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Taxonomy of Serpulidae (Annelida, Polychaeta): The state of affairs

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Abstract

The Serpulidae are a large group of sedentary polychaetes inhabiting calcareous tubes. The relationships within the group are poorly understood and taxonomy of the group is very confused which is a major obstacle to accessing their phylogeny. This review provides up-to-date information on the current state of taxonomy of Serpulidae *sensu lato* (not including Spirorbinae). The morphology of the group is reviewed with special reference to the features that can provide characters for future phylogenetic analyses. Scanning electron micrographs illustrate the structure of the chaetae and uncini. The list of 46—in our opinion valid—genera is accompanied by detailed generic diagnoses, species composition and distribution (checklist), and remarks on major taxonomic literature. A taxonomic key to the genera and a list of invalid genera with synonymy is also provided.

Key words: Annelida, Polychaeta, Serpulidae, taxonomy, morphology, SEM ultrastructure of chaetae and uncini

Introduction

The family Serpulidae is a discrete group of sedentary calcareous tubeworms within the large clade Sabellida, which shares a presence of radiolar crown and separation of the body into thoracic and abdominal regions, as divergence from the usually rather uniformly segmented motile polychaete form. The views on the relationships within Serpulidae have undergone many changes over the years (see Kupriyanova *et al.* 2006 for the details). The Serpulidae Rafinesque, 1815 had been traditionally divided into subfamilies Serpulinae Rafinesque, 1815 (although probably in most papers attributed to MacLeay, 1840) and Spirorbinae Chamberlin, 1919 until Rioja (1923) established the subfamily Filograninae. Pillai (1960) included 5 brackish-water serpulid genera in the subfamily Ficopomatinae but ten Hove & Weerdenburg (1978) revised the group and placed all its genera in the genus *Ficopomatus*. Uchida (1978) created 11 sub-families and numerous new genera, but his scheme, strongly criticized by ten Hove (1984) has not been accepted widely. Pillai (1970) elevated Spirorbinae to the family Spirorbidae, but later a number of authors suggested that Spirorbidae are more closely related to Serpulinae than to Filograninae (ten Hove 1984, Fitzhugh 1989, Smith 1991, Rouse & Fitzhugh 1994) and that the maintenance of the family Spirorbidae is not justified. Recent phylogenetic analyses confirmed the position of Spirorbinae as a subfamily of Serpulidae (Kupriyanova 2003, Kupriyanova *et al.* 2006, Lehrke *et al.* 2007, Kupriyanova & Rouse 2008). Ten Hove (1984) regarded the Filograninae as paraphyletic and a morphology-based cladistic analysis of some Serpulidae (Kupriyanova 2003) supported his conclusions. Moreover, the most recent phylogenetic analyses of Serpulidae using 18S ribosomal DNA (Lehrke *et al.* 2007) and another using combined molecular and morphological data (Kupriyanova *et al.* 2006) suggested that both traditionally formulated sub-families Serpulinae and Filograninae are not monophyletic. Kupriyanova *et al.* (2006) refrained from revising the serpulid classification and suggested that a major revision of serpulid taxonomy is needed based on more genera than used in their study.

The major obstacle to a comprehensive phylogenetic analysis of the Serpulidae remains the state of its alpha taxonomy. It is almost proverbial to say that serpulid taxonomy is very confused and most currently recognized serpulid genera have long and convoluted taxonomic histories. Within Serpulidae, specific identification has traditionally been based on a combination of characters such as morphology of the operculum and opercular peduncle (if present), degree of development of the collar and thoracic membranes, structure of collar chaetae and tube and, to a lesser degree, structure of chaetae and uncini. Serpulid genera have been described on the basis of unique characters or on unique combinations of characters (even on absence of characters) rather than on presence of shared derived characters. Although traditionally only few characters have been used in serpulid taxonomy, variability of these characters remains largely unstudied.

There have been very few reviews of serpulid taxonomy. The very first revision (Mörch 1863) was followed by early reviews by Saint-Joseph (1894), Bush (1905), and Pixell (1912, 1913). Chamberlin (1919) gave a key to the serpulid genera without attempting to revise the family, and so did Southward (1963), half a century later. Fauchald (1977) compiled a list of generic diagnoses and a key to genera for all polychaetes, including serpulids and spirorbids. In addition to the Spirorbidae, he acknowledged 331 species of serpulids, divided into 3 sub-families; the Serpulinae with 44 genera, the Filograninae with 5 genera, and the Ficopomatinae with 5 genera. Of these 54 genera, 22 were monotypic and another 13 had only 2 species. Uchida (1978) provided a systematic review of the group with a description of new species and new genera, but gave no key. He mentioned only 233 species, as compared to the 331 of Fauchald (1977). Of the 61 genera distinguished by Uchida (1978), 26 were monotypic, and 15 had only two species. No attempts to review Serpulidae have been made ever since and now, thirty years later, Fauchald (1977) still remains the most commonly used source of information on the generic composition of serpulids. During the last three decades serpulid taxonomy underwent significant changes, with numerous taxa being synonymized, older diagnoses emended and extended, new species described and about 10 genera added.

Material and methods

The aim of this review is to provide up-to-date information on the current state of taxonomy of Serpulidae *sensu lato*. Although the position of Spirorbinae within Serpulidae has been determined (Kupriyanova 2003, Kupriyanova *et al.* 2006, Lehrke *et al.* 2007), spirorbins are not included in the present paper because composition and phylogenetic relationships within this monophyletic group recently have been treated elsewhere (Macdonald 2003). The morphology of serpulids (and variability of morphological characters) is reviewed with respect to features that can be used as characters in forthcoming cladistic analyses. "Not observed" in the diagnoses below indicates that no data have been given in the literature and material either could not be (re-) examined by us, or was not preserved well enough.

Since a mere literature compilation would not be sufficient when dealing with a group with such a complex taxonomic history, we examined with use of light microscopy representatives (mostly previously unpublished material) of all genera currently considered valid in Serpulidae *sensu lato*. It should be noted that some of the characters are subject to interpretation, changing gradually rather than in distinct steps. Moreover, while structure of chaetae and uncini do provide important characters for serpulid taxonomy, many existing descriptions, especially the early ones, were published with very sketchy line-drawings of chaetal structures made under a compound light microscope. These illustrations often do not provide adequate details of chaetal ultrastructure, and even can give a wrong impression when compared with images done with scanning electron microscopy (SEM) (ten Hove & Jansen-Jacobs 1984: 147; compare for instance Fauvel 1927 fig. 121q with Breton & Vincent 1999 fig. 10). Therefore, chaetae and uncini of at least one representative of the genus were re-examined with SEM, enabling to catch the dentition of uncini in a dental formula, see glossary. Note that SEM photographs of many currently known serpulids have never been published before. Existing descriptions of two monotypic genera, *Chitinopomoides* and *Paumotella*, were that incomplete that full redescriptions of their type-species have been included.

Authors' names and year of publication for valid serpulid taxa can be found in the Table of Contents and in the relevant sections and lists of species. For the remaining taxa, this information is given with their first occurrence in the text.

The material examined for this review is deposited in the following museums:

BMNH	collection number of the Natural History Museum, London, United Kingdom, formerly the **B**ritish **M**useum of **N**atural **H**istory
DIZMSU	**D**epartment of **I**nvertebrate **Z**oology, **M**oscow **S**tate **U**niversity, Moscow, Russia
HUJ	the **H**ebrew **U**niversity of **J**erusalem, Biological Collections, Israel
LACM-AHF	**L**os **A**ngeles County **M**useum of Natural History, **A**llan **H**ancock **F**oundation, California, USA
MCZ	**M**useum of **C**omparative **Z**oology, Harvard University, Cambridge, USA
NHMW	Natural History Museum Vienna, **N**atur**h**istorisches **M**useum **W**ien, Vienna, Austria
QM	**Q**ueensland **M**useum, Brisbane, Queensland, Australia
RMNH	collection number of the Nationaal Natuurhistorisch Museum Naturalis, Leiden, the Netherlands, formerly the **R**ijks **M**useum voor **N**atuurlijke **H**istorie
SAM	**S**outh **A**ustralian **M**useum, Adelaide, Australia
SIO RAS	**S**hirshov **I**nstitute of **O**ceanology, **R**ussian **A**cademy of **S**ciences, Moscow, Russia
USNM	collection number of the Smithsonian National Museum of Natural History (NMNH), Washington, formerly **U**nited **S**tates **N**ational **M**useum
ZMA	**Z**oological **M**useum of **A**msterdam, Amsterdam, the Netherlands
ZMH	Zoologisches Institut und **Z**oologisches **M**useum, **H**amburg, Germany.

Morphology

The tube

Whereas tubes of the closely related sabellid family are constructed of mucus and muddy or sandy sediments (e.g., Bonar 1972; with the exception of the calcareous tube in the sabellid *Glomerula* Nielsen, 1931 (including *Calcisabella* Perkins, 1991), e.g., Vinn *et al.* 2008), all serpulids build tubes of crystalline calcium carbonate and a mucopolysaccharide matrix using calcium glands located on the collar (e.g., Neff 1968, 1971, Nott & Parkes 1975, Vovelle *et al.* 1991). Tube additions are molded by the collar folds when the worm is in a feeding position, at the entrance of the tube. The resulting tube shape depends upon the degree of rotation of the worm within the tube and upon the morphology of the collar folds themselves (Faouzi 1930, Hanson 1948b, Hedley 1956a, b, 1958).

In spirorbins the tubes are coiled either dextrally or sinistrally in a tight flat spiral (the character that gave the name to the group) and are usually completely attached to the substrate (*Helicosiphon* Gravier, 1907 is an exception having the tube with erect distal end). In serpulins the tube shape is quite variable and coiling, when present, is irregular (maybe with the exception of *Nogrobs grimaldii* (de Montfort, 1808), but the tube of this taxon starts and ends with a straight part). In almost all serpulids the tubes are attached to the substrate by at least the proximal older parts. The only known exceptions are the free-living *Ditrupa* (Fig. 1A), and maybe *Bathyditrupa*, *Nogrobs grimaldii*, and *Serpula crenata* (Ehlers, 1908; possibly including *S. sinica* Wu & Chen, 1979). Very likely larvae of these taxa settle on a pebble or a shell (as observed for *D. arietina* by Charles *et al.* (2003) and for *S. crenata* by ten Hove & Ben-Eliahu, unpublished), and break free later. Some serpulids have tubes attached to the substrate throughout their entire length (e.g., *Pomatoceros triqueter* (Linnaeus, 1758)) while others have free erect distal parts (e.g., *Hyalopomatus* spp.). The direction of tube growth is apparently affected by environmental conditions (e.g., Knight-Jones 1981). Serpulids are able to deal with high rates of sedimentation by changing the shape and direction of tube growth (e.g., Hartmann-Schröder 1967, 1971). Standing erect tubes are observed in waters with low current and high sedimentation rate; the most extreme example being that of *Serpula israelitica* Amoureux, 1976, with up to 10 cm long erect tubes embedded in sand (ten Hove, 16 June 1982, observation on Van Veen grab sample, CANCAP Expedition VI, Sta. 111, South of Santa Luzia, 55–62 m, sand). Tubes completely attached to the substrate may be indicative of water movements (currents, tides) with low rates of sedimentation (Kupriyanova & Badyaev 1998). A high density of tubes may result in the distal parts growing away from the substrate (e.g., Jackson 1977, Table 3). Tubes of some taxa, such as *Floriprotis* (Fig. 1E) and several *Spirobranchus* spp. (Fig. 1D) may be completely embedded in scleractinian corals (see review by Martín & Britayev 1998, Ben-Tzvi *et al.* 2006). These are not boring organisms, but settle on a dead coral part and become overgrown later.

The importance of tubes in serpulid taxonomy is underestimated and adequate descriptions and figures are mostly absent in Recent descriptions. In some genera (e.g., *Hydroides*) the tube morphology is too uniform for general taxonomic use, but locally some *Hydroides* species can be recognized in the field by their tubes. In other genera (such as *Filogranula*, *Pyrgopolon*, *Pseudovermilia*) the tubes provide excellent diagnostic characters.

Tube shapes. In external cross-section, tubes of many serpulids are circular or sub-circular when a flattened area of attachment is present. However, in some taxa the tube cross-sections may be notably triangular (*Pomatoceros*, *Pomatostegus*, *Placostegus*, *Pseudovermilia*, Fig. 2E) or sub-triangular with one major longitudinal keel (*Laminatubus alvini* ten Hove & Zibrowius, 1986). Tubes of *Galeolaria* having two major longitudinal keels can be considered as trapezoidal. *Bathyditrupa hovei* Kupriyanova, 1993b and *Nogrobs grimaldii* are unusual in having tubes rectangular in cross-section. Within a single tube changes may occur from trapezoidal to polyangular (*Pyrgopolon differens* (Augener, 1922): ten Hove 1973 Pl. IIB) or from triangular respectively trapezoidal/semicircular to circular (e.g., *Pseudovermilia occidentalis* (McIntosh, 1885); *Hydroides brachyacanthus* Rioja, 1941a: ten Hove 1975 Pl. VII g, k; Imajima & ten Hove 1984 fig. 5).

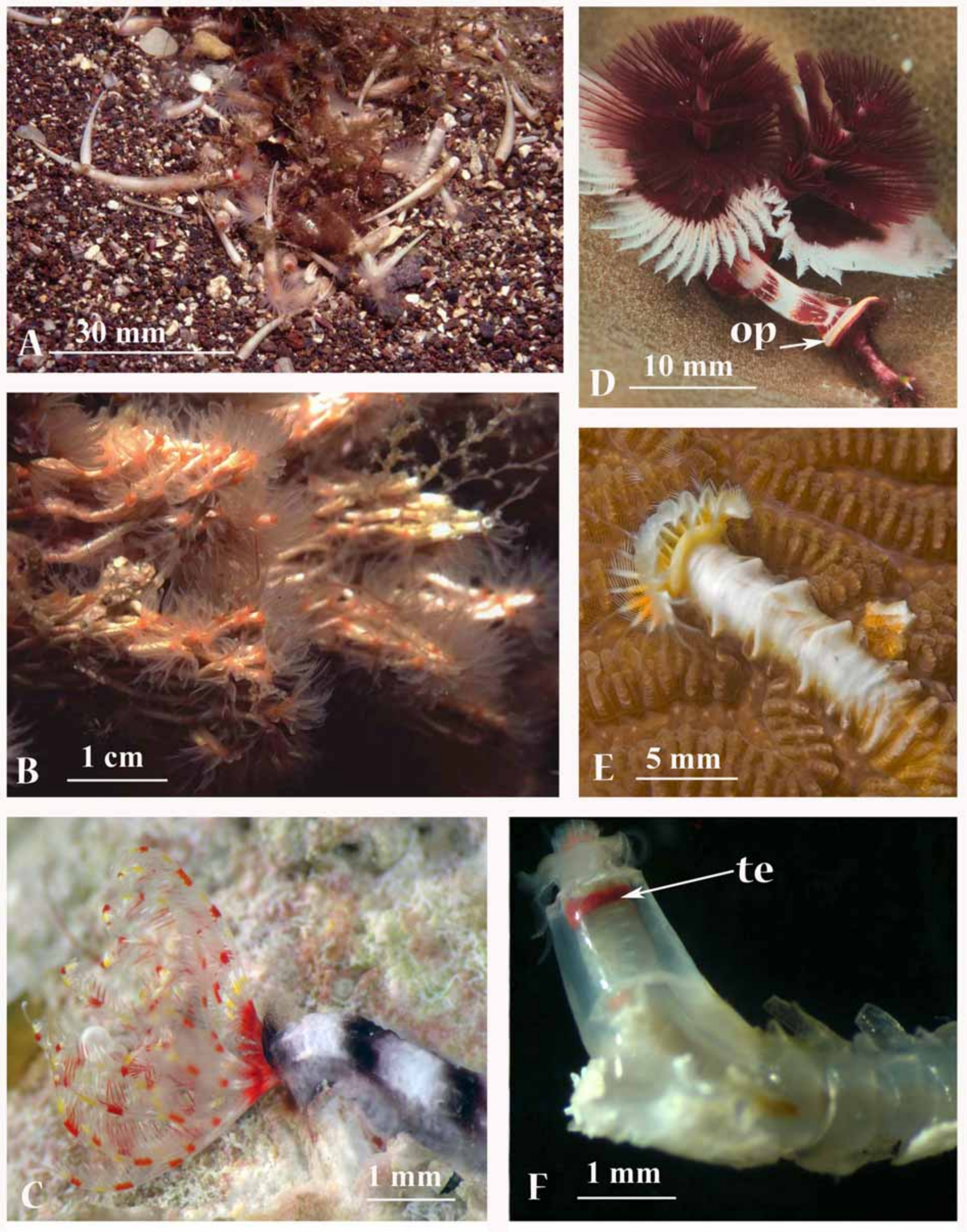

FIGURE 1. Serpulids in their tubes. A—*Ditrupa arietina*, *in situ*, tubes not attached to substrate, from Madeira Island (photo P. Wirtz), B—*Filograna implexa*, *in situ* from Portugal, Sesimbra (photo P. Wirtz), C—*Serpula vittata*, from Australia, Queensland, Lizard Island (photo G. Rouse), D—*Spirobranchus gardineri*, from the Seychelles Exp. oceanic reefs, Amirantes, Alphonse Atoll, SE part of lagoon, 7º03'S, 52º44'E, 4–6 January 1993; patch reef and reef flat, 4 m, near Sta. 787 (photo J. Randall), E—*Floriprotis sabiuraensis*, from Indonesia, North Sulawesi, tube embedded into coral (photo M. Boyer), F—*Placostegus* sp., in transparent tube, from Australia, Queensland, Lizard Island, branchial crown and operculum missing, orange belt of thoracic eyes is well seen (photo G. Rouse). Abbreviations: op—operculum, te—girdle of thoracic eyes.

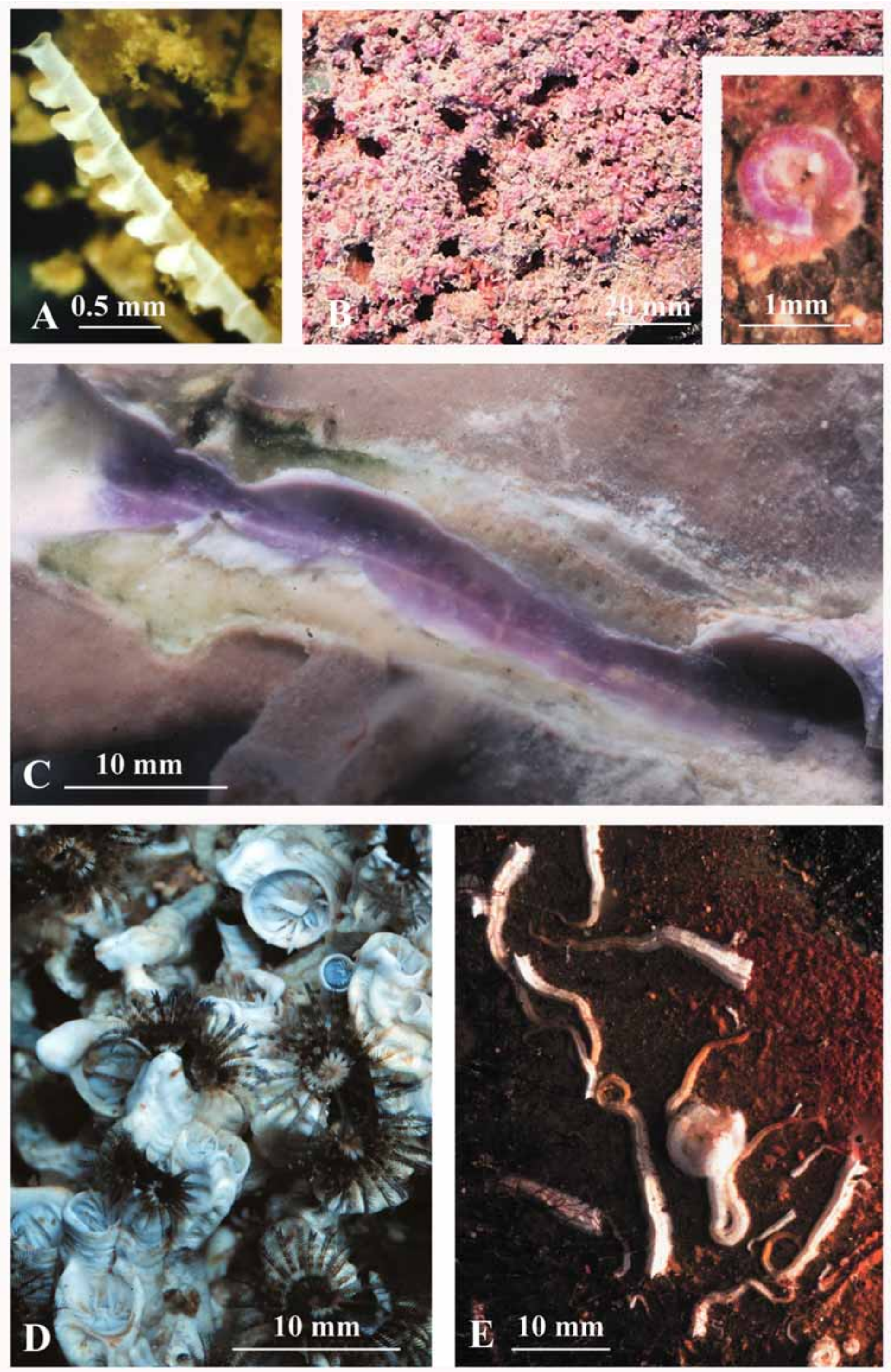

FIGURE 2. Variability of serpulid tube morphology. A—*Rhodopsis pusilla*, tube with brood chambers from Japan, Okinawa (photo E. Nishi), B—*Spiraserpula caribensis*, aggregations (pink/purple) mixed with *Homotrema rubens* (Lamarck, 1816; red) and some filogranids (white) from the Netherlands Antilles, Curaçao, St. Jorisbaai, about 100 m from sea; from undersides of boulders and large metal poles in surf (legit & photo H. A. ten Hove), the insert shows a single *Spiraserpula caribensis* tube from the Netherlands Antilles, Curaçao, Zakitó (legit and photo H.A. ten Hove), C—Internal colouration of *Spirobranchus giganteus* tube, the Netherlands Antilles, Curaçao, Bullenbaai, E, near swimming pool, 28 April 1970; sandflat, 5–6 m, from living *Millepora*, legit H.A. ten Hove, St. 2048A (photo C. Roessler), D—*Galeolaria caespitosa* aggregation from Australia, Sydney, Balmoral (photo N. Tait), E—Tubes of *Pseudovermilia occidentalis* (triangular) and *Hydroides bispinosus* (enrolled on itself) from the Netherlands Antilles, Curaçao, Bullenbaai, near swimming pool, from rusted can in sand, Sta. 2048 (legit & photo H.A. ten Hove).

The inside of the tube, the lumen, is even more underexploited as a character than the outside. The internal cross-section of the tube lumen in serpulids is mostly circular. However, in species of the genus *Spiraserpula* Pillai & ten Hove, 1994, the lumen can also be oval with a "waist", the cross-section is like a ∞ without the middle line dividing it in two parts (Fig. 7E). Such a lumen shape is a result of the internal tube structures (ITS) in the form of ridges and crests that are known only for this genus. There is a single observation of a *Protula* species with a dorso-ventrally compressed lumen (Netherlands Antilles, Curaçao, Piscadera Bay, 20 m, reef, 12 Jan. 1990, ten Hove unpublished). Finally, two series of small pits in the substrate-side of the lumen have been described for *Spirobranchus corrugatus* (see ten Hove & Nishi 1996).

Tabulae or transverse tube elements (Fig. 7C) may partition the oldest parts of the tube as response to tube damage in *Pyrgopolon*, *Pomatoceros*, *Spirobranchus*, and *Serpula* (e.g., Lamarck 1818: 362, McIntosh 1923 fig. 168, Mörch 1863: 349, ten Hove 1973, ten Hove & van den Hurk 1993: 27), and rarely so in *Hydroides* (Perkins pers. comm.; Breton & Vincent 1999 fig. 14), as well as in *Crucigera*, *Ficopomatus*, *Hyalopomatus*, and *Neovermilia* (present paper).

Attached parts of the tubes are often flattened and may contain alveolar structures as for instance in *Filogranula*, *Pomatoceros*, *Semivermilia*, and *Spirobranchus* (e.g., Bianchi 1981 figs 32c, 36a, 42b, 43b; McIntosh 1923 fig. 169–170; Thomas 1940 Plate 1 figs 2, 3). According to Thomas (1940: 7) it is probable that alveoles are left to economize the amount of material used.

The ornamentation of the external tube surface of the serpulid tubes is variable within populations and may be quite elaborate (e.g., *Janita fimbriata*, see Bianchi 1981 fig. 39), but most typically consists of longitudinal and transverse elements (see Bianchi 1981 fig. 6 for possibilities). Serpulids may have a single major prominent longitudinal keel (as in *Pomatoceros* or *Laminatubus*, e.g., ten Hove & Zibrowius 1986 fig. 1) or two identical major keels may be present (as in *Galeolaria*, e.g., Dew 1959 figs 11, 12), even though such keels may be indistinct as in some *Hydroides* spp. In other cases, the major longitudinal keel is supplemented by secondary more subtle ones (compare *Pomatoceros triqueter* with *P. lamarckii* in Bianchi 1981 figs 42a, b, 43a, b). Finally, a number of longitudinal keels may be present (*Metavermilia multicristata*, *Serpula vermicularis*, e.g., Bianchi 1981 figs 29, 13). The keels may either be sharp (*Semivermilia agglutinata*: Bianchi 1981 fig. 33) or smooth (*S. pomatostegoides*: Bianchi 1981 fig. 34), straight (*Hydroides uniformis* Imajima & ten Hove, 1986 fig. 1) or wavy (as in *Semivermilia crenata*: Bianchi 1981 fig. 31), or in the form of longitudinal rows of larger denticles and smaller tubercules (*Spirobranchus lima*: Bianchi 1981 fig. 40).

Transverse tube ornamentation includes simple growth striations such as in *Protula*, circular growth rings (*Josephella marenzelleri*: Bianchi 1981 fig. 50), flaring smooth trumpet peristomes directed toward the distal end of the tube as seen in *Ficopomatus enigmaticus*. The most complex denticulate peristomes are found in *Filogranula stellata, F. calyculata,* and *F. gracilis* (e.g., Bianchi 1981 figs 35–38).

A combination of numerous longitudinal keels and transverse ridges may form structures as in *Metavermilia arctica* Kupriyanova (1993d fig. 1K) or *Vermiliopsis labiata* (see Imajima 1977 fig. 4). Tube ornamentation in the free distal and attached proximal parts of one tube may differ (e.g., *Filogranula annulata*: Bianchi 1981 fig. 37, *Placostegus incomptus* Ehlers (1887 pl. 60 fig. 8) or *Pyrgopolon differens* (ten Hove, 1973 pl. IIb)). Tube ovicells used for brooding such as found in *Rhodopsis* (Fig. 2A), *Chitinopoma*, and *Pseudovermilia* (Fig. 7D) are also a form of tube ornamentation.

The tube wall is usually uniformly opaque, but in species such as, for example, *Ditrupa arietina* and *Laminatubus alvini*, the walls consist of two distinct layers: an inner opaque and outer hyaline layer; the latter may cause a shiny surface in tubes of e.g., *Bathyvermilia* and *Serpula crenata*. A hyaline granular overlay is present in tubes of *Spiraserpula* species (see ten Hove & Pillai 1994), as well as in *Serpula oshimae* and *S. hartmanae*, in *Hydroides mongeslopezi* and also in an undescribed species of *Apomatus* (ten Hove unpubl.). It may have been overlooked in other taxa. *Placostegus* (Fig. 1F), *Vitreotubus*, and *Neomicrorbis* have entirely transparent tubes, and this situation also may occur in some spirorbins (e.g., *Paradexiospira vitrea* (Fabricius, 1780) and *Protolaeospira striata* (Quiévreux, 1963)). Scanning electron microscopy observation of some of these tubes (ten Hove & Zibrowius 1986) suggested that transparency is caused by preferred orientation of large crystals in the structure of the tube, while small, disorderly arranged crystals give an opaque appearance. Most recently, Vinn *et al.* (2008) described up to four different layers found in 34% of serpulid tubes, based on SEM and they also found a positive correlation between regular crystal orientation and tube transparency.

Aggregated tubes. Serpulids like *Salmacina*, *Filograna*, and *Filogranella* build characteristic open aggregates made of numerous tiny branching tubes (Fig. 1B). Nishi (1992c) illustrated that the "colonies" are the result of combination of asexual budding and gregarious larval settling. Asexual reproduction also leads to a chain of tubes in *Filogranula* (cf. ten Hove 1979: 286) or a network of branching tubes in *Josephella marenzelleri* and *Rhodopsis pusilla* (see George 1974, Ben-Eliahu & ten Hove 1989, Nishi 1992c, Nishi & Yamasu 1992). Asexual reproduction also has been reported for *Spiraserpula* (Pillai & ten Hove 1994 fig. 16B). These "colonies" are different from dense aggregations such as found in *Galeolaria caespitosa* (Fig. 2D), *Ficopomatus enigmaticus* or some or some *Hydroides* spp. resulting from gregarious larval settling only. For a review of serpulid "colonies" see ten Hove & van den Hurk (1993).

Tube colour. Serpulid tube colour is most commonly white, however in some species completely or partly pink, bluish, orange (e.g., *Spirobranchus*, *Serpula* and one *Hydroides*), or purple (Fig. 2B), as well as mustard (both *Spiraserpula*), or even white with dark-brown cross-striation as in *Serpula vittata* (as *S. palauense* Imajima, 1982 fig. 2m; Fig. 1C). Sometimes inner tube parts can be coloured as in tropical *Spirobranchus* spp. (ten Hove 1970, Smith 1985, Fig. 2C). In individual tubes of small *Serpula* spp. colour can change from pink to white in a few millimeters near the entrance of the tube (ten Hove unpublished).

The general morphology of the body

Serpulids (and sabellids) have a body that is clearly divided into three regions: branchial crown, thorax, and abdomen (Fig. 5A–D). The branchial crown is composed of a number of radioles each bearing a double row of ciliated pinnules. One of the radioles is usually transformed into the opercular peduncle (Fig. 5C, D, pd) and distally bears the operculum (Fig. 5B–C, op). The base of the branchial crown is surrounded by the collar, which continues as the thoracic membranes, a structure found only in serpulids. The border between thorax and abdomen is marked by chaetal inversion, with the dorsal notochaetae and ventral comb-shaped neurochaetae (uncini) of the thorax changing places such that abdominal uncini become dorsal (notopodial) and abdominal chaetae become ventral (neuropodial) in the abdomen.

Although serpulids are often very brightly coloured and the colour of the animals indeed may be useful in the field (Fig. 1), as a taxonomic character the type of colouration is of little use as colour is rapidly lost in preservatives, particularly in alcohol. The colouration may also be a subject to significant interspecific variability (e.g., in the *Spirobranchus corniculatus* complex: Fosså & Nilsen 2000: 140, 147; Song 2006, as *S. giganteus*). It may even vary within a single specimen, for instance, in *Spirobranchus* the colour of both lobes of a branchial crown may be so different as blue and red (ten Hove unpubl.). Føyn & Gjøen (1953) describe a Mendelian pattern found in the colouration of branchial crowns of *Pomatoceros triqueter,* with 2628 brown, 218 blue, and only 2 orange branchial crowns.

The branchial crown

The branchial crown, used for feeding and respiration, with each radiole bearing rows of paired ciliated pinnules is a distinct feature of sabellids and serpulids. The crown is considered to be prostomial (cf. Segrove 1941). The radioles of the branchial crown are attached to paired lobes (Fig. 6F, bl) located laterally on both sides of the mouth. The branchial lobes are completely separate from one another in serpulids, but are fused together in some sabellids (e.g., *Chone* Bush, 1905 and *Sabella* Linnaeus, 1767, see Fitzhugh (1989)).

The number of radioles used to delineate some taxa (e.g., *Salmacina tribranchiata*) is an unreliable character. In individual species, the lower limit of the number of radioles has no value, since all juveniles have fewer radioles than adults. The upper limit is possibly an exponent of size, possibly genetically determined. However, the variation within individuals of larger species (e.g., *Spirobranchus* and *Protula*) is enormous. Kupriyanova (1999) showed that within some *Serpula* species number of radioles (as well as number of opercular radii) is directly correlated with animal size.

The bases of the radioles in some sabellids and serpulids may be joined with an inter-radiolar membrane (Fig. 3A, E, mb). In serpulids, the inter-radiolar membrane is very high in *Pomatoleios* and it unites radioles for up to half of their length in *Pyrgopolon.* The membrane is also well developed in *Spirobranchus* (and may bear processes in some *Spirobranchus* spp.), *Pomatoceros*, *Pomatostegus*, *Galeolaria*, *Dasynema*, and *Neovermilia*. It is also commonly found in species of *Serpula*, *Spiraserpula*, and *Crucigera*, but is very rare in *Hydroides* (see Bastida-Zavala & ten Hove 2002). The membrane is absent in the serpulid genera *Ficopomatus*, *Filograna*, *Pseudochitinopoma*, *Pseudovermilia*, *Salmacina*, and *Vermiliopsis*.

Eyes. Photoreceptors may be found not only in the anterior region but almost anywhere in annelids, including Sabellida, from ephemeral eye-spots on epitokous segments (notably in Eunicidae) to those on pygidia (e.g., *Fabricia* Blainville, 1828; *Augeneriella* Banse, 1957 (both in Fitzhugh 1989)). The serpulids are no exception to this plasticity, as e.g., shown by the girdle of thoracic (peristomial?) red-pigmented ocelli in *Placostegus* (Fig. 1F, te). One difficulty is that the eyespots may disappear in preservative in a comparatively short time. In the diagnoses given below, “presence” or “absence” has been observed in fresh material; “not observed” indicates that no data have been given in the literature and material could not be (re-)examined by us. Another difficulty is that there has been no consistent terminology, “eye” or “eyespot” can have any of the meanings given below.

Prostomial ocellar clusters. Many serpulids possess a pair of brain-associated clusters of ocelli in the prostomium, apparently the continuation of the larval “eyes” (Smith 1984a, b). For instance, more than 20 preserved specimens of *Filograna implexa* showed 2 rows of 4–6 pigmented cells in the prostomial area, presumed to be prostomial “eyespots”, however without lenses; on the other hand, more than 20 non-operculate specimens of *Salmacina* spec. from Marseille lacked pigmented spots in the prostomial area (ten Hove & Pantus 1985). *Metavermilia multicristata* has prostomial “eyes” (Zibrowius 1968a: 86, 128, as *Vermiliopsis*), presumably simple ocelli. On the other hand, in fresh *M. multicristata* specimens from the Seychelles “eyespots” were invisible (ten Hove unpublished).

Branchial eyes. In serpulids, most photoreceptors are associated with the branchial crown (including the operculum), and these could be termed collectively “*branchial eyes*”. Apart from ultrastructural differences, and although intermediate types do occur, photoreceptors may roughly be grouped into three groups for which we propose the following “standard” terms:

Ocelli: single eyespots with (or without a single lens). These may occur on the axis of radioles (e.g., *Vermiliopsis* spp., some taxa of the *Spirobranchus tetraceros*-complex), but also near the inter-radiolar membrane (Fig. 6D), on the peduncle or the operculum (e.g., a hundred or more ocelli, not rigidly patterned, on the ventral rim of the opercula of *Pomatostegus stellatus* and *Spirobranchus corrugatus*).

Ocellar clusters: loose, bulging groupings of approximately 2–20 ocelli, generally with as many lenses. Occurrence on various radioles (notably *Apomatus* spp.), or peduncle (e.g., *Semivermilia pomatostegoides*, on border between peduncle and opercular ampulla). *Dasynema chrysogyrus* has 5–6 pairs of ocellar clusters, with 2–11 lenses each (Imajima & ten Hove 1984). Uchida (1978) reports *Microprotula ovicellata* as having 8–11 pairs of “eyespots” (ocellar clusters) on each radiole, and a red "eye" (probably a simple ocellus) in the base of each branchial tuft.

Compound eyes: more or less rigidly patterned groupings of ocelli (Fig. 6A). In the *Spirobranchus giganteus*-complex *sensu lato*, for instance, there are 600–1000 lenses in a compound eye, located at the base of each branchial lobe (Fig. 6E), proximally on the first left and right radiole. These might very well be capable of receiving visual impressions in a similar way as in crustaceans (Smith 1984a). The radii of the opercular funnel in *Hydroides lambecki* and of the operculum of *Pyrgopolon ctenactis* show circular groupings of 20–30 red pigmented bulging structures (Fig. 6B), which certainly are very reminiscent of small compound eyes. The knobs at the base of the radioles in *Protula balboensis* (illustrated by Monro 1933 fig.

30A) most probably too are a series of large ocellar clusters or small compound eyes, as is evident from syntypes (BMNH 1933:7:10:265–266) and additional material in LACM-AHF (present paper).

Some interesting literature observations could not be confirmed by us. For example, *Protula intestinum* is reported to have two elliptical compound eyespots at both sides of the head by Radl (1912: 246, as *P. protula*), but we cannot confirm this observation. In *Protula* spp. we found scattered single ocelli along the rhachis, radioles with two rows of single red ocelli ("eyespots"), to radioles with up to 9 bright red transverse bands, marking paired bulging ocellar clusters (Fig. 6F). *Janita fimbriata* is reported as sometimes with stalked "eyes" on the base of the pinnules (as *Omphalopoma spinosa* by Langerhans 1884, fig. 45a; by Fauvel 1927, Rioja 1931, both as *Omphalopomopsis*); these presumably ocellar clusters could not be found by us in preserved material.

Field notes on about 80 serpulid taxa made by one of us (HAtH) also show no overall consistent patterns. For instance, in *Crucigera tricornis* observations are contradictory, from a single medial row of transparent lenses on the rhachis of each radiole in one specimen to the same plus a row of bulbous bright red spots, presumably large ocellar clusters or small compound eyes, above the inter-radiolar membrane in another. There are indications that occurrence of photoreceptors may be dependent on the (dorsal to ventral) position of radioles in the branchial crown as exemplified by the different observations in *Spiraserpula paraypsilon*, where there are up to 6 eyespots (type not specified) at the base of radioles, however, neither in dorsal-most radiole nor in the 3 ventral radioles, while in other specimens no lenses were seen (not looked for in the correct position?).

In conclusion, compiled data from the literature and field notes, altogether from almost a hundred species in 30 genera, show no consistent patterns. Moreover, eyespots and eyes are difficult to find in preserved material. These characters have not been systematically studied in most serpulids nor mentioned in taxonomic descriptions. They may be useful in some taxonomic decisions, but need more consistent study.

Stylodes. An unusual feature found on serpulid radioles is external unpaired finger-like stylodes (Fig. 14A), an autapomorphy found in the serpulid genus *Dasynema* only (Imajima & ten Hove 1984); paired stylodes are known in the sabellid genera *Pseudobranchiomma* Jones, 1962 and *Branchiomma* Kölliker, 1858 (e.g., Tovar-Hernández & Knight-Jones 2006, figs 1C–F).

The radiole arrangement. In most small serpulids, radioles are arranged in two semi-circles when outside the tube in the feeding position (Hartman 1969 frontispiece, present Fig. 1E). Depending on the length of branchial lobes, short pectinate arrangement (as in *Semivermilia* spp.: Zibrowius 1968a Plate 4 fig. 26) and long pectinate arrangement (*Pseudovermilia occidentalis*: ten Hove 1975 Plate II f) of radioles is possible in serpulids. Spiralled arrangement of radioles occurs when the ventral margins of the branchial lobe continue to grow, adding radioles and spiralling along the inner margin of the crown. In some large serpulids, especially in the large species of the genus *Spirobranchus*, the crown is a pair of beautiful spiralled cones (hence the name), the arrangement that is responsible for the common name "Christmas-tree worm" for *Spirobranchus* (Fig. 1D). Some *Protula* species, such as the huge *Protula bispiralis* (including *P. magnifica* (Straughan, 1967b)) also have distinctly spiral branchiae. Perkins (1984) and Knight-Jones & Perkins (1998) suggested that spiralling of branchiae is an exclusively size-related phenomenon. However, Fitzhugh (1989) pointed out that whereas in juveniles of some sabellid species the branchial base is semi-circular and begins to spiral ventrally with increase in size, other small species of the same genus never exhibit spiralling when mature.

Filamentous tips. Long filiform ends of radioles (filamentous tips) are sometimes mentioned in serpulid descriptions, however, there has been no systematic documentation of these structures across the group. Bastida-Zavala & ten Hove (2002) distinguished 4 size classes of filamentous tips in *Hydroides*. They found the character to be variable on the infraspecific level: 4 taxa showed filamentous tips in a single size class, 12 in two, 6 in three, while in one species the size ranged through all 4 sizes, from absent to very long.

Mouth palps. The presence of filiform dorsal mouth palps is a character not commonly used in serpulid systematics (ten Hove 1973). These processes are held facing anteriorly and ventrally across the mouth into the centre of the branchial crown on each side. Although considered to be typically absent by some authors (Day 1967, Pettibone 1982), these palp-like processes are likely to be a consistent feature of serpulids, albeit inconspicuous in larger species. Orrhage (1980: 155–156) distinguished three types of palps: 1) lip associated radioles (*Sabella*, *Potamilla* Malmgren, 1866, *Euchone* Malmgren, 1866, *Chone*); 2) lip associated pinnules (*Potamilla*, *Euchone*, *Chone*, *Pomatoceros*, *Ditrupa*, *Hydroides*, *Placostegus*, *Serpula*, in the latter almost invisible); 3) *de novo* outgrowths of the dorsal lip (*Apomatus*, *Protula*, ?*Filograna*). Unfortunately Orrhage studied only a few genera, but apparently in serpulids all "palps" may not be homologous. As opposed to these dorsal palps, ventral mouth palps have been reported for *Pseudovermilia madracicola* and *Rhodopsis* by ten Hove (1989) and Ben-Eliahu & ten Hove (1989). However, re-studying the types of *P. madracicola*, it becomes apparent that the palps are attached to the dorsal lip (which already could be suspected from ten Hove's figure (1989 fig. 23)), and that it having been attributed to being connected to a ventral lip is incorrect. In absence of well preserved material of *Rhodopsis* we have not been able to check the position here, but we would not be surprised if the same applies to the "ventral" palp of Ben-Eliahu & ten Hove (1989). "Not observed" in the diagnoses below indicates that no data have been given in the literature and material either could not be (re-) examined by us, or was not preserved well enough.

The operculum

A modified radiole, the operculum, serving as a tube plug when a worm withdraws into its tube, is generally present in serpulids (Fig. 4A–F), but is always absent in sabellids and sabellariids. The opercular structure in serpulids has traditionally been considered one of the most important taxonomic characters.

Some serpulid taxa are non-operculate: *Salmacina*, *Protula* (Fig. 5A, 6F), *Protis*, *Filogranella* (Fig. 6C), *Floriprotis* (Fig. 1E), and *Microprotula*. However, *Salmacina* and *Protula* are practically indistinguishable from the nominal operculate taxa *Filograna* and *Apomatus* (Fig. 5B) respectively. As a consequence, some authors considered *Apomatus* to be a synonym of *Protula*, and mentioned individual specimens of what was considered to be *Protula tubularia* with soft globular opercula (Zibrowius 1968a, Hong 1984, Bianchi 1981). However, based on the examination of thoracic blood-vessel patterns in over a hundred specimens ten Hove & Pantus (1985) regarded operculate and non-operculate forms found in the Mediterranean as belonging to two different genera, *Protula* and *Apomatus*. Differences have been elucidated in a key by Ben-Eliahu & Fiege (1996: 27). Whether *P. tubularia* really shows operculate and non-operculate individuals remains unclear.

Normally non-operculate species may include operculate individuals and normally non-operculate genera may include operculate species, as mentioned for *Protis* (by Kupriyanova 1993b, Ben-Eliahu & Fiege 1996, Kupriyanova & Jirkov 1997) and for *Paraprotis* (by Imajima 1979). Normally operculate genera occasionally include non-operculate species (e.g., ten Hove 1989: 136, Fiege & ten Hove 1999 for *Spirobranchus nigranucha*, Lechapt 1992 for *Neovermilia anoperculata*, Knight-Jones *et al.* 1997 for *Hyalopomatus cancerum*). In *Vermiliopsis striaticeps*, the functional operculum is accompanied by a rudimentary operculum on a normal pinnulate radiole, or a modified, almost smooth radiole on the opposite lobe (Bianchi 1981 fig. 26). Ludwig (1957) showed that if the operculum in *Vermiliopsis* is amputated, a new one is formed at the tip of the opposite radiole. *Apomatus* spp. also may have a slightly modified radiole, a pseudoperculum, opposite the functional operculum. *Protis polyoperculata* has up to 6 opercula, some of them smaller, which probably can be classified as pseudopercula.

The serpulid genera *Crucigera*, *Hydroides*, *Serpula*, and *Spiraserpula* are uniformly characterized by a pseudoperculum (Fig. 5C, ps), a club-shaped underdeveloped operculum carried on short modified (rudimentary) radiole on the opposite side of the opercular crown. The pseudoperculum can develop into a functional operculum if the latter is shed or lost (Okada 1932, Schochet 1973a, b). Sometimes, two functional opercula can be found simultaneously, for example, in *Hydroides* bioperculate forms are not uncommon (Zeleny 1902, Ichikawa & Takagaki 1942, Schochet 1973a, b, ten Hove & Ben-Eliahu 2005), or some taxa from that group may have two rudimentary opercula only. For instance, in a population of *Hydroides spongicola*, 75%–95% of the individuals possess two small pseudopercula instead of one functional and one rudimentary operculum; a similar phenomenon has been reported for populations of *Crucigera inconstans* (see ten Hove & Jansen-Jacobs 1984: 164).

Throughout *Spiraserpula*, there is a trend of opercular loss. In *S. massiliensis*, for instance, Pillai & ten Hove (1994: 53) found 12 operculate specimens and 25 non-operculate ones, although mostly two pseudopercula are present. The trend culminates in some specimens of *S. paraypsilon*, where even the pseudopercula may be lost (Pillai & ten Hove 1994).

One wonders if this loss of a functional defence mechanism has some relation to the gain of an alternative defence mechanism such as grab-footholds in the tube for *Spiraserpula*; the extremely irritating chemical defence mechanism of the host sponge *Neofibularia nolitangere* (Duchassaing & Michelotti, 1864) as extra protection for *Hydroides spongicola*; the occurrence deep down branches of species of *Acropora* Oken, 1815 protecting *S. nigranucha* against predation; and the symbiotic *Floriprotis* may have extra protection of its host corals. Knight-Jones *et al.* (1997) also suggested that in serpulids secondary loss of the operculum could be an adaptation to certain environmental conditions, such as low oxygen concentration in some habitats.

Opercular structure and reinforcement vary widely from simple vesicular and lacking any reinforcement (*Apomatus* (Fig. 5B), some *Hyalopomatus* (Fig. 3C), some *Metavermilia* spp. and *Protis*) or spoon-shaped (*Filograna implexa*)), to very elaborate ones. Quite commonly, serpulid opercula are reinforced with flat or slightly concave chitinous endplates (*Bathyditrupa*, *Ditrupa*, some *Filogranula* spp., *Janita*, *Marifugia*, *Placostegus*, *Pseudochitinopoma*, and *Chitinopoma*) or elongated distal caps (*Vermiliopsis* (Fig. 3F), *Semivermilia*) with or without distal thorns (*Pseudovermilia*, some *Metavermilia* spp.). *Ficopomatus* and *Rhodopsis* show a large number of chitinous spines sometimes imbedded in or inserted into a chitinous base. In *Bathyvermilia*, *Dasynema*, and *Vermiliopsis labiata* the chitinous endplates are additionally reinforced by encrusted calcareous deposits. Several serpulid genera have opercular reinforcements in the form of calcareous endplates (*Pomatoleios*), sometimes adorned with non-movable horns of varying complexity (*Pomatoceros*, *Spirobranchus*: Fig. 3E, 4A). The two species of *Galeolaria* (Figs 2D, 4B) are the only serpulids that have opercula armed with very elaborate movable calcareous spines. In the genus *Metavermilia* a range of opercular forms is found (see Nishi *et al.* 2007), from a spherical soft operculum in *M. inflata*, to an inverse conical ampulla with a horny distal cap in *M. multicristata*, with a complex multi-tiered chitinous structure in some other species such as *M. acanthophora* (Fig. 4C). Another multi-tiered opercular reinforcement in *Pomatostegus* spp. forms one of the most complex opercula known in Serpulidae (see Imajima 1977 fig. 7).

Finally, calcareous opercular reinforcement is extreme in *Pyrgopolon* (Fig. 6B, including *Sclerostyla*, and the nominal fossil genera *Hamulus* Morton, 1834 and *Turbinia* Michelin, 1845), where both the operculum and opercular talon (reaching deep into the peduncle) are entirely calcified (ten Hove 1973). Calcareous talons are otherwise only found in spirorbins (e.g., Bianchi 1981 figs 54, 56, 58, 64) and *Neomicrorbis* (present paper); Pillai (1965 fig. 22H) and ten Hove (1973 fig. 43) report small talons in *Pomatoleios*, however, these do not reach beyond the opercular ampulla.

The nature of opercular reinforcement is still unclear in some serpulids, for example, in *Laminatubus* and *Neovermilia globula* (Fig. 4E) the opercular distal cap is made of stouter material than the proximal soft bulbous part (ampulla), however, without either calcareous or chitinous reinforcement. It might be a thickened cuticle similar to that found in the opercula of *Serpula* (Thorp *et al.* 1991) and *Crucigera*.

The funnel-shaped opercula of *Crucigera*, *Hydroides*, *Serpula*, and *Spiraserpula* are very distinct in being composed of numerous fused radii (Figs 3A, D, 4F, 5C). While in species of *Serpula* and *Spiraserpula* the opercular funnel is simple, it possesses basal bulbous processes in *Crucigera* and is armed with a distal verticil of chitinous spines in *Hydroides* (Fig. 4D). The basal processes of *Crucigera* (Fig. 3D, bk) are thought to be homologous to the proximal funnel of *Hydroides* by ten Hove (1984). The similar basal knobs in the operculum of *Janita* (Fig. 24A) may be a convergent development. The calcareous long stalked funnel-shaped operculum of *Pyrgopolon* (Fig. 6B) appears superficially similar to the funnels of the *Serpula*-group (e.g., Fig. 5C), but this similarity is of a convergent nature.

Ontogeny of operculum and peduncle. Which radiole is ontogenetically modified into the peduncle has been a matter of debate. Pillai (1970) argued that the opercular peduncle of spirorbins is a modified second radiole, whereas, in his opinion, it always is the first radiole in serpulins. He suggested, therefore, that spirorbin operculum is not homologous to the serpulin operculum.

However, to determine which radiole is modified into the peduncle, ontogenetic studies are needed, and these do not give a clear-cut answer. According to the embryological literature, the operculum is formed from the 3rd radiolar bud dorsally (e.g., Zeleny 1905 for *Hydroides*; Segrove 1941 for *Pomatoceros*; Vuillemin 1965 for *Ficopomatus* and spirorbins). Salensky (1884) is less clear for spirorbins, but contrary to Vuillemin (1965) seems to indicate an origin from the second dorsal bud. According to Matjašič & Sket (1966), in *Marifugia*, the operculum even may be formed from the 4th radiolar bud dorsally. However, it cannot be excluded that the differences in specifying the buds are due to confusion between radiolar and pinnular buds, such as the later lip-associated pinnule (see different types of mouth-palps, p. 13). Another explanation for the differences in numbering might be found in Smith (1985: 148): “The operculum arises completely independently of the existing radioles. It starts as a small bud at the left side of the prostomium between radioles 2 and 3 [in Smith’s perception radiole 1 becomes the dorsal palp of the mouth], but dorsal to them [thus outside the normal range of radioles], in what is essentially the dorsal position. This bud grows out into a cylindrical opercular stalk with distal swelling, … From the outset it is devoid of pinnules and no corresponding opercular stalk is found on the right side.”

Partly based on the papers above, ten Hove (1984) argued that the peduncle in serpulids is actually the modified second dorsal-most radiole, but in large-bodied serpulids the peduncle migrates during development in such a way that it appears to be formed from the first radiole (or even completely outside the branchial crown, such as the position in *Pomatoceros*).

Ten Hove (1984, 1989) distinguishes between indirect and direct opercular ontogeny. In some serpulids (*Hydroides*, *Serpula*) juveniles develop an operculum on a pinnulated radiole; later, the peduncle loses its pinnules and becomes smooth (= indirect development, e.g., Mörch 1863, ten Hove & Ben-Eliahu 2005). When a functional operculum is lost, the rudimentary operculum develops into a functional one. Direct development means that the peduncle and operculum develop directly from a knob, without a pinnule-bearing stage (Segrove 1941: *Pomatoceros*; Vuillemin 1965: *Ficopomatus*, spirorbins; Matjašič & Sket 1966: *Marifugia*; Smith 1985: 148 *Spirobranchus*). In the event of damage, a new operculum is regenerated from the same peduncle (e.g., ten Hove 1970, figs 122, 123). Marsden & Anderson (1981) gave a figure of the metamorphosing larva of *Galeolaria*; unfortunately they do not specify which of the 3 pairs of buds figured will be the later operculum, but the figure does not essentially differ from that of *Pomatoceros* in Segrove (1941 text/fig. 20). Most probably the opercular development in *Galeolaria* is direct, from a bud without a pinnulate stage, just as in *Pomatoceros*, *Marifugia*, *Ficopomatus*, and spirorbids.

The opercular peduncle

In some serpulid taxa, the branchial radiole that bears the operculum is identical to the other radioles (*Filograna*, *Apomatus*, *Josephella* (Fig. 3B; however, not in *Josephella* populations from the E. Mediterranean (Ben-Eliahu & Payiatas 1999)) and in *Protis*). In most serpulids the operculum is borne on a distinct peduncle (Fig. 3A, C, D, E, F). The peduncle may gradually merge into the basal fleshy part of the operculum (Figs 3E, 5C), or be separated from it by a more or less clear constriction (Fig. 3F).

Morphologically, an opercular peduncle is usually inserted more or less below and between the first and second normal radiole, outside the line of radioles (Fig. 3F). In some genera, the peduncle is located at the base of branchial crown, covering several radioles (*Pomatoceros*, *Spirobranchus*, and *Galeolaria*). In other taxa, such as *Semivermilia*, *Metavermilia* and *Bathyvermilia*, the peduncle is clearly positioned as the second modified radiole (ten Hove 1975). In small specimens/species the insertion of peduncle may be very difficult to observe. In *Semivermilia pomatostegoides* the peduncle is either the second radiole, or inserted below and between first and second.

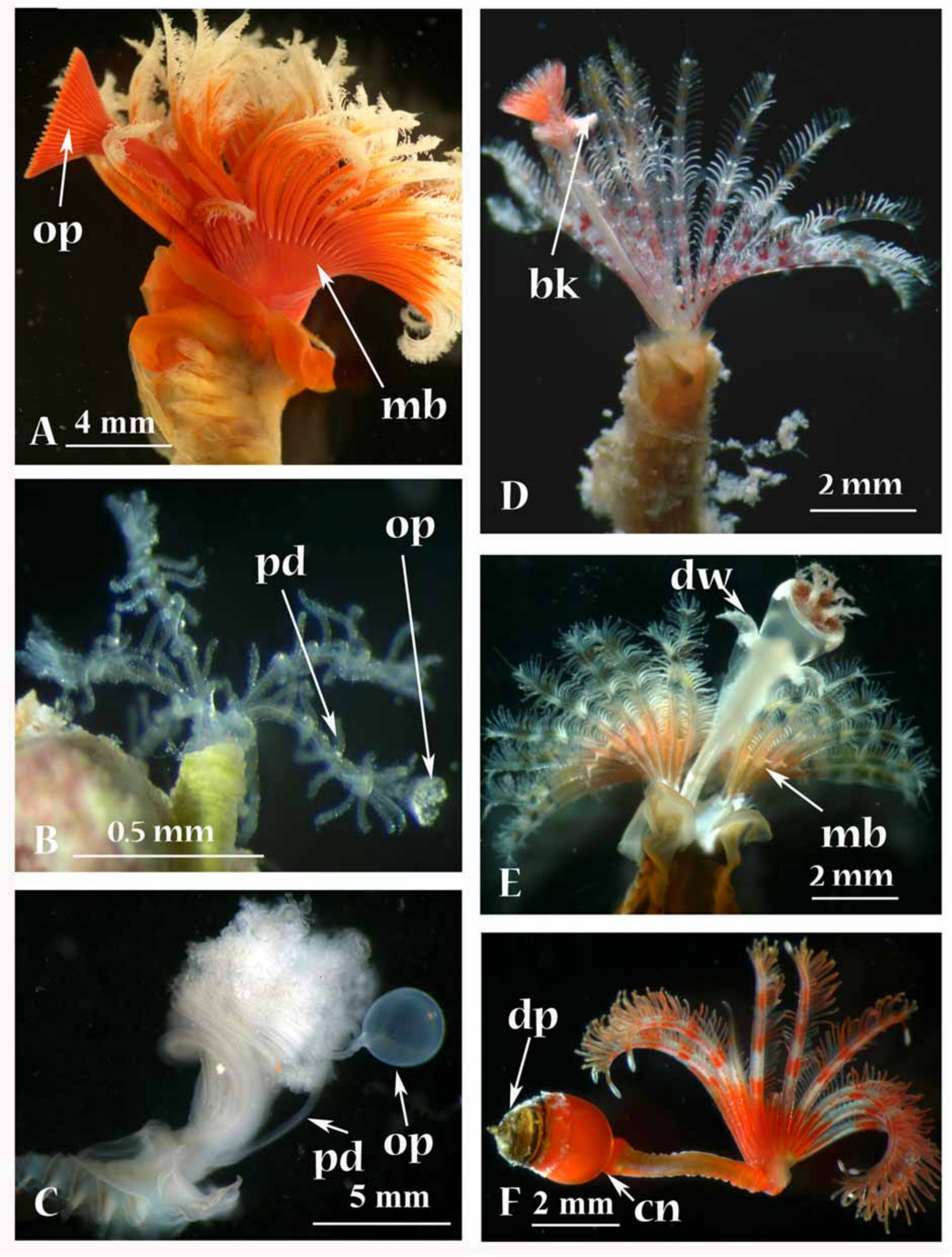

FIGURE 3. Morphology of serpulid anterior ends, removed from tube unless stated otherwise. A—*Serpula jukesii*, from Edithburgh, South Australia, B—*Josephella marenzelleri*, in tube, from Australia, Queensland, Lizard Island, C—*Hyalopomatus* sp., hydrothermal vents, North Fiji Basin, D—*Crucigera tricornis*, from Australia, Queensland, Lizard Island, E—*Spirobranchus tetraceros*, from Australia, Queensland, Lizard Island, F—*Vermiliopsis glandigerus-pygidialis*-complex, branchial lobe with operculum, from Australia, Queensland, Lizard Island (all photos G. Rouse). Abbreviations: op—operculum, mb—inter-radiolar membrane, bk—basal knobs, pd—peduncle, dp—endplate of operculum, dw—distal peduncular wing, cn—constriction between operculum and opercular peduncle.

