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Serpulidae (Annelida) of the Australian Indian Ocean Territories

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ABSTRACT. Research voyages onboard RV '*Investigator*' in 2021 (IN2021_V08) and 2022 (IN2022_V04) sampled benthic communities of seamounts off Christmas Island and Cocos (Keeling) Islands, also known as the Australian Indian Ocean Territories (IOT). Over 150 specimens of the family Serpulidae (Annelida) collected during the voyages were deposited in the Australian Museum. The animals belonged to the filogranin genera *Apomatus*, *Bathyvermilia*, *Bathyvermilioides* n. gen., *Filogranula*, and *Protis,* as well as to serpulin genera *Hyalopomatus*, *Placostegus* and *Vitreotubus*. In total, 12 species were identified, including three named serpulids *Bathyvermilia challengeri*, *Filogranula stellata,* and *Vitreotubus digeronimoi.* Nine species *Apomatus nishii* n. sp., *Bathyvermilia rolandobastidai* n. sp., *Bathyvermilioides juliebrockae* n. sp., *Protis melmackenzieae* n. sp., *P. perneti* n. sp., *Hyalopomatus nogueirai* n. sp., *H. rossanae* n. sp., *H. suelindsayae* n. sp., and *Placostegus leslieharrisae* n. sp. were described. All species descriptions are accompanied by DNA sequence data and their phylogenetic positions in the family Serpulidae have been assessed.

Introduction

The family Serpulidae Rafinesque, 1818 (including Spirorbinae) is a group of sedentary annelids inhabiting self-secreted calcareous tubes. The family is composed of ~70 genera and over 500 species (Capa *et al.,* 2021). These animals are most common and abundant in subtidal and shelf habitats, but occur from intertidal to hadal depths (Kupriyanova *et al.*, 2010, 2011, 2014; Kupriyanova & Ippolitov, 2015; Gunton *et al.*, 2021; Kupriyanova & Flaxman, 2023). Serpulids from bathyal and abyssal depths belong to the genera *Bathyditrupa*, *Bathyvermilia*, *Filogranula*, *Hyalopomatus*, *Laminatubus, Protis*, *Spirodiscus*, *Vitreotubus* and *Zibrovermilia* (Kupriyanova & Ippolitov, 2015; Capa *et al.*, 2021), but only representatives of *Bathyditrupa*, *Bathyvermilia*, *Hyalopomatus*, and *Protis* are typical abyssal taxa also penetrating into the upper hadal zone (Kupriyanova *et al.*, 2010; 2011). *Laminatubus alvini* ten Hove & Zibrowius, 1986*, L. paulbroocksi* Rouse & Kupriyanova, 2021 and *L. joycebrooksae* Rouse & Kupriyanova, 2021 as well as *Protis hydrothermica* ten Hove & Zibrowius, 1986 are commonly found in the vicinity of hydrothermal vent and cold seep communities (ten Hove & Zibrowius, 1986; Rouse & Kupriyanova, 2021). Kupriyanova *et al.* (2010) reported two serpulids (*Hyalopomatus* cf. *mironovi* and *Protis* sp.) from vicinity

Keywords: Serpulinae, Filograninae, 18S, cytochrome b, seamounts, abyssal, bathyal
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of hydrothermal vents of North Fiji and the phylogeny presented by Kupriyanova *et al.* (2023) includes *Filogranula stellata* (Southward, 1963) from the vicinity of Lost City hydrothermal field in the Atlantic Ocean.

The shallow-water (intertidal to shelf) serpulid fauna of Australia is well documented, with 45 genera and ~ 180 species recorded from Australian waters, but only four deep-sea species have been reported by MacIntosh *et al.* (2018) from the Great Australian Bight. In Gunton *et al.* (2021) over 900 serpulid specimens belonging to 12 species were recorded from the Australian lower bathyal and abyssal environment, nine of them appear to be new to science, but so far only one (*Spirodiscus ottofinamusi* Kupriyanova & Flaxman, 2023) has been described. The aims of this study were to: 1) to report on the serpulid species collected from seamounts of the Christmas and Cocos (Keeling) Islands, collectively known as Australian Indian Ocean Territories (IOT), and 2) formally describe new taxa.

Material and methods

Morphological examination

Specimens collected during the IOT voyages on board RV "*Investigator*" in 2021 and 2022 and deposited in the Australian Museum (**AM**) were examined. Initially specimens were photographed in their intact tubes, then the tubes were removed from the substrate and posterior abdomens were cut for DNA analysis. Later, selected specimens were removed from tubes, stained with methyl blue and 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. Selected paratypes were dehydrated in ethanol, critical-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

Specimens preserved in 95% ethanol were used for the molecular part of the study (Table 1). 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 mitochondrial (*Cyt b*) was used as these markers evolve at a different rate and thus provides a different level of resolution.

The *18S* rRNA genes (approximately 1800 bp) were amplified in two overlapping fragments, one of approximately 1100 bp with the primers TimA (AMCTGGTTGATCCTGCCAG) and 1100R2 (CGGTATCTGATCGTCTTCGA) from Nóren and Jordelius (1999); the other of approximately 1300 bp using 18s2F (GTTGCTGCAGTTAAA) and 18s2R (ACCTTGTTAGCTGTTTTACTTCCTC) from Kupriyanova *et al*. (2006). The *18S* fragments were combined using Geneious Prime v2022.2.2. The *Cyt b* gene fragments (approximately 350 bp) were amplified with the primer pair Cytb424F (GGWTAYGTWYTWCCWTGRGGWCARAT) and cobr825 (AARTAYCAYTCYGGYTTRATRTG) (Halt *et al.*, 2009). PCR conditions were as follows: an initial denaturation step at 94°C for 3 min (*18S* and *Cyt b*), 40 cycles at 94°C for 30 s (*18S*) respectively 45 cycles at 94°C for 1 min (*Cyt b*), 52°C for 30 s (*18S*) respectively, 50°C for 30 s (*Cyt b*), 72°C for 30 s (*18S*) respectively, 72 °C for 1 min (*Cyt b*), with a final extension at 72 °C for 5 min (*18S*) respectively, 8 min (*Cyt b*). 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, South Korea where they were purified, and standard Sanger sequencing was performed. Sequences were edited using Geneious and were aligned in Geneious (*Cyt b*) or using MAFFT (*18S*; Katoh & Standley, 2013). BLAST search confirmed the correct gene regions had been amplified (Altschul *et al.*, 1990) and the new sequences were submitted to GenBank (Table 1).

Phylogenetic analysis

The concatenated analysed dataset included 1616 bp long *18S* and 347 bp *Cyt b* long gene fragments. The phylogenetic relationships were inferred using Maximum Likelihood analysis in IQ-TREE (Minh *et al.*, 2020). Separate nucleotide substitution models selected using the Bayesian information criterion in ModelFinder (Kalyaanamoorthy *et al.*, 2017) for Maximum Likelihood analysis were HKY+F+I+G4 for *Cyt b* and TNe+I for *18S*. Branch support was estimated using 1000 ultrafast bootstraps (Hoang *et al.*, 2018).

Results

Molecular results

The consensus phylogram produced from the concatenated dataset is shown in Fig. 1. Maximum Likelihood analysis resulted in a topology where the Serpulidae are divided into three well-supported clades (subfamilies *sensu* Kupriyanova *et al.,* 2023). One included the taxa belonging to the subfamily Serpulinae (with tribes Serpulini and Ficopomatini). Another major clade included the subfamily Filograninae that constituted the sister to the subfamily Spirorbinae. Within the Filograninae, genus *Apomatus* was recovered as a highly supported monophyletic clade. *Apomatus nishii* n. sp. (3 terminals, Table 1) was nesting (with low support) *A. voightae* Kupriyanova & Nishi, 2010 in a fully supported (bs 100) clade, in turn recovered as the sister group to *A. globifer* Théel, 1879. For further comments see the taxonomy of individual genera.

The genus *Bathyvermilia* was not recovered as a monophyletic clade. Instead, while the type species of the genus, *B. challengeri* (1 terminal), formed the sister to *B. eliasoni* (Zibrowius, 1970), the fully supported (bs 100) *Bathyvermilia rolandobastidai* n. sp. clade (2 terminals) was positioned as the sister to a well-supported (bs 94) *Protis–Filograna–Salmacina* clade. *Bathyvermilioides juliebrockae* n. g. and n. sp. (1 terminal) formed the sister to *Rhodopsis pusilla* Bush, 1905 in a fully supported (bs 100) clade, also containing *Semivermilia* and *Pseudovermilia*.

Filogranula stellata previously collected from the hydrothermal vent Lost City in the Mid-Atlantic ridge was recovered nested in a fully supported clade (bs 100) with

Table 1. Terminals with vouchers and GenBank accession numbers. AM–Australian Museum, Sydney, NSW; FMNH–Field Museum of Natural History, Chicago, IL, USA; SAM–South Australian Museum, Adelaide, SA; SIO–Scripps Institution of Oceanography, San Diego, CA, USA; ZM– Zoological Museum of University of Amsterdam, nowadays Naturalis Biodiversity Centre; USNM–United States National Museum, Washington DC, USA.

Species	Vouchers	Locality	*18S*	*Cyt b*
Apomatus globifer	ZMA V.Pol. 5250	Atlantic Ocean	EU195378	OQ427448
Apomatus nishii n. sp.	AM W.53423	IOT	PP883399	PP893247
Apomatus nishii n. sp.	AM W.54373	IOT	PP883415	PP893248
Apomatus nishii n. sp.	AM W.54510	IOT	PP883437	PP893246
Apomatus voightae	FMNH 6217	Alaska, USA	GU441856	OQ427450
Bathyvermilia challengeri	AM W.49721	NSW, Australia	PP883392	–
Bathyvermilia eliasoni	FMNH 6189	Alaska, USA	GU441857	–
Bathyvermilia rolandobastidai n. sp.	AM W.53398	IOT	PP883393	–
Bathyvermilia rolandobastidai n. sp.	AM W.53399	IOT	PP883395	–
Bathyvermilioides juliebrockae n. sp.	AM W.54380	IOT	PP883438	–
Chitinopoma serrula	SAM E3524	Norway	DQ317112	–
Crucigera inconstans	SAM E3525	SA, Australia	DQ317113	EU190464
Crucigera tricornis	SAM E3587	Qld, Australia	EU184056	EU190474
Dasynema chrysogyrus	AM W.45087	Qld, Australia	OQ379429	–
Ditrupa arietina	SAM E3527	France	DQ317114	–
Ficopomatus enigmaticus	SAM E3356	SA, Australia	DQ317115	OQ427451
Ficopomatus miamiensis	SAM E3617	Florida, USA	EU167531	KP863779
Filograna implexa	SAM E3528	France	DQ317116	OQ427452
Filogranella elatensis	SAM E3661	Israel	EU195385	–
Filogranula stellata	SAM E3606	Atlantic Ocean	EU195374	–
Filogranula stellata	AM W.53407	IOT	PP883404	–
Filogranula stellata	AM W.54390	IOT	PP883412	–
Filogranula stellata	AM W.53403	IOT	PP883401	–
Filogranula stellata	AM W.53462	IOT	PP883398	–
Floriprotis sabiuraensis	SAM E3659	Japan	EU195386	OQ427453
Galeolaria caespitosa	SAM E3529	SA, Australia	OQ379431	EU184054
Galeolaria hystrix	SAM E3526	SA, Australia	EU200441	EF192931
Helicosiphon biscoensis	SIO-BIC A4000	Antarctic	OQ379432	–
Hyalopomatus cf. *mironovi*	SAM E3728	North Fiji	GU063862	–
Hyalopomatus mironovi	AM W.50990	Kuril–Kamchatka Trench	OP598070	–
Hyalopomatus nogueirai n. sp.	AM W.54508	IOT	PP883435	PP893258
Hyalopomatus nogueirai n. sp.	AM W.53396	IOT	PP883396	–
Hyalopomatus nogueirai n. sp.	AM W.55300	IOT	PP883424	PP893260
Hyalopomatus nogueirai n. sp.	AM W.55297	IOT	PP883416	PP893259
Hyalopomatus nogueirai n. sp.	AM W.55293	IOT	PP883406	–
Hyalopomatus nogueirai n. sp.	AM W.55296	IOT	PP883425	–
Hyalopomatus nogueirai n. sp.	AM W.54368	IOT	PP883418	–
Hyalopomatus nogueirai n. sp.	AM W.54420	IOT	PP883431	PP893263
Hyalopomatus nogueirai n. sp.	AM W.54383	IOT	PP883427	PP893261
Hyalopomatus nogueirai n. sp.	AM W.54396	IOT	PP883411	PP893262
Hyalopomatus nogueirai n. sp.	AM W.55295	IOT	PP883413	–
Hyalopomatus rossanae n. sp.	AM W.54378	IOT	PP883419	–
Hyalopomatus rossanae n. sp.	AM W.54394	IOT	PP883409	–
Hyalopomatus rossanae n. sp.	AM W.55292	IOT	PP883430	–
Hyalopomatus rossanae n. sp.	AM W.53459	IOT	PP883402	–
Hyalopomatus rossanae n. sp.	AM W.54392	IOT	PP883408	–
Hyalopomatus rossanae n. sp.	AM W.53432	IOT	PP883400	–
Hyalopomatus rossanae n. sp.	AM W.54374	IOT	PP883420	–
Hyalopomatus rossanae n. sp.	AM W.54369	IOT	PP883417	–
Hyalopomatus sp. 1	SIO A1434	Jaco Summit	MT472387	–
Hyalopomatus sp. 2	SIO A1566	Guayamas Basin	MT472386	–
Hyalopomatus suelindsayae n. sp.	AM W.54366	IOT	PP883414	–
Hyalopomatus suelindsayae n. sp.	AM W.54438	IOT	PP883410	–
Hydroides elegans	SAM E3616	Florida, USA	EU195384	OQ427455

Table 1. *Continued ...*

Table 1. *Continued.*

Species	Vouchers	Locality	*18S*	*Cyt b*
Hydroides ezoensis	SAM E3584	Vladivostok, Russia	EU184062	OQ427456
Janita fimbriata	AM W.42388	Spain	OQ379433	OQ427457
Josephella marenzelleri	SAM E3620	Qld, Australia	EU195375	OQ427458
Laminatubus alvini	SAM E3531	East Pacific Rise	DQ317118	OQ427459
Marifugia cavatica	SAM E3612	Bosnia and Herzegovina	EU167530	OQ427460
Metavermilia acanthophora	SAM E3533	SA, Australia	DQ317119	OQ427461
Neomicrorbis azoricus	AM W.54342	IOT	PP002544	–
Neovermilia globula	SAM E3586	SA, Australia	EU195379	–
Paraprotis dendrova	SAM E3591	Qld, Australia	EU195377	–
Paraprotis pulchra	SAM E3665	Japan	OQ379434	OQ427462
Placostegus leslieharrisae n. sp.	AM W.54407	IOT	PP883434	–
Placostegus sp.	SAM E3589	Qld, Australia	OQ379435	–
Placostegus tridentatus	SAM E3585	Norway	OQ379436	–
Pomatostegus actinoceras	AM W.42378	Qld, Australia	OQ379437	–
Pomatostegus stellatus	SAM E3607	Mexico	EU195382	–
Protis hydrothermica	SAM E3541	East Pacific Rise	DQ317122	–
Protis melmackenzieae n. sp.	AM W.53456	IOT	PP883394	PP893252
Protis melmackenzieae n. sp.	AM W.55299	IOT	PP883432	PP893256
Protis melmackenzieae n. sp.	AM W.55291	IOT	PP883429	PP893255
Protis melmackenzieae n. sp.	AM W.54415	IOT	PP883422	PP893253
Protis melmackenzieae n. sp.	AM W.55298	IOT	PP883433	PP893257
Protis melmackenzieae n. sp.	AM W.54414	IOT	PP883428	PP893254
Protis melmackenzieae n. sp.	AM W.55294	IOT	PP883407	–
Protis perneti n. sp.	AM W.54408	IOT	PP883423	–
Protis perneti n. sp.	AM W.54384	IOT	PP883426	PP893249
Protis perneti n. sp.	AM W.53482	IOT	PP883405	–
Protis perneti n. sp.	AM W.53480	IOT	PP883397	PP893250
Protis perneti n. sp.	AM W.53467	IOT	PP883403	PP893251
Protis sp. 1	SAM E3727	North Fiji	OQ379438	–
Protis sp. 2	SIO A6319	Alarcon Rise	KY706465	–
Protolaeospira cf. *tricostalis*	SAM E3487	NSW, Australia	DQ242557	–
Protula atypha	SAM E3549	Hawaii, USA	DQ318595	–
Protula bispiralis	SAM E3657	Japan	OQ379439	OQ427464
Protula palliata	SAM E3540	SA, Australia	DQ317124	–
Protula tubularia	SAM E3542	Spain	DQ317123	OQ427465
Pseudochitinopoma occidentalis	SAM E3501	Washington, USA	DQ242542	OQ427466
Pseudochitinopoma pavimentata	SAM E3660	Japan	OQ379440	OQ427467
Pseudovermilia occidentalis	SAM E3613	Mexico	EU195383	OQ427468
Pyrgopolon ctenactis	SIO-BIC A25451	Panama	OQ379441	–
Rhodopsis pusilla	SAM E3621	Qld, Australia	EU195376	OQ427469
Romanchella quadricostalis	SAM E3491	SA, Australia	DQ242559	–
Salmacina sp.	SAM E3499	SA, Australia	DQ317126	OQ427470
Semivermilia elliptica	SAM E3664	Japan	EU195387	OQ427472
Semivermilia lylevaili	SAM E3629	Qld, Australia	OQ389601	–
Serpula jukesii	SAM E3536	SA, Australia	DQ317129	EU190465
Serpula vittata	SAM E3594	Qld, Australia	EU184057	EU190479
Spiraserpula iugoconvexa	AM W.42093	Qld, Australia	OQ379444	OQ427473
Spirobranchus kraussii	AM W.49977	South Africa	MK308673	MK308658
Spirobranchus taeniatus	SAM E3532	SA, Australia	DQ317120	OQ427480
Spirodiscus ottofinamusi	AM W.50871	NSW, Australia	OP598071	–
Turbocavus secretus	USNM 251863	Virgin Islands	OQ379448	OQ427483
Vermiliopsis labiata	SAM E3543	France	DQ317131	OQ427485
Vermiliopsis pygidialis	SAM E3544	Qld, Australia	DQ317132	–
Vitreotubus digeronimoi	AM W.54409	IOT	PP883421	–
Vitreotubus digeronimoi	AM W.55301	IOT	PP883436	–
Schizobranchia insignis	GenBank	Washington, USA	AY732222	–

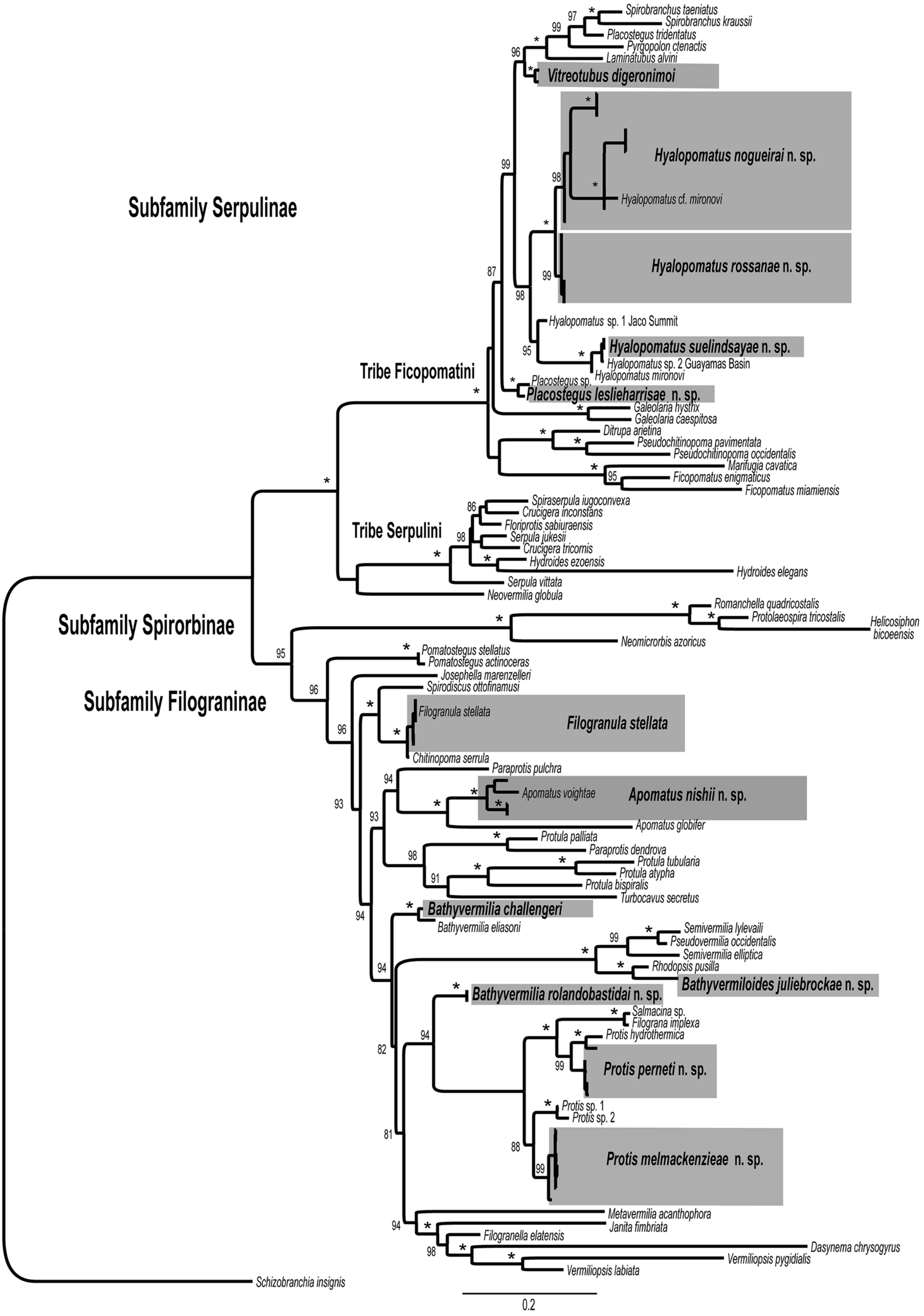

Figure 1. Maximum Likelihood consensus phylogram of the concatenated (*18S* and *Cyt b*) data set. Only nodes with bootstrap values > 70 are indicated. Nodes with bootstrap values 100 are indicated by *(asterisk).

