i.e. the stolon/ progenitor joining segment). These two protuberances were formed by several segments having achaetigerous parapodia, smaller than the normal ones and bearing only one oval to digitiform cirrus (Fig. 10A). Even after the stolon release, the two protuberances remained separated and the stolon/progenitor joining point was still visible between them (Fig. 10B). At this stage, each protuberance already showed one anal cirri. At the end of the process the pygidial region of the progenitor showed almost no traces of the fusion of the two protuberances, and was formed by a few prepygidial achaetigerous segments (Fig. 10C).

Female stolons had 11–15 chaetigers (Figs 5D, 10D). Male stolons reached up to 33 chaetigers. Although the colour pattern in preserved worms did not differ from that of the adults, the reddish-violet marks were usu ally more extensive in male than in female stolons (Fig. 5D). The stolons had a bilobed head with two small, dorsal digitiform antennae (Fig. 10E,F), two small ventral semi-spherical palps and two latero-ventral pairs of reddish eyes (Fig. 5E,F), the diameter of the ventral-most being twice the diameter of the lat ero-dorsal ones. The head, parapodia and laterals of the body were covered by tufts of cilia (Fig. 10E–G). The parapodia were similar to those of the progenitors, except in size (they appeared larger than in the pro genitor, probably owing to the presence of sexual products inside) and the presence of swimming chaetae (Fig. 5G, 10G). These chaetae were already present in the stolons before being separated from the adult and occurred from the second segment to the end of the body. The parapodia had a distally pointed, single notoaciculum, which was thinner than the neuroaciculum. Both oocytes and spermatozoa were present from the first segment to the end of the body, being usually absent from the last two. The pygidium was semi-spherical. None of the studied specimens had anal cirri, although the marks of the attachment point were visible in the pygidium.

Remarks on stolon formation: According to Laubier (1960), the stolons of *H. chamaeleon* were of *Chaetosyllis* type (i.e. with two antennae, palps absent). Our observations showed that both male and female sto lons clearly had palps. Thus, they should be considered as tetracerous stolons (i.e. with two antennae and two palps). Although little information is available concerning the reproduction of syllids, there are a number of papers describing larval development, stolon formation process and/or the stolons themselves (e.g. Heacox, 1980; Estapé & San Martín, 1991). Most authors studying the stolon-formation process care fully described the stolons, but failed to mention how this process may affect the parental adults, i.e. whether they are able to recover after releasing the stolons or how this recovery may be

accomplished. Our observations on *H. chamaeleon* are thus the first report on this aspect, together with a recent paper describing a new genus and species of Syllidae, *Alcyonosyllis phili*, also associated to a host gorgonian (Glasby & Watson, 2001). Previous discussions between one of us (D. Martin) and these authors caused them to pay particular attention to the stocks of *A. phili*, which were also shown to undertake a regeneration process similar to that observed in *H. chamaeleon*. Although equivalent, the processes dif fer in that the two protuberances remain separated even after stolon release in *H. chamaeleon*, whereas in *A. phili*, the two protuberances fuse at a very early stage before the stolon is released. Accordingly, the adult worms may survive the stolon-formation pro cess, regenerating their posterior end until it is not possible to distinguish if a stolon was released or not. We thus agree with Glasby & Watson (2001) in that, although rare in the literature, the observations on syllid stocks during the respective stolon formation process may be a useful taxonomic character (at spe cies or, even, at genus level) and, also, in that the dis covery of adult worms surviving after stolon release indirectly implies that they might have an iteroparous life-cycle. Unfortunately, however, no reproductive specimens were found among the ***H. villogorgicola*** **sp. nov.** specimens, so that the existence of a regeneration process could not be currently assessed for the species.

Regeneration processes linked to asexual reproductive activities are frequently reported among polychaetes (Giangrande, 1997). However, they differ from the processes observed in *H. chamaeleon* and *A. phili* in that regeneration always starts after bud releasing. A well-illustrated example is the fragmentation of the spionid *Pigospio elegans* Claparède (Gibson & Harvey, 2000). Asexual reproduction occurs after spontaneous transverse fission of the adult body in several fragments (most often two), followed by extension of the blastema to regenerate the lost body regions. The formation of sexual stolons is always a more complex pro cess, which implies strong modifications of the posterior-most body segments (Estapé & San Martín, 1991), as well as migration of the sexual products (spermatozoans and oocytes) from the coelom of the anterior and mid-body regions to the stolonizing region (Wissocq, 1966). The whole process occurs under a complex endocrine control (Giangrande, 1997), which probably acts to trigger the regeneration of the last segments and pygidium in parallel with the stolon formation.

Ecology: Haplosyllis chamaeleon lives on the branches of its host gorgonian *Paramuricea clavata*, often reaching densities of no more than ten worms per host colony. The worms usually extend their bodies along the longitudinal axes of the host branches, preferably near zones with a high number of living polyps (mainly the apical parts) and they have been observed with the anterior ends inside the gastric cavity of gorgonian polyps. When separated from the gorgonian, the polychaetes remain particularly immobile and coiled around themselves. Only after contacting a host branch do they start to crawl and reach their habitual position on the branches. The colouring of the worms varied from yellow to dark red or violet, with dark violet dorsal marks, matching exactly the colours of its host. However, hybrid specimens showing different colour combinations may occur. Uniform colourings may be related to symbionts growing on the same gorgonian branch, and then moving to different parts of the colony without having any branch colour preference. Hybrid forms may be the result of bitten (by predators), autotomized or stolonizing worms, which regenerate their posterior ends on a differently coloured branch.

This suggests that the source of the colour matching may be the worms feeding on the host gorgonian, in a similar way as happens in *Branchiosyllis oculata* Elhers (Pawlik, 1983). This species, how ever, lives in association with several host species (i.e. sponges) having different colours instead of a single two-coloured one.

HAPLOSYLLIS ANTHOGORGICOLA UTINOMI (1956)

(FIGS 11–13)

Haplosyllis anthogorgicola (Imajima, 1966): 220; (Imajima & Hartman, 1964): 119–120; (Utinomi, 1956); 247–249, fig. 2.

Material examined: Syntypes: Seto, Wakayama Pref., Honsyû (Japan) collected from *Anthogorgia bocki* by H. Utinomi, three (*anth*-1, *anth*-2 and *anth*-3, mounted for SEM, SMBL) and more than 80 (Type 161, SMBL) specimens.

Description: Length up to 3 mm, width 0.18–0.24 mm (anterior region, without parapodia), up to 38–42 cha etigers (Fig. 11A). Body short, slightly flattened dorso ventrally in the anterior region. Colour *in vivo* light orange. Preserved specimens whitish to dark brown.

Prostomium oval, about twice as wide as long (Figs 11A, 12A); two pairs of eyes in trapezoidal arrangement. Palps broad, fused at their base but clearly distinguishable one from another (Fig. 12B), with several small ciliary tufts distributed in non-regular rows. Cilia with slightly swollen tips (Fig. 12F). Median antenna inserted in the middle of prostomium, three times as long as the lateral ones, with 25–28 articles; lateral antennae inserted near anterior margin of prostomium, similar in length to the prostomium and palps together, with ten articles (Figs 11A, 12B). Nuchal organs consisting of two very small dorso-lateral ciliary regions located at the junction between the prostomium and the peristomium (Fig. 12E). Peristomium half as long as the remaining segments. Dorsal tentacular cirri about twice long as the ventral cirri, having up to 15 articles; ventral tentacular cirri similar in length to lateral antennae, having eight articles (Figs 11A, 12B). Dorsal cirri of the first fourth of the body much longer than the remaining ones; of these, those from segments one to six were the longest; these cirri show a highly characteristic alternation in length, which is well represented by the number of articles (cirri ordered from first to 12th): 30–35, 7–8, 5–7, 10–15, 3–6, 5–10, 3–5, 3, 4, 3, 4, 3 (Figs 11A, 12B). All dorsal cirri from segments 10–11 to 25–30 short, similar in length, slightly articulated or pseudo-articulated, having a slight alternation in the number of articles (three to four and two to three) (Figs 11A, 12C,D). Dorsal cirri from segments 25–30 to the posterior end similar to the preceding ones but shorter, alternatively having one or two articles. Ventral cirri oval, minute, not extending beyond the parapodial lobe. One (rarely two) simple chaetae per parapodium, having two small teeth and a main fang. Chaetae from the first 4–5 chaetigers slightly thinner than the remaining ones, with the main fang deeply incised near its apex and a triangular swelling with a deep fold in the shaft, opposite to the main fang (Figs 11D, 12G). Chaetae from chaetigers 6–7 similar to the anterior ones, but with a less pronounced incision in the main fang (or with only traces

of it) (Fig. 12H). Remaining chaetae slightly wider than the anterior-most, often having a minute proximal tooth at their tips and a slightly incised or entire main fang (Figs 11E, 12I). Acicula from the first 6–7 chaetigers as wide as the chaetae, with a round 90 degrees bent tip (Fig. 11F), becoming progressively more pointed at mid-body (Fig. 11G), and hooked and wider than the chaetae in the posterior-most parapodia (Fig. 11H). Pygidium triangular, with two anal cirri similar in length to the dorsal ones but thinner and showing traces of articulation (up to five articles) (Fig. 11B). Pharynx short and narrow, the distal end provided with a small, pyriform dorsal tooth and a crown of nine to ten soft papillae. Cilia on papillae and at the papillae basis not seen. Proventriculum cylindrical similar in length to the pharynx, extending through out three to four chaetigers, almost twice as long as wide, with about 35 muscular cell-rows (Fig. 13K).

Remarks: The species was originally described as hav-sisted of a large main fang and a bidentate tip. ing one simple chaeta with bidentate tip on each Although the *H. anthogorgicola* chaetae are certainly parapodium. However, the observation of the syntype simple, their particular outline may have originated revealed that the chaetae were closer to the 'spongi-as a result of fusing the blade and shaft of a typical cola' type than originally thought, as their outline con-articulate syllid chaetae, as occurs in other syllid spe cies (e.g. *Syllis gracilis* Grube). Blade and shaft fusion might only be one of the possible explanations of the evolution of the simple chaetae of *Haplosyllis* from the compound syllid falciger chaetae. Other possibilities may be loss of the blade of compound falcigers, or evolution of the simple chaetae 'de novo'. In *H. anthogorgicola*, however, fusion is the most likely explanation, as suggested by the presence of a bifid apical tooth, the incision in the main fang and the deep fold on the back and lateral sides of some chaetae (Figs 11D, 12G). An additional difference with the original description is that the median and posterior dorsal cirri were defined as having a single article, whereas all observed specimens proved to have pseudo-articulated dorsal cirri, the articles being clearly distinguishable under a light microscope (Fig. 12C) but difficult to perceive or not visible under SEM (Fig. 12D). The posterior-most dorsal cirri (which are probably still growing) appeared to be uniarticulated.

