

A New Species of the Mysterious Genus *Spirodiscus* (Annelida: Serpulidae) of the Eastern Australian Abyss

ELENA K. KUPRIYANOVA^{1,2}  AND BETH FLAXMAN^{1,3} 

¹ Australian Museum Research Institute,
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

² Department of Biological Sciences,
Macquarie University, North Ryde NSW 2109, Australia

³ School of Life and Environmental Sciences,
The University of Sydney NSW 2006, Australia

ABSTRACT. In May–June 2017 an expedition on board RV *Investigator* sampled benthic communities along the lower slope and abyss of Australia’s eastern margin from off mid-Tasmania to the Coral Sea. Over 200 annelids of the family Serpulidae collected during the voyage were collected and deposited in the Australian Museum in Sydney. Among them there was a new species of the poorly known abyssal (3754–4378 m) genus *Spirodiscus*. 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, 1993 with quadrangular tusk-shaped tubes, and *Spirodiscus groenlandicus* (McIntosh, 1877) with octagonal tusk-shaped tubes. The new species, *S. ottofinamusi* sp. nov. has very characteristic thin tusk-shaped unattached fluted tubes similar to those found in *S. groenlandicus*, but it differs by the details of collar, thoracic tori and abdominal chaetae. Morphologically, it has a pinnulated opercular peduncle and flat geniculate abdominal chaetae like filogranin serpulids but lacks thoracic *Apomatus* chaetae like serpulins. The first DNA sequences of this mysterious taxon places the new species within the filogranins in sister group relationship with *Chitinopoma serrula*.

Introduction

The family Serpulidae Rafinesque, 1815 (including Spirorbinae Chamberlin, 1919) is a group of sedentary annelids inhabiting self-secreted calcareous tubes. The family is composed of c. 70 genera and more than 500 species (Capa *et al.* 2021). These animals are most common in subtidal and shelf habitats, but can occur from intertidal to hadal depths (Kupriyanova *et al.*, 2010, 2011, 2014; Kupriyanova & Ippolitov, 2015). Serpulids from bathyal and abyssal depths belong to the genera *Bathyvermilia* Zibrowius, 1973;

Bathyditrupa Kupriyanova, 1993; *Filogranula* Langerhans, 1884; *Hyalopomatus* Marenzeller, 1878; *Laminatubus* ten Hove & Zibrowius, 1986; *Spirodiscus* Fauvel, 1909; *Protis* Ehlers, 1887; *Vitreotubus* Zibrowius, 1979; and *Zibrovermilia* Kupriyanova & Ippolitov, 2015 (see Capa *et al.*, 2021).

Among these abyssal taxa, two genera, *Spirodiscus* and *Bathyditrupa*, are the most mysterious ones. Chronologically, *Spirodiscus groenlandicus* (McIntosh, 1877) was first to be collected in 1875 as an empty unattached tusk-shaped tube with distinct eight ridges from an abyssal location in the Labrador Sea. The species was described as *Ditrypa* [sic]

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ORCID: Elena K. Kupriyanova <https://orcid.org/0000-0003-0336-4718>; Beth Flaxman <https://orcid.org/0000-0002-0329-9525>

Corresponding author: Elena K. Kupriyanova Elena.Kupriyanova@Australian.Museum

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groenlandica by the author 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 ... It differs from any other *Ditrypa* known to me in its slender form and the well-marked longitudinal ridges.” In his review of abyssal serpulids, 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”. Whether the mysterious tubes belonged to a scaphopod mollusc or a serpulid remained enigmatic for over a century, the type being lost (Kupriyanova & Ippolitov, 2015).

The genus *Spirodiscus*, and species *S. grimaldii*, were described by Fauvel (1909, 1914) from lower bathyal depths off the Azores, based on material collected from RV *Princesse Alice* during the Prince of Monaco expeditions. The generic name referred to the tube that is unusual for serpulids, in that it is coiled into a flat spiral (like in spirorbins), unattached to a substrate, and quadrangular in cross-section. The species also had an unusual peduncle—much thicker than normal radioles, but with pinnules. *Spirodiscus grimaldii* had only been known by the type material until Hartman & Fauchald (1971) reported additional specimens from the western Atlantic Ocean. Ten Hove & Kupriyanova (2009) reported unpublished topotypical material from 2440 m deposited in the Zoological Museum of University of Amsterdam (ZMA). Both published and unpublished records of this mysterious species have been summarized by Kupriyanova & Nishi (2011).

Simultaneously with *Spirodiscus grimaldii*, Fauvel (1909, 1914) collected unnamed empty tubes (“tube de Serpulien”) that “like the coiled tubes were quadrangular in cross-section but straight”. Nearly a century later, Kupriyanova (1993) described the genus *Bathyditrupa* and species *B. hovei* from the abyssal depths of Kuril-Kamchatka Trench. *Bathyditrupa hovei* is characterized by quadrangular tusk-shaped tubes as mentioned by Fauvel (1909). Kupriyanova (1993) had not recognized the similarity between *Spirodiscus grimaldii* and *Bathyditrupa hovei*, however, ten Hove (in litt. pers. comm.) was the first to propose that *Bathyditrupa* might be a synonym of *Spirodiscus* and suggested that tube coiling in *Spirodiscus* is not a distinctive character for the genus despite its name. Additional records of *Bathyditrupa hovei* were reported by ten Hove & Kupriyanova (2009) and Kupriyanova *et al.* (2011).

The long-standing mystery of deep-sea serpulids living in polygonal unattached tubes was finally resolved by Kupriyanova & Ippolitov (2015). The authors revised numerous specimens with tetragonal (and secondary octagonal) tubes, both spirally coiled and tusk-shaped ones, collected over years (1969–1989) in the Atlantic, Indian, and Pacific Oceans by various French deep-sea expeditions and kindly provided by Dr Helmut Zibrowius (Marseille, France). The revision of the Recent material has revealed six species in five genera, and among them, Kupriyanova & Ippolitov (2015) found that the animals in coiled tetragonal (*Spirodiscus grimaldii*, Fig. 1C), tusk-shaped tetragonal (*Bathyditrupa hovei*, Fig. 1A, B) and tusk-shaped octagonal (*Ditrypa groenlandica*, Fig. 1D) have identical chaetation patterns, very similar morphology of the animals (operculum, peduncle, and thoracic membranes), general appearance of tube wall ultrastructure (crystal size, orientation, structure), and the outer layer in tubes. Thus, *Ditrypa groenlandica* was transferred to the genus *Spirodiscus* and the generic diagnosis was amended to include species with both coiled tetragonal

and straight octagonal tubes. A significant difference between the nominal genera *Spirodiscus* and *Bathyditrupa* is the structure of abdominal chaetae that are typical flat geniculate in the former, but are unusual, simple capillary in the latter. Thus, Kupriyanova & Ippolitov (2015) maintained *Bathyditrupa* as a valid genus until new data contradicting this assumption became available.

