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Amazing Diversity of *Nothria* (Annelida, Onuphidae) in the Australian Deep Sea

Hannelore Paxton[1,2], Nataliya Budaeva[3], and Laetitia M. Gunton[2]

[1] School of Natural Sciences, Macquarie University, Sydney NSW 2109, Australia

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

[3] Department of Natural History, University Museum of Bergen,
University of Bergen, Allégaten 41 5007, Bergen, Norway

Abstract. The epibenthic onuphid genus *Nothria* Malmgren, 1867 presently comprises 21 accepted species. We are reporting here on specimens collected during six deep-sea expeditions of the RV *Investigator* from 2015–2018 to the Great Australian Bight (GAB) and off eastern Australia from Tasmania to Queensland, describing eight new species of *Nothria*. This is the first integrated study of the genus, sequencing the markers COI, 16S rDNA and 28S rDNA from 37 specimens and employing conventional and exploratory morphological characters as well as tube consistency and structure for identification. Molecular data provided strong support for recognition of the eight new species and the *Nothria otsuchiensis* Imajima, 1986 species complex. Since the analysis of morphology between the specimens of this complex has not revealed any obvious differences, it may represent a complex of cryptic species. *Nothria digitata* sp. nov. was collected at a depth of 400 m whilst the remaining seven new species are from depths of 980–2751 m. *Nothria deltasigma* sp. nov., *N. digitata* sp. nov. and *N. minima* sp. nov. were collected at a single station each, while *N. josae* sp. nov. and *N. simplex* sp. nov. were found at two stations. However, *N. delta* sp. nov. displayed the widest distribution, occurring at GAB, Tasmania and Jervis Bay Marine Park, NSW. Most stations yielded only one species, Jervis Bay Marine Park and south of Brians, Tasmania, harboured two, but an astounding example of sympatry was discovered at Huon Marine Park, Tasmania, where three species, *N. delta* sp. nov., *N. lizae* sp. nov. and *N. orensanzi* sp. nov. were collected together in one station.

Introduction

Onuphid annelids of the genus *Nothria* Malmgren, 1867 construct distinctive dorsoventrally flattened tubes, externally covered mainly with shell fragments, foraminiferans, sand grains, spines and other materials. As they extend their greatly enlarged anterior parapodia from this tube, moving along the sea floor in a caterpillar-like fashion, they are known as epibenthic crawlers and have been reported worldwide from shallow subtidal waters to abyssal depths (Kucheruk, 1980, 1985; Paxton, 1986a; Budaeva & Paxton, 2013). The number of recognized species of *Nothria* was listed as 19 by Budaeva & Paxton (2013) and rose to the presently accepted 21 species with the description of *N. nikitai* Budaeva, 2014 and the addition of *N. edwardsi* (Roule, 1898) originally described as *Hyalinoecia* and transferred to *Nothria* by Arias & Paxton (2016).

Six *Nothria* species have been reported from depths below

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ORCID iD: Hannelore Paxton 0000-0001-7086-5219; Nataliya Budaeva 0000-0001-9748-2285; Laetitia M. Gunton 0000-0003-4758-4974
Corresponding author: Laetitia M. Gunton Laetitia.Gunton@Australian.Museum
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2000 m. It is interesting to note that *N. edwardsi,* collected by the Research Vessel (RV) *Talisman* between the Azores archipelago and the Iberian Peninsula in 1883 is the first deep-water species collected and near the greatest depth (4255 m) (Arias & Paxton, 2016). *Nothria solenotecton* (Chamberlin, 1919) was described from off Panama at 2323 m and *N. atlantica* (Hartman, 1965) from the Mid-Atlantic-Ridge at 3200 m depth. Three species with great depth and distributional ranges, *Nothria abyssia* Kucheruk, 1978 (to 5200 m), *N. anoculata* Orensanz, 1974 (to 900 m) and *N. otsuchiensis* Imajima, 1986 (to 2900 m) may represent species complexes and will be discussed below.

The convoluted taxonomy of the genus and the difficulties with species determination were discussed in detail by Budaeva & Paxton (2013). *Nothria* demonstrates a significant variation in most morphological characters which has at times defeated its investigators. Kucheruk (1980) attempted to estimate the morphological variation based on examination of 1200 specimens collected worldwide in 45–2930 m and was forced to refer them all to *N. conchylega.* Jirkov & Yermolaev (1989) examined ca. 200 *Nothria* specimens from the North Atlantic and the Arctic, analyzing 12 morphological characters and ended up identifying two distinct morphotypes, A and B. The variation in morphological characters is complicated by ontogenetic variation where characteristics used for species identification change with the development of the worm and become stabilized at different points in development for different species. This has been recognized by Kucheruk (1980), Jirkov & Yermolaev (1989) and Orensanz (1990), and in studies of *N. abyssia* and *N. otsuchiensis* by Budaeva & Paxton (2013) and *N. maremontana* André & Pleijel, 1989 by Paxton & Arias (2014). Ideally, the ontogeny of each species should be known to allow correct identification.

The fact that only one species, *N. nikitai*, has been described during the last twenty years may be related to the taxonomic problems of the genus. No molecular phylogenetic studies have yet been carried out on the group. The only molecular data available on GenBank are for the type species *Nothria conchylega* (Budaeva *et al*., 2016; Worsaae *et al.,* 2005; Dahlgren *et al*., 2001). A possible case of cryptic diversity within *N. conchylega* was reported based on barcode data of a population from British Columbia differing in 11.2 % from the North Atlantic populations (Carr *et al.,* 2011).

The Australian *Nothria* biodiversity is largely unknown. At least two species, one from shallow water and one from 2900 m were known to occur, but not identified to species (Paxton, 2000). Two species, *N. abyssia* and *N. otsuchiensis* from eastern Australia were subsequently recognized and examined for a study of ontogenetic variation of diagnostic characters (Budaeva & Paxton, 2013).

In the present study we describe eight new species belonging to the genus *Nothria* from the deep waters of the Great Australian Bight and along the Australian eastern continental margin from Tasmania to southern Queensland. We present the first integrative study of the genus. The species are defined on the basis of three molecular markers and qualitative and quantitative morphological characteristics.

Material and methods

Field sampling

Specimens were collected during six expeditions on the Research Vessel (RV) *Investigato*r from 2015–2018 to deep-water environments around Australia (Table S1). These surveys included; IN2015_C01, IN2015_C02 and IN2017_C01 to the Great Australian Bight (GAB) during the Great Australian Bight Deepwater Marine Program (GABDMP), a CSIRO led research program sponsored by Chevron Australia. The GAB is a large, relatively flat, submarine plain that covers most of Australia's southern coastline extending from Cape Pasley in Western Australia to Cape Catastrophe in South Australia. The crescent-shaped continental shelf (<200 m depth) of the GAB covers an area of around 150,000 km^2 (Rogers *et al.,* 2013). The shelf break descends to the continental slope, which contains two main terraces; in the west the Eyre Terrace and in the east the larger Ceduna Terrace. The Ceduna Terrace, where the present study samples were collected, slopes gently to the southwest and has numerous submarine valleys dissecting its surface (Tilbury & Fraser, 1981).

The eastern continental margin of Australia from Tasmania to southern Queensland was sampled during "Sampling the Abyss" survey, IN2017_V03. The Australian eastern continental margin is relatively narrow and can be as close as 60 km from the coast (Heap & Harris, 2008). The base of the continental slope and beginning of abyssal floor starts around 3500–4500m.

"Seamount Coral Survey" voyage IN2018_V06 sampled the Tasmanian seamounts and trial cruise IN2015_E02 the Tasmanian outer continental shelf and slope. At the far south of the eastern Australian continental margin, on the continental slope to the east and south of Tasmania, lie clusters of 191 volcanic seamounts (Williams *et al.*, 2020a). These seamounts range in size from < 0.2 to c. 20 km^2 base area, and peak at around 570 to 2400 m depth (Williams *et al*., 2020a). Deep-sea reefs formed by the matrix-building scleractinian coral *Solenosmilia variabilis* Ducan, 1873 are common on the peaks and flanks of these seamounts (Koslow *et al*., 2001, Williams *et al*., 2020b), making these deep-water areas vulnerable marine ecosystems (VME) (Williams *et al*., 2020b).

Biological sampling

Most samples were collected using a CSIRO 4 m wide × 0.5 m high Beam Trawl (Lewis, 2010), and a Geoscience Australia design rock dredge with mouth-size 0.90 m wide × 0.35 m high (for details see MacIntosh *et al.,* 2018). Collected specimens were live sorted on board the RV *Investigator* into higher taxa on ice in chilled (5°C) seawater and annelids in the family Onuphidae were separated out. Specimens were fixed in either 95% ethanol or in 10% buffered formalin and shipped to the Australian Museum, Sydney. In the laboratory, formalin-fixed specimens were rinsed in water and then preserved in 80% ethanol.

Morphological studies

Specimens were examined under a dissecting stereo microscope in 80% or 95% ethanol. Temporary slides of small specimens or body parts were mounted in glycerol and examined under a compound light microscope. Line drawings were prepared with the aid of a camera lucida. Specimens used for scanning electron microscopy (SEM)

were dehydrated in an ascending series of graded ethanol, critical-point-dried, mounted on stubs or pins, gold coated and imaged with a JEOL JSM-6480LA scanning electron microscope at Macquarie University, Sydney. Chaetal and prostomial appendages terminology generally follows Paxton (1986a, 1998 respectively). The figures of the first treated species are completely labelled for reference (Figs 2–4). The description of certain characters has been refined with respect to detail and size as below:

Anterior simple, pseudocompound and compound hooks. These are the specialized hooks of the anterior modified parapodia of onuphids that have generally been referred to as "pseudocompound hooks" (Fauvel, 1923; Hartman, 1944; Day, 1967; Fauchald, 1982; Paxton, 1986a; Orensanz, 1990). Budaeva & Fauchald (2010) suggested the term "falciger" to describe simple or pseudocompound hooded dentate chaetae present in the ventral fascicle of the anterior modified parapodia and to distinguish them from the subacicular simple bidentate chaetae appearing in median and posterior unmodified parapodia. In our opinion, the term "falciger" is somewhat misleading since it is defined as a compound chaeta with a stout, hooked blade or apex (Glasby *et al.,* 2000) but is in usage (Budaeva & Fauchald, 2011; Budaeva & Paxton, 2013; Paxton & Budaeva, 2013; Zanol *et al.,* 2021).

Falcigers or compound hooks do occur among onuphid anterior hooks during ontogeny in several genera where they may be present as transitory provisional hooks as in *Rhamphobrachium ehlersi* Monro, 1930 (Paxton 1986a: table 2) or may be retained as permanent hooks by the mature worm into the next one or two chaetigers following pseudocompound anterior hooks as in *R. diversosetosum* Monro, 1937 and *R. hutchingsae* Paxton, 1986 (Paxton, 1986b); *Hirsutonuphis armillaris* Paxton, 1986 (Paxton, 1996); *Aponuphis willsiei* Cantone & Bellan, 1996 (Arias & Paxton, 2015), and indeed a number of *Nothria* species. These compound anterior hooks of onuphids are strongly reminiscent of eunicid falcigers in presenting a free blade or apex rather than being ancylosed as well as being finely serrated along the upper shafts and appendages, sharing the plesiomorphic characteristics of their sister family.

The three (rarely two) pairs of modified anterior *Nothria* parapodia are an important aid to the worms benthic crawling. Their hooks range from very slender to robust; even in the same parapodium the more superior hooks are usually thicker in diameter than the inferior ones. We found that the width of the anterior hooks can be a diagnostic character that has previously been largely under-utilized. In the descriptions we define the width of a hook as very slender (diameter less than 15 μm), slender (diameter 15–30 μm) and robust (diameter more than 30 μm). We are presenting figures of the anterior hooks of all new species drawn to the same scale (for a given species) for ease of comparison. Hooks of chaetiger 1 and 2 can be simple or pseudocompound. The hooks of the last modified pair of parapodia (usually chaetiger 3) are usually true falcigers, they are very rarely simple, range from pseudocompound to compound, and part of their upper shaft and hood are covered with tiny serrations or knobs, showing their ancient relationship with eunicids (Fig. 21D).

Pectinate chaetae. The pectinate chaetae of most *Nothria* species are so-called "scoop-shaped" or with rolled margins; rarely flat. Of the species collected during the present study, *N.* cf. *paxtonae* is the only species having flat pectinate chaetae. Scoop-shaped pectinate chaetae extend their lateral flanges, creating almost a total circle or even overlapping the edges (Fig. 21C), occurring in most cases in great numbers in chaetiger 3 (Fig. 12C). In the descriptions we are reporting the number of teeth per chaeta, ranging from 14–25, indicate their approximate number in chaetiger 3 (3–30) and illustrate selected species. As their shape is not as informative as that of their eunicid sister we do not consider it necessary to illustrate them for each species.

Jaw features. The maxillae have been illustrated for completeness of descriptions. Although they display specific differences, these differences are hard to quantify and use as diagnostic characters. In some species the distal tooth of the left maxilla II forms a large fang (Fig. 13F), whilst in most species there is no such distinction. However, the mandibles show more promise than the maxillae. In an attempt to discover new characters, we have compared the length of the protomandibles, the initial sclerotized tiny mandibles (Fig. 4H) as well as the shafts, in particular the relationship of the length of the mandible to length of the maxillary apparatus. In most onuphid genera the length of the mandible equals the length of the maxilla, whilst *Nothria* species have unusually long mandibular shafts. Exploring the possibility of a new distinctive character, we have included the ratio of length of mandible (base of shaft to lateral tip of sclerotized cutting plate) over length of maxillae (base of carrier to tip of maxilla I) in the descriptions (Fig. 4H,I).

The material examined, i.e. list of specimens used in this study with GenBank Accession numbers, BOLD process ID, and data on their sampling and storage is presented in Table S1. Information for the holotypes (date of sampling, place name, geographical coordinates and depth) has been listed with the registration and station numbers for each new species as it defines the type locality.

Measurements and counts in the description are of the holotype; the range for the paratypes is given in parentheses. Body width (without parapodia) is of chaetiger 10. Types of newly described species and other material examined are deposited in the Australian Museum, Sydney (AM) and the South Australian Museum, Adelaide (SAMA).

DNA extraction, amplification and sequencing

Molecular analyses included sequences obtained from 37 specimens of *Nothria* from deep Australian waters, five specimens of *Nothria conchylega* from various localities in the Northern Hemisphere and two outgroup onuphid species: *Australonuphis teres* (Ehlers, 1868) and *Hyalinoecia tubicola* (O. F. Müller, 1776) (Table S1). Genomic DNA was extracted from the 95% ethanol-fixed tissue samples using QuickExtract™ DNA Extraction Solution following the protocol: 100 μl of QuickExtract solution was added to each sample air-dried from ethanol, incubated for 45 min at 65°C, followed by 2 min at 98°C. Amplification of the targeted regions of COI, 16S rDNA and 28S rDNA was performed with TaKaRa Ex Taq HS kit in a 25 μl reaction consisting of 1 μl of DNA template, 17.35 μl of purified water, 2.5 μl of 10x Ex Taq buffer, 2 μl of dNTP mixture, 1 μl of each primer and 0.15 μl of TaKaRa Ex Taq HS. Amplification protocols and primers used for each marker are shown in Table S2. The amplified products were purified and bidirectionally sequenced by Macrogen Europe (Amsterdam, Netherlands). GenBank accession numbers and BOLD process IDs of all obtained sequences are listed in Table S1.

Sequence analysis

Sequences were manually edited using Sequencher v. 4.5 (Gene Codes, Ann Arbor, Michigan) and aligned with MUSCLE algorithm (Edgar, 2004) in MEGA7 (Kumar *et al.,* 2016) with the following settings: –400 gap opening penalty, –50 gap extension penalty. Substitution models for each marker were selected in jModelTest v. 2.1.5 (Guindon & Gascuel, 2003; Darriba *et al.,* 2012) based on corrected Akaike Information Criterion (AICc). The following models were selected: 16S and 28S: GTR+G, COI 1st codon position: SYM+G+I, 2nd codon position: F81+I, 3rd codon position: HKY+G. Phylogenetic analysis of individual markers and combined dataset of three markers was done using Bayesian inference in MrBayes v3.2.2 (Ronquist *et al*., 2012). Two independent and simultaneous runs with flat prior probabilities and four chains were run for 10,000,000 generations. Convergence between the runs was verified using the Average Standard Deviation of Split Frequencies (ASDSF) calculated in MrBayes. Tracer v. 1.7 (Rambaut *et al*., 2018) was used to examine MCMC sampling statistics and parameter estimates and to verify stationarity with plots of log likelihoods. An effective sample size (ESS) higher than 200 for the log likelihood and all other parameters when the two runs were combined was considered a good mixing and the results of analyses were accepted. Trees were sampled every 1000th generation. Tracer v. 1.7 was used to identify the burn-in phase and the first 25% resulting trees were excluded. The remaining trees were summarized into a majority rule consensus tree with posterior probabilities (PP) indicating the support for each clade. The trees were visualized using FigTree v.1.3.1 (Rambaut, 2010) and later edited in CorelDraw.

Mean uncorrected pairwise genetic distances (p-distances) for each of the main clades (within clade mean distances) and between the main clades were calculated in MEGA7 (Kumar *et al*., 2016).

The single-marker trees generated in MrBayes v3.2.2 were used as the input trees in the species delimitation analyses with Bayesian implementation of the Poisson Tree Processes (bPTP) model (Zhang *et. al*., 2013). All analyses were run on the bPTP web server (http://species.h-its.org/) with default settings and pruned outgroups. Final species delimitation hypotheses were formulated based on the combined evidence from morphology and three independent bPTP analyses of individual molecular markers.

Results

Species delimitation results

The combined data of the three concatenated markers set has 1821 aligned positions (COI with 658 positions, 16S rDNA with 497 positions, and 28S rDNA with 666 positions). The Bayesian analysis of the combined dataset yielded ten well supported clades (A–J) (Fig. 1) with PP = 1.00 which we interpret as putative species with an exception of clade C. The same ten clades with support of PP = 0.99–1.00 were present on the three single gene trees except the clade H which was absent on the 16S tree due to missing data (Figs S1–S3). Three larger and well supported (PP = 0.99–1.00) clades combining several species (clade J+D+I, clade B+E+H, and clade A+F) were recovered on the tree constructed based on the combined dataset. Notably, these clades were not recognized or not well supported on the single marker trees, except the clade J+D+I highly supported (PP = 1.00) on the 16S tree (Fig. S2) and the clade B+E+H highly supported (PP = 1.00) on the 28S tree (Fig. S3).

Initial morphological analysis indicated the presence of nine morphotypes in the studied material. Clades D and I demonstrated the most similar morphology but were later re-examined and found to have minor differences in anterior hooks (see taxonomic remarks). One of the clades was assigned to the previously described species *Nothria otsuchiensis* (clade C). Further, the well-known Northern Hemisphere species *Nothria conchylega*, that was added for comparison, was distinguished by a separated clade (clade J). Specimens from other clades did not match the morphology of any of the known *Nothria* species.

With the exception of clade C (*Nothria otsuchiensis* complex), which was comprised of highly divergent sequences, all other clades had significantly lower values of within clade mean p-distances than between clade mean p-distances (Table S3). The within mean p-distances in the *N. otsuchiensis* complex were 14.9% in COI, 5.75% in 16S and 0.41% in 28S, while in all other species they ranged 0–3.88% in COI, 0–0.94% in 16S, and 0–0.26 % in 28S. The between clade p-distances were 13.6–23.7% in COI, 5.5–23.9% in 16S and 0.8–9.3% in 28S.

Thirteen putative species were recovered in the COI bPTP analysis with the marker missing from two molecular operational taxonomical units (MOTUs) (Fig. S4), twelve putative species were recovered in 16S (Fig. S5) and 28S (Fig. S6) analyses (marker missing from two and one MOTUs respectively). Delimitation of eight putative species (Clades A, D–J) was congruent in all analyses, including morphology (Fig. 1). Clade C comprised four putative species in each gene analysis. Notably, results of the COI and 16S delimitations were similar while the 28S analysis gave a conflicting delimitation scheme. Clade B was delimited as a single species in the 28S analysis and also based on morphology, however, the COI and 16S analyses recovered the specimen W.49030 as a separate putative species.

Overall posterior delimitation probability (PDP) in the COI analysis ranged from 0.94 to 1.00 except for clades C and B; in 16S between 0.81 and 0.99. In the 28S analysis, PDP values were low, ranging from 0.43 to 0.88, which is significantly lower than the recommended cut-off value of 0.91 (PTP web portal) (Figs S4–S6).

The combination of species delimitation results based on morphology and three individual markers allowed recognition of eight new species of *Nothria* and the *Nothria otsuchiensis* species complex which potentially may constitute several species (Fig. 1). The detailed descriptions of all species are provided below.

