



## Bathy- and mesopelagic annelida from the Arctic Ocean: Description of new, redescription of known and notes on some “cosmopolitan” species



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### ARTICLE INFO

#### Keywords:

Deep sea  
Biodiversity  
Lopadorrhynchidae  
Typhloscolecidae  
Iospiliidae  
Polynoidae  
Molecular systematics  
Morphology  
Pelagic polychaeta  
18S rDNA  
28S rDNA  
16S rDNA

### ABSTRACT

Pelagic polychaetes collected in the deep Arctic Ocean between 2011 and 2016 during three expeditions of R/V *Polarstern* were investigated using morphological taxonomic and molecular methods based on DNA sequences for portions of the mitochondrial 16S and nuclear 18S and 28S rDNA genes. A comparison of our results on arctic *Pelagobia* cf. *longicirrata* Greeff, 1879, (Lopadorrhynchidae) and *Typhloscolex* cf. *muelleri* Busch, 1851 (Typhloscolecidae) with the data on *P. cf. longicirrata* and *T. cf. muelleri* from the Atlantic, Antarctic and Pacific, suggests the presence of species complexes within each of them instead of cosmopolitan species. We infer the validity of *Phalacroforus borealis* Reibisch, 1895 (Iospiliidae), synonymized earlier by several authors with cosmopolitan *P. pictus* Greeff, 1879 as a subspecies. Also, we describe a new Lopadorrhynchidae genus, *Bathypelagobia* gen. nov. with a redescription of *Pedinosoma polaris* (Buzhinskaja, 2017). Finally, we describe a new Polynoidae species, *Bathypolaria kondashovi* sp. nov. with some notes on the reproductive biology of the latter species.

### 1. Introduction

In the XIX and first half of the XX centuries, with the beginning of an active discovery of marine zooplankton, many species of pelagic invertebrates were described from different regions of the marine realm (Wagner, 1872; Greeff, 1879; Viguer, 1886, 1911; Reibisch, 1895; Southern, 1909; Bergström, 1914; Fauvel, 1916; Augener, 1922). These initial descriptions based mainly on morphological data were often brief and lacking details, and the respective holotypes were often lost (Wagner, 1872; Greeff, 1879; Viguer, 1886, 1911; Reibisch, 1895; Southern, 1909; Bergström, 1914; Fauvel, 1916; Augener, 1922). This situation was compounded in the first third of the XX century, when the idea of wide distribution areas and high intraspecific variation of pelagic animals widely disseminated among taxonomists (Kramp, 1961; Dales, 1957; Tebble, 1962; Russell, 1970; Nygren, 2014; Hutchings and Kupriyanova, 2017). Particularly, this idea was applied to pelagic polychaetes that were considered showing unusually wide geographic distributions, and, subsequently, many of closely related species from different parts of the world were synonymized (Knox, 1959; Fauvel, 1959; Dales, 1957; Tebble, 1962; Day, 1967; Nygren, 2014; Hutchings

and Kupriyanova, 2017). During the last three decades, however, the widespread adoption of molecular methods in zoology has led to another increase in the species diversity, due to rediscovering of misidentified species, having morphological variation, that not considered of inter-specific importance.

In fact, some species may be sympatric and very similar, whereas other species may be widely-distributed and morphologically variable (Kramp, 1961; Russell, 1970; Knowlton, 1993, 2000; Nygren, 2014; Kolbasova et al., 2014; Hutchings and Kupriyanova, 2017). Molecular methods help to avoid an incorrect synonymisation of different species and a needless production of new species, but as the data on pelagic polychaetes in the genetic databases are few, there is often nothing to compare to make a decision on a species status.

During this study, we focused on investigation of pelagic polychaetes collected with plankton nets in three expeditions to deep basins of the Arctic Ocean in 2011, 2015, and 2016. Our study was aimed to better document diversity of pelagic polychaetes for this region based on critical comparison with data on their diversity that has accumulated over the years of morphological-based taxonomic and systematic studies before the widespread use of molecular approaches (Burnette et al.,

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2005).