4 terminals from IOT obtained for this study. *Filogranula stellata* formed a clade with *Chitinopoma serrula* (Stimpson, 1853) and the *Filogranula–Chitinopoma* was recovered as the sister to *Spirodiscus ottofinamusi* (bs 100).

The *Filograna–Salmacina* clade was nested within *Protis*, forming a well-supported clade, and thus making the genus *Protis* paraphyletic. Within his clade, *Protis perneti* n. sp. (5 terminals) was recovered nesting *Protis hydrothermica* from East Pacific Rise with high support (bs 99) and *Protis melmackenzieae* n. sp. (7 terminals) formed the sister clade with two unnamed *Protis* spp. from Fiji and the Alarcon Rise with the same level of support (bs 99).

The fully supported (bs 100) subfamily Serpulinae was split into fully-supported sister clades, the tribes Serpulini and Ficopomatini. All specimens from this study were recovered in the Ficopomatini. The clade of *Vitreotubus digeronimoi* (2 terminals) was recovered with high support as the sister to the clade that also included *Spirobranchus*, *Laminatubus*, *Pyrgopolon* and *Placostegus tridentatus* (Fabricius, 1779). The genus *Placostegus*, however, was not recovered as monophyletic since *P. leslieharrisae* n. sp. (1 terminal), although forming a well-supported clade with *Placostegus* sp. from Lizard Island off Queensland, did not group with *P. tridentatus*, the type species of the genus.

The genus *Hyalopomatus* was recovered as a monophyletic clade forming the sister to the *Spirobranchus–Placostegus tridentatus–Pyrgopolon–Laminatubus–Vitreotubus* clade. Within the genus *Hyalopomatus,* the *H. nogueirai* n. sp. clade (11 terminals) showed notable population structure and nested *H.* cf. *mironovi* from hydrothermal vents off North Fiji. The species *H. nogueirai* n. sp. was recovered as the sister to *H. rossanae* n. sp. (8 terminals) with full support (bs 100). *Hyalopomatus suelindsayae* n. sp. (2 terminals) formed the clade with *Hyalopomatus* sp. 2 from the Guayamas Basin hydrothermal vent and *Hyalopomatus mironovi* from Kuril-Kamchatka Trench. The above clade was the sister to *Hyalopomatus* sp. 1 collected from Jaco Summit hydrothermal seep.

Taxonomy

Phylum Annelida Lamarck, 1802

Class Polychaeta Grube, 1850

Subclass Sedentaria Lamarck, 1818

Infraclass Canalipalpata

Rouse & Fauchald, 1997

Order Sabellida Levinsen, 1884

Family Serpulidae Rafinesque, 1815

Subfamily Filograninae Rioja, 1923 *sensu* Kupriyanova *et al.*, 2023

Subfamily diagnosis. Tube not spirally coiled; body symmetrical; thoracic sickle (*Apomatus*) chaetae present; abdominal chaetae flat geniculate.

Remarks. The subfamily Filograninae was proposed by Rioja (1923: 107) who stated that presence of pinnules on the opercular peduncle “indicates that the species included in this subfamily are very primitive, …, corroborated by a hardly developed operculum”. However, molecular phylogenetic studies (e.g., Kupriyanova *et al.*, 2006; Lehrke *et al.*, 2007; Kupriyanova *et al.*, 2023) found that both traditional subfamilies Serpulinae and Filograninae were not monophyletic, so Kupriyanova *et al.* (2023) re-classified and re-formulated the sub-family diagnoses and based these on chaetal structures.

Genus *Apomatus* Philippi, 1844

Types species. *Apomatus ampulliferus* Philippi, 1844

Generic diagnosis (after Kupriyanova & Nishi, 2010). Tube white, opaque, circular in cross-section, keels and collar-like rings absent. Granular overlay may be present. Operculum a soft membranous vesicle without endplate borne on unmodified pinnulated radiole. Opercular constriction may be present. Pseudoperculum may be present on unmodified radiole. Radioles may be exceptionally flat ribbon-like. Arrangement of radioles in semi-circles (may be up to ¾ of a circle), maximum number up to 40 per lobe in larger species. Inter-radiolar membrane present. Radiolar eyes present. Stylodes absent. Mouth palps present. Seven thoracic chaetigerous segments. Collar trilobed or unlobed with smooth edge. Thoracic membrane long, forming ventral apron across anterior abdominal segments. Tonguelets between ventral and lateral collar lobes absent. Collar chaetae limbate, of two sizes (thus, in the classical terminology capillary and limbate), may exceptionally be supplemented by *Apomatus* chaetae. *Apomatus* chaetae usually present from chaetiger 3 onward. Thoracic uncini saw-to-rasp-shaped with approximately 30 teeth in profile, up to 3 (exceptionally 4) teeth in a row above and continuing onto peg; anterior peg very long, blunt, almost rectangular. Ventral thoracic triangular depression absent. Abdominal chaetae sickle-shaped with finely denticulate blades; uncini rasp-shaped with approximately 30 teeth in profile. Short achaetous anterior abdominal zone present. Posterior capillary chaetae present. Posterior glandular pad present.

Apomatus nishii n. sp.

urn:lsid:zoobank.org:act:71533B4E-A8AA-40F4-AB6B-1417E25C0FED

Fig. 2A–G

Material examined. Holotype: W.54373 (extraction number LK287), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°14'32"S, 96°17'31"E), depth 932–965 m, 21/10/2022.

Paratypes: W.53423 (LK259), Christmas Island SW (10°32'59"S, 105°31'59"E), depth 1388–1533 m, 09/07/2021 (1 spec., radiolar crown missing, prepared for SEM); W.54510 (LK318), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°16'41"S, 96°04'06"E), depth 1395–1459 m, 20/10/2022 (1 spec).

Description. Tube: white opaque or slightly reddish, circular in cross section, attached to substrate throughout its length, with smooth surface, without either collar-like rings or flaring

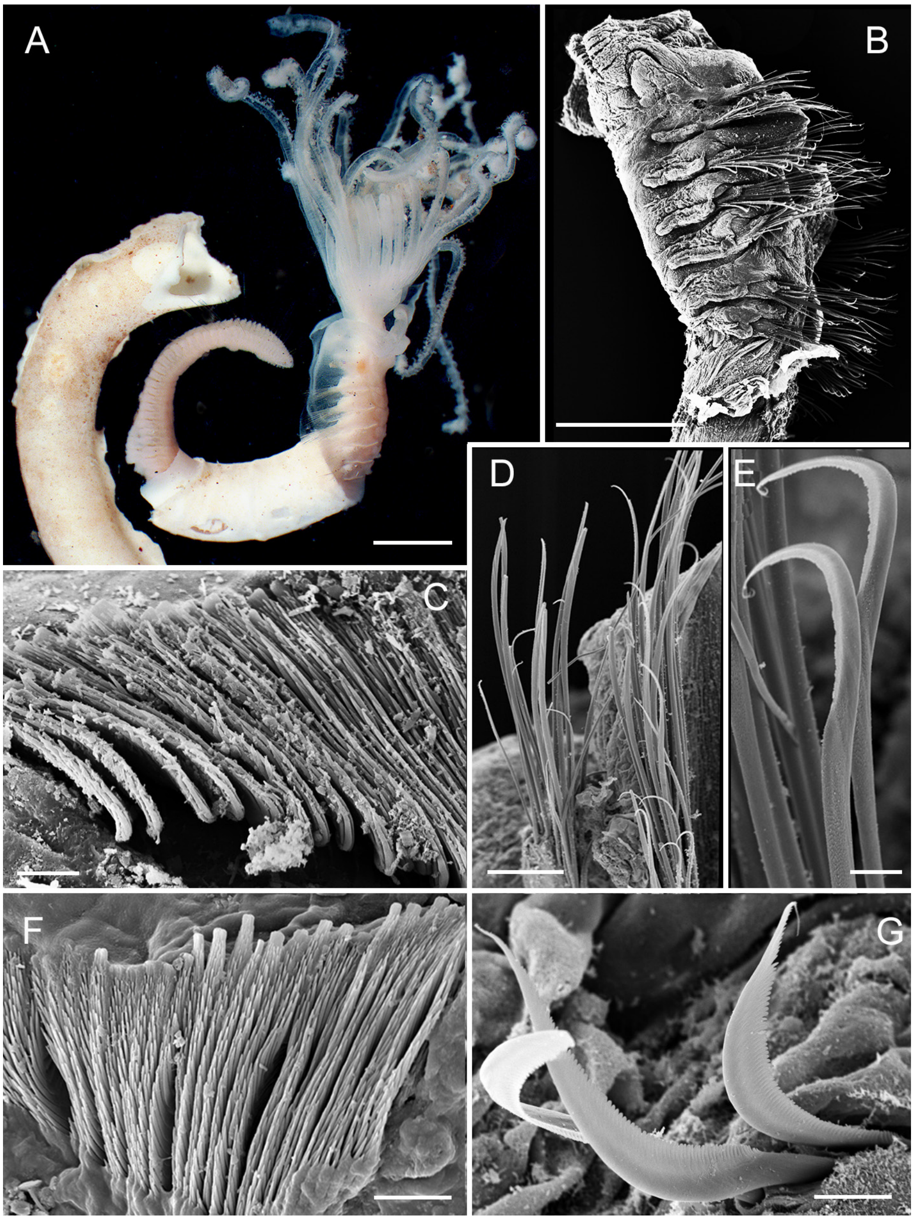

Figure 2. *Apomatus nishii* n. sp. A – photograph of holotype W.54373. B-C – SEM images of paratype W.53423: B – lateral view of the thorax, C – thoracic uncini, D – collar chaetae (left) and thoracic chaetal bundle (right); E – close-up view of *Apomatus* chaetae from chaetiger 3; F – abdominal uncini; G – abdominal chaetae. Scale: A – 1 mm; B – 0.5 mm; C – 5 µm; D – 100 µm; E – 20 µm; F, G – 10 µm.

peristomes. Median keels absent (Fig. 2A).

Radioles: flat ribbon-like, wide (Fig. 2A); each lobe with up to 12 pairs of radioles, arranged in semicircles, fused basally (connected by short inter-radiolar membrane) for about 1/20 of their length. Pinnules short and thin; each radiole ending into thin short filamentous tip (Fig. 2A, not well visible here). Radiolar eyes not observed in the preserved material. Stylodes absent.

Operculum: absent or lost (Fig. 2A), no distinct peduncle observed. Pseudoperculum absent.

Collar and thoracic membranes: collar unlobed, with entire edge, short, barely covering radiolar lobes (Fig. 2A, B); continuous with wide thoracic membranes (Fig. 2C, D) forming an apron across anterior abdominal chaetigers 1 or 2. Pairs of small, wart-like protuberances of collar chaetiger absent, calcium-secreting glands visible on collar.

Thorax: with collar chaetiger and 6 uncinigerous chaetigers (Fig. 2A, B). Uncinigerous tori positioned close to each other, ventral thoracic triangular depression absent. Collar chaetae (Fig. 2B, D) simple capillary (limbate) of two sizes, *Apomatus* chaetae absent (Fig. 2D). Subsequent chaetal bundles with *Apomatus* chaetae (Fig. 2E) and simple capillary and limbate chaetae (Fig. 2D). Uncini predominantly rasp-shaped (Fig. 2C), with approximately 20 teeth in profile, 2 teeth in posterior-most row and up to 5 teeth in a row above and continuing onto peg; anterior peg long, blunt, almost rectangular (Fig. 2C). Pair of prostomial eyes not observed.

Abdomen: up to 40 abdominal chaetigers. Short achaetous anterior abdominal zone present. Uncini rasp-shaped with 3–6 rows of teeth and up to 25 teeth in profile view, long blunt almost rectangular peg (Fig. 2F). Chaetae flat sickle-shaped with finely denticulate blades (Fig. 2G). Long capillary chaetae in posterior chaetigers absent. Posterior glandular pad not observed.

Size: body length (without radioles) up to 20 mm, width of thorax up to 0.8 mm. Radioles and operculum accounting for one third of entire length. Tube up to 1.2 mm wide with lumen of up to 1.0 mm diameter.

Diagnostic remarks. The new species resembles *Apomatus voightae* Kupriyanova & Nishi, 2010 from the Patton-Murray seamounts (Gulf of Alaska) that differs from all other serpulid species by its very characteristic flat ribbon-like radioles. An unusual feature of *A. voightae* is the presence of *Apomatus* chaetae in the collar chaetae bundle. Normally in the genus *Apomatus* chaetae are present in abundance throughout most thoracic segments but are absent in the collar bundle (Kupriyanova & Nishi, 2010). *Apomatus* chaetae are absent in the collar bundle of *Apomatus nishii* n. sp. and an operculum is also lacking in this species, but soft vesicular opercula in this genus are easily lost, so this character is unreliable.

Molecular data support monophyly of the genus *Apomatus* and placement of the new species in the genus. However, the relationship between the morphologically distinct species *Apomatus voightae* and *A. nishii* n. sp. need to be examined in further studies.

Etymology. The species is named in honour of Professor Eijiroh Nishi (Yokohama National University, Japan) in recognition of his numerous important contributions to taxonomic and reproductive studies of Serpulidae.

Distribution. Only known from seamounts off Christmas and Cocos (Keeling) Islands, 932–1533 m.

Genus *Bathyvermilia* Zibrowius, 1973

Type species. *Bathyvermilia challengeri* Zibrowius, 1973

Generic diagnosis (after Kupriyanova & Ippolitov, 2015 emended). Tube white, opaque, circular to quadrangular in cross-section, keel(s) may present. Collar-like rings present. Operculum sub-globular, with simple flat to slightly conical chitinous endplate, sometimes encrusted by calcareous deposit. Peduncle cylindrical, either smooth or wrinkled, distal wings absent; inserted as 2nd dorsal radiole on either side, constriction present. Pseudoperculum absent. Up to 35 radioles per lobe arranged in semi-circles. Inter-radiolar membrane, radiolar eyes, and stylodes absent. Mouth palps may present. Seven thoracic chaetigerous segments, six of which uncinigerous. Trilobed collar (may be not divided into lobes) with straight edge, tonguelets absent. Thoracic membranes of variable length, extending to 2nd–7th thoracic segment. Collar chaetae limbate capillaries. *Apomatus* chaetae present. Thoracic uncini saw-shaped (rarely saw-to-rasp shaped), with 6–12 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 present. Posterior capillary chaetae present. Posterior glandular pad present.

Remarks. Ten Hove and Kupriyanova (2009) listed five bathyal and abyssal species in this genus (*Bathyvermilia challengeri*, *B. islandica* Sanfilippo, 2001, *B. kupriyanovae* Bastida-Zavala, 2008, *B. langerhansi* (Fauvel, 1909), and *B. zibrowiusi* Kupriyanova, 1993a). Kupriyanova and Nishi (2010) added a species from the Patton-Murray Seamount, Gulf of Alaska by transferring *Vermiliopsis* (?) *eliasoni* Zibrowius, 1970 to the genus *Bathyvermilia*. Further Kupriyanova and Ippolitov (2015) added *Bathyvermilia gregrousei* to the genus and emended the generic diagnosis to include the species with tetragonal, slightly spirally twisted tubes.

Bathyvermilia challengeri Zibrowius, 1973

Fig. 3A–F

Placostegus ornatus (not Sowerby in Mörch, 1863: 420) McIntosh, 1885: 522–524, pl. 55, fig. 5–6, pl. 30A, fig. 25–27.

Bathyvermilia challengeri Zibrowius, 1973: 428–430, fig. 1a–e; Kupriyanova *et al.*, 2011; Gunton *et al.*, 2021: 214–25, fig. 28A.

Material examined. W.53395, Christmas Island SE (10°33'00"S, 105°42'11"E), depth 1225–1626 m, 06/07/2021 (1 spec. in tube, photo and prepared for SEM).

Species diagnosis. Very recognisable tubes with characteristic sculpture made of numerous transverse ridges close to each other (Fig. 3A). Thoracic membranes rounded, extending to 3rd thoracic segment (Fig. 3B). Operculum conical, covered with simple slightly raised chitinous endplate having distinct rims (Fig. 3B). Peduncle smooth cylindrical, constriction obvious (Fig. 3C). Collar chaetae simple limbate (Fig. 3D). *Apomatus* chaetae present in thorax (Fig. 3E). Thoracic uncini saw-to-rasp shaped, with 12 teeth in lateral view and simple, pointed anterior fang (Fig. 3F).

Remarks. This species is easily recognisable by its very characteristic tube with numerous conspicuous transverse ridges (not anteriorly directed peristomes), positioned close to each other, encircling the tube interrupted by a longitudinal groove cutting transverse ridges near the base. The original records of this species came from three HMS "*Challenger*" stations in the North and South Pacific Ocean taken at 4246–5719 m (Zibrowius, 1973). Most recently a specimen was collected in the Eastern Australian Abyss (Gunton *et al.*, 2021); this specimen was sequenced for the present study because DNA amplification of the *B. challengeri* specimen from IOT examined here was unsuccessful.

