



Deep-sea serpulids (Annelida: Polychaeta) in tetragonal tubes: on a tube convergence path from the Mesozoic to Recent

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Abstract

Serpulids typically build cylindrical calcareous tubes attached to hard substrates. Until now, only three serpulid species inhabiting free-lying polygonal tubes were reported from the deep sea: *Spirodiscus grimaldii* Fauvel, 1909 with quadrangular spirally coiled tubes, *Bathyditrupa hovei* Kupriyanova, 1993a with quadrangular tusk-shaped tubes, and *Ditrupa groenlandica* McIntosh, 1877 with octagonal tusk-shaped tubes. Similar free-lying tubes with tetragonal cross-section, both coiled and tusk-shaped, are described from shallow-water Mesozoic deposits as *Nogrobs* de Montfort, 1808, *Tetraserpula* Parsch, 1956, *Tetraditrupa* Regenhardt, 1961, *Glandifera* Regenhardt, 1961 and *Tubulostium* Stoliczka, 1868. We have revised deep-sea serpulids with tetragonal (and secondary octagonal) tubes and compared their tube ultrastructures and mineralogies with those of morphologically similar fossils. Revision of the Recent material has revealed six species in five genera: *Spirodiscus grimaldii*, *S. groenlandicus* **comb. nov.**, *Bathyditrupa hovei*, *Bathyvermilia gregrousei* **sp. nov.**, *Hyalopomatus dieteri* **sp. nov.** and *Zibrovermilia zibrowii* **gen. et sp. nov.** Comparisons showed significant ultrastructural and mineralogical differences between Recent and Mesozoic species. Similar tetragonal tube morphology of the Recent forms appears to be a result of convergence due to adaptation to similar soft-sediment habitats of the deep sea. None of Recent genera should be synonymised with any fossil genus, and the genus *Spirodiscus* Fauvel, 1909, previously synonymised with fossil *Nogrobs*, should be re-instated. However, a huge stratigraphic gap (66 Myr) between the earliest known fossil tetragonal tubes and their Recent counterparts still allows the possibility that such essentially different structures is a result of ultrastructural evolution, a hypothesis that could be verified by discovery and further study of Cenozoic material.

Key words: Serpulidae, bathyal, abyssal, tube ultrastructures, taxonomy, mineralogy, Jurassic, Cretaceous

Introduction

The diversity of bathyal and abyssal marine organisms is still poorly known and this holds true also for calcareous tube-worms of the polychaete family Serpulidae, a group known as common inhabitants of shallower seas. The serpulid genus *Spirodiscus* Fauvel, 1909 is a good illustration of this statement. Fauvel (1909, 1914) described *Spirodiscus grimaldii* gen. et sp. nov. from lower bathyal depths off the Azores, based on the material from the Prince of Monaco expeditions. The generic name referred to the unusual for serpulids tube, quadrangular in cross-section, unattached, and coiled into a flat spiral (Fig. 1A). The species also had an unusual peduncle—thick, but with pinnules. The very few subsequent records of this mysterious species have been recently summarised by Kupriyanova & Nishi (2011). Simultaneously with *Spirodiscus*, also from lower bathyal depths in the Azores, Fauvel (1909, 1914) collected unnamed empty tubes ("tube de Serpulien") that "like the coiled tubes were quadrangular in cross-section but straight". Almost a century later, Kupriyanova (1993a) described from the abyssal depths of Kuril-Kamchatka Trench *Bathyditrupa hovei* gen. et sp. nov., the species characterised by quadrangular tusk-shaped tubes (Fig. 1B,C) similar to those mentioned by Fauvel (1909). Additional records of *Bathyditrupa hovei* were reported only recently (ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2011).

Kupriyanova (1993a) had not recognised the similarity between *Spirodiscus grimaldii* and *Bathyditrupa hovei*, however, ten Hove (pers. comm.) proposed that *Bathyditrupa* might be a synonym of *Spirodiscus* based on the characters used in serpulid taxonomy (chaetae, operculum, opercular peduncle) and suggested that tube coiling in

Spirodiscus is not a distinctive character for the genus. Even in Fauvel's specimens of *S. grimaldii* (as evident from his drawings) initial and terminal parts of the tube are not coiled. Both coiled and straight specimens were obtained in the Azores by the bathyscaph *Archimede* in 1971 and subsequently collected in the Atlantic, Indian and Pacific Oceans by French deep-sea expeditions. Based on his preliminary examination of this material, Dr Helmut Zibrowius (Marseille, France, pers. comm.) hypothesised a total of at least four species that he tentatively attributed to *Spirodiscus*, both with spirally coiled tubes similar to those of *Spirodiscus* and straight tubes similar to those of *Bathyditrupa* (see Kupriyanova *et al.* 2011). In addition to *S. grimaldii* and *B. hovei*, he found an undescribed species with straight quadrangular in cross-section tubes from bathyal depths off New Caledonia and a tiny species with octagonal straight tubes (Fig. 1D) from the northern Atlantic, originally described as *Ditrypa groenlandica* McIntosh, 1877. Several other Recent shallow-water species occasionally show ostensibly free polygonal tubes, *e.g.*, *Pyrgopolon differens* (Augener, 1922) with 8–13 keels (ten Hove 1973) and *Serpula crenata* (Ehlers, 1908) with 6 keels (ten Hove & Smith 1990).

Fossil free-lying tetragonal tubes, both with significant coiled parts, like *Spirodiscus*, and simply curved, like *Bathyditrupa*, are common in shallow-water deposits of Mesozoic (Jurassic to Cretaceous, Fig. 1H–T) age. They are mainly known under the names of *Nogrobs* de Montfort, 1808 and *Tetraserpula* Parsch, 1956 or *Tetraditrupa* Regenhardt, 1961, respectively and include over 10 species (Ippolitov *et al.* 2014). The genera *Tubulostium* Stoliczka, 1868 and *Glandifera* Regenhardt, 1961 have also been used to classify fossil tetragonal tubes, but received little attention in literature. Jäger (2005) suggested synonymising the extant genus *Spirodiscus* Fauvel, 1909 with the fossil *Nogrobs* de Montfort, 1808 based on striking morphological similarity of their spirally coiled tetragonal tubes. Moreover, he suggested that Recent tusk-shaped tubes of *Bathyditrupa hovei* might belong to *Tetraditrupa* Regenhardt, 1961, which he classified as a subgenus of *Nogrobs*. This idea looks even more appealing considering that ancient faunal elements (“living fossils”), widely distributed in shallow water communities during some geological times, nowadays inhabit deep sea refugia, as known for some brachiopods, monoplacophorans, coelacanth, and stalked crinoids (*e.g.*, Gage & Tyler 1991; Manceñido 1997; Yoshida 2002; Wisshak *et al.* 2009). Following Jäger (2005), in their review of serpulid taxonomy ten Hove & Kupriyanova (2009) used the generic name *Nogrobs* for the former *Spirodiscus grimaldii*, but retained *Bathyditrupa* as a valid genus, despite its similarity to fossil *Tetraserpula* and *Tetraditrupa*. Ippolitov (2007) interpreted morphological similarity between fossil and Recent tetragonal tubes more cautiously: he proposed to keep Recent *Bathyditrupa* and fossil *Tetraserpula* separate until comparative data on tube ultrastructures become available.

The idea to evaluate generic affiliation of fossil species using tube ultrastructures was proposed by Sanfilippo (1998b). Studies over the last three decades revealed significant ultrastructural diversity in serpulid tubes (*e.g.*, ten Hove & Zibrowius 1986; Zibrowius & ten Hove 1987; Sanfilippo 1998a, b; 2001; Vinn 2005, 2007, 2008; Vinn *et al.* 2008, Ippolitov & Rzhavsky 2014). Tube ultrastructures tend to show significant variability, sometimes even making species identification possible (Vinn 2007; Ippolitov & Rzhavsky 2008), and may have more or less clear adaptive significance (Vinn *et al.* 2008; Vinn & Kupriyanova 2011), although intra-generic variability of ultrastructures is still poorly understood. Mineralogical composition of serpulid tubes that can be represented by different modifications of CaCO₃—calcite, aragonite or their mixture in various proportions (Bornhold & Milliman 1973; Vinn *et al.* 2008; Smith *et al.* 2013)—provides another potential tool for decrypting phylogenetic positions of fossils (Ippolitov *et al.* 2014).

This study had two aims. First, we revised Recent deep-sea serpulids living in tetragonal and octagonal tubes to determine whether they all are closely related as suggested by Zibrowius (pers. comm.). Second, we compared tube ultrastructures and mineralogy in these species with those of tetragonal fossil species to determine whether Recent and fossil species are so closely related that their generic names should be synonymised as suggested by Jäger (2005).

Material and methods

The study is based on unpublished Recent material kindly provided by Dr. Helmut Zibrowius (Marseille, France) and collected during various, mostly French oceanographic expeditions (mentioned if otherwise): on board R/V VALOROUS (UK) in 1875; by bathyscaph ARCHIMEDE in 1969; R/V JEAN CHARCOT, cruise INCAL in 1976, cruise WALVIS in 1978–79, cruise DEMERABY in 1980 and cruise BIOGAS 11 in 1981; R/V KNORR (USA), cruise 25 in 1972; R/V DISCOVERY (UK), cruise 92 in 1978 and cruise 105 in 1979; R/V MARION DUFRESNE,

cruise MD 20 in 1979; R/V CRYOS, cruise ABYPLAINE in 1981 and 1983; R/V CHALLENGER (UK), cruise 5/82 in 1982; R/V LE SUROIT, cruise EPI 1 in 1984 and cruise SEAMOUNT 2 in 1993; R/V JEAN CHARCOT, cruise BIOCAL in 1985; R/V VAUBAN, cruise MUSORSTOM 4 in 1985; R/V MARION DUFRESNE, cruises MD50 and MD32 in 1986; R/V CORIOLIS, cruise MUSORSTOM 5 in 1986 and cruise BIOGEOCAL in 1987; R/V ALIS, cruise MUSORSTOM 6 in 1989. We also included unpublished material collected by Russian oceanographic expeditions on board R/V VITYAZ in 1954–1975 and VITYAZ-2 in 1982.

The examined material of fossil tetragonal tubes from the collections of the second author (API) and Dr. Manfred Jäger (Rosenfeld, Germany) comprised 13 species (Table 1) and included the type species for four out of five known genera with free tetragonal tubes. The samples were collected from Europe (Central Russia, Central Ukraine, Crimea Peninsula, South-western Germany, Northern Germany, and England) and Asia (South India) and covered the geological interval from the Bajocian stage of Middle Jurassic (~169 Myr) to Maastrichtian Stage of Upper Cretaceous (~66 Myr). This material represents the entire variety of fossil tetragonal tubes so far described because in younger Cenozoic rocks (66 Myr to Recent) such tubes are still unknown.

The material is deposited in the following museum collections: **AM**—Australian Museum, Sydney, Australia; **ARI**—Agarkar Research Institute, Pune, India; **LACM-AHF**—Los Angeles County Museum of Natural History, Allan Hancock Foundation, California, USA; **MNHN**—Muséum National d'Histoire Naturelle, Paris, France; **MOM**—Musée Océanographique de Monaco; **NBCL**—Naturalis Biodiversity Center, Leiden, the Netherlands (including ZMA V.Pol., former collection numbers of the Zoological Museum Amsterdam, now incorporated in **Naturalis** Biodiversity Center, Leiden); **NHMUK**—The Natural History Museum, London, UK; **PIN**—Paleontological Institute of Russian Academy of Sciences, Moscow, Russia; **SIO**—P. P. Shirshov Institute of Oceanology of Russian Academy of Sciences, Moscow, Russia; **SMF**—Senckenberg Museum and Institute, Frankfurt, Germany; **USNM**—United States National Museum of Natural History, Washington, D.C., USA; **ZMA**—Zoologisch Museum Amsterdam, now incorporated in the **Naturalis** Biodiversity Center, Leiden, the Netherlands.

The type specimens of *Bathyditrupa hovei* were re-examined at **SIO** by both authors (API and EKK). The type material of *Spirodiscus grimaldii* was examined by EKK at **MNHN** and at **MOM** by Helmut Zibrowius who shared his unpublished observations with us. The material of *Spirodiscus grimaldii* reported in Hartman & Fauchald (1971) was re-examined by EKK at **LACM-AHF** and the material of *Bathyditrupa* mentioned in ten Hove & Kupriyanova (2009) was studied at **ZMA** by EKK.

Before examination, serpulids were removed from their tubes and stained with methylene blue to increase contrast. Specimens were examined under a dissecting microscope Leica MZ8 and selected specimens were photographed with a Nikon 4300 Coolpix camera mounted on a Leica MZ8 stereomicroscope at **AM**. Selected specimens were prepared for scanning electron microscopy (SEM) by critical point drying, coated with palladium, and observed under a Leo 435VP at **AM**.

Tube ultrastructures in all Recent and fossil species were studied with a CamScan and Tescan SEM in **PIN** by API. Two to four specimens were examined for most species to assess variability, and for one species with abundant material (*Bathyditrupa hovei*) ontogenetic series of sections were studied. All tubes have been sectioned in transverse and longitudinal directions, and were coated with gold for SEM study. No special etching was used to prepare the sections. Ultrastructural descriptions followed the terminology of Carter *et al.* 1990 adapted for serpulids by Vinn *et al.* 2008 (see Table 2 for abbreviations of structure names). To facilitate direct species to species comparisons in the future, we adopted the approach of Weedon (1994) who provided descriptions of not only crystal arrangement (ultrastructural types), but also of crystal shapes for each studied species. Therefore, descriptions of all Recent species are accompanied by data on their tube ultrastructures.

Mineralogy was studied by X-ray diffraction analysis in the laboratory of Geological Department of Moscow State University (**MSU**). One or two tubes of each Recent and selected fossil species from the samples used for SEM were desintegrated into powder and analysed with DRON-3M X-ray diffractometer. Signal was obtained in the interval 30–36° 2 θ with step 0.1°, containing major peaks of both calcite (34.35° 2 θ ; corresponding spacing between diffracting planes $d=3.04$ Å) and aragonite (31.00° and 31.65 2 θ ; corresponding spacing between diffracting planes $d=3.40$ Å and $d=3.29$ Å, respectively). Calcite/aragonite ratio was calculated using Ca/Ar main peaks intensity ratio. To demonstrate the data reliability, we provided values of absolute intensity (I) of reflection

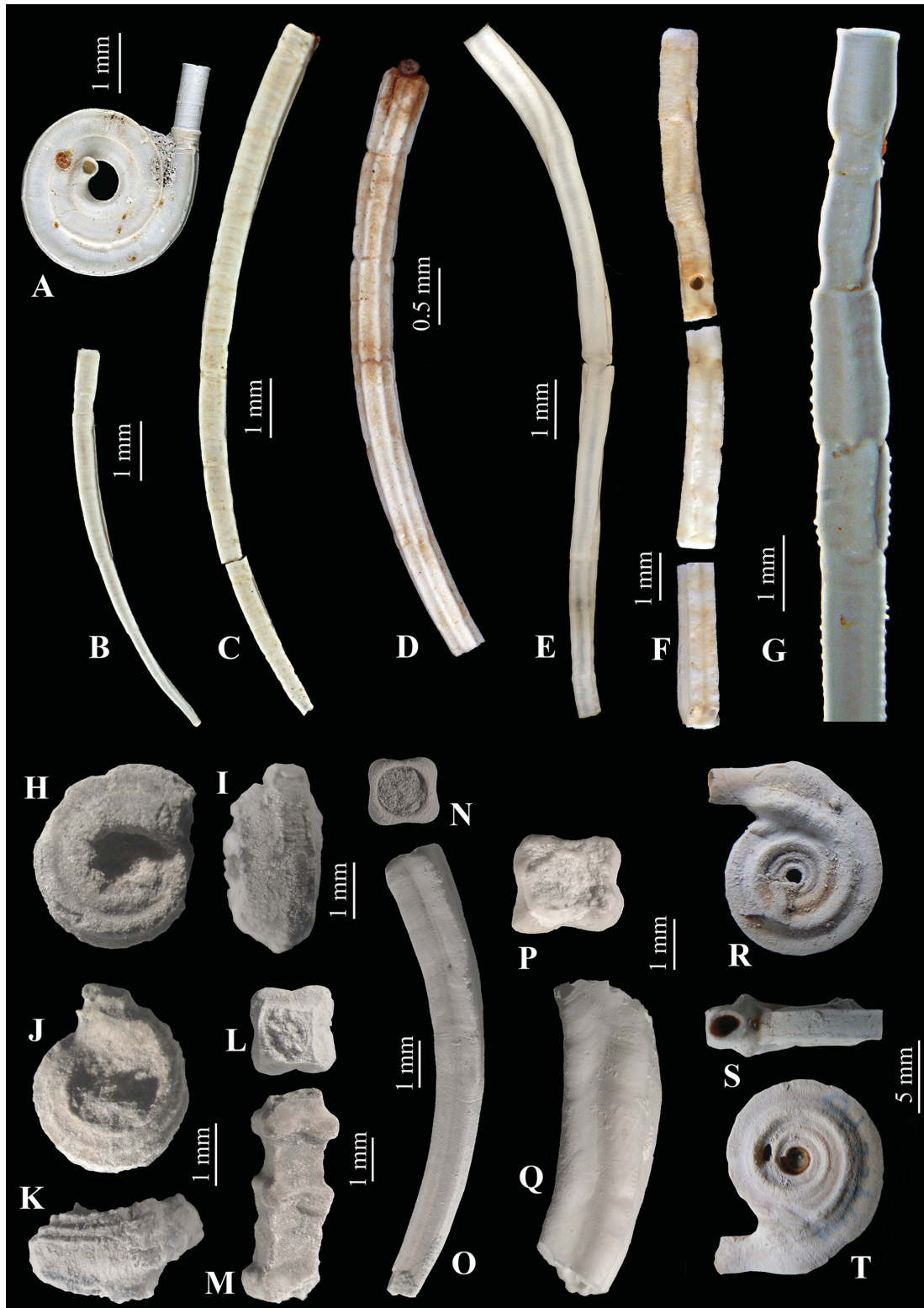


FIGURE 1. External morphology of polygonal serpulid tubes. Recent species: A—*Spirodiscus grimaldii*, R/V VITYAZ-2, St. 78. B, C—*Bathyditrupa hovei*, R/V VITYAZ-2, St. 79. D—*Spirodiscus groenlandicus* **comb. nov.**, R/V VITYAZ-2, St. 79. E—*Bathyvermilia gregrousei* **sp. nov.**, R/V VITYAZ, St. 5074. F—*Hyalopomatus dieteri* **sp. nov.**, R/V JEAN CHARCOT, cruise BIOCAL, St. CP27. G—*Zibrovermilia zibrowii* **gen. et sp. nov.**, R/V ALIS, cruise MUSORSTOM 6, St. CP438. Fossil tubes: H, I—*Nogrobs* cf. *vermicularis*, PIN 5485/23. J–K—*Glandifera* cf. *vertebralis*, spirally coiled juvenile tube with median keel running along the lateral tube side, PIN 5485/02. L, M—*Glandifera* cf. *vertebralis*, a fragment of straight adult tube with regular peristomes, PIN 5485/01. N, O—*Tetraserpula barremica*, PIN 5485/06. P, Q—*Tetraditrupa canteriata*, PIN 5485/04. R–T—*Tubulostium discoideum*, ARI Od 224/70 (the specimen figured by Chiplonkar & Tapaswi, 1973, pl. 11, fig. 15).

TABLE 1. Fossil material studied with SEM. Absolute geological ages follow official site of International Commission on Stratigraphy

(http://stratigraphy.org/GSSP/index.html), accessed 06-04-2014.

*type species of *Nogrobs* de Montfort, 1808, ** type species of *Tetraserpula* Parsch, 1956, ***type species of *Tubulostium* Stoliczka, 1868, ****type species of *Tetratirupa* Regenhardt, 1961.

| Fossil species | Registration and figure numbers | Appearance | Geological age | Locality | Coordinates | Tube ultrastructures |
|---------------------------------------------------------------------|-------------------------------------------------------------------------------------------------|-----------------------------------------------------------------|----------------------------|---------------------------------------------------|--------------------------------------------------------|------------------------|
| <i>Tetraserpula</i> sp. 1 | PIN 5485/37 PIN 5485/38 | Straight fragments up to 1.5 mm in diameter, no peristomes | Early Bajocian (~169 Ma) | Delkhofen near Balingen, Germany | 47°09'34"N 08°46'39"E | Unilayered SP |
| <i>Nogrobs</i> cf. <i>vermicularis</i> de Montfort, 1808* | PIN 5485/18 (Fig. 15A-D) PIN 5485/23 (Fig. 1H, I) PIN 5485/44 | Spirally coiled in juveniles, straight in adults, no peristomes | Late Bathonian (~165 Ma) | Lechstedt near Hildesheim, Germany | ~52°06'N ~10°01'E | Unilayered SP |
| <i>Glandifera</i> cf. <i>vertebralis</i> (J. de C. Sowerby, 1829) | PIN 5485/01 (Fig. 1L, M) PIN 5485/02 (Fig. 1J, K) PIN 5485/03 (Fig. 15E-H) PIN 5485/43 | Straight fragments with regular peristomes | Early Callovian (~164 Ma) | Egesheim near Balingen, Germany | 48°06'49"N 08°51'39"E | Unilayered SP |
| <i>Tetraserpula</i> sp. 2 | PIN 5485/19 (Fig. 16A-D) PIN 5485/47 | Straight fragments, no peristomes | Early Callovian (~164 Ma) | Znamenka, Kostroma Region, Russia | 58°24'45"N 44°53'02"E | Unilayered SP |
| <i>Tetraserpula</i> sp. 3 | PIN 5485/26 PIN 5485/27 | Straight fragments up to 4 mm in diameter, no peristomes | Early Callovian (~164 Ma) | Trahtemirov, Cherkassy, Ukraine; Kandern, Germany | 49°59'31"N 31°22'57"E / 47°43'08"N 07°39'53"E | Unilayered SP |
| <i>Nogrobs tumidus</i> (J. de C. Sowerby, 1829) | PIN 5485/20 (Fig. 16E-H) PIN 5485/41 PIN 5485/49 | Spirally coiled tubes up to 3.5 mm in diameter, no peristomes | Late Callovian (~162 Ma) | Solnechnaya Dolina, Crimea, Ukraine | ~44°52' N ~35°06'E | Diagenetically altered |
| <i>Tetraserpula</i> cf. <i>tetragona</i> (J. de C. Sowerby, 1829)** | PIN 5485/46 | Tusk-shaped tubes, no peristomes | Middle Oxfordian (~158 Ma) | Schurovo, Moscow Region, Russia | 55°01'36"N 38°47'09"E | Unilayered SP |

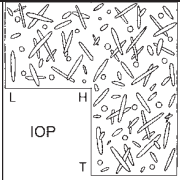
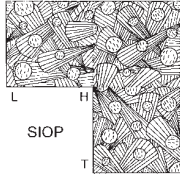
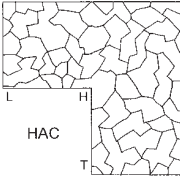
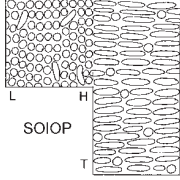
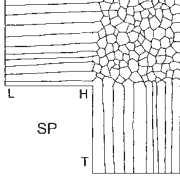
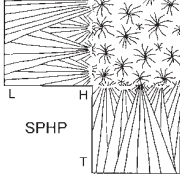
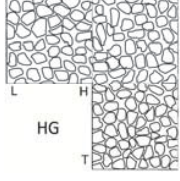
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TABLE 1. (Continued).

| Fossil species | Registration and figure numbers | Appearance | Geological age | Locality | Coordinates | Tube ultrastructures |
|---------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------|-----------------------------|--------------------------------------------|----------------------------|-----------------------------------------------------------------|
| <i>Tetraserpula</i> sp. 4 | PIN 5485/21 (Fig. 17A-D) | Straight fragments, no peristomes | Late Berriasian (~141 Ma) | Balki, Crimea, Ukraine | 44°59'30"N 34°28'10"E | Diagenetically altered |
| <i>Tetraserpula</i> sp. 5 | PIN 5485/39 | Straight fragments, no peristomes | Early Hauterivian (~133 Ma) | Engelbostel near Hannover, Germany | ~52°26'N ~09°39'E | Diagenetically altered |
| <i>Tetraserpula barremica</i> (Sasonova, 1958) | PIN 5485/06 (Fig. 1N, O) PIN 5485/07 (Fig. 17E-H) PIN 5485/25 | Straight fragments, no peristomes | Late Barremian (~127 Ma) | Bolshaya Fedorovka, Saratov Region, Russia | ~51°50'N ~45°30'E | Partly altered, originally unilayered SP |
| <i>Tetraditirupa rustica</i> (J. de C. Sowerby, 1829) | PIN 5485/22 (Fig. 18A-D) PIN 5485/31 | Straight fragments up to 2.5 mm in diameter, no peristomes | Cenomanian (~95 Ma) | Folkestone/Dover, England | ~51°06'N ~01°15'E | Two-layered (outer SPHP + main HG). ?Diagenetically altered. |
| <i>Tubulostium discoideum</i> Stoliczka, 1868*** | ARI Od224/70 (Fig. 1R-T) PIN 5485/24 (Fig. 19A-H) PIN 5485/48 | Spiral tubes with coil diameter up to 10 mm | Turonian (94–90 Ma) | Kunnam, Tamil Nadu, India | 11°14'392"N 79°00'472"E | Three-layered (outer SP, middle HG, inner SP) |
| <i>Tetraditirupa canteriata</i> (von Hagenow, 1840)**** | PIN 5485/04 (Fig. 1P, Q) PIN 5485/05 (Fig. 18E-H) PIN 5485/28 PIN 5485/29 PIN 5485/30 | Large curved tubes, no peristomes | Late Maastrichtian (~66 Ma) | Rügen Island, Germany | unknown | Partly altered, originally unilayered SP |

peaks. When the intensities of calcite (I_{calc}) and/or aragonite (I_{arag}) major peaks were close to the background intensity ($I_{\text{bgr}}=5-6$), the calculations of calcite/aragonite ratio for the corresponding sample were deemed unreliable.

