





New Species of *Melinna* (Melinnidae, Annelida) from the Australian Abyss with Comments on *M. albicincta*, *M. cristata* and *M. elisabethae*

LAETITIA M. GUNTON¹ , WILLIAM ZHANG² ,
ELENA K. KUPRIYANOVA^{1,3} , AND PAT A. HUTCHINGS^{1,3} 

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

² School of Life and Environmental Sciences,
University of Sydney NSW 2006, Australia

³ Department of Biological Sciences,
Macquarie University, North Ryde NSW 2109, Australia

ABSTRACT. A new species of *Melinna* (family Melinnidae) is described from the abyssal depths off the east coast of Australia. All material was collected during the RV *Investigator* voyage “Sampling the abyss” (IN2017_V03) in May–June 2017 from Bass Strait, Tasmania/Victoria using a beam trawl at 4197–4133 m depth. The new species *Melinna hamulus* sp. nov. differs from all other species of *Melinna* by having around 45 abdominal segments, dorsal membrane with 13–17 projections, four pairs of branchiae completely free and occurring in depths of over 4000 m. Phylogenetic relationships between our new species and other species within the family Melinnidae were assessed using the nuclear 18S and the mitochondrial 16S and cytochrome oxidase subunit I (COI) gene fragments. The results revealed that *Melinna hamulus* sp. nov. was genetically distinct from all other species of Melinnidae. This is the first species of *Melinna* to be described from Australian waters. We provide a new standard for description of species of *Melinna* and provide further detail on three existing species: *Melinna albicincta* Mackie & Pleijel, 1995, *Melinna elisabethae* McIntosh, 1914 and the type species of the genus *Melinna cristata* (Sars, 1851) using morphological characters illustrated with light and scanning electron microscopy photographs. We provide a table with the main diagnostic characters of all described species of *Melinna* together with type localities and depths.

Introduction

Traditionally, Melinninae Chamberlin, 1919 and Ampharetinae Malmgren, 1866 were treated as two subfamilies within the family Ampharetidae Malmgren, 1866 and Ebbe & Purschke (2021) who provided a brief description of the family Ampharetidae accepted these two subfamilies. However,

Stiller *et al.* (2020) undertook a phylogenetic analysis of a selected number of Terebelliformia using both molecular and morphological data. They found that the subfamily Melinninae was sister to the Terebellidae Johnston, 1846 and not closely related to other ampharetids. Thus, they raised Melinninae to a new family, Melinnidae. This new family includes all the five genera previously included in the subfamily Melinninae,

Keywords: Melinnidae; *Melinna*; deep-sea; Australia; new species

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ORCID: Gunton, 0000-0003-4758-4974; Zhang, 0000-0001-9990-6520; Kupriyanova, 0000-0003-0336-4718; Hutchings, 0000-0001-7521-3930

Corresponding author: Laetitia M. Gunton Laetitia.Gunton@AustralianMuseum

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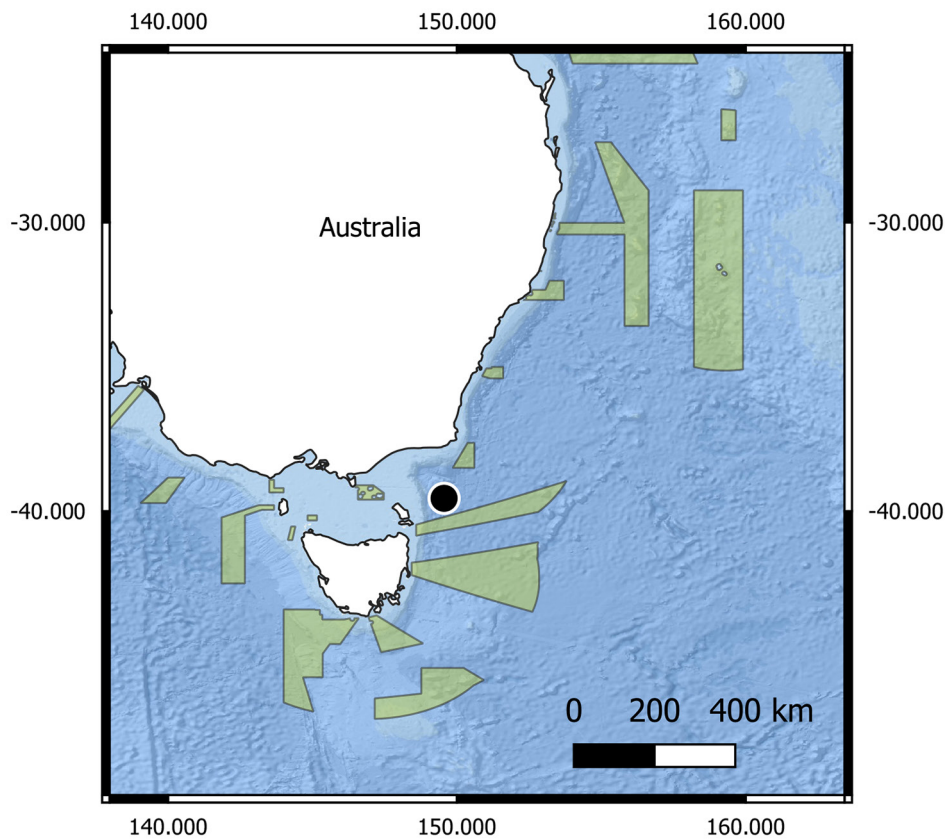


Figure 1. Map of southeastern Australia showing type locality (black dot) of the species *Melinna hamulus* sp. nov. collected during the RV *Investigator* voyage “Sampling the Abyss” (IN2017_V03), operation 030. Green polygons represent Australian Marine Parks.

although molecular data for Melinninae used in Stiller *et al.* (2020) was limited. The authors used molecular data from 41 taxa of Ampharetinae and only six taxa of Melinninae. All other genera previously classified in the Ampharetinae have been elevated to the Ampharetidae and, within this, Stiller *et al.* (2020) recognized three clades: Ampharetinae, Amaginae, and Amphicteinae, although it is unclear if these should be considered as subfamilies, given the limited numbers of species in this family sequenced.

Currently, the Melinnidae consists of the following five genera and 51 species: *Melinnopsides* Day, 1964 (1 species), *Melinantipoda* Hartman, 1967 (1 species), *Melinnopsis* McIntosh, 1885 (18 species), *Isolda* Müller, 1858 (6 species), and *Melinna* Malmgren, 1866 (25 species) (WoRMS). This number of described species as listed by WoRMS differs considerably from the number (6) which Ebby & Purschke (2021) list.

Melinna are tubicolous annelids and members of the genus share the presence of strongly recurved dorsal hooks behind their branchiae. The resemblance of these curved hooks to grappling hooks gives them their common name “grapple worms” (O’Reilly & Nowacki, 2008). Members of the genus have been recorded in very high densities, for example, in Galway Bay, Ireland animals were found in densities of around 1500 individuals/m² (Grehan *et al.*, 1991) and even 5000 individuals/m² off the Northumberland coast, UK (Buchanan, 1963; Hutchings, 1973) where they are an important food source for cod. Furthermore, their high densities make them

key sediment stabilizers of intertidal mudflats as seen in the Arcachon Bay, France (Bernard *et al.*, 2014).

Here we report one new species belonging to the genus *Melinna* from deep waters along the Australian eastern continental margin. The phylogenetic position of the new species within Melinnidae is assessed using molecular data.

Material and methods

Study area

Samples were collected during the research vessel RV *Investigator* voyage “Sampling the Abyss” (IN2017_V03) to deep-waters (900–4,800 m depth) off the east Australian coast (O’Hara, 2017) using a CSIRO 4 m wide × 0.5 m high Beam Trawl (Lewis, 2010). From 15 May to 16 June 2017 samples were taken along a south to north latitudinal transect of 18 degrees along the east coast of Australia, from 42° to 24°S (Fig. 1, showing type locality relative to the Australian coast) at target depths 2,500 m and 4,000 m. Specimens of *Melinna* were collected during operation (OPS 30) from Bass Strait, Tasmania/Victoria at 4,197–4,133 m. Onboard specimens were live sorted into higher taxa on ice in chilled (5°C) seawater, annelids were sorted to families, then fixed in either 95% ethanol or in 10% buffered formalin. At the Australian Museum Research Institute laboratory, formalin-fixed specimens were soaked in water and preserved in 80% ethanol. All material was then sorted to genera.

Morphological analysis

Comparative material of *Melinna cristata* and *M. elisabethae* was examined from the Australian Museum collections. *Melinna albicincta* was loaned from the National Museum of Wales (NMW).

The specimens were examined in ethanol using a dissecting microscope (OLYMPUS SZX7) and compound microscope (OLYMPUS BX53). Specimens were extracted from their tubes, measured (length from prostomium to pygidium), stained with methyl blue and photographed using an OLYMPUS DP74 camera attached to dissecting and compound microscopes with the imaging software OLYMPUS cellSens Standard 1.17.

One of the paratypes of *Melinna hamulus* sp. nov. and material listed in Mackie & Pleijel (1995) including a paratype of *M. albicincta* and other material of *M. cristata* and *M. elisabethae* was 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. All material of the new species is lodged at the Australian Museum, Sydney (AM); all AM registered specimens are prefixed “AM W”. Material fixed in 95% ethanol was used for molecular analysis.

DNA extraction, amplification, and sequencing

Tissue samples were taken from three specimens of *Melinna hamulus* sp. nov. (Table 1). DNA extraction was performed using a Bioline Isolate II genomic DNA kit following the manufacturer’s protocols. PCR amplification of the COI, 16S and 18S gene fragments was conducted using six sets of primers (Table 2). Polymerase chain reaction (PCR) mixtures consisted of 0.4 µl of each primer (forward and reverse), 1 µl of template DNA, 2 µl Coral Load Qiagen PCR buffer, 1.5 µl MgCl₂, 1.5 µl dNTPs, 0.1 MyTaq DNA Polymerase Bioline and 13.1 µl water, making a total volume of 20 µl. PCRs were conducted in a Thermal Cycler with the following conditions; COI: 94°C/1 min, 5 cycles 94°/40 s, 45°/40 s, 72°/60 s, followed by 35 cycles 94°/40 s, 51°/40 s, 72°/60 s, and finally 72°/5 min. 16S: 94°/3 min, 35 cycles of 94°/30 s, 50°/30 s, 72°/90 s, and finally 72°/7 min. 18S: 94°/3 min, 40 cycles of 94°/30 s, 52°/30 s, 72°/30 s and finally 72°/5 min. The quantity of PCR products was detected using gel electrophoresis 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.

Sequence analysis

Overlapping fragments were assembled into consensus sequences and edited in Geneious Prime 2019.0.4 (<https://www.geneious.com>). A BLAST analysis (Altschul *et al.*, 1990) was performed to confirm the correct region had been amplified, to compare with other sequences on GenBank, and to check for contamination. New sequences were submitted to GenBank (Table 1). Additional sequences from the family Melinnidae (10 taxa) were downloaded from GenBank (Table 1). Two species, *Polycirrus carolinensis* and *Terebella lapidaria*, were used as an outgroup.

Sequences were aligned using the Geneious plugins with the default settings: MAFFT (Katoh *et al.*, 2002) for 16S and 18S and MUSCLE (Edgar, 2004) for COI. Pairwise genetic

distances for 16S and COI were calculated for aligned sequences in Geneious. Concatenated sequences for all three genes were made in Geneious. JModelTest (Darrriba *et al.*, 2012) was used to find the best model using the Akaike information criteria. The model GTR + I + G was selected as the best model for each gene. Phylogenetic trees were constructed in IQTREE. Trees were visualized in FigTree v1.4.4 (Rambaut, 2018) and edited in Adobe Illustrator.

Molecular results

Genomic DNA was successfully amplified and sequenced from three specimens of *Melinna hamulus* sp. nov. (AM W.50732, AM W.50353 and AM W.50382). The combined data of three concatenated markers had 2918 aligned positions (COI with 654 positions, 18S rDNA with 1778 positions and 16S rDNA with 486 positions).

Maximum Likelihood analysis of combined COI, 16S and 18S sequence data formed two major clades within Melinnidae (Fig. 2). The first clade included *Melinnopsis* sp., *Melinnopsis gardelli*, *Melinnopsis chadwicki*, *Isolda pulchella*, *Melinna palmata*, *Melinna oculata* and *Melinna albicincta* and was not supported (SH-aLRT: 10.4%, UFBoot: 20%). Within this group, *Melinna albicincta*, *M. oculata* and *M. palmata* were recovered in a poorly supported clade with *Isolda pulchella* (SH-aLRT: 96.9%, UFBoot: 50%). The second major clade included *Melinna hamulus* sp. nov. with *M. cristata* and *M. heterodonta* and was also poorly supported (SH-aLRT: 91.4%, UFBoot: 94%). The sequences belonging to specimens identified as *Melinna hamulus* sp. nov. formed a strongly supported clade (SH-aLRT: 98%, UFBoot: 100%), these were recovered as sister clade to *M. cristata* and *M. heterodonta*.

Estimates of evolutionary divergence between sequences revealed the COI intraspecific pairwise genetic distances within *Melinna hamulus* sp. nov. ranged from 0.005–0.02. The closest COI sequence to *Melinna hamulus* sp. nov. was *M. heterodonta* (ranged 0.076–0.083 difference).

Taxonomy

Family Melinnidae Chamberlin, 1919

Melinninae Chamberlin, 1919: 443. Emended Day, 1964: 103–107.

Melinnidae Stiller *et al.*, 2020: 6, figs 4, 5; Rouse *et al.*, 2022: 238–241.

Diagnosis. Tubicolous. Hood like prostomium lying over the buccal region, with eye spots present or absent and nuchal organs present. Retractable buccal tentacles. Peristomium clearly demarcated from an achaetous segment. Typically, with 4 pairs of tapering conical branchiae (2–3 pairs in some species) on segments 2–5, although may appear to arise from segments 2 and 3. Neuropodia on segments 2–5 with acicular chaetae, from segment 6 neuropodia with pectinate uncini. Notopodia with capillary notochaetae from segment 4 or 5 and continuing with a variable number of thoracic segments (10–16). Variable number of abdominal segments (20–90) with only neuropodia. Often with a more or less distinct membrane across dorsum at level of segments 2–3. Postbranchial dorsal recurved hooks present or absent.