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) age. They are mainly known under the names of *Nogrobs* de Montfort, 1808, *Tetraserpula* Parsch, 1956 or *Tetradyditrupa* Regenhardt, 1961, respectively and include over 10 species (Ippolitov *et al.*, 2014). Jäger (2005) suggested synonymizing the extant genus *Spirodiscus* with the fossil *Nogrobs* based on striking morphological similarity of their spirally coiled tetragonal tubes. However, the results of comparative SEM studies of tube wall ultrastructures (Kupriyanova & Ippolitov, 2015) show very different crystal arrangement in *Spirodiscus* and in the type species of genus *Nogrobs*, indicating that these genera should not be synonymized.

In this study we report a new species of the mysterious genus *Spirodiscus* from eastern Australian abyss. In addition to the detailed illustrated description, we obtained 18S and 28S ribosomal RNA sequences for this species. The sequences were added to a phylogenetic data set of published serpulid 18S and 28S rRNA genes (Kupriyanova *et al.*, 2006, 2009, 2010; Kupriyanova & Nishi, 2010; Sun *et al.*, 2016) to examine the phylogenetic position of the species within the family Serpulidae.

Material and methods

Serpulids in octagonal tubes collected by Brenke Epibenthic Sledge, during the *Sampling the Abyss* cruise on board RV *Investigator* in May–June 2017 and fixed in formalin and ethanol. All specimens deposited in the Australian Museum (AM) were examined. Specimens were stained with methyl blue for photographing. The types were photographed using a Canon EOS 7D digital camera with a Macro EF 100 mm lens and the Spot Flex CCD 15.2 fitted on a Leica MZ16 Stereo microscope in the Australian Museum. Paratype W.49511 was dehydrated in ethanol, critically point dried, coated with 20 nm of gold, and examined under the Scanning Electron Microscope (SEM) JEOL JSM-6480 at Macquarie University, Sydney.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from posterior parts of abdomens using the Bioline Isolate II genomic DNA kit according to the manufacturer’s protocol. Stock DNA was diluted 1:10 with deionized water to produce template strength DNA for Polymerase Chain Reactions (PCR). A combination of ribosomal (18S and 28S) genes were used as these markers evolve at a conservative rate and thus show greater resolution at the family level (e.g., Simon *et al.*, 2019).

The 18S rRNA genes (c. 1,800 bp) were amplified in two overlapping fragments, one of approximately 1100 bp with the primers TimA (AMCTGGTTGATCCTGCCAG) and 1100R2 (CGGTATCTGATCGTCTTCGA) from

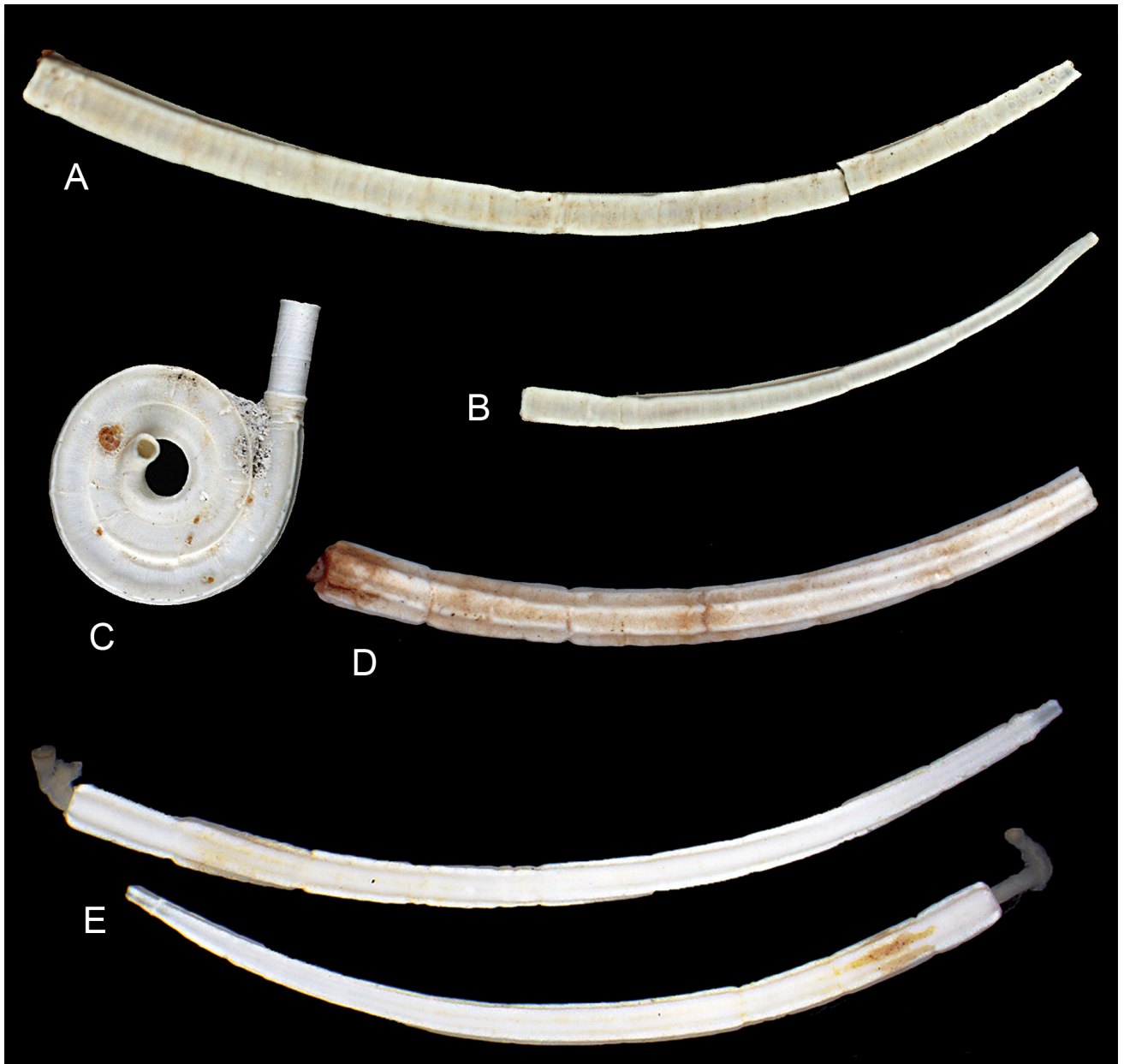


Figure 1. External morphology of *Bathyditrupa* and *Spirodiscus* tubes. (A, B) *Bathyditrupa hovei* (from Kupriyanova & Ippolitov, 2015); (C) *Spirodiscus grimaldii* (from Kupriyanova & Ippolitov, 2015); (D) *Spirodiscus groenlandicus* (from Kupriyanova & Ippolitov, 2015); (E) *Spirodiscus ottofinamusi* sp. nov. W.49511.