TABLE 2. Main types of serpulid tube structures found or discussed during this study (based on Vinn *et al.* 2008). Abbreviations: H: horizontal section; L: longitudinal section; T: transverse section.
*main direction of orientation may be different from illustrated.

| Nature | Group | Structure name | | Principal structural units | Schematic diagram |
|---------|--------------------|----------------|----------------------------------------------|----------------------------------|---------------------------------------------------------------------------------------|
| | | abbreviation | full | | |
| Primary | Unoriented | IOP | Irregularly oriented prismatic | rice grain-shaped crystals |  |
| | | SIOP | Spherulitic irregularly oriented prismatic | sectorial spherulites |  |
| | | HAC | Homogenous angular crystal | irregular angular crystals |  |
| | Semi-oriented | SOIOP* | Semi-oriented irregularly oriented prismatic | rice grain-shaped crystals |  |
| | Oriented prismatic | SP | Simple prismatic | long rod-like prismatic crystals |  |
| | | SPHP | Spherulitic prismatic | sectorial spherulites |  |
| | Altered (?) | HG | Homogenous granular | isometric granules |  |

Taxonomy of Recent species

Genus *Bathyditrupa* Kupriyanova, 1993a

Bathyditrupa Kupriyanova 1993a: 21–22.—ten Hove & Kupriyanova 2009: 29.—Kupriyanova *et al.* 2011: 2–3.

Type species: *Bathyditrupa hovei* Kupriyanova, 1993a

Diagnosis (after ten Hove & Kupriyanova 2009): Tube white, opaque, free-lying, curved but not coiled, rectangular in cross-section; peristomes absent. Operculum inverse conical, with flat or slightly concave brown chitinous endplate. Opercular ampulla gradually merges (constriction absent) into thick, rather triangular peduncle with pinnules, but without wings. Peduncle inserted as 2nd dorsal radiole on either side. Pseudoperculum absent. Up to six radioles per lobe in semi-circular arrangement. Radiolar eyes not observed. Inter-radiolar membrane and stylodes absent. Mouth palps not observed. 5 thoracic chaetigerous segments, 4 of which uncinigerous. Collar not divided into lobes (=unlobed), short, with straight edge. Tonguelets between ventral and lateral collar parts absent. Thoracic membranes short, ending at 2nd chaetiger. Collar chaetae limbate capillaries. *Apomatus* chaetae absent. Thoracic uncini saw-to-rasp-shaped, with up to 4 (6) teeth in a transverse row above anterior peg, with about 15 curved teeth in a row in profile view. Anterior peg flat gouged. Thoracic triangular depression absent. Abdominal chaetae all capillaries, posterior ones slightly longer. Abdominal uncini rasp-shaped. Achaetous anterior abdominal zone short, just one or two segments. Posterior glandular pad absent.

Remarks. Morphology of the animals (operculum, peduncle, and thoracic membranes), general appearance of tube wall (crystal size, orientation, structure), and the outer layer in tubes of *Bathyditrupa hovei* are similar to those of *Spirodiscus grimaldii* and *S. groenlandicus* **comb. nov.** (see below), thus suggesting a close relationship of *Bathyditrupa* to *Spirodiscus*. However, a significant difference between *Spirodiscus* and *Bathyditrupa* is the structure of abdominal chaetae that are typical flat geniculate in the former, but are very unusual, simple capillary in the latter. Because of this difference, we propose maintaining *Bathyditrupa* as a valid genus until new data contradicting this assumption become available.

Bathyditrupa hovei Kupriyanova, 1993a

Figures 1B, C, 2, 3

Bathyditrupa hovei Kupriyanova, 1993a: 22–23, fig. 1.

Bathyditrupa hovei.—ten Hove & Kupriyanova 2009: 29, fig. 9; Kupriyanova *et al.* 2011: 46, fig. 2, 3.

Spirodiscus grimaldii.—Hartman & Fauchald 1971: 183 [in part, only in R/V CHAIN St. 100, ATLANTIS-II St. 118].

?*Filogranula* spp.—Hartman & Fauchald 1971: 182 [in part, R/V CHAIN St. 85, St. 100, R/V ATLANTIS-II, St. 155].

Material examined. R/V VITYAZ, North Pacific: St. 5620, 44°48'N, 156°33'E, 5070 m (11 spec. **SIO**, 1 tube used for SEM **PIN** 5485/08, 5485/09, and X-ray diffraction analysis, sample # 1); St. 5622, 45°14'N, 155°15'E, 5110 m (**holotype** and 1 **paratype SIO**); St. 5624, 45°26'N, 154°12'E, 5020 m (2 spec. **SIO**); St. 4279, 19°46'N, 120°17'W, 4104 m (1 tube **SIO**); St. 4281, 20°01'3"N, 121°59'W, 4370 m (4 spec. **SIO**); St. 6015, 26°51'5"N, 165°32'1"E, 5850 m (1 spec. **SIO**); St. 5074, 10°28'N, 140°01'W, 4833 m (1 tube **SIO**); St. 7391, 24°08'N, 143°46'1"E, 6330 m (3 spec. **SIO**); St. 4370, 26°04'2"N, 153°49'3"W, 6050 m (1 spec. **ZMA** V.Pol. 5325); St. 3151, 44°28'3"N, 170°07'E, 5237 m (3 tubes **ZMA** V.Pol. 5326).

R/V VITYAZ-2, North Atlantic: St. 79, 34°54.3'N, 45°39'W, 4440 m (2 spec. **SIO**, 1 tube used for SEM, **PIN** 5485/14, 5485/15, 5485/34, 5485/40, and X-ray diffraction analysis, sample # 2).

R/V CHAIN, North-West Atlantic: St. CH 85, 37°59.2'N, 69°26.2'W, 3834 m (14 spec. **LACM-AHF**); St. CH 100, 33°56.8'N, 65°47'W, 4892–4743 m (1 tube **LACM-AHF**).

R/V ATLANTIS-II, West Atlantic: St. 118, 32°19.4'N, 64°34.9'W, 1135–1153 m (5 spec. **LACM-AHF**); St. A155, 0°0.3'S, 27°78.0'W, 3730–3783 m (2 spec. **LACM-AHF**).

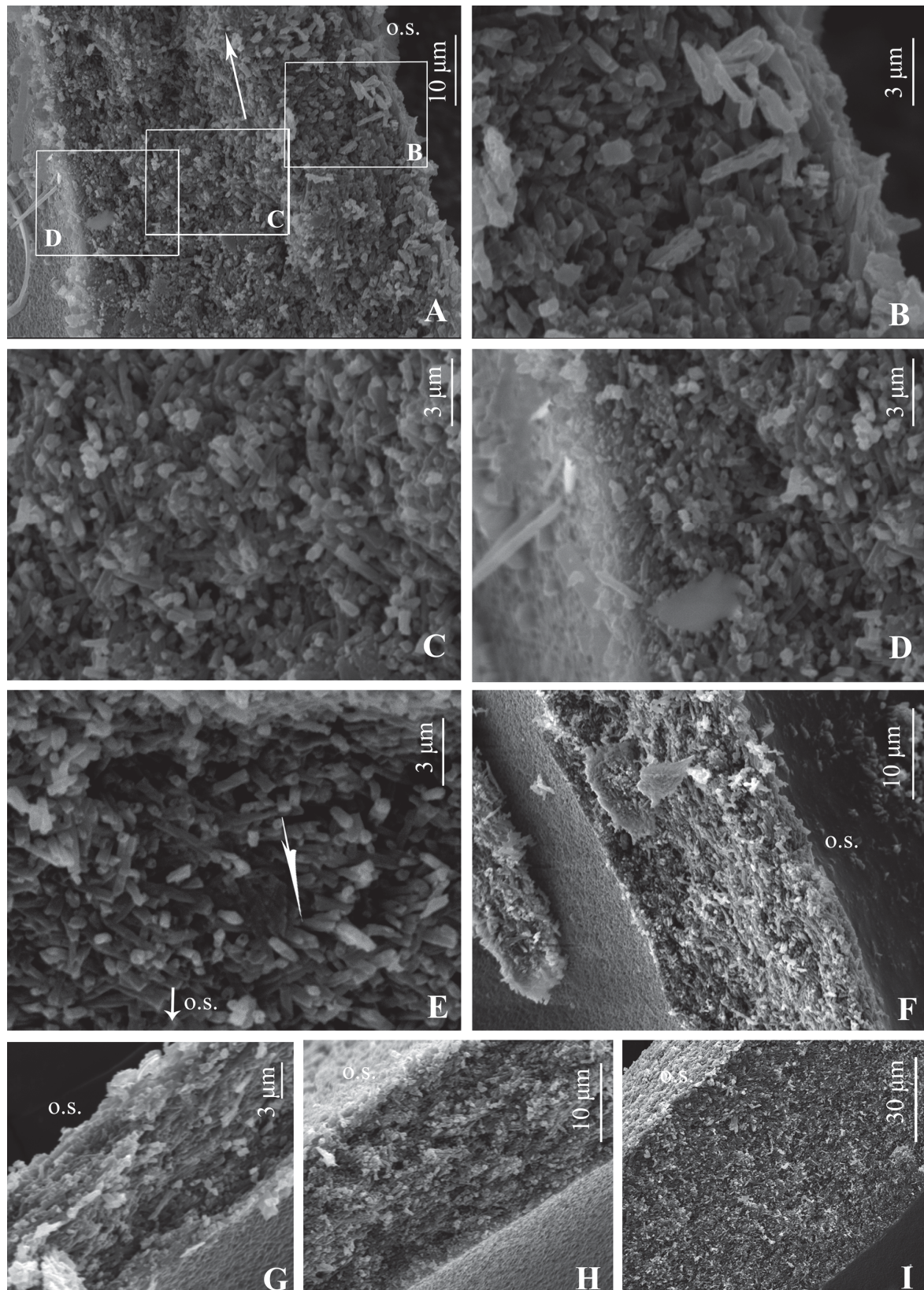


FIGURE 2. Tube ultrastructures of *Bathyditrupa hovei*. A–D: **PIN 5485/08**, A—longitudinal wall section, B—enlarged outer wall part, C—enlarged middle wall part consisting of elongated crystals, D—enlarged inner wall part showing a thin layer of smaller isometric crystals. E: **PIN 5485/09**, middle wall part showing loose transverse orientation of crystals (oblique section). F: **PIN 5485/11**, longitudinal wall section. G–I: **PIN 5485/15**, a series of tube fragments of different sizes (may belong to different specimens) showing no principal ultrastructural ontogenetic changes. Arrows indicate direction of tube growth. Abbreviation: o. s.—outer tube surface.

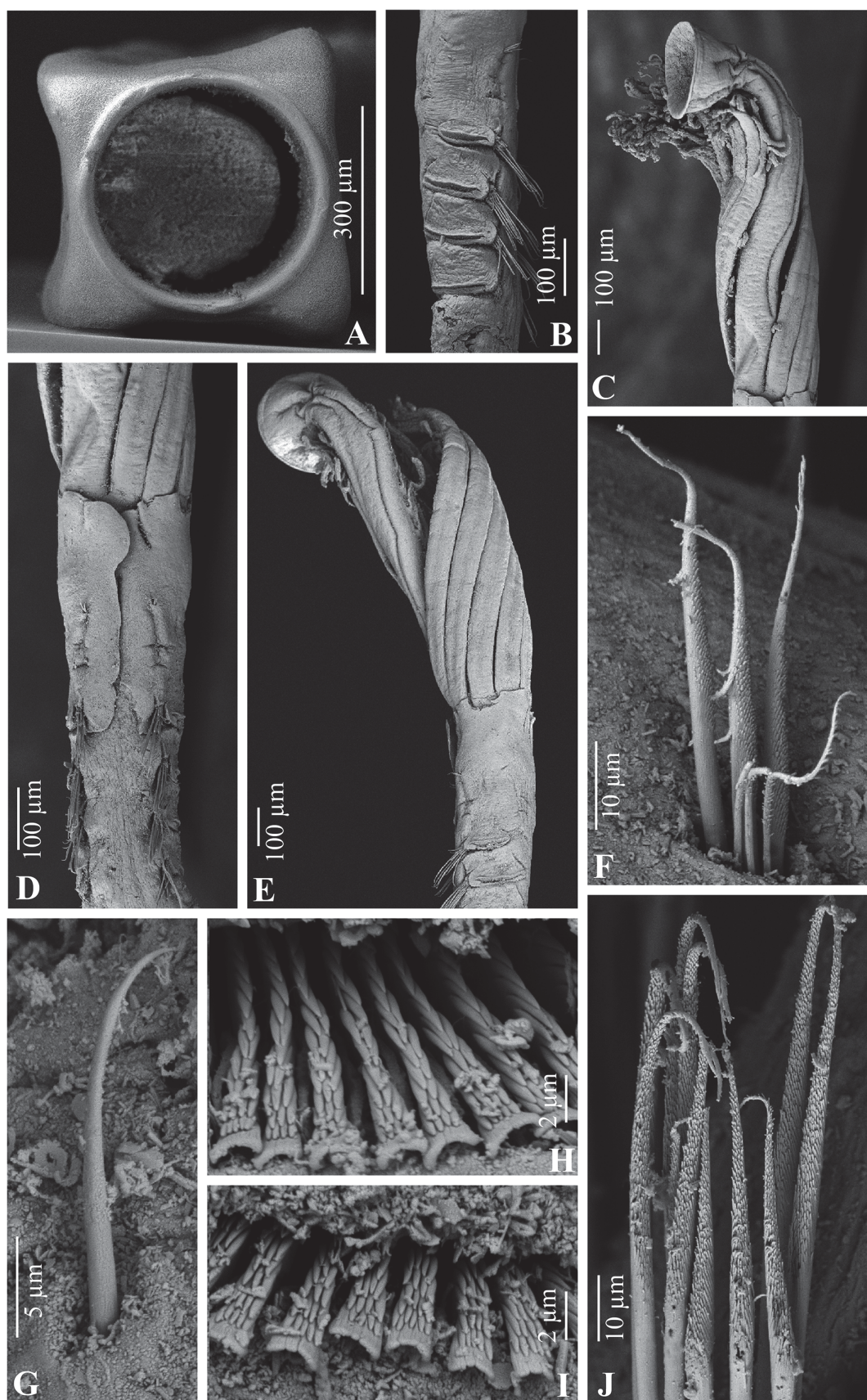


FIGURE 3. SEM images of *Bathyditrupa hovei* AM W.46394. A—anterior tube part, B—lateral view of thorax, C—radioles with operculum, D—dorsal view of thorax showing thoracic membranes, E—lateral view of thorax and radioles showing pinnulated peduncle, F—collar chaetae, G—abdominal chaeta, H—thoracic uncini, I—abdominal uncini, J—thoracic chaetae.

R/V KNORR, cruise 25, North-West Atlantic: St. 288, 25.2.1972, 11°02.2'N, 55°05.5'W, 4417–4429 m (1 spec. **MNHN** PNT 39).

R/V CRYOS, cruise ABYPLAINE, North-East Atlantic: St. 10-CP17, 11.6.1981, 42°44.5'N, 15°58.5'W, 4480 m (1 broken tube **MNHN** PNT 43); St. 10-CP18, 11.6.1981, 42°52.3'N, 15°53.1'W, 4330 m (2 spec., including 1 removed from broken into pieces tube **MNHN** PNT 42); St. 8-DS7, 30.5.1981, 34°06'N, 17°04'W, 4270 m (1 spec. in decalcified tube **MNHN** PNT 44); St. 12-DS13, 21.7.1983, 44°41.2'N, 17°49.0'W, 4990 m (2 spec. **MNHN** PNT 45); St. 11-DS11, 12.6.1981, 42°59.7'N, 14°05.4'W, 5260 m (2 spec. in decalcified tubes **MNHN** PNT 40); St. 12-DS12, 20.7.1983, 44°39.9'N, 17°52.9'W, 4990 m (3 spec. without tubes **MNHN** PNT 46); St. 11-CP20, 12.6.1981, 42°59.7'N, 14°07.2'W, 5260 m (1 dry specimen in brittle tube **MNHN** PNT 41); St. 2-DS1, 17.5.1981, 37°18'N, 15°33'W, 4260–4450 m (1 spec. **AM** W.46391); St. 8-CP11, 30.5.1981, 34°06.1'N, 17°06.3'W, 4270 m (8 spec. **AM** W.46392, 1 prepared for SEM **AM** W.46393 and **PIN** 5485/11); St. 10-DS10, 11.6.1981, 42°51.2'N, 15°55.3'W, 4270–4360 m (10 spec., 1 spec. prepared for SEM **AM** W.46394, 10 spec. **NBCL ZMA** V.Pol. 5549, 10 spec. **SMF** 23989, 5 spec. **NHMUK ANEA** 2015.927-936, 5 spec. **LACM-AHF** Poly 7021, 5 spec. **USNM** 1283058).

R/V JEAN CHARCOT, cruise WALVIS, South Atlantic, Cape Basin and Angola Basin: St. C-Pr44-DS7, 3.1.1979, 26°59.7'S, 1°07.1'E, 5100–5214 m (1 spec. **SMF** 23983); St. B-Pr37-DS5, 30.12.1978, 33°20.5'S, 2°34.9'E, 4560 m (1 spec. **SMF** 23982); same, cruise INCAL, SW Ireland - off Brittany: St. 2.4-Pr48-OS3, 4.8.1976, 46°02.5'N, 10°19.5'W, 4798 m (1 spec. **SMF** 23984); St. 2.3-Pr67-WS8, 9.8.1976, 47°30.5'N, 9°33.7'W, 4287–4301 m (1 spec. in decalcified tube **SMF** 23986); St. 2.4-Pr48-OS3, 4.8.1976, 46°02.9'N, 10°18.7.1'W, 4798 m (1 spec. **SMF** 23985); same, cruise DEMERABY: St. A-Pr29-DS2, 14.9.1980, 8°09.23'N, 49°04.37'W, 4430 m (1 spec. in decalcified tube **SMF** 23987); St. A-Pr51-KG9, 16.9.1980, 8°09.91'N, 49°03.47'W, 4440 m (1 spec. in decalcified tube **SMF** 23988).

Description. *Tube*: white opaque, free-lying, slightly curved (Fig. 1B, C), open at both ends; quadrangular in cross-section outer part, with flat to slightly concave sides (Fig. 2A), entirely opaque. Tube surface with transversal growth lines.

Tube ultrastructure: wall essentially unilayered with irregularly oriented prismatic ultrastructure (IOP *sensu* Vinn *et al.* 2008 = “criss-cross” *sensu* ten Hove & Zibrowius 1986; Sanfilippo 1998a, b; 2009, Fig. 2A), consisting of elongated cigar-shaped (most common) to isometric crystals. Innermost wall part (~1/5 of total thickness; Fig. 2D) made of smaller isometric crystals sized 0.5–1 µm consolidated by amorphous cement. Middle part of wall (Fig. 2C) with larger elongated rice grain-like crystals (length ~1.5–2 µm, diameter 0.5 µm). In some transverse sections elongated crystals oriented loosely parallel to tube surface (Fig. 2E, G). Outer part of wall (Fig. 2B) similar to middle one, but with a characteristic thin outer layer of ordered elongated rice grain-like crystals oriented more or less along tube length with their axes (SOIOP structure, see Table 2). No distinct border between inner, middle, and outer wall parts, all structures changing gradually. Crystal shapes and sizes not changing significantly during ontogeny (Fig. 2G–I). Parabolic growth lamellae indistinct, with parabolic axis displaced centrally within wall.

Tube mineralogy: sample # 1: 5% calcite ($I_{\text{calc}}=1$); 95% aragonite ($I_{\text{arag}}=20$); sample # 2: 8% calcite ($I_{\text{calc}}=3$); 92% aragonite ($I_{\text{arag}}=36$);

Radiolar crown: arrangement of radioles semi-circular, up to 4–6 pairs of radioles not joined by inter-radiolar membrane. Radiolar eyes not observed. Mouth palps absent.

Peduncle: inserted as 2nd dorsal radiole, three to five times thicker than radioles, slightly flattened, with pinnules (Fig. 3C, D).

Operculum: funnel-shaped, covered with concave brown chitinous endplate (Fig. 3C); opercular bulb continuing smoothly into peduncle, constriction absent.

Collar and thoracic membranes: collar not subdivided into lobes (entire), slightly shorter laterally than dorsally. Medium-sized incision along the ventral mid-line may be present. Thoracic membranes reaching up to 2nd chaetiger, about same width throughout (Fig. 3D).

Thorax: with 5 thoracic chaetigers, 4 of which uncinigerous (Fig. 3B). Collar chaetae a few short capillaries (Fig. 2F); other thoracic notochaetae limbate, with short slightly bent distal blades; *Apomatus* chaetae absent (Fig. 3J). Thoracic uncini saw-to-rasp-shaped with numerous (12–5) teeth in profile view (Fig. 3H); front uncinal view triangular, starting with one tooth posteriorly and ending in up to 5 teeth over wide gouged blunt anterior peg, dental formula P:5:4:3:3:3:2:2:1:1:1:1.

Abdomen: abdominal chaetigers 30–40. Uncini similar to thoracic ones, but rasp-shaped (Fig. 2I), dental formula P: 5(6):4(5):4:4:4:3:3:3:2:?:?. Chaetae short capillaries, slightly longer on posterior segments (Fig. 2G); each chaetiger with a single chaeta.

Size: total body length up to 15 mm, including up to 3 mm long radioles, width of thorax up to 0.35 mm. Tube length up to 25 mm. Maximum external tube diameter across angular margins up to 0.65 mm, in between up to 0.5 mm, corresponding lumen diameter 0.35–0.4 mm. Thickness of tube wall in between angular margins about 1/10th of outer diameter.

Distribution. Atlantic Ocean, bathyal—lower abyssal, 1135–5260 m, North and Central Pacific Ocean, 4104–6330 m.

Remarks. This species, characterised by distinct tusk-shaped quadrangular in cross-section tubes was originally described from depths of 5050–5620 m in the Kuril-Kamchatka Trench (Kupriyanova 1993a). Recently Kupriyanova *et al.* (2011) summarised published data and provided new records of this species from the North and Central Pacific Ocean. In this study the distribution range of *B. hovei* is extended to the bathyal-abyssal of the Atlantic Ocean.

Kupriyanova & Nishi (2011) showed that material reported as *Spirodiscus grimaldii* from three stations (R/V CHAIN St. 100, R/V ATLANTIS-II St. 118 and 119) in the Western Atlantic by Hartman & Fauchald (1971: 183) was in fact a mixture of several species and that two of these stations (CH100 and A118) had included *Bathyditrupa hovei*. Similarly, animals identified in Hartman & Fauchald (1971: 183) as ?*Filogranula* from stations CH85 and A155, also partly belonged to *B. hovei* as it is clear even from the description by Hartman & Fauchald (1971: 182): “Long, straight tubes, from Sta. Ch 85, are square in cross section, externally smooth and have a cylindrical lumen. The small, slender body measures less than 10 mm long, consists of 5 thoracic and 30 to 40 abdominal setigers; the crown consists of four or five pairs of radioles, of which the dorsalmost is modified as an operculum, with thick, fleshy stalk and sparse numbers of barbules limited to its ventro-basal part. The opercular disk is circular, infundibular, lightly chitinized and minutely crenulated at its margin. The collar segment is the longest; it has simple collar setae, and the last four setigers are uncinigerous. Abdominal segments are short and crowded”. In addition to *Bathyditrupa hovei*, station CH85 also included numerous specimens of *Spirodiscus groenlandicus* **comb. nov.** in octagonal tubes (see below).

Kupriyanova *et al.* (2014) reported *Bathyditrupa hovei* to have aragonitic tubes with IOP structure, therefore, data herein principally agree with the earlier ones. However, as we used X-ray diffraction (direct quantitative method), precise calcite/aragonite ratios are now available for this species for the first time. Details of crystal arrangement along the outer tube surface were also observed for the first time.

Ten Hove (pers. comm.) noticed 10 oblong eggs, 120–140 µm long and 50–60 µm wide, inside the tube of along the abdomen of the specimen from **NBCL ZMA V.Pol. 5325**, which suggests that the species is a lecithotrophic intratubular brooder.

Genus *Spirodiscus* Fauvel, 1909

Spirodiscus Fauvel, 1909: 56–57.—Fauchald 1977: 147.

Nogrobs.—ten Hove & Kupriyanova 2009: 68–69.—Kupriyanova & Nishi 2011: 1–2.

Type species: *Spirodiscus grimaldii* Fauvel, 1909

Diagnosis (after Kupriyanova & Nishi 2011, emend.): Tube white, free-lying, polygonal in cross-section, quadrangular or octagonal (= modified quadrangular), straight to slightly curved (tusk-shaped), or initially cylindrical, then quadrangular in cross-section and coiled clockwise into a flat spiral, finally with short cylindrical straight distal part. Peristomes absent. Operculum inverse cone (ampulla) with chitinous endplate and central depression. Peduncle thick, pinnulated, without distal wings, with dorsal 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, radiolar eyes, and stylodes absent. Mouth palps absent. 5 or 6 thoracic chaetigerous segments. Collar non-lobed with straight edge, no clear separation towards thoracic membranes that end at second chaetiger; tonguelets between ventral and lateral collar parts absent. No apron. Collar chaetae limbate. *Apomatus* chaetae absent. Thoracic uncini saw-to-rasp-shaped with numerous teeth (> 12) in profile, 2–3 teeth per row; anterior peg gouged. Thoracic

triangular depression absent. Abdominal chaetae short, with flat triangular denticulate blade; uncini similar to thoracic ones. Achaetous anterior abdominal zone absent. Long posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. The Recent genus *Spirodiscus* Fauvel, 1909, characterised by an unattached quadrangular tube coiled into a flat spiral (hence the generic name), was synonymised with the fossil *Nogrobs* de Montfort, 1808 by Jäger (2005). This was supported by ten Hove & Kupriyanova (2009) and Kupriyanova & Nishi (2011). However, tubes of Recent *Spirodiscus grimaldii* are strictly clockwise coiled (when looking from the upper side), while known populations of fossil representatives of genus *Nogrobs* demonstrate a mixture of clockwise and anticlockwise coiled specimens (Ippolitov, unpubl.). At the same time, although coiling direction appears to be a morphological argument against Jäger's synonymy, this character is not very important taxonomically. The results of comparative SEM studies of tube wall ultrastructures (see below) show very different crystal arrangement in *Spirodiscus* and in the type species of genus *Nogrobs*, thus indicating that these genera should not be synonymised.

Spirodiscus grimaldii and *S. groenlandicus* **comb. nov.** (formerly *Ditrupa groenlandica*) described below, have very different tube morphologies: coiled tetragonal in the former and tusk-shaped octagonal in the latter. However, the animals inhabiting these tubes are very similar (except for five thoracic chaetigers in *S. groenlandicus* **comb. nov.** and six in *S. grimaldii*) and have identical chaetation patterns. Their tube walls also show similar ultrastructures having a well-defined outer layer with characteristic crystal orientation (see below). All this indicates that *S. grimaldii* and *S. groenlandicus* **comb. nov.** are closely related and justifies placing them into one genus. The generic diagnosis here has been emended to include species with both coiled tetragonal and straight octagonal tubes.

***Spirodiscus grimaldii* Fauvel, 1909**

Figures 1A, 4, 5

Spirodiscus grimaldii Fauvel, 1909: 56–57, fig. 4.