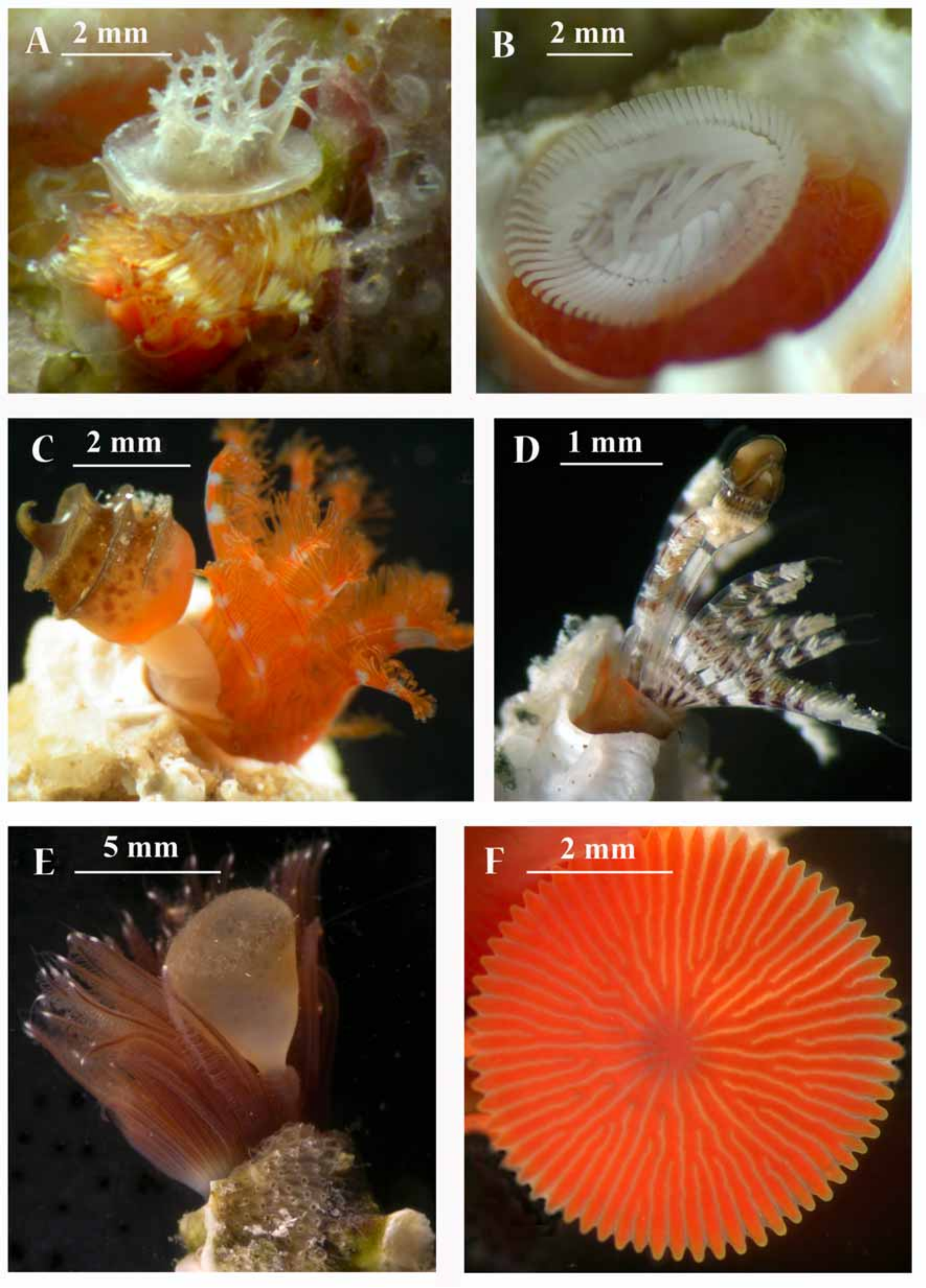

FIGURE 4. Opercular variability in Serpulidae. A—Operculum of *Spirobranchus coronatus*, from Australia, Queensland, Lizard Island, showing calcareous endplate and branching calcareous spines, B—Operculum of *Galeolaria hystrix*, from South Australia, Edithburgh, with elaborate calcareous plates and numerous movable spines, C—Multi-tiered operculum of *Metavermilia acanthophora*, from South Australia, Edithburgh, D—Operculum of *Hydroides tuberculatus*, from Australia, Queensland, Lizard Island, E—Operculum of *Neovermilia globula* in tube, from South Australia, Edithburgh, F—Frontal view of *Serpula jukesii* operculum, from South Australia, Edithburgh, showing numerous radii (all photos G. Rouse).

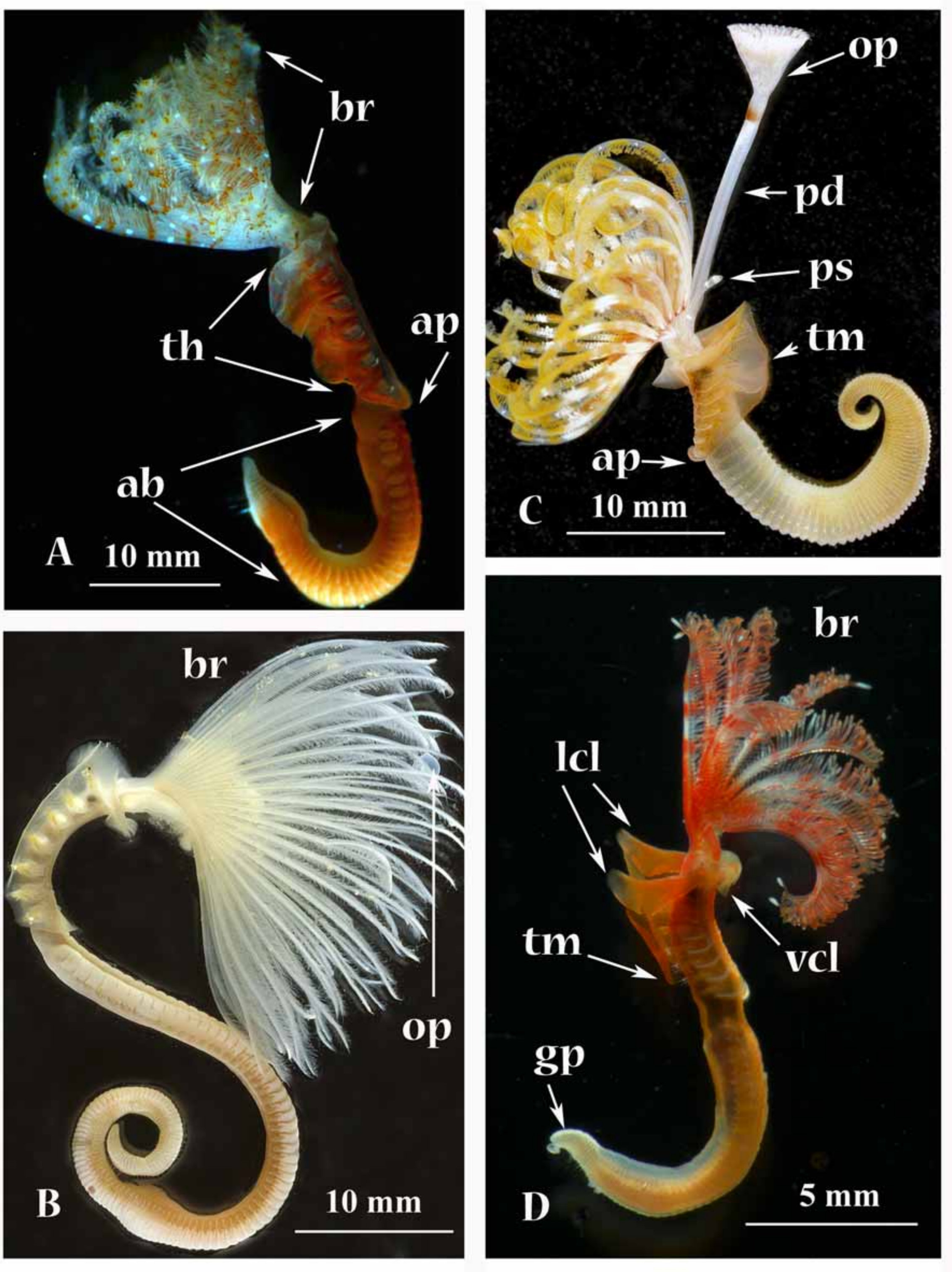

FIGURE 5. General morphology of serpulids removed from their tubes. A—Lateral view of *Protula* sp., removed from tube, Australia, Queensland, Lizard Island (photo G. Rouse), B—Lateral view of *Apomatus* sp., removed from tube, Cape Verde Islands, SE of Cima, 14º57'N, 24º39'W, 165 m, hard bottom with some yellow calcareous sand, van Veen grab, CANCAP St. 7.030 (photo F. Verbiest), C—Lateral view of *Serpula vermicularis*, removed from tube, Cape Verde Islands, SW of Ilha do Maio, Pta Inglez/Pta Preta, 15º07'N, 23º14'W, 69 m, calcareous nodules, CANCAP Sta. 7.058 (photo F. Verbiest), D—*Vermiliopsis glandigerus-pygidialis*-complex, missing branchial lobe and operculum (shown in Fig. 3F), from Australia, Queensland, Lizard Island (photo G. Rouse). Abbreviations: op—operculum, br—branchial crown, ap—apron, th—thorax, ab—abdomen, tm—thoracic membranes, gp—glandular pad, pd—peduncle, lcl—lateral collar lobes, vcl—ventral collar lobe, ps—pseudoperculum.

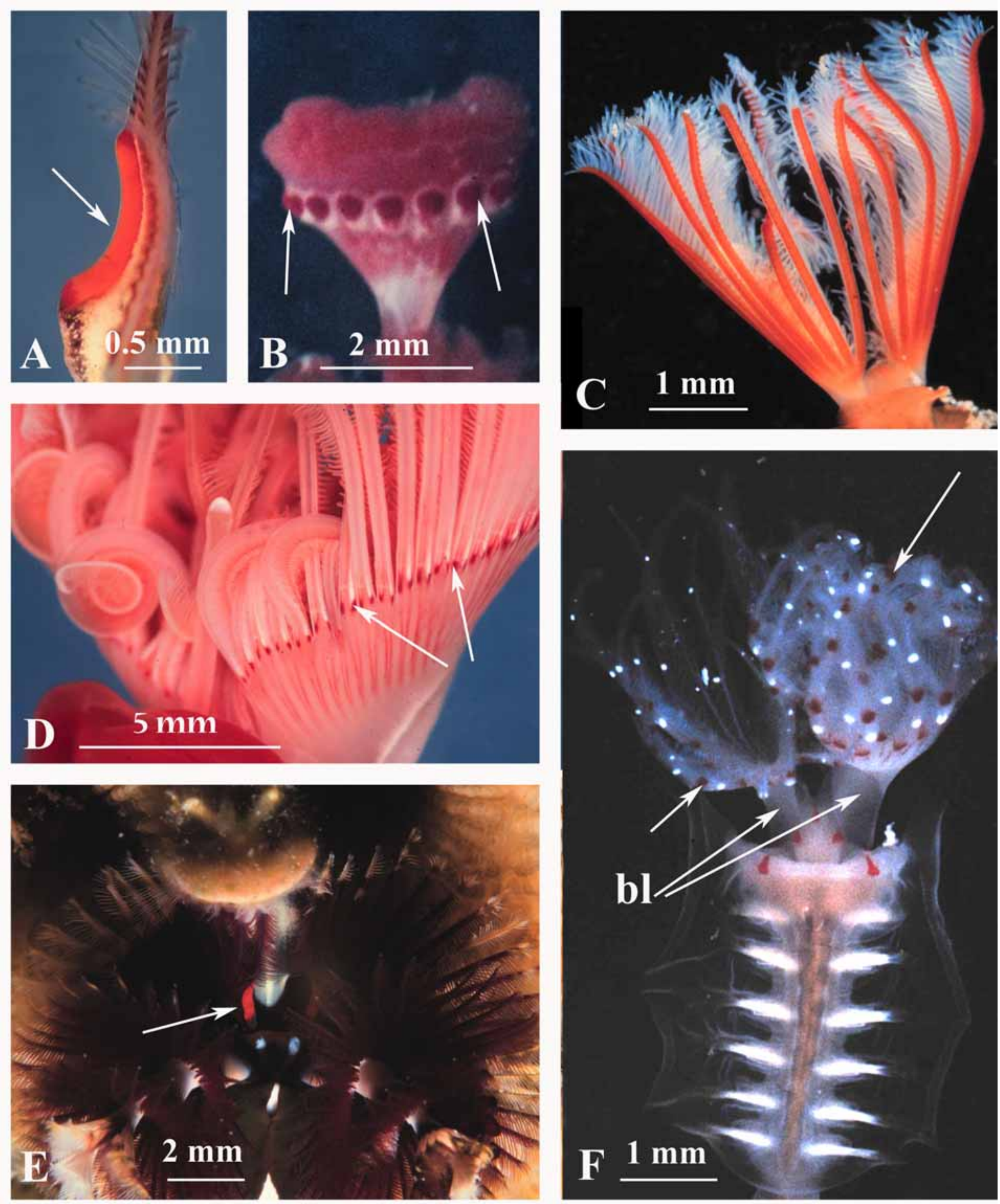

FIGURE 6. Serpulid eyes. A—*Spirobranchus corniculatus*, details of compound eye, Australia, Townsville, 10.1984 (photo R. Smith), B—*Pyrgopolon ctenactis*, with compound eyes on opercular brim, Netherlands Antilles, Curaçao, Boca Hulu, SE, 14.09.1970. Reef, little sand; 28–30 m. From limestone and corals, St. 2041C (legit & photo H.A. ten Hove), C—?*Filogranella elatensis*, branchial crown lacking eyes, Cape Verde Islands, SW of Ilha do Maio, Pta Inglez/ Pta Preta, 15º07'N, 23º13'W, 70 m, calcareous red algae, 1.2 m Agassiz trawl, 25 July1986, CANCAP St. 7.046 (photo F. Verbiest), D—*Serpula jukesii*, branchial crown showing single eyespots at base of radioles, Australia, Queensland, Magnetic Island (photo R. Smith), E—*Spirobranchus cruciger*, showing red compound eye at base of radioles, Israel, Elat in front of Marine Biology Laboratory, 1993 (photo U. Frank), F—*Protula* sp., with red ocellar clusters on radioles, Cape Verde Islands, S of Branco, 16º38'N, 24º41'W, 159 m, 1.2 m Agassiz trawl, CANCAP Sta. 7.152 (photo F. Verbiest). Arrows point to the eyes. Abbreviation: bl—branchial lobes.

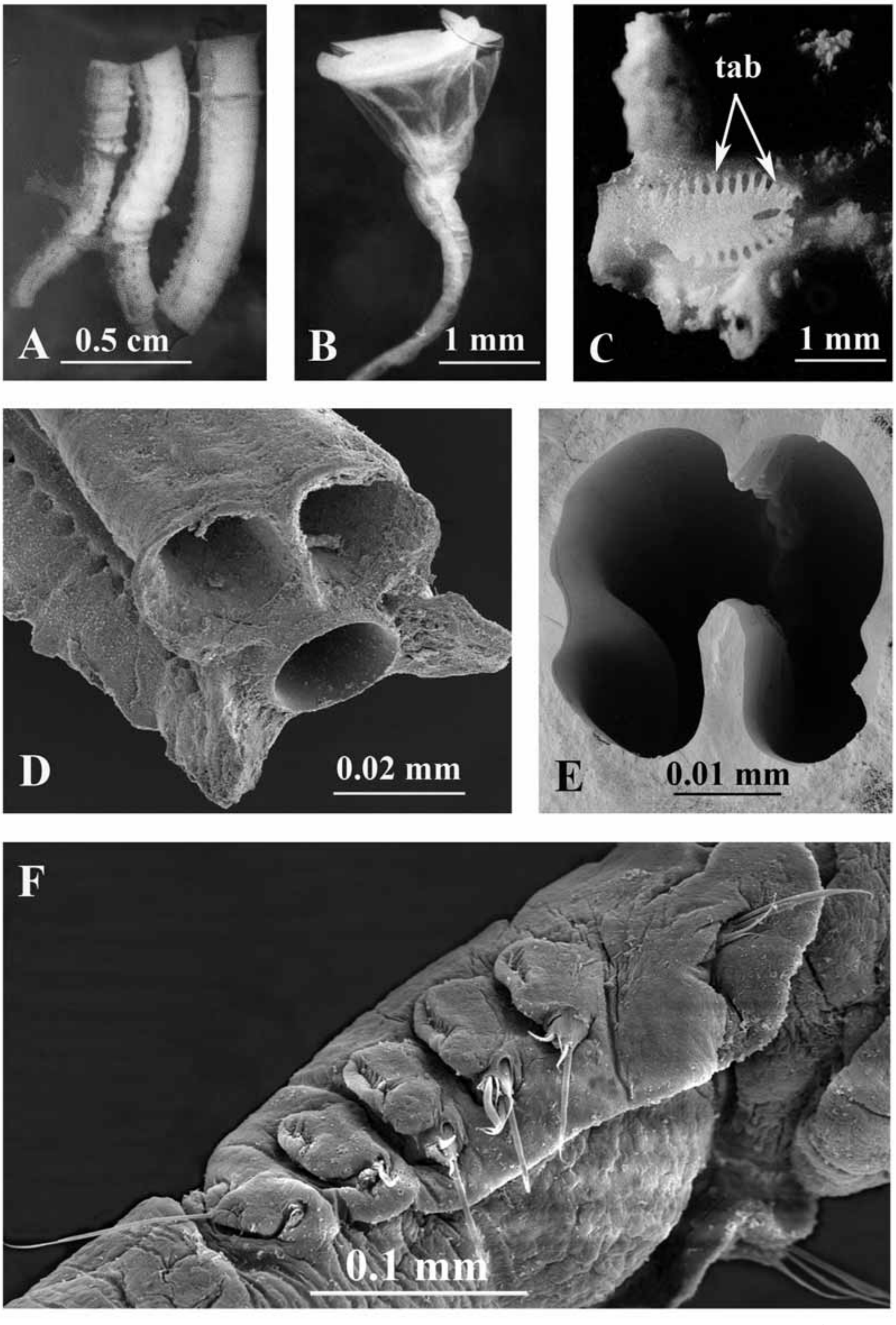

FIGURE 7. Serpulid morphology (continued). *Omphalopomopsis langerhansii,* holotype, a—tube fragments (photo H. Zibrowius), B—Operculum with calcareous endplate and opercular peduncle (photo H. Zibrowius), C—Tabulae in *Pyrgopolon ctenactis* tube, the Netherlands Antilles, Bonaire, Santa Barbara (near Hato), 25 June 1970; basis of reef, 41 m; from dead and living corals, Sta. 2112Ja (legit & photo H.A. ten Hove), D—SEM showing external tube structures (ovicells?) in *Semivermilia* sp., Australia, Queensland, Lizard Island, E—SEM micrograph showing internal tube structures in *Spiraserpula lineatuba* from Australia, New South Wales, Sydney, Long Reef, legit Straughan, det. H.A. ten Hove, exchange from Australian Museum W 4019, ZMA V.Pol. 3450, F—SEM micrograph of morphallaxis (transformation abdominal segments into thoracic ones) during asexual budding in *Salmacina* from Hawaii, Pearl Harbor, Middle Loch, rust bucket, Waikiki of Ingerson, legit R.E. Brock, 12 April 2000 (ZMA stub H94, photo H.A. ten Hove).

Peduncular shape. Normally, the opercular peduncle is lacking pinnules and it is 1.5–3 times thicker than normal unmodified radioles. One of the notable exceptions is the genus *Hyalopomatus*, with the peduncle as wide as the normal radioles (Fig. 3C). However, a number of serpulids, such as *Paraprotis pulchra*, *Filogranula exilis*, *Nogrobs grimaldii*, and *Bathyditrupa hovei*, possess pinnules on the operculum-bearing peduncle. *Filogranula* species other than *F. exilis* typically have smooth peduncles, although Zibrowius (1968a) mentions that a pinnulated peduncle may occasionally occur. In *Nogrobs grimaldii* and *Bathyditrupa hovei*, an inverse conical opercular ampulla is reinforced with a chitinous endplate as in many serpulins, and the peduncle, though pinnulated, is very thick and is clearly a modified radiole (Fauvel 1909, Kupriyanova 1993b). A peduncle without pinnules is smooth in most genera, but it is clearly wrinkled in *Neovermilia globula* (Fig. 4E) and *Janita fimbriata*.

In cross-section, the opercular peduncle is most often cylindrical or slightly sub-cylindrical, but in some serpulids (e.g., *Pomatoceros*), it is nearly triangular. It is flattened in *Bathyditrupa*, *Dasynema*, *Janita*, *Neovermilia*, and *Pomatostegus*. The genus *Metavermilia* has a very characteristic flat ribbon-like peduncle (Fig. 4C).

Peduncular distal wings. Below the operculum, the peduncle may be modified to form distal wings (*Pomatoceros*, *Spirobranchus*, *Galeolaria*, *Pomatoleios*, and *Pomatostegus*). These wings can be narrow, spine-shaped (*Pomatoceros*), or wide and flattened (*Galeolaria*) and running the entire length of the peduncle (*Pomatostegus*). In some *Spirobranchus* species, the wings are rounded, entire, in others they are distally digitated (Fig. 3E, dw) or crenulated. It is unclear whether small latero-dorsal distal “winglets” found on the peduncle of *Dasynema*, *Neovermilia* (Fig. 4E) and the syntypes of *Vermiliopsis glandigerus* are homologous to the larger wings described above or are caused by flattening of the peduncle.

Peduncular proximal wings. *Dasynema*, *Paumotella*, *Vermiliopsis glandigerus* (as observed by us in the syntypes, though not explicitly mentioned by Gravier 1906), and *V. leptochaeta* show a long, one-sided lateral extension along the basal 2/3rds of the peduncle, which also might be termed a wing. In *Vermiliopsis striaticeps*, the presence of this proximal wing appears to be size related, being absent in small specimens, and present in large ones. The character is not always mentioned in existing descriptions. However, being unpaired and basal, the proximal wing most probably is not homologous with the distal ones discussed above.

The collar and the thoracic membranes

Collar. The base of the branchial crown of sabellids and serpulids is surrounded by a membranous peristomial collar, which is absent in sabellariids. The collar in serpulids is usually trilobed, sub-divided into one medio-ventral and two latero-dorsal lobes (Fig. 5D, lcl, vcl). Commonly, the medio-ventral lobe is wider and longer than the lateral ones. The medio-ventral lobe may have an additional incision as in *Floriprotis* and *Tanturia*, thus making the collar quadrilobed. Also, the ventral lobe may bear an additional tongue with 2 lateral incisions, thus making the collar pentalobed as in *Janita fimbriata*. Rarely, the serpulid collar is non-lobed as in *Ditrupa*, *Ficopomatus*, *Paraprotis*, and *Bathyditrupa*. The collar edge is normally smooth in most serpulids (see note under thoracic membranes).

Tonguelets. Small tongue-shaped outgrowths, tonguelets, located between the dorso-lateral and ventral lobes of the collar are present in *Spirobranchus*, *Pyrgopolon* (ten Hove 1970, 1973 fig. 35, as *Sclerostyla*), *Pomatoceros* (termed lappets: Thomas 1940 pl. I fig. 5) and *Pomatoleios*. According to ten Hove (1973), they are not found in *Ditrupa*, *Hydroides*, *Ficopomatus*, *Pomatostegus*, *Serpula*, and *Vermiliopsis*. Thomas (1940: 9, 39) hypothesizes a possible sensory function, since a nerve is seen to enter each tonguelet.

Collar segment. In almost all Sabellida, the first chaetiger is the collar segment lacking neuropodial uncini and bearing only notopodial chaetae (termed collar chaetae). It appears that uncini are secondarily lost in the collar segment, the biramous condition being original in Polychaeta and Oligochaeta. Mainly because the first chaetiger in *Ditrupa* bears both chaetae and uncini, ten Hove & Smith (1990: 103) argue that it is not the collar segment, but actually the second segment. Secondary loss of collar chaetae has been reported to occur incidentally in *Pomatoceros*, *Spirobranchus*, and *Pyrgopolon* (ten Hove 1970, 1973, as *Sclerostyla*). Collar chaetae are absent in the genera *Ditrupa* (see above), *Marifugia*, *Placostegus*, *Pomatoleios*, and *Rhodopsis*), however, juvenile specimens of *Pomatoleios* sometimes do bear collar chaetae. *Placostegus* spp. have a girdle of ocelli (Fig. 1F) resembling a compound eye in the first segment (e.g., Langerhans 1884: 275).

Thoracic membranes. The latero-dorsal collar lobes continue into the thoracic membranes (Fig. 5C, D, tm), a feature found only in serpulids, thus, the presence of thoracic membranes is a synapomorphy for the family (ten Hove 1984 fig. 4). It should be noted that spirorbin taxonomists (e.g., Knight-Jones & Knight-Jones 1977 fig. 1b) do not distinguish between thoracic membranes and the collar, they use the term "collar" collectively for both. The degree of thoracic membrane development varies significantly within the Serpulidae. The membranes may be very short, ending at the first (*Ditrupa*, *Josephella*, *Rhodopsis*) or the second thoracic chaetiger (*Chitinopoma*, *Pseudovermilia*, *Semivermilia*). In some serpulids thoracic membranes reach the mid-thorax (e.g., *Pomatostegus*, *Vermiliopsis* (Fig. 5D, tm), some *Metavermilia*), while in others they continue throughout the length of the thorax and end posterior to the last thoracic segment (some *Spiraserpula* and *Metavermilia* spp.). Thoracic membranes continuing past the end of the thorax often fuse over the first abdominal segment(s), forming a ventral apron (e.g., *Serpula* (Fig. 5C, ap), *Hydroides*, *Protula* (Fig. 5A, ap), *Galeolaria*, *Ficopomatus*, *Spirobranchus*, and *Pomatoceros*). Aprons tend to be absent in juvenile individuals of a species. Ben-Eliahu & Fiege (1996) regard the presence of an apron to be a full expression of a size-related character in *Protis*.

In Serpulinae, margins of thoracic membranes are fused dorsally only in *Ficopomatus uschakovi*. In Spirorbinae the fused condition is more common, occurring in the nominal genera *Neodexiospira* Pillai, 1970, *Romanchella* Caullery & Mesnil, 1897, and *Velorbis* Knight-Jones & Knight-Jones, 1995. The genus *Floriprotis* shows pockets on the inside of the thoracic membranes (see remarks *Floriprotis*).

The thorax

Number of chaetigers. The number of thoracic chaetigers is fairly constant in most serpulid taxa and traditionally constitutes an important character in serpulid taxonomy. In most genera, the thorax of adults consists of 7 thoracic chaetigerous segments (Fig. 5A–D), including the collar segment lacking uncini (thus, 6 thoracic uncinigerous segments), although juvenile specimens may have fewer chaetigers (e.g., *Semivermilia cribrata* and *S. pomatostegoides* with 5–6 chaetigers, present paper). Some serpulid taxa have 5 chaetigerous segments (*Bathyditrupa*, *Josephella*, *Tanturia*), 6 (*Laminatubus*, *Hyalopomatus* (Fig. 3C)), 9 (*Protula setosa*, ?*Filogranella prampramiana*) or even more (*Filogranella*, Fig. 18A, see below). In spirorbins the number of thoracic chaetigers generally varies from 3 to 5 (Knight-Jones & Knight-Jones 1977, Bianchi 1981), but *Neomicrorbis* (Fig. 29A) has 5–6 chaetigers. Sabellidae usually display a distinct constancy of 8 thoracic segments, even though deviations from this number have been noted as an intraspecific phenomenon (Fitzhugh 1989).

Some serpulid taxa have a variable number of thoracic chaetigers, such as *Filograna* and *Salmacina* (6–12 segments); *Filogranella* (11–14); *Nogrobs*, *Rhodopsis* (4–6); and *Spiraserpula* (5–11). This situation can be a result of asexual reproduction, where numbers of thoracic chaetigers in clones of *Salmacina* are congruent with those of their ancestors, as demonstrated by Vannini & Ranzoli (1961). Moreover, some genera with an otherwise fixed number of thoracic segments (7) occasionally show species with a variable number of thoracic segments: for example, three *Hydroides* species (*H. bisectus* and 2 as yet undescribed species) have 7–9 chaetigers (Imajima & ten Hove 1989: 13), three species of *Serpula* (*S. israelitica, nanhaiensis, oshimae*) have 9-12, while *Vermiliopsis notialis* has only 5 thoracic chaetigers.

Thoracic chaetae. The terminology relating to the structure of serpulid chaetae has been inconsistent. Various interpretations of their shape by earlier taxonomists are most likely due to the fact that many details of chaetal structure are near the limits of the optical resolution of a compound microscope. In the last two decades, wide use of scanning electron microscopy in zoological research allowed clarification of even the smallest chaetal structures.

Notochaetae of thoracic chaetigerous segments are usually termed simple capillary and narrow limbate (or hooded) chaetae in all serpulids and sabellids. Under the high magnification of a compound microscope a distal hood (or limbus) looks like a transparent finely striated blade structure (e.g., Fig. 33A, C). However, with SEM it is obvious that the limbus (or hood) in fact consists of a large number of fibers, more loosely packed than in the shaft, ending in tiny needle-shaped teeth (e.g., Figs 37A, 50A). Moreover, the usual thoracic chaetae (including collar chaetae, if any) are all limbate, but of two sizes: the smaller being called capillary, but clearly "limbate" as well. We have not specified this again in the generic diagnoses, and referred to them as "limbate".

In posterior thoracic segments (usually from the third backwards), these limbate chaetae (of two sizes) can be supplemented in some species by special chaetae termed "*Apomatus*" chaetae (Figs 10A, 11B, 12E, 14C, 18C, 19B, 24C, 25A, 28B, 30C, 33B, 37E, 41A, 44B). These chaetae are typically sigmoid to sickle-shaped with a proximal denticulate zone (looking like fine striation under a compound microscope) and a long flat curved blade with a row of blunt regular teeth. In the spirorbin literature (e.g., Knight-Jones 1981) sigmoid chaetae of both thorax and abdomen are called "sickle-chaetae". However, the proximal denticulate zone is an order of magnitude shorter in abdominal sigmoid chaetae; therefore we propose to restrict "sickle-chaetae" to abdominal chaetae, to discern them from the thoracic *Apomatus* chaetae. Sometimes these *Apomatus* chaetae are almost straight.

The bundle of collar chaetae may contain special chaetae in addition to simple limbate ones. These special chaetae have a more-or-less distinct boss at the base of the distal limbate blade. Like the "hoods" of the limbate blades, the basal bosses are made of fibres, ending in tips forming teeth. Depending on the number and size of the teeth in the boss, four types of special collar chaetae have been distinguished in serpulids.

1. Bayonet-type chaetae generally have one or two (sometimes more) large proximal bosses at the base of the distal limbate zone: *Serpula* (Fig. 46A), *Spiraserpula*, *Crucigera* (Fig. 13A), *Hydroides* (Fig. 23A), and *Floriprotis* (Fig. 20A), sometimes small auxiliary teeth present.
2. Fin-and-blade chaetae have the basal boss ("fin") made of relatively few teeth of intermediate size; the basal fin may or may not be separated by a toothless zone (a gap) from the distal blade: *Chitinopoma* (Fig. 11A), *Chitinopomoides* (Fig. 12A), *Filograna* (Fig. 17A), *Filogranula* (Fig. 19A).
3. *Spirobranchus*-type chaetae have a proximal boss consisting of very numerous tiny hair-like spines: *Spirobranchus* (Fig. 47A) and *Laminatubus* (Fig. 26A).
4. *Ficopomatus* has unusual collar chaetae, with coarse curved teeth alongside the distal part of chaetae (Fig. 16A).

Thoracic uncini. The uncini are arranged side by side in a single row in a torus, transverse relative to the long axis of the body, with the dentate distal edge of the uncini directed anteriorly. Thoracic uncinigerous tori generally are positioned along the lateral side of the thorax, but in some taxa they are widely separated in front, gradually approaching one another posteriorly, so that the posterior thoracic tori may touch each other, forming a triangular depression on the ventral side of the thorax. In other taxa (e.g., *Neovermilia globula*) thoracic tori are completely shifted to the ventral part of the thorax. Some species of *Protula* may completely lack thoracic uncini (e.g., *P. bispiralis* and, occasionally, *P. intestinum* as well (Fauvel 1927)).

Serpulid uncini are flattened comb-shaped structures with a number of curved teeth on their edge. Each uncinus in our view possesses four characters: 1) the number of teeth visible in profile (from 4 to well over 30); 2) the (maximum) number of teeth in a transverse row; 3) the shape of the anterior-most tooth ("fang" or "peg"); 4) overall shape of the edge of the uncinus. Depending on the number of vertical rows of teeth in the uncini they are termed saw-shaped (one row of teeth along the edge, e.g., thorax *Hydroides*), saw-to-rasp-shaped (from 1 tooth on edge distally to a row of 5 teeth proximally above the peg, e.g., *Filogranula*, dental formula P:5:3:3:2:1:1:1:1:1:1:1:1:1, Fig. 19C, *Semivermilia*) or rasp-shaped (several rows of teeth along the entire edge, e.g., *Hyalopomatus*) (ten Hove 1975, ten Hove & Wolf 1984). In some taxa, thoracic uncini normally have teeth in a single row (saw-shaped, e.g., Figs 23B, 38B, 46B). However, towards the end of a row uncini occasionally may change from saw-shaped to saw-to-rasp-shaped, in which case the distal tooth (teeth) may be single, while the teeth proximal to the fang may be in 2–3 rows or uncini even change to completely rasp-shaped (Knight-Jones & Fordy 1979 figs 73, 77, for spirorbins). Also, juvenile specimens of otherwise "saw-shaped" species may show rasp-shaped uncini (see also Ben-Eliahu & Fiege 1996). Finally, the shape of the uncini may change from saw-shaped to rasp-shaped from the anterior to the posterior thorax (this is a more or less normal situation in the abdomen). This especially is the case for juvenile specimens of otherwise saw-shaped taxa because posterior chaetigers are formed later in ontogeny; however, it may be a specific character in other taxa as well.

The shape (profile) of a serpulid uncinus is roughly triangular or rectangular; these uncini never have the long proximal handles typical for some sabellids (Fitzhugh 1989). A serpulid uncinus roughly consists of the outer surface with the teeth, the lower base embedded into the torus, the anterior side below the main fang or peg (the breast *sensu* Fitzhugh 1989), and the posterior side (straight as in *Spirobranchus*, concave as in *Protula*, convex as in *Serpula*). The shape of the uncinus appears to be a character related to the number of teeth, and it is difficult to observe unless the uncinus is removed from the tissue and mounted in a flat position.

The shape of the anterior tooth of uncini is believed to be of taxonomic importance (e.g., ten Hove 1975); this structure is usually referred to in earlier publications as being either simple or bifurcate. However, SEM examinations here reveal that ultrastructure of the anterior tooth is very variable. The serpulid anterior tooth is simple pointed (acute) and termed a fang in such genera as, for example, *Filograna* (Fig. 17B), *Hydroides* (Fig. 23B), *Neovermilia* (Fig. 30A, B), *Salmacina* (Fig. 44C), and *Serpula* (Fig. 46B).

However, what -depending on the orientation of the uncini on the slide- under a compound microscope appears to be a bifurcate or blunt anterior tooth may in fact be gouged, that is, a bluntly truncate flattened structure with lateral edges curved underneath (e.g., *Pomatoceros*, Fig. 35B, *Pseudovermilia*, Fig. 41B, and *Spirobranchus*, Fig. 47C). Examination with SEM shows that blunt (not pointed) anterior teeth of serpulid uncini may also be either flat, rounded, spatulate (as in *Galeolaria*, Fig. 21 B, C), rectangular or even trapezoidal in appearance (*Ficopomatus*, Fig. 16D), bilobed to quadrilobed (as in *Hyalopomatus marenzelleri*, Fig. 22B, C); or truncated, rounded or indented anteriorly (*Chitinopoma* Fig. 11C, *Pyrgolopon*, Fig. 42A, B, *Vermiliopsis*, Fig. 49C); or elongated, blunt, rounded to squarish, with transverse rows of teeth continuing over almost its entire length (*Apomatus*, *Protula*, Fig. 8A, 39A). For all these "wedge" shaped, not acute anterior teeth, we propose the collective term peg.

The abdomen

Number of segments. The abdomen consists of numerous segments, the number of which is very variable depending on size and age; it can be as low as 10 in small spirorbins and serpulins to over 200 segments in large species of *Spirobranchus* (e.g., *S. corniculatus, S. giganteus*) and *Protula* (*P. bispiralis, P. pacifica*). The maximal number of abdominal chaetigers is a function of age, but may well be genetically defined too.

Several anterior abdominal segments may lack chaetae and uncini, forming a so called achaetous abdominal zone. Some taxa have a glandular zone on the dorsal side of the last abdominal segments called the posterior glandular pad (Fig. 5D, gp). Its function is unknown, it might be involved in closing off damaged posterior tube parts, though a positive correlation between the glandular pad and occurrence of tabulae (see p. 10, **Tube shapes**) has not been found. The pygidium is usually bilobed and bears a terminal slit-like anus.

Abdominal chaetae. After the achaetous region, if present, each anterior and middle abdominal segment bears a dorsal uncinigerous torus and a ventral bundle of chaetae. Abdominal chaetae are normally less numerous per bundle than the thoracic ones. The simplest forms of abdominal chaetae are capillary (Fig. 23D), nearly capillary (e.g., *Hyalopomatus*, Fig. 22D), or acicular (*Paumotella*, Fig. 33F).

The term "trumpet-shaped chaetae", commonly used by various authors to describe the abdominal chaetae in the genera *Crucigera* (Fig. 13D), *Hydroides* (Fig. 23C), *Serpula* (Fig. 46D) and *Spiraserpula*, is misleading. Although the distal parts of these chaetae, when examined under a compound microscope, are widened into what in profile looks like a chalice or trumpet edged with apparently two rows of thin teeth, examination with SEM shows that these chaetae are not hollow as the name might suggest, but rather flat, with a single row of marginal acute teeth. The second row of teeth observed under a compound microscope is an optical (refractory) illusion. Therefore, following ten Hove & Jansen-Jacobs (1984), where a more extensive discussion can be found, they are termed here flat trumpet-shaped chaetae.

Truly trumpet-shaped chaetae, however, are distally hollow, with two parallel rows of sharp denticles, extending into a long lateral spine; they may be smoothly bent (e.g., in *Ficopomatus* Fig. 16C; *Galeolaria* Fig. 21E), or abruptly bent (e.g., in *Pomatoceros* Figs 35C, D; *Spirobranchus* Fig. 47D). Fauvel (1927) used the term “en cornet comprimé à longue pointe latérale” for the latter, but used “geniculate chaetae” for *Ficopomatus*. In dictionaries, geniculate generally is defined as “having a knee-like joint” or “bent sharply”. In its first meaning this term is slightly misleading for this type of chaetae since a joint between the proximal and distal part of the chaetae is absent in all serpulid chaetae. “Bent sharply” applies to part of these abdominal chaetae. Again, it is extremely difficult to see with a compound microscope whether such chaetae have a single or double row of teeth bordering the blade (Fauvel 1927: 348; our observations). Therefore it is not surprising that in older literature true trumpet chaetae have been lumped together with the completely different flat geniculate abdominal chaetae. For instance Dew (1959) used the same term “geniculate” for the abdominal chaetae of *Galeolaria* and *Neovermilia globula* (as *Vermiliopsis*), both with, in our terminology, “true trumpets”, as well as for *Metavermilia acanthophora* (as *Vermiliopsis*), with “narrow flat trumpets”. Bianchi (1981) generally used “genicolate” consistently for truly trumpet chaetae, but also for *Josephella*, which has flat narrow geniculate abdominal chaetae as defined below.

In reality, “geniculate” chaetae in our narrowed definition (flat geniculate, not hollow) possess a capillary proximal shaft and a bent blade, sometimes only bent slightly so (Day 1967: 799, geniculate setae have gradually tapering blades set at a slight angle to the shaft); the blade has a single row of blunt rounded to sharp denticles along its edge. These “flat geniculate” chaetae are not uniform in their structure and depending on the shape of the distal blade the following types can be distinguished:

a) sickle-shaped: fairly straight to weakly sickle-shaped abdominal chaeta with long concave edge bordered by very regular rounded teeth (“en faucille” *sensu* Fauvel 1927; e.g., *Apomatus*, Fig. 8E, Ben-Eliahu & Fiege (1996) fig. 9D, and *Protula*, Fig. 39B); however, see ten Hove & Pantus (1985).

b) flat triangular, with a knee-like bend and with dentition on the outside of a wide triangular distal blade (e.g., *Chitinopoma*, Fig. 11E; *Filogranula*, Fig. 19E).

c) flat narrow geniculate, as above b), but with the blade not so sharply bent and more elongated (e.g., *Filograna*, Fig. 17C; *Josephella*, Fig. 25D; *Salmacina*, Fig. 44D; *Vermiliopsis*, Figs 49E, F).

d) retro-geniculate chaeta, as c) above, but with a recurved hook on the outside (anterior side) of the knee, directed proximally (e.g., *Protula balboensis* Monro, 1933 and *Neomicrorbis*, Fig. 29F).

Abdominal chaetae usually become progressively longer towards the pygidium, and the posterior abdominal chaetae tend to be either true capillaries (e.g., *Hydroides*, Fig. 23D) or elongated and “unbent” modified chaetae. If capillary chaetae of the most posterior abdominal segments are at least an order of magnitude longer than the chaetae of anterior and middle abdominal segments, they are referred to as “long capillary chaetae”.

Abdominal uncini. In lateral view, anterior abdominal uncini in serpulids are usually similar to thoracic ones, but may be slightly smaller. However, the shape of the edge of the uncini (saw- and/or rasp- shaped) may vary strongly according to their position in the abdomen. Zibrowius (1968a) suggested that presence of rasp-shaped uncini in the abdomen was of prime importance for generic classification of serpulids. However, rasp-shaped uncini are almost invariably found in the most posterior and thus, in the youngest, segments. Since polychaetes increase body length by addition of segments posteriorly (e.g., Parapar *et al.* 1993), this uncinal variability implies that serpulids can shed or resorb their juvenile rasp-shaped uncini and replace them with saw-to-rasp-shaped uncini and finally with saw-shaped adult uncini as they grow. Thus, when examining specimens, consideration should be taken of their ontogenetic state, the size of the individual.

Valid genera with diagnoses and lists of species

The Serpulidae *sensu lato*, but excluding spirorbins, currently contain about 350 nominal species in 46 "valid" genera (see below); of which 19 include only one species (e.g., *Chitinopomoides, Paumotella, Microprotula*) and/or are known from one or two records only. Others (e.g., *Bathyditrupa, Bathyvermilia, Laminatubus*) are found only in abyssal locations. Whether serpulid genera constitute monophyletic groups remains unknown, so no assumption of their monophyly has been made here. Instead, the serpulid taxa that are currently recognized as valid by us are listed below; in some cases, considered as "valid" only because some have not been formally synonymized or are too poorly described to synonymize here. A list of invalid serpulid genera with their synonyms is given separately. Each generic diagnosis is accompanied by the list of "valid" species with notes on their distribution. Generic remarks concern the current state of the taxonomy and major taxonomic studies.

1. *Apomatus* Philippi, 1844

(Fig. 8)

Type-species: *Apomatus ampulliferus* Philippi, 1844
Number of species: 7

Tube white, opaque, circular in cross-section, keels and collar-like rings absent. Granular overlay may be present. Operculum a soft membranous vesicle without endplate borne on unmodified pinnulated radiole. Opercular constriction may be present. Pseudoperculum may be present on unmodified radiole. Arrangement of radioles in semi-circles (may be up to ¾ of a circle), maximum number up to 40 per lobe in larger species. Inter-radiolar membrane present. Branchial eyes present in the form of ocellar clusters. Stylodes absent. Mouth palps present. 7 thoracic chaetigerous segments. Collar trilobed with smooth edge. Thoracic membrane long, forming ventral apron across anterior abdominal segments. Tonguelets between ventral and lateral collar lobes absent. Collar chaetae limbate, of two sizes (thus, in the classical terminology capillary and limbate). *Apomatus* chaetae present (Fig. 8C, D). Thoracic uncini saw-to-rasp-shaped with approximately 30 teeth in profile, up to 3 (exceptionally 4) teeth in a row above and continuing onto peg; anterior peg very long, blunt, almost rectangular (Fig. 8A, B). Ventral thoracic triangular depression absent. Abdominal chaetae sickle-shaped with finely denticulate blades (Fig 8E, F); uncini rasp-shaped with approximately 30 teeth in profile. Short achaetous anterior abdominal zone present. Posterior capillary chaetae present. Posterior glandular pad present.

Remarks. A controversy exists whether *Protula* and *Apomatus* should be regarded as separate genera (ten Hove & Pantus 1985) or synonymized under *Protula* (Kupriyanova & Jirkov 1997). The genera are separated mainly by the presence (*Apomatus*) or absence (*Protula*) of a soft vesicular operculum on an unmodified radiole. Hanson's (1948a) study on the pattern of blood vessels showed that *P. tubularia*, *A. ampulliferus*, and *A. similis* are similar to each other, but dissimilar to *P. intestinum*. She proposed that these genera should be fused. However, ten Hove & Pantus (1985) studied over a 100 fresh specimens and found consistent differences in blood-vessel patterns between operculate and non-operculate specimens. They suggested that *Protula* and *Apomatus* are valid genera and that Hanson (1948a) mistook an *Apomatus* specimen that incidentally lost its operculum for *P. tubularia*. This controversy is yet to be resolved, probably with the aid of molecular genetics.

1. *Apomatus ampulliferus* Philippi, 1844 Mediterranean, Atlantic
2. *Apomatus elisabethae* McIntosh, 1885 New Zealand
3. *Apomatus enosimae* Marenzeller, 1885 South Japan, South China Sea
4. *Apomatus geniculata* (Moore & Bush, 1904), incl. *A. timsii*, North Pacific, Japan to California

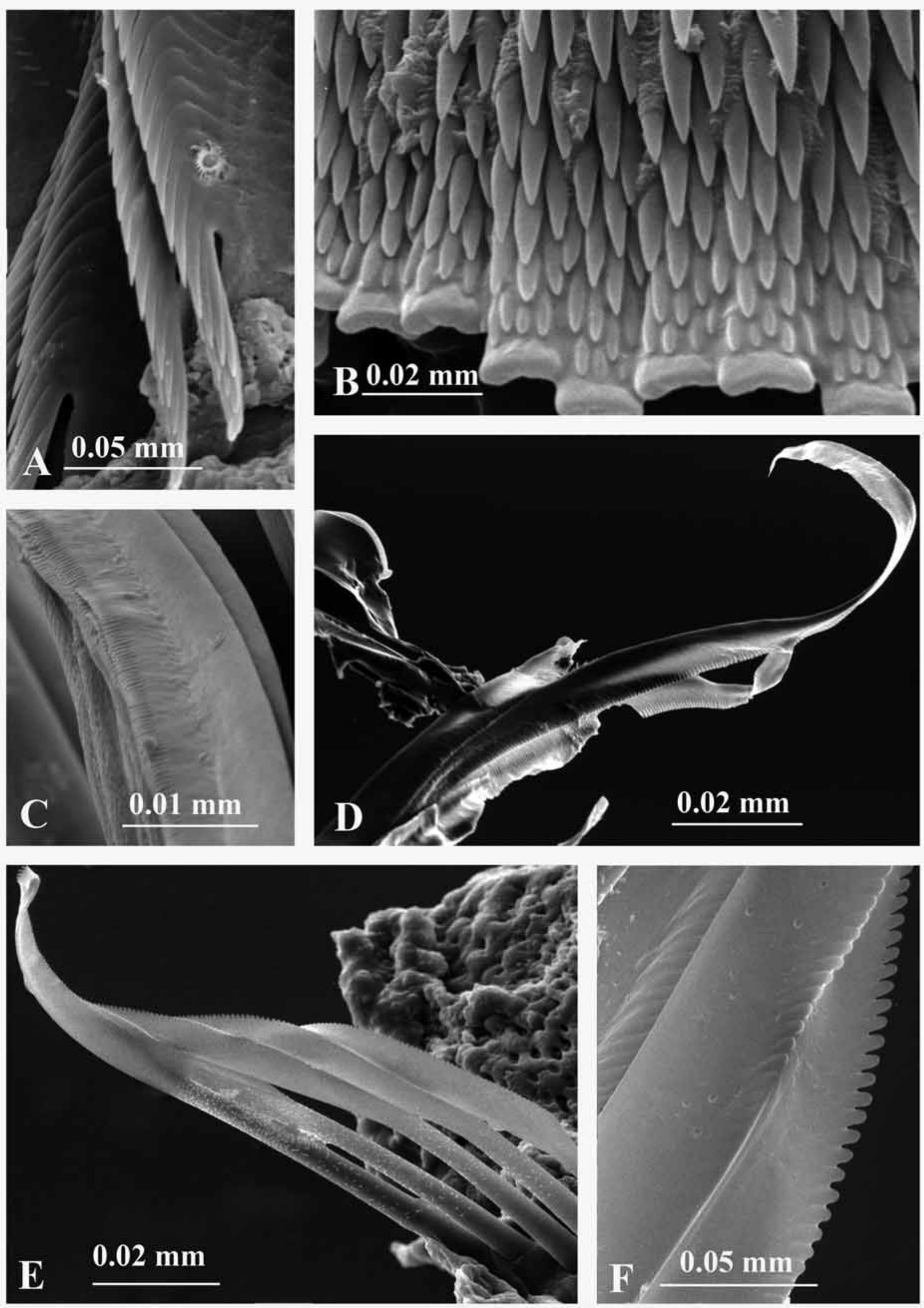

FIGURE 8. SEM micrographs of chaetae in *Apomatus ampulliferus*. France, Marseille, 200 m, legit F.J.A. Pantus, ZMA V.Pol. 3812. A—uncini of 4th thoracic chaetiger, B—anterior abdominal uncini, details of peg, C—details of *Apomatus* chaetae in 7th thoracic chaetiger, D—details of *Apomatus* chaetae in 4th thoracic chaetiger, E—middle abdominal chaetae, F—details of E.

5. *Apomatus globifer* Théel, 1878, Arctic, Norway; probably see *A. similis*
6. *Apomatus lilliei* Benham, 1927, North Cape, New Zealand
7. *Apomatus similis* Marion & Bobretzky, 1875, Mediterranean Atlantic; probably includes *A. globifer*

2. *Bathyditrupa* Kupriyanova, 1993b
(Fig. 9)

Type-species: *Bathyditrupa hovei* Kupriyanova, 1993b
Number of species: 1

Tube free, curved but not coiled, white, opaque, rectangular in cross-section; collar-like rings absent. Granular overlay absent. Operculum inverse conical, with brown chitinous endplate, flat or slightly concave. Opercular ampulla gradually merges (constriction absent) into thick, rather triangular peduncle with pinnules, but without wings. Peduncle inserted as the second dorsal radiole on one side. Pseudoperculum absent. Arrangement of radioles semi-circular, up to 6 per lobe. Branchial eyes not observed. Inter-radiolar membrane and stylodes absent. Mouth palps not observed. 5 thoracic chaetigerous segments. Collar non-lobed, short, with entire edge. Tonguelets absent. Thoracic membranes short, ending at second thoracic segment. Collar chaetae limbate (Fig. 9A). *Apomatus* chaetae absent (Fig. 9B). Thoracic uncini saw-to-rasp-shaped, with up to 4 (?6) teeth in a row above peg, with about 15 curved teeth in a row in profile (Fig. 9D). Anterior peg bifurcate in high-power microscopy, but clearly gouged when studied by SEM (Fig. 9E). Thoracic triangular depression absent. Abdominal chaetae all capillary (Fig. 9C), posterior ones slightly longer; abdominal uncini rasp-shaped (Fig. 9F). Achaetous anterior abdominal zone short, just one or two segments. Posterior glandular pad absent.

Remarks. This abyssal species had only been reported from the Kurile-Kamchatka trench (Kupriyanova 1993b). We studied 2 additional specimens from the North Pacific Ocean, collected by the R/V *Vityaz,* Sta. 3151, near the Emperor Seamounts, 44°28'3" N 170°07'0"E, grab, 5237 m, ZMA V.Pol. 5326; Sta. 4370, NE off Hawaii, 26°04'2" N, 153°49'3" W, grab, 6050 m, ZMA V.Pol. 5325. The characteristic feature of the genus is a free, unattached tube similar to that of *Ditrupa*, but rectangular in cross-section and without an outer hyaline layer (see **The tube**, p. 7). It is probably synonymous with *Nogrobs fide* Jäger (2004: 140), see remarks below (p. 69).

Bathyditrupa hovei Kupriyanova, 1993b, Kurile-Kamchatka trench and North Pacific Ocean; abyssal.

3. *Bathyvermilia* Zibrowius, 1973a
(Fig. 10)

Type-species: *Bathyvermilia challengeri* Zibrowius, 1973a
Number of species: 5.

Tube white, opaque, circular in cross-section, longitudinal keel may be present. Collar-like rings present. Granular overlay absent. Operculum sub-globular, with simple flat to slightly conical chitinous endplate, which may be encrusted by calcareous deposit. Peduncle cylindrical, smooth or wrinkled, without distal wings; inserted as second dorsal radiole on one side, constriction present. Pseudoperculum absent. Arrangement of radioles in semi-circles, up to 35 per lobe. Inter-radiolar membrane absent. Branchial eyes not observed. Stylodes absent. Mouth palps may be present. 7 thoracic chaetigerous segments. Collar trilobed (may be non-lobed) with entire edge, tonguelets absent. Thoracic membranes variable, ending at 2nd—7th thoracic segment. Collar chaetae limbate. *Apomatus* chaetae present (Fig. 10A). Thoracic uncini saw-shaped

(Fig. 10B), with few teeth (6 to 10). Anterior fang simple, pointed. Abdominal chaetae flat, narrow geniculate with blunt teeth (Fig. 10D); abdominal uncini saw-shaped, except in a few far posterior segments, with rasp-shaped uncini (Fig. 10C). Short achaetous anterior abdominal zone present. Posterior capillary chaetae present. Posterior glandular pad present.

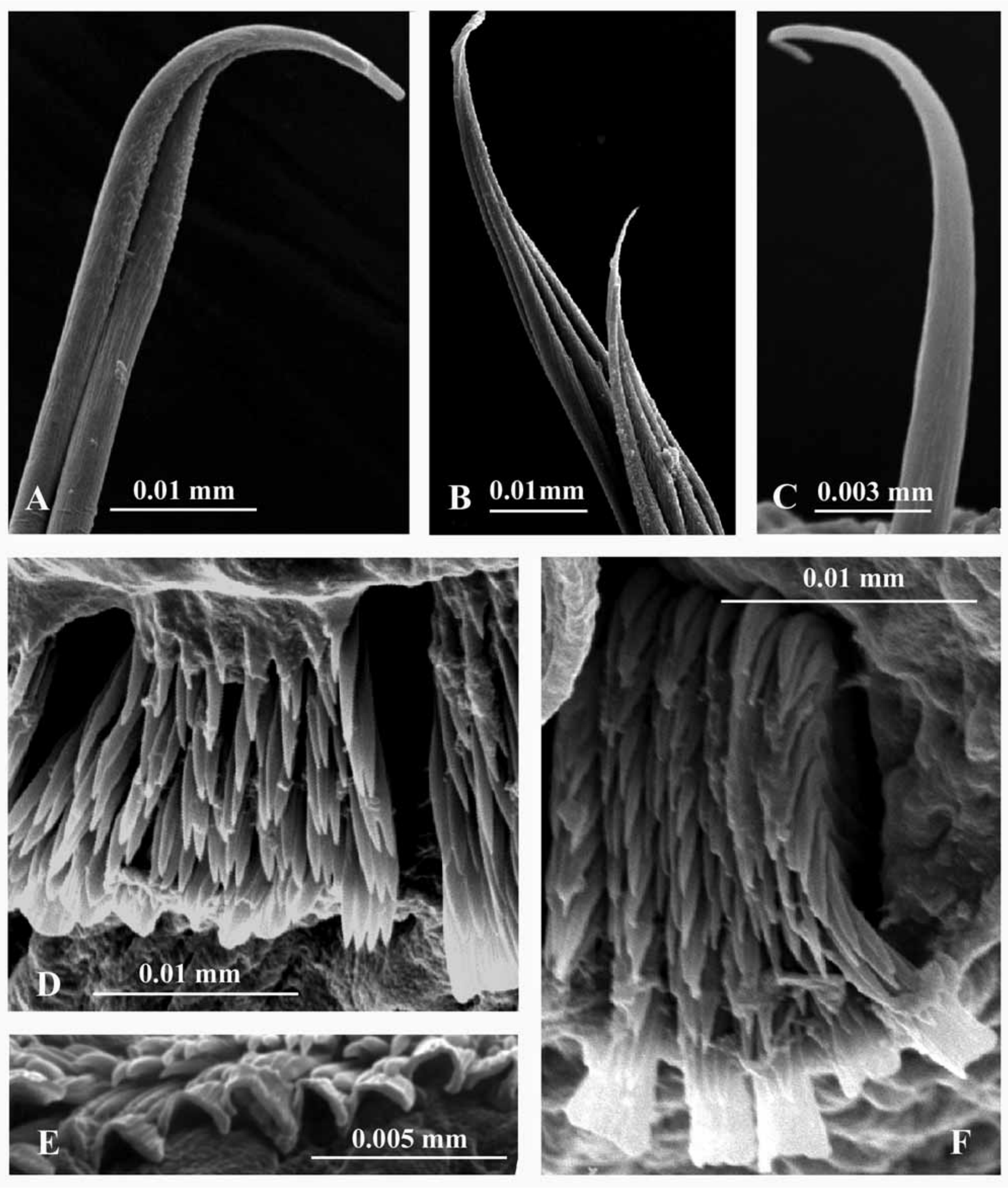

FIGURE 9. SEM micrographs of chaetae in *Bathyditrupa hovei*, ZMA V.Pol.5325 . A—collar chaetae, B—fourth bundle of thoracic chaetae, C—anterior abdominal chaeta, D—third row of thoracic uncini, E—gouged pegs of posterior thoracic uncini from below, F—first row of abdominal uncini.