Nóren & Jordelius (1999); the other of approximately 1,300 bp using 18s2F (GTTGCTGCAGTTAAA) and 18s2R (ACCTTGTTAGCTGTTTTACTTCCTC) from Kupriyanova *et al.* (2006). The 18S fragments were combined using Geneious Prime v2022.2.2. The 28S genes, of approximately 1,200 bp, were amplified using the primers LSUD1F (ACCCGCTGAATTTAAGCATA) and D3ar (ACGAACGATTTGCACGTCAG) from Lenaers *et al.* (1989).

PCR conditions were as follows: an initial denaturation step at 94°C for 3 min (18S) or 2 min (28S), then 40 cycles of 94°C for 30 s, 52°C for 30 s, 72°C for 30 s (18S) or 35 cycles

of 94°C for 30 s, 61°C for 30 s, 72°C for 1 min (28S), with a final extension at 72°C for 5 min (18S) or 2 min (28S). PCR success was detected using gel electrophoresis (1% agarose gel stained with gel red (Biotium TM, San Francisco)) and visualized using a Bio-Rad XR+ Gel Documentation System. Successful PCR products were sent to Macrogen TM, South Korea where they were purified and standard Sanger sequencing was performed. Sequences were edited using Geneious and were aligned with Clustal Omega in Geneious 2022.2.2. A BLAST search confirmed the correct gene regions had been amplified (Altschul *et al.*, 1990) and the new sequences were submitted to GenBank (Table 1).

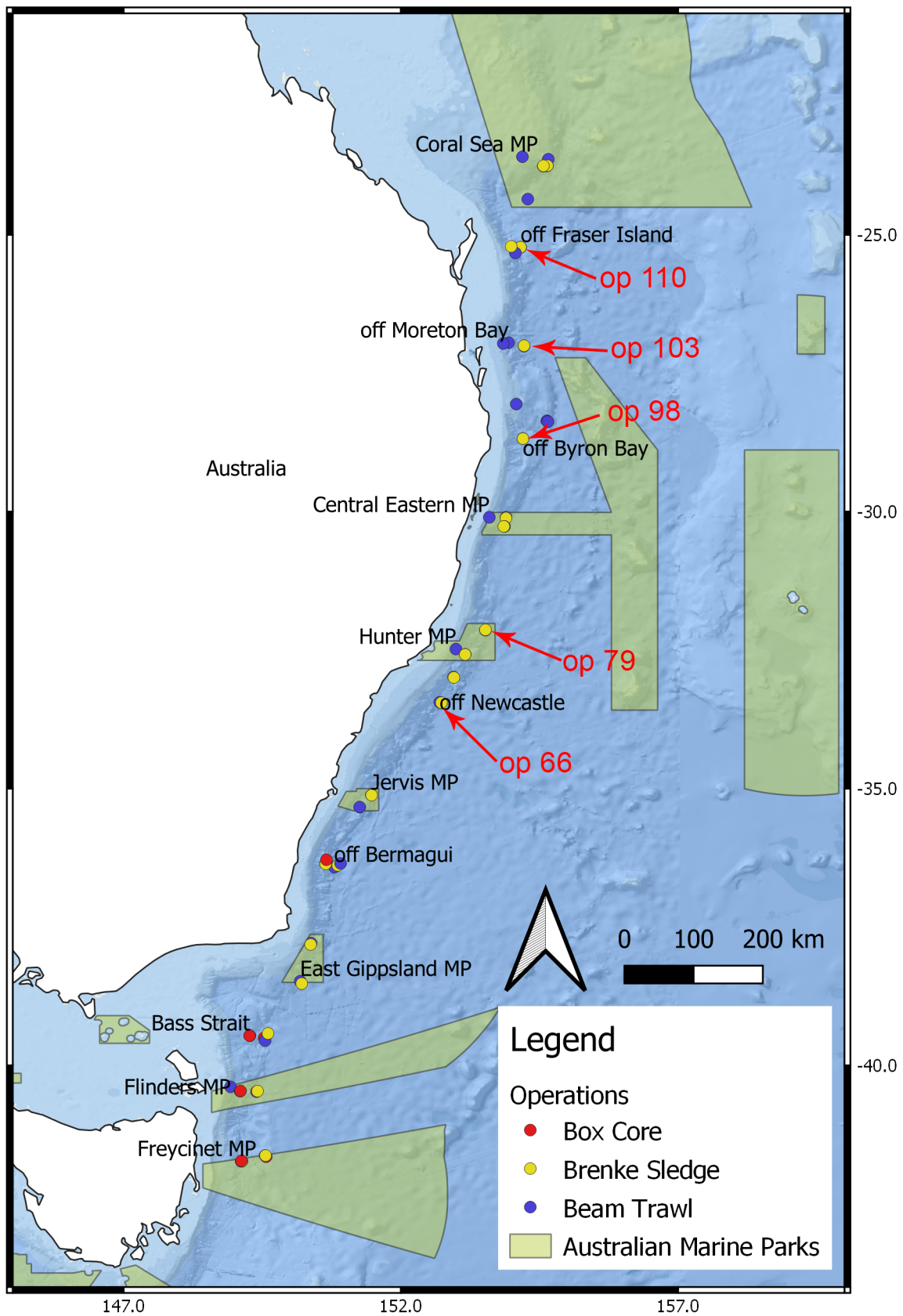


Figure 2. Map of sampling sites from RV *Investigator* voyage IN2017_V03 along eastern Australia. Red arrows indicate stations where *Spirodiscus ottofinamusi* sp. nov. was found.

Table 1. Terminals used in phylogenetic analysis with registration numbers, collection localities and GenBank numbers. *AM*, Australian Museum, Sydney; *FMNH*, Field Museum of Natural History, Chicago; *SAM*, South Australian Museum, Adelaide; *ZMA*, Zoological Museum of Amsterdam, now Naturalis, Leiden, The Netherlands. Sources: {1} the present paper; {2} Kupriyanova & Nishi (2010); {3} Kupriyanova *et al.* (2006); {4} Kupriyanova *et al.* (2009); {5} Kupriyanova *et al.* (2008); {6} Kupriyanova *et al.* (2010); {7} Rouse & Kupriyanova (2021); {8} Sun *et al.* (2016); {9} Struck *et al.* (2005).

