

Nothria and *Anchinothria* (Annelida: Onuphidae) from eastern Australian waters, with a discussion of ontogenetic variation of diagnostic characters

NATALIYA BUDAIEVA^{1,2} AND HANNELORE PAXTON^{1,3}

¹Australian Museum, 6 College Street, Sydney, NSW 2010, Australia, ²P.P. Shirshov Institute of Oceanology Russian Academy of Sciences, Nakhimovsky pr. 36, 117997, Moscow, Russia, ³Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Nothria and *Anchinothria*, two sister genera of onuphid worms were studied from eastern Australian waters. *Nothria abyssia*, with a wide distribution in Pacific and Antarctic waters is reported from slope depths south-east of Australia, while *N. otsuchiensis*, described from Japanese waters, was found along the eastern coast of Australia from shallow subtidal to deep slope areas. *Anchinothria parvula* sp. nov. is described, based on the presence of uni- and bidentate pseudocompound falcigers in the first three pairs of parapodia, absence of branchiae and appearance of limbate chaetae from chaetiger 2, subacicular hooks from chaetigers 6–8 and pectinate chaetae from chaetiger 14. The new species represents the first record of the genus in Australian waters. Ontogenetic variation of chaetal composition and morphology of parapodia was estimated in two *Nothria* species examined. Three size-related morphotypes with different chaetal composition and morphology of anterior falcigers were revealed in *N. abyssia* and *N. otsuchiensis*. The number of chaetigers with pseudocompound falcigers is the only character independent of size of the specimens in both examined species. Distribution of subacicular hooks and postchaetal lobes is shown to be size-dependent. The following characters are considered of diagnostic value only when scored in adults: presence/absence of simple falcigers in anterior parapodia; chaetiger of origin of limbate chaetae, pectinate chaetae, and subacicular hooks; and number of chaetigers with auricular prechaetal lobes and digitiform postchaetal lobes. The use of adult specimens with the final set of definitive morphological structures for diagnoses of *Nothria* species is suggested.

Keywords: polychaetes, new species, slope, deep sea, distribution, parapodia, redescription, chaetal replacement

Submitted 11 November 2012; accepted 5 December 2012; first published online 26 March 2013

INTRODUCTION

The short-bodied onuphids of the genus *Nothria* Malmgren, 1867, inhabiting distinctive dorsoventrally flattened tubes, adorned with large shell fragments and foraminiferans, are well known as epibenthic crawlers and have been reported worldwide from shallow subtidal waters to abyssal depths (Kucheruk 1980, 1985; Paxton 1986). Less well known is their sister genus *Anchinothria* Paxton, 1986, also widely distributed, with most species occurring deeper than 500 m, constructing flattened soft muddy tubes, often encrusted with elongated foreign objects (Paxton, 1986; Orensanz, 1990). The generic name *Nothria* was widely used in the older onuphid literature for species having only single branchial filaments (Hartman, 1944; Day, 1967; Fauchald, 1968) until Pettibone (1970) redefined the genus. She recognized the close relationship between *Nothria* and *Paradiopatra* Ehlers, 1887, in both having enlarged anterior parapodia, although modified in different ways. Pettibone (1970) suggested the

lobes of the anterior parapodia as diagnostic characters, and recognized auricular prechaetal lobes in *Nothria* and bi- to trilobed prechaetal lobes in *Paradiopatra*. The first attempt to revise both genera was undertaken by Fauchald (1982a) who re-examined the type material, referred eight species to *Nothria* and 11 species to *Paradiopatra*. Paxton (1986) revised the whole family Onuphidae, uncovered that the name '*Paradiopatra*' was already in use, and proposed the new name *Anchinothria* for species previously placed in *Paradiopatra sensu* Pettibone (1970). Paxton's phylogenetic analysis of the generic relationships within onuphids based on morphological characters confirmed Pettibone's earlier observation in revealing two sister genera: *Nothria* and *Anchinothria*, sharing a number of synapomorphies. Both genera comprise short-bodied onuphid worms with enlarged anterior parapodia, distally wide so-called 'scoop-shaped' pectinate chaetae with rolled lateral margins, and subacicular hooks inserted medially in the posterior parapodia between two bundles of limbate chaetae.

Paxton (1986) re-evaluated the morphology of the anterior parapodia of species revised by Fauchald (1982a), re-assigned them among the two genera, and recognized 13 species of *Nothria* and 12 species of *Anchinothria*. Seven more species of *Nothria* have been described during the following two

Corresponding author:

N. Budaeva

Email: nataliya.budaeva@gmail.com

decades, and two were later synonymized by Orensanz (1990) increasing the total number of species in the genus to 19. Of the 12 species referred to *Anchinothria*, three were later synonymized by Orensanz (1990), and Imajima (1999) described a new *Anchinothria* species from Japan, bringing the total number of species in the genus up to 11 (Table 1).

Nothria demonstrates a significant variation in the majority of morphological characters which was underestimated in the early species descriptions and revisions of the genus (Fauchald, 1982a; Kucheruk, 1985). Several attempts to estimate the morphological variation based on the examination of large material were performed. Kucheruk (1980) analysed 1200 specimens of *Nothria* collected worldwide at depths from 45 to 2930 m. He referred all the examined specimens to *Nothria conchylega* (Sars, 1835) despite the significant variability found in the studied material. Kucheruk (1980) reported that the chaetal composition (presence or absence of falcigers, limbate, and pectinate chaetae) in the anterior three pairs of parapodia was invariable in all specimens studied while the shape of falcigers in three anterior chaetigers was size-related. Jirkov & Yermolaev (1989) examined extensive collections of *Nothria* specimens from the northern hemisphere and identified two distinct morphotypes (A and B) differing from each other in the presence/absence of limbate and pectinate chaetae on the second pair of parapodia. They have analysed 12 morphological characters in 191 specimens belonging to morphotype A and 62 specimens assigned to morphotype B. Three characters were found to be size-dependent while eight characters, including chaetal composition in anterior pairs of parapodia, lacked significant correlation with the size (expressed by body width) of studied worms. Orensanz (1990) discussed the ontogenetic variation in *Nothria anoculata* Orensanz, 1974 and demonstrated the gradual replacement of pseudocompound falcigers by simple falcigers in the first two pairs of parapodia with increasing size of specimens. The segment number of the first appearance of subacicular hooks and branchiae was also variable in the examined material, with positive correlation with the size of the worms. In contrast, the morphology of *N. abyssia* was shown to be less variable and became stabilized earlier in the development in comparison with *N. anoculata* (Orensanz, 1990).

Intertidal and shallow water onuphids of Australia have been studied by Paxton (1979, 1993, 1996). The present study focuses on *Nothria* and *Anchinothria* which are better represented in low subtidal and slope depths. The genus *Nothria* has been reported from New Zealand for *N. conchylega* (Knox & Hicks, 1973), was known to occur in Australia, but had not been identified to species (Paxton, 2000), whilst *Anchinothria* has never been reported from Australian waters.

The present study aims to revise the species of *Nothria* and *Anchinothria* collected from shelf and slope depths off south-eastern Australia. The detailed description of intraspecific variability in at least four different species of *Nothria* (Kucheruk, 1980; Jirkov & Yermolaev, 1989; Orensanz, 1990) showed several different patterns of size-dependency of major diagnostic characters. We also aim to analyse the ontogenetic variation of the major diagnostic morphological characters in Australian *Nothria* such as chaetal morphology and composition in the anterior three pairs of parapodia, morphology and distribution of branchiae, prechaetal and postchaetal parapodial lobes, and appearance of the subacicular hooks. The description of size-dependent morphological variation in *Nothria* from Australian waters will become a basis for future

revision of diagnostic characters in other species of the genus with subsequent generic revision of *Nothria*.

MATERIALS AND METHODS

Specimens were stained with methylene blue solution in 30% ethanol and examined under a dissecting stereomicroscope. Methylene blue staining increased the contrast of some morphological structures, such as ceratophores, branchiae, and parapodial lobes and cirri. After examination stained specimens were transferred to 70% ethanol, which led to the complete loss of the stain from the specimens. Unstained specimens were examined under a compound light microscope. Temporary glycerol slides of specimens smaller than 1.3 mm wide were used for the detailed examination of chaetal distribution and the morphology of parapodia along the body. Permanent slides of anterior parapodia embedded into Hydro-Matrix® mounting medium were made for the examination of chaetae in worms larger than 1.3 mm wide. Line drawings were made with the aid of a camera lucida and digital photography.

Specimens used for scanning electron microscopy (SEM) analysis were initially fixed with 4% formalin and then transferred into 70% ethanol. They were run through the series of ethanol: 70%, 80%, 90%, 100%, 100%, 100%, 30 minutes at each step, critically point dried with a Bal-Tec CPD 030 Critical Point Dryer, mounted on stubs, coated with gold using Emitec K550 Gold Sputter Coater and imaged with a Zeiss EVO LS15 scanning electron microscope with a Robinson Backscatter Detector.

Kucheruk (1980) demonstrated strong positive correlation between the width and the length of the body and the number of chaetigers in *Nothria*. He suggested that the width of a worm can be used for size estimation since posterior regions were frequently missing or in poor shape in the studied samples. Following Kucheruk (1980) the width of the sixth chaetiger measured as a distance between the inner parts of dorsal cirri was used as an estimation of the size of the worms.

We followed chaetal terminology suggested by Budaeva & Fauchald (2010). The term 'falciger' was used to describe simple or pseudocompound hooded dentate chaetae present on anterior modified parapodia. The term 'hook' was used to define simple bidentate chaetae appearing in median position in posterior unmodified parapodia. The terminology for prostomial appendages followed that of Paxton (1998).

Specimens borrowed from the following institutions have been examined: Australian Museum, Sydney, New South Wales, Australia (AM); Museum Victoria, Melbourne, Victoria, Australia (MV); and Senckenberg Museum, Frankfurt-am-Main, Germany (SMF). The holotype and paratypes of the new species were deposited in the Marine Invertebrate Collection of the Australian Museum, Sydney (AM). Station details of the material from the RV 'Franklin' SLOPE expedition (MV) are given in Table 2.

SYSTEMATICS

Order EUNICIDA Dales, 1962
 Family ONUPHIDAE Kinberg, 1865
 Subfamily HYALINOECIINAE Paxton, 1986
 Genus *Anchinothria* Paxton, 1986

Table 1. Species composition and distribution of *Nothria* and *Anchinotheria*.

Species	Authority	Type locality	Depth-range (m)	Distribution
<i>Nothria abyssia</i>	Malmgren, 1867 Kucheruk, 1978	South-eastern Pacific sector of Antarctica, 65°31'S 152°26' E, 2800 m	400–5200	North Pacific: off Aleutian Islands, Japan, New Guinea, and Chile (Kucheruk, 1978); Subantarctic: Pacific–Antarctic Ridge, Macquarie Ridge, southern part of south-eastern Pacific basin; Antarctica: Scotia Sea (Kucheruk, 1978, Orensanz, 1990); off south-eastern Australia, Atlantic sector of Antarctica (present study)
<i>Nothria africana</i>	(Augener, 1918)	Atlantic, off Dahomey, Great Popo	?	Western Africa (Augener, 1918)
<i>Nothria anoculata</i>	Orensanz, 1974	Western Atlantic, off Argentina, Buenos Aires Province, 700–900 m	75–1887	Subantarctic: Tierra del Fuego, off slope of Argentina, north of Drake–Passage, South Georgia shelf, Pacific–Antarctic Ridge, Macquarie Ridge, Antipodes–Bounty shelf, Prince Edward–Marion shelf; Antarctica: Ross Sea (Orensanz, 1990)
<i>Nothria atlantica</i>	(Hartman, 1965)	Northern Atlantic, Mid-Atlantic Ridge, 35°37'N 30°51'W, 3200 m	2560–3236	Northern Atlantic, Mid-Atlantic Ridge (Hartman, 1965)
<i>Nothria benthophyla</i>	Lana, 1991	South-western Atlantic, off Brazil, 29°3'S 48°0'W, 183 m	35–183	Off south-eastern Brazil (Lana, 1991)
<i>Nothria brittanica</i>	(McIntosh, 1903)	Northern Atlantic, Shetland, St Magnus Bay, 182 m,	?	Type locality, other records unconfirmed
<i>Nothria conchylega</i>	(Sars, 1835)	North-eastern Atlantic, Norway, Florø, 15–18 m (lectotype, designated by Fauchald, 1982c)	?	North-eastern Atlantic (Fauchald, 1982c), other records unconfirmed
<i>Nothria grossa</i>	Imajima, 1989	North-western Pacific, off Japan, off Sanriku, 39°12.9'N 142°16.0'E – 39°13.9'N 142°16.4'E, 562 m	330–1680	North-western Pacific, off Japan (Imajima, 1999)
<i>Nothria hawaiiensis</i>	Pettibone, 1970	Central Pacific, west coast of Hawaii, 20°06'10"N 155°59'40"W, 463–699 m	463–730	Central Pacific, off Hawaii (Pettibone, 1970)
<i>Nothria hyperborea</i>	(Hansen, 1878)	Northern Atlantic, 62°44'N 1°48'E, 412–753 m (lectotype, designated by Fauchald, 1982a); 64°36'N 10°22'W, 299–547 m (paratypes, designated by Fauchald, 1982a)	?	Reported from type locality (Hansen, 1882), other records unconfirmed
<i>Nothria itoi</i>	Maekawa & Hayashi, 1989	North-western Pacific, off Japan, Wakasa Bay, 89–90 m	20–300	North-western Pacific, Japan (Imajima, 1999)
<i>Nothria mannarensis</i>	Rangarajan & Mahadevan, 1961	Indian ocean, off south-eastern India, Gulf of Mannar, opposite Pudumadam, 9°16'N 79°01'E, 4 m	4	Reported only from type locality
<i>Nothria maremontana</i>	Andre & Pleijel, 1989	Northern Atlantic, Seine Seamount, 33°48.03'N 14°23.03'W, 450–455 m	255–455	Northern Atlantic, Seine Seamount, Josephine Seamount (Andre & Pleijel, 1989)
<i>Nothria oblonga</i>	Imajima, 1999	North-western Pacific, Japan, off Kushimoto, Wakayama Prefecture, 33°27.3'N 135°44.6'E–33°27.5'N 135°44.1 E, 45–68 m	25–110	North-western Pacific, off Japan (Imajima, 1999)