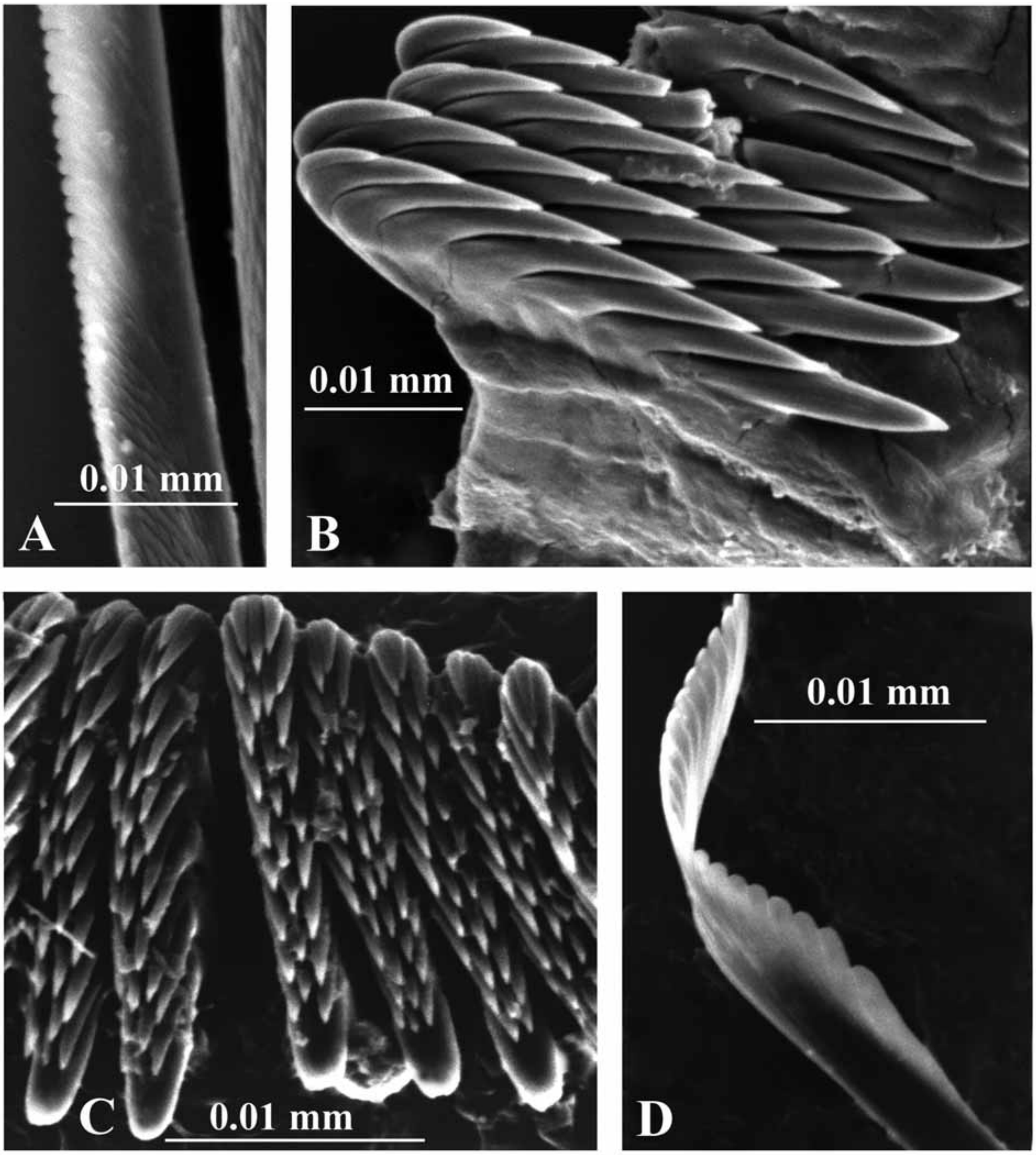

FIGURE 10. SEM micrographs of chaetae in *Bathyvermilia kupriyanovae*. USA, off California, 34°41' N, 123°08' W, 4100 m, legit K.L. Smith, R/V *New Horizon*, det. H.A. ten Hove, Natural History Museum of LA County, USA. A—details of *Apomatus* chaetae of 4th thoracic chaetiger, B—uncini of 4th thoracic chaetiger, C—posterior abdominal uncini, D—detail of middle abdominal chaeta.

Remarks. Zibrowius (1973a) established the genus *Bathyvermilia* for the deep-water *Vermiliopsis langerhansi* Fauvel, 1909 and the newly described *Bathyvermilia challengeri* (new name for *Placostegus ornatus* not Mörch, 1863 but *sensu* McIntosh, 1885). Later, three species (see list below) were added. Zibrowius (1973a) provided a table summarizing the differences for the genera *Bathyvermilia*, *Metavermilia*, *Pseudovermilia*, and *Vermiliopsis*, previously all united under *Vermiliopsis*.

1. *Bathyvermilia challengeri* Zibrowius, 1973a, Mid Pacific; abyssal
2. *Bathyvermilia islandica* Sanfilippo, 2001, Iceland; bathyal-abyssal

3. *Bathyvermilia kupriyanovae* Bastida-Zavala, 2008, off California; bathyal
4. *Bathyvermilia langerhansi* (Fauvel, 1909), Atlantic; bathyal-abyssal
5. *Bathyvermilia zibrowiusi* Kupriyanova, 1993b, Kurile-Kamchatka trench; abyssal.

4. *Chitinopoma* Levinsen, 1884

(Fig. 11)

Type-species: *Chitinopoma fabricii* Levinsen, 1884 = junior synonym of *Vermilia serrula* Stimpson, 1854.
Number of species: 3 (possibly 4)

Tube white, opaque, with single longitudinal keel, triangular or sub-triangular in cross-section, with brood chambers. Hyaline granular overlay absent. Operculum inverse conical, with chitinous endplate. Peduncle cylindrical, smooth, without distal wings, constriction present; inserted as second dorsal radiole on one side. Pseudoperculum absent. Radioles arranged in semi-circles, up to 7 radioles per lobe, inter-radiolar membrane absent. Branchial eyes and stylodes absent. Mouth palps not observed. 7 thoracic chaetigerous segments. Collar trilobed with entire edge, tonguelets between ventral and lateral collar lobes absent. Thoracic membranes short, ending at second thoracic chaetiger. Collar chaetae fin-and-blade, fin well separated from blade, and limbate (Fig. 11A). *Apomatus* chaetae present (Fig. 11B). Thoracic uncini saw-shaped, with about 12 teeth (Fig. 11C); anterior peg simple, rounded. Thoracic triangular depression absent. Abdominal chaetae with large flat triangular denticulate blade (Fig. 11E); uncini rasp-shaped (Fig. 11D). Achaetous anterior abdominal zone absent. Posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. The partial revision of the genus by Zibrowius (1969a) showed that the brooding *Chitinopoma serrula* is a species widely distributed in the Arctic and boreal North Atlantic. Later, brooding *C. arndti* Zibrowius, 1983 was added and *C. rzhavskii* (Kupriyanova, 1993a) was transferred from *Filogranula* (Kupriyanova *et al.* 2001). However, various forms of brooding of embryos, the main character distinguishing *Chitinopoma* from *Filogranula*, are very common for small serpulid species (Kupriyanova *et al.* 2001). Additional studies are needed to determine whether these two genera should be synonymized. Probably the nominal taxon *Ficopomatus capensis* Day, 1961 belongs here as well (*fide* ten Hove & Weerdenburg 1978: 101).

1. *Chitinopoma arndti* Zibrowius, 1983, St. Paul, Amsterdam Island, southern Atlantic
2. ?*Chitinopoma capensis* (Day, 1961), South Africa
3. *Chitinopoma rzhavskii* (Kupriyanova, 1993a), Kamchatka
4. *Chitinopoma serrula* (Stimpson, 1854), Arctic, North Atlantic.

5. *Chitinopomoides* Benham, 1927

(Figs 12, 51A–D)

Type-species: *Chitinopoides wilsoni* Benham, 1927
Number of species: 1

Tube white, opaque, triangular in cross-section, with a smooth longitudinal keel and sometimes 2 poorly-defined smooth ridges along the sides. Tube with irregularly placed former peristomes, questionably with brood care function. Granular overlay not observed. Operculum fig-shaped with bilaterally symmetrical concave chitinous endplate. Peduncle smooth, subtriangular in cross-section, without distal wings; inserted just below and between 1st and 2nd radiole (=second radiole). Pseudoperculum absent. Arrangement of radioles short pectinately, up to 10 pairs of radioles. Inter-radiolar membrane absent. Branchial eyes unknown. Stylodes absent. Mouth palps not observed. 7 thoracic chaetigerous segments. Collar trilobed with entire edge, tonguelets between ventral and lateral collar lobes absent. Thoracic membranes short, ending at second chaetiger; no apron. Collar chaetae fin-and-blade (Benham (1927): "with a large knob and few proximal additional teeth below the limbate zone", Fig. 12A), and limbate. *Apomatus* chaetae present (Fig. 12E). Thoracic uncini saw-shaped with about 12 teeth, anterior peg blunt, seemingly bifurcate (slightly gouged?) (Fig. 12B). Triangular depression absent. Abdominal chaetae flat geniculate with large distal triangular blade (Fig. 12D). Abdominal uncini all rasp-shaped (Fig. 12C), with more teeth in posterior segments than in the anterior ones, with at least 12 teeth seen in profile. Achaetous anterior abdominal zone absent. Posterior capillary chaetae short, glandular pad present.

Remarks. *Chitinopomoides wilsoni* was previously known from a single specimen dredged in the Ross Sea. Zibrowius (1969a) re-examined the specimen and expanded Benham's description of the chaetae and uncini. However, as the collar chaetae of the specimen were all broken, Zibrowius could not re-examine their structure and thus, generic justification of *Chitinopomoides* was questionable. A redescription (below) based on new unpublished material allowed us to elucidate the ultrastructure of collar (and other) chaetae with use of SEM. A possible relationship with other genera will be discussed in (a) forthcoming paper(s) by us.

Chitinopomoides wilsoni Benham, 1927, Antarctic.

Chitinopomoides wilsoni Benham, 1927: 156–158, Pl. 5 figs 162–173 [McMurdo Sound, 366 m, British Antarctic "Terra Nova" Exp. Sta. 348, BMNH 1928:2:29:174]; Hartman 1966: 129–130, Pl. 43 figs 4–7 [same, no new data]; Zibrowius, 1969a: 9–10, fig. 3 [re-examined holotype]; Fauchald, 1977: 144 [generic diagnosis]; Uchida, 1978: 74 [name in list].

Material studied. Antarctica, Davis Sea, Wilkes Land, Burton Island, 66°32.94'S, 93°90'E, 80 m, Deep Freeze III, legit R.R. Starr, Sta. 5, Russian St. Mirny, 29.I.1958, det. H.A. ten Hove 1971 (3 thoraxes, 3 abdomens, 1 small spec., tubes, USNM 51505, ZMA V.Pol. 3166); Ross Sea, Victoria Land, Robertson Bay area, 77°26'S, 169°30'E, Deep Freeze I, legit Wiston-W.H. Littlewood, R/V "*Edisto*" 1955/56, Sta. 8, 9.II.1956, USNM 51506, det. H.A. ten Hove 1971 (1 broken specimen); Argentina, Ushuaia, 54°48'S, 68°19'W, 18 m (10 Faden) legit H. Mag. Samm. 122, don. W. Michaelsen, det. H.A. ten Hove 1982, ZMH P-17557 (2 spec., tubes, separated from ZMH V 4963, *Serpula* spec., det. Augener 1921).

Description. TUBE: white, up to 1.4 mm wide with lumen of maximally 0.8 mm. Triangular in cross-section when attached, to almost semicircular when free; may bear wide, three-lobed, collar-like peristomes (2 mm across, Fig. 51A), not unlike those figured for *Pseudovermilia conchata* (ten Hove, 1975 pl. VIIIe, h). Smooth undulating medial keel present. Entire tube-wall (approx. 0.28 mm thick) appearing opaque in stereomicroscopy, though thin (0.03 mm) outer and inner layers are slightly more transparent, milky.

BRANCHIAE: each lobe with 9–10 branchial radioles, arranged short pectinately or almost semi-circular, not connected by branchial membrane. Rachis of radiole rounded triangular in cross-section, extended into flange to which pinnules are attached. Pinnules all more or less equal in size; terminal filament about twice as long as pinnule. Mouth palps not observed. Pair of prostomial eyes not observed. Branchial eyes not observed. Stylodes absent.

PEDUNCLE: smooth, subtriangular in cross section, inserted at left side just between first and second normal radiole, slightly wider than these. The distal part of the peduncle gradually swelling to about 1/2 the width of the opercular ampulla, separated from the latter by a clear constriction. Peduncular wings absent. Pseudoperculum absent.

OPERCULUM: fig-shaped, bilaterally symmetrical, with a distal concave endplate, almost an oblique funnel reaching halfway down into the ampulla (Fig. 51B–D). Distal plate chitinous, without ornamentation. Length of the operculum about 1.8 mm, width 1.4 mm.

COLLAR and thoracic membranes: collar low, with laciniate edge; continuous with thoracic membranes, ending at chaetiger 2 (1st row of uncini). Pockets in thoracic membranes absent. Pairs of wart-like protuberances of collar chaetiger absent; tonguelets between ventral and lateral collar lobes absent.

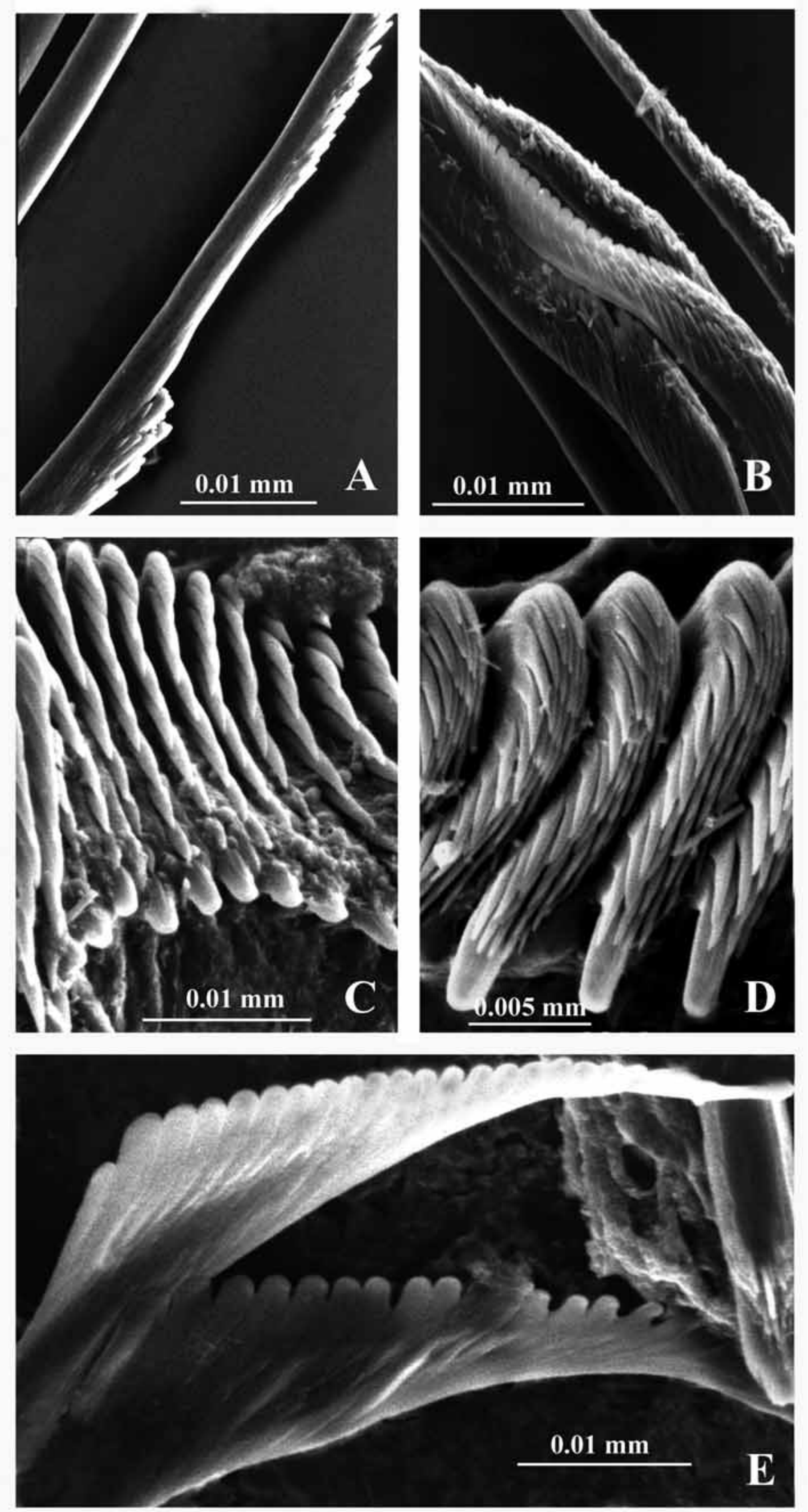

FIGURE 11. SEM micrographs of chaetae in *Chitinopoma serrula*. Greenland, det. H. Zibrowius, ZMA V.Pol. 3832. A—details of fin-and-blade collar chaeta, B—details of *Apomatus* chaetae of 4th chaetiger, C—1st row of thoracic uncini, D—middle abdominal uncini, E—middle abdominal chaetae.

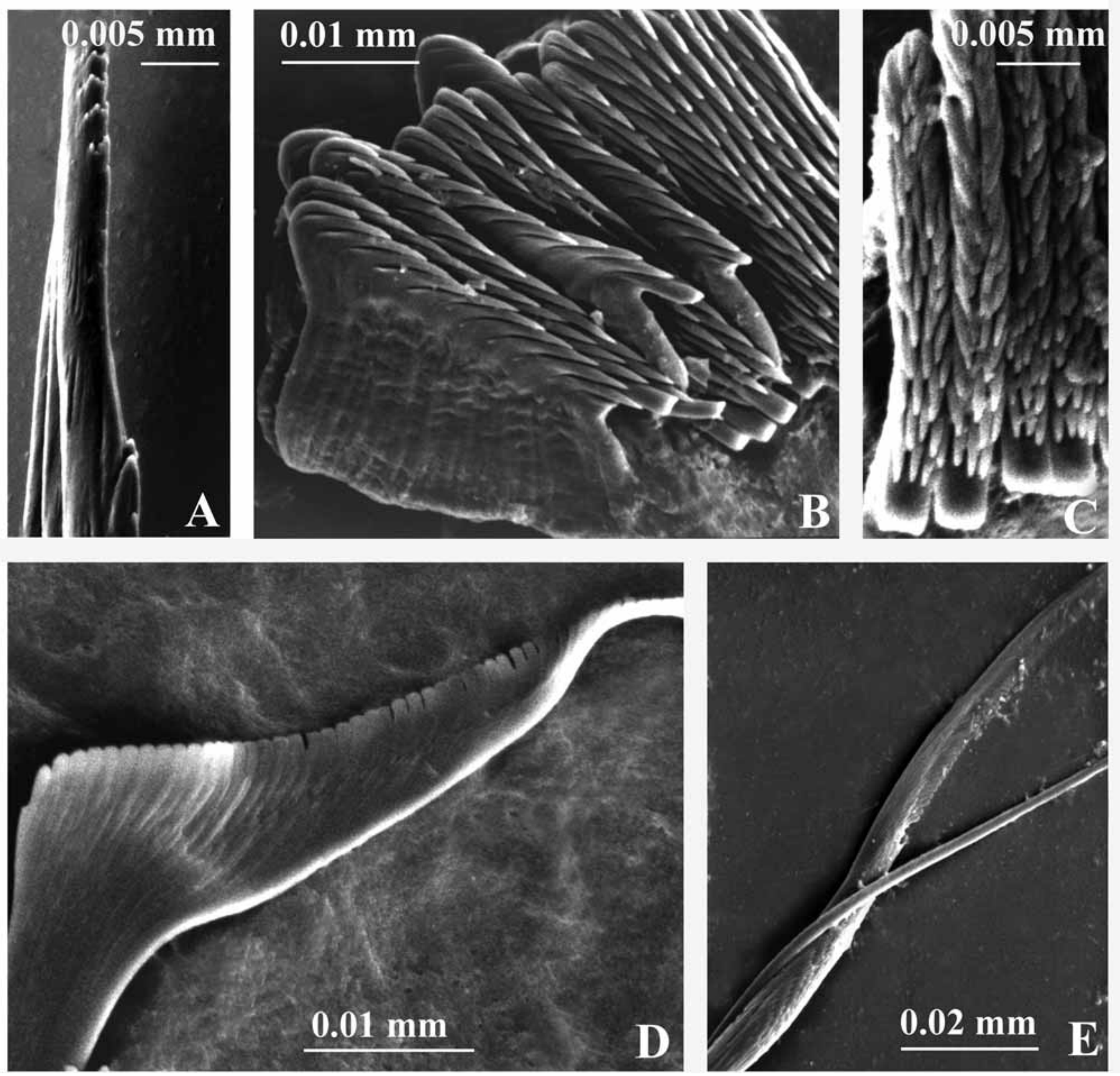

FIGURE 12. SEM micrographs of chaetae in *Chitinopomoides wilsoni*. Antarctic, ZMA V.Pol. 3166. A—fin-and-blade collar chaeta, B—1st row of thoracic uncini, C—abdominal uncini, D—middle abdominal chaeta, E—“capillary” and *Apomatus* chaetae of 4th thoracic chaetiger.

THORAX: with collar chaetiger, and 6 uncinigerous chaetigers. Collar chaetae of two types: fin-and-blade and hooded (limbate). Subsequent chaetae hooded, of two sizes. *Apomatus* chaetae from chaetiger 3 onwards. Uncini along entire thorax saw-shaped, with 12 curved teeth, with blunt, apparently bifurcated peg (dental formula P + 12).

ABDOMEN: abdominal chaetigers up to 62 at least (broken). Anterior uncini rasp-shaped, with peg and 12 teeth when seen in profile; posterior uncini with up to 5 teeth in a row. Chaetae flat geniculate. Short capillary chaetae and glandular pad present in about 12 posterior chaetigers. Pygidium bilobed.

Size: length up to 24 mm. Width of thorax up to 0.8 mm. Branchiae and operculum accounting for 1/5th of entire length.

Colour: no records.

Ecology: no data except for depth, 18–366 m. The USNM material was removed from tubes of *Serpula narconensis* by H. Zibrowius.

Remarks. All literature records are based on the same specimen, the holotype. Our seven additional specimens are all broken (or juvenile), but none of the thoraxes still have significant parts of the abdomen attached, at most 1 or 2 chaetigers; the numbers of abdominal chaetigers (40, 45, 53, 62) as counted on the loose abdomens thus probably represent almost complete counts. The specimen collected on 9.II.1956 showed eggs in its abdomen.

6. *Crucigera* Benedict, 1887

(Fig. 13)

Type-species: *Crucigera websteri* Benedict, 1887
Number of species: 5

Tube white or yellowish, opaque, circular to semi-circular in cross-section, with or without longitudinal keels and/or peristomes; tabulae may be present. Granular overlay absent, but outer layer may be shiningly hyaline. Operculum soft, funnel shaped, formed of fused radii. Base of funnel with 2–4 finger-like bosses. Peduncle smooth, cylindrical, without wings, separated from operculum by constriction; inserted proximal from first and/or second dorsal radiole on one side. Pseudoperculum present. Arrangement of radioles in two half to complete circles, up to 50 radioles per lobe in larger taxa. Inter-radiolar membrane present. Branchial eyes may be present. Stylodes absent. Mouth palps absent. 7 thoracic chaetigerous segments. Collar trilobed, tonguelets between ventral and lateral collar lobes absent. Thoracic membranes long, forming apron. Collar chaetae bayonet-shaped and limbate (Fig. 13A). Thoracic chaetae limbate, *Apomatus* chaetae absent (Fig. 13B). Thoracic uncini saw-shaped with 5–7 teeth, including simple pointed anterior fang (Fig. 13C). Triangular depression present. Abdominal chaetae flat trumpet-shaped, with denticulate edge (Fig. 13D). Abdominal uncini saw-shaped with 4–6 teeth anteriorly (Fig. 13E); rasp-shaped with 2–4 rows, 7–8 teeth in profile posteriorly. Long posterior capillary chaetae present. Achaetous anterior abdominal zone absent. Posterior glandular pad absent.

Remarks. The genus, with 5 species, was thoroughly revised by ten Hove & Jansen-Jacobs (1984). However, Kupriyanova *et al.* (2008) demonstrate that the traditional genera *Crucigera* and *Serpula* most probably are paraphyletic.

1. *Crucigera inconstans* Straughan, 1967b, Queensland, New South Wales, Western Australia
2. *Crucigera irregularis* Bush, 1905, Arctic North Pacific, Kamchatka to Washington State
3. *Crucigera tricornis* Gravier, 1906, widely distributed in the Indo-West Pacific
4. *Crucigera websteri* Benedict, 1887, Gulf of Mexico, Caribbean, Brazil; Pacific Colombia, California
5. *Crucigera zygophora* (Johnson, 1901), North Japan, Arctic North Pacific, Kamchatka to Washington State.

7. *Dasynema* Saint-Joseph, 1894

(Fig. 14)

Type-species: *Serpula chrysogyrus* Grube, 1876
Number of species: 1

Tube white, opaque, with some orange, semi-circular in cross-section, with peristomes and (5) irregular longitudinal keels. Hyaline granular overlay of the tube absent. Operculum with fleshy globular ampulla proximally, calcium carbonate infested chitinous cone distally. Peduncle smooth, without pinnules, broadly flattened, with unpaired basal wing for 2/3rds of its length and paired small distal wings, separated from ampulla by constriction; inserted at the base of branchial crown below and between 1st and 2nd radioles. Pseudoperculum absent. Radioles arranged in two semi-circles and connected by short inter-radiolar membrane. Radioles with ocellar clusters and unpaired outwardly directed stylodes, up to 15 radioles per lobe (Fig. 14A). Mouth palps not observed. 7 thoracic chaetigerous segments. Collar trilobed, tonguelets absent. Thoracic membranes ending at 5th chaetiger, no apron. Collar chaetae limbate (Fig. 14B). *Apomatus* chaetae present (Fig. 14C). Thoracic uncini saw-shaped (Fig. 14D), with numerous (approximately 17) teeth, anterior peg blunt (not gouged or pointed). Triangular depression present. Abdominal chaetae (Fig. 14E) flat narrow geniculate with blunt teeth along blade (*Vermiliopsis* type). Abdominal uncini saw-shaped anteriorly, with 11–12 teeth, posteriorly rasp-shaped with 2–4 rows of teeth, 14–15 teeth in profile (Fig. 14G). Achaetous anterior abdominal zone absent. Posterior capillary chaetae present, very long (Fig. 14F). Posterior glandular pad present.

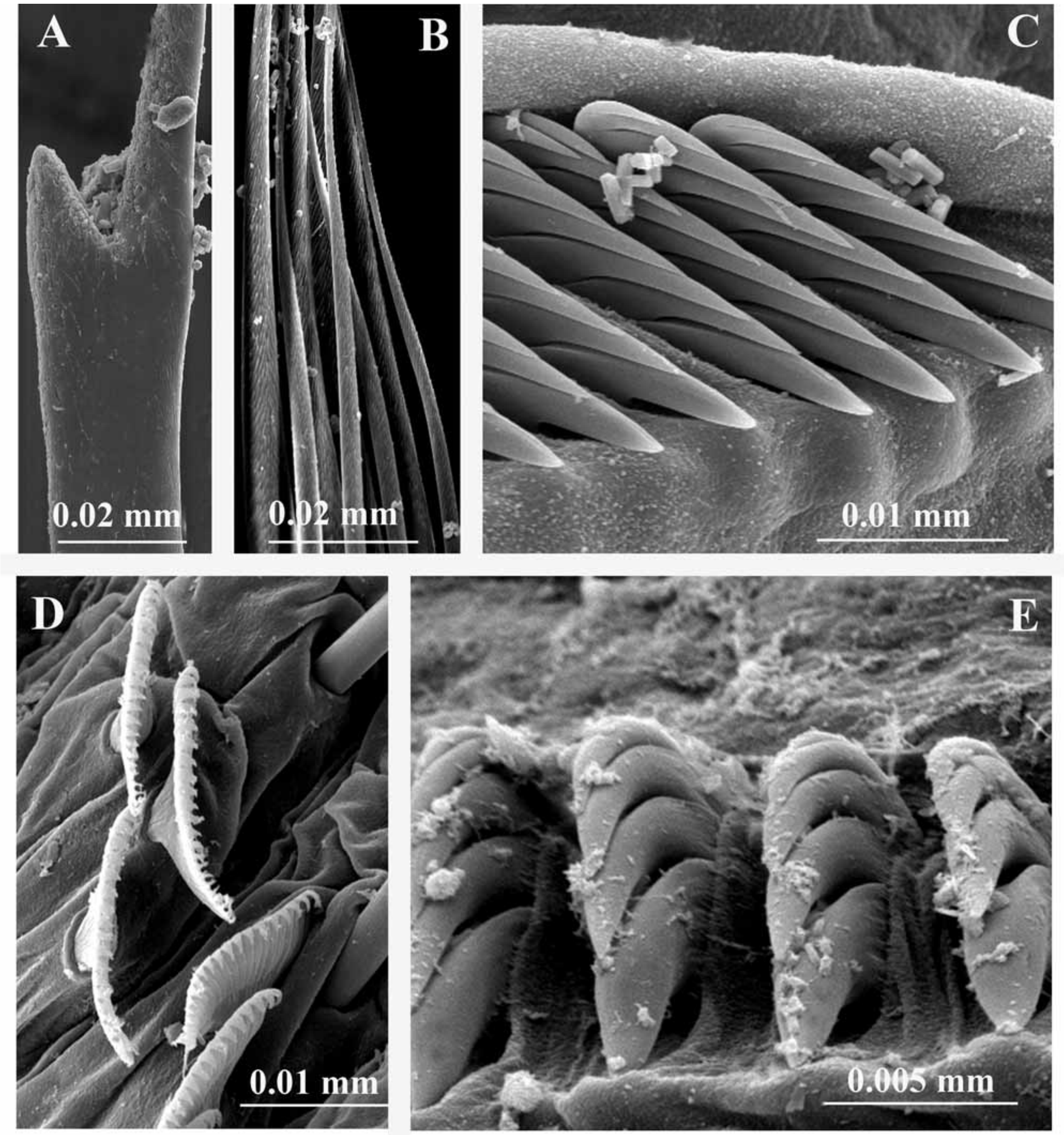

FIGURE 13. SEM micrographs of chaetae in *Crucigera websteri*. Australia, Queensland, Lizard Island, legit & det. E. Kupriyanova. A—bayonet collar chaeta, B—thoracic chaetae, C—thoracic uncini; *Crucigera zygophora* (Johnson, 1901), Canada, British Columbia, Barkley Sound, legit T. Macdonald, det. E. Kupriyanova, D—flat trumpet-shaped abdominal chaetae, E—anterior abdominal uncini.

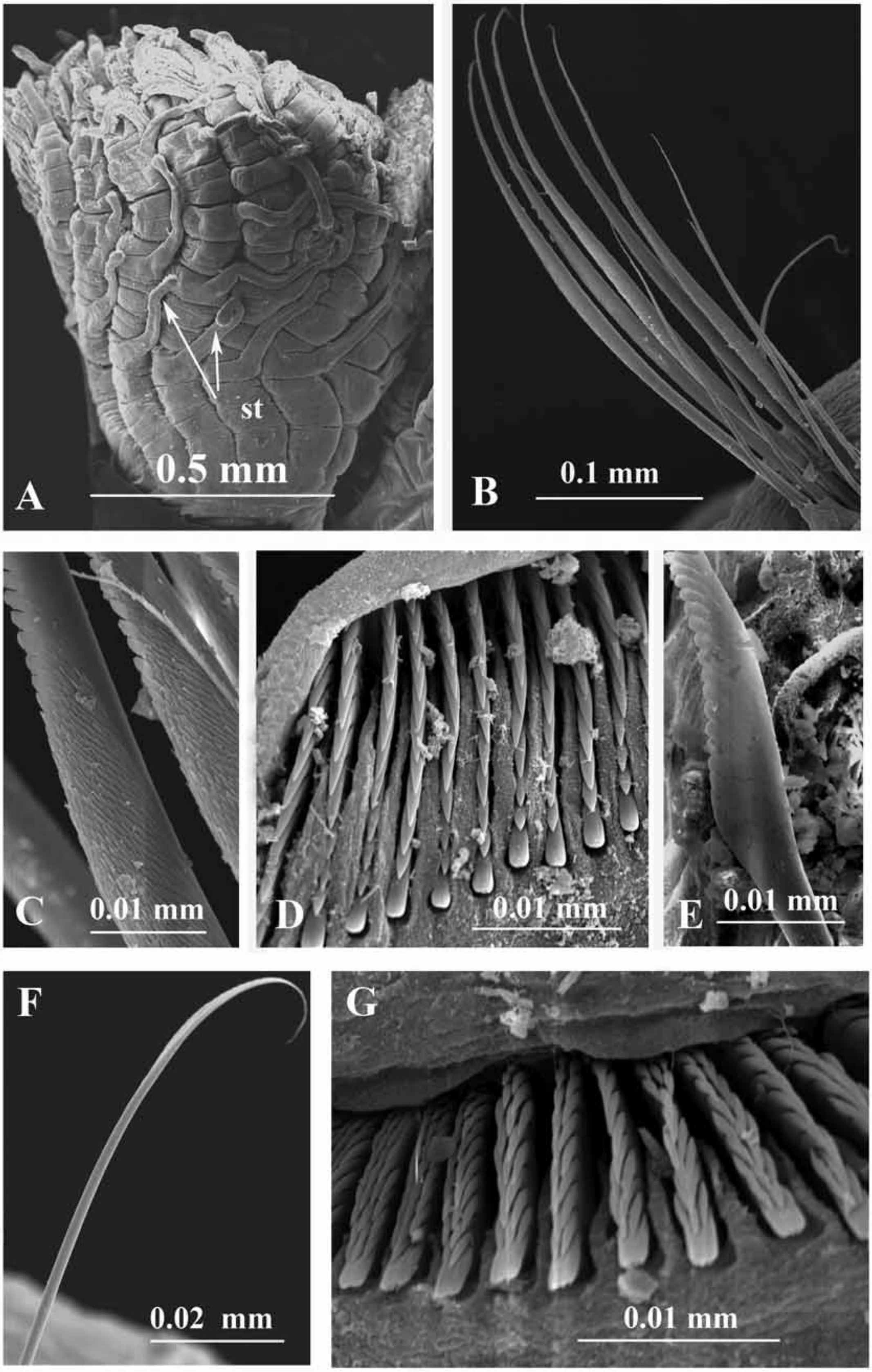

FIGURE 14. SEM micrographs of *Dasynema chrysogyrus*. Australia, Queensland, Lizard Island, legit & det. H.A. ten Hove. ZMA V.Pol. 4540. A—Branchial crown with stylodes (st), B—bundle of collar chaetae, C—details of thoracic chaetae (“limbate” and *Apomatus*), D—thoracic uncini, E—anterior abdominal chaetae, F—posterior capillary abdominal chaeta, G—middle abdominal uncini.

Remarks. This relatively poorly known monotypic genus is recorded from the Indo-West Pacific (see Imajima & ten Hove 1984, Nishi 1993). Its characteristic feature, outwardly directed stylodes on the radioles, is unique for serpulids. Paired stylodes are found elsewhere only in the sabellid genera *Branchiomma* and *Pseudobranchiomma*. See also discussion by Imajima & ten Hove (1984).

Dasynema chrysogyrus (Grube, 1876), Japan, Philippine Islands, Ponape, Indonesia.

8. *Ditrupa* Berkeley, 1835

(Fig. 15)

Type-species: *Dentalium subulatum* Deshayes, 1826 = junior synonym of *Dentalium arietinum* Müller, 1776; designated by Bush 1905: 223.
Number of species: 2

Tube free, tusk-like, not attached to substratum, circular in cross-section, open at both ends, broadening anteriorly though exterior tapers just prior to tube mouth. Outer layer hyaline or white, inner layer opaque. Granular overlay of the tube absent. Operculum inverse conical with chitinous endplate. Peduncle cylindrical, smooth, without wings, gradually merging into operculum, no constriction; it is positioned as first dorsal left radiole. Pseudoperculum absent. Radioles arranged pectinately; up to 15 radioles per lobe. Inter-radiolar membrane, branchial eyes, and stylodes absent. Pair of filiform mouth palps present. 6 thoracic chaetigerous segments. Large entire (non-lobed) collar continuous with short thoracic membranes, ending at first chaetiger (second thoracic segment); tonguelets absent. Collar chaetae absent (see **Collar segment**, p. 22). First thoracic chaetiger biramous (see **Collar segment**, p. 22) with limbate chaetae (Fig. 15A, B) and with uncini; sometimes with special chaetae (see remarks). *Apomatus* chaetae absent. Thoracic uncini saw-to-rasp-shaped (dental formula P:2:2:2:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1 or P:3:2:2:1……1) or rasp-shaped; about 25 teeth in profile, with 2 or 3 teeth in a row above peg (P); peg blunt, curved upwards and gouged underneath (Fig. 15C). Triangular depression absent. Abdominal chaetae and certainly posterior ones thin, almost capillary, with very faint narrow geniculate tip (to completely capillary in *D. gracillima*). Abdominal uncini rasp-shaped, with 20–25 in profile, up to 8 teeth in a row above peg; anterior peg blunt, almost rectangular (Fig. 15D). Achaetous anterior abdominal zone absent; however, anterior half of abdomen with uncini only. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. The genus is found living unattached (Fig. 1A) in soft sediment marine environments around the world. Like many serpulid genera, *Ditrupa* has a history of taxonomic confusion to the extent that its tubes were included in the Mollusca by some authors. The generic diagnosis was emended by ten Hove & Smith (1990). An unattached free tube similar to that of *Ditrupa* is known only in two (?three) other serpulids, *Bathyditrupa hovei* and *Serpula crenata* (possibly incl. *S. sinica*). Unlike the circular in cross-section tubes of *Ditrupa*, those of *Bathyditrupa* and *S. crenata* are rectangular to multi-angular in cross-section (see **The tube**, p. 7).

Ten Hove & Smith (1990: 113, 115) describe 2 populations of *Ditrupa gracillima* in which the first thoracic chaetiger shows special chaetae, one almost geniculately terminating in an oblique frayed narrow limbus, the other stoutly acicular. In view of the limited distributions of these two forms they question whether these populations might be in the process of speciation.

1. *Ditrupa arietina* (Müller, 1776), Northern Norway to Azores and Canary Islands, Mediterranean
2. *Ditrupa gracillima* Grube, 1878, widely distributed in Indo-West Pacific.

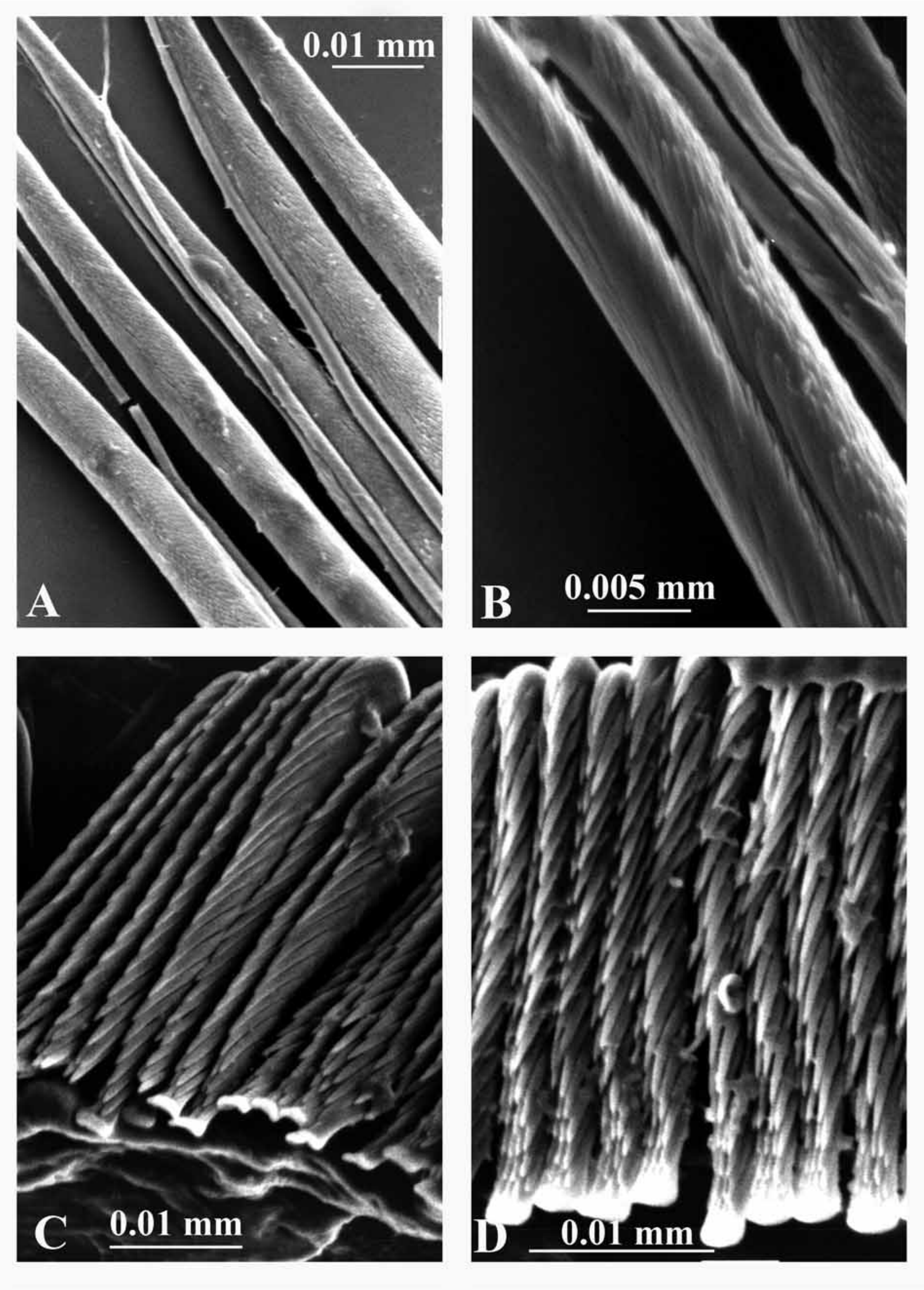

FIGURE 15. SEM micrographs of chaetae in *Ditrupa arietina*. Canary Islands, SW of Palma, 28°39' N 17°58' W, 60-80 m, legit H.A. ten Hove, ZMA V.Pol. 3559. A—chaetae of 4th chaetiger, two sizes, B—chaetae of 1st chaetiger, two sizes, C—uncini of 1st thoracic chaetiger, D—anterior abdominal uncini.

9. *Ficopomatus* Southern, 1921
(Fig. 16)

Type-species: *Ficopomatus macrodon* Southern, 1921
Number of species: 5

Tube white (exceptionally orange), opaque, circular to triangular in cross-section, keels, peristomes, and tabulae may be present. Granular overlay of the tube absent. Operculum a bulbous fleshly ampulla, uncovered or covered with either a chitinous, non-calcified endplate or with numerous chitinous spines in the distal tissue. Peduncle smooth, sub-triangular, with dorsal groove, without distal wings, gradually merging into the opercular ampulla; inserted just below left branchial lobe, near medial line. Pseudoperculum absent. Radioles arranged in semi-circles, up to 11 per lobe, not united by inter-radiolar membrane. Branchial eyes, stylodes, and mouth palps absent. 7 thoracic chaetigerous segments. Collar non-lobed, with entire edge, tonguelets absent. Thoracic membranes long, forming ventral apron across anterior abdominal segments. Dorsal edges of thoracic membranes fused in *F. uschakovi*. Collar chaetae coarsely serrated (Fig. 16A) and limbate. *Apomatus*

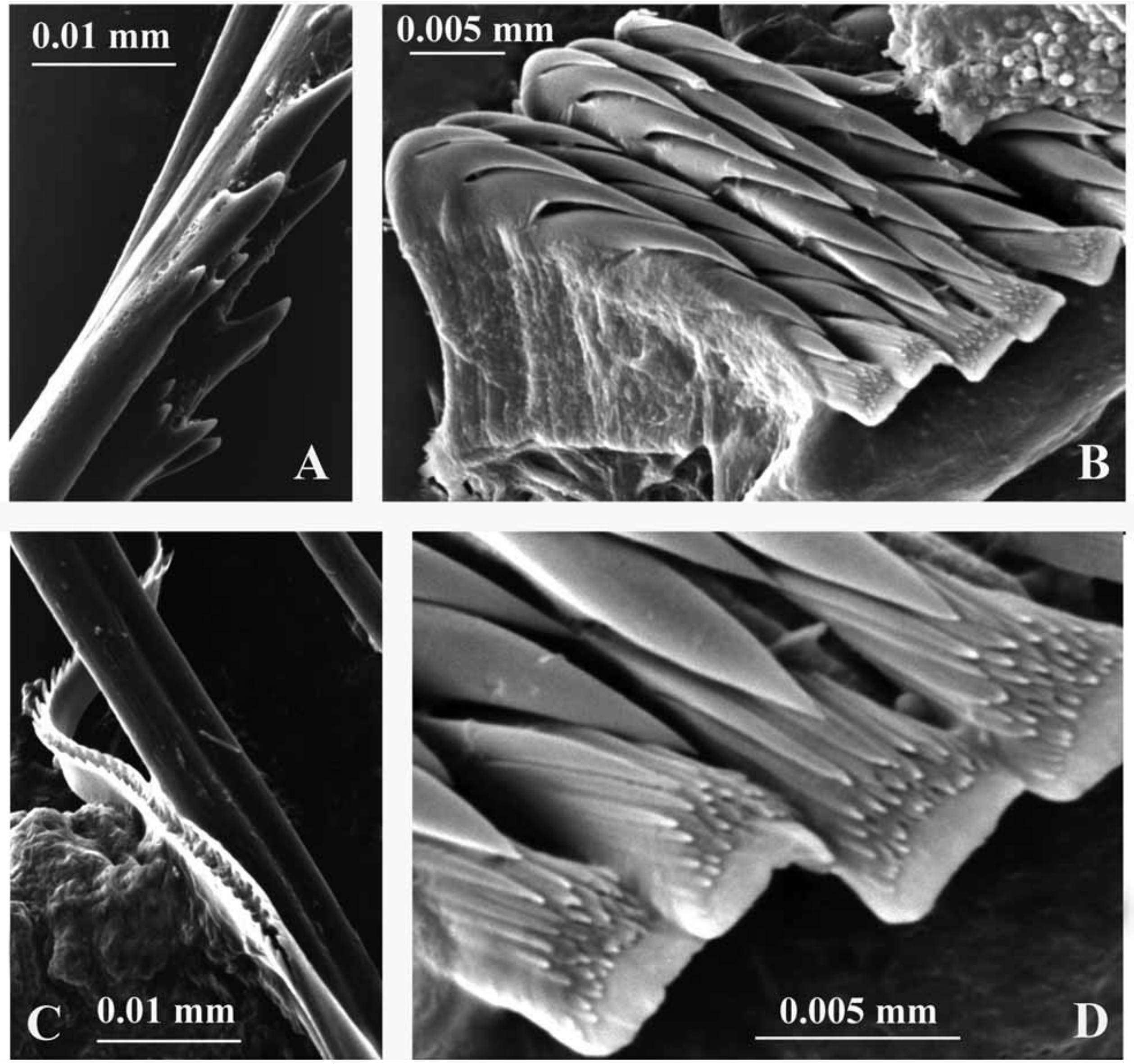

FIGURE 16. SEM micrographs of chaetae in *Ficopomatus enigmaticus*. The Netherlands, Vlissingen, Keersluisbrug near power station, legit H.A. ten Hove, ZMA V.Pol. 3069. A—details of *Ficopomatus* collar chaetae, B—uncini of 4th thoracic chaetiger, C—posterior abdominal chaeta with double row of teeth (hollow tip), D—detail of peg, uncini of 4th thoracic chaetiger.

chaetae absent. Thoracic uncini saw-shaped (Fig. 16B), rarely partly rasp-shaped, with 6–12 teeth; anterior peg flat trapezoidal, blunt, with numerous tiny auxiliary teeth above peg (Fig. 16D). Triangular depression absent. Abdominal chaetae truly trumpet-shaped, smoothly bent, with denticulate edge (Fig. 16C); uncini saw- or rasp-shaped. Achaetous anterior abdominal zone absent. Posterior capillary chaetae and glandular pad absent.

Remarks. Ten Hove & Weerdenburg (1978) revised in detail the monotypic brackish-water genera *Mercierella* Fauvel, 1923, *Sphaeropomatus* Treadwell, 1934, *Mercierellopsis* Rioja, 1945, and *Neopomatus* Pillai, 1960 and synonymized them under *Ficopomatus* Southern, 1921. It should be noted that Pillai (2008) reinstated the genus *Neopomatus*, based on the autapomorphy of thoracic membranes joined over the dorsal thorax, for its single species *uschakovi*. In *Ficopomatus* species there is a continuous series in opercular development from unadorned ampulla without any endplate to a fully developed chitinous plate, even with spines (ten Hove & Weerdenburg 1978). The nominal species *Ficopomatus capensis* Day, 1961 more probably should be placed in *Chitinopoma* (*fide* ten Hove & Weerdenburg 1978: 101).

1. *Ficopomatus enigmaticus* (Fauvel, 1923), worldwide subtropical-temperate, Northern and Southern Hemisphere; brackish
2. *Ficopomatus macrodon* Southern, 1921, India, Sri Lanka; tropical; brackish
3. *Ficopomatus miamiensis* (Treadwell, 1934), Gulf of Mexico, Caribbean; SE Gulf of California; tropical; brackish
4. *Ficopomatus talehsapensis* Pillai, 2008 Taléh Sap, Gulf of Thailand; tropical; brackish
5. *Ficopomatus uschakovi* (Pillai, 1960), Africa, Indo-Pacific; tropical; brackish.

10. *Filograna* Berkeley, 1835

(Fig. 17)

Type species: *Filograna implexa* Berkeley, 1835
Number of species: 1

Worms form open aggregates consisting of large numbers of small whitish tubes, circular in cross-section. Granular overlay and keels absent. A pair of membranous spoon-shaped opercula on first unmodified pinnulate radioles. Radioles arranged into semi-circles, up to 4 radioles per lobe. Branchial eyes absent. Inter-radiolar membrane and stylodes absent. Prominent prostomium with ocellar clusters. Mouth palps present. 6–12 thoracic chaetigerous segments. Collar trilobed, tonguelets between ventral and lateral collar lobes absent. Thoracic membranes long, forming apron. Collar chaetae fin-and-blade (Fig. 17A) and limbate. *Apomatus* chaetae present. All uncini rasp-shaped with up to 10 teeth in profile, 2–4 teeth in a transverse row; anterior fang pointed (Fig. 17B). Triangular depression absent. Achaetous anterior abdominal zone present, short. Abdominal chaetae flat narrow geniculate with rounded teeth along edge (Fig. 17C). Long posterior capillary chaetae and glandular pad absent.

Remarks. The genus *Filograna* has been attributed by e.g., Mörch (1863; as *Filigrana*) and Hartman (1959) to Oken (1815). However, Oken used *filograna* as species name in the combination "*Clymene filograna*, *Serpula filograna*"; the species name was elevated to generic rank by Berkeley (1835). The nominal genera *Filograna* and *Salmacina* are distinguished mainly by the presence of two (rarely one) membranous opercula in the former and absence of an operculum in the latter. Some authors consider them distinct genera (Iroso 1921, Fauvel 1927, Pillai 1960, Straughan 1967b), whereas others treat them as a single species (McIntosh 1923, Faulkner 1929, Day 1955, 1967). More recent authors (Nelson-Smith 1967, Gee 1963, Zibrowius 1968a, 1973b, Uchida 1978, Kupriyanova & Jirkov 1997) regard operculate and non-operculate forms to be separate species within the genus *Filograna*. Nogueira & ten Hove (2000) gave an extensive discussion and synonymy and adapted the heuristic view that the operculate cold-temperate Atlantic *Filograna* better be kept separate from the non-operculate ubiquitous *Salmacina*.

Filograna implexa M. Berkeley, 1835. Weymouth, English Channel, UK; cold temperate-subtropical Atlantic, Mediterranean; other locations doubtful.

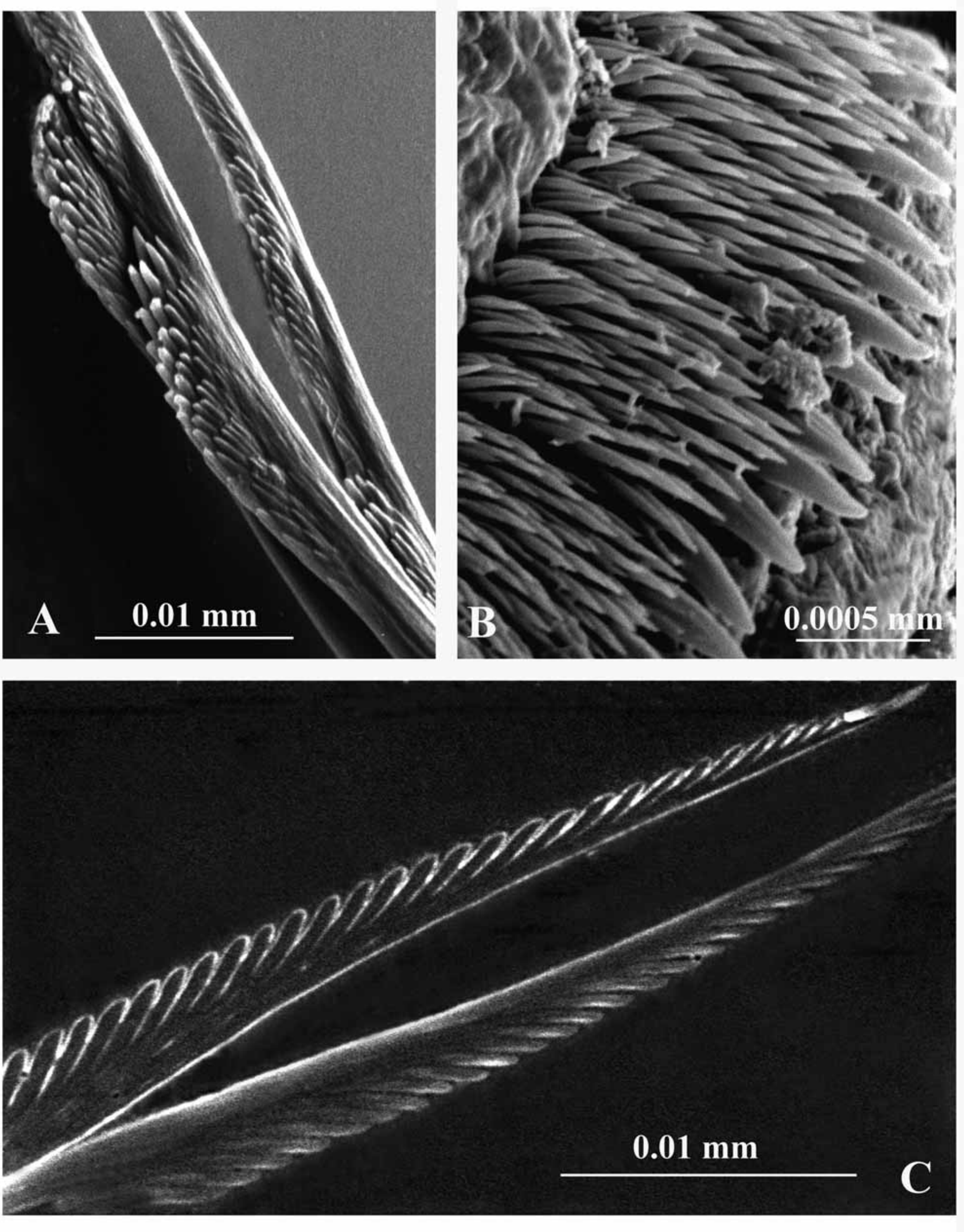

FIGURE 17. SEM micrographs of chaetae in *Filograna implexa*. United Kingdom, Orkney Islands, Head of Work, 22 m, legit M.J. de Kluyver, ZMA V.Pol. 3767. A—fin-and-blade collar chaetae, B—1st row of thoracic uncini, C—middle abdominal chaetae, imprint of tip.