| species | registration number | collection locality | 18S | 28S | source |
|--|---------------------|------------------------------|----------|----------|---------------|
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.50871 | off Moreton Bay, Australia | OP598071 | OP598085 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49740.001 | off Moreton Bay, Australia | OP598072 | OP598086 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49740.002 | off Moreton Bay, Australia | OP598073 | OP598087 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49740.003 | off Moreton Bay, Australia | OP598074 | OP598088 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49684.001 | off Moreton Bay, Australia | OP598075 | OP598089 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49684.002 | off Moreton Bay, Australia | OP598076 | OP598090 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49684.003 | off Moreton Bay, Australia | OP598077 | OP598091 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49686.001 | off Fraser Island, Australia | OP598078 | OP598092 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49686.002 | off Fraser Island, Australia | OP598079 | OP598093 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49686.003 | off Fraser Island, Australia | OP598080 | OP598094 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49687.001 | off Byron Bay, Australia | OP598081 | OP598095 | {1} |
| <i>Spirodiscus ottofinamusi</i> sp. nov. | W.49687.002 | off Byron Bay, Australia | OP598082 | OP598096 | {1} |
| <i>Apomatus globifer</i> | ZMA V.Pol. 5250 | Atlantic Ocean | EU195378 | EU195362 | {2} |
| <i>Apomatus voightae</i> | FMNH 5201 | Patton-Murray Seamounts | GU441856 | — | {2} |
| <i>Bathymetilia eliasoni</i> | FMNH 6189 | Patton-Murray Seamounts | GU441857 | — | {2} |
| <i>Chitinopoma serrula</i> | SAM E3524 | Iceland | DQ317112 | EU195350 | {3}, {4} |
| <i>Crucigera inconstans</i> | SAM E3525 | SA, Australia | DQ317113 | EU184071 | {3}, {4} |
| <i>Crucigera zygophora</i> | SAM E3503 | BC, Canada | DQ242543 | DQ242577 | {3}, {4} |
| <i>Ditrupa arietina</i> | SAM E3527 | France | DQ317114 | EU195351 | {3}, {4} |
| <i>Ficopomatus enigmaticus</i> | SAM E3356 | SA, Australia | DQ317115 | EU195373 | {3}, {4} |
| <i>Ficopomatus macrondon</i> | SAM E3618 | Thailand | EU167532 | EU167535 | {4} |
| <i>Ficopomatus miamiensis</i> | SAM E3617 | FL, USA | EU167531 | EU167534 | {4} |
| <i>Filograna implexa</i> | SAM E3528 | France | DQ317116 | EU195347 | {3}, {4} |
| <i>Galeolaria caespitosa</i> | SAM E3529 | SA, Australia | AB106257 | EU184080 | {3} |
| <i>Galeolaria hystrix</i> | SAM E3526 | SA, Australia | DQ314839 | EU256550 | {3}, {4} |
| <i>Hyalopomatus mironovi</i> | AM W.50990 | Kurile-Kamchatka Trench | OP598070 | OP598083 | {7}, {1} |
| <i>Hydroides ezoensis</i> | SAM E3584 | Sea of Japan, Russia | EU184062 | EU184077 | {5} |
| <i>Hydroides minax</i> | SAM E3597 | Qld, Australia | EU184063 | EU184074 | {5} |
| <i>Hydroides nikae</i> | SAM E3530 | SA, Australia | DQ317117 | EU184072 | {3}, {4}, {8} |
| <i>Hydroides sanctaerucis</i> | SAM E3625 | FL, USA | EU184061 | EU184076 | {5} |
| <i>Hydroides trivesiculosa</i> | SAM E3601 | Qld, Australia | EU184060 | EU184073 | {3}, {4} |
| <i>Laminatubus alvini</i> | SAM E3531 | East Pacific Rise | DQ317118 | EU195355 | {3}, {4} |
| <i>Marifugia cavatica</i> | SAM E3612 | Bosnia and Herzegovina | EU167530 | EU167533 | {4} |
| <i>Metavermitia acanthophora</i> | SAM E3533 | SA, Australia | DQ317119 | EU195352 | {3}, {4} |
| <i>Neovermitia globula</i> | AM W.49842 | NSW, Australia | MT472384 | OP598084 | {7}, {1} |
| <i>Protis hydrothermica</i> | SAM E3541 | East Pacific Rise | DQ317122 | EU195356 | {3}, {4} |
| <i>Protis</i> sp. | SAM E3727 | North Fiji | GU063863 | — | {6} |
| <i>Protolaeospira eximia</i> | SAM E3482 | BC, Canada | DQ242556 | DQ242584 | {4} |
| <i>Protula tubularia</i> | SAM E3542 | Mediterranean | DQ317123 | EU195349 | {3}, {4} |
| <i>Pseudochitinopoma occidentalis</i> | SAM E3501 | BC, Canada | DQ242542 | DQ242575 | {3} |
| <i>Salmacina</i> sp. 1 | SAM E3499 | SA, Australia | DQ317126 | EU256545 | {3}, {4} |
| <i>Serpula columbiana</i> | SAM E3505 | BC, Canada | DQ317127 | DQ242576 | {3} |
| <i>Serpula jukesii</i> | SAM E3536 | SA, Australia | DQ317129 | EU184069 | {3}, {4} |
| <i>Serpula vermicularis</i> | SAM E3537 | France | DQ317128 | EU184070 | {3}, {4} |
| <i>Spirobranchus corniculatus</i> | SAM E3608 | Qld, Australia | EU195381 | EU195366 | {3}, {4} |
| <i>Spirobranchus lima</i> | SAM E3538 | France | DQ317130 | EU256547 | {3}, {4} |
| <i>Spirobranchus taeniatus</i> | SAM E3532 | SA, Australia | DQ317120 | EU195353 | {3}, {4} |
| <i>Spirorbis tridentatus</i> | SAM E3477 | BC, Canada | DQ242573 | DQ242602 | {4} |
| <i>Vermiliopsis labiata</i> | SAM E3543 | France | DQ317131 | EU256549 | {3}, {4} |
| <i>Vermiliopsis pygidialis</i> | SAM E3544 | Qld, Australia | DQ317132 | EU256546 | {3}, {4} |
| <i>Vermiliopsis striaticeps</i> | SAM E3545 | France | DQ317133 | EU256548 | {3}, {4} |
| Outgroups | | | | | |
| Sabellaridae | | | | | |
| <i>Gunnarea gaimardi</i> | SAM E3360 | South Africa | DQ317111 | EU256544 | {3}, {4} |
| Sabellidae | | | | | |
| <i>Schizobranchia insignis</i> | GenBank | WA, USA | AY732222 | AY732225 | {9} |