Exploratory morphological features

In the search for new diagnostic characters, we evaluated the widths of the anterior hooks and defined them as very slender (diameter less than 15 μm), slender (diameter 15–30 μm) and robust (diameter more than 30 μm). These criteria may prove helpful and have been incorporated into diagnoses and descriptions. Five of the eight new species have robust and three species have slender hooks on chaetiger 1. Seven species have at least some simple hooks on chaetiger 1, while only the smallest species, *N. minima* sp. nov., has only

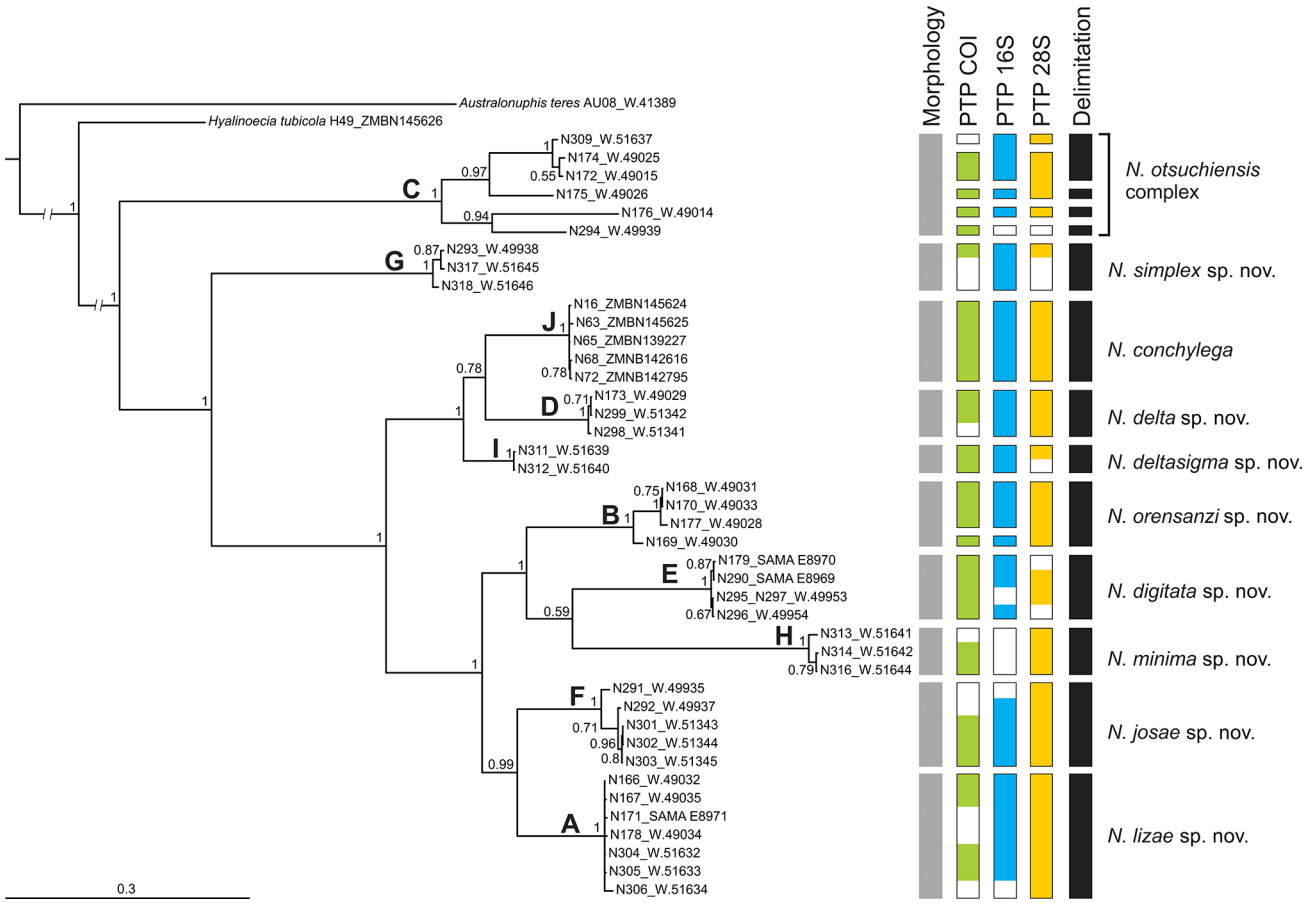

Figure 1. Consensus tree from the Bayesian analysis of the combined COI, 16S and 28S dataset; numbers on nodes indicate Bayesian posterior probabilities; capital letters correspond with the clades discussed in the text. Species delimitation results inferred by morphology and DNA-based methods (COI, 16S, and 28S) are indicated right to the consensus tree followed by the final hypothesis based on all evidence combined. White bars indicate missing data.

pseudocompound to compound hooks on chaetiger 1. Only two species, *N. delta* sp. nov. and *N. deltasigma* sp. nov., have robust simple unidentate or almost unidentate hooks on chaetiger 1 like the Northern Hemisphere *N. conchylega* while all other species in the study have clearly bidentate hooks.

Other newly explored characteristics were certain jaw features. The maxillary apparatuses of all new species are fully illustrated, and the maxillary formulae are presented in the descriptions. However, the only scorable characteristic of the maxillae is that the left maxilla II of five species terminates into a distal fang while in the other three species the regular dentation continues to the top. The mandibles are also very similar to each other. They are illustrated in ventral view, showing the long shafts and the calcium-covered cutting plates. The cutting plates end distally in two median teeth and the large distal tooth in all species. The sclerotized protomandibles visible through the calcium cutting plate is an interesting feature. The protomandibles are the first mandibular structures laid down in the early developmental stages and are retained as the mandible develops around them (Paxton & Safarik, 2008). These protomandibles are in a dorsal position and are also visible in ventral view through the calcium cutting plate. In most species they are short, reaching no further than the posterior end of the cutting plate (Fig. 10F) while in *N. delta* sp. nov. and *N. deltasigma* sp. nov. they are longer, being visible beyond the cutting plates (Fig. 4H).

Comparing the length of the mandibles to the length of the maxillary apparatus, we find it striking that in *Nothria* species the mandibles are always longer than the maxillae while in most other genera they are equally long (see illustrations in Paxton, 1986a). This led us to explore whether the ratio of length of mandibles/length of maxillae could present a possible new discriminatory character. The ratio was calculated for all species and varied from 1.20 in *N. josae* sp. nov. to 1.34 in *N. orensanzi* sp. nov. To test the reproducibility of this feature we tested several specimens of a species and found that the results were not constant within a species. The greatest discrepancies were found for *N. minima* sp. nov. where the results for three jaw apparatuses ranged from 1.11 to 1.19 but a fourth result was 1.44, giving a mean of 1.22. In view of this variability of individual specimens it cannot be considered a reliable character. However, the ratios are included in the descriptions to encourage other workers to explore it further.

A hitherto little utilized feature is the consistency and structure of the tubes which are constructed by the inhabitants. Of course, the materials used depend on the availability in the particular habitat, but the structure of the tube is often distinctive and species specific. In this study, the tubes of all new species are illustrated with colour photographs to highlight the different types of construction.

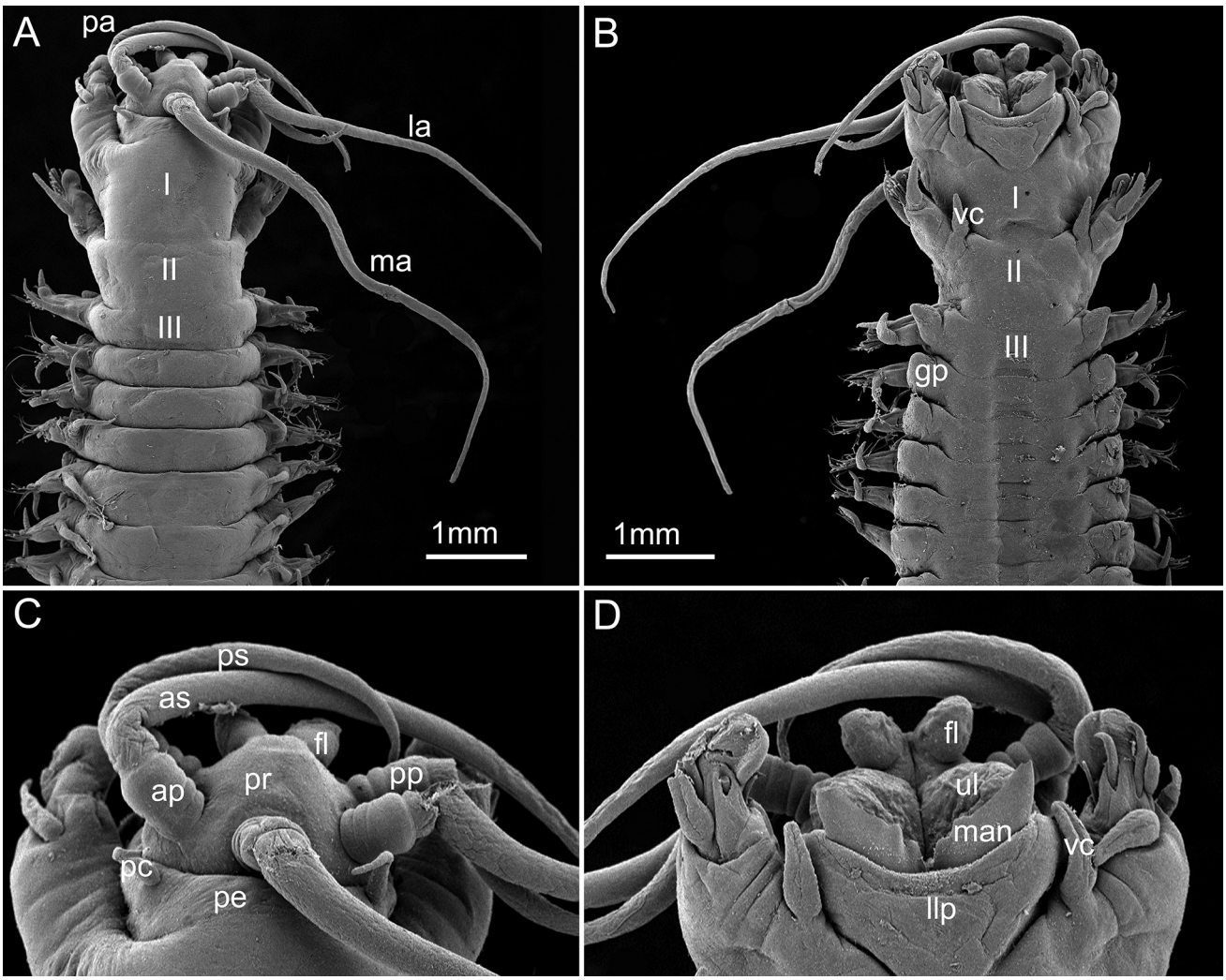

Figure 2. *Nothria delta* sp. nov. SEM micrographs of paratype AM W.51448. (*A*) anterior part, dorsal view; (*B*) same, ventral view; (*C*) enlargement of prostomium and associated structures, dorsal view; (*D*) same, ventral view. *ap*, antennophore; *as*, antennostyle; *fl*, frontal lip; *gp*, glandular pad; *la*, lateral antenna; *llp*, lower lip; *ma*, median antenna; *man*, mandible; *pa*, palp; *pc*, peristomial cirrus; *pe*, peristomium; *pp*, palpophore; *ps*, palpostyle; *pr*, prostomium; *ul*, upper lip; *vc*, ventral cirrus; *I–III*, chaetigers 1–3.

Distribution remarks

Three species (*N. deltasigma* sp. nov., *N. digitata* sp. nov. and *N. minima* sp. nov.) were collected only in a single station and thus at one location and depth only. Two species (*N. josae* sp. nov. and *N. simplex* sp. nov.) were found in two stations each; the former at 999–1093 m and the latter at 2350–2518 m depth, both off northern NSW and southern Queensland. Although *N. lizae* sp. nov. was collected in six stations, five were from off Tasmania in 1422–2028 m and one far apart in the GAB in 1570–1636 m depth. *Nothria orensanzi* sp. nov. was collected off Tasmania in three samples in 2010–2820 m and in one station off southern NSW in 2636–2650 m. *Nothria delta* sp. nov. was the most widely distributed species, being collected in four stations, of which two were off Tasmania in 2010–2028 m, one off southern NSW in 2636–2650 and one in the GAB in 1772–1808 m depth.

By far the richest general area for *Nothria* collection was off Tasmania, followed by the GAB, southern NSW, northern NSW, and Queensland. This could be related to the collecting effort as Tasmania was visited by the RV *Investigator* during IN2015_E02 (Trial Cruise), IN2017_V03 (Sampling the Abyss) and IN2018_V06 (Seamount Coral Survey). Furthermore, the Seamount Coral Survey concentrated on a completely different habitat than the other cruises. This is borne out by the results as *N. deltasigma* sp. nov. and *N. minima* sp. nov. were only collected during the Seamount cruise, while *N. orensanzi* sp. nov. was collected during the Trial and Abyss cruises, *N. lizae* sp. nov. during the Trial and Seamount cruises, and *N. delta* only during the Trial cruise. Most stations yielded only one species of *Nothria* while IN2017_V03_056 from Jervis Marine Park harboured *N. delta* sp. nov. and *N. orensanzi* sp. nov. However, the most astounding examples of sympatry were discovered off Tasmania. *Nothria delta* sp. nov., *N. lizae* sp. nov. and *N. orensanzi* sp. nov. were collected together in each of the stations IN2015_E02_021 and 022 from the Huon Marine Park as well as *N. lizae* sp. nov. and *N. deltasigma* sp. nov. in station IN2018_V06_169 from the flat area south of Brians.

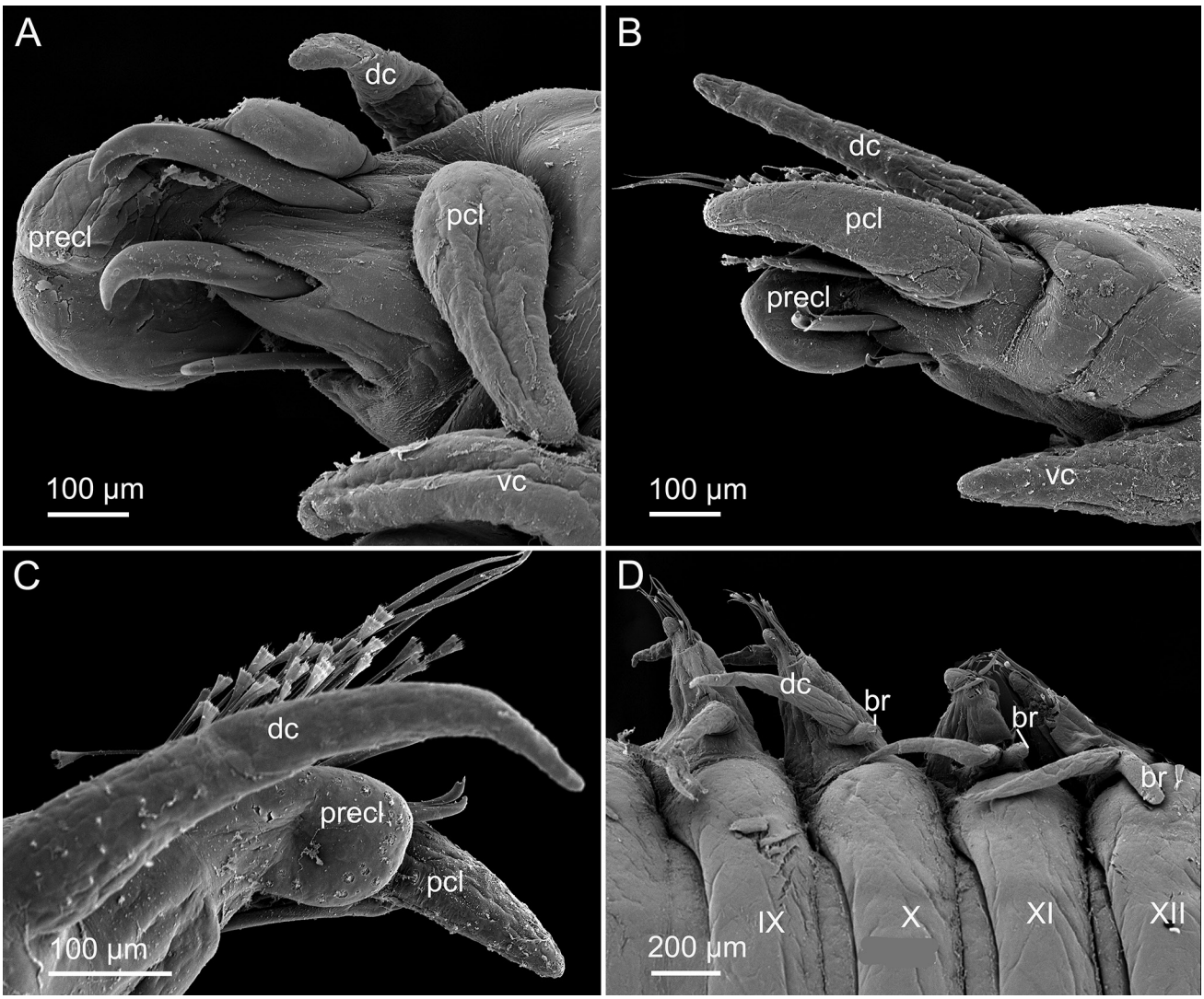

Figure 3. *Nothria delta* sp. nov. SEM micrographs of paratype AM W.51448. (*A*) parapodium of chaetiger 1, posterior view; (*B*) parapodium of chaetiger 2, same view; (*C*) parapodium of chaetiger 3, anterior view; (*D*) parapodia 9–12 to show appearance of branchiae, dorsal view. *br*, branchia; *dc*, dorsal cirrus; *pcl*, postchaetal lobe; *precl*, prechaetal lobe; *vc*, ventral cirrus; *IX–XII*, chaetigers 9–12.

Taxonomy

Family Onuphidae Kinberg, 1865

Subfamily Hyalinoeciinae Paxton, 1986

Genus *Nothria* Malmgren, 1867

Diagnosis (adapted from Budaeva & Paxton, 2013). Body short, up to 100 segments. Prostomium anteriorly rounded to subtriangular, palps short, antennae moderately long; palpophores and antennophores with 2–5 rings. Peristomial cirri present; nuchal grooves straight. Anterior 2–3 pairs of parapodia modified, enlarged and directed anteroventrally, with large auricular prechaetal lobes. Dorsal cirri digitate to subulate, ventral cirri subulate on anterior 2–3 chaetigers. Branchiae present or absent, usually with single filaments. Uni- to bidentate (rarely tridentate) simple, pseudocompound or compound hooks on anterior modified parapodia, usually with hoods. Pectinate chaetae usually with rolled margins, so-called "scoop-shaped", rarely flat, from chaetigers 2–3, rarely later. Subacicular hooks in median position from chaetigers 7–15, rarely later. Tubes dorsoventrally flattened with thin inner parchment-like layer covered with shell fragments, small stones and foraminiferans.

Nothria delta sp. nov.

urn:lsid:zoobank.org:act:6A42BD06-7979-44A8-90EC-D0806F0632AF

Figs 1, 2–5, Tables 1, 2, S1

Nothria sp. nov. 2.—Gunton *et al.*, 2021:75, fig. 16E.

Holotype. Australian Museum (AM) W.51342, IN2015_E02_22; 11 Apr 2015; Australia, Tasmania, Huon Marine Park; 44.3°S 147.36°E; 2010 m depth. **Paratypes** (3): AM W.49029, IN2015_E02_21 (1); AM W.51341, IN2015_E02_21 (1); AM W.51448.001, mounted for SEM, AM W.51448 worm tube, IN2017_C01_207 (1).

Other material examined (13). AM W.53845, IN2017_C01_207 (9); SAMA E8968, IN2017_C01_207 (3); AM W.49933, IN2017_V03_56 (1).

Comparative material. AM W.198975. *Nothria conchy-*

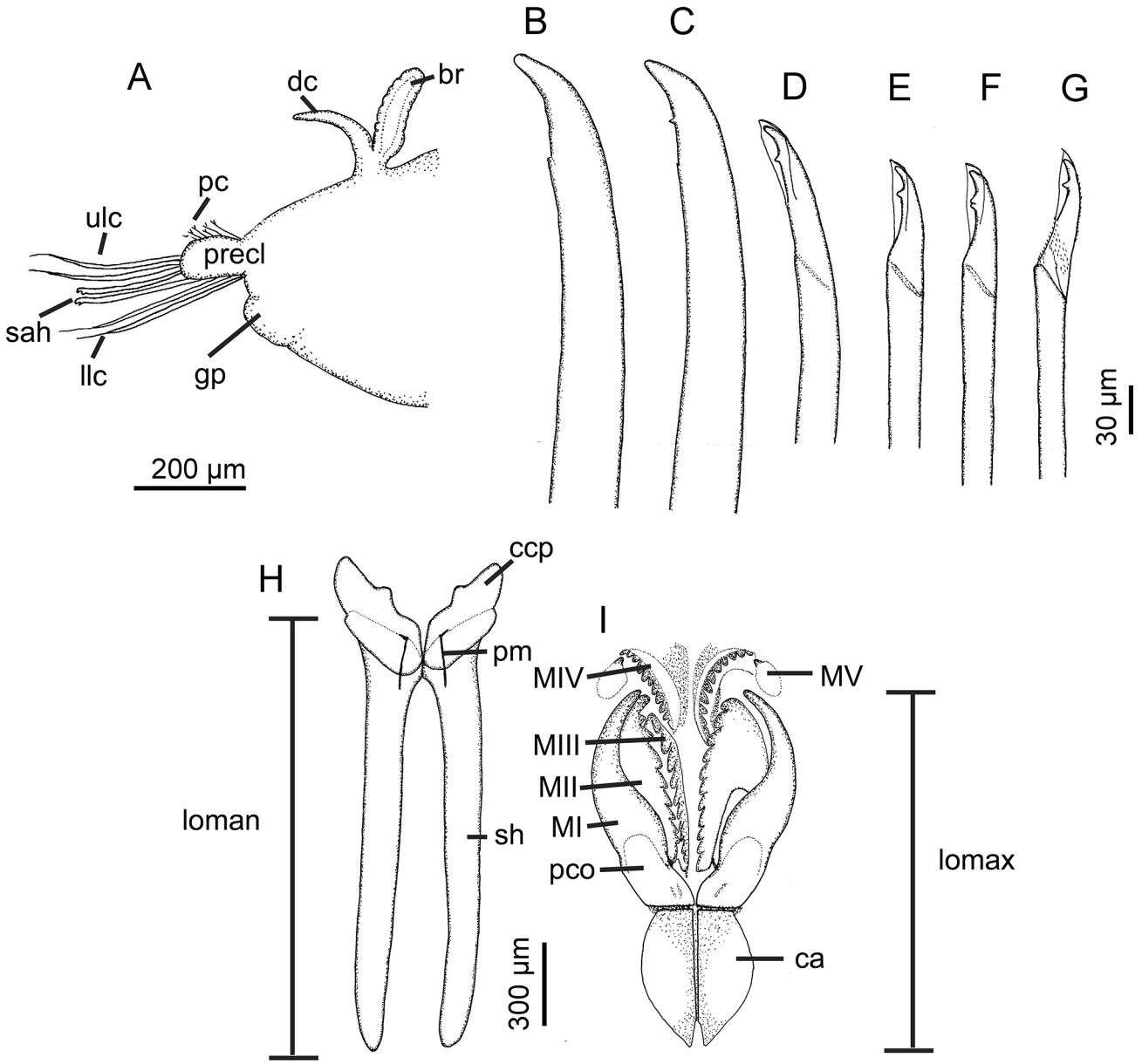

Figure 4. *Nothria delta* sp. nov. Line drawings of paratype AM W.51341. (*A*) parapodium of chaetiger 17 to show small branchia; (*B*) robust unidentate simple hook from chaetiger 1; (*C*) robust weakly bidentate simple hook from chaetiger 1; (*D*) slender bidentate pseudocompound hook from chaetiger 1; (*E*) slender bidentate pseudocompound hook from chaetiger 2; (*F*) slender tridentate pseudocompound hook from chaetiger 2; (*G*) slender bidentate compound hook from chaetiger 3; (*H*) mandibles, ventral view; (*I*) maxillae, dorsal view. *br*, branchia; *ca*, carrier; *ccp*, calcareus cutting plate; *dc*, dorsal cirrus; *gp*, glandular pad; *llc*, lower limbate chaetae; *loman*, length of mandible; *lomax*, length of maxillae; *pc*, pectinate chaetae; *pco*, pulp cavity opening; *pm*, protomandible; *precl*, prechaetal lobe; *sah*, subacicular hooks; *sh*, shaft; *ulc*, upper limbate chaetae.

lega. Norway, Ramfjord near Tromsø, 63.55°N 19.08°E, in mud and sand, 50 m depth, coll. Eivind Oug, 23 Jan 1978 (5).