## 2. Materials and methods

### 2.1. Sampling and preservation

Specimens of polychaetes examined in this study were collected during three cruises of the R/V *Polarstern* to the deep Arctic Ocean: PS78 in August-September 2011 in the Nansen and Makarov Basins (stations 1 and 7), PS94 in September-October 2015 in the Nansen and Amundsen Basins (stations 2, 3, 5, and 6), and PS101 in September-October 2016 in the Amundsen Basin (station 4) (Fig. 1).

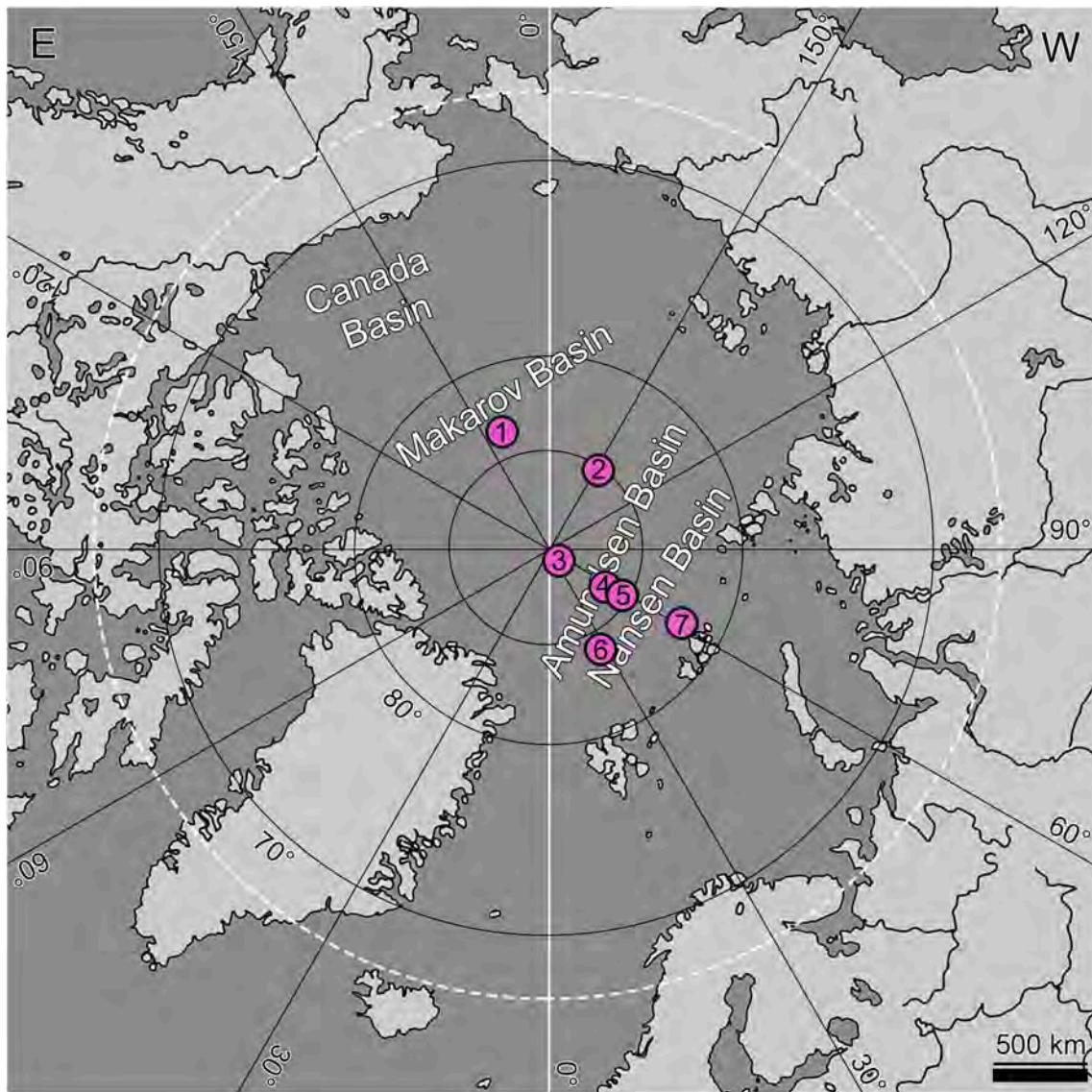
During these expeditions, zooplankton was collected with vertical casts of a plankton net (0.5 m<sup>2</sup> mouth opening, 150 µm mesh size). Nine layers were sampled: bottom (3000 m)-2000, 2000-1000, 1000-750 (500), 750 (500)-300, 300-200, 200-100, 100-50, 50-25, 25-0 m. Additional integral catches were obtained with a bongo net (150 µm mesh size) towed from the bottom (4830 m) and from layers 4400-2800, 3800-3000 or from 1500 m to the surface.