Spirodiscus grimaldii.—Fauvel 1914: 335–338, pl. 29, fig. 7–21.—Belloc 1953: 8.—Hartman & Fauchald 1971: 183 [in part, R/V ATLANTIS-II, St. 119 only, see Kupriyanova & Nishi 2011 for discussion of Hartman & Fauchald 1971 material].—in Zibrowius 1977: 299 [comments on Hartman & Fauchald 1971 material].—in Garcia-Diez *et al.* 2005: 44: [name only].—in Fabri *et al.* 2006 [database name only].

Serpulidae A.—Maurer & Williams 1988: 692.

Spirodiscus.—ten Hove, 1984: 189 [mentioned specimen off the Cape Verde Islands].

Nogrobs grimaldii.—ten Hove & Kupriyanova 2009: 68–69, fig. 31; Kupriyanova & Nishi 2011: 2, fig. 1.

Material examined. Prince of Monaco, cruises 1896, 1902, off Azores: St. 1334, 13.8.1902, 39°30'N, 29°02'15"W, 1900 m (1 syntype in tube MNHN POLY TYPE 237, 4 syntypes, including 3 tubes and 1 spec. without tube MOM 18 0883); St. 698, 18.7.1896, 39°11'N, 30°44'40"E, 1846 m (2 syntypes in tubes and 4 tube fragments MOM 18 0475); St. 683, 7.7.1896, 38°20'N, 28°04'45"W, 1550 m (3 spec. MOM); St. 703, 19.7.1896, 39°21'20"N, 31°05'45"W, 360 m (3 spec. MOM); St. 719, 27.7.1896, 39°11'N, 30°24'15"W, 1600 m (3 spec. MOM); St. 738, 7.8.1896, 37°40'N, 26°26'15"W, 1919 m (1 spec. MOM).

R/V ATLANTIS-II, off Bermuda, cruise 24: St. A119, 19.8.1966, 32°15.8' to 32°16.1'N, 64°31.6' to 64°32.6'W, 2095–2223 m (2 tubes LACM-AHF).

Bathyscaph ARCHIMEDE, cruise 1969, Azores: Dive 12, 19.8.1969, 38°03.0'N, 25°28.3'W, 1990–2110 m (1 spec. MNHN PNT 37); Dive 15, 29.8.1969, 37°20.2'N, 25°27.5'W, 2000 m (1 spec. in broken tube MNHN PNT 38).

R/V JEAN CHARCOT, cruise BIACORES, Azores: St. 54A, 13.10.1971, 38°12'N, 28°15'W, 1810 m (1 empty tube MNHN PNT 34); St. 86, 17.10.1971, 39°25.5'N, 28°01.5'W, 1670 m (1 spec. MNHN PNT 35); St. 92, 17.10.1971, 39°03.5'N, 28°27.5'W, 2450 m (10 spec. MNHN PNT 36, 7 spec. AM W.46395, 1 spec. used for SEM AM W.46396); St. 95, 18.10.1971, 39°03.5'N, 28°25.5'W, 2440 m (5 spec. AM W.46397, 5 spec. NBCL ZMA V.Pol 5548, 5 spec. SMF 23974, 5 spec. NHMUK ANEA 2015.922–926, 5 spec. LACM-AHF Poly 7020, 5 spec. USNM 1283057); St. 120, 20.10.1971, 39°03.5'N, 32°43.5'W, 2100 m (1 empty tube SMF 23975); St. 126, 23.10.1971, 39°19.5'N, 32°47'W, 3360 m (6 spec. SMF 23976); St. 171, 1.11.1971, 37°58.5'N, 26°07'W, 3215 m (1 spec. SMF 23977); St. 173, 2.11.1971, 37°57'N, 26°08'W, 3225 m (4 spec. NBCL ZMA V.Pol 5547, 3 spec.

LACM-AHF Poly 7019); St. 174, 2.11.1971, 38°06'N, 26°15'W, 3050–3100 m (3 empty tubes **SMF** 23978); St. 206, 7.11.1971, 37°21'N, 26°28.5'W, 2085–2096 m (1 spec. **SMF** 23979); St. 227, 10.11.1971, 37°10'N, 26°19.5'W, 2160–2180 m (2 spec. **NBCL ZMA** V.Pol 5546).

R/V **MARION DUFRESNE**, cruise MD50, Amsterdam Island: St. 5-DC34, 13.7.1986, 37°40.33'S, 77°30.50'E, 2200 m (2 spec. **MNHN** PNT 33); same, cruise MD32, Reunion Island: St. DR104, 30.8.1982, 20°48.6'S, 55°01.4'E, 1875–1920 m (1 spec. **SMF** 23980); St. DR139, 3.9.1982, 20°46.5'S, 55°38.3'E, 1575–1600 m (1 empty old tube **SMF** 23981).

R/V **LE SUROIT**, cruise SEAMOUNT 2, Atlantis Seamount: St. TS 267: 4.2.1993, 34°22.48'N, 30°22.48'W, 2235 m (1 spec. **MNHN** PNT 32).

R/V **VITYAZ-2**, south-west of Azores, St. 78, 34°41'1" N, 40°38'6" W, 3160 m (1 tube prepared for SEM and for X-ray diffraction analysis **PIN** 5485/10).

Description. *Tube*: white opaque, free-lying, its most obvious part clockwise coiled into a flat spiral of 2.5 whorls (Fig. 1A). However, initial tube straight, with circular cross-section (these posterior parts always broken off and lost, at best parts about 1 mm long may be preserved), growing straight upwards, abruptly turning to flat spiral perpendicular to initial tube, and with cross-section becoming quadrangular. Anterior tube part straight, pointing away from spiral in plane of coiling, smooth and circular in cross-section. Sides of quadrangular section flat to slightly convex. Outer convex side of spiral part with a median rib. Peristomes absent.

Tube ultrastructure: wall unilayered, structure is mostly irregularly oriented prismatic (IOP). Inner wall part (Fig. 4D, H) made of more or less isometric crystals up to 0.5 µm in diameter. Middle part consisting of crystals of rice grain-like shape (length 2–2.5 µm, diameter 0.5 µm) loosely oriented parallel to tube surface (Fig. 4C, I) and thus ultrastructure is transforming to semi-ordered irregularly oriented prismatic (SOIOP). Outer part of wall made of larger crystals (length 3–3.5 µm, diameter 1 µm), oriented subparallel to tube surface (Fig. 4B, J). Neighbouring crystals with the same orientation may form “packets” (Fig. 4J), such pattern sometimes can present in the middle part of wall (Fig. 4I), but with smaller crystals and less definite orientation. Parabolic growth lamellae indistinct.

Tube mineralogy: 8% calcite ($I_{\text{calc}}=12$), 92% aragonite ($I_{\text{arag}}=134$).

Radiolar crown: radiole arrangement semi-circular, up to 8 per lobe.

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 (Fig. 5A, B).

Operculum: inverse cone (ampulla) with chitinous endplate and central depression (Fig. 5A). Pseudoperculum absent.

Thorax: with 6 thoracic chaetigerous segments, 5 of which uncinigerous (Fig. 5A, B). Collar non-lobed with entire edge, no clear separation towards thoracic membranes that end at second chaetiger. No apron. Collar chaetae and remaining thoracic chaetae limbate, of two sizes; *Apomatus* chaetae absent (Fig. 5C, D). Thoracic uncini saw-to-rasp-shaped with numerous teeth (> 12) in profile, 4–5 teeth per row above flattened gouged anterior peg, one tooth per row posteriorly (dental formula P:4:4:4:3:3:2:1:1:1:1:1:1:1)(Fig. 5E).

Abdomen: with up to 40 chaetigers. Chaetae short, with flat triangular denticulate blade (Fig. 5F). Long posterior capillary chaetae absent. Uncini similar to thoracic ones, but rasp-shaped, dental (formula P:6:5:5:4:4:4:3:3:3:2:2:2:2) (Fig. 5G). Achaetous anterior abdominal zone absent. Posterior glandular pad absent.

Size: total body length up to 10 mm, including up to 3.5 mm long radioles, width of thorax up to 0.35 mm. Diameter of tube spiral 3–4 mm, tube outer diameter within coiled part 0.5–0.55 mm, corresponding lumen diameter 0.35–0.4 mm. Thickness of tube wall in between angular margins about 1/10th of outer diameter.

Distribution. North Atlantic Ocean, Indian Ocean (Amsterdam Island, Reunion Island), 360–3550 m.

Remarks. *Spirodiscus grimaldii* was described and illustrated by Fauvel (1909) based on multiple specimens (syntypes) from two stations of the Prince of Monaco expeditions to the Azores (St. 698 and St. 1334). In the catalogue of the polychaete type collection at **MOM**, Belloc (1953) mentioned material from four additional stations in the Azores (St. 683, 703, 719, 738), but did not provide any further information. These samples have been verified by Helmut Zibrowius (pers. comm.) who did not record the number of specimens in each sample (numbers of specimens were kindly provided by Michele Bruni, **MOM**), but confirmed them to be typical *S. grimaldii* already identified and labelled by Fauvel (labels are in his handwriting). However, specimens from these four stations did not appear to be the syntypes of *S. grimaldii* (Bruni, **MOM**, pers. comm.) as claimed by Belloc (1953). Kupriyanova & Nishi (2011) followed Zibrowius (pers. comm.) who stated that the label of the type at

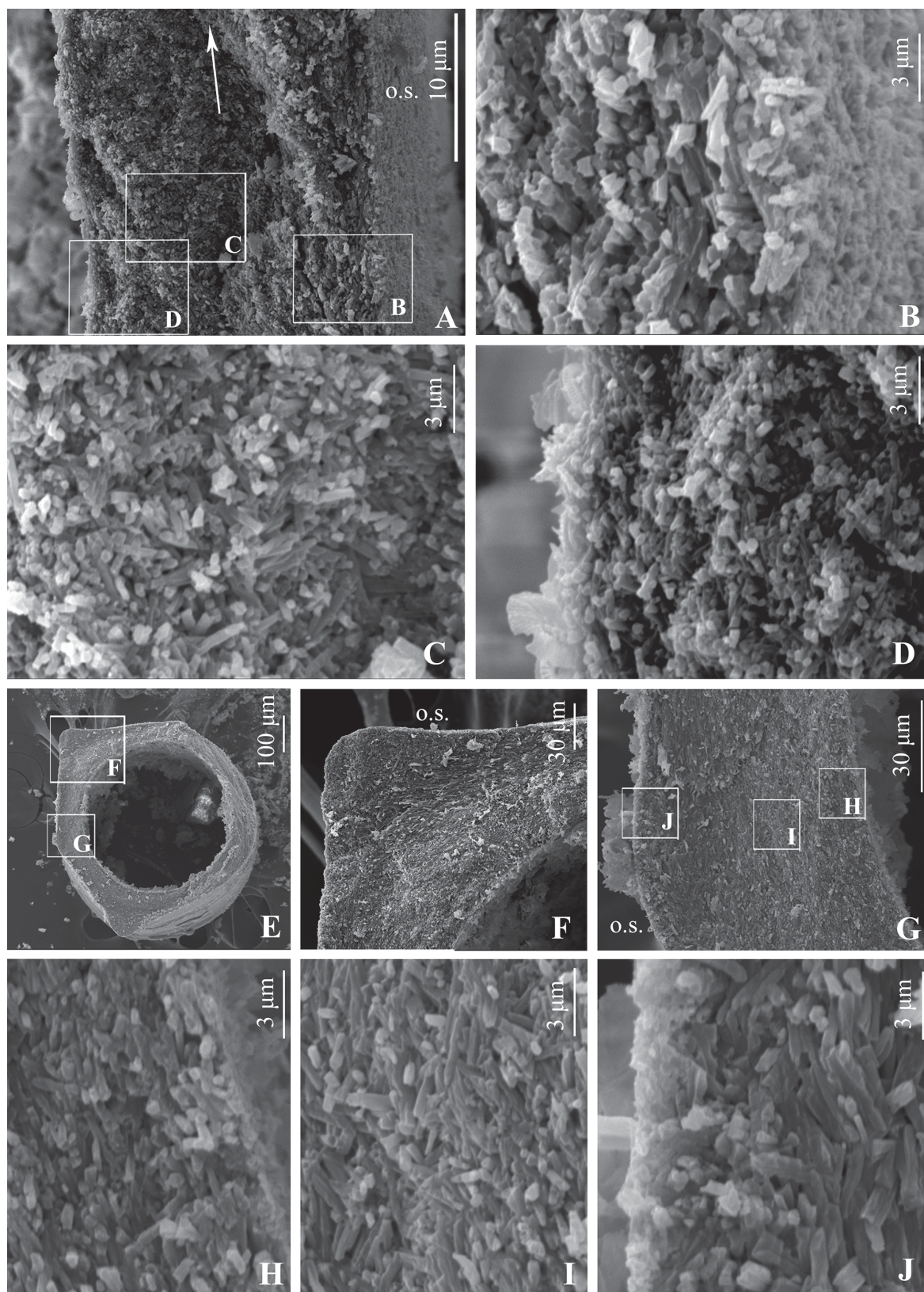


FIGURE 4. Tube ultrastructures of *Spirodiscus grimaldii*. A–J: PIN 5485/10, A—longitudinal wall section, B—enlarged outer part with a layer of crystals oriented in two directions subparallel to surface, C—enlarged middle wall part consisting of elongated crystals, D—enlarged inner wall part showing consolidated isometric crystals, E—tube cross-section, median rib clearly visible to the left, F—enlarged tube wall section through lateral keel, G—enlarged tube wall section through median keel, H—enlarged inner wall part, I—middle wall part, J—outer wall part, layer with two-direction crystal orientation resembling a pile of isometric crystals. Arrows indicate direction of tube growth. Abbreviation: o. s.—outer tube surface.

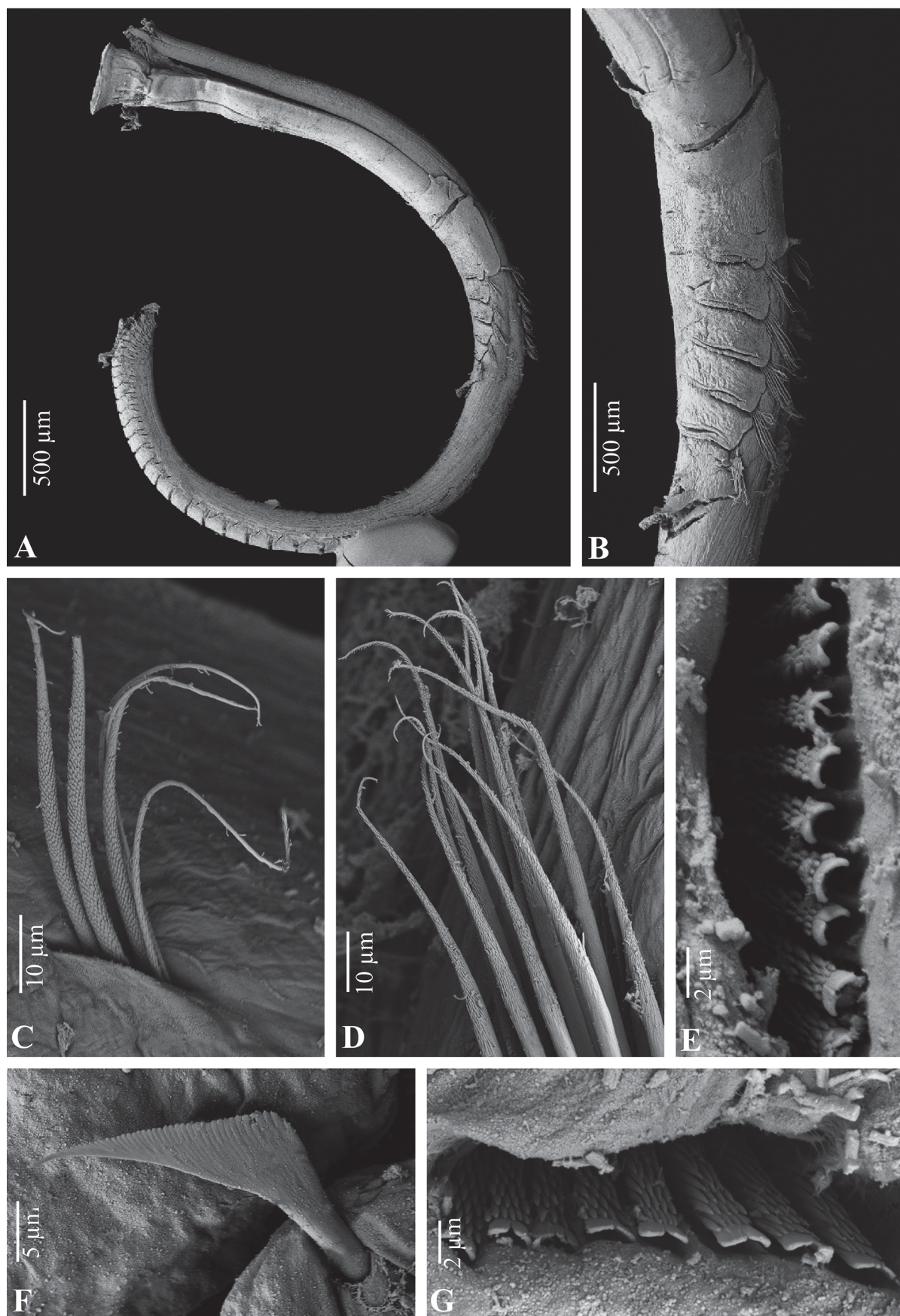


FIGURE 5. SEM images of *Spirodiscus grimaldii* AM W.46396. A—lateral view of entire animal, B—close-up view of the thorax, C—collar chaetae, D—thoracic uncini, E—thoracic uncini, F—anterior abdominal chaeta, G—abdominal uncini.

MNHN did not indicate the station of origin, but suggested the specimens were likely to be from St. 1334, as no material from this station had been deposited at **MOM** (Zibrowius, pers. comm.). However, the material from St. 1334 is present at **MOM** (Bruni, pers. comm.) and also the origin of the syntype **MNHN** POLY TYPE 237 is clearly indicated as St. 1334 (Mezaine, **MNHN**, pers. comm.).

The material (R/V JEAN CHARCOT, ZMA V.Pol. 3906) reported in ten Hove & Kupriyanova (2009) was collected in 1971 from the Azores and thereby is almost topotypical. Recently, Kupriyanova & Nishi (2011) summarised and refuted all previous records of *S. grimaldii* and provided several new ones, including topotypical material from the Azores collected by R/V VITYAZ-2. Hartman & Fauchald (1971: 183) reported *Spirodiscus grimaldii* from 3 stations in the western Atlantic. The specimen from R/V CHAIN, St. 100 from **LACM-AHF** available to Zibrowius (1977), proved to be a straight tube of *Bathyditrupa hovei* (see Kupriyanova & Nishi 2011). Material from R/V ATLANTIS-II stations not available to Zibrowius (1977) was re-examined by EKK (Kupriyanova & Nishi 2011), who confirmed that it was also partly misidentified since R/V ATLANTIS-II, St. A118 did not contain *Spirodiscus grimaldii* at all, whereas St. A119 contained two apparently empty coiled *S. grimaldii* tubes mixed with tubes of two unidentified species. The material reported here as new records was obtained in the Indian Ocean, near Reunion and Amsterdam Islands.

Kupriyanova & Nishi (2011) provided a new record of two *Spirodiscus* specimens in spiral tubes from the Pacific Ocean (**LACM-AHF** collection), but stated that specific attribution of these animals was uncertain. According to ten Hove & Kupriyanova (2009), the specimens from off the Galapagos (**ZMA** V.Pol. 3859) belong to an undescribed species of *Spirodiscus*. A specimen from the Pacific St. H361 of ECHO-1 survey (**LACM-AHF**) had a typical *Spirodiscus*-type tube, with six thoracic chaetigers and a thick pinnulated peduncle bearing typical for this species operculum covered with a concave endplate. It might also belong to the same species as **ZMA** V.Pol. 3859, and thus, further detailed comparative study is needed.

The form of coiling typical for *S. grimaldii* is similar to that found in some species of fossil *Nogrobs*, including *N. vermicularis* de Montfort, 1808 (the type species), *N. tumidus* (J. de C. Sowerby, 1829), and *Tubulostium discoideum* Stoliczka, 1868, that also have straight anterior tube parts. However, straight anterior parts are common for all free-lying spirally coiled medium-sized fossil genera, even those lacking tetragonal sections (e.g., Regenhardt 1961, pl. 8, fig. 9, 12). In the also spirally coiled tubes of spirorbins, the initial tube parts (if preserved at all) are not perpendicular to the whorls, but more or less in line with them (compare Malaquin 1904: 66 fig.1).

***Spirodiscus groenlandicus* (McIntosh, 1877) comb. nov.**

Figures 1D, 6, 7

Ditrypa [sic!] *groenlandica* McIntosh, 1877: 219.

Ditrypa groenlandica.—McIntosh 1879: 509, fig. 1A–B.—Hartman 1959: 573.—1971: 1426.—Zibrowius 1977: 292.

Ditrypa grönlandica.—Ditlevsen 1914: 732.

?*Filogramula* spp.—Hartman & Fauchald 1971: 182 [in part, only in R/V CHAIN St. 85].

Material examined. R/V DISCOVERY, cruise 92, North-East Atlantic, south-west of Ireland: St. 9756 #14, 15.4.1978, 50°04.0'N, 13°55.6'W, 3680–3697 m (**neotype** **NHMUK** ANEA 2015.972, 1 spec. prepared for SEM **AM** W.46398).

R/V CRYOS, cruise ABYPLAINE: St. 10-DS10, 11.6.1981, 42°51.2'N, 15°55.3'W, 4270–4360 m (4 spec. **MNHN** PNT 26, 3 spec. **SMF** 23973, 1 spec. prepared X-ray diffraction analysis sample #1).

R/V LE SUROIT, cruise BENTHEDI, North Madagascar: St. 87CH, 3.4.1977, 11°44'S, 47°35'E, 3716 m (5 spec. **NBCL** **ZMA** V.Pol. 5542, 3 spec. **LACM-AHF** Poly 7015, 3 spec. **NHMUK** ANEA 2015. 973–975); St. 90CH, 4.4.1977, 11°44'S, 47°30'E, 3700 m (3 spec. in tubes plus 1 removed, **AM** W.46399, tube fragments prepared for SEM **PIN** 5485/12 and X-ray diffraction analysis sample #2, 2 spec. **USNM** 1283053).

R/V MARION DUFRESNE, cruise MD 20, South-Eastern Madagascar: St. 15-CP8, 2.9.1979, 31°52.0'S, 48°28.8'E, 3825 m (1 spec. **SMF** 23972).

R/V CHAIN, St. 85, 37°59.2'N, 69°26.2'W, 3834 m (53 spec. and tubes **LACM-AHF**).

R/V VITYAZ-2, North Atlantic Ocean, St. 79, 34°54.3'N, 45°39.0'W, 4440 m (1 dry spec. in tube **SIO**).

Description. *Tube*: white opaque, free-lying, tusk-shaped, slowly expanding, octagonal in cross-section, with 8 smooth keels (longitudinal ridges) arranged all around the tube and grouped by pairs (Fig. 6F, 7B). In spaces

between two neighbouring keels (forming one pair) walls slightly thicker than in spaces separating different pairs. Sides between keels concave. Short growth stops resembling tiny irregularly displaced transverse constrictions present.

Tube ultrastructure: wall (Fig. 6A) with two layers consisting of elongated rice grain-shaped crystals. Inner layer of irregularly oriented prismatic structure (IOP), crystal length up to 1.5–2.5 μm , diameter 0.5 μm . Innermost part of inner layer (Fig. 6D) with isometric or slightly elongated crystals less than 0.5 μm long, with long axes oriented more or less along growth lines of parabolic lamellae. Middle and outer parts of inner layer (Fig. 6C) consisting of elongated crystals of slightly larger size, oriented more or less along the growth lines with their long axes. Transition from inner to middle part of wall gradual, size of crystals gradually increasing towards outer tube surface. Outer layer (Fig. 6B, E) very distinct, consisting of largest crystals, 4–5 μm long, 0.75–1 μm in diameter. Crystals of outer layer tending to form “bundles” of uniform orientation, lying more or less longitudinally along the surface (SOIOP structure). In transverse sections this layer usually looking like a pile of isometric crystals (Fig. 6H) and hardly recognizable. Thickness of outer layer 5–12 μm (corresponding wall thickness 50 μm), no distinct boundary with inner layer. Parabolic lamellae often clearly visible (Fig. 6A), marked by orientation of elongated crystals.

Tube mineralogy: sample #1: 100% aragonite ($I_{\text{arag}}=71$); sample #2: 6% calcite ($I_{\text{calc}}=2$), 94% aragonite ($I_{\text{arag}}=30$).

Radiolar crown: 3–5 pairs of radioles not joined by inter-radiolar membrane. Radiolar eyes not visible in preserved material.

Peduncle: inserted as 2nd dorsal radiole, about twice as thick as radioles, with pinnules (Fig. 7C, F).

Operculum: funnel-shaped, covered with concave brown chitinous endplate (Fig. 7C, F); opercular bulb continuing smoothly into peduncle, constriction absent.

Collar and thoracic membranes: collar four-lobed, short, continuing into thoracic membranes reaching up to 2nd chaetiger (Fig. 7E).

Thorax: with 5 thoracic chaetigers, 4 of which uncinigerous (Fig. 7C). Collar chaetae simple limbate only (Fig. 7F), of two sizes. Chaetae thick with distal limba, of two sizes, *Apomatus* chaetae absent (Fig. 7G). Uncini saw-to-rasp-shaped, with 3–5 rows above wide peg divided into 2 (occasionally 3) lobes; with 14–15 teeth in profile view (Fig. 7H). Dental formula slightly variable within a row of uncini, P:4:4:4:3:3:3:2:2:2:1:1:1:1, or similar (e.g. P:4:3:3:2:..., etc). Achaetigerous zone between thorax and abdomen absent.

Abdomen: with up to 40 segments. Chaetae short, with flat triangular denticulate blade (Fig. 7I), slightly longer on posteriormost segments (Fig. 7L); each torus with a single chaeta. Uncini rasp-shaped, with 9–12 teeth in profile view and 5–6 rows, dental formula P:6:5:5:5:5:4:4:3:3:3 (Fig. 7J).

Size: total body length up to 12 mm, including up to 1.5 mm long radioles, width of thorax up to 0.2 mm. Tube length up to 13 mm. Maximum external tube diameter in between angular margins up to 0.45 mm, corresponding lumen diameter 0.25 mm. Thickness of tube wall in between keels about 1/4–1/5th of the outer diameter, up to 1/2 when measured across keels.

Distribution. North Atlantic Ocean, 3404–4400 m; Indian Ocean, Madagascar, 3404–3716 m.