Diagnosis. Eyes absent; antennae extending to chaetiger 10–14; short branchiae from chaetiger 10–12; first 3 chaetigers with anterior hooks: robust uni- to weakly bidentate simple and slender bidentate pseudocompound hooks on chaetiger 1; slender bi- to weakly tridentate pseudocompound hooks on chaetiger 2 and very slender bidentate pseudocompound to compound hooks on chaetiger 3; pectinate and limbate chaetae from chaetiger 2; subacicular hooks from chaetiger 10–14.

Description. All examined specimens lacking posterior ends. Length of holotype 18 mm for 29 chaetigers, width 2.7 mm; paratypes 7.5–18 mm (15–32 chaetigers) long, 2.5 mm wide. Non-type material ranging from 1.2–2.2 mm in width. Alcohol-stored specimens overall cream-coloured. Holotype lacking any pigmentation but some specimens with brown spot dorsally on anterior part of prostomium. Prostomium anteriorly rounded to subtriangular, wider than long, with 2 ovoid frontal lips, separated from each other by small space (Fig. 2A–D). Palpo- and antennophores with 2–3 proximal rings and longer distal ring. Palpostyles tapering, extending to chaetiger 1, lateral antennostyles to chaetiger 10 (4–10), median antennostyle extending to chaetiger 14 (9–14); antennostyles tapering gradually, becoming very thin towards distal end (Fig. 2A–B). Nuchal grooves straight, with small middorsal separation. Eyes absent. Ventral upper lip rounded,

lower lip subtriangular, neither with median section (Fig. 2D). Peristomium short, peristomial cirri inserted subdistally on peristomium, about as long as peristomium.

First chaetiger greatly enlarged, about three times as long as peristomium, chaetiger 2 about twice length of peristomium, chaetigers 3–6 about as long as peristomium, subsequent ones slightly longer (Fig. 2A,B). Anterior 3 pairs of parapodia modified; first pair greatly enlarged, directed forward, extending slightly beyond anterior margin of prostomium, with large auricular prechaetal lobes, subulate postchaetal lobes, dorsal and ventral cirri (Fig. 3A). Second pair of parapodia similar but smaller, with smaller prechaetal lobes (Fig. 3B). Third pair (Fig. 3C) only slightly larger than subsequent parapodia, directed laterally, with further reduced prechaetal lobes; ventral cirri transitioning to glandular pads. From chaetiger 4 onwards parapodial structures becoming more uniform; dorsal cirri gradually becoming thinner and shorter, prechaetal lobes becoming short and rounded, postchaetal lobes gradually decreasing, last on chaetigers 15 (13–15), ventral cirri replaced by round glandular pads from chaetiger 4 (Fig. 2B). Simple branchiae present as very short oval filament from chaetiger 12 (10–12) (Fig. 3D), increasing only slightly in length (Fig. 4A) to remain as relatively short structure to end of incomplete worms; total extent unknown.

First pair of parapodia with 2 robust uni- (Fig. 4B) to weakly bidentate simple (Fig. 4C) and 1–2 slender bidentate pseudocompound (Fig. 4D) hooded hooks. Second pair of parapodia with slender bi- (Fig. 4E) to occasionally tridentate (Fig. 4F) pseudocompound hooks, as well as 2 limbate and many pectinate chaetae with 18–20 teeth. Third pair of parapodia with 2–4 slender, bidentate pseudocompound to compound hooks with serrated upper shaft and appendage (Fig. 4G), 3–4 limbate chaetae and numerous (up to 30) scoop-shaped pectinate chaetae with 18–20 teeth (Fig. 3C). Hooks absent from chaetiger 4, limbate and pectinate chaetae present in reduced numbers presumably to end of body. Subacicular hooks present singly from chaetigers 14 (10–14), as pairs from chaetiger 16 (12–16). Pygidium unknown.

Mandibles (Fig. 4H) highly calcified, almost white, except for darkly sclerotized, unusually long protomandibles. High cutting plates with weakly defined median and large distal tooth. Maxillae (Fig. 4I) with little sclerotization except for teeth and attachment lamellae. Maxillary formula: MI = 1+1; MII = 9+10; MIII = 9+0; MIV = 10+10; MV = 1+1. Ratio of mandibles/maxillae = 1.2. Flattened tube (Fig. 5A), covered with small pieces of shells and foraminiferans, lining transparent.

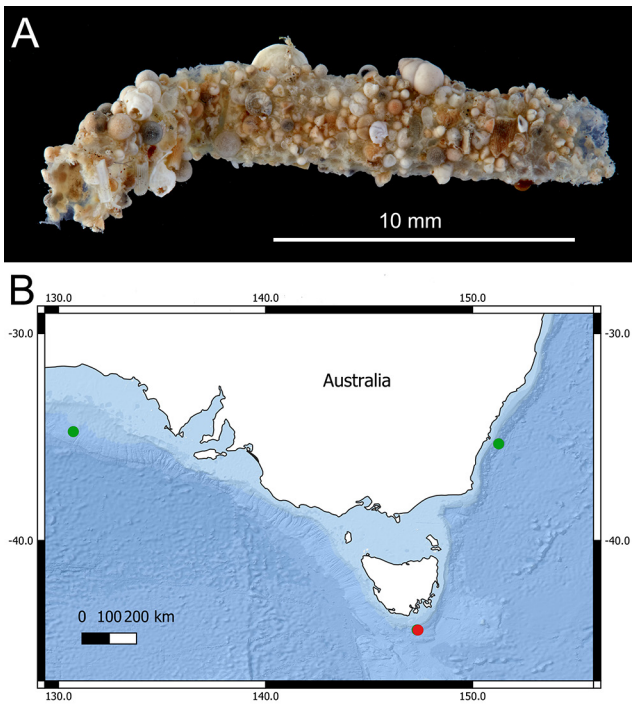

Figure 5. *Nothria delta* sp. nov. (*A*) photograph of tube of paratype AM W.51448. (*B*) map of distribution; red dot represents type locality, green dots other sites of collection.

Remarks. The new species shares the possession of unidentate or falcate simple anterior hooks with five *Nothria* species: *N. conchylega, N. edwardsi, N. occidentalis* Fauchald, 1968, *N. anoculata* Orensanz, 1974 and *N. grossa* Imajima, 1989. *Nothria edwardsi* can be most easily distinguished from the group by having only two pairs of anterior parapodia bearing hooks (Arias & Paxton, 2016) while the others have three. Although the morphometric and meristic characteristics of the remaining species are

Table 1. Distinguishing features of *Nothria anoculata, N. delta* sp. nov., and *N. deltasigma* sp. nov. Abbreviations: *C*, compound; *PC*, pseudocompound.

character	*Nothria anoculata* Orensanz, 1974	*Nothria anoculata fide* Orensanz, 1990	*Nothria delta* sp. nov.	*Nothria deltasigma* sp. nov.
maximum width (mm)	1.2	2.0	2.7	2.4
start of branchiae	chaetiger 10–12	chaetiger 10–14	chaetiger 10–12	chaetiger 10–12
branchiae, relative length	twice length of dorsal cirrus	twice length of dorsal cirrus	branchia = dorsal cirrus	branchia = dorsal cirrus
antennae, antennoph.rings	incompletely ringed	2–3 rings	3–4 rings	3–4 rings
antennae, to chaetiger	lateral to 7; median to 10	lateral to 9; median to 6	lateral to 10; median to 14	lateral to 11; median to 13
last postchaetal lobe	chaetiger 12	chaetiger 13–15	chaetiger 13–15	chaetiger 13–16
hooks on chaetiger 1	robust simple only	robust simple only	robust simple & slender PC	robust simple & slender simple
hooks on chaetiger 2	PC only	simple & PC	PC only	simple & PC
hooks on chaetiger 3	PC to C	PC to C	PC to C	PC to C
no. of teeth on pectinates	14	12	18–20	18–20
start of subacicular hooks	chaetiger 9–11	chaetiger 11–13	one ch. 10–14; two ch. 12–16	one ch. 11–14; two ch. 12–16
distribution	off Buenos Aires, Argentina	subantarctic areas	off Tasmania, Jervis Bay MP and Great Australian Bight	Tasmanian seamounts
depth	700–900 m	75–900 m	1772–2650 m	1286–1414 m

Table 2. Distinguishing features of Australian deep-water *Nothria* species collected during present study. *n/a*, not applicable; *PC*, pseudocompound; *C*, compound.

character	*delta*	*deltasigma*	*digitata*	*josae*	*lizae*	*minima*	*orensanzi*	*otsuchiensis* complex	cf *paxtonae* Imajima, 1999	*simplex*
maximum width (mm)	2.7	2.4	2.3	2.0	4.0	1.6	2.6	3.0	1.3	2.8
shape of anterior prostomium	rounded to subtriangular	rounded to subtriangular	rounded	subtriangular	rounded	rounded to subtriangular	rounded to subtriangular	rounded to subtriangular	rounded	rounded
antennae, to chaetiger	median 9–14; lateral 4–10	median 13; lateral 11	median 7–9; lateral 7–8	median 9–11; lateral 7–9	median 11–18; lateral 9–14	median 6–9; lateral 4–7	median 8–15; lateral 6–11	median 4–5; lateral 3–4	median 6; lateral 5	median 5; lateral 4
rings of palps and antennae	3–4	3–4	4–5	3–4	3–4	2–3	2–3	2–3	2–3	3–4
eyes	absent	absent	small anterior; large posterior	large posterior	absent	absent	absent	sm.ant.pres/abs la.post.pres/abs	none visible	absent
branchiae from chaetiger	10–12	10–12	9–10	11–13	12–14	absent	absent	8–9	absent	10
branchiae, length	short	short	long	short	short	n/a	n/a	short to long	n/a	long
last postchaetal lobe on chaetiger	13–15	13–16	11–12	13–16	13–15	8–12	11–13	15	19	11–13
anterior chaetigers with hooks	3	3	3	3	3	3	3	3	2	2
hooks of chaetiger 1	simple & PC	simple	simple & PC	simple & PC	simple & PC	PC to C	simple & PC	simple & PC	PC	simple
tips of hooks chaetiger 1	uni- bidentate	uni- tridentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate
hooks of chaetiger 2	PC only	simple & PC	PC	simple & PC	simple & PC	PC to C	PC	simple & PC	PC	simple & PC
tips of hooks chaetiger 2	bi- to tridentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate
hooks of chaetiger 3	PC to C	PC to C	PC to C	PC to C	PC to C	PC to C	PC to C	PC to C	absent	absent
tips of hooks chaetiger 3	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	bidentate	n/a	n/a
pectinates from chaetiger	2	2	3	3	3	2	2	3	8	3
number of teeth on pectinates	18–20	18–20	14–16	18–20	20–22	16–20	20–25	20	12	20–25
subacicular hooks from chaetiger	10–14	11–14	10–11	9–12	10–13	9–10	11–13	10–15	8–9	13–14
left maxilla II	no distal fang	no distal fang	no distal fang	distal fang	distal fang	distal fang	distal fang	distal fang	?	distal fang
ratio mandibles/maxillae	1.2	1.3	1.2	1.2	1.2	1.2	1.3	1.3	?	1.2
tube	forams and small shells	large shell fragments	large shells	mixed sized shells	large shell fragments, pavement-like	similarly sized shells	mixed shells, elongate pieces placed transversely	small shell fragments and forams	forams	forams & shells
depth (m)	1772–2650	1422–1443	400	1013–1093	1422–2028	1202–1221	2010–2850	400–1761	1772–2650	2342–2518

exceedingly similar, all but *N. anoculata* possess two large posterior eyes, leaving *N. anoculata* as the morphologically most similar species to *N. delta* sp. nov.

Directly below, we are describing another anoculate species with unidentate simple anterior hooks that also closely resembles *N. anoculata.* The relationship between the three species will be detailed in Table 1 and discussed in the Remarks section of the next new species.

Etymology. The specific epithet refers to the manuscript name "D" of the new species in the Greek language.

Distribution. The holotype and paratypes (AM W.49029 and AM W.51341) were collected from off southern Tasmania in 2010–2028 m depth. Paratype AM W.51448 and 11 specimens were collected from the GAB, 1772–1808 m, while W.49933 was collected at Jervis Bay Marine Park in 2636–2650 m depth (Fig. 5B).

Nothria deltasigma sp. nov.

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Figs 1, 6–8, Tables 1, 2, S1

Holotype. Australian Museum (AM) W.51639, IN2018_V06_169; 14 Dec 2015; Australia, Tasmania, flat area south of Brians, 44.24–44.23°S 147.29–147.30°E; 1422–1443 m depth. **Paratypes** (2): AM W.51640, IN2018_V06_169 (1). AM W. 53497, mounted for SEM, IN2018_V06_169 (1).

Other material examined (7). AM W.53846, IN2018_V06_169 (7).

Diagnosis. Eyes absent; antennae extending to chaetiger 11–13; short branchiae from chaetiger 10–12; first 3 chaetigers with anterior hooks: robust uni- to weakly tridentate and slender bidentate simple hooks on chaetiger 1; robust uni- to bidentate simple hooks and slender bidentate weakly pseudocompound hooks on chaetiger 2 and very slender bidentate pseudocompound to compound hooks on chaetiger 3; pectinate and limbate chaetae from chaetiger 2; subacicular hooks from chaetiger 11–14.

Description. All examined specimens lacking posterior ends. Length of holotype 11 mm for 23 chaetigers, width 2.4 mm; paratypes 10 and 16 mm (15 and 32 chaetigers) long, 1.8 and 2.2 mm wide respectively. Non-type material ranging from 1.7–2.3 mm in width. Alcohol-stored specimens overall cream-coloured. Holotype lacking any pigmentation but some specimens with brown spot dorsally on anterior part of prostomium. Prostomium anteriorly rounded to subtriangular, wider than long, with 2 ovoid frontal lips, separated from each other by small space (Fig. 6A,B). Palpo- and antennophores with 2–3 proximal rings and a longer distal ring. Palpostyles tapering, extending to chaetiger 1, lateral antennostyles extending to chaetiger 11, median antennostyle to chaetiger 13 (in holotype); antennostyles tapering gradually, becoming very thin towards distal end (Fig. 6A). Nuchal grooves straight, with small middorsal separation. Eyes absent. Ventral upper lips rounded, lower lips subtriangular, neither with median section (Fig. 6B). Peristomium short, peristomial cirri inserted subdistally on peristomium, slightly longer than peristomium.

First chaetiger greatly enlarged, about three times as long as peristomium, chaetiger 2 about twice length of peristomium, subsequent chaetigers about 1.5 times as long as peristomium (Fig. 6A,B). Anterior 3 pairs of parapodia modified; first pair greatly enlarged, directed forward, extending slightly beyond anterior margin of prostomium (Fig. 6A,B), with large auricular prechaetal lobes, subulate postchaetal lobes, dorsal and ventral cirri. Second pair of parapodia similar but smaller, with smaller prechaetal lobes (Fig. 6C). Third pair only slightly larger than subsequent parapodia, directed laterally, with further reduced, tongue-like prechaetal lobes; ventral cirri transitioning to glandular pads (Fig. 6B). From chaetiger 4 onwards parapodial structure becoming more uniform; dorsal cirri gradually becoming thinner and shorter, prechaetal lobes becoming short and rounded, postchaetal lobes gradually decreasing, last on chaetigers 16 (13–16), ventral cirri replaced by round glandular pads from chaetiger 4. Simple branchiae present as short filament from chaetiger 11 (10–12), increasing only slightly in length (Figs 6D, 7G) remaining as relatively short structure until end of incomplete worms; total extent unknown.

First pair of parapodia with 2–3 robust uni- to weakly bi- (Fig. 7A) to tridentate (Fig. 7B) simple hooded hooks and a lower slender bidentate simple hook (Fig. 7C). Second pair of parapodia with 2–3 robust bidentate simple hooks (Fig. 7D), a slender bidentate weakly pseudocompound hook (Fig. 7E), as well as 2 limbate and numerous pectinate chaetae with 18–20 teeth. Third pair with 3–5 slender, bidentate pseudocompound to compound hooks with serrated upper shaft and appendage (Fig. 7F), limbate chaetae and numerous scoop-shaped pectinate chaetae (Fig. 6E). Hooks absent from chaetiger 4, limbate and pectinate chaetae present in reduced numbers presumably up to end of body. Subacicular hooks present singly from chaetiger 12 (11–14), as pairs from 14 (12–16). Pygidium unknown.

Mandibles (Fig. 7H) highly calcified, almost white, except for darkly sclerotized, unusually long protomandibles. High cutting plates with weakly defined median and large distal tooth. Maxillae (Fig. 7I) lightly sclerotized except for teeth and attachment lamellae; carriers with unusually dark outer edges and curved basal extensions, perhaps indicating imminent moult of jaws. Maxillary formula: MI = 1+1; MII = 8+8; MIII = 9+0; MIV = 8+11; MV = 1+1. Ratio of mandibles/maxillae = 1.3. Flattened tube (Fig. 8A), covered mainly with larger pieces of shells dorsally and ventrally, sides filled in with foraminiferans; lining transparent.

Remarks. Orensanz (1974) described the subspecies *N. conchylega anoculata* lacking the eyes that are present in the stem species from off Buenos Aires, Argentina from a depth of 700–900 m; Fauchald (1982) subsequently raised the subspecies to full specific level. *Nothria delta* sp. nov. and *N. deltasigma* sp. nov. are morphologically similar to each other and to *N. anoculata*. Some of the noticeable differences are in the presence of simple vs. pseudocompound anterior hooks on chaetiger 1 and 2 (Table 1). This could be interpreted as a function of size and thus a pseudocompound hook could be a juvenile characteristic as discussed by Orensanz (1990) and Budaeva & Paxton (2013). However, extrapolating from his drawings, the original Argentinian specimens consisted of a width of 1.2 mm (Orensanz, 1974: pl 7, fig 1) while our material measured 1.7–2.7 mm in width, having three chaetigers with anterior hooks, and thus representing the adult stage.

The differences between the three species are detailed in Table 1 and to the remaining species in Table 2. They can

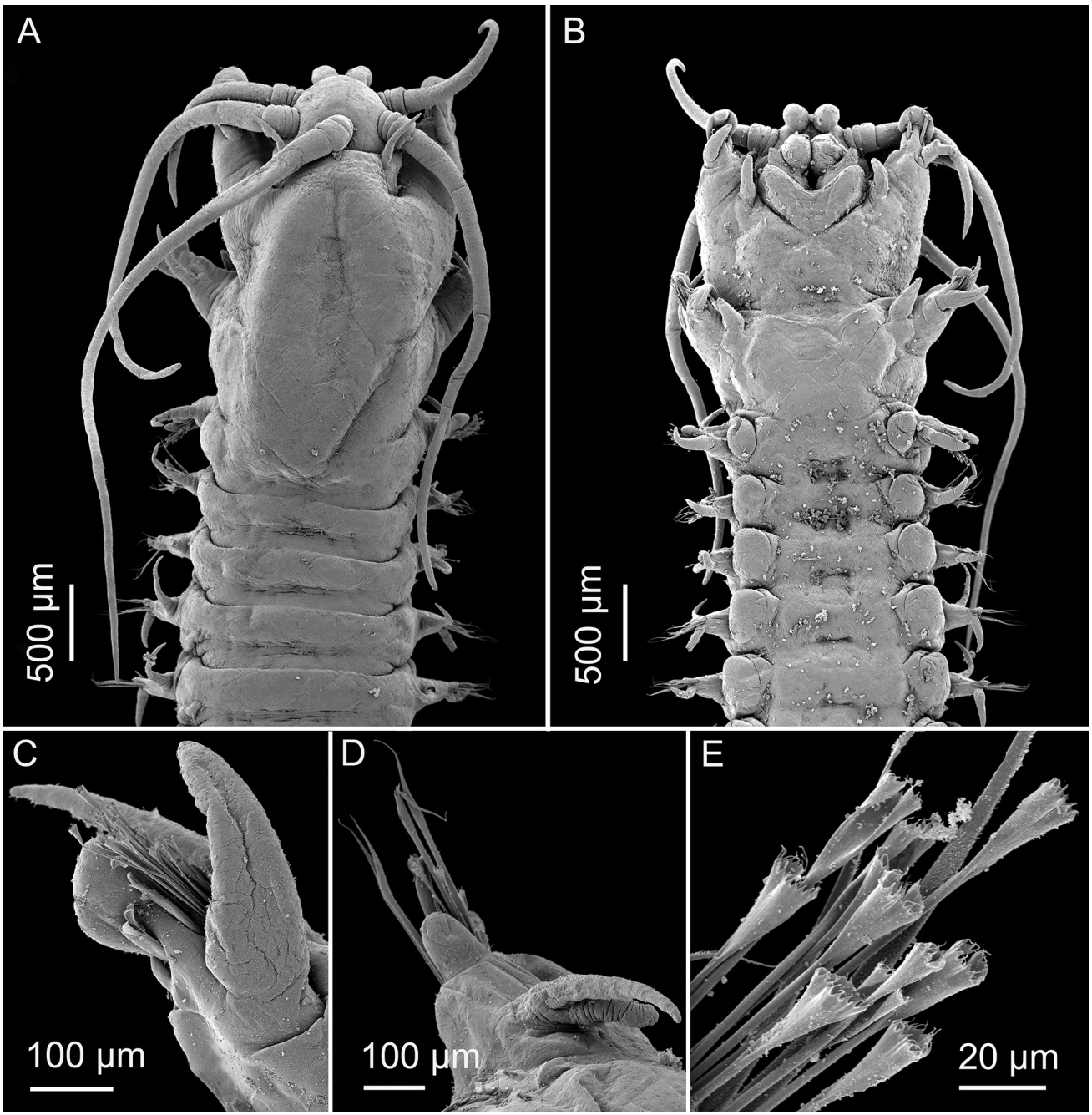

Figure 6. *Nothria deltasigma* sp. nov. SEM micrographs of paratype AM W.53497. (*A*) anterior part, dorsal view; (*B*) same, ventral view; (*C*) parapodium of chaetiger 2, posterior view; (*D*) chaetiger 14 to show branchia; (*E*) pectinate chaetae of chaetiger 3.

be summarized as follows: hooks of chaetiger 1 are only simple in *N. anoculata* and *N. deltasigma* sp. nov, simple and pseudocompound in *N. delta* sp. nov.; hooks of chaetiger 2 are only pseudocompound in *N. anoculata* and *N. delta* sp. nov, and simple and pseudocompound in *N. deltasigma* sp. nov.; hooks of chaetiger 3 are pseudocompound to compound in all three species. The antennae are shorter in *N. anoculata* (median to chaetiger 10) and longer (median to chaetiger 13–14) in *N. delta* sp. nov. and *N. deltasigma* sp. nov. Branchiae are about twice as long in *N. anoculata* as in the other two species.