11. *Filogranella* Ben-Eliahu & Dafni, 1979
(Fig. 18)

Type-species: *Filogranella elatensis* Ben-Eliahu & Dafni, 1979
Number of species: 1, maybe 3

Tubes white, opaque, circular in cross-section, with 5 longitudinal keels; peristomes absent. Granular overlay of the tube absent. Operculum and pseudoperculum absent (but see Remarks). Radioles arranged in semi-circles, up to 9 per lobe. Inter-radiolar membrane and stylodes absent. Branchial eyes absent. Prominent prostomium with ocellar clusters. Mouth palps absent. 11–14 thoracic chaetigerous segments (Fig. 18A). Well-developed trilobed collar continuous with thoracic membranes ending in mid-thorax, around 5th–6th thoracic chaetiger. Tonguelets absent. Collar chaetae limbate (Fig. 18B). *Apomatus* chaetae present (Fig. 18C). Thoracic uncini saw- to rasp-shaped with about 16 teeth in profile and up to 4 teeth in a row above peg. Triangular depression absent. Abdominal chaetae flat sickle shaped with blunt teeth on the edge (Fig. 18E). Abdominal uncini rasp-shaped with > 20 teeth in profile, up to 7 teeth in a row; anterior peg blunt, slightly gouged underneath (Fig. 18D). Achaetous anterior abdominal zone short. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. *Filogranella* forms aggregations that resemble those of *Filograna*, but worms and their tubes are larger. However, *Filograna* differs from *Filogranella* in having fin-and-blade collar chaetae with proximal denticulate wing well separated from the distal limbate zone, a pair of well-developed thoracic membranes with apron, and rasp-shaped thoracic uncini (Ben-Eliahu & Dafni 1979). *Filogranella* aggregations have been mentioned from various locations around the world in diving guides (e.g., Allen & Steene 1994, 1996, Colin & Arneson 1995, Gosliner *et al.* 1996, Weinberg 1996, Debelius 1998, Fosså & Nilsen, 2000: Red Sea, Indonesia, Philippines, Caribbean). Some colonies have specimens with opercula with flat chitinous endplates, on a flat peduncle (more or less like that of *Metavermilia*) inserted as the second dorsal radiole. We suspect it is a complex of related species that needs to be sorted out. *Vermiliopsis prampramiana* Augener, 1918, regarded to be undeterminable by Zibrowius (1973b), might belong here by its general chaetation pattern and 9 thoracic chaetigers. *Neovermilia aberrans* Rullier & Amoureux, 1979, might rather belong in this genus.

1. ?*Filogranella aberrans* (Rullier & Amoureux, 1979), Brazil
2. *Filogranella elatensis* Ben-Eliahu & Dafni, 1979, Elat, Gulf of Aqaba; Indo-West Pacific, Central Atlantic, Caribbean; probably more than one species
3. ?*Filogranella prampramiana* (Augener, 1918), Gold Coast, Africa.

12. *Filogranula* Langerhans, 1884
(Fig. 19)

Type-species: *Filogranula gracilis* Langerhans, 1884
Number of species: 6

Tube white, opaque, with elaborate peristomes; keel present. Granular overlay absent. Operculum with chitinous endplate, may have additional spines in the center. Peduncle cylindrical, smooth, without wings (however, see Remarks); inserted as second dorsal radiole on one side. Opercular constriction present (but for *F. stellata*, absent). Pseudoperculum absent. Radioles arranged in semi-circles, up to 7 per lobe. Inter-radiolar membrane and stylodes absent. Branchial eyes may be present. Mouth palps not observed. 7 thoracic chaetigerous segments. Collar generally non-lobed (may be trilobed) with entire edge, continuous with short thoracic membranes, ending at second thoracic chaetiger. Tonguelets absent. Collar chaetae fin-and-blade (Fig. 19A) and limbate. *Apomatus* chaetae present (Fig. 19B). Thoracic uncini saw- or saw-to-rasp-shaped with 12–14 teeth in profile, up to 5 teeth in a row above anterior peg (P), blunt, gouged underneath (e.g., dental formula P:5:3:3:2:1:1:1:1:1:1:1:1:1, Fig. 19C). Triangular depression absent. Abdominal chaetae short, flat triangular with wide distal denticulate blade (Fig. 19E); abdominal uncini rasp-shaped (Fig. 19D). Achaetous anterior abdominal zone present. Long posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. Zibrowius (1983) and Kupriyanova (1993a) remark that the genera *Chitinopoma* and *Filogranula* are very similar in general structure of the operculum, chaetal structure, and length of the thoracic membranes. See also comments to *Chitinopoma*. *Filogranula exilis* is unusual as it shows a pinnulate radiole functioning as peduncle.

1. *Filogranula annulata* (O.G. Costa, 1861), Mediterranean, Portugal
2. *Filogranula calyculata* (O.G. Costa, 1861), Mediterranean, Lusitania, Mauretania
3. *Filogranula exilis* Imajima, 1979, Japan, Seychelles
4. *Filogranula gracilis* Langerhans, 1884, Eastern Atlantic, Hawaii?
5. *Filogranula revizee* Nogueira & Abbud, 2009, South Brazil
6. *Filogranula stellata* (Southward, 1963), Mediterranean Atlantic

13. *Floriprotis* Uchida, 1978

(Fig. 20)

Type-species: *Floriprotis sabiuraensis* Uchida, 1978
Number of species: 1

Tube white, opaque, circular in cross-section, normally completely embedded into living corals; granular overlay absent. Operculum and pseudoperculum absent. Radioles arranged (semi-circular to) short pectinately, up to 20 per lobe. Inter-radiolar membrane present. Stylodes absent. Branchial eyes absent. Mouth palps absent. 7 thoracic chaetigerous segments. Collar trilobed with entire edge, tonguelets absent. Thoracic membranes long, apron present. A pair of pockets on the inner side of each thoracic membrane, between the second and third thoracic segments. Collar chaetae bayonet, with elongate rounded teeth at base of very short blade (Fig. 20A), and limbate. *Apomatus* chaetae absent. Thoracic uncini of *Serpula* type, with 4–5 teeth and pointed fang (Fig. 20B). Triangular depression present. Abdominal chaetae flat trumpet-shaped with denticulate edge as in *Serpula* (Fig. 20D). Abdominal uncini similar to thoracic ones, saw-shaped with 4–5 teeth anteriorly, but rasp-to-saw-shaped (dental formula F:1:1:2:3:3:3:4:3) posteriorly (Fig. 20C), with 1 tooth proximally above fang (F) to 3 (exceptionally 4) teeth per row distally, 7–8 teeth in profile. Achaetous zone absent. Long posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. The species is an obligate symbiont of corals in the Indo-West Pacific (Uchida 1978, Bailey-Brock 1985, Nishi 1992b). The chaetation pattern of this species is very similar to that typical for *Crucigera*-*Hydroides*-*Serpula*-*Spiraserpula* group and, as it was suggested by its author, *F. sabiuraensis* is likely to be closer to that clade than to *Protis*.

The unusual characteristic feature of this monotypic genus is the presence of pockets in the thoracic membranes, however, see Remarks following *Serpula*. Bailey-Brock (1985) noted that one *Floriprotis* specimen from Fiji did contain eggs in pockets with a few eggs under the overlapping flaps of thoracic membranes, but whether these eggs were fertilized remains unknown. Thus, there is no hard evidence that the pockets are used for incubation.

Another special feature according to Uchida (1978, Plate V A) would be the presence of wart-like protuberances laterally in the collar segment. However, though never reported before, wart-like protuberances are found in some larger species of *Hydroides* and *Serpula* and in *Protis hydrothermica* (ten Hove & Zibrowius 1986, fig. 6q); the character had not been noted before in these taxa.

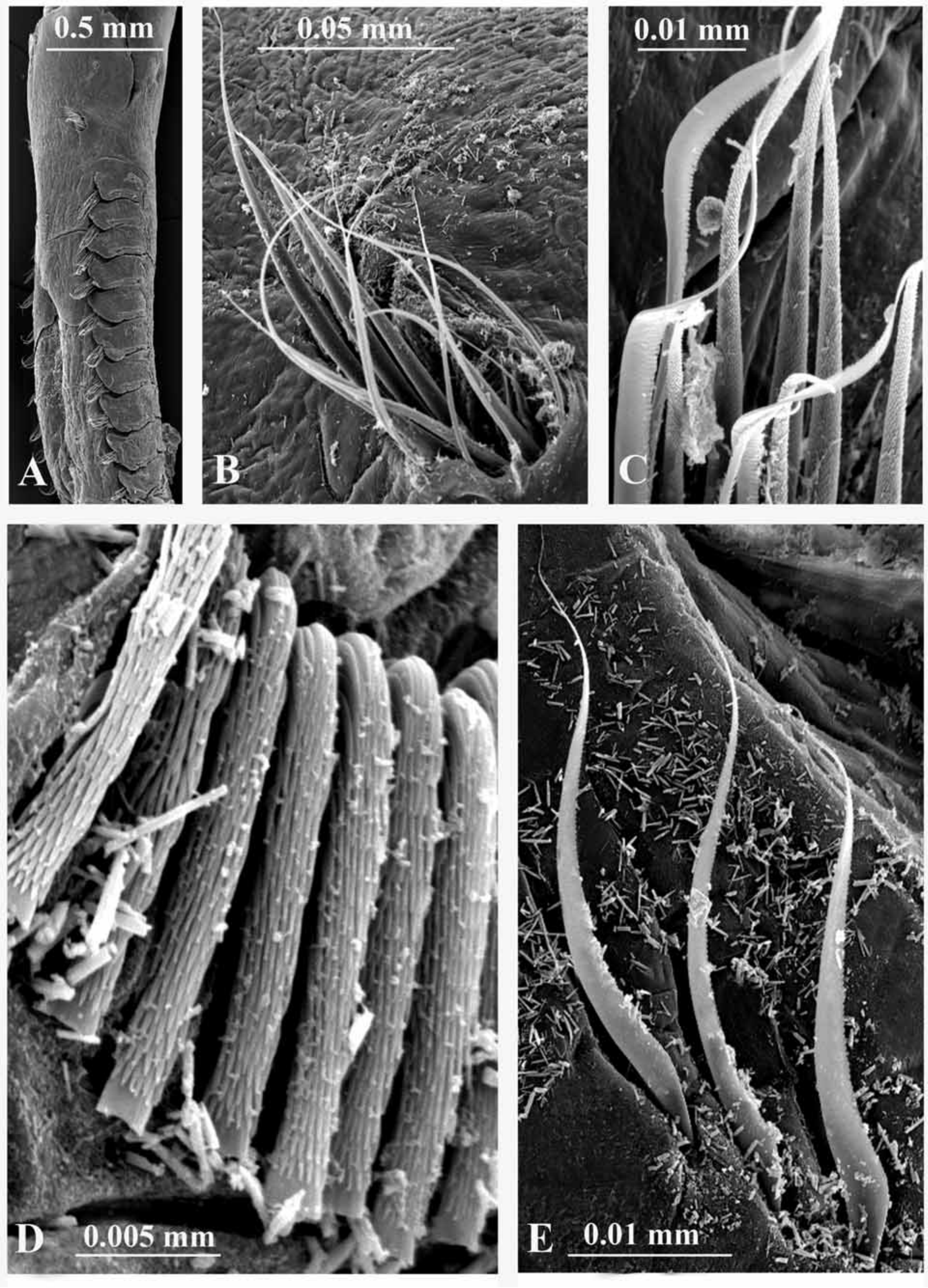

FIGURE 18. SEM micrographs of *Filogranella elatensis*. Israel, Elat, 10 m, legit J. Dafni, det. H.A. ten Hove, ex HUJ, SAM E3661. A—Lateral view of thorax, B—bundle of collar chaetae, C—thoracic chaetae of 4th chaetiger (*Apomatus* and "limbate"), D—anterior abdominal uncini, E—anterior abdominal chaetae.

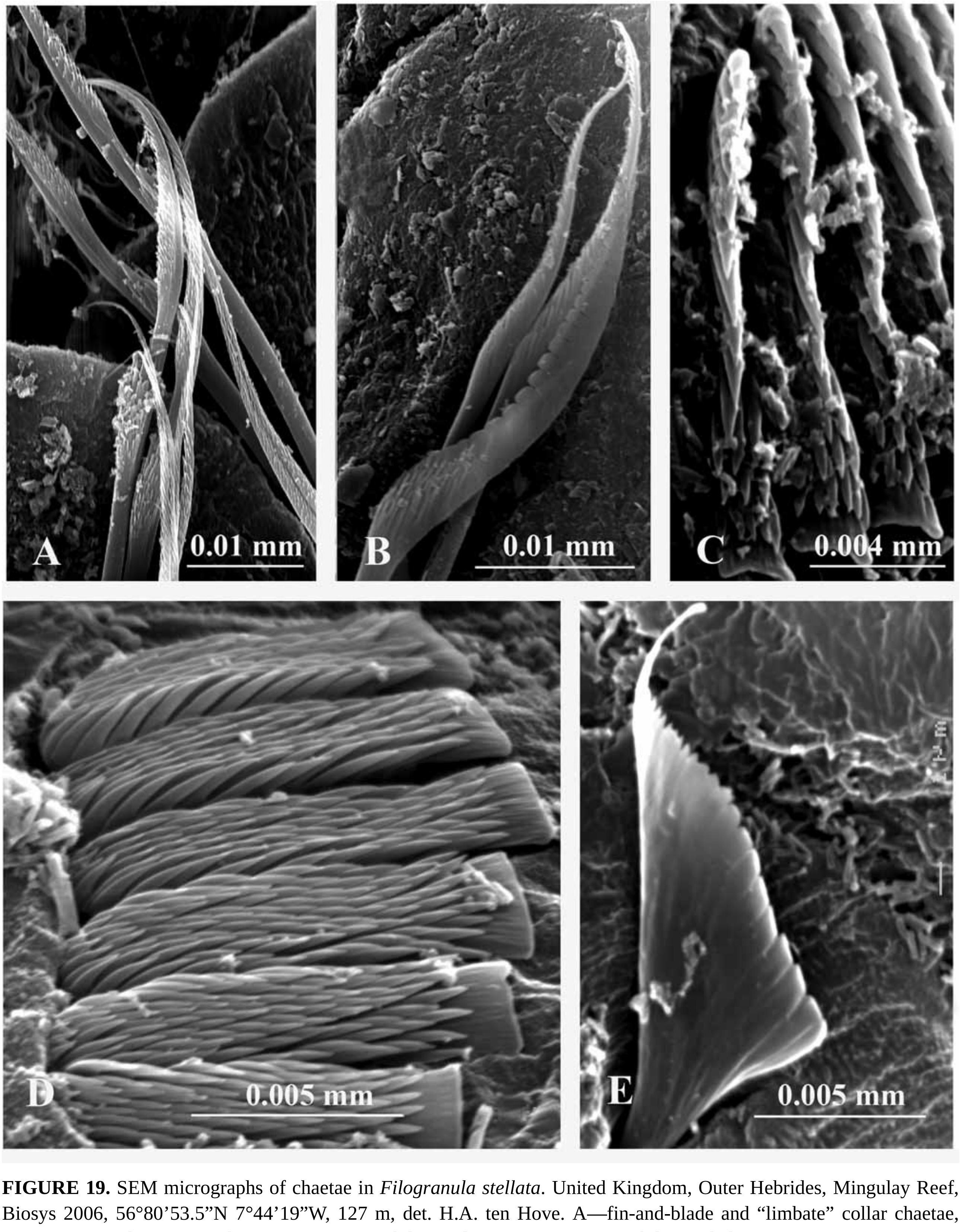

FIGURE 19. SEM micrographs of chaetae in *Filogranula stellata*. United Kingdom, Outer Hebrides, Mingulay Reef, Biosys 2006, 56°80’53.5”N 7°44’19”W, 127 m, det. H.A. ten Hove. A—fin-and-blade and “limbate” collar chaetae, B—*Apomatus* chaetae, C—thoracic uncini, D—abdominal uncini, E—anterior abdominal chaeta.

Floriprotis has been reported from southern Japan (Uchida 1978, Nishi 1992b) and Fiji (Bailey-Brock 1985) and Indonesia (herein). At least some of the latter material, however, shows abraded *Serpula*-type collar chaetae (e.g., Nishi 1992b fig. 2C) rather than the typical *Floriprotis* bayonets (e.g., Uchida 1978 Pl. V C;

Bailey-Brock 1985 fig. 13e; this paper), and either a pair of small pseudopercula or even a half developed *Serpula*-type operculum. The presence of warts on the collar segment makes this material even more confusing, all should be rechecked and variability (if any) of collar chaetae and (pseud)opercula should be documented.

Floriprotis sabiuraensis Uchida, 1978, Japan, Indonesia, Fiji.

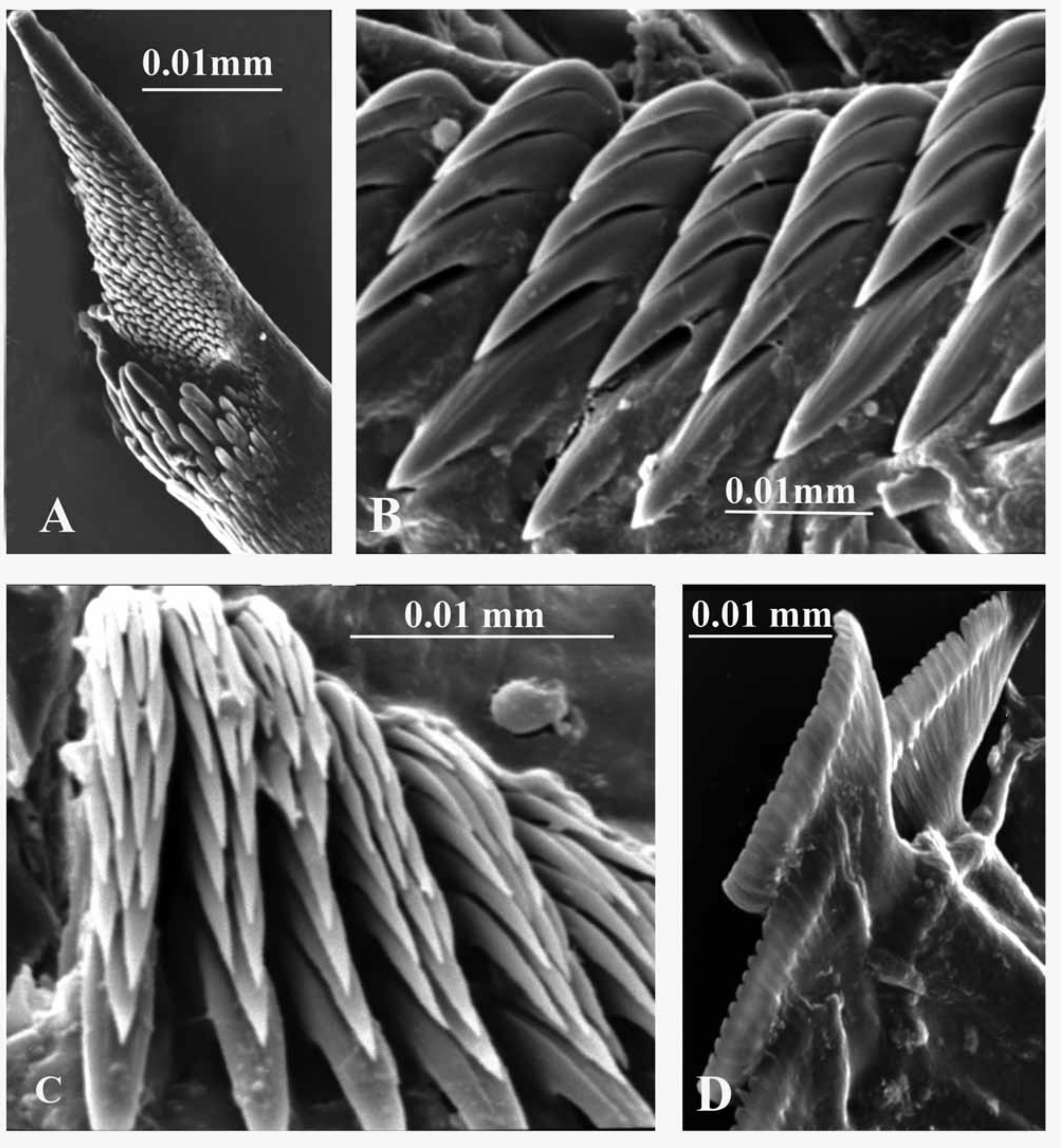

FIGURE 20. SEM micrographs of chaetae in *Floriprotis sabiuraensis*. Indonesia, Ambon, 03°39' S, 128°3' E, inner bay West of Halong, Snellius II Expedition, 2-15 m, legit H.A. ten Hove, ZMA V.Pol. 3801. A—bayonet collar chaeta, B—uncini of 1st thoracic row, C—posterior abdominal uncini, D—anterior abdominal chaetae.

14. *Galeolaria* Lamarck, 1818

(Fig. 21)

Type-species: *Galeolaria caespitosa* Lamarck, 1818
Number of species: 2
.

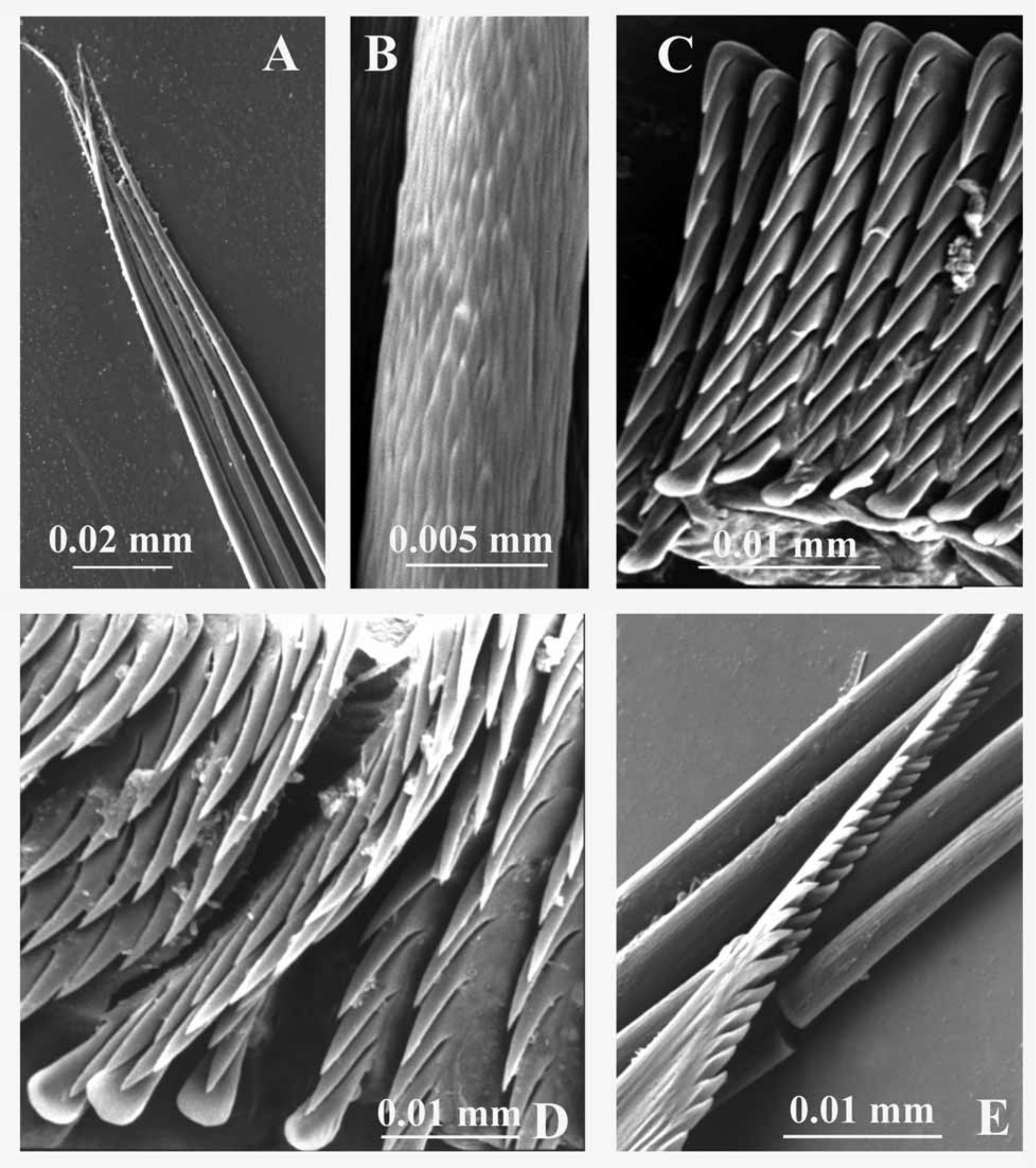

FIGURE 21. SEM micrographs of chaetae in *Galeolaria caespitosa*. Australia, Sydney, Port Jackson, intertidal, Th. Mortensen's Pacific Expedition 14-16, exchange Zoological Museum Copenhagen, ZMA V.Pol. 3637. A—bundle of collar chaetae, B—detail of thoracic limbate chaeta, C—1st row of thoracic uncini, D—anterior abdominal uncini, E—details of anterior abdominal chaeta with a hollow tip.

Tube white or pink, opaque, with 2 longitudinal keels, trapezoidal in cross-section. Granular overlay absent. Operculum rather flat ampulla with distal calcareous plate, armed with elaborate movable spines. Peduncle thick, triangular in cross-section, with distal wings; inserted almost medio-dorsally, covering the base of up to 3–4 dorsal radioles; constriction absent. Pseudoperculum absent. Radioles arranged almost in spirals (1.25 whorl), up to 42 per lobe. Stylodes and branchial eyes absent. Inter-radiolar membrane present. Mouth palps absent. 7 thoracic chaetigerous segments. Collar trilobed, collar edge entire, smooth, occasionally with frilly edge (*G. hystrix*). Tonguelets absent. Thoracic membranes forming apron. Collar chaetae small, limbate (Fig. 21A). *Apomatus* chaetae absent. Thoracic uncini saw-shaped with 7–10 teeth, anterior peg stout, rounded to spatulate (Fig. 21C). Triangular depression absent. Abdominal chaetae true trumpet-shaped, smoothly bent, with two rows of denticles separated by a hollow groove and extended into a long lateral spine (Fig. 21E). Abdominal uncini with 11–15 teeth, anterior peg stout, rounded (Fig. 21D), posterior ones rasp-shaped with 2–3 rows. Long posterior capillary chaetae absent. Achaetous anterior abdominal zone short (2–3 segments). Posterior glandular pad absent.

Remarks. The genus *Galeolaria* is one of the taxa that has been attributed to Savigny by various authors (e.g., Fauchald 1977: 144). The Code, however, is very clear on the point of priority of publication, Lamarck (1818) precedes Savigny (1820), and is the author of *Galeolaria* (cf. Fauchald 1992: 2–3).

The genus *Galeolaria* is endemic to the southern half of Australia and New Zealand. *G. caespitosa* is gregarious and intertidal, whereas *G. hystrix* is solitary and subtidal, rarely forming “reefs” (see Smith *et al.* 2005). The uncorroborated records of *Galeolaria caespitosa* from New Caledonia by Fauvel (1947) and of *G. hystrix* from N.W. Spain by Alvariño (1951) are most probably erroneous.

1. *Galeolaria caespitosa* Lamarck, 1818, temperate and cold southern part of Australia
2. *Galeolaria hystrix* Mörch, 1863, New Zealand, temperate and cold southern part of Australia.

15. *Hyalopomatus* Marenzeller, 1878
(Fig. 22)

Type-species: *Hyalopomatus claparedii* Marenzeller, 1878
Number of species: 11 or 12

Tube white, opaque, sometimes with external hyaline layer, but granular overlay absent; (semi) circular in cross-section. Tabulae may be present. Operculum globular, soft, without distinct endplate or consisting of proximal ampulla with slightly chitinized distal cap; well separated from peduncle by constriction; sometimes operculum absent. Peduncle very thin, cylindrical, smooth, without wings; inserted outside branchial crown proper in front of first dorsal radiole on one side. However, for *H. langerhansi* we observed “between base of first and second radiole”. Pseudoperculum absent. Arrangement of radioles short pectinate, up to 15 pairs of radioles. Inter-radiolar membrane absent. Branchial eyes rarely present. Stylodes absent. Mouth palps present. 6 thoracic chaetigerous segments. Collar trilobed, tonguelets absent. Thoracic membranes short, ending at first or second thoracic chaetiger. Collar chaetae fin-and-blade (Fig. 22A), or without gap between fin and blade and thus with uniform distal denticulate wing, and limbate. *Apomatus* chaetae absent (contrary to Ben-Eliahu & ten Hove 1989). Thoracic uncini rasp-shaped with numerous small teeth, approximately 20 in profile, up to 9 teeth in a row above peg; anterior peg made of two rounded lobes with a shallow incision in between, flat or slightly gouged in the middle (Fig. 22B). Triangular depression absent. Abdominal chaetae almost capillary with only tip flat narrow geniculate with pointed teeth (Fig. 22D); uncini rasp-shaped, similar to thoracic ones, but their anterior peg with 3–4 flat rounded lobes (Fig. 22C). Achaetous anterior abdominal zone may be present. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. This genus is poorly known probably because it includes mainly bathyal and abyssal species. Zibrowius (1969a) revised the genus to include six species. Kupriyanova (1993c) described three new species and provided a key to all species known at that time. More recently, three new species were added to the genus, *H. variorugosus* Ben-Eliahu & Fiege (1996), who also discuss the then known species, the non-operculate *H. cancerum* Knight-Jones *et al*. (1997) and *H. madreporae* Sanfilippo (2009), known by tubes only. Non-operculate specimens of *Hyalopomatus*, apparently accidental, were reported in the review by Zibrowius (1969a: 13).

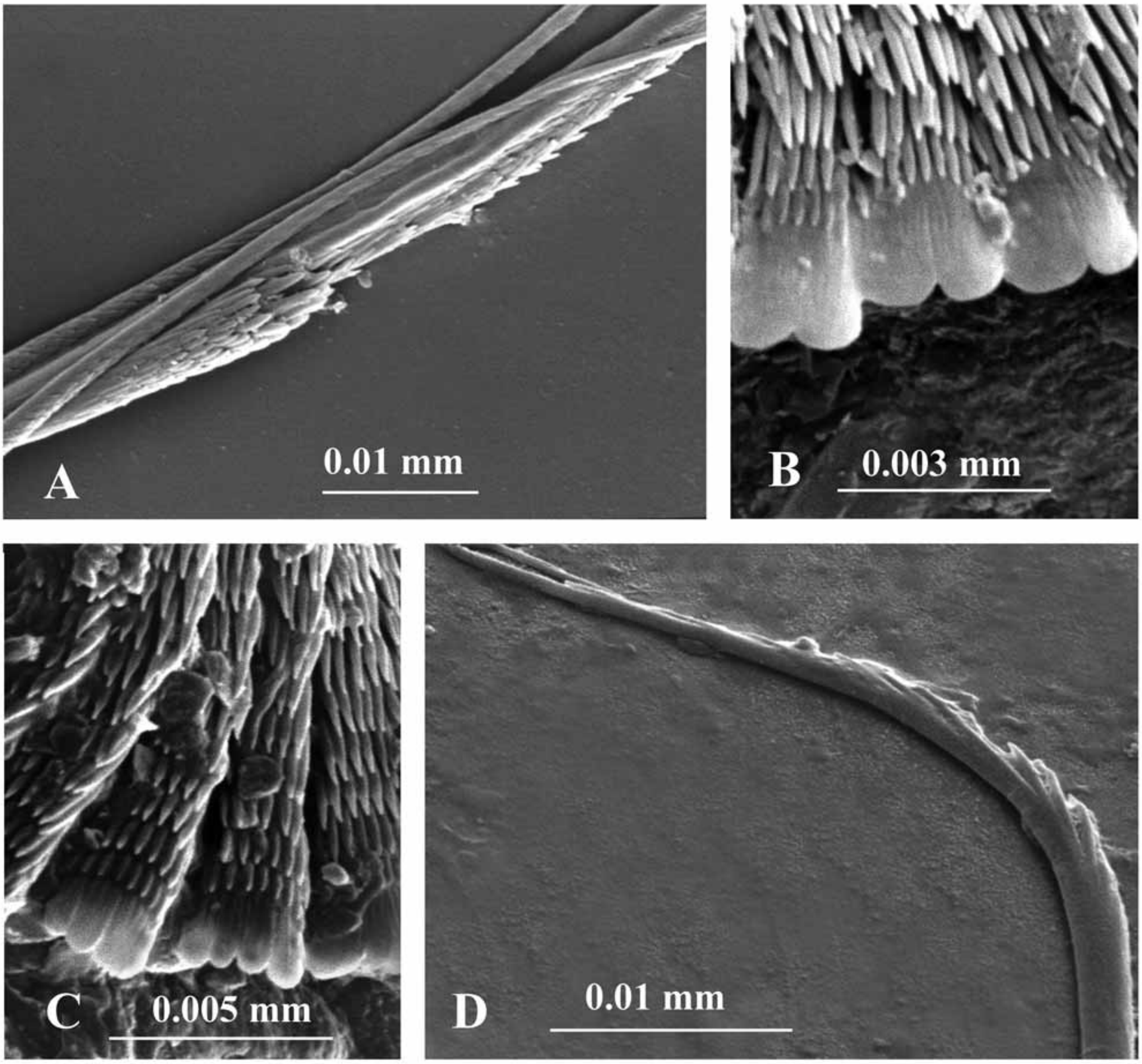

FIGURE 22. SEM micrographs of chaetae in *Hyalopomatus marenzelleri*. Canary Islands, SE of Lanzarote, 28°45' N, 13°19' W, 1134-1315 m, legit H.A. ten Hove, RMNH 18332. A—fin-and-blade and “capillary” collar chaetae, B—detail of peg in last (6th) thoracic uncini, C—posterior/middle abdominal uncini, D—posterior/middle abdominal chaetae.

1. *Hyalopomatus biformis* (Hartman, 1960), S. California
2. *Hyalopomatus cancerum* Knight-Jones *et al.,* 1997, off Oman
3. *Hyalopomatus claparedii* Marenzeller, 1878, Arctic; bathyal
4. *Hyalopomatus jirkovi* Kupriyanova, 1993c, Kurile-Kamchatka trench; abyssal/hadal
5. *Hyalopomatus langerhansi* Ehlers, 1887, off Cuba; compare *H. sombrerianus*
6. *Hyalopomatus macintoshi* (Gravier, 1911), Antarctic
7. *Hyalopomatus madreporae* Sanfilippo, 2009, Mediterranean
8. *Hyalopomatus marenzelleri* Langerhans, 1884c, Canary Islands to S. off Ireland, ?Mediterranean
9. *Hyalopomatus mironovi* Kupriyanova, 1993, Kurile-Kamchatka trench, off California; abyssal/hadal
10. *Hyalopomatus nigropileatus* (Ehlers, 1900c), South Chile, Antarctica

11. *Hyalopomatus sikorskii* Kupriyanova, 1993c, Kurile-Kamchatka trench; abyssal/hadal
12. *Hyalopomatus sombrerianus* (McIntosh, 1885), off Sombrero, St. Thomas, Caribbean; compare *H. langerhansi*
13. *Hyalopomatus variorugosus* Ben-Eliahu & Fiege, 1996, Mediterranean, Atlantic.

16. *Hydroides* Gunnerus, 1768

(Fig. 23)

Type species: *Hydroides norvegicus* Gunnerus, 1768
Number of species: 89 (one with 2 subspecies)

Tube white (sometimes bluish), more or less circular to trapezoidal (with flattened upper surface) in cross-section, peristomes and shallow longitudinal ridges may be present, no distinct keels. A granular overlay may be present. Operculum two-tiered, composed of basal funnel of fused radii and distal verticil (crown) of chitinized spines. Peduncle cylindrical, smooth, without wings, may or may not be separated from opercular funnel by a constriction; formed from second dorsal radiole on one side. Pseudoperculum present. Arrangement of radioles in semi-circles, up to 33 per lobe. Branchial eyes absent. Inter-radiolar membrane generally absent, rarely present (Bastida-Zavala & ten Hove 2002, mention only one species where it is present). Stylodes absent. Mouth palps absent. 7 thoracic chaetigerous segments, exceptionally more (9 in *H. bisectus* Imajima & ten Hove, 1989 and *Hydroides* sp.2 Bastida-Zavala & ten Hove 2002; 7–9 in *H. bannerorum* Bailey-Brock, 1991). Collar trilobed, tonguelets absent. Thoracic membranes long, forming ventral apron. Collar chaetae bayonet-type (Fig. 23A) and limbate. *Apomatus* chaetae absent. All uncini saw-shaped with relatively few (up to 7) teeth; anterior fang simple pointed (Fig. 23B). Triangular depression present. Abdominal chaetae flat trumpet-shaped with denticulate edge (Fig. 23C). Achaetous anterior abdominal zone absent. Posterior capillary chaetae present (Fig. 23D). Posterior glandular pad absent.

Remarks. *Hydroides* is the largest serpulid genus with a mainly tropical to sub-tropical distribution. Species in the genus are distinguished by well-differentiated opercula and differences in chaetal and tube structure. Although a complete world-wide revision of the genus is yet to be completed, Bastida-Zavala & ten Hove (2002, 2003) recently published revisions of the *Hydroides* species from the Western Atlantic region, respectively Eastern Pacific region and Hawaii. Also, Bastida-Zavala & ten Hove (2002) provided a detailed historical review of taxonomic studies of the genus.

1. *Hydroides alatalateralis* (Jones, 1962), Jamaica, Caribbean, Colombian Pacific
2. *Hydroides albiceps* (Grube, 1870), Red Sea, widely distributed in the Indo-West Pacific; compare *H. trivesiculosus*
3. *Hydroides ancorispinus* Pillai, 1971, Sri Lanka; compare *H. malleolaspinus*
4. *Hydroides arnoldi* Augener, 1918, Annobón, Sao Tome, Congo, Zaire, Ghana, Liberia; NB. part of Augener 1918, Tebble 1956, and all Uschakov 1970 belongs to *H. augeneri*
5. *Hydroides augeneri* Zibrowius, 1973b, Congo, Dahomey, Ghana, Liberia, Guinea; see remark *H. arnoldi*
6. *Hydroides azoricus* Zibrowius, 1972d, Azores; sometimes confused with *H. norvegicus*
7. *Hydroides bandaensis* Zibrowius, 1972c, Banda Sea; compare *H. novaepommeraniae*
8. *Hydroides bannerorum* Bailey-Brock, 1991, Hawaii
9. *Hydroides bifurcatus* Pixell, 1913, Maldives, South Africa, Madagascar, ?Sri Lanka, ?New Caledonia
10. *Hydroides bisectus* Imajima & ten Hove, 1989, Okinawa, Japan
11. *Hydroides bispinosus* Bush, 1910, Bermuda, Gulf of Mexico, Eastern USA and Caribbean
12. *Hydroides brachyacanthus* Rioja, 1941a, Western Mexico to Ecuador, ?Hawaii; circum(sub)tropical records from elsewhere probably belong to a complex of species (Bastida-Zavala & ten Hove 2002, 2003)
13. *Hydroides* cf. *brachyacanthus* Rioja, 1941a, Lesser Antilles, Venezuela, South Brazil

14. *Hydroides bulbosus* ten Hove, 1990, Gulf of Oman
15. *Hydroides calopoma* Zibrowius, 1973b, Annobón
16. *Hydroides capensis* Zibrowius, 1972d, Cape, Ghana, Nigeria, Senegal; sometimes confused with *H. norvegicus*
17. *Hydroides centrospina* Wu & Chen, 1981b, South China, Tonga; see remarks under *H. elegans*
18. *Hydroides chilensis* Hartmann-Schröder, 1962, Arica, Chile, Colombia
19. *Hydroides cruciger* Mörch, 1863, Punta Arenas Pac., Baja California to Colombia, Hawaii; N.B. all Caribbean records belong to *H. bispinosus* and/or *H. parvus*
20. *Hydroides dafnii* (Amoureux, Rullier & Fishelson, 1978), Red Sea; compare *H. perezi, tuberculatus*
21. *Hydroides deleoni* Bastida-Zavala & ten Hove, 2003, Punta San Juanico, Baja California Sur to Ecuador
22. *Hydroides dianthus* (Verrill, 1873), New Jersey to Massachusetts, temperate to subtropical Atlantic coasts of North America; probably ship-transported to Curaçao, Atlantic coasts of Europe, Africa, and the Mediterranean; complicated synonymy, see Zibrowius (1971a)
23. *Hydroides dipoma* (Schmarda, 1861), tropical West Africa, South Africa, Suez
24. *Hydroides diramphus* Mörch, 1863, St. Thomas, Caribbean, probably ship-transported to a circum (sub)tropical distribution; complicated synonymy, see Bastida-Zavala & ten Hove 2002, 2003
25. *Hydroides elegans* (Haswell, 1883), Port Jackson, Australia probably ship-transported to a circum(sub) tropical distribution; very confused synonymy, see e.g., ten Hove (1974), all (sub)tropical records of *H. norvegicus* belong here; N.B. In tropical Indo-Pacific regions the species can easily be confused with *H. centrospina*, *H. longispinosus*, *H. multispinosus*, and *H. nanhaiensis*
26. *Hydroides elegantulus* (Bush, 1910), Bermuda Islands
27. *Hydroides exaltatus* (Marenzeller, 1885), widely distributed in the Indo-West Pacific
28. *Hydroides externispina* Straughan, 1967a, Queensland, South-Western Japan; compare *H. ralumianus*
29. *Hydroides ezoensis* Okuda, 1934, Northern Sea of Japan, Vladivostok, South China, imported in France and Southern United Kingdom, and temperate Australia
30. *Hydroides floridanus* (Bush, 1910), Florida, Gulf of Mexico and Eastern USA
31. *Hydroides furcifer* (Grube, 1878), Philippines, Palau Island
32. *Hydroides fuscus* Imajima, 1976, South Japan, Palau Island, Red Sea, South China
33. *Hydroides fusicola* Mörch, 1863, Japan, South China
34. *Hydroides gairacensis* Augener, 1934, La Guayra, Venezuela; South Florida to South Brazil, Pacific Panama
35. *Hydroides glandifer* Rioja, 1941a, Acapulco, West Mexico, Baja California Sur
36. *Hydroides gracilis* (Bush, 1905), Pacific Groove, California to Baja California Sur
37. *Hydroides helmatus* (Iroso, 1921), Naples, Mediterranean
38. *Hydroides heterocerus* (Grube, 1868), Red Sea, Zanzibar, Madagascar, Iranian Gulf, Sri Lanka, ?New Caledonia, Lessepsian migrant to the Levant Mediterranean
39. *Hydroides heterofurcatus* Pillai, 1971, Sri Lanka
40. *Hydroides homoceros* Pixell, 1913, Maldives, Zanzibar, Seychelles, Sudan, Iranian Gulf, Lessepsian migrant to the Levant Mediterranean, once mentioned from ship's hull in Toulon, Mediterranean
41. *Hydroides huanghaiensis* Sun & Yang, 2000, Yellow Sea
42. *Hydroides humilis* (Bush, 1905), Gulf of California, Baja California to Panama
43. *Hydroides inermis* Monro, 1933, Galapagos, North Peru
44. *Hydroides inornatus* Pillai, 1960, Sri Lanka, India, Hong Kong; most probably synonym of *H. operculatus*
45. *Hydroides lambecki* Bastida-Zavala & ten Hove, 2003, Curaçao, Caribbean
46. *Hydroides longispinosus* Imajima, 1976, South Japan, South China, Ponape, Tonga, Queensland; see remark under *H. elegans*
47. *Hydroides longistylaris* Chen & Wu, 1980, South China Sea; compare *H. rectus*
48. *Hydroides malleolaspinus* Straughan, 1967b, Queensland, tropical Australia, Sri Lanka; compare *H. ancorispinus*; not *sensu* Imajima 1982, see *H. novaepommeraniae*

49. *Hydroides microtis* Mörch, 1863, North America, North Carolina, Gulf of Mexico, Guyana
50. *Hydroides minax* (Grube, 1878), widely distributed in the Indo-West Pacific, Lessepsian migrant to the Levant Mediterranean
51. *Hydroides mongeslopezi* Rioja, 1959, Vera Cruz, Gulf of Mexico, Caribbean
52. *Hydroides monroi* Zibrowius, 1973b, Congo, Cabinda
53. *Hydroides mucronatus* Rioja, 1959, Veracruz, Gulf of Mexico
54. *Hydroides* cf. *mucronatus* Rioja, 1959; ten Hove, 1984 Caribbean; status uncertain, see Bastida-Zavala & ten Hove (2002), probably new (sub?)species
55. *Hydroides multispinosus* Marenzeller, 1885, Enoshima, Japan; see remark under *H. elegans*
56. *Hydroides nanhaiensis* Wu & Chen, 1981b, South China Sea; see remark under *H. elegans*
57. *Hydroides niger* Zibrowius, 1971a, Mediterranean
58. *Hydroides nodosus* Straughan, 1967b, Queensland
59. *Hydroides norvegicus* Gunnerus, 1768, Boreal European species; very confused synonymy, all harbour and Indo Pacific records see *H. elegans*
60. *Hydroides novaepommeraniae* Augener, 1925, New Britain, Palau and Truk Island, Philippines, South Japan; confused synonymy, see Imajima & ten Hove (1984)
61. *Hydroides ochoterena* Rioja, 1941a, Acapulco, Western Mexico to Pacific Colombia
62. *Hydroides operculatus* (Treadwell, 1929), probably incl. *H. inornatus*; Somalia, Moçambique, Queensland, Lessepsian migrant to the Levant Mediterranean
63. *Hydroides panamensis* Bastida-Zavala & ten Hove, 2003, Pacific Panama, Ecuador
64. *Hydroides parvus* (Treadwell, 1902), Puerto Rico, South Florida to Brazil
65. *Hydroides perezi* Fauvel, 1918, Iranian Gulf, Red Sea, Tonga; not *sensu* Straughan 1967b, compare *H. dafnii, H. tuberculatus*
66. *Hydroides plateni* (Kinberg, 1867), South Brazil to Patagonia
67. *Hydroides protulicola* Benedict, 1887, Cape Hatteras, North Carolina, Eastern USA and northern Gulf of Mexico
68a. *Hydroides pseudouncinatus africanus* Zibrowius, 1971a, Morocco, Guinee, Senegambia, ?Madagascar
68b. *Hydroides pseudouncinatus pseudouncinatus* Zibrowius, 1968a, Marseille, Mediterranean
69. *Hydroides ralumianus* Augener, 1927, New Caledonia; compare *H. externispina*
70. *Hydroides rectus* Straughan, 1967b, Queensland, Northern Territories; compare *H. longistylaris*
71. *Hydroides recurvispina* Rioja, 1941a, Acapulco, West Mexico, Gulf of California to Panama
72. *Hydroides rhombobulus* Chen & Wu, 1980, South China Sea, Hong Kong; compare *H. uniformis* and *H. xishaensis*
73. *Hydroides rostratus* Pillai, 1971, Sri Lanka; N.B. preoccupied by *H. rostratus* Iroso, 1921, *nov. nom*. for *H. uncinatus* Ehlers, 1887, = *H. floridanus*
74. *Hydroides salazarvallejoi* Bastida-Zavala & ten Hove, 2003, Colombia, Caribbean and Pacific Costa Rica to Ecuador
75. *Hydroides sanctaecrucis* Krøyer [in] Mörch, 1863, St. Croix, Caribbean, both sides of Mexico and Panama, ?Hawaii, ship-transported to Singapore and tropical Australia; confused synonymy, see Bastida-Zavala & ten Hove (2002)
76. *Hydroides similis* (Treadwell, 1929), Baja California to Panama
77. *Hydroides similoides* Bastida-Zavala & ten Hove, 2003, Puerto Rico, Caribbean
78. *Hydroides sinensis* Zibrowius, 1972c, Yellow Sea
79. *Hydroides spongicola* Benedict, 1887, Gulf of Mexico, Caribbean, Bahamas
80. *Hydroides steinitzi* Ben-Eliahu, 1972, Suez Canal, Philippines, found once on ship's hull in Toulon, Mediterranean
81. *Hydroides stoichadon* Zibrowius, 1971a, Provence, Mediterranean
82. *Hydroides tambalagamensis* Pillai, 1961, widely distributed in the Indo-West Pacific
83. *Hydroides tenhovei* Bastida-Zavala & de Leon Gonzalez, 2002, Cabo San Lázaro, Baja California Sur

84. *Hydroides trilobulus* Chen & Wu, 1978, Guandong, South China Sea
85. *Hydroides trivesiculosus* Straughan, 1967a, Queensland; tropical Australia, Tanzania, Red Sea; compare *H. albiceps*
86. *Hydroides trompi* Bastida-Zavala & ten Hove, 2003, Baja California to Panama
87. *Hydroides tuberculatus* Imajima, 1976, widely distributed in the Indo-West Pacific; compare *H. dafnii, H. perezi*
88. *Hydroides uniformis* Imajima & ten Hove, 1986, Solomon Islands, ?Queensland; compare *H. rhombobulus* and *H. xishaensis*
89. *Hydroides xishaensis* Chen & Wu, 1978, Guandong, China; compare *H. rhombobulus* and *H. uniformis.*

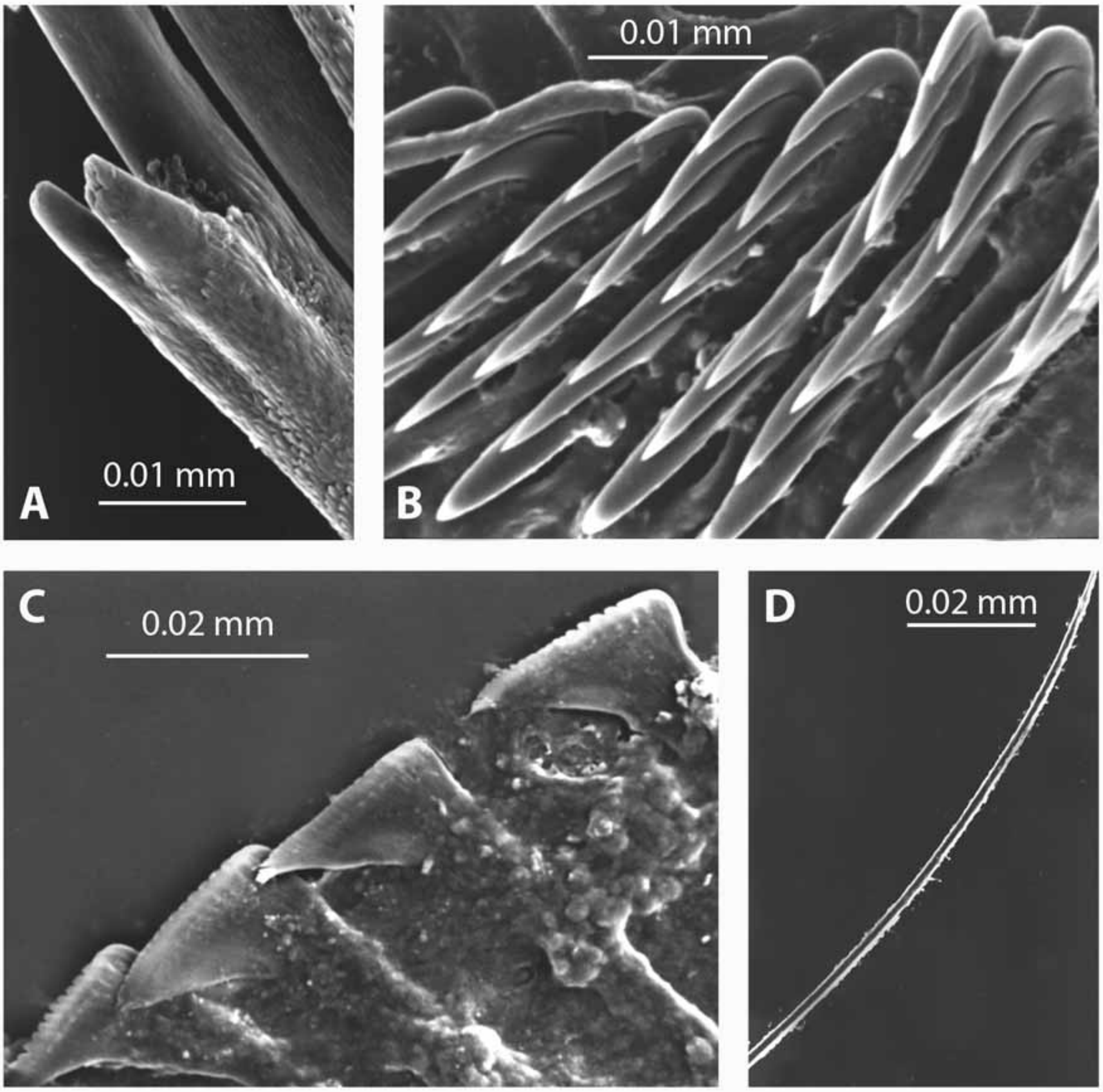

FIGURE 23. SEM micrographs of chaetae in *Hydroides norvegicus*. Norway, South of Island Fosenheia, 63°37’ N, 9°27’ E, 30 m, Scandinavia Expedition 1961, det. H.A. ten Hove 1969, ZMA V.Pol. 3090. A—details of bayonet collar chaetae, B—anterior abdominal uncini, C—middle abdominal chaetae, D—tip of posterior abdominal capillary chaeta.

17. *Janita* Saint-Joseph, 1894
(Fig. 24)

Type-species: *Omphalopoma spinosa* Langerhans, 1884, = junior synonym of *Serpula fimbriata* delle Chiaje, 1822
Number of species: 1

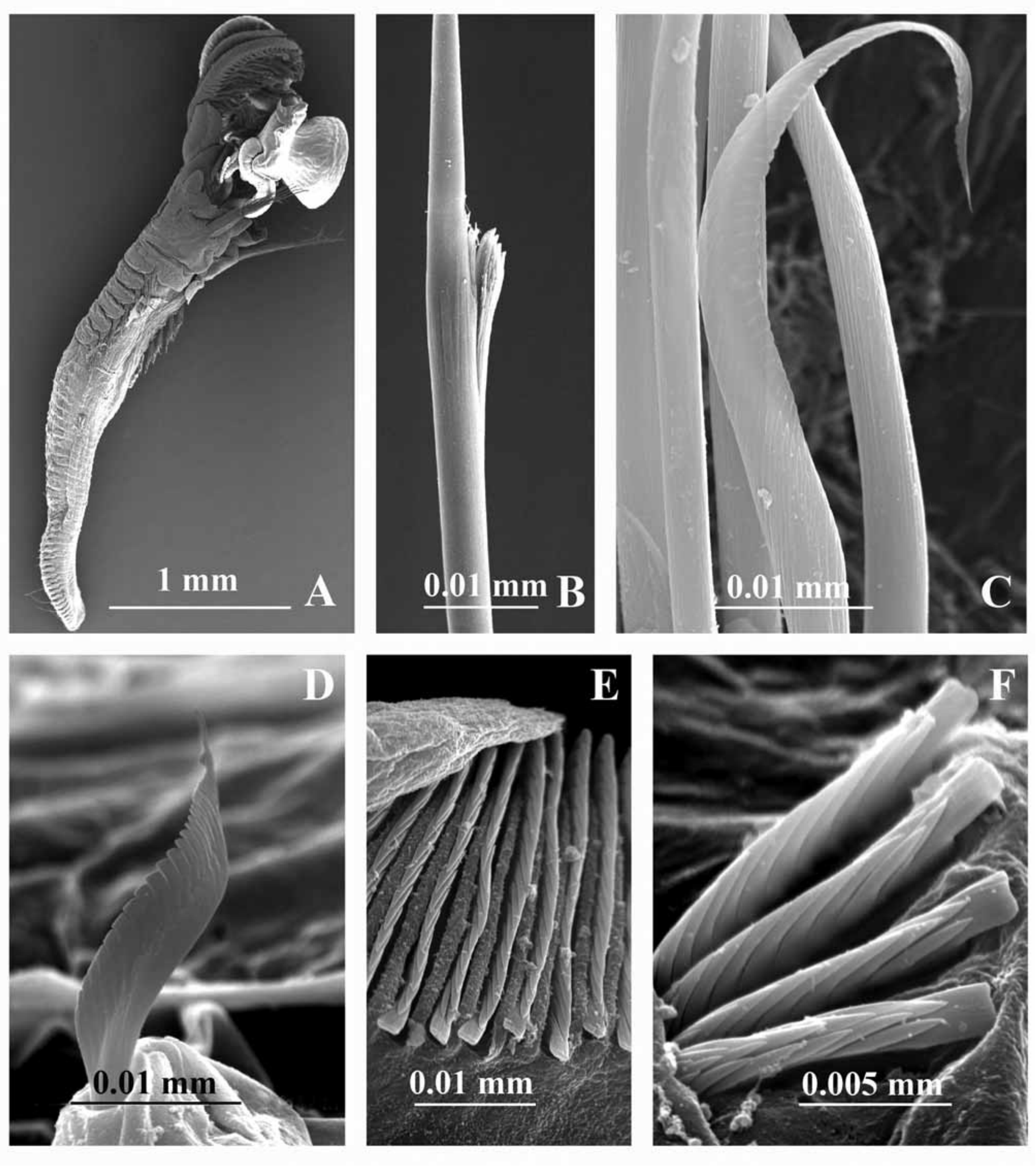

FIGURE 24. SEM micrographs of chaetae in SEM micrographs of *Janita fimbriata*. France, Marseille, det. and don. H. Zibrowius, ZMA V.Pol. 3033. A—lateral view of entire animal, B—*Spirobranchus* type collar chaeta, C—*Apomatus* chaeta, D—anterior abdominal chaeta, E—thoracic uncini, F—posterior abdominal uncini.

Tube white, sub-circular in cross-section, with 5 longitudinal winding ridges. Granular overlay absent. Operculum bell-shaped, ending in simple thick brown concave endplate; opercular base surrounded by three fleshy processes, one triangular and two rounded ones, not unlike those figured for *Crucigera zygophora* by ten Hove & Jansen-Jacobs (1984 fig. 9C). Peduncle cylindrical, slightly compressed dorso-ventrally and wrinkled; inserted below and between first and second normal radiole (below second in larger specimens). Pseudoperculum absent. Arrangement of radioles short pectinate, up to 12 radioles per lobe. Inter-radiolar membrane and stylodes absent. Branchial eyes present, reported as stalked eyes at base of pinnules by Langerhans (1884 fig. 45a). Mouth palps present. 7 thoracic chaetigerous segments. Collar pentalobate, medioventral lobe divided by deep median and two shallow incisions. Tonguelets absent. Thoracic membranes short, ending at second thoracic chaetiger. Collar chaetae of *Spirobranchus* type (Fig. 24B), acicular and limbate. *Apomatus* chaetae present (Fig. 24C). Thoracic uncini saw-shaped with up to 16 teeth, anterior peg blunt, questionably gouged (Fig. 24E). Triangular depression absent. Anterior abdominal uncini saw-shaped, posterior rasp-shaped (Fig. 24F), with approximately 13 teeth in profile, 3–5 teeth per row. Abdominal chaetae flat narrow geniculate, with a more or less crenulated edge to the blade (Fig. 24D). Achaetous anterior abdominal zone very short or absent. Long posterior capillary chaetae absent. Posterior glandular pad present.