Remarks. This species is currently listed as *nomen dubium* in WORMS (ten Hove 2010). It was first found in 1875 as an empty tube from an abyssal location (3404 m or 2660 m) in the North-West Atlantic, Labrador Sea (R/V VALOROUS, St. 12, 56°11'N, 57°41'W). The origin was incorrectly given as Davis Strait by Ditlevsen (1914) and Hartman (1959, 1971). In fact, it had been collected considerably further south in the North-West Atlantic on the return trip of an expedition to Davis Strait. The species was originally described as *Ditrypa groenlandica* by McIntosh (1877) who wrote: “The tube is about half an inch in length, not much thicker than a thread, and curved from end to end like a bow (fig. 1). It tapers very gradually from the anterior to the posterior end, contrasting in this respect with the more decided diminution in *D. arietina*. The oval aperture (fig. 2) forms a smooth slightly constricted rim, which is narrower than the tube almost by the depth of the ridges. The latter are eight in number, and run from the anterior to the posterior end of the tube, though, it must, be added, none of the specimens were quite perfect. It was obtained from station ISTo. 12 (1450 fathoms). It differs from any other *Ditrypa* known to me in its slender form and the well-marked longitudinal ridges.”

Zibrowius (1977: 292) commented: “looks strange for a serpulid, but C. P. Palmer (in litt.) suggested that it is not a scaphopod mollusc because of the unusually low expansion rate”. The species remained enigmatic for decades, the type being lost. The problem is resolved now, as specimens that fit McIntosh's description and

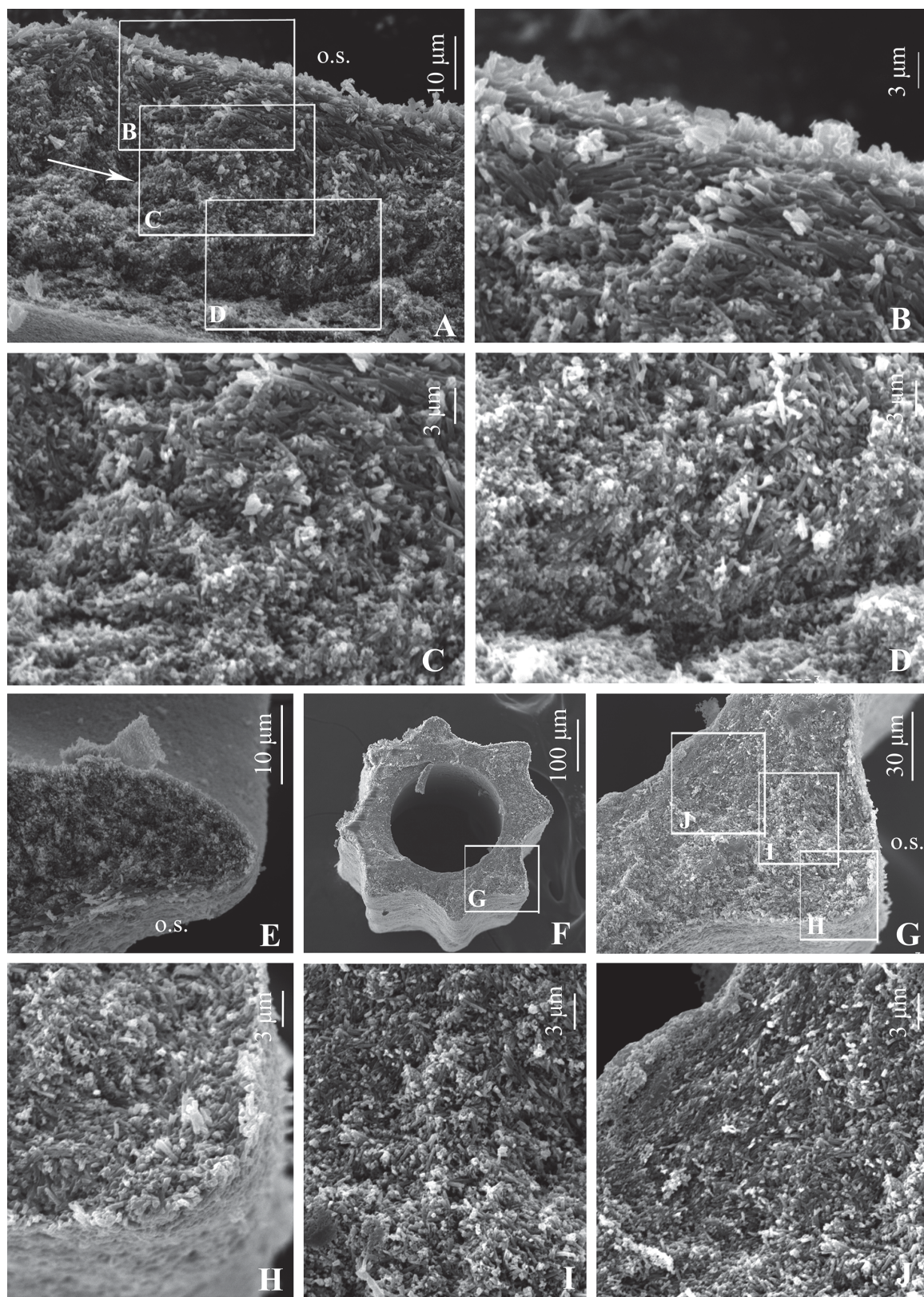


FIGURE 6. Tube ultrastructures of *Spirodiscus groenlandicus* **comb. nov.** A–J: PIN 5485/12, A—longitudinal wall section, B—enlarged outer part with a layer consisting of large cigar-shaped crystals packed in bundles oriented in two directions, C—enlarged middle wall part consisting of small elongated crystals, D—enlarged middle (right) and inner (left) parts of tube wall, the latter consisting of very small consolidated isometric crystals, E—longitudinal wall section near tube mouth, F—tube cross-section, edges grouped by two, G—enlarged edge section, H—enlarged outer wall part, outer layer resembling a pile of isometric crystals, I—details of middle wall part, J—details of inner wall part. Arrows indicate direction of tube growth (where known). Abbreviations: o. s.—outer tube surface.

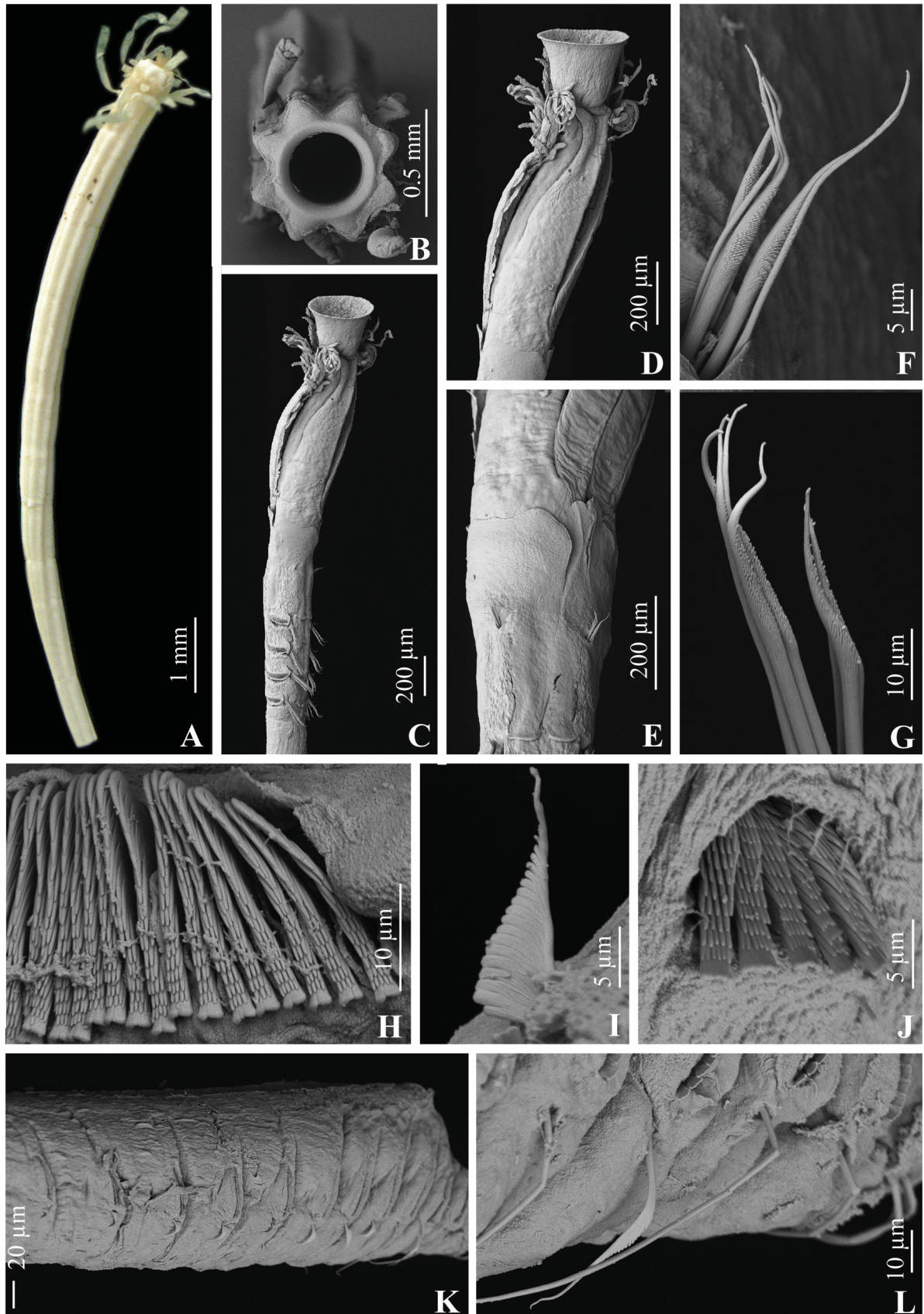


FIGURE 7. Photos and SEM images of *Spirodiscus groenlandicus* **comb. nov.** AM W.46398. A: tube photo, B–L: SEM images, B—anterior view of the tube entrance, C—anterior view of an animal, D—close-up view of radiolar crown with operculum, E—thoracic membranes, F—collar chaetae, G—thoracic uncini, H—thoracic uncini, I—abdominal chaeta, J—abdominal uncini, K and L—posterior part of abdomen showing flat geniculate and capillary chaetae.

illustration are available from deep dredging in the North-East Atlantic. Moreover, material of Hartman & Fauchald (1971) from the North-Western Atlantic reported as ?*Filogranula* spp. and re-examined by EKK contained numerous specimens of *S. groenlandicus* **comb. nov.** in typical free tusk-shaped octagonal tubes. An additional dried specimen in the tube collected from North-Western Atlantic was found in SIO collections (Fig. 1D). Very similar free small-sized serpulid tubes with 8 longitudinal ridges from the SW Indian Ocean (depth about 3000 m) appear to be the same species.

The fact that tube keels are grouped by pairs (Fig. 6F; Fig. 7B) suggests that tetragonal cross-section probably was plesiomorphic, and subsequent bifurcation of keels resulting in octagonal cross-section is a secondary, apomorphic, modification. Fossil material provides examples of species with a similar morphology. Regenhardt (1961) established a taxon "Octogonae" of uncertain rank, but with the "generotype" *Dentalium octocostatum* Fraas, 1867, for octagonal tubes from the Late Cretaceous of Europe. Ziegler (2006) redescribed the same group of species as the genus *Octogonella* nov. gen., but designated another type species, *Ditrupula faxensis* Brünnich Nielsen, 1931. *D. octocostatum* has long large tubes (outer diameter up to 7–8 mm), curved somewhat irregularly, and clearly is not related to *S. groenlandicus* **comb. nov.** Instead, it is likely a member of the genus *Pyrgopolon* de Montfort, 1808 *sensu* Jäger 2005. *Ditrupula faxensis* has smaller tubes (outer diameter about 2 mm), but they are still extremely large relative to those of *S. groenlandicus* **comb. nov.** In conclusion, *Octogonella* Ziegler, 2006 is unlikely to be a junior synonym of *Spirodiscus* Fauvel, 1909, but this needs to be verified with examination of the type material.

Genus *Bathyvermilia* Zibrowius, 1973

Bathyvermilia Zibrowius, 1973: 428.—Sanfilippo 2001: 177–178.—ten Hove & Kupriyanova 2009: 29–30.—Kupriyanova *et al.* 2011: 4, 7.

Type-species: *Bathyvermilia challengerii* Zibrowius, 1973

Diagnosis (after ten Hove & Kupriyanova 2009, emend.): Tube white, opaque, circular to quadrangular in cross-section. Peristomes may be present. Operculum sub-globular, with simple flat to slightly conical chitinous endplate, sometimes encrusted by calcareous material. Peduncle cylindrical, smooth or wrinkled, distal wings absent; inserted as 2nd dorsal radiole on either side, constriction present. Pseudopericulum absent. Up to 35 radioles per lobe arranged in semi-circles. Inter-radiolar membrane, radiolar eyes, and stylodes absent. Mouth palps present or absent. Seven thoracic chaetigerous segments, 6 of which uncinigerous. Trilobed collar (may be not divided into lobes in some taxa) with straight edge, tonguelets between ventral and lateral collar parts absent. Thoracic membranes of variable length, extending to 2nd–7th thoracic segment. Collar chaetae limbate capillaries. *Apomatus* chaetae present. Thoracic uncini saw-shaped, with 6–10 teeth and simple, pointed anterior fang. Abdominal chaetae flat, narrow geniculate with blunt teeth. Anterior and mid-abdominal uncini saw-shaped, uncini on few far posterior segments rasp-shaped. Short achaetous anterior abdominal zone may be present. Posterior capillary chaetae present. Posterior glandular pad usually present, but may be absent.

Remarks. The genus currently includes 6 bathyal and abyssal species (Kupriyanova *et al.* 2011). The diagnosis has been emended to include the species with tetragonal tubes.

Bathyvermilia gregrousei sp. nov.

Figures 1E, 8–10

?"tube de serpulien".—Fauvel 1909: 74–75.—Fauvel 1914: 338–339, pl. 29, fig. 2–6.

Spirodiscus grimaldii.—Hartman & Fauchald 1971: 183 [in part, R/V ATLANTIS-II, St. A119].

Material examined. Prince of Monaco, cruise 1896: Azores; St. 663, 27.6.1896, 37°28'30"N, 25°31'45"W, 1732 m (empty tubes, MOM 18 2642); St. 698, 18.7.1896, 39°11'N, 30°44'40"E, 1846 m (empty tubes, MOM 18 0475).

R/V JEAN CHARCOT, cruise INCAL, SW Ireland - off Brittany: St. 2.1-Pr34-WS1, 30.7.1976, 50°19.4'N, 13°08.1'W, 2539–2550 m (**holotype** MNHN POLY TYPE 1567, >50 paratypes MNHN POLY TYPE 1568, 1 paratype prepared for SEM AM W.46401, > 100 paratypes AM W.46400, 3 tubes of this set prepared for SEM PIN 5485/13, PIN 5485/35, PIN 5485/36 and X-ray diffraction analysis sample #1, > 50 paratypes NBCL ZMA V.Pol

5550, > 50 paratypes **SMF** 23990, > 50 paratypes **NHMUK** ANEA 2015. 937–946, >50 paratypes **LACM-AHF** Poly 7022, > 50 paratypes **USNM** 1283059); St. 2.1-Pr29-CP9, 27.7.1976, 50°15.4'N, 13°15.8'W, 2659–2691 m (> 30 spec. **MNHN** PNT 51, >50 spec. **AM** W.46402, >30 spec. **NBCL ZMA** V.Pol 5554, >30 spec. **SMF** 23991, 12 spec. **NHM UK** ANEA 2015.955–964, > 30 spec. **LACM-AHF** Poly 7024, >30 spec. **USNM** 1283062); St. 2.2-Pr37-CP10, 31.7.1976, 48°25.5'N, 15°10.7'W, 4823 m (5 spec. broken in pieces **SMF** 23992); St. 2.2-Pr39-DS11, 1.8.1976, 48°18.8'N, 15°11.5'W, 4823 m (1 spec. **SMF** 23933); St. 2.4-Pr48-OS3, 4.8.1976, 46°02.9'N, 10°18.7.1'W, 4798 m (tube fragments **SMF** 23994). Same, cruise BIACORES, Azores: St. 92, 17.10.1971, 39°03.5'N, 28°27.5'W, 2450 m (fragments of 1 empty tube **MNHN** PNT 48); St. 165, 1.11.1971, 37°33'N, 25°58'W, 2050–2085 m (2 spec. in tubes **MNHN** PNT 47); St. 171, 1.11.1971, 37°58.5'N, 26°07'W, 3215 m (9 spec. **SMF** 23977); St. 173, 2.11.1971, 37°57'N, 26°08'W, 3225 m (5 spec. **NBCL ZMA** V.Pol 5552, 5 spec. **USNM** 1283060, 5 spec. **LACM-AHF** Poly 7023); St. 174, 2.11.1971, 38°06'N, 26°15'W, 3050–3100 m (1 spec. in fragmented tube, **SMF** 23996). Same, cruise BIOGAS 11, off Brittany: St. CP37, 11.10.1981, 47°33.8'N, 8°39.2'W, 2175 m (2 spec. **SMF** 23999).

R/V DISCOVERY, cruise 105 (biology), off Brittany: St. 10112#1, 9.9.1979, 50°25.0'N, 13°19.1'W, 2640–2660 m (7 spec. in tubes **SMF** 24000); St. 10112#3, 9.9.1979, 50°19.1'N, 13°25.8'W, 2740–2755 m (1 spec. and tube fragment **MNHN** PNT 49).

R/V CHALLENGER, cruise 5/82 (biology cruise 514), off Brittany: St. 51416: 31.3.1982, 50°16.8'N, 13°31.4'W, 2770–2780 m (5 spec. **MNHN** PNT 50, 5 spec. **USNM** 1283061, 5 spec. **NHM UK** ANEA 2015.950–954, 3 spec. **AM** W.46405, 5 spec. **NBCL ZMA** V.Pol 5553).

R/V LE SUROIT, cruise EPI 1, off Brittany: St. CP39, 30.3.1984, 47°32.0'N, 8°38.4'W, 2100 m (1 spec. **SMF** 23998).

R/V CRYOS, cruise ABYPLAINE, North-East Atlantic: St. 2-DS1, 17.5.1981, 37°18'N, 15°33'W, 4260–4450 m (tube fragments **SMF** 23997); St. 8-CP11, 30.5.1981, 34°06.1'N, 17°06.3'W, 4270 m (5 spec. **NBCL ZMA** V.Pol 5551); St. 10-DS10, 11.6.1981, 42°51.2'N, 15°55.3'W, 4270–4360 m (3 spec. **AM** W.46403); St. 10-CP18, 11.6.1981, 42°52.3'N, 15°53.1'W, 4330 m (3 spec. **NHM UK** ANEA 2015. 947–949).

R/V ATLANTIS-II, North-West Atlantic: St. A119, 19.8.1966, 32°15.8' to 32°16.1'N, 64°31.6' to 64°32.6'W, 2095–2223 m (7 spec. **LACM-AHF**); St. A155, 00°03'S, 27°48'W, 3730–3783 m (8 spec., 1 spec. prepared for SEM, **LACM-AHF**).

R/V MARION DUFRESNE, cruise MD 50, Amsterdam Island: St. 5-DC34, 13.7.1986, 37°40.33'S, 77°30.50'E, 2200 m (7 spec. **MNHN** PNT 52, 7 spec. **AM** W.46404, 7 spec. **NBCL ZMA** V.Pol. 5555, 7 spec. **SMF** 24001, 7 spec. **NHM UK** ANEA 2015.965–971, 7 spec. **LACM-AHF** Poly 7025, 7 spec. **USNM** 1283063).

R/V VITYAZ, Pacific Ocean: St. 3243, 11.5.1955, 39°43.8'N, 159°48.0'E, 5542 m (1 spec. **SIO**); St. 4191, 8.12.1958, 40°22.5'N, 135°49.9'W, 4472–5072 m (2 spec. **SIO**); St. 4265, 13.01.1959, 24°57.6'N, 113°24.8'W, 3315–3340 m (2 spec. **SIO**); St. 4279, 19.1.1959, 19°46'N, 120°17.4'W, 4104 m (1 spec. **SIO**); St. 4281, 21.01.1959, 20°01.3'N, 121°59.6' W, 4370 m (1 spec. **SIO**); St. 4370, 3.3.1959, 26°04.2'N, 153°49.3'W, 6127–6107 m (1 tube **SIO**); St. 5937, 0°20.2'N, 179°52'W, 5480 m (2 spec. **SIO**); St. 6298-56, 22°41.9'N, 160°50.8'W, 4270–4350 m (2 tube pieces **SIO**).

(?) R/V VITYAZ-2, Atlantic Ocean: St. 79, 34°54.3'N, 45°39'W, 4440 m (1 tube studied with SEM, **PIN** 5485/14 and X-ray diffraction analysis, sample # 2).

Description. *Tube*: white, opaque, ostensibly free, with shiny surface, open at both ends, straight or slightly curved, slowly increasing in diameter, slightly twisted spirally (Fig. 8C, D, H, I). Cross-section tetragonal (Fig. 8J). Sides of tube slightly concave, but cross-section becomes almost circular anteriorly (Fig. 8J). Some tubes showing growth stops marked by tiny constrictions, not peristomes, accompanied by sudden turns around growth axis up to 45° (Fig. 8C, D), some tubes can be slightly twisted (Fig. 8H, I). Wall thickness varying between tube sides, with one side (lateral?) being significantly thinner (Fig. 9F), making tube cross-section bilaterally symmetrical (see *Size* as well).

Tube ultrastructure: wall unilayered, with irregularly oriented prismatic (IOP) structure consisting mostly of elongated cigar-shaped crystals, but appearance and orientation of crystals throughout the wall not uniform. Inner part thin (1/10–1/15 of wall, Fig. 9D), but clearly distinct; consisting of consolidated rice grain-shaped crystals oriented more or less along growth direction by their axes. Length of crystals about 3–4 µm, diameter 0.5 µm. Middle wall part separated from inner layer by characteristic zone with numerous elongated “cavities”, positioned along growth lamellae of tube wall (Fig. 9A, D, E). These cavities entirely surrounding lumen also visible in transverse sections (Fig. 9G, J). Middle part of tube wall (Fig. 9C, I) consisting of unoriented crystals similar in

shape and size to crystals of inner and outer parts. Outer wall part (Fig. 9B, H) composed of elongated crystals similar to crystals of inner layer, also oriented loosely parallel to tube wall. All variations of wall thickness produced by middle and outer wall parts (Fig. 9G), thickness of inner part and “cavities” zone being stable. Parabolic growth lamellae indistinct, but visible (Fig. 9A, C) in sections.

Tube mineralogy: sample # 1: 20% calcite ($I_{\text{calc}}=9$), 80% aragonite ($I_{\text{arag}}=37$); sample # 2: 55% calcite ($I_{\text{calc}}=56$) and 45% aragonite ($I_{\text{arag}}=44$).

Radiolar crown: 4–6 pairs of radioles arranged in semicircles to pectinately, not joined by inter-radiolar membrane. Radiolar eyes not visible in preserved material. Long naked tips of radioles absent.

Peduncle: inserted slightly in front between 1st and 2nd dorsal radioles, about same thickness as radioles, smooth (no pinnules), slightly longer than radioles (Fig. 8E).

Operculum: elongated, covered with convex yellow-brown chitinous cap, sometime with a knob in the centre (Fig. 8A, E); opercular bulb gradually narrowing towards peduncle, but separated by shallow conspicuous constriction.

Collar and thoracic membranes: collar short, subdivided into 2 latero-dorsal and 1 ventral lobe, the latter slightly incised. Thoracic membranes reaching up to 2nd chaetiger, about same width throughout.

Thorax: with 7 thoracic chaetigers, 6 of which uncinigerous (Fig. 8B, F, G). Tori widely separated, first and second slightly closer to each other. Thoracic tori of similar size along thorax. Collar chaetae as few short capillaries (Fig. 10B); other thoracic chaetae limbate, with short slightly bent distal blades; *Apomatus* chaetae present (Fig. 10C). Uncini saw-shaped with 9–11 teeth in profile view, dental formula P:1:1:1:1:1:1:1:1 (Fig. 10D); anterior peg pointed.

Abdomen: with up to 45 segments. Uncini similar to thoracic ones, but rasp-shaped, with 3–4 rows, dental formula P:3:3:4:4:4:4:3:3:3 (Fig. 10F). Chaetae flat triangular blade with rounded denticles, only slightly longer on posterior segments (Fig. 10K); each chaetiger usually with a single chaeta. No achaetigerous zone between thorax and abdomen. Posterior glandular pad absent.

Size: total body length up to 15 mm, including up to 11 mm long radioles, width of thorax up to 0.4 mm. Maximum tube fragment length observed 35 mm (tubes incomplete). External tube diameter up to 0.67 mm with corresponding lumen diameter up to 0.45 mm. Thickness of tube wall in between angular margins about 1/7th of outer diameter at thinner sides, and ~1/6th at thicker sides.

Distribution. North Atlantic, low bathyal to abyssal depths (1732–4823 m), Indian Ocean (Amsterdam Island), 2200 m, Pacific Ocean, 3315–6127 m.

Etymology. The species is named after Professor Greg Rouse (Scripps Institution of Oceanography, USA) who made important contributions to serpulid phylogeny and deep-sea biology.

Remarks. This species apparently was first characterised by Fauvel (1909, 1914) from empty tubes only: “quadrangular in cross-section and thereby similar to *Spirodiscus grimaldii* but straight”. Similar tubes from the Indian Ocean (near Amsterdam Island, 2200 m) were found co-occurring with typical coiled *S. grimaldii*. These Indian Ocean specimens of *B. gregrousei* **sp. nov.** also have the distal parts of their tubes smooth and circular in cross-section. Occasionally these parts can be proportionally very long.

The tubes of *Bathyvermilia gregrousei* **sp. nov.** resemble quadrangular tusk-shaped tubes of *Bathyditrupa hovei* in size and tube diameter (compare Fig. 1B, C with E). However, tubes of *B. hovei* have a very regular slightly curved shape, a quadrangular tube cross-section with tube edges forming straight angles throughout and distal parts of the tube never become circular in cross-section. The tubes of *Bathyvermilia gregrousei* **sp. nov.**, although more or less straight and quadrangular in cross-section, have more variable and less regular shapes (Fig. 11C, D), normally slightly spirally twisted (Fig. 11H, I), and distal tube parts often become smooth and circular in cross-section. However, the morphology of the animals removed from their tubes is very different.