Continued

Table 1. Continued

Species	Authority	Type locality	Depth-range (m)	Distribution
<i>Nothria occidentalis</i>	Fauchald, 1968	Eastern Pacific, off Ensenada, Mexico, 31°53'20"N 116°48'15"W, 75 m	75–119	Eastern Pacific, Southern California, south to Colombia, Pacific side of Baja California (Fauchald, 1968)
<i>Nothria otsuchiensis</i>	Imajima, 1986	North-western Pacific, off Japan, Otsuchi Bay, 48–79 m	26–2900	Western Pacific: Japan (Imajima, 1999); New Caledonia, off south-eastern Australia (present study)
<i>Nothria paxtonae</i>	Imajima, 1999	North-western Pacific, Japan, off Emi, Boso Peninsula, 35°00.1'N 140°06.8'E–35°00.5'N 140°07.5'E, 145–150 m	90–175	North-western Pacific, off Japan (Imajima, 1999)
<i>Nothria solenotecton</i>	(Chamberlin, 1919)	Eastern Pacific, off Panama, 7°05.5'N 79°40'W, 2323 m	2323	Type locality, other records unconfirmed
<i>Nothria textor</i>	Hartman & Fauchald, 1971	West Atlantic east of Bermuda, from 32°19.4'N 64°34.9'W–32°19.0'N 64°34.8'W, 1135–1153	1135–1153 m	Type locality, other records unconfirmed
<i>Anchinotheria</i>	Paxton, 1986			
<i>Anchinotheria cirrobranchiata</i>	(Moore, 1903)	North-western Pacific, off Japan, Suruga Bay, 306 m	100–980	North-western Pacific, off Japan (Imajima, 1999)
<i>Anchinotheria cobra</i>	(Chamberlin, 1919)	Eastern Pacific, off Panama, 4°56'N 80°52.5'W, 3225 m	3225	Reported only from type locality
<i>Anchinotheria crassisetosa</i>	(Chamberlin, 1919)	Syntype, eastern Pacific off Panama 6°36'N 81°45'W, 1057 m (syntype); off Galapagos Islands, 0°59'S 88°58.5'W, 718 m (syntype)	718–2530	Eastern Pacific, off Panama, off Galapagos Islands (McIntosh, 1885); off Japan, 2530 m (Imajima, 1999)
<i>Anchinotheria fissurata</i>	(Fauchald, 1972)	North-eastern Pacific, off Mexico, Baja California, 22°48'20"N 109°52'40"W, 898 m	898–1865	Eastern Pacific, off Mexico, Baja California, off Cabo San Lucas; off Panama (Fauchald, 1972)
<i>Anchinotheria glutinatrix</i>	(Ehlers, 1887)	Western Atlantic, Caribbean Sea, off the Sambos, 432 m	432	Reported only from type locality
<i>Anchinotheria hiatidentata</i>	(Moore, 1911)	Eastern Pacific, off southern California, 32°32'40"N 118°04'20"W, 1927 m	1927	Reported only from type locality
<i>Anchinotheria macrobranchiata</i>	(McIntosh, 1885)	North-western Pacific, off Japan, south of Yedo, 35°11'N 139°28'E, 631 m	435–1350	North-western Pacific, off Japan (Imajima, 1999)
<i>Anchinotheria parvula</i>	sp. nov.	Off south-eastern Australia, 33°16.85'S 159°09.15'E, 244 m	244	Reported only from type locality
<i>Anchinotheria pourtalesii</i>	(Ehlers, 1879)	Western Atlantic, off Cuba, 23°11'N 82°23'W, 531 m (2 syntypes), off Cuba, 23°02.5'N 83°11'W, 522 m (syntype); off Florida, Sand Keys, 557 m (syntype), and off the Sambos, 435 m (syntype)	36–918	Western Atlantic, Caribbean region, off Florida, and Gulf of Mexico (Pettibone, 1970)
<i>Anchinotheria pycnbranchiata</i>	(McIntosh, 1885)	Eastern Pacific, off the Chilean coast, 34°7'S 73°56'W, 4069 m	2433–4464	Antarctic and Subantarctic waters: southern border of south-east Pacific basin, Pacific–Antarctic Ridge, Chile Ridge, Scotia Sea, western part of Atlantic–Indian basin (Orensanz, 1990)
<i>Anchinotheria sombreroana</i>	(McIntosh, 1885)	Western Pacific, West Indies, off Sombrero and St Thomas, 713–860 m	713–860	Reported only from type locality
<i>Anchinotheria tosaensis</i>	Imajima, 1999	North-western Pacific, off Japan, Tosa bay, 33°13.6'N 133°36.4'E–33°13.3'N 133°35.8'E, 200–198 m	200–423	North-western Pacific, off Japan (Imajima, 1999)

Table 2. Details of RV ‘Franklin’ epibenthic sled stations (Poore *et al.*, 1994).

Station	Latitude, S	Longitude, E	Depth (m)
6	34°53.57′	151°12.60′	770
7	34°52.29′	151°15.02′	1096
22	37°00.60′	150°20.70′	363
25	38°25.90′	148°58.60′	1850
32	38°21.90′	149°20.00′	1000
33	38°19.60′	149°24.30′	930
34	38°16.40′	149°27.60′	800
45	42°02.20′	148°38.70′	800
46	42°00.20′	148°37.70′	720
48	41°57.50′	148°37.90′	400
66	38°40.29′	149°18.06′	2900
67	38°23.95′	149°17.02′	1277
69	38°29.33′	149°19.98′	1840
81	42°00.25′	148°43.55′	1264
82	41°57.30′	148°58.54′	1770

DIAGNOSIS

Body short, up to 100 segments. Median antenna longer and thicker than lateral antennae. Ceratophores short, consisting of 2–5 rings. Nuchal grooves straight. Anterior 2–3 pairs of parapodia enlarged, directed anteroventrally with bi- to trilobed prechaetal lobes. Uni- or bidentate simple or pseudocompound falcigers on first 2–4 pairs of anterior parapodia, in one species on first seven pairs of parapodia. Subacicular hooks in median position from chaetigers 4–16. Pectinate chaetae wide with rolled margins, so-called ‘scoop-shaped’, from chaetigers 2–3, in one species from chaetiger 14. Branchiae present or absent, single to up to 10 filaments. Tubes dorsoventrally flattened with parchment-like inner layer covered with mud and often incrustated with scattered large elongated foraminiferans, glass sponge spicules or echinoid spines attached along longitudinal margins of tubes.

Anchinothria parvula sp. nov.
(Figures 1–3)

TYPE MATERIAL

AM: W.41478, Tasman Sea, Taupo Seamount, RV ‘Franklin’ Station 8, 33°16.85′S 159°09.15′E, 244 m, 2 October 1989 (holotype); W.41475.001, the same location as holotype (1 paratype gold-coated for SEM); W.41476, the same location as holotype (1 paratype with dissected maxillae); W.41476.001, the same location as holotype (microscopic slide with dissected parapodia 1–3, 7, and 13 from paratype W.41476); W.41477, the same location as holotype (10 paratypes).

DIAGNOSIS

First pair of parapodia with pseudocompound uni- or bidentate falcigers. Second and third pairs of parapodia with pseudocompound bidentate falcigers and limbate chaetae. Pectinate chaetae flat, from chaetiger 14. Branchiae absent. Subacicular hooks from chaetigers 6–8. Prechaetal lobes as low rounded ridges on all chaetigers. Postchaetal lobes present on first three chaetigers. Two pairs of eyes.

TYPE LOCALITY

Off south-eastern Australia, 33°16.85′S 159°09.15′E, 244 m.

DESCRIPTION

All specimens examined represented by anterior fragments. Holotype, largest specimen, consisting of 17 chaetigers, 0.73 mm wide and 5.9 mm long (Figure 1A–C). Paratypes consisting of 9–18 chaetigers with width varying from 0.4 to 0.73 mm. Specimens pale yellowish in colour with dark brown strap along lateral posterior margin of prostomium and anterior margin of peristomium; light brown spots located dorsally at bases of first pair of parapodia (Figure 1C). Some specimens without coloration.

Prostomium with rounded anterior margin, globular frontal lips not visible from dorsal side, projecting anteroventrally (Figures 1A–C; 2A). Palps reaching chaetiger 1 (1–2); lateral antennae reaching chaetiger 5 (3–7); median antenna longer and thicker than lateral antennae reaching chaetiger 9 (6–9). Ceratophores consisting of 3 (2–4) rings (Figure 1C). Nuchal grooves straight with narrow middorsal separation. Two pairs of eyes present, large dark eyes located laterally near bases of lateral antennae (Figure 1A); pair of small eyespots located dorsally at anterior margin of peristomium (Figure 1C). Peristomium half as long as first chaetiger, bearing short, tapering peristomial cirri (Figure 1A, C).

First pair of parapodia slightly larger than subsequent parapodia projecting lateroventrally and directed anteriorly (Figures 1C; 2A, B). Anterior pair of parapodia with short rounded prechaetal lobe, subulate dorsal cirri, digitiform postchaetal lobes and ventral cirri (Figures 1D; 2C–D). Second pair of parapodia similar in size with posterior parapodia bearing short, rounded prechaetal lobes, subulate dorsal cirri, digitiform postchaetal lobes and conical ventral cirri (Figures 1E; 2E). Third pair of parapodia with very short rounded prechaetal lobes, bearing subulate dorsal cirri, digitiform postchaetal lobes and slightly conical ventral cirri with distal glandular pads (Figures 1F; 2E). Prechaetal lobes becoming invisible after chaetiger 3 (Figures 1F; 2E); postchaetal lobes abruptly disappearing from chaetiger 4 (Figure 2F). Ventral cirri subulate on first two chaetigers (Figures 1D, E; 2C–E), slightly conical with round glandular tips on chaetiger 3 (Figures 2E) transforming into flat, round glandular pads from chaetiger 4 (Figure 2F, I, J).

First pair of parapodia of holotype and seven paratypes with 3 (4) bidentate clearly pseudocompound falcigers (Figures 1D, J; 3A); six paratypes with unidentate falcigers (Figure 1I). Falcigers with wide, short distal parts, covered with short blunt hoods. Second tooth, when present, relatively small, widely separated from distal tooth (Figure 1J). Shafts of anterior falcigers smooth with scattered small spines. Second and third pairs of parapodia bearing single dorsal limbate chaetae (Figure 1E, F, L) and three pseudocompound clearly bidentate falcigers with short blunt hoods and group of small spines located beyond pseudoarticulation (Figures 1E, F, K; 2E; 3B). Single bundle of bilimbate chaetae with wide distal parts from chaetiger 4 (Figures 2F; 3C). Subacicular hook starting from chaetiger 8 (6–8) in median position with single limbate chaeta located dorsally and ventrally (Figures 1G, N, M; 3D, E). Subacicular hooks first present singly in parapodium (Figures 1G; 2G), becoming paired posteriorly (Figures 1H; 2H). Pectinate chaetae first present on chaetiger 14, flat, slightly bent with approximately 18–20

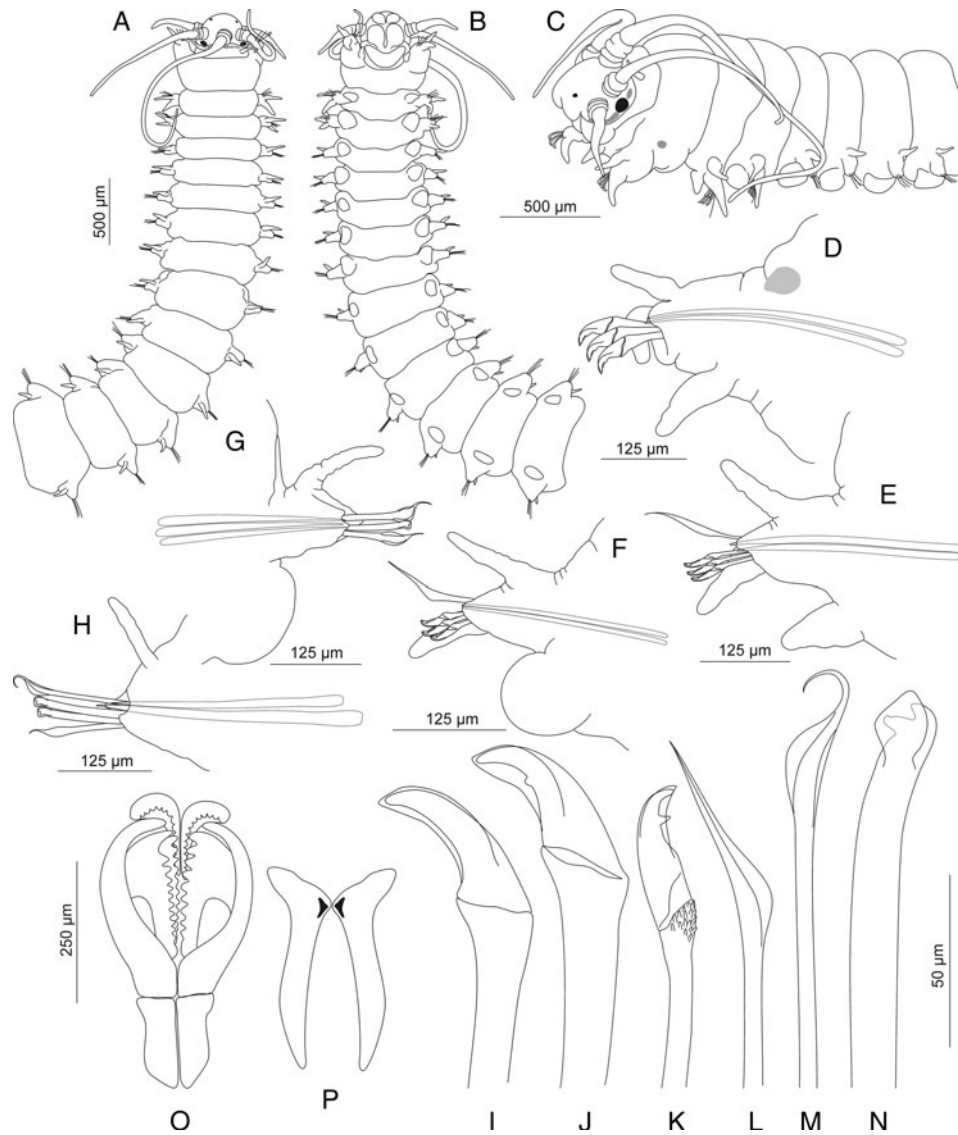


Fig. 1. *Anchinothria parvula*, new species: (A) anterior part of body, dorsal view; (B) same, ventral view; (C) same, lateral view; (D) parapodium of chaetiger 1, anterior view; (E) parapodium of chaetiger 2, anterior view; (F) parapodium of chaetiger 3, anterior view; (G) parapodium of chaetiger 7, posterior view; (H) parapodium of chaetiger 13, anterior view; (I–J) pseudocompound falcigers from chaetiger 1; (K) same from chaetiger 2; (L) limbate chaeta from chaetiger 3; (M) same from chaetiger 13; (N) subacicular hook from chaetiger 13; (O) maxillae; (P) mandibles.

denticles, one per parapodium (Figures 2H; 3F, G). Neuroaciculae pale yellow with pointed tips (Figure 3G), 2–3 per parapodium (Figure 1D–H).

Mandibles white with short shafts (Figure 1P). Maxillae very delicate almost transparent with approximately 10 teeth in each plate of MxII–MxIV. Mx V not observed (Figure 1O). Branchiae absent. Pygidium and tubes unknown.

ETYMOLOGY

The species name '*parvula*' meaning 'little', 'pretty', 'young' in Latin refers to the small size and dainty appearance of individuals of the new species.

REMARKS

Anchinothria parvula belongs to a group of species with falcigers on the first three pairs of parapodia. This group comprises the following species: *Anchinothria crassisetosa*

(Chamberlin, 1919), *A. hiatidentata* (Moore, 1911), *A. macrobranchiata* (McIntosh, 1885), and *A. pycnbranchiata* (McIntosh, 1885). The new species can be distinguished from *A. crassisetosa*, *A. pycnbranchiata* and *A. hiatidentata* in the origin of the subacicular hook. They are present from chaetiger 4 in the two former species and from chaetiger 12 in the latter, while *A. parvula* sp. nov. has subacicular hooks starting from chaetigers 6–8. *Anchinothria parvula* sp. nov. differs from *A. macrobranchiata* in lacking rather than having long branchiae from chaetiger 8 and being much smaller in size. The largest specimen of *A. parvula* is 0.73 mm wide without parapodia while *A. macrobranchiata* reaches 6 mm in width including parapodia (McIntosh, 1885).

DISTRIBUTION

Anchinothria parvula is known from a single locality, off south-eastern Australia, at a depth of 244 m.