Table 1. Melinnidae taxa used in molecular phylogenetic analysis with museum voucher number, sampling location, depth, GenBank or BOLD accession numbers. Institutional abbreviations: *RUB*, Ruhr-Universität Bochum; *SIO-BIC*, Scripps Institution of Oceanography Benthic Invertebrate Collection; *ZMBN*, Department of Natural History, University Museum of Bergen; *AM*, Australian Museum. Em-dashes indicate no data available.

species	voucher	sampling location	depth (m)	GenBank or BOLD accession number			publication
				COI	16S	18S	
Melinnidae							
<i>Isolda bipinnata</i> Fauchald, 1977	SIO- BIC:A9437	Belize	—	MT166993	MT166809	MT166867	Stiller <i>et al.</i> , 2020
<i>Isolda pulchella</i> Müller, in Grube, 1858	ZMBN 105698	Morocco	35	MG270119	MG253081	MG253135	Eilertsen <i>et al.</i> , 2017
<i>Isolda pulchella</i> Müller, in Grube, 1858	ZMBN 105697	Morocco	35	MG270120	MG253082	MG253136	Eilertsen <i>et al.</i> , 2017
<i>Melinna albicincta</i> Mackie & Pleijel, 1995	SIO-BIC:A1113	Trondhejmsfjord, Norway	—	JX423767	JX423679	JX423649	Stiller <i>et al.</i> , 2013
<i>Melinna cristata</i> (M. Sars, 1851)	ZMBN 95306	Skagerrak, Norway	212	MG270118	MG253102	MG253147	Eilertsen <i>et al.</i> , 2017
<i>Melinna cristata</i> (M. Sars, 1851)	NTNU-VM 68699	Trondhejmsfjord, Norway	40	—	MG253103	MG253148	Eilertsen <i>et al.</i> , 2017
<i>Melinna cristata</i> (M. Sars, 1851)	SIO-BIC:A9438	Gullmaren, Sweden	—	GQ229117	DQ779624	MT166877	Canales-Aguirre <i>et al.</i> , 2011 (COI), Rousset <i>et al.</i> , 2007 (16S), Stiller <i>et al.</i> , 2020 (18S)
<i>Melinna heterodonta</i> (Moore, 1923)	SIO-BIC:A4546	California, USA	—	MT167004	MT166818	MT166878	Stiller <i>et al.</i> , 2020
<i>Melinna oculata</i> Hartman, 1969	SIO-BIC:A9439	California, USA	—	MT167005	MT166819	MT166879	Stiller <i>et al.</i> , 2020
<i>Melinna palmata</i> Grube, 1870	—	France	—	—	—	KJ182970	Cowart <i>et al.</i> , 2015
<i>Melinna hamulus</i> sp. nov.	AM W.50732	Bass Strait, Australia	4197–4133	OP561681	OP584503	OP584506	this study
<i>Melinna hamulus</i> sp. nov.	AM W.50353	Bass Strait, Australia	4197–4133	OP561679	OP584501	OP584504	this study
<i>Melinna hamulus</i> sp. nov.	AM W.50382	Bass Strait, Australia	4197–4133	OP561680	OP584502	OP584505	this study
<i>Melinnopsis</i> sp.	RUB Msp_01	Antarctica	2057	RUMS096-09	—	—	unpublished
<i>Melinnopsis</i> sp.	RUB Msp_09	Antarctica	2057	RUMS104-09	—	—	unpublished
<i>Melinnopsis</i> sp.	RUB Msp_27	Antarctica	2057	RUMS122-09	—	—	unpublished
<i>Melinnopsis</i> sp.	RUB Msp_28	Antarctica	2057	RUMS123-09	—	—	unpublished
<i>Melinnopsis</i> sp.	RUB Msp_29	Antarctica	2057	RUMS124-09	—	—	unpublished
<i>Melinnopsis chadwicki</i> Gunton <i>et al.</i> , 2020	AM W.50414	off Moreton Bay, Australia	1071–1138	MT556172	MT556641	MT561568	Gunton <i>et al.</i> , 2020
<i>Melinnopsis chadwicki</i> Gunton <i>et al.</i> , 2020	AM W.52949	Coral Sea Marine Park, Australia	1013–1093	MT556174	MT556643	MT561570	Gunton <i>et al.</i> , 2020
<i>Melinnopsis chadwicki</i> Gunton <i>et al.</i> , 2020	AM W.52948	Coral Sea Marine Park, Australia	1013–1093	MT556173	MT556642	MT561569	Gunton <i>et al.</i> , 2020
<i>Melinnopsis gardelli</i> Gunton <i>et al.</i> , 2020	AM W.52539	Jervis Marine Park, Australia	2650–2636	MT556177	MT556646	MT561573	Gunton <i>et al.</i> , 2020
<i>Melinnopsis gardelli</i> Gunton <i>et al.</i> , 2020	AM W.50735	Jervis Marine Park, Australia	2650–2636	MT556175	MT556644	MT561571	Gunton <i>et al.</i> , 2020
<i>Melinnopsis gardelli</i> Gunton <i>et al.</i> , 2020	AM W.51476	Freycinet Marine Park, Australia	2820–2751	MT556176	MT556645	MT561572	Gunton <i>et al.</i> , 2020
outgroup species							
<i>Polycirrus carolinensis</i> Day, 1973	SIO-BICA1101	Curlew Bank, Belize	15–17	JX423769	JX423681	JX423651	Stiller <i>et al.</i> , 2013
<i>Terebella lapidaria</i> Linnaeus, 1767	SIO-BICA1102	Plymouth, UK	low tide	JX423771	JX423683	JX423653	Stiller <i>et al.</i> , 2013

Table 2. Primers used for PCR and sequencing.

gene	primer	sequence 5'-3'	direction	reference
16S	Ann16SF	GCGGTATCCTGACCGTRCWAAGGTA	forward	Sjölin <i>et al.</i> (2005)
	16SbrH	CCGGTCTGAACTCAGATCACGT	reverse	Palumbi (1991)
18S	18e	CTGGTTGATCCTGCCAGT	forward	Hillis & Dixon (1991)
	18L	GAATTACCGCGGCTGCTGGCACC	reverse	Halanych <i>et al.</i> (1995)
	18F509	CCCCGTAATTGGAATGAGTACA	forward	Struck <i>et al.</i> (2002)
	18R	GTCCCTTCCGCAATTYCTTTAAG	reverse	Passamaneck <i>et al.</i> (2004)
	18F997	TTCGAAGACGATCAGATACCG	forward	Struck <i>et al.</i> (2002)
	18R1843	GGATCCAAGCTTGATCCTTCTGCAGGTTACCTAC	reverse	Struck <i>et al.</i> (2005)
	TimA	AMC TGG TTG ATC CTG CCA G	forward	Noren & Jondelius (1999)
	1100R2modified	CGG TAT CTG ATC GTC TTC GA	reverse	Kupriyanova <i>et al.</i> (2006)
COI	polyLCO	GAYTATWTTCAACAAATCATAAAGATATTGG	forward	Carr <i>et al.</i> (2011)
	polyHCO	TAMACTTCWGGGTGACCAAARAATCA	reverse	Carr <i>et al.</i> (2011)

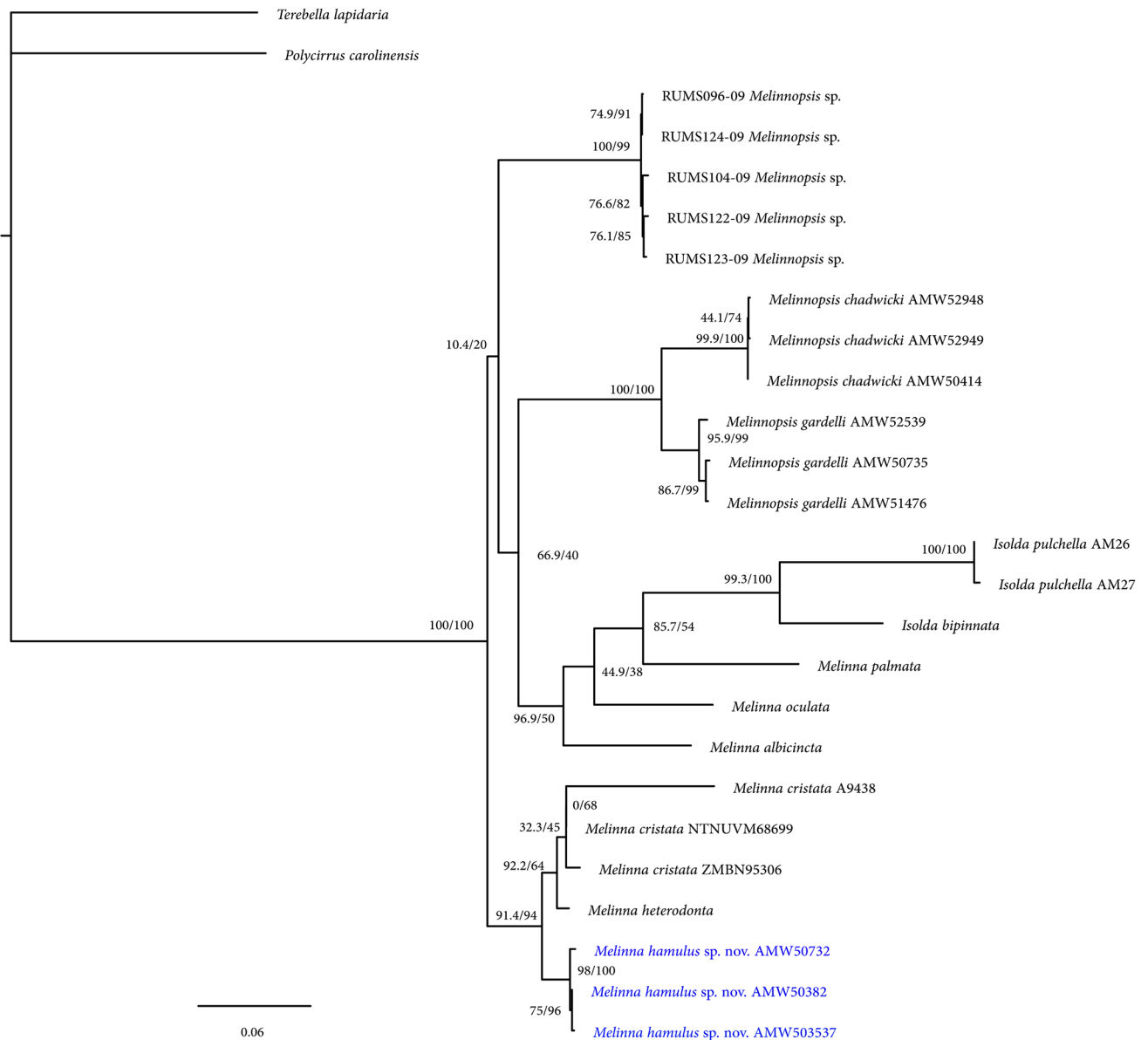


Figure 2. Phylogeny of the family Melinnidae obtained from Maximum Likelihood analysis of combined dataset of COI, 16S and 18S gene fragments in IQ-TREE. Node labels show SH-aLRT support (%) / ultrafast bootstrap support (%).

Remarks

The family Melinnidae was originally a subfamily within the family Ampharetidae Chamberlin, 1919. Day (1964) emended the diagnosis of the subfamily and provided two tables listing the characters of genera and type species in the subfamily. As Day (1964) states, many new genera have been described since Chamberlin erected the subfamily. Day (1964) emended the diagnosis to include all members that have acicular neurochaetae on segments 2–5 (Day incorrectly numbers them as present on segments 3–6) and indicated that members of this subfamily may or may not have dorsal hooks and paleae are always absent. Later, as a result of a molecular and morphological study of the Terebelliformia, Stiller *et al.* (2020) elevated this subfamily to a full family, although they did not formally provide a diagnosis of the new family. Subsequently Rouse *et al.* (2022) provided a description of the family, including morphology, physiology, natural history and systematics, but no diagnosis.

The above family diagnosis is based on Stiller *et al.* (2020) and Rouse *et al.* (2022) although there are comments in Rouse *et al.* (2022) such as “some species show unusual neurochaetae on anterior segments”, thus it is unclear if these characters are restricted to particular genera or not. Furthermore, Rouse *et al.* (2022) clearly state that all Melinnidae have straight acicular spine-like neurochaetae on 2nd to 4th or 5th segments (chaetigers 1–4) which is contradictory to the previous statement. Similarly, Rouse *et al.* (2022) suggest that notopodia can begin on segment 4, although usually they begin on segments 5 or 6 and it is unclear if this is a generic character or not. Rouse *et al.* (2022) neither indicate the segments on which the dorsal hooks occur nor the genera in which they occur. According to Holthe (1986), these hooks are present on segments 3 and 4, but Rouse *et al.* (2022) do not agree with the segmental numbering system of Holthe (1986) who did not recognize the achaetous segment 1, thus all Holthe’s numbering is one number out. We suggest that all the genera in this newly erected family need to be rechecked to clarify the above characters, but this is beyond the scope of this paper.

Melinna Malmgren, 1865

Diagnosis (after Mackie & Pleijel, 1995). Melinnidae with 4 pairs of apinnate branchiae on segments 2–5. Single pair of postbranchial dorsal hooks on segment 3. Segments 4 to 7 forming dorsal depression, posteriorly delimited by transverse membranous fold. Eighteen pairs of thoracic chaetigers, segments 2–5 with neuropodia with slender acicular chaetae, subsequent neuropodia with uncini. Notopodia from segment 4 or 5, with capillary notochaetae. Four pairs of nephridia on segments 4–7. Abdomen with variable number of neuropodia with uncini. Pygidium lobulate, anal cirri absent.

Type species *Sabellides cristata* Sars, 1851 by monotypy.

Remarks. The above diagnosis is based on Mackie & Pleijel (1995), but is modified with regards to segment number, as Rouse *et al.* (2022) state that there is an achaetous segment (segment 1) before the first chaetiger (segment 2). While the branchiae arise from segments 2–4, they appear to arise from a dorsal ridge at the level of segments 2–3, and they exhibit varying levels of basal fusion. Nephridia are on segments 4–7. With regard to the segment on which the dorsal hooks appear we do not follow Holthe (1986), instead we follow Stiller *et al.* (2020) and Rouse *et al.* (2022) to indicate that they begin on segment 3.

Earlier descriptions of *Melinna* species can be quite confusing regarding the numbering of segments and chaetigers. Most authors of previous descriptions have failed to recognize or neglected the anterior achaetous segment behind the peristomium, while the anterior notopodia are small and ventrally displaced so may have been missed. While the definition of Mackie & Pleijel (1995) indicates that notopodia begin from segment 4 or 5, we cannot find any records of species with notopodia from segment 5, and the confusion in the literature about anterior segment numbering does not help. Table 3 lists the numbering of anterior segments which will facilitate the interpretation of earlier descriptions of species of *Melinna* as many lack the presence of an anterior achaetous segment.

We have also followed more recent papers in referring to segments by numbers and not by Roman numerals. Given the confusion of some species from northern Europe, including the type species of the genus *Melinna*, *M. cristata*, we have provided expanded descriptions and figures to supplement those provided by Mackie & Pleijel (1995).

Table 3. Numbering of anterior segments in *Melinna* species.

segment number	neuropodia	notopodia	chaetiger number	branchiae
peristomium	—	—	—	—
achaetous segment 1	—	—	—	—
segment 2	present as acicular spines	—	chaetiger 1	present ^a
segment 3	present as acicular spines	—	chaetiger 2	present
segment 4	present as acicular spines	notopodia 1st very small	chaetiger 3	present
segment 5	present as acicular spines	notopodia 2nd very small	chaetiger 4	present
segment 6	present as uncini	notopodia becoming more dorsal & larger	chaetiger 5	—
segment 19	present as uncini	last notopodia	chaetiger 18	—

^a branchiae appear as on segments 2–3

Melinna hamulus sp. nov.

urn:lsid:zoobank.org:act:04B34BFC-0464-4B96-B935-EC26699040F8

Figs 1, 3–5; Tables 4, 5

Melinna cf. *armandia* Gunton *et al.*, 2021: 63, fig. 4D,d.
Non McIntosh, 1885.