Although the original description was inaccurate, the new data reported here still allows *H. anthogorgicola* to be distinguished from all previously known *Haplosyllis* species, including those that are currently known to form the 'spongicola' complex (D. Martin, personal observations). Therefore, we con sider that the species is still a valid one.

Ecology: Living worms are light orange and their colour exactly mimics that of the host colonies. Up to 77 worms were visible in a small fragment of *A. bocki*, whose branches measured a total of 12.5 cm (Fig. 13A,B). However, a small fragment of about 1 cm2 with only one worm visible on the surface was revealed to harbour about 15 worms inside the host (Fig. 13J). *Haplosyllis anthogorgicola* inhabits galler ies inside the coenchym, between the surface covered by spicules and the host skeleton (Fig. 13E–J). The origin of these galleries is not clear. Although they may initially result from worms' excavating activity, they ultimately appear as well-structured tubes, whose tissue-built walls may be easily distinguished from the remaining unaltered coenchym (Fig. 13E). The galleries may thus be the result of a protective

response by the host to the continuous movements of the symbionts through its coenchym. The galleries protrude from the host bark in abnormal outgrowths, which open near to the polyps forming tube-like swellings or flaps (Figs 11I, 13C,D). The outgrowths are irregularly covered by fusiform spicules and the tubular projection, usually bent slightly, does not exceed the height of the polyp verrucae. The origin of these structures is probably the same as the galleries, i.e. a host protection, but in this case as a response to the worms moving between the outside and inside of the host bark. From one to five outgrowths may be found surrounding a given polyp (Fig. 13C,D). Most worms are located inside the galleries, but some of them may be observed with the anterior end emerging from the outgrowths (Figs 11I, 13G,H). More than an adapta tion to inhabit galleries, as suggested by Utinomi (1956), the particular morphology of the worms (with the anterior-most appendages clearly longer than the posterior-most and bearing more sensory organs) seems to be an adaptation to being frequently in that position (i.e. partly protruding from the outgrowths) in order to have a better access to the nearby polyp when feeding. Some other worms have been observed with their posterior ends outside outgrowths, which are more often located far from the polyps (Fig. 13I). This suggests that, in addition to the galleries, the worms may use the bark surface for their movements.

Taking into account the enormous infestation intensities and the particular disposition of galleries and outgrowths in the host, the possibility of the worms feeding on the host polyps or tissues (i.e. true parasitic behaviour) may certainly be discarded, while a kleptoparasitic, commensal or, even, mutualistic (i.e. cleaner) behaviour seems much more probable. An additional possibility may be that the worms feed by perforating the gastric tubes which communicate between the different polyps of the host colony and then suck the gut contents, in a similar way as occurs in some associations between *Haplosyllis spongicola* and its aplysinid host sponges (Tsurumi & Reiswig, 1997). However, this possibility does not explain both the existence of the outgrowths and the worm's morphology so, even if feeding from the gut occurs, it is presumably in combination with one of the other food sources outside the host bark.

According to Utinomi (1956), the presence of out growths near to the polyps has been reported in all previous descriptions of *A. bocki*, including the origi nal one. This strongly supports the existence of the symbiosis throughout the distributional area of the host, i.e. the Pacific coast of southern Japan and the Bonin Islands. The outgrowths are apparently absent from all other species of *Anthogorgia* (Utinomi, 1956) so that the association seems to be highly specific.

DISCUSSION

HAPLOSYLLIS VILLOGORGICOLA SP. NOV VS. *HAPLOSYLLIS CHAMAELEON*

There were a number of characters allowing ***H. villogorgicola* sp. nov.** to be distinguished from *H. chamaeleon*, ranging from morphological to ecological and morphometric features. A classical morphological characteristic is the shape of the chaetae. In the anterior-most parapodia, ***H. villogorgicola* sp. nov.** had chaetae with clearly bidentate tips, while in *H. chamaeleon* these chaetae were markedly

more hooked, with one hair-like distal tooth. In the mid body parapodia, the new species still had bidentate chaetae, which became more hooked. Conversely, in *H. chamaeleon* these chaetae were clearly less hooked and showed a hair-like distal tooth similar to that in the anterior ones. These differences in chaetal appearance were hardly visible under a light microscope (Fig. 5A–C) but were evident when comparing SEM micrographs (Fig. 4D–J vs. Figs 8D–J, 9A–J). Another classical morphological character is the shape and length pattern of dorsal cirri. In the case of the two species studied here, however, the differences found were very subtle and were only revealed after a statistical analysis of these characters at the population level. The length pattern is the same in both species, this probably being characteristic of the genus. Nevertheless, with the exception of the second one, the cirri of *H. villogorgicola* are consistently shorter than those of *H. chamaeleon*. Although this is not the main purpose of this study, some recent observations on other *Haplosyllis* species strongly support the view that these types of morphometric analyses may be a very useful taxonomic tool, significantly contributing to the characterization of different species of the genus (D. Martin, personal observations).

The use of SEM enabled the description of the species-specific presence and distribution of the cephalic sensory organs. *Haplosyllis chamaeleon* had ciliary rows and ciliary tufts on each pharyngeal papilla and on the edges and ventral side of the palps, respectively, while ***H. villogorgicola* sp. nov.** had smooth papillae, the lateral ciliary tufts were absent from the palps and the ciliary regions below palps were replaced by areas showing gland pore openings, often partly covered by a mucus layer. Although ciliation is seldom considered as a character with taxonomic value, it may be related to the mode of life of the species. Different types of sensory organs may reflect differences in the interactions of the worm with the surrounding environment and, especially, with the host. Thus, we may assume that the differences in sensory organs are the morphological representation of ecological or behavioural differences. The behaviour of *H. chamaeleon* clearly points to the existence of short-distance host recognition. Although behavioural tests were not undertaken for ***H. villogorgicola* sp. nov.**, their different sensory organs may be the result of a different degree of symbiotic specialization. Accord ingly, only ***H. villogorgicola* sp. nov.** appeared to induce the host to form gall-like structures and *H. anthogorgicola* (which lives inside its host coen chym) also has different sensory organs (i.e. ciliary tufts of palps irregularly distributed in rows and formed by cilia with swollen tips).

Haplosyllis chamaeleon and its host *P. clavata* are considered as Mediterranean endemics (López *et al*., 1996). Conversely, the host gorgonian harbouring ***H. villogorgicola sp. nov.***, *V. bebrycoides*, is known to occur both in the Mediterranean and in the eastern Atlantic Ocean, between 63 and 700 m (Grasshoff, 1977a; Brito, 1985). Although there are no records of the presence of symbiotic *Haplosyllis* for the Mediterranean populations of *V. bebrycoides*, the presence of symbionts is also possible. We may thus hypothesize that the new association described here is the original one (as the host/symbiont relationships appears to be more complex), so that the association between *P. clavata* and *H. chamaeleon* (which still feeds on its host and does not induce any response to its activity) has evolved more recently in the particular Mediterranean conditions (viz. new environment, new host). However, further research should be carried out to test this hypothesis, either by looking at the particular characteristics of the different populations of both spe cies or by analysing their genetic structure.

In summary, our approach allowed us to combine different features – morphological (e.g. shape of chaetae, shape and distribution of sensory organs), morphometric (e.g. statistical analysis of dorsal cirri length pattern), and ecological (e.g. cryptic colouring, host-symbiont relationships) – to define the *Haplosyllis* specimens found in the Canary Islands living in symbiotic association with the gorgonian *V. bebrycoides* as a new species. An interesting additional study would be to assess the possible presence of symbiotic *Haplosyllis* populations along the whole geographical range of distribution (Mediterranean included) of *V. bebrycoides*, as well as the reproductive biology of the new species.

ON THE ASSOCIATIONS BETWEEN SYLLID POLYCHAETES AND GORGONIANS

The association between *H. chamaeleon* and *P. clavata* may be considered as the only well-described example of a monoxenous (i.e. one symbiotic species associated with a single host species) relationship among symbi otic polychaetes (Martin & Britayev, 1998). In fact, although all symbiotic species of *Haplosyllis* associ ated with cnidarians seem to be monoxenous, most are poorly known. Like *H. chamaeleon* and *H. anthogorgicola*, ***H. villogorgicola sp. nov.*** may also be a monoxenous symbiont. It was only harboured by *V. bebrycoides* and was absent from the sympatric gorgonian *Paramuricea grayi*, the only known species of the genus reported from the Canary Islands (Grasshoff, 1977b; Brito, 1985). In agreement with its strictly symbiotic mode of life, a remarkable colour mimicry occurred in the three gorgonian-associated *Haplosyllis* species. The type of mimicry appears to be related to the type of association. Monoxenous relationships such as those in ***H. villogorgicola sp. nov.***, *H. chamaeleon* and *H. anthogorgicola* often display an exact colour matching mimicry. A striking example has recently been described for the polynoid *Medioantena clavata* Imajima in the host hydroid *Solanderia misakiensis* (Inaba). The host has reddish branches and polyps with black basis and white tips, while the worms have reddish bodies and dorsal cirri with black basis and white tips (Nishi & Tachikawa, 1999). Polyxenous symbionts may also show an exact colour matching mimicry but, at the same, time they must be able to change their body colour depending on the colouring of their different hosts. In some cases, this ability may be related to a low degree of specificity, with the source of the colour matching being the host themselves through the symbionts feeding activities (e.g. *Branchiosyllis oculata* and its host sponges, see Pawlik, 1983). A more evolved network of polyxenous relationships occurs between *Gastrolepidia clavigera* Schmarda and its 13 host holothuroids from the fam ilies Stichopodidae and Holothuridae (Britayev & Zamyshliak, 1996). The symbionts also adopt the host colour, probably by partly feeding on them or by incorporating some host secretions. However, the symbionts have developed behavioural adaptations (e.g. they are usually located near anterior or posterior ends of their holothurian host's body and quickly hide in the oral or cloacal openings when threatened) as well as morphological adaptations (e.g. shield-like ventral lobes functioning like suckers, swollen elytral tubercles and appendages exactly mimicking the holothurian papillae with its attached white sand grains). *Gastrolepidia clavigera*, however, is not able to alter its body colour in a short time period, such as octopus or flatfish do. A more sophisticated mimicry is displayed by *Alcyonosyllis phili*, a cnidarian-associated syllid (Glasby & Watson, 2001). This worm has a striking white and brown banding pattern, with a blue to purple pigment

spot at base of appendages that are whitish with brown tips. Although the worms may be easily seen on all hosts in some circumstances, they do appear to be able to alter the intensity of their colour pattern to more closely resemble that of the host.