In Table 1 we have listed the values stated in the original description of *N. anoculata* from Argentina separately from those given later for the subantarctic records by Orensanz (1990) as they do not always agree and seem to represent an expansion of the original *N. anoculata* definition to fit the wider distribution. Thus, it supports our suspicion that rather than a widely distributed species in the southern seas, *N. anoculata* as characterized by Orensanz (1990) represents a species complex.

Etymology. The specific epithet refers to the manuscript name "Ds" of the new species, referring to its great similarity and thus second version of "D" in the Greek language.

Distribution. The new species was only collected on the flat area south of Brians, south of Tasmania in 1422–1443 m depth (Fig. 9B).

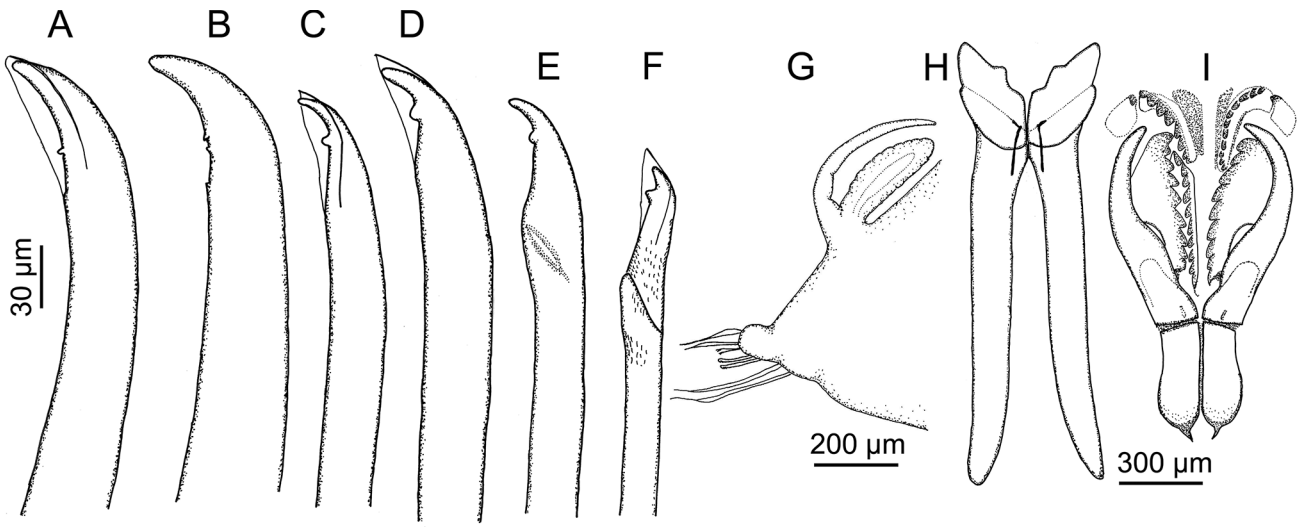

Figure 7. *Nothria deltasigma* sp. nov. Line drawings of holotype AM W.51639 (*A, C, F*) and paratype AM W. 51640 (*D, E, G, I*). (*A*) robust weakly bidentate simple hook from chaetiger 1; (*B*) robust weakly tridentate simple hook from chaetiger 1; (*C*) slender bidentate simple hook from chaetiger 1; (*D*) robust bidentate simple hook from chaetiger 2; (*E*) slender bidentate pseudocompound hook from chaetiger 2; (*F*) slender bidentate compound hook from chaetiger 3; (*G*) parapodium of chaetiger 17 to show branchia; (*H*) mandibles, ventral view; (*I*) maxillae, dorsal view.

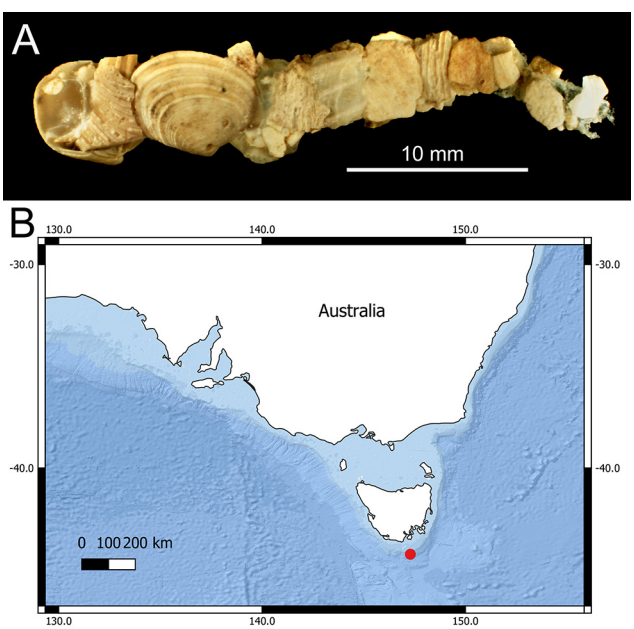

Figure 8. *Nothria deltasigma* sp. nov. (*A*) photograph of tube of AM W.53846. (*B*) map of distribution; red dot represents type locality.

Nothria digitata sp. nov.

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Figs 1, 9–11, Tables 2, S1

Holotype. SAMA E8969, IN2015_C02_174; 8 Dec 2015; Australia, Southern Ocean, Great Australian Bight, 34.25–34.24°S 132.62°E; 400 m depth. **Paratypes** (3): SAMA E8970, IN2015_C02_174 (1); AM W.49953, IN2015_C02_174 (1, anterior part on SEM pin, posterior part wet specimen); AM W.49954, IN2015_C02_174 (1).

Diagnosis. Eyes present, ventral upper lip with median section; antennae extending to chaetiger 7–9; branchiae long, digitate, from chaetiger 9–10; 3 first chaetigers with anterior hooks: robust bidentate simple and very slender bidentate pseudocompound hooks on chaetiger 1; slender and very slender bidentate pseudocompound hooks on chaetiger 2 and very slender bidentate pseudocompound to compound hooks on chaetiger 3; pectinate and limbate chaetae from chaetiger 3; subacicular hooks from chaetiger 10–11.

Description. All specimens lacking posterior ends. Length of holotype 18 mm for 22 chaetigers, width 2.3 mm; paratypes 9–19 mm (13–24 chaetigers) long, 2.2–2.3 mm wide.

Alcohol-stored specimens overall whitish without any pigmentation. Prostomium anteriorly rounded, wider than long, with 2 ovoid frontal lips separated by small space (Fig. 9A,B). Palpo- and antennophores with 3–4 proximal rings and longer distal ring. Palpostyles tapering, extending to chaetiger 1, antennostyles tapering gradually, lateral antennostyles extending to chaetiger 8 (7–8), median antennostyle generally longest, extending to chaetiger 9 (7–9); slightly shorter one in W.49953 (Fig. 9A) atypical. Nuchal grooves straight, with small middorsal separation. Small anterior eyespots on anterior part of prostomium between palps and lateral antennae (only left one visible in holotype), large posterior eyes between bases of palps and lateral antennae next to peristomium. Ventral upper lip squared with median section, lower lip subtriangular (Fig. 9B). Peristomium short, peristomial cirri inserted subdistally on peristomium, about twice as long as peristomium (Fig. 9A).

First chaetiger enlarged, slightly more than twice as long as peristomium, chaetiger 3 similar in length to following chaetigers. Anterior three pairs of parapodia modified (Fig. 9A,B). First pair greatly enlarged, directed forward, extending beyond anterior margin of prostomium, with large auricular prechaetal lobes and subulate postchaetal lobes. Parapodia 2 and 3 similar but smaller, with smaller prechaetal lobes. Third pair similar to subsequent parapodia, with small

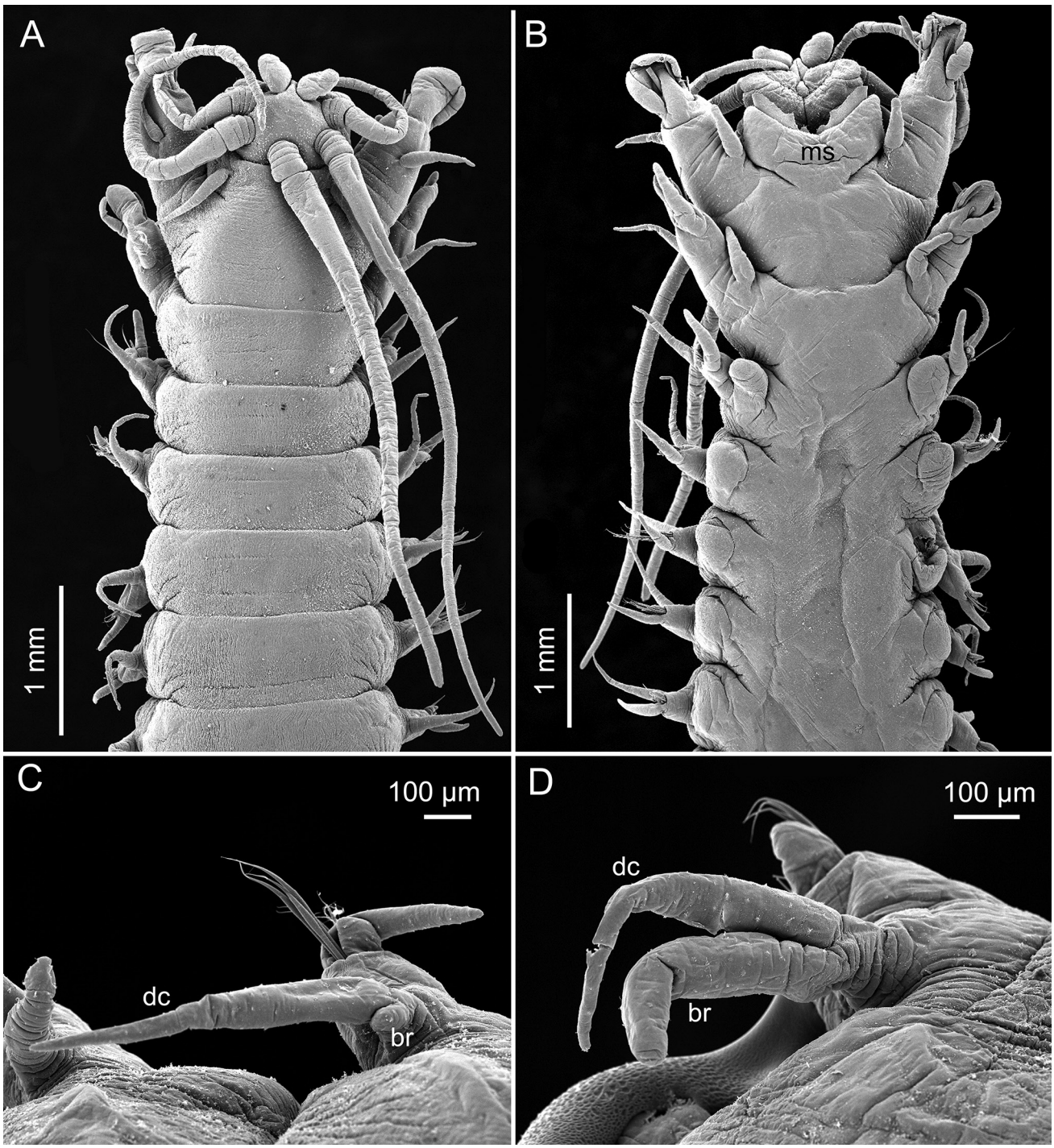

Figure 9. *Nothria digitata* sp. nov. SEM micrographs of paratype AM W.49953. (*A*) anterior part, dorsal view; (*B*) same, ventral view; (*C*) parapodium of chaetiger 9, showing first branchia, dorsal view; (*D*) parapodium of chaetiger 12, showing fully developed branchia, dorsal view; *br*, branchia; *dc*, dorsal cirrus; *ms*, median section of ventral upper lip.

tongue-like prechaetal lobes present into posterior region, last postchaetal lobes on chaetiger 12 (11–12). Ventral cirri of first two chaetigers subulate, becoming rounded on chaetiger 3 as transitioning to glandular pads (Fig. 9B). Dorsal cirri subulate from chaetiger 1, becoming cirriform, gradually thinner and shorter. Branchiae starting from chaetiger 9, 10 (9–10) as short filament (Fig. 9C), increasing to length of dorsal cirrus by chaetiger 12–14 (Fig. 9D); branchiae retaining length, dorsal cirrus becoming smaller and slenderer, by chaetiger 22–24 (end of largest types) branchia about 2–3 times as long as dorsal cirrus.

First pair of parapodia with 2 robust bidentate simple (Fig. 10A) and 1–2 very slender bidentate pseudocompound hooks (Fig. 10B). Second pair of parapodia with 2 slender (Fig. 10C) and 1–2 very slender bidentate pseudocompound hooks (Fig. 10D). Third pair of parapodia with 2–3 upper limbate chaetae, 3–5 scoop-shaped pectinate chaetae with 14–16 teeth, and 2–3 bidentate pseudocompound to compound

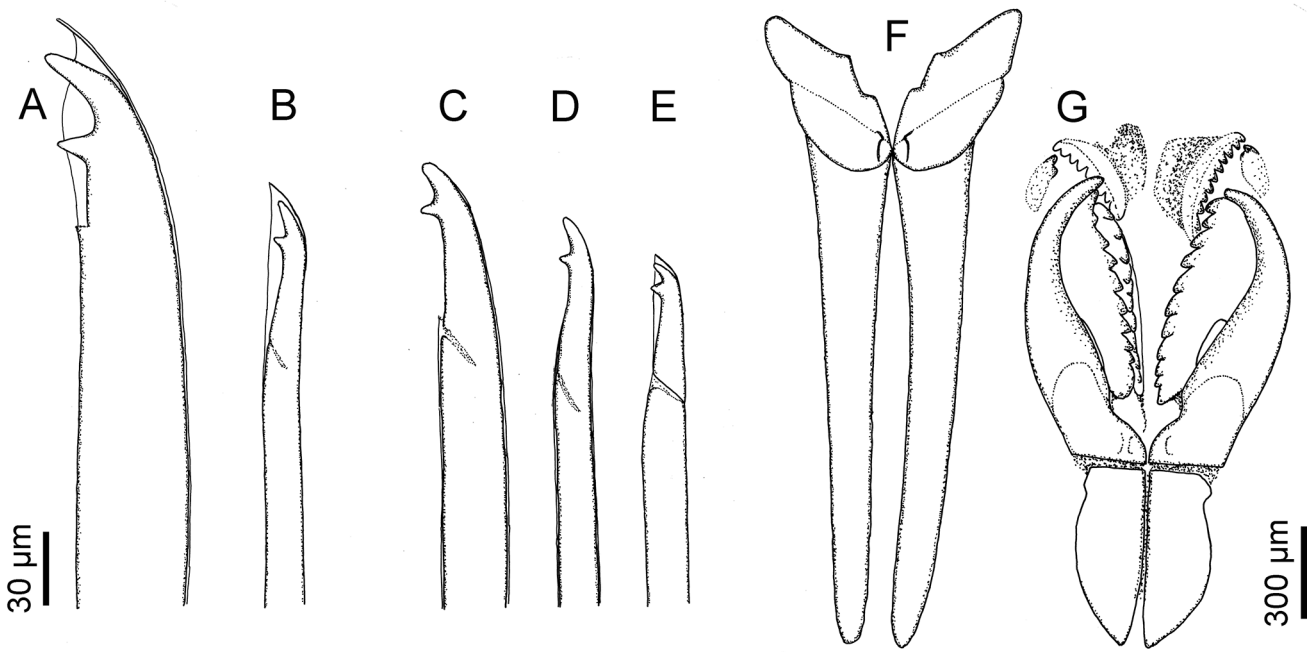

Figure 10. *Nothria digitata* sp. nov. Line drawings of holotype SAMA E8969. (*A*) robust bidentate simple hook from chaetiger 1; (*B*) very slender bidentate pseudocompound hook from same; (*C*) slender bidentate pseudocompound hook from chaetiger 2; (*D*) very slender bidentate pseudocompound hook from same; (*E*) slender bidentate compound hook from chaetiger 3; (*F*) mandibles, ventral view; (*G*) maxillae, dorsal view.

hooks (Fig. 10E). Anterior hooks absent from chaetiger 4, upper and lower limbate chaetae and pectinate chaetae present to end of fragments (presumably end of body). Subacicular hooks present singly from chaetiger 11 (10–11), as pairs from chaetiger 13 (11–13). Pygidium unknown.

Mandibles (Fig. 10F) highly calcified, white, except for short darkly sclerotized protomandibles; shafts long and slender, cutting plates high with weakly defined median and large distal tooth. Maxillae (Fig. 10G) overall whitish, fangs and teeth light brown, ligaments and attachment lamellae more sclerotized, appearing dark brown. Maxillary formula (based on holotype): MI = 1+1, MII = 9+10; MIII = 10+0, MIV = 8+9, MV = 2+2. Ratio of mandibles/maxillae = 1.2. Flattened tube, lining transparent, covered with pieces of shells (often larger than width of worm), laterally filled in with foraminiferans and other small fragments (Fig. 11A).

Remarks. *Nothria digitata* sp. nov. resembles *N. otsuchiensis* in having eyes, long branchiae from chaetiger 9–10 and subacicular hooks from chaetiger 10 (Table 2). The two species differ in that *N. digitata* sp. nov. has digitate rather than flat branchial filaments, 11–12 postchaetal lobes rather than 14–17, pseudocompound hooks on chaetiger 2 rather than simple and pseudocompound hooks. Furthermore, the new species displays no pigmentation pattern while *N. otsuchiensis* has a brown spot on each segment.

Etymology. The name of the new species is suggested by its long, digitate branchiae.

Distribution. *Nothria digitata* sp. nov. was collected from the GAB, in 400 m depth (Fig. 11B).

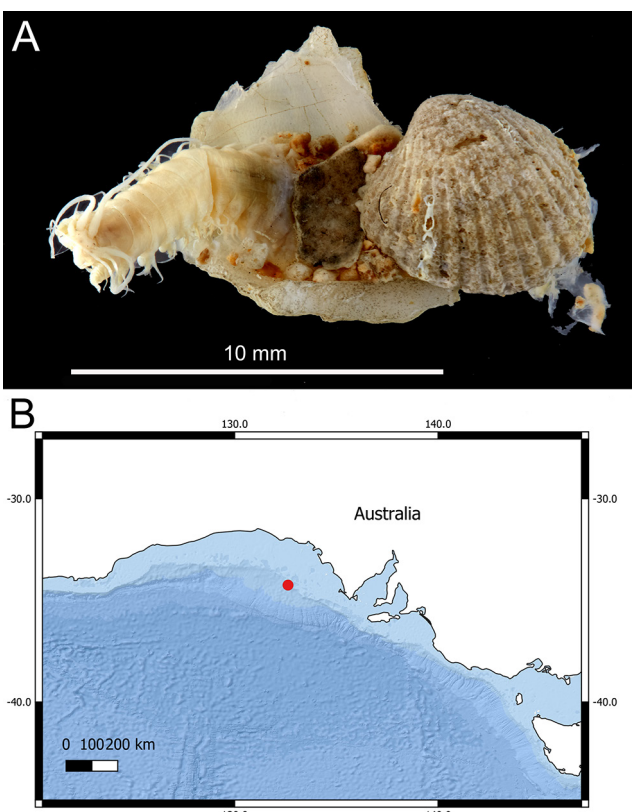

Figure 11. *Nothria digitata* sp. nov. (*A*) photograph of paratype AM W.49954, specimen in tube, dorsal view; (*B*) map of distribution; red dot represents type locality.

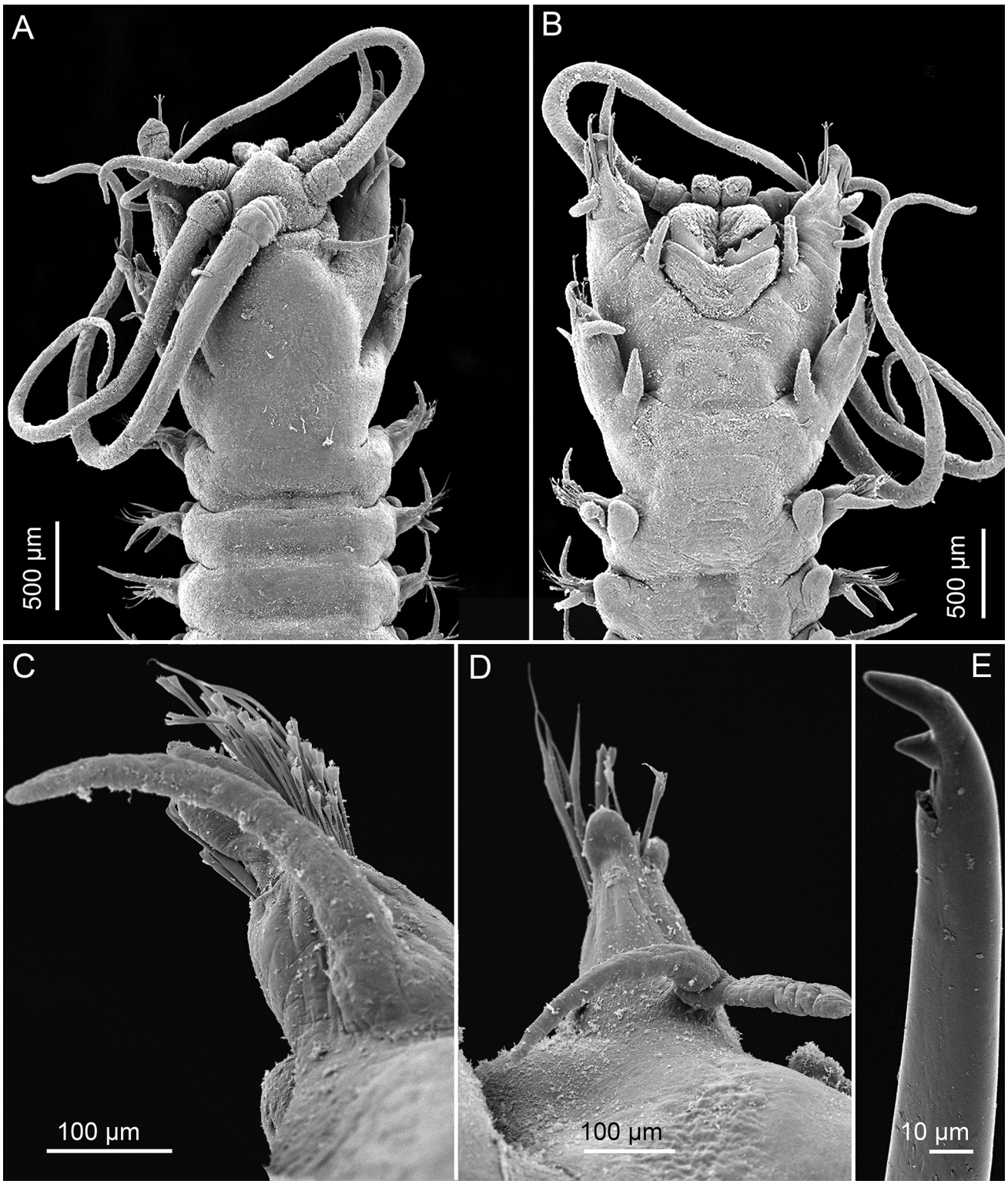

Figure 12. *Nothria josae* sp. nov. SEM micrographs of paratype AM W.51445. (*A*) anterior part, dorsal view; (*B*) same, ventral view; (*C*) parapodium of chaetiger 3, dorsal view; (*D*) parapodium of chaetiger 14, dorsal view; (*E*) slender bidentate simple hook from chaetiger 1.