The specimen of *B. challengeri* from IOT shows at least 12 teeth in lateral view of thoracic uncini, moreover, these uncini are saw-to-rasp shaped (Fig. 3F). The original description of *B. challengeri* (Zibrowius,1973) states "thoracic uncini saw-shaped with about 7 to 10 teeth". The generic diagnosis in Kupriyanova and Ippolitov (2015) gives saw-shaped thoracic uncini with 6–10 teeth, while 9–11 teeth were reported for *B. gregrousei*. Thus, we emended the diagnosis of the genus *Bathyvermilia* to reflect the observed variability.

The specimen collected off Johnston Atoll near Hawaii at 380 m (Kupriyanova *et al.*, 2011) is currently the shallowest record for this nominal species. Although the specimen from the upper bathyal off Johnston Atoll fits the original description of *B. challengeri* and is morphologically very similar to the specimens collected from the lower abyssal zone, such a disjunct bathymetric distribution is unusual (reviewed in Capa *et al.*, 2021). Further collecting and

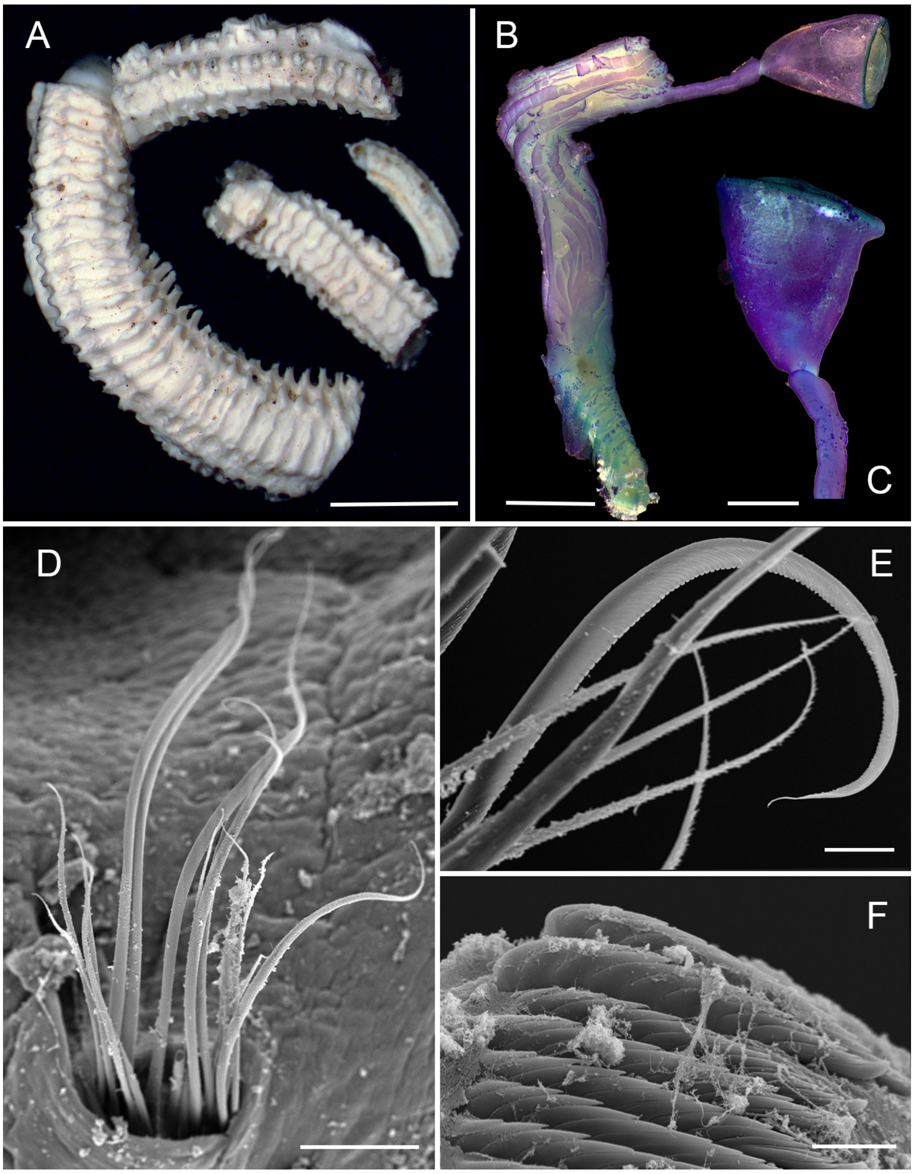

Figure 3. *Bathyvermilia challengeri* W.53395. A – tube fragments, B – lateral view of thorax with radioles and operculum, C – close-up view of the operculum (stained), D – SEM of collar chaetae, E – *Apomatus* chaetae, F – thoracic uncini. Scale: A, B – 1 mm; C – 0.5 mm. D – 50 µm; E, G – 10 µm.

additional taxonomic studies of deep-sea serpulids are needed to determine whether *B. challengeri* does have disjunct or wide bathymetric distribution or whether at least two morphologically similar species are present in the Pacific Ocean.

Distribution. Mid-Pacific Ocean, 4246–5719 m, Johnston Atoll (about 1400 km west of Hawaii), 380 m; South Pacific Ocean off NSW, Australia, 2562–2587 m; South Indian Ocean, off Christmas Island, Australia, 1225–1626 m.

Bathyvermilia rolandobastidai n. sp.

urn:lsid:zoobank.org:act:D04FC5F4-442A-4B90-8CF7-723ACB7891C5

Fig. 4A–H

Material examined. Holotype: W.53399 (LK250), Christmas Island SE (10°34'13"S, 105 41'23"E), depth 643–997 m, 06/07/2021.

Paratypes: W.53398 (LK247), same as above (1 spec, photo and SEM); W.54907 (1 spec).

Description. Tubes: white or slightly brownish, opaque, circular in internal in cross-section, more or less semicircular in external cross-section with attachment area narrowly wider than tube width (Fig 4A, B), attached to substrate throughout their length. Tube surface with numerous (6–7) low keels and some occasional, slightly elevated peristomes (Fig. 4A, B).

Radioles: 10–11 pairs arranged in two semicircles. Interradiolar membrane and stylodes absent. Each radiole ending in a thick filamentous tip as long as pinnules.

Peduncle: smooth circular in cross-section, slightly thicker than normal radioles and inserted as a 2nd radiole.

Operculum: semi-globular, with flat or slightly depressed chitinous endplate (Fig. 4A, B). Constriction at junction of basal part of operculum and peduncle present. Pseudoperculum absent.

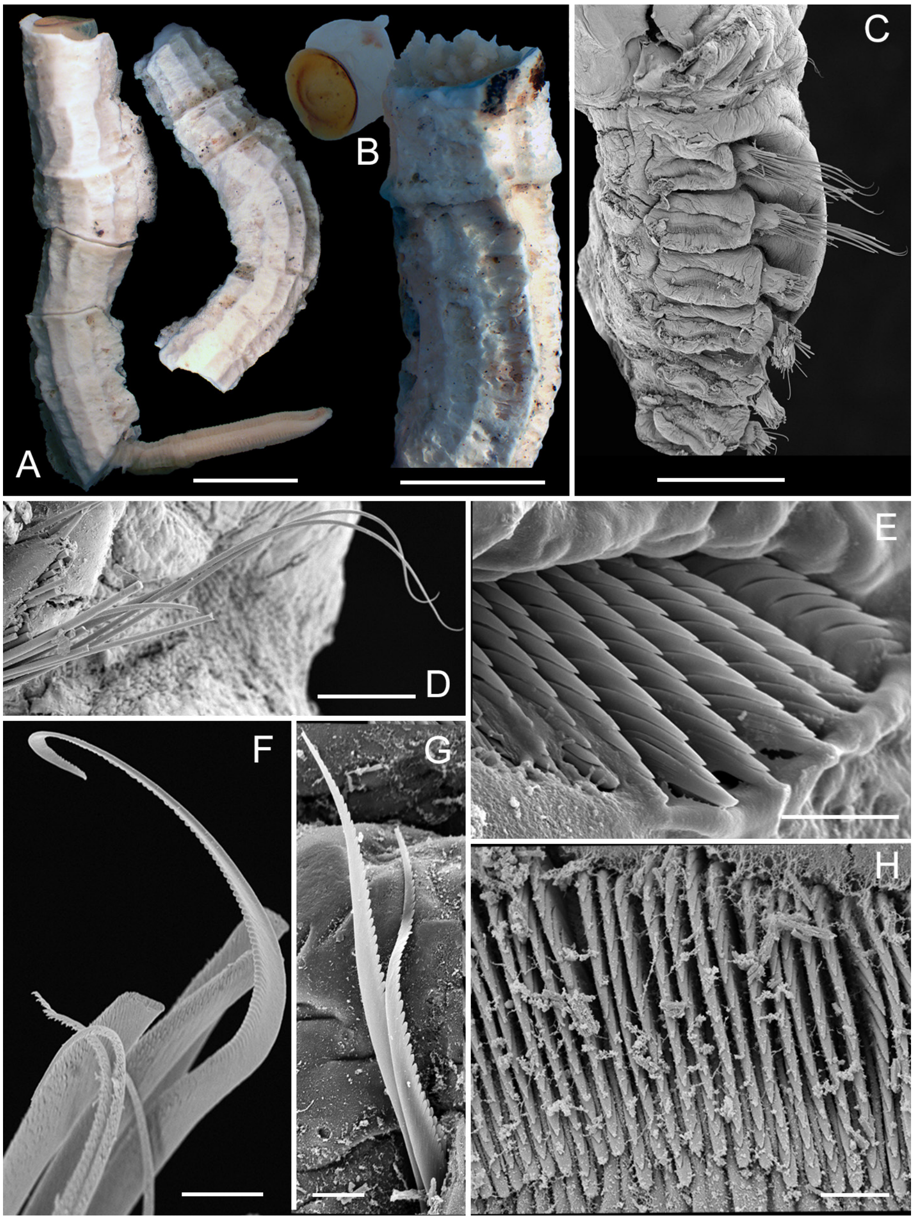

Figure 4. *Bathyvermilia rolandobastidai* n. sp., light microscopy photograph of animals in tubes, A – holotype W.53399; SEM, B – paratype W.53398, C – lateral view of thorax, D – collar chaetae, E – thoracic uncini, F – *Apomatus* chaetae of thorax, G – abdominal chaetae, H – abdominal uncini. Scale: A, B – 1 mm; C – 0.5 mm; D – 100 µm; E, G, H – 10 µm; F – 20 µm.

Collar and thoracic membranes: collar trilobed, with ventral and two latero-dorsal lobes. Thoracic membranes continuing to thoracic chaetiger 5.

Thorax: Seven thoracic segments, 6 with uncini (Fig. 4C). Collar chaetae limbate of two sizes (Fig. 4D). Rest of chaetae limbate plus *Apomatus* chaetae (Fig. 4F). Thoracic tori positioned along mid-lateral line of thorax, triangular depression absent. Thoracic uncini saw-shaped with 8–9 teeth and pointed anterior fang (Fig. 4E).

Abdomen: with up to 60 chaetigers. Anterior abdominal chaetae flat narrow geniculate with blunt teeth (Fig. 4G), replaced by capillary chaetae on posterior segments. Anterior abdominal uncini saw-shaped with 12 teeth and simple pointed fang (Fig. 4H). Uncini of middle and posterior abdominal segments rasp-shaped, with up to 13 teeth in profile and 2–3 teeth per row. Short achaetous anterior abdominal zone present. Posterior glandular pad present.

Size: total body length up to 15 mm, width of thorax up to 0.8 mm. Radioles and operculum accounting for one third of entire length. Tube up to 1.2 mm wide with lumen of up to 1.0 mm in diameter.

Diagnostic remarks. The species in the genus are distinguished by tube structure, and to a lesser degree, by the length of the thoracic membranes and details of opercular structure. The new species is easily recognisable from all congeners by its characteristic tube with numerous low keels and occasional transverse ridges/peristomes. Tubes are also very distinct in *B. challengeri* (with numerous transverse ridges close to each other), *B. eliasoni* (with three longitudinal ridges raised into curved spines), *B. gregrousei* (tetragonal in cross-section, slightly spirally twisted) and *B. langerhansi* (with smooth shiny surface, sub-triangular in cross-section with a median keel, but lacking lateral keels, peristomes, and transverse ridges).

Bathyvermilia islandica, B. kupriyanovae and *B. zibrowiusi* are similar in having tubes circular in cross-section, with smooth shiny surface and distal peristomes. The tube of *B. islandica* is attached to the substrate for all its length, forming a distinct peripheral basal flange and undulated peristomes are sometimes present along the tube but are rare. *Bathyvermilia islandica* is also distinct in having long thoracic membranes ending at the 7th thoracic chaetiger, they are wide up to the 2nd segment, and then narrow sharply. *Bathyvermilia zibrowiusi* is most similar to *B. kupriyanovae* as both species have tubes with wide peristomes and thoracic membranes extending to the 4th chaetiger. The main difference between them is the opercular endplate with developed concentric ridges in *B. zibrowiusi*, as opposed to simple chitinous endplate with some calcareous inclusions in *B. kupriyanovae*.

The molecular results of this study did not support monophyly of the genus *Bathyvermilia*; alternatively, the data suggest that the new species does not belong to the genus *Bathyvermilia*. However, because morphology of *Bathyvermilia rolandobastidai* n. sp. fits the generic diagnosis of the genus *Bathyvermilia* well, we decided against the change in nomenclature until further molecular data become available.

Distribution. Only known off Christmas Island, South Indian Ocean, 643–997 m.

Etymology. The species is named after Professor Rolando Bastida-Zavala (Universidad de Mar, Oaxaca, Mexico) to honour his important contributions to taxonomic studies of Serpulidae.

Genus *Bathyvermilioides* n. gen.

urn:lsid:zoobank.org:act:6965D659-044F-4247-83DA-B031CDACDA0C

Type species. *Bathyvermilioides juliebrockae* n. sp.

Generic diagnosis. Tube white, opaque, tusk-shaped, quadrangular in cross-section, without peristomes. Operculum very hard, semi-globular shiny endplate. Peduncle cylindrical, smooth, without wings; inserted as 2nd dorsal radiole on one side. Pseudoperculum absent. Radioles arranged in semi-circles, up to 12 per lobe. Inter-radiolar membrane and stylodes absent. Radiolar eyes and mouth palps absent. Seven thoracic chaetigerous segments. Collar trilobed, with entire edge, continuous with short thoracic membranes ending at 2nd thoracic chaetiger. Tonguelets absent. Collar chaetae limbate. *Apomatus* chaetae present. Thoracic uncini saw-shaped with 9–10 teeth in profile, anterior fang pointed. Triangular depression absent. Abdominal chaetae short, flat triangular with wide distal denticulate blade; abdominal uncini rasp-shaped, anterior fang pointed. Achaetous anterior abdominal zone absent. Long posterior capillary chaetae absent. Posterior glandular pad absent.

Remarks. The new genus *Bathyvermilioides* has tusk-shaped quadrangular in cross-section tubes resembling those of nominal *Bathyditrupa* and *Spirodiscus*, but the similarities end here, and quadrangular tubes are apparently convergent in several genera of deep-sea serpulids (Kupriyanova & Ippolitov, 2015). The genus clearly belongs to the subfamily Filograninae as indicated by the presence of the thoracic *Apomatus* chaetae and flat geniculate abdominal chaetae and which is supported by molecular results here (Fig. 1).

The results of the phylogenetic analysis here (Fig. 1) showed that the new taxon does not fall into the *Bathyvermilia* clade (type species *B. challengeri*) but belongs to the well supported clade with *Rhodopsis pusilla, Semivermilia,* and *Pseudovermilia*. The phylogenetic position of *B. juliebrockae* n. gen., n. sp. suggests that the new taxon could have been included in the genus *Rhodopsis.* However, the taxa are very different morphologically, as the two currently valid species of the genus *Rhodopsis* are tiny, with the tubes <0.2 mm in diameter and often bearing unpaired brood chambers. The operculum in *Rhodopsis* is usually covered with a well-developed soft chitinous endplate bearing spines, the number of thoracic chaetigerous segments varies from four to six, and the achaetous anterior abdominal zone is long. Chaetal characters also differ in the two taxa as in *Rhodopsis* collar chaetae are absent, both thoracic and abdominal uncini are rasp-shaped, and abdominal chaetae are flat narrow geniculate.

Morphologically the new species most closely resembles *Bathyvermilia gregrousei*, a deep-sea species inhabiting similarly quadrangular, although smaller and slightly spirally twisted, tubes. It is likely that the *Bathyvermilia gregrousei* also should be transferred to the new genus, but molecular data are needed to confirm this hypothesis. Because of these morphological similarities with *Bathyvermilia* and phylogenetic position of the new species we established the new genus *Bathyvermilioides*. The suffix -oides means “similar to”. This taxonomical decision will again be tested in future molecular studies of deep-sea serpulids.

Bathyvermilioides juliebrockae n. sp.

urn:lsid:zoobank.org:act:89CE3532-DE97-48F9-94E2-AB89015526AA

Fig. 5A–L

Material examined. Holotype: W.54380, Cocos (Keeling) Islands Territory, Investigator Ridge Abyssal (11°15'26"S, 97°58'08"E), depth 4980–4990 m, 12/10/2022 (not removed from the tube). Paratype: W.55302 (LK319), same as above (specimen removed for DNA, photos, and SEM).

Description. Tube: white opaque, ostensibly free, with shiny surface, tusk-shaped, thick-walled, mostly quadrangular in cross-section, edges rounded and never denticulate (Fig. 5A).

Radiolar crown: with 11 pairs of radioles in holotype, 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, slightly thicker than remaining radioles, distal wings absent; inserted on left side between base of 1st and 2nd radioles.

Collar and thoracic membranes: collar covering bases of radiolar lobes, thin; four-lobed, with ventral lobe made of two lobes and distinctly higher than lateral ones (Fig. 5B–D). Collar continuous with short rounded thoracic membranes ending at 2nd chaetiger (Fig. 5E).