Holotype. Australian Museum (AM) W.50352, IN2017_V03, OPS 030, Australia, Bass Strait between Tasmania and Victoria, Beam Trawl (start: 39°33'07"S 149°33'11"E, 4,197 m, end: 39°29'46"S 149°35'53"E, 4,133 m), 23 May 2017; specimen posteriorly complete, although body wall damaged in a few places, 45 mm in length, 4 mm max width in thorax, muddy tube present, formalin fixed. All paratypes collected from the same location as holotype. **Paratypes.** AM W.50366 (1 specimen), fixed in formalin, pale yellow lacking any pigmentation, damaged in 2 pieces, anterior end 20 mm in length, 4 mm maximum width, with 14 thoracic neuropodia, plus posterior fragment to pygidium. AM W.53257 (2 specimens) fixed in formalin, one specimen 15 mm in length, plus tube, anterior portion covered in fine mud, posterior part flimsy chitinous tube, another specimen mounted for SEM AM W.53257.001 posteriorly incomplete, 25 mm in length, 4 mm maximum width. AM W.50351 (2 specimens), fixed in formalin, anterior fragment 12 mm in length, thorax 3 mm in width, plus posterior fragment, anterior fragment 5 mm in length, plus tube fragments. AM W.50732 (1 specimen), fixed in 95% ethanol, 12 mm in length, thorax complete 4 mm max width, abdomen damaged from tissue collection for molecular analysis. AM W.53871 (1 specimen), fixed in 95% ethanol, damaged posterior thorax, max width 4 mm and anterior abdomen with posterior abdomen intact with 40 + segments, with tube. AM W.53872 (1 specimen), fixed in 95% ethanol, sequenced, anterior thorax, max width 4.5 mm, 135+ abdominal segments. AM W.50353 (1 specimen), thorax max width 4 mm plus separated abdomen, abdomen damaged from tissue collection for molecular analysis. AM W.50382 (1 specimen), fixed in 95% ethanol, posteriorly incomplete, abdomen damaged from tissue collection for molecular analysis, max width 3 mm. AM W.50354 (2 specimens), fixed in formalin, 1 specimen complete with regenerating posterior end, but mid body damaged, 30 mm in length, 3 mm max width, tube present with damaged posterior end, other incomplete, only thorax 7 mm in length, max width 3 mm. AM W.50383 (1 specimen), fixed in formalin, thorax only, 12 mm in length, 4 mm max width. AM W.53880 (1 specimen), fixed in formalin, in two pieces, anterior part 16 mm in length, max width 4 mm, plus posterior part 13 mm in length. AM W.53881 (1 specimen), fixed in formalin, posteriorly incomplete, 12 mm in length, max width of thorax 3 mm, plus tube.

Other material examined. *Melinna albicincta* (NMWZ1989-125-22, NMWZ1989-125-26); *M. cristata* (AM W.21791); *M. elisabethae* (AM.W.21793) for comparative purposes, details given for each under the expanded descriptions of each of these species.

Description

Description based on holotype with variation observed among paratypes indicated. Prostomium with well-defined anterior and posterior parts, separated by pair of transverse nuchal slits (Fig. 3F), anterior part distally trilobed, followed by achaetous segment forming a glandular collar dorsally

with smooth margin (Fig. 3B,F). Buccal tentacles almost completely withdrawn with tips exposed (Figs 3F, 4A,B). Lateral wings of anterior body between prostomium and segment 5 highly arched (Fig. 3A,B,C). First four segments glandular, subsequent seven segments with discrete ventral glandular shields (Figs 3C, 4A,C). Four pairs of smooth branchiae on segments 2–5, although appearing to arise on a dorsal ridge on segments 2 and 3, arranged two in front and two behind. Completely separated from each other. All branchia similar in both width and length, tapering to fine tips distally and having slightly swollen bases with slightly crenulated surfaces (Fig. 4F,G,I). Branchia circular in cross section. Incomplete dorsal membranous fold on segment 4 (Fig. 3B,C). Postbranchial dorsal membrane with 13 (17) triangular lobes or projections, all similar in size, except for the slightly larger middle one, some bilobed, and middle larger one with small lateral lobes at base so appearing as tricorn (Figs 3A,B, 4F,G). Pair of short dorsal curved hooks, pale yellow with darker slightly curved pointed tip, base triangular (one missing on holotype), no canal inside tooth visible (Figs 3B,b, 4H,I). Segmentation visible dorsally in postbranchial area. No visible nephridial papillae. Capillary notochaetae present in 23 thoracic chaetigers starting from segment 4. First notopodia (segment 4) very small. Following notopodia inserted more laterally (Figs 3A, 4C), becoming progressively larger and reaching maximum size by segment 8 (Fig. 3B). Subsequent notopodia (from segment 8 onwards) continuing for 15 segments. Notopodia well-developed, each bearing paired notopodial lobes and long golden capillary notochaetae (Figs 4D,E, 5D). Notochaetae arranged in two tiers of capillary chaetae (Figs 4D,E, 5D). Abdominal notochaetae lacking. Small, rounded projections evident in notopodial positions, no cilia observed (Fig. 3D). Neurochaetae as an elongated row of simple acicular short spines on slightly raised glandular ridge and inserted progressively more dorsally from segment 2–5 (Fig. 3A,B). Neuropodia with pectinate uncini from segment 6, present in 21 pairs of thoracic uncinigers (to end of abdomen, segment 26). Numbers of pairs of abdominal neuropodia 45, based on AM W.53257. Abdominal neuropodia elongate and basally swollen, without any rudimentary notopodia (Fig. 5E,G). Thoracic uncini from segment 6 with 30 uncini within a row. Abdominal neuropodia with 31 uncini in torus. Dentition of uncini within a row varies slightly (Fig. 5F,H). Thoracic uncini avicular with two teeth in a vertical row over rostral tooth, sub-rostral process and basal prow (Figs 3G, 5A,B,C). Side of uncini with marked ornamentation (Fig. 5C). Abdominal uncini with conspicuous long tendons attaching them to body and visible through body wall. Uncini arranged on elevated neuropodia in curved row (Fig. 5E,G). Uncini with four to six teeth (Fig. 5F,H). Posterior segments compacted, none of the paratypes complete. Pygidium with two lateral lobes and 4–5 smaller lobes surrounding them (Fig. 3H). No anal cirri present.

Tube. Composed of fine-grained sediment and lined with a thin, stiff clear membrane. Length of tube at least 2 times specimen (Fig. 3E).

Methyl blue staining pattern. Use of methyl blue staining reveals strong staining of the prostomium and segments 1–4, branchiae lightly speckled at tips and transverse rings at bases. Stained band behind dorsal membrane from segments 5–6. Light staining elsewhere on thorax and on abdomen. Light staining on ventral shields, staining stronger laterally on shields.

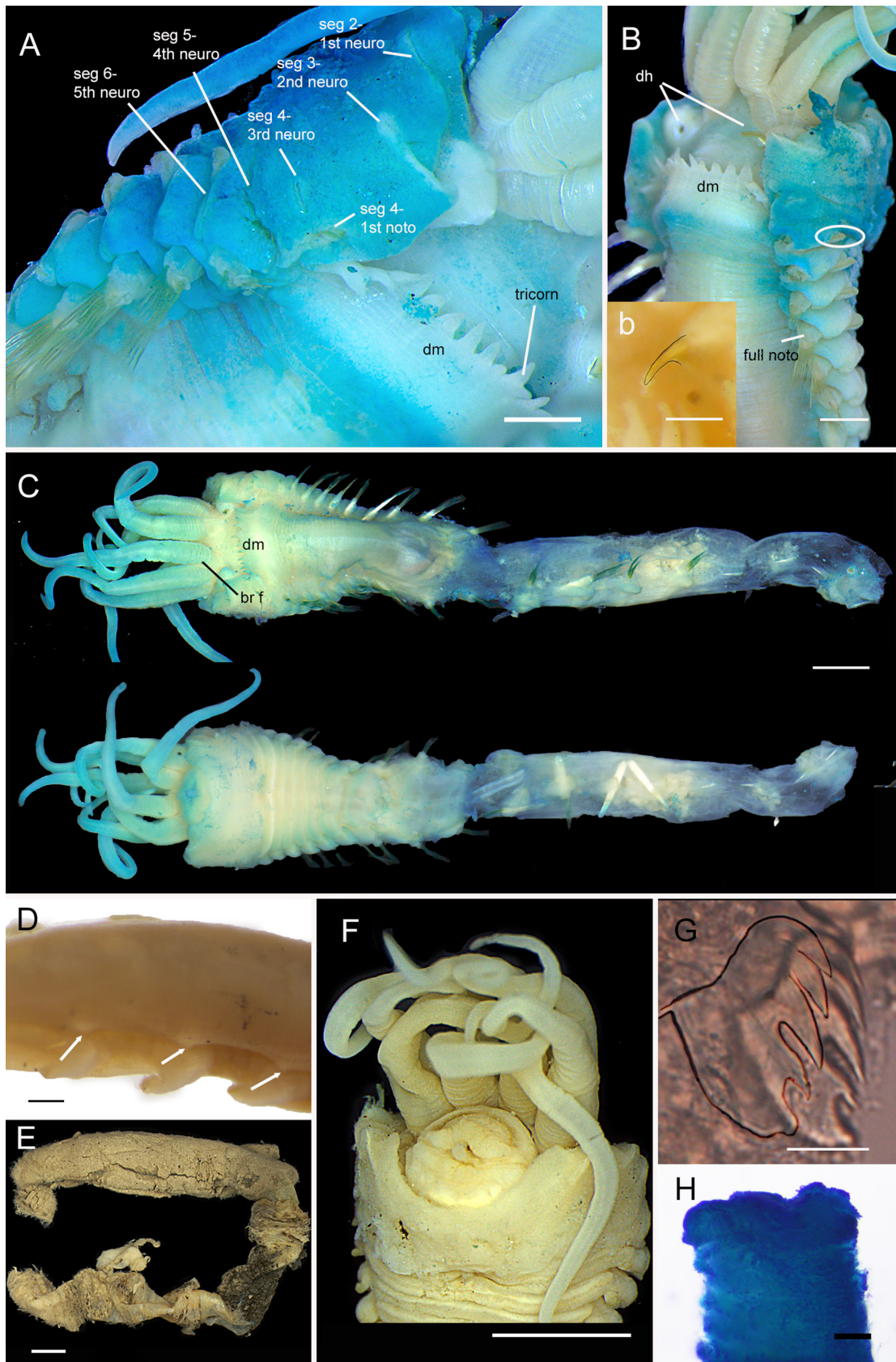


Figure 3. Light microscopy images of *Melinna hamulus* sp. nov. (A) AM W.50366, dorsal view of anterior end showing positions of first neuro- and notochoetae, in specimen stained with methyl blue. (B) AM W.50366, dorsal view of anterior end stained with methyl blue. Ellipsoid shows raised thoracic neuropodia. (b) AM W.53880, dorsal hook outlined to highlight shape. (C) AM W.50366, whole specimen, upper-dorsal view stained with methyl blue, lower-ventral view stained with methyl blue. (D) AM W.53257, abdomen, arrows indicate notopodia as small rounded projections. (E) AM W.50366, tube. (F) AM W.50366, ventral view anterior. (G) AM W.53257, thoracic uncini of segment 9. (H) AM W.50366, pygidium stained with methyl blue. Scale bars: A, 500 µm; B, C, F, 1 mm; b, H, 200 µm; E, 2 mm; G, 20 µm. Abbreviations: *seg*, segment; *noto*, notochoetae; *neuro*, neurochaetae; *es*, eyespots; *bf*, branchiae completely free; *dm*, dorsal membrane; *dh*, dorsal hooks; *full noto*, fully developed notopodia.

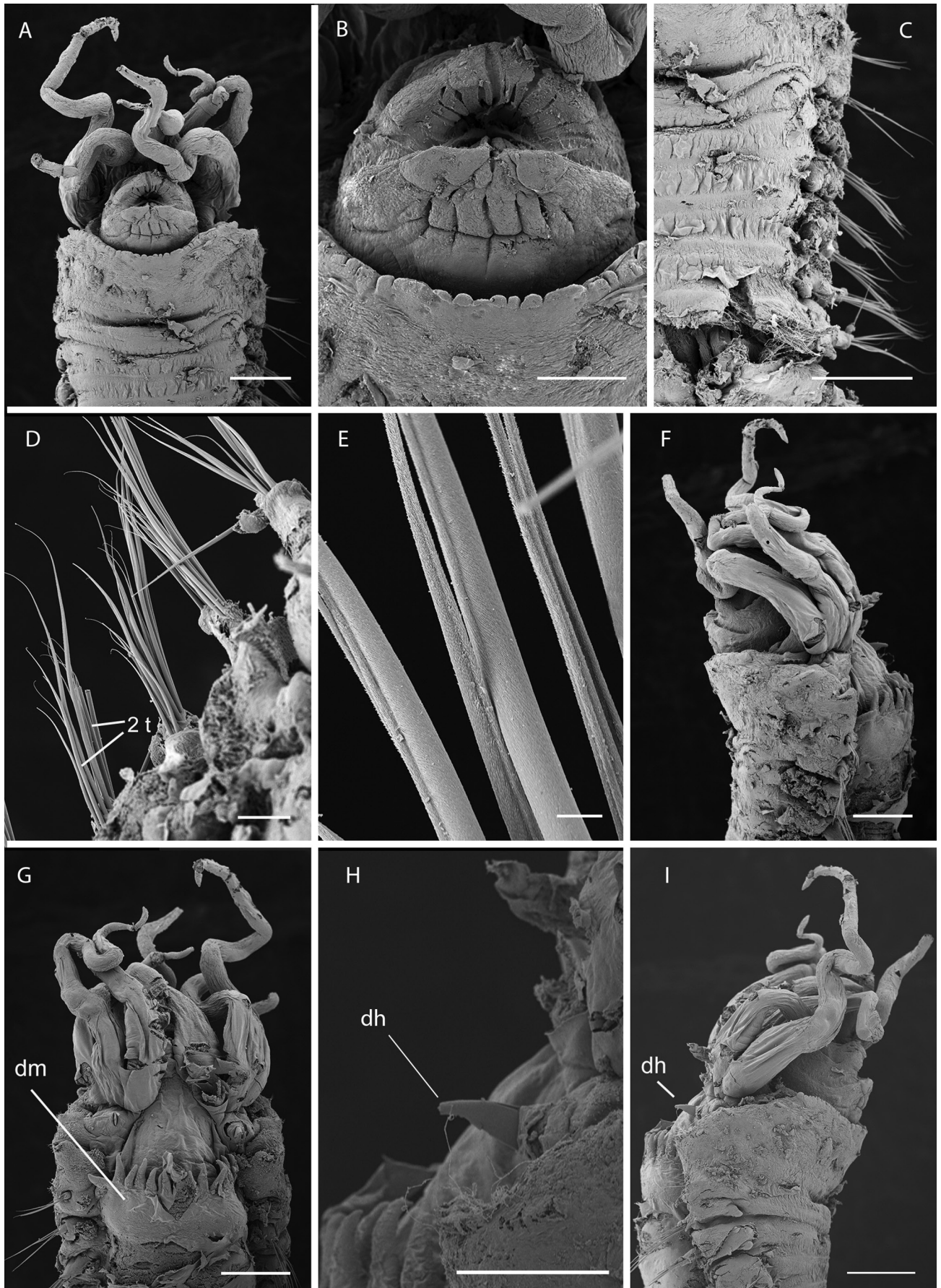


Figure 4. SEM images of *Melinna hamulus* sp. nov. (AM W.53257.001). (A) Ventral view of anterior end. (B) Ventral view of lips. (C) Lateral view of anterior notopodia. (D) Anterior notopodia. (E) Surface of notochaetae. (F) Lateral view of anterior end. (G) Dorsal view of anterior end. (H) Dorsal hook. (I) Lateral view of anterior end including dorsal hooks. Scale bars: A, C, F, G, I, 1 mm; B, H, 500 μ m; D, 200 μ m; E, 20 μ m. Abbreviations: *dm*, dorsal membrane; *dh*, dorsal hook; *2t*, two tiers of notochaetae.