Nothria josae sp. nov.

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Figs 1, 12–14, Tables 2, S1

Nothria sp. nov. 3.—Gunton *et al.,* 2021:76, fig 16F.

Holotype. Australian Museum (AM) W.51343, IN2017_V03_100; 9 Jun 2017; Australia, New South Wales, Byron Bay, 28.05–28.10°S 154.08°E; 999–1013 m depth. **Paratypes** (5): AM W.49935, IN2017_V03_100 (1); AM W.49937, IN2017_V03_100 (1); AM W.51344, IN2017_V03_100 (1); AM W.51345, IN2017_V03_100 (1); AM W.51445, IN2017_V03_121 (1 mounted on SEM pin).

Other material examined (31). AM W.49936, IN2017_V03_100 (25); AM W.49934, IN2017_V03_121 (2); AM

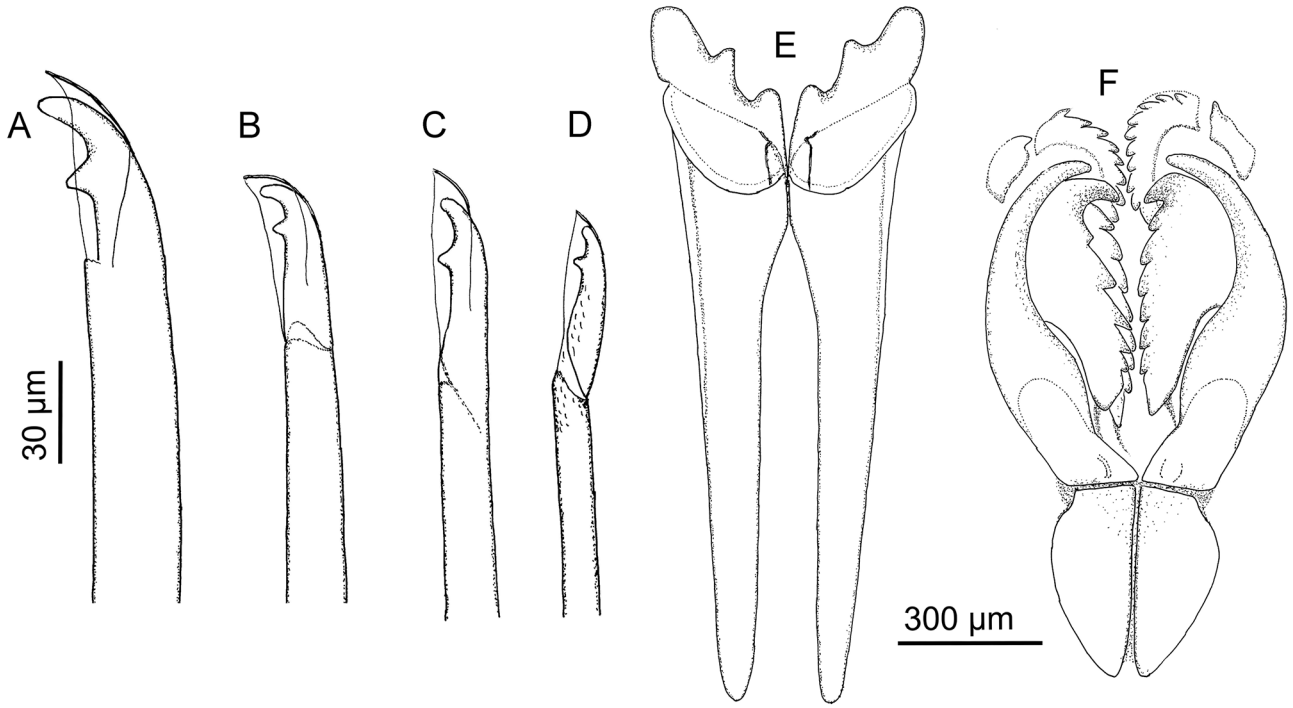

Figure 13. *Nothria josae* sp. nov. Line drawings of AM W.49934. (*A*) slender bidentate simple hook from chaetiger 1; (*B*) very slender bidentate pseudocompound hook from same; (*C*) very slender bidentate pseudocompound hook from chaetiger 2; (*D*) bidentate serrated compound hook from chaetiger 3; (*E*) mandibles; (*F*) maxillae.

W.51449, IN2017_V03_121 (3 in tubes); AM W.53850. IN2017_V03_121 (1).

Diagnosis. Large posterior eyes present; antennae extending to chaetiger 7–11; branchiae short digitate filaments, from chaetiger 11–13; 3 first chaetigers with anterior hooks: slender, bidentate simple and pseudocompound hooks on chaetiger 1; slender bidentate pseudocompound hooks on chaetiger 2 and very slender bidentate pseudocompound to compound hooks on chaetiger 3; pectinate and limbate chaetae from chaetiger 3; subacicular hooks from chaetiger 9–12.

Description. All specimens lacking posterior ends. Length of holotype 5.5 mm for 13 chaetigers, width 1.5 mm; paratypes 4.5–15 mm (12–30 chaetigers) long, 1.5–2.0 mm wide. Non-type material ranging from 1.0–1.8 mm in width. Alcohol-stored specimens overall whitish to cream-coloured. Few specimens with pale brown median spot on prostomium, pale brown splotches on first parapodia and on ventral upper and lower lips; holotype and most other specimens without any pigmentation. Subdermal brown pigment or blood in jaw region, sometimes visible through epidermis dorsally. Prostomium subtriangular, wider than long, with 2 closely spaced ovoid frontal lips (Fig. 12A,B). Palpo- and antennophores with 2–3 proximal rings and longer distal ring (Fig. 12A). Palpostyles tapering, extending to chaetiger 1, antennostyles tapering gradually, lateral antennostyles extending to chaetiger 9 (7–9), median antennostyle noticeably thicker than laterals (Fig. 12A), extending to chaetiger 11 (9–10). Nuchal grooves straight, with small middorsal separation. Large posterior pair of eyes at bases of lateral antennae, faded in holotype but darkly pigmented in paratypes and other specimens. Ventral upper lips rounded, lower lips subtriangular, neither with median section (Fig. 12B). Peristomium short, peristomial cirri

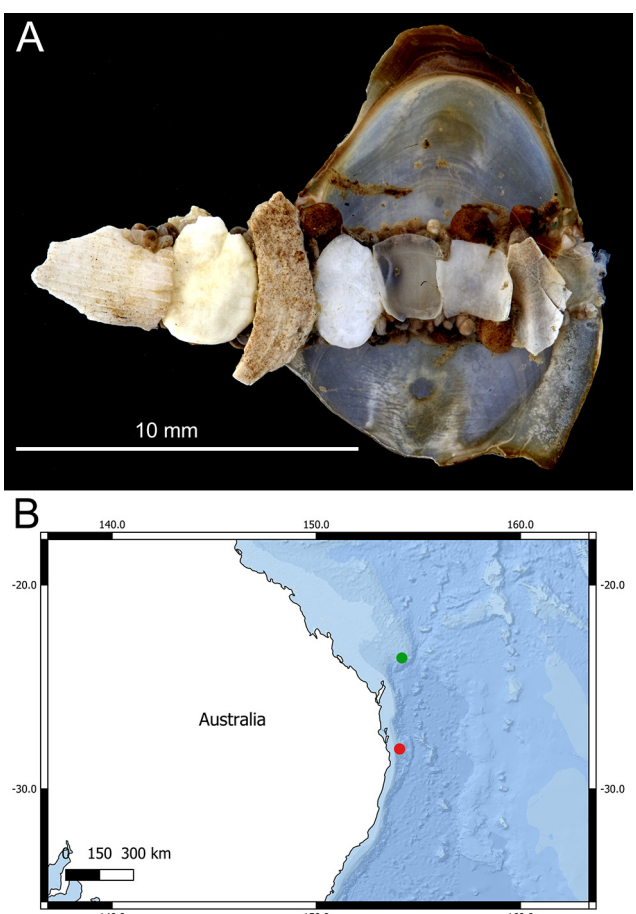

Figure 14. *Nothria josae* sp. nov. (*A*) photograph of tube AM W.51449; (*B*) map of distribution; red dot represents type locality, green dot other site of collection.

inserted subdistally on peristomium, about twice as long as peristomium (Fig. 12A).

First chaetiger enlarged, about twice as long as peristomium, chaetiger 2 much shorter, chaetiger 3 similar in length to following ones. Anterior three pairs of parapodia modified (Fig. 12A,B). First pair greatly enlarged, directed forward, extending well beyond prostomium, with large auricular prechaetal lobes, subulate postchaetal lobes, dorsal and ventral cirri (Fig. 12A,B). Parapodia 2 similar but smaller, with smaller prechaetal, digitate postchaetal lobes and subulate ventral cirri (Fig. 12A,B). Parapodia 3 only slightly larger than subsequent ones (Fig. 12A,B), directed anterolaterally, with tongue-like prechaetal lobes (Fig. 12C). From chaetiger 4 onwards parapodial structures becoming more uniform; prechaetal lobes continued into posterior region, last postchaetal lobes on chaetiger 14 (13–16). Dorsal cirri long and slender to chaetiger 10–12, thereafter becoming gradually shorter, by chaetiger 30 reduced to tiny stumps. Ventral cirri transitional on chaetiger 3, replaced by glandular pads from chaetiger 4 (Fig. 12B). Branchiae beginning on chaetiger 11 (11–13, most often 12) as little stump, becoming short digitate filament (Fig. 12D) by chaetiger 15–17, continuing as tiny stump to end of incomplete specimens.

First pair of parapodia with 2 bidentate almost slender simple hooded hooks (Figs 12E, 13A) and 1 slender bidentate pseudocompound (Fig. 13B) hook. Parapodia 2 with 3 slender simple to pseudocompound (Fig. 13C) bidentate hooks. Parapodia 3 (Fig. 12C) with 2–4 upper limbate chaetae, about 20–30 scoop-shaped pectinate chaetae with 18–20 teeth, 2–3 very slender bidentate pseudocompound to compound hooks with serrated upper shafts and appendages (Fig. 13D). Following parapodia (Fig. 12D) with 5–6 upper limbate, several pectinate and lower limbate chaetae; subacicular hook present singly from chaetiger 12 (9–12) and as pairs from chaetiger 15 (12–16). Pygidium unknown.

Mandibles (Fig. 13E) highly calcified, white, except for darkly sclerotized protomandibles; shafts long and slender, cutting plates high with pronounced median and large distal tooth. Maxillae (Fig. 13F) overall beige coloured, fangs and teeth brown, ligaments and attachment lamellae more sclerotized, appearing dark brown. Maxillary formula (based on 3 paratypes): MI = 1+1; MII = 6–7 + 7–8 (left most distal tooth fang-like); MIII = 7–8 + 0; MIV = 6–7 + 8–10; MV = 1+1. Ratio of mandibles/maxillae = 1.2. Flattened tube, lining transparent, covered on outside with different sized shell fragments (some much larger than diameter of tube), lateral spaces between shells filled in with small particles (Fig. 14A).

Remarks. Below we describe a sister species to *N. josae* sp. nov., where morphological similarities and differences between the two species will be discussed.

Etymology. *Nothria josae* sp. nov. is named for Josie Paxton, granddaughter of the first author.

Distribution. The new species was collected from the Coral Sea Marine Park, Queensland and off Byron Bay, New South Wales, in 999–1013 m and the Coral Sea Marine Park in 1013–1093 m depth (Fig. 14B).

Nothria lizae sp. nov.

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Figs 1, 15–17, Tables 2, S1

Holotype. Australian Museum (AM) W. 49032, IN2015_E02_22; 11 Apr 2015; Australia, Tasmania, Huon Marine Park, 44.32°S 147.32–147.31°E; 2010 m depth. **Paratypes** (8): AM W.49034, IN2015_E02_21 (1). AM W.49035, IN2015_E02_21 (1). AM W.51446, IN2015_E02_22 (1 SEM on pin). SAMA E8971, IN2015_C01_69 (1). AM W.51566, IN2018_V06_74 (1). AM W.51632, IN2018_V06_169 (1). AM W.51633, IN2018_V06_169 (1). AM W.51634, IN2018_V06_169 (1).

Other material examined (102). AM W.53854, IN2015_E0_21 (2). AM W.53855, IN2015_E0_22 (1). AM W.53853, IN2015_E0_22 (2). AM W.51565, IN2018_VO6_037 (1). AM W.53856, IN2018_V06_ 169 (2). AM W.53857, IN2018_V06_169 (94).

Diagnosis. Eyes absent; antennae extending to chaetiger 9–18; short branchiae from chaetiger 12–14 onwards on some or all chaetigers; first 3 chaetigers with anterior hooks: robust, bidentate simple and slender pseudocompound hooks on chaetiger 1; slender bidentate simple and pseudocompound hooks on chaetiger 2; bidentate pseudocompound to compound hooks on chaetiger 3; pectinate and limbate chaetae from chaetiger 3; subacicular hooks from chaetiger 10–13.

Description. Holotype almost complete, measuring 20 mm for 42 chaetigers, width 2.8 mm; 3 complete paratypes (16–30 mm long for 48–57 chaetigers, width 2.6–4.0 mm); 5 incomplete paratypes (7–19 mm long for 15–39 chaetigers, width 2.2–3.0 mm). Non-type material ranging from 1.9–3.0 mm in width. Alcohol-stored specimens overall whitish to cream coloured with brown splotches on head structures, parapodia and dorsum. Prostomium anteriorly rounded, wider than long with 2 ovate frontal lips close together in holotype and most specimens but separated in some by small space. Palpo- and antennophores with 2–3 proximal rings and a slightly longer distal ring (Fig. 15A,B). Palpostyles tapering, extending to chaetiger 1, lateral antennostyles to chaetiger 10 (9–14), median antennostyle to 12 (11–18); antennostyles tapering gradually, ending in blunt tips. Nuchal grooves straight, with small middorsal separation. Eyes absent. Ventral upper lip rounded to oval, lower lip subtriangular, neither with median section. Peristomium short, peristomial cirri inserted subdistally on peristomium, about twice as long as peristomium (Fig. 15A).

First chaetiger enlarged, slightly more than twice as long as peristomium, chaetiger 2 about half as long as chaetiger 1, chaetiger 3 similar in length to following ones. Anterior 3 pairs of parapodia modified; first pair greatly enlarged, directed forward, extending far beyond anterior margin of prostomium with large auricular prechaetal lobes, subulate postchaetal lobes, digitate dorsal and subulate ventral cirri (Fig. 15A,B). Prechaetal lobes of holotype and most paratypes with small lip-like extension between two large hooks (Fig. 15C). Second pair of parapodia similar to first but smaller, with smaller prechaetal lobes. Third pair only slightly larger than subsequent parapodia, with further reduced, tongue-like prechaetal lobes; ventral cirri ovate, transitioning to glandular pads (Fig. 15A,B). From chaetiger 4 onwards parapodial structures becoming more

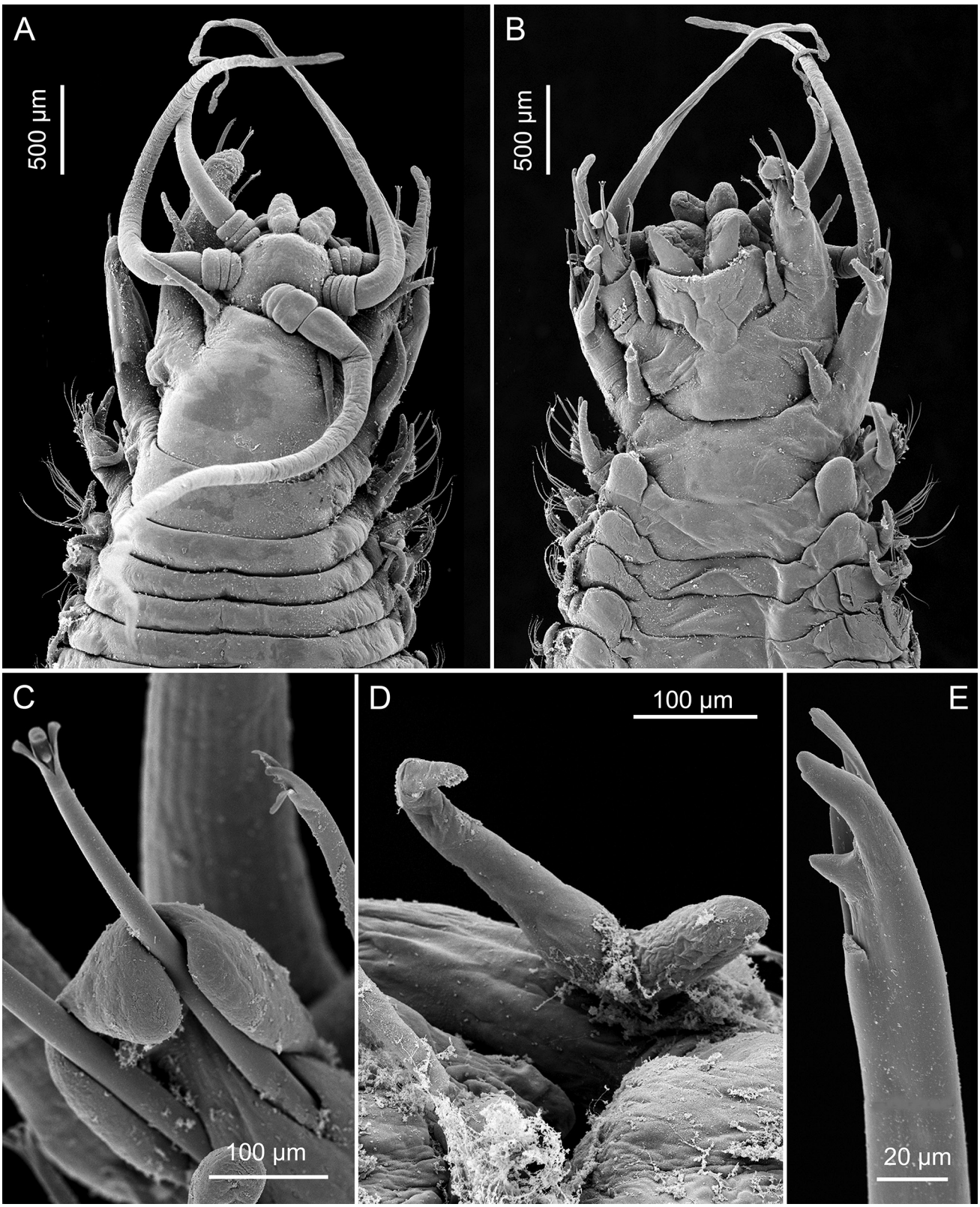

Figure 15. *Nothria lizae* sp. nov. SEM micrographs of paratype AM W.51446. (*A*) anterior part, dorsal view; (*B*) same, ventral view; (*C*) parapodium of chaetiger 1 showing lip-like extension of prechaetal lobe, ventral view; (*D*) parapodium of chaetiger 15 showing small branchia, dorsal view; (*E*) almost robust (< 30 µm wide) bidentate simple hook from chaetiger 1.

uniform; dorsal cirri gradually becoming thinner and shorter, prechaetal lobes becoming short and rounded, postchaetal lobes gradually decreasing in length, last one on chaetiger 14 (13–15), ventral cirri replaced by oval glandular pads. Branchiae present as short, filaments; in holotype tiny branchia from chaetiger 12, increasing slightly to chaetiger 30 where it is equal in length to greatly reduced dorsal cirrus, then decreasing in size but present until end of fragment. In paratypes branchial filament starting from chaetiger 12–14 (Fig. 15D), sometimes only for a few segments, thereafter

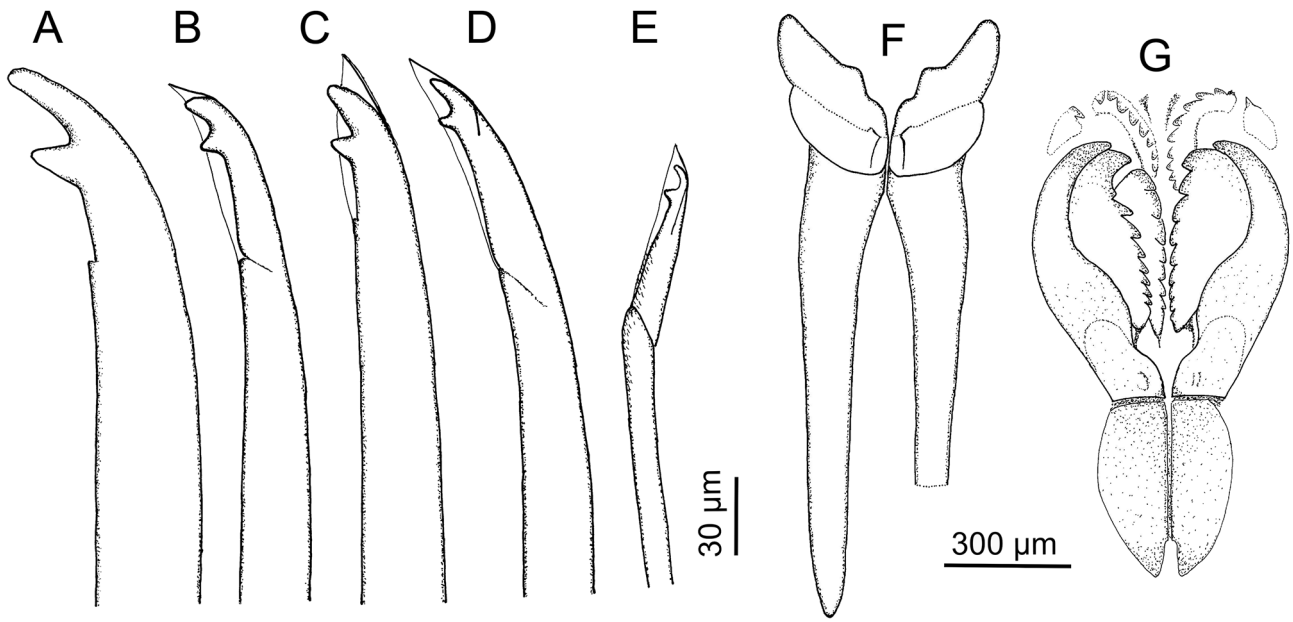

Figure 16. *Nothria lizae* sp. nov. Line drawings of paratype SAMA E8971. (*A*) robust bidentate simple hook from chaetiger 1; (*B*) slender bidentate pseudocompound hook from chaetiger 1; (*C*) slender bidentate simple hook from chaetiger 2; (*D*) slender bidentate pseudocompound hook from chaetiger 2; (*E*) very slender bidentate serrated compound hook from chaetiger 3; (*F*) mandibles; (*G*) maxillae.