Operculum: with soft membranous semi-transparent ampulla and distal part distinctly differentiated from basal part. Distally operculum covered with very hard, brownish semi-globular endplate with shiny surface (Fig. 5F);

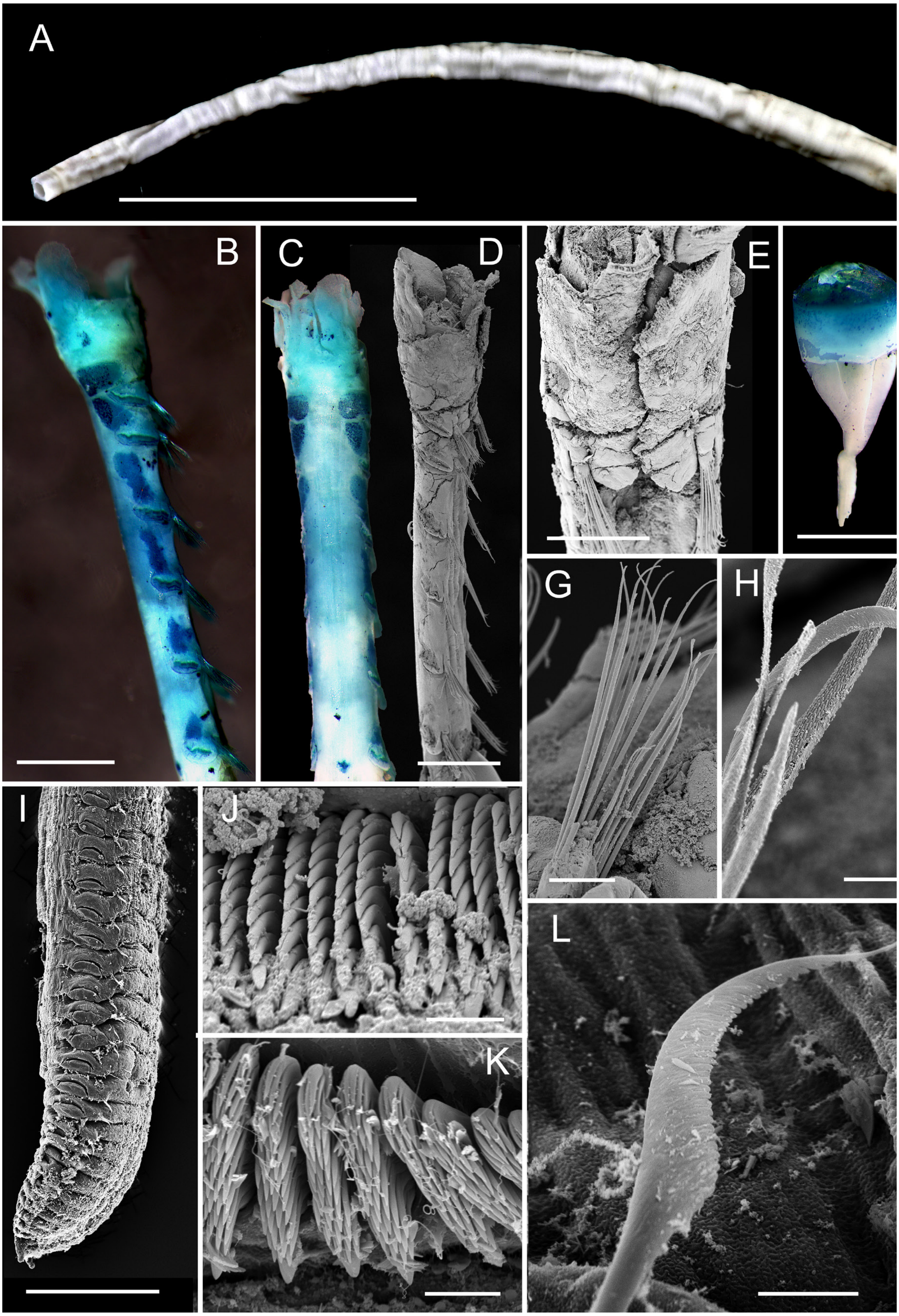

Figure 5. *Bathyvermilioides juliebrockae* n. sp. holotype W.54380. A – tube; W.55302. B – photos, lateral view of thorax, C – operculum, D – ventral view of thorax, E – SEM, lateral view of thorax, F – dorsal view of thorax showing length of thoracic membranes, G – thoracic chaetae with *Apomatus* chaetae, H – close-up view of *Apomatus* chaeta, I – thoracic uncini, J – abdominal uncini, K – abdomen, L – abdominal chaeta. Scale: A – 1 mm; B, C, D, F – 0.5 mm; E – 0.2 mm; G – 50 µm; H, L – 10 µm; I – 0.5 mm; J, K – 5 µm.

conspicuous constriction between operculum and peduncle present (Fig. 5F). Pseudoperculum absent.

Thorax: with 7 chaetigerous segments, 6 of which uncinigerous (Fig. 5B–D). Small bundle of limbate collar chaetae. Subsequent chaetae limbate, of two sizes, *Apomatus* chaetae present (Fig. 5G, H, e.g., the strongly bent chaeta). Uncini saw-shaped, with 9–10 teeth in profile view and pointed anterior fang (Fig. 5J). Pair of prostomial eyes absent. Triangular depression absent (Fig. 5C), thoracic tori widely separated and almost parallel to mid-lateral line of thorax.

Abdomen: paratype with 56 segments. Abdominal chaetae short, flat triangular with wide distal denticulate blade (Fig. 5L). Long capillary chaetae absent in posterior chaetigers (Fig. 5I). Uncini rasp-shaped with 9–10 teeth in profile and up to 5 rows of teeth above pointed anterior fang (Fig. 5K). Achaetous anterior abdominal zone absent.

Size: total body length of paratype 13.8 mm, including 4.4 mm long radioles, 4.0 mm long thorax, 5.4 mm long abdomen, width of thorax 1.1 mm. Complete tube of holotype 22 mm long (Fig. 5A). In holotype external tube diameter of tube mouth 1.5 mm, corresponding lumen diameter 1.1 mm.

Species diagnosis. The species is characterised by distinct quadrangular tusk-shaped tubes and the operculum covered with a very hard (questionably calcified) convex (semi-globular) brown endplate. This very hard endplate distinguishes the new species from other quadrangular-tubed taxa that have soft endplates. The diameter of the open posterior end suggests that the specimen originally settled on a small pebble or even a sand granule, and later broke free.

Distribution. Only known from seamounts off Cocos (Keeling) Islands, Indian Ocean, 4980–4990 m.

Etymology. The abyssal species is named in honour of Professor Julie Brock (University of Hawaii at Manoa, USA) for her numerous and important contributions to taxonomy of deep-sea serpulids.

Genus *Filogranula* Langerhans, 1884

Type species. *Filogranula gracilis* Langerhans, 1884

Generic diagnosis (from ten Hove & Kupriyanova, 2009). Tube white, opaque, with elaborate peristomes; keel present. Granular overlay absent. Operculum with chitinous endplate, may have additional spines in the centre. Peduncle cylindrical, smooth, without wings; inserted as 2nd dorsal radiole on one side. Pseudoperculum absent. Radioles arranged in semi-circles, up to 7 per lobe. Inter-radiolar membrane and stylodes absent. Radiolar eyes may be present. Mouth palps not observed. Seven thoracic chaetigerous segments. Collar generally non-lobed (may be trilobed) with entire edge, continuous with short thoracic membranes ending at 2nd thoracic chaetiger. Tonguelets absent. Collar chaetae fin-and-blade and limbate. *Apomatus* chaetae present. Thoracic uncini saw- or saw-to-rasp-shaped with 12–14 teeth in profile, up to 5 teeth in a row above anterior peg, blunt, gouged underneath. Triangular depression absent. Abdominal chaetae short, flat triangular with wide distal denticulate blade; abdominal uncini rasp-shaped. Achaetous anterior abdominal zone present. Long posterior capillary chaetae present. Posterior glandular pad absent.

Remarks. Zibrowius (1983) and Kupriyanova (1993b) noticed that the genera *Chitinopoma* Levinsen, 1884 and *Filogranula* are very similar in general opercular and chaetal structure, as well as in the length of thoracic membranes. Ten Hove and Kupriyanova (2009) mentioned that additional studies are needed to determine whether these two genera should be synonymised. The most recent multigene molecular phylogeny of Kupriyanova *et al.* (2023) showed that *F. stellata* and *C. serrula* are sister groups, thus supporting the hypothesis.

Filogranula stellata (Southward, 1963)

Fig. 6A–F

Ompalopoma stellata Southward, 1963: 576–578, fig. 3 (Atlantic Ocean, continental slope of the UK, between 46° and 52°N, 320–1775 m).

Filogranula stellata – Bianchi, 1981: 99–100, fig. 38a-c (Mediterranean); Ben-Eliahu & Fiege, 1996: 11–12 (Central and Eastern Mediterranean); ten Hove & Kupriyanova, 2009: 45 (name only), 47, fig. 19A–E (SEM micrographs of chaetae); Kupriyanova *et al.*, 2023 (DNA, phylogeny, Lost City Hydrothermal field, Mid-Atlantic Ridge, SAM E3606): Rosso *et al.*, 2021 (Mediterranean, submarine caves).

Filogranula cf. *stellata* – Kupriyanova *et al.*, 2011: 52, fig. 5J (tube only, RV "*Vityaz*" Stn. 6348-2, Pacific Ocean, 18º35'N, 175º05'W, 1600–1900 m).

Material examined. W.53461, Territory of Christmas Island, Clara Marie Seamount (13°34'35"S, 105°19'39"E), depth 2189–2264 m, 12/07/2021 (1 tube); W.53462 (LK257), same as above (1 spec.); W.53403 (LK261), Christmas Island SE (10°33'22"S, 105°45'51"E), depth 3200–3345 m, 07/07/2021 (1 spec.); W.53407 (LK269), same as above (1 spec.); W.54390 (LK280), Cocos (Keeling) Islands Territory (12°13'32"S, 96°57'36"E), depth 1113–1343 m, 17/10/2022 (1 spec. prepared for SEM).

Species diagnosis. Tube white, opaque, with elaborate star-like peristomes; denticulate keel present (Fig. 6A). Operculum with chitinous concave endplate (Fig. 6A, C). Peduncle smooth cylindrical, without wings, gradually continuing into operculum without constriction (Fig. 6C), inserted as 2nd dorsal radiole on one side. Seven thoracic chaetigerous segments (Fig. 6C). Collar non-lobed with entire edge, continuous with short thoracic membranes, ending at 2nd thoracic chaetiger (Fig. 6D). Collar chaetae fin-and-blade and limbate (Fig. 6F). *Apomatus* chaetae present (Fig. 6E). Illustrations of uncini and abdominal chaetae are given by ten Hove and Kupriyanova (2009, fig. 19).

Remarks. This species with very characteristic tubes bearing denticulate collars was originally described from the Northern Atlantic. Kupriyanova *et al.* (2011) provided the first (tentative as based on an empty tube only) record of the species from the Pacific Ocean. Most recently, the molecular phylogeny of Kupriyanova *et al.* (2023) included sequences of a specimen from Lost City Hydrothermal field located on Mid-Atlantic Ridge (Table 1). This study provided the first record of the species from the Indian Ocean. The phylogenetic results of this study support placement of the collected specimens into *Filogranula stellata*.

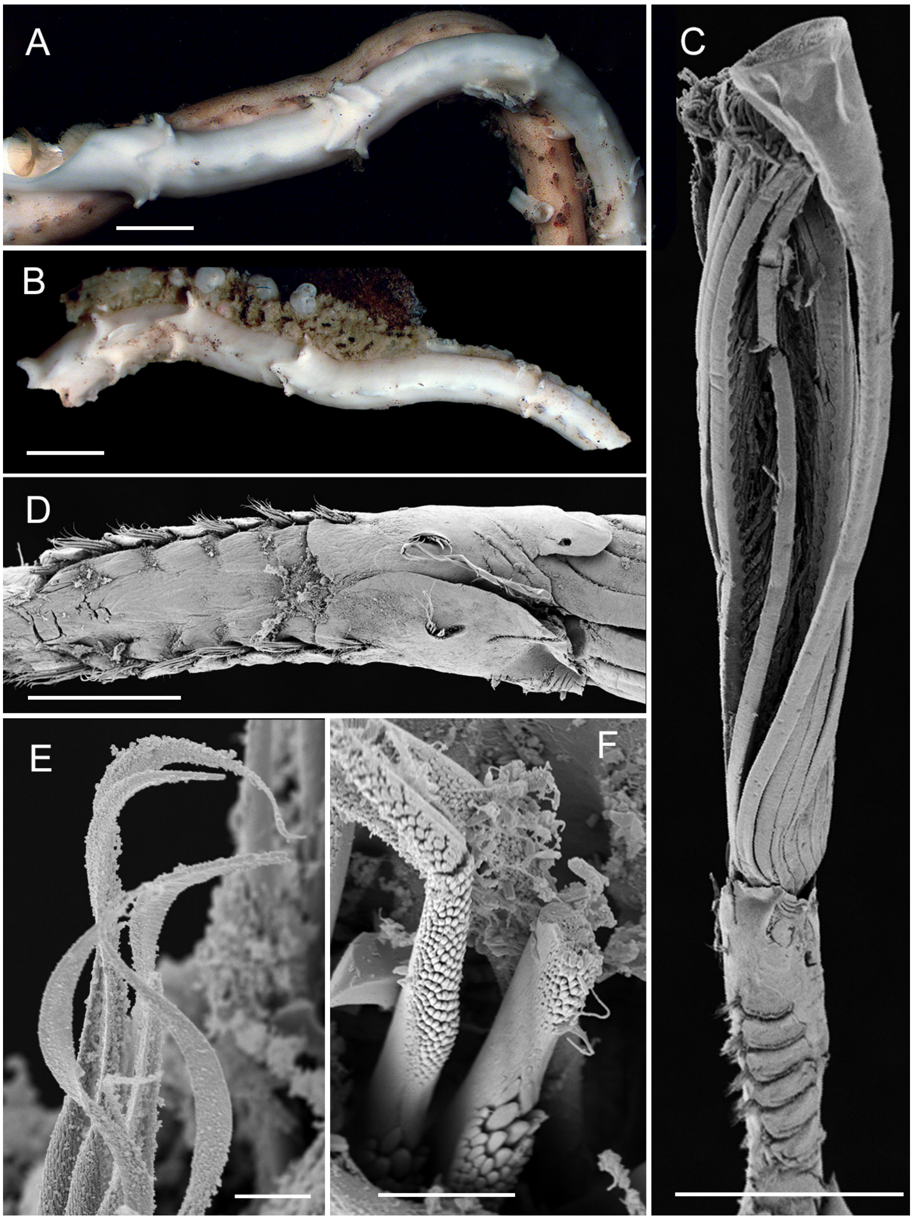

Figure 6. *Filogranula stellata*. Photo of tubes with typical star-shaped peristomes, A – W.53462, B – W.53461. SEM, W.54390, C – lateral view of anterior end, D – dorsal view showing length of thoracic membranes, E – *Apomatus* chaetae, F – special collar chaetae. Scale: A, B, C – 1 mm; D – 0.5 mm; E – 20 µm, F – 10 µm.

Distribution. North Atlantic Ocean, 320–1775 m; Mediterranean, 700–2485 m; Pacific Ocean, 1600–1900 m; Indian Ocean, Territories of Christmas and Cocos (Keeling) Islands, 1113–3345 m.

Genus *Protis* Ehlers, 1887

Type species. *Protis simplex* Ehlers, 1887

Generic diagnosis (from Rzhavsky *et al.,* 2013 emended). Tube white, opaque, without peristomes, keel present in *P. akvaplani*. Operculum absent or one or more membranous globular opercula present on normal pinnulate radiole(s). Arrangement of radioles pectinate, up to 20 per lobe. Inter-radiolar membrane absent. Radiolar eyes not observed. Stylodes absent. Mouth palps absent. Seven (six in *P. akvaplani*) thoracic chaetigers. Collar trilobed with entire edge, tonguelets absent. Thoracic membranes variable, ending at chaetiger 3 in *P. akvaplani* and in *P. melmackenzieae* n. sp. or long, at least to end of thorax and usually forming ventral apron across anterior abdominal segments. Collar chaetae fin-and-blade and limbate. *Apomatus* chaetae present. Thoracic uncini saw-shaped with about 6 (up to 12 in *P. melmackenzieae* n. sp.) teeth, anterior fang simple pointed. Triangular depression absent. Abdominal chaetae flat narrow geniculate with rounded teeth, slightly more triangular blade in *P. hydrothermica*. Abdominal uncini rasp-shaped in all segments or saw-shaped in anterior segments, with up to 6 teeth in profile, approximately 5–7 teeth in a row above fang. Achaetous anterior abdominal zone absent. Long posterior capillary chaetae present. A posterior glandular pad may be present.

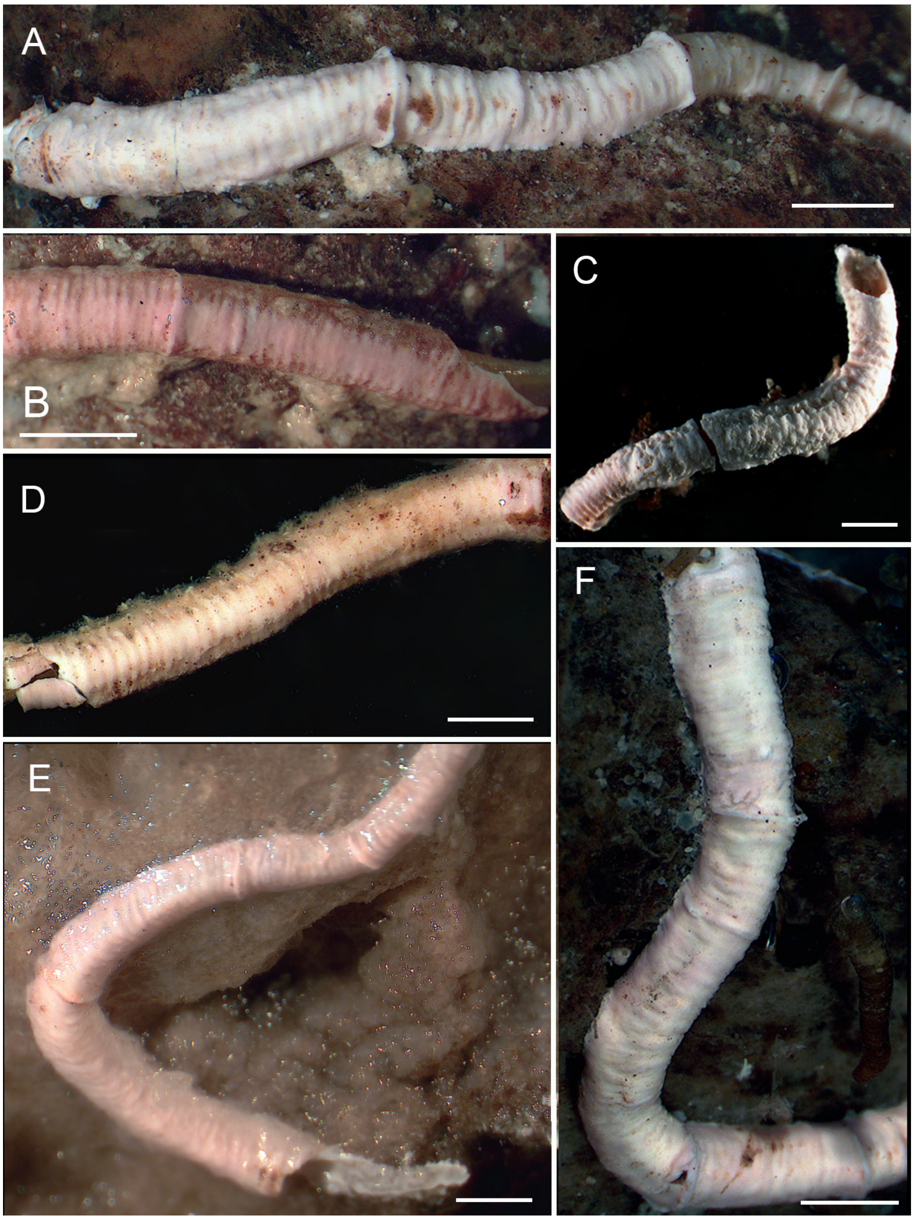

Figure 7. Tube colour variability of *Protis melmackenzieae* n. sp. A – W.54412, B – W.55298, C – W.53456, D – W.55299, E – W.54414, F – W.54411. Scale: 1 mm.

Remarks. Ehlers' original diagnosis does not mention an operculum at all, the lack of an operculum thus was considered a characteristic feature of *Protis*. Kupriyanova and Jirkov (1997) extended the diagnosis to include individuals with one or more opercula, following the description of the abyssal *P. polyoperculata* by Kupriyanova (1993a). Rzhavsky *et al*. (2013) emended the diagnosis to include their newly described *P. akvaplani,* having tubes with a very distinct high keel and six thoracic segments. Here we further emended the diagnosis to reflect the short thoracic membranes in *P. akvaplani* and *P. melmackenzieae* n. sp.

Protis melmackenzieae n. sp.

urn:lsid:zoobank.org:act:A25072A1-D8D4-42D3-A4F5-F390D236725A

Fig. 7A–F, 8A–F

Material examined. Holotype: W.54485, Cocos (Keeling) Islands Territory, Cocos (Keeling) (12°13'32"S, 96°57'36"E), depth 1113–1343 m, 17/10/ 2022, complete specimen with operculum.