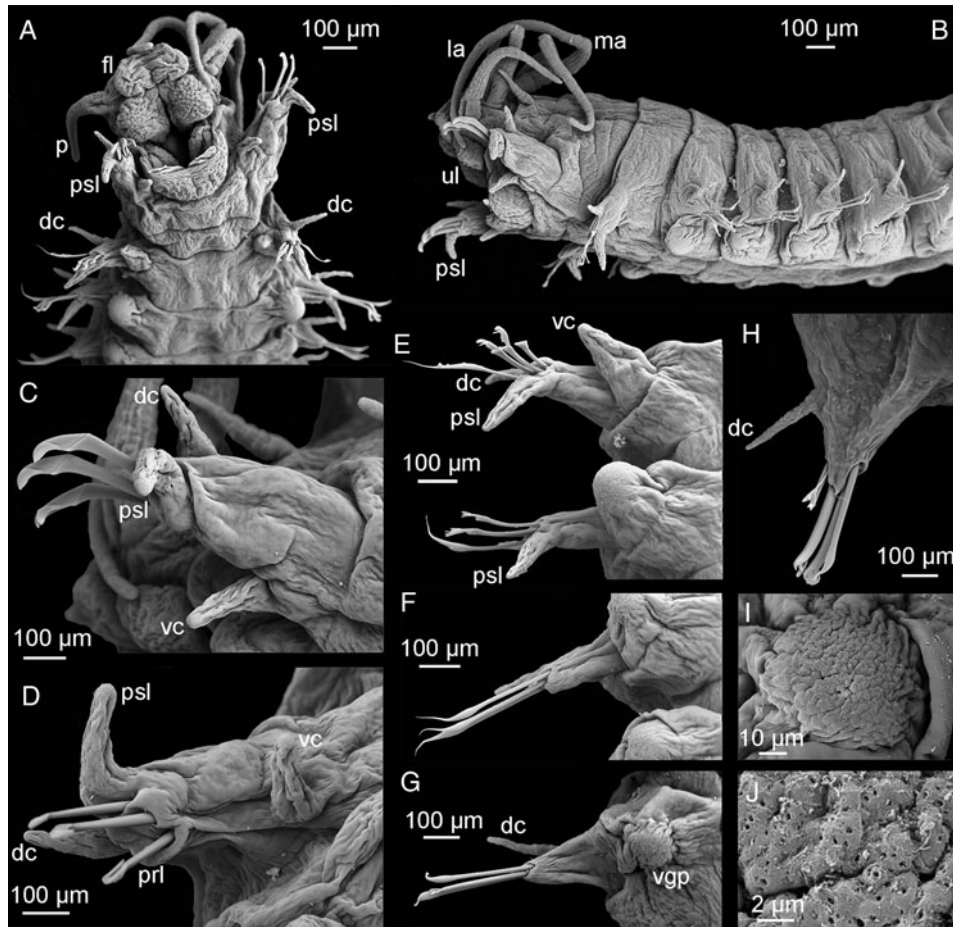


Fig. 2. *Anchinothria parvula*, new species: (A) anterior part of body, ventral view; (B) same, lateral view; (C) parapodium of chaetiger 1, posterior view; (D) same, anteroventral view; (E) parapodia of chaetigers 2–3, ventral view; (F) parapodium of chaetiger 4, ventral view; (G) parapodium of chaetiger 7, ventral view; (H) parapodium of chaetiger 15, anterior view; (I–J) ventral glandular pad of chaetiger 5; dc, dorsal cirrus; fl, frontal lip; la, lateral antenna; ma, median antenna; p, palp; psl, postchaetal lobe; ul, upper lip; vc, ventral cirrus; vgp, ventral glandular pad.

Genus *Nothria* Malmgren, 1867

DIAGNOSIS

Body short, up to 100 segments. Median antenna longer and thicker than lateral antennae. Ceratophores short, consisting

of 2–5 rings. Nuchal grooves straight. Anterior 2–3 pairs of parapodia enlarged, directed anteroventrally with large auricular prechaetal lobes. Uni-, bi- or tridentate simple or pseudocompound falcigers on first 2–3 pairs of anterior parapodia. Subacicular hooks in median position from

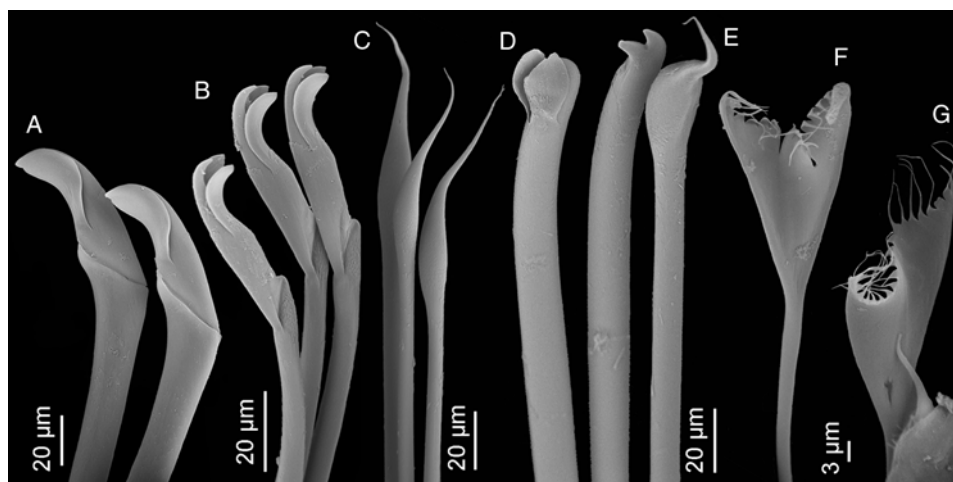


Fig. 3. *Anchinothria parvula*, new species: (A) pseudocompound falcigers from chaetiger 1; (B) pseudocompound falcigers from chaetiger 3; (C) limbate chaetae from chaetiger 4; (D) subacicular hooks from chaetiger 13; (E) limbate chaeta from chaetiger 13; (F) pectinate chaeta from chaetiger 15; (G) pectinate chaeta and emerging acicula from chaetiger 14.

chaetigers 7–15. Pectinate chaetae wide with rolled margins, so-called ‘scoop-shaped’, from chaetigers 2–3, in one species from chaetiger 9. Branchiae present or absent, single to up to five filaments. Tubes dorsoventrally flattened with thin inner parchment-like layer covered with large shell fragments, small stones and foraminiferans.

Nothria abyssia Kucheruk, 1978
(Figures 4–10)

Nothria abyssia Kucheruk, 1978: 101–103, figures 4, 5.—Orensanz 1990: 48–50, pl. 10, chart 5B.

Nothria abranchiata – Hartman 1964: 112, pl. 24, figures 1–3.—non *Nothria abranchiata* McIntosh, 1885: 314–317, pl. 21A, figure 27; pl. 22A, figures 1–3, pl. 40, figures 1–12.

Onuphis (*Nothria*) *abranchiata*—Averincev 1972: 178.—Averincev 1974: 219.

Onuphis (*Nothria*) *australatlantica* Fauchald, 1982b: 238, figure 1, table 1.

Paradiopatra abyssia—Fauchald 1982a: 83.

MATERIAL EXAMINED

AM: W42762, RV ‘Franklin’ SLOPE Station 69 (2), W42763.001, RV ‘Franklin’ SLOPE Station 69 (2 specimens gold-coated for SEM); W42764.001, RV ‘Franklin’ SLOPE Station 69 (1 specimen gold-coated for SEM).

MV: F183731, RV ‘Franklin’ SLOPE Station 82 (2); F183732, RV ‘Franklin’ SLOPE Station 67 (1); F183733, RV ‘Franklin’ SLOPE Station 25 (1); F183734, RV ‘Franklin’ SLOPE Station 69 (35); F183735, RV ‘Franklin’ SLOPE Station 48 (3); F183736, RV ‘Franklin’ SLOPE Station 66 (1); F192362, RV ‘Franklin’ SLOPE Station 69 (one slide with dissected parapodia).

ZMH: P.26039, ANDEEP III, RV ‘Polarstern’ ANT XXII-3 Station 59-5, 67°29.81′S 0°00.23′W, 4651 m, 14 February 2005, epibenthic sledge, supranet (2); P.26040, ANDEEP III, RV ‘Polarstern’ ANT XXII-3 Station 59-5, 67°29.81′S 0°00.23′W, 4651 m, 14 Feb 2005, epibenthic sledge, epinet (2); P.26041, ANDEEP III, RV ‘Polarstern’ ANT XXII-5 Station 102-13, 65°33.18′S 036°31.05′W, 4817 m, 6 March 2005, epibenthic sledge, epinet (1); P.26042, ANDEEP III, RV ‘Polarstern’ ANT XXII-5 Station 102-13, 65°33.18′S 036°31.05′W, 4817 m, 6 March 2005, epibenthic sledge, supranet (1); P.260043, ANDEEP III, RV ‘Polarstern’ ANT XXII-4 Station 81-8, 70°31.08′S 14°34.82′W, 4419 m, 24 February 2005, epibenthic sledge, supranet (1); P.26044, ANDEEP II, RV ‘Polarstern’ ANT XIX-4 Station 141-10, 58°25.08′S 25°00.77′W, 2313 m, 23 March 2002, epibenthic sledge, epinet (1).

DIAGNOSIS

Based on specimens wider than 1.0 mm at chaetiger 6 excluding parapodia: first pair of parapodia extending beyond frontal margin of prostomium, with simple and pseudocompound bidentate falcigers. Second pair of parapodia with bidentate pseudocompound falcigers and limbate chaetae. Third pair of parapodia with limbate and pectinate chaetae. Pectinate chaetae flat. Branchiae absent. Subacicular hooks from chaetigers 7–9. Auricular prechaetal lobes on first chaetiger only, chaetigers 2–3 with conical prechaetal lobes, reduced posteriorly. Postchaetal lobes present on first 2–3 chaetigers. Paired eyespots may be present on dorsal side of prostomium.

TYPE LOCALITY

Antarctic Ocean, 65°31′S 152°26′E, 2800 m.

DESCRIPTION

All examined specimens represented by anterior fragments varying in width from 0.4 to 1.53 mm. Specimens light brownish, lacking colour pattern. Following description based on specimens wider than 1.0 mm at chaetiger 6 excluding parapodia.

Prostomium anteriorly rounded with paired ovoid to oval frontal lips, palps reaching chaetiger 1, lateral antennae reaching chaetiger 4 and median antenna reaching chaetigers 3–6 (Figure 4A). Ceratophores short, consisting of 2–3 indistinct rings. Two little eyespots present on dorsal side of prostomium (Figure 4A). Some specimens without eyes. Nuchal grooves wide and straight, with narrow mid-dorsal separation. Upper lips oval; ventral lip wide and massive. Peristomium half as long as first chaetiger (Figure 4A). Peristomial cirri as long as peristomium.

First pair of parapodia enlarged, prolonged significantly extending beyond anterior margin of prostomium, bearing large truncate auricular prechaetal lobes, short digitiform postchaetal lobes, subulate dorsal cirri and short digitiform ventral cirri (Figures 4C; 5C; 6C). Second pair of parapodia similar in size to subsequent parapodia, bearing very short foliose prechaetal lobes, well developed digitiform postchaetal lobes, dorsal cirri and conical ventral cirri (Figures 4D; 7C). Third pair of parapodia with smaller but distinct prechaetal lobes, digitiform postchaetal lobes, dorsal cirri and transitional slightly conical ventral cirri (Figures 4E; 8C). Dorsal cirri present on all chaetigers of specimens examined, gradually decreasing in size and becoming subulate. Prechaetal lobes decreasing in size considerably from chaetigers 3–4, becoming short and rounded, almost invisible from chaetigers 4–5. Postchaetal lobes gradually decreasing posteriorly, visible on up to 24 chaetigers in longest specimens examined. Ventral cirri replaced by round glandular pads from chaetiger 4 (Figure 4B).

First pair of parapodia with one simple and 2–3 indistinctly pseudocompound bidentate falcigers (Figures 4C; 6F). Subdistal tooth on anterior falcigers small and often broken (Figure 6F). Anterior falcigers bearing paired short hood with blunt tips, in some falcigers hoods missing, presumably broken (Figures 4C, 6F). Second pair of parapodia with 3–4 clearly bidentate pseudocompound falcigers with short, paired hoods and 1–4 simple, thin limbate chaetae (Figures 4D; 7G). Third pair of parapodia with 5–8 thin limbate chaetae and 2–3 flat and wide pectinate chaetae with 17–20 denticles (Figures 4E; 8D). Subsequent parapodia with numerous limbate and pectinate chaetae. Subacicular hooks starting from chaetigers 7–9, two per parapodium. Neuroaciculae yellow with pointed tips, 2–3 per parapodium.

Branchiae absent. Tubes flattened, covered by numerous foraminiferan tests; no large pieces of shell fragments were observed.

ONTOGENETIC VARIATION

Thirty-two specimens of *Nothria abyssia* ranging in width from 0.4 to 1.53 mm (Figure 5) were examined (SLOPE Station 69).

Chaetal composition of the first pair of parapodia

Specimens smaller than 1.0 mm wide had 3–4 (rarely up to 5) pseudocompound falcigers in the parapodia of the first chaetiger (Figure 4F; 6D, E). In specimens larger than 1.0 mm wide, a single pseudocompound falciger was replaced by a simple

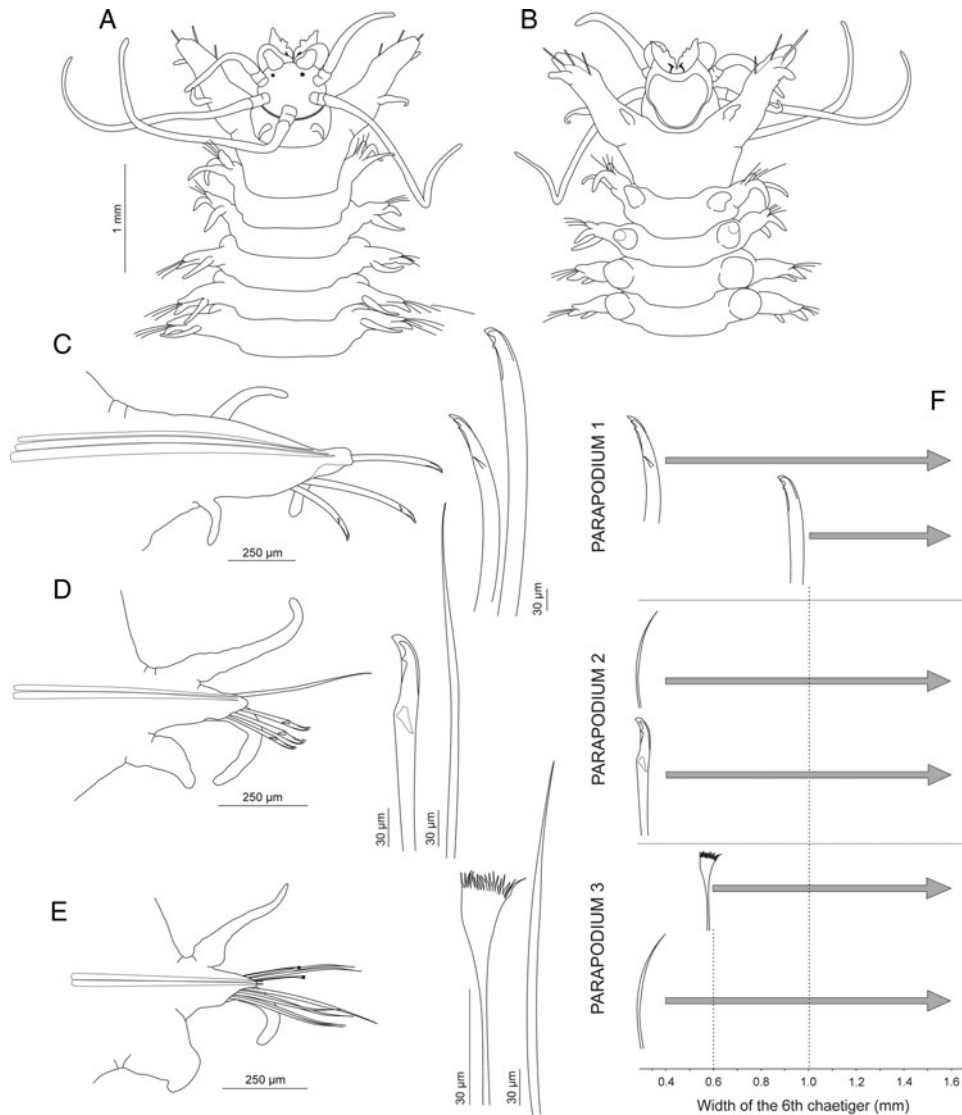


Fig. 4. *Nothria abyssia* Kucheruk, 1978, morphology and chaetal composition: (A) anterior region, dorsal view; (B) same, ventral view; (C) parapodium and chaetae from chaetiger 1; (D) parapodium and chaetae from chaetiger 2; (E) parapodium and chaetae from chaetiger 3; (F) diagram of chaetal replacement in relation to body width of worms.

falciger (Figures 4F; 6F). Both simple and pseudocompound falcigers frequently were with partly broken or worn subdistal tooth and lacked hoods in the largest specimens examined (Figure 6F). No truly unidentate falcigers were observed in the studied material.