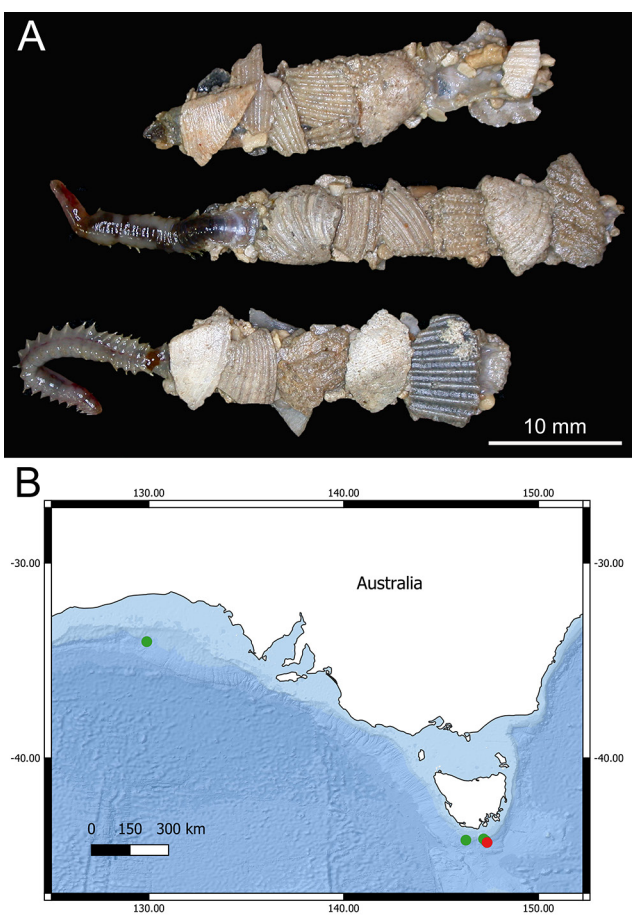

Figure 17. *Nothria lizae* sp. nov. (*A*) photograph of tube AM W.51446; (*B*) map of distribution; red dot represents type locality; green dots other sites of collection.

absent or later reappearing again to near end of body.

First pair of parapodia with 2 almost robust (shaft < 30 µm wide) (Fig. 15E) to robust bidentate simple (Fig. 16A) and 1 slender bidentate pseudocompound hooded hook (Fig. 16B). Second pair of parapodia with slender, bidentate simple (Fig. 16C) and pseudocompound hooks (Fig. 16D). Third pair of parapodia with 3–4 very slender pseudocompound to compound bidentate hooks with serrated upper shaft and appendages (Fig. 16E), as well as 2–3 limbate chaetae and numerous (about 30) scoop-shaped pectinate chaetae with about 20–22 teeth. Anterior hooks absent from chaetiger 4, limbate and pectinate chaetae present in reduced numbers to end of body. Subacicular hooks present singly from chaetiger 12 (10–13) and as pairs from chaetiger 14 (12–15). Pygidium with 2 long anal cirri.

Mandibles (Fig. 16F) highly calcified, almost white, except for darkly sclerotized protomandibles; shafts long and slender, cutting plates high with weakly defined lower teeth and large distal tooth. Maxillae (Fig. 16G) overall light brown with darker sclerotized teeth and attachment lamellae; maxillary formula: MI = 1+1; MII = 7–10 + 9–10 (left most distal tooth fang-like), MIII = 7–8 + 0; MIV = 1+1 (based on 5 specimens). Ratio of mandibles/maxillae = 1.2. Flattened tube (Fig. 17A), covered mainly with evenly sized shell fragments dorsally and ventrally giving the appearance of a pavement, sides filled in with foraminiferans; lining transparent.

Remarks. *Nothria lizae* sp. nov. and *N. josae* sp. nov. (described directly above) are two sister species that are similar morphologically (Table 2). They both have short branchiae from about chaetiger 12–13, a similar distribution of bidentate simple and pseudocompound hooks on chaetigers 1–3, pectinate chaetae from chaetiger 3 and subacicular hooks from about chaetiger 12. However, they can be distinguished in that *N. josae* sp. nov. is a smaller

species (maximum width to 2 mm), has a subtriangular prostomium, large posterior eyes, shorter antennae (median to chaetiger 9–11), tube with oversized shells, and was collected at a depth of about 1000 m, while *N. lizae* sp. nov. has a rounded prostomium, lacks eyes, has longer antennae (median to chaetiger 11–18), tube with evenly sized shell fragments and occurs at about 1500–2000 m depth.

Etymology. *Nothria lizae* sp. nov. is named for Liza Paxton, granddaughter of the first author.

Distribution. The new species has been collected south of Tasmania in the flat area south of Brians, in 1443–1422 m, the Huon Marine Park in 2010–2028 m and in the Great Australian Bight in 1569.6–1636 m (Fig. 17B).

Nothria minima sp. nov.

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Figs 1, 18–20, Tables 2, S1

Holotype. Australian Museum (AM) W.51642, IN2018_V06_184; 17 Dec 2018; Australia, Tasmania, St. Helen's flat; 41.21–41.20°S 148.80–148.78°E; 1221–1202 m depth. **Paratypes** (8): AM W.51641, IN2018_V06_184 (1). AM W.51643, IN2018_V06_184 (1). AM W.51644, IN2018_V06_184 (1). AM W.53498, IN2018_V06_184 (1 SEM on pin). AM W.53849, IN2018_V06_184 (4).

Other material examined (82). AM W.51567, IN2018_V06_184 (76). AM W.53848, IN2018_V06_184 (6 in tubes).

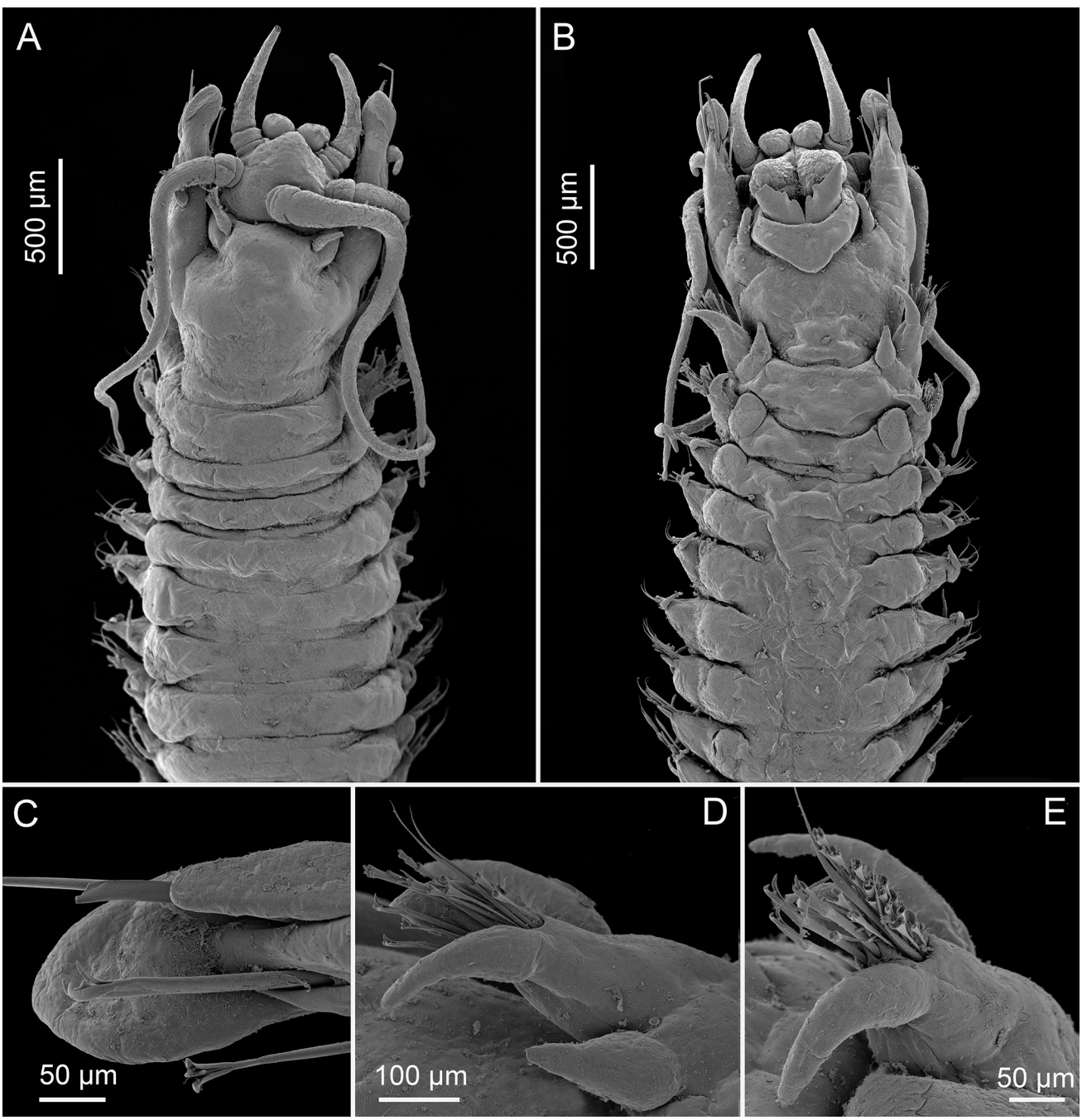

Figure 18. *Nothria minima* sp. nov. SEM micrographs of paratype AM W.53498. (*A*) anterior part, dorsal view; (*B*) same, ventral view; (*C*) parapodium of chaetiger 1, posterior view; (*D*) parapodium of chaetiger 2, same view; (*E*) parapodium of chaetiger 3, same view.

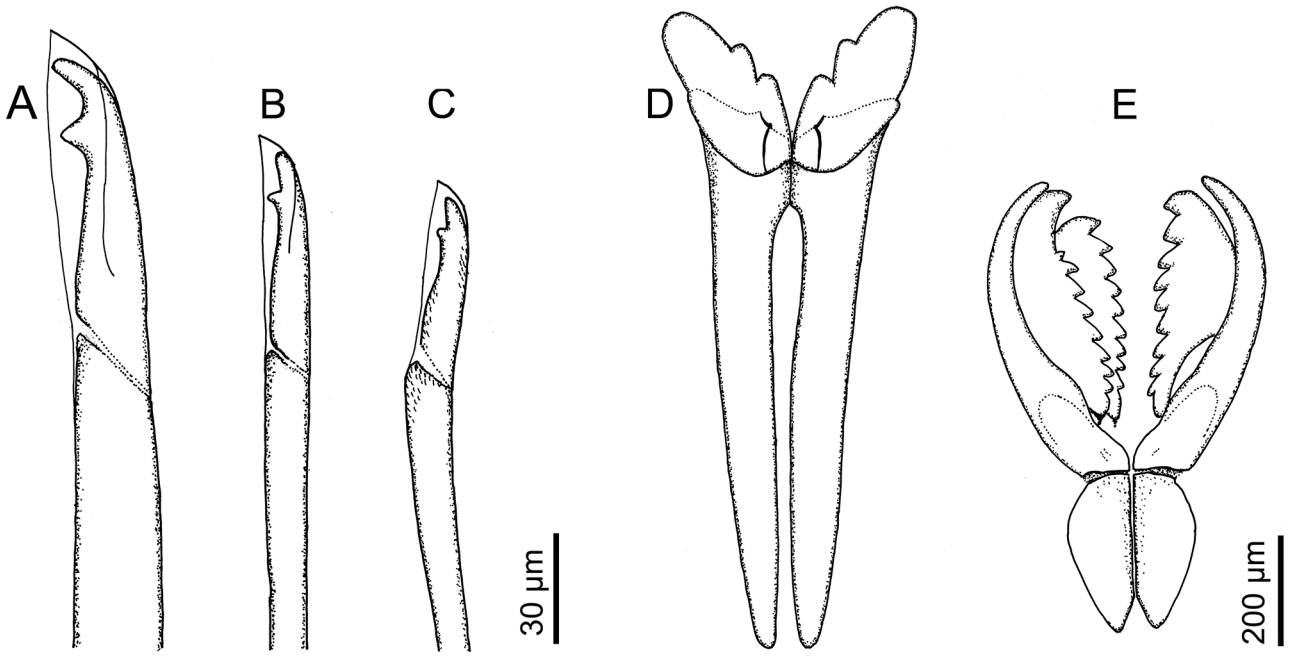

Figure 19. *Nothria minima* sp. nov. Line drawings of holotype AM W.51642 (*A–C*) and AM W.53849 (*D, E*). (*A*) slender bidentate pseudocompound to compound hook from chaetiger 1; (*B*) very slender bidentate pseudocompound to compound hook from chaetiger 2; (*C*) slender bidentate compound hook from chaetiger 3; (*D*) mandibles; (*E*) maxillae (delicate with little sclerotization; MIV and MV hard to make out, hence not included in drawing).

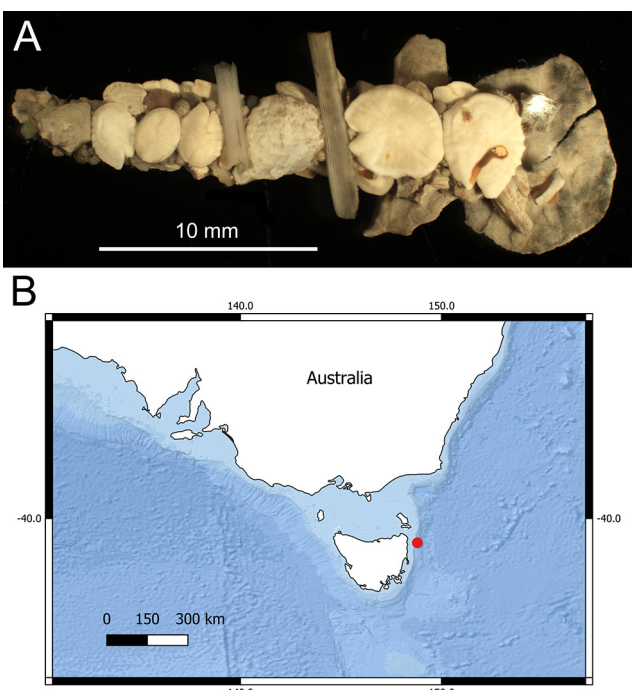

Figure 20. *Nothria minima* sp. nov. (*A*) photograph of tube AM W.51567; (*B*) map of distribution; red dot represents type locality.

Diagnosis. Eyes absent; antennae extending to chaetiger 5–9; branchiae absent; dorsal cirri absent from chaetiger 14–20; first 3 chaetigers with anterior hooks: slender bidentate pseudocompound to compound hooks on chaetiger 1 and 2; very slender bidentate compound hooks on chaetiger 3; pectinate and limbate chaetae from chaetiger 2; subacicular hooks from chaetiger 9–10.

Description. All examined specimens lacking posterior ends. Length of holotype 7.5 mm for 17 chaetigers, width 1.4 mm; paratypes 6.0–9.0 mm (17–22 chaetigers) long, 1.2–1.6 mm wide, non-type material ranging from 1.0–1.8 mm in width.

Preserved specimens overall whitish to cream coloured without any colour pattern. Prostomium anteriorly rounded in holotype, rounded to subtriangular in other specimens, wider than long, with 2 rounded to ovoid frontal lips (Fig. 18A,B). Palpo- and antennophores very short, with 1–2 proximal rings and slightly longer distal ring. Palpostyles tapering, extending to chaetiger 1, antennostyles tapering gradually, lateral antennostyles extending to chaetiger 6 (4–7), median antennostyle with broken tip, reaching chaetiger (6–9). Nuchal grooves straight, with small middorsal separation. Eyes absent. Ventral upper lip rounded, lower lip subtriangular, neither with median section (Fig. 18B). Peristomium short, peristomial cirri inserted subdistally on peristomium, about as long as peristomium (Fig. 18A).

First chaetiger enlarged, about twice as long as peristomium, chaetiger 2 and 3 progressively shorter, following ones about as long as peristomium. Anterior 3 pairs of parapodia modified; first pair greatly enlarged, directed forward, extending far beyond anterior margin of prostomium (Fig. 18A,B) with narrow auricular, almost tongue-like prechaetal lobes and subulate postchaetal lobes (Fig. 18C). Second pair of parapodia much smaller, hardly prolonged, with smaller tongue-like prechaetal lobe (Fig. 18D). Third pair of parapodia (Fig. 18E) only slightly larger than subsequent ones, with prechaetal lobes further reduced, present as little knobs to posterior part of body, last postchaetal lobes on chaetigers 9 (8–12). Ventral cirri of first two chaetigers subulate, becoming rounded on chaetiger 3, as transitioning to glandular pads (Fig. 18B). Dorsal cirri weakly subulate to cirriform from chaetiger 1, becoming thinner and shorter, abruptly absent from chaetiger 15 (14–20). Branchiae absent.

First pair of parapodia (Fig. 18C) with 3–5 slender bidentate pseudocompound to compound hooks (Fig. 19A). Second pair (Fig. 18D) with 3 very slender bidentate pseudocompound to compound hooks (Fig. 19B), 2–3 limbate and 15–20 scoop-shaped pectinate chaetae with 16–20 teeth. Third pair of parapodia (Fig. 18E) with 3–5 very slender, bidentate compound hooks with serrated upper shafts and appendages (Fig. 19C), 2–3 limbate chaetae and numerous (up to 30) scoop-shaped pectinate chaetae (Fig. 18E). From chaetiger 4 anterior hooks absent, limbate and pectinate chaetae present to end of fragments, presumably end of body, although number of pectinate chaetae greatly reduced. Subacicular hooks present singly from chaetigers 9 (8–10), as pairs from chaetiger 10 (9–11). Pygidium unknown.

Mandibles (Fig. 19D) highly calcified, almost white, except for darkly sclerotized protomandibles. High cutting plates with two median teeth and large distal tooth. Maxillae (Fig. 19E) delicate with little sclerotization (MIV and MV hard to make out hence not included in drawing); MI very slender maxillary formula (based on 3 specimens): MI = 1+1; MII = 9 + 9 (left most distal tooth fang-like); MIII = 9 + 0; MIV = 7+8; MV = 1+1. Ratio of mandibles/maxillae = 1.2 (ratio for 3 jaw apparatuses ranged from 1.11–1.19 but a fourth result was 1.44, giving a mean of 1.22). Flattened tube (Fig. 20A), covered with similarly sized shells dorsally and ventrally, gaps filled in with foraminiferans; lining transparent.

Remarks. *Nothria minima* sp. nov. resembles *N. solenotecton* (Chamberlin, 1919), a deep-sea species from off Panama, as well as the new species to be described directly below, where the morphological similarities and differences between the three species are discussed.

Etymology. This species is the smallest, most delicate one encountered in the study, hence the epithet "*minima",* meaning "small" in Latin.

Distribution. The new species was only collected in station 184 of cruise IN2018_V06, "St. Helens flat" in 1202–1221 m depth (Fig. 20B).

Nothria orensanzi sp. nov.

urn:lsid:zoobank.org:act:A8958CCC-64F4-421F-903E-E229D5E62B23

Figs 1, 21–23, Tables 2, S1

Nothria sp. nov. 1.—Gunton *et al.*, 2021:75, fig. 16C,D.
?Nothria sp., near *solenotecton* Chamberlin, 1919.—Orensanz 1990: 130, pl. 42, figs g–i.

Holotype. Australian Museum (AM) W.49031, IN2015_E02_22; 11 Apr 2015; Australia, Tasmania, Huon Marine Park; 44.33°S 147.36°E; 2010 m depth. **Paratypes** (7): AM W.49028, IN2015_E02_21 (1). AM W.49033, IN2015_E02_21 (1). AM W.51447, IN2015_E02_22 (1 SEM on pin). AM W.51444, IN2015_E02_22 (1 SEM on pin). AM W.53851, IN2015_E02_22 (3).

Other material examined (91). AM W.47917, IN2015_E02_021 (19). AM W.47920, IN2015_E02_21 (3). AM W.47918, IN2015_E02_22 (17). AM W.49030, IN2015_E02_22 (1). AM W.47919, IN2015_E02_022 (48). AM W.53852, IN2017_V03_004 (1). AM W.49940, IN2017_V03_056 (2).

Diagnosis. Eyes absent; antennae extending to chaetiger 8–15; branchiae absent; first 3 chaetigers with anterior hooks; dorsal cirri absent from about chaetiger 30; slender bidentate simple and pseudocompound hooks on chaetiger 1, slender bidentate pseudocompound hooks on chaetiger 2; very slender bidentate pseudocompound to compound hooks on chaetiger 3; pectinate and limbate chaetae from chaetiger 2; subacicular hooks from chaetiger 11–13.

Description. All examined specimens lacking posterior ends. Length of holotype 10 mm for 21 chaetigers, width 2.5 mm; paratypes 13–18 mm (26–29 chaetigers) long, 2.3–2.6 mm wide. Non-type material ranging from 1.7–2.6 in width.