Paratypes: W.53456 (LK248), Territory of Christmas Island, Karma Seamount (12°49'33"S, 107°02'48"E), depth 2760–2850 m, 11/07/2021 (1 spec. prepared for SEM); W.55294 (LK274), Cocos (Keeling) Islands Territory, Rudist Seamount (11°03'47"S, 99°26'36"E), depth 3780–3839 m, 12/10/2022 (1 spec.); W.55299 (LK309), same locality (1 spec); W.55298 (LK310), same locality (1 spec.); W.54414 (LK305), same locality (1 spec.); W.55291 (LK306), same locality (1 spec.); W.54415 (LK298), same locality (1 spec.).

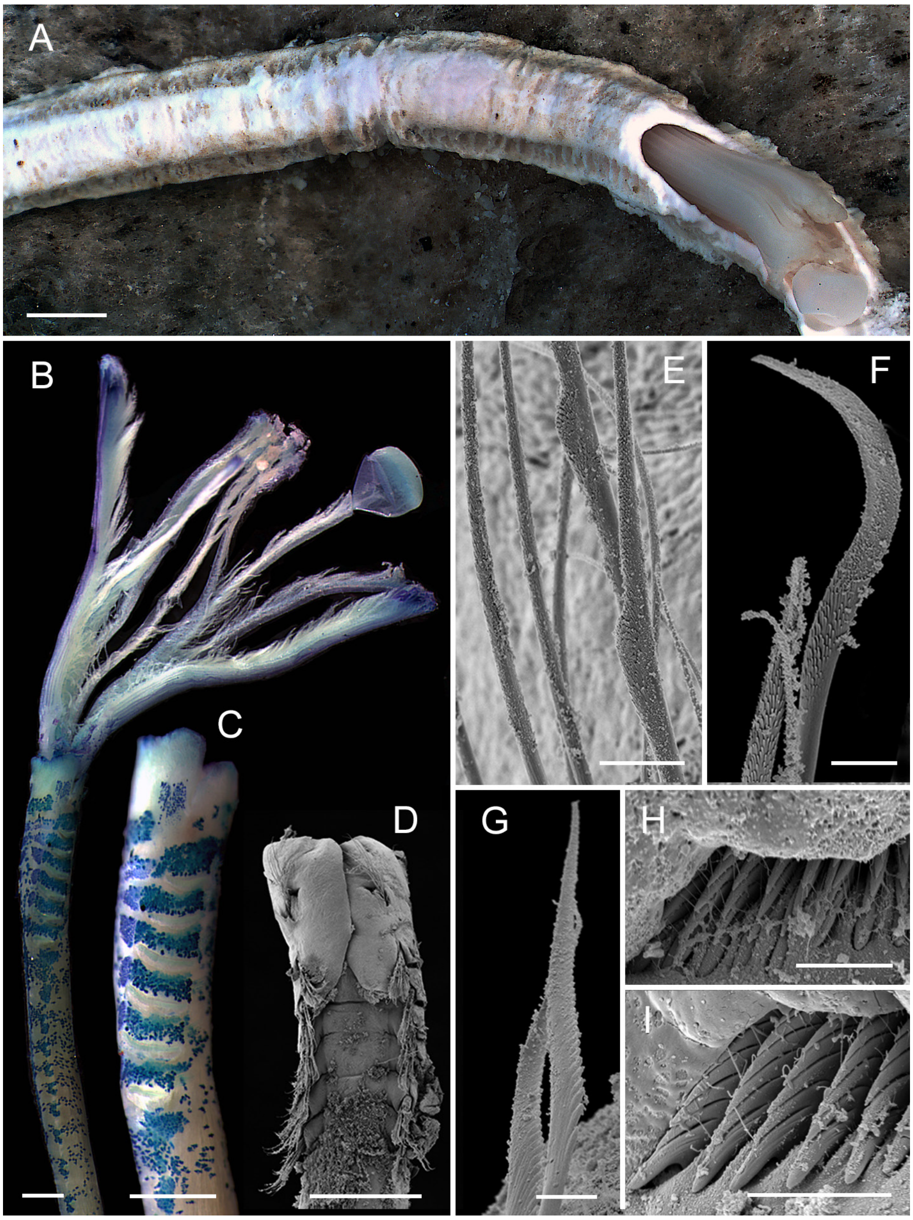

Figure 8. *Protis melmackenzieae* n. sp. A – photos of holotype W.54485 with globular operculum in tube; B – holotype removed from tube and stained with methyl blue, C – close-up view of lateral thorax. SEM of paratype W.53456, D – dorsal view of thorax showing length of thoracic membranes, E – special collar chaetae, F – *Apomatus* chaeta, G – abdominal chaetae, H – thoracic uncini, I – anterior abdominal uncini. Scale: A, B, C, D – 0.5 mm; E – 20 µm; F, G, H, I – 10 µm.

Description. Tube: pink, although tube colour ranging from nearly white, only slightly pinkish to distinctly pink (Fig. 7A–F), entirely opaque, circular in cross section, attached to substrate throughout its length (Fig. 7A–F). Tube surface rough (not smooth), with growth ridges and occasional narrow peristomes; with attachment area narrowly wider than tube width.

Radioles: each lobe bearing 8–10 radioles arranged pectinately, not connected by inter-radiolar membrane (Fig. 8B). Radiolar eyes and distinct long terminal pinnules absent.

Operculum: if present, a membranous transparent globular vesicle with slightly differentiated distal endplate (Fig. 8A, B) on a normally pinnulated left 2nd radiole. Pseudoperculum absent.

Collar and thoracic membranes: collar with entire edge, short, barely covering radiolar lobes. Trilobed, medio-ventral lobe slightly higher and wider than lateral lobes (Fig. 8B, C); collar continuous with short thoracic membranes ending as rounded flaps at 3rd thoracic segment, no apron (Fig. 8D). Pairs of small, wart-like protuberances of collar chaetiger absent; tonguelets between ventral and lateral collar parts absent.

Thorax: with collar chaetiger and 6 uncinigerous chaetigers (Fig. 8B, C). Collar chaetae limbate and fin-and-blade, distal blade not separated from proximal dentate zone (Fig. 8E). Subsequent chaetae limbate, of two sizes. *Apomatus* chaetae present in posterior thoracic segments (Fig. 8F). Uncini along entire thorax saw-shaped, with 5–6 slightly curved teeth and simple pointed fang (Fig. 8H). Prostomial eyes not observed.

Abdomen: up to 40 abdominal chaetigers. Achaetous anterior abdominal zone absent. Anterior uncini saw-shaped, with 7–8 teeth in profile and simple pointed fang (Fig. 8I), posterior rasp-shaped. Abdominal chaetae flat narrow geniculate with rounded teeth and tapered tip (Fig. 8G). Long capillary chaetae of posterior chaetigers not observed. Posterior glandular pad present.

Size: total body length up to 14 mm, including up to 4.0 mm long radioles, 3.2 mm long thorax 6.8 mm long abdomen, width of thorax 0.6 mm. In holotype external diameter of tube mouth 1.2 mm, corresponding lumen diameter 1.0 mm.

Species diagnosis. The new species is clearly different from the rest of the genus *Protis* due to the distinctly pinkish tube. This is one of the first newly described species (along with *H. perneti* n. sp.) of the genus in which a detailed illustrated description is accompanied by the molecular sequence data from the type series.

Etymology. The species is named after Melanie Mackenzie, collection manager at Museums Victoria, Melbourne, Australia.

Distribution. Only known from seamounts off Christmas and Cocos (Keeling) Islands, Indian Ocean, 1113–3839 m.

Protis perneti n. sp.

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Fig. 9A–G

Material examined. Holotype: W.53467 (LK268), Territory of Christmas Island, Apollo Seamount (11°24'45"S, 104°56'32"E), depth 1285–1350 m, 13/07/2021 (prepared for SEM).

Paratypes: W.53480 (LK254), Territory of Christmas Island, Balthazar Seamount (11°24'16"S, 104°26'25"E), depth 1237–1290 m, 16/07/2021 (1 spec.); W.53482 (LK270), same locality (1 spec.); W.54384 (LK303), Cocos (Keeling) Islands Territory (11°49'56"S, 96°37'36"E), depth 1589–1896 m, 14/10/2022 (1 spec.); W.54408 (LK300), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°16'41"S, 96°04'06"E), depth 1459–1595 m, 20/10/2022 (1 spec.).

Description. Tube: white or slightly brownish, entirely opaque, circular in cross section, attached to substrate throughout its length. Tube surface with some growth lines, but without distinct ridges and peristomes (Fig. 9a).

Radioles: each lobe bearing 8–10 radioles arranged pectinately, not connected by an inter-radiolar membrane (Fig. 9A). Radiolar eyes and distinct long terminal pinnules absent.

Operculum: absent or lost in examined specimens (Fig. 9A).

Collar and thoracic membranes: collar with entire edge, short, barely covering radiolar lobes. Trilobed, medio-ventral lobe slightly higher and wider than lateral lobes (Fig. 9B, C); collar continuous with long thoracic membranes ending as long apron (Fig. 9B, C). Pairs of small, wart-like protuberances of collar chaetiger absent; tonguelets between ventral and lateral collar parts absent.

Thorax: with collar chaetiger and 6 uncinigerous chaetigers (Fig. 9A–C). Collar chaetae limbate and fin-and-blade, distal blade well separated from proximal dentate zone (Fig. 9E). Subsequent chaetae simple limbate, of two sizes. *Apomatus* chaetae present in posterior thoracic segments (Fig. 9F). Uncini along entire thorax saw-shaped, with 5–6 slightly curved teeth and simple pointed fang (Fig. 9D). Prostomial eyes not observed.

Abdomen: up to 40 abdominal chaetigers. Achaetous anterior abdominal zone absent. Uncini rasp-shaped, with 3-4 teeth in a row, 7–8 teeth in profile and simple pointed fang (Fig. 9G). Abdominal chaetae flat narrow geniculate with rounded teeth and tapered tip (Fig. 9H). Distinct long capillary chaetae of posterior chaetigers present. Posterior glandular pad not observed.

Size: total length up to 9.4 mm, including up to 3.6 mm long radioles, 2.8 mm long thorax, 3.0 mm long abdomen, width of thorax 0.9 mm. In holotype external diameter of tube mouth 1.2 mm, corresponding lumen diameter 1.0 mm.

Diagnostic remarks. According to World Register of Marine Species (Read & Fauchald, 2024), the genus *Protis* contains seven poorly known species mainly from bathyal and abyssal locations. The taxonomy of the genus is problematic because the chaetae, uncini, and tubes are very similar and opercula, if present, are normally undifferentiated membranous vesicles. Both operculate and non-operculate species are described, however, soft vesicular opercula are easily lost. Moreover, *Protis arctica* (Hansen, 1879) and *P. polyoperculata* Kupriyanova, 1993a have been reported to contain both operculate and non-operculate specimens (Kupriyanova, 1993a; Ben-Eliahu & Fiege, 1996; Kupriyanova & Jirkov, 1997). *Protis hydrothermica* ten Hove & Zibrowius, 1986 shows two characters not known for the other species: warts between ventral and lateral collar lobes and a pair of pockets in the medio-ventral collar. *Protis akvaplani* Rzhavsky *et al*., 2013 shows very distinct characters: it has only six thoracic chaetigerous segments, short thoracic membranes ending after the 3rd thoracic chaetiger, and tube with a high longitudinal keel. *Protis melmackenzieae* n. sp. differs from all other species of the genus by very distinct pink tubes. *Protis pacifica* Moore, 1923 of Southern California (below 500 m) is recognisable because of its large size (body size up to 65 mm long). However, distinguishing *Protis simplex* Ehlers, 1887 and *P. brownii* (Pixell, 1913) from *P*. *perneti* n. sp. is not straightforward because descriptions of the former two taxa are brief and generic, lacking indications of obvious diagnostic characters. Moreover, *P. browni* from Antarctica was even suggested as a possible synonym of *P. simplex* from the bathyal off Florida (ten Hove & Kupriyanova, 2009).

There are two obvious morphological differences between *P. melmackenzieae* n. sp. and *P. perneti* n. sp. First, the thoracic membranes are short ending at chaetiger 3 in the former but are with very long apron in the latter. Second, the distal blade of special collar chaetae is not separated from proximal dentate fin in *P. melmackenzieae* n. sp. *versus* very well separated in almost bayonet-like special collar chaetae of *P. perneti* n. sp.

With this in mind, we described here *Protis perneti* n. sp. as a species distinct from both nominal *P. brownii* and *P. simplex* mostly based on geographical information. This taxonomical decision will be tested in future molecular studies of deep-sea serpulids. This is one of the first newly described species of the genus in which a detailed illustrated description is accompanied by the molecular sequence data from the type series.

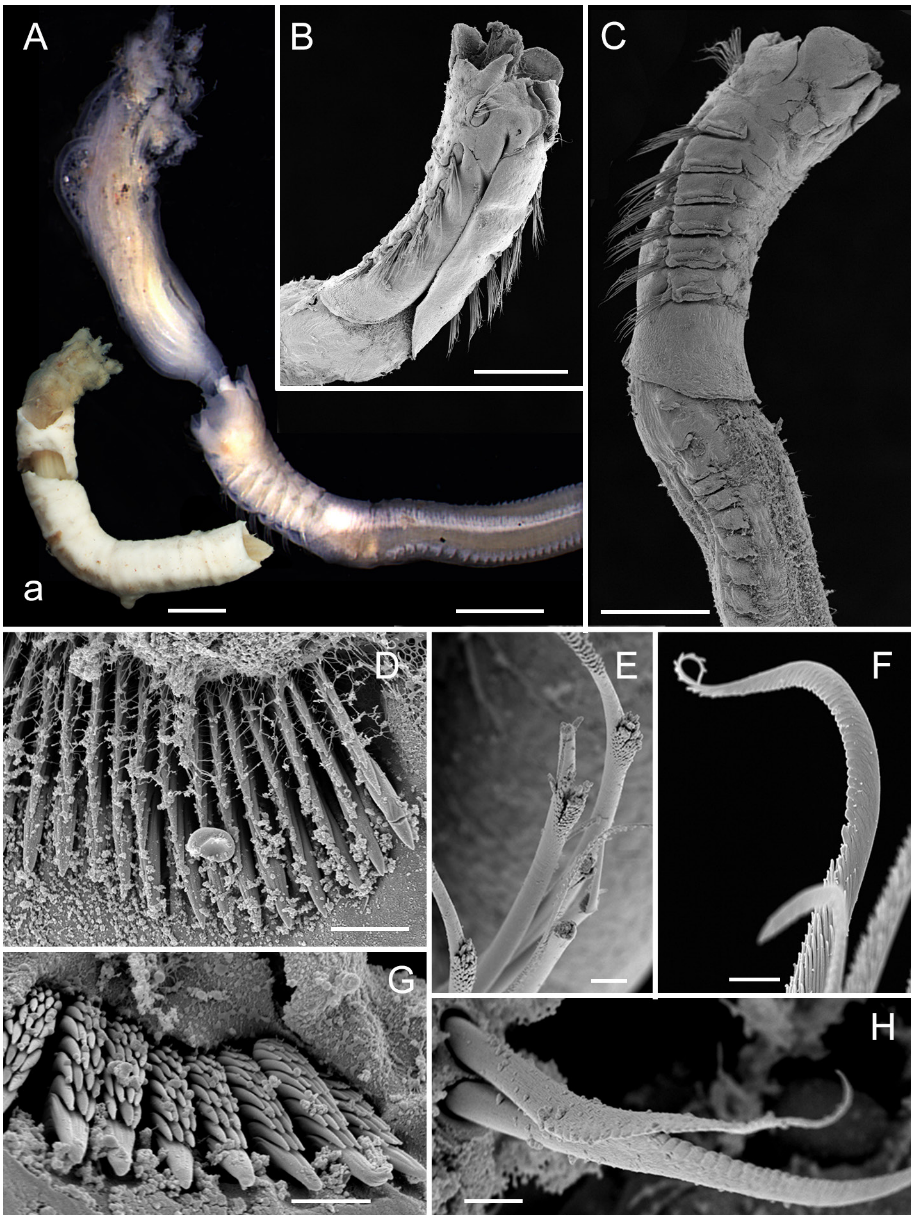

Figure 9. *Protis perneti* n. sp. W.53467, A – general view of holotype without tube, a – holotype in tube, B – dorsal view of thorax showing length of thoracic membranes, C – lateral view of thorax, thoracic uncini, D – thoracic uncini, E – special collar chaetae, F – *Apomatus* chaeta, G – posterior abdominal uncini, H – abdominal chaetae. Scale: A, a – 1 mm, B, C – 0.5 mm, D, E, F – 10 µm, G, H – 5 µm.

The results of the phylogenetic analysis (Fig. 1) suggest that one of the terminals of *P. perneti* n. sp. is more closely related to *Protis hydrothermica*. Clearly, the relationships between these taxa need to be examined in further studies when additional specimens of the former species become available.

Etymology. The species is named after Professor Bruno Pernet (California State University at Long Beach, California, USA) for his important contributions to serpulid larval ecology and evolution.

Distribution. Only known from seamounts off Christmas and Cocos (Keeling) Islands, Indian Ocean, 1237–1896 m.

Subfamily Serpulinae Rafinesque, 1815 *sensu* Kupriyanova *et al.*, 2023

Subfamily diagnosis. Tube not spirally coiled, body symmetrical; thoracic sickle (*Apomatus*) chaetae absent; abdominal chaetae either true trumpet-shaped or flat trumpet-shaped.

Tribe Ficopomatini Pillai, 1960 *sensu* Kupriyanova *et al.*, 2023

Tribe diagnosis. Tube not spirally coiled; body symmetrical; thoracic sickle (*Apomatus*) chaetae always absent; abdominal chaetae true trumpet-shaped.

Genus *Hyalopomatus* Marenzeller, 1878

Type species. *Hyalopomatus claparedii* Marenzeller, 1878

Generic diagnosis (after Kupriyanova & Ippolitov, 2015). Tube white, opaque, sometimes with external hyaline layer; (semi) circular or quadrangular with rounded edges in cross-section. 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 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 lobes 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 9 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 14 nominal species mainly from bathyal and abyssal depths (ten Hove & Kupriyanova, 2009; Kupriyanova *et al*., 2011, Kupriyanova & Ippolitov, 2015). Likely because of the deep-sea habitat, these animals are poorly known. In fact, six (*Hyalopomatus cancerum* Knight-Jones *et al*., 1997; *H. dieteri* Kupriyanova & Ippolitov, 2015; *H. langerhansi* Ehlers, 1887; *H. nigropileatus* Ehlers, 1900; *H. macintoshi* Gravier, 1911; and *H. sombrerianus* (McIntosh, 1885)) out of 14 currently valid species are known only by few specimens.

Morphologically, the species of *Hyalopomatus* are characterized by six thoracic chaetigers, short thoracic membranes, vesicular opercula on thin non-pinnulated peduncle, fin-and-blade special collar chaetae and, most importantly, uncini with very distinct flat crenulated pegs. A smooth tube with a breaking point (likely a former peristome) (as in Fig. 12A) appears to be characteristic for the genus *Hyalopomatus* as such breaks are frequently illustrated (e.g., *Hyalopomatus biformis*, *H. claparedii*, *H. madreporae*, *H. marenzelleri*, and *H. variorugosus*).

While the species of the genus are relatively easily distinguishable from representatives of other serpulid genera, the species within this genus tend to be morphologically similar to each other. The distinct species are *Hyalopomatus madreporae* Sanfilippo, 2009 and *H. cancerum* that lack opercula. Tube structure provides further characters to distinguish species within this genus: *H. dieteri* has characteristic quadrangular in cross-section tubes, tube surface of *H. variorugosus* is distinctly rugose because of characteristic minute flap-like structures, while the attached part of the *H. biformis* (Hartman, 1960) tube has a high keel (Bastida-Zavala, 2008) and tubes of *H. langerhansi* have slight lateral keels in the part attached to the substrate (Zibrowius, 1969). The remaining 8 species have simple circular in cross-section tubes with smooth surface and differ by the details of opercular morphology, length of thoracic membranes, and collar structure. See remarks to new species described below.