Chaetal composition of the second pair of parapodia

Parapodia of all specimens examined were with the same set of chaetae consisting of 3–4 pseudocompound bidentate falcigers (Figures 4D, F; 7D, F, G) and 1–2 limbate chaetae (Figure 7E). Pectinate chaetae were absent in all studied specimens. No variation was observed.

Chaetal composition of the third pair of parapodia:

Parapodia of all specimens examined lacked falcigers (Figure 4E, F). Specimens smaller than 0.6 mm wide were with limbate chaetae only (Figure 8A), the larger specimens had both limbate and pectinate chaetae, 2–4 per parapodium (Figure 8C, D). Pectinate chaetae were flat with approximately 20 long teeth.

Presence of subacicular hooks

The segment of the first presence of subacicular hooks varied from six to nine with positive correlation with the body size (Figure 9).

Distribution of prechaetal and postchaetal parapodial lobes

Well-developed auricular prechaetal lobes were present only on the first pair of parapodia in all specimens examined, independently of their size (Figure 6A–C). Short foliose prechaetal lobes were distinguishable on the second and the third pairs of parapodia in specimens larger than 1.5 mm wide (Figures 7C; 8C). In smaller specimens they were present as short rounded ridges (Figures 7B; 8A, B). All subsequent parapodia were with very short prechaetal lobes in all material examined, independently of the size of the worms. Postchaetal lobes were digitiform on the first two pairs of parapodia in all the specimens. In specimens smaller than 0.5 mm wide they became short conical or knob-shaped from chaetiger 3 (Figure 8A), gradually decreasing in size posteriorly. In larger specimens the anterior 5–6 chaetigers were with digitiform postchaetal

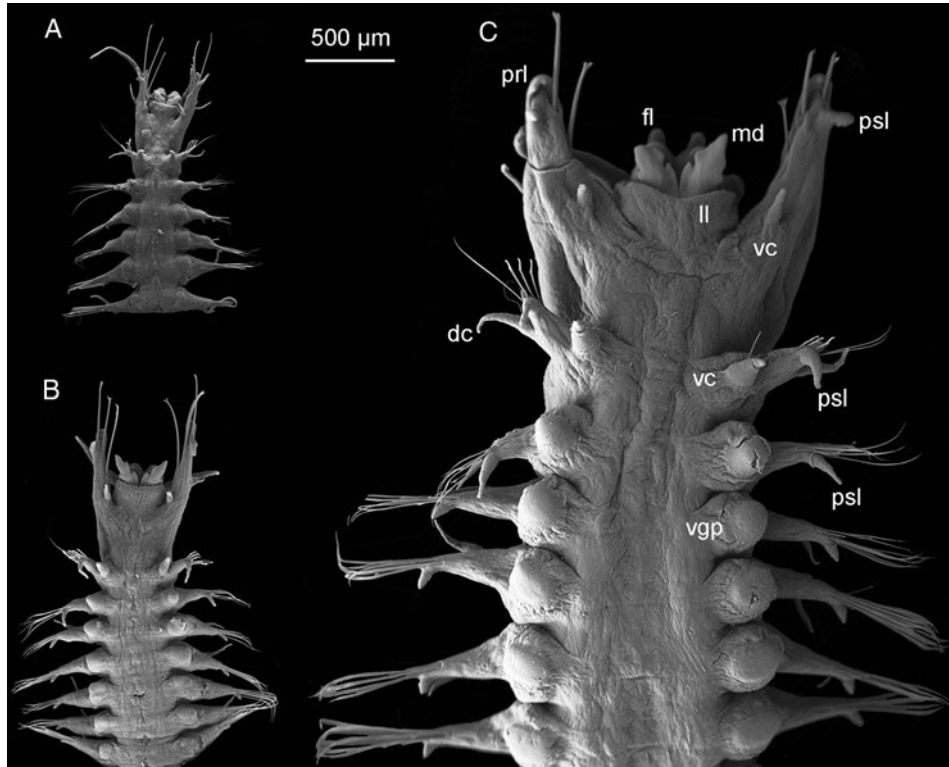


Fig. 5. *Nothria abyssia* Kucheruk, 1978, ventral view: (A) specimen of 0.4 mm width; (B) specimen of 0.6 mm width; (C) specimen of 1.57 mm width; dc, dorsal cirrus; fl, frontal lip; ll, lower lip; md, mandibles; prl, prechaetal lobe; psl, postchaetal lobe; vc, ventral cirrus; vgp, ventral glandular pad.

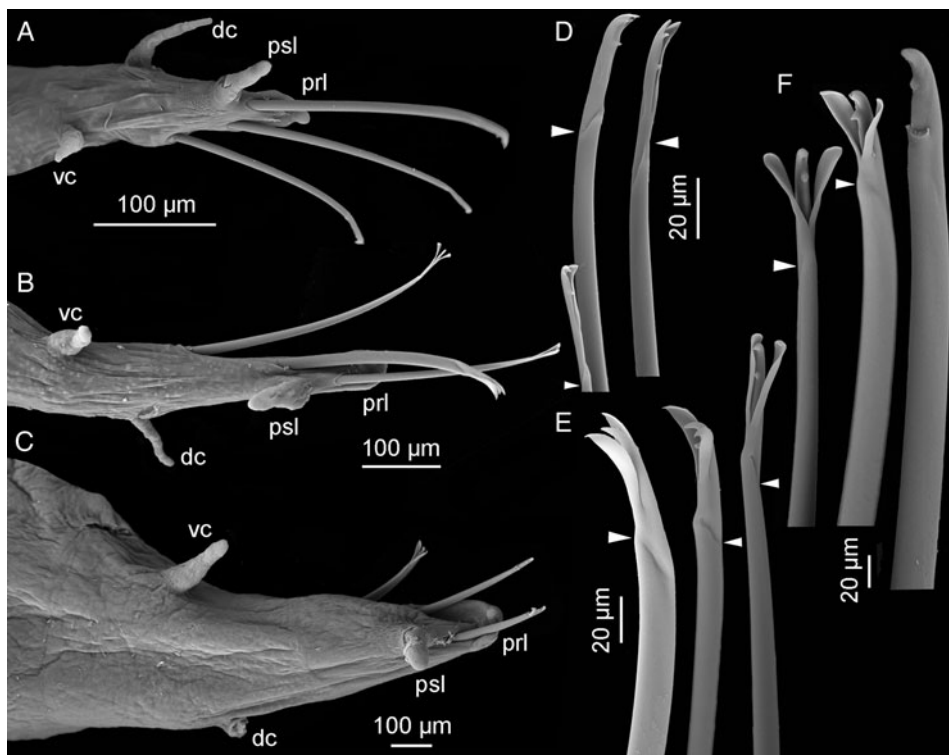


Fig. 6. *Nothria abyssia* Kucheruk, 1978, parapodia and chaetae from chaetiger 1 of specimens of different sizes: (A) parapodium from chaetiger 1 of specimen of 0.4 mm width, posterior view; (B) same of specimen of 0.6 mm width; (C) same of specimen of 1.57 mm width; (D) pseudocompound falcigers of specimen of 0.4 mm width; (E) pseudocompound falcigers of specimen of 0.6 mm width; (F) simple and pseudocompound falcigers of specimen of 1.57 mm width. Arrow heads indicate pseudoarticulation of falcigers; dc, dorsal cirrus; prl, prechaetal lobe; psl, postchaetal lobe; vc, ventral cirrus.

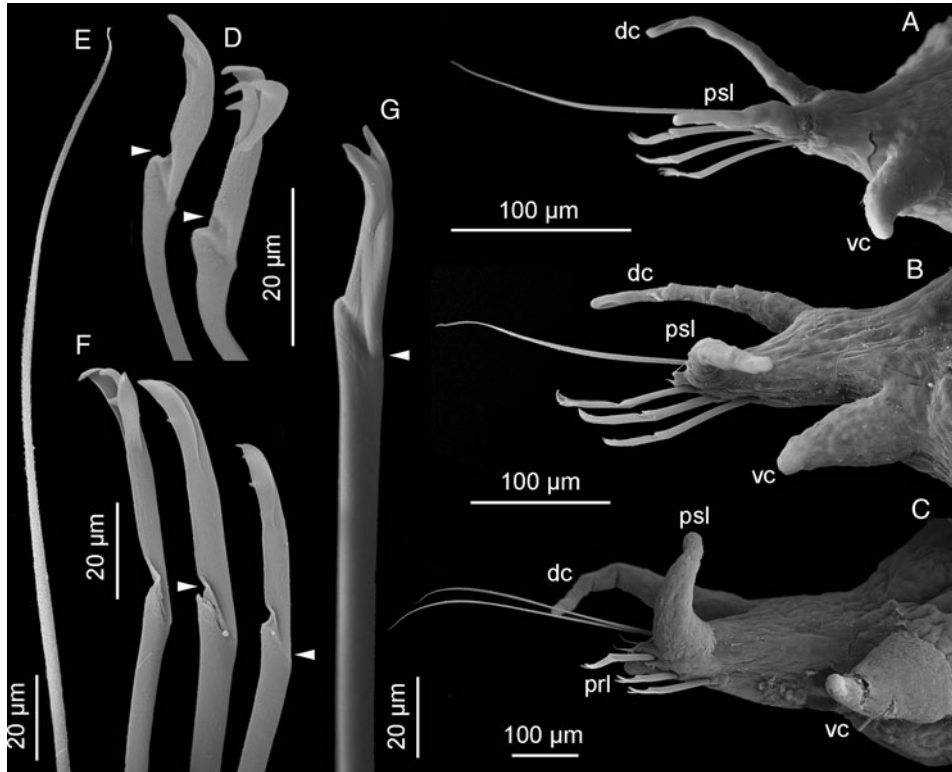


Fig. 7. *Nothria abyssia* Kucheruk, 1978, parapodia and chaetae from chaetiger 2 of specimens of different sizes: (A) parapodium from chaetiger 2 of specimen 0.4 mm width, posterior view; (B) same of specimen of 0.6 mm width; (C) same of specimen of 1.57 mm width; (D) pseudocompound falcigers of specimen of 0.4 mm width; (E) limbate chaeta of specimen of 0.6 mm width; (F) pseudocompound falcigers of specimen of 0.6 mm width; (G) pseudocompound falciger of specimen of 1.57 mm width; dc, dorsal cirrus; prl, prechaetal lobe; psl, postchaetal lobe; vc, ventral cirrus.

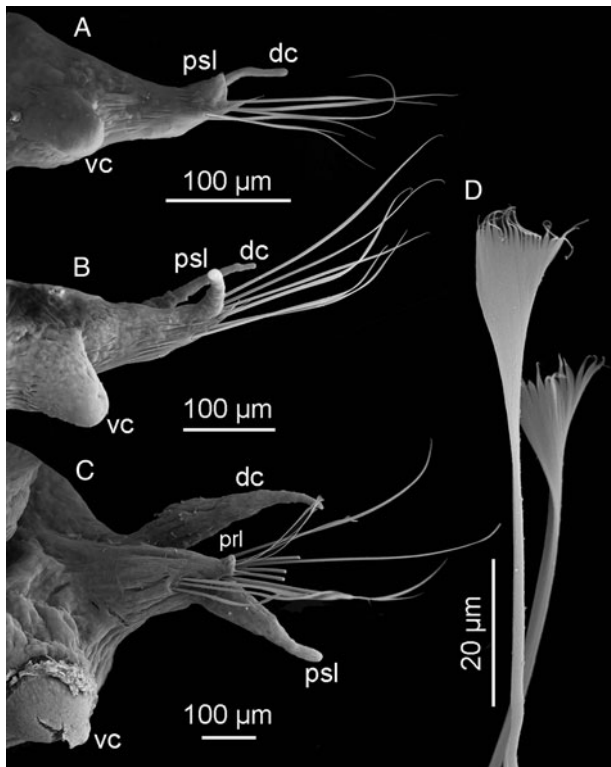


Fig. 8. *Nothria abyssia* Kucheruk, 1978, parapodia and chaetae from chaetiger 3 of specimens of different sizes: (A) parapodium from chaetiger 3 of specimen of 0.4 mm width, ventral view; (B) same of specimen of 0.6 mm width, posterior view; (C) same of specimen of 1.57 mm width, anterior view; (D) pectinate chaetae of specimen of 1.57 mm width; dc, dorsal cirrus; prl, prechaetal lobe; psl, postchaetal lobe; vc, ventral cirrus.

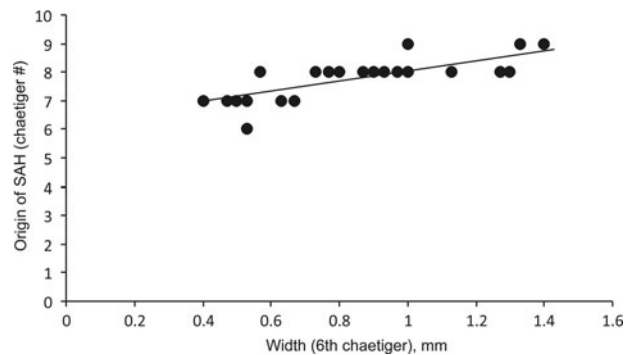


Fig. 9. *Nothria abyssia* Kucheruk, 1978: relationship between body width of specimens and origin of subacicular hooks (SAH), $R^2 = 0.556$.

lobes, becoming short and conical posteriorly, present at least till chaetiger 24 in the longest specimen examined.

REMARKS

Nothria abyssia is similar to *N. paxtonae* Imajima, 1999 in lacking branchiae, having falcigers present on the first two pairs of parapodia and limbate chaetae starting from chaetiger 2. Both species share the presence of flat pectinate chaetae rather than scoop-shaped pectinate chaetae characteristic of other species of *Nothria*. In *N. abyssia* pectinate chaetae were reported on chaetiger 2 by Kucheruk (1978) however were found only on chaetiger 3 in the examined material. Imajima (1999) reported pectinate chaetae starting from chaetiger 9 in *N. paxtonae*. In addition, *N. paxtonae* has eight

papillae surrounding the anus. Anal papillae were never reported in *N. abyssia*.

Three specimens from SLOPE Station 48 (400 m) were with two pairs of eyes, one large pair located laterally and a pair of small dorsal eyespots. This record represents the shallowest finding of *N. abyssia* and the presence of eyes could have an adaptive value. Other specimens examined lacked eyes or had a single pair of small eyespots on the dorsal side of the prostomium.

DISTRIBUTION

Nothria abyssia has been reported worldwide at bathyal and abyssal depths. It has been reported by Kucheruk (1978) from the Antarctic Ocean, off the Aleutian Islands, Japan, New Guinea, and Chile at depths from 2700 to 5200 m. Orensanz (1990) reported *N. abyssia* from the Pacific–Antarctic Ridge, the Macquarie Ridge, southern part of the South-east Pacific Basin, the Scotia Sea, depth-range 609–4370 m. In the present study *Nothria abyssia* is reported from slope depths (400–2900 m) south-east of Australia and from bathyal–abyssal depths (2313–4817 m) from the Atlantic sector of Antarctica (Figure 10).