Preserved specimens overall whitish to cream coloured. Holotype and some paratypes with weak brown pigment splotches/spots laterally on prostomium, peristomium and first few segments. Prostomium anteriorly rounded to subtriangular, wider than long, with 2 ovoid frontal lips (Fig. 21A,B). Palpo- and antennophores with 1–2 proximal rings and longer distal ring. Palpostyles tapering, extending to chaetiger 1, antennostyles tapering gradually, lateral antennostyles extending to chaetiger 7 (6–11), median antennostyle to chaetiger 9 (8–15). Nuchal grooves straight, with small middorsal separation. Eyes absent. Ventral upper lip rounded to squared, lower lip subtriangular, neither with median section (Fig. 21B). Peristomium relatively long, peristomial cirri inserted subdistally on peristomium, about as long as peristomium (Fig. 21A).

First chaetiger greatly enlarged, about twice as long as peristomium, chaetiger 2 about as long as peristomium, chaetiger 3 and subsequent ones slightly shorter than peristomium. First 3 pairs of parapodia enlarged and modified; first pair greatly so, directed forward, extending slightly beyond anterior margin of prostomium, with large auricular prechaetal lobes and subulate postchaetal lobes (Fig. 21A,B). Second pair of parapodia similar but smaller, with smaller prechaetal but larger subulate postchaetal lobes. Third pair of parapodia only slightly larger than subsequent ones, with further reduced prechaetal lobes; prechaetal lobes present as little knobs to posterior part of body, last postchaetal lobes on chaetiger 13 (11–13). Ventral cirri of the first two chaetigers subulate, becoming rounded on chaetiger 3 as transitioning, glandular pads from chaetiger 4 (Fig. 21B). Dorsal cirri weakly subulate to cirriform from chaetiger 1 (Fig. 21A), becoming gradually thinner and shorter, very short by chaetiger 15, absent from chaetiger 20–30. Branchiae absent.

First pair of parapodia with 3–4 slender bidentate simple (Fig. 22A), almost simple (Fig. 22B) and pseudocompound hooks (Fig. 22C). Second pair with 2–3 similar sized bidentate pseudocompound hooks (Fig. 22D), 2–4 limbate and up to 10 scoop-shaped pectinate chaetae with 20–25 teeth (Fig. 21C). Third pair of parapodia with 3–4 very slender bidentate pseudocompound to compound hooks with serrated upper shafts and appendages (Figs 21D, 22E), 3–4 limbate chaetae and up to 20 pectinate chaetae. From chaetiger 4 anterior hooks absent, limbate and reduced number of pectinate chaetae present to end of fragments, presumably end of body, although number of pectinate chaetae greatly reduced. Subacicular hooks present singly from chaetigers 12 (11–13), as pairs from chaetiger 13 (12–14). Pygidium unknown.

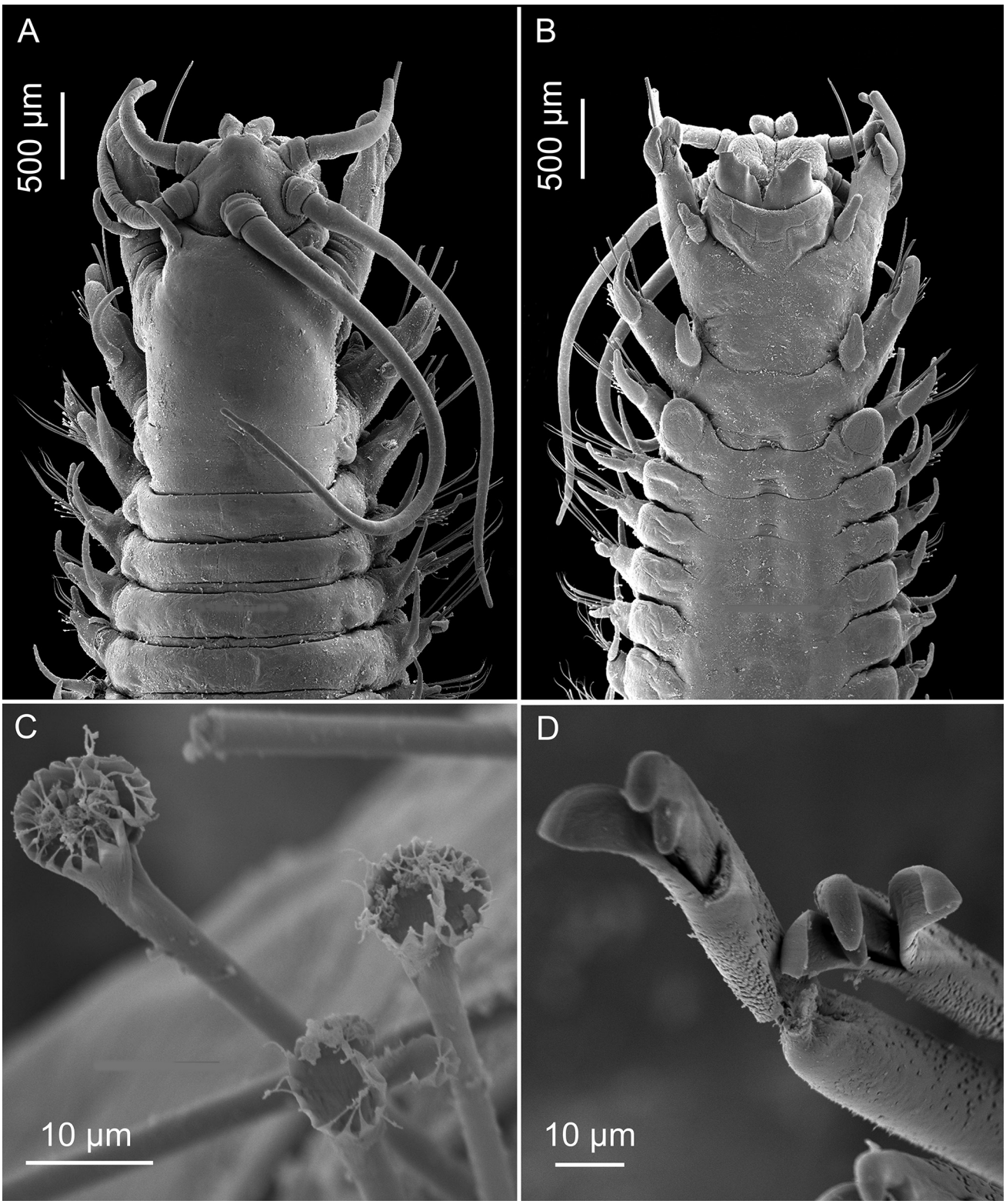

Figure 21. *Nothria orensanzi* sp. nov. SEM micrographs of paratype AM W.51444. (*A*) anterior part, dorsal view; (*B*) same, ventral view; (*C*) pectinate chaetae from chaetiger 2; (*D*) bidentate serrated compound hooks from chaetiger 3.

Mandibles (Fig. 22F) highly calcified, almost white, except for darkly sclerotized protomandibles. High cutting plates with 2 median teeth and large distal tooth. Maxillae (Fig. 22G) also highly calcified with little sclerotization; left MII with distinct distal fang; maxillary formula: MI = 1+1; MII = 6+10; MIII = 9+0; MIV = 9+9; MV = M1+1. Ratio of mandibles/maxillae = 1.3. Flattened tube (Fig. 23A), made up of clear but strong inner secreted layer, covered with pieces of shells and pebbles dorsally and ventrally, with elongate fragments usually placed transversely, laterally filled in with foraminiferans and other small fragments; tubes very sturdy due to strong cementing substance.

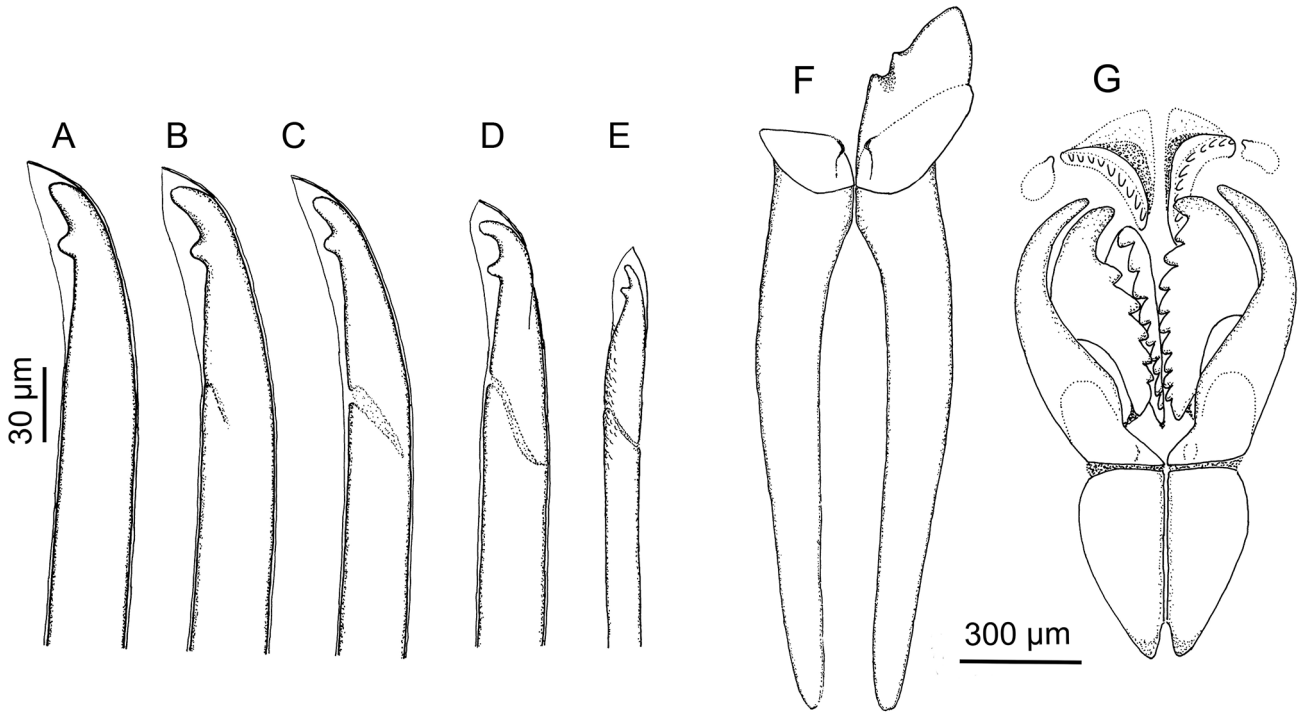

Figure 22. *Nothria orensanzi* sp. nov. Line drawings of paratype AM W.53851. (*A*) slender bidentate simple hook from chaetiger 1; (*B*) slender bidentate weakly pseudocompound hook from chaetiger 1; (*C*) slender bidentate pseudocompound hook from chaetiger 1; (*D*) slender bidentate pseudocompound hook from chaetiger 2; (*E*) very slender bidentate serrated compound hook from chaetiger 3; (*F*) mandibles; (*G*) maxillae.

Remarks. Prior to the present study only four abranchiate species of *Nothria* were known: *Nothria abyssia* Kucheruk, 1978, *N. paxtonae* Imajima, 1999, *N. solenotecton* (Chamberlin, 1919) and *N. textor* Hartman & Fauchald, 1971. *Nothria abyssia* and *N. paxtonae* are species with anterior hooks limited to the first two chaetigers. Both occur in Australian waters; they are treated below and are distinguished further from *N. minima* sp. nov. and *N. orensanzi* sp. nov. (both with anterior hooks on the first three chaetigers) in Table 2. *Nothria textor* is a very small species (width 0.84 mm) from the North Atlantic. It differs from the two new species in having pectinate chaetae only on chaetigers 2 and 3 and subacicular hooks from chaetiger 7. The two new species resemble most closely *N. solenotecton*, a deep-sea species from off Panama. This goes particularly for *N. orensanzi* sp. nov.; however, the latter differs from the former in having longer antennae with well defined, rather than obscurely ringed or smooth ceratophores and simple and pseudocompound hooks rather than only pseudocompound hooks on chaetiger 1. Orensanz (1990) discussed *N. solenotecton* when reporting three specimens of a closely related species from South of Tasmania (2800–3000 m) and around New Zealand ("lower bathyal") that he listed as *Nothria* sp., near *solenotecton* Chamberlin, 1919, but did not formally describe. We have examined a large number of specimens of *N. orensanzi* sp. nov. from off eastern Australia ranging from southern Tasmania to Jervis Bay Marine Park, concluding that our new species is most probably identical with his material and describe the new species in his honour.

Nothria orensanzi sp. nov., *N. minima* sp. nov. and *N. solenotecton* are all abranchiate, anoculate, have ceratophores with few rings, bidentate hooks on the first three chaetigers and pectinate chaetae from chaetiger 2. Despite these similarities, *N. minima* sp. nov. differs from

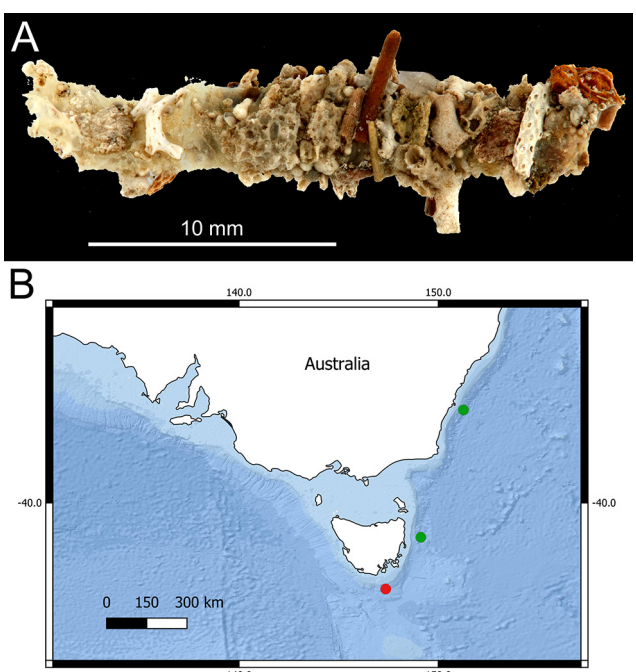

Figure 23. *Nothria orensanzi* sp. nov. Photograph of tube AM W.51564; (*B*) map of distribution; red dot represents type locality, green dots other sites of collection.

N. orensanzi sp. nov. in its second pair of parapodia being hardly prolonged, having no simple hooks on chaetiger 1 and having pectinate chaetae with 16–20 rather than 20–25 teeth. *Nothria minima* sp. nov. is a smaller, more delicate species than *N. orensanzi* sp. nov. as is evident by having a maximum width of 1.6 mm rather than 2.6 mm. This does not

mean that the former is a juvenile of the latter since members of both species contained mature gametes. Furthermore, the tubes of *N. minima* sp. nov. consist of similarly sized shells (Fig. 20A) while those of *N. orensanzi* sp. nov. are constructed from mixed shells with elongated pieces placed transversely (Fig. 23A).

Etymology. We dedicate this species to the late José M. Orensanz in recognition of his valuable contributions to the study of eunicemorph polychaetes.

Distribution. *Nothria orensanzi* sp. nov. appears to be widely distributed. It was collected off southern Tasmania, Freycinet and Huon Marine Parks, and New South Wales, Jervis Marine Park, at 2010–2820 m depth (Fig. 23B).

Nothria otsuchiensis Imajima, 1986 complex

Figs 1, 24, Tables 2, 3, S1

Nothria otsuchiensis Imajima, 1986: 108, fig. 8.—Imajima 1999: 46, fig 26.—Budaeva & Paxton 2013: 1492, figs 11–17.

Material examined (21). AM W.49014, IN2015_C01_110 (1). AM W.49037, IN2015_C01_110 (1). AM W.49038, IN2015_C01_114 (1). AM W.49015, IN2015_C01_117 (1). AM W.49025, IN2015_C02_196 (1). AM W.49026, IN2015_C02_330 (1). AM W.49939, IN2017_V03_128 (1). AM W.51635, IN2018_V06_184 (1). AM W.51636, IN2018_V06_184 (1). AM W.51637, IN2018_V06_184 (1). AM W.51638, IN2018_V06_184 (1). AM W.53847, IN2018_V06_184 (10).

Diagnosis. Prostomium anteriorly rounded to subtriangular. Small anterior and large posterior eyes present or absent. Palpo- and antennophores with 2–3 rings, median antennae extending to chaetiger 4–5, lateral to 3–4. Branchiae with short to long filaments, from chaetiger 8–9, most often 9. First 2 chaetigers enlarged, parapodia directed anteriorly, often surpassing peristomium. Last postchaetal lobe on chaetiger 15. Robust bidentate simple and slender pseudocompound hooks on chaetiger 1; slender bidentate simple and pseudocompound hooks on chaetiger 2; bidentate pseudocompound to compound hooks on chaetiger 3; pectinate chaetae with about 20 teeth and limbate chaetae from chaetiger 3; subacicular hooks from chaetiger 10–15.

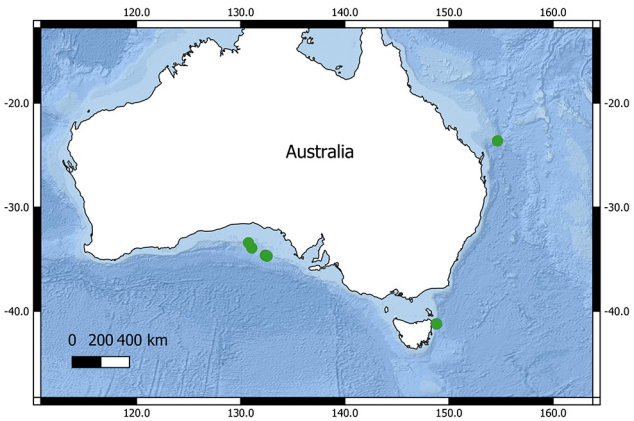

Figure 24. *Nothria otsuchiensis* Imajima, 1986 complex. Map of distribution of RV *Investigator* collections; green dots represent sites of collection.

Remarks. All of our specimens are anterior fragments measuring 1.9 to 3 mm in width. *Nothria otsuchiensis* was described from Otsuchi Bay, in 48–79 m depth based on the holotype and 27 paratypes. The complete holotype measured 18 mm in length for 49 chaetigers and 3 mm in width including parapodia, the morphological characteristics are here presented in Table 3. In a monograph of the Onuphidae from Japan, Imajima (1999) reported numerous additional

Table 3. Distinguishing features of the *Nothria otsuchiensis* complex. *C*, compound; *PC*, pseudocompound.

character	Imajima, 1986	Imajima, 1999	Budaeva & Paxton, 2013	present study
max. width (mm)	3.0 with parapodia	3.0 with parapodia	2.1 without parapodia	3.0 without parapodia
shape of anterior prostomium	rounded	rounded	subtriangular	rounded to subtriangular
antennae, to chaetiger	median 10; lateral 5	median 10; lateral 5	median 6–12; lateral 4–9	median 4–5; lateral 3–4
eyes	small anterior & large posterior	small anterior & large posterior	small anterior absent; large posterior present	small anterior pres./absent large posterior pres./absent
branchiae from chaetiger	10	9–10	9	8–9
branchiae, shape and length	flat; long	flat; long	flat; long	flat; short to long
last postchaetal lobe on chaetiger	14	14	14–17	15
anterior chaetigers with hooks	3	3	3	3
hooks of chaetiger 1	simple & PC	simple & PC	simple & PC	simple & PC
tips of hooks chaetiger 1	bidentate	bidentate	bidentate	bidentate
hooks of chaetiger 2	simple & PC	simple & PC	simple & PC	simple & PC
tips of hooks chaetiger 2	bidentate	bidentate	bidentate	bidentate
hooks of chaetiger 3	PC	PC	PC	PC to C
tips of hooks chaetiger 3	bidentate	bidentate	bidentate	bidentate
pectinates from chaetiger	3	3	3	3
number of teeth on pectinates	20	not stated	18–22	20
subacicular hooks from chaetiger	10	10–12	10–13	10–15
depth (m)	48–79	26–1070	24–2900	400–1761
distribution	Otsuchi Bay, Japan	Otsuchi Bay to Kagoshima Bay, Japan	Eastern Australia; New Caledonia	Eastern Australia; Great Australian Bight

records of the species from Otsuchi Bay to Kagoshima Bay, in 26–1070 m depths. In spite of the huge increase of material examined and range of distribution and depth, the diagnostic features were almost identical. The only widening of parameters were the start of branchiae from chaetiger 9–10 rather than 10, and subacicular hooks from chaetiger 10–12 rather than 10 in the original description. In a study of ontogenetic variation of diagnostic characters Budaeva & Paxton (2013) examined a large number of *N. otsuchiensis* from off eastern Australia in 24–2900 m and a single specimen from New Caledonia in 440–450 m depth. Again, the morphological characteristics were basically the same, showed only a slightly wider range in the length of the antennae, last postchaetal lobes and start of subacicular hooks from the original description (Table 3). As far as diagnostic characters could be evaluated, in spite of the large geographical and depth ranges all specimens examined appeared to match the description of *N. otsuchiensis.*

In the present study we examined material from three research cruises to the Great Australian Bight and eastern Australia in 400–1761 m depth with similar results (Table 3). Several specimens were sequenced as discussed in the "Molecular Results" section. We obtained several clades, indicating that we are dealing with a species complex that can only be resolved with a deeper molecular investigation of a larger number of specimens.

Distribution. Eastern Australia and Great Australian Bight, in 400–1761 m depth (Fig. 24).

Nothria cf. *paxtonae* Imajima, 1999

Fig. 25, Tables 2, S1

?Nothria paxtonae Imajima, 1999: 51, figs 27–29.
Nothria cf. *paxtonae.*—Gunton *et al.,* 2021:75, fig 16B.

Material examined (4). AM W.53844, IN2017_V03_56 (3). AM W.53843, IN2017_C01_207 (1).

Diagnosis. No eyes visible. Palpo- and antennophores with 2–3 rings, lateral antennae extending to chaetiger 5, median antenna to 6. Branchiae absent. First chaetiger and parapodia greatly enlarged, parapodia directed anteriorly, surpassing prostomium. Bidentate pseudocompound hooks only present on chaetigers 1 and 2; limbate chaetae from chaetiger 2; flat pectinate chaetae with about 12 teeth present on chaetiger 8; subacicular hooks from chaetiger 8–9. Tube with thin transparent lining, covered closely with foraminiferans.

Remarks. All of our specimens are anterior fragments, measuring 4–5 mm in length for 8–11 chaetigers, 1.0–1.3 mm in width. The specimens were fixed in formalin, hence could not be sequenced. The alcohol-stored specimens are overall whitish without any pigmentation. The delicate jaws were not examined.