As often stated for many symbiotic associations (syllids guests included), there is a frustrating lack of information on their biological and ecological charac teristics (Martin & Britayev, 1998). Trophic interactions between syllids and their hosts have only been documented for *Branchiosyllis oculata*, *Haplosyllis* cf. *spongicola* (Tsurumi & Reiswig, 1997) and *Proceraea rzhavsky* (Britayev & San Martín, 2001). The first two feed on their host sponges, whilst the third shares the hydrothecae with a polyp of its host hydroid during the first developmental stages, then feeds on the polyp and remains alone inside the hydrothecae until the adult stage, when it goes out to build a tube attached to the hydroid colony. *Haplosyllis chamaeleon* was observed with its anterior end inside the gastric cavity of the gorgonian polyps (Laubier, 1960; D. Martin personal observations). However, it is not clear whether the worms were feeding on the prey inside the polyp's stomach (i.e. commensalistic or kleptoparasitic behaviour) or on the polyps themselves (i.e. strictly parasitic behaviour). A similar behavioural dichotomy may be assumed for ***Haplosyllis villogorgicola* sp. nov.**

There is, however, a remarkable difference in the host/symbiont relationship between ***H. villogorgicola* sp. nov.** and *H. chamaeleon*. The specimens of both species may be found extending their body along the longitudinal axes of the branches, usually near zones with living polyps. However, the former species may have induced the formation of gall like structures in the host and is more commonly found inside these structures, while this behaviour was never observed for the latter. Accordingly, ***H. vil logorgicola sp. nov.*** should be included among the symbiotic polychaetes that stimulate host cnidarians to react and build protective structures (such as tunnels, gall-like structures or enlarged previously exist ing formations) around them. This has been reported for commensal polychaetes, such as *Eunice floridana* Portuales, *Harmothoe melanicornis* Britayev, *Malmgreniella dicirra* Hartman and several species of *Gorgonyapolynoe*, but also for parasitic worms, such as *Autolytus penetrans* Wright & Woodwick, and *Proceraea rzhavsky* (Britayev & San Martín, 2001) and, particularly, for the congeneric species *H. anthogorgicola*. The formation of structures implies that the host is able to recognize (and to react to) the presence of the symbiont. Among polychaetes, none of the known associations reported have any indication of possible host benefits that might allow the formation of structures to be characterized as the host contribution to a mutualistic relationship. Conversely, most studies indicate that the structures are formed as a result of disturbance of the normal growth of the host induced by the presence of the symbiont, thus making possible parasitic behaviour a more likely explanation. The reasons why two closely related symbionts (i.e. ***H. villogorgicola* sp. nov**. and *H. chamaeleon*) which have similar (i.e. low) infestation intensities differ fundamentally in their induction of this host reaction are unknown and justify further studies. We may hypothesize that ***H. villogorgicola* sp. nov.** has more consistently evolved towards a kleptoparasitic behaviour, as the worms occur in a fixed position with the same polyps available nearby. Gorgonians are not fast growing organisms so that the formation of gall-like structures in *V. bebrycoides* must be related to a relatively stable position of the symbiont on the host, which would not be maintained long-term if they feed on the polyps (being thus forced to frequently change their position,

searching for a new food source). Conversely, *H. chamaeleon* does not have a fixed position in the gorgonian so that a true parasitic behaviour seems more likely in that case. In *H. anthogorgicola*, the situation differs significantly. The small size of the worms (much smaller than in the other two species), their appendage arrangement, the highest infestation intensities (i.e. probably thousands of worms per host colony), the presence of a complex network of galleries inside the very thin host coenchym and the openings surrounding the polyps, allow us to discard a strict parasitic behaviour, which would not be supported by its slow-growing gorgonian host. A kleptoparasitic or mutualistic (i.e. cleaner) behaviour may be possible in this case although, again, neither biological nor behavioural data have been reported so far.

Therefore, a detailed comparison of the three known species of *Haplosyllis* living symbiotically with gorgonians indicates that they may represent three differ ent adaptation models to a similar habitat. In light of our observations, *H. villogorgicola*, *H. chamaeleon* and *H. anthogorgicola* have apparently evolved towards kleptoparasitic (stealing food from the host), true parasitic (feeding on the host) and kleptoparasitic or mutualistic (cleaning the host) behaviour, respectively. We also suggest that the first two species may share a common origin, while *H. anthogorgicola* certainly represent a parallel evolutionary line, which gave rise to different solutions (i.e. morphological, ecological, behavioural) to the problem of living associated to gorgonians. An interesting topic for further research would be to study these associations (or other similar) in order to assess the real meaning of the relation ships established between the hosts and their respective symbionts, particularly from a behavioural point of view.

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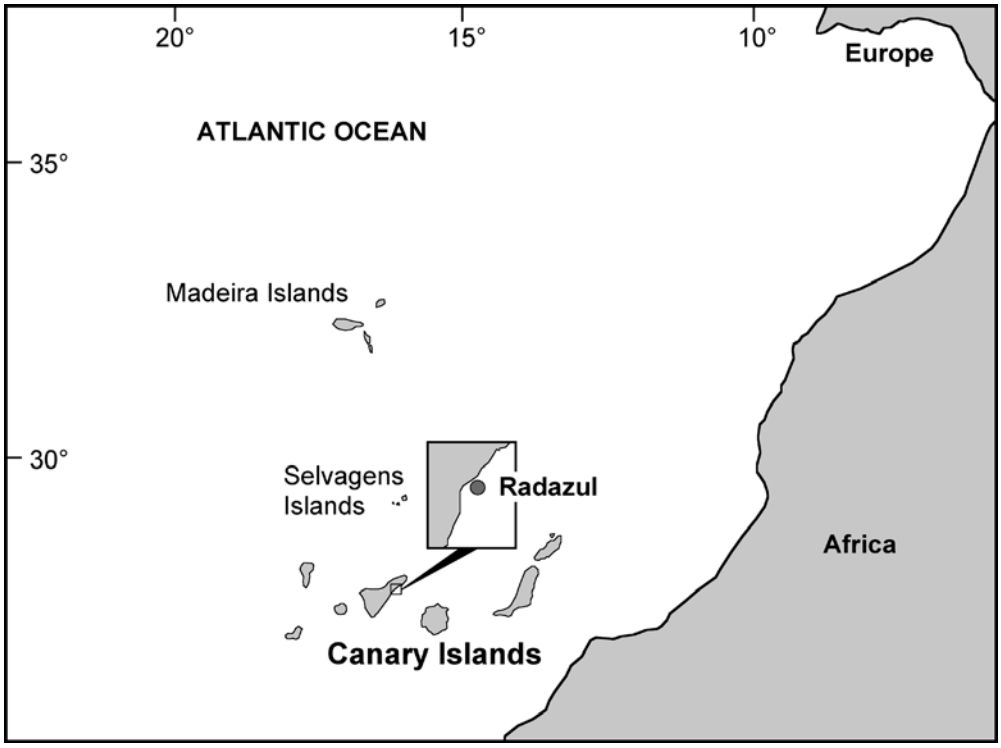

Figure 1. Map of situation of Canary Islands and location of sampling site.