Known ultrastructures for *Bathyvermilia* cover three species—*B. islandica* Sanfilippo, 2001 (tube structure is illustrated in the original description), *B. langerhansii* (Fauvel, 1909) figured by Vinn (2008) and Vinn *et al.* (2008) and *Bathyvermilia challengerii* Zibrowius, 1973 (figured in Kupriyanova *et al.* 2014), thus allowing intrageneric comparison. All three species have tubes with well-developed homogeneous angular crystal ultrastructure (HAC) at least in the outer layer. This highly specialized structure has nothing to do with the IOP ultrastructure described herein for *B. gregrousei* **sp. nov.** IOP ultrastructure constituting the inner layer of *B. islandica* and the entire tube of *B. gregrousei* **sp. nov.** is widely distributed among serpulids (Vinn *et al.* 2008, table 2) and seems to be less specialized, which suggests that HAC ultrastructure may be an apomorphy inside a certain group of *Bathyvermilia* species.

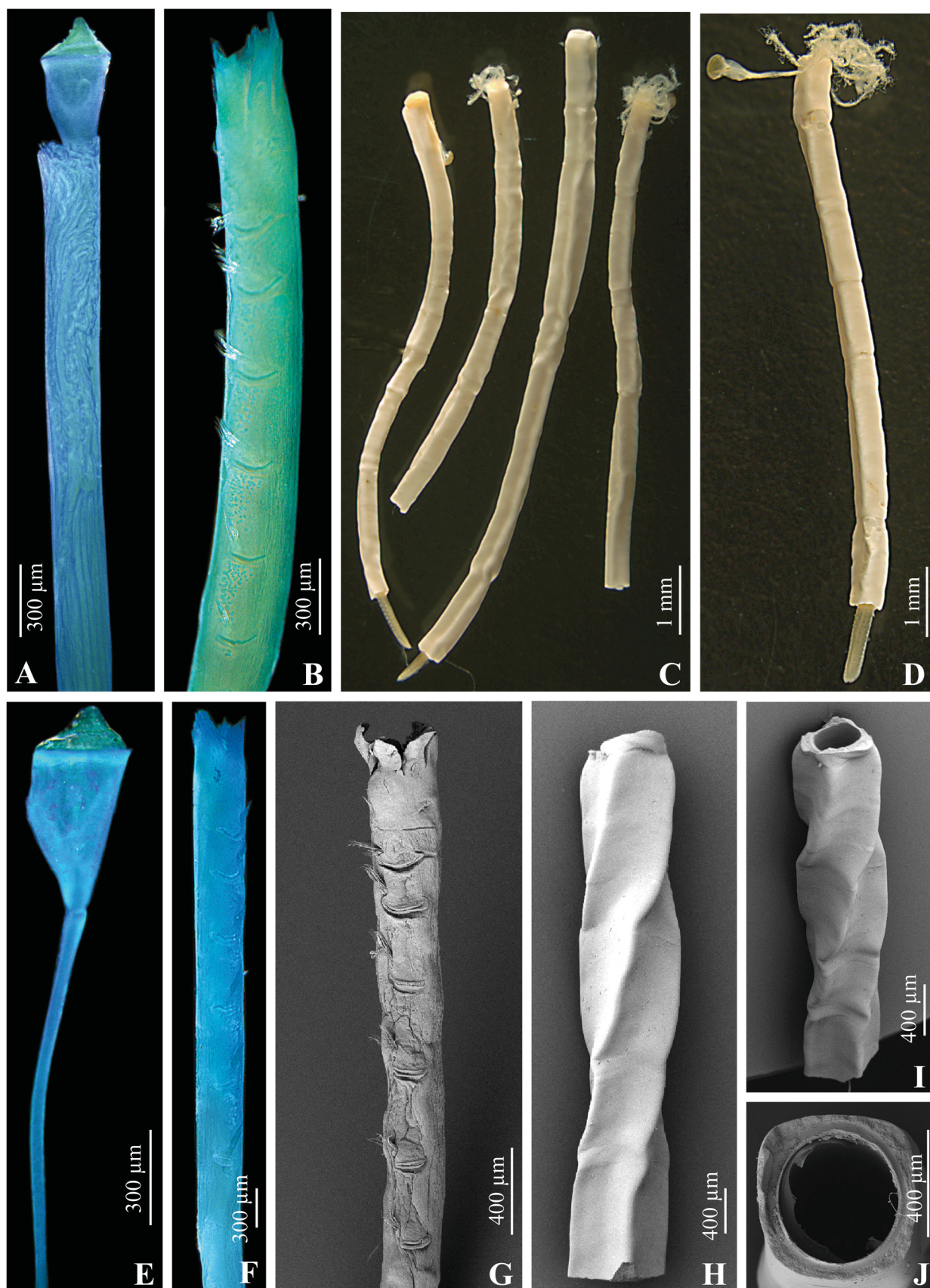


FIGURE 8. Photos and SEM images of *Bathyvermilia gregrousei* sp. nov. A–F: AM W.46400, photos, A—radiolar crown with operculum, B—lateral view of thorax, C, D—tubes with animals inside, E—operculum on thin smooth opercular peduncle, F—lateral view of thorax. G–J: AM W.46401, SEM images, G—lateral view of the thorax, H, I—tube fragments, J—tube cross-section.

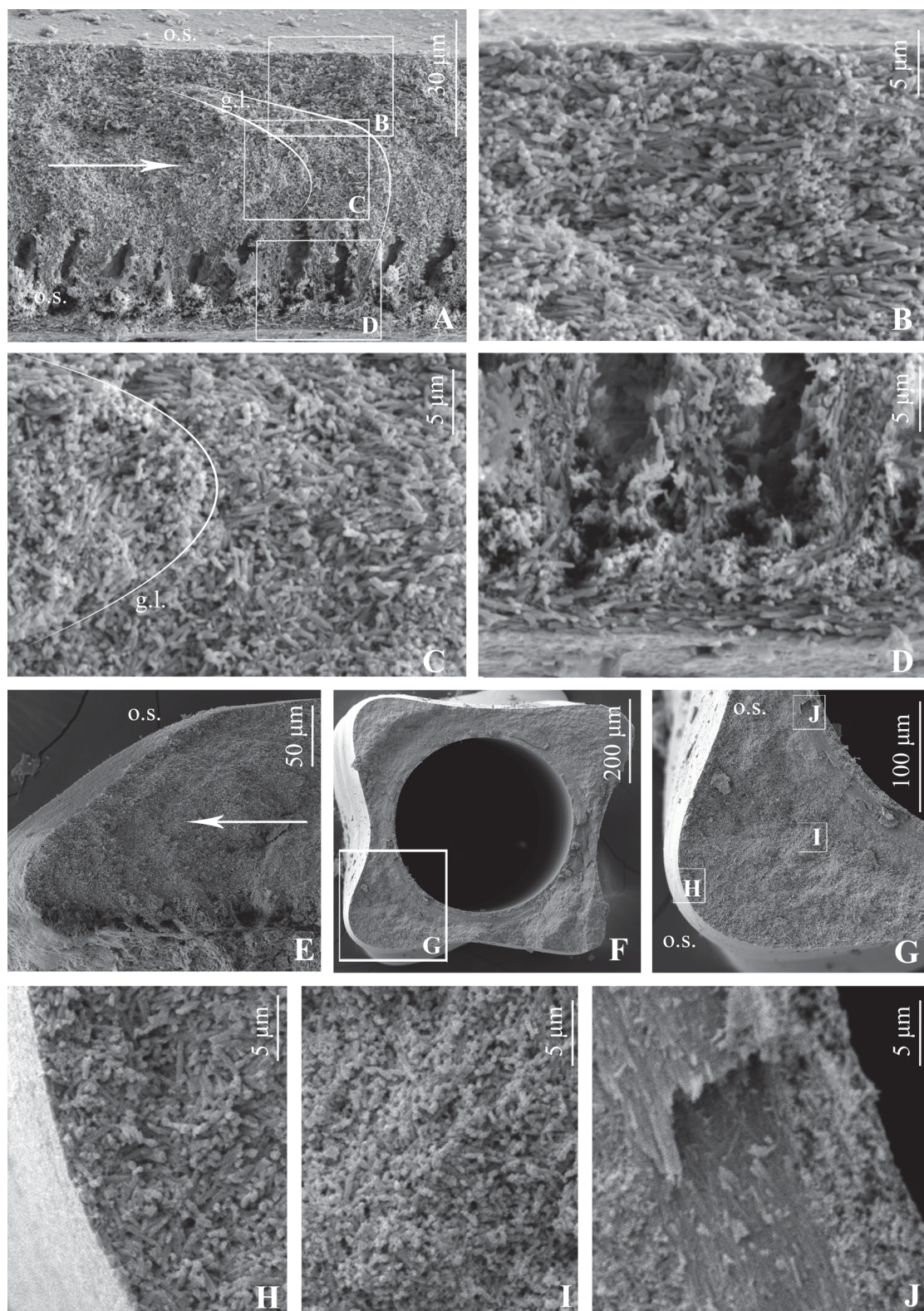


FIGURE 9. Tube ultrastructures of *Bathyvermilia gregrousei* **sp. nov.** A–D and F–J: **PIN 5485/13**, A—general view of longitudinal wall section, B—enlarged outer wall part consisting of elongated crystals positioned parallel to direction of tube growth, C—enlarged middle wall part consisting of elongated loosely oriented crystals, D—details of inner wall part with clearly visible cavities and thin inner layer, F—transverse section, G—enlarged edge showing inner layer with cavities, H—details of outer wall part, I—middle part of tube wall with unoriented crystals, J—details of wall inner part, including cavities and innermost layer. E: **PIN 5485/14**, empty tube of (?)*Bathyvermilia gregrousei* **sp. nov.** identified by ultrastructure only, longitudinal section of anterior tube end showing diagnostic inner layer with cavities. Arrows indicate direction of tube growth. Abbreviations: g. l.—growth lamellae, o. s.—outer tube surface.

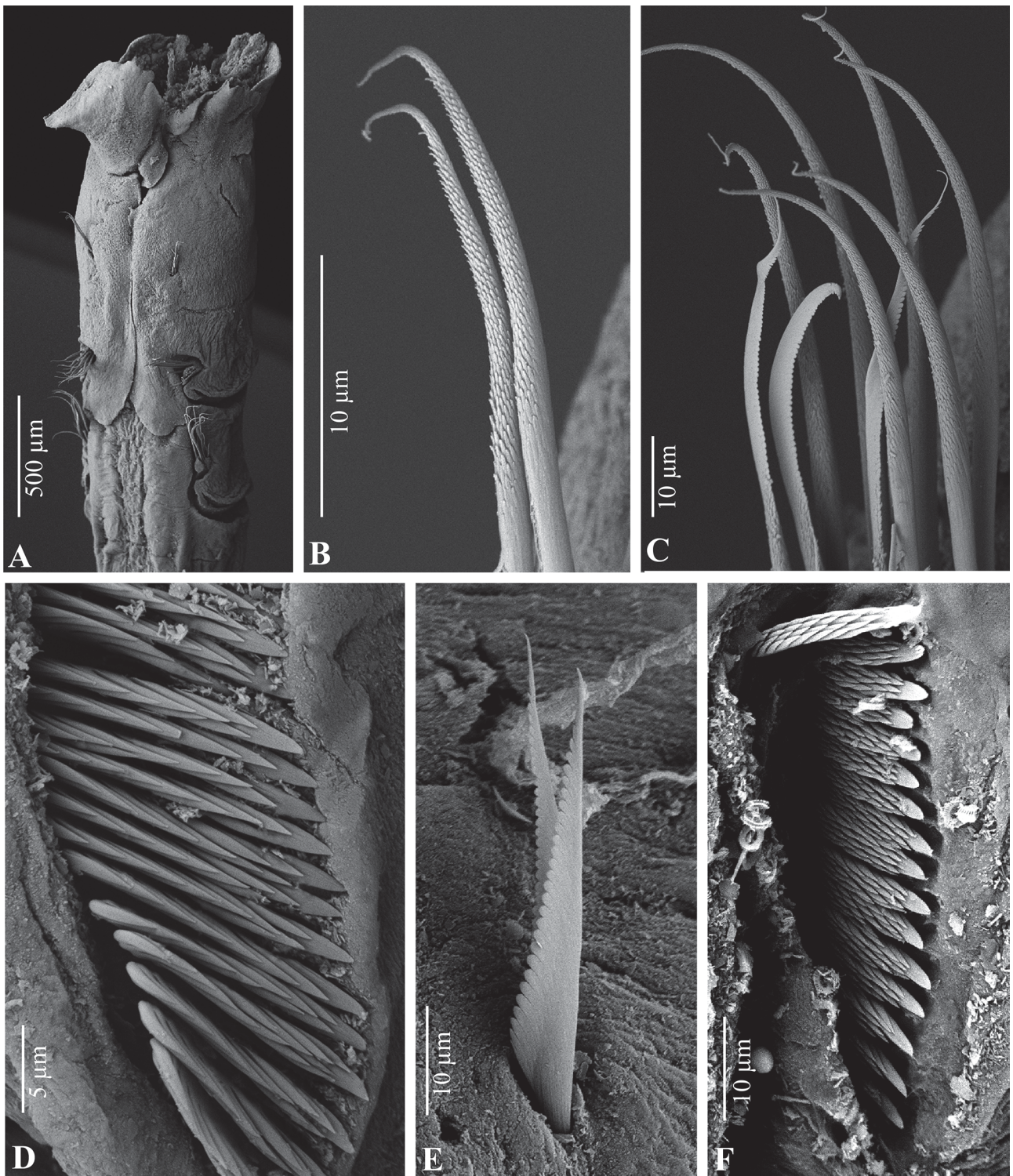


FIGURE 10. SEM images of *Bathyvermilia gregrousei* sp. nov. AM W.46401. A—dorsal view of anterior thorax showing thoracic membranes, B—collar chaetae, C—bundle of thoracic chaetae with *Apomatus* chaetae, D—thoracic uncini, E—anterior abdominal chaetae, F—abdominal uncini.

Tube ultrastructure of *B. gregrousei* sp. nov. in general is similar to those described for *Bathyditrupa* and *Spirodiscus*, being also composed of elongated crystals similar in size and shape. However, the inner part of the wall of *B. gregrousei* sp. nov. is made of larger elongated, not smaller isometric crystals. Moreover, an outer layer with SOIOP structure representing crystal “bundles” oriented subparallel to the tube surface and growth direction, characteristic for *Spirodiscus* and *Bathyditrupa*, is absent in *B. gregrousei*. At the same time, unilayered tube walls

built of more or less chaotically oriented elongated crystals are not unique to *Bathyvermilia* but known for a wide range of serpulid taxa (see Vinn *et al.* 2008). While making comparisons based on descriptions only is difficult, among figured ultrastructures the most similar one is known for *Protis hydrothermica* (see ten Hove & Zibrowius 1986, fig. 4a, b) that seems to be relatively close to *Bathyvermilia* (Kupriyanova & Nishi 2010). Very diagnostic for the *B. gregrousei* **sp. nov.** are microcavities surrounding the lumen and observed in all three specimens studied with SEM. Although cavities of various morphology are known in some taxa (*e.g.*, Bianchi 1981: fig. 27b, c, 32a–c), such tiny ones surrounding the entire lumen were not previously described for any other serpulid.

Genus *Hyalopomatus* Marenzeller, 1878

Hyalopomatus Marenzeller, 1878: 393.—Zibrowius 1969: 13.—Kupriyanova 1993b: 146.—Ben-Eliahu & Fiege 1996: 13.—Kupriyanova & Jirkov 1997: 211.—Knight-Jones *et al.* 1997: 146.—ten Hove & Kupriyanova 2009: 50–52.—Sanfilippo 2009: 151.—Kupriyanova *et al.* 2010: 58–59.—2011: 56.

Cystopomatus Gravier, 1911: 149.

Hyalopomatopsis de Saint-Joseph, 1894: 261 [in part].

Type species: *Hyalopomatus clapedii* Marenzeller, 1878

Diagnosis (after Kupriyanova *et al.* 2010, emend.): Tube white, opaque, sometimes with external hyaline layer; (semi) circular or quadrangular with rounded edges in cross-section. *Hyalopomatus variorugosus* Ben-Eliahu & Fiege, 1996, characterised by tubes with minute flap-like structures, and *H. biformis* (Hartman, 1960), which tubes have a longitudinal keel, are exceptions on this general pattern. Tabulae may be present. Operculum globular, soft, without distinct endplate or consisting of proximal ampulla with slightly chitinized distal cap; conspicuous constriction between operculum and peduncle; sometimes operculum absent. Peduncle sometimes thin (same thickness as radioles), cylindrical, smooth, wings absent; inserted outside radiolar crown proper in front of 1st dorsal radiole on either side or between base of 1st and 2nd radioles. Pseudoperculum absent. Up to 15 pairs of radioles, in pectinate arrangement. Inter-radiolar membrane absent. Radiolar eyes rarely present. Stylodes absent. Mouth palps present. Six thoracic chaetigerous segments, 5 of which uncinigerous. Collar trilobed, tonguelets between ventral and lateral collar parts absent. Thoracic membranes short, ending at 1st or 2nd chaetiger. Collar chaetae simple limbate capillaries and fin-and-blade, with or without gap between fin and blade. *Apomatus* chaetae absent. Thoracic uncini rasp-shaped with about 20 small teeth in profile view, up to nine teeth in a transverse row above flat or slightly gouged anterior peg, made of two or more rounded lobes with shallow incision(s) in between. Triangular depression absent. Abdominal chaetae ending in long narrow tip made of pointed teeth that at least partly arranged in two rows on anterior and mid-abdominal segments, long capillaries on posterior chaetigers. Abdominal uncini rasp-shaped, similar to thoracic ones, but their anterior peg with 3–6 flat rounded lobes. Achaetous anterior abdominal zone may be present. Posterior glandular pad absent.

Remarks. The genus *Hyalopomatus* currently contains 13 nominal species mainly from bathyal and abyssal depths (ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2011).

Hyalopomatus dieteri **sp. nov.**

Figures 1F, 11, 12

Material examined. R/V CORIOLIS, cruise BIOGEOCAL, 1987, East of New Caledonia, St. CP260: 17.4.1987, 21°00.00'S, 167°58.34'E, 1820–1980 m (**holotype** MNHN POLY TYPE 1564, 1 tube fragment prepared for SEM and X-ray diffraction analysis PIN 5485/16).

R/V JEAN CHARCOT, cruise BIOCAL, 1985, approximately 100 km South of New Caledonia, St. CP27, 29.8.1985, 23°05.52'S, 166°26.41'E, 1900 m (1 **paratype** without radioles AM W.46386, partly prepared for SEM).

Description. *Tube:* white opaque, ostensibly free, with shiny surface, straight, thick-walled, mostly quadrangular in cross-section, edges rounded and never denticulate. Juvenile tubes with sharper keels, becoming rounded in adults. Tubes slightly twisted, growth stops accompanied by sudden turns of tube around growth axis. Sides usually slightly convex, sometimes slightly concave.

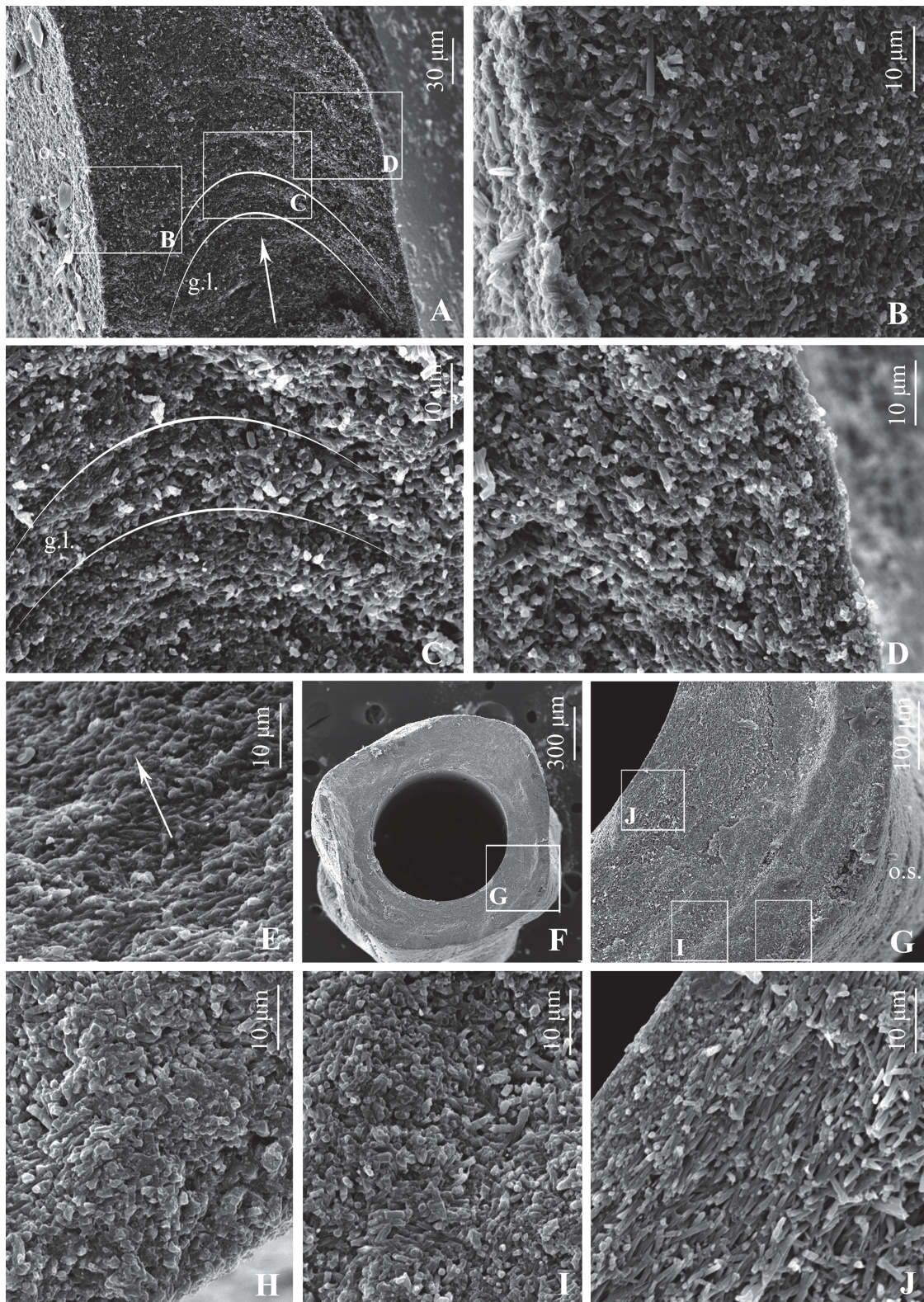


FIGURE 11. Tube ultrastructures of *Hyalopomatus dieteri* sp. nov. A–E: PIN 5485/16, A—longitudinal wall section with parabolic texture in middle wall part, B—enlarged outer part consisting of larger slightly elongated and isometric crystals, C—enlarged middle wall part, parabolic texture produced by orientation of elongated crystals along growth lines, D—enlarged inner wall part showing slight transition to isometric smaller crystals, E—oblique longitudinal section through inner wall part showing orientation of crystals transversely to growth axis, F—tube cross-section, G—enlarged cross-section across tube edge, H—enlarged outer wall part, I—details of middle wall part consisting of isometric to slightly elongated crystals in tube edge area, J—details of inner wall part showing layer with ordered cigar-shaped crystals. Arrows indicate direction of tube growth (where known). Abbreviations: g. l.—growth lamellae, o. s.—outer tube surface.

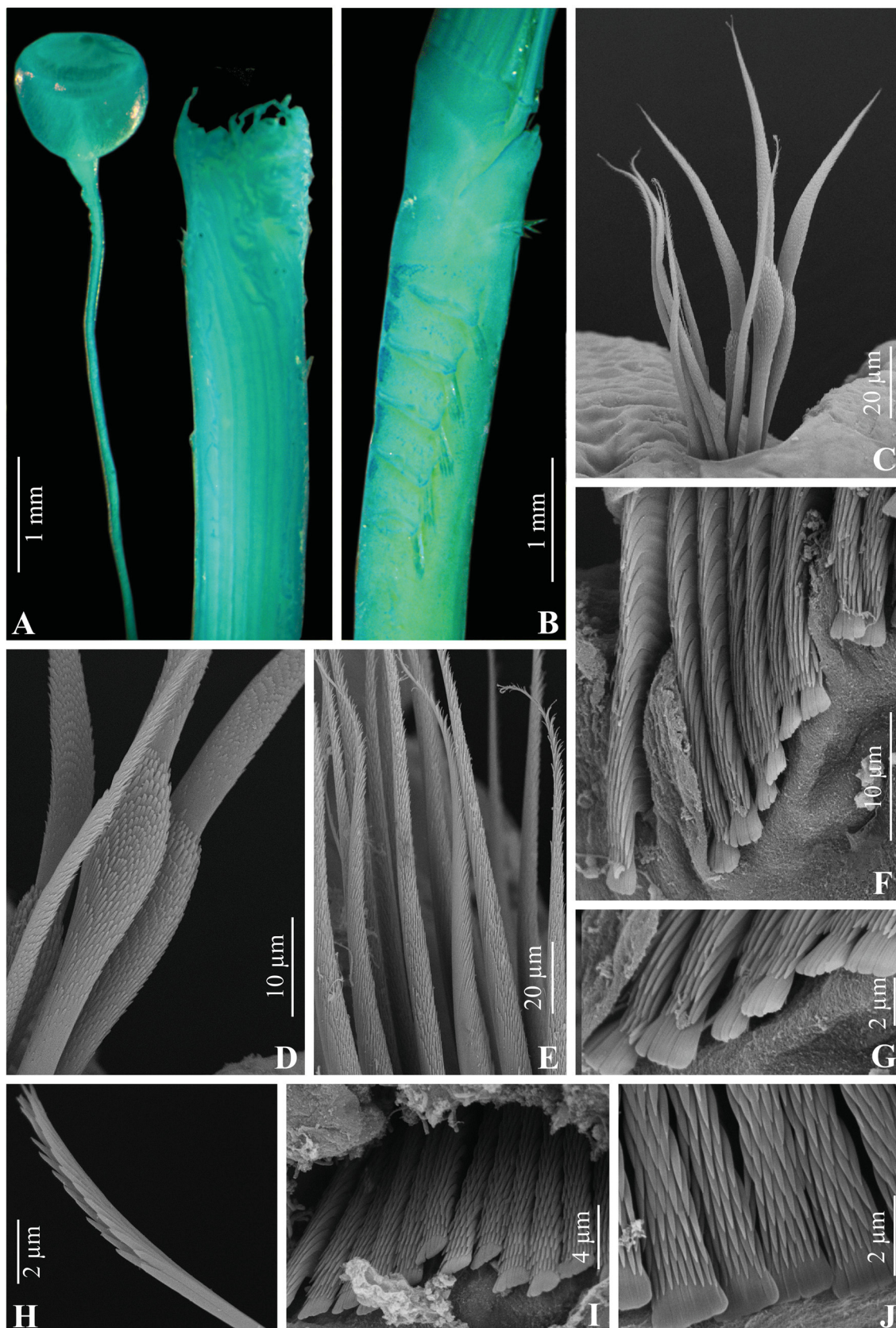


FIGURE 12. Photos and SEM images of *Hyalopomatus dieteri* sp. nov. A–B: MNHN POLY TYPE 1564, photos, A—distal view of radioles and operculum on thin smooth peduncle, B—lateral view of thorax and basal part of radiolar lobes. C–J: paratype AM W.46386, SEM images, C—bundle of collar chaetae with fin-and-blade chaetae, D—close-up view of fin-and-blade collar chaetae, E—thoracic chaetae, F—anterior thoracic uncini, G—close-up view of anterior pegs of thoracic uncini, H—distal part of abdominal chaeta, I—abdominal uncini, J—anterior pegs of abdominal uncini.