Live polychaete specimens were preserved in Bouin's solution or in 4% formalin for morphological examination, and in 96% undenatured

ethanol for genetic analysis. Species identification was provided using keys by Ushakov (1972) and Fauchald (1977) for pelagic families, and Bonifácio and Menot (2019) for Macellicephalinae. Specimens of *Pelagobia* cf. *longicirrata* Greeff, 1879 examined in the present study are deposited in the collections of the Zoological Museum of Moscow State University (Moscow, Russia) with numbers ZMMU WS3644-WS3652, WS4058-4059, *Typhloscolex* cf. *muelleri* Busch, 1851 with numbers ZMMU WS3653-ZMMU WS3661 and ZMMU WS4060, *Phalacrophorus pictus borealis* Reibisch, 1895 with the number ZMMU WS3643, and *Bathypolaria kondrashovi* sp. nov. with numbers ZMMU WS11183-ZMMU WS11185, ZMMU WS3641, ZMMU WS3673, and ZMMU WS4057. Specimens for new genus *Bathypelagobia polaris* gen. nov. comb. nov. are deposited with accession numbers ZMMU WS11198-ZMMU WS11200.

### 2.2. Morphological analysis

The specimens preserved in 4% formalin or in Bouin's solution were examined under a stereomicroscope Leica M 165 C and a microscope Leica DM 2500. Drawings were edited using Adobe Illustrator software. For scanning electron microscopy, specimens were critically-point dried



**Fig. 1.** Sampling area during cruises R/V *Polarstern* PS78 (Makarov and Nansen Basins), PS94 (Nansen and Amundsen Basins) and PS101 (Amundsen Basin). Stations 1 – PS78/239, 2 – PS94/125, 3 – PS94/081, 4 – PS101/183, 5 – PS94/058, 6 – PS94/050, 7 – PS78/188.

with CO<sub>2</sub>, Au–Pd-coated and examined using scanning electron microscope Cam Scan S-2.

### 2.3. DNA amplification and sequencing

Genomic DNA was extracted from seven specimens of *P. cf. longicirrata*, five specimens of *Bathypelagobia polaris* gen. nov. comb. nov. one specimen of *P. pictus borealis*, three specimens of *T. muelleri*, and three specimens of *B. kondrashovi* sp. nov. The Promega Wizard SV Genomic DNA Purification Kit and protocol (Promega Corporation, Madison, USA) were used for tissue lysis and DNA purification. Polymerase chain reaction (PCR) amplification of nuclear 18S rDNA, fragments of 28S rDNA and mitochondrial 16S rDNA was accomplished with the standard primers.

The 18S rDNA gene was PCR amplified in three overlapping fragments using primer pairs 1 F-5R, 3 F-18Sbi and 18Sa2.0–9 R (Giribet et al., 1996, 1999). For the 28S rDNA gene we used C1' and C2 primers (Lê et al., 1993). The universal primers 16Sar-L and 16Sbr-H (Palumbi and Kessing, 1991) did not yield products that could be sequenced, therefore for the 16S rDNA gene we used the primer pair 16SAnnF-16SAnnR (Sjölin et al., 2005). All PCR primers used in amplification and sequencing are given in Table 1.