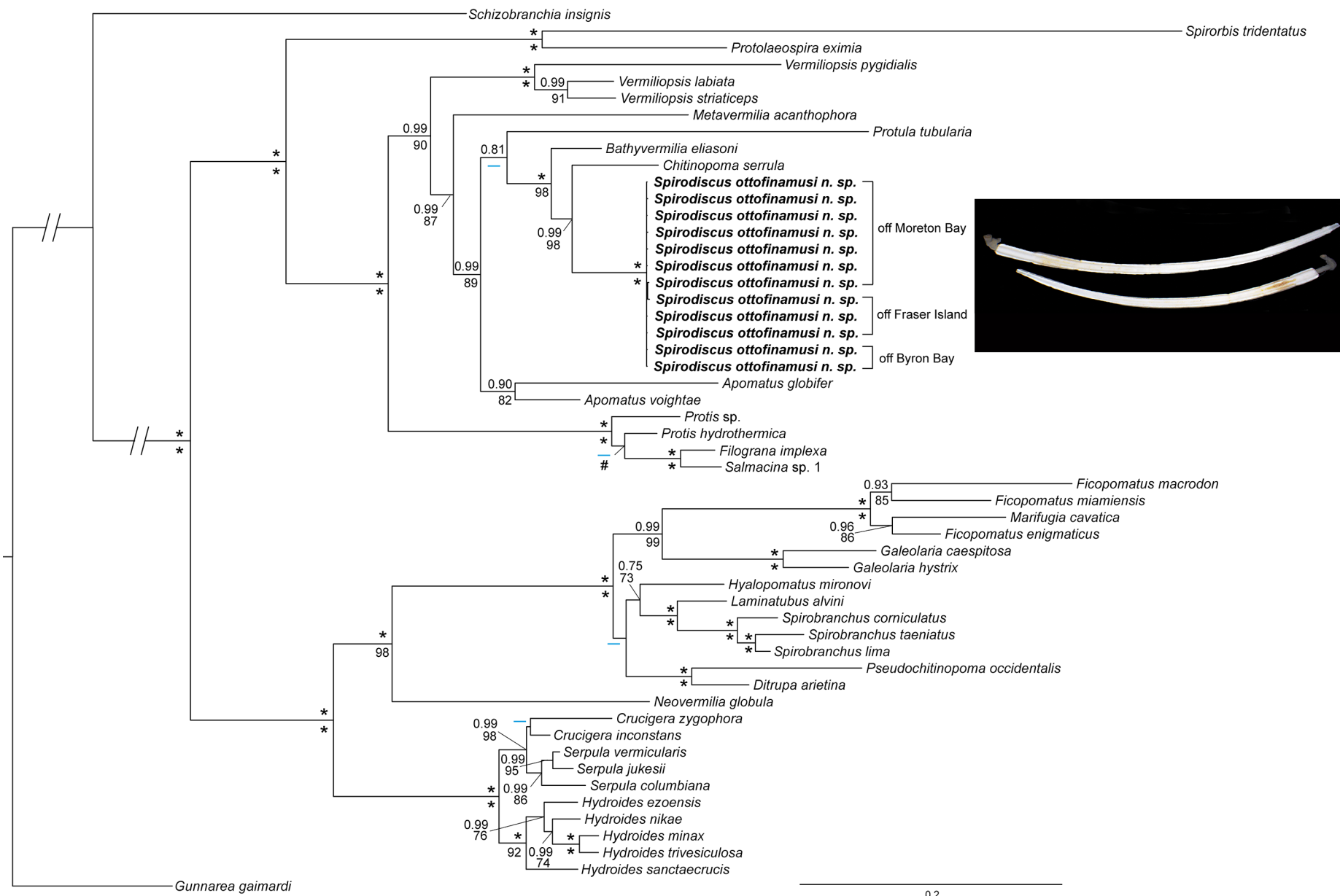


Figure 3. Bayesian majority rule consensus phylogram of the concatenated data set. Nodes with posterior probabilities < 0.70 or bootstrap values < 70 are indicated by blue dashes. Nodes with posterior probabilities 1.0 or bootstrap values 100 are indicated by * (asterisk). Numbers above branches are posterior probabilities, obtained from Bayesian Inference analysis; numbers below branches are bootstrap values obtained from Maximum Likelihood analysis.

Phylogenetic analyses

The concatenated analysed dataset included 1846 bp long 18S and 1,158 bp long 28S gene fragments. The phylogenetic relationships were inferred using maximum likelihood analysis (ML) in IQ-TREE (Minh *et al.*, 2020) and Bayesian inference (BI) in MrBayes (Ronquist *et al.*, 2012). Separate nucleotide substitution models for maximum likelihood analysis, selected using the Bayesian information criterion in ModelFinder (Kalyaanamoorthy *et al.*, 2017), were TIM3+F+I+R3 (18S) and TIM3+F+I+R4 (28S). Branch support was estimated using 1000 ultrafast bootstraps (Hoang *et al.*, 2018). For Bayesian inference, substitution models TrN+I+G and GTR+I+G were used for 18S and 28S, respectively (Keane *et al.*, 2006). A Markov chain Monte Carlo analysis was run for 10 million generations, with samples drawn every 1,000 generations and the first 1,000 samples removed as burn-in. Nodal support was indicated by posterior probabilities (BI) and bootstrap values (ML).

Results

Molecular results

The consensus phylogram produced from the concatenated dataset is shown in Fig. 3. Maximum likelihood and Bayesian inference methods resulted in similar topologies, where the Serpulidae is divided into two major well supported clades, “Filograninae” and “Serpulinae” (BI pp 1, ML bs 100). *Spirodiscus ottofinamusi* sp. nov. was recovered within the major “filogranin” clade as sister group to *Chitinopoma serrula* in a clade with *Bathyvermilia*. *Protula* was positioned outside of the *Spirodiscus*-*Chitinopoma*-*Bathyvermilia* clade, however this position was poorly supported (pp 0.81, bs 67). The remaining filogranin clades (Spirorbinae, *Vermiliopsis*, *Metavermilia*, *Apomatus* and *Protis-Filograna-Salmacina*) were recovered with high values of support (pp > 0.90, bs > 87). The only discrepancy between the results of the two analyses was found at the poorly supported *Protis hydrothermica* node, which is grouped with *Protis* sp. in maximum likelihood results (bs 69) but placed as a sister group to the *Filograna-Salmacina* clade with Bayesian inference (pp 0.66). Within the second major serpulid clade (“Serpulinae”), most clades were well-supported (pp > 0.99, bs > 98): *Ficopomatus-Marifugia-Galeolaria*, *Neovermilia*, *Crucigera-Serpula* and *Hydroides*. However, the positions of *Hyalopomatus*, *Laminatubus-Spirobranchus* and *Pseudochitinopoma-Ditrupe* were poorly supported (pp 0.75, 0.60, bs 73, 67 respectively).

Taxonomy

Genus *Spirodiscus* Fauvel, 1909

Spirodiscus Fauvel, 1909: 56–57.—Fauchald, 1977: 147; Kupriyanova & Ippolitov, 2015: 162–163.
Nogrobs (not Montfort, 1808).—ten Hove & Kupriyanova, 2009: 68–69; Kupriyanova & Nishi, 2011: 1–2.