Tube ultrastructure: wall unilayered with irregularly oriented prismatic (IOP) structure, in inner wall part transforming into semi-ordered irregularly oriented prismatic (SOIOP). Tube wall not clearly subdivided into layers, in longitudinal section revealing only larger isometric to slightly elongated crystals with size up to 5 µm long (Fig. 11A–D). Crystal size smallest near lumen (Fig. 11D), increasing in middle (Fig. 11C), and becoming largest in outer part of the wall (Fig. 11B). Cross-section showing distinct zone in inner wall part consisting of highly ordered cigar-shaped crystals (5–6 µm in length, 1–1.5 µm in diameter, Fig. 11J) with long axes oriented parallel to tube surface (Fig. 11E, J) resulting in SOIOP ultrastructure; in longitudinal sections this structure is unrecognizable. Transition from IOP to SOIOP structure gradual (Fig. 11J). Parabolic growth lamellae (Fig. 11A, C) present in all studied sections, axis of parabolae located in wall centre.

Tube mineralogy: 97–100% aragonite ($I_{\text{arag}}=69$), doubtful calcite content.

Radiolar crown: with 7 pairs of radioles in holotype (radioles mostly missing in paratype), arranged pectinately, easily detachable from short radiolar lobes. Inter-radiolar membrane and stylodes absent. Terminal filaments of radioles thin, spirally twisted. Radiolar eyes and mouth palps not observed.

Peduncle: smooth, cylindrical, thin (approximately same thickness as radioles), distal wings absent; inserted conspicuously outside radiolar crown proper, between base of 1st and 2nd radioles (Fig. 12B).

Collar and thoracic membranes: collar covering radiolar lobes, thin; trilobed, with ventral lobe slightly higher than the lateral ones (Fig. 12B). Collar continuous with short thoracic membranes ending at 2nd chaetiger.

Operculum: soft membranous, semi-transparent, mostly globular, but with flattened top, slightly differentiated from the basal part; conspicuous constriction and additional small vesicular ampulla between operculum and peduncle (Fig. 12A). Pseudoperculum absent.

Thorax: with 6 chaetigerous segments, 5 of which uncinigerous. Small bundle of collar chaetae, of two types: simple limbate and fin-and-blade with the distal blade separated from the basal fin by a short gap (Fig. 12C, D). Subsequent chaetae limbate, of two sizes, *Apomatus*-chaetae absent (Fig. 12E). Uncini along entire thorax rasp-shaped, with 20–25 small teeth in profile view, with 6–8 teeth in the row above flat anterior peg made of 3–4 rounded lobes, dental formula P:8:7:7:7:6:6:6:6:6:6:6:6:?:?:?:?:? (Fig. 12F, G). Pair of prostomial eyes absent. Triangular depression absent, thoracic tori almost parallel to mid-ventral line of the thorax.

Abdomen: with up to 60 segments. Chaetae long, nearly capillary with only narrow geniculate tip clearly made of two rows of pointed teeth (Fig. 12I). Capillary chaetae present in posterior chaetigers. Uncini rasp-shaped with over 20 teeth in profile and up to 9 rows of teeth (Fig. 12J, K) above anterior peg flat divided into 3–5 rounded lobes (crenulated). Dental formula P:9:7:5:4:3:4:3:2:?:? or P:8:5:5:5:4:4:4:?:?. Achaetous anterior abdominal zone long.

Size: total body length up to 15 mm, including up to 9 mm long radioles, width of thorax up to 0.5 mm. Tubes incomplete and broken into fragments, maximum total length of fragments (in paratype) 40 mm. External tube diameter up to 1.3 mm, corresponding lumen diameter 0.9 mm. Thickness of tube wall in between the angular margins about 1/3–1/4th of outer diameter, and up to 1/2 when measured across keels.

Etymology. The species is named after Dr. Dieter Fiege (SMF) in recognition of his important contributions to taxonomy of Serpulidae.

Distribution. Coral Sea off New Caledonia, 1820–1980 m.

Remarks. The new species from New Caledonia resembles *H. macintoshi* (Gravier, 1911) in having a globular transparent, only slightly differentiated operculum. However, the tube of *H. dieteri* **sp. nov.** is distinct in being polygonal (quadrangular).

Four other *Hyalopomatus* spp. with known tube ultrastructures are *H. variorugosus* Ben-Eliahu & Fiege, 1996 (see Sanfilippo 1998a; Vinn *et al.* 2008), *H. clapedii* Marenzeller, 1878, *H. marenzelleri* Langerhans, 1884 and *H. madreporae* Sanfilippo, 2009 (see Sanfilippo 2009). Ultrastructural type and shape of crystals of *H. variorugosus* are very similar to those of *H. dieteri* **sp. nov.**, despite chaotic orientation of crystals without defined SOIOP ultrastructure in the former. *H. marenzelleri* demonstrates squat prismatic crystal shapes, but the ultrastructure type is still the same (IOP). The closest to *H. dieteri* **sp. nov.** is *H. clapedii* that has a well-defined SOIOP ultrastructure near the lumen (Sanfilippo 2009, fig. 6E) with a gradual transition to IOP ultrastructure in the outer part of the tube wall. The tube of *H. madreporae* also shows a similar pattern, but its SOIOP zone (Sanfilippo 2009, fig. 4G) seems to be relatively wider than those in both *H. dieteri* **sp. nov.** and *H. clapedii*. All *Hyalopomatus* spp. studied to date have very similar tube ultrastructures supporting the generic placement of the new species described herein.

Genus *Zibrovermia* gen. nov.

Type-species: *Zibrovermia zibrowii* gen. et sp. nov.

Diagnosis. Tube white opaque, quadrangular in cross-section; with 4 denticulate keels, distal parts circular in cross-section, without ring-like peristomes. Operculum an inverse conical ampulla, with chitinous endplate; borne on 2nd normal pinnulated radiole. Pseudoperculum absent. Radioles arranged pectinately, inter-radiolar membrane absent. Radiolar eyes not observed. Stylodes absent. Mouth palps not observed. Seven thoracic chaetigerous chaetigers, including six uncinigerous. Collar trilobed, tonguelets between ventral and lateral collar parts absent. Thoracic membranes short, ending at 2nd–3rd thoracic chaetiger. Collar chaetae limbate, of two sizes. *Apomatus* chaetae present. Thoracic uncini rasp-shaped with up to 15 teeth in profile and 4–5 teeth in frontal view above blunt peg. Triangular depression absent. Abdominal chaetae flat narrow geniculate, blade with a more or less crenulated edge (rounded teeth). Abdominal uncini rasp-shaped, anterior peg blunt. Achaetous anterior abdominal zone absent. Long posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. The new species is attributed to a new genus mainly because of its very peculiar quadrangular tubes with serrated edges, its pinnulated peduncle and its rasp-shaped thoracic uncini. *Zibrovermia* gen. nov. is most similar to *Bathyvermia* Zibrowius, 1973 and *Vermiliopsis* de Saint-Joseph, 1894 in the chaetation pattern (except for rasp-shaped thoracic and abdominal uncini in *Zibrovermia* gen. nov.), length of thoracic membranes, and opercular morphology (Table 3). According to Zibrowius (1973), the main differences between *Bathyvermia* and *Vermiliopsis* are the insertion of smooth opercular peduncle as second radiole in the former and as the first in the latter. However, ten Hove & Kupriyanova (2009) argue that the peduncle is ontogenetically formed from second dorsal radiole on one side, but in adults it often located at base of radiolar crown covering 3–6 normal radioles, which would undermine Zibrowius' rather absolute "difference".

TABLE 3. Comparisons of *Zibrovermia* gen. nov. with morphologically similar serpulid genera.

| Genus | Pinnules on peduncle | Peduncle shape | Peduncle inserted | Thoracic membrane | Thoracic uncini |
|-------------------------------------------|----------------------|---------------------|---------------------------------------------------------------|-----------------------------------|-------------------------------------------|
| <i>Bathyvermia</i> Zibrowius, 1973 | absent | smooth, cylindrical | as 2 nd radiole | ending at chaetiger 2 | saw-shaped with simple peg |
| <i>Metavermia</i> Bush, 1905 | absent | flat, ribbon-shaped | as 2 nd radiole | to chaetiger 4, may be with apron | saw-shaped with simple peg |
| <i>Pseudovermia</i> Bush, 1907 | absent | smooth, cylindrical | below and between 1 st and 2 nd radiole | ending at chaetiger 2 | saw-shaped with gouged peg |
| <i>Semivermia</i> ten Hove, 1975 | absent | smooth, cylindrical | as 2 nd radiole | ending at chaetiger 2 | saw-to-rasp-shaped with gouged peg |
| <i>Vermiliopsis</i> de Saint-Joseph, 1894 | absent | smooth, cylindrical | below and between 1 st and 2 nd radiole | ending at chaetiger 2 or 3 | saw-shaped with simple peg |
| <i>Zibrovermia</i> gen. nov. | present | normal radiole | as 2 nd radiole | ending between chaetigers 2 and 3 | rasp-shaped with flattened crenulated peg |

In *Zibrovermia* gen. nov. the second normal (pinnulated) radiole bears the operculum with a chitinous endplate lacking any calcification. Ten Hove (1984, 1989) distinguishes between indirect (juveniles develop an operculum on a pinnulated radiole that later loses its pinnules and becomes smooth) and direct (peduncle and operculum develop directly, without a pinnule-bearing stage) opercular ontogeny. It is unclear what kind of opercular ontogeny is typical for the genera of the *Vermiliopsis*-group, but in the case of indirect development the "diagnostic" pinnulated peduncle of *Zibrovermia* might be neotenic and thus not very reliable.

The assignment of the newly described species, *Z. zibrowii* gen. et sp. nov., to a new monospecific genus is a result of a unique combination of its characters. Although the tube of *Z. zibrowii* gen. et sp. nov. is quadrangular in cross-section and the peduncle is pinnulated like that in *Spirodiscus* and *Bathyditrupa*, the similarities end here. The operculum-bearing radiole in *Z. zibrowii* gen. et sp. nov. is similar to other radioles, not modified into a thick

peduncle as seen in *Spirodiscus* and *Bathyditrupa* and the tubes are large and thick-walled, with denticles on the edges. The new species is similar to *Bathyvermilia gregrousei* **sp. nov.** in having 7 thoracic segments, thoracic *Apomatus* chaetae, and very typical *Bathyvermilia* or *Vermiliopsis* -type abdominal chaetae. The blunt slightly indented pegs of uncini in *Z. zibrowii* **gen. et sp. nov.** are reminiscent of those observed in *Vermiliopsis infundibulum* (Philippi, 1844) (compare fig. 49C in ten Hove & Kupriyanova 2009). However, thoracic uncini of the new genus are rasp-shaped, not saw-shaped as in *Vermiliopsis* and *Bathyvermilia*. Pinnulated peduncles are not found either in *Bathyvermilia* or in *Vermiliopsis*. Table 3 summarises characters found in the *Vermiliopsis*-group genera. When molecular data on phylogenetic position of the species become available, the taxonomic position of *Zibrovermilia* **gen. nov.** may have to be reconsidered.

Etymology. The genus is named after Dr Helmut Zibrowius who made important contributions to serpulid taxonomy and provided most of material for this study; *-vermilia* stresses the similarity with other genera (Table 3), with this stem.

***Zibrovermilia zibrowii* sp. nov.**

Figures 1G, 13, 14.

Material examined. R/V ALIS, cruise MUSORSTOM 6, Coral Sea: St. CP438: 18.2.1989, 20°23.00'S, 166°20.10'E, 780 m (**holotype** MNHN POLY TYPE 1565, >30 **paratypes** MNHN POLY TYPE 1566, including 1 prepared for SEM **AM** W.46387, > 30 **paratypes** NBCL **ZMA** V.Pol 5543, >30 **paratypes** SMF 24002, 10 **paratypes** NHMUK ANEA 2015.902–911, >30 **paratypes** LACM-AHF Poly 7016, >30 **paratypes** USNM 1283054, tubes prepared for SEM and X-ray diffraction analysis **PIN** 5485/17, 5485/32, 5485/33, 5485/45).

R/V CORIOLIS, cruise BIOGEOCAL, Coral Sea: St. CP272, 20.4.1987, 21°00.04'S, 166°56.94'E, 1615–1710 m (2 spec. **MNHN** PNT 29); St. CP308, 1.5.1987, 20°40.07'S, 166°58.05'E, 510–590 m (1 spec. **MNHN** PNT 30).

R/V VAUBAN, cruise MUSORSTOM 4, Coral Sea: St. DC168, 16.5.1985, 18°48.2'S, 163°10.8'E, 720 m (5 spec. **MNHN** PNT 31, 5 spec. **AM** W.46390, 4 spec. NBCL **ZMA** V.POL 5545, 5 spec. SMF 24007, 5 spec. NHMUK ANEA 2015.917–921, 5 spec. LACM-AHF Poly 7018, 4 spec. USNM 1283056).

R/V CORIOLIS, cruise MUSORTSOM 5: St. CP323, 14.10.1986, 21°18.52'S, 157°57.62'E, 970 m (15 spec. SMF 24008).

R/V ALIS, cruise MUSORSTOM 6, Coral Sea: St. DW394, 13.2.1989, 20°49.46'S, 167°09.11'E, 570 m (1 spec. SMF 24003); St. DW410, 15.2.1989, 20°38.05'S, 167°06.65'E, 490 m (9 spec. **AM** W.46388); St. CP427, 17.2.1989, 20°23.35'S, 166°20.00'E, 800 m (1 old empty tube SMF 24004); St. DW468, 21.2.1989, 21°05.86'S, 167°32.98'E, 600 m (9 spec. NBCL **ZMA** V.Pol 5544); St. DW469, 21.2.1989, 21°03.64'S, 167°34.67'E, 630 m (1 spec. SMF 24005); St. DW483, 23.2.1989, 21°19.80'S, 167°47.80'E, 600 m (5 spec. **MNHN** PNT 28, 5 spec. NHMUK ANEA 2015. 912–916, 5 spec. LACM-AHF Poly 7017, 5 spec. USNM 1283055, 3 spec. **AM** W.46389); DW484, 23.2.1989, 21°20.80'S, 167°50.05'E, 520 m (6 spec. **MNHN** PNT 27); DW489, 24.2.1989, 20°48.37'S, 167°05.86'E, 700 m (6 spec. SMF 24006).

Description. *Tube*: white, straight, ostensibly free, quadrangular in cross-section, occasionally and locally pentagonal. Edges may be slightly serrate, especially in younger tube parts. Tube sides slightly concave. Distal part of tube circular in cross-section, smooth, with small peristomes resembling circular rings (Fig. 14A, D).

Tube ultrastructure: wall two-layered, inner layer occupying almost entire thickness, with spherulitic irregularly oriented prismatic ultrastructure (SIOP) containing abundant micritic cement. Inner layer made of small 1 µm or less densely packed spherulites of irregular shape, but more or less isometric. Spherulites appear as aggregates of very small crystals with common crystallization centre, precise shape of spherulites unclear, their size uniform throughout wall (Fig. 13A–D), but relatively large near the tube edges, especially in middle part of the wall (compare Fig. 13I and Fig. 13J). Outer layer uniformly thin (~5 µm; corresponding wall thickness 180 µm), having spherulitic prismatic structure (SPHP), consisting of elongated spherulites with growth direction perpendicular to tube surface (Fig. 13B, H).

Tube mineralogy: 100% calcite ($I_{\text{calc}}=447$).

Radiolar crown: 5–7 pairs of radioles arranged pectinately, not joined by inter-anterior membrane. Stylodes absent.

Peduncle: inserted as 2nd dorsal radiole, with about same thickness as other radioles, with pinnules (Fig. 14C). Pair of lateral wings proximal to opercular bulb absent.

Operculum: inverted cone covered with flat or slightly concave chitinous endplate, constriction distinct (Fig. 14C). Pseudoperculum absent.

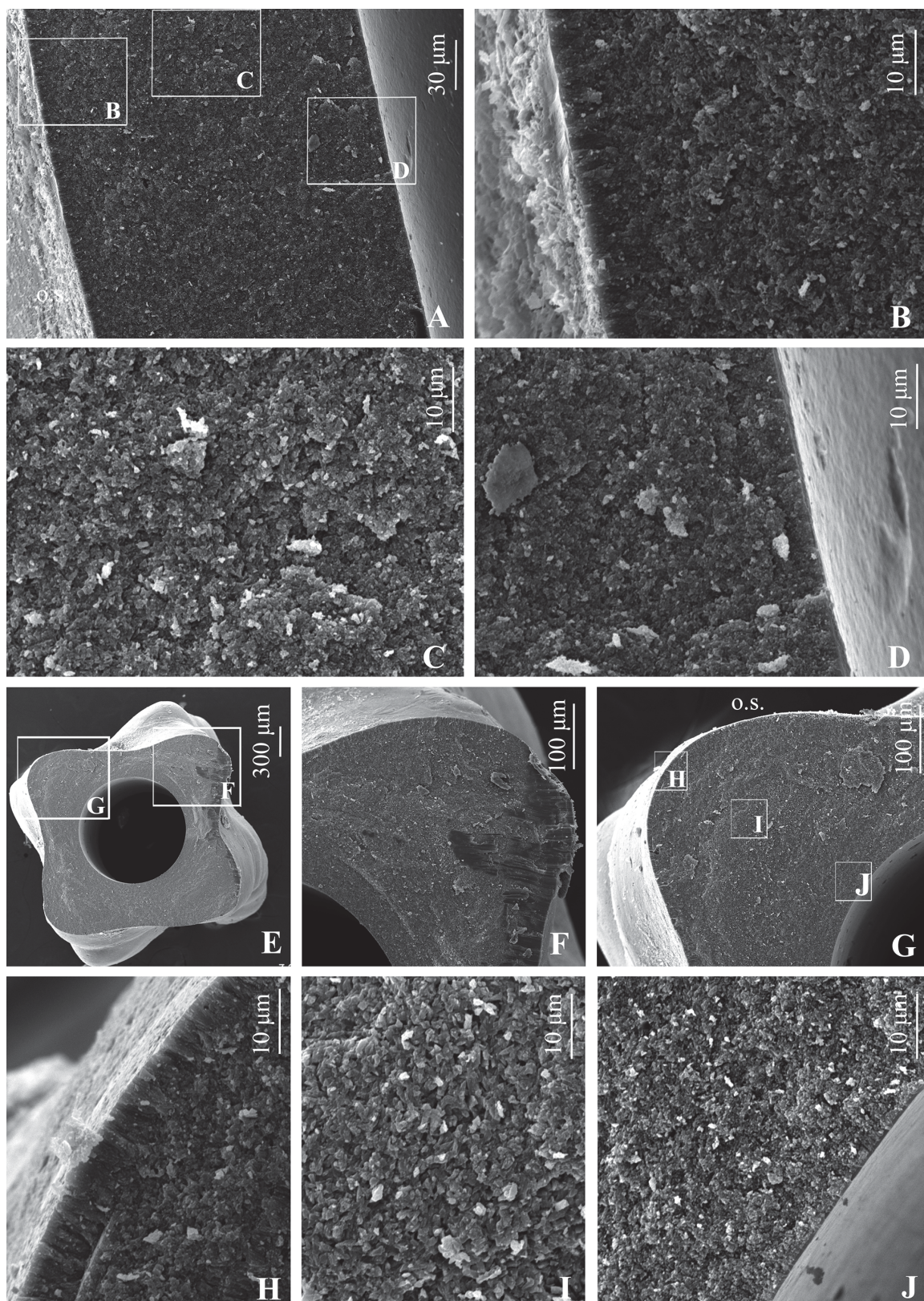


FIGURE 13. Tube ultrastructures of *Zibrovermia zibrowii* **gen. et sp. nov.** PIN 5485/17. A—longitudinal wall section, B—enlarged outer part showing outer layer consisting of elongated crystals orientated perpendicular to outer surface, C—enlarged middle wall part consisting of small isometric crystals, D—enlarged inner wall part with smallest isometric crystals, E—tube cross-section, G—enlarged cross-section through edge showing separation of inner wall layer, dark area to the right is an artefact (cutting trace), F—another enlarged cross-section through edge, H—details of outer wall part with clearly visible outer layer, I—details of middle wall part, J—details of inner wall part showing layer consisting of smallest isometric crystals. Abbreviation: o. s. – outer tube surface.

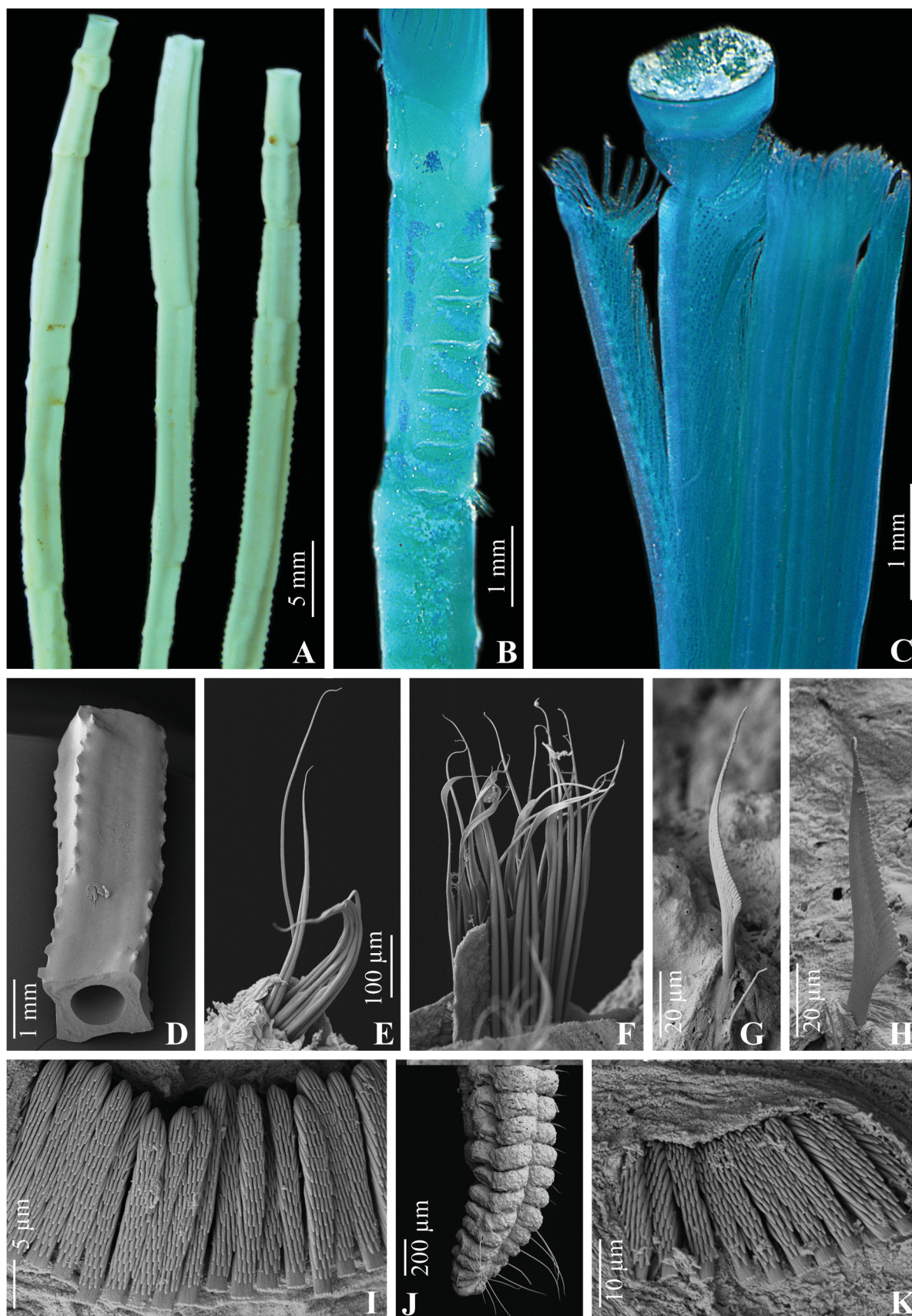


FIGURE 14. Photos and SEM images of *Zibrovermilia zibrowii* gen. et sp. nov. AM W.46387. A–C: photos, A—tubes, B—lateral view of thorax stained with methyl blue, C—radiolar crown with operculum and pinnulated opercular peduncle similar to other radioles, D–K: SEM images, D—tube fragment with denticulate edges, E—collar chaetae, F—thoracic chaetae, G, H—abdominal chaetae, I—thoracic uncini, J—posterior abdomen, K—abdominal uncini.

Collar and thoracic membranes: collar subdivided into 3 lobes, 2 small latero-dorsal and wide and longer ventral one (Fig. 14B). Thoracic membranes relatively wide, about same width throughout, ending between 2nd and 3rd chaetiger.

Thorax: with 7 thoracic chaetigers, 6 of which uncinigerous (Fig. 14B). Thoracic tori of similar size along thorax, parallel, not shifted dorso-ventally (no triangular depression). Collar chaetae limbate of two sizes, special chaetae absent (Fig. 14E); other thoracic notochaetae limbate of two sizes and *Apomatus* chaetae (Fig. 14F). Uncini rasp-shaped with around 15 teeth in profile view and 4–5 teeth in frontal view, dental formula P:4:5:5:5:5:5:5:5:4 (Fig. 14I); anterior peg rectangular flattened with crenulated edge.

Abdomen: up to 70 segments. Abdominal uncini rasp-shaped, with 12–14 teeth in profile view and 4–5 rows in frontal view, anterior peg rectangular flattened with crenulated edge, dental formula P:3(4):4:4:4:5:5:5:5:5 (Fig. 14K). Abdominal chaetae flat geniculate with edge made of rounded denticles (Fig. 14G, H), replaced by longer limbate capillaries only on very last 10–12 posterior segments (Fig. 14J); each chaetiger normally with a single chaeta. Posterior glandular pad absent (Fig. 14J).