Remarks. The genus *Janita* was erected by Saint-Joseph for *Omphalopoma spinosa* Langerhans, 1884, which is a junior synonym of *Serpula fimbriata* delle Chiaje, 1822 (see e.g., Fauchald, 1977: 144, Lommerzheim 1979: 157). There was a considerable confusion about generic attribution of this species, generally it has been attributed to *Omphalopomopsis*. Zibrowius (1972b) points out that the distinction between *Janita* and *Omphalopomopsis* is justified due to having very different opercula: *O. langerhansi* has a simple globular operculum with a shallow concave calcareous endplate, *J. fimbriata* has a more complex operculum with a deeply cupped chitinous endplate, which has a horny talon into the fleshy opercular ampulla (Imajima, 1979).

It should be noted that Rioja (1923) and Fauvel (1927) mentioned both "*Spirobranchus*" type and acicular collar chaetae for *Janita fimbriata* (as *Omphalopomopsis*); (Zibrowius (1968a) on the other hand regarded the "acicular" chaetae as misinterpretation of "*Spirobranchus*" type, observed from the back (not in lateral view). Martín (1989) assumed that specimens with acicular collar chaetae and those with "*Spirobranchus*" type chaetae belong to different taxa. Ben-Eliahu & Fiege (1996) mentioned specimens with one or the other type of collar chaetae from a single population of what they regard to be *J. fimbriata*; ten Hove (in Ben-Eliahu & Fiege 1996) mentioned a specimen with both types. The phenomenon merits further attention.

The monotypic genus is distributed in the (sub) tropical Atlantic, Mediterranean (Zibrowius 1972b, 1973b, Bianchi 1981, Bianchi *et al.* 1984), and Indo-West Pacific (Imajima & ten Hove, 1984, 1986, ten Hove 1994). See also remarks following *Omphalopomopsis*.

Janita fimbriata (delle Chiaje, 1822), (sub)tropical Atlantic, Mediterranean, Indo-West Pacific.

18. *Josephella* Caullery & Mesnil, 1896

(Fig. 25)

Type-species: *Josephella marenzelleri* Caullery & Mesnil, 1896
Number of species: 1

Tube white, opaque, circular in cross-section, with small peristomes; tube diameter approximately 0.1 mm. Granular overlay absent. Operculum delicate membranous cup with a flat distal surface surmounted by a marginal crown of fine teeth joined by a transparent membrane. Peduncle second non-modified pinnulate radiole, though Bush (1905) and Ben-Eliahu & Payiatas (1999: 109) mention a non-pinnulate radiole (the first as *J. humilis*). Pseudoperculum absent. Radioles arranged in semi-circles, up to 3 per lobe. Inter-radiolar membrane absent. Branchial eyes absent, a pair of red ocellar clusters at the base of collar. Stylodes absent. Mouth palps absent. 5 thoracic chaetigerous segments. Collar non-lobed. Tonguelets absent. Thoracic membranes short, ending at first chaetiger. Collar chaetae limbate. *Apomatus* chaetae present (Fig. 25A). Uncini rasp-shaped, with 10–12 teeth seen in profile, 4 teeth in a row distally to 7 above peg (Fig. 25B, C). Anterior peg gouged, widened into a rectangular to trapezoid base, flat, but with sharp angles that sometimes curve underneath (thus giving a bifurcate appearance under compound microscope). Triangular depression absent. Abdominal chaetae flat narrow geniculate with pointed denticulate edge (Fig. 25D). Abdominal uncini with 9–10 teeth in a row. Achaetous anterior abdominal zone long. Posterior capillary chaetae absent. Posterior glandular pad absent.

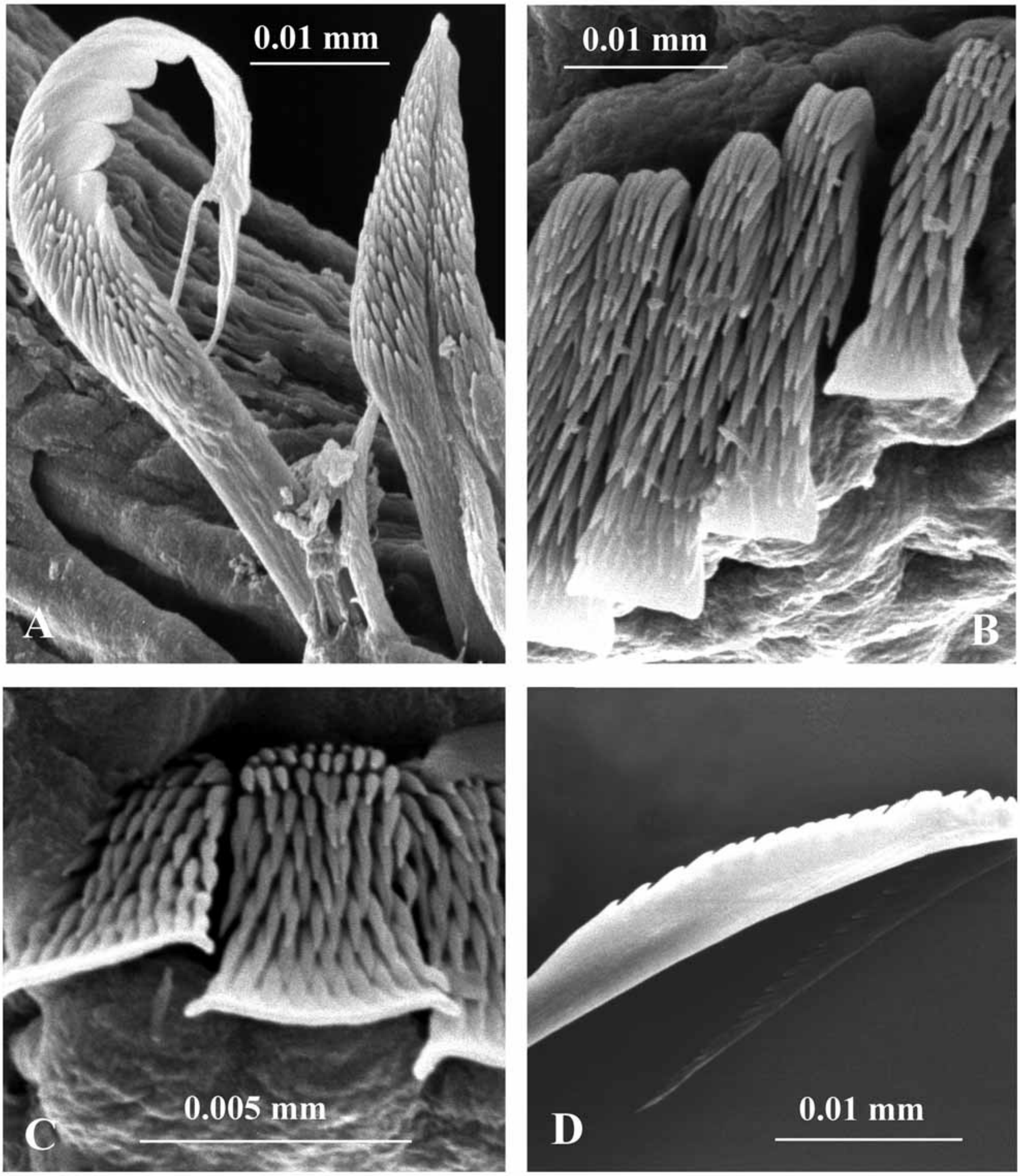

FIGURE 25. SEM micrographs of chaetae in *Josephella marenzelleri*. France, Marseille, Vieux Port, legit H. Zibrowius, ZMA V.Pol. 3030. A—*Apomatus* and "limbate" chaetae of 3rd thoracic chaetiger, B—4th (and last) thoracic row of uncini, C—anterior abdominal uncini, D—tip of anterior abdominal chaeta.

Remarks. This tiny serpulid is known from numerous circum(sub)tropical, temperate locations around the world: Australia (Dew 1959), Japan (Uchida 1978, Imajima 1979), Hawaii (Bailey-Brock 1991), Israel (Ben-Eliahu 1976), Italy (Bianchi 1981), Cyprus (Ben-Eliahu & Payiatas 1999), Germany (Hartmann-

Schröder 1971), France (Fauvel 1927, Zibrowius 1968a), west coast of Africa (Zibrowius 1973b), north coast of Tunis (Zibrowius 1979a). The species was confused with *Rhodopsis* (by Straughan 1967a fig. 5i). Ben-Eliahu & Payiatas (1999) provided SEMs of *Josephella* chaetae. Dew (1959) mentioned a single specimen with two opercula equal in size.

Josephella marenzelleri Caullery & Mesnil, 1896, circum(sub)tropical, temperate.

19. *Laminatubus* ten Hove & Zibrowius, 1986

(Fig. 26)

Type-species: *Laminatubus alvini* ten Hove & Zibrowius, 1986
Number of species: 1

Tube white, more or less triangular in cross-section, with large undulating longitudinal keel; consisting of two layers: an inner opaque layer and an outer (not granular) hyaline one. Operculum globular, with bulbous proximal ampulla and more or less flattened distal part with thickened cuticle. Peduncle cylindrical, gradually merging into opercular ampulla, constriction absent; inserted to left side, proximal from first and second normal radiole. Pseudoperculum absent. Radioles not connected by inter-radiolar membrane, arranged into slightly ascending spiral of up to two whorls. Up to 33 radioles per lobe. Stylodes and branchial eyes absent. Mouth palps not observed. 6 thoracic chaetigerous segments. Collar with medio-ventral and two latero-dorsal lobes, continuous with thoracic membranes, forming apron. Tonguelets absent. Collar chaetae *Spirobranchus*-type (Fig. 26A) and limbate. *Apomatus* chaetae absent. All uncini saw-shaped with 5–7 teeth, anterior fang simple, pointed (Fig. 26D, C). Thoracic tori converging posteriorly, forming triangular depression. Abdominal chaetae long, with hollow trumpet-shaped tip, smoothly bent (Fig. 26D). Posterior chaetae become longer, but posterior capillary chaetae absent. Achaetous anterior abdominal zone absent. Posterior glandular pad absent.

Remarks. The species is a common element of the bathyal hydrothermal vent communities found in the Galapagos rift and the East Pacific Rise.

Laminatubus alvini ten Hove & Zibrowius, 1986, East Pacific, 1–21° N; bathyal.

20. *Marifugia* Absolon & Hrabě, 1930

(Fig. 27)

Type-species: *Marifugia cavatica* Absolon & Hrabě, 1930
Number of species: 1

Tube white, opaque, circular in cross-section; irregular longitudinal keel and collar like rings may be present. Thin hyaline granular overlay of the tube present. Operculum fig-shaped to inverse conical, with (or without) chitinous endplate. Peduncle flattened cylindrical, smooth, without distal wings, gradually merging into opercular ampulla; inserted just below and between first and second dorsal radiole on left side (in large specimen almost covering base of branchial lobe). Pseudoperculum absent. Radioles arranged in semi-circles, up to 6 per lobe. Inter-radiolar membrane, branchial eyes and stylodes absent. Mouth palps not found. 6 thoracic chaetigerous segments. Collar non-lobed but with low medio-ventral projection. Thoracic membranes narrow but forming apron. Tonguelets absent. Collar chaetae absent. Thoracic chaetae limbate, *Apomatus* chaetae absent (Fig. 27A). Thoracic uncini saw-to-rasp-shaped, with about 8 teeth in profile, up to 4 in a row above blunt almost square shallowly gouged anterior peg (dental formula P:4:3:2:1:1:1:1:1, Fig. 27B). Triangular depression absent. Abdominal chaetae trumpet-shaped, long, smoothly bent, with hollow tip bordered with pointed teeth (Fig. 27D). Posterior abdominal capillaries not observed. Uncini saw-to-rasp-shaped; anterior peg simple rounded (Fig. 27C). Achaetous anterior abdominal zone, long posterior capillary chaetae and glandular pad absent.

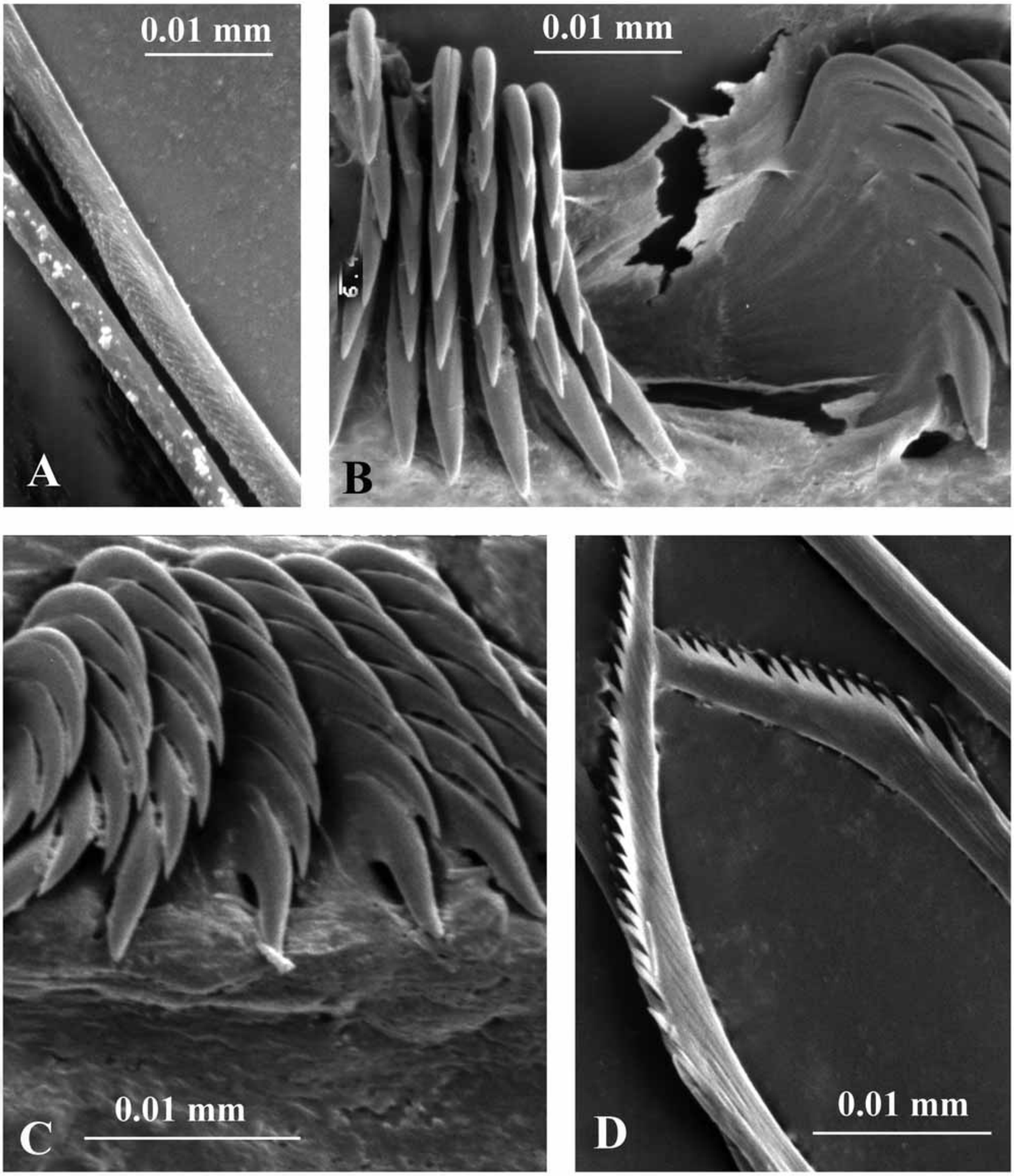

FIGURE 26. SEM micrographs of chaetae in *Laminatubus alvini*. Galapagos rift, "*Alvin*" dive 884, Garden of Eden, hydrothermal vent areas, 0°47.69' N, 80°07.74' W, 2482 m, ZMA V.Pol. 3480. A—details of *Spirobranchus* collar chaeta, B—uncini of 4th thoracic chaetiger, C—anterior abdominal uncini, D—anterior abdominal chaetae, details of hollow tip.

Remarks. *Marifugia cavatica* is unique in being the world's only fresh-water serpulid, of presumably marine origin (Sket 1983), inhabiting subterranean waters of the Dinaric karst of the former Yugoslavia. The most recent study (Kupriyanova *et al.*, in prep.) summarises data on ecology, distribution, and reproduction of the species and shows its close relationship with *Ficopomatus*.

Marifugia cavatica Absolon & Hrabě, 1930, Bosnia and Herzegovina, Croatia, Slovenia to extreme N.E. Italy; fresh-water subterranean caves.

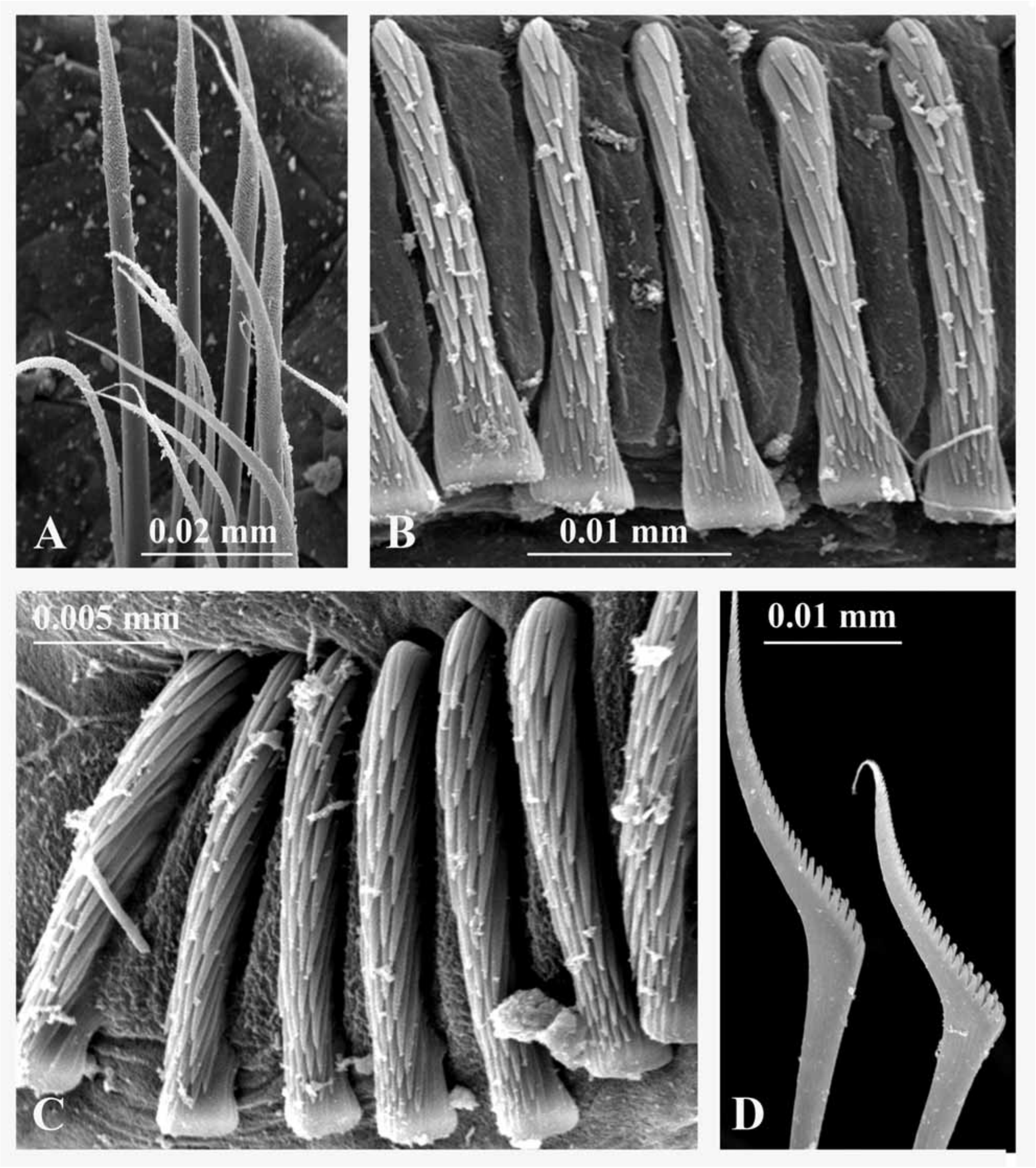

FIGURE 27. SEM micrographs of chaetae in *Marifugia cavatica*. Bosnia & Herzegovina, Ravno, Zavala, Vjetrenica, Ravanjski kanal, legit M. Zagmajster, det. E. Kupriyanova, SAM E3612. A—thoracic chaetae, B—thoracic uncini, C—anterior abdominal uncini, D—anterior abdominal chaetae with hollow tips.

Membranopsis Bush, 1910

Type-species: *Membranopsis inconspicua* Bush, 1910
Number of species: 1

Tube not known. Specimen without branchial crown, thus all radiolar characters not known. Mouth palps not known. 9 thoracic chaetigerous segments. Collar quadrilobed; thoracic membranes wide, forming apron; tonguelets between ventral and lateral collar lobes not known. Collar chaetae damaged, apparently limbate. Subsequent chaetae limbate. *Apomatus* chaetae present from 7th chaetiger onwards. Uncini [along entire body?] similar to those in *Protula* and *Apomatus*. Abdominal chaetae "curved somewhat in crescent shape rather narrow and abruptly tapering toward the tip" [? thus sickle-shaped?]. Achaetous anterior abdominal zone, long posterior capillary chaetae and glandular pad not known.

Remarks. This monotypic taxon is ill-defined and known from Bush's (1910) very sketchy original description only. Based on type comparison (by Gayle Playa, pers. comm.), *Membranopsis inconspicua* is most likely synonymous with *Salmacinopsis setosa* Bush, 1910, also with 9 thoracic chaetigers, probably a *Protula* species, an opinion shared with Chamberlin (1919a: 479); the latter taxon was referred to *Protula setosa* by Perkins (1998: 95). Since the generic name had not been formally synonymized yet, we mention it in this account, without number, but we regard it to be an invalid genus.

21. *Metavermilia* Bush, 1905
(Fig. 28)

Type-species: *Vermilia multicristata* Philippi, 1844
Number of species: 14

Tube white, opaque, peristomes may be present, as well as several longitudinal keels, sometimes denticulate. Granular overlay generally absent. Operculum with chitinous, non-calcified endplate, sometimes with complex multi-tiered structures, or endplate may be absent. Peduncle flattened, ribbon-like, without distal wings; formed from second dorsal radiole on one side. Constriction may be present. Pseudoperculum may be present. Radioles arranged in semi-circles to short pectinate, up to 18 per lobe. Inter-radiolar membrane and stylodes absent. Branchial eyes may be present. Mouth palps absent. 7 thoracic chaetigerous segments. Collar trilobed, tonguelets between ventral and lateral collar lobes absent. Length of thoracic membranes variable, ending at thoracic segments 3–7, sometimes forming ventral apron on anterior abdominal segments. Collar chaetae limbate (Fig. 28A). *Apomatus* chaetae present (Fig. 28B). Thoracic uncini saw-shaped with up to 15 teeth, anterior tooth blunt, rounded (Fig. 28C). Triangular depression absent. Abdominal chaetae with flat narrow geniculate blade with rounded teeth (Fig. 28E); uncini saw- or rasp-shaped (Fig. 28D). Achaetous anterior abdominal zone absent. Posterior capillary chaetae and glandular pad present.

Remarks. The genus *Metavermilia* was revised and emended by Zibrowius (1971b) for four species; since then 10 more species have been added (see Nishi *et al.* 2007 for history and literature review). Specimens of *M. acanthophora* have a pseudoperculum (as mentioned for AM W3629 by Dew (1959) and ZMA V.Pol. 4701); another in the Queensland Museum (G 3905) has 2 opercula, one elaborate with three chitinous diabolos and spine, the other simple with a single chitinous endplate with spine.

1. *Metavermilia acanthophora* (Augener, 1914), Indo-West Pacific, South Japan to Australia
2. *Metavermilia annobonensis* Zibrowius, 1971b, Annobón, Western Africa; records from elsewhere should be checked
3. *Metavermilia arctica* Kupriyanova, 1993d, off Greenland, off Norway, Arctic Ocean
4. *Metavermilia gravitesta* Imajima, 1978, Izu Islands, Japan

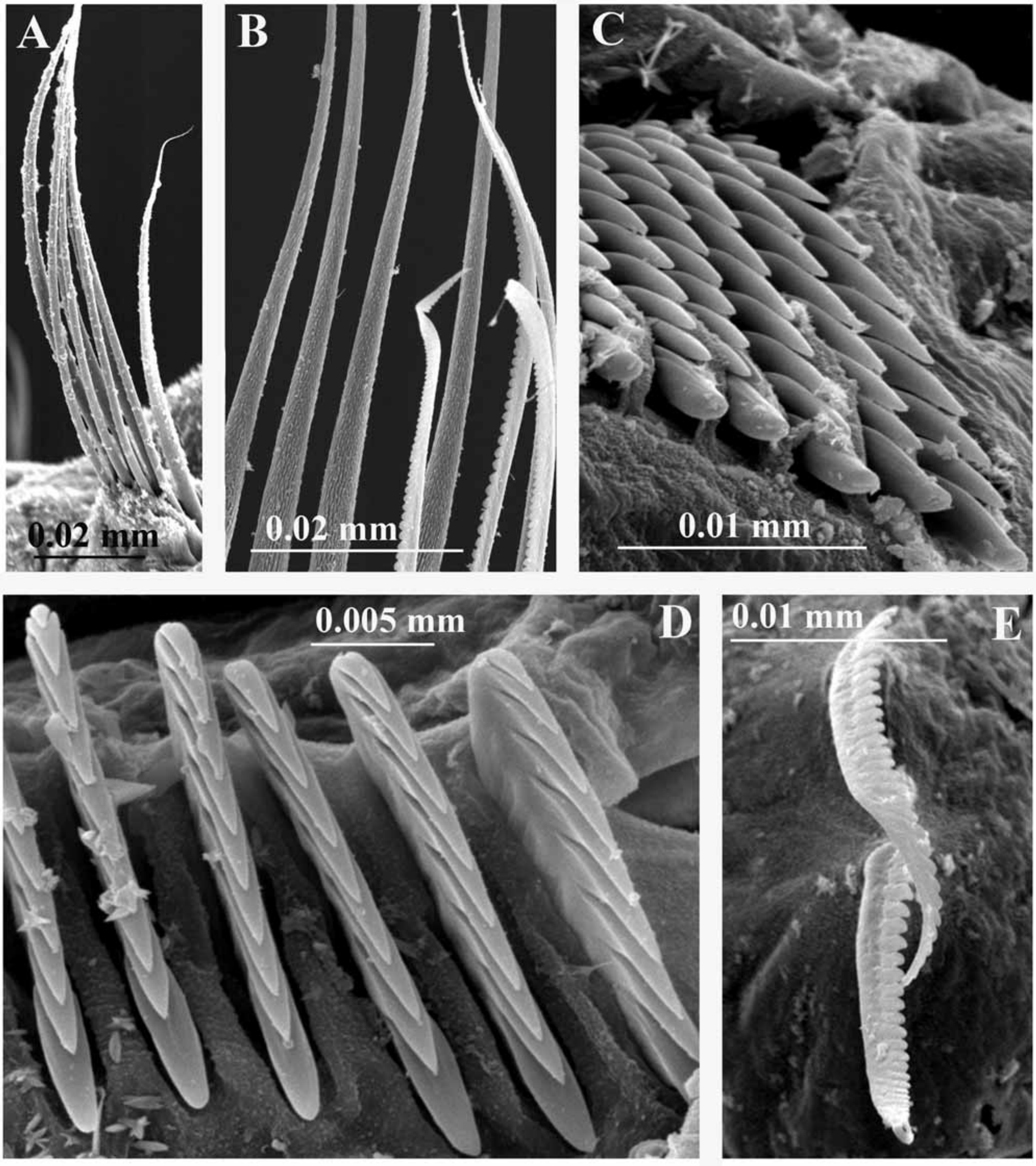

FIGURE 28. SEM micrographs of chaetae in *Metavermilia acanthophora*. Australia, Queensland, Lizard Island, legit G. Rouse and E. Kupriyanova, det. E. Kupriyanova. A—bundle of collar chaetae, B—thoracic "limbate" and *Apomatus* chaetae, C—thoracic uncini, D—anterior abdominal uncini, E—anterior abdominal chaetae.

5. *Metavermilia inflata* Imajima, 1977, Ogasawara Islands, Japan; bathyal
6. *Metavermilia multicristata* (Philippi, 1844), (sub)tropical Atlantic, Mediterranean, West Indian Ocean
7. *Metavermilia nanshaensis* Sun, 1998, China
8. *Metavermilia nates* Zibrowius, 1971b, Europa Island, Tanzania; Red Sea, Ponape; Honshu, Japan
9. *Metavermilia ogasawaraensis* Nishi, Kupriyanova & Tachikawa, 2007, Ogasawara Islands, Japan
10. *Metavermilia ovata* Imajima, 1978, Japan, Seychelles

11. *Metavermilia spicata* Imajima, 1977, Japan
12. *Metavermilia taenia* Zibrowius, 1971b, Josephine Bank, East Atlantic
13. *Metavermilia truncata* Imajima, 1978, Izu Islands, Japan
14. *Metavermilia yamazatoi* Imajima & ten Hove, 1989, Okinawa, North-West Pacific.

22. *Microprotula* Uchida, 1978

Type-species: *Microprotula ovicellata* Uchida, 1978
Number of species: 1

Tube white, opaque, circular in cross-section, proximal part irregularly coiled and attached to substrate, distal erect and free. Granular overlay absent. Globular ovicells around erect distal part of the tube. Operculum and pseudoperculum absent. Arrangement of radioles semi-circular, up to 4 per lobe. Inter-radiolar membrane and stylodes absent. 8–12 pairs of red ocellar clusters present on both sides of each radiole. Mouth palps absent. 7 thoracic chaetigerous segments. Collar well developed, with 4 weakly expressed lobes. Tonguelets absent. Thoracic membranes narrow, but forming apron. Collar chaetae limbate. *Apomatus* chaetae present. Thoracic and abdominal uncini rasp-shaped, *Protula* type, up to approximately 20 teeth in profile, up to 6 in a row; anterior peg elongated, blunt, questionably gouged. Triangular depression absent. Abdominal chaetae sickle-shaped with blunt teeth. Achaetous anterior abdominal zone short. Long posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. This poorly known tiny species has never been found in the field, the material described by Uchida (1978) comes from a population found in a marine aquarium. Some more questionable specimens (without typical ovicells) came from “reef rock in aquarium shop in Germany, origin probably Central Indo-Pacific” (Fosså & Nilsen 2000: 151, ZMA V.Pol. 4046). The type material was re-examined by EK. The species is morphologically very similar to small representatives of the genus *Protula* (hence the name). The major reason of its elevation into a separate genus has been the presence of tube ovicells used to brood embryos. *Microprotula* may not have a phylogenetic basis, as some *Protula* species do show incubation of embryos (Kupriyanova *et al.* 2001), admittedly not in special brood-chambers but in gelatinous masses.

Microprotula ovicellata Uchida, 1978, Sabiura, Japan.

23. *Neomicrorbis* Rovereto, 1904
(Fig. 29)

Type-species: *Serpula crenatostriata* Münster in Goldfuss, 1831 (*fide* Regenhardt 1961: 89); a fossil taxon
Number of Recent species: 1

Tube transparent (vitreous), circular in cross-section, with numerous longitudinal ridges consisting of small denticles (Fig. 29C). Tube spiral, either dextral or sinistral. Granular overlay absent. Operculum with distal calcareous plate and large talon projecting into proximal ampulla, merging into peduncle without constriction (Fig. 29B). Peduncle second radiole right, two small distal wings. Pseudoperculum absent. Arrangement of radioles semi-circular, 10 radioles left, 7 right. Inter-radiolar membrane, branchial eyes, and stylodes absent. Mouth palps absent. Number of thoracic chaetigers asymmetric, 5 to the left and 6 to the right (Fig. 29A). Collar non-lobed, tonguelets and length of thoracic membranes not known. Collar chaetae fin-and-blade and limbate. *Apomatus* chaetae present in posterior thoracic segments (Fig. 29E). Thoracic uncini saw-shaped with 12–15 teeth and rounded peg. Thoracic depression is not known. Abdominal chaetae retro-geniculate (Fig. 29F). Abdominal uncini rasp-shaped with 14–17 teeth in profile, 3–5 in a row (Fig. 29D). Long anterior achaetous abdominal zone. Posterior capillary chaetae present. Posterior glandular pad absent.

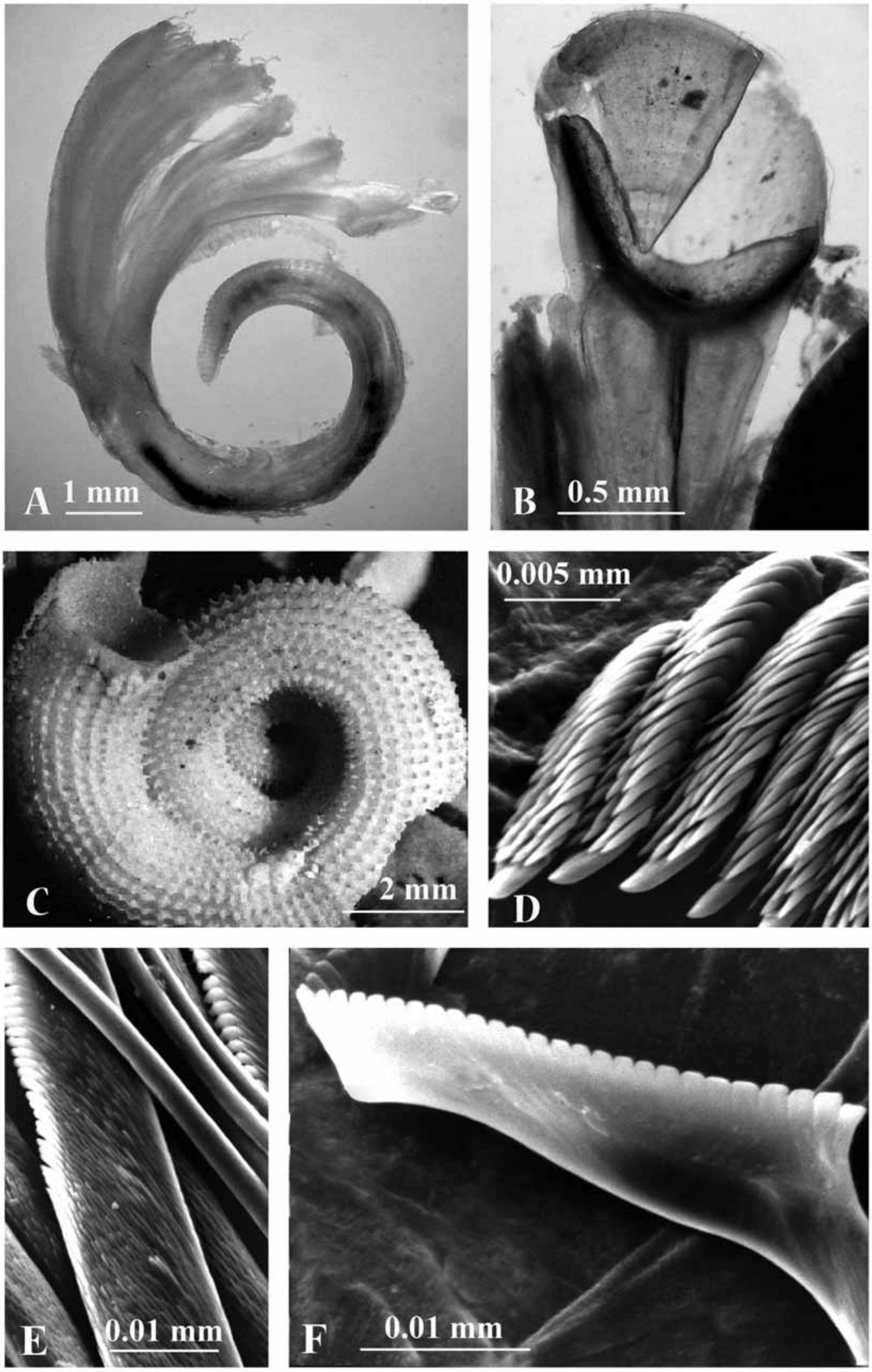

FIGURE 29. Photos and SEMs of chaetae of *Neomicrorbis azoricus*. Azores, 37°18'N 24°45.5'W, 610 m, R/V "*Jean Charcot*", det. and don. H. Zibrowius, ZMA V.Pol. 3905. A—Lateral view of entire animal removed from its tube (photo R. Bastida-Zavala), B—operculum (photo R. Bastida-Zavala), C—tube (photo H. Zibrowius), D—anterior abdominal uncini, E—4th thoracic bundle of thin "capillary" and *Apomatus* chaetae, F—anterior abdominal chaeta.

Remarks. The diagnosis above is partly based on a personal communication by R. Bastida-Zavala. This is a poorly known monotypic genus with unclear affinities. According to Rzhavsky (pers. comm.), *Neomicrorbis* belongs to the Spirorbidae (Paralaeospirinae) because of its incomplete chaetal inversion typical for spirorbins. Reproduction is unknown, which makes placement within spirorbins difficult. Zibrowius (1972a) regards it as something intermediate between a "serpulid" and a spirorbin.

Neomicrorbis azoricus Zibrowius, 1972a, Azores, St. Paul Island, West Indian Ocean.

24. *Neovermilia* Day, 1961

(Fig. 30)

Type-species: *Neovermilia capensis* Day, 1961
Number of species: 6

Tube white, opaque, triangular to subcircular in cross-section, medial keel may be present. Granular overlay absent, though hyaline inner (bordering lumen) and hyaline outer layers may be present. Tabulae occasionally present. Operculum globular, soft proximally, at most with slightly chitinized, or sclerotized, or calcified cap. Operculum absent in one species. Peduncle sub-cylindrical to triangular, wrinkled (annulated), sometimes with small distal latero-dorsal "winglets" (flattened parts of the peduncle), constriction present; inserted at base of first to fourth normal radiole. Pseudoperculum absent (but see remarks). Radioles arranged in semi-circles to short spiral (1.5 whorls), up to 50 per lobe. Inter-radiolar membrane present (that is, radioles fused basally for about 1/20th of their length). Stylodes absent. Branchial eyes not observed. Mouth palps absent. 7 thoracic chaetigerous segments. Collar trilobed, tonguelets between ventral and lateral collar lobes absent. Thoracic membranes forming ventral apron across anterior abdominal segment. Collar chaetae limbate. *Apomatus* chaetae absent. Thoracic uncini saw-shaped with 5–6 teeth above pointed anterior fang (Fig. 30A); saw-to-rasp shaped in one species. Triangular depression absent, but rows of thoracic tori converge, completely touching each other medioventrally. Abdominal chaetae long, trumpet-shaped, smoothly bent, with hollow end bordered by two rows of pointed teeth (Fig. 30C). Abdominal uncini similar to thoracic ones, with 7 teeth above fang (Fig. 30B). Achaetous anterior abdominal zone absent. Posterior capillary chaetae and glandular pad absent.

Remarks. Ten Hove (1975) tabulated the known species of *Neovermilia*. Later, two more species were described and attributed to this genus, *N. aberrans* Rullier & Amoureux, 1979 and *N. anoperculata* Lechapt, 1992. Uncini of *N. aberrans* were figured with a bifid anterior peg; contrary to the description, *Apomatus* chaetae are present, and the number of thoracic chaetigers is higher than 7 (Zibrowius, pers. comm.), it might rather belong to *Filogranella*. The taxon *anoperculata* agrees well with the diagnosis of *Neovermilia*, but for the absence of an operculum and its thoracic uncini which are saw-to-rasp-shaped. One specimen of *N. globula* from Taronga Park checked by one of us (HAtH; Australian Museum) had a pseudoperculum in addition to the normal peduncle.

1. *Neovermilia anoperculata* Lechapt, 1992, New Caledonia; SEM photos of chaetae in original description
2. *Neovermilia capensis* Day, 1961, False Bay, South Africa
3. *Neovermilia dewae* (Straughan, 1967b), Heron Island, Queensland, Australia
4. *Neovermilia falcigera* (Roule, 1898), Cape Bojador; East Atlantic from off Ireland to North Africa, Mediterranean; bathyal
5. *Neovermilia globula* (Dew, 1959), Port Jackson, New South Wales, Australia
6. *Neovermilia sphaeropomatus* (Benham, 1927), New Zealand.

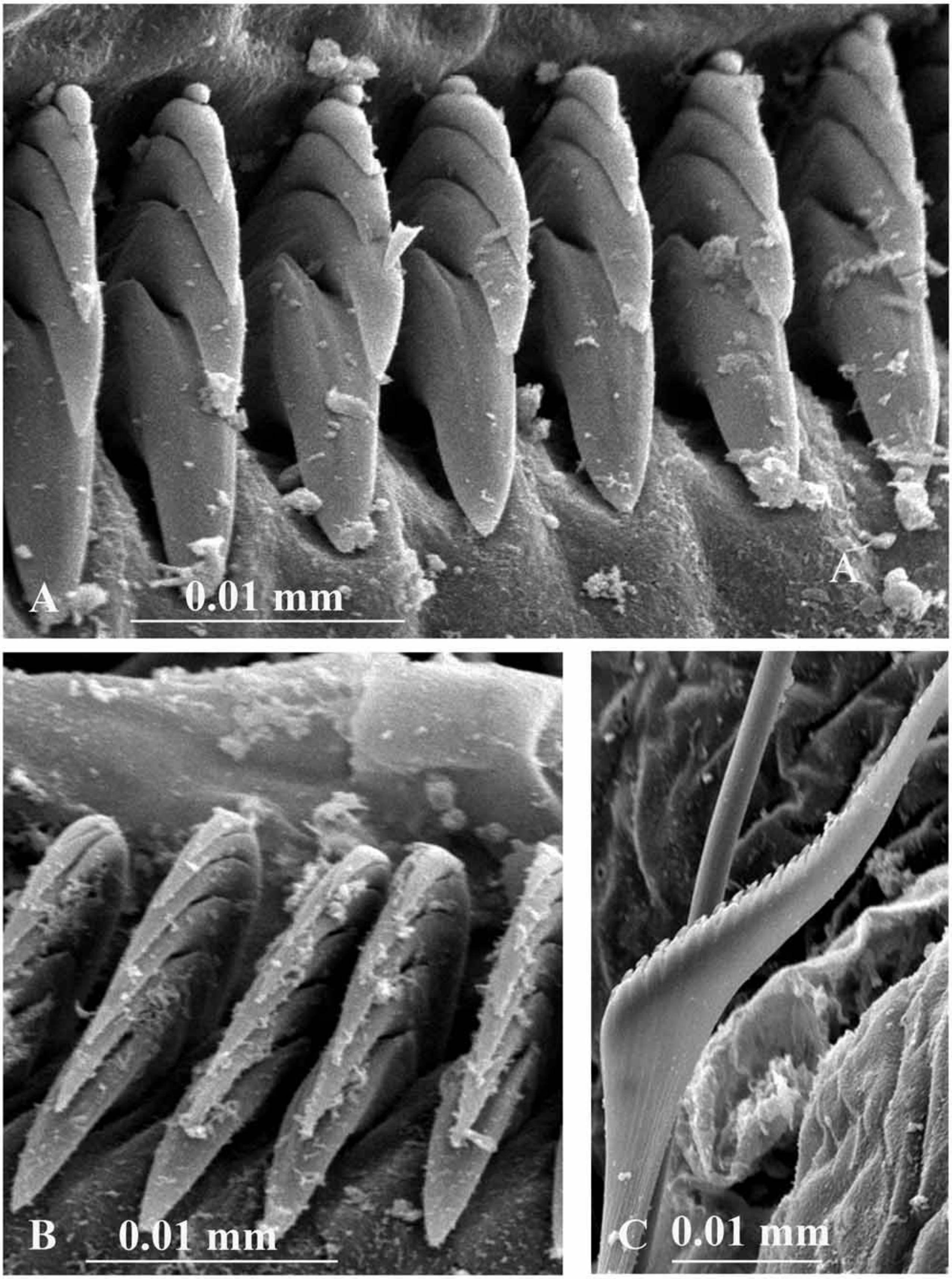

FIGURE 30. SEM micrographs of chaetae in *Neovermilia globula*. Australia, New South Wales, Sydney, Bondi Beach, legit G. Rouse, det. E. Kupriyanova. A—thoracic uncini, B—abdominal uncini, C—hollow tip of abdominal chaeta.

25. *Nogrobs* de Montfort, 1808

(Fig. 31)

Type-species: *Nogrobs vermicularis* de Montfort, 1808 (a fossil taxon)
Number of (Recent) species: 1

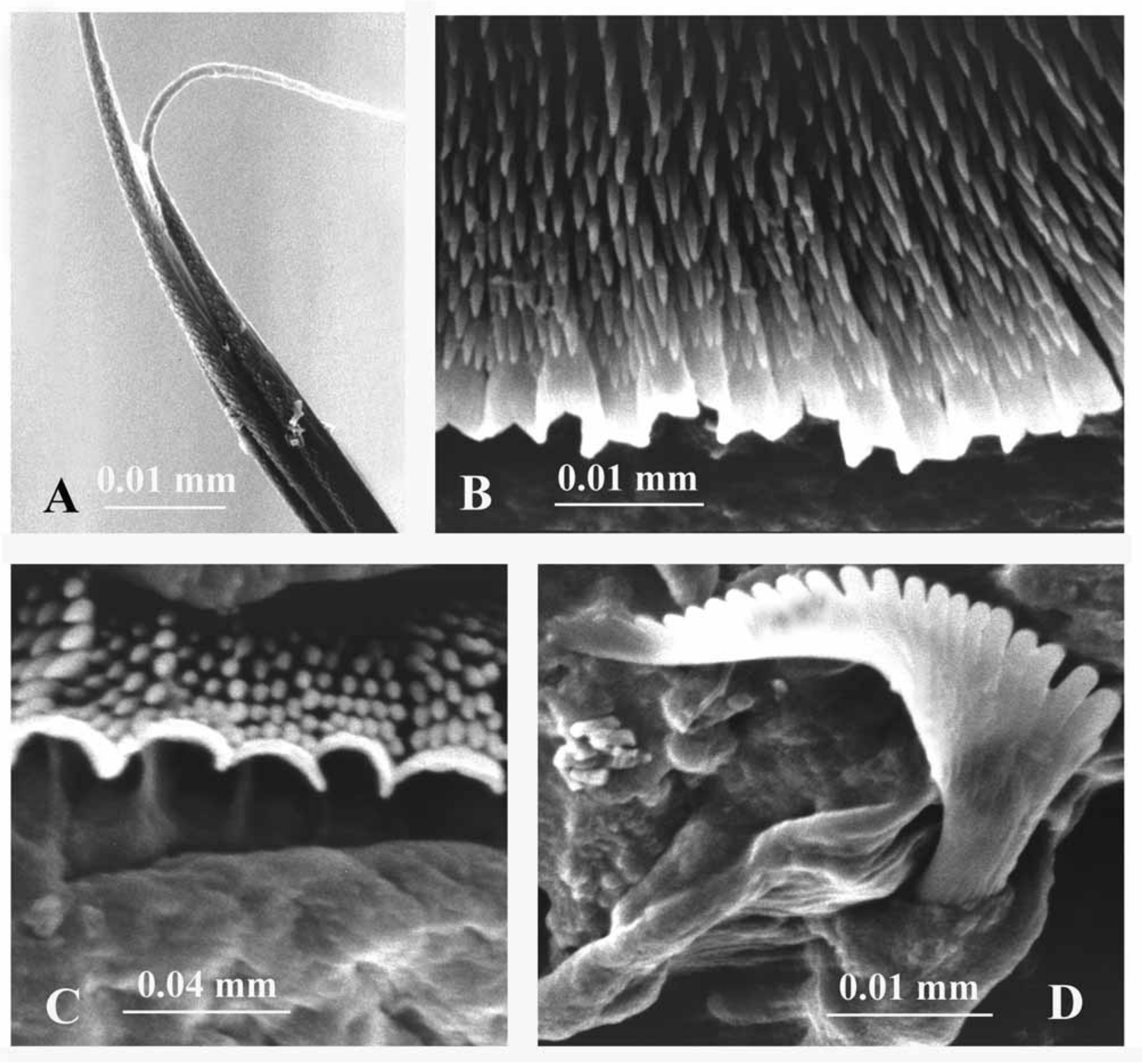

FIGURE 31. SEM micrographs of chaetae in *Nogrobs grimaldii*. Azores, 39°03.5' N, 28°25.5' W, 2440 m, R/V "*Jean Charcot*", det. H. Zibrowius 1972, ZMA V.Pol. 3906. A—collar chaetae, B—6th row of thoracic uncini, C—anterior abdominal uncini, D—anterior abdominal chaeta.

Tube free, white, sinistrally coiled, initially cylindrical, then prismatic (quadrangular in cross-section), finally with short cylindrical straight distal part. Collar like rings and granular overlay absent. Operculum inverse cone (ampulla) with chitinous endplate and central depression. Peduncle pinnulated, without distal wings, with outer groove distally, with or without constriction beneath ampulla; inserted as second right radiole, up to 3 times as wide as other radioles. Pseudoperculum absent. Arrangement of radioles semi-circular, up to 8 per lobe. Inter-radiolar membrane, branchial eyes, and stylodes absent. Mouth palps absent. 4–6 thoracic chaetigerous segments. Collar non-lobed with entire edge, no clear separation towards thoracic membranes that end at second chaetiger. No apron, no tonguelets. Collar chaetae limbate (Fig. 31A). *Apomatus* chaetae absent. Thoracic uncini saw-to-rasp-shaped with numerous teeth (> 12) in profile, 2–3 teeth per row (dental formula P:3:3:3:2:2:1:1:1:1:1:1:1:1); anterior peg gouged (*Pomatoceros* type) (Fig. 31B). Abdominal chaetae short, with flat triangular denticulate blade (Fig. 31D). Thoracic triangular depression absent. Abdominal uncini similar to thoracic ones (Fig. 31C). Achaetous anterior abdominal zone absent. Long posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. The diagnosis above is based on the description of the only Recent species thus far described - from specimens collected at depths of 1846–1900 m off the Azores. Topotypical material from 2440 m is present in the collections of the ZMA (V.Pol. 3906, presented by H. Zibrowius), additional material from the Central Atlantic was mentioned by Hartman & Fauchald (1971), they, however, counted 4 thoracic chaetigers only. A possible second undescribed species was found at 4124 m south-east off the Galapagos Islands (ZMA V.Pol. 3859). Zibrowius (pers. comm.) suspects a total of 4 different species, partly with not coiled quadrangular tubes.

Jäger (2004) synonymized the Recent genus *Spirodiscus* Fauvel, 1909 with the Fossil *Nogrobs* de Montfort, 1808. Jäger also suggested that the Recent *Bathyditrupa hovei* might belong to the subgenus *Nogrobs* (*Tetraditrupa*) Regenhardt, 1961, without further argumentation.

Nogrobs grimaldii (Fauvel, 1909), Central Atlantic, off Azores; bathyal, abyssal.

26. *Omphalopomopsis* Saint-Joseph, 1894

(Fig. 7A, B)

Type-species: *Omphalopoma langerhansii* Marenzeller, 1885
Number of species: 1

Tube subcylindrical, white, opaque, with 3 denticulate keels and an occasional low collar-like ring. Granular overlay not observed. Operculum bulbous with slightly convex brilliantly white calcareous endplate. Peduncle cylindrical, broadening and wrinkled towards opercular ampulla, constriction present; without wings; insertion unknown. Pseudoperculum not mentioned in original description, presumably absent. Up to 25 pairs of radioles, arranged in two circles/short spires. Inter-radiolar membrane absent. Branchial eyes, stylodes, and mouth palps not observed. 7 thoracic chaetigerous segments. Collar trilobed, well developed, especially medio-ventrally; thoracic membranes wide till 3rd segment, further unknown (damaged), apron apparently absent. Tonguelets unknown. Collar chaetae bayonet-like with numerous hair-like processes basally, *Spirobranchus*-type and limbate. *Apomatus* chaetae present. Thoracic uncini saw-shaped, with 7–8 teeth above anterior pointed fang. Triangular depression unknown. Abdominal chaetae geniculate, SEM details unknown, probably *Vermiliopsis*-type (then flat narrow geniculate), apparently with almost smooth edge, very long posteriorly. Uncini saw-shaped anteriorly with 7 teeth and fang, rasp-shaped posteriorly. Achaetous zone not known. Long posterior capillary chaetae present. Posterior glandular pad not observed.

Remarks. The taxon is known only from the single holotype deposited in the Natural History Museum of Vienna, NHMW A.N.14552, Inv. no. 2054 (Fig. 7A, B). The description by Marenzeller (1885) leaves doubt about the shape of the anterior uncinal tooth, it may be either pointed as in *Hydroides*, or blunt as in *Vermiliopsis*.

Specimens attributed to *Omphalopomopsis* by Fauvel (1930, 1953) and Pillai (1960) in reality belong to *Pomatostegus actinoceras* (*fide* Zibrowius (1973b), as *P. stellatus*).

Omphalopomopsis langerhansii (Marenzeller, 1885), South Japan, Enoshima, 366 m.

27. *Paraprotis* Uchida, 1978
(Fig. 32)

Type-species: *Paraprotis dendrova* Uchida, 1978
Number of species: 2, maybe 1

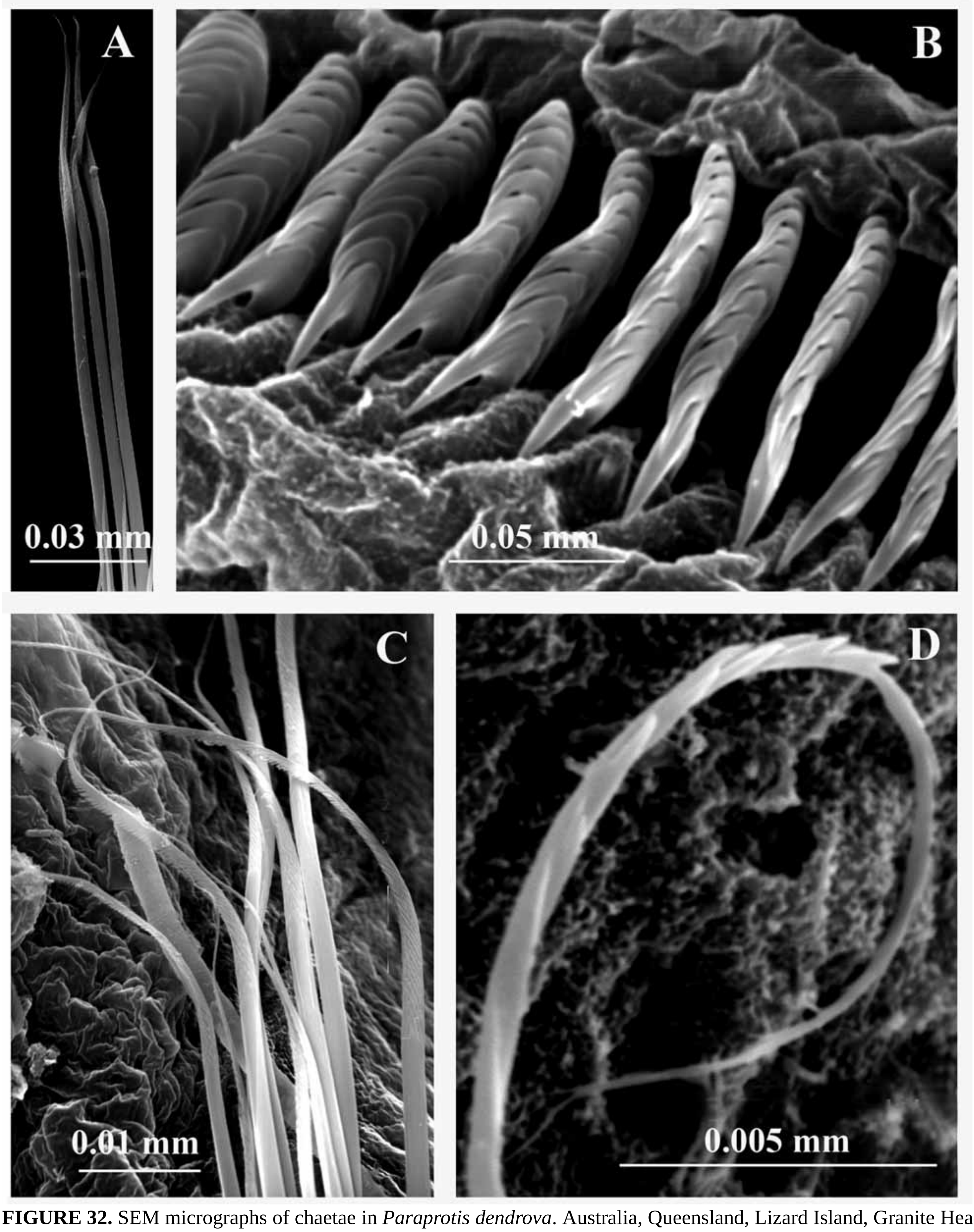

FIGURE 32. SEM micrographs of chaetae in *Paraprotis dendrova*. Australia, Queensland, Lizard Island, Granite Head, from underside of boulders on rock, little sand, subtidally, legit H.A. ten Hove, 18.06.1983, det. D. Makhan. A—bundle of collar chaetae, B—thoracic uncini, C—thoracic chaetae, D—abdominal chaeta.