Type species. *Spirodiscus grimaldii* Fauvel, 1909

Diagnosis (after Kupriyanova & Ippolitov, 2015). 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 three times as wide as other radioles. Pseudopericulum absent. Arrangement of radioles semi-circular, up to eight per lobe. Inter-radiolar membrane, branchial eyes, and stylodes absent. Mouth palps absent. Five to six 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. Jäger (2005) synonymized the Recent monotypic at the time genus *Spirodiscus* with the fossil *Nogrobs* de Montfort, 1808. In their review, ten Hove & Kupriyanova (2009) followed Jäger (2005) and used the name *Nogrobs* for *Spirodiscus grimaldii*. Zibrowius (pers. comm.) expressed doubts that the name *Nogrobs* should be used for the extant material suggesting that the fossil tubes of “*Nogrobs*” may be so convergent that synonymizing the Recent *Spirodiscus* would result in a loss of a well-defined genus. This point of view was supported by Kupriyanova & Ippolitov (2015), who demonstrated significant ultrastructural and mineralogical differences between in tubes of Recent and Mesozoic species. The authors concluded that similar tetragonal tube morphology of the Recent forms is a result of convergence due to adaptation to similar soft-sediment habitats of the deep sea and reinstated the genus *Spirodiscus*, previously synonymized with fossil *Nogrobs*.

Spirodiscus ottofinamusi sp. nov.

urn:lsid:zoobank.org:act:D1A2535B-20DD-4B68-BEE0-CB12A63DE5F4

Figs 1–5

Holotype Op 98, Australia, New South Wales, off Byron Bay (28°22'17"S 154°38'50"E), 8 June 2017, 3811–3754 m, Australian Museum (AM) W.54171. **Paratypes** AM W.49511, as above (5 spec.).

Additional material. Op. 66, Australia, New South Wales, off Newcastle (33°26'54"S 152°43'58"E), 30 May 2017, 4378–4195 m: W.49691 (2 spec.). Op 79, Australia, New South Wales, Hunter Commonwealth Marine Reserve (32°7'51"S 152° 31'38"E), 4 June 2017, 4031 m: W.49683 (2 spec.). Op 98, Australia, New South Wales, off Byron Bay (28°22'17"S 154°38'50"E), 8 June 2017, 3811–3754 m: W.49704 (20 spec.), W.49687 (6 spec.). Op 103, Australia, Queensland, off Moreton Bay (27°1'S 154°13'23"E), 10 June 2017, 4260–4280 m: W.49671 (1 spec.), W.49684 (16 spec.).

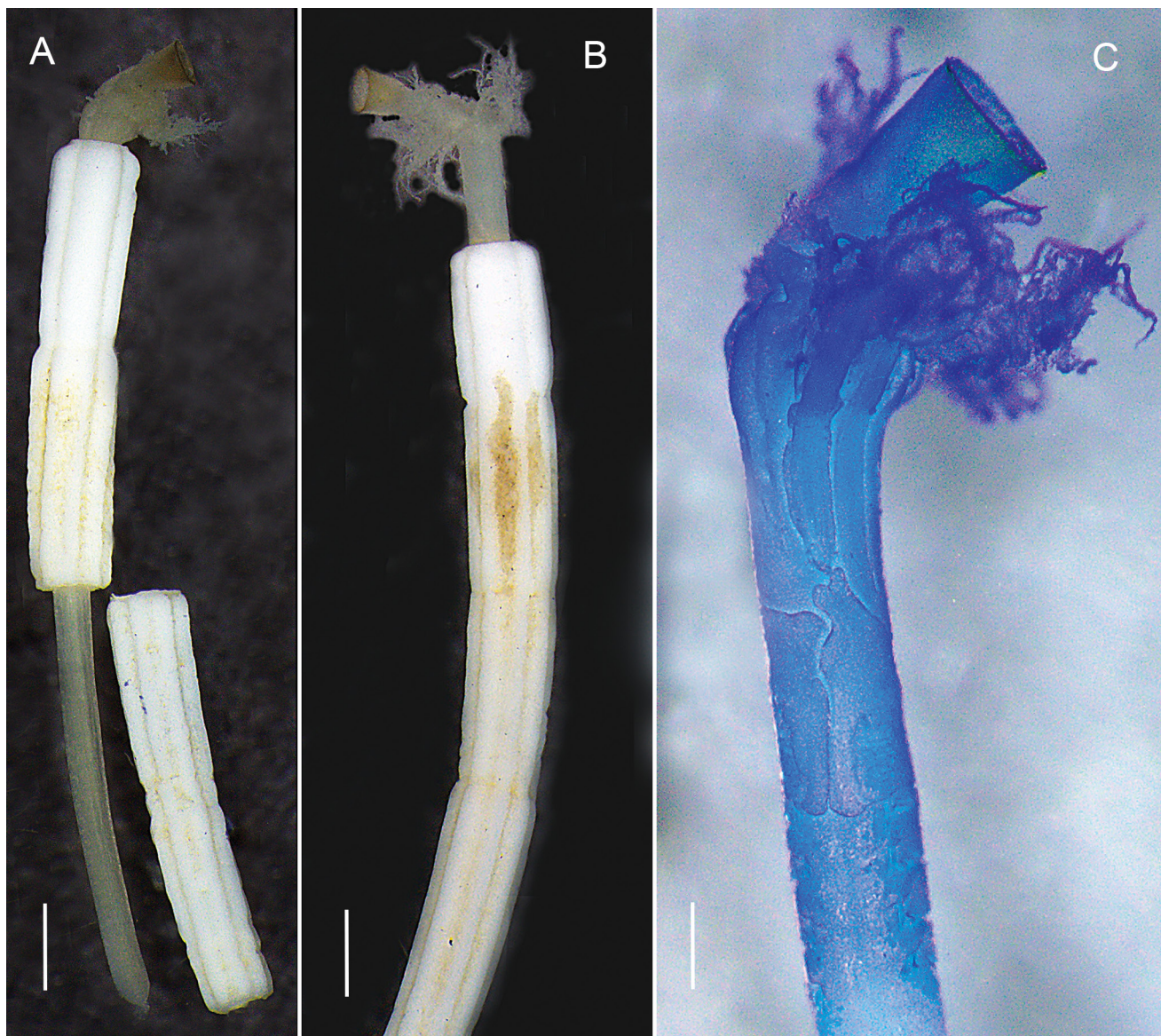


Figure 4. Light microscopy photographs of the holotype of *Spirodiscus ottofinamusi* sp. nov. (A, B) Specimens in tube; (C) close-up of the dorsal view of the specimen removed from the tube, stained with methyl blue. Scale bars: A, B, 500 μ m; B, 200 μ m.