Size: Total body length up to 18 mm, including up to 6 mm long radioles, width of thorax up to 0.65 mm. Tube total length up to 50 mm, outer diameter up to 0.9 mm, corresponding lumen diameter 0.55 mm. Thickness of tube wall in between angular margins varies in range 1/8–1/4th of outer diameter.

Distribution. Coral Sea, New Caledonia area, including Loyalty Islands, 490–1710 m.

Etymology. Named after Dr Helmut Zibrowius who initiated this study.

Remarks. SIOP tube ultrastructure was reported for a large number of serpulid genera (Vinn *et al.* 2009), many of which are unrelated. Two species reasonably close to the new species and having reported SIOP structure are *Vermiliopsis infundibulum* (Philippi, 1844) and *Pseudovermilia madracicola* ten Hove, 1989. However, both of them have unilayered tubes, without an external SPHP layer (Vinn *et al.* 2008) and thus, cannot be confused with *Zibovermilia zibrowii* **gen. et sp. nov.** The differentiation of SIOP structure from a relatively more common IOP structure may be difficult when spherulites are small and irregularly shaped as in the studied species. For example, in Vinn *et al.* (2008) *V. infundibulum* is reported to have IOP structure in one paragraph (Vinn *et al.* 2008: 645), but SIOP structure in another (*ibid.*: 635, table 2).

Fossil species with tetragonal tubes

Taxonomic composition of examined fossil material. Five generic names: *Nogrobs* de Montfort, 1808, *Tubulostium* Stoliczka, 1868, *Tetraserpula* Parsch, 1956, *Tetraditrupa* Regenhardt, 1961, and *Glandifera* Regenhardt, 1961 –are used in paleontological literature for tetragonal tubes, and all these genera were covered in the present ultrastructural study.

The name *Nogrobs* is the most commonly used for tetragonal tubes coiled into a spiral and having straight posterior parts (Fig. 1H–I), like in *Spirodiscus grimaldii*. Uncoiled tetragonal tubes are treated as either *Tetraserpula* (Fig. 1N–O) or *Tetraditrupa* (Fig. 1P–Q). Although Jäger (2005) considered *Tetraserpula* a synonym of *Nogrobs* *s. str.* and used the subgenus *Nogrobs (Tetraditrupa)* for all Jurassic-Cretaceous species having uncoiled free tetragonal tubes, there is no clear morphological difference between *Tetraserpula* (having type species from the Late Jurassic) and *Tetraditrupa* (type species from the Late Cretaceous). Therefore, these genera most probably are synonyms, and the older name *Tetraserpula* should replace *Tetraditrupa*. However, the demarcation between coiled *Nogrobs* and uncoiled *Tetraserpula/Tetraditrupa* is not obvious because of a variety of transitional forms between typical coiled and uncoiled forms, including uncoiled species with juvenile spirals. For heuristic reasons we have followed the “stratigraphical” tradition: *Tetraserpula* is used here for Jurassic-Lower Cretaceous uncoiled species, *Tetraditrupa* for Upper Cretaceous ones.

Glandifera Regenhardt, 1961, originally described as a subgenus of pentagonal *Genicularia* Quenstedt, 1857 (not closely related to the *Nogrobs-Tetraserpula-Tetraditrupa* group), includes tetragonal tubes with frequent and well-defined peristomes. It shows a combination of initial spiral coiling (Fig. 1J–K), like found in *Nogrobs*, with long straight anterior part (Fig. 1L–M), similar to those in *Tetraserpula* and *Tetraditrupa*. The only character separating *Glandifera* from the mentioned genera is regular peristomes that can be environmentally induced as hypothesized by ten Hove & Smith (1990) for Recent similarly unattached *Ditrupa* Berkeley, 1835. Therefore, the validity of *Genicularia* is doubtful and this name possibly should be synonymised with *Nogrobs* and/or

Tetraserpula. Juvenile spiral stages in some species of both *Nogrobs* and *Glandifera* demonstrate median keels (Fig. 1H-K) similar to those found in Recent *Spirodiscus grimaldii*.

Tubulostium Stoliczka, 1868 (Fig. 1R-T), originally described as a gastropod from the Upper Cretaceous (Turonian) of South India, is rarely mentioned in paleontological literature. It was never discussed in the context of tetragonal tubes classification and neither Jäger (2005), nor Ippolitov (2007) noted its striking similarity with fossil *Nogrobs* and Recent *Spirodiscus*. Starting from Rutsch (1939), this genus was classified as a synonym of *Rotularia* Defrance, 1827, the fossil genus that includes large spirally coiled tubes with variable (round to polygonal) cross-sections. Most recently, *Tubulostium* was tentatively treated either as a synonym of *Rotularia* s. str. or as a separate subgenus of *Rotularia* (Jäger 2005: 142), but it also may be convenient to treat it as a separate genus because *Rotularia* seems to be a “waste bin” of taxa with similar coiling by convergence (Ippolitov *et al.* 2014). To conclude, the composition of the genus *Tubulostium* is unclear and needs to be revised.

All five fossil genera have different type species, and therefore, all the names can be considered available according to ICZN, but their validity and relationships should be investigated. Thus, the generic names used for examined fossil species (Table 1) are provisional and in most cases our material is determined in open nomenclature. A revision of the entire *Tetraserpula*-*Nogrobs*-*Tetraditrupa*-*Glandifera*-*Tubulostium* fossil complex will constitute a separate paper (Jäger & Ippolitov in prep.).

Ultrastructures and mineralogy of examined fossil tubes. The studied fossil material can be subdivided into three groups based on tube ultrastructures. Group 1 includes Jurassic species of *Tetraserpula* (*T.* sp. 1, *T.* sp. 2, *T.* sp. 3, *T.* cf. *tetragona* (J. de C. Sowerby, 1829)), as well as *Nogrobs* cf. *vermicularis* de Montfort, 1808 and *Glandifera* cf. *vertebralis* (J. de C. Sowerby, 1829). This group is characterised by simple prismatic ultrastructures (SP) in outer and inner parts of the tube wall (Fig. 15A-H, 16A-D), while irregularly shaped isometric crystals (Fig. 15C, G, 16C), probably of secondary nature, may form a homogenous granular structure (HG *sensu* Vinn 2007) in the axial part of the parabolic growth lamellae. Crystals in well preserved tubes are prismatic, 10–12 µm long and 4–5 µm wide, and even show smallest growth lines (Fig. 15B, 16B). In badly preserved tubes, crystals appear to be slightly etched, often irregularly shaped (Fig. 15E-H).

Group 2 includes the Jurassic *Nogrobs tumidus* (J. de C. Sowerby, 1829) and two Lower Cretaceous species, *Tetraserpula* sp. 4 and *T.* sp. 5 (Fig. 16E-H; 17A-D). Ultrastructures are homogenous granular (HG) throughout the entire wall, without visible parabolic growth lamellae.

Ultrastructures of the Lower Cretaceous *Tetraserpula barremica* (Sasonova, 1958) and both Upper Cretaceous *Tetraditrupa rustica* (J. de C. Sowerby, 1829) and *T. canteriata* (von Hagenow, 1840) are somewhat intermediate between Group 1 and Group 2 (Fig. 17E-H, 18E-H). In *Tetraserpula barremica* (Fig. 17E-H) there is a gradual transition from the outer tube wall with simple prismatic (SP) ultrastructure to the inner part composed of isometric small crystals (homogenous granular structure, HG). *T. rustica* (Fig. 18A-D) has a thin outer layer of spherulitic prismatic structure (SPHP) similar to SP, while most part of the wall has a homogenous granular structure. In *T. canteriata* (Fig. 18E-H) crystals have an elongated shape throughout the wall, but their shapes are not prismatic and look like being strongly etched (Fig. 18F). Granular isometric crystals are especially numerous near outer and inner wall surfaces and are intermixed with elongated crystals.

Group 3 includes the only studied species of genus *Tubulostium*. In longitudinal section its tube wall is composed of three distinct layers characterised by different types of structures. The thickest outer layer—occupying up to 80% of the wall—has a homogenous angular crystal structure (HAC, Fig. 19B). Crystals are up to 20–25 µm long and irregularly shaped. In the axial zone of the parabolic growth lines the structure gradually transforms into simple prismatic (SP, Fig. 19C). However, only SP structure is observed in transverse section near the upper tube side (Fig. 19H), while HAC structure is present in the lateral sides, and there is no clear boundary between these two types of structure. Middle wall layer occupying 20% of wall width demonstrate homogenous granular structure (HG) with uniform crystals 1–1.5 µm long. There is no rectilinear boundary between outer and middle layers, and in some wall parts numerous segments of SP structure are chaotically interspersed within the middle HG layer (Fig. 19D). The inner layer does not exceed 20 µm (2–5% of the wall) in total width and has a simple prismatic (SP) or spherulitic prismatic structure (SPHP), which can be inferred from the general appearance of elongated crystals (Fig. 19E, G), but seems to be significantly recrystallised into aggregates of more or less isometric granular crystals.

Mineralogy of fossil tubes was analysed for five species: *Tetraserpula* sp. 1, *Nogrobs* cf. *vermicularis*, *Glandifera* cf. *vertebralis* (Group 1), *Tetraserpula* sp. 5 (Group 2) and *Tetraserpula barremica* (intermediate between Groups 1 and 2). In all cases tubes were found to consist of 100% calcite with high confidence.

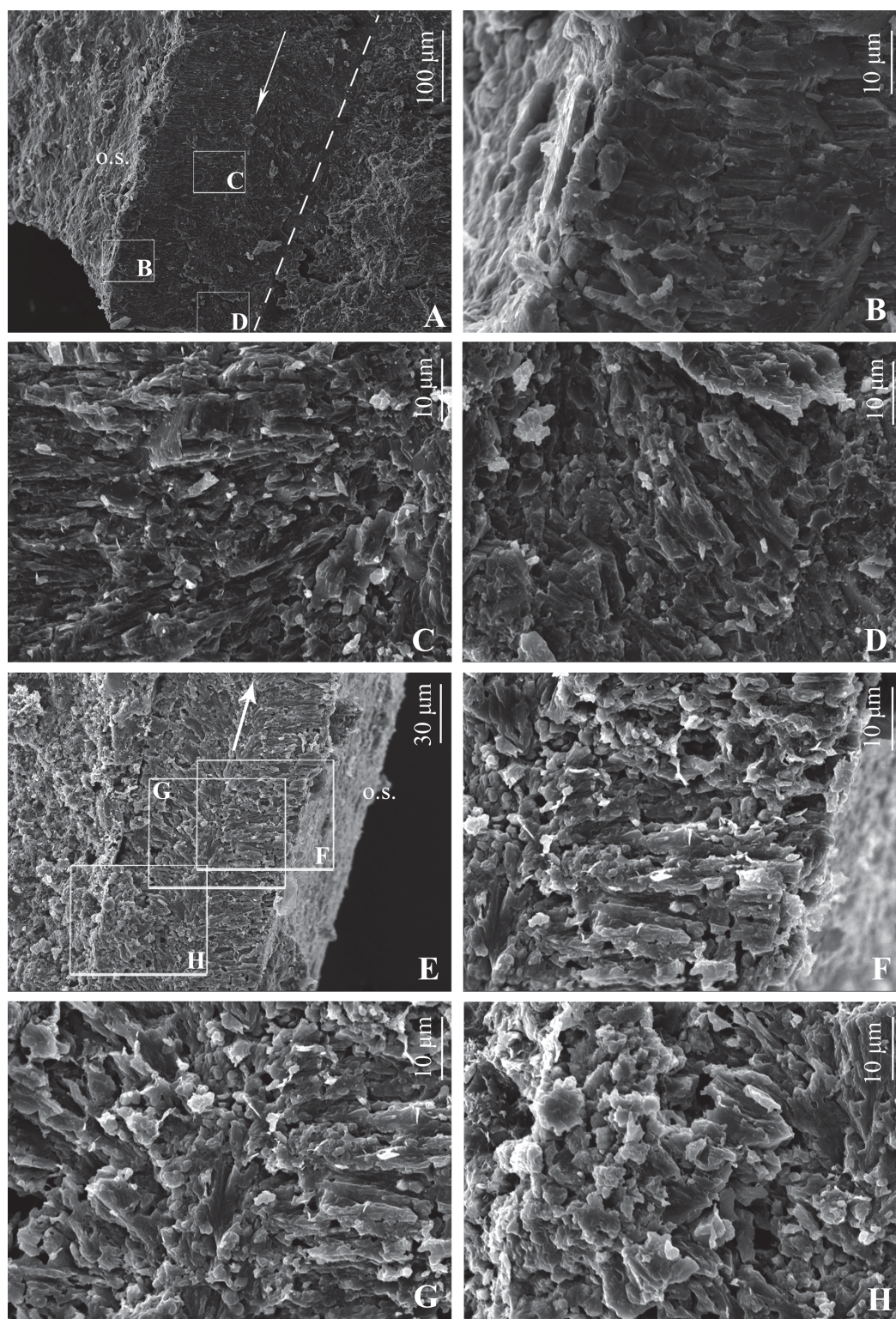


FIGURE 15. Tube ultrastructures of fossil tetragonal serpulids from the Middle Jurassic. A-D: *Nogrobs* cf. *vermicularis* PIN 5485/18. A—longitudinal wall section, B—enlarged outer part consisting of consolidated crystal aggregates, crystal growth lines are visible; C—enlarged middle wall part containing irregularly-shaped and isometrical crystals; D—enlarged middle (left) and inner (right) wall parts. E-H: *Glandifera* cf. *vertebralis*, PIN 5485/03. E—longitudinal wall section; F—enlarged outer to middle part consisting of consolidated aggregates in the outer part, with appearance of isometric crystals in the middle part; G—enlarged middle part of the wall, containing irregularly-shaped and isometrical crystals; H—enlarged inner part of tube wall. Arrows indicate the direction of growth and placed along the axis of parabolic growth lamellae, dashed line marks the inner margin of tube wall. Abbreviation: o. s.—outer tube surface.

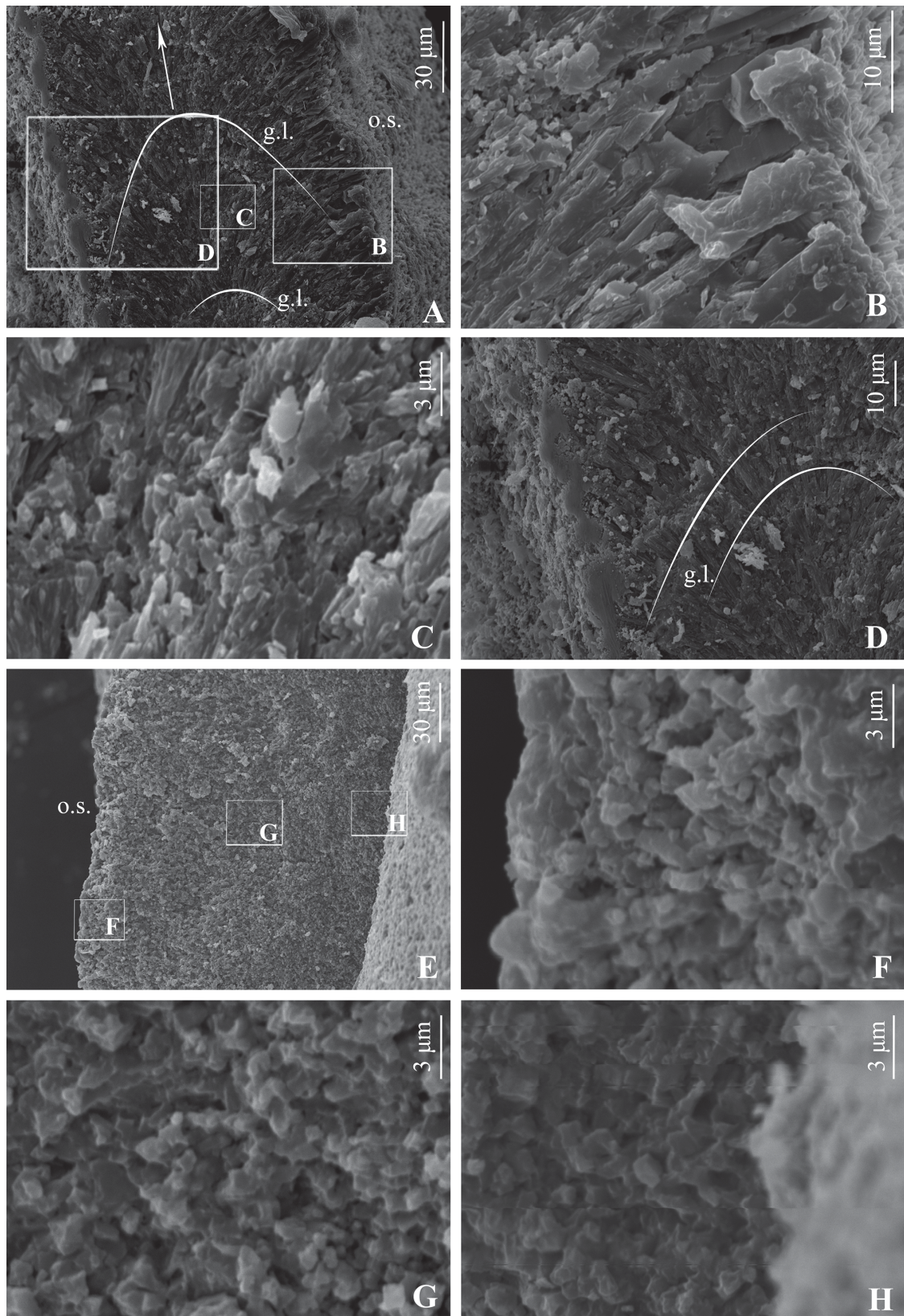


FIGURE 16. Tube ultrastructures of fossil tetragonal serpulids from the Middle Jurassic. A-D: *Tetraserpula* sp. 2 PIN 5485/19, A—longitudinal wall section, B—enlarged outer part showing large consolidated crystal aggregates, C—enlarged middle wall part containing isometrical crystals, D—enlarged inner wall part. E-H: *Nogrobs tumidus* PIN 5485/20, E—longitudinal wall section, F—enlarged outer wall part, G—enlarged middle wall part, H—enlarged inner wall part. Arrows indicate direction of tube growth and are placed along the axis of parabolic growth lamellae. Abbreviation: g. l.—growth lamellae; o. s.—outer surface of the tube.

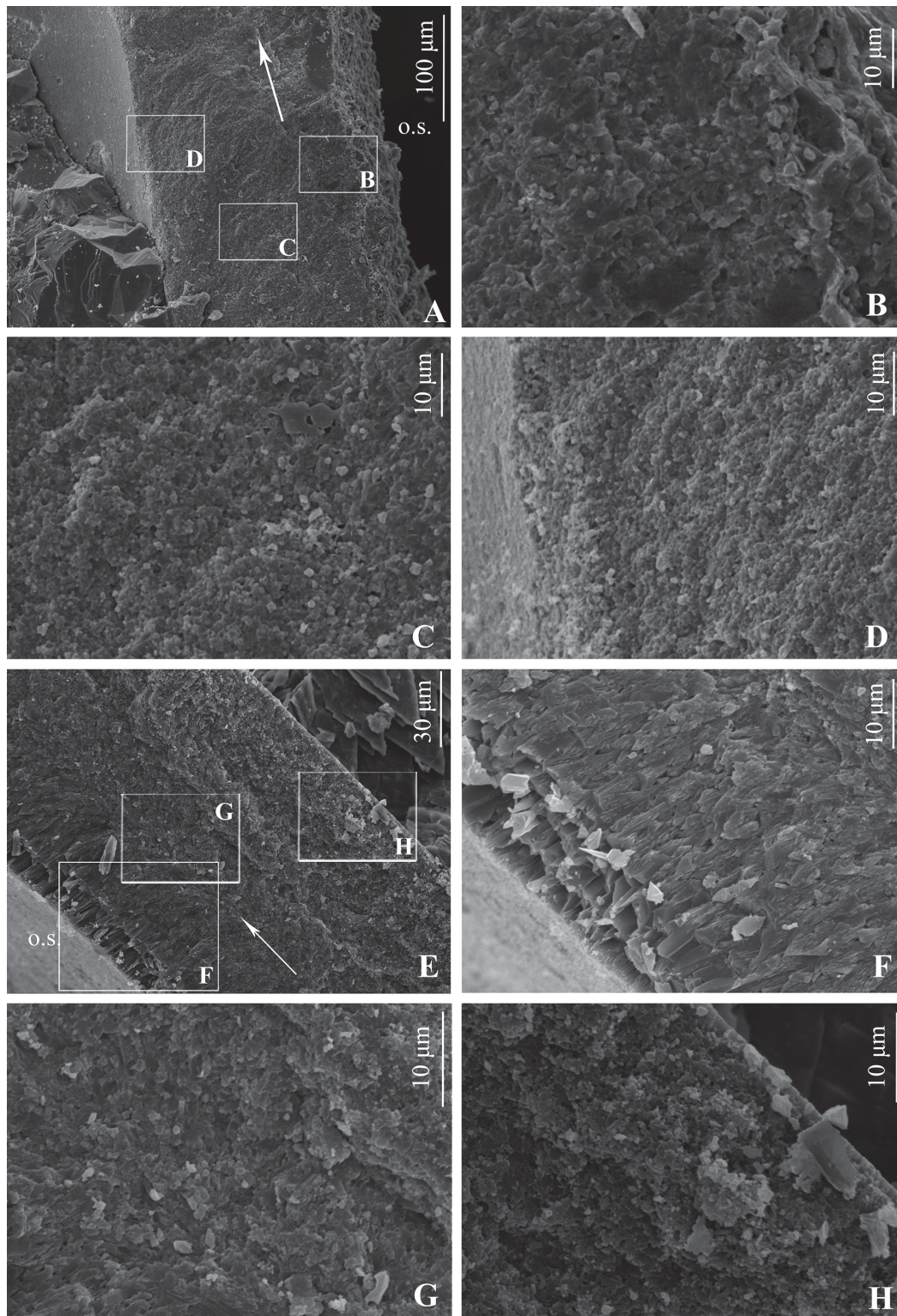


FIGURE 17. Tube ultrastructures of fossil tetragonal serpulids from the Lower Cretaceous. A-D: *Tetraserpula* sp. 4 PIN 5485/21, A—longitudinal wall section, B—enlarged outer wall part showing isometric crystals forming homogenous granular (HG) ultrastructure, C—enlarged middle part consisting of isometric crystals, D—enlarged inner wall part. E-H: *Tetraserpula barremica* PIN 5485/07, E—longitudinal wall section showing a transition from prismatic crystals in outer wall to isometric in inner wall, F—enlarged outer (unaltered) wall part showing elongated oriented crystals near wall surface and isometric crystals near axial part of parabolic lamellae, G—enlarged axial wall part (slightly recrystallised) consisting mostly of small slightly elongated crystals, H—inner wall part (heavily recrystallised) consisting of small isometric crystals. Arrows indicate direction of tube growth and are placed along axis of parabolic growth lamellae. Abbreviation: o. s.—outer tube surface.

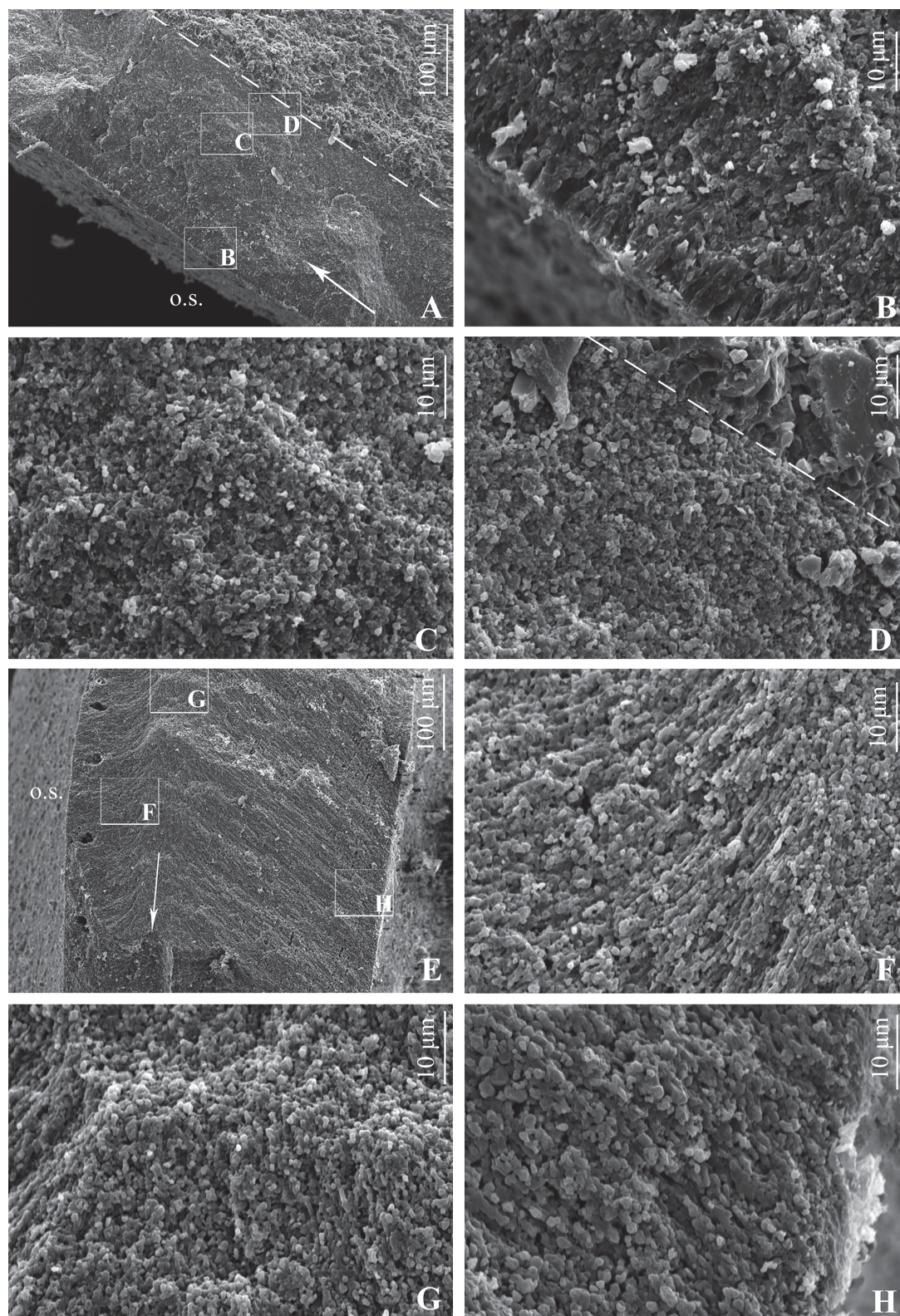


FIGURE 18. Tube ultrastructures of fossil tetragonal serpulids from the Upper Cretaceous. A-D: *Tetradietropa rustica* PIN 5485/22, A—longitudinal wall section, B—enlarged outer part with a layer of crystals oriented perpendicular to outer surface, C—enlarged middle wall part consisting of isometric crystals, D – enlarged inner wall part. E-H: *Tetradietropa canteriata* PIN 5485/05, E—longitudinal wall section, F—enlarged outer wall part showing elongated oriented crystals and isometric crystals near outer wall, G – enlarged axial wall part made of small isometric crystals, H—enlarged inner wall part made of (?) partly recrystallised elongated oriented crystals. Arrows indicate direction of tube growth, and are placed along axis of parabolic growth lamellae, dashed line marks inner wall margin. Abbreviation: o. s.—outer tube surface.