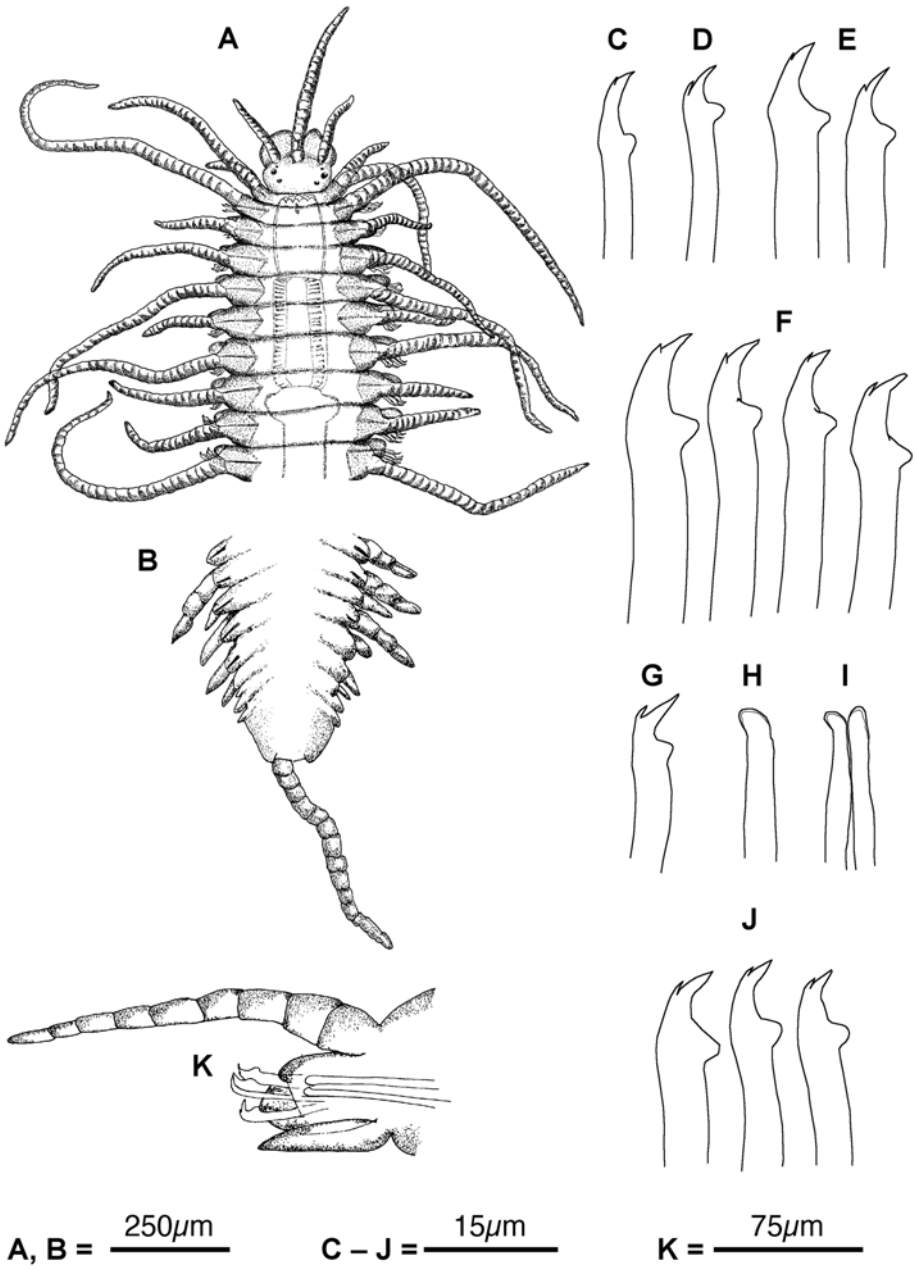

Figure 2. ***Haplosyllis villogorgicola*** **sp. nov.** (holotype). (A) Anterior end, dorsal view. (B) Posterior end, dorsal view. (C) Dorsal chaeta, first chaetiger. (D) Ventral chaeta, same chaetiger. (E) Ventral chaetae, chaetiger 11. (F) Dorsal to ventral chaetae, median parapodium. (G) Ventral chaeta, chaetiger 30. (H) Aciculum, same parapodium. (I) Acicula, median parapodium. (J) Chaetae, posterior parapodium. (K) Median parapodium.

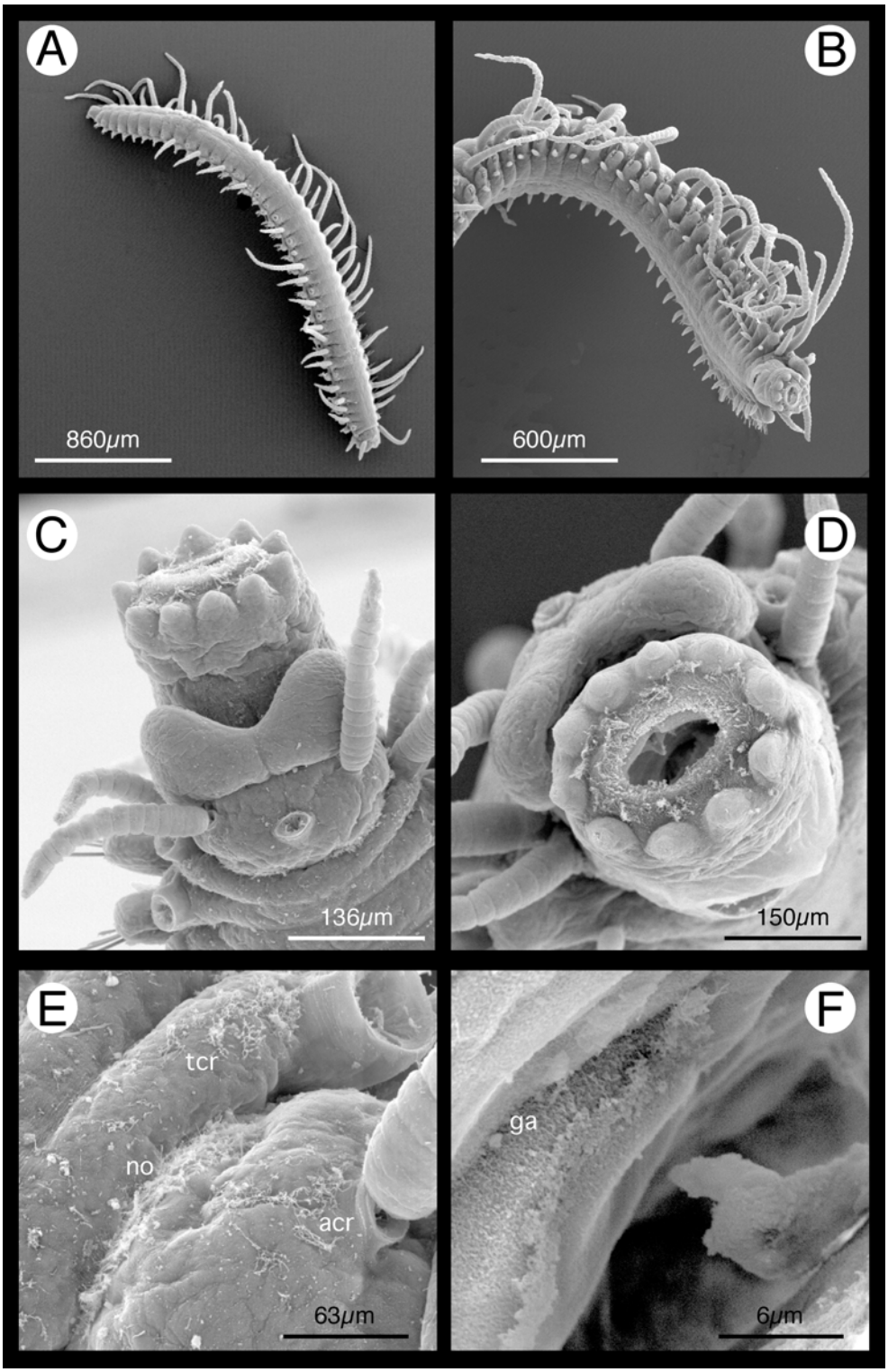

Figure 3. ***Haplosyllis villogorgicola*** **sp. nov.** (A) Entire worm (dorsal view). (B) Anterior end (ventral view). (C) Detail of prostomium (dorsal view). (D) Pharynx (frontal view). (E) Nuchal organ (no) and ciliated regions at the basis of antennae (acr) and tentacular cirri (tcr). (F) Perforated glandular area (ga) at the ventral side of palps.

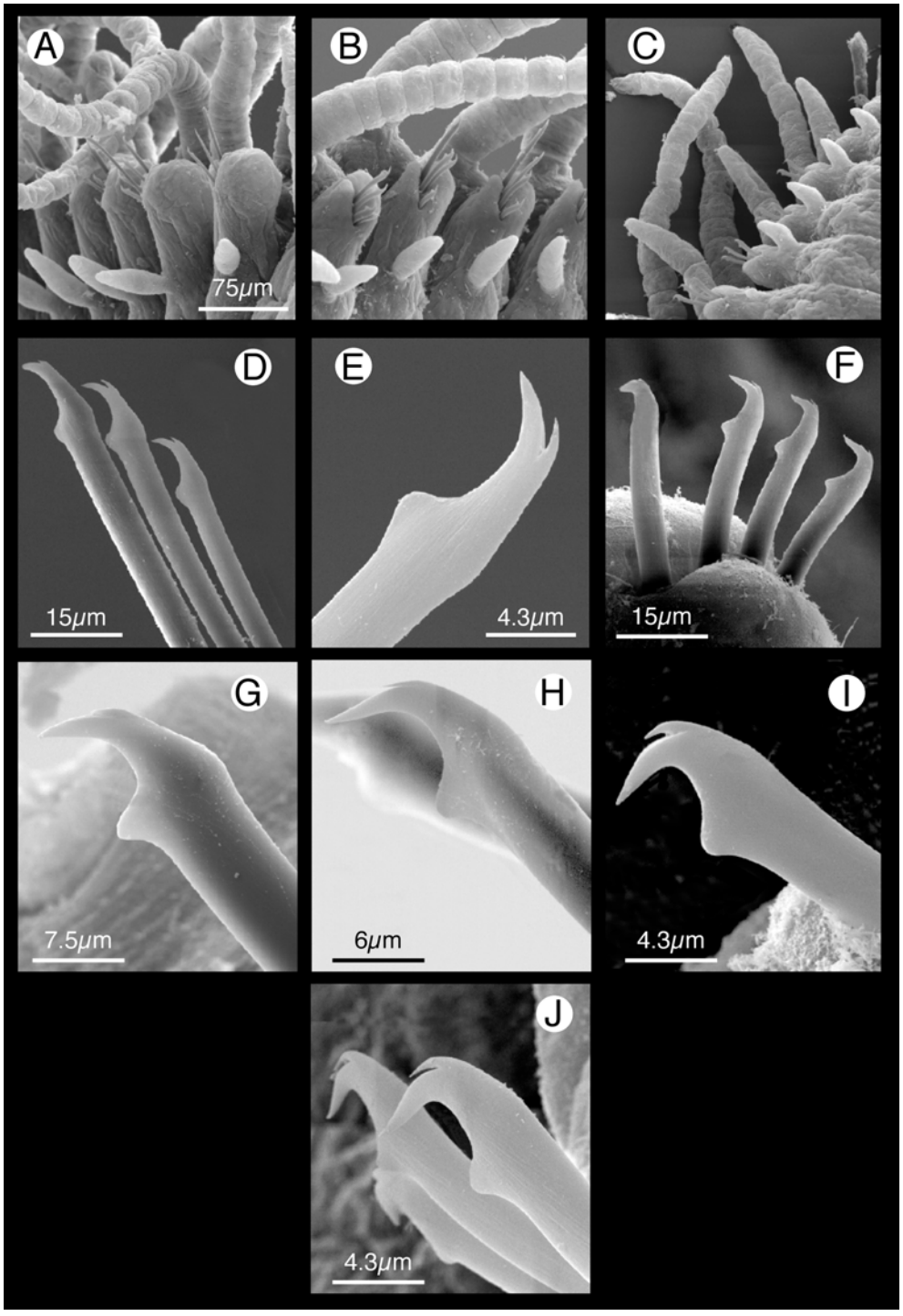

Figure 4. ***Haplosyllis villogorgicola*** **sp. nov.** (A) First three parapodia (ventral view). (B) Mid-body parapodia (ventral view). (C) Posterior-most parapodia (ventral view). (D) Chaetae from the first chaetiger. (E) Tip of a chaeta from the first parapodium. (F) Mid-body chaetae. (G) Tip of a dorsal mid-body chaeta. (H) Tip of a middle mid-body chaeta. (I) Tip of ventral mid-body chaetae. (J) Chaetae from a posterior-most chaetiger.