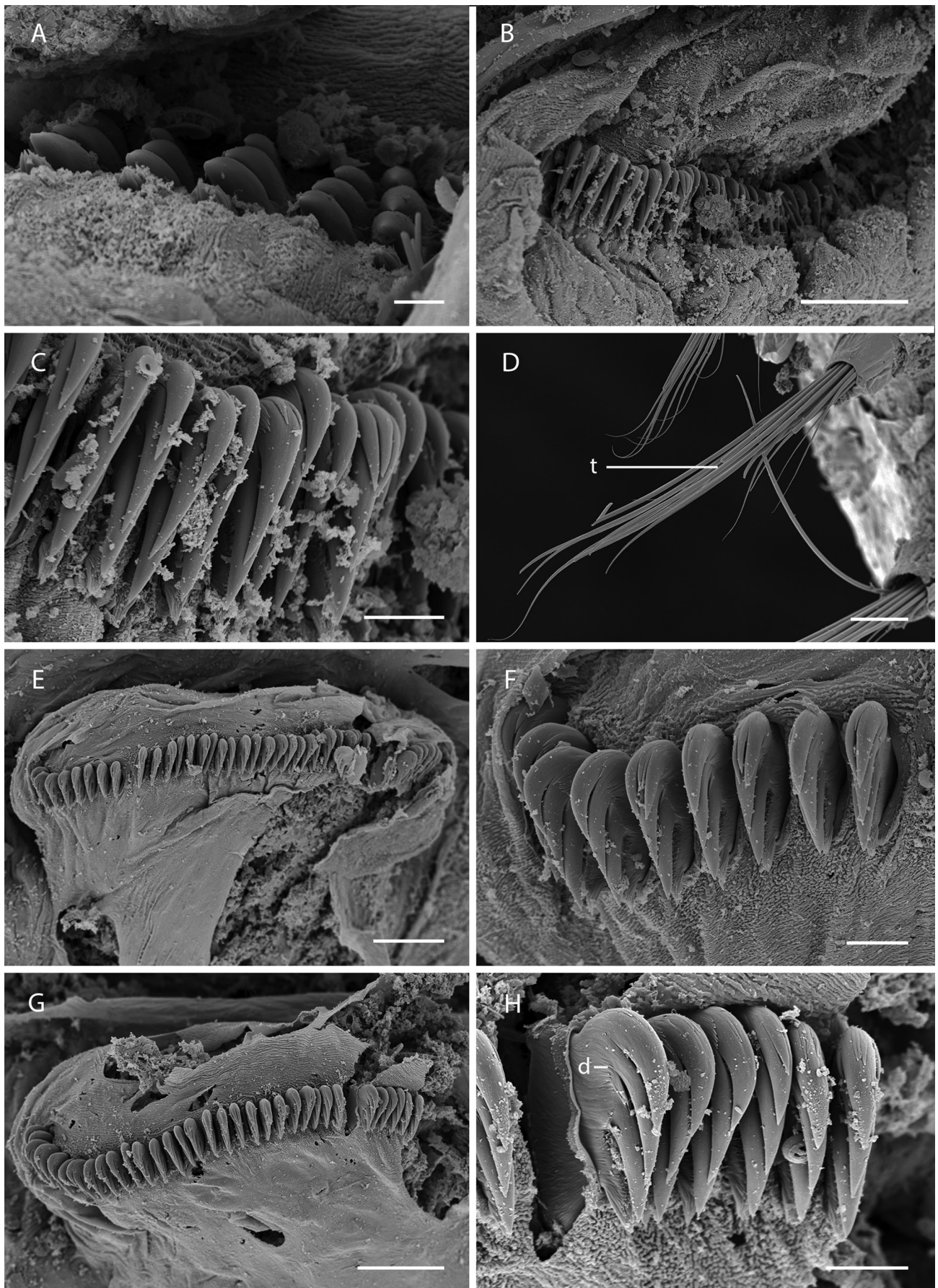


Figure 5. SEM of *Melinna hamulus* sp. nov. (AM W.53257.001). (A) Neurochaeta of chaetiger 10. (B) Neurochaetae of chaetiger 13. (C) Neurochaetae of chaetiger 13. (D) Notochaetae of chaetiger 13. (E) Anterior abdominal neurochaetae. (F) Close-up view of anterior abdominal neurochaetae. (G) Posterior abdominal neurochaetae. (H) Close-up view of posterior abdominal neurochaetae. Scale bars: A, C, F, H, 10 µm; B, 20 µm; D, 200 µm; E, G, 50 µm. Abbreviations: *d*, dentition; *t*, two tiers of notochaetae.

Remarks

Melinna hamulus sp. nov. is characterized by the following characters: around 45 abdominal segments, dorsal membrane with 13–17 triangular projections, four pairs of branchiae completely free, one pair of curved dorsal hooks with pointed tips lacking a canal, and a pygidium with two large lateral lobes surrounded by four or five smaller lobes, which distinguishes it from all other described species where the data are available (Table 5). We compare the morphological characters along with type locality and depth of our new species with the other currently accepted 26 species of *Melinna* (Tables 4, 5).

Gunton *et al.* (2021) recorded this species as *M. cf. armandi* McIntosh, 1885, which was originally described from west of North Island, New Zealand in a depth of 2,012 m. However, while having a similar number of abdominal segments, *M. armandi* has the dorsal membrane with only eight large projections, far fewer than in the new species (13–17) and the dorsal hooks have a distinct canal which is absent in *M. hamulus* sp. nov. The only other *Melinna* species recorded in the region is *M. arnaudi* Parapar & San Martín, 1997 from Livingston Island in Antarctica from 104–422 m, which has 72 abdominal chaetigers and so easily distinguished from *M. hamulus* sp. nov., which has 45 abdominal segments and occurs below 4,000 m depth.

Type locality and habitat. Bass Strait, SE Australia, 4,133–4,197 m, no sediment data was collected due to gear failure.

Etymology. The new species is named *hamulus* meaning little hook in Latin, a reference to the small dorsal hooks of this new species.

Melinna albicincta Mackie & Pleijel, 1995

Figs 6–8; Tables 4, 5

Melinna albicincta Mackie & Pleijel, 1995: 116–120, fig. 3, 5, table 1.

Material examined. Paratypes NMWZ1989-125-26, one mounted for SEM, NMWZ1989-125-22, type locality Southwest of Yttre Vattenholmen, Kosterfjord, Sweden (58°52'30"N 11°06'18"E), sand/mud/gravel, dredged from 60–80 m, coll. A.S. Mackie & F. Pleijel, 28 October 1989. AM W.21794, 1 specimen, collected same locality, same date, same collectors, sandy mud/stones/gravel, 40–50 m, dredge. In Mackie & Pleijel, 1995 this paratype is listed as AM W.21791, this is incorrect, the correct registration number for this specimen is AM W.21794.

Remarks

The original description only provided line drawings, here we give additional information based on light and SEM photographs.

Prostomium with two elongate transverse nuchal slits (Fig. 6A,B). The first segment achaetous, forming a ventral collar with an elevated crenulated anterior margin (Fig. 6D). Segments 2, 3, 4 and 5 with neurochaetae as short acicular spines with neuropodia becoming more lateral, on segment 6 elongated raised tori with neurochaetae as uncini (Figs 6D, 7B). First notopodia on segment 4, very small with short

capillary chaetae, and gradually becoming more dorsal and better developed by segment 6 with two tiers of capillary chaetae (as seen in chaetiger 11, Fig. 7C). This numbering of anterior segments differs from that given by Mackie & Pleijel (1995) as they did not recognize an achaetous segment 1 which forms a ventral glandular collar (Fig. 6D). Pair of short dorsal curved hooks (Fig. 6E, F). Four pairs of elongate branchiae ending in tapered pointed tips (Fig. 6A,D,E), with inner and anterior most pair basally fused (35–40%) (Figs 6E, 7E,F); two conspicuous white bands present on inner pairs (Fig. 6A,B) but absent on other branchiae. Segment 5 with dorsal membrane (Fig. 7E) bearing large number of small projections. Larger mid-dorsal papilla beneath dorsal membrane (Figs 6E, 7E,F), as also shown in Fig. 5A of Mackie & Pleijel (1995). Ventrums with anterior margins of segments elevated and glandular (Fig. 7A). Notopodia with elevated lobes and notochaetae arranged in two tiers (Fig. 8A,D). Anterior neuropodia forming raised tori with uncini arranged in a curved row (Fig. 7B), with four teeth in longitudinal row on chaetiger 11 and 13 (Figs 7D, 8B respectively). Rudimental notopodia on the abdomen as small rounded projections (Fig. 6C). Mid- and posterior neuropodia becoming increasingly elevated (Fig. 8A,F). Abdominal uncini with four teeth in a longitudinal row (Fig. 8B,C,E). Pygidium with terminal anus and surrounded by a pair of large lateral lobes and a number of smaller ones (Fig. 8F). Living in muddy tube with attached shell fragments (Fig. 6G).

Melinna cristata (Sars, 1851)

Figs 9–12; Tables 4, 5

Sabellides cristata M. Sars, 1851: 205–206; 1856: 19–23, pl. 2, fig. 1–7.

Melinna cristata Malmgren, 1866: 371–372, pl. 20, fig. 50. For complete synonymy see Mackie & Pleijel, 1995.

Material examined. AM W.21791, 3 specimens, including one prepared for SEM (AM W.21791.001), west of Salto, Kosterfjord, Sweden (59°00'N 11°00'E), mud, 110 m, coll. A. S. Mackie & F. Pleijel, 26 October 1989.

Remarks

The redescription by Mackie & Pleijel (1995) only provided line drawings, here we give additional information based on light and SEM photographs.

Prostomium with well-defined anterior and posterior parts followed by an achaetous segment 1 with anterior elevated margin (Fig. 9A,B). Segments 2–5 with short row of acicular neurochaetae progressively becoming more laterally inserted (Fig. 9B). From segment 6 onwards neuropodia with uncini on raised tori (Fig. 11D). Notopodia present from segment 4 (chaetiger 3), very small with few notochaetae, gradually increasing in size and becoming conspicuous and laterally arranged by segment 7 onwards (Figs 9D, 10G, 11D, 12A,B,C). Notopodia bearing two tiers of notochaetae with finely spinulose surface (Fig. 11A,B). Dorsal membrane with at least 8 equal triangular projections (Figs 10B, 11C). A single pair of slightly curved dorsal hooks with prominent internal canal (Fig. 10B,C,D,E). Four pairs of branchiae (Fig. 10A,E), annulated with distinct longitudinal bands of cilia (Fig. 10F) and fused basally for about 10% of their length (Figs 9C,D, 10A,E, 11D). Thoracic neuropodia (Fig. 11D,E)

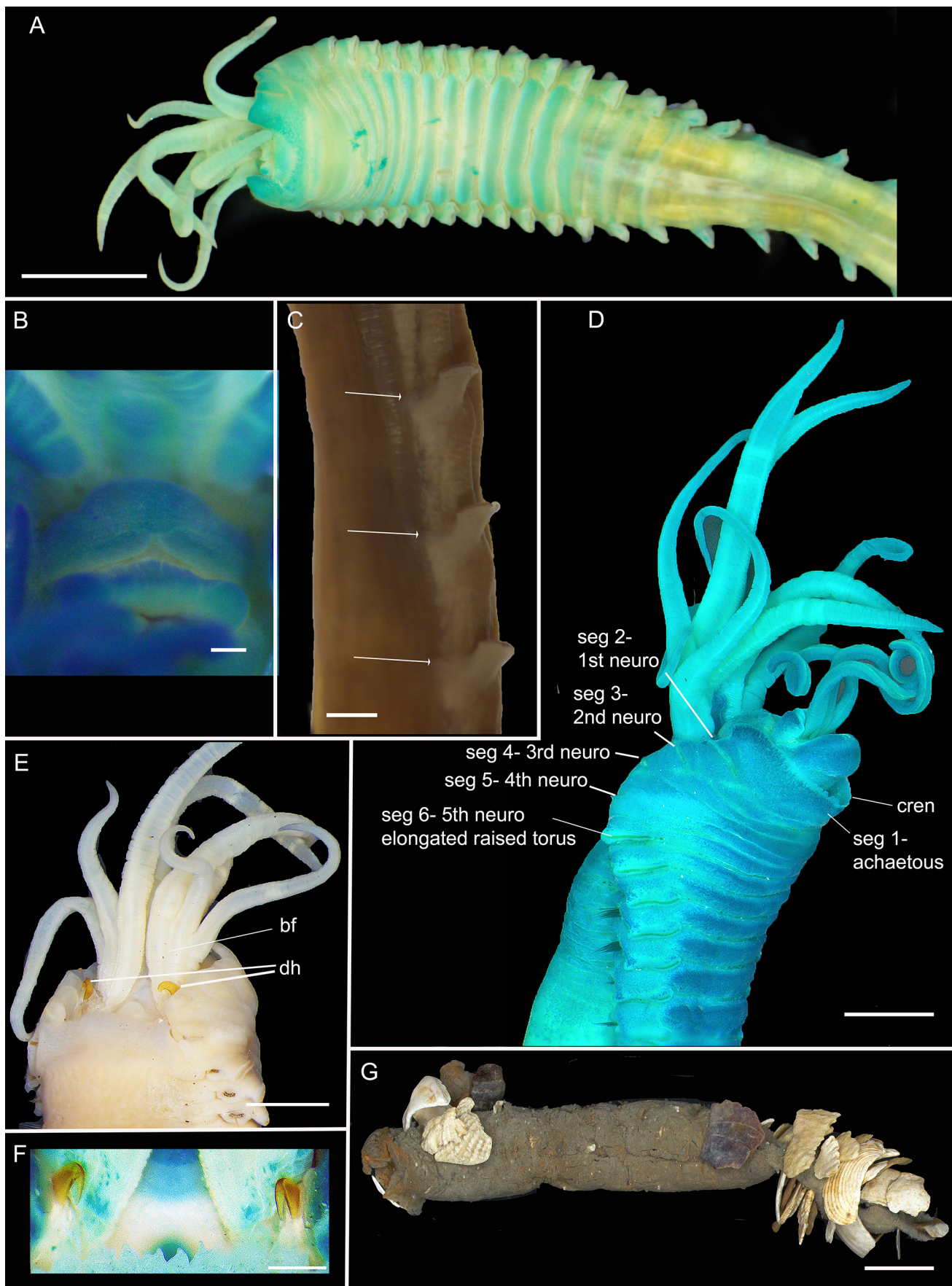


Figure 6. Light microscopy images of *Melinna albicincta* (NMWZ1989-125-26). (A) Ventral view of anterior end with methyl blue staining. (B) Dorsal view of prostomium showing transverse nuchal slits. (C) Lateral view of abdomen, arrows showing rudimental notopodia. (D) Lateral view of anterior end stained with methyl blue. (E) Dorsal view of anterior end. (F) Dorsal hooks. (G) Tube. Scale bars: A, D, E, 1 mm; B, 200 µm; C, 500 µm; F, 250 µm; G, 3 mm. Abbreviations: *seg*, segment; *neuro*, neurochaetae; *es*, eyespots; *bf*, branchial fusion; *dh*, dorsal hooks; *cren*, crenulated anterior margin.