Tube white, opaque, circular in cross-section, without longitudinal keels. Granular overlay not observed. Operculum and pseudoperculum absent (or soft globular operculum may be present on second unmodified radiole in *P. pulchra*). Arrangement of radioles semi-circular or short pectinate, up to 6 per lobe (up to 32 per lobe in *P. pulchra*). Inter-radiolar membrane absent. Branchial eyes (ocellar clusters) present. Stylodes absent. Mouth palps absent, but a spiral projection for brood attachment originates from the right side of the mouth. Collar non-lobed, tonguelets absent. Thoracic membranes narrowing at third chaetiger but continuing to the 7th thoracic chaetiger, a narrow apron is probably present (neither Uchida's description nor an additional specimen SAM E3591 give a definite answer). 7 thoracic chaetigerous segments. Collar chaetae limbate (Fig. 32A). *Apomatus* chaetae absent (Fig. 32C). Thoracic uncini of *Protis* type, saw-shaped with about 10 teeth, anterior fang with pointed tip (Fig. 32B). Thoracic triangular depression not observed. Anterior abdominal chaetae flat narrow geniculate with a row of sharp teeth along its free margin (Fig. 32D). Abdominal uncini similar to thoracic ones but rasp-shaped. Achaetous anterior abdominal zone present, short (2–4 segments). Long posterior capillary chaetae present. Posterior glandular pad not observed.

Remarks. The diagnosis has been taken from Uchida (1978) who in the name for his new genus implied some similarity to *Protis*, mainly in the shape of thoracic uncini and lack of operculum, even though *Protis* has special fin-and-blade collar chaetae and thoracic *Apomatus* chaetae. Imajima (1979) described a second *Paraprotis* species, *P. pulchra* from Japan. Both species have a similar chaetation pattern; however, some specimens of *P. pulchra* have a thin globular operculum. Also, *P. pulchra* has a well developed trilobed collar, an inter-radiolar membrane, and uniformly wide thoracic membranes unlike *P. dendrova*, with its poorly developed non-lobed collar, bright ocellar clusters on its radioles but lacking an inter-radiolar membrane, and thoracic membranes that narrow at the 3rd thoracic chaetiger. Spiral brooding projections typical for *P. dendrova* have not been mentioned for *P. pulchra*. Because of all the differences, *P. pulchra* very likely does not belong to the genus *Paraprotis* (*fide* ten Hove, 1984). Nishi (1992b) provided SEM micrographs of chaetae of *P. dendrova*, additional figures are given in this paper (Fig. 32).

1. *Paraprotis dendrova* Uchida, 1978, Sabiura, South Japan
2. ?*Paraprotis pulchra* Imajima, 1979, Honshu, Japan.

28. *Paumotella* Chamberlin, 1919

(Figs 33, 51E)

Type-species: *Paumotella takemoana* Chamberlin, 1919
Number of species: 1

Tube unknown. Operculum inverse conical, the distal chitinous endplate slightly depressed, without processes. Opercular peduncle smooth, oval (flattened circular) in cross-section, with long basal lateral wing (Fig. 51E); insertion just outside radioles, covering base of 4–5 radioles. Pseudoperculum absent. Arrangement of radioles in semi-circles, up to 21 per lobe. Inter-radiolar membrane absent. Branchial eyes not found in preserved material, stylodes absent. Mouth palps present. 7 thoracic chaetigerous segments. Collar trilobed, with entire edge. Thoracic membranes narrowing abruptly between 4th and 5th segment, where they end; no apron. Tonguelets absent. Collar chaetae limbate (Fig. 33A). *Apomatus* chaetae present (Fig. 33B, C). Thoracic uncini saw-shaped, with 12 teeth above rounded peg (Fig. 33D). Thoracic triangular depression present. Anterior and median abdominal regions with stout, moderately curved, acute, slightly compressed acicular chaetae (Fig. 33F); posteriorly long capillaries with distal limbus; uncini rasp-shaped, with about 10 teeth in profile, 2–3 teeth in a row above peg (Fig. 33E). Achaetous anterior abdominal zone short, 2–3 segments only. Posterior glandular pad absent.

Remarks. The original description of this monotypic genus is not up to the present standards, a new description is given below. The characteristic features of the genus, according to Chamberlin (1919) are the abdominal chaetae that are neither denticulate nor geniculate, but acicular, as well as the shape of the operculum; however, the latter is not very characteristic, being similar to that of some *Vermiliopsis* spp., as well as that of *Ditrupa*.

Paumotella takemoana **Chamberlin, 1919, French Polynesia, Paumotu Archipelago.**

Paumotella takemoana Chamberlin, 1919: 481–483, pl. 78 figs 1–5; Southward, 1963: 586 (in key only); Fauchald, 1977: 145 (opercular peduncle with wings); Uchida, 1978: 71–72 (associated with *Vermiliopsis*).

Material studied. French Polynesia, Paumotu Archipelago, Makemo, coral, at bottom of lagoon, 24 m (13 fm), R/V "Albatross" E. Pac. Exp. 1899–1900 ident. by Chamberlin (further details not present in internet list of stations) (holotype, USNM 19432; 2 slides (schizotypes) MCZ).

Description. TUBE: absent, and not described by Chamberlin either.

BRANCHIAE: each lobe with 20–21 branchial radioles, arranged in semi-circles, not connected by branchial membrane. Radioles too convoluted to observe details of pinnules, terminal filament long. Branchial eyes not observed. Stylodes absent. Pair of mouth palps present.

PEDUNCLE: smooth, flattened circular in cross section, inserted just below left branchial lobe, covering base of 4–5 radioles. A single lateral wing along proximal 2/3^{rds} of peduncle (Fig. 51E), exactly like figured for *Vermiliopsis leptochaeta* Pillai, 1971; showing clear constriction just below ampulla. Pseudoperculum absent.

OPERCULUM: globular to inverse conical with a distal slightly concave chitinous endplate, with smooth margin, and with flat central area without further ornamentation (Fig. 51E). Length of operculum and peduncle 4–5 mm; opercular bulb 1.4 mm, width 1.8 mm.

COLLAR and thoracic membranes: collar high, with entire edge; deep incision between ventral and lateral collar lobes, the latter continuous with thoracic membranes, ending between chaetiger 4 and 5. Tonguelets between ventral and lateral collar lobes absent. Internal pockets in thoracic membranes and wart-like protuberances of collar chaetiger as in *Floriprotis* absent.

THORAX: with collar chaetiger, and 6 uncinigerous chaetigers. Pair of prostomial eyes not observed. Collar chaetae broken off, but according to Chamberlin they are limbate, of two sizes. Subsequent chaetae hooded (limbate), of two sizes. *Apomatus* chaetae occur in addition as well, both in slides of the type (MCZ) as well as in rest of holotype (contrary to Chamberlin's description, and Fauchald (1977). Uncini along entire thorax saw-shaped, with 12 curved teeth and rounded peg. Thoracic uncinigerous tori gradually approaching one another posteriorly, forming a triangular depression on the ventral side of the thorax.

ABDOMEN: abdominal chaetigers 56, anterior three achaetigerous. Uncini rasp-shaped, with peg and 10 teeth in profile, 2–3 teeth in a row. Chaetae faintly curved, rounded acute aciculae, 3–4 per bundle. Long capillary chaetae present in 10–15 posterior chaetigers, broken, thus extent not entirely clear. Pygidium clearly bilobed. Posterior glandular pad absent.

Size: length up to 23.5 mm. Width of thorax 2.1 mm. Branchiae and operculum accounting for 1/6 of entire length.

Colour: the general colour is brownish yellow, with the parapodial processes paler. The thoracic collar is transparent. The branchiae yellow. Operculum yellow, with the rim black (Chamberlin 1919: 482).

Ecology: no data except for those in label: coral, at bottom of lagoon, 24 m.

Remarks. Chamberlin´s original label gives as locality "Takemo", hence the specific name of the taxon; this mistake already was corrected in his paper to the atoll of Makemo. From the fact that Fauchald (1977: 145) attributes wings to the opercular peduncle, a character not mentioned by Chamberlin, we infer that he probably saw the holotype. But for the presence of the absolutely unique abdominal chaetae the taxon could easily be mistaken for a species of the genus *Vermiliopsis*. Uchida (1978: 71–72) also associates the genus tentatively with *Vermiliopsis* sensu lato (his subfamily Vermiliopsinae). Possible relationship will be discussed in (a) forthcoming paper(s) by us.

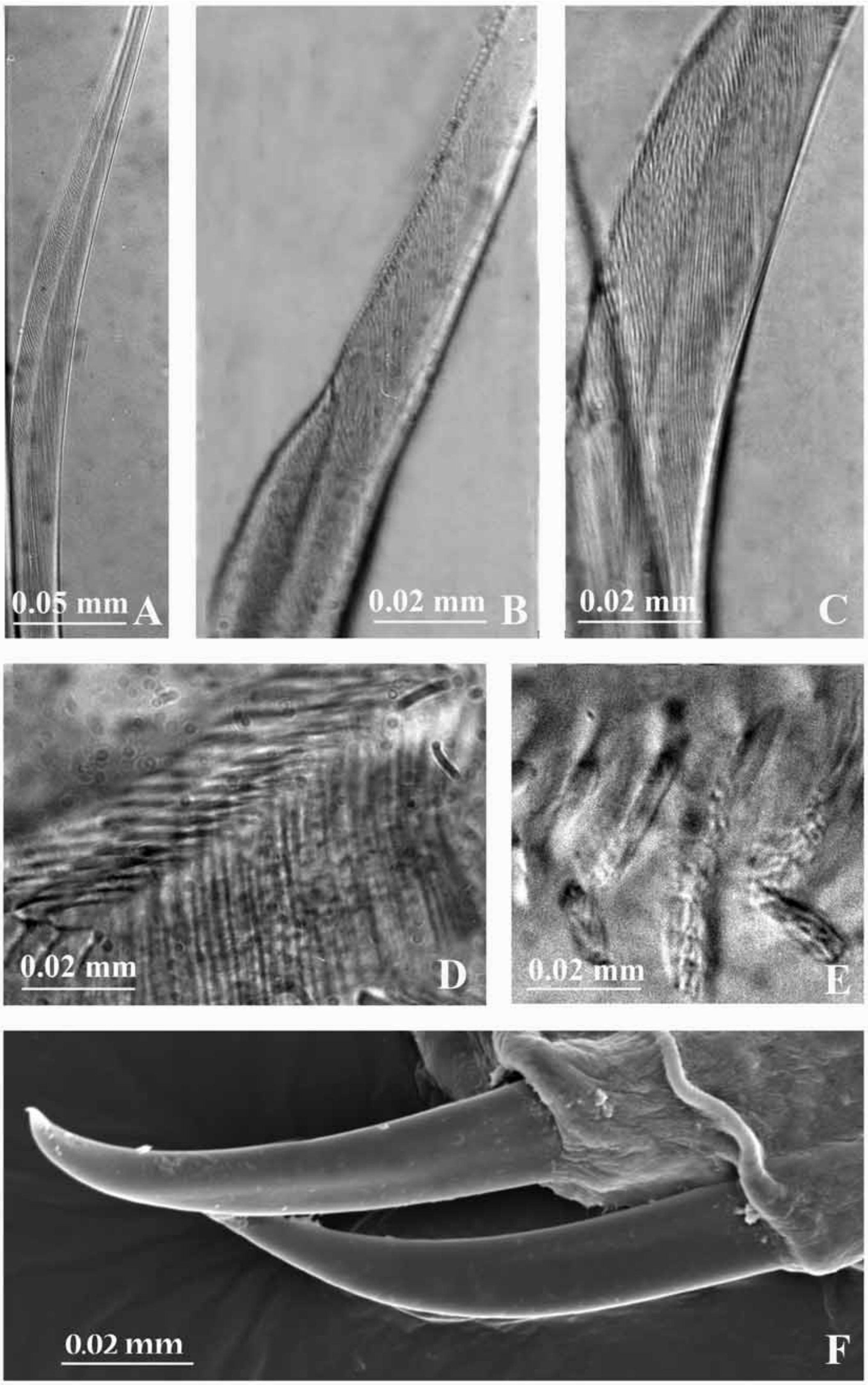

FIGURE 33. Photos (A–E) and a SEM micrograph (F) of chaetae in *Paumotella takemoana*. Holotype, USNM and MCZ (slides). A—"limbate" chaeta of 6th thoracic chaetiger, B—*Apomatus* chaeta of 6th chaetiger, C—same *Apomatus* chaeta as in B, but different focus, D—lateral view of thoracic uncini, E—frontal view of abdominal uncini, F—acicular abdominal chaetae.

29. *Placostegus* Philippi, 1844
(Fig. 34)

Type-species: *Serpula tridentata* Fabricius, 1780
Number of species: 7 (-8)

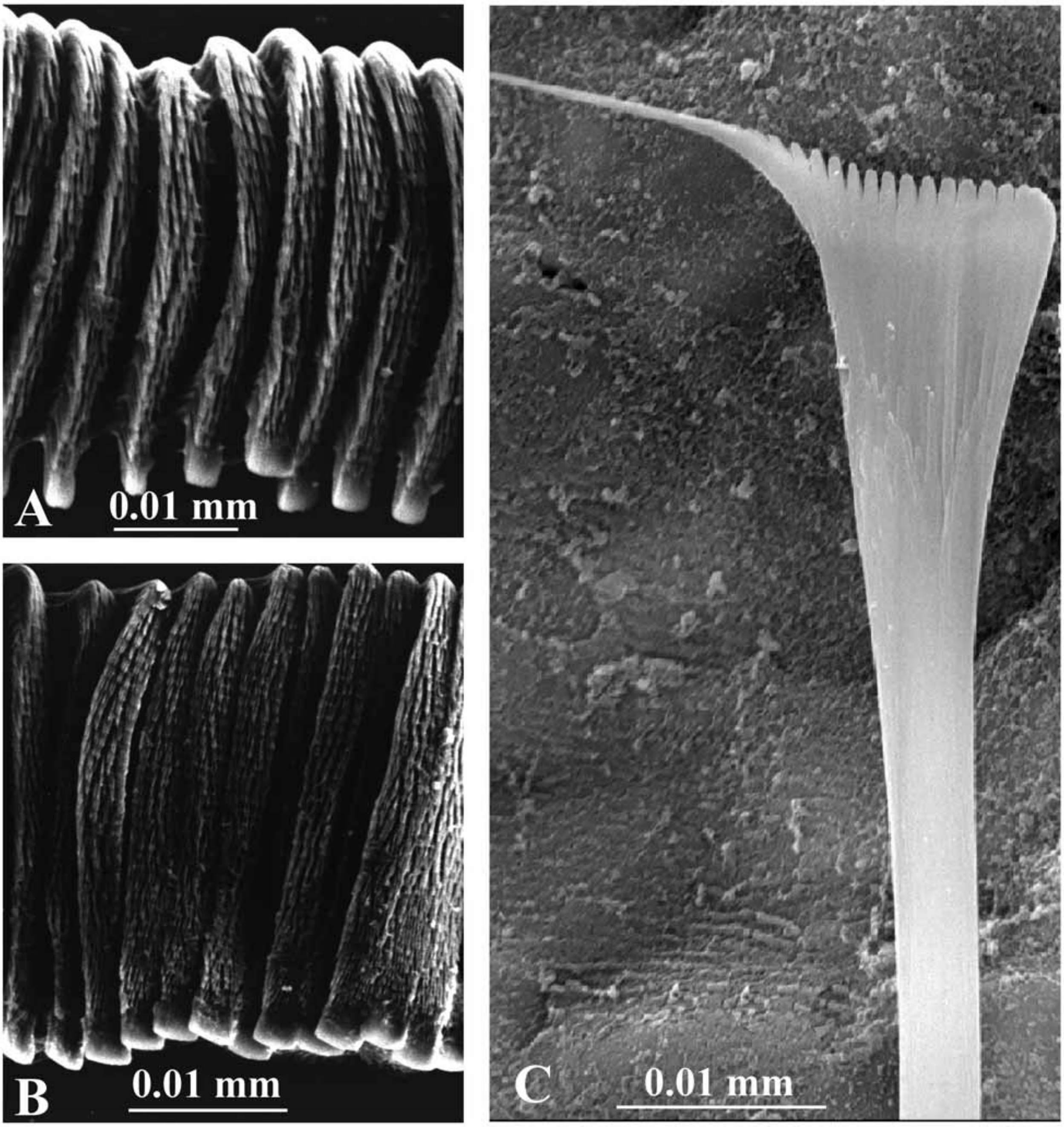

FIGURE 34. SEM micrographs of chaetae in *Placostegus tridentatus*. Norway, Bolsøy galten, S. of Hamarøy, 67°57.0' N, 15°23.8' E, 115 m, legit H. Lemche, det. H.A. ten Hove, ZMA V.Pol. 3643. A—1st row of thoracic uncini, B—anterior abdominal uncini, C—anterior abdominal chaeta with a hollow tip.

Tube triangular in cross-section, with denticulate keels, transparent or semi-transparent, often only attached to substratum at the base, collar-like rings absent. Granular overlay absent. Operculum inverse conical, with chitinous cup-shaped endplate. Peduncle cylindrical, smooth, without wings, gradually merging into operculum, at most with shallow constriction; inserted at base of radioles on one side between first and second normal radiole and maximally covering base of first three radioles. Pseudoperculum absent. Radioles arranged in semi-circles, up to 24 per lobe; inter-radiolar membrane, branchial eyes, and stylodes absent. Mouth palps present. 6 thoracic chaetigerous segments. Collar tri- to penta-lobed, collar edge may be almost laciniate; tonguelets between ventral and lateral collar lobes present. Thoracic membranes long, forming ventral apron across anterior abdominal segment. Collar chaetae absent; collar region with girdle of reddish ocelli. *Apomatus* chaetae absent. All uncini sub-rectangular, rasp-shaped with > 20 teeth in profile, and up to 8 small teeth in a row; anterior peg wide, flat, bluntly truncate, almost rectangular (Fig. 34A). Thoracic triangular depression absent. Abdominal chaetae truly trumpet, with distal hollow triangular blade, abruptly bent (Fig. 34C). Achaetous anterior abdominal zone present. Long posterior capillary chaetae may be present. Posterior glandular pad absent.

Remarks. *Placostegus* is one of three serpulid genera (see also *Neomicrorbis* and *Vitreotubus*) with an entirely vitreous tube; completely transparent, glass-like in live animals, it may become milky-white semi-transparent after preservation in formalin. The tube in *P. incomptus* shows a remarkable dual appearance, proximally with closely set transverse ribs, distally smoothly triangular. Fauvel (1927 fig. 128i) and Imajima (1978 fig. 9c) mention a chitinous talon projecting from the endplate into the opercular bulb.

Placostegus has one evident diagnostic autapomorphy—the belt of bright red ocelli in the region where in other genera collar-chaetae are found (e.g., Langerhans 1884 fig. 38b, Ehlers 1887 fig. 3, Hartman 1969 fig. 2; our Fig. 1F).

1. *Placostegus assimilis* McIntosh, 1885, off Bermudas; bathyal
2. *Placostegus californicus* Hartman, 1969, Southern California
3. *Placostegus crystallinus* (Scacchi, 1836) *sensu* Zibrowius, 1968a, Eastern North Atlantic, Mediterranean; ?Red Sea, Indian Ocean, these reports might belong to a different species (Ben-Eliahu, pers. comm.)
4. ? *Placostegus grayi* Baird, 1865, no location given; generic status uncertain
5. *Placostegus incomptus* Ehlers, 1887, off Cuba; bathyal
6. *Placostegus langerhansi* Marenzeller, 1893, Madeira, Canary Islands
7. *Placostegus tridentatus* (Fabricius, 1780), Atlantic, Mediterranean, Indo-West Pacific.

30. *Pomatoceros* Philippi, 1844

(Fig. 35)

Type-species: *Serpula triquetra* Linnaeus, 1758
Number of species: 5

Tube generally white, opaque, though blue, purplish and pink parts may occur; usually with longitudinal keel(s), may be with more or less regular series of pits, triangular or sub-triangular in cross-section; granular overlay absent. Operculum with inverse conical to rather shallow ampulla, with calcified endplate, sometimes bearing spines. Peduncle thick, triangular in cross-section, with distal lateral wings; a constriction between peduncle and ampulla may be present; peduncle inserted almost medio-dorsally, covering the base of up to three dorsal radioles. Pseudoperculum absent. Radioles arranged in semi-circles and up to 20 per lobe. Branchial eyes and stylodes absent. Mouth palps present. 7 thoracic chaetigerous segments. Collar trilobed; tonguelets between ventral and lateral collar lobes present. Thoracic membranes long, forming ventral apron across anterior abdominal segment. Collar chaetae small, limbate. *Apomatus* chaetae absent. All uncini saw-shaped with 10–11 teeth, anterior peg blunt gouged (Fig. 35A, B). Thoracic triangular depression present. Abdominal chaetae true trumpet-shaped, abruptly bent, distally with two rows of denticles separated by hollow groove (Fig. 35C, D). Achaetous anterior abdominal zone absent. Long posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. See remarks for *Spirobranchus*.

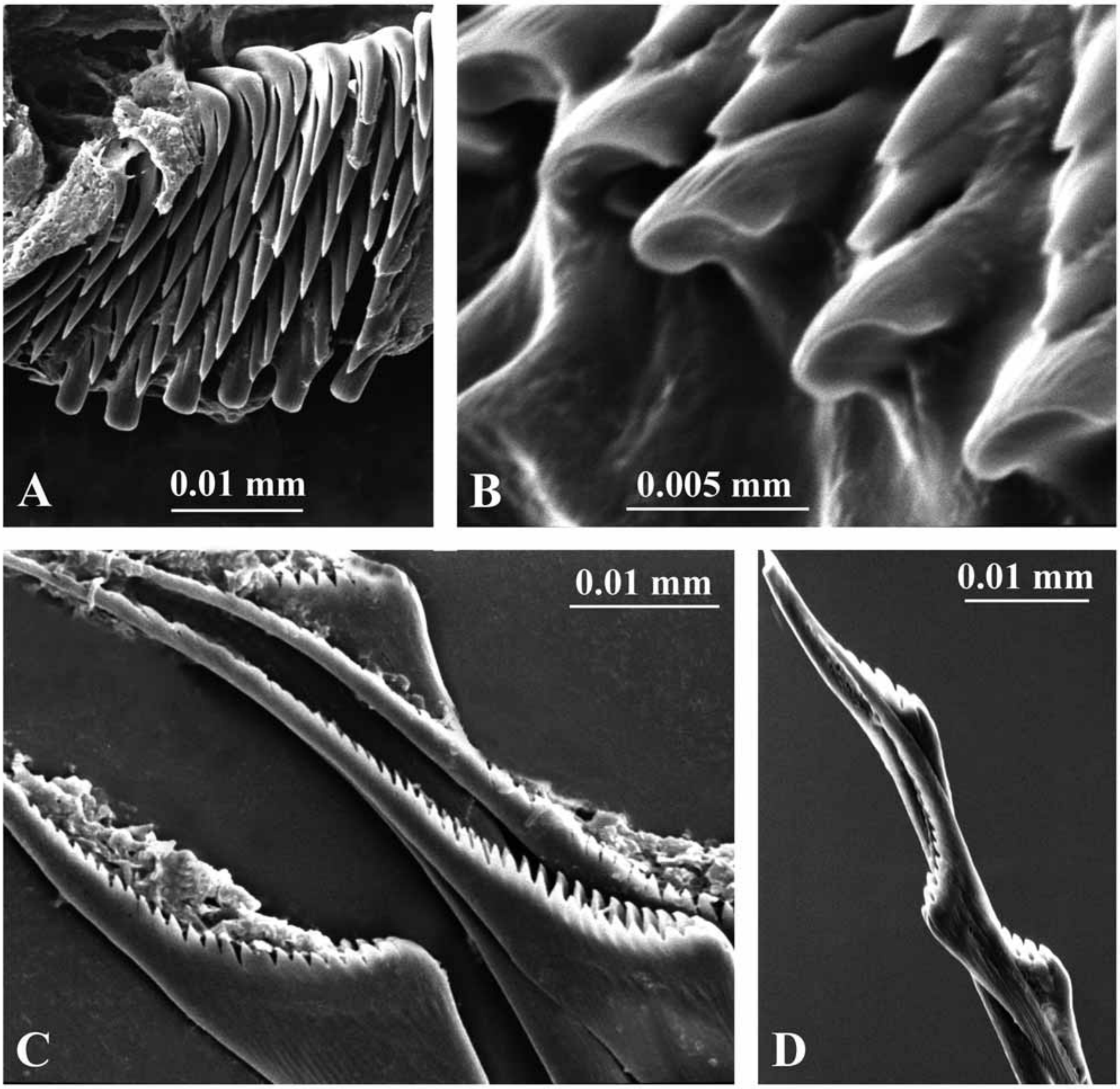

FIGURE 35. SEM micrographs of chaetae in *Pomatoceros triqueter.* United Kingdom, Liverpool Bay, 53˚50’ N, 3˚50’ W, legit S.J. de Groot, ZMA V.Pol. 3201. A—anterior abdominal uncini, B—detail of pegs in last row of uncini, view from below, C—anterior abdominal chaetae with hollow tips, D—posterior abdominal chaetae.

1. *Pomatoceros americanus* Day, 1973, Beaufort, North Carolina; temperate Eastern USA
2. *Pomatoceros lamarckii* (Quatrefages, 1866), Guettary, France; Mediterranean-Atlantic, U.K., English Channel
3. *Pomatoceros minutus* Rioja, 1941b, Acapulco, West Mexico; Gulf of California, Gulf of Mexico, Caribbean to Brazil
4. *Pomatoceros taeniatus* (Lamarck, 1818), Tasmania; South Australia, New South Wales, New Zealand, South Trinidad Islands; a remarkable and questionable distribution, Trinidad might be explained by a label error by Benham (1927, as *P. terraenovae*)
5. *Pomatoceros triqueter* (Linnaeus, 1758), Norway to and including Mediterranean-Atlantic, Black Sea; records from other areas questionable.

31. *Pomatoleios* Pixell, 1913
(Fig. 36)

Type-species: *Pomatoleios crosslandi* Pixell, 1913, junior synonym of *Placostegus cariniferus* var. *kraussii* Baird, 1865
Number of species: 1

Tube white or bluish, opaque, triangular in cross-section, with medial keel projecting into flap over the entrance. Granular overlay absent. Operculum inverse conical with flat calcareous plate; sometimes with talon projecting into opercular ampulla (best seen if operculum is cleared in glycerine). Peduncle thick, triangular in cross-section, with distal wings, without constriction, inserted almost medially, slightly left, covering base of up to five radioles. Pseudoperculum absent. Radioles arranged in semi-circles, up to 19 per lobe, connected by very high inter-radiolar membrane. Branchial eyes present (single ocelli visible in fresh material only). Stylodes absent. Mouth palps present. 6 thoracic chaetigerous segments (in juveniles 7). Collar with entire edge, tonguelets between ventral and lateral collar lobes present; thoracic membranes forming ventral apron. Collar chaetae absent (limbate ones present in juveniles only). *Apomatus* chaetae absent. Uncini saw-shaped with fairly numerous (10–11) teeth, anterior peg wide and blunt, gouged (Fig. 36B). Triangular depression present. Abdominal chaetae true trumpet-shaped, abruptly bent, distally with two rows of denticles separated by a groove (Fig. 36A). Achaetous anterior abdominal zone absent. Posterior capillary chaetae and posterior glandular pad absent.

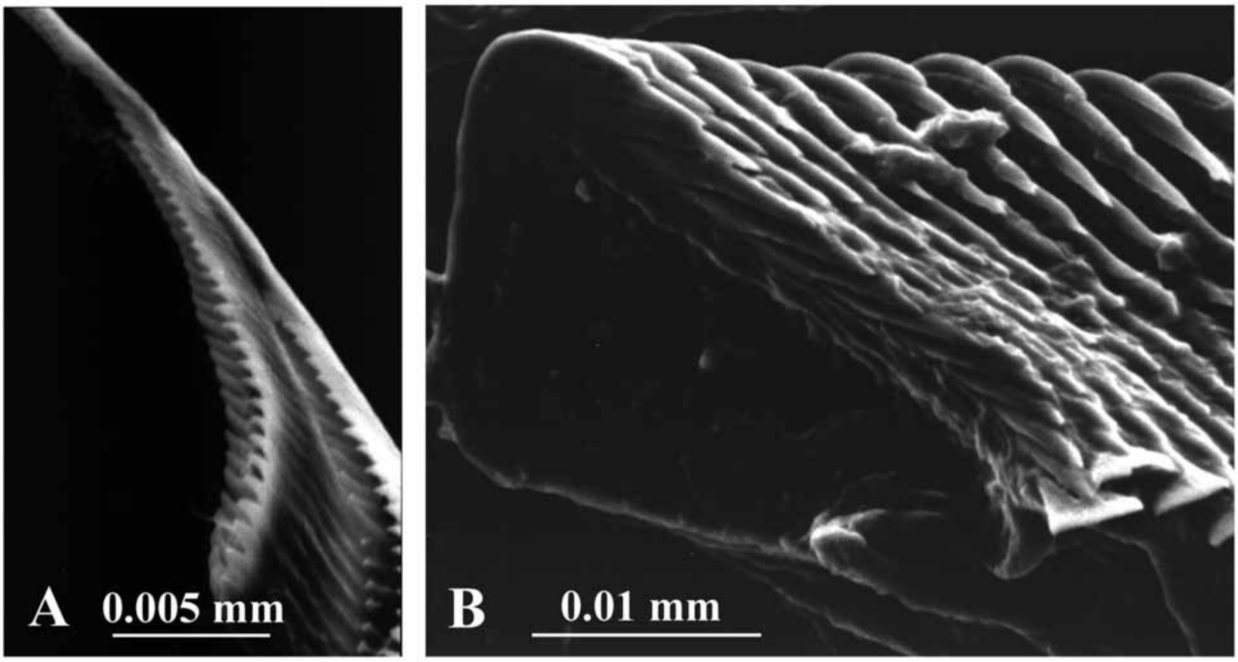

FIGURE 36. SEM micrographs of chaetae in *Pomatoleios kraussii*. Madagascar, Tuléar, littoral, det. and don. H. Zibrowius, legit J. Picard, ZMA V.Pol. 3068. A—anterior abdominal chaetae with hollow tips, B—thoracic uncini of 1st row.

Remarks. Opercular talons as reported by Pillai (1965 fig. 22H) and ten Hove (1973 fig. 43) are not consistenly mentioned (nor looked for) in the literature. Whether or not the presence of such a talon is a character distinguishing between populations or even taxa should be investigated.

Pomatoleios kraussii is widely distributed in the Indo-Pacific forming intertidal aggregations. The only difference between *Pomatoceros* and *Pomatoleios* is the more or less consistent lack of collar chaetae in the latter. However, collar chaetae may be present in juvenile specimens (Zibrowius 1968a, Crisp 1977, ten Hove & Nishi 1996), and occasionally absent in *Pomatoceros* (e.g., 9 specimens from the Irish Sea, ZMA V.Pol. 3201) as well as in *Spirobranchus* (e.g., as *Olga elegantissima* Jones, 1962), thus this monotypic genus likely lacks a phylogenetic basis. See further remarks for *Spirobranchus*. SEM photos of *Pomatoleios* are published in Fiege & Sun (1999).

Pomatoleios kraussii (Baird, 1865), South Africa; widely distributed in the Indo-Pacific; Lessepsian migrant to the Levant Mediterranean.

32. *Pomatostegus* Schmarda, 1861

(Fig. 37)

Type-species: *Pomatostegus macrosoma* Schmarda, 1861, junior synonym of *Terebella stellata* Abildgaard, 1789
Number of species: 3

Tube white, opaque, semi-circular to roughly triangular in cross-section, with up to 5 longitudinal keels; granular overlay absent. Operculum a very flat ampulla covered with chitinous disk bearing a column with several serrated disks alternating with circlets of spines proximally and closely applied to each disk. Peduncle flatly triangular in cross-section with broad latero-distal wings along its entire length; inserted to the left or right at the basis of the branchial lobe; from the fact that the first and second radiole separated by the base of the peduncle, it is inferred that it is derived from the second normal radiole. Constriction absent. Pseudoperculum absent. Arrangement of radioles in (semi-)circles, up to 90 per lobe. Inter-radiolar membrane present. Branchial eyes present. Stylodes absent. Mouth palps absent. 7 thoracic chaetigerous segments. Collar tri- to penta-lobed, well developed with an entire smooth margin. Tonguelets absent. Thoracic membranes short, ending just posterior to the second row of uncini (segment 3). Collar chaetae *Spirobranchus*-type, with basal pilose fin and distal blade, and limbate (Fig. 37B). *Apomatus* chaetae present (Fig. 37E). Thoracic uncini saw-shaped, with 9–13 teeth, anterior peg blunt (Fig. 37C). Thoracic tori meet ventrally in larger specimens; in juveniles the ventral space between thoracic tori narrowing towards last rows that almost fused, leaving a triangular depression. Abdominal chaetae flat narrow geniculate, with long blade (Fig. 37F). Abdominal uncini smaller than thoracic ones, with about 8 teeth in profile, 3 teeth in a row (Fig. 37D). Achaetous anterior abdominal zone absent. Long posterior capillary chaetae absent, but posterior chaetae longer. Posterior glandular pad absent.

Remarks. According to the recent literature there is but a single circumtropical species, *Pomatostegus stellatus*. However, an unpublished study by P. Valentijn (former student to HAtH, University Utrecht), re-instigated two species regarded to be synonymous with the type-species to full specific rank: *P. actinoceras*, from the Indo-West Pacific Region, and *P. krøyeri*, from tropical Pacific America, leaving a tropical Atlantic distribution only for *P. stellatus*. The latter taxon has been recorded from Atlantic Africa by Augener (1918), Amoureux (1973), and Zibrowius (1973b), however, the single specimen studied from Western Africa by Valentijn and ten Hove could not be attributed with certainty to either *P. actinoceras* (likely) or *P. stellatus* (less likely).

1. *Pomatostegus actinoceras* Mörch, 1863, Indo-West Pacific, ?Western Africa; generally synonymised with *P. stellatus*
2. *Pomatostegus krøyeri* Mörch, 1863, tropical Pacific America; generally synonymised with *P. stellatus*
3. *Pomatostegus stellatus* (Abildgaard, 1789), West Indies; Caribbean; usually including preceding 2 species.

33. *Protis* Ehlers, 1887

(Fig. 38)

Type-species: *Protis simplex* Ehlers, 1887
Number of species: 6 (or 7)

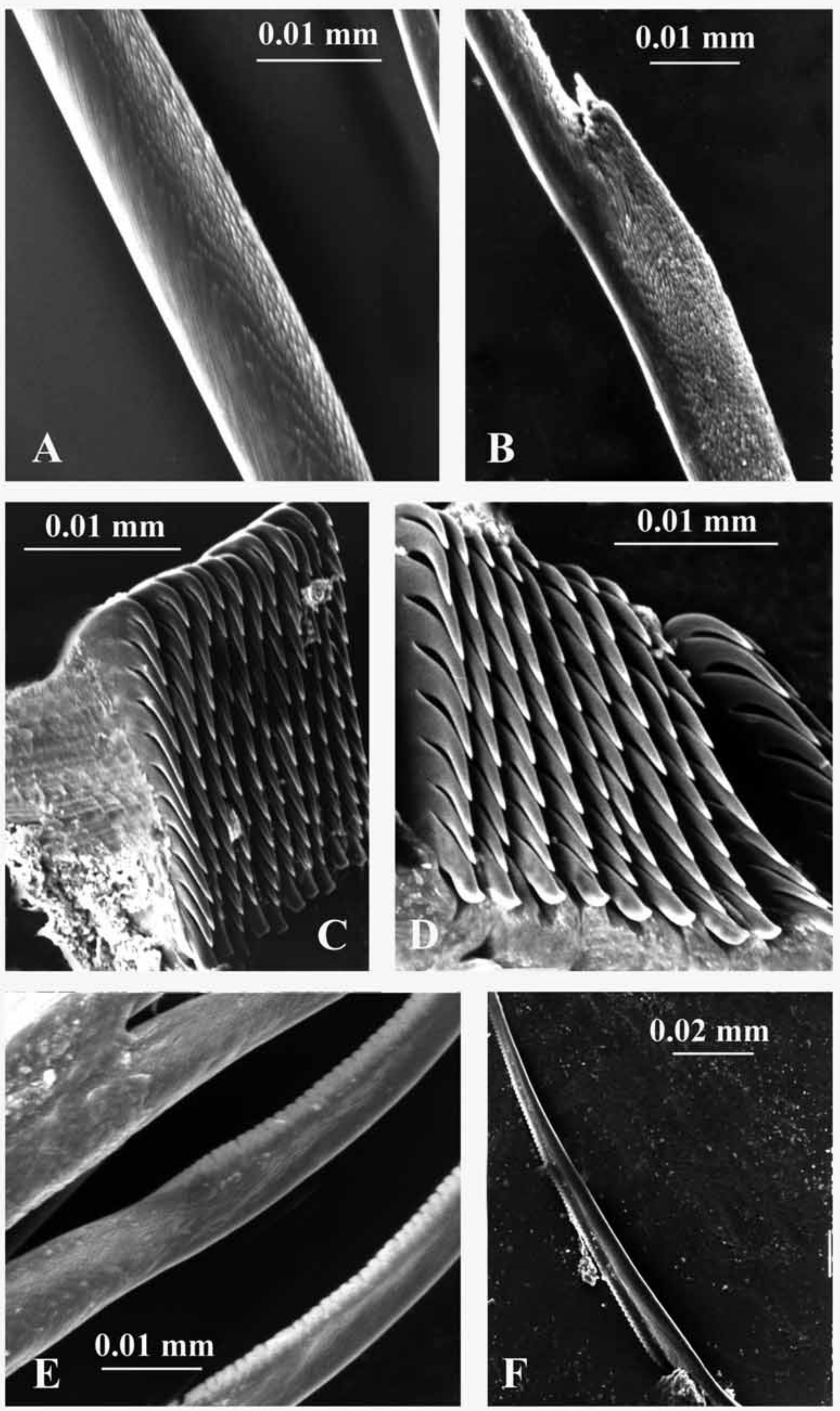

FIGURE 37. SEM micrographs of chaetae in *Pomatostegus stellatus*. Cuba, South-East, Isla de la Juventud, Cayo Boca de Alonso, 4 m, legit G. San Martin, ZMA V.Pol. 3840. A—“limbate” chaeta of 2nd thoracic bundle, B—*Spirobranchus* collar chaeta, C—1st row of thoracic uncini, D—middle abdominal uncini, E—*Apomatus* chaetae of 7th thoracic bundle, F—anterior abdominal chaeta.

Tube white, opaque, without keels or flaring peristomes. Granular overlay absent. Operculum absent or one or more membranous globular opercula present on normal pinnulate radiole. Arrangement of radioles pectinate, up to 20 per lobe. Inter-radiolar membrane absent. Branchial eyes not observed. Stylodes absent. Mouth palps absent. 7 thoracic chaetigers. Collar trilobed with entire edge, tonguelets absent. Thoracic membranes long, at least to the end of thorax and usually forming ventral apron across anterior abdominal segments. Collar chaetae fin-and-blade (Fig. 38A) and limbate. *Apomatus* chaetae present. Thoracic uncini saw-shaped with about 6 teeth, anterior fang simple pointed (Fig. 38B). Triangular depression absent. Abdominal chaetae flat narrow geniculate with rounded teeth (Fig. 38D), slightly more triangular blade in *P. hydrothermica*. Abdominal uncini rasp-shaped in all segments, with up to 6 teeth in profile, approximately 5–7 teeth in a row above fang (Fig. 38C). Achaetous anterior abdominal zone absent. Long posterior capillary chaetae present. A posterior glandular pad may be present.

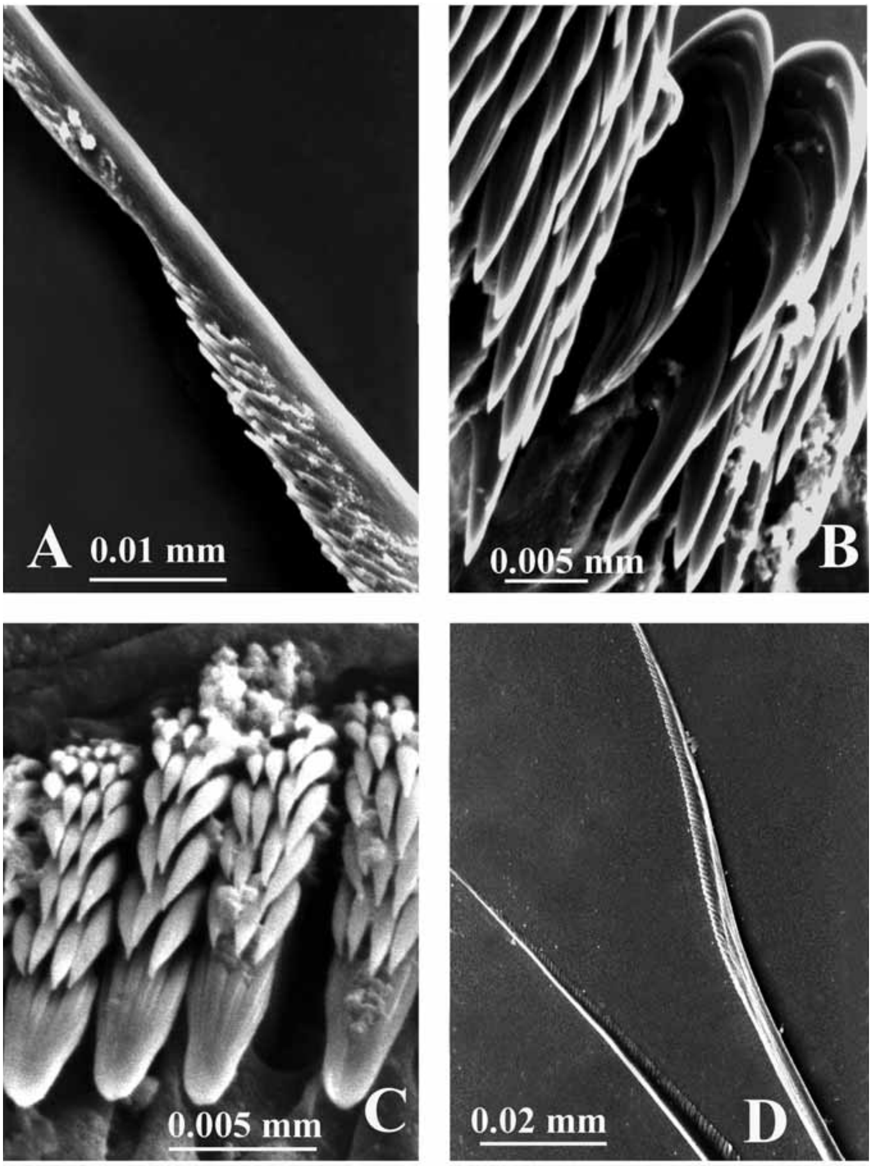

FIGURE 38. SEM micrographs of chaetae in *Protis arctica*. North East off Iceland, 60°33' N, 7°25' W, 1802 m, R/V "*Ingolf*", det. E. Wesenberg-Lund, redet. M.N. Ben-Eliahu, exchange with Zoological Museum Copenhagen, ZMA V.Pol. 3833. A—details of fin-and-blade collar chaeta, B—uncini of 4th thoracic chaetiger, C—posterior abdominal uncini, D—anterior abdominal chaetae.

Remarks. According to the original diagnosis, the lack of an operculum is considered a characteristic feature of *Protis* Ehlers, 1887. Ten Hove & Zibrowius (1986) reformulated the diagnosis, Kupriyanova &

Jirkov (1997) further extended it to include individuals with one or more opercula following the description of the abyssal *P. polyoperculata* by Kupriyanova (1993b). Ben-Eliahu & Fiege (1996) and Kupriyanova & Jirkov (1997) report both operculate and non-operculate specimens of *P. arctica*. The nominal taxon *Salmacina chilensis* Gallardo, 1969 better would fit here (or in *Chitinopoma*). The taxonomy of the genus is difficult because chaetae, uncini and tubes are very similar and opercula, if present, are undifferentiated. *Protis hydrothermica* shows two characters not mentioned for the other species: warts between ventral and lateral collar lobes (see remarks *Floriprotis*), and a pair of pockets in the medio-ventral collar.

1. *Protis arctica* (Hansen, 1879), Arctic to Central Atlantic, Mediterranean; bathyal; compare *P. simplex*
2. *Protis brownii* (Pixell, 1913), Antarctic; maybe synonym of *P. simplex*
3. ?*Protis chilensis* (Gallardo, 1969), off Punta Patache, Northern Chile; bathyal (*fide* Nogueira & ten Hove 2000)
4. *Protis hydrothermica* ten Hove & Zibrowius, 1986, East Pacific; near hydrothermal vents
5. *Protis pacifica* Moore, 1923, Southern California; bathyal
6. *Protis polyoperculata* Kupriyanova, 1993b, Kurile-Kamchatka trench; abyssal
7. *Protis simplex* Ehlers, 1887, off Florida, 1500 m; compare *P. arctica*.

34. *Protula* Risso, 1826
(Fig. 39)

Type-species: *Protula rudolphi* Risso, 1826, junior synonym of *Serpula tubularia* Montagu, 1803
Number of species: ?23

Tube white, opaque, may be up to 2 cm across and 40 cm long, (semi-)circular in cross-section, longitudinal keels and flaring peristomes absent. Operculum and pseudoperculum absent. Radioles arranged in two semi-circles to a spire of up to 6 whorls, up to 320 per lobe (*P. superba*). Inter-radiolar membrane present. Branchial eyes may be present. Stylodes absent. Mouth palps present. 7 thoracic chaetigerous segments (however, see remarks). Collar trilobed, tonguelets absent. Thoracic membranes long and wide, with undulating edge, forming ventral apron across anterior abdominal segments. Collar chaetae limbate. *Apomatus* chaetae present. Thoracic and abdominal uncini rasp-shaped with approximately 30 teeth in profile, up to 6 rows of teeth above and continuing onto elongated rounded peg (Fig. 39A, C). Thoracic triangular depression absent. Abdominal chaetae sickle-shaped, with finely denticulate blades (Fig. 39B), may be retro-geniculate in some taxa. Achaetous anterior abdominal zone absent. Long posterior capillary chaetae present. Posterior glandular pad present.

Remarks. The genus *Protula* is the most problematic serpulid taxon and it has been pointed out that the phylogenetic basis for this genus is ill-defined (ten Hove 1984). The generic characters are based mainly on the negative characters, such as lack of operculum, lack of special collar chaetae and any characteristic ornamentation of the tubes. Because reliable species-level morphological characters are missing, species in the genus *Protula* have been described based on small differences in the shape of collar, number and arrangement of radioles, and even body and tube size. These differences may have been caused by varying state of preservation, variation in age, a different way of figuring and interpretation by the authors. Moreover, some species distinctions have been based on presumed differences in chaetation. For instance, Uchida (1978) relies heavily on literature data on absence or presence of *Apomatus* chaetae, a character used for generic distinction in his “subfamily Protulinae”. However, ten Hove & Pantus (1985) showed that *Apomatus* chaetae are extremely difficult to discern in the thick bundles of limbate chaetae, and if present occur at best in the chaetigers 5–7 in the Mediterranean *Protula tubularia sensu auct.* Within one population, specimens with and without *Apomatus* chaetae may occur, as well as specimens with or without thoracic uncini. Thus, the scanty literature data should be viewed with more caution than was done by Uchida (1978). For instance, his genus

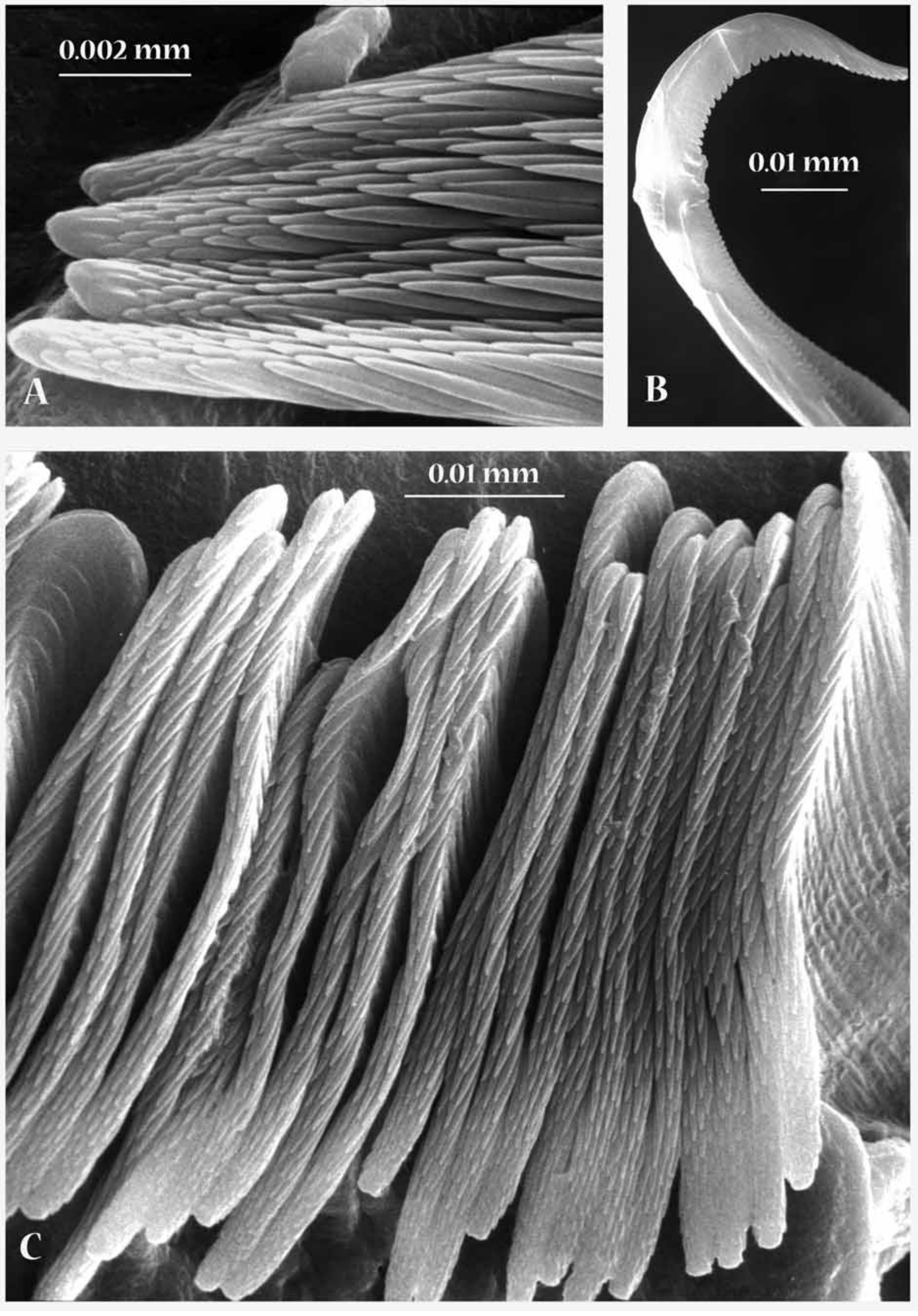

FIGURE 39. SEM micrographs of chaetae in *Protula tubularia*. France, Banyuls, ZMA V.Pol. 3816. A—thoracic uncini of 1st row, details of pegs, B—tip of anterior abdominal chaetae, C—thoracic uncini of 1st row.

Paraprotula was based on the absence of the character "capillary" chaetae in thoracic segments in literature descriptions of *Protula*. However, "capillary" chaetae do occur in all serpulid genera we observed, including *Protula*. A further difference according to Uchida would be the abdominal chaetae, sickle shaped in *Protula*, retro-geniculate ("with a notch at the base of the free margin") in *Paraprotula apomatoides*; however, this retro-geniculate chaetal type is known from *Protula balboensis* as well. Therefore we included his taxon *Paraprotula apomatoides* in the genus *Protula*. The number of 9 thoracic chaetigers, in our opinion, is insufficient to maintain a separate genus, *Salmacinopsis*, for the nominal taxon *setosa*, it would fit in the genus *Protula*.

A very necessary revision of the genus should be based upon a comparison of all available types and as well as a statistical study of variability and should be confirmed with molecular data. Some of the names given below as "valid" had been synonymised in the past, on the misconception that widespread distributions of polychaetes were very common.

1. *Protula alba* Benedict, 1887, West Indies; perhaps see *P. longiseta*
2. *Protula alberti* Fauvel, 1909, off Azores; bathyal
3. *Protula americana* McIntosh, 1885, Nova Scotia, Eastern Canada
4. *Protula antennata* Ehlers, 1887, off South Florida; bathyal; compare *P. longiseta*
5. *Protula apomatoides* (Uchida, 1978), Sabiura, South Japan
6. *Protula appendiculata* Schmarda, 1861, Jamaica; questionable
7. *Protula atypha* Bush, 1905, California, Hawaii; compare *P. superba*
8. *Protula balboensis* Monro, 1933, Gulf of Panama, Pacific Colombia, ?Brazil
9. *Protula bispiralis* (Savigny, 1820), widely distributed in the Indo-West Pacific, New Zealand; probably complex of species
10. *Protula diomedeae* Benedict, 1887, Eastern USA; shelf depths to bathyal; compare *P. submedia*
11. *Protula intestinum* (Lamarck, 1818), Mediterranean-Atlantic, southern U.K.
12. *Protula longiseta* Schmarda, 1861, West Indies; compare *P. alba* and *P. antennata*
13. *Protula lusitanica* McIntosh, 1885, off Portugal; bathyal; indeterminable, specimen lost
14. *Protula media* Stimpson, 1854, Eastern Canada, Arctic
15. *Protula pacifica* Pixell, 1912, West Canada, North Japan Sea
16. *Protula palliata* (Willey, 1905), Sri Lanka, Indo-West Pacific
17. ?*Protula setosa* (Bush, 1910), Bermuda Islands; the generic and specific status of *Salmacinopsis setosa* is uncertain, but most probably *Protula*
18. ?*Protula soofita* Ben-Eliahu, 1976, Gulf of Elat (= Gulf of Aqaba); generic attribution uncertain, shows affinities with *Vermiliopsis* as well
19. *Protula submedia* Augener, 1906, West Indies; bathyal; compare *P. diomedeae*
20. *Protula superba* Moore, 1909, Gulf of California, California; compare *P. atypha*
21. *Protula tubularia* (Montagu, 1803), England, Atlantic, questionably worldwide
22. *Protula tubularia anomala* Day, 1955, South Africa; probably a full species
23. *Protula tubularia caeca* Imajima, 1977, Ogasawara Islands, Japan; probably a full species.

35. *Pseudochitinopoma* Zibrowius, 1969a

(Fig. 40)

Type-species: *Hyalopomatopsis occidentalis* Bush, 1905
Number of species: 2

Tube white opaque, with longitudinal keel, sub-triangular or triangular in cross-section, with occasional scooped peristomes (brood-care?). Hyaline granular overlay may be present. Operculum inverse conical with

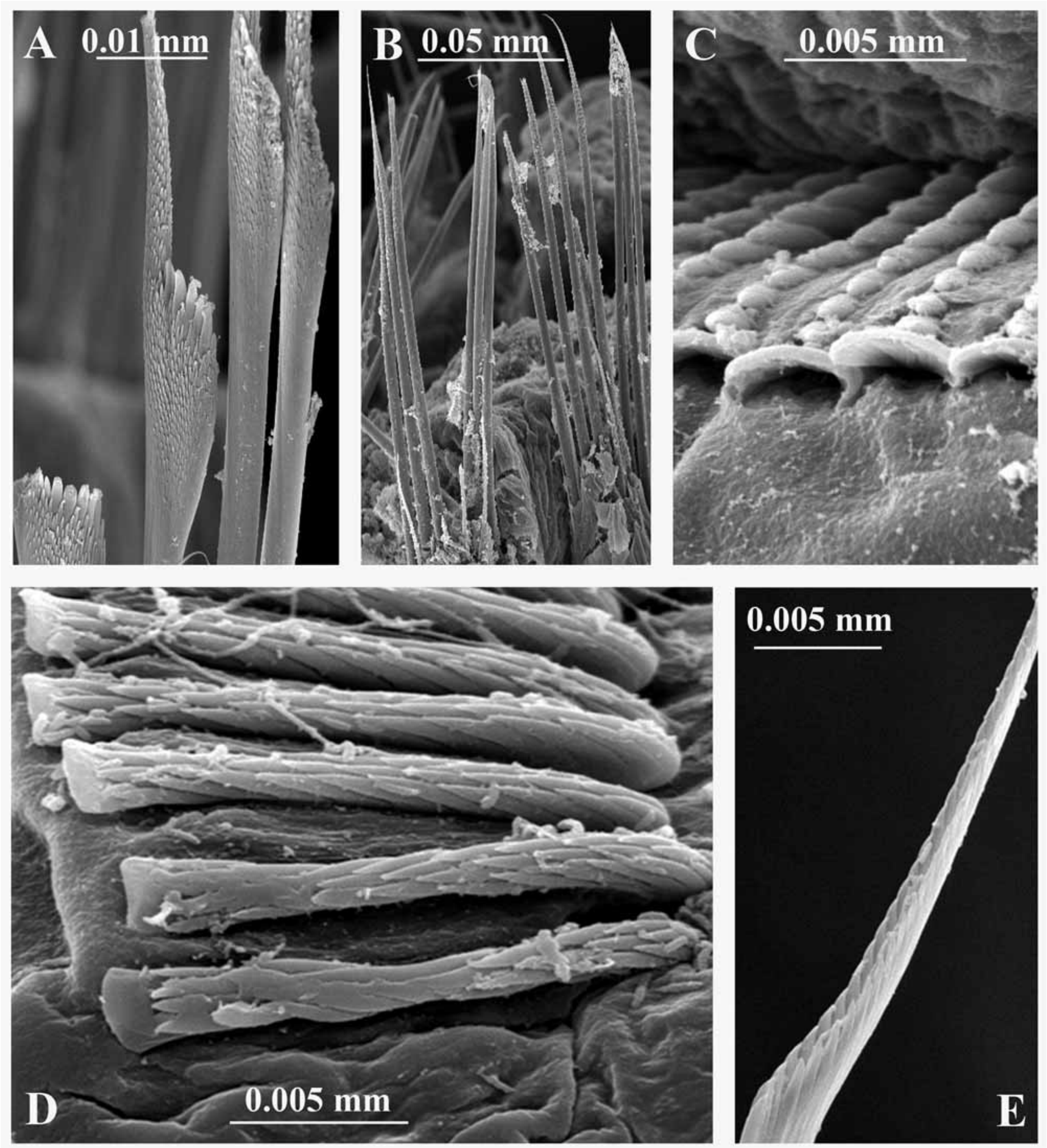

FIGURE 40. SEM micrographs of chaetae in *Pseudochitinopoma occidentalis*. Canada, British Columbia, Barkley Sound, legit T. Macdonald, det. E. Kupriyanova. A—fin-and-blade collar chaetae, B—thoracic chaetae, C—thoracic uncini, D—abdominal uncini, E—abdominal chaeta with a hollow tip.

distal chitinous shallow cap. Peduncle circular to rounded triangular in cross-section, about twice as wide as radiole, without wings or pinnules, separated from ampulla by constriction; inserted at base of left branchial lobe, in front of first radiole or almost midway between branchial lobes. Pseudoperculum absent. Radioles in semi-circles to short pectinate arrangement, with up to 10 radioles per lobe, inter-radiolar membrane absent. Branchial eyes absent. Mouth palps absent. 7 thoracic chaetigerous segments. Collar trilobed, tonguelets between median and latero-dorsal lobes absent. Thoracic membranes short, ending at the chaetiger 2. Collar chaetae fin-and-blade, with a distal limbate zone and a proximal wing not well separated (Fig. 40A), and limbate chaetae. *Apomatus* chaetae absent. Thoracic uncini saw-shaped, with about 12 teeth above gouged peg (Fig. 40C). Triangular depression absent. Abdominal chaetae hollow trumpet-shaped, narrow and smoothly bent, with long lateral tip (Fig. 40E). Abdominal uncini rasp-shaped, with 12–14 teeth in profile, 3–6 teeth in a row above gouge shaped peg (Fig. 40D). Achaetous anterior abdominal zone absent. Long posterior capillary chaetae and posterior glandular pad absent.