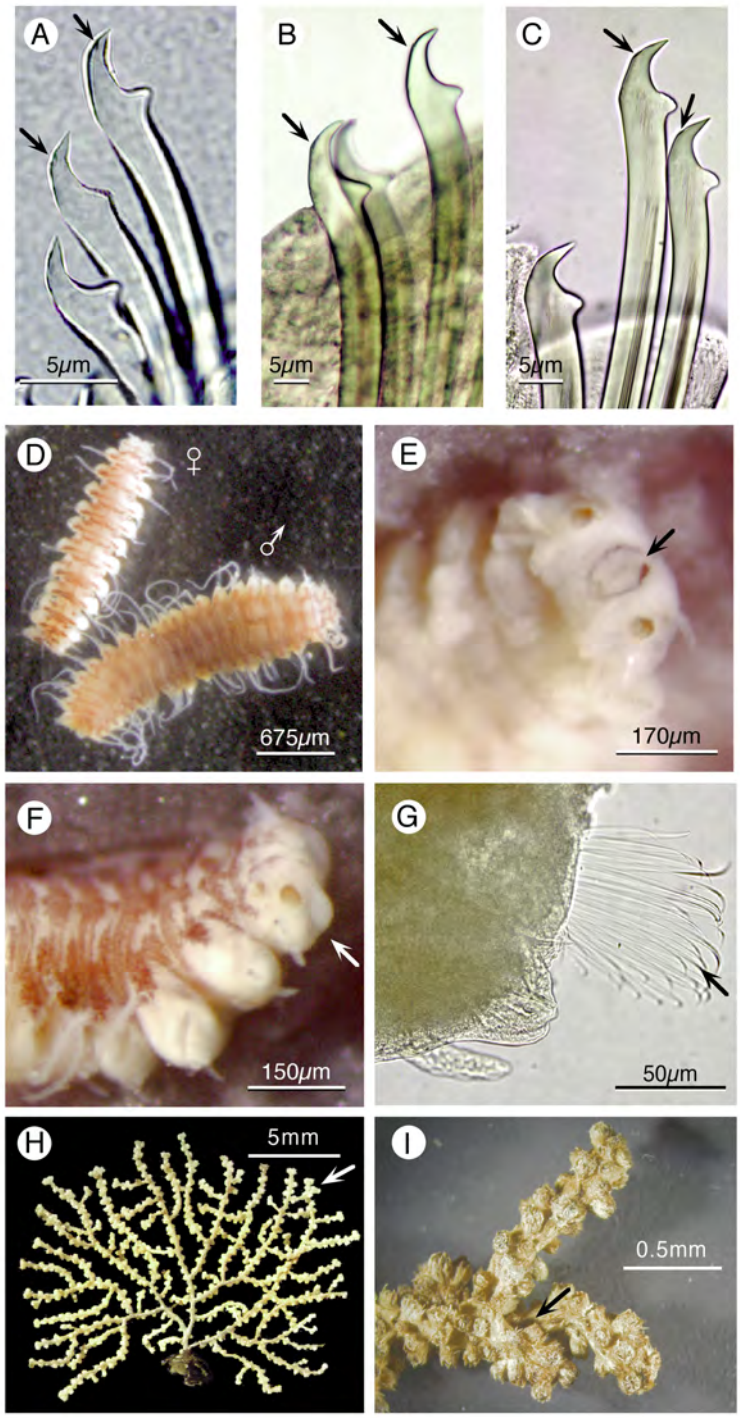

Figure 5. Light microscope photographs. (A) ***Haplosyllis villogorgicola* sp. nov.** Mid-body chaetae. (B–G) *Haplosyllis chamaeleon*. (B) Mid-body chaetae of a Cape of Creus specimen. (C) Mid-body chaetae of a Chafarinas Islands specimen. (D) Male and female stolons. (E) Head of a recently separated female stolon (ventral view). (F) Head of a male stolon (lateral view). (G) Parapodium of a stolon (dorsal cirri absent). (H,I) *Villogorgia bebrycoides*. (H) Entire specimen. (I) Detail of anastomosed branches. The arrows indicate: the location of the distal tooth (A, B, C); the former point of union of the stolon to the progenitor (E), the palp (F), the swimming chaetae (G) and the gall-like structures formed by anastomosed branches (H,I).

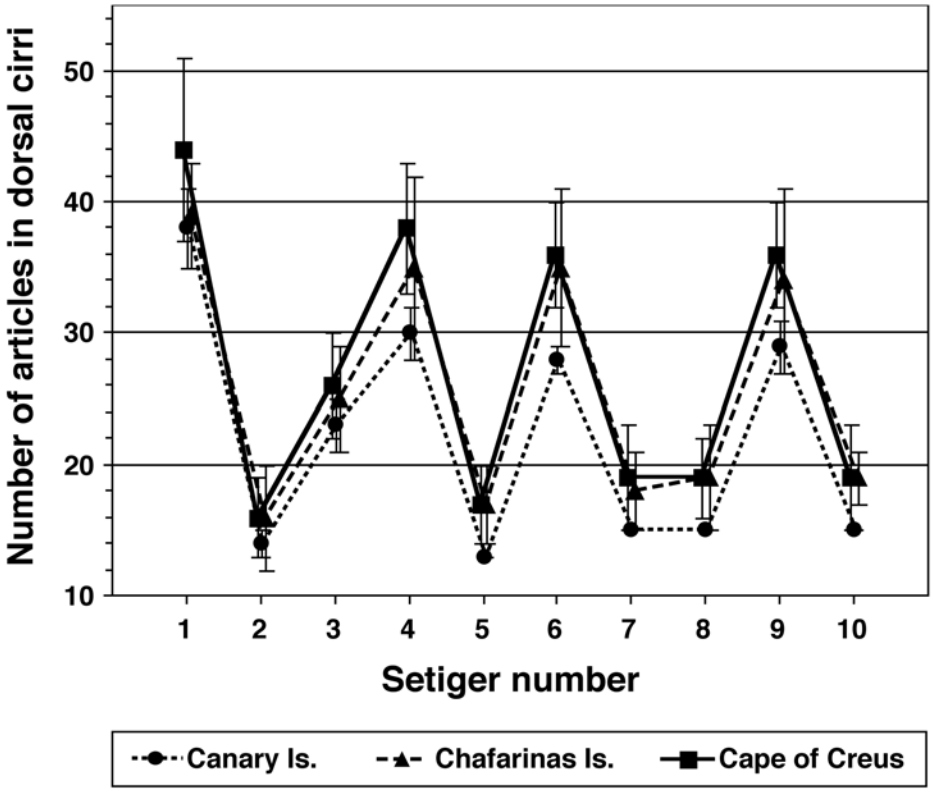

Figure 6. Graphical representation of the length pattern of the first ten dorsal cirri in ***Haplosyllis villogorgicola* sp. nov.** (from Canary Islands) and *Haplosyllis chamaeleon* (from Chafarinas Islands and Cape of Creus).

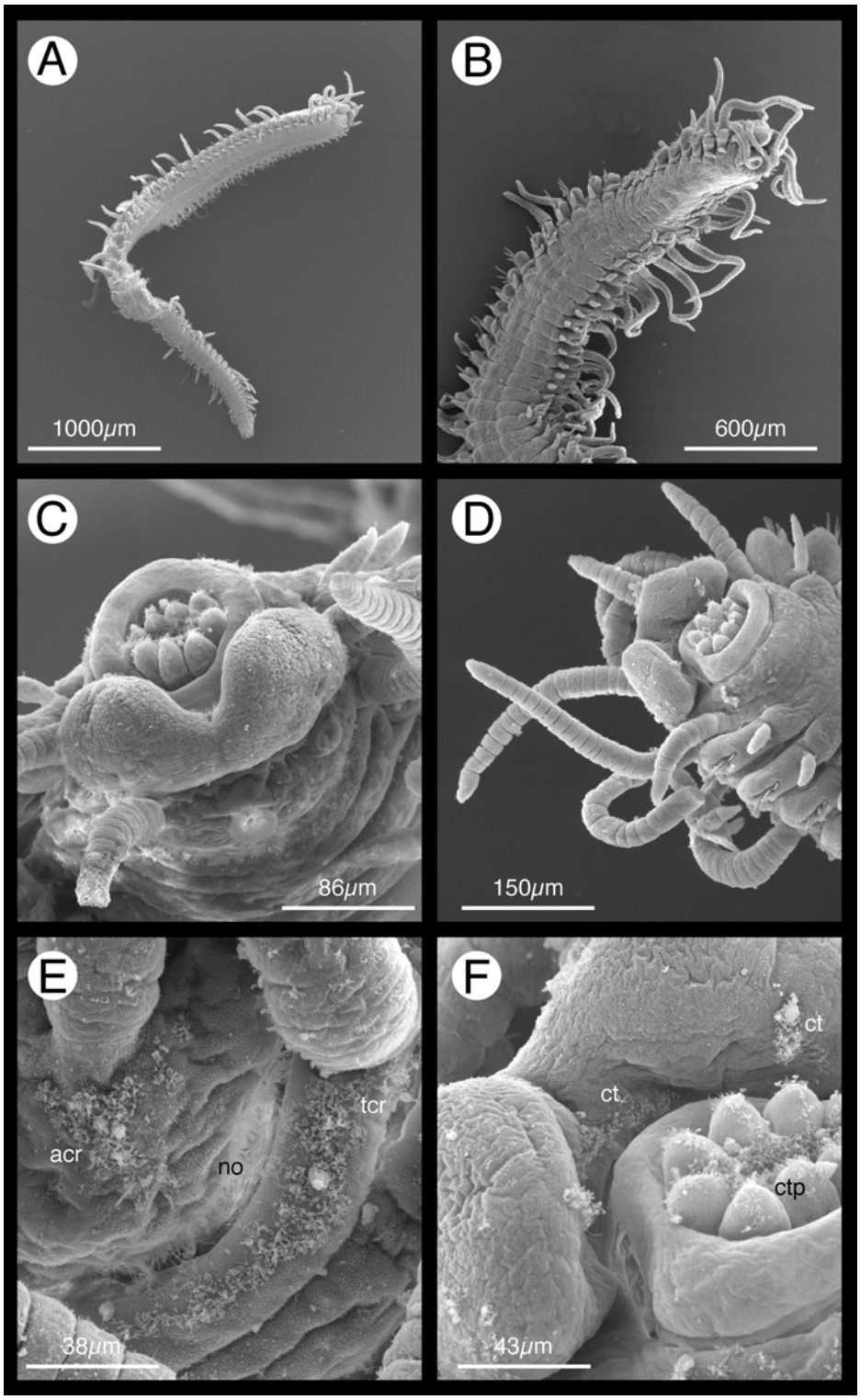

Figure 7. *Haplosyllis chamaeleon* from the Cape of Creus. (A) Entire worm (ventral view). (B) Anterior end (ventral view). (C) Detail of prostomium (frontal view). (D) Detail of anterior end (ventral view). (E) Nuchal organ (no) and ciliated regions at the basis of antennae (acr) and tentacular cirri (tcr). (F) Ciliated tufts at the ventral side of palps (ct) and on the pharyngeal papillae (ctp).