W.49685 (3 spec.), W.49740 (53 spec.). Op 110, Australia, Queensland, off Fraser Island (25°13'11"S 154°9'37"E), 11 June 2017, 4005–4010 m: W.49512 (3 empty tubes.), W.49686 (15 spec.), W.52131 (1 spec.).

Comparative material examined

Spirodiscus groenlandicus (McIntosh, 1877)—W.46398, North Atlantic Ocean, Porcupine Seabight, off Brittany (50°4'N 13°55'36"W), 15 April 1978; W.46399, western Indian Ocean, Mozambique Channel, north of Madagascar, south-east of Glorioso Islands (11°44'S 47°30'E), 4 April 1977.

Bathyditrupa hovei Kupriyanova, 1993—W.46391, North Atlantic Ocean, Iberian Basin, west of southern Spain (37°18'N 15°33'W), 17 May 1981; W.46392, North Atlantic Ocean, Iberian Basin, north of Madeira (34°6'N 17°6'18"W), 30 May 1981; W.46394, North Atlantic Ocean, Iberian Basin, west of northern Spain (42°51'12"N 15°55'18"W), 11 Jun 1981.

Description

Tube: Less than 1 cm long, 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 (Figs 1E, 4A,B). 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.

Radiolar crown: 3–5 pairs of radioles not joined by inter-radiolar membrane (Figs 4C, 5B). Radiolar eyes absent.

Peduncle: inserted as 2nd dorsal radiole, 3–4 times as thick as radioles (Fig. 5B), with pinnules.

Operculum: funnel-shaped (bell-shaped), covered with concave brownish endplate (Figs 4A,B,C, 5B); opercular ampulla continuing smoothly into peduncle or with slight constriction.

Collar and thoracic membranes: collar five-lobed, two latero-dorsal lobes and ventral one clearly subdivided into

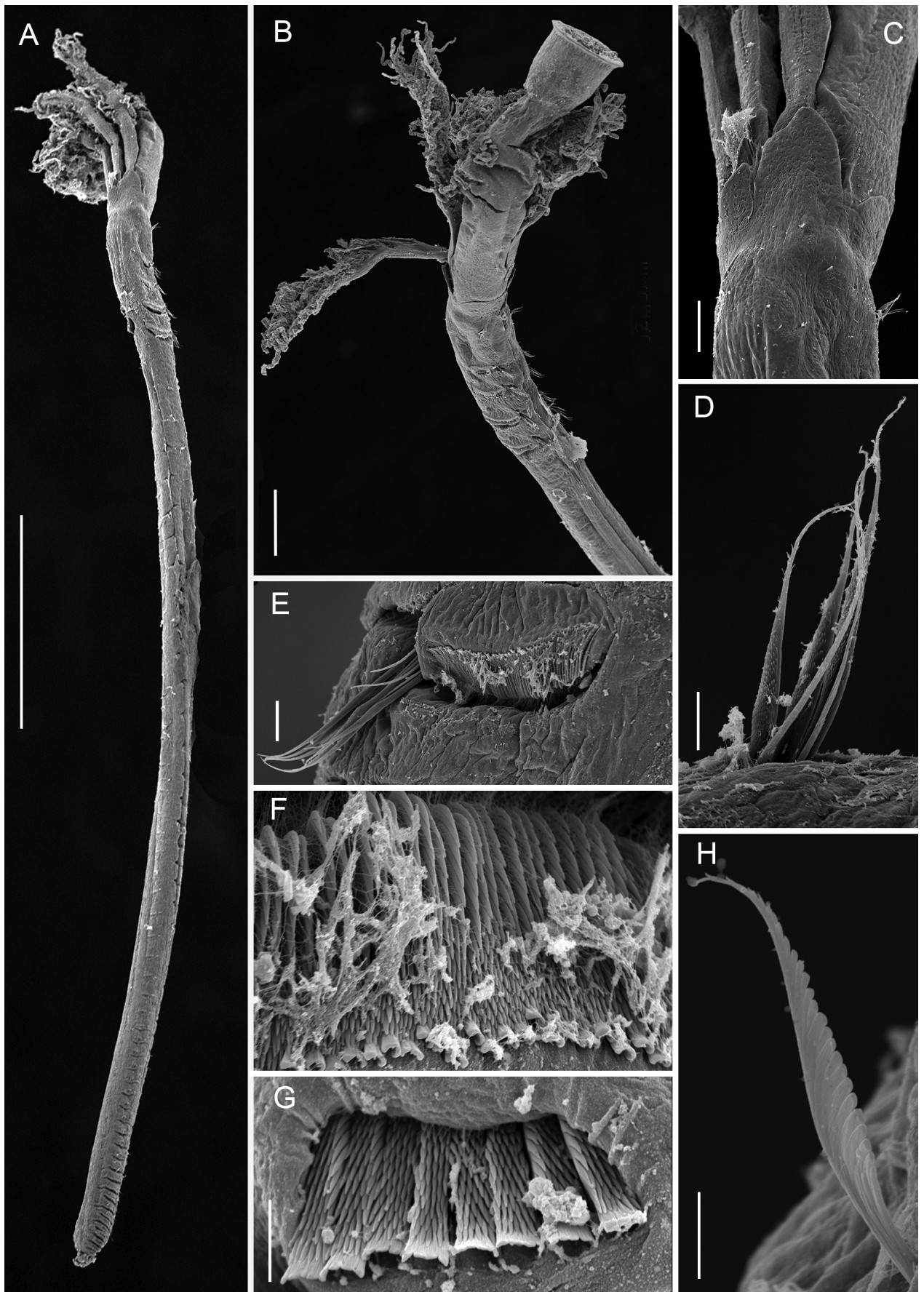


Figure 5. SEM micrographs of *Spirodiscus ottofinamusi* sp. nov. paratype W.49511. (A) Entire specimen, ventral view; (B) anterior view of the specimen, showing the operculum and thick pinnulated peduncle; (C) view of the ventral collar lobe subdivided into three lobes; (D) collar chaetae; (E) chaetae and uncini of the second thoracic chaetiger; (F) close-up view of saw-to-rasp thoracic uncini; (G) anterior abdominal uncini; (H) anterior abdominal chaeta. Scale bars: A, 1 mm; B, 200 µm; C, 50 µm; D, 10 µm; E, 20 µm; F, G, H, 5 µm.

a longer middle and two shorter lateral lobes (Fig. 5B,C), continuing into thoracic membranes reaching up to 2nd chaetiger (Fig. 4C). Collar chaetae simple limbate only (Fig. 5D), of two sizes.

Thorax: with five thoracic chaetigers, four of which uncinigerous (Fig. 5A, B). Thoracic tori decreasing in length towards abdomen, with the second chaetiger being twice as short as the fourth chaetiger (Fig. 5B). Chaetae thick with distal limba, of two sizes, *Apomatus* chaetae absent (Fig. 5E). Uncini saw-to-rasp-shaped, with 3–4 rows above wide gouged underneath anterior peg divided into two lobes; with 12–14 teeth in profile view (Fig. 5F). Dental formula P:3:3:3:2:2:2:1:1:1:1:1:1 or similar (e.g., P:4:3:3:2: ...). Achaetigerous zone between thorax and abdomen absent (Fig. 5A).