Nothria otsuchiensis Imajima, 1986 (Figures 11–17)

Nothria otsuchiensis Imajima, 1986: 108–110, figure 8.—Imajima 1999: 46–51, figure 26.

Nothria otsuchiensis binocolata Maekawa & Hayashi, 1989: 66–68, figure 4a–m.

Nothria conchylega—Imajima 1970: 116.—Imajima 1982: 157.—Imajima 1997: 177–178.

MATERIAL EXAMINED

AM: W.24760, RV ‘Tangaroa’, NZOI, East of Newcastle, NSW, 32°49′18″S 152°49′6″E, 9 October 1982 (11);

W.24762, RV ‘Kapala’, Sydney–Newcastle, NSW, 33°37′S 152°4′E – 33°39′S 152°2′E, 896–924 m, 10 December 1980, benthic dredge (17); W.16567, RV ‘Kapala’, east of Port Stephens, NSW, K78-26-09, 32°50′S 152°40′E, 274 m, 6 December 1978 (1); W.198982, RV *Kimbla*, 32 km north of Fraser Island., QLD, Station 25, 24°22.3′S 153°17.1′E, 192–229.5 m, 15 December 1977. Coll.: W. Ponder, I. Loch, P. Terrill (3); W.41761, RV ‘Kimbola’, south-east of Percy Island, QLD, 21°47′S 150°34′E, 59 m, 13 December 1977, coarse shell and bryozoa substrate, Coll.: W. Ponder, I. Loch, P. Terrill (6); W.41764, RV ‘Kimbola’, east of Broad Sound, QLD, 22°6′S 150°49′E, 53 m, coarse shell, 13 December 1977, Coll.: W. Ponder, I. Loch, P. Terrill (6); W.41762, Off Cape Bowling Green Light, QLD, 19°17′S 147°32′E, 24 m, coarse shells, foraminiferans, 20 November 1977, Coll.: P. Colman, F. Lowe (1); W.41763, 96 km north-north-east of Port Headland, WA, 20°35′S 118°34′E, 36–37 m, sand, 24 October 1988, Coll.: B.W. Jenkins (1); W.41766, RV ‘Franklin’ Station 22, 18°11.01′S 147°25.5′E, 472–490 m, 26 August 1988, sledge, (1); W.41484, BIOCAL Station DW44, New Caledonia, 22°47′S 167°14′E, 440–450 m, 30 August 1985 (25, one slide with dissected parapodia); W.41481, off Japan: Shimoda, Station 12 34°38.875′N 138°57.123′E–34°38.625′N 138°56.750′E, 45–40 m, dredge, 20 October 1999. Coll.: R. Ueshima (3); W.41482, off Japan: Shimoda, Station 43 34°36.380′N 138°57.722′E–34°36.375′N 138°58.265′E, 93–109 m, 14 July 2000, Coll.: R. Ueshima (1); W.41483.001, off Japan: Shimoda, Station 43 34°36.380′N 138°57.722′E–34°36.375′N 138°58.265′E, 93–109 m, 14 July 2000, Coll.: R. Ueshima (1 specimen gold-coated for SEM); W.42765.001, RV ‘Franklin’ SLOPE Station 32 (1 specimen gold-coated for SEM); W.42766.001, RV ‘Franklin’ SLOPE Station 32 (1 specimen gold-coated for SEM); W.42767.001, RV ‘Franklin’ SLOPE Station 32

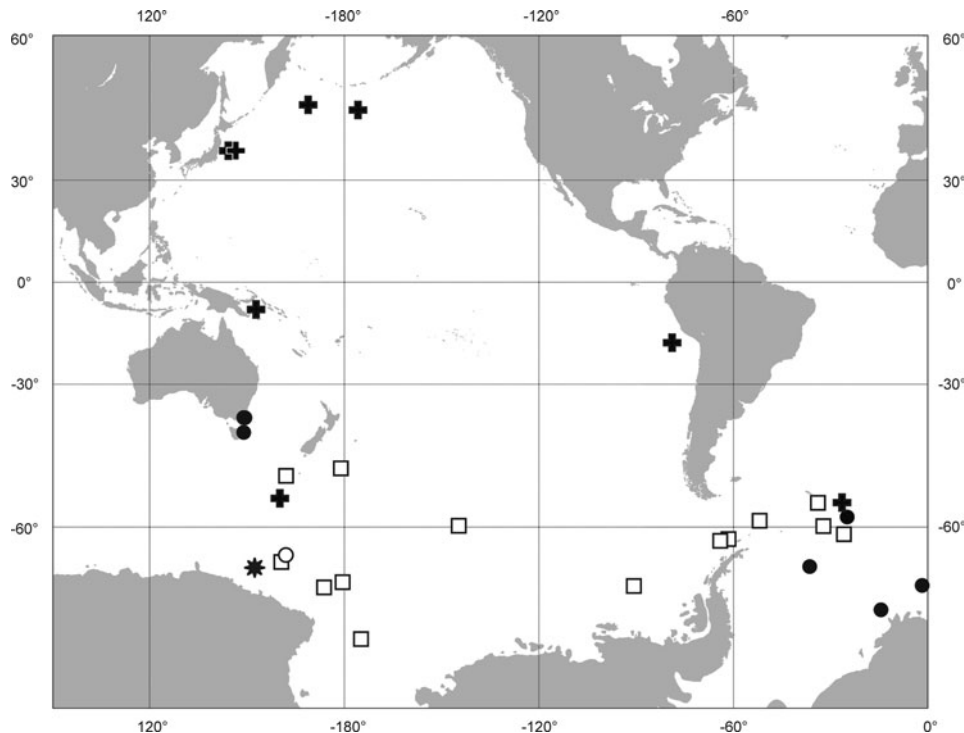


Fig. 10. Distribution of *Nothria abyssia* Kucheruk, 1978: black asterisk – type locality; black circles – examined material; black crosses – records from Kucheruk (1978); white squares – records from Orensanz (1990); white circles – record from Averincev (1972).

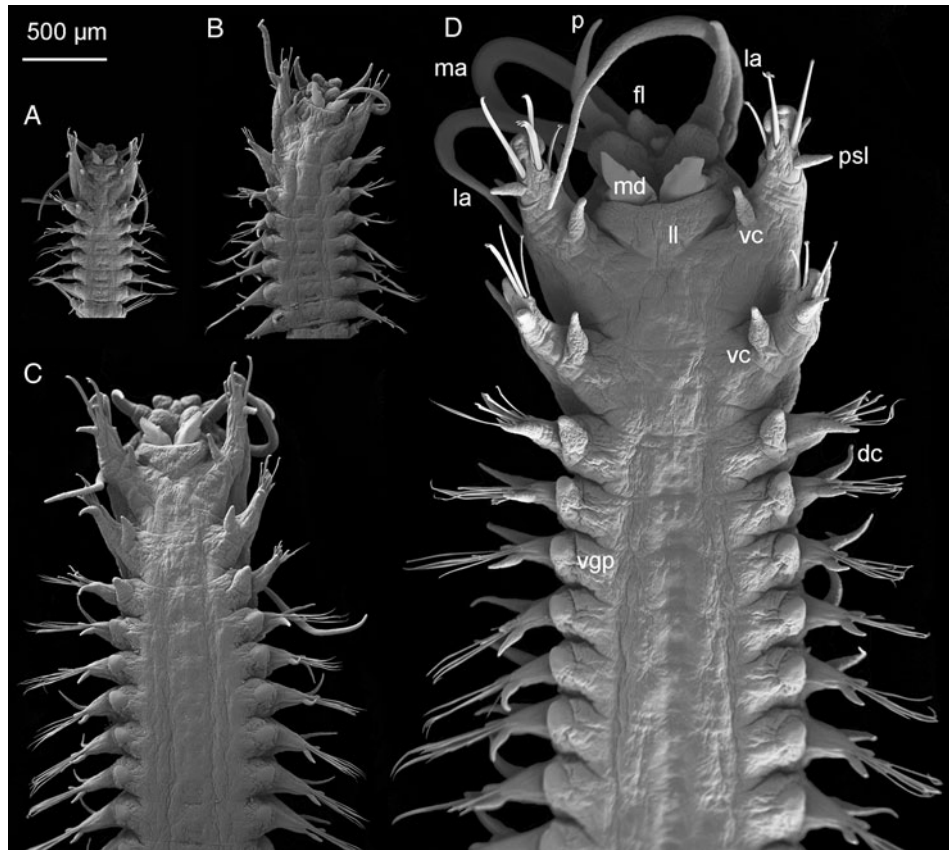


Fig. 11. *Nothria otsuchiensis* Imajima, 1986, ventral view: (A) specimen of 0.35 mm width; (B) specimen of 0.54 mm width; (C) specimen of 0.97 mm width; (D) specimen of 1.49 mm width; dc, dorsal cirrus; fl, frontal lip; la, lateral antenna; ll, lower lip; ma, median antenna; md, mandibles; p, palp; psl, postchaetal lobe; vc, ventral cirrus; vgp, ventral glandular pad.

(4 specimens gold-coated for SEM); W.42768.001, RV ‘Franklin’ SLOPE Station 32 (2 specimens gold-coated for SEM); W.42769.001, RV ‘Franklin’ SLOPE Station 32 (2 specimens gold-coated for SEM).

MV: F183649, Bass Trait, RV ‘Tangaroa’ Cruise 81-T-1 Station 177, 38°53.7’S 147°06.5’E, 59 m, 18 November 1981, coarse shell, Agassiz trawl (1); F43639, Bass Strait, RV ‘Tangaroa’ Cruise 81-T-1 Station 177, 38°53.7’S 147°06.5’E, 59 m, 18 November 1981, sled (2); F43648, Bass Trait, RV ‘Tangaroa’ Cruise 81-T-1 Station 193, 39°16.7’S 143°06.7’E, 95 m, 21 November 1981, shelly sand, Zock dredge (1); F43613, Bass Strait, FV ‘Sadra’ GCB Poore Cruise 80-Sa-1 Station 117, 40°38.0’S 145°23.0’E, 4 November 1980, muddy shell, grab (1); F183647, Bass Strait, RV ‘Tangaroa’ Cruise 81-T-1 Station 170, 31°51.8’S 148°26.5’E, 130 m, 15 November 1981, sled (3); F183648, Bass Strait, RV ‘Tangaroa’ Cruise 81-T-1 Station. 171, 38°53.7’S 147°55.2’E, 71 m, 17 November 1981, sled (3); F183646, Bass Strait, FRV ‘Hai Kung’ Cruise 81-HK-1 Station 120, 39°01.0’S 143°22.1’E, 84 m, 31 January 1981 (1); F183737, RV ‘Franklin’ SLOPE Station 46 (19); F183738, RV ‘Franklin’ SLOPE Station 67 (5); F183739, RV ‘Franklin’ SLOPE Station 33 (99); F183740, RV ‘Franklin’ SLOPE Station 22 (2); F192351, RV ‘Franklin’ SLOPE Station 66 (4); F192352, RV ‘Franklin’ SLOPE Station 82 (4); F192353, RV ‘Franklin’ SLOPE Station 34 (15); F192354, RV ‘Franklin’ SLOPE Station. 81 (18); F192355, RV ‘Franklin’ SLOPE Station 69 (4); F192356, RV ‘Franklin’ SLOPE Station 32 (398);

F192357, RV ‘Franklin’ SLOPE Station 7 (46); F192358, RV ‘Franklin’ SLOPE Station. 6 (2); F192359, RV ‘Franklin’ SLOPE Station 45 (91); F192363–F192375, RV ‘Franklin’ SLOPE Station 32 (13 slides with dissected parapodia); F192376, RV ‘Franklin’ SLOPE Station 7 (one slide with dissected parapodia); F192377, RV ‘Franklin’ SLOPE Station 45 (one slide with dissected parapodia).

DIAGNOSIS

Based on specimens wider than 1.4 mm at chaetiger 6 excluding parapodia: first pair of parapodia reaching frontal margin of prostomium. First and second pair of parapodia with simple and pseudocompound bidentate falcigers. Third pair of parapodia with pseudocompound bidentate falcigers, limbate and pectinate chaetae. Pectinate chaetae with rolled lateral margins. Branchiae from chaetiger 9. Subacicular hooks from chaetigers 10–13. Auricular prechaetal lobes on first chaetigers, becoming foliose on chaetiger 2, gradually reduced posteriorly, present till end of body. Postchaetal lobes present on first 14–16 chaetigers. One or two pairs of eyes.

TYPE LOCALITY

Japan, Otsuchi Bay, 49–79 m.

DESCRIPTION

All specimens in samples from Australian waters incomplete anterior fragments from 0.35 to 2.1 mm wide (Figure 11A–D). Largest complete specimen from BIOCAL Station

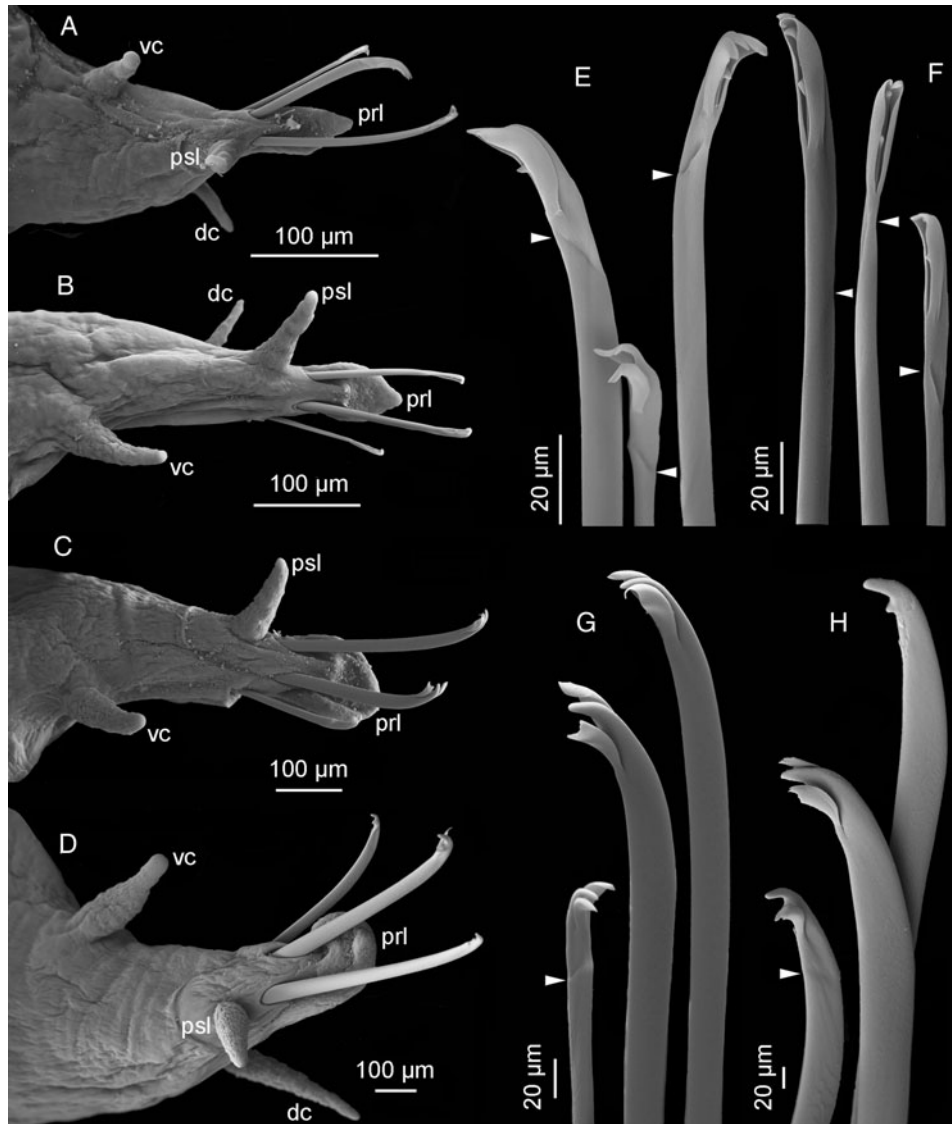


Fig. 12. *Nothria otsuchiensis* Imajima, 1986, parapodia and chaetae from chaetiger 1 of specimens of different sizes: (A) parapodium from chaetiger 1 of specimen of 0.35 mm width, posterior view; (B) same of specimen of 0.54 mm width; (C) same of specimen of 0.97 mm width; (D) same of specimen of 1.49 mm width; (E) pseudocompound falcigers of specimen of 0.35 mm width; (F) same of specimen of 0.54 mm width; (G) simple and pseudocompound falcigers of specimen of 0.97 mm width; (H) same of specimen of 1.49 mm width; dc, dorsal cirrus; prl, prechaetal lobe; psl, postchaetal lobe; vc, ventral cirrus.