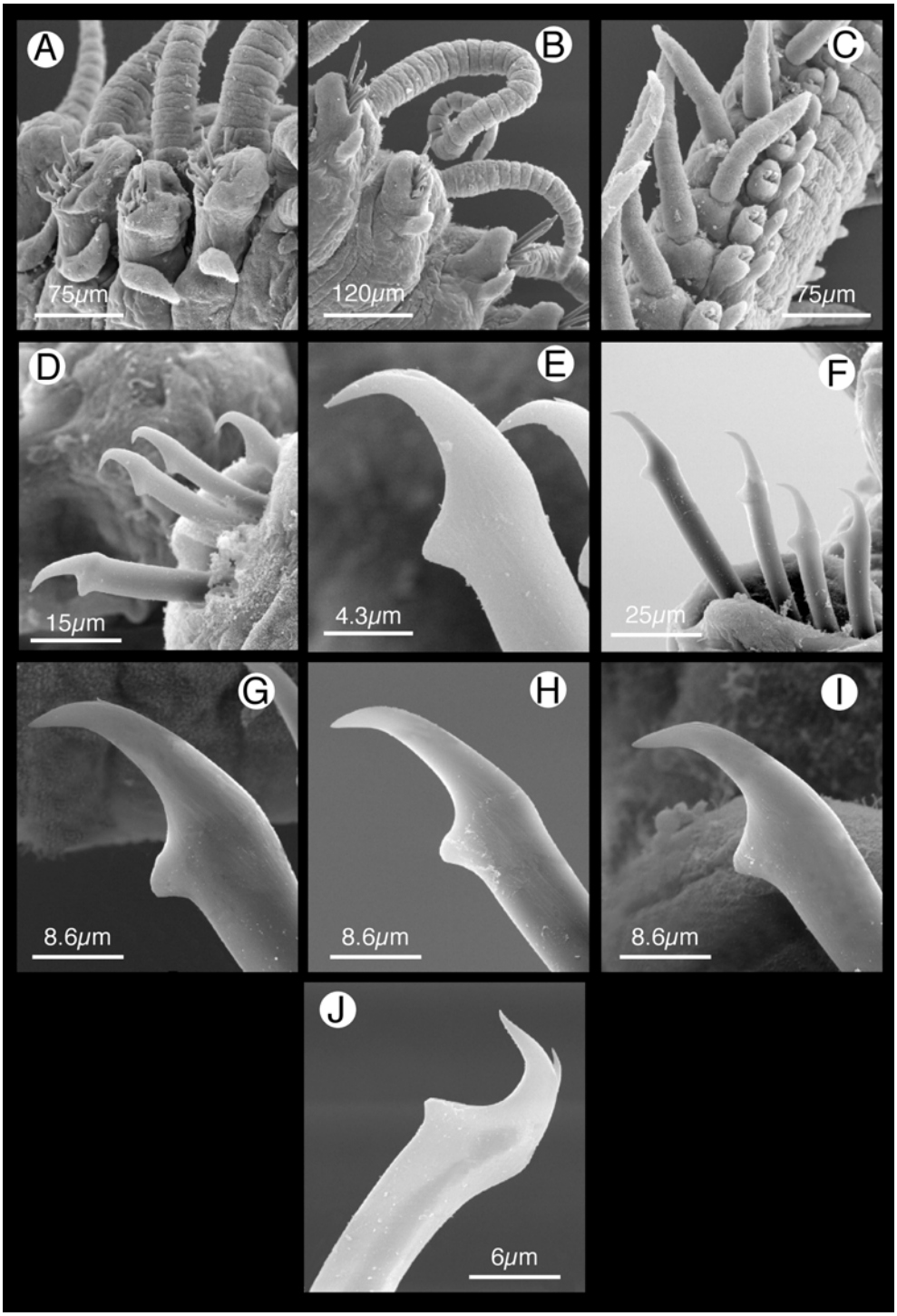

Figure 8. *Haplosyllis chamaeleon* from the Cape of Creus. (A) First three parapodia (ventral view). (B) Mid-body parapodia (ventral view). (C) Posterior-most parapodia (ventral view). (D) Chaetae from the first chaetiger. (E) Tip of chaetae from the first parapodium. (F) Mid-body chaetae. (G) Tip of a dorsal mid-body chaeta. (H) Tip of a middle mid-body chaeta. (I) Tip of a ventral mid-body chaeta. (J) Tip of a chaeta from posterior-most chaetigers.

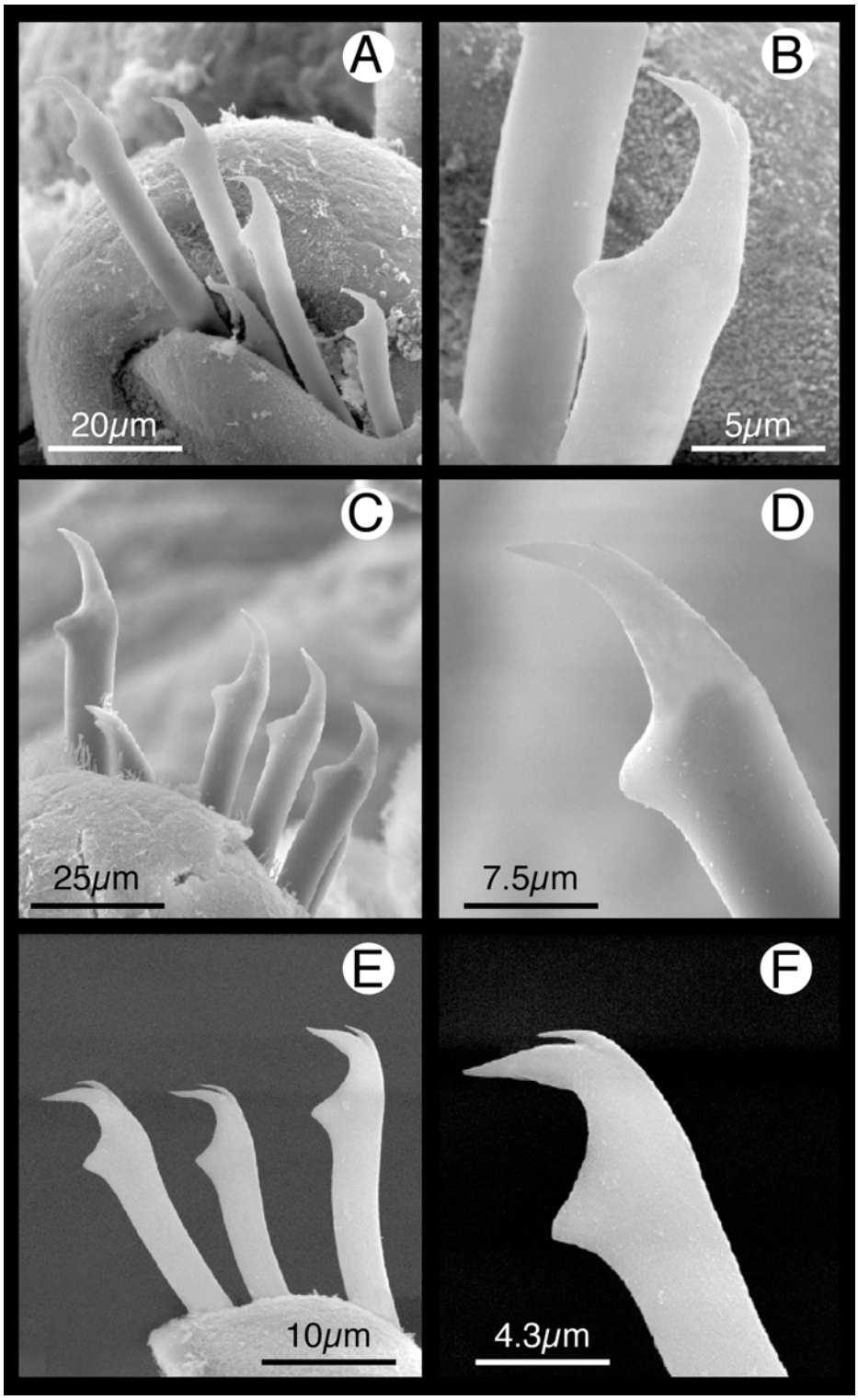

Figure 9. *Haplosyllis chamaeleon* from Chafarinas Islands. (A) Chaetae from the first chaetiger. (B) Tip of a chaeta from the first parapodium. (C) Mid-body chaetae. (D) Tip of a mid-body chaeta. (E) Chaetae from a posterior-most chaetiger. (F) Tip a posterior-most chaeta.