Kupriyanova *et al.* (2010) emended the diagnosis of the genus *Hyalopomatus* because SEM of the abdominal chaetae of *H.* cf. *mironovi* Kupriyanova, 1993c revealed that their tips have the teeth arranged in two rows, at least at the base of the chaetal tip and are not “flat narrow geniculate with pointed teeth”. Thus, the abdominal chaetae appear to be a variation of true trumpet-shaped (*sensu* ten Hove & Kupriyanova, 2009) chaetae normally characterised by two rows of denticles separated by a hollow groove and extended into a long lateral spine. The tips of abdominal chaetae in *H. biformis* are similarly not flat but are arranged into at least two irregular rows (Kupriyanova & Nishi, 2010, fig.6C), and these tips are clearly true trumpet-shaped in *H. dieteri* (Kupriyanova & Ippolitov, 2015, fig. 12H). This type of abdominal chaetae is typical for representatives of tribe Ficopomatinae, which is also supported by molecular sequence data here (Fig. 1) and in Kupriyanova *et al.* (2023).

Hyalopomatus nogueirai n. sp.

urn:lsid:zoobank.org:act:7BFB27A6-D9F1-43B1-83A9-EF16AC0B89A7

Fig. 10A–I

Material examined. Holotype: W.55296 (LK302), Cocos (Keeling) Islands Territory, Rudist Seamount (11°03'47"S, 99°26'36"E), depth 3780–3839 m, 12/10/2022 (specimen with operculum in tube).

Paratypes: W.53396 (LK252), Christmas Island SE (10°33'00"S, 105°42'11"E), depth 1225–1626 m, 06/07/2021 (1 spec.); W.55297 (LK288), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°14'32"S, 96°17'31"E), depth 932–965 m, 21/10/2022 (1 spec.); W.55295 (LK281), Christmas Island Territory, Balthazar Seamount (11°21'33"S, 104°2'53"E), depth 3510–3611 m, 7/10/2022 (1 spec.); W.54396 (LK279), Cocos (Keeling) Islands Territory, Rudist Seamount (11°03'47"S, 99°26'36"E), depth 3780–3839 m, 12/10/2022 (1 spec.); W.55300 (LK301), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°16'41"S, 96°04'06"E), depth 1459–1595 m, 20/10/2022 (1 spec. prepared for SEM); W.55293 (LK272), Cocos (Keeling) Islands Territory, Rudist Seamount (11°03'47"S, 99°26'36"E), depth 3780–3839 m, 12/10/2022 (1 spec.); W.54368 (LK291), Cocos (Keeling) Islands Territory, Rudist Seamount (11°03'47"S, 99°26'36"E), depth 3780–3839 m, 12/10/2022 (1 spec.); W.54420 (LK308), Cocos (Keeling) Islands Territory, Rudist Seamount (11°03'47"S, 99°26'36"E), depth 3780–3839 m, 12/10/2022 (1 spec.); W.54383 (LK304), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°26'12"S, 96°18'17"E), depth 3948–4047 m, 24/10/2022 (1 spec.); W.54508 (LK314), Christmas Island Territory, Attention Seamount (11°45'25"S, 103°16'49"E), depth 1401–1408 m, 9/10/2022 (1 spec. not removed from tube).

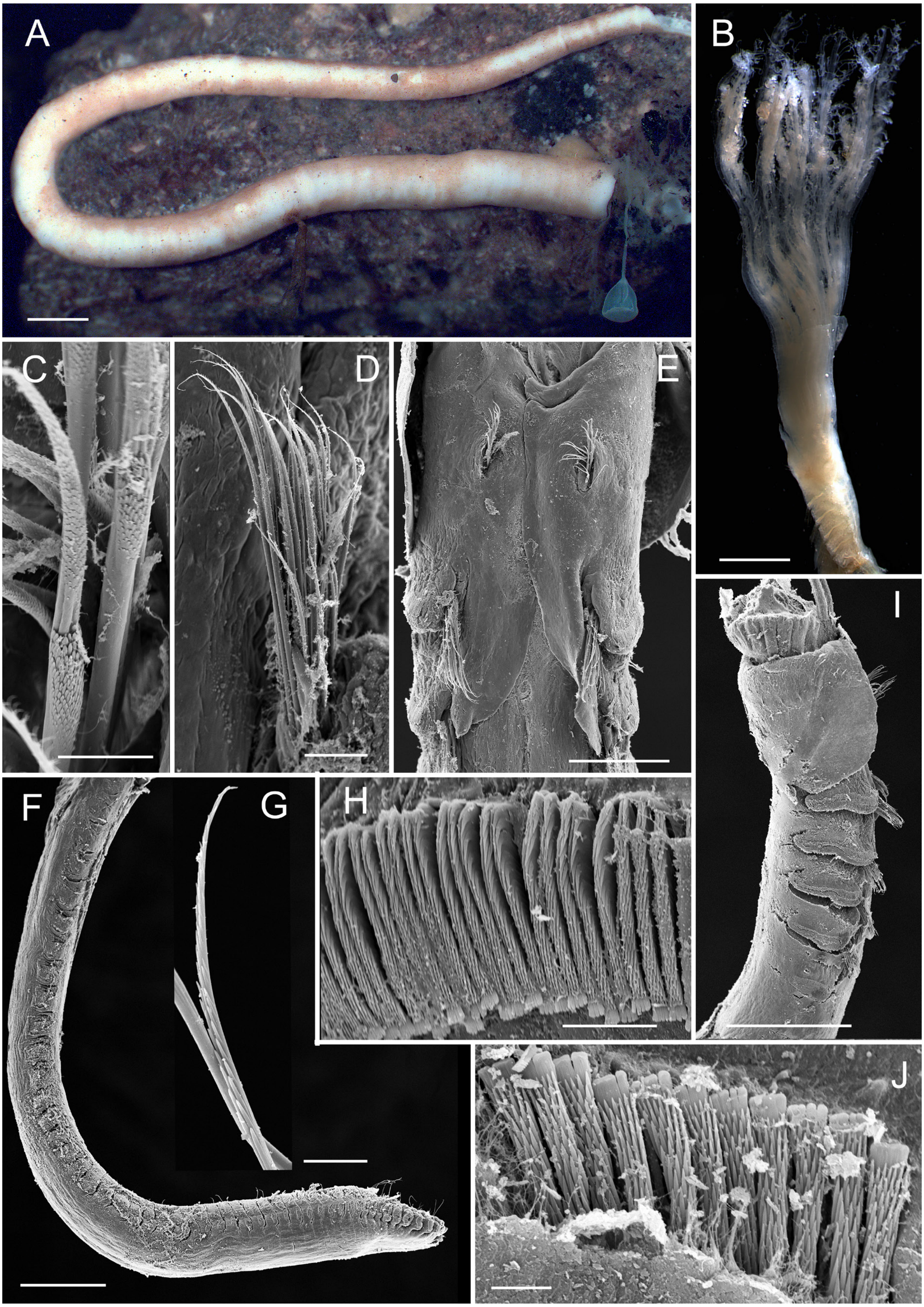

Figure 10. *Hyalopomatus nogueirai* n. sp. A – photo of the holotype W.55296 with operculum sticking out of tube. B – photos of anterior end of paratype W.55300. SEM W.54396: C – special collar chaetae, D – thoracic chaetae of 2nd chaetiger, E – thoracic membranes, F – abdomen, G – tip of an abdominal chaeta from end of abdomen, H – thoracic uncini, I – lateral view of thorax, J – abdominal uncini. Scale: A, B, F, I – 0.5 mm, D – 50 µm, E – 200 µm; C, G, H – 10 µm; J – 5 µm.

Description. Tube: white or slightly brownish opaque, with smooth surface, circular in cross-section, attached to substrate throughout its entire length (Fig. 10A).

Radiolar crown: with up to 10 pairs of radioles (Fig. 10B), arranged pectinately, easily detachable from short radiolar lobes. Inter-radiolar membrane and stylodes absent. Terminal filaments of radioles thin. Radiolar eyes and mouth palps not observed.

Peduncle: smooth, cylindrical, thin (approximately same thickness as radioles) (Fig. 10A); inserted outside radiolar crown proper, between base of 1st and 2nd radioles.

Collar and thoracic membranes: collar long, completely covering radiolar lobes and distinctly unlobed (Fig. 10B, I). Collar continuous with short thoracic membranes ending at 2nd chaetiger (Fig. 10E).

Operculum: soft membranous, semi-transparent, semi-globular, with flattened top, slightly differentiated from basal part; conspicuous constriction and additional small vesicular ampulla between operculum and peduncle present (Fig. 10A). Pseudoperculum absent.

Thorax: with 6 chaetigerous segments, 5 of which uncinigerous (Fig. 10I). Small bundle of collar chaetae (Fig. 10E) of two types: limbate and fin-and-blade with distal blade separated from basal fin by a short gap (Fig. 10C). Subsequent chaetae limbate, of two sizes, *Apomatus* chaetae absent (Fig. 10D). Uncini along entire thorax rasp-shaped, with 20–25 small teeth in profile view, with 6 teeth in row above flat anterior peg made of 3–4 rounded lobes (Fig. 10H). Pair of prostomial eyes absent. Triangular depression absent, thoracic tori almost parallel to mid-lateral line of thorax (Fig. 10B, I).

Abdomen: with up to 55 segments. Chaetae long, nearly capillary with only narrow geniculate tip made of two rows of pointed teeth (Fig. 10G). Capillary chaetae present in posterior chaetigers (Fig. 10F). Uncini rasp-shaped with over 20 teeth in profile and up to 8 rows of teeth (Fig. 10J) above anterior peg flat divided into 3–5 rounded lobes (crenulated). Achaetous anterior abdominal zone present.

Size: total body length up to 11 mm, including up to 5.9 mm long radioles, 1.2 mm long thorax, 4.2 mm long abdomen, width of thorax 0.5 mm. External tube diameter up to 0.6 mm, corresponding lumen diameter 0.5 mm.

Diagnostic remarks. *Hyalopomatus nogueirai* n. sp. has an operculum with a differentiated endcap flattened at the top and a clearly unlobed collar. A distinct character of the new species is the multilobed pegs of thoracic uncini because other species of the genus tend to have two-lobed pegs of such uncini. The multilobed pegs of thoracic uncini are also found in *H. dieteri*, the species that is distinct in having thick-walled, quadrangular in cross-section tubes. However, at least some two-lobed uncini in older literature may be due to high power microscope observations, misinterpreting the real structure of the "gouged" peg.

The multilobed thoracic uncini formally separate the new species from other congeners having globular or pear-shaped vesicular opercula without differentiated distal caps (*H. claparedii* Marenzeller, 1878*, H. langerhansi* Ehlers, 1887*,* and *H. sombrerianus* (McIntosh, 1885)). It is distinct from *H. nigropileatus* (Ehlers, 1900) having an elongate spindle-shaped operculum covered with dark violet or black distal cap with a net-like structure, and *H. sikorskii* having an operculum with distal dark cap flat on top resembling a brimless domed hat without net-like structure. *Hyalopomatus jirkovi* Kupriyanova, 1993c has elongate operculum and its collar's ventral lobe has a deep medial incision, thus making the collar four-lobed. *Hyalopomatus nogueirai* n. sp. is most similar to *H. macintoshi* (Gravier, 1911) from Antarctica and *H. mironovi* from Kuril-Kamchatka Trench as both species have globular transparent opercula, slightly flattened on top. However, both these species have tri-lobed collars, while in *H. macintoshi* tubes bear with well-developed flaring peristomes.

The phylogenetic results also show that that *H.* cf. *mironovi* from North Fiji is nested inside the *Hyalopomatus nogueirai* n. sp. clade instead of forming a clade with *H. mironovi* from Kuril-Kamchatka Trench (the type locality). This suggests that the specimen attributed to *H. mironovi* by Kupriyanova *et al.* (2010) likely belongs to *Hyalopomatus nogueirai* n. sp.

Etymology. The species is named after Professor João Miguel de Matos Nogueira (Universidade de São Paulo, Brazil) for his important contributions to serpulid systematics.

Distribution. Only known from seamounts off Christmas and Cocos (Keeling) Islands, Indian Ocean, 932–4047 m.

Hyalopomatus rossanae n. sp.

urn:lsid:zoobank.org:act:9675EECD-427B-4398-9C2C-1A123B8B9C6E

Fig. 11A–J

Material examined. Holotype: W.54369 (LK289), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°26'12"S, 96°18'17"E), depth 3948–4047 m, 24/10/2022.

Paratypes: W.53432 (LK260), Territory of Christmas Island, Karma Seamount (12°49'33"S, 107°02'48"E), depth 2860–2850 m, 11/07/2021 (1 spec.); W.53459 (LK267), Territory of Christmas Island, Clara Marie Seamount (13°34'35"S, 105°19'39"E), depth 2189–2264 m, 12/07/2021 (1 spec.); W.54374 (LK294), Cocos (Keeling) Islands Territory, Investigator Ridge Abyssal (11°15'26"S, 97°58'08"E), depth 4980–4990 m, 12/10/2022 (1 spec.); W.54378 (LK292), Cocos (Keeling) Islands Territory (12°13'32"S, 96°57'36"E), depth 1113–1343 m, 17/10/2022 (1 spec. prepared for SEM); W.54392 (LK276), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°05'33"S, 96°21'09"E), depth 2889–2923 m, 23/10/2022 (1 spec.); W.54394 (LK277), Cocos (Keeling) Islands Territory, Investigator Ridge Abyssal (11°15'26"S, 97°58'08"E), depth 4980–4990 m, 12/10/2022 (1 spec.); W.55292 (LK307), Cocos (Keeling) Islands Territory, Rudist Seamount (11°03'47"S, 99°26'36"E), depth 3780–3839 m, 12/10/2022 (1 spec.).

Description. Tube: white opaque, with shiny surface, thin-walled, circular in cross-section, attached to substrate throughout entire length, no keels, peristomes or obvious transverse ridges or growth lines (Fig. 11C, D).

Radiolar crown: with 6–7 pairs of radioles, 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, approximately same thickness as normal radioles (Fig. 11B), inserted outside

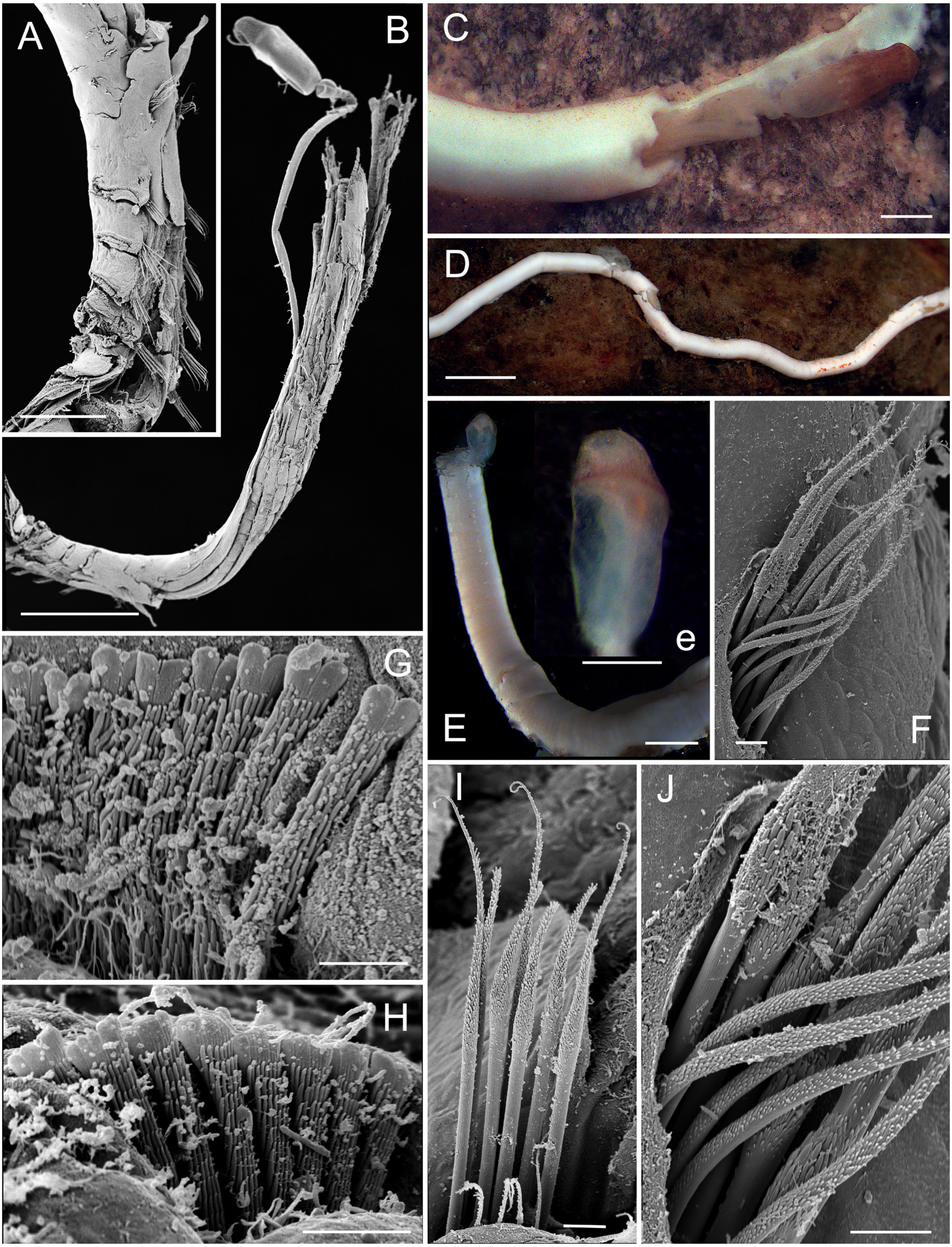

Figure 11. *Hyalopomatus rossanae* n. sp. SEM, W.54378, A–lateral view of anterior end, B–close-up view of thorax showing length of thoracic membranes. Photo, C – holotype, operculum in tube W.54369; D – tube W.54392; E – operculum in tube W.54378, e – close-up view of an operculum W.54378. SEM, W.54378, F – bundle of collar chaetae, G – thoracic uncini, H – abdominal uncini, I – thoracic chaetae, J – close-up view of special collar chaetae. Scale: A, C – 0.2 mm; B – 0.5 mm; D – 1 mm; E – 0.3 mm; e – 0.2 mm; G, H – 5 µm; F, I, J – 10 µm.

radiolar crown, between base of 1st and 2nd radioles.

Collar and thoracic membranes: collar long covering radiolar lobes, trilobed, with ventral lobe at least twice as long as lateral ones (Fig. 11B). Collar continuous with short rounded thoracic membranes ending at 2nd chaetiger (Fig. 11A, B).

Operculum: soft membranous, semi-transparent, elongated with convex brown cap, distinctly differentiated from basal part; conspicuous constriction and additional small vesicular ampulla between operculum and peduncle (Fig. 11B, C, E, e). Pseudoperculum absent.

Thorax: with 6 chaetigerous segments, 5 of which uncinigerous (Fig. 11A, B). Small bundle of collar chaetae of two types: simple limbate and fin-and-blade with distal blade separated from basal fin by a short gap (Fig. 11F, J). Subsequent chaetae limbate, of two sizes, *Apomatus* chaetae absent (Fig. 11I). Uncini along entire thorax rasp-shaped, with 20–25 small teeth in profile view, with 6–8 teeth in row above flat peg made of two rounded lobes (Fig. 11G). Pair of prostomial eyes absent. Triangular depression absent, thoracic tori almost parallel to mid-lateral line of thorax.