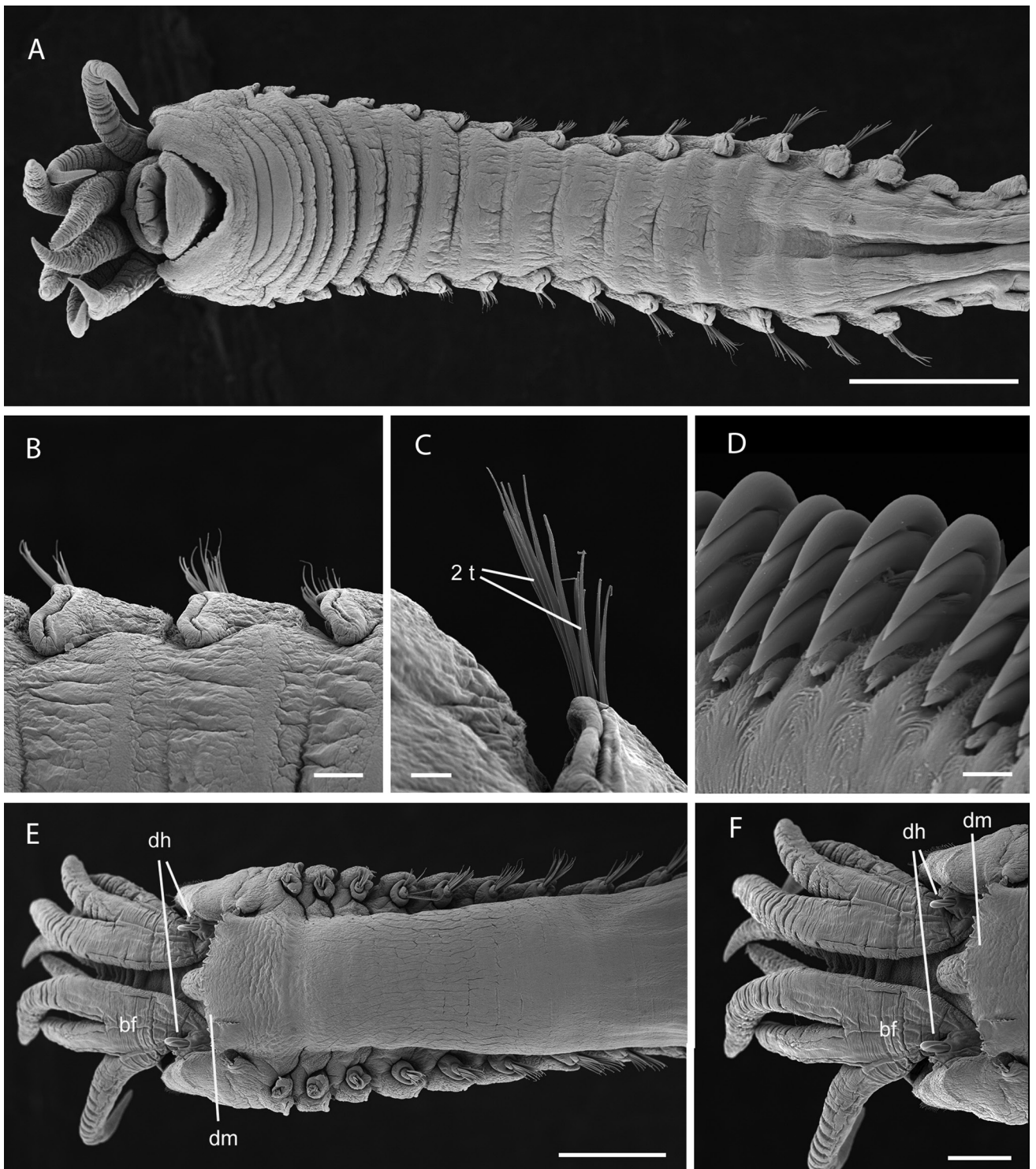


Figure 7. SEM of *Melinna albicincta* (NMWZ-1989-125-22). (A) Ventral view of anterior end. (B) Lateral view of chaetiger 6–8. (C) Notochaetae of chaetiger 11. (D) Neuropodia of chaetiger 11. (E) Dorsal view of anterior end. (F) Dorsal view of anterior end with dorsal hooks. Scale bars: A, 1 mm; B, 500 μ m; C, 200 μ m; D, F, 100 μ m; E, 10 μ m. Abbreviations: *2t*, two tiers of notochaetae; *bf*, branchial fusion; *dh*, dorsal hooks; *dm*, dorsal membrane.

raised, glandular tori with over 40 uncini, uncini with a single row of 3–4 teeth and a sub-rostral ornamented process (Fig. 11F,G). Rudimental notopodia on the abdomen as small rounded projections (Fig. 9F). Abdominal segments with elevated neuropodia decreasing in size posteriorly (Fig. 9E). Abdominal uncini with rostral tooth surrounded by strongly denticulated head (Fig. 12D,E). Pygidium with terminal

anus, bounded by glandular lobes (Figs 9E,e, 12F,G) with no anal cirri. Methyl blue staining shows extensive ventral and lateral thoracic glandular areas (Fig. 9A,E). No tube present.

This numbering of anterior segments differs from that given by Mackie & Pleijel (1995) as they did not recognize an achaetous segment 1 forming a ventral glandular collar (Fig. 11D).

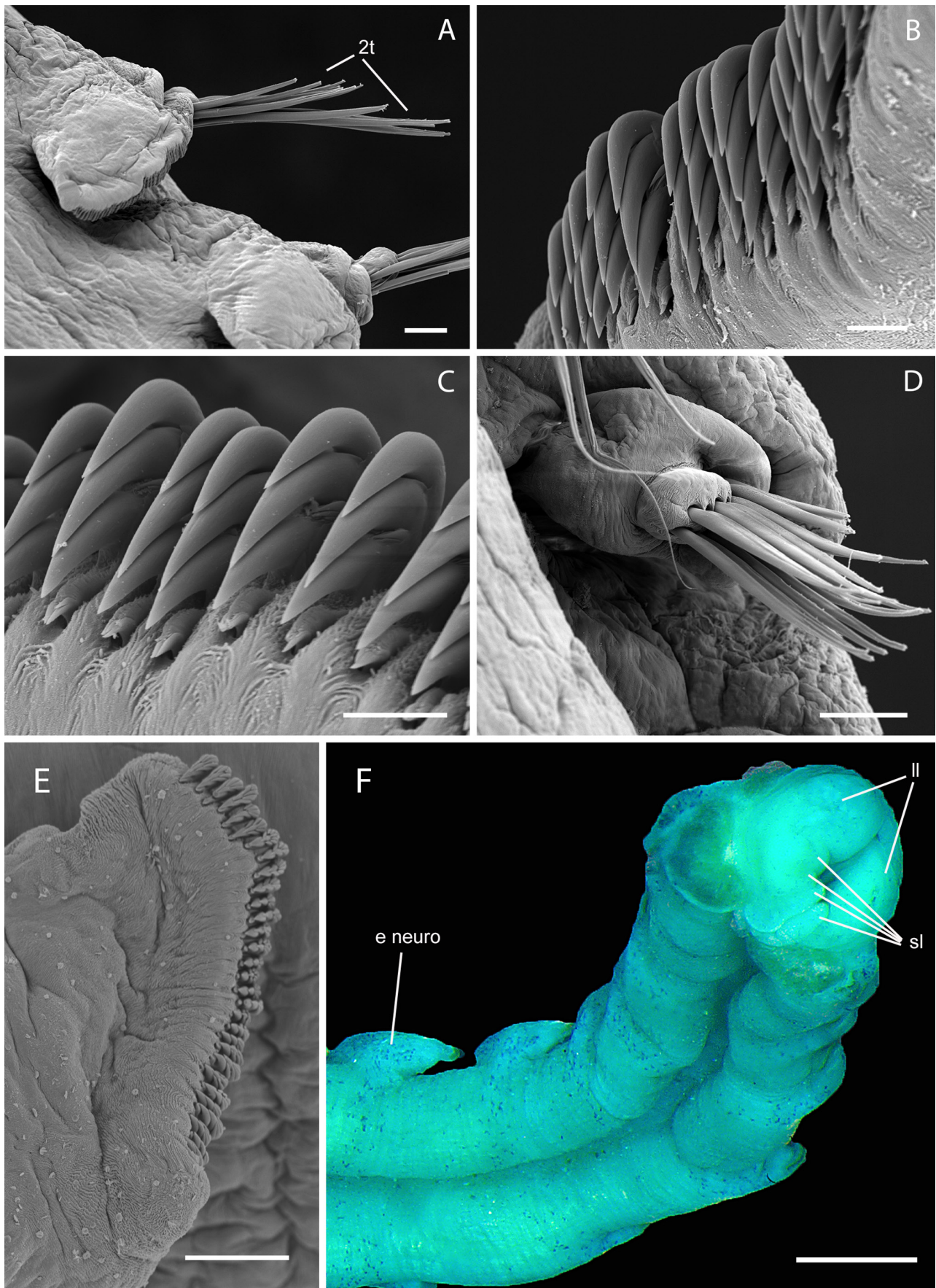


Figure 8. SEM images of *Melinna albicincta* (NMWZ-1989-125-22). (A) Notochaetae of two tiers + neurochaetae. (B) Neurochaetae of chaetiger 13. (C) Neurochaetae of chaetiger 13. (D) Base of chaetiger 6, no nephridial papillae. (E) Abdominal neuropodia. (F) (NMWZ1989-125-26), light microscopy image of pygidium and far posterior abdominal segments showing elongated neuropodia. Scale bars: A, D, 100 μm; B, C, 10 μm; E, 50 μm; F, 200 μm. Abbreviations: 2t, two tiers of notochaetae; e neuro, elongated neuropodia; ll, large lobes; sl, small lobes.

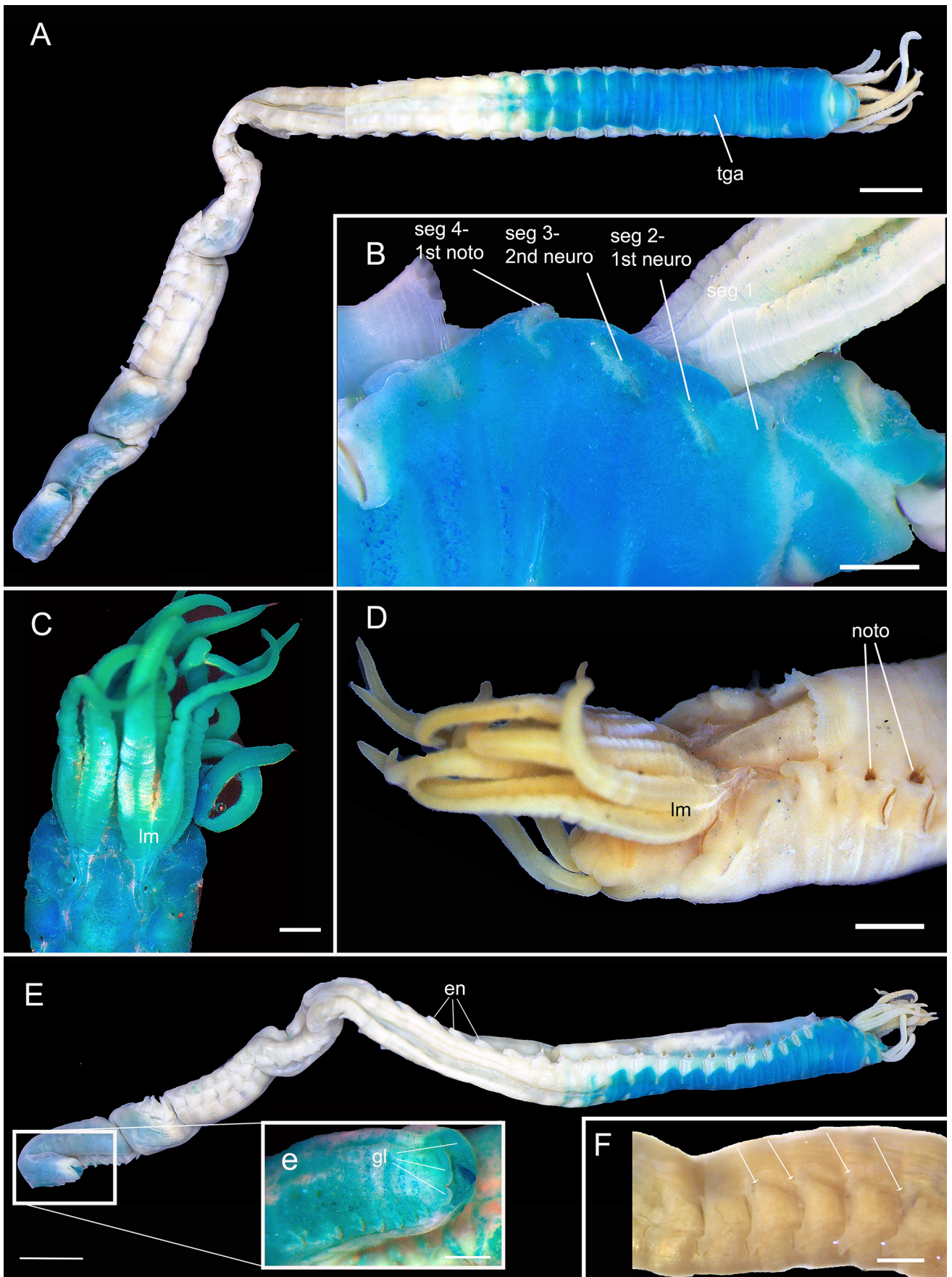


Figure 9. Light microscopy images of *Melinna cristata* (AM W.21971). (A) Ventral view, entire specimen. (B) Lateral view, anterior end. (C) Dorsal view of branchiae. (D) Lateral view of anterior end. (E) Lateral view of entire specimen. (e) Pygidium. (F) Lateral view of abdomen, arrows indicate rudimental notopodia. Scale bars: A, 2 mm; B, C, e, F, 500 μ m; D, 1 mm; E, 3 mm. Abbreviations: *tga*, thoracic glandular areas (glandular shields); *seg*, segment; *noto*, notochaetae; *neuro*, neurochaetae; *lm*, low membrane basal fusion; *en*, elevated neuropodia; *gl*, glandular lobes.