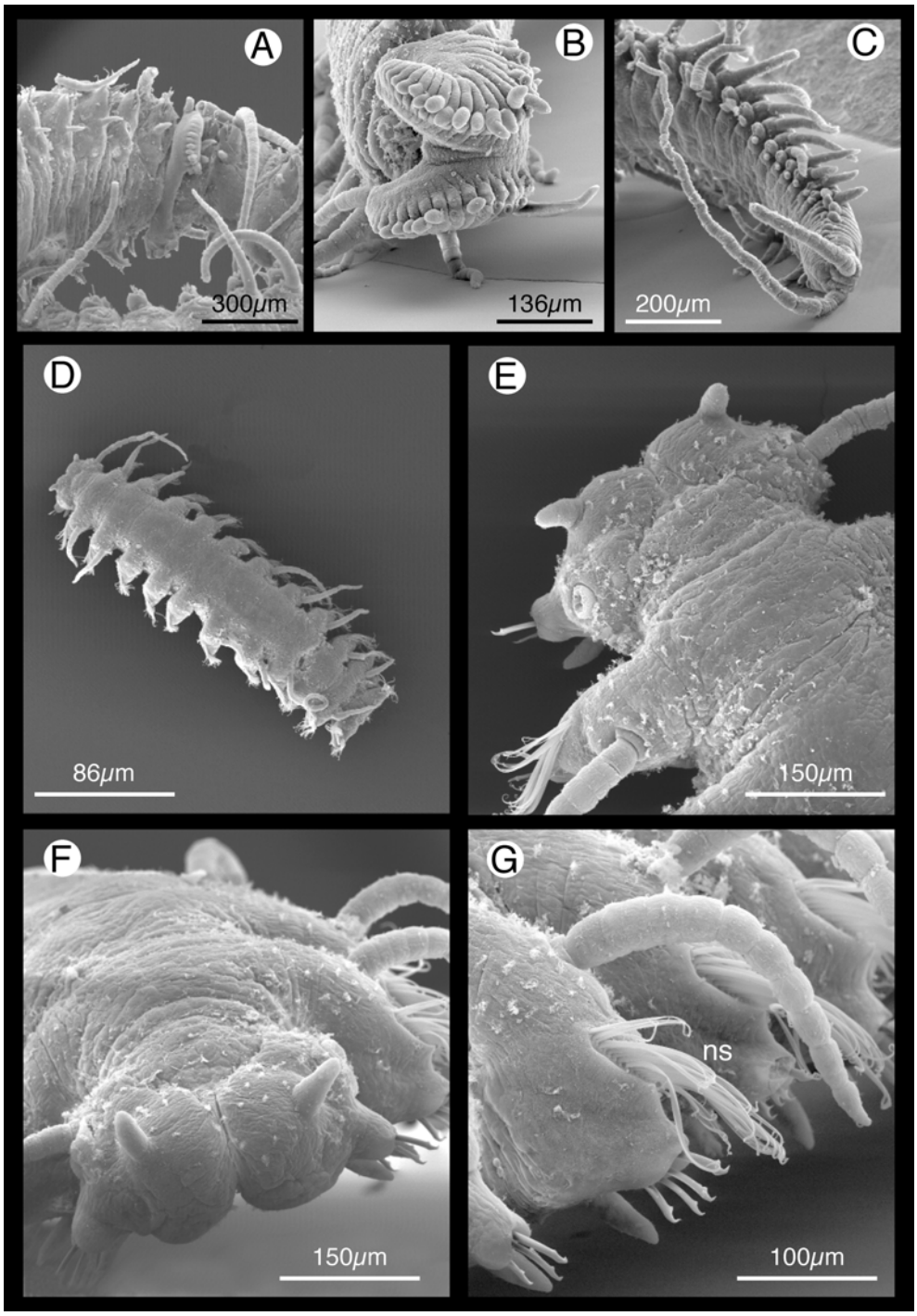

Figure 10. Stolonization in *Haplosyllis chamaeleon* (specimens from Chafarinas Islands). (A) Adult worm during the process (ventral view). (B) Posterior end of an adult just after releasing the stolon. (C) Posterior end of an adult some time after releasing the stolon. (D) Released stolon (dorsal view). (E) Head of the stolon (dorsal view). (F) Head of the stolon (frontal view). (G) Parapodium of the stolon showing the swimming chaetae.

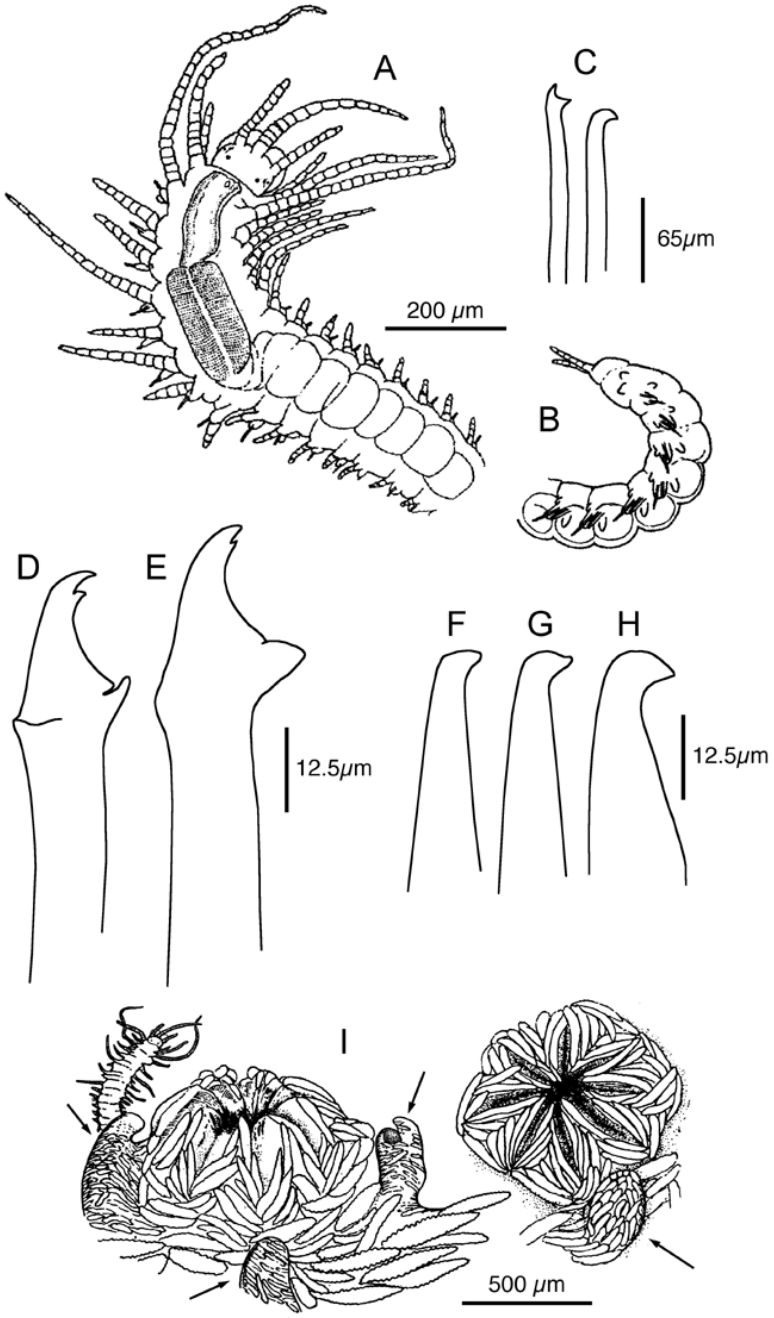

Figure 11. *Haplosyllis anthogorgicola*. (A) Anterior end. (B) Posterior end.(C) Original figures for the chaetae and acic ulum. (D) Chaetae from chaetiger two. (E) Chaetae from mid-body. (F) Aciculum from chaetiger two. (G) Aciculum from mid-body. (H) Aciculum from a posterior-most chaeti ger. (I) Detail of two polyp verrucae of *Anthogorgia bocki* showing the surrounding outgrowths (pointed by arrows) and a protruding specimen of *H. anthogorgicola*. A, B, C and I are redrawn from Utinomi (1956).

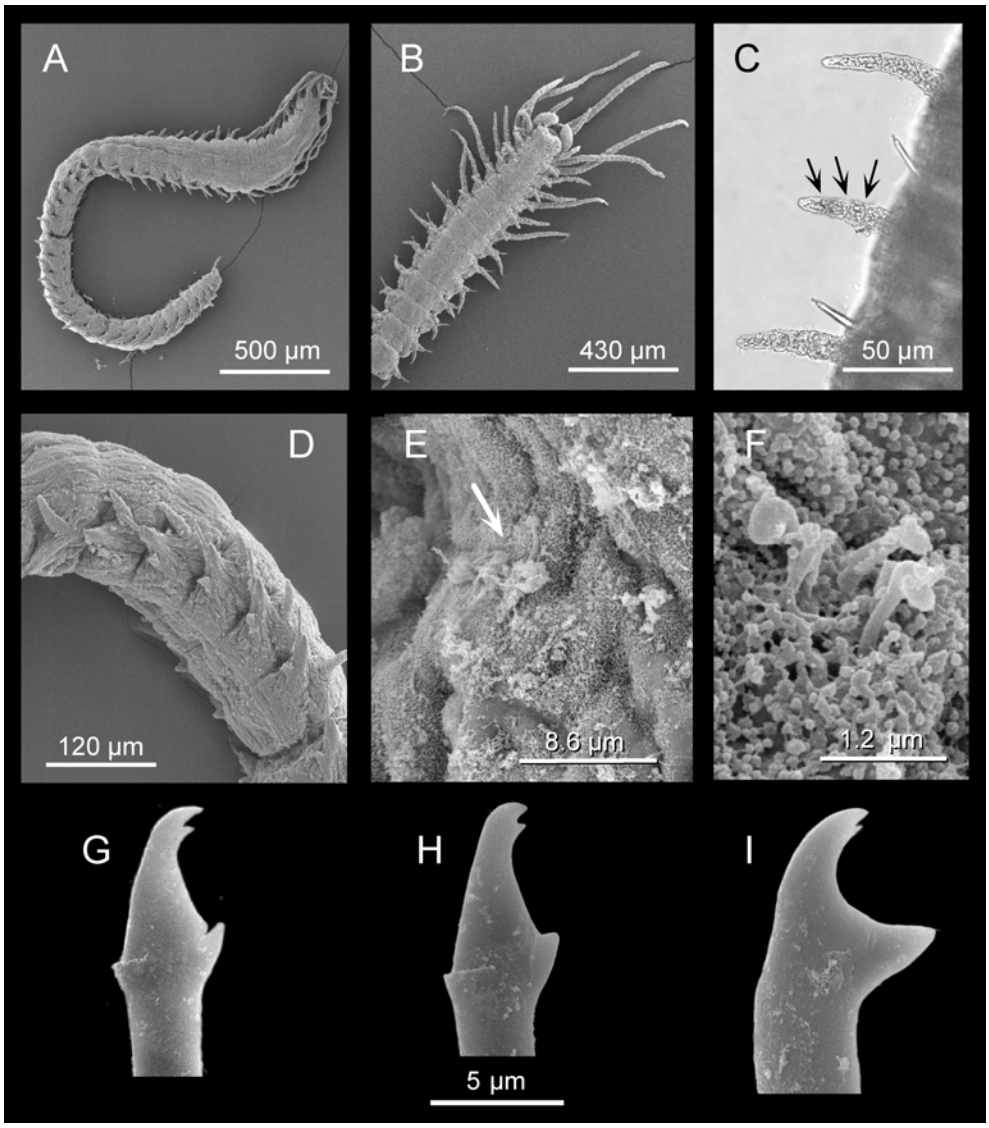

Figure 12. *Haplosyllis anthogorgicola*. (A) Entire worm (dorsal view). (B) Anterior end (ventral view). (C) Light microscope micrograph of the mid-body dorsal cirri. (D) SEM micrograph of the mid-body dorsal cirri. (E) Nuchal organ. (F) Ciliary tuft on palps. (G) Chaetae of the first chaetiger. (H) Chaetae of chaetiger six. (I) Mid-body chaetae. Black arrows indicate the joining of dorsal cirri articles; the white arrow indicates the position of the nuchal organ.