DW44 (New Caledonia) 2.2 mm wide, 28 mm long consisting of 52 chaetigers. All specimens light brownish lacking distinct colour pattern. The following description based on specimens wider than 1.4 mm at chaetiger 6 excluding parapodia.

Prostomium distally slightly tapering, forming triangle with ovoid frontal lips projecting anteroventrally (Figure 11C). Palps reaching chaetiger 1, lateral antennae reaching chaetigers 4–9, median antenna thicker and longer than lateral antennae, reaching chaetigers 6–12. Ceratophores with 2–4 rings. One pair of large dark eyes present laterally on prostomium near bases of lateral antennae. One of specimens examined (SLOPE Station 22) with second pair of small eyes dorsally on prostomium. Nuchal grooves straight with narrow mid-dorsal separation. Peristomium half as long as first chaetiger. Peristomial cirri thin and slender, longer than peristomium. All specimens examined light beige lacking distinct colour pattern.

First pair of parapodia enlarged projecting lateroventrally, directed anteriorly with large auricular prechaetal lobes, digitiform postchaetal lobes and dorsal and ventral cirri (Figures

11D; 12D; 15A). Second pair of parapodia slightly enlarged projecting anteriorly with foliose distally tapering prechaetal lobes, digitiform postchaetal lobes and subulate dorsal and ventral cirri (Figures 11D; 13D; 15C). Third pair of parapodia similar in size with subsequent parapodia, directed laterally with foliose distally tapering prechaetal lobes, well developed digitiform postchaetal lobes, subulate dorsal cirri and conical ventral cirri (Figures 11D; 14D; 15D). Prechaetal lobes present on all parapodia of longest anterior fragment (up to chaetiger 28) gradually reduced posteriorly. Postchaetal lobes reduced in size towards posterior region, completely disappearing from chaetigers 15–18. Dorsal cirri present on all chaetigers, becoming shorter and thinner posteriorly. Transitional ventral cirri present on chaetigers 3 and 4, replaced by oval glandular pads from chaetiger 5 (Figure 11D).

First pair of parapodia with 1–2 simple bidentate falcigers and 1–2 bidentate pseudocompound falcigers bearing paired short pointed hoods. Frequently hoods on anterior falcigers

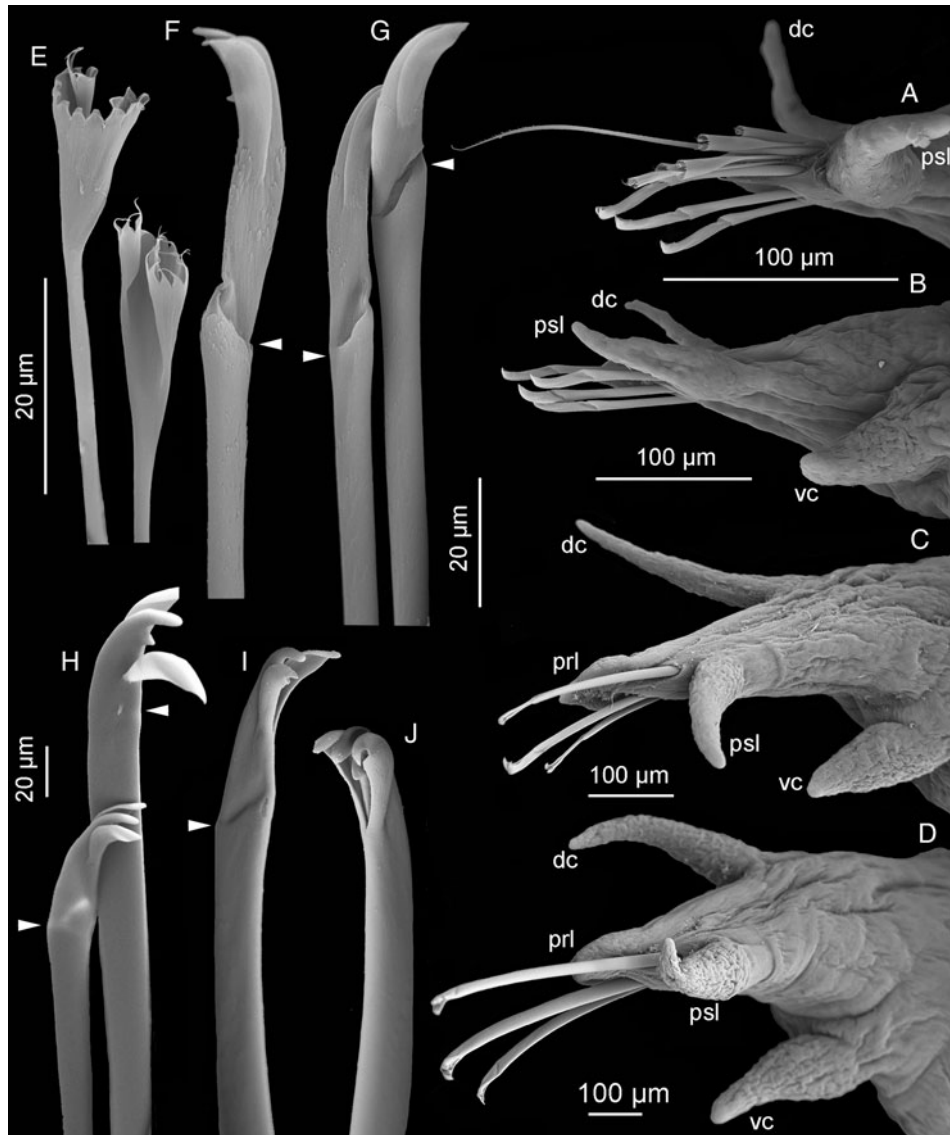


Fig. 13. *Nothria otsuchiensis* Imajima, 1986, parapodia and chaetae from chaetiger 2 of specimens of different sizes: (A) parapodium from chaetiger 2 of specimen of 0.35 mm width, posterior view; (B) same of specimen of 0.54 mm width; (C) same of specimen of 0.97 mm width; (D) same of specimen of 1.49 mm width; (E) pectinate chaetae of specimen 0.35 mm width; (F) pseudocompound falciger of specimen of 0.35 mm width; (G) same of specimen of 0.54 mm width; (H) same of specimen of 0.97 mm width; (I) same of specimen of 1.49 mm width; (J) simple falciger of specimen of 1.49 mm width; dc, dorsal cirrus; prl, prechaetal lobe; psl, postchaetal lobe; vc, ventral cirrus.

broken (Figures 12D, H; 15A). Second pair of parapodia with one simple and two pseudocompound bidentate falcigers with paired hoods (Figures 13D, I, J; 15C). Third pair of parapodia with two bundles of chaetae: dorsal bundle of 1–2 slender limbate chaetae and 5–10 pectinate chaetae with 18–22 denticles and rolled lateral margins; ventral bundle of 3–4 bidentate pseudocompound falcigers with paired short and pointed hoods (Figures 14D, H; 15D). Only limbate and pectinate chaetae present from chaetiger 4. Paired bidentate subacicular hooks appearing in median position within ventral bundle of limbate chaetae from chaetigers 10–13. Neuroaciculae pale yellow with pointed tips, 2–3 per parapodium.

Branchiae starting from chaetiger 9 in all specimens examined from Australian waters, single, strap-like, becoming longer and wider towards median body section and reduced in size posteriorly. Specimens from BIOCAL Station DW44 with branchiae starting from chaetigers 9–12. Pygidium

with dorsal anus and one pair of anal cirri. Tubes dorsoventrally flattened, covered with shell fragments of various size, foraminiferans and large sand particles.

ONTOGENETIC VARIATION

Seventy-six specimens of *Nothria otsuchiensis* ranging in width from 0.35 to 2.1 mm (Figure 11A–D) were examined (SLOPE Stations 7(5), 32(49), 33(8), 45(14)). A number of morphological characters were size related.

Chaetal composition of the first pair of parapodia

Specimens smaller than 0.6 mm wide had 3–4 pseudocompound falcigers in the parapodia on the first chaetiger (Figures 12A, B, E, F; 15E). Left and right parapodia were asymmetrical in chaetal composition in 33% of specimens examined (N = 21). In specimens larger than 0.6 mm wide 1–2 pseudocompound falcigers were replaced by simple

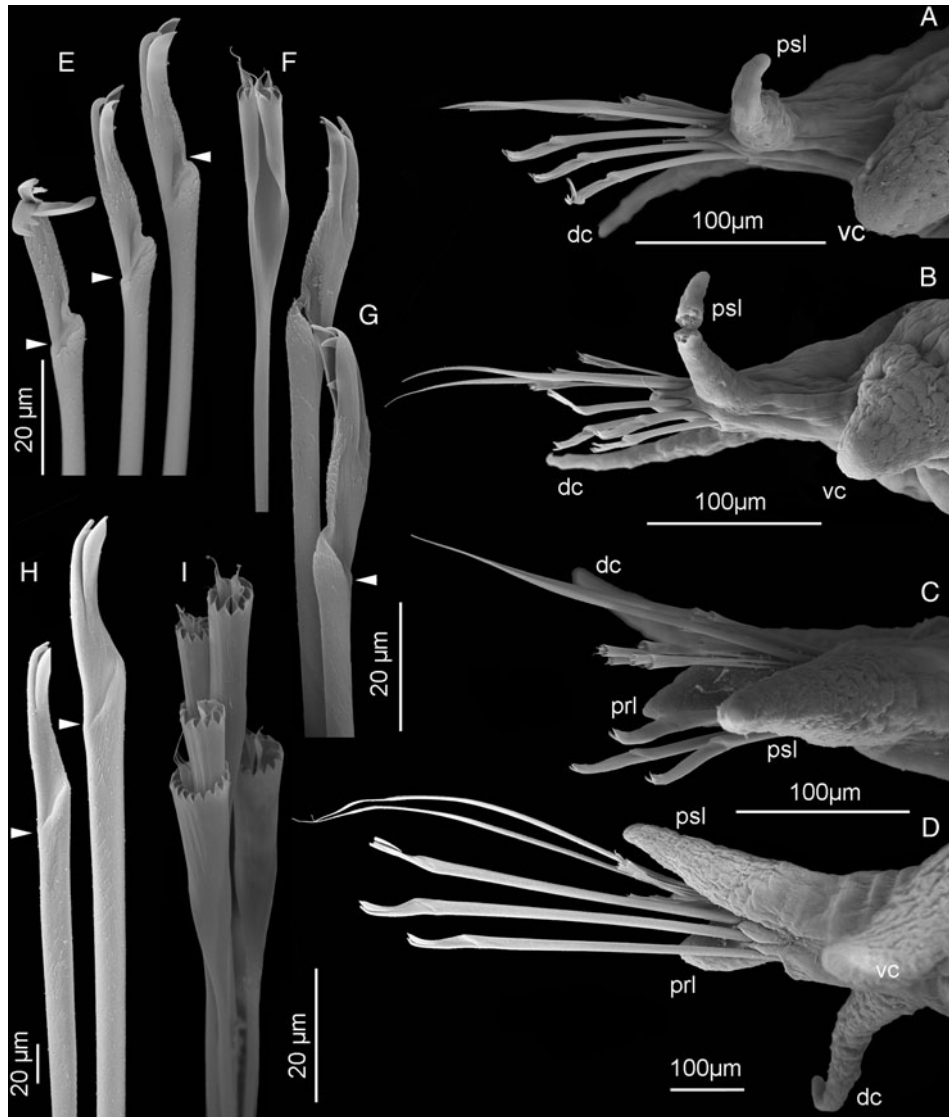


Fig. 14. *Nothria otsuchiensis* Imajima, 1986, parapodia and chaetae from chaetiger 3 of specimens of different sizes: (A) parapodium from chaetiger 3 of specimen of 0.35 mm width, posterior view; (B) same of specimen of 0.54 mm width; (C) same of specimen of 0.97 mm width; (D) same of specimen of 1.49 mm width; (E) pseudocompound falcigers of specimen of 0.35 mm width; (F) pectinate chaetae of specimen of 0.54 mm width; (G) pseudocompound falcigers of specimen of 0.54 mm width; (H) same of specimen of 1.49 mm width; (I) pectinate chaetae of specimen 0.97 mm width; dc, dorsal cirrus; prl, prechaetal lobe; psl, postchaetal lobe; vc, ventral cirrus.

falcigers (Figures 12 C, D, G, H; 15A, E). The most frequent composition of anterior chaetae was two simple falcigers and one pseudocompound falciger which was found in both parapodia in 50% of specimens examined ($N = 45$). In other specimens the chaetal composition was asymmetrical in the left and right parapodia with various combinations of simple and pseudocompound falcigers, but not exceeding five chaetae in total per parapodium. In nine of the largest specimens (wider than 1.33 mm) only left parapodia were observed, and the combination of two simple and one pseudocompound falcigers was found in eight of them. Simple falcigers of the largest specimens often lacked their hoods, which presumably were broken (Figure 12H).

Chaetal composition of the second pair of parapodia

Specimens smaller than 0.6 mm wide had limbate and pectinate chaetae starting from chaetiger 2 (Figures 13 A, E; 15B, E). Occasionally limbate and pectinate chaetae were found

in the second parapodia of larger specimens (up to 0.77 mm wide) but never in both right and left parapodia and rarely together. No limbate and/or pectinate chaetae were observed in specimens larger than 0.8 mm wide. Specimens of all sizes had three (up to five) pseudocompound falcigers in the parapodia of the second chaetiger (Figures 13A–D, F–I; 15A–E). One or two simple falcigers replaced pseudocompound falcigers in specimens larger than 1.4 mm wide (Figures 13D, J; 15C, E). The total number of falcigers in the largest specimens was always three per parapodium. Neither simple nor pseudocompound falcigers in the second pair of parapodia lost their hoods (Figure 13F–J).