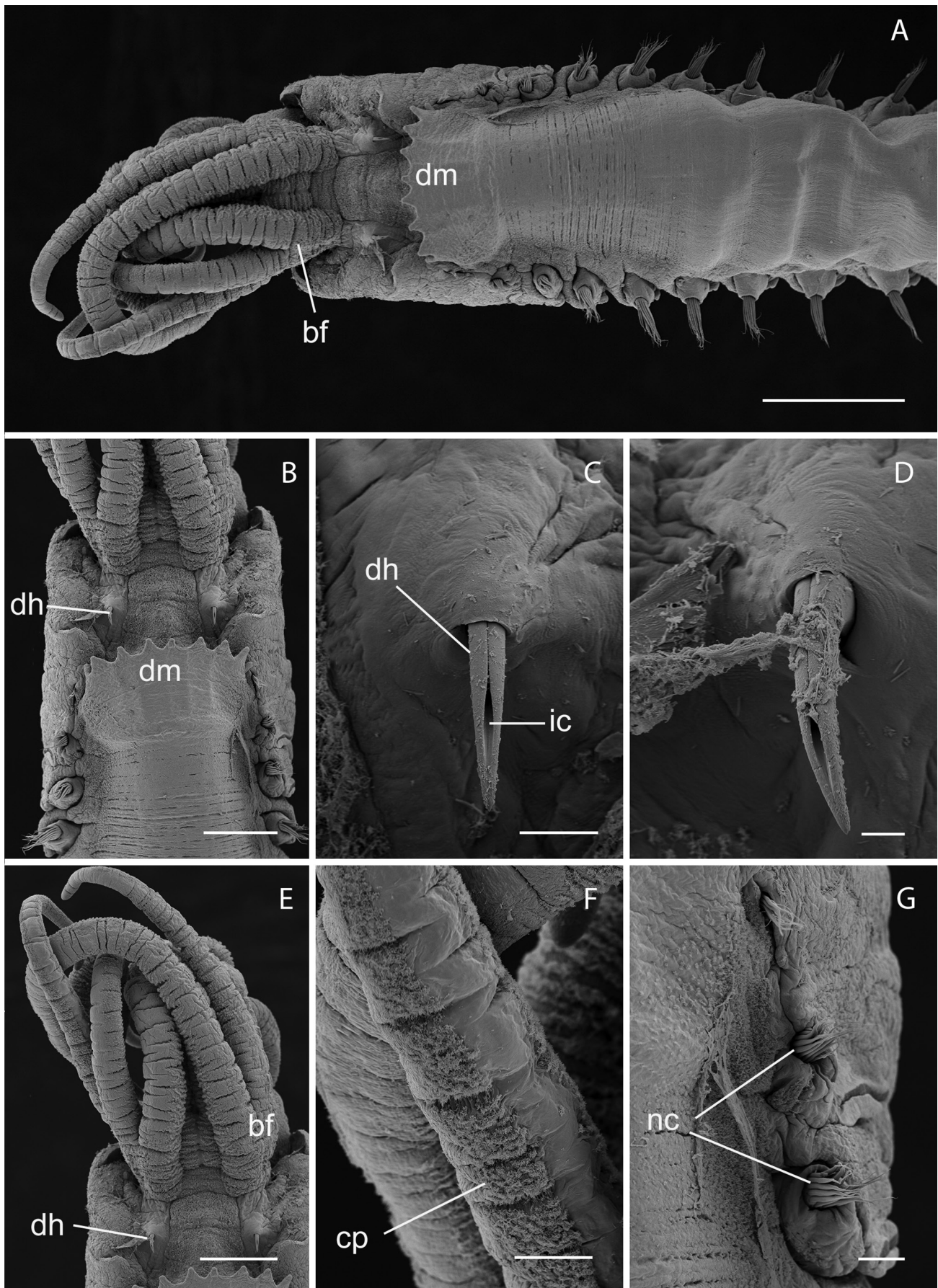


Figure 10. SEM of *Melinna cristata* (AM W.21791.001). (A) Dorsal view of anterior end. (B) Dorsal view of anterior end. (C) Dorsal hook. (D) Dorsal hook. (E) Dorsal view of branchiae. (F) Branchial surface. (G) Chaetigers 1–3. Scale bars: A, 1 mm; B, E, 500 µm; C, 50 µm; D, 20 µm; F, G, 100 µm. Abbreviations: *bf*, basal fusion; *dh*, dorsal hooks; *dm*, dorsal membrane; *ic*, internal canal; *cp*, rows of cilia on branchiae; *nc*, notochaetae.

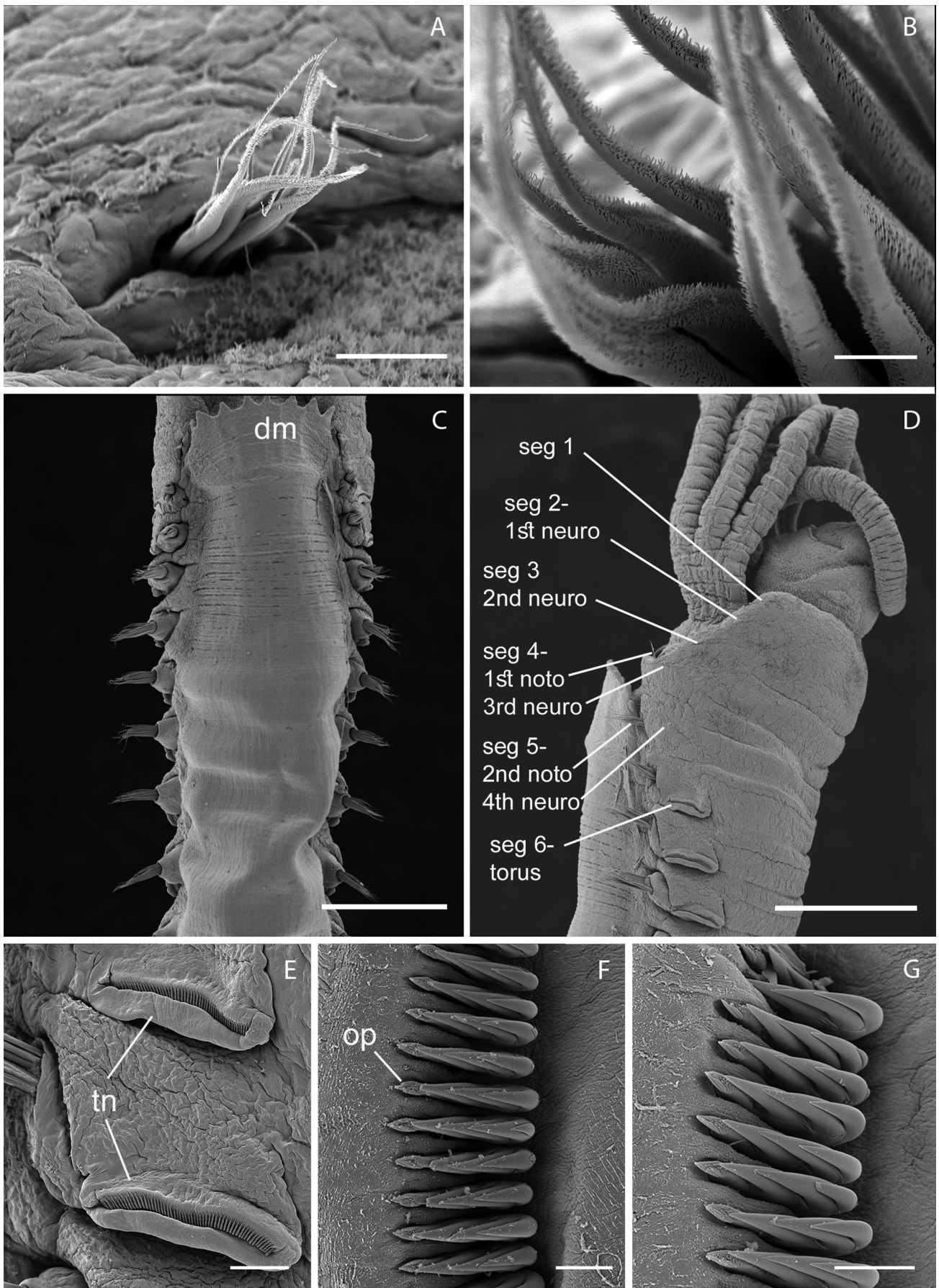


Figure 11. SEM of *Melinna cristata* (AM W.21791). (A) Chaetiger 11. (B) Close-up view of chaetae from chaetiger 11. (C) Dorsal view of entire specimen. (D) Lateral view of anterior end. (E) 1st and 2nd neuropodia. (F) Close-up view of 2nd neuropodia. (G) Close-up view of 2nd neuropodia. Scale bars: A, 50 µm; B, F, G, 10 µm; C, D, 1 mm; E, 100 µm. Abbreviations: *dm*, dorsal membrane; *seg*, segment; *noto*, notochaetae; *neuro*, neurochaetae; *tn*, thoracic neuropodia; *op*, sub-rostral ornamented process.

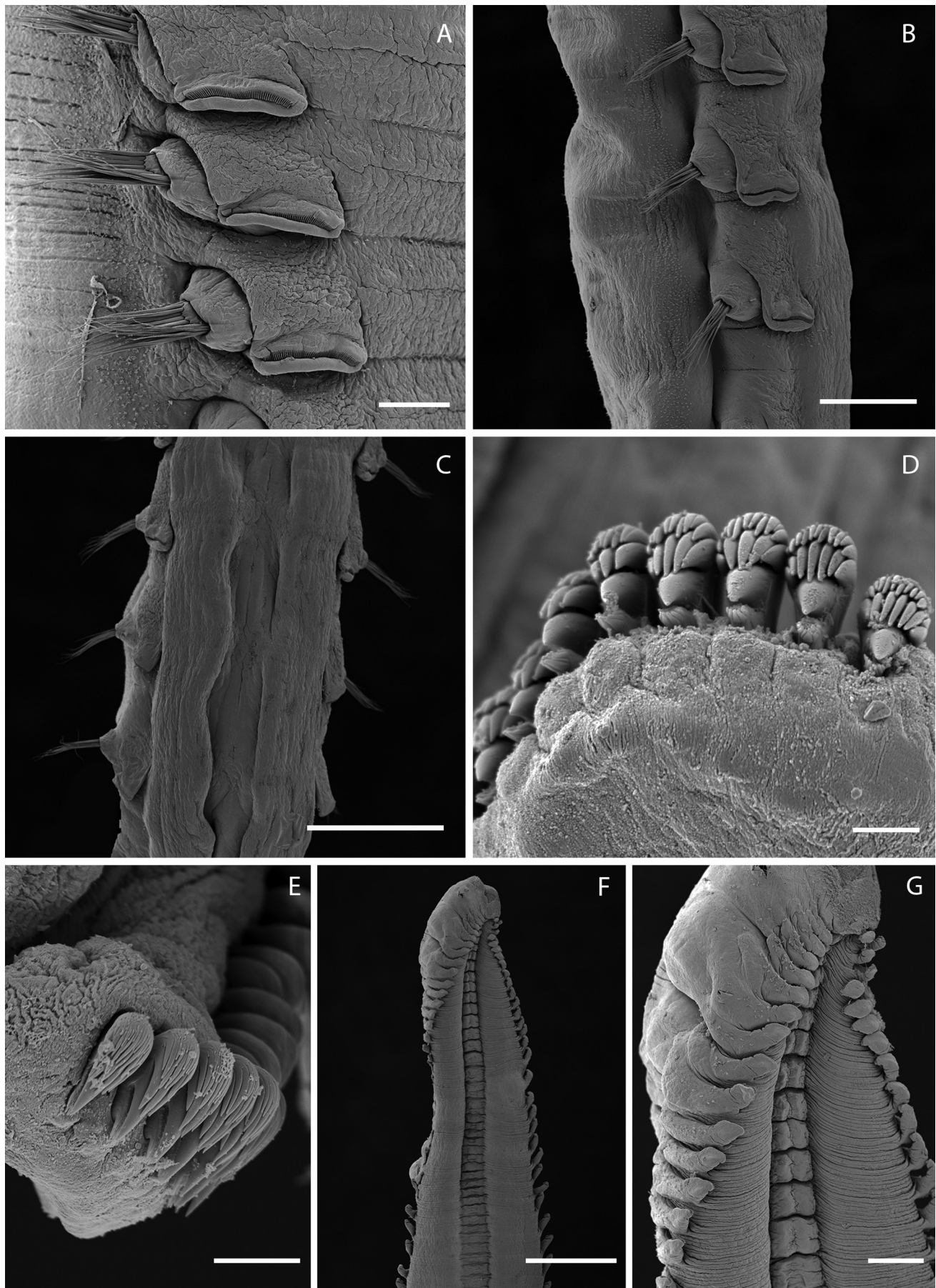


Figure 12. SEM of *Melinna cristata* (AM W.21791). (A) Chaetigers 11–14. (B) Lateral view of posterior end. (C) Junction of thorax and abdomen. (D) Far posterior abdominal neurochaetae. (E) Far posterior abdominal neurochaetae. (F) Pygidium. (G) Close-up view of pygidium. Scale bars: A, G, 200 µm; B, 500 µm; C, F, 1 mm; D, 5 µm; E, 10 µm.

Melinna elisabethae McIntosh, 1885

Figs 13–15; Tables 4, 5

Melinna elisabethae McIntosh, 1885: 438; 1914 106–107 (in part).

For complete synonymy see Mackie & Pleijel, 1995.

Material examined. AM W.21793, 4 specimens, including prepared for SEM, Cleveland, Tees Bay, England (54°36'N 1°48'W), gravelly mud/rock, 44 m, coll. Analytical & Environmental Services, 7 September 1984.

Remarks

The original description by Mackie & Pleijel (1995) only provided line drawings, we give additional information based on light and SEM images.

Prostomium well-developed and divided into anterior and posterior parts, anterior part trilobed (Fig. 15B), posterior part raised triangular glandular with anterior margin bearing longitudinal slits (Fig. 15B). Buccal tentacles numerous and equal in length to the branchiae (Fig. 13B). Four pairs of branchiae annulated with distal surface exhibiting cilia patches (Fig. 14A,C). Branchiae circular in cross-section, anterior pair showing 40% of basal fusion and outer pair 20% fusion (Figs 13B,C, 14C). One pair of dorsal hooks strongly curved and with pointed tips (Figs 13B,D,E, 14B,C), solid without internal canal. Dorsal membrane with about 12 triangular projections on anterior margin (Figs 13E, 14A). First segment achaetous (Fig. 14A) with crenulated ventral margin (Fig. 15B). Segments 2–5 with acicular neurochaetae arranged in elongated tori, progressively inserted more laterally (Fig. 13B,C). From segment 6 neuropodia with uncini continuing to pygidium. Notopodia present from segment 4, initially very small with short notochaetae, then progressively becoming larger, more laterally inserted and well-developed by segment 7 (Figs 13D, 14A, 15C) and on all subsequent ones. Notochaetae arranged in two tiers (Fig. 14H) with tips of longer ones curved (Fig. 15A) and with blades finely ornamented (Figs 14F,H, 15A,E). Notopodia globular with posterior lobe longer than anterior one (Fig. 14D,E,F) and well separated from neuropodia (Figs 14E, 15C). Thoracic neuropodia raised glandular tori slightly curved, bearing about 26 uncini (Fig. 14E). Thoracic uncini with a single row of four teeth with ornamentation on lateral face and becoming marked and behind anterior tooth strongly ornamented with small teeth (Figs 14G, 15D,F). Abdominal rudimentary notopodia not observed as in Mackie & Pleijel (1995), specimens very small and thin (Fig. 15G). Abdominal neuropodia well-developed but not elevated, anteriorly bearing four teeth arranged in a single row (Fig. 15H,I). Terminal anus bounded by pair of large lateral lobes and several smaller lateral ones (Fig. 13a) and lacking anal cirri. Methyl blue stain shows extensive ventral glandular areas (Fig. 13F). Tube with attached shell fragments on anterior end and rest of tube made of smaller sand grains and mud (Fig. 13G).

Discussion

To date 26 species of *Melinna* have been described and accepted including this new species *Melinna hamulus* sp. nov. This is the first species of *Melinna* to be described from

Australian waters. We have described our material as a new species, based on the morphology and that the new species is genetically distinct from all other species of *Melinna* for which DNA sequence data are available.

When comparing species of *Melinna* using morphology, we noted that many species were poorly described and illustrated, and in some cases no figures were provided (Table 5). We used the numbering system from the original descriptions as it is unclear if the original descriptions' numbering system recognizes the presence of the first anterior achaetous segment or not. These poor original descriptions have not prevented some of these species, such as the type species of the genus *M. cristata* (Sars, 1851), being widely recorded from localities far away from the Norwegian type locality (see Parapar & San Martín, 1997) and for a subspecies *Melinna cristata australis* Hartmann-Schröder, 1965 being described from Chile. Mackie & Pleijel (1995) began a revision on just the species occurring in northern Europe and found that the species complex of *M. cristata* included a new species *M. albicincta* Mackie & Pleijel (1995). These authors resurrected *M. elisabethae* McIntosh, 1885, a species previously synonymized with *M. cristata*. Mackie & Pleijel (1995) concluded that another species from Iceland, *M. islandica* Saemundsson, 1918, whose type is lost, must be considered as a *nomen nudum*. Following on from Mackie & Pleijel (1995), Parapar & San Martín (1997) described a new species *M. arnaudi* from the Antarctic and discussed at length how the Antarctic records of *M. cristata* probably do not belong to this species, while the records from South Africa by Day (1967), may represent a sibling species of their new species. We suggest that all these records from the Antarctic and sub-Antarctic (Ehlers, 1887, 1908; Monro, 1930; Hartmann-Schröder & Rosenfeldt, 1965 as *M. cristata australis*; Hartman, 1966, 1967; Hartmann-Schröder & Rosenfeldt, 1989, 1991) should be re-examined.