Remarks. Zibrowius (1969a) erected the genus *Pseudochitinopoma* for *Hyalopomatopsis occidentalis* Bush, 1905 to stress its superficial similarity to the genus *Chitinopoma*. He tabulated the differences between these two genera in the shape of anterior tooth of thoracic uncini, the structure of the special collar chaetae and abdominal chaetae, as well as the presence of *Apomatus* chaetae. However, morphologically, *Chitinopoma* appears to be closer to *Filogranula* than to *Pseudochitinopoma* (Kupriyanova & ten Hove in prep.), see remarks for *Filogranula*. Moreover, Kupriyanova *et al.* (2006) provided preliminary molecular evidence that *Pseudochitinopoma* and *Chitinopoma* are not closely related.

1. *Pseudochitinopoma occidentalis* (Bush, 1905), Prince William Sound, Eastern North Pacific
2. *Pseudochitinopoma pavimentata* Nishi, 1999, off Tateyana, Tokyo Bay, Formosa Strait, Japan.

36. *Pseudovermilia* Bush, 1907
(Fig. 41)

Type-species: *Spirobranchus occidentalis* McIntosh, 1885
Number of species: 10

Tube white (in one species with transverse brown bands), opaque, with longitudinal keel(s), sub-triangular or triangular in cross-section; generally with regular ornamentation of ribs, pits, or teeth. Double or single brooding scoops may be present. Granular overlay absent. Operculum consisting of bulbous ampulla terminated by chitinous endplate or cap, usually with spine(s). Pseudoperculum absent. Peduncle smooth, cylindrical, without wings, clearly separated from ampulla by constriction; inserted just below and between first and second radiole on one side. Arrangement of radioles pectinate, up to 17 per lobe, inter-radiolar membrane absent. Branchial eyes not known. Stylodes absent. Filiform mouth palps present. 7 thoracic chaetigerous segments. Collar with unpaired medio-ventral lobe and two latero-dorsal lobes continuous with short thoracic membranes, continuing to second thoracic chaetiger. Tonguelets between ventral and lateral collar lobes absent. Collar chaetae limbate. *Apomatus* chaetae present from second or third chaetiger onward (Fig. 41A). Thoracic uncini saw-shaped, with 9–17 teeth above gouged peg (seemingly bifurcate). Triangular depression absent. Abdominal chaetae flat narrow geniculate, with rounded teeth on edge (Fig. 41D). Abdominal uncini rasp-shaped with 9–13 teeth in profile view, up to 6 teeth in a row above gouged peg (Fig. 41B, C). Short achaetous anterior abdominal zone may be present. Long posterior capillary chaetae present. Posterior glandular pad may be present.

Remarks. The original diagnosis of Bush (1905) was emended by Zibrowius (1970b) and further emended by ten Hove (1975).

1. *Pseudovermilia babylonia* (Day, 1967), Vema Sea Mount, South Africa
2. *Pseudovermilia conchata* ten Hove, 1975, California, Baja California Sur; ? South China Sea
3. *Pseudovermilia fuscostriata* ten Hove, 1975, Bonaire, Netherlands Antilles; Caribbean
4. *Pseudovermilia harryi* Nogueira & Abbud, 2009, South Brazil
5. *Pseudovermilia holcopleura* ten Hove, 1975, Barbados, Caribbean; ?Tonga
6. *Pseudovermilia madracicola* ten Hove, 1989, Bonaire, Netherlands Antilles; Caribbean
7. *Pseudovermilia multispinosa* (Monro, 1933), Gorgona Island, Gulf of Panama; Florida to South Brazil
8. *Pseudovermilia occidentalis* (McIntosh, 1885), Bermuda, (sub)tropical Atlantic, ?Indo-West Pacific

9. *Pseudovermilia pacifica* Imajima, 1978, Izu Island, Indo-West Pacific
10. *Pseudovermilia xishaensis* Sun & Yang, 2001, Xisha Islands, South China Sea.

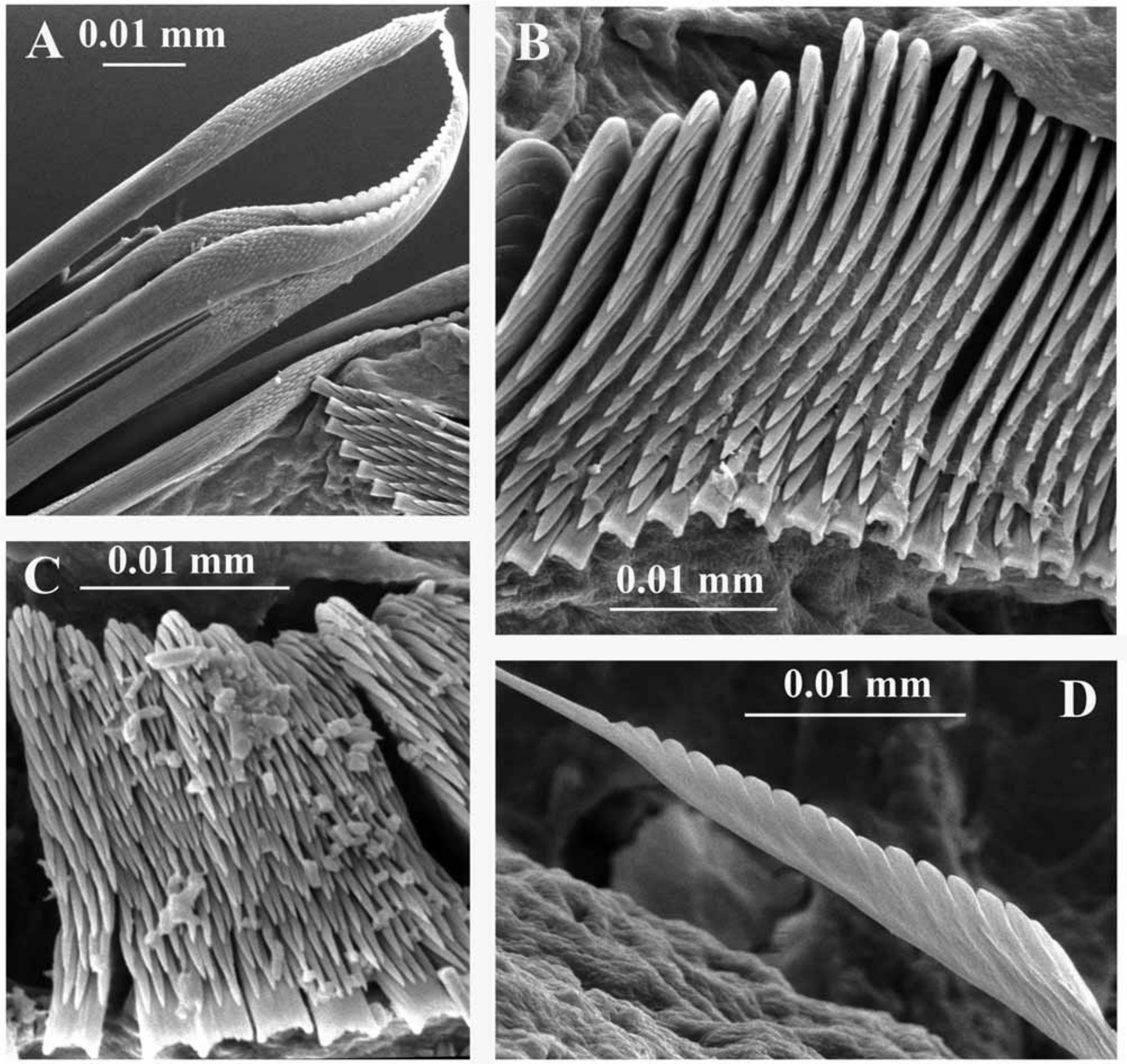

FIGURE 41. SEM micrographs of chaetae in *Pseudovermilia occidentalis*. Puerto Rico, off Isla Matei, 17°53' N, 60°59' W, 20-25 m, legit & det. H.A. ten Hove, ZMA V.Pol. 3138. A—*Apomatus* and "limbate" chaetae of 4th thoracic chaetiger, B—anterior abdominal uncini, C—posterior abdominal uncini, D—anterior abdominal chaeta.

37. *Pyrgopolon* de Montfort, 1808

(Fig. 42)

Type-species: *Pyrgopolon mosae* de Montfort, 1808 (a fossil taxon)
Number of (Recent) species: 3

Tube white or pinkish/red, opaque, generally with longitudinal ridges and/or transverse rims; tabulae may be present. Cross-section semi-circular to trapezoidal, erect part polygonal. A hyaline, granular overlay may be present. Operculum funnel-shaped, with numerous radial ridges on inner side; operculum and peduncle

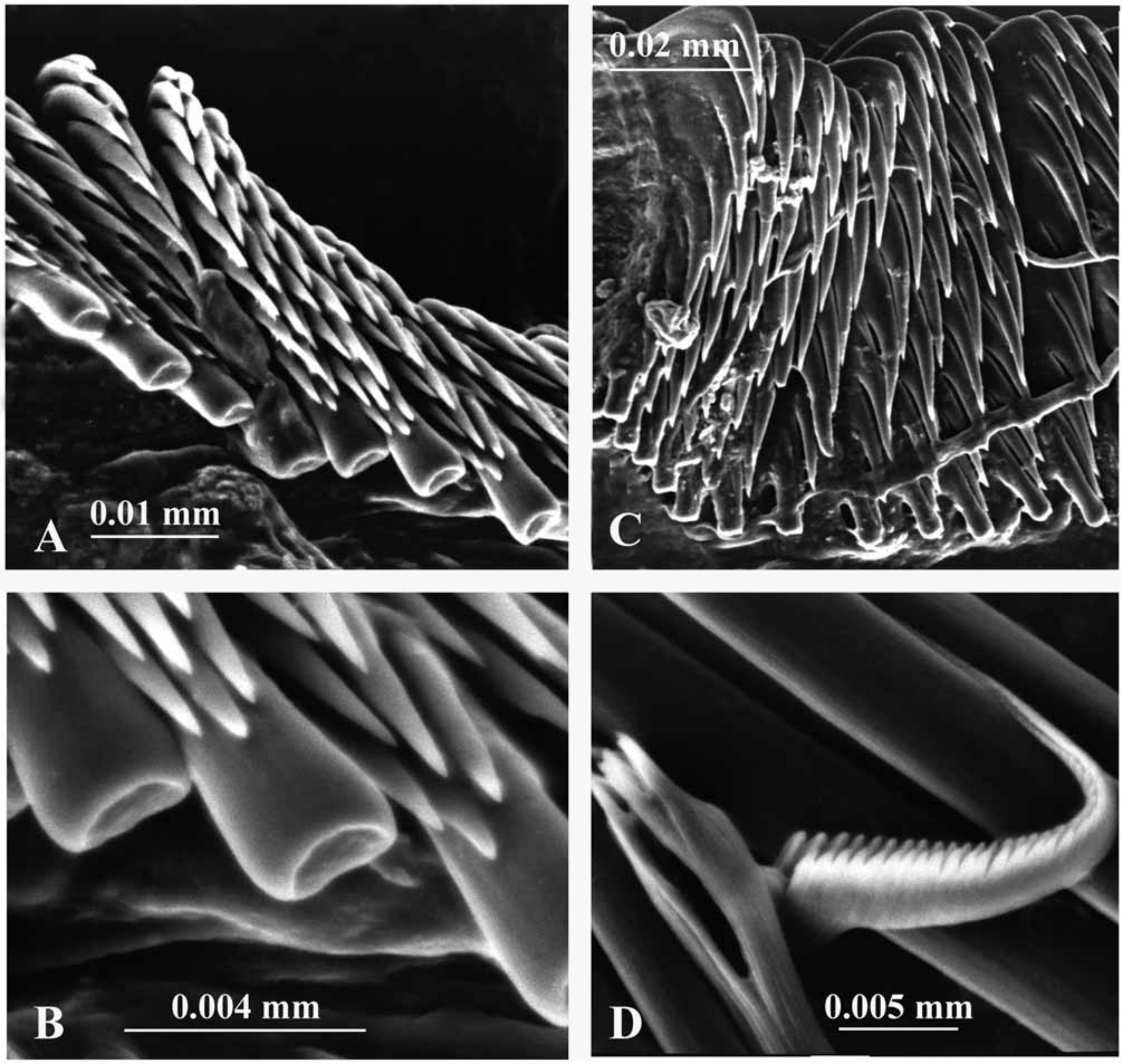

FIGURE 42. SEM micrographs of chaetae in *Pyrgopolon ctenactis*. The Netherlands Antilles, Bonaire, North of Witte Pan, legit H.A. ten Hove, Sta. 2117, ZMA V.Pol. 4969. A—middle abdominal uncini, B—same as A, detail of pegs, C—1st row of thoracic uncini, D—detail anterior abdominal chaeta with double row of teeth.

entirely calcified; with an extremely long calcareous talon embedded into the tissue of the peduncle that is inserted medially. Pseudoperculum absent. Radioles arranged in semi-circles, up to 38 per lobe, united by inter-radiolar membrane for 1/4–1/2 of their length, surrounding pair of well-developed mouth palps. Branchial eyes have not been observed but the brim of the skin around the operculum is scalloped, due to a circle of compound eyespots (Fig. 6B). Stylodes absent. 7 thoracic chaetigerous segments, though collar chaetae generally missing. Collar with large, bilobed ventral part; tonguelets between lateral and ventral collar lobes present. Thoracic membranes very wide anteriorly, narrowing at 3rd or 4th segment, and united ventrally on first abdominal segment forming an apron. Collar chaetae (if present) *Spirobranchus*-type and limbate. *Apomatus* chaetae absent. Thoracic uncini saw-shaped, with 8–9 teeth, anterior peg bluntly truncated, indented anteriorly (Fig. 42C). Thoracic tori almost touching ventrally in posterior thoracic segments of larger specimens, leaving a clear triangular depression. Abdominal chaetae almost capillary, with short hollow trumpet-shaped tips, smoothly bent and with double row of pointed teeth extending in long lateral spine (Fig.

42D). Abdominal uncini rasp-shaped with 8–11 teeth in profile, 2–3 teeth in a row (Fig. 42A, B). Achaetous anterior abdominal zone absent. Short capillary chaetae present posteriorly. Posterior glandular pad, if present, hardly visible.

Remarks. *Sclerostyla* Mörch, 1863 has been synonymized with *Pyrgopolon*, according to Jäger (1993, 2004) including the genera *Hamulus* and *Turbinia*, known only from the fossil record. This opinion is shared by Belokrys (1994). Fossils have been mentioned from the Maastrichtian (Cretaceous) from e.g., the Southern Netherlands, Northern Belgium, and the Crimean Mountains. The Recent distribution of the genus is the tropical seas of the Americas and is little known because the animals are difficult to find as their tubes are usually embedded into substrate. The distinguishing feature (autapomorphy) of the genus is the funnel-shaped calcareous operculum continuing into a calcareous peduncle (talon). Opercular talons, but shorter, are also known in *Pomatoleios* and *Neomicrorbis*. The bright red “glandular fields” around the brim of the operculum mentioned by ten Hove (1973 figs 32–33) in the meantime have been found to be compound eyespots (HAtH, SEM observations); ten Hove’s (1973) revision still remains the most comprehensive source of information about this genus.

1. *Pyrgopolon ctenactis* (Mörch, 1863), St. Thomas, Caribbean and tropical Pacific America
2. *Pyrgopolon differens* (Augener, 1922), Barbados, Shelf of Surinam
3. *Pyrgopolon semiannulatum* (ten Hove, 1973), Barbados.

38. *Rhodopsis* Bush, 1905
(Fig. 43)

Type-species: *Rhodopsis pusilla* Bush, 1905
Number of species: 2

Tube white, circular in cross-section, thin-walled, not increasing in diameter, distal part sometimes erect, unattached, with peristomes; granular overlay absent. Animals with tube diameter < 0.2 mm. Some tubes may have one or more unpaired, inverted brood-chambers associated with peristomial rings. Operculum pear-shaped, laterally compressed, usually with well-developed chitinous plate bearing spines. Opercular plate may be deeply infolded and sunk, angled, within the opercular ampulla, then with halves closely appressed; plate rarely flat and terminal. Rarely operculum a simple ampulla only. Peduncle smooth, cylindrical, without wings, separated from ampulla by constriction; inserted proximal to 1st radiole on one side. Pseudoperculum absent. Arrangement of radioles short pectinate, only 2–3 radioles per lobe. Inter-radiolar membrane absent. Branchial eyes not observed. Stylodes absent. Mouth palps present. 4–6 thoracic chaetigerous segments present. Collar (tri-)quadri-lobed. Thoracic membranes short, reaching 1st thoracic chaetiger. Collar chaetae absent. *Apomatus* chaetae present from second chaetiger onward. Thoracic and abdominal uncini rasp-shaped, with 6–8 teeth in a row in edge view and about 8 teeth in profile, anterior fang simple pointed (Fig. 43A, B). Triangular depression absent. Single capillary chaeta in middle abdominal chaetigers accompanied by single flat narrow geniculate chaeta with blunt teeth (Fig. 43C). Achaetous anterior abdominal zone long, followed by up to 15 chaetigers. Posterior capillary chaetae present (Fig. 43D). Posterior glandular pad not observed.

Remarks. This little known species was incompletely described by Bush (1905) from a tiny worm collected on corals off Bermuda, characterized by numerous irregular spines in chitinous opercular plate. The type material was lost. Ben-Eliahu & ten Hove (1989) designated the neotype and re-described the species in detail. They also referred the monotypic *Apomatolos* Uchida, 1978 to *Rhodopsis*.

1. *Rhodopsis pusilla* Bush, 1905, Bermuda, Caribbean, Mediterranean, Indo-West Pacific
2. *Rhodopsis simplex* (Uchida, 1978), Kushimoto, Japan.

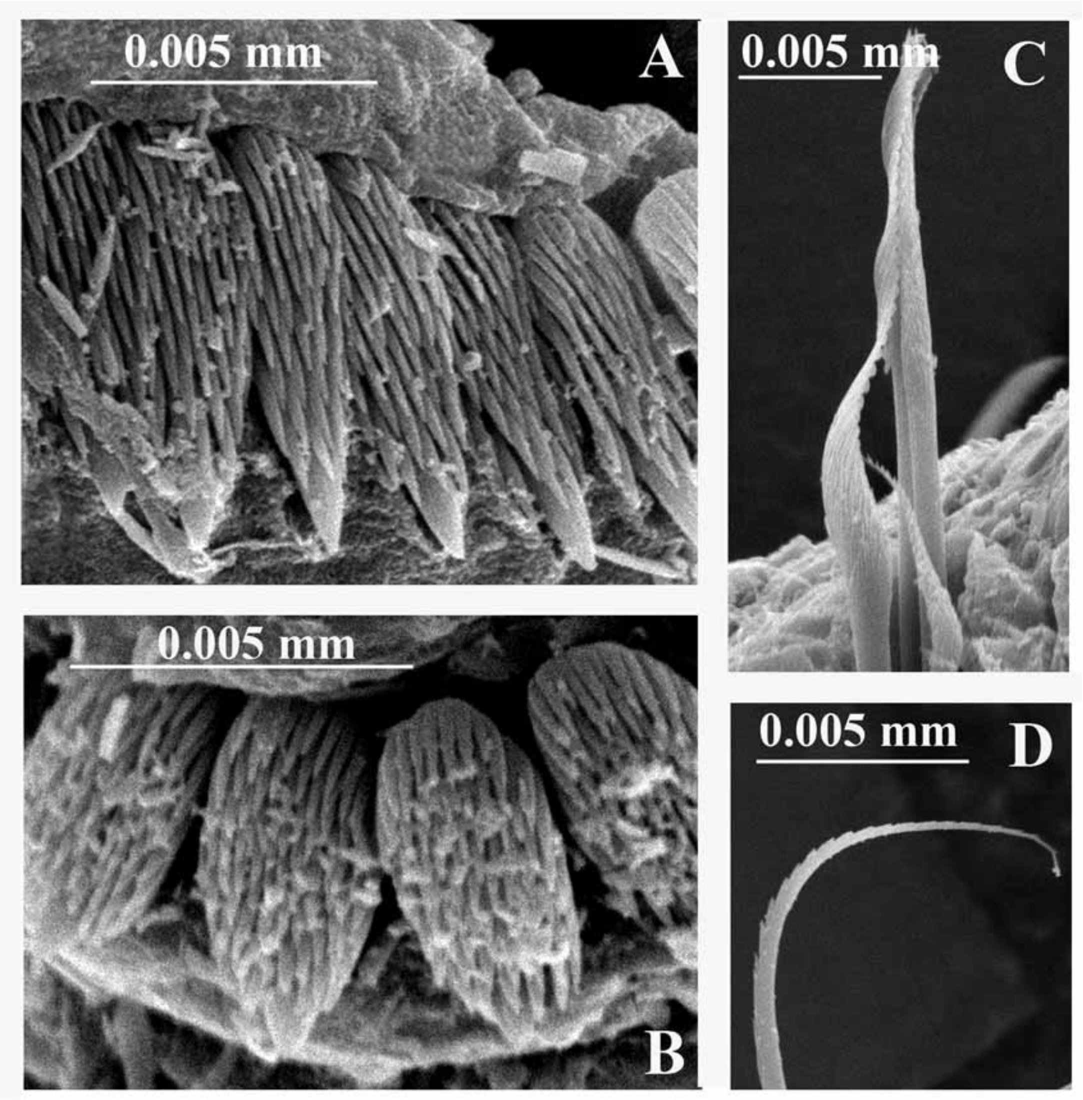

FIGURE 43. SEM micrographs of chaetae in *Rhodopsis pusilla*. Australia, Queensland, Lizard Island, legit & det. E. Kupriyanova. A—thoracic uncini, B—abdominal uncini, C—anterior abdominal chaetae, D—posterior abdominal chaeta.

39. *Salmacina* Claparède, 1870
(Fig. 44)

Type-species: *Salmacina incrustans* Claparède, 1870
Number of species: 11 (?10)

Worms form open aggregates consisting of large numbers of tiny whitish tubes, circular in cross-section without further diagnostic features; granular overlay absent. Operculum and pseudoperculum absent, sometimes swollen tips of radioles present. Radioles arranged in semi-circles, up to 4 radioles per lobe. Inter-radiolar membrane and stylodes absent. Branchial eyes may be present. Mouth palps present. 6–12 thoracic chaetigerous segments. Collar trilobed, tonguelets absent. Thoracic membranes forming apron. Collar chaetae fin-and-blade, distal blade well separated from fin, and limbate (Fig. 44A). *Apomatus* chaetae present (Fig. 44B). Thoracic uncini rasp-shaped, rectangular to wedge-shaped (triangular) in frontal view, with 2–12 teeth in a transverse row, with up to 10 teeth in profile view; anterior fang pointed (Fig. 44C). Thoracic triangular depression absent. Achaetous anterior abdominal zone present. Abdominal chaetae flat narrow geniculate with pointed teeth along edge (Fig. 44D). Uncini similar to thoracic ones, with more teeth in the transverse rows, and squarish peg. Long posterior capillary chaetae and posterior glandular pad absent.

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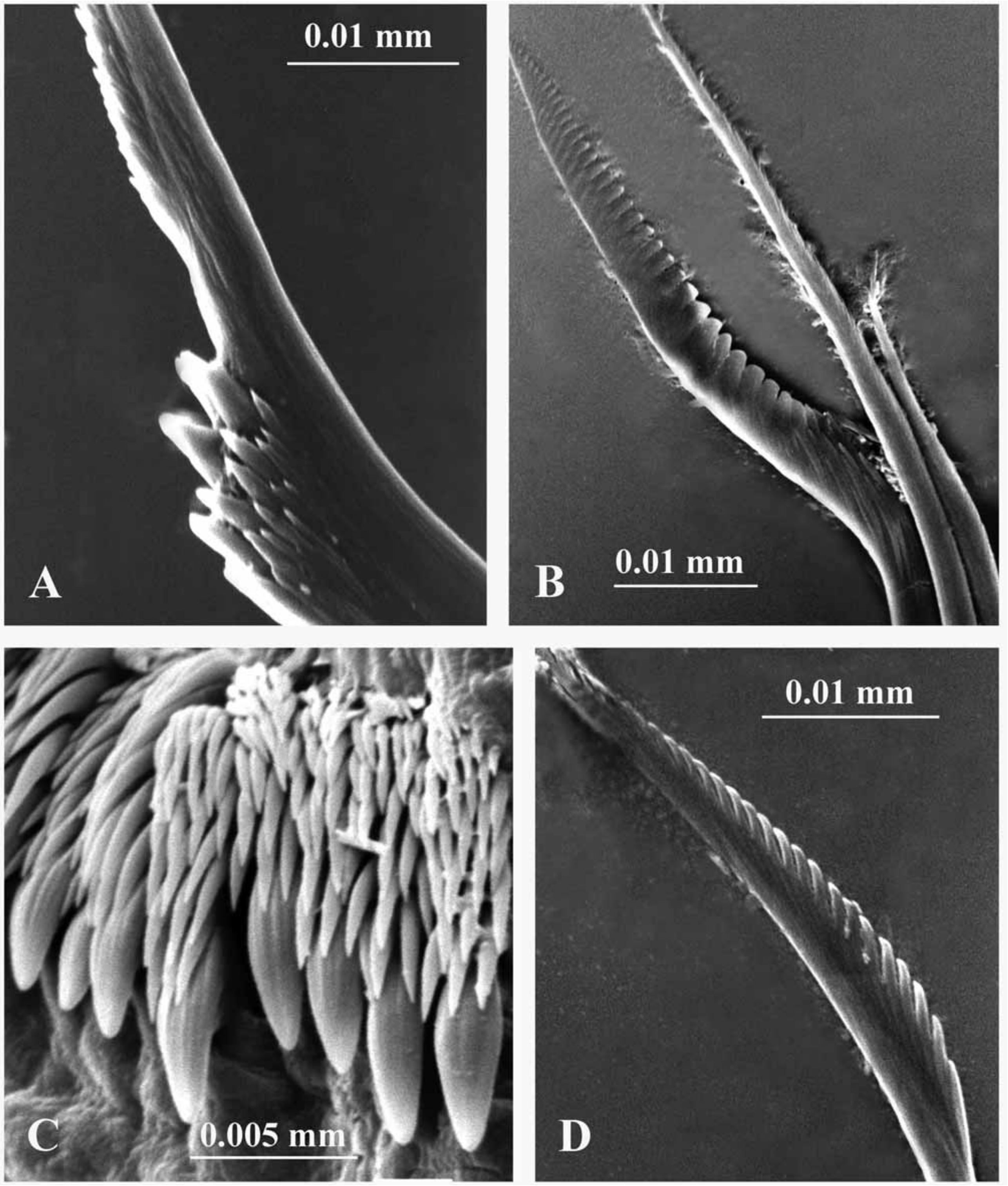

FIGURE 44. SEM micrographs of chaetae in *Salmacina incrustans*. Spain, Costa Brava, Playa de San Pol, legit & det. H.A. ten Hove, ZMA V.Pol. 3814. A—details of fin-and-blade collar chaeta, B—*Apomatus* and "capillary" chaetae of 7th thoracic chaetiger, C—uncini of 4th thoracic chaetiger, D—middle/posterior abdominal chaeta.

Remarks. See remarks for *Filograna,* and Nogueira & ten Hove (2000) for a discussion on the *Filograna*/*Salmacina* complex. The generic attribution of *Salmacina chilensis* is doubtful, probably it belongs in *Protis* or *Chitinopoma*.

1. *Salmacina amphidentata* Jones, 1962, Port Royal, Jamaica; Caribbean; ?South China, ?Japan
2. *Salmacina australis* Haswell, 1885, Port Jackson, Australia; temperate-cold Southern part of Australia, New Zealand; compare *S. dysteri*
3. *Salmacina ceciliae* Nogueira & ten Hove, 2000, Alcatrazes, Sao Paulo, Brazil
4. ?*Salmacina chilensis* Gallardo, 1969, off Punta Patache, Northern Chile; bathyal; generic attribution doubtful, *Protis* (or *Chitinopoma*)?
5. *Salmacina dysteri* (Huxley, 1855) Tenby, Bristol Channel, Wales; not "worldwide", but complex of species (Ben-Eliahu & ten Hove, in prep.)
6. *Salmacina dysteri falklandica* Monro, 1930, East Falkland Island; collar chaetae aberrant, generic attribution questionable
7. *Salmacina huxleyi* (Ehlers, 1887), Tortugas; Loggerhead Key, Florida; Bahamas, Caribbean
8. *Salmacina incrustans* Claparède, 1870, Gulf of Naples, Italy; "worldwide"; probably complex of species
9. *Salmacina piranga* (Grube, 1872), Estreite, Desterro, Brazil
10. *Salmacina setosa* Langerhans, 1884, Madeira; West off England; bathyal
11. *Salmacina tribranchiata* (Moore, 1923), Santa Rosa Island, South California; British Columbia, ?Japan.

40. *Semivermilia* ten Hove, 1975

(Fig. 45)

Type-species: *Vermiliopsis pomatostegoides* Zibrowius, 1969b
Number of species: 8

Tube triangular to sub-triangular in cross-section, keels present, otherwise variable; without flaring peristomes; granular overlay absent. Operculum inverse conical with chitinous endplate, more often a cap or series of diabolo-like plates; sometimes with terminal spine. Peduncle inserted as second radiole, cylindrical in cross-section; constriction present. Pseudoperculum absent. Radiolar arrangement short pectinately, up to 7 radioles per lobe. Inter-radiolar membrane absent. Branchial eyes may be present. Stylodes absent. Mouth palps present. (5-)7 thoracic chaetigerous segments. Collar tri- to penta-lobed, tonguelets absent. Thoracic membranes end at chaetiger 2. Collar chaetae limbate. *Apomatus* chaetae present in posterior thoracic segments (Fig. 45A). Thoracic uncini saw- to-rasp-shaped; with about 15 teeth in profile view, 1 tooth at the apex of the uncinus to 5 teeth in the row above the wide gouged peg (dental formula e.g., P:5:3:2:2:1:1:1:1:1:1:1:1:1:1; Fig. 45B). Triangular depression absent. Abdominal chaetae flat narrow geniculate, with rounded teeth on edge (Fig. 45D, E); abdominal uncini smaller than thoracic ones, entirely rasp-shaped, with about 13 teeth in profile view, up to 8 teeth in a row (Fig. 45C). Achaetous anterior abdominal zone, if present, very short. Long posterior capillary chaetae absent. Posterior glandular pad may be present.

Remarks. Within the group of *Vermiliopsis*-like genera, Zibrowius (1972b, 1973a, b) distinguished 4 genera (*Bathyvermilia*, *Metavermilia*, *Pseudovermilia*, and *Vermiliopsis*) and a group of aberrant species that he termed ?*Vermiliopsis*. Ten Hove (1975) erected a new genus *Semivermilia* for part of the latter (leaving the attribution of ?*Vermiliopsis glacialis* Monro, 1939, *V. notialis* Monro, 1930, and *V. eliasoni* Zibrowius, 1970a uncertain) and provided a table that allows distinguishing between the five genera above and *Neovermilia*.

In small specimens/species, such as *Semivermilia pomatostegoides* (this paper), and certainly *S. cribrata* (as *Josephella carenata* Zibrowius, 1968a: 176) the number of thoracic chaetigers may be 5 or 6. Contrary to statements in the literature that the peduncle is the first radiole (e.g., Zibrowius (1968a) for *S. crenata* as *Vermiliopsis undulata*, respectively Zibrowius (1969b) as *V. pomatostegoides*), we checked material (Canary Islands, SW coast of La Palma, Punta del Hombre, 8–12 m, May 29, 1980, CANCAP Sta. 4.D10, ZMA V.Pol. 4213), and found it to be the second normal radiole, or to be inserted just below the first and second normal radiole (thus probably migrated down from the second position). The character is difficult to observe, and may be subject to prejudice.

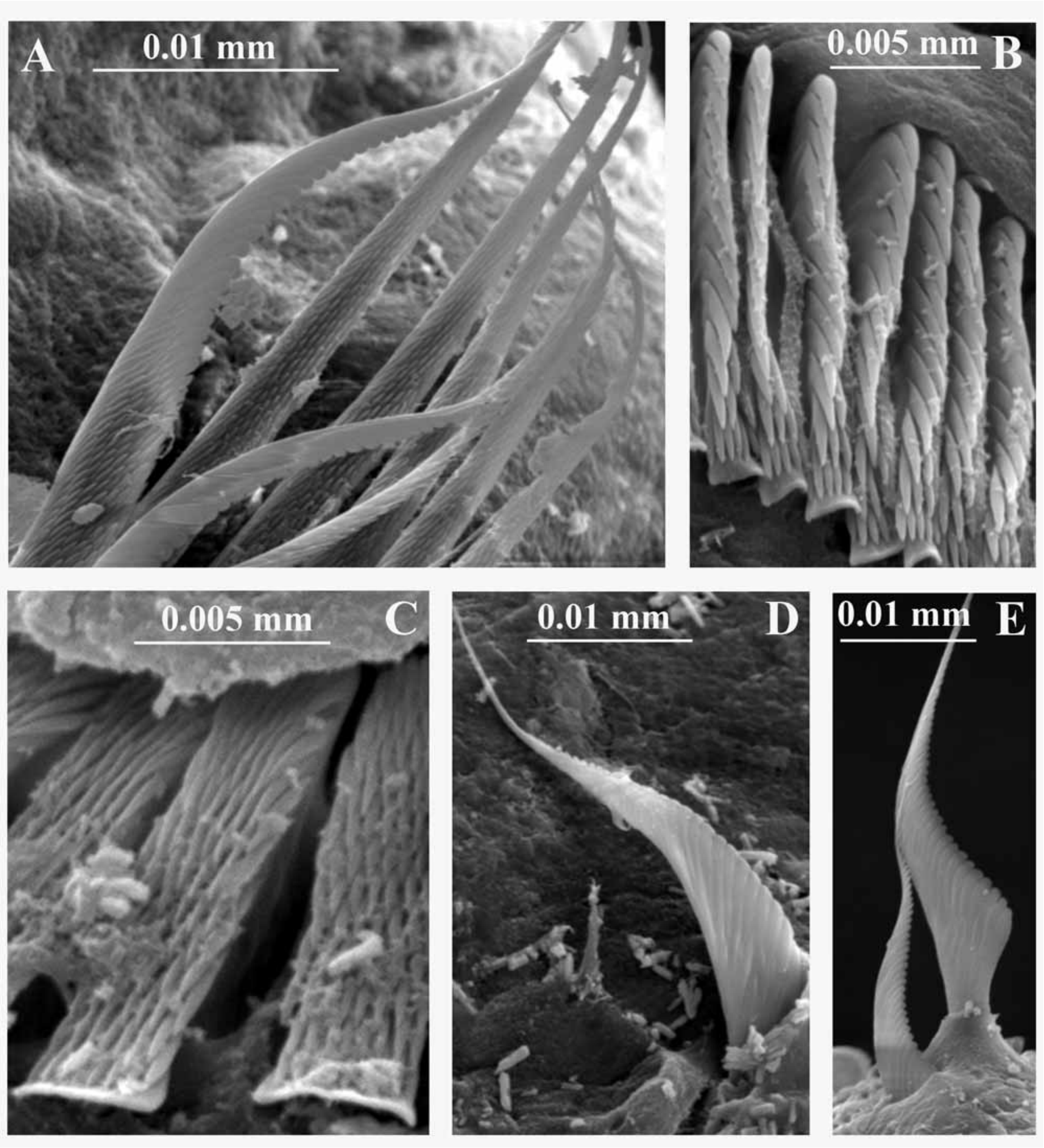

FIGURE 45. SEM micrographs of chaetae in *Semivermilia elliptica*. Japan, Shirohama, Seto Marine Biological Laboratory, marine aquarium, legit E. Kupriyanova, det. H.A. ten Hove, SAM E3664. A—4th thoracic bundle, B—uncini of 4th thoracic chaetiger, C—abdominal uncini, D—anterior abdominal chaeta, E—posterior abdominal chaetae.

1. *Semivermilia agglutinata* (Marenzeller, 1893), Benghazi, Mediterranean; bathyal
2. *Semivermilia crenata* (O.G. Costa, 1861), Mediterranean, Mauretania
3. *Semivermilia cribrata* (O.G. Costa, 1861), Mediterranean, Mauretania
4. *Semivermilia elliptica* Imajima, 1978, Izu Island, Japan
5. *Semivermilia parapomatostega* Wu & Chen, 1981a, South China Sea
6. *Semivermilia pomatostegoides* (Zibrowius, 1969b), Tripolis, Mediterranean, Central Atlantic, Indo-West Pacific

7. *Semivermilia torulosa* (delle Chiaje, 1822), Mediterranean, Mauretania
8. *Semivermilia uchidai* Imajima & ten Hove, 1986, Solomon Islands, ?Seychelles.

41. *Serpula* Linnaeus, 1758
(Fig. 46)

Type-species: *Serpula vermicularis* Linnaeus, 1767, designated by Heppell, 1963.
Number of species: 29

Tube white, pink, orange, or yellowish, opaque; (semi)circular to trapezoidal in cross-section, rarely polygonal; longitudinal keels, peristomes, a hyaline outer layer or granular overlay may be present. Operculum soft to cartilaginous, funnel shaped with crenulated edge (fused radii). Peduncle smooth, cylindrical, without wings; inserted just below and between first and second dorsal radiole on one side. In large specimens the insertion outside the normal radioles, seemingly the first radiole. Radioles arranged in semi-circles, up to 50 per lobe in larger species. Pseudoperculum and inter-radiolar membrane present. Branchial eyes may be present. Mouth palps present, though only to be observed with histological techniques (Orrhage, 1980). Stylodes absent. 7 (rarely up to 12) thoracic segments. Collar trilobed. Tonguelets absent, though wart-like protuberances may be present at base of cleft between ventral and latero-dorsal collar lobes. Thoracic membranes long, forming ventral apron across anterior abdominal segments. Collar chaetae bayonet-shaped (Fig. 46A) and limbate. *Apomatus* chaetae absent. Uncini saw-shaped, with approximately 5 teeth, anterior fang simple pointed (Fig. 46B). Thoracic triangular depression present. Abdominal chaetae flat trumpet-shaped with denticulate edge (Fig. 46D); uncini similar to thoracic ones, smaller, anteriorly saw-shaped but becoming rasp-shaped towards the pygidium, with up to 12 teeth in profile, up to 8 teeth in a row (Fig. 46C). Achaetous anterior abdominal zone absent. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. This is another serpulid genus that poses serious taxonomic difficulties. Although attribution of any given specimen to the genus *Serpula* is easy due to a very characteristic funnel-shaped operculum with rounded radii (but see below), the number of useful taxonomic characters within the genus is limited and their variability is not documented enough to ensure the validity of many described species (see discussion in ten Hove & Jansen-Jacobs 1984). Many of the original descriptions are very limited and vague, and the characters typical for all species of the genus (such as the presence of bayonet-chaetae and a funnel-shaped operculum) have been used for specific diagnoses. As a consequence, the nominal species *S. vermicularis* has been reported from Arctic to tropical conditions, neither ecologically nor biogeographically a likely distribution. Some nominal species were based on incomplete or juvenile specimens; juvenile *Hydroides* species, also characterised by an operculum with a single scalloped operculum only, were often attributed to *Serpula* too (ten Hove & Ben-Eliahu 2005). The most commonly used meristic character, the number of opercular radii, appears to have limited taxonomic value for discriminating species because of its population and ontogenetic variability (Kupriyanova 1999). A much-needed revision of the genus is currently under way (Pillai, pers. com.), and the list of “valid” species below is tentative only. Unpublished field notes by ten Hove state that some larger *Serpula* species (i.e. *S.* cf. *jukesii*) have thoracic membrane pockets similar to those found in *Floriprotis*, see also remarks to *Floriprotis*. Finally, a recent study by Kupriyanova *et al.* (2008) demonstrates that the traditional genus *Serpula* most probably is paraphyletic.

1. *Serpula cavernicola* Fassari & Mollica, 1991, Messina, Italy; compare *S. vermicularis*-complex
2. *Serpula columbiana* Johnson, 1901, incl. *S. nannoides* Chamberlin, 1919, Puget Sound, North-West coast of Americas

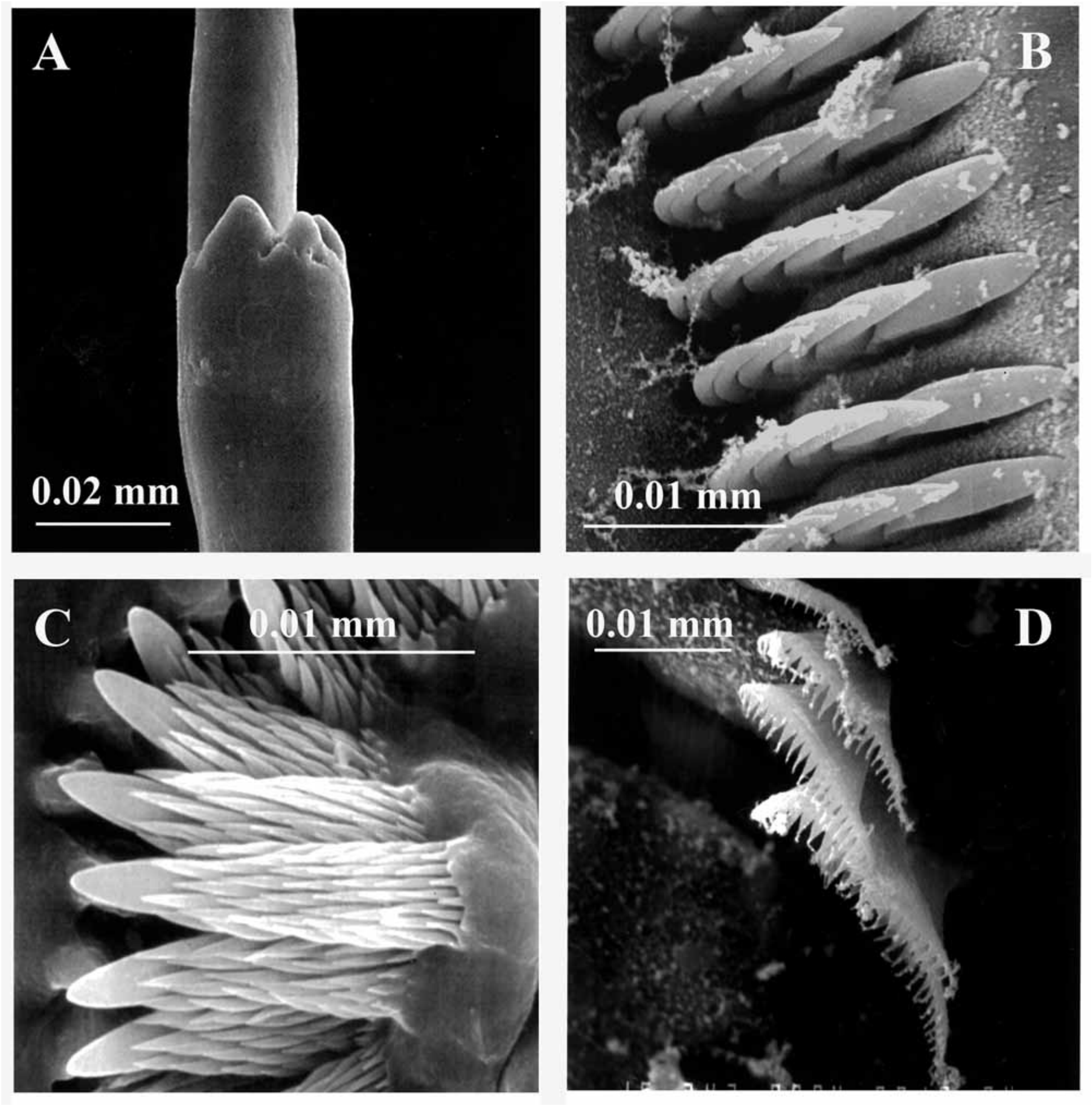

FIGURE 46. SEM micrographs of chaetae in *Serpula columbiana*. USA, Washington State, Puget Sound, San Juan Island, Friday Harbor Laboratories, legit & det. E. Kupriyanova. A—bayonet collar chaetae, B—thoracic uncini, C—posterior abdominal uncini, D—anterior abdominal flat trumpet-shaped chaetae.

3. *Serpula concharum* Langerhans, 1880, Madeira, Atlantic-Mediterranean; other records probably belong to different species
4. *Serpula crenata* (Ehlers, 1908), Zanzibar, Indo-West Pacific; bathyal; possibly incl. *S. sinica*
5. *Serpula granulosa* Marenzeller, 1885, Kagoshima and Enoshima, Japan, Indo-West Pacific
6. *Serpula hartmanae* Reish, 1968, Bikini, Indo-West Pacific
7. *Serpula indica* Parab & Gaikwad, 1989, India
8. *Serpula israelitica* Amoureux, 1976, Haifa, Levant Basin
9. *Serpula japonica* Imajima, 1979, Honshu, Japan; questionably Seychelles
10. *Serpula jukesii* Baird, 1865, Indo-West Pacific
11. *Serpula lobiancoi* Rioja, 1917, Mediterranean-Atlantic
12. *Serpula longituba* Imajima, 1979, Honshu, Japan

13. *Serpula maorica* (Benham, 1927), New Zealand; doubtful *fide* ten Hove & Jansen-Jacobs (1984: 151)
14. *Serpula nanhaiensis* (Sun & Yang, 2001), South China Sea
15. *Serpula narconensis* Baird, 1865, Narcon Island, Antarctica, subantarctic
16. *Serpula oshimae* Imajima & ten Hove, 1984, Indo-West Pacific
17. *Serpula pacifica* (Uchida, 1978), Sabiura, Japan; questionable *fide* ten Hove (1984: 103–104) and Pillai & ten Hove (1994: 40, 100)
18. *Serpula philippensis* McIntosh, 1885, Philippine Islands; bathyal; questionable
19. *Serpula planorbis* (Southward, 1963), Irish Sea; bathyal
20. *Serpula rubens* Straughan, 1967b, Queensland, New South Wales, Australia
21. *Serpula sinica* Wu & Chen, 1979 (in Wu, Sun & Chen 1979), South China Sea; possibly synonym of *S. crenata*
22. *Serpula tetratropia* Imajima & ten Hove, 1984, Palau and Caroline Island
23. *Serpula uschakovi* Kupriyanova, 1999, Gilderbrandt Island, Sea of Japan; Moneron, Sakhalin
24. *Serpula vasifera* Haswell, 1885, Port Jackson, New South Wales, Australia
25. *Serpula vermicularis* Linnaeus, 1767, Western Europe; and probably restricted to this area, not worldwide as reported
26. *Serpula vittata* Augener, 1914, Sharks Bay, Australia; Indo-West Pacific
27. *Serpula watsoni* Willey, 1905, Trincomalee, Sri Lanka; Indo-West Pacific
28. *Serpula willeyi* Pillai, 1971, Pearl Banks, Sri Lanka
29. *Serpula zelandica* Baird, 1865, New Zealand.

42. *Spiraserpula* Regenhardt, 1961

Type-species: *Spiraserpula spiraserpula* Regenhardt, 1961 (a fossil taxon)
Number of Recent species: 18

Tube variable in colour, from white to orange and mustard, or with pink lateral longitudinal stripes; opaque; circular to trapezoidal in cross-section, rarely with small peristomes. Rounded longitudinal keels may be present; hyaline granular overlay present. Tube with internal longitudinal keels or other structures (Fig. 7E) and/or rows of teeth. Operculum soft, funnel shaped, formed of fused radii, endplate absent. Operculum absent in some species. Peduncle smooth, cylindrical, without wings; it is formed from the second dorsal radiole on one side. Pseudoperculum present. Radioles arranged in semi-circles, up to 8 per lobe. Inter-radiolar membrane present. Branchial eyes may be present. Stylodes absent. Mouth palps absent. 5–14 thoracic chaetigerous segments. Collar trilobed, tonguelets absent. Thoracic membranes ending in mid-thorax. Collar chaetae bayonet-shaped and limbate. *Apomatus* chaetae absent. Thoracic uncini saw-shaped, with up to 7 teeth above anterior pointed fang. Thoracic triangular depression present. Abdominal chaetae flat trumpet-shaped with denticulate edge. Abdominal uncini similar to thoracic ones, smaller, anteriorly saw-shaped but becoming rasp-shaped towards the pygidium, with up to 8 teeth in profile, up to 7 teeth in a row. Achaetous anterior abdominal zone absent. Posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. The genus *Spiraserpula* Regenhardt, 1961 was previously known only from fossils. Its species are closely related to the genus *Serpula*. Pillai & ten Hove (1994) referred to the genus *Spiraserpula* those *Serpula* species that lack an apron and possess sharp ridges and spines on the inner walls (“internal tube structures”, ITS, Fig. 7E) of their tubes.

1. *Spiraserpula capeverdensis* Pillai & ten Hove, 1994, Sao Vicente, Cape Verde Islands, Central Atlantic
2. *Spiraserpula caribensis* Pillai & ten Hove, 1994, Curaçao, Netherlands Antilles, Caribbean, Florida, Pacific Panama
3. *Spiraserpula deltoides* Pillai & ten Hove, 1994, Sumba, Indonesia, Central Indo-West Pacific

4. *Spiraserpula discifera* Pillai & ten Hove, 1994, Sydney, New South Wales, Australia
5. *Spiraserpula iugoconvexa* Pillai & ten Hove, 1994, North-East Flores Sea, Indonesia, Central Indo-West Pacific
6. *Spiraserpula karpatensis* Pillai & ten Hove, 1994, Bonaire, Netherlands Antilles, Caribbean
7. *Spiraserpula lineatuba* (Straughan, 1967b), Sydney, New South Wales, Australia
8. *Spiraserpula massiliensis* (Zibrowius, 1968a), Marseille, France, Mediterranean, Eastern North Atlantic
9. *Spiraserpula minuta* (Straughan, 1967b), Port Douglas, Queensland, Australia, Indo-West Pacific
10. *Spiraserpula nudicrista* Pillai & ten Hove, 1994, Bonaire, Netherlands Antilles, Caribbean
11. *Spiraserpula paraypsilon* Pillai & ten Hove, 1994, Klein Bonaire, Netherlands Antilles, Caribbean
12. *Spiraserpula plaiae* Pillai & ten Hove, 1994, Curaçao, Netherlands Antilles, Caribbean
13. *Spiraserpula singularis* Pillai & ten Hove, 1994, Puerto Rico, Caribbean
14. *Spiraserpula snellii* Pillai & ten Hove, 1994, Taka Bone Rate, Indonesia, Indo-West Pacific
15. *Spiraserpula sumbensis* Pillai & ten Hove, 1994, Sumba, Indonesia, Central Indo-West Pacific
16. *Spiraserpula vasseuri* Pillai & ten Hove, 1994, Europa Island, the French Southern and Antarctic Lands, SW Indian Ocean
17. *Spiraserpula ypsilon* Pillai & ten Hove, 1994, Brava, Cape Verde Islands, Central Atlantic, Caribbean, Gulf of Mexico
18. *Spiraserpula zibrowii* Pillai & ten Hove, 1994, Curaçao, Netherlands Antilles, Caribbean.

43. *Spirobranchus* de Blainville, 1818

(Fig. 47)

Type-species: *Serpula gigantea* Pallas, 1766
Number of species: 20+

Tube colour white, blue, pink or salmon, inside and/or outside. Tube typically (sub)triangular in cross-section, with median keel, rarely (sub)circular. Granular overlay absent. Operculum with inverse conical to rather shallow ampulla, covered by calcified endplate, with or without group of spines, sometimes branching. Peduncle broad, thickly triangular in cross-section, with distal lateral wings; inserted at base of branchial crown just left of medial line (formed between first and second normal dorsal radiole on left side, see **Ontogeny of operculum and peduncle**, p. 15). above. Pseudoperculum absent. Operculum rarely lacking. Radioles may be arranged in a clear spiral of up to 8 whorls, but in most small species as well as in *Spirobranchus tetraceros* arranged in a circle. Up to 50–60 pairs of radioles in larger species. Inter-radiolar membrane present. Branchial eyes may be present; stylodes absent. Mouth palps present. 7 thoracic chaetigerous segments. Collar trilobed (exceptionally pentalobed). Tonguelets present. Thoracic membranes forming ventral apron across anterior abdominal segment. Collar chaetae bayonet-like, with numerous hair-like processes on its basal portion (*Spirobranchus* chaetae, Fig. 47A), and limbate. *Apomatus* chaetae absent. All uncini saw-shaped (9–25 teeth), incidentally with 2 teeth above peg (Fig. 47B); anterior peg blunt, clearly gouged underneath (Fig. 47C). Ventral ends of thoracic uncinigerous tori widely separated anteriorly, gradually approaching one another towards the end of thorax, thus leaving a triangular depression. Abdominal chaetae true trumpet-shaped, abruptly bent distally, with two rows of denticles separated by a hollow groove and forming long lateral spine (Fig. 47D). Achaetous anterior abdominal zone absent. Chaetae becoming increasingly longer posteriorly, but posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. Species of this genus commonly occur in subtropical and tropical waters, but their taxonomy is confused because of significant variability in the opercular morphology. The major difference between the genera *Pomatoceros, Pomatoleios* and *Spirobranchus* is in the collar chaetae that are absent in *Pomatoleios*, simple limbate in *Pomatoceros*, and special with a knob consisting of numerous hair-like teeth in *Spirobranchus*. However, collar chaetae are occasionally absent in *Pomatoceros* and *Spirobranchus* and present in juvenile *Pomatoleios*.

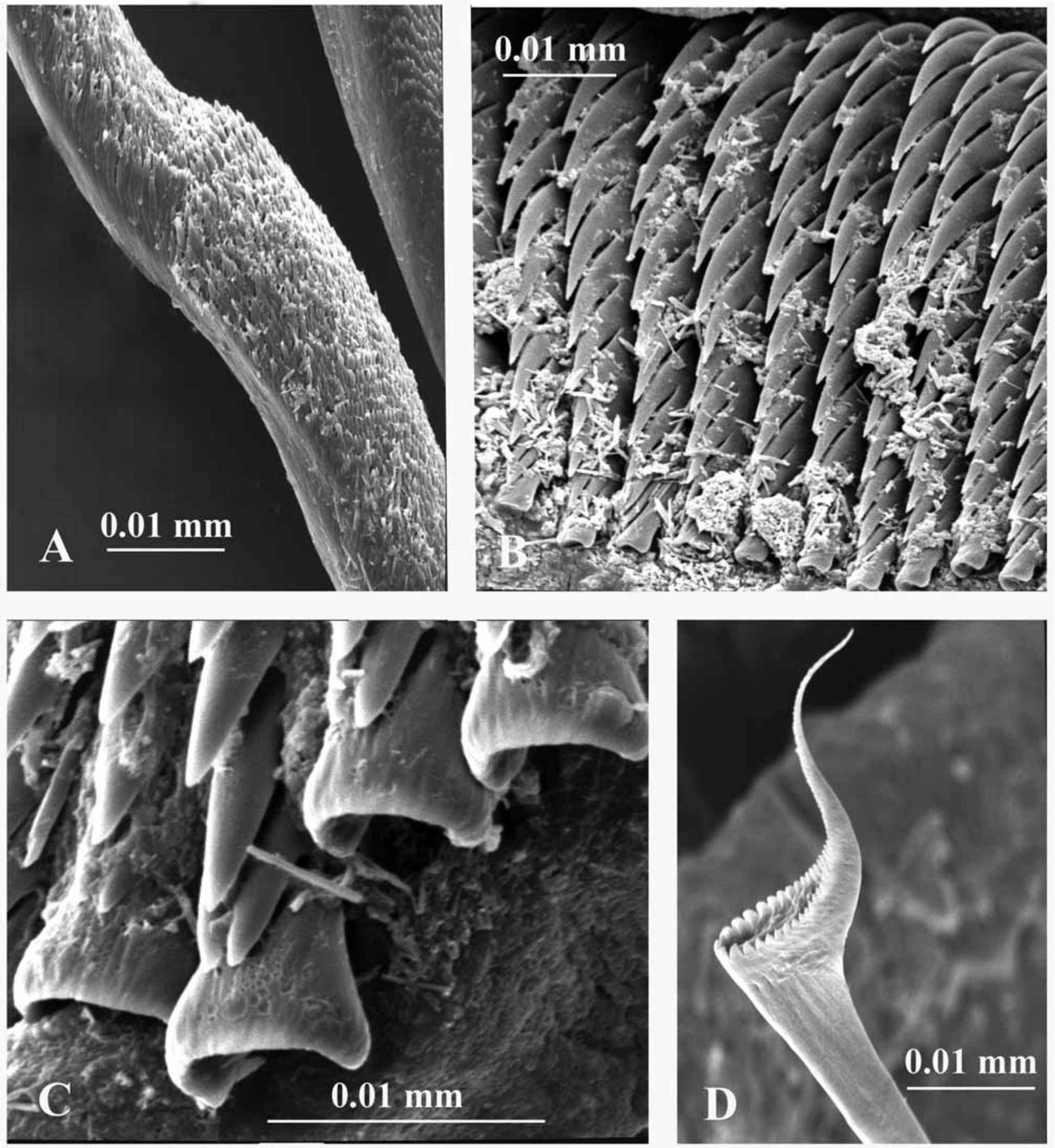

FIGURE 47. SEM micrographs of chaetae in *Spirobranchus giganteus*. The Netherlands Antilles, Curaçao, Piscadera Baai, outer bay, piling, iron & wooden poles, 0-1 m, legit P. Wagenaar Hummelinck, ZMA V.Pol. 3021. A—*Spirobranchus* collar chaeta, B—middle abdominal uncini, C—detail of gouged anterior peg of thoracic uncini, D—posterior abdominal chaeta with a hollow tip.