All loci were amplified using the Encyclo PCR kit (Evrogen Joint Stock Company, Russia). We amplified a 25 µl reaction mix containing 1 x PCR buffer, 1 µl of 10 µM of primer pair mix, 1 µl of template, 0.2 mM of each dNTP and 0.5 units Taq polymerase. Reaction mixtures were heated on Veriti® Thermal Cycler to 94°C for 300 s, followed by 35 cycles of 15 s at 94°C, 30 s at a specific annealing temperature, and 45–60 s at 72°C, depending on the length of fragment, and then a final extension of 7 min at 72°C. Annealing temperature was set to 49°C for the 18S primer pairs 1 F-5R and 18Sa2.0–9 R, 52°C for the 18S primer pair 3 F-18Sbi and for the 28S primer pair C1'-C2, 60°C for the 16S primer pair 16SAnnF and 16SAnnR (Roussett et al., 2007).

We used the Promega PCR Purification Kit and protocol (Promega) to purify our amplification products, which were sequenced in both directions. Each sequencing reaction mixture included 1 µl of BigDye (Applied Biosystems, PerkinElmer Corporation, Foster City, CA), 1 µl of 1 µM primer and 1 µl of DNA template, and was processed for 40 cycles of 96°C (15 s), 50°C (30 s) and 60°C (4 min). Samples were purified prior to sequencing by ethanol precipitation to remove unincorporated primers and dyes. Products were re-suspended in 12 µl formamide and electrophoresed in an ABI Prism 3500 sequencer (Applied Biosystems). All new DNA sequences have been submitted to the NCBI GenBank repository and accession numbers have been assigned (Table 2).

### 2.4. Data analysis

Data analysis was conducted in MEGA Ver. 6.06 (Tamura et al., 2013), and included 72 sequences from this study and sequences

**Table 1**  
PCR primers used in amplification and sequencing.

Name	Sequence 5'-3'	Source
<b>18S</b>		
1 F	TACCTGGTTGATCCTGCCAGTAG	Giribet et al. (1996)
5R	CTTGGCAATGCTTTCGC	Giribet et al. (1996)
3 F	GTTCGATTCCGGAGAGGGA	Giribet et al. (1996)
18Sbi	GAGTCTCGTCGTTATCGGA	Giribet et al. (1999)
18Sa2.0	ATGGTTGCAAAGCTGAAAC	Giribet et al. (1999)
9R	GATCCTCCGCAGGTTCACCTAC	Giribet et al. (1996)
<b>28S</b>		
C1'	ACCCGCTGAATTAAAGCAT	Lê et al. (1993)
C2	TGAACCTCTCTTCAAAGTTCTTTTC	Lê et al. (1993)
<b>16S</b>		
AnnF	GCGGTATCCTGACCGTRCWAAGGTA	Sjölin et al. (2005)
AnnR	TCCTAACGCCAATCGAGGTGCCAA	Sjölin et al. (2005)

obtained from GenBank for species of other polychaete families, including Phyllodocidae Örsted, 1843, Polynoidae Malmgren, 1867, Lopadorrhynchidae Claparède, 1870 and Typhloscolecidae Uljanin, 1878. The analysis involved 58 nucleotide sequences for 18S rDNA, 38 nucleotide sequences for the 28S rDNA and 72 nucleotide sequences for mt16S rDNA. All ambiguous positions were removed for each sequence pair. For the holopelagic polychaetes 18S tree *Nereis pelagica* Linnaeus, 1758 and *Eulalia viridis* Linnaeus, 1767 were included as outgroup species; for Polynoidae combined 16S and 18S tree the outgroup is *Pholoe baltica* Örsted, 1843.

Nucleotide sequences were edited using the software CodonCode Aligner v. 5.0.2 (CodonCode Corporation) and checked for identity against the nuclear redundant (default) database of GenBank using BLASTn (Altschul et al., 1990). Multiple nucleotide alignments were made with MUSCLE (Edgar, 2004) and corrected with Alter (Glez-Peña et al., 2010) algorithms. The combined data set alignments were manually stripped of ambiguously aligned positions and Gblocked (Castresana, 2000). For Lopadorrhynchidae-Typhloscolecidae-Iospididae group the final length for individual alignments was 1199, 420 and 220 bp for the 18S, 28S and 16S rDNA genes respectively. For Polynoidae group the length of 18S alignment was 1810 bp, for 16S rDNA 404 bp. The average evolutionary divergence over sequence pairs was calculated within species (intraspecific variation) and between species (interspecific variation) using the Kimura two-parameter (Kimura, 1980).