Chaetal composition of the third pair of parapodia

Parapodia of all specimens examined were with the same set of chaetae consisting of 1–5 pseudocompound bidentate falcigers (Figures 14A–H; 15D, E), 1–3 limbate chaetae and

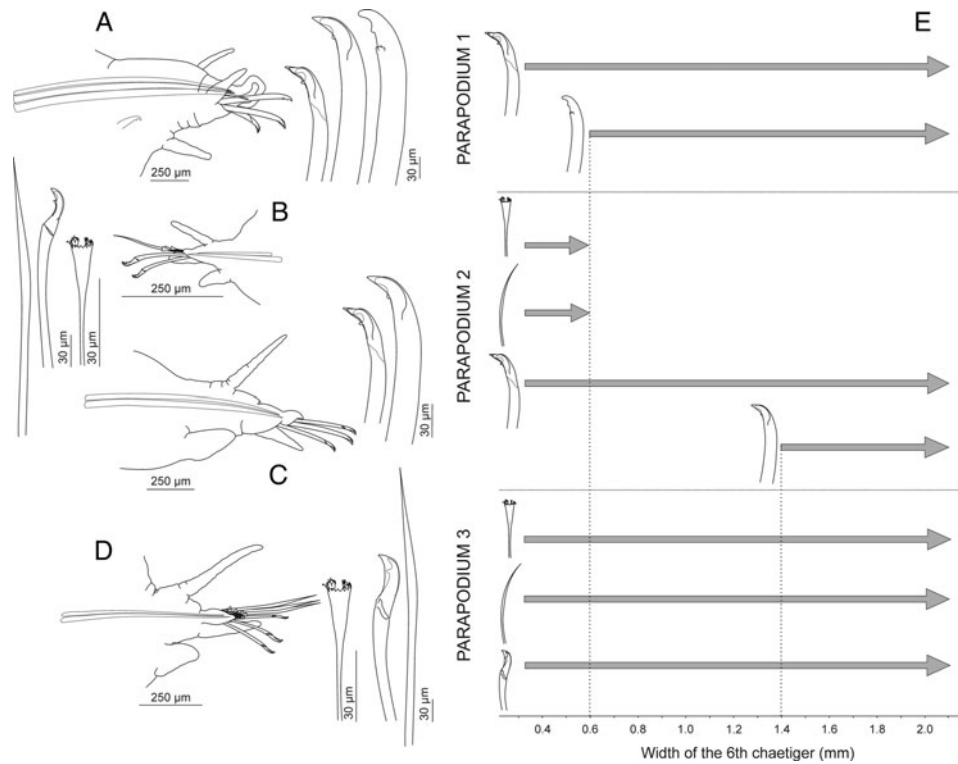


Fig. 15. *Nothria otsuchiensis* Imajima, 1986, parapodia and chaetal composition: (A) parapodium and chaetae from chaetiger 1 of specimen of 1.6 mm width; (B) parapodium and chaetae from chaetiger 2 of specimen of 0.5 mm width; (C) same of specimen of 1.6 mm width; (D) parapodium and chaetae from chaetiger 3 of specimen of 1.6 mm width; (E) diagram of chaetal replacement in relation to body width of worms.

pectinate chaetae (Figures 14A–D, I; 15D, E). No variation was observed.

Distribution of prechaetal and postchaetal parapodial lobes

All specimens examined consisted of anterior fragments. Therefore, we estimated the variation in distribution of the parapodial lobes in the anterior body region. All specimens, independently of their size, had enlarged auricular prechaetal lobes on the first pair of parapodia (Figure 12 A–D) becoming foliose and slightly tapering on the second and the third pairs of parapodia (Figures 13A–D; 14A–D). In the specimens smaller than 0.6 mm wide prechaetal lobes were visible on the anterior 7–9 chaetigers and almost untraceable posteriorly. All the larger specimens had prechaetal lobes on all segments, gradually reduced posteriorly, but distinguishable.

Twenty-six specimens examined were anterior fragments with a sufficient number of segments allowing estimation of the variation of the distribution of postchaetal lobes. The number of chaetigers with digitiform postchaetal lobes was a size-dependent character varying from four chaetigers in specimens of 0.37–0.5 mm wide to 16 chaetigers in specimen of 2.1 mm wide (Figure 16A).

Presence of subacicular hooks

The first presence of subacicular hooks was a size-dependent character. The variation of this character ranged from hooks starting from chaetiger 6 to chaetiger 13 (Figure 16B).

Presence of branchiae

Branchiae were totally absent in five specimens smaller than 0.5 mm wide. In specimens from Australian waters, branchiae started strictly from chaetiger 9 with no variation observed.

Specimens from New Caledonia had branchiae starting from chaetigers 9–12 independent of size of worms.

REMARKS

Nothria otsuchiensis is similar to *Nothria oblonga* Imajima, 1999 in having at least one pair of large eyes and sharing the presence of falcigers in the first three pairs of parapodia and the presence of limbate and pectinate chaetae from the third pair of parapodia. The former species can be distinguished from the latter in having simple and pseudocompound falcigers rather than exclusively pseudocompound falcigers on the first two pairs of parapodia. Imajima (1999) reported that *N. oblonga* resembles the juveniles of *N. otsuchiensis* bearing pseudocompound and compound falcigers on the anterior parapodia. However, he stated that the holotype of *N. oblonga* was a mature specimen with oocytes in the body cavity. Consequently, he considered it as a valid species. Imajima reported the holotype of *N. oblonga* being the largest specimen at 2 mm wide (presumably with parapodia). The body width of the holotype at the level of the sixth chaetiger without parapodia estimated from the original illustration (Imajima, 1999, p. 45, figure 24a) was 1.5 mm. Simple falcigers were found in the first pair of parapodia of the examined specimens of *N. otsuchiensis* larger than 0.6 mm wide. Therefore, *N. oblonga* does not fall within the described pattern of the ontogenetic variation of *N. otsuchiensis* and is considered to be a valid species.

Imajima (1986) described two pairs of eyes in *N. otsuchiensis*, one large pair of eyes located laterally near the bases of the lateral antennae and a pair of small eyespots located dorsally on the prostomium near the bases of the palps. Brown patches on the dorsal side of the anterior parapodia were

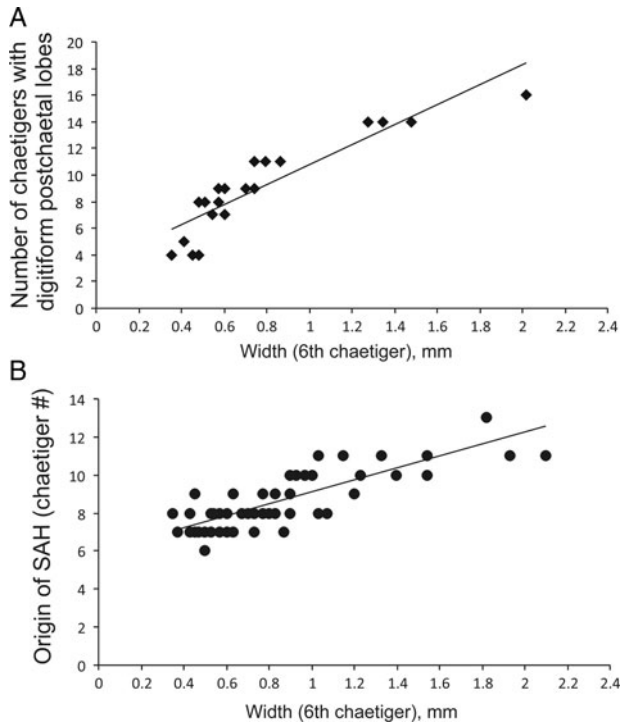


Fig. 16. *Nothria otsuchiensis* Imajima, 1986: (A) relationship between body width of specimens and number of chaetigers with digitiform postchaetal lobes, $R^2 = 0.812$; (B) relationship between body width of specimens and origin of subacicular hooks (SAH), $R^2 = 0.677$.

also observed by Imajima (1986) in *N. otsuchiensis*. *Nothria otsuchiensis binocolata* Maekawa & Hayashi (1989) lacking the dorsal pair of eyes and brown pigmentation on the parapodia was reported from Wakasa Bay, Japan. Imajima (1999) re-examined the type specimens of the new subspecies and reported two pairs of eyes, stating the pigmentation can disappear in the preserved specimens. All the specimens examined in the present study from Australia and New Caledonia lacked the dorsal pair of eyespots. The only specimen with two pairs of eyes was found at Slope Station 22. All specimens from Japan examined in the present study had two pairs of eyes. No specimens with brown pigmented patches on the dorsal side of parapodia were found in the present material.

DISTRIBUTION

Nothria otsuchiensis was widely reported from Japan from Otsuchi to Kagoshima Bay at water depth from 26 to 1070 m (Imajima, 1986, 1999). In Australian waters it was found along the western and south-western coast, depth range 24–2900 m. A single record was reported from New Caledonia, 440–450 m (Figure 17).

DISCUSSION

Ontogenetic variation of morphological characters involving changes in chaetal and parapodial morphology has been widely reported for onuphid worms (Paxton, 1986, 1993, 1996, 1998; Orensanz, 1990; Budaeva & Fauchald, 2010, 2011). Chaetae of onuphids undergo replacement during the worm's growth and maturation. Onuphid larvae and early

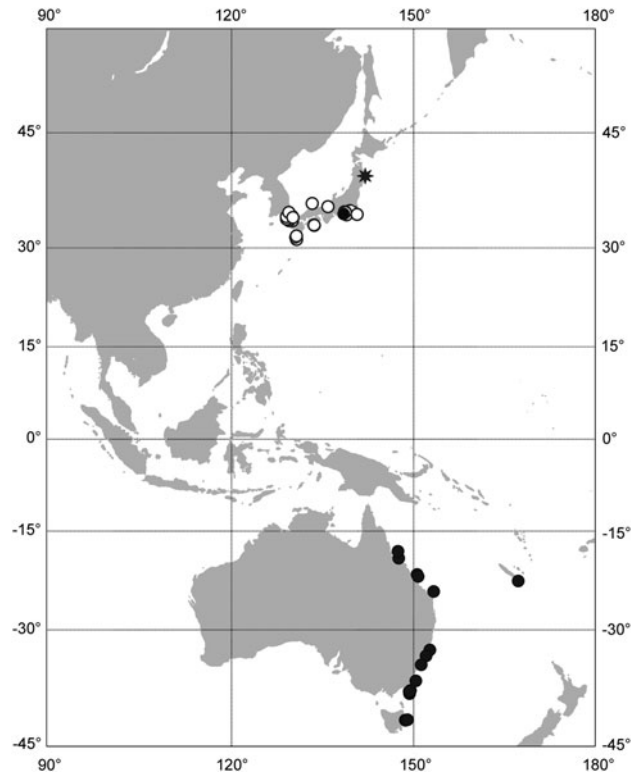


Fig. 17. Distribution of *Nothria otsuchiensis* Imajima, 1986: black asterisk, – type locality; black circles, – examined material; white circles, – records from Imajima (1999).

juveniles bear various provisional chaetae that are subsequently replaced by definitive chaetae in later juveniles and adults. Provisional larval chaetae differ significantly from adult chaetae and can be clearly distinguished from the latter (Budaeva & Fauchald, 2010). Chaetal replacement continues in later development of onuphids: anterior falcigers replace each other, increasing in size and slightly changing in morphology, limbate and pectinate chaetae increase in numbers, subacicular hooks frequently shift posteriorly (Paxton, 1986, 1993, 1996, 2005; Hsieh & Simon, 1987; Budaeva & Fauchald, 2010). The general pattern of growth related changes in parapodial morphology is represented by the increasing number of modified parapodia and spreading of digitiform postchaetal lobes towards the posterior end of the body (Jirkov & Yermolaev, 1989; Orensanz, 1990). In a number of onuphid genera (e.g. *Paradiopatra*, *Diopatra*, *Onuphis*, *Kinbergonuphis* and *Mooreonuphis*) branchiae tend to appear in the anterior part of the body and spread more anteriorly and/or posteriorly with increasing worm size (Blake, 1975; Fauchald, 1982c; Hsieh & Simon, 1987; Fadlaoui *et al.*, 1995; Budaeva & Fauchald, 2010). However, in *Nothria* the segment of the first appearance of branchiae remains variable but not size-dependent (Kucheruk, 1980; Jirkov & Yermolaev, 1989; Orensanz, 1990).

Intraspecific variability has never been studied thoroughly in *Anchinotria*, presumably due to insufficient material, as was also the case during the present study. Nevertheless, the investigation of morphological variation in this genus is desirable to re-evaluate the taxonomic status of a number of species. Examination of 95 specimens of *Anchinotria* including non-type material and types of *Anchinotria*

pycnobranchiata (McIntosh, 1885), *A. abbranchiata* (McIntosh, 1885) and *A. antarctica* (Hartman, 1967) revealed significant variation in the presence/absence of branchiae, a character used to distinguish these three species (Orensanz, 1990). The diameter of subacicular hooks was shown to be strongly size-dependent in *A. pycnobranchiata* (Orensanz, 1990) but an analysis of variation of other diagnostic characters was never performed.

We followed Kucheruk (1980) and Jirkov & Yermolaev (1989) in distinguishing variation in two parameters of chaetal distribution in the anterior parapodia of *Nothria*. The first parameter was chaetal composition, i.e. presence or absence of different types of chaetae: falcigers, limbate and pectinate chaetae. The second parameter was morphology of falcigers, e.g. dentition, presence or absence of pseudoarticulation and hoods. Chaetal composition was previously reported independent of the size of specimens. Only morphology of falcigers was shown to be size-dependent (Kucheruk, 1980; Jirkov & Yermolaev, 1989; Orensanz, 1990). Consequently, chaetal composition of the anterior parapodia was used as a major diagnostic character in species of *Nothria*. Kucheruk (1985) recognized four different types of chaetal composition in the anterior three pairs of parapodia and presented them as four formulas with different letters indicating several types of chaetae. He assigned nine *Nothria* species to the four types based on literature data. Imajima (1999) distinguished five species of *Nothria* reported from Japanese waters based on the presence/absence of different types of chaetae in the anterior parapodia.

The cases of invariance of chaetal composition in *Nothria* were presumably reported due to unavailability of small specimens for examination. The smallest specimens studied by Jirkov & Yermolaev (1989) were 0.7 mm wide, at the level of chaetiger 10. Kucheruk (1980) included specimens 1.0–3.3 mm wide into his analysis. The size of the smallest specimens examined by Orensanz (1990) was not reported. Examination of the wide size-range (0.35–2.1 mm) in two *Nothria* species in the present study demonstrated that chaetal composition can vary significantly in specimens of different sizes. No provisional chaetae were found in the studied material, demonstrating that all the specimens examined were juveniles and adults. Hence, ontogenetic changes in morphology associated with the transition from larval stages to juveniles could not be considered in the present study.

The general pattern of falciger morphology in *Nothria* specimens of various sizes represents three growth related chaetal replacement tendencies: replacement of bidentate falcigers of smaller specimens by unidentate falcigers in larger specimens, replacement of pseudocompound falcigers by simple falcigers, and loss of paired hood in the largest specimens examined (Kucheruk, 1980; Jirkov & Yermolaev, 1989;

Orensanz, 1990). A similar pattern was found in the two species examined in the present study. Pseudocompound falcigers were gradually replaced by simple falcigers in the larger specimens of both species. Falcigers on the first pair of parapodia frequently lacked hoods in both species and the second tooth in *N. abyssia*.

The patterns of chaetal morphology and composition elucidated during the present study have been summarized in Figure 4 for *Nothria abyssia* and Figure 15 for *N. otsuchiensis*, and compared to each other in Figure 18. In *N. abyssia* the third pair of parapodia lacked pectinate chaetae in specimens smaller than 0.5 mm wide, having only limbate chaetae on the third chaetiger. Pectinate chaetae appeared from chaetiger 3 in *N. abyssia* larger than 0.5 mm wide. Specimens of *N. otsuchiensis* smaller than 0.6 mm wide had limbate and pectinate chaetae in addition to falcigers on the second pair of parapodia, while in adults only pseudocompound falcigers were found on the second chaetiger. Kucheruk (1978) reported pectinate chaetae starting from chaetiger 2 in *N. abyssia*. His largest specimen examined was 4 mm wide and could potentially represent the next stage of chaetal replacement with pectinate chaetae emerging on chaetiger 2.

As a result, three size-related morphotypes can be recognized in *Nothria otsuchiensis* and *N. abyssia* based on both chaetal composition and morphology of falcigers (Figure 18). The patterns of chaetal replacement in the two examined species differed from each other. In *N. abyssia* new types of chaetae (pectinate chaetae and simple falcigers) appeared in the anterior parapodia with the growth of a worm. In *N. otsuchiensis* emergence of simple falcigers was combined with disappearance of limbate and pectinate chaetae. Assessment of ontogenetic variation in other species of *Nothria* may reveal patterns of chaetal replacement different from the patterns described here. Therefore, examination of every species within the genus is required for accurate evaluation of their validity.