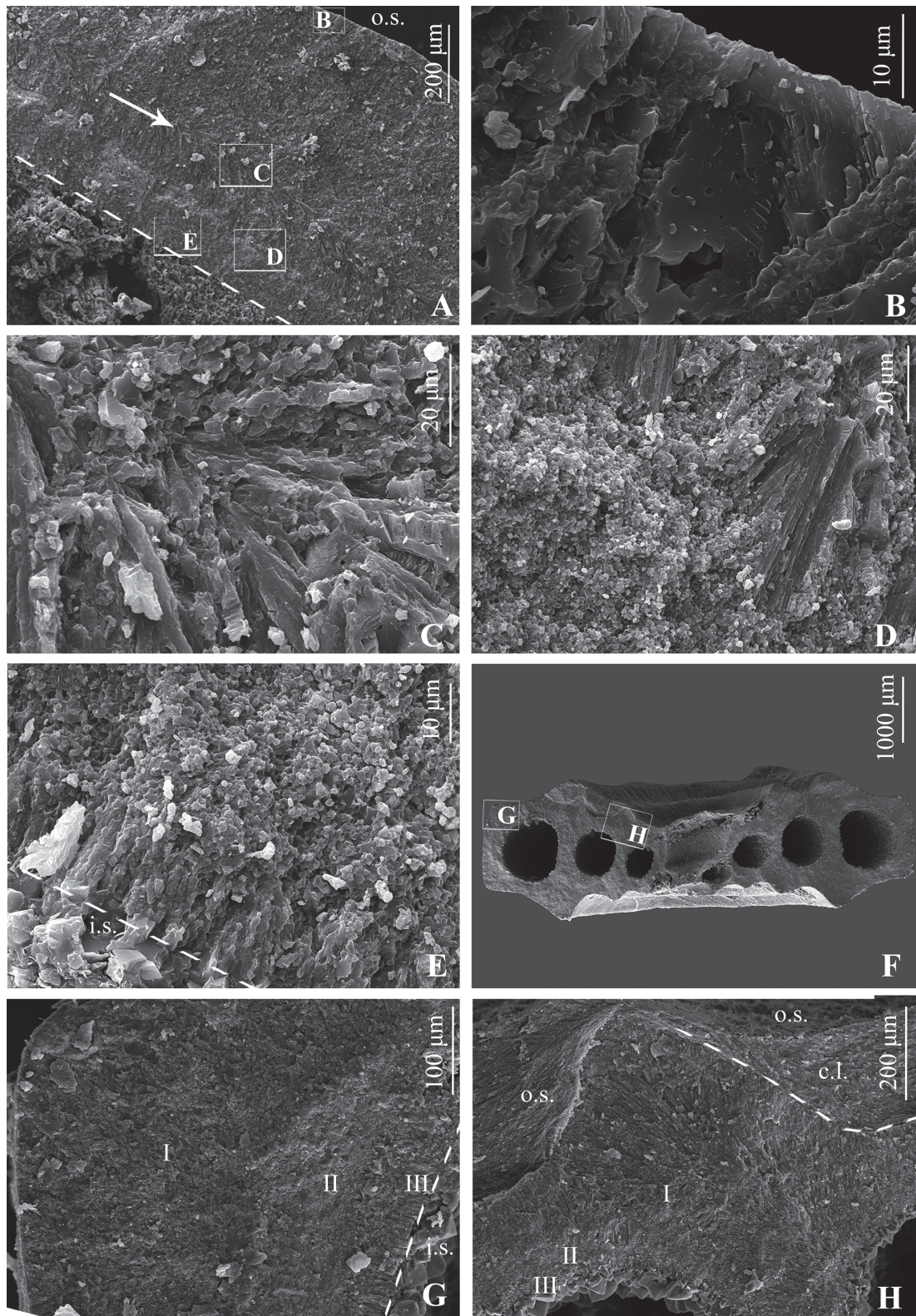


FIGURE 19. Tube ultrastructures of fossil tetragonal serpulid *Tubulostium discoideum* PIN 5485/24. A-E: longitudinal wall section, A—general view, B—enlarged outer part showing irregularly shaped crystals forming homogenous angular crystal (HAC) structure, C—enlarged axial part of parabolic growth lamellae showing simple prismatic (SP) structure, D—contact zone between outer layer and middle layer with homogenous granular (HG) structure, marked with non-rectilinear appearance of boundary between layers, E—internal wall part showing middle layer with HG structure and thin inner layer with slightly recrystallized simple prismatic (SP) or spherulitic prismatic (SPHP) structure; F-H: transverse section, F—view of sectioned spiral tube, G—view of wall cross-section through lateral side, H—same, through upper tube side. Abbreviations: o. s.—outer tube surface, i. s.—inner tube surface, c. l.—cementing layers, I—outer tube layer, II—middle tube layer, III—inner tube layer.

Discussion

Diversity and phylogenetic relationships of Recent serpulids in tetragonal tubes. The current revision of Recent deep-sea serpulids characterised by polygonal (tetragonal or octagonal) tubes revealed at least six species inhabiting bathyal to abyssal depths. Only one of them, *Spirodiscus grimaldii*, has partially spiral tubes, while the remaining five are characterised by more or less regular straight or tusk-shaped tubes, with four or eight (the latter only in *Spirodiscus groenlandicus* **comb. nov.**) edges. Contrary to our original expectations, only three of those species (*Bathyditrupa hovei*, *Spirodiscus groenlandicus* **comb. nov.**, and *S. grimaldii*) are morphologically similar to suggest close relationships. Ultrastructurally, all three of them characterised by IOP structure in the inner and middle part of the tube wall and thin layer having SOIOP structure near the outer side. The latter structure previously was recorded for *Protula diomedea* Benedict, 1887 by Vinn *et al.* (2008), and for some species of *Hyalopomatus*, including the new species described herein (see Remarks for *H. dieteri* **sp. nov.**). However, in all the taxa mentioned above the dominant orientation of crystal axes is transverse, not longitudinal like in *Bathyditrupa* and *Spirodiscus*, thus, indicating substantial difference in organization of crystal matter and convergent nature of nominally the same ultrastructural type in the *Bathyditrupa-Spirodiscus* clade. Mineralogically, all the members of *Bathyditrupa-Spirodiscus* clade are similar and predominantly aragonitic with aragonite content 92–100%.

The other three species with quadrangular tubes belong to the genera *Bathyvermilia*, *Hyalopomatus*, and *Zibovermilia* **gen. nov.** Tube ultrastructures of these genera are so different that a combination of tube morphology with ultrastructural characters allows confident identification of their empty tubes. Except for *Zibovermilia zibrowii* **gen. et sp. nov.** having a two-layered tube constructed of spherulites (SPHP+SIOP structures) and thus easily recognizable, all other species have tubes built of rice grain-like elongated crystals. *Bathyvermilia gregrousei* **sp. nov.** is distinct because of its unilayered tube with IOP structure and the unique “cavity belt” surrounding the lumen, while *Hyalopomatus* has a combination of IOP and SOIOP structures in the wall, like *Bathyditrupa* and *Spirodiscus* do. *Hyalopomatus dieteri* **sp. nov.** differs from them by the tinternal position of the SOIOP zone and transverse, not longitudinal orientation of crystals constituting the SOIOP structure. We suggest that data on tube ultrastructures—as introduced by ten Hove & Zibrowius (1986) and Zibrowius & ten Hove (1987)—should become a standard part of serpulid taxonomic descriptions.

Mineralogically, all three species are different and therefore are recognizable as well. *Hyalopomatus dieteri* **sp. nov.** is close to members of *Bathyditrupa-Spirodiscus* clade (aragonite content 97–100%), *Bathyvermilia gregrousei* **sp. nov.** has a more balanced calcite-aragonite ratio (aragonite content varies from 80% to (?) 45%), while the tube of *Zibovermilia zibrowii* **gen. et sp. nov.** is 100% calcitic.

All molecular phylogenetic analyses (*e.g.*, Kupriyanova *et al.* 2006, 2009; Lehrke *et al.* 2007; Kupriyanova & Nishi 2010) inferred two major clades within Serpulidae. Clade A comprised two clades, the *Serpula-Crucigera-Hydroides* (Clade AI, “*Serpula*-group”), and the *Spirobranchus-Ficopomatus-Ditrupa* (Clade AII, “*Spirobranchus*-group”). Clade B included monophyletic Spirorbinae as the sister group to the *Protis-Protula-Vermiliopsis* clade (BI, “*Protula*-group”). Although no molecular data were available for the species examined in this study, we assume that *Hyalopomatus dieteri* **sp. nov.** belongs to Clade AI along with *H. bififormis* (see Kupriyanova & Nishi 2010), but unlike all known members of the clade (see Smith *et al.* 2013), this new species of *Hyalopomatus* has an aragonitic mineralogy. *Bathyvermilia* is a member of Clade BI (see Kupriyanova & Nishi 2010), therefore, we assume that both *Bathyvermilia gregrousei* **sp. nov.** and the morphologically similar *Zibovermilia zibrowii* **gen. et sp. nov.** also belong to Clade BI, even though the latter has an outer SPHP layer not characteristic for members of this clade (see Vinn & Kupriyanova 2011) and 100% calcitic composition, also untypical for this clade (see Smith *et al.* 2013). The phylogenetic position of *Bathyditrupa* and *Spirodiscus* remains uncertain because these taxa lack thoracic *Apomatus* chaetae typical for Clade BI, but at least *Spirodiscus* has flat geniculate abdominal chaetae characteristic for this clade. Tube ultrastructures do not provide any indication of phylogenetic position either because unilayered tubes with IOP structure, principally similar to those of *Bathyditrupa* and *Spirodiscus*, are found in both clades AII and BI (Vinn & Kupriyanova 2011: tab. 1). However, predominantly aragonitic mineralogy observed for all three species is common in clade BI (see Smith *et al.* 2013), but some members of clades AI (two species of *Hydroides*, see Bornhold & Milliman 1973; Vinn *et al.* 2008; Smith *et al.* 2013: tab. 1) and AII (*Hyalopomatus dieteri* **sp. nov.** herein) have predominantly aragonitic tubes as well, while some members of clade BI may have calcitic tubes (*e.g.*, *Bathyvermilia challengerii*, see Kupriyanova *et al.* 2014).

The best known Recent free-living subtidal serpulid is *Ditrupa* Berkeley, 1835 (Clade AII) with species *Ditrupa arietina* (O. F. Müller, 1776) and *D. gracillima* Grube, 1878, characterised by tusk-shaped tubes circular in cross-section. Larvae of *D. arietina* species settle on small particles and early juveniles are attached, but as the animals grow, their tubes soon break free (Charles *et al.* 2003). Other examples of secondarily free-living serpulids include *Serpula crenata* (Ehlers, 1908) with curved hexagonal tubes (Clade AI) and *Spirobranchus latiscapus* (Marenzeller, 1885) with curved triangular in cross-section tubes (Clade AII). Juvenile specimens of the latter species are commonly found attached to small pebbles (Kupriyanova, unpubl.). Ten Hove & Smith (1990) hypothesized that curved tubes are likely to be an adaption to a soft sediment existence and, therefore, can be convergent. While three closely related Recent tetragonal species *Bathyditrupa hovei*, *Spirodiscus grimaldii*, and *S. groenlandicus* **comb. nov.** are true free-lying soft-bottom dwellers, *Bathyvermilia gregrousei* **sp. nov.**, *Hyalopomatus dieteri* **sp. nov.** and *Zibrovermilia zibrowii* **gen. et sp. nov.** are treated as “ostensibly free” because available material is represented by long, more or less straight, not tusk-shaped, anterior fragments. It is unclear whether such straight tubes were horizontally lying on the surface of soft substrates or were attached posteriorly and growing upwards as typical in environments with low currents and high sedimentation rate (*e.g.*, Kupriyanova & Badyaev 1998) for *e.g.*, *Hyalopomatus* spp. (see Kupriyanova & Jirkov 1997; Sanfilippo 2009). Both free-lying species and those that have a small area of attachment for growing away from the substrate (presumably unattached) represent a continuum of adaptations to soft sediments of the deep-sea. Similar tube morphology, discovered in phylogenetically distant Recent species studied here, appears to be a result of convergence due to similar habitats.

Preservation of fossil material. Recrystallization is a form of diagenetic (occurring during its lithification) and post-diagenetic changes that presents a serious problem for fossil ultrastructural studies. As a result of recrystallization, fossil serpulid tube ultrastructures may become significantly different from their original state (Zibrowius & ten Hove 1987; Weedon 1994; Sanfilippo 1998b, Vinn 2005, 2007; Vinn & Furrer 2008). Diagenetically altered material is characterised by isometric crystals more or less uniform in size and the disappearance of growth lamellae (Vinn & Furrer 2008), although Vinn (2007) suggested that HG ultrastructure, having such characters, might be original for some ancient serpulids.

For all examined Jurassic tubes from Group 1 diagenetic recrystallization can be ruled out because material from distant geographic locations shows a high degree of ultrastructural similarity. Preservation of fine growth lamellae and even growth lines of individual prismatic crystals is also indicative of unaltered ultrastructures. Moreover, all studied Jurassic tubes of Group 1 originated from clay mudstones, the type of rocks most suitable for preventing any alteration of carbonate material, and in most localities serpulid tubes were accompanied by ammonite shells with preserved aragonitic nacre (Ippolitov, field obs.). Aragonite usually quickly transforms into calcite during recrystallization, and thus, presence of nacre indicates potentially good preservation. This also means that mineralogy of examined 100% calcitic fossil tubes with SP structure is probably unaltered. Recent species *Placostegus tridentatus* (Fabricius, 1780) and *Vitreotubus digeronimoi* Zibrowius, 1979 having unilayered tubes with SP structure also have 100% calcitic tubes (see Vinn *et al.* 2008), which supports the idea of unaltered mineralogy for fossils from Group 1.

As the tube wall of the only member of Group 3, *Tubulostium discoideum*, has three distinct layers, each with a well-defined type of structure, this wall is likely to have an unaltered structure as well. Only the inner SP/SPHP layer is slightly recrystallized, which, however, does not significantly affect its primary structure. Homogenous ultrastructures of Group 2 seem to be mostly diagenetically altered as suggested by the isotropic appearance of the wall fabric, absence of any elongated prismatic crystals characteristic for serpulids, and lack of visible growth lamellae. Calcitic composition of the only species with studied mineralogy, *Tetraserpula* sp. 5, can be either primary or secondary.

Lower Cretaceous *Tetraserpula barremica* and Upper Cretaceous *Tetraditrupa canteriata*, being somewhat intermediate between Group 1 and Group 2 (Fig. 17E-H, 18E-H), probably show different stages of recrystallization. The early stage is well-illustrated by *Tetraserpula barremica* (Fig. 17E-H) that has an almost unaltered outer tube wall with a preserved simple prismatic (SP) ultrastructure, but likely a recrystallized inner part. Lumens of serpulid tubes were filled with secondary calcite, while the general sediment was a siltstone. This suggests that after being buried, empty tube cavities were affected by fluids circulating in the sediment. This then resulted in formation of large calcite crystals filling the lumen and the wall part immediately underlying it became most heavily recrystallized, while the outer wall part remained unaltered. In case of *T. canteriata* (Fig. 18E-H) just

after burial the inner cavity was filled with thin carbonate sediment, consisting mainly of coccoliths. Isometric (=diagenetically altered) crystals are common near tube surfaces, whereas traces of a likely original structure are found in the middle part of the parabolic axis. The observed ultrastructure in *T. canteriata* is probably a result of long-term diagenetic and post-diagenetic infiltration through the rocks resulting in a slow dissolution and recrystallization of the wall material.

The nature of the wall in *Tetraserpula rustica* (Fig. 18A-D), another Late Cretaceous species from carbonate sediment, is uncertain. The layer of spherulitic prismatic structure (SPHP) that could be a remnant of the primary structure is uniformly thin and located on the outer side of the tube wall, which is not the best position for protection from diagenetic agents. Thus, the entire wall structure can be either primary or secondary with an outer layer of diagenetic origin as a result of the effect of diagenetic agents from the outside of the surface.

To conclude, only fossil material from Groups 1 and 3 have preserved primary ultrastructures and thus can be used for direct ultrastructural comparisons with the Recent material.

Comparison of tube ultrastructures, mineralogy and morphology of Recent and fossil species. Our study showed that fossil tubes of Group 1 – including representatives of spirally coiled *Nogrobs*, most species of tusk-shaped *Tetraditrupe*/*Tetraserpula* lacking peristomes, and peristome-bearing *Glandifera* – demonstrated very similar unilayered walls with simple prismatic (SP) structure and 100% calcitic mineralogy. Unilayered SP structure is characteristic for Recent members of Clade AII (e.g., *Placostegus* Philippi, 1844 (see ten Hove & Zibrowius 1986; Vinn 2007; Vinn *et al.* 2008), *Vitreotubus digeronimoi* Zibrowius, 1979) as well as for some spirorbins of Clade B (Ippolitov & Rzhavsky 2008), belongs to a group of oriented prismatic structures (*sensu* Vinn *et al.* 2008) and results in tube transparency. In contrast, Recent species with tetragonal and octagonal tubes show a variety of tube ultrastructures, mainly of unoriented and semi-oriented types (*sensu* Vinn *et al.* 2008), but none of them have an unilayered tube with oriented SP structure typical for fossils of Group 1. Among all studied Recent species, only *Zibovermilia zibrowii* **gen. et sp. nov.** has 100% calcitic tube, thus being similar to the studied fossils, but its tube structure is still very different.

Morphological comparison of fossil and Recent uncoiled tetragonal tubes shows that the tube shapes of fossil *Tetraditrupe* and *Tetraserpula* are closer to those of *Hyalopomatus dieteri* **sp. nov.** and *Zibovermilia zibrowii* **gen. et sp. nov.**, than to those of *Bathyditrupe hovei*, the species previously considered as a possible descendant of fossil tetragonal forms (Jäger 2005; Ippolitov 2007). In all studied Mesozoic species, tubes can slightly twist around their growth axis, have obvious growth stops marked by constrictions or by massive peristomes (in *Glandifera*), their tubes tend to become rounded in late growth stages, and the tube shapes are not strictly tusk-like. None of these characters are observed in Recent *Bathyditrupe*. However, most fossil species with variously curved tetragonal tubes seem to be truly free-lying, not ostensibly free as can be inferred for the long straight tubes of *Hyalopomatus dieteri* **sp. nov.**, *Bathyvermilia gregrousei* **sp. nov.** and *Zibovermilia zibrowii* **gen. et sp. nov.**

The ultrastructure of the three-layered tube of *Tubulostium discoideum* (Group 3) also has no direct analogues among studied Recent forms. Like members of Group 1, it also seems to belong to Clade A judging by oriented SP structure and multiple layers in tube wall. Unlike Recent coiled *Spirodiscus grimaldii*, *Tubulostium* has larger tubes and layers cementing the coils (Fig. 19H).

Ultrastructurally, *Tetraditrupe rustica* is the only fossil species that closely resembles a certain Recent species, *Zibovermilia zibrowii* **gen. et sp. nov.** Both species have thin external SPHP layers, while for the most part the wall is made of unoriented structure represented by spherulitic irregularly oriented prismatic ultrastructure (SIOP) in the Recent species and homogenous granular structure (altered SIOP?) in the fossil one. However, an external SPHP structure is common for many serpulids of clade AII (Vinn & Kupriyanova 2011) and cannot imply an affinity itself. Given that a primary nature of *T. rustica*'s ultrastructure is doubtful, the affinity of *T. rustica* and *Zibovermilia* **gen. nov.** also remains doubtful.

Taxonomic and phylogenetic implications of ultrastructural comparisons. The presence of an unilayered SP tube structure in fossil tetragonal tubes of Group 1 is fully concordant with published data on other fossil tetragonal species from the Middle-Upper Jurassic of Europe, determined as “*Nogrobs* cf. *vertebralis*” (J. de C. Sowerby, 1829), “*Tetraserpula planorbiformis*” (Münster in Goldfuss, 1831) and “*Nogrobs?* *hydrocarbonicus*” (respectively in Vinn 2005, Vinn & Furrer 2008 and Vinn *et al.* 2012). Such a similarity among all species of Group 1 (*Nogrobs*, *Tetraserpula*, *Glandifera* and, questionably, *Tetraditrupe*) suggests close relationships. This result supports the opinion of Jäger (2005) who treated both planospirally coiled and simply curved tubes as subgenera within the genus *Nogrobs*. The number of tube layers in the only member of Group 3, *Tubulostium discoideum*, is

strikingly different from those of Group 1, suggesting that *Tubulostium* is not closely related to similarly coiled *Nogrobs* and should not be synonymised with it.

The ultrastructural diversity discovered in Recent serpulids with tetragonal tubes does not include unilayered tubes with SP structure common for most fossils, which makes synonymization of Recent *Spirodiscus* with fossil *Nogrobs*, as accepted in ten Hove & Kupriyanova (2009), doubtful. The same is true for synonymization of Recent *Bathyditrupa* with fossil *Tetraserpula*/*Tetraditrupa* supposed by Jäger (2005) and Ippolitov (2007). Tubes of fossil *Tubulostium*, also similar to *Spirodiscus* in coiling and general morphology, have a very different three-layered structure, and thus, cannot be synonymised with *Spirodiscus* either.

Significant ultrastructural differences found in Recent and fossil tubes suggest that appearance of spirally coiled tetragonal tubes and related tusk-shaped forms in Jurassic and Recent seas is likely a result of convergence, confirming the earlier suggestions of relatively low taxonomical significance of external tube characters (*e.g.*, ten Hove & van den Hurk 1993). The ultrastructural similarity of fossil species *Tetraditrupa rustica* to Recent *Zibrovermilia zibrowii* **gen. et sp. nov.** may indicate that fossil “*Serpula rustica*” J. de C. Sowerby, 1829 should be placed within the genus *Zibrovermilia* **gen. nov.**, but this warrants further studies. To conclude, based on differences in tube ultrastructures, we reject Jäger’s (2005) hypothesis that extant *Spirodiscus* is synonymous with fossil *Nogrobs*, thus re-instating the Recent genus as a valid taxon.

All researchers who discussed the connection of fossil tetragonal tubes with Recent ones of *Spirodiscus* and *Bathyditrupa* (Jäger 2005; Ippolitov 2007; ten Hove & Kupriyanova 2009) were unaware that tetragonal tubes can be found in a number of Recent genera. Therefore, all earlier phylogenetic interpretations based on this character need to be re-evaluated. All fossil species belong to Clade AII and thus are clearly unrelated to Recent tetragonal *Bathyvermilia* and *Zibrovermilia* **gen. nov.** representing clade BI. However, a close relationship of fossil species with Recent tetragonal members of Clade A (*Hyalopomatus* and questionably *Bathyditrupa* and *Spirodiscus*) still cannot be excluded. Unoriented (IOP) and semi-oriented (SOIOP) ultrastructures of Recent *Bathyditrupa*, *Spirodiscus*, and *Hyalopomatus dieteri* **sp. nov.**, are considered to be plesiomorphic relative to highly ordered oriented (SP) structures (Vinn & Kupriyanova 2011: 144) characteristic for studied fossil *Nogrobs* and *Tetraserpula*/*Tetraditrupa*. Therefore, linking fossil tetragonal tubes of Group 1 to Recent *Bathyditrupa*/*Spirodiscus* or *Hyalopomatus* would indicate drastic simplification of ultrastructures. Accepting that Jurassic coiled tetragonal tubes belonged to direct ancestors of Recent *Spirodiscus*, while uncoiled tusk-like Jurassic species may be ancestors of *Bathyditrupa* or tetragonal *Hyalopomatus dieteri* **sp. nov.**, would mean parallel ultrastructural simplification that occurred at least in two lineages. This assumption makes linking fossil species with tetragonal tubes to any Recent members of Clade A with similar tubes unlikely. However, a large stratigraphical gap covering the entire Caenozoic (66 Myr) between the youngest known fossil tetragonal tubes (Late Cretaceous *Tetraditrupa canteriata*) and Recent species with similar tubes still allows the possibility of a gradual evolution in ultrastructures. Also, the fact that fossil species inhabited shallow-water subtidal environments, while Recent species are found in bathyal and abyssal zones should be reflected in any hypotheses explaining ultrastructural evolution of serpulid tubes.

Conclusions

1. Morphological, ultrastructural and mineralogical studies of Recent serpulids with tetragonal tubes have revealed their significant taxonomic and morphological diversity. Three new species of three genera (including one new), *Bathyvermilia gregrousei* **sp. nov.**, *Hyalopomatus dieteri* **sp. nov.**, *Zibrovermilia zibrowii* **gen. et sp. nov.** have been described.
2. Tubes of all examined Recent species have markedly different ultrastructures and different tube mineralogy, which allows recognition of species with similar tetragonal tube morphologies. However, ultrastructures and mineralogy of three closely related species (*Spirodiscus grimaldii*, *S. groenlandicus* **comb. nov.** and *Bathyditrupa hovei*) are very similar.
3. New species with tetragonal tubes belong to genera, for which tetragonal tubes were previously unknown (*Bathyvermilia*, *Hyalopomatus*), thus suggesting that the similar tube morphology is a result of convergence in deep-sea serpulids.
4. Two newly established deep-sea species (*Hyalopomatus dieteri* **sp. nov.** and *Zibrovermilia zibrowii* **gen. et sp. nov.**) have tube mineralogies untypical for the clades they belong to (AII and B, respectively), indicating much higher plasticity of this character than previously thought.

5. Tube ultrastructures of most fossil serpulids with tetragonal tubes, including coiled *Nogrobs* and straight *Tetraserpula*/*Tetraditrupa*, are similar to each other, but differ markedly from all extant taxa with such tubes. This indicates a common origin for the entire fossil *Nogrobs*-*Tetraserpula* group, which is unlikely to be a mixture of unrelated morphologically convergent taxa, as shown for Recent species.
6. Ultrastructural and mineralogical differences between fossil and Recent material mean that synonymization of Recent *Spirodiscus* and *Bathyditrupa* with fossil *Nogrobs*, as suggested by Jäger (2005), should be rejected.

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