Many of the accepted species of *Melinna* have not been recorded since they were described or only listed as names in benthic surveys (Tables 4, 5). Indeed, some descriptions have morphed over the years, like that of *M. palmata* Grube, 1870. Mackie & Pleijel (1995) indicate that *M. palmata* Grube, 1870 has a denticulated margin on the dorsal membrane whereas the original description clearly states that the margin is smooth not denticulated.

Only a limited number of *Melinna* taxa have been sequenced and not all sequenced specimens were collected from the type locality. In the large transcriptomic data analysis of the main groups of Terebelliformia, Stiller *et al.* (2020) used only one taxon from Melinnidae, *Melinna oculata* Hartman, 1969. In a second phylogenetic analysis six taxa of Melinnidae were used; (1) *Isolda bipinnata* Fauchald, 1977, specimen A9437 collected from Belize, the type locality is Galeta Reef, Laurencia Zone off Panama in the Caribbean Sea (Fauchald, 1977); (2) *Isolda pulchella* Müller in Grube, 1858, specimen ZMBN 105697, collected from Morocco, the type locality is Santa Catharina Island, Brazil; (3) *Melinna albicincta* Mackie & Pleijel, 1995, specimen A1113 collected from Trondheim Fjord, Norway, the type locality is Kosterfjord, Sweden (Mackie & Pleijel, 1995); (4) *Melinna cristata* (Sars, 1851), specimen A9438 collected from Gullmaren, Sweden, type locality Bergen or Finnmark, Norway (*vide* Holthe, 1986), neotype location Hjeltefjord Norway (Mackie & Pleijel, 1995); (5) *Melinna heterodonta*, specimen A4546 collected from California

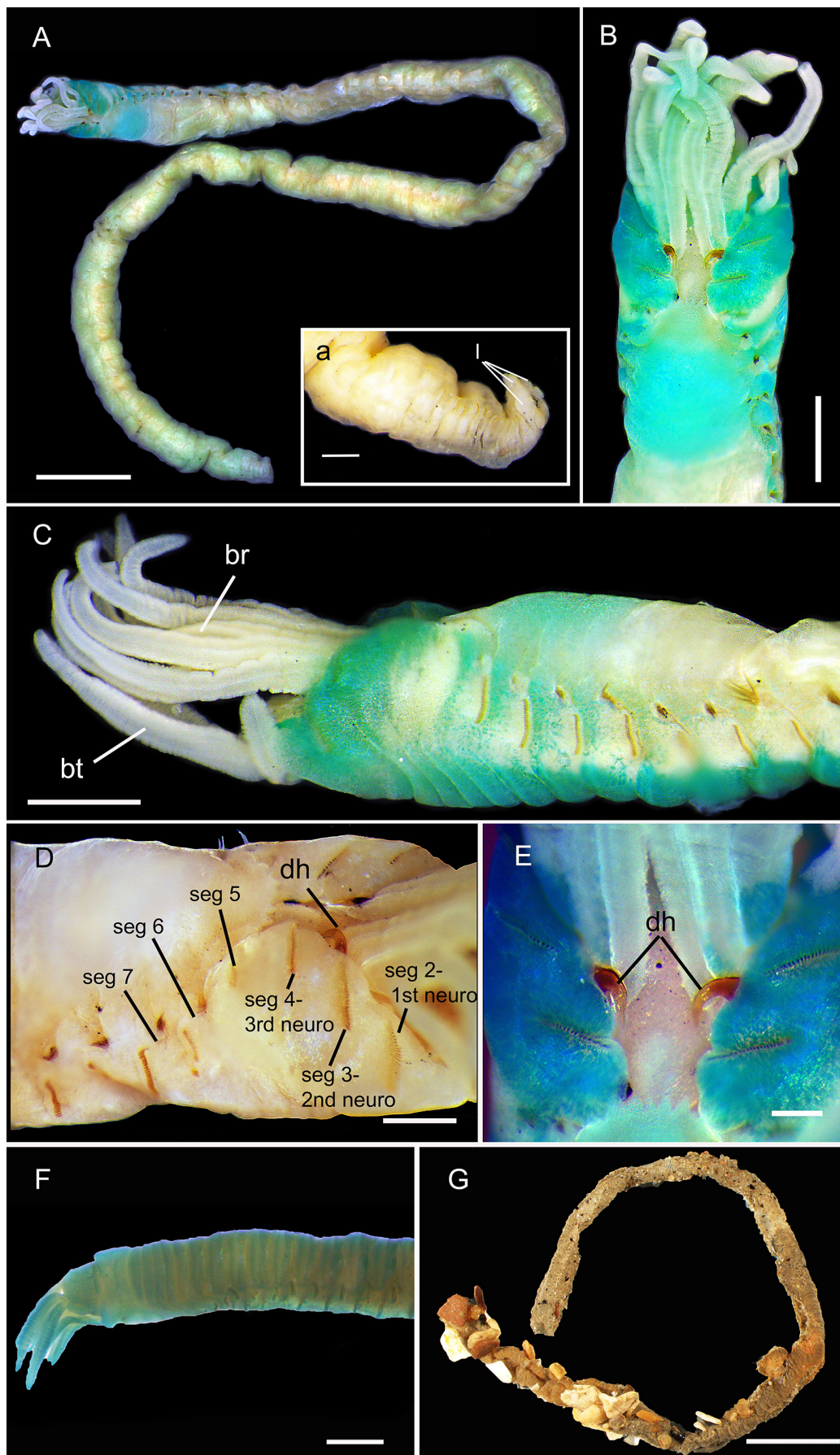


Figure 13. Light microscopy images of *Melinna elisabethae* (AM W.21793). (A) Whole specimen. (a) Pygidium. (B) Anterior end dorsal view, stained with methyl blue. (C) Lateral view of anterior end stained with methyl blue. (D) Lateral view of anterior end. (E) Dorsal hooks. (F) Anterior end ventral view, stained with methyl blue. (G) Tube. Scale bars: A, 2 mm; a, 250 µm; B, C, F, 500 µm; D, 250 µm; E, 100 µm; G, 3 mm. Abbreviations: *l*, lobes; *br*, branchiae; *bt*, buccal tentacles; *seg*, segment; *neuro*, neurochaetae; *dh*, dorsal hooks.

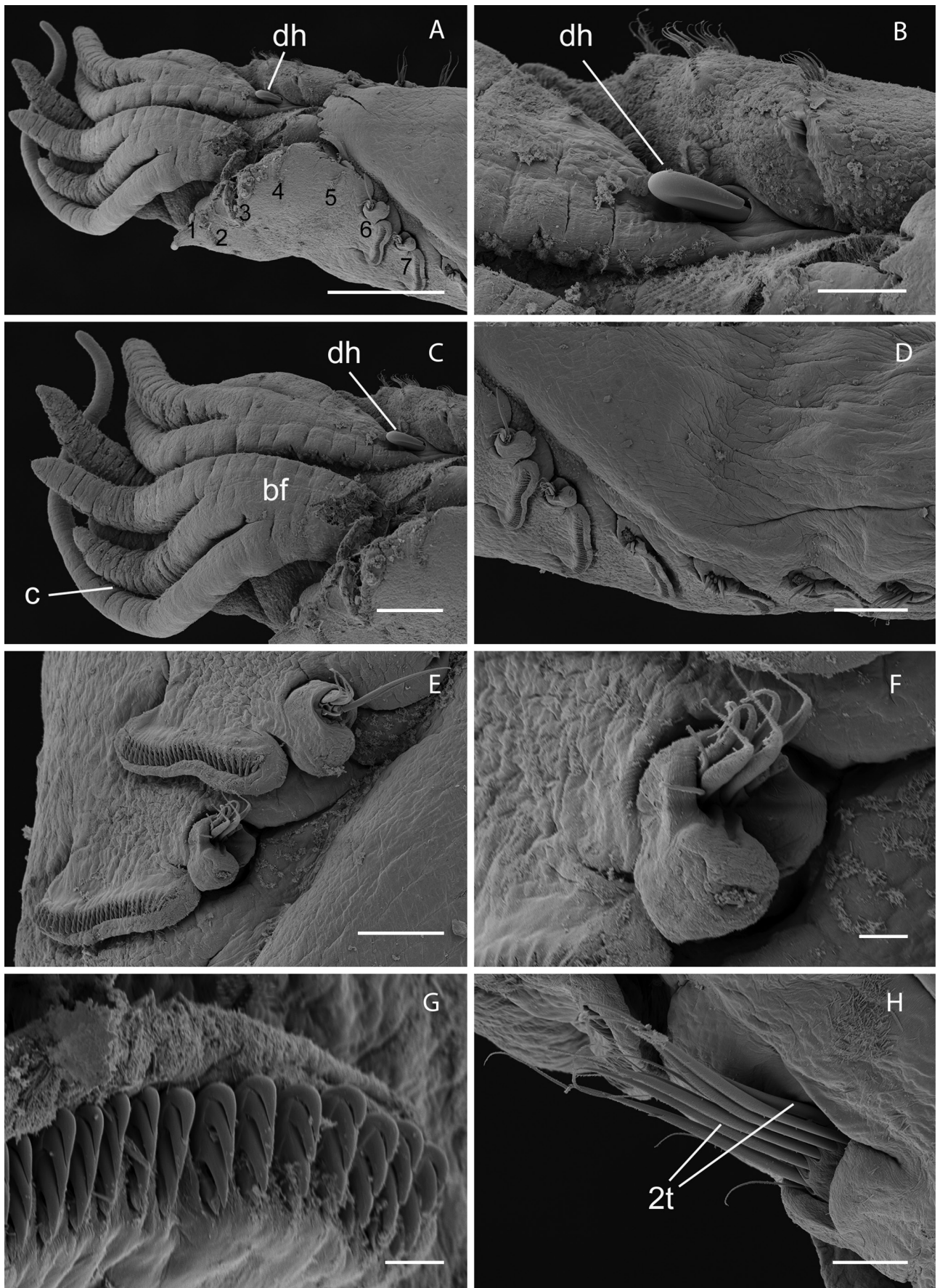


Figure 14. SEM of *Melinna elisabethae* (AM W.21793.002). (A) Dorsal view of anterior end with segments numbered. (B) Dorsal hook. (C) Surface of branchiae. (D) Lateral view of chaetigers 5–10. (E) Chaetigers 5 and 6. (F) Notochaetae chaetiger 6. (G) Anterior neurochaetae of chaetiger 6. (H) Mid-thoracic notopodium showing two types of chaetae. Scale bars: A, 500 μ m; B, E, 100 μ m; C, D, 200 μ m; F, 20 μ m; G, 10 μ m; H, 50 μ m. Abbreviations: *dh*, dorsal hooks; *bf*, branchial fusion; *2t*, notochaetae of 2 tiers + neurochaetae; *c*, cilia patches.

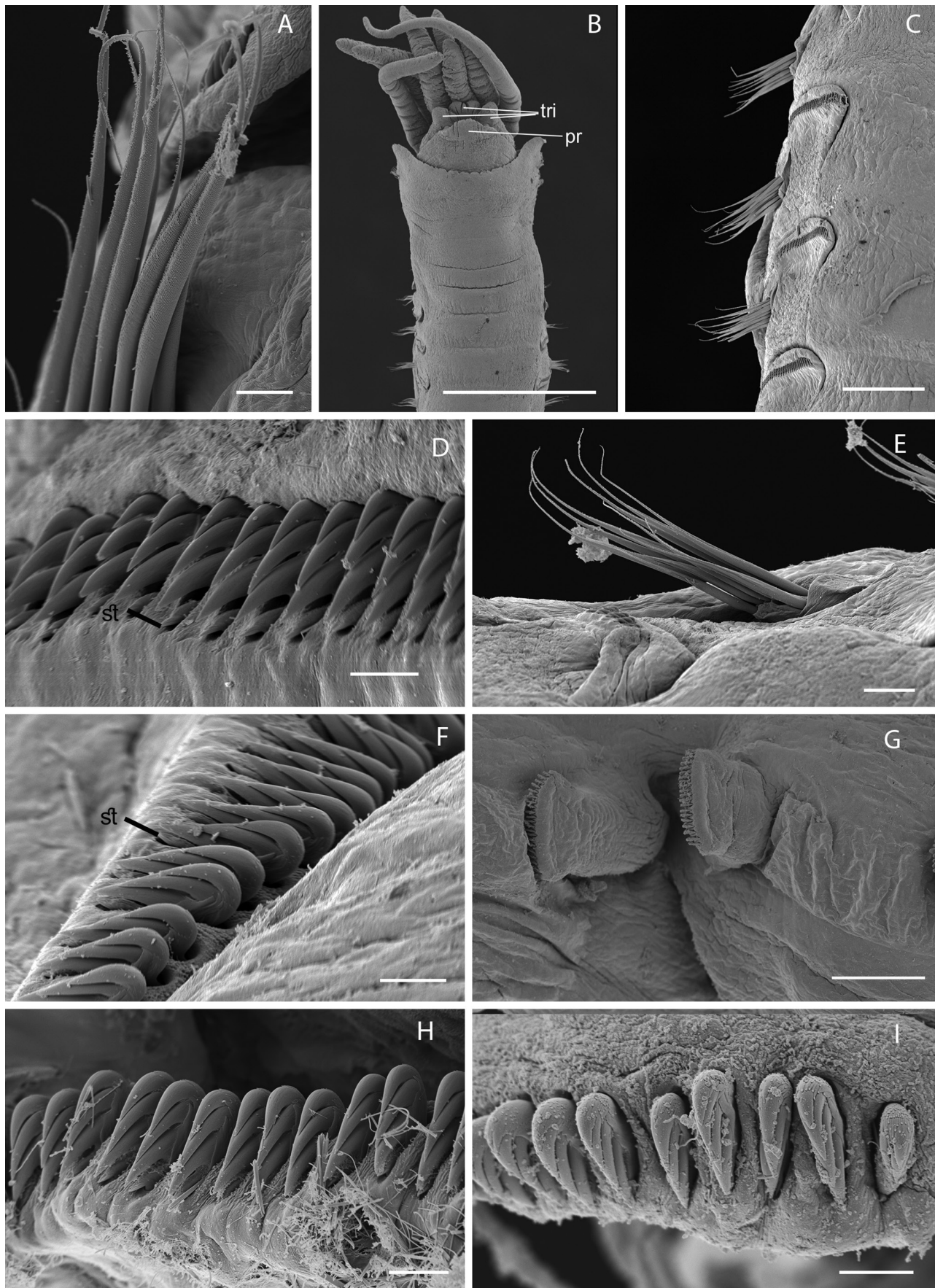


Figure 15. SEM of *Melinna elisabethae* (AM W.21793.002). (A) Close-up view of notopodial chaetal surface of chaetiger 14. (B) Ventral view of anterior end. (C) Dorsal view of chaetigers 6, 7, 8, 9. (D) Neurochaetae chaetiger 7. (E) Chaetiger 11. (F) Posterior thoracic neurochaetae. (G) Abdominal chaetigers showing lack of notopodia. (H) Posterior neurochaetae. (I) Close-up view of posterior neurochaetae. Scale bars: A, 20 μ m; B, 1 mm; C, 200 μ m; D, 10 μ m; E, 50 μ m; G, 100 μ m; H, I, 10 μ m. Abbreviations: *tri*, trilobed prostomium; *pr*, triangular glandular prostomium with anterior margin bearing longitudinal slits; *st*, small teeth.