Although *Spirobranchus* has special collar chaetae, the range of chaetal forms in what traditionally is included in *Spirobranchus* is quite wide and includes species with almost simple limbate chaetae. Moreover, the sperm morphology of *Spirobranchus* and *Pomatoleios* is very similar (Nishi 1992a). Thus, although it is very likely that the three genera are synonymous, for the purpose of this review we have treated them as separate taxa.

A schematic presentation of the *Spirobranchus giganteus*-complex in its largest sense is given in Fiege & ten Hove (1999). According to Marsden (1992), the two morphotypes described by ten Hove (1970) as *S. polycerus* and *S. polycerus* var. *augeneri* are reproductively isolated, they thus probably should be regarded as full species.

1. *Spirobranchus carinifer* (Gray, 1843), New Zealand
2. *Spirobranchus corniculatus* (Grube, 1862), Java, Indonesia, Indo-West Pacific; part of a complex of species, often as *S. giganteus*
3. *Spirobranchus coronatus* Straughan, 1967b, Queensland, Fiji, Seychelles; compare *S. tetraceros*
4. *Spirobranchus corrugatus* Straughan, 1967a, Queensland, widely distributed in Indo-West Pacific
5. *Spirobranchus cruciger* (Grube, 1862), Red Sea, Indo-West Pacific; part of *S. corniculatus*-complex, often as *S. giganteus*
6. *Spirobranchus decoratus* Imajima, 1982, Palau Islands, widely distributed in Indo-West Pacific
7. *Spirobranchus eitzeni* Augener, 1918, Cameroon, tropical East Atlantic
8. *Spirobranchus gardineri* Pixell, 1913, North of Madagascar, widely distributed in Indo-West Pacific; maybe complex of 2 species
9. *Spirobranchus gaymardi* (Quatrefages, 1866), unknown type locality, widely distributed in Indo-West Pacific; part of *S. corniculatus*-complex
10. *Spirobranchus giganteus* (Pallas, 1766), West Indies, widely distributed in tropical Western Atlantic; not in Pacific, where specimens belong to the *S. corniculatus*-complex
11. *Spirobranchus incrassatus* Krøyer [in] Mörch, 1863, Puntarenas, Colombia, tropical American Pacific; part of *S. giganteus*-complex
12. *Spirobranchus latiscapus* (Marenzeller, 1885), South Japan, widely distributed in Indo-West Pacific
13. *Spirobranchus lima* (Grube, 1862), Adriatic Sea, Mediterranean; records from elsewhere are incorrect
14. *Spirobranchus maldivensis* Pixell, 1913, Maldive Islands, Indian Ocean, Central Indo-Pacific; compare *S. latiscapus*
15. *Spirobranchus nigranucha* (Fischli, 1903), Ternate, Indonesia, Indo-West Pacific
16. *Spirobranchus paumotanus* (Chamberlin, 1919), Paumotu Islands, widely distributed in Indo-West Pacific
17. *Spirobranchus polycerus* (Schmarda, 1861), Jamaica, Caribbean; probably “var. *augeneri* ten Hove, 1970” is a full species
18. *Spirobranchus polytrema* (Philippi, 1844), Mediterranean, Atlantic; records from Indo-West Pacific probably complex of species by themselves
19. *Spirobranchus spinosus* Moore, 1923, Sta. Barbara Isl., California; belongs to *S. giganteus*-complex
20. *Spirobranchus tetraceros* (Schmarda, 1861), New South Wales, circumtropical complex of species; Lessepsian migrant to Eastern Mediterranean and ship-transported to Senegal (Zibrowius, pers. comm.).

44. *Tanturia* Ben-Eliahu, 1976
(Fig. 48)

Type-species: *Tanturia zibrowii* Ben-Eliahu, 1976
Number of species: 1

No details of tube available, tiny specimens (0.9–2.17 mm in length) were extracted from vermetid reefs. Operculum globular to inverse conical, with flat to convex chitinous endplate. Peduncle smooth, without distal wings, inserted as second radiole; constriction absent. Pseudoperculum absent. Arrangement of radioles in semi-circles, up to 3 per lobe. Inter-radiolar membrane and stylodes absent, branchial eyes not observed. Mouth palps unknown. 5 thoracic chaetigerous segments. Collar trilobed, with 2 deep lateral incisions; tonguelets absent. Thoracic membranes unknown. Collar chaetae fin-and-blade, with well-separated distal limbate zone and proximal wing (Fig. 48A), and limbate. *Apomatus* chaetae present from 3rd chaetiger on (Fig. 48B). Thoracic uncini saw-to-rasp-shaped with about 15 teeth in profile, up to 4 teeth in a row above peg (dental formula P:4:3:3:1:2:1:1:1:1:1:1:1:1:1:1, Fig. 48C); peg bifurcate under compound microscope but blunt, almost trapezoidal in SEM. Triangular depression absent. Abdominal chaetae with flat triangular blades with blunt teeth (Fig. 48E). Abdominal uncini rasp-shaped, with 7 teeth in profile, up to 8 fine teeth in row above blunt apparently bifurcate (gouged?) anterior fang (Fig. 48D). Achaetous anterior abdominal zone present. Posterior capillary chaetae absent. Posterior glandular pad not observed.

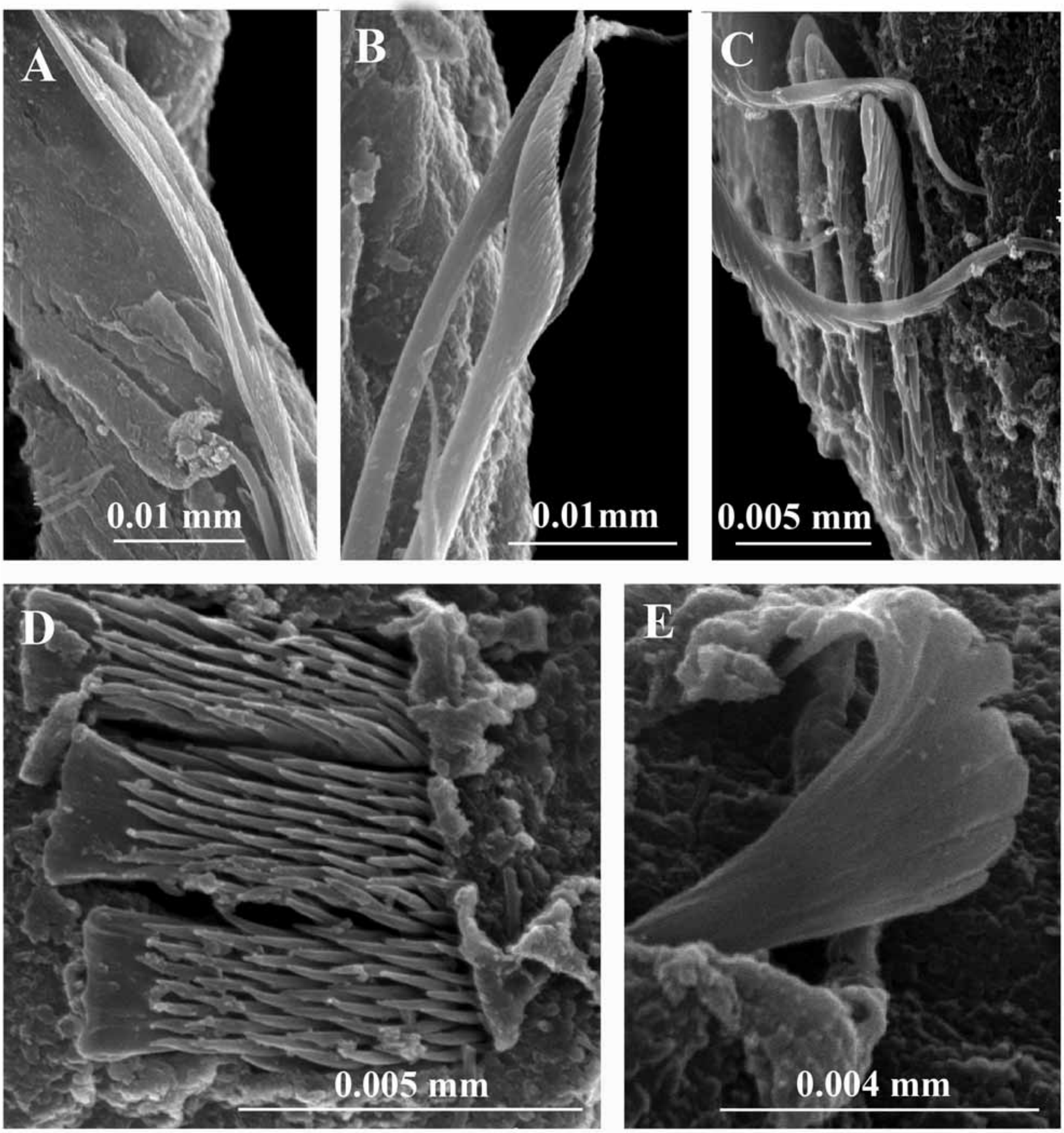

FIGURE 48. SEM micrographs of chaetae in *Tanturia zibrowii*. Israel, Gulf of Aqaba (Elat), Sinai coast, infauna of *Dendropoma*, paratype, exchange with HUJ, ZMA V.Pol. 4668. A—fin-and-blade collar chaetae, B—thoracic chaetae, C—thoracic uncini, D—abdominal uncini, E—abdominal chaeta.

Remarks. This monotypic genus is known only from 14 specimens (type series) collected from vermetid reefs near Elat, Red Sea.

Tanturia zibrowii Ben-Eliahu, 1976, Elat, Gulf of Aqaba, Sinai coast.

45. *Vermiliopsis* Saint-Joseph, 1894

(Fig. 49)

Type-species: *Vermilia multivaricosa* Mörch, 1863, new name for *Vermilia infundibulum sensu* Philippi, 1844
Number of species: 13 (-19)

Tube white, opaque, circular to sub-quadrangular in cross-section; generally with 3–7 longitudinal keels and peristomes. Granular overlay absent. Operculum an inverse conical ampulla, with flat to conical chitinous endplate, sometimes a partitioned cap. Peduncle wrinkled, cylindrical, separated from opercular ampulla by a constriction; without distal wings, but a proximal wing may be present. Peduncle ontogenetically formed from second dorsal radiole on one side, but in adults at base of branchial crown covering 3–6 normal radioles. Pseudoperculum generally absent (but present as under-developed second radiole in *V. striaticeps*). Radioles arranged in (semi-)circles, up to 20 per lobe. Inter-radiolar membrane absent. Branchial eyes (single pigmented ocelli) along dorsal side of rhachis. Stylodes absent. Mouth palps may be present. 7 thoracic chaetigerous segments present. Collar trilobed, tonguelets absent. Thoracic membranes short, continuing to 3rd–5th thoracic chaetiger. Collar chaetae limbate (Fig. 49A). *Apomatus* chaetae present. Thoracic uncini saw-shaped with up to 10–15 teeth above blunt indented peg (Fig. 49B, C). Triangular depression present. Abdominal chaetae flat narrow geniculate, with a more or less crenulated edge (rounded teeth) to the blade (Fig. 49E, F). Abdominal uncini rasp-shaped, anterior peg blunt (Fig. 49D). Achaetous anterior abdominal zone absent. Long posterior capillary chaetae present. Posterior glandular pad present.

Remarks. As early as 1776 a summary description of *Serpula infundibulum* was given by Martini (1776: 359, pl. 12 fig. 1). “Serpula Infundibulum. Tubulus vermicularis testaceus, in formâ infundibulorum triplici gyro convolutus”. From his description and figure it is impossible to decide whether this tube belongs to the genus *Serpula s.str.*, *Vermiliopsis s.str.*, or *Dasynema*. His material “a nice group of Eastindian seatophus [= tuff] obtained in an auction” apparently has been lost, it was not found in the musea in Copenhagen and Berlin where some of Martini's mollusks still are. The species was subsequently mentioned by various authors (e.g., Gmelin 1791, Lamarck 1818, Philippi 1844, Chenu 1842–55), generally miscited as *S. infundibulum* Gm., although Gmelin explicitly refers to Martini in his 13th edition of Systema Naturae.

Mörch (1863: 389) apparently thought that Philippi's (1844: 193) “*Vermilia infundibulum* Gm.” was not the same as Martini's species, since he proposed a new name *Vermilia multivaricosa* Mörch for Philippi's and other Mediterranean records of this nominal species. Unfortunately Mörch does not give reasons why, and except for a listing as extant species (p. 453) *Serpula infundibulum* Martini is not discussed further by him, though he reidentified some other “*Serpula infundibulum*” as vermetid or probable *Hydroides* species. Although *Vermilia multivaricosa* has been used in the literature about 20 times, the great majority (150 records) of the authors still used the name *Vermiliopsis infundibulum*, generally attributed to Philippi (1844), probably to indicate that they wanted to confine the name to Mediterranean-Lusitanian material.

Saint-Joseph (1894: 262) erected a new genus *Vermiliopsis* to contain a number of *Vermilia* species, the first he included was *Vermilia multivaricosa* Mörch, 1863. This species was subsequently formally designated as type species of the genus *Vermiliopsis* by Bush (1905: 223), in line with Saint-Joseph's intentions.

Many species included in *Vermiliopsis* by various authors, catalogued by Hartman (1959, 608–609), in the meantime have been referred to the above mentioned genera *Metavermilia*, *Bathyvermilia*, *Pseudovermilia*, *Semivermilia*, and *Neovermilia* by Zibrowius (1971b, 1973a) and ten Hove (1975). The traditional “*Vermiliopsis infundibulum* Philippi” from the Mediterranean as for instance in Fauvel (1927: 362–363) and

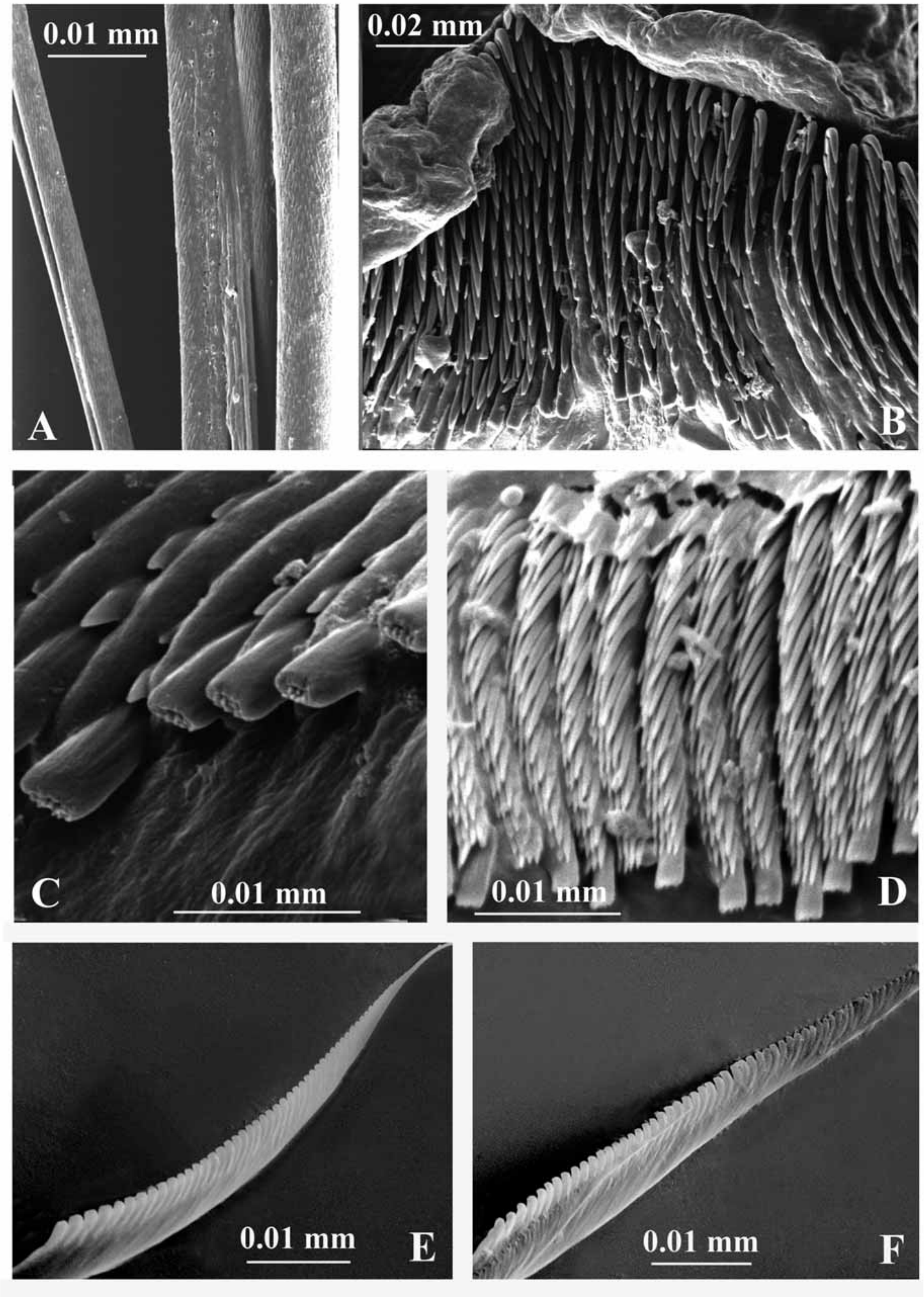

FIGURE 49. SEM micrographs of chaetae in *Vermiliopsis*. *V. infundibulum*. France, Marseille, legit & det. H. Zibrowius. ZMA V.Pol. 3041. A—"limbate" collar chaetae of two sizes, B—1st row of thoracic uncini, C—uncini of 4th thoracic chaetiger, details of blunt indented pegs, D—posterior abdominal uncini. *Vermiliopsis* sp., Cayman Islands, Little Cayman, legit Paul Humann, det. T. Perkins and H.A. ten Hove, ZMA V.Pol. 3807, E—anterior abdominal chaeta, F—middle abdominal chaeta.

Zibrowius (1968a: 121–124) was found to contain two different species "*Vermiliopsis infundibulum* Philippi *s.str.*" and *Vermiliopsis striaticeps* Grube, 1862 (Zibrowius 1973b: 44–45, ten Hove 1975: 57–58; Bianchi 1981: 74–75). Apparently both the genus *Vermiliopsis* and the species *infundibulum* are ill-defined, and designation of a neotype is unavoidable. The binomen *Vermiliopsis infundibulum* generally has been used for Mediterranean-Lusitanian forms, and only rarely for Indo-Pacific forms which normally are identified as *Vermiliopsis glandigera* Gravier, 1906 or *Vermilia/Vermiliopsis pygidialis* Willey, 1905. The origin of Martini's specimen is ill defined at least, maybe even doubtful (obtained in an auction). In view of the Preamble of the International Code of Nomenclature, the object of it being to promote stability, it appears fitting to choose a neotype from the Mediterranean to preserve a well known name. This, however, should be done in the context of a much-needed revision of the problematic genus, and falls outside the scope of present account.

According to Zibrowius (1973a), *Vermiliopsis sensu stricto* is characterized by a peduncle formed from the first dorsal radiole. On closer inspection (by us) it appeared to be derived from the second, covering radioles 1–4. There is one species, *V. labiata*, where the distal chitinous plate of the operculum is reinforced with calcareous matter like a coral-theca.

The attribution of the taxa *Vermiliopsis* (?) *eliasoni*, *glacialis*, and *notialis* to this genus has been questioned by Zibrowius (1968b, 1970a). *V. prampramiana*, from the Gold Coast (Africa), is regarded to be undeterminable by Zibrowius (1973b), however, see remarks *Filogranella*.

1. *Vermiliopsis annulata* (Schmarda, 1861), Jamaica, Caribbean; complex of at least 2 species, with the next taxon
2. *Vermiliopsis* cf. *annulata sensu* ten Hove & San Martín (1995), Caribbean; see above
3. ? *Vermiliopsis eliasoni* Zibrowius, 1970a, Banc Joséphine, Central Atlantic; generic attribution uncertain
4. ? *Vermiliopsis glacialis* Monro, 1939, Antarctic; bathyal; generic attribution uncertain
5. *Vermiliopsis glandigerus* Gravier, 1906, Red Sea, Indo-West Pacific; part of complex with *V. pygidialis*, *V. infundibulum*
6. *Vermiliopsis infundibulum* (Philippi, 1844), Mediterranean, North Atlantic; part of complex with *V. pygidialis*, *V. glandigerus*
7. *Vermiliopsis labiata* (Costa, 1861), Mediterranean, tropical Atlantic, Indo-West Pacific
8. *Vermiliopsis leptochaeta* Pillai, 1971, Sri Lanka; part of complex with *V. pygidialis, V. glandigerus*
9. ? *Vermiliopsis longiseta* (Bush, 1910), Bermuda Islands; questionable
10. ? *Vermiliopsis minuta* Straughan, 1967a, Heron Island, Queensland; doubtful, maybe composite
11. *Vermiliopsis monodiscus* Zibrowius, 1968c, Mediterranean, North Atlantic
12. *Vermiliopsis multiannulata* (Moore, 1923), South California to the Galapagos; part of complex with *V. glandigerus*, *V. infundibulum*
13. ? *Vermiliopsis notialis* Monro, 1930, South Georgia, (sub)antarctic; generic attribution uncertain
14. ? *Vermiliopsis producta* (Benham, 1927), New Zealand; status uncertain
15. *Vermiliopsis pygidialis* (Willey, 1905), Sri Lanka, Indo-West Pacific; part of complex with *V. glandigerus, V. infundibulum*
16. *Vermiliopsis spirorbis* (Langerhans, 1884), Madeira; part of *V. infundibulum*-complex
17. *Vermiliopsis striaticeps* (Grube, 1862), Mediterranean, Atlantic
18. *Vermiliopsis torquata* Treadwell, 1943, Hawaiian Islands; part of complex with *V. glandigerus*, *V. infundibulum*
19. *Vermiliopsis zibrowii* Nogueira & Abbud, 2009, South Brazil.

46. ***Vitreotubus*** **Zibrowius, 1979b**
(Fig. 50)

Type-species: *Vitreotubus digeronimoi* Zibrowius, 1979b
Number of species: 1

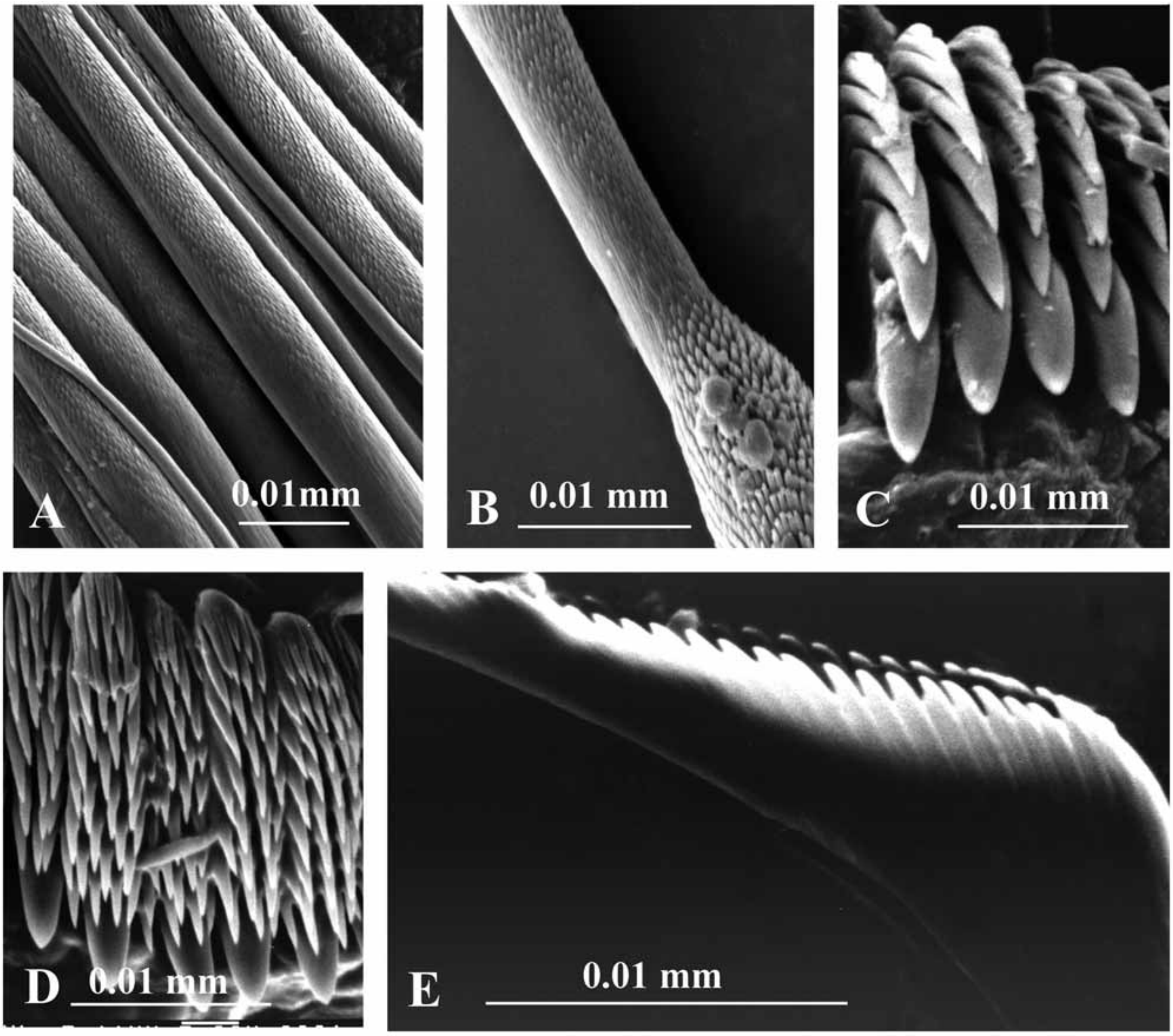

FIGURE 50. SEM micrographs of chaetae in *Vitreotubus digeronimoi*. Indian Ocean, East Amsterdam Island, 37°47.20' N, 77°38.98' E, 1680-940 m, R/V "*Marion Dufresne*" cruise MD 50, don. & det. Zibrowius, ZMA V.Pol. 3907. A—chaetae of 7th thoracic bundle, two sizes, B—*Spirobranchus* collar chaeta, C—middle abdominal uncini, D—posterior abdominal uncini, E—abdominal chaeta with a hollow tip.

Tube entirely vitreous, more or less quadrangular in cross-section by its two ample undulating lateral keels, and with a dorsal row of teeth. Granular overlay absent. Operculum inverse conical with chitinous diabolo-like endplate. Peduncle smooth, cylindrical, merging gradually into operculum, without wings, inserted as first radiole (at base of left branchial lobe, in line with first radiole). Pseudoperculum absent. Arrangement of radioles short pectinate, up to 11 per lobe. Inter-radiolar membrane and stylodes absent. Branchial eyes not observed. Mouth palps present. 7 thoracic chaetigerous segments. Collar trilobed. Medial lobe of collar with scalloped edge and lateral projections, separated from lateral lobes by deep incision (tonguelets absent), latter continuous with thoracic membranes extending all along the thorax, but narrow in the posterior segments,

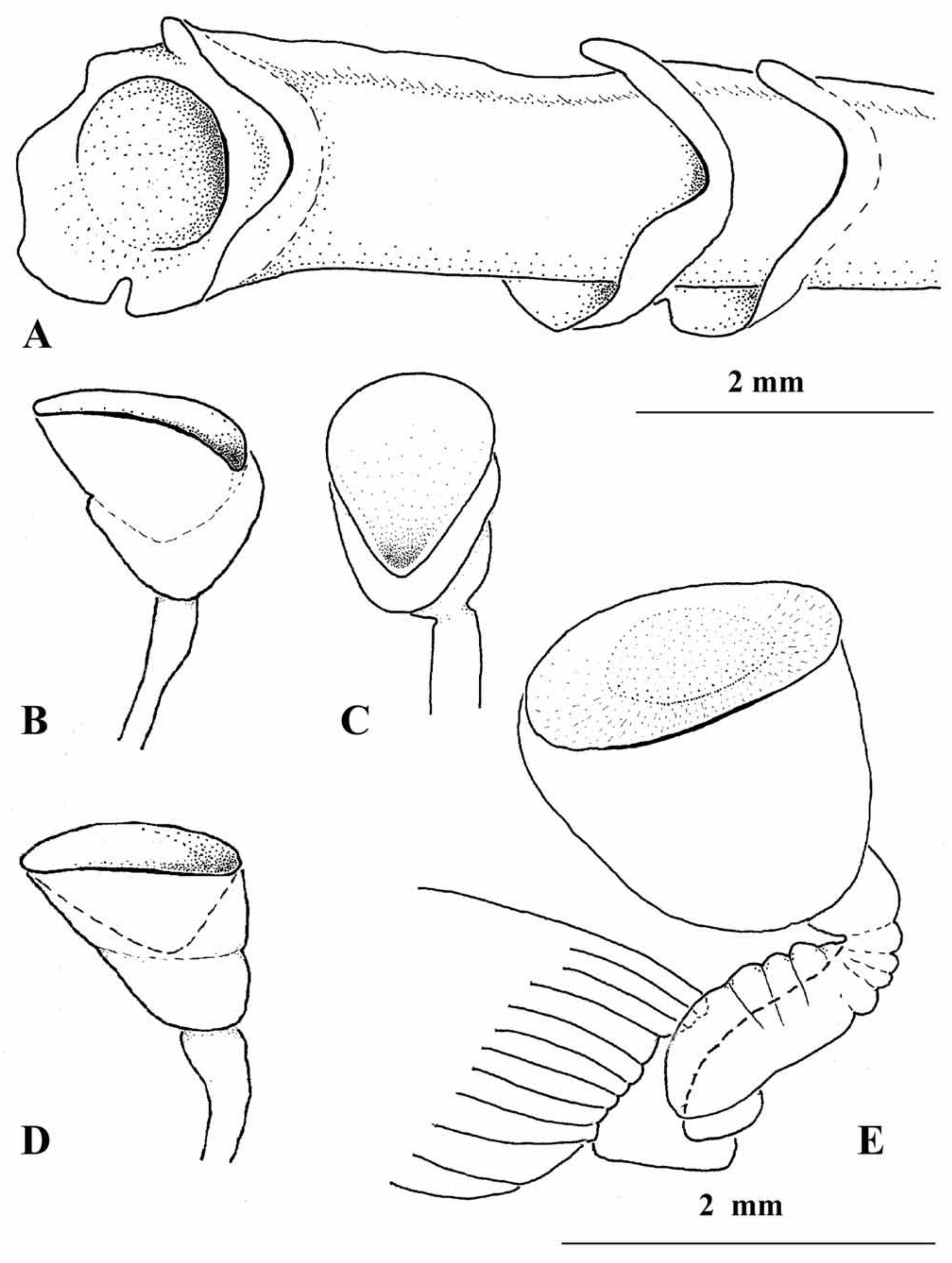

FIGURE 51. Drawings of serpulids redescribed herein. *Chitinopomoides wilsoni*, USNM 51505. A—tube, B–D—opercula, B–C—lateral and dorsal view of same specimen, D—lateral view of second specimen. *Paumotella takemoana*, holotype. E—lateral view of operculum, peduncle and its insertion.

forming ventral apron. Collar chaetae *Spirobranchus*-type (Fig. 50B) and simple limbate. *Apomatus* chaetae absent. Thoracic uncini saw-shaped with 6–7 teeth above pointed fang. Triangular depression present. Abdominal chaetae true trumpet-shaped, with two rows of pointed teeth bordering hollow groove and extended into a long lateral spine (Fig. 50E). Abdominal uncini saw-shaped with about 6 teeth anteriorly (Fig. 50C), rasp-shaped with about 10 teeth in profile, 3–4 teeth in a row posteriorly (Fig. 50D). Achaetous anterior abdominal zone absent. Posterior capillary chaetae absent, but geniculate chaetae long at the end of abdomen. Posterior glandular pad absent.

Remarks. The monotypic genus was originally described from fossil records and Recent material from the bathyal zone of the Azores and the Indian Ocean (Zibrowius, 1979b), more recent records are given by ten Hove (1994). It has a very characteristically shaped transparent tube.

Vitreotubus digeromimoi Zibrowius, 1979b, Central Atlantic, Indian Ocean; bathyal.

Invalid genera (as Serpulid)

Actinocerus (error pro *–ras* Bronn, 1835) Quatrefages, 1866 Mollusca*
Amphiserpula Uchida, 1978 see *Serpula*
Anatomus Montfort, 1810 not spirorbin but Mollusca: Scissurellidae
Anisomelus Templeton, 1835 indeterminable, depositfeeding, not serpulid
Antalium not Garsault, 1764 (Mollusca), *sensu* Guettard, 1770 see *Serpula*
Apomatolos Uchida, 1978 see *Rhodopsis*
Apomatopsis Saint-Joseph, 1894 see *Apomatus*
Bonhourella Gravier, 1905 see *Ditrupa gracillima* Grube, 1878
Bunodus Guettard, 1770 (Mollusca), erroneously mentioned as synonym of *Protula*
Calcareopomatus Straughan, 1967a see *Neovermilia*
Clymene Oken, 1815 see *Hydroides* and *Filograna*
Codonytes not delle Chiaje, 1828 (Bryozoa), *sensu* de Quatrefages, 1866 see *Hydroides*
Conchoserpula Blainville, 1818 erected for *Serpula triquetra* Linnaeus, see *Pomatoceros*
Conopomatus Pillai, 1960 see *Spirobranchus*
Crinoserpula Uchida, 1978 see *Serpula*
Crosslandiella Monro, 1933 see *Pseudovermilia*
Cymospira Blainville, 1828 see *Spirobranchus* and *Pomatostegus*
Cystopomatus Gravier, 1911 see *Hyalopomatus*
Dipomatus Ehlers, 1913 see *Serpula*
Ehlerprotula Uchida, 1978 see *Protula*
Eucarphus Mörch, 1863 see *Hydroides*
Eupomatus Philippi, 1844 see *Hydroides*
Filigrana Mörch, 1863 see correct spelling *Filograna*
Filipora Fleming, 1825 variant spelling *Filopora*, see *Filograna*
Glomerula Nielsen, 1931 (incl. *Calcisabella* Perkins, 1991) see Sabellidae**
Glossopsis Bush, 1905 see *Hydroides*
Helena Castelnau, 1842 see *Serpula*
Hyalopomatopsis Saint-Joseph, 1894 see *Hyalopomatus* and *Pseudochitinopoma* (*occidentalis*)
Isovermilia Rosenfeldt, 1979 error for *Semivermilia*
Lemintina Risso, 1826 (Mollusca), erroneously mentioned as synonym of *Protula*
Membranopsis Bush, 1910 see *Protula*
Mercierella Fauvel, 1923 see *Ficopomatus*
Mercierellopsis Rioja, 1945 see *Ficopomatus*

Miroserpula Dons, 1930, variant spelling *Microserpula*, 1931 see *Chitinopoma*
Neopomatus Pillai, 1960 see *Ficopomatus,* and note p. 42
Olga Jones, 1962 see *Spirobranchus*
Olgaharmania Rioja, 1941b see *Hydroides*
Omphalopoma Mörch, 1863 type species undeterminable (*fide* Zibrowius 1973b), other taxa see *Filogranula*, *Janita*, *Omphalopomopsis*
Paraprotula Uchida, 1978 see *Protula*
Paraserpula Southward, 1963 see *Serpula*
Paravermilia Bush, 1905 see *Vermiliopsis*
Philippiprotula Uchida, 1978 see *Protula*
Piratesa Templeton 1835, indeterminable
Pixellgrana Uchida, 1978 see *Protis*
Placostegopsis Saint-Joseph, 1894 see *Placostegus*
Podioceros Quatrefages, 1866 see *Pomatoceros*
Polyphragma Quatrefages, 1866 see *Hydroides*
Pomatoceroides Munier-Chalmas *in* Ferronière, 1901 is chironomid larva (*fide* Zibrowius, Botosaneanu & ten Hove 1995)
Pomatoceropsis Gravier, 1905 see *Spirobranchus*
Pomatoceropsis Holly, 1935 homonym of *Pomatoceropsis* Gravier, 1905 also see *Spirobranchus*
Pomatocerus Mörch, 1863 variant spelling of *Pomatoceros*
Protoplacostegus Bush, 1905 see *Placostegus*
Protohydroides Uchida, 1978 see *Hydroides*
Protoserpula Uchida, 1978 see *Serpula* or *Spiraserpula* (*fide* Pillai & ten Hove 1994: 40, 100)
Protulopsis Saint-Joseph, 1894; re-instated Uchida, 1978 see *Protula*
Pseudopomatoceros Holly, 1936, erected for homonym *Pomatoceropsis* Gravier, see *Spirobranchus*
Pseudoserpula Straughan, 1967b see *Spiraserpula* and *Crucigera*
Psygmobranchus Philippi, 1844 see *Protula*
Salmacinopsis Bush, 1910, ill-defined but referred to *Protula* by Perkins (1998: 95)
Sclerostyla Mörch, 1863 see *Pyrgopolon*
Schizocraspedon Bush, 1905 see *Hydroides*
Semiserpula Imajima, 1979 homonym of the fossil genus *Semiserpula* Wetzel, 1957; Recent species placed in *Serpula*
Siliquaria not Bruguière, 1789 (Mollusca, Siliquariidae) *sensu* Lamarck, 1818, confused, partly siliquariid mollusc (*Pyxipoma*), partly indeterminable polychaete
Sphaeropomatus Treadwell, 1934 see *Ficopomatus*
Spiramella Blainville, 1828 see *Protula*
Spirodiscus Fauvel, 1909 see *Nogrobs*
Stoa de Serres, 1855 questionable vermetid (or spirorbid)
Subprotula Bush, 1910 confused, type-species questionably see *Vermiliopsis*, other taxa see *Protula*
Temporaria Straughan, 1967b see *Spirobranchus*
Vermilia Lamarck, 1818 confused, *V. rostrata* see *Spirobranchus*, other taxa referrable to *Vermiliopsis sensu lato*, *Pomatoceros*, *Hydroides*, and even to vermetid gastropods
Zopyrus Kinberg, 1867 see *Serpula*

*The genus *Actinoceras* Bronn, 1835 has been mistakenly attributed to Mörch, 1863 by e.g., Hartman (1959: 568). However, the genus was erected for nautiloid molluscs from the Silurian-Carboniferous, not for a serpulid. Mörch (1863: 400) mentioned *Actinoceras Bigsbyi* Chenu, 1859 as a synonym of the serpulid *Pomatostegus actinoceras* Mörch, 1863; in reality Chenu (1859: 64–65, fig. 230) depicted a fossil siphon of a nautiloid, probably correctly under the genus *Actinoceras,* which indeed shows a superficial resemblance to the operculum of the recent serpulid *P. actinoceras*.

** According to Ippolitov (2007: 260), the name *Glomerula* Nielsen, 1931 should be “unavailable according to ICZN 13.3)”. No further explanation is given by Ippolitov. If he is referring to Article 13 (iii), the full text of that is: “Article 13. Names published after 1930.- (a) Names in general.- In addition to satisfying the provisions of Article 11, a name published after 1930 must be either . . . (iii) proposed expressly as a replacement fro a pre-existing available name”. Nielsen (1931: 85) defines the genus *Glomerula* in a key, and (p. 88) attributes a single species (*Serpulites gordialis* von Schlotheim, 1820) to his genus. Nielsen, who did not give any explanation for his action at all, either replaced the generic name *Serpulites*, a name explicitly unavailable according to “Article 20. Genus-group names ending in *–ites* . . . given to fossils.”, or he simply placed the species *gordialis* in a new genus. Both ways we do not see conflict with the Code, certainly not with 13 (iii), and in our opinion the name *Glomerula* is available, though not being a serpulid.

Key to serpulid genera (described before 2008)

Although we have included the most obvious exceptions to the generic diagnoses with a double, even sometimes treble pathway (e.g., *Hyalopomatus* (in part)), it is impossible to provide for every exception. For instance, juveniles may show fewer thoracic segments than adults, while the adult number of segments has been used in this key. The genera *Pomatoceros* and *Spirobranchus* occasionally show specimens without collar chaetae, which then would key out with *Pomatoleios*. Specimens with two minute pseudopercula instead of one pseudoperculum and a full grown operculum have been reported for all genera of the *Serpula*-clade. A generic name found with this (any) key always should be checked carefully against its diagnosis. Spirorbins have been included as category only.

1	Body symmetrical	2
-	Body asymmetrical	49
2 (1)	Operculum present	3
-	Operculum absent	40
3 (2)	Collar chaetae absent	4
-	Collar chaetae present	8
4 (3)	Opercular peduncle without wings	5
-	Peduncle with wings	*Pomatoleios*
5 (4)	Tube free (see 30 as well), tusk-shaped, smooth, thoracic membranes short	*Ditrupa*
-	Tube otherwise, mostly attached to the substrate	6
6 (5)	Operculum inverse conical, with brown(ish) endplate lacking spines	7
-	Operculum pear-shaped, laterally compressed, and if bearing chitinous plate at all, than with multiple spines	*Rhodopsis*
7 (6)	Tube (semi) transparent, apron present, collar region with reniform band of reddish ocelli	*Placostegus*
-	Tube white opaque, apron absent	*Marifugia*
8 (3)	Opercular peduncle with well developed membranous distal wings	9
-	Opercular peduncle without well developed distal wings	12
9 (8)	Collar chaetae few, fine and capillary	10
-	Collar chaetae numerous, *Spirobranchus*-type	11
10 (9)	Operculum with calcareous endplate, sometimes with non-movable spines	*Pomatoceros*
-	Operculum with elaborate calcareous movable spines	*Galeolaria*
11 (9)	Operculum with calcareous endplate, sometimes with non-movable spines	*Spirobranchus*
-	Operculum with chitinous column bearing several serrated disks	*Pomatostegus*
12 (8)	Pseudoperculum (rudimentary operculum) present	13
-	Pseudoperculum (rudimentary operculum) absent	17
13 (12)	Collar chaetae simple, peduncle with distal latero-dorsal winglets, opercular ampulla slightly chitinized distally.	*Neovermilia globula* (in part)
-	Collar chaetae simple, peduncle without winglets, opercular ampulla with brown horny distal cap	*Vermiliopsis* (in part, *striaticeps*)
-	Collar chaetae simple and fin-and-blade-type, one to six vesicular opercula	*Protis* (in part, *polyoperculata*)
-	Collar chaetae simple and bayonet-type	14

14 (13) Operculum two-tiered (in mature specimens), with proximal funnel of fused radii and distal verticil of spines .... *Hydroides*
- Operculum a simple funnel made of fused radii 15

15 (14) Tube with internal structures .... *Spiraserpula*
- Tube without internal structures 16

16 (15) Basal processes on opercular funnel absent .... *Serpula*
- Basal processes on opercular funnel present .... *Crucigera*

17 (12) Collar chaetae coarsely serrated and simple .... *Ficopomatus*
- Collar chaetae fin-and-blade and simple 18
- Collar chaetae simple only 29

18 (17) Colonies of branching tubes, 2 membranous spoon-shaped opercula on pinnulated radioles .... *Filograna*
- Tubes do not form colonies of branching tubes, opercula otherwise 19

19 (18) 7 thoracic segments 20
- Less than 7 thoracic segments 27

20 (19) Operculum and peduncle not calcified 21
- Operculum and peduncle calcified .... *Pyrgopolon*

21 (20) Opercular base surrounded by three fleshy processes .... *Janita*
- Opercular base without fleshy processes 22

22 (21) Tube transparent .... *Vitreotubus*
- Tube opaque 23

23 (22) Anterior tooth of thoracic uncini a pointed fang, operculum with calcareous endplate .... *Omphalopomopsis*
- Anterior tooth otherwise 24

24 (23) Anterior peg of thoracic uncini bifurcate, gouged 25
- Anterior peg of thoracic uncini simple, rounded 26

25 (24) Operculum with flat to hollow endplate, abdominal chaetae flat triangular .... *Filogranula*
- Operculum with conical endplate, abdominal chaetae hollow trumpet shaped .... *Pseudochitinopoma*

26 (24) Posterior glandular pad absent .... *Chitinopoma*
- Posterior glandular pad present .... *Chitinopomoides*

27 (19) 6 thoracic segments 28
- 5 thoracic segments .... *Tanturia*

28 (27) Thoracic membranes long, apron .... *Laminatubus*
- Thoracic membranes reaching segment 2 .... *Hyalopomatus* (in part)

29 (17) Opercular peduncle pinnulate 30
- Peduncle smooth, without pinnules 34

30 (29) Peduncle non-modified radiole, tube attached 31
- Peduncle modified, thicker than normal radioles, tube mostly free 33

31 (30) Operculum delicate membranous cup with a flat distal surface surmounted by a marginal crown of fine teeth joined by a transparent membrane, 5 thoracic chaetigerous segments *Josephella* (in part)
- Operculum simple membranous vesicle, 7 thoracic segments 32

32 (31) Thoracic uncini saw-shaped with pointed fang .... *Paraprotis*
- Thoracic uncini saw-to-rasp-shaped with elongated peg .... *Apomatus*

33 (30) 5 thoracic segments .... *Bathyditrupa*
- 6 thoracic segments .... *Nogrobs*

34 (29) Stylodes present .... *Dasynema*
- Stylodes absent 35

35 (34) Abdominal chaetae short stout curved spines .... *Paumotella*
- Abdominal chaetae otherwise 36

36 (35) Opercular peduncle flat, ribbon-like, 7 thoracic segments .... *Metavermilia*
- Opercular peduncle flat, ribbon-like, 11–14 thoracic segments .... *Filogranella* (in part)
- Peduncle cylindrical or sub-cylindrical 37

37 (36) Peduncle with latero-dorsal winglets, apron present, *Apomatus* chaetae absent .... *Neovermilia*
- Peduncle without winglets, thoracic membranes not forming apron, *Apomatus* chaetae absent .... *Hyalopomatus* (in part)
- Peduncle without winglets, thoracic membranes not forming apron, *Apomatus* chaetae present 38

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Glossary

Essentially adapted from Fauchald (1977), ten Hove & Jansen-Jacobs (1984), Glasby *et al.* (2000), Rouse & Pleijel (2001), and Bastida-Zavala & ten Hove (2002), this glossary aims to standardize terminology by using preferential and more precisely defined terms. Preferential terms are given in bold.

abdomen: body region posterior to the thorax.

achaetous: without chaetae.

acicular chaeta: stout, projecting chaeta.

annulated: ringed or marked with transverse grooves.

ampulla: proximal living part of operculum, mostly bulbous, distally often covered by calcareous or chitinous plate.

***Apomatus* chaeta:** sigmoid to overall sickle shaped thoracic chaeta, with a proximal denticulate limbate zone and distal zone with fine rectangular teeth (compare sickle-chaeta).

apron: thoracic membranes joined ventrally past the last thoracic chaetigers, across anterior abdominal segments.

basal membrane, basal web, see preferred term: interradiolar membrane.

bayonet chaeta: special chaeta in first thoracic chaetiger of overall bayonet shape: collar chaeta, generally with one or two (sometimes more) large proximal bosses (or "teeth") at the base of a distal limbate zone.

biramous: parapodium consisting of two (chaetae bearing) parts, a ventral neuro- and a dorsal notopodium.

blade: distal, seemingly flat portion of a chaeta (see, however, hooded (capillary) chaeta).

boss: small projection or knob-like process in collar chaeta.

branchiae: see branchial crown

branchial crown: a bilaterally symmetrical branched structure formed by prostomial palps. In serpulids consisting of two lobes, each with a number of (branchial) radioles bearing pinnules; often including an operculum with peduncle on one lobe and sometimes also a pseudoperculum on the opposite lobe.

branchial eyes: all photoreceptors of the branchial crown (and operculum).

branchial filament, see preferred term: radiole.

branchial membrane, see preferred term: interradiolar membrane.

capillary chaeta: slender, often long, chaeta tapering to a fine point; in the literature the term has been used as collective term for elongate, needle-like chaetae of otherwise variable shape and ontogeny. See explanation hooded as well. It is very unlikely that the "capillaries" of a thorax are homologous with the types of "capillaries" as occurring in the posterior abdomen of various genera.

chaeta (*pl.* chaetae): chitinous bristle protruding from an epidermal pocket in the body wall.

chaetal inversion: in Serpulidae (and Sabellidae) the thorax bears chaetae dorsally (in notopodia) and uncini ventrally (neuropodial); in the abdomen the position of chaetae and uncini is reversed.

chaetiger: segment bearing chaetae.

collar segment: first chaetiger, with an anterior **collar,** an encircling fold or flap covering the base of the branchial crown (see thoracic membranes too). Usually longer than other thoracic chaetigers; uniramous, lacking uncini.

compound eye: a more or less rigidly patterned groupings of ocelli.

constriction: narrowing of the opercular peduncle or a transverse groove, at basis of funnel or ampulla.

crenulated: having a margin with small, low, rounded teeth.

crown: see branchial crown.

cuticle: thin, non-cellular protective layer produced by, and overlying, the epidermis; probably not chitinous but consisting of scleroprotein.

dental formula: notation showing the distribution of teeth on the crest of an uncinus, first used by Ben-Eliahu & Dafni (1979). For instance: F + 4 means Fang + 4 teeth (seen in profile), alternatively F:1:1:1:1; P + 10 means Peg + 10 teeth (seen in profile), which may be detailed as P:1:1:1:1:1:1:1:1:1:1 if saw-shaped, P:3:2:2: 1:1:1:1:1:1:1 if saw-to-rasp-shaped, P:4:4:4:4:4:4:4:4:3:2 if rasp-shaped.

dentate: toothed.

denticulate: with small teeth.

entire edge (margin): smooth edged, without projections.

eye, eyespot: photoreceptor or light-receptive organ, usually occurring on prostomium, but may occur on the pygidium or almost anywhere along the body.

fang: sharply pointed anterior (or primary) tooth of uncinus.

filamentous: shaped like a filament or fine thread.

filiform: thread-like, very slender.

fin-and-blade chaeta: collar chaeta with basal boss ("fin") made of relatively few teeth of intermediate size; the basal fin may or may not be separated by a toothless zone (a gap) from the distal blade.

flat-trumpet-shaped chaeta: chaeta with a thin, flat distal part with small teeth on its edge.

funnel: descriptive term used to indicate the inverted cone-like proximal part of the operculum in *Hydroides*, the ditto distal part in *Crucigera*, and the entire operculum in *Serpula*.

geniculate: "having a knee-like joint" or "bent sharply". In serpulids traditionally used for a variety of bent chaetae, see discussion and specification of types of chaetae in the introductory part of this paper.

glandular pad: glandular zone on the dorsal side of the last abdominal segments in some serpulids.

hooded (capillary) chaetae, hooded (limbate) chaetae: type of thoracic chaetae, stiff, elongate, narrowly hooded and tapering to a fine point (usually called "limbate"), or slender, elongate, very narrowly hooded and tapering (usually called "capillaries"). These chaetae consist of densely packed fibrils; distally they seem to have a limbus or flat blade, which on close inspection is an outer layer where the fibrils are packed less tightly than in the central axis (or shaft), enveloping 1/2 to 2/3 of the axis.

internal tube structures: in the narrow sense, ridges and crests inside *Spiraserpula* tubes; in a wider sense, any internal structure such as the small pits in the substrate-side of the lumen in *Spirobranchus corrugatus*.

interradial groove: groove on outside of a funnel, marking radius insertion (*Serpula*-clade).

interbranchial membrane, preferred term: interradiolar membrane.

interradiolar membrane: thin membrane connecting basal parts of radioles in some Sabellida.

lappet: lobe or flap-like projection.

limbate: condition of chaetae, in which a longitudinal flange appears to be present; however, this is an artifact of light microscopy, see hooded.

limbus: flattened distal border of chaetae, longitudinal flange (Latin = edge, border), however, see hooded.

mouth: anterior opening of the alimentary canal; in serpulids also used for anterior opening (or entrance) of the tube.

mouth palp: filiform projections of the dorsal lip of the Sabellida mouth.

neurochaeta: chaeta of a neuropodium.

neuropodium (*pl.* neuropodia): ventral branch or ramus of a parapodium.

notochaeta: chaeta of a notopodium.

notopodium (*pl.* notopodia): dorsal branch or ramus of a parapodium.

ocellar clusters: loose groupings of approximately 2–20 ocelli, generally with as many lenses.

ocellus (*pl.* ocelli): single eyespot with (or without a single lens).

operculum (*pl.* opercula): tip of modified radiole used to plug the tube when the worm is retracted.

opercular plate: terminal reinforcement of opercular ampulla, often chitinous or calcareous.

opercular stalk, see preferred term: peduncle.

palmar or palmate membrane, see preferred term: interradiolar membrane.

parapodium (*pl.* parapodia): fleshy lateral projection from a body segment which usually bears chaetae.

pectinate: comb-like; with series of projections like the teeth of a comb. In serpulids an arrangement of radioles.

peduncle: modified radiole bearing the operculum.

peduncular wings: collective term for all flattened lateral wing-like appendages of peduncle.

peg: wedge shaped, not sharply pointed anterior tooth of uncinus

peristome: collar-like widening of tube (former tube-mouth).

peristomium: pre-segmental region of the body surrounding the mouth (alimentary canal).

pinnules: small paired side branches of the radioles, giving each radiole a feathery appearance.

primary tooth, see fang.

prostomium: anteriormost, presegmental region of body, bearing the branchial radioles and sometimes eyes.

pseudoperculum (*pl.* pseudopercula) [variant, but not preferred spelling pseudo-operculum]**:** modified radiole (generally the second dorsal one), generally without pinnules; can develop into a new functional operculum when the functional operculum is lost.

pygidium: post-segmental terminal body-part surrounding the anus.

radiolar crown, see preferred term: branchial crown.

radiolar web or webbing, see preferred term: interradiolar membrane.

radioles: pinnulate filaments of branchiae, used for respiration and feeding.

radius (pl. radii): radial projection of the funnel (*Serpula*-clade).

rasp-shaped uncinus: uncinus with two (biseriate) or more rows of teeth (multiseriate), see dental formula.

reniform: kidney-shaped.

rudimentary operculum, see preferred term: pseudoperculum.

saw-shaped uncinus: uncinus with only one row of teeth (uniseriate), see dental formula.

segment: one of the serially repeated units comprising the trunk; often separated internally by septa or dissepiments.

seta (*pl.* setae), see: chaeta, term preferentially adopted by the 1st International Polychaete Conference in Australia.

shaft: proximal part of a chaeta.

sickle-chaeta: a recurved abdominal chaeta with tiny dentition on the inside of the curve. N.B. used in spirorbin literature for both thoracic *Apomatus* chaetae and abdominal sickle-chaetae

spinule: each of the tubercular or tooth-like projections of a spine in the verticil of the genus *Hydroides*. By their position relative to the axis, spinules may be internal, lateral, or external. By their position along the spine they may be proximal, medial, or distal.

***Spirobranchus*-type chaeta:** bayonet-like collar chaeta with a proximal boss consisting of very numerous tiny hair-like spines.

stylode: finger-like outward projection of radioles in some Sabellida.

tabulae: transverse internal tube elements partitioning off the oldest parts of the tube, generally as response to tube damage.

thoracic membranes: thin folds on both sides of thorax, extending from dorsal part of collar to lateral and/or ventral side of posterior thorax. N.B. Thoracic membranes have been included in the the term collar by some spirorbin taxonomists.

thorax: anterior region of the body behind the head.

tonguelet: special form of lappet, between dorso-lateral and ventral lobes of the collar in some serpulid genera.

torus (*pl.* tori): transverse elevation of parapodium surrounding the uncini.

transversal ridge: annular elevation of tube, less pronounced than peristome.

triangular depression: depressed area between thoracic uncinigerous tori when gradually approaching and almost touching one another posteriorly and ventrally.

trumpet chaetae: abdominal chaetae in e.g., *Serpula*, *Hydroides*, formerly thought to be hollow (like a trumpet; in French "soies en calice comprimé"); however, more recently proven to be flat, not hollow at all. See preferred term: flat-trumpet-shaped chaetae.

truly trumpet-shaped chaetae: distally hollow chaetae, with two parallel rows of sharp denticles, extending into a long lateral spine.

unciniger: segment carrying uncini.

uncinus (*pl.* uncini): deeply embedded comb-shaped chaeta with only its dentate edge protruding from the body wall; uncini usually arranged in tori, elevated rows transverse to the axis of the animal.

uniramous: parapodium with only one (chaetae bearing) part.

verticil: distal part of operculum in *Hydroides*.

verticil spine: any of the radial elements, generally around a central disc, together forming the verticil in *Hydroides*.

wing: in the genus *Hydroides* used in the restricted sense of lateral and flat expansion of verticil spine.

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