Abdomen: with up to 40 segments. Abdominal chaetae not observed, likely absent. Uncini rasp-shaped with over 20 teeth in profile and up to 9 rows of teeth (Fig. 11H) above anterior peg flat divided into 3–4 rounded lobes (crenulated). Achaetous anterior abdominal zone long.

Size: total body length up to 7.0 mm, including up to 3.0 mm long radioles, up to 1.0 mm long thorax, 3.0 mm long abdomen, width of thorax up to 0.2 mm. External tube diameter in holotype 0.3 mm, corresponding lumen diameter 0.25 mm.

Diagnostic remarks. The tiny new species is most similar to *Hyalopomatus nigropileatus*, *H. jirkovi* Kupriyanova, 1993c, and *H. sikorskii* Kupriyanova, 1993c by having an elongate operculum covered with a darker distal cap. *Hyalopomatus rossanae* n. sp. differs from *H. nigropileatus* that is distinct in having dark violet or black cap with a net-like structure. The new species differs from *H. sikorskii* (having operculum with a distal dark cap flat on top) by having a trilobed collar with very long ventral lobe, whereas *H. sikorskii* has short collar with lobes of equal length. Finally, although both *Hyalopomatus rossanae* n. sp. and *H. jirkovi* have the collar with the ventral lobe much longer than the lateral ones, the ventral lobe of collar in *H. jirkovi* has a deep medial incision, thus making the collar four-lobed.

The molecular results here supported monophyly of the genus *Hyalopomatus* and placement of *Hyalopomatus rossanae* n. sp. in this genus.

Etymology. The species is named in honour Professor Rossana Sanfilippo (University of Catania, Italy), an expert on systematics and palaeoecology of Serpulidae and other tube-dwelling polychaetes.

Distribution. Only known from seamounts off Christmas and Cocos (Keeling) Islands, Indian Ocean, 1113–4990 m.

Hyalopomatus suelindsayae n. sp.

urn:lsid:zoobank.org:act:414F6723-28BD-4EA0-9989-C6C4F93128F5

Fig. 12A–F

Material examined. Holotype: W.54438 (LK278); Cocos (Keeling) Islands Territory, Cocos (Keeling) (12°1'10"S, 96°50'11"E), depth 754–890 m, 16/10/2022. Paratype: W.54366 (LK285), same as above (1 spec. prepared for SEM).

Description. Tube: white opaque, with shiny surface, straight, thin-walled, brittle, circular in cross-section, keels and peristomes absent, distinct breaks present (Fig. 12A).

Radiolar crown: with 7 pairs of radioles in holotype, 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) (Fig. 12A, a).

Collar and thoracic membranes: collar long, covering radiolar lobes, trilobed, with ventral lobe distinctly higher than lateral ones. Collar continuous with short thoracic membranes ending at 3rd chaetiger.

Operculum: soft membranous, semi-transparent, distinctly globular, no distal cap; conspicuous constriction and additional small vesicular ampulla between operculum and peduncle absent (Fig. 12A). Pseudoperculum absent.

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

Abdomen: with up to 35 segments. Chaetae long, nearly capillary with only narrow geniculate tip made of two rows of pointed teeth (Fig. 12F). Capillary chaetae present in posterior chaetigers. Uncini rasp-shaped with over 20 teeth in profile and up to 9 rows of teeth (Fig. 12E) above anterior peg flat divided into 3–5 rounded lobes (crenulated). Achaetous anterior abdominal zone absent.

Size: total body length up to 7.0 mm, including up to 1.4 mm long radioles, 1.2 mm long thorax, 4.4 mm abdomen, width of thorax up to 0.3 mm. External tube diameter in holotype 0.4 mm, corresponding lumen diameter 0.35 mm.

Diagnostic remarks. The new species is characterised by its distinctly globular operculum lacking any differentiated distal cap and its straight tube with smooth shiny surface, attached only by the posterior part to substrate. Other similar *Hyalopomatus* spp. having opercula without differentiated distal caps are *H. claparedii* Marenzeller, 1878 from the Arctic Ocean and *H. mironovi* Kupriyanova, 1993c from the Kuril-Kamchatka Trench in the North-West Pacific Ocean. *Hyalopomatus suelindsayae* n. sp. having a globular operculum differs from *H. claparedii* and *H. mironovi* that have pear-shaped opercula. *Hyalopomatus mironovi* also has tubes with slight transverse ridges and special collar chaetae with a distinct large fin well separated from the distal blade.

The new species also appears to be morphologically different from the poorly known taxa *H. sombrerianus* and *H. langerhansi,* both from West Atlantic Ocean. *Hyalopomatus sombrerianus*, originally described as *Serpula sombreriana* McIntosh, 1885, was based on a single dry non-operculate

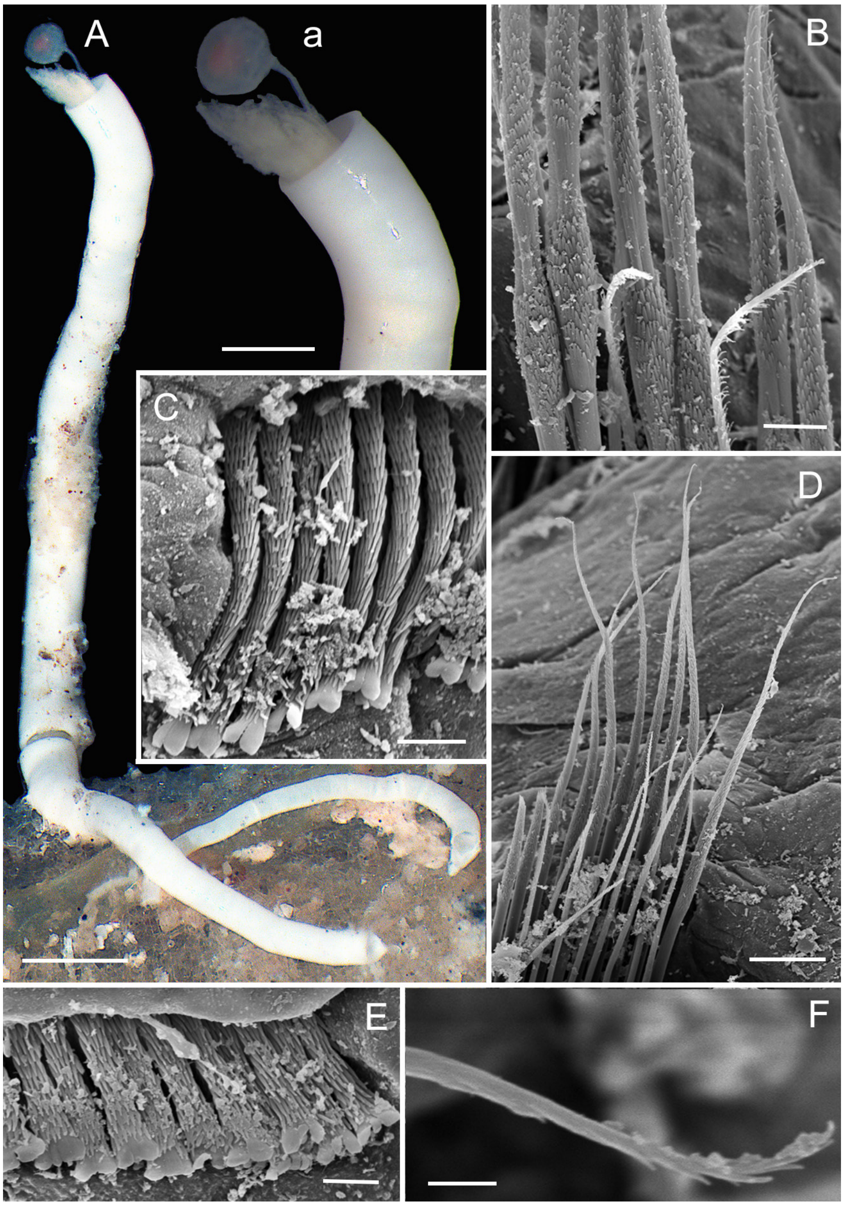

Figure 12. *Hyalopomatus suelindsayae* n. sp. W.54438. A – holotype in tube, a – close-up view of the same animal. Paratype SEM W.54366. B – special collar chaetae, C – thoracic uncini, D – thoracic chaetae, E – abdominal uncini, F – tip of abdominal chaeta. Scale: A– 0.5 mm; a – 0.2 mm; B, C, E – 5 µm; D – 20 µm; F– 2 µm.

specimen 12 mm long, dredged off Sombrero, St. Thomas, the Caribbean Sea, in 859–713 m. The taxon was transferred to *Hyalopomatus* by ten Hove in Ben-Eliahu and Fiege (1996). The type examined by ten Hove proved to be a mutilated specimen with broken chaetae (*fide* Ben-Eliahu & Fiege, 1996). The status of this species is uncertain, both Ben-Eliahu and Fiege (1996) and ten Hove and Kupriyanova (2009) suggested that the species is probably includes *H. langerhansi.* The description of the latter species was based on two finds collected by the "*Blake*" expedition (1868), northwest of Cuba (near Havana in 535 m, and 23°42'N 83°19'W, in 1572 m) (*fide* Zibrowius, 1969). According to Hartman (1938), the type material is badly damaged. The specimens have tubes with a sub-quadrangular section in its attached part, having two slight keels, which is a potential diagnostic character. As in *H. claparedii*, the operculum of *H. langerhansi* is a transparent pear-shaped vesicle.

Molecular results of this study indicate that *H. suelindsayae* n. sp. from IOT is most closely related to an unnamed *Hyalopomatus* sp. 1 from the Jaco Summit hydrothermal seep on the Costa Rica margin and to *H. mironovi* collected from the Kuril-Kamchatka trench. The taxonomic status of *Hyalopomatus* spp. populations from these localities needs to be examined into further studies.

Etymology. The species was named to honour Sue Lindsay, formerly Australian Museum, now SEM laboratory manager at Macquarie University, Sydney for her invaluable help and support over years.

Distribution. Only known from Cocos (Keeling) Islands Territory, Indian Ocean, 754–890 m.

Genus *Placostegus* Philippi, 1844

Type species. *Placostegus tridentatus* (Fabricius, 1779)

Generic diagnosis (from ten Hove & Kupriyanova, 2009). Tube triangular in cross-section, with denticulate keels, transparent or semi-transparent, often only attached to substratum at base, collar-like rings absent. Granular overlay absent. Operculum inverse conical, with chitinous cup-shaped endplate. Peduncle cylindrical, smooth, without wings, gradually merging into operculum, at most with shallow constriction; inserted at base of radioles on one side between 1st and 2nd normal radiole and maximally covering base of first three radioles. Pseudoperculum absent. Radioles arranged in semi-circles, up to 24 per lobe; inter-radiolar membrane, radiolar eyes, and stylodes absent. Mouth palps present. Six thoracic chaetigerous segments. Collar tri- to penta-lobed, collar edge may be almost laciniate; tonguelets between ventral and lateral collar lobes present. Thoracic membranes long, forming ventral apron across anterior abdominal segments. Collar chaetae absent; collar region with girdle of reddish ocelli. *Apomatus* chaetae absent. All uncini sub-rectangular, rasp-shaped with > 20 teeth in profile, and up to 8 small teeth in a row; anterior peg wide, flat, bluntly truncate, almost rectangular. Thoracic triangular depression absent. Abdominal chaetae true trumpet-shaped, with distal hollow triangular blade, abruptly bent. Achaetous anterior abdominal zone present. Long posterior capillary chaetae may be present. Posterior glandular pad absent.

Remarks. *Placostegus* and *Vitreotubus* (see below) are the only two serpulins with an entirely vitreous tube. *Placostegus* has one evident diagnostic autapomorphy – the belt of bright red ocelli in the region where in other genera collar chaetae are found (ten Hove & Kupriyanova, 2009, fig. 1F).

Unexpectedly, despite clear morphological similarities and identifiable synapomorphies, the genus was not recovered as a monophyletic clade in this study. However, because this phylogenetic position−based on *18S* sequence data alone−contradicts monophyly of the genus *Placostegus* demonstrated in the multigene analysis of Serpulidae in Kupriyanova *et al.*, 2023, here we did not change the nomenclature until further molecular data on *Placostegus* spp. become available.

Placostegus leslieharrisae n. sp.

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Fig. 13A–E

Material examined. Holotype: W.54407 (LK311), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°10'06"S, 96°11'14"E), depth 271–311 m, 22/10/2022 (photo, DNA and SEM). Paratype: W.54410, Cocos (Keeling) Islands Territory, Muirfield Seamount (13°11'13"S, 96°08'51"E), depth 367 m, 23/10/2022 (1 empty tube).

Description. Tubes: triangular in cross section, thick-walled, nearly transparent (Fig. 13, A, a; smaller empty white tubes unidentifiable). Tube attached to substrate for most of its length, only distal-most part free, tube mouth rounded, lacking any denticles.

Radiolar crown: 22 radioles not connected by inter-radiolar membrane at base.

Peduncle: smooth cylindrical, only slightly wider than normal radioles (Fig. 13A, a, B), inserted medio-dorsally at base of radiolar lobe.

Collar and thoracic membranes: collar trilobed, long, covering radiolar lobes and proximal part of radioles. Lobes approximately of same length, dorsal lobe wider than lateral lobes. Collar margin smooth. Collar chaetae absent.

Operculum: elongated inverted cone covered with a slightly concave brown chitinous endplate (Fig. 13A, a, B). Constriction between operculum and peduncle present (Fig. 13A, a, B).

Thorax: short, compact, thoracic notopodia positioned close to each other, along mid-lateral line of thorax, triangular depression absent. Collar segment with girdle of red-pigmented ocelli (Fig. 13b). Thoracic membranes continuing to end of thorax forming short apron ventrally. Thoracic chaetae (Fig. 13C) simple limbate of two sizes, *Apomatus* chaetae absent. Thoracic uncini (Fig. 13D) rasp-shaped, with over 200 small teeth in profile view and up to 10 teeth per row, anterior peg wide with rounded edges.

Abdomen: chaetae with long shafts (Fig. 13E) and distal tips with 2–3 rows of small denticles (Fig. 13e). Chaetae of posterior abdominal segments slightly longer than more anterior ones. Abdominal uncini similar to thoracic uncini. Achaetous anterior abdominal zone present. Long posterior capillary chaetae present. Posterior glandular pad absent.

Size: total body length of holotype 16.9 mm, including up to 5.2 mm long radioles, up to 1.6 mm long thorax, 10.1 mm long abdomen, width of thorax 0.7 mm. External tube diameter in holotype 1.3 mm, corresponding lumen diameter 1.1 mm.

Diagnostic remarks. According to WoRMS (Read & Fauchald, 2024)**,** six species are currently considered valid in the genus *Placostegus*. The best known species *Placostegus tridentatus* originally described from Northern Europe is recognisable by its transparent triangular tube with keels extended into three denticles at the mouth and radially symmetrical operculum. The species has been widely reported not only from the Mediterranean and the Atlantic Ocean, but also from the Indo-West Pacific, an unlikely distribution for a shallow-water species. However, the only record from Japan was reported by Imajima (1978), who stressed that he referred his material to *P. tridentatus* only tentatively and that a revision of the genus is needed.

Placostegus assimilis McIntosh, 1885 from the Bermudas has a radially symmetrical operculum and tube with a denticulate mouth, according to the original illustration, but the tube mouth of *P. assimilis* has more than three main denticles unlike that of *P. tridentatus*. Both *Placostegus langerhansi* Marenzeller, 1893 from Madeira and *Placostegus californicus* Hartman, 1969 from California have distinctly zygomorphic (bilaterally symmetrical) opercula and tubes with tri-denticulate mouths, but apparently these species differ by the collar having seven lobes in the former and three lobes in the latter. *Placostegus crystallinus* (non-Scacchi, 1837) *sensu* Zibrowius, 1968 (likely an undescribed species) has a recognisable tube with numerous rounded transverse ridges and somewhat similar ridges in the posterior part of the tube have been reported for *Placostegus incomptus* Ehlers, 1887.

The new species is distinct from all described species

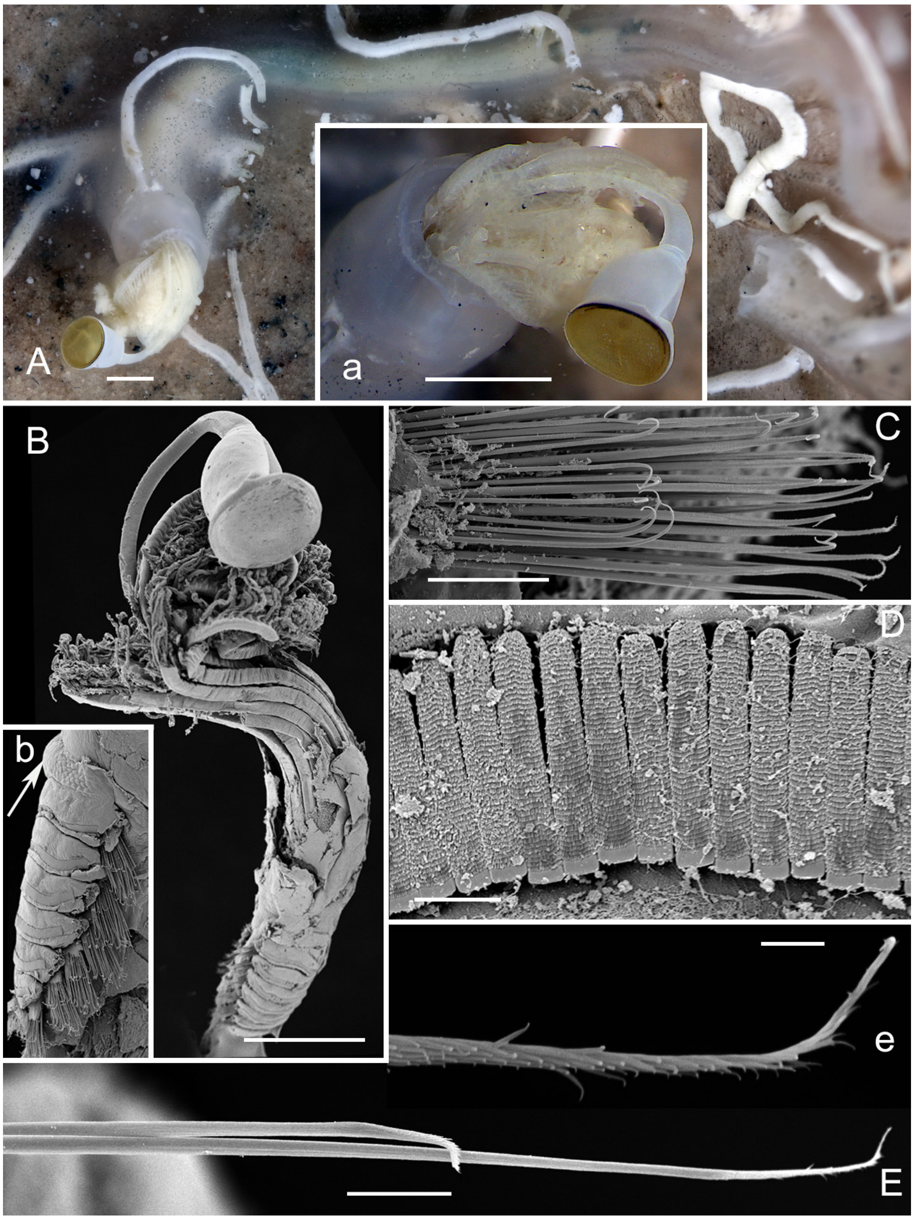

Figure 13. *Placostegus lesliehsarrisae* n. sp. W.54407, A – photo, holotype in tube, a – close-up view of anterior end of the tube showing operculum; B – SEM of anterior end of the same specimen, b – close-up view thorax showing a band of eyes (arrow), C – thoracic chaetae, D – thoracic uncini, E – long abdominal chaetae, e – close-up view the tip of abdominal chaeta. Scale: A, a, B – 1 mm; b – 100 µm; C – 50 µm; D, E – 10 µm; e – 2 µm.

of the genus because of the combination of radially symmetrical operculum and the tube with a rounded mouth lacking any denticles. In this respect the new species resembles *Placostegus* sp. from Lizard Island, Qld, Australia (Kupriyanova *et al*., 2015, fig. 14B, C). Also, abdominal chaetae in *P. lesliehsarrisae* n. sp. are similar to the abdominal chaetae found in some *Hyalopomatus* spp. (see above) in having distal tips with 2–3 rows of small denticles. The tips (Fig. 13E) are not hollow and are very different from the almost rectangular angle of the true trumpet-shaped chaetae as illustrated in ten Hove and Kupriyanova (2009, fig. 34C) for *P. tridentatus*. This is the first newly described species of the genus in which a detailed illustrated description is accompanied by the molecular sequence data from the type specimen.