Table 4. List of described *Melinna* species with type localities, depths, and coordinates (decimal degrees).

<i>Melinna</i> species	type locality (habitat)	depth (m)	latitude	longitude
<i>M. aberrans</i> Fauvel, 1932	Visakhapatnam Channel, India	—	c.17.6900°	83.3000°
<i>M. albicincta</i> Mackie & Pleijel, 1995	Kosterfjord, Sweden (sand/mud/gravel)	60–80	58.8750°	11.1050°
<i>M. armandi</i> McIntosh, 1885	west of North Island, New Zealand (mud)	2012	-40.4667°	177.7167°
<i>M. arnaudi</i> Parapar & San Martín, 1997	off Falsa Bay and Sur Bay, Livingston Island, Antarctic (mixed bottom)	386	-62.4419°	-60.3229°
<i>M. buskii</i> McIntosh, 1922	RV <i>Challenger</i> St. 157, midway between Antarctic and Australia (diatom ooze)	3566	-53.9167°	108.5833°
<i>M. collare</i> Detinova, 1986	North Atlantic	1895	58.3333°	-31.5483°
<i>M. cristata cristata</i> (M. Sars, 1851)	Norway, Bergen or Finnmark (not specified) neotype Hjeltefjord (mud)	78	60.6147°	4.8642°
<i>M. c. australis</i> Hartmann-Schröder, 1965	Gulf of Ancud, Chile	264	-42.0000°	-73.0000°
<i>M. denticulata</i> Moore, 1908	Funter Bay, Lynn Canal, southeast coast of Alaska, USA ^f	549	c.58.2700°	-134.9500°
<i>M. elisabethae</i> McIntosh, 1914	St Andrews, Fife, Scotland (holotype from stomach of haddock)	7–120	c.56.3474°	-2.7949°
<i>M. exilia</i> Fauchald, 1972	Guaymas Basin, Gulf of California, USA	1609–1646	27.4750°	-111.7250° ^a
<i>M. fauchaldi</i> Gallardo, 1968	Nha Trang, South Viet Nam (mud)	9	12.1736°	109.2122°
<i>M. heterodonta</i> Moore, 1923	off Point La Jolla, California, USA (mud/sand)	201–2560	30.5833°	-117.4000° ^b
<i>M. maculata</i> Webster, 1879	off Sombbrero and St Thomas, West Indies	713–860	—	—
<i>M. malmgreni</i> Caullery, 1944	Sulu Archipelago, Philippines	275	6.1333°	121.3167°
<i>M. marchadi</i> Fauvel & Rullier, 1959	Cape of Gorée, Senegal; Station 559-AB	190–220	c.14.6700°	-17.4000°
<i>M. monoceroides</i> Fauvel, 1936	Morocco	224	30.4750°	-10.0639°
<i>M. ochotica</i> Uschakov, 1950	southern part of Okhotsk Sea, Russia	1366	—	—
<i>M. oculata</i> Hartman, 1969	Palos Verdes shelf (mixed sediment, shelf to shallow slope)	0.02	33.7200°	-118.3458°
<i>M. pacifica</i> McIntosh, 1885	mid Pacific (<i>Globigerina</i> ooze)	3749	36.1667°	178.0000°
<i>M. palmata</i> Grube, 1870	St Malo, France	—	c.48.6500°	-2.0350°
<i>M. parumdentata</i> Ehlers, 1887	off Florida, USA	587	25.7000°	-88.1667°
<i>M. plana</i> Fauchald, 1972	Guaymas Basin, Gulf of California, USA	1609–1646	27.4750°	-111.7250° ^d
<i>M. profunda</i> Augener, 1906	West Indies	2756	—	—
<i>M. tentaculata</i> Fauchald, 1972	southern part of Gulf of California, USA	2432	24.3333°	-109.9750°
<i>M. uruguayi</i> Hessle, 1917	off coast of Uruguay	80	-35.0000°	-51.1667°
<i>M. hamulus</i> sp. nov.	southeastern Australia	4133–4197	-39.5519°	149.5531° ^e

^a trawl ends at 27.3000° -111.5917°

^b trawl ends at 33.0264° -121.4750°

^d trawl ends at 27.3000° -111.5917°

^e trawl ends at -39.4961° 149.5981°

^f Steamer *Albatross* 1903 voyage St. 4258

USA, the type locality is off Point La Jolla, California and (6) *Melinna oculata*, specimen SIO-BIC:A9439 collected from California, the type locality is Palos Verdes shelf off California (Stiller *et al.*, 2020). We stress that sequencing material from the type locality is essential. Nygren *et al.* (2018) highlighted that high cryptic diversity was recorded even in the relatively well-studied area of the northeast Atlantic. A molecular investigation of the genus *Terebellides* Sars, 1835 revealed 27 species, from a previously reported

seven species based on morphology alone (Nygren *et al.*, 2018). Many of the species occurred in sympatry with several other species in the species complex.

The misidentifications, lack of detail in early descriptions and lack of genetic material from type localities all highlight the need for a revision of the genus *Melinna*, and indeed of the whole family Melinnidae. Type material of all species should be re-examined or fresh topotypical collected examined and sequenced.

Table 5. Diagnostic characters of *Melinna* species. Column headings are abbreviated as follows: *corrected*, numbering of anterior segments corrected; *hooks*, numbers of pairs of dorsal hooks; *fusion*, numbers of branchiae and degree of fusion; *projections*, dorsal membrane on segments 5—numbers of projections; *neurochaetae*, numbers of neuropodia with acicular neurochaetae; and *segments*, numbers of abdominal segments. *Numbering of segments as stated in original paper indicating lack of recognition of achaetous segments, difficult to reconcile with Rouse *et al.* (2022).

species	corrected	hooks	eye spots	fusion	projections	neurochaetae	segments	pygidium	references	comments
<i>M. aberrans</i>	no	1 pair, bent tip	transverse row of many eye spots	4 pairs, in 2 groups joined basally for at least ½ length	smooth and convex	segments, 2,3 and 5 with acicular neurochaetae	30	not recorded	Fauvel, 1932, 1953	
<i>M. albicincta</i>	yes	1 pair, posteriorly directed, sharply pointed, strongly curved tips, no internal canal	absent	4 pairs, on dorsal ridge segment 2, inner and anterior—most ones of each group basally fused (35–40%), other group fused for < 10%	15–25 unequal triangular projections, often arranged in groups of 3	segments 2–5, fine acicular with long lanceolate tips	49 neuropodia, small rounded notopodial projections on anterior 10–15 segments	terminal anus bounded dorsolaterally by pair large rounded lobes, ventrally by 8–12 smaller lobes, anal cirri absent, no pigment spots	Mackie & Pleijel, 1995	
<i>M. armandi</i>	no	1 pair stout, canal present	not recorded	4 pairs stout, not tapering	8 large projections	not recorded	42–43	simple, wide funnel, no cirri	McIntosh, 1855	few details given, only compared with <i>M. cristata</i> . Reported in Probert <i>et al.</i> (1996) from Chatham Rise, New Zealand. considerable variation in dentition of uncini along body
<i>M. arnaudi</i>	yes	1 pair, slightly curved tip, canal absent	absent	4 pairs in 2 groups, inner & anterior—most inserted more anteriorly, joined 20–30% basally, posterior group < 10% basally fused	serrated free margin with 5–11 equal triangular projections	segments 2–5, none on elevated lobes	72 neuropodia, with small rounded projecting notopodia without notochaetae	terminal anus, bounded dorsolaterally by pair of large lobes, and ventrally by 6 smaller lobes, cirri absent	Parapar & San Martín, 1997	
<i>M. buskii</i>	no	not recorded	not recorded	not recorded	smooth edge	not recorded	not recorded	with 2 anal cirri	McIntosh, 1985	minimal figs & description suggest indeterminate
<i>M. collare</i>	no	1 pair golden	not recorded	4 pairs, schematic figure suggests basal fusion of branchiae	8 projections	chaetigers 1–4 with acicular neurochaetae, notochaetae present from chaetiger 3, first 2 pairs with thin, short notochaetae	32	anus surrounded by 5 poorly developed irregularly shaped lobes	Detinova, 1986	brief description and minimal figures

Table 5 continued ...

species	corrected	hooks	eye spots	fusion	projections	neurochaetae	segments	pygidium	references	comments
<i>M. cristata cristata</i>	yes	1 pair, sharply pointed with gently curved tips, internal canal	present, small cluster	4 pairs, in 2 basally fused groups, inner and anterior-most branchiae of each group basally fused (< 20%)	serrated free margin with 8–14 equal triangular projections	segments 2–5, acicular with long lanceolate tips, those on segment 4 on elevated lobes	57 neuropodia, with small distally ciliated papilliform projections in notopodial positions	terminal anus, bounded dorsolaterally by pair of large lobes, and ventrally by 2–4 small lobes, anal cirri absent, no pigment spots with 2 lappets	Mackie & Pleijel, 1995 designated neotype	Holthe, 1986, type material probably lost
<i>M. cristata australis</i>	no	yellowish hook with bent tip	present, small ocelli	4 pairs, thick annulated, touching medially at base, distally tips thread-like	18 rounded projections	difficult to interpret	about 50		Hartmann-Schröder, 1965	
<i>M. denticulata</i>	no	straighter than other species and more tapering	not recorded	4 pairs, thick taper to bluntly pointed tip, some basal fusion	18 prominent projections	difficult to interpret	55+, posteriorly incomplete	posteriorly incomplete	Moore, 1908, 1905	incorrectly named <i>M. cristata</i> in Moore, 1905, in Moore, 1908 name changed to <i>M. denticulata</i> , only uncini figured
<i>M. elisabethae</i>	yes	1 pair sharply pointed, strongly curved tips, no internal canal	present, along edge of nuchal slits	4 pairs, arranged in 2 basally fused groups	crenulated margin, 6–12 triangular variable projections, usually unequal, sharply tapering to narrow points.	segments 2–5, acicular with long lanceolate tips	72, anterior 10–15 with small rounded projection in notopodial position, then absent	terminal anus, bounded dorso laterally by pair of large lobes, ventrally by 6–8 smaller lobes, anal cirri absent, 1 pair of black pigment spots laterally	Mackie & Pleijel, 1995; this paper	found in UK, Sweden and Iceland, widely reported elsewhere but not confirmed
<i>M. exilia</i>	no	1 pair	not recorded	4 pairs arranged in 2 groups, connected by low branchial membrane	dentate margin forming deep funnel shaped pocket, with 5–6 blunt projections	1st 3 neuropodia with acicular chaetae	15 (approximately)	not recorded	Fauchald, 1972	minimal figures. Recorded from southeastern Gulf of California, Mexico in Méndez (2006)
<i>M. fauchaldi</i>	no	1 pair, terminates in filiform tip	absent	4 pairs, no fusion, reach back to chaetiger 7	smooth edge	segments 3–6*	incomplete specimen, 39+	incomplete specimen	Gallardo, 1968	minimal figures

Table 5 continued ...

species	corrected	hooks	eye spots	fusion	projections	neurochaetae	segments	pygidium	references	comments
<i>M. heterodonta</i>	no	1 pair large	not recorded	4 pairs, anterior innermost pairs fused basally	14–16 unequal triangular projections	1st 4 anterior neuropodia with acicular chaetae	54 (Hartman records 73)	not recorded	Moore, 1923	minimal figures, Fauchald, 1972, Hartman, 1969
<i>M. maculata</i>	no	not recorded	not recorded	not recorded	not recorded	not given	55	not recorded	Webster, 1879	very brief description, similar to <i>M. cristata</i> no other records
<i>M. malmgreni</i>	yes	1 pair (not illustrated)	present as convex arc of pigment by nuchal organs	4 pairs not fused basally	dentate, number of projections not recorded	segments 2–5 with acicular neuropodial chaetae	incomplete with 12+	incomplete specimen	Caullery, 1944	
<i>M. marchadi</i>	no	1 pair (not illustrated)	present, as 4 black spots	4 pairs, with deep canal	smooth	3 segments with acicular spines	damaged specimen, 50–60	damaged specimen	Fauvel & Rullier, 1959	indicates abdominal uncini arranged in double rows back to back
<i>M. monoceroides</i>	no	1 pair schematic figure	absent	4 pairs, posterior 3 of each group well connected basally	smooth	2,3 and 5 with acicular neurochaeta	numerous chaetigers but no count given	not recorded	Fauvel, 1936	
<i>M. ochotica</i>	no	1 or 2 hooks (unclear), narrow, elongated tips not strongly bent	not recorded	4 pairs, distal membrane at base	3–4 projections	segments 2,3,4 and 6 with acicular neurochaetae, notopodia from segment 5	40	elongated, ventral anus	Ushakov, 1950	no figures
<i>M. oculata</i>	no	1 pair with sharply curved tip pointed	present in front of nuchal ridges	4 pairs inserted on common stalk, with anterior-most medial, other forming crescent behind, 1st pair fused for most of length, others for <50%	dentate with about 10 projections	1st 4 neuropodia with acicular chaetae	55–58	large anal pore bounded by short flange with middorsal cleft and ventral crenulations	Hartman, 1969, recorded by Hartman, 1966 as <i>M. denticulata</i> (in part)	
<i>M. pacifica</i>	no	not recorded	present as crescentic bands of pigment spots	4 pairs	projections filiform	not recorded	not recorded, but poorly preserved	not recorded	McIntosh, 1885	minimal figures

Table 5 continued ...

species	corrected	hooks	eye spots	fusion	projections	neurochaetae	segments	pygidium	references	comments
<i>M. palmata</i>	no	1 pair, strongly hooked	longitudinal row of small eye spots	4 pairs, connected by membrane for half of length	smooth margin	not recorded	not recorded	not recorded	Grube, 1870	no figures Mackie & Pleijel (1995) state it has scalloped margin to the dorsal crest although the original description says smooth
<i>M. parumdentata</i>	no	present but no details given	not recorded	4 pairs forming half circle, no mention of any fusion	8–10 large teeth appear as triangular lappets	no precise details given	40	not recorded although complete specimen	Ehlers, 1887	refers to 58 chaetigers, how many thoracic unclear
<i>M. plana</i>	no	1 pair present in figure 63a (Fauchald, 1972) but no details given in description	absent	4 pairs, arranged in semi-circle of 3 enclosing 4th anterior-most, all free to base	smooth	1st 4 neuropodia with acicular chaetae	incomplete specimen	incomplete specimen	Fauchald, 1972	minimal figures
<i>M. profunda</i>	no	not present, perhaps lost	not recorded	4 pairs	not well preserved	not recorded	incomplete specimen, 22+	incomplete specimen	Augener, 1906	minimal figs & description
<i>M. tentaculata</i>	no	1 pair attached to small medial lobe at edge of lateral flange	absent	4 pairs, fused into 2 groups dorsolaterally	8 projections	1st 3 neuropodia with acicular chaetae	incomplete specimen, abdominal segments with no notopodial papillae	incomplete specimen	Fauchald, 1972	minimal figures, pair of large oral tentacles and numerous short smooth tentacles
<i>M. uruguayi</i>	no	not recorded	not recorded	not recorded	not recorded	not recorded	40 segments, anterior uncini with 5 teeth	not recorded	Hessle, 1917	minimal figures only of uncini
<i>M. hamulus</i> sp.nov.	yes	1 pair short curved pointed tips, no canal visible	present as 2 elongated patches of small spots	4 pairs, all completely separated, slightly swollen bases, tapering to fine tips	13–17 triangular projections	1st 4 neuropodia with acicular chaetae	45	anal cirri absent, 2 large lateral lobes surrounded by 4 or 5 smaller lobes	this paper	previously reported by Gunton <i>et al.</i> (2021) as <i>M. cf. armandia</i>

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