Origin of subacicular hooks in *Nothria* was shown to be size-dependent in several species. Generally subacicular hooks appear in more posterior segments in larger specimens (Jirkov & Yermolaev, 1989; Orensanz, 1990). Growth related increase of the number of chaetigers with digitiform postchaetal lobes in two species of *Nothria* was reported by Jirkov & Yermolaev (1989). Our results confirm the observations made by previous authors. Both *N. abyssia* (Figure 9) and *N. otsuchiensis* (Figure 16B) showed positive correlation between the segment of the first appearance of subacicular hooks and the body width. *Nothria otsuchiensis* displayed positive correlation between the size of worms and number of chaetigers with postchaetal lobes (Figure 16A). Relationship between the size of worms and number of

	<i>Nothria abyssia</i> Kucheruk, 1978			<i>Nothria otsuchiensis</i> Imajima, 1986		
Width, mm	0.4 - 0.6	0.5 - 1.0	1.0 - 1.53	0.35 - 0.6	0.6 - 1.4	1.4 - 2.1
Chaetiger 1	pF	pF	pF sF	pF	pF sF	pF sF
Chaetiger 2	L pF	L pF	L pF	P L pF	pF	pF sF
Chaetiger 3	L	P L	P L	P L pF	P L pF	P L pF

Fig. 18. Chaetal composition and morphology in anterior parapodia of *Nothria abyssia* Kucheruk, 1978 and *N. otsuchiensis* Imajima, 1986: (L) limbate chaetae; (P) pectinate chaetae; (pF) pseudocompound falcigers; (sF) simple falcigers.

chaetigers with postchaetal lobes in *N. abyssia* was not estimated due to the poor condition of the specimens examined.

The number of chaetigers with pseudocompound falcigers was the only character independent of size of the specimens in both examined species. The chaetiger of the first appearance of branchiae in *N. otsuchiensis* was also unrelated to the size of worms. However, both characters display very low variation among species of *Nothria* and can only be used in separation of the groups of closely related species. Additional diagnostic characters are required for the differentiation of *Nothria* species. The following characters are considered of diagnostic value only when scored in adults: absence/presence of simple falcigers in anterior parapodia; chaetiger of origin of limbate and pectinate chaetae; chaetiger of origin of subacicular hooks; number of chaetigers with auricular prechaetal lobes and digitiform postchaetal lobes. We suggest that both chaetal composition and chaetal morphology be used in species diagnoses within *Nothria*. The diagnoses should be based on adult specimens with the final set of definitive morphological structures. The revision of the genus involving examination of type material and ontogenetic variation of chaetal composition in the anterior parapodia is required to clarify the status of all *Nothria* species. Species described based on small specimens (e.g. *Nothria textor* Hartman & Fauchald, 1971; *Nothria mannarensis* Rangarajan & Mahadevan, 1961) may potentially represent the juveniles of other species retaining the provisional set of chaetae.

ACKNOWLEDGEMENTS

We are grateful to Pat Hutchings, Stephen Keable and the staff of the Australian Museum for providing facilities and assistance during the duration of the research project. We are also thankful to the following individuals and institutions for the loan and exchange of specimens: Robin Wilson and Chris Rowley (Museum Victoria), Eijiroh Nishi (Yokohama National University), Karin Meißner (German Centre for Marine Biodiversity Research, Hamburg); Angelika Brandt and Petra Wagner (Zoological Museum of Hamburg), Jean-Paul Lechapt (Marine Laboratory, Dinard), Tarik Meziane (National Museum of Natural History, Paris). We would like to thank Sue Lindsay (Australian Museum) for assistance with SEM.

FINANCIAL SUPPORT

This work was supported by an Endeavour Research Fellowship (N.B.), the Russian Foundation for Basic Research (grants number 10-04-01687, 12-05-33049) and by the Ministry of Education and Science of the Russian Federation (contract number 8132).

REFERENCES

- Andre C. and Pleijel F.** (1989) *Nothria maremontana*, a new onuphid species off the Portuguese coast. *Cahiers de Biologie Marine* 30, 11–16.
- Augener H.** (1918) Polychaeta. *Beiträge zur Kenntnis der Meeresfauna Westafrikas* 2, 67–625.
- Averincev V.G.** (1972) Benthic polychaetes Errantia from the Antarctic and Subantarctic collected by the Soviet Antarctic Expedition. *Issledovaniya fauny morei, Zoologicheskii Institut Akademii Nauk USSR* 11, 88–292. [In Russian.]
- Averincev V.G.** (1974) The polychaetous annelids of the abyssal and bathyal zones of the Scotian arc based on the 11th cruise of R/V Akademik Kuchatov. *Trudy Instituta Okeanologia Akademia nauk SSSR* 98, 213–227. [In Russian.]
- Blake J.A.** (1975) The larval development of Polychaeta from the northern California coast. II. *Nothria elegans* (Family Onuphidae). *Ophelia* 13, 43–61.
- Budaeva N. and Fauchald K.** (2010) Larval development of *Mooreonuphis stigmatis* (Treadwell 1922) (Polychaeta: Onuphidae) from the north-east Pacific. *Marine Biology Research* 6, 6–24.
- Budaeva N. and Fauchald K.** (2011) Phylogeny of the *Diopatra* generic complex with a revision of *Paradiopatra* Ehlers [sic], 1887 (Polychaeta: Onuphidae). *Zoological Journal of the Linnean Society*, 163, 319–436.
- Chamberlin R.V.** (1919) The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology at Harvard College* 48, 1–514.
- Day J.H.** (1967) A monograph on the Polychaeta of southern Africa. Part I. Errantia. *British Museum (Natural History) Publications* 656, 1–458.
- Ehlers E.** (1879) Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the United States Coastal Survey Steamer *Blake*, Lieutenant-Commander C.D. Sigsbee, U.S.N., commanding. 4. Preliminary report on the worms. *Bulletin of the Museum of Comparative Zoology at Harvard College* 5, 269–274.
- Ehlers E.** (1887) Reports on the results of dredging, under the direction of L.F. Poutales, during the years 1868–1870, and of Alexander Agassiz, in the Gulf of Mexico (1877–78), and in the Caribbean Sea (1878–79), in the U.S. Coast Survey Steamer *Blake*, Lieutenant-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 31. Report on the annelids. *Memoirs of the Museum of Comparative Zoology at Harvard College* 15, 1–335.
- Fadlaoui S., Lechapt J.-P. and Retière C.** (1995) Larval development of the onuphid *Diopatra marocensis* (Annelida: Polychaeta) from the Atlantic coast of Morocco. *Journal of the Marine Biological Association of the United Kingdom* 75, 957–966.
- Fauchald K.** (1968) Onuphidae (Polychaeta) from Western Mexico. *Allan Hancock Monographs in Marine Biology* 3, 1–82.
- Fauchald K.** (1972) Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the Eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology* 7, 1–575.
- Fauchald K.** (1982a) Revision of *Onuphis*, *Nothria*, and *Paradiopatra* (Polychaeta: Onuphidae) based upon type material. *Smithsonian Contributions to Zoology* 356, 1–109.
- Fauchald K.** (1982b) Description of *Mooreonuphis jonesi*, a new species of onuphid polychaete from shallow water in Bermuda, with comments on variability and population ecology. *Proceedings of the Biological Society of Washington* 95, 807–825.
- Fauchald K.** (1982c) Some species of *Onuphis* (Polychaeta: Onuphidae) from the Atlantic Ocean. *Proceedings of the Biological Society of Washington* 95, 238–250.
- Hansen G.A.** (1878) Annelider fra den norske Nordhavsexpedition i 1876. *Nyt magasin for naturvidenskaberne (Christiania)* 24, 133–192.
- Hansen G.A.** (1882) Annelida. *The Norwegian North-Atlantic Expedition 1876–1878 Volume Bd. 3. VII. Zoology*. Christiania: Gröndahl & Son, pp. 1–54.

- Hartman O.** (1944) Polychaetous Annelids. Part V. Eunicea. *Allan Hancock Pacific Expeditions* 10, 1–237.
- Hartman O.** (1964) Polychaeta Errantia of Antarctica. *Antarctic Research Series* 3, 1–131.
- Hartman O.** (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occasional Papers of the Allan Hancock Foundation* 28, 1–378.
- Hartman O.** (1967) Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic Seas. *Allan Hancock Monographs in Marine Biology* 2, 1–387.
- Hartman O. and Fauchald K.** (1971) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas, Pt. 2. *Allan Hancock Monographs in Marine Biology* 6, 1–327.
- Hsieh H.-L. and Simon J.L.** (1987) Larval development of *Kinbergonuphis simoni*, with a summary of development patterns in the family Onuphidae (Polychaeta). *Bulletin of the Biological Society of Washington* 7, 194–210.
- Imajima M.** (1970) Errant polychaetous annelids collected from the areas around the Tsushima Islands. *Memoirs of the National Science Museum, Tokyo* 3, 113–122.
- Imajima M.** (1982) Polychaetous annelids around Shimoda, Izu Peninsula. *Memoirs of the National Science Museum, Tokyo* 15, 155–161.
- Imajima M.** (1986) Eight species of Onuphidae (Polychaeta) in and off-shore of Otsuchi Bay, Northeastern Japan. *Bulletin of the National Science Museum, Tokyo A (Zoology)* 12, 93–116.
- Imajima M.** (1989) Two new Species of *Nothria* (Polychaeta, Onuphidae) from off Sanriku, Northeastern Honshu, Japan. *Bulletin of the National Science Museum, Tokyo A (Zoology)* 15, 1–10.
- Imajima M.** (1997) Polychaetous annelids of Suruga Bay, Central Japan. *National Science Museum Monographs* 12, 149–228.
- Imajima M.** (1999) Onuphidae (Annelida, Polychaeta) from Japan, excluding the genus *Onuphis*. *National Science Museum Monographs* 16, 1–115.
- Jirkov I.A. and Yermolaev I.G.** (1989) Analysis of variation of taxonomic characters in the genus *Nothria* (Polychaeta, Onuphidae). *Zoologicheskij Zhurnal* 68, 5–13. [In Russian with English abstract.]
- Knox G.A. and Hicks K.** (1973) The polychaetes of New Zealand. Part 5. Onuphidae. *Journal of the Royal Society of New Zealand* 3, 281–294.
- Kucheruk N.V.** (1978) Deep-water Onuphidae (Polychaeta) from the collections of the 16th Cruise of the R/V Dmitry Mendeleev (to the generic classification of the family Onuphidae). *Trudy Instituta Okeanologia Akademia nauk SSSR* 113, 88–106. [In Russian with English abstract.]
- Kucheruk N.V.** (1980) Age and bathymetric variability of *Nothria conchylega* (Polychaeta, Onuphidae). In Kuznetsov A.P. (ed.) *Ecological investigations of the shelf* Moscow: IO AN SSSR, pp. 63–72. [In Russian.]
- Kucheruk N.V.** (1985) Polychaetous annelids of genus *Nothria* (Onuphidae): systematic characters, species composition and distribution. *Issledovaniya fauny morej* 34, 83–87. [In Russian.]
- Lana P.** (1991) Onuphidae (Annelida: Polychaeta) from southeastern Brazil. *Bulletin of Marine Science* 48, 280–295.
- Maekawa N. and Hayashi I.** (1989) Onuphid polychaetes from Wakasa Bay, Sea of Japan. *Memoirs of the College of Agriculture, Kyoto University* 134, 61–93.
- Malmgren A.J.** (1867) *Annulata Polychaeta Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita*. Helsingfors: Ex Officina Frenckelliana.
- McIntosh W.C.** (1885) Report on the Annelida Polychaeta collected by H.M.S. *Challenger* during the years 1873–1876. In Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the years 1872–76. *Zoology* 12, 1–554.
- McIntosh W.C.** (1903) Notes from the Gatty Marine Laboratory, St. Andrews, no 24. 1. On the frequency of the occurrence of pearls in the mussel (*Mytilus edulis*). 2. The effects of marine piscatorial birds on the food fishes. 3. On the British Euniceidae. *The Annals and Magazine of Natural History, Series 7* 11, 549–565.
- Moore J.P.** (1903) Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea. *Proceedings of the Academy of Natural Sciences, Philadelphia* 55, 401–490.
- Moore J.P.** (1911) The polychaetous annelids dredged by the U.S.S. 'Albatross' off the coast of southern California in 1904. III. Euphrosynidae to Goniadidae. *Proceedings of the Academy of Natural Sciences, Philadelphia* 62, 234–318.
- Orensanz J.M.** (1974) Los anelidos poliuetos de la provincial biogeografica Argentina. V. Onuphidae. *Physis, Secciyon A* 33, 75–122.
- Orensanz J.M.** (1990) The Eunicemorph polychaete annelids from Antarctic and Subantarctic Seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Antarctic Research Series—Biology of the Antarctic Seas XXI* 52, 1–183.
- Paxton H.** (1979) Taxonomy and aspects of the life history of Australian beachworms (Polychaeta: Onuphidae). *Australian Journal of Marine and Freshwater Research* 30, 265–294.
- Paxton H.** (1986) Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta). *Records of the Australian Museum* 38, 1–74.
- Paxton H.** (1993) *Diopatra* Audouin and Milne Edwards (Polychaeta, Onuphidae) from Australia, with a discussion of developmental patterns in the genus. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 10, 115–154.
- Paxton H.** (1996) *Hirsutonuphis* (Polychaeta: Onuphidae) from Australia, with a discussion of setal progression in juveniles. *Invertebrate Taxonomy* 10, 77–96.
- Paxton H.** (1998) The *Diopatra chiliensis* confusion—redescription of *D. chiliensis* (Polychaeta, Onuphidae) and implicated species. *Zoologica Scripta* 27, 31–48.
- Paxton H.** (2000) Family Onuphidae. In Beesley P.L., Ross G.J.B. and Glasby C.J. (eds) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Volume 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. Melbourne: CSIRO Publishing, pp. 99–104.
- Paxton H.** (2005) *Fauchaldonuphis*, a new genus for the enigmatic polychaete *Diopatra paradoxa* Quatrefages, 1866. *Marine Ecology* 26, 209–215.
- Pettibone M.H.** (1970) Polychaeta Errantia of the Siboga Expedition. Part IV. Some additional polychaetes of the Polynoidae, Hesionidae, Nereidae, Goniadidae, Euniceidae, and Onuphidae, selected as new species by the late Dr. Hermann Augener with remarks on other related species. *Siboga-Expeditie Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch gebied verzameld in de Oost-Indische Archipel 1899–1900 aan boord H.M. Siboga onder commando van Luitenant ter zee 1e kl. G.F. Tydeman* 24, 27–72.
- Poore G.C.B., Just J. and Cohen B.F.** (1994) Composition and diversity of Crustacea Isopoda of the southeastern Australian continental slope. *Deep-sea Research I* 41, 677–693.

Rangarajan K. and Mahadevan S. (1961) On a new species of *Nothria* Malmgren (Polychaeta, Annelida) from the Gulf of Mannar. *Journal of the Marine Biological Association of India* 3, 179–185.

and

Sars M. (1835) *Beskrivelser og Iagttagelser over nogle mærkelige eller nye i Havet ved den Bergenske Kyst levende Dyr af Polypernes, Acalephernes, Radiaternes, Annelidernes og Molluskernes Classer, men en kort Oversigt over de hidtil af Forfatteren sammesteds*

fundne Arter og deres Forekommen. Bergen: Thorstein Hallagers Forlag.

Correspondence should be addressed to:

N. Budaeva
P.P. Shirsov Institute of Oceanology
Russian Academy of Sciences
Nakhimovsky pr. 36, 11797 Moscow, Russian
email: nataliya.budaeva@gmail.com