Abdomen: with up to 50 segments. Chaetae short, with flat narrow denticulate blade (Fig. 5H), each torus with a single chaeta. Chaetae slightly longer on posterior-most segments (Fig. 5A), but long posterior capillary chaetae absent. All uncini rasp-shaped, with 9–12 teeth in profile view and 5–6 rows, dental formula P:6:5:5:5:4:4:3:3:3 (Fig. 5G); flat anterior peg subdivided in 5–6 shallow lobes (Fig. 5G). Posterior glandular pad absent.

Size: total body length up to 10 mm, including up to 1.5 mm long branchia, width of thorax up to 0.2 mm. Tube length up to 12 mm.

Etymology. The species is named in honour of Otto Nielson Simpson, whose parent's generous donation to the Australian Museum Research Institute made this research possible.

Distribution. Southern Pacific Ocean, along east coast of Australia, 3754–4378 m.

Remarks. The new species is the third species described in the deep-sea genus *Spirodiscus*. The two previous species, *Spirodiscus grimaldii* and *S. groenlandicus*, have very similar morphology (except for five thoracic chaetigers in *S. groenlandicus* and six in *S. grimaldii*) and have identical chaetation patterns but differ remarkably by their tube morphologies (coiled tetragonal in the former and tusk-shaped octagonal in the latter).

Spirodiscus ottofinamusi sp. nov. from the eastern Australian abyss is morphologically most similar to *S. groenlandicus* originally described from the bathyal of North Atlantic Ocean. Both *S. ottofinamusi* sp. nov. and *S. groenlandicus* species have five thoracic chaetigers, thick pinnulated peduncles bearing opercula in the shape of inverse cone with chitinous convex endplate, and short thoracic membranes. Both species have tusk-shaped unattached tubes with eight longitudinal ridges. However, they show relatively subtle, but clear morphological differences. Collar four-lobed with straight edge in *S. groenlandicus*, while it is five-lobed in *S. ottofinamusi* sp. nov. In *S. groenlandicus* thoracic tori are of the same size, but they decrease in length towards abdomen in *S. ottofinamusi* sp. nov. Finally, abdominal chaetae are elongated flat narrow geniculate in *S. ottofinamusi* sp. nov. but are short flat triangular geniculate in *S. groenlandicus* (and in *S. grimaldii*).

Discussion

This is the first study in over a century to describe a new species of the poorly known and unusual deep-sea genus *Spirodiscus*. While these animals inhabiting unattached tubes are likely to be common in soft-sediment bathyal and abyssal localities around the world (see Gunton *et al.*, 2021), they are probably overlooked due to their small size and/or confused with scaphopod molluscs. Moreover, this is the first study to report DNA sequence data for this mysterious genus and to infer its phylogenetic position in the family Serpulidae.

Morphology provided mixed signals regarding phylogenetic relationships of *Spirodiscus*. Traditionally the family Serpulidae has been subdivided into the subfamilies Serpulinae and Filograninae (reviewed in Capa *et al.* 2021). The former included the genera that bear the operculum enforced with chitinous or calcareous endplates on thickened smooth peduncle (e.g., *Hydroides*, *Serpula*, *Spirobranchus*). The latter was originally erected by Rioja (1923) for genera that lack an operculum or have a simple membranous operculum on an unmodified pinnulate radiole (e.g., *Apomatus*, *Filograna*, *Protula*, *Protis*). However, in *Spirodiscus*—as in serpulins—the operculum is reinforced with a chitinous distal endplate, but the peduncle, although thickened resembling a typical serpulid opercular peduncle, bears pinnules as in filogranins. Thus, it is unclear which subfamily *Spirodiscus* should be referred to based on Rioja's (1923) criterion. As a result of this confusion, for example, Hartman (1959) classified *Spirodiscus* as Serpulinae, while Fauchald (1977) included *Spirodiscus* in Filograninae. Clearly, additional evidence such as molecular data were needed to resolve this puzzle.

The first formal phylogenetic analysis using DNA data (Kupriyanova *et al.*, 2006) significantly changed our understanding of relationships within the family. It inferred two major clades within Serpulidae. The clade A (“Serpulinae”) comprised two clades: Clade AI “*Serpula*-group” and Clade AII “*Spirobranchus*-group”. The Clade B (“Filograninae”) included a monophyletic Spirorbinae as sister group to the clade BI “*Protula*-group”. Positions of serpulid genera, such as *Vermiliopsis* and *Chitinopoma* within clade BI along with typical filogranins, made both traditionally formulated Filograninae and Serpulidae paraphyletic. As expected, the same relationships were inferred in our study. Importantly, the first DNA sequences of *S. ottofinamusi* sp. nov. obtained in this study unequivocally places the new species within the “filogranins” (clade BI *sensu* Kupriyanova *et al.*, 2006) in sister group relationship with *Chitinopoma serrula*. Thus, the long-standing puzzle of phylogenetic position of *Spirodiscus* has been resolved, further supporting the notion that the morphological characters traditionally used in serpulid taxonomy, especially opercular structures, may be misleading.

It appears that morphological synapomorphies that support the serpulid subfamilies can be found in the chaetal characters, as flat geniculate abdominal chaetae and thoracic *Apomatus* chaetae are observed in filogranins, while serpulins (clade A *sensu* Kupriyanova *et al.*, 2006) lack *Apomatus* chaetae and have either flat trumpet (clade AI *sensu* Kupriyanova *et al.*, 2006) or true trumpet abdominal chaetae (clade AII *sensu* Kupriyanova *et al.*, 2006). However, the generality of this statement needs to be tested with more extensive taxon sampling.

Spirodiscus ottofinamusi sp. nov. is morphologically similar to *S. groenlandicus* described from the North Atlantic, and later reported from the abyssal zone of the southern Indian Ocean by Kupriyanova & Ippolitov (2015). Whether this bathyal-abyssal species indeed has such a wide distribution or whether multiple species are involved remains to be determined in future studies. The degree of genetic connectivity and variability over long distances among deep-sea serpulids is unknown, although bathyal *Laminatubus alvini*, associated with hydrothermal vent communities, showed little genetic variation from the Alarcon Rise vents in Gulf of California (c. 23°N), to at least a point at 38°S on the East Pacific Rise (Rouse & Kupriyanova, 2021).

In conclusion, the results of this study shed new light on phylogenetic position of a mysterious abyssal taxon within the family Serpulidae and call for further research addressing biodiversity and genetic connectivity of deep-sea serpulids.

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