Nothria paxtonae was described from off Boso Peninsula to Suruga Bay, Japan, in 90–175 m depth, having small anterior eyespots and larger posterior eyes, pectinate chaetae from chaetiger 9, and uniquely for the genus, eight foliaceous papillae surrounding the anus.

Since our specimens are all incomplete, we were unable to confirm this identifying characteristic. Furthermore, none of our specimens appeared to have eyes and only one specimen has one pectinate chaeta on chaetiger 8. In view

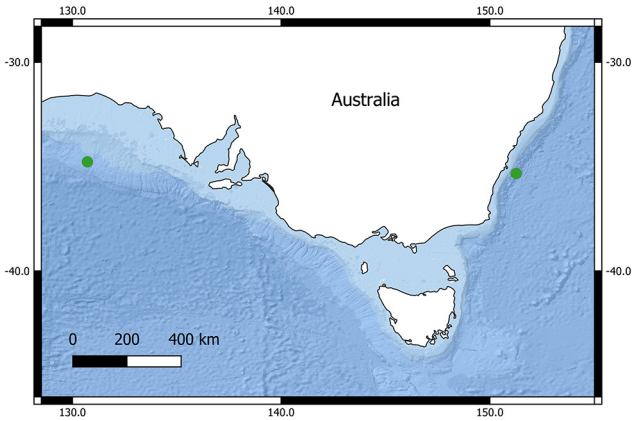

Figure 25. *Nothria* cf. *paxtonae* Imajima, 1999. Map of Australian distribution; green dots sites of collection.

of these uncertainties, we are reporting the specimens as *N.* cf. *paxtonae* for the present time.

Budaeva & Paxton (2013) reported *N. abyssia* from off south-eastern Australia; it is very similar to *N. paxtonae*; both species lack branchiae, have hooks present on the first two pairs of parapodia only, limbate chaetae starting from chaetiger 2 and have flat pectinate chaetae. They differ in that anal papillae are absent and pectinate chaetae have 17–20 teeth, starting on chaetiger 2–3 in *N. abyssia* whilst they have only 12 teeth and start on chaetiger 9 in *N. paxtonae.* However, they were not collected in the material of the present study.

Distribution. Off Jervis Marine Park, New South Wales, and Great Australian Bight, in 1772–2650 m depth (Fig. 25).

Nothria simplex sp. nov.

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Figs 1, 26–27, Tables 2, S1

Holotype. Australian Museum (AM) W.49938, IN2017_V03_86; 11 Jun 2017; Australia, Queensland, off Fraser Island; 25.33–25.35°S 154.07–154.08°E; 2350–2342 m depth. **Paratypes** (2). AM W.51645, IN2017_V03_86(1). AM W.51646, IN2017_V03_115 (1).

Diagnosis. Eyes absent; antennae extending to chaetiger 4–5; branchiae from chaetiger 10, becoming long and flat by chaetiger 15–20; 2 first chaetigers with anterior hooks: robust and slender bidentate simple hooks on chaetiger 1; slender bidentate simple and bidentate pseudocompound hooks on chaetiger 2; pectinate and limbate chaetae from chaetiger 3; subacicular hooks from chaetiger 13–14.

Description. All specimens lacking posterior ends. Length of holotype 10 mm for 18 chaetigers, width 2.5 mm; paratypes 9 mm (14 chaetigers) and 15 mm (24 chaetigers), 2.8 and 2.7 mm in width respectively. Alcohol-stored specimens overall cream-coloured. Paratype W.49938 with pale brown median spot on prostomium, some splotches on ventral lower lip and on sides of parapodia (Fig. 26A). Prostomium anteriorly rounded, wider than long, with 2 circular frontal lips, slightly separated from each other. Palpo- and antennophores with 2–3 proximal rings and longer distal ring. Antennostyles of holotype lost, greatly damaged or lost in paratypes; remaining

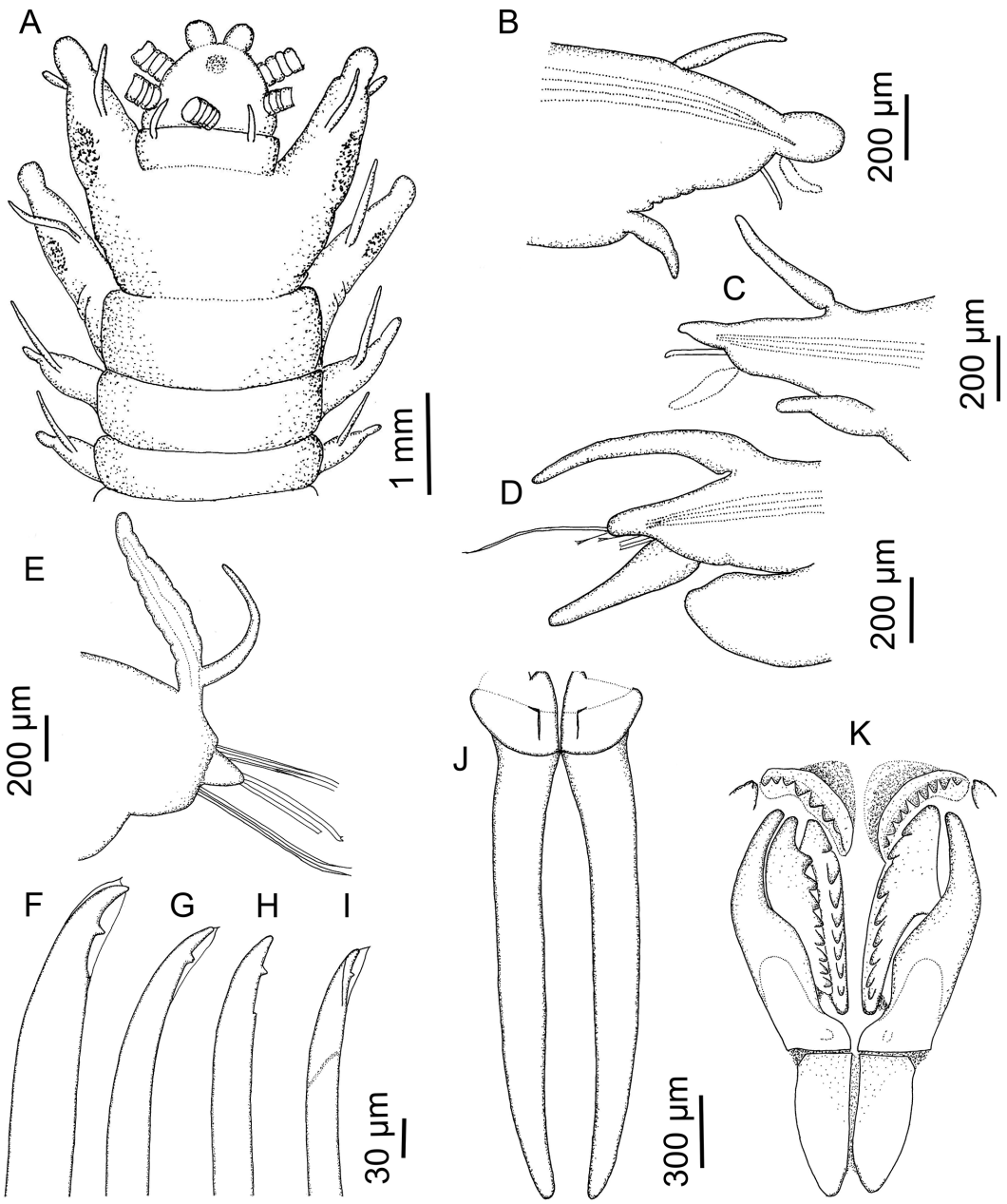

Figure 26. *Nothria simplex* sp. nov. Line drawings of paratype AM W.51646 (*A*), holotype AM W.49938 (*B, E, F–I*), and paratype AM W.51645 (*D, J, K*). (*A*) anterior part, dorsal view; (*B*) parapodium of chaetiger 1, anterior view (missing postchaetal lobe dotted); (*C*) parapodium of chaetiger 2, anterior view (missing postchaetal lobe dotted); (*D*) parapodium 3, anterior view; (*E*) parapodium 15, anterior view; (*F*) robust bidentate simple hook from chaetiger 1; (*G*) slender bidentate simple hook from same; (*H*) slender bidentate simple hook from chaetiger 2; (*I*) slender bidentate weakly pseudocompound hook from same; (*J*) mandibles, ventral view; (*K*) maxillae, dorsal view.

ones short, tapering gradually, palpostyles to chaetiger 1, lateral antennostyles extending to about chaetiger 4, median to chaetiger 5. Nuchal grooves straight, with small middorsal separation. Eyes absent. Ventral upper lips globular, lower lips subtriangular, neither with median section. Peristomium short, peristomial cirri inserted subdistally on peristomium, about as long as peristomium (Fig. 26A).

First chaetiger greatly enlarged, about four times as long as peristomium, chaetiger 2 about three fourths as long as chaetiger 1, third only slightly longer than following ones (Fig. 26A). Anterior 2 pairs of parapodia modified; first pair greatly enlarged, directed forward, extending slightly beyond anterior margin of peristomium in paratype W.51646 (Fig. 26A). First pair of parapodia with large auricular prechaetal lobes, digitate postchaetal lobes and dorsal cirri, subulate ventral cirri (Fig. 26B). Second pair of parapodia almost as long but much slenderer with tongue-like prechaetal lobes, digitate postchaetal lobes, dorsal cirri and subulate ventral cirri (Fig. 26C). Third pair of parapodia directed laterally, with small prechaetal lobes, subulate postchaetal lobes and dorsal cirri; ventral cirri almost transitioned to oval glandular pads (Fig. 26D). From chaetiger 4 onwards parapodial structures becoming more uniform; prechaetal lobes continued to end of fragments, postchaetal lobes absent from chaetiger 11 (11–13), dorsal cirri decreasing in size, ventral cirri as glandular pads. Branchiae beginning on chaetiger 10 as small stump, increasing in size to about chaetiger 20 becoming long and flat (Fig. 26E) when becoming shorter again.

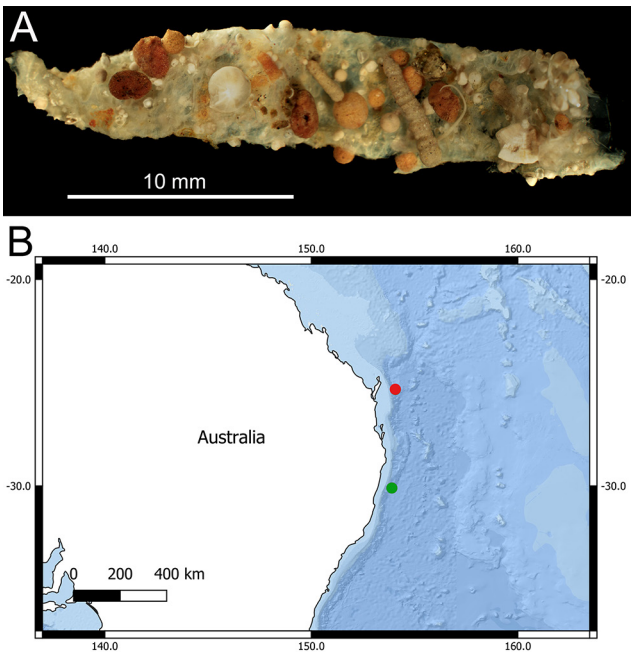

Figure 27. *Nothria simplex* sp. nov. (*A*) Photograph of tube of paraype AM W.51646; (*B*) map of distribution; red dot represents type locality, green dot other site of collection.

First pair of parapodia with 2 robust (Fig. 26F) and 1 slender bidentate simple hooded hooks (Fig. 26G). Parapodia 2 with 2 slender simple (Fig. 26H) and 1 very slender bidentate weakly pseudocompound hooded hooks (Fig. 26I). Anterior hooks absent from chaetiger 3; upper limbate chaetae, scoop-shaped pectinate chaetae with 20–25 teeth and lower limbate chaetae present. Subacicular hooks present singly from chaetiger 13(14–15), as pairs from chaetiger 14.

Mandibles (Fig. 26J) highly calcified, white, except for sclerotized protomandibles; shafts long and slender, cutting plates distally incomplete. Maxillae (Fig. 26K) calcified, almost white, except teeth, ligaments and attachment lamellae more sclerotized, appearing dark brown. Maxillary formula: MI = 1+1; MII = 9 + 8 (left most distal tooth fang-like); MIII = 8 + 0; MIV = 7 + 9; MV = 1+1. Ratio of mandibles/maxillae = 1.2. Pygidium unknown. Tube with parchment-like inner layer, covered on outside with foraminiferans and shell fragments (Fig. 27A).

Remarks. Only three damaged anterior fragments were available for study. Although some appendages and chaetae were absent or damaged, we were able to describe the morphology of this unusual species, albeit without any SEM images.

Six species of *Nothria* have only two pairs of parapodia with anterior hooks. Of these, *N. abyssia* and *N. paxtonae* are very slender, abranchiate species, whilst the new species is larger and has branchiae. *Nothria edwardsi* from the North Atlantic differs from *N. simplex* sp. nov. in having uni- to bidentate hooks on chaetiger 1 and only pseudocompound to compound hooks on chaetiger 2 rather than clearly bidentate hooks on chaetiger 1 and simple and weakly pseudocompound hooks on chaetiger 2. *Nothria atlantica* (Hartman, 1965) from the Mid-Atlantic Ridge differs in a number of features, most notably in having cirriform prechaetal lobes on chaetiger 1 and almost unidentate anterior hooks whilst the new species has auricular prechaetal lobes on chaetiger 1 and distinctly bidentate anterior hooks.

That leaves *N. mannarensis* Rangarajan and Mahadevan, 1961 from the Gulf of Mannar and *N. hawaiiensis* Pettibone, 1970 from off Hawaii collected at depths of 4 m and 463–730 m respectively. The former species was described on the basis of two tiny complete specimens measuring 8 and 13 mm in length for 25 and 38 chaetigers respectively while the holotype of the latter is a complete specimen of 60 mm length for 64 segments and a width of 7 mm. *Nothria mannarensis* differs from the new species in having large posterior eyes, an earlier start of branchiae and subacicular hooks, simple and pseudocompound hooks on chaetiger 1 and most likely represents juveniles. *Nothria hawaiiensis,* although twice as large as *N. simplex,* resembles the new species in some quantitative characteristics, e. g., beginning of branchiae and subacicular hooks and absence of postchaetal lobes. However, the anterior hooks have delicate distal fang and second tooth, and the maxillae are calcified and white in *N. simplex* sp. nov. while those of *N. hawaiiensis* are thick and blunt, and the maxillae are strongly sclerotized and dark.

Orensanz (l990) discussed a sample of "*Nothria,* unnamed species" from South of New Zealand, from a depth of 1026 m having only two anterior pairs of parapodia with hooks. It is similar to the new species but differs in having well developed eyespots, branchiae from chaetiger nine, 16 postchaetal lobes, composite hooks on chaetiger 2, and subacicular hooks from chaetiger 10–12.

Etymology. The name of the new species is suggested by having almost only simple hooded hooks on the anterior modified parapodia.

Distribution. *Nothria simplex* sp. nov. was collected from off Central Eastern Marine Park in 2429–2518 m and off Fraser Island in 2342–2350 m depth (Fig. 27B).

Discussion

The type-species of *Nothria, N. conchylega*, was described from shallow waters in western Norway (M. Sars, 1835). The original description is very general, giving few characters presently known to be of taxonomic importance. Fauchald (1982) redescribed the species and designated a lectotype from Florø, Western Norway.

Species of *Nothria* are superficially very similar and their lack of clear diagnostic features has hampered and complicated the taxonomy of the genus (Pettibone, 1970; Fauchald, 1982; Kucheruk, 1985). Chaetae, which are usually such useful characters in specific polychaete classification, are too generalized in this genus to be of much help. The specialized hooks of the anterior three, or rarely two, pairs of modified parapodia are distally almost all bidentate and the state of their fracture, i.e. whether they are simple, pseudocompound or compound, can be dependent on their stage during ontogeny where the final or adult state is only reached at a certain size (Orensanz, 1990; Budaeva & Paxton, 2013; Arias & Paxton, 2016). However, during the present study this problem did not arise since we encountered few juvenile specimens.

This is the first integrative study of the genus, sequencing the markers COI, 16S rDNA and 28S rDNA from 37 specimens and employing conventional and exploratory morphological characters as well as tube structure for

Key to Australian deep-water *Nothria* species collected by RV *Investigator*

1	Branchiae absent	2
——	Branchiae present	4
2	Anterior 2 pairs of parapodia with hooks	*N.* cf. *paxtonae* Imajima, 1999
——	Anterior 3 pairs of parapodia with hooks	3
3	Parapodia 1 and 2 prolonged; hooks of chaetiger 1 simple and pseudocompound; robust species (max. width 2.6 mm); tube with smallish fragments and rubble (Fig. 23A)	*N. orensanzi* sp. nov.
——	Parapodia 1 greatly prolonged, parapodia 2 hardly so; hooks of chaetiger 1 pseudocompound to compound; slender, delicate species (max. width 1.6 mm); tube covered with similarly sized shells (Fig. 20A)	*N. minima* sp. nov.
4	Anterior 2 pairs of parapodia with hooks	*N. simplex* sp. nov.
——	Anterior 3 pairs of parapodia with hooks	5
5	Hooks of chaetiger 1 uni- to bi- or tridentate	6
——	Hooks of chaetiger 1 clearly bidentate	7
6	Hooks of chaetiger 1 simple and pseudocompound; tube with foraminiferans and other small fragments (Fig. 5A)	*N. delta* sp. nov.
——	Hooks of chaetiger 1 simple only; tube with large shell fragments (Fig. 8A)	*N. deltasigma* sp. nov.
7	Branchiae short, starting from chaetiger 11–14	8
——	Branchiae long, starting from chaetiger 8–10	9
8	Prostomium subtriangular; large posterior eyes present; tube with some very large shells (Fig. 14A)	*N. josae* sp. nov.
——	Prostomium anteriorly rounded; eyes absent; tube with evenly sized shell fragments, resembling pavement (Fig. 17A)	*N. lizae* sp. nov.
9	Branchiae from chaetiger 9–10; ventral upper lip with median section (Fig. 9B); postchaetal lobes on first 11–12 chaetigers	*N. digitata* sp. nov.
——	Branchiae from chaetiger 8–9; ventral upper lip without median section; postchaetal lobes on first 14–17 chaetigers	*N. otsuchiensis* Imajima, 1986 complex

identification. In search for the exploration of new diagnostic features we evaluated the widths of the anterior hooks, certain jaw features with respect to mandibles and maxillae, and the consistency and structure of the tubes which are constructed by their inhabitants. These characters have been incorporated into the taxonomic descriptions.

Molecular data provided strong support for recognition of the eight new species with high posterior probability values for all clades and with congruent results between species delimitation analyses based on two mitochondrial and one nuclear marker. The *Nothria otsuchiensis* species complex clade (Fig. 1, clade C) showed conflicting delimitation results due to high divergence in sequences, missing sequence data for some specimens/markers and insufficient taxon sampling. If more specimens from this complex are analyzed in the future, it might result in splitting it into several well delimited species. The analysis of morphology has not revealed any obvious differences between the specimens within the complex. Thus, *N. otsuchiensis* may represent a complex of cryptic species, alternatively, such characters could be found after examination of a large amount of material containing various ontogenetic stages. Another delimitation conflict was recovered within *Nothria orensanzi* sp. nov. (Fig. 1, clade B) which contained one specimen delimited as a separate species in 16S and COI analyses. Adding more sequences may potentially lead to splitting this species into two. Nevertheless, here we recognize the whole clade B as a single species based on the data available at hand.

Three larger clades were highly supported in the analysis based on the combined dataset of three markers. Clade B+E+H showed no synapomorphic morphological characters. Clade F+A contains two sister species *N. josae* sp. nov. and *N. lizae* sp. nov. that share a similar distribution of simple and pseudocompound hooks on chaetigers 1–3, pectinate chaetae from chaetiger 3, have short protomandibles and maxilla IIL with a distal fang. Clade J+D+I comprising *Nothria conchylega*, *N. delta* sp. nov. and *N. deltasigma* sp. nov. is the only larger clade that showed synapomorphic characters. The latter three species shared the presence of robust unidentate simple hooks on chaetiger 1 and lacking a distal fang on maxilla II left. *Nothria delta* sp. nov. and *N. deltasigma* sp. nov. have long protomandibles, in contrast to the other new species described here. Although the protomandibles of *N. conchylega* do not surpass the lower

end of the cutting plates, they are equal in length to those in *Nothria delta* sp. nov. and *N. deltasigma* sp. nov. Our tree represents only a third of species diversity in *Nothria* which might be even higher than is currently known. A better taxon coverage would be required to aid in understanding of phylogeny and evolution of morphological characters within the genus.

While we recognized that we might be dealing with eight new species, it was the certainty of the genetic results that substantiated it. As stated above, *Nothria* has 21 recognized species. To this number we are adding eight new deep-water species, almost half as many as the previously known diversity. This underscores that a large proportion of *Nothria* inhabit the deep oceanic waters that are still understudied. At the same time, it demonstrates the advantage of integrated studies. While presently we can only reconcile the clades D, I and J (*N. delta* sp. nov.*, N. deltasigma* sp. nov. and *N. conchylega*) on genetic and morphological grounds, we feel certain that with future studies that can be extended to other clades as more known species are sequenced and included.

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Supplementary data

Figures S1–S6 are published separately online at *figshare*, see Paxton *et al*. (2023a) and the link below. Figs S1–S3: Consensus trees from the Bayesian analysis of the COI dataset (Fig. S1); of the 16S dataset (Fig. S2); and of the 28S dataset (Fig. S3) (in each, the numbers on nodes indicate Bayesian posterior probabilities). Figs S4–S6: PTP species delimitation trees built based on COI dataset (Fig. S4); on the 16S dataset (Fig. S5); and on the 28S dataset (Fig. S6) (in each, red clades represent putative species; and numbers on each node are posterior probabilities of the inner taxa forming one species):

https://doi.org/10.6084/m9.figshare.22596004

Tables S1–S3 are published separately online at *figshare,* see Paxton *et al*. (2023b) and the link below. List of specimens used in this study with GenBank Accession numbers, BOLD process ID, and data on their sampling and storage (Table S1); primer sequences and PCR parameters used for amplification of COI, 16S, and 18S (Table S2); and estimates of average evolutionary divergence over sequence pairs (p-distance) within and between the clades A–J calculated for individual markers (COI, 16S, and 28S) (Table S3):

https://doi.org/10.6084/m9.figshare.22589299