Etymology. The species was named in honour of Leslie Harris (Senior Collection Manager, Natural History Museum of Los Angeles County, CA, USA) for her remarkable dedication to studies of polychaetes and her important contributions to the field of polychaete taxonomy.

Distribution. Only known from Muirfield Seamount, Cocos (Keeling) Islands, Indian Ocean, 271–367 m.

Genus *Vitreotubus* Zibrowius, 1979

Type species. *Vitreotubus digeronimoi* Zibrowius, 1979

Generic diagnosis (from ten Hove & Kupriyanova, 2009). Tube entirely vitreous, more or less quadrangular in cross-section by its two large undulating lateral keels, and with a median keel made of a row of teeth. Operculum inverse conical with chitinous diabolo-like endplate. Peduncle smooth, cylindrical, merging gradually into operculum, without wings, inserted as first radiole. Pseudoperculum absent. Arrangement of radioles short pectinate, up to 11 per lobe. Inter-radiolar membrane and stylodes absent. Radiolar eyes not observed. Mouth palps present. Seven thoracic chaetigerous segments. Collar trilobed. Medial lobe of collar with scalloped edge and lateral projections, separated from lateral lobes by deep incision (tonguelets absent), latter continuous with thoracic membranes extending all along thorax, but narrow in posterior segments, forming ventral apron. Collar chaetae *Spirobranchus*-type and simple limbate. *Apomatus* chaetae absent. Thoracic uncini saw-shaped with 6–7 teeth above pointed fang. Triangular depression present. Abdominal chaetae true trumpet-shaped, with two rows of pointed teeth bordering hollow groove and extended into a long lateral spine. Abdominal uncini saw-shaped with about 6 teeth anteriorly, rasp-shaped with about 10 teeth in profile, 3–4 teeth in a row posteriorly. Achaetous anterior abdominal zone absent. Posterior capillary chaetae absent, but geniculate chaetae long at end of abdomen. Posterior glandular pad absent.

Remarks. The monotypic genus was originally described from fossil records and Recent material collected in the bathyal zone off the Azores and in the Indian Ocean (Zibrowius, 1979), more recent records are given by ten Hove (1994).

Vitreotubus digeronimoi Zibrowius, 1979

Figs. 14A–C, 15A–E

Vitreotubus digeronimoi Zibrowius, 1979: 184, figs 1–2.

Vitreotubus digeronimoi – ten Hove 1994:113 (Seychelles,

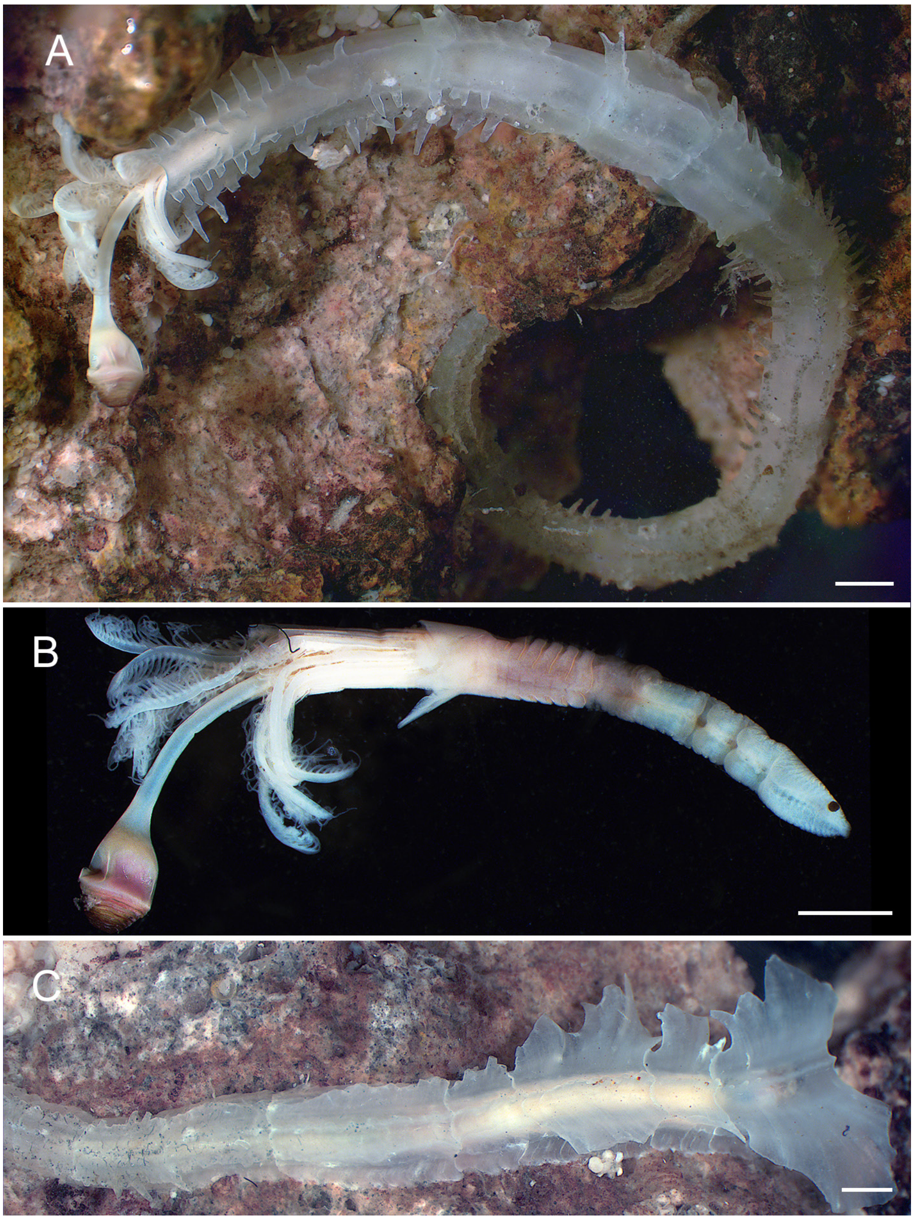

Figure 14. Photo of *Vitreotubus digeronimoi* W.54409, A – specimen in atypical tube. B – the same specimen removed from tube. W.55301, C – specimen in typical tube. Scale: A, B, C – 1 mm.

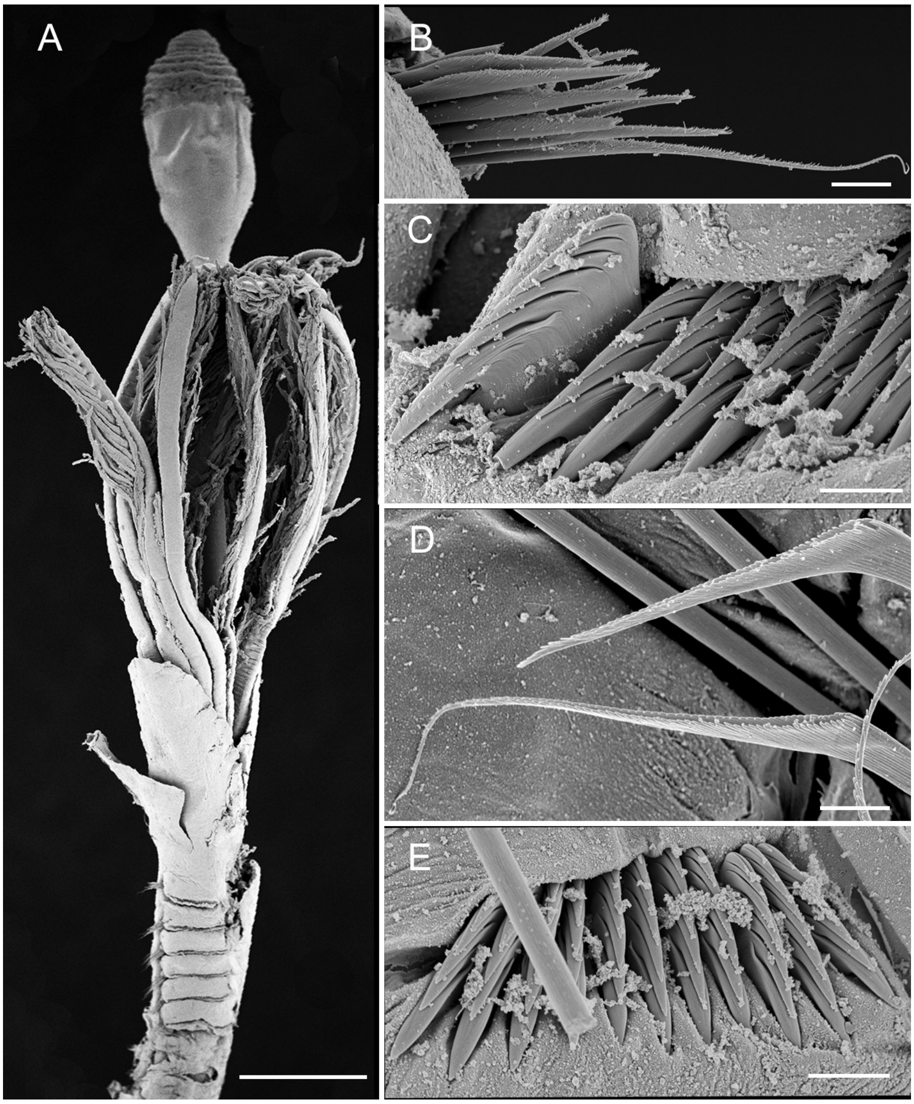

Figure 15. SEM of *Vitreotubus digeronimoi* W.55301, A – lateral view of anterior end, B – thoracic chaetae, C – thoracic uncini, D – tips of long true trumpet-shaped abdominal chaetae, E – abdominal uncini. Scale: A – 1 mm; B – 20 µm; C, D, E – 10 µm.

empty tubes only); Vinn, 2005: 262–262, fig. 5 (tube ultrastructure); ten Hove & Kupriyanova, 2009: 103–104, fig. 50 (SEM of chaetae).

Material examined: W.54402, Cocos (Keeling) Islands Territory, Muirfield Seamount (13°10'28"S, 96°14'14"E), depth 528 m, 21/10/2022 (1 tube); W.54409 (LK295), Cocos (Keeling) Islands Territory, Muirfield Seamount (13°10'28"S, 96°14'14"E), depth 528 m, 21/10/2022 (1 spec); W.55301 (LK317), same locality (1 spec. prepared for SEM).

Species diagnosis. Tube entirely vitreous (Fig. 14A, C), more or less quadrangular in cross-section, by its two large undulating (Fig. 14C) or distinctly denticulate lateral keels (Fig. 14C), and with a median keel made of a row of short teeth. Operculum inverse conical with chitinous diabolo-like endplate (Fig. 14B, 15A). Seven thoracic chaetigerous segments. Collar trilobed. (Fig. 14B, 15A). *Apomatus* chaetae absent (Fig. 15B). Thoracic uncini saw-shaped with 6–7 teeth above pointed fang (Fig. 15C). Abdominal chaetae true trumpet-shaped, with two rows of pointed teeth bordering hollow groove and extended into a long lateral spine (Fig. 15D). Abdominal uncini saw-shaped with about 6 teeth anteriorly (Fig. 15E).

Remarks. The species has a very characteristically shaped transparent tube. Not surprisingly, the irregular spherulitic prismatic tube ultrastructure of *Vitreotubus* closely resembles that of *Placostegus tridentatus*, a species with similarly transparent tube (Vinn, 2005).

Zibrowius (1979) designated the station 229/9.11.1971 of RV "*Jean Charcot*" Campagne Biaçores collected NW of Santa Maria, Azores (37°01.5'N, 25°14'W, 600 m) as the type locality of *V. digeronimoi*, but his additional material came from Northern (off Kuria Muria Islands off Oman coast) and Southern (Mayotte) Indian Ocean localities. The depth range reported for the species is 500–1415 m. Here we provide a new record from Southern Indian Ocean (Muirfield Seamount) of this poorly known, but apparently widely distributed bathyal species and, more importantly, we provide the first DNA sequence data for this species.

Distribution. Central Atlantic and Indian Ocean; bathyal (500–1415 m).

Discussion

This is the first study examining serpulid polychaetes from seamounts of the Australian Indian Ocean Territories. It demonstrated previously unknown diversity and calls for further research in this area. We reported here 12 species, including nine newly described ones. Importantly, this study also reports DNA sequence data unequivocally linked with type material for all newly described serpulid species, thus providing molecular vouchers that will significantly facilitate future comparisons in taxonomic studies. Previously such data were only available for four deep-sea species: *Apomatus voightae*, *Laminatubus joicebrooksae*, and *L. paulbrooksi* (bathyal) and *Spirodiscus ottofinamusi* (abyssal) (Kupriyanova & Nishi, 2010; Rouse & Kupriyanova 2021; Kupriyanova & Flaxman, 2023). This study also provides the first DNA sequences for the poorly known serpulid species *Bathyvermilia challengeri* and monotypic *Vitreotubus digeronimoi*.

The first formal phylogenetic analysis using DNA sequence data of Serpulidae (Kupriyanova *et al.*, 2006) significantly changed our understanding of relationships within the family. The most recent study based on a nearly comprehensive sampling of serpulid genera (Kupriyanova *et al.*, 2023) resulted in a large-scale re-classification of the family. However, though monophyly of several serpulid genera (e.g., *Spirobranchus, Galeolaria, Pseudochitinopoma, Hydroides, Laminatubus,* and *Pomatostegus*) has been confirmed, others, such as e.g., *Paraprotis*, were recovered as polyphyletic or as paraphyletic (e.g., *Semivermilia*, *Serpula*, and *Crucigera*), and monophyly of most genera still remains untested (Kupriyanova *et al.*, 2023).

Out of six non-monotypic genera (*Apomatus*, *Bathyvermilia*, *Filogranula*, *Hyalopomatus*, *Placostegus,* and *Protis*) examined in the present study, monophyly was confirmed for *Apomatus* and *Hyalopomatus*) whereas *Protis* was recovered as paraphyletic (including nominal genera *Filograna* and *Salmacina*) and other two (*Bathyvermilia* and *Placostegus*) were suggested as polyphyletic. Clearly, monophyly of most serpulid genera needs to be tested in future phylogenetic studies. We suggest that further studies of deep-sea serpulids and descriptions of new species should proceed in the context of integrative taxonomic revisions of poorly known genera typical for deep-sea habitats (such as. e.g., *Bathyditrupa*, *Bathyvermilia*, *Protis*, and *Spirodiscus*).

Importantly, the study was based mostly on *18S* sequences (mitochondrial *Cyt b* sequences were not available for many specimens, see Table 1) that are too conservative to be used for species delimitation analysis. As a result, here only phylogenetic positions of newly described species in the family Serpulidae have been assessed and their morphology-based attribution to the respective genera has been confirmed.

The sampling of the IOT seamount fauna covered a wide range of depths and recovered serpulids starting from the continental slope (270 m, *Placostegus lesliebarrisae* n. sp.) and upper and lower bathyal (500 m, *Vitreotubus digeronimoi*; 643–997 m, *Bathyvermilia rolandobastidai* n. sp.; 754–890 m, *Hyalopomatus suelindsayae* n. sp., 932–1533 m, *Apomatus nishii* n. sp.; 1237–1896 m, *Protis perneti* n. sp.) to the abyssal (nearly 5000 m, *Bathyvermilioides juliebrockae* n. gen., n. sp.) depths. However, only bathymetric data for taxa for which multiple specimens were available (*H. rossanae* n. sp.: 1113–4990 m, *H. nogueirai* n. sp.: 932–4047 m, *P. melmackenzieae* n. sp.: 1113–3839 m) are likely to be informative. For examined taxa found below approximately 1000 m these data suggest wide bathymetric distributions spanning from the lower bathyal to the abyssal zone.

In terms of geographic distribution, any conclusions about biogeographic patterns of the new species described here would be premature due to limited sampling coverage. Discovery of new species on seamounts is not surprising given that essentially seamounts are islands separated by great depths and isolation of such habitats maybe enhanced by the currents that help retain larvae near the seamount (e.g., Mullineaux & Mills, 1997). As a result, seamounts may be subject to isolating mechanisms resulting in development of highly endemic taxa and ecosystems (e.g., De Forges *et al*., 2000; Shank, 2010). On the other hand, seamounts may also provide stepping stone habitats for dispersal across ocean divides (McClain, 2007). Moreover, both hypotheses can be valid as a group of seamounts can function either as isolated islands or stepping stones for dispersal for different taxa (e.g., Miller & Gunasekera, 2017).

Endemicity of the IOT seamount serpulids cannot be hypothesised not only because of the ecological and evolutionary complexities of seamount systems, but also due to our generally insufficient knowledge of deep-sea serpulid diversity. Until this study, 37 nominal named species had published records below 1000 m and 28 of them were reported from depths below 2000 m (Capa *et al.*, 2021, table 5; Kupriyanova & Flaxman, 2023). Five of these 28 abyssal species were suggested to be endemic for the Kuril-Kamchatka Trench (Paterson *et al.* 2009). However, four of these species have been subsequently reported from numerous bathyal and abyssal localities of the Pacific Ocean (Kupriyanova *et al.*, 2011).

Of particular interest for this study are previously described *Bathyvermilia challengeri*, *Filogranula stellata*, and *Vitreotubus digeronimoi*. These taxa have been reported from both Pacific and Indian Oceans (*B. challengeri*), both Atlantic and Indian Oceans (*V. digeronimoi*) and even from the Atlantic, Indian and Pacific Oceans (*F. stellata*). These patterns suggest that at least some abyssal and bathyal serpulids found in the vicinity of seamounts have distributions spanning over several oceans as generally suggested for abyssal polychaetes (e.g., Glover *et al.*, 2001). However, it is also become increasingly clear that species delimitation within deep-sea polychaetes is problematic, if not impossible, without DNA sequence data providing information on genetic connectivity. Recent genetic studies confirmed extensive distribution ranges of some deep-sea polychaetes (e.g., Budaeva *et al.*, 2024; Guggolz *et al.*, 2020; Meißner *et al.*, 2023), especially of those associated with reducing chemosynthetic environments (Eilertsen *et al.*, 2018; Georgieva *et al.*, 2015; Rouse & Kupriyanova, 2021). Continuing collecting and morphological work coupled with DNA sequencing efforts is needed to determine whether the new species described here are endemic to seamount of IOT or have wide distributions.

In conclusion, further genetic studies are needed to test monophyly of most serpulid genera, determine bathymetric and geographic ranges of deep-sea serpulids, and to test wide distributions suggested by earlier morphology-based studies. We suggest that further international collaboration and funding for taxonomic research are essential to achieve these goals.

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