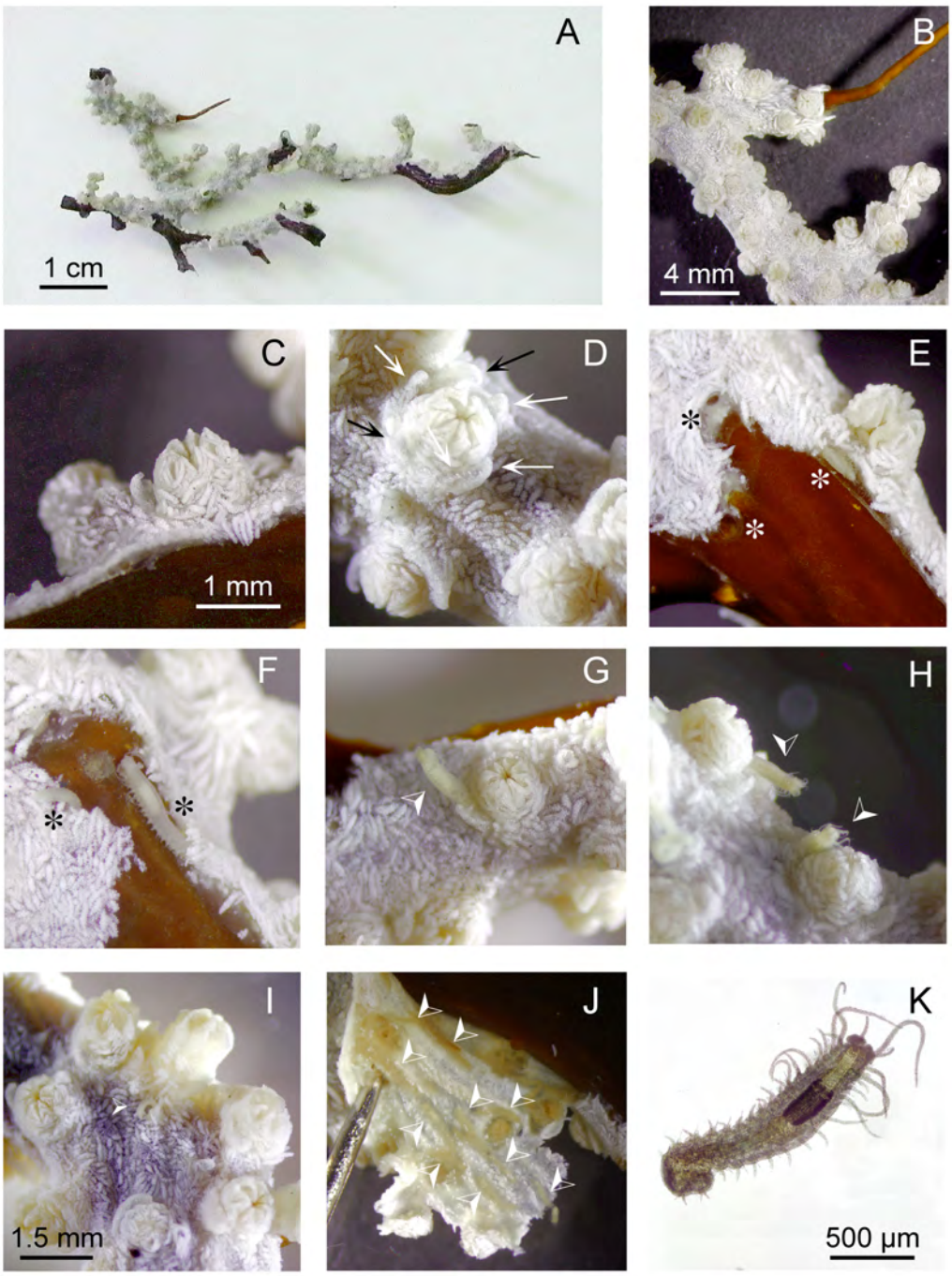

Figure 13. *Haplosyllis anthogorgicola*. (A) Fragment of the host gorgonian *Anthogorgia bocki*. (B) Detail of the same fragment showing the polyp verrucae. (C,D) Different views of the abnormal outgrowths caused by the symbionts (marked by the arrows). (E,F) Detail of the symbionts and the galleries (broken bark). (G,H) Anterior ends of the symbionts protruding from the host outgrowths. (I) Posterior end of a symbiont in a outgrowth far from the polyp verrucae. (J) Detail of the symbionts and their galleries seen through the inner side of the host bark. (K) Light microscope micrograph of the symbiont. C–H and I–J share the same scale bar, respectively. The arrows indicate the position of the outgrowths; the asterisks indicate the position of the galleries; the pointers indicate the position of worms.

.- Summary of measurements of the most relevant morphological features of *Haplosyllis villogorgicola* sp. n. and *Haplosyllis chamaeleon* and Chafarinas Islands). n: number of measured specimens; min: minimum; max: maximum; avg.: average; std: standard deviation.

	H. villogorgicola sp. n.					*H. chamaeleon (Cape of Creus)*					*H. chamaeleon (Chafari*			
	n	**min**	**max**	**avg**	**std**	**n**	**min**	**max**	**avg**	**std**	**n**	**min**	**max**	**avg**
th	23	3.87	13.25	7.84	2.58	11	3.87	11.5	8.7	2.28	3	4.25	13.25	8.97
h	23	0.27	0.72	0.54	0.11	11	0.42	0.7	0.55	0.09	11	0.35	0.78	0.61
f setigers	23	30	79	54.61	13.7	11	38	104	74	21.77	3	47	80	59.33
central	21	0.35	0.92	0.63	0.15	9	0.38	0.64	0.49	0.09	9	0.45	0.88	0.68
central	21	13	30	21.76	4.68	9	16	27	20.67	3.54	9	14	28	21.1
lateral	23	0.2	0.66	0.3	0.11	10	0.19	0.33	0.26	0.05	10	0.24	0.39	0.32
lateral	23	9	16	11.87	1.98	10	10	15	12.9	1.52	10	5	16	13
r cirri														
ventral	22	0.2	0.71	0.31	0.11	10	0.17	0.3	0.23	0.04	11	0.15	0.31	0.26
ventral	22	10	33	12.82	4.82	10	8	15	10.9	2.42	11	3	18	10.33
dorsal	23	0.32	1.83	0.84	0.32	11	0.36	0.7	0.54	0.1	11	0.425	1.13	0.71
dorsal	23	16	47	27.52	6.57	11	18	35	25.18	4.77	11	16	36	26.83
irri									0					0
ventral	23	0.08	0.15	0.11	0.02	11	0.06	0.1	0.09	0.01	11	0.06	0.12	0.1
ong dorsal	15	0.81	1.47	1.04	0.18	11	0.53	0.9	0.75	0.12	11	0.58	1.275	1.03
short dorsal	8	0.46	0.83	0.56	0.13	11	0.23	0.38	0.32	0.05	11	0.21	0.575	0.46
long dorsal	15	25	42	32.07	5.73	11	27	39	32.55	4.27	11	14	51	34.73
short dorsal	8	15	30	19.25	4.71	11	11	19	15.82	3.16	11	5	27	18.91
cirri														
ventral	22	0.05	0.15	0.09	0.02	11	0.07	0.12	0.09	0.01	11	0.06	0.12	0.09
ong dorsal	12	0.71	1.53	1	0.23	11	0.48	1	0.72	0.15	11	0.64	1.6	1.11
short dorsal	11	0.48	0.76	0.59	0.07	11	0.29	0.45	0.36	0.05	11	0.26	0.75	0.49
long dorsal	12	14	44	27.33	8.38	11	21	41	29	5.67	11	17	49	32.92
short dorsal	11	15	21	18.36	1.96	11	12	20	16	2.49	11	8	28	17.67
cirri														
ventral	19	0.03	0.12	0.06	0.02	11	0.05	0.115	0.08	0.03	3	0.05	0.112	0.09
ong dorsal	7	0.51	1.19	0.78	0.24	11	0.44	1.15	0.75	0.22	3	0.55	1.25	1.02
short dorsal	15	0.2	0.66	0.46	0.15	11	0.24	0.55	0.37	0.09	3	0.31	0.68	0.55
long dorsal	7	15	30	20.57	6.6	11	11	40	23.82	8.62	3	13	34	24.33
short dorsal	15	7	22	13.87	4.47	11	6	21	12.46	5.11	3	7	18	13.67
ength	23	0.2	0.61	0.45	0.11	11	0.3	0.62	0.41	0.1	11	0.19	0.55	0.44
culum														
	23	0.3	0.87	0.6	0.13	11	0.36	0.85	0.58	0.14	11	0.3	0.96	0.64
	23	0.12	0.4	0.26	0.07	11	0.19	0.35	0.24	0.05	11	0.14	0.35	0.28

Table 2.- Summary of the results of the post-hoc test (Tukey HSD) to assess the differences in cirri length for the first 10 parapodia. • = $p < 0.05$; •• = $p < 0.001$; ••• = $p < 0.0001$; NS = non-significant differences.

Chaetigers	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
2	•••								
3	•••	•••							
4	•	•••	•••						
5	•••	NS	•••	•••					
6	••	•••	•••	NS	•••				
7	•••	NS	•••	•••	NS	•••			
8	•••	•	•••	•••	NS	•••	NS		
9	••	•••	•••	NS	•••	NS	•••	•••	
10	•••	•	•••	•••	NS	•••	NS	NS	•••