GenBank Accession Numbers for sequences obtained in the present study are given in Table 3. The best-fitting nucleotide evolution model for each partition was tested using the MEGA7 toolkit. Topologies were constructed under Bayesian inference (BI) and maximum likelihood (ML) criteria. The Bayesian analysis was done using MrBayes Version 3.2.0 (Ronquist et al., 2011), Markov chains were sampled at intervals of 500 generations, the analysis was started with random starting trees and 10<sup>7</sup> generations. Chains convergence was verified by the TRACER (Rambaut et al., 2018). The ML analysis was conducted with RAxML version 0.6.0 (Kozlov, 2018) using the GTR model for 18S and 28S, and HKY + I model for 16S; a partition scheme letting the parameters be optimized for all three genes separately, with 100 replication trials (0.03 bootstrapping cutoff). Final phylogenetic tree images were rendered in FigTree 1.4.4. (Rambaut, 2006).

Species delimitation analysis. Minimum and maximum uncorrected p-distances were calculated with MEGA 6 software. We also applied the Automatic Barcode Gap Discovery (Puillandre et al., 2011) method to detect species-level clusters with the default settings ( $P = 0.001\text{--}0.1$  and  $X = 1.5$ ) to generate a preliminary partition of sequences using the 18S alignment and excluding outgroups.

## 3. Results

### 3.1. Lopadorrhynchidae Claparède, 1870.

*Bathypelagobia* gen. nov. Kolbasova, 2020.

Type species. *Pedinosoma polaris* (Buzhinskaja, 2017) [gender: feminine].

**Diagnosis.** Prostomium and peristomium fused; two antennae and two palps. Nine segments. Eyes absent, pharyngeal jaws present. Two pairs of tentacular cirri on one segment, chaetae and aciculae present on tentacular segment. Second segment without dorsal cirri. Parapodia uniramous, acicular; dorsal and ventral cirri shorter than parapodial lobes; all chaetae compound spinigers with smooth shafts and serrated blades. Pygidium with two rudimentary appendages.

**Remarks.** *Bathypelagobia* gen. nov. clearly differs from all remaining Lopadorrhynchidae, Iospididae Bergström, 1914 and Pontodorididae Bergström, 1914 genera by the combination of key characters, such as prostomium fused with peristomium, shape of chaetae and parapodia and the number of segments and tentacular cirri. Among the non-valid lopadorrhynchid genera, *Halyplanella* Treadwell, 1943 and *Halyplanes*

**Table 2**

Specimens used in the molecular analysis.

Species name	Museum catalog number	GenBank 16S accession number	GenBank 18S accession number	GenBank 28S accession number	Sampling location	Depth (m)
<i>Typhloscolex cf. muelleri</i>	ZMMU WS3654	–	–	MK660161	84°23,00' N, 29°46,50' E	500–0
	ZMMU WS3655	–	MK660170	MK660160	84°23,00' N, 29°46,50' E	500–0
	ZMMU WS3656	–	MK660169	MK660159	84°23,00' N, 29°46,50' E	500–0
<i>Phalacrophorus pictus borealis</i>	ZMMU WS3643	MK559883	MK660179	MK660155	89°0,62' N, 61°26,15' E	4300–0
<i>Pelagobia cf. longicirrata</i>	ZMMU WS3644	MK559884	MK660178	–	85°18,10' N.,59°55,26' E	500–100
	ZMMU WS3645	MK559885	MK660177	–	85°18,10' N.,59°55,26' E	500–100
	ZMMU WS3646	MK559886	MK660176	–	85°18,10' N, 59°55,26' E	500–100
	ZMMU WS3647	MK559887	MK660175	–	85°18,10' N, 59°55,26' E	500–100
	ZMMU WS3648	MK559888	MK660174	–	85°18,10' N, 59°55,26' E	500–100
	ZMMU WS3649	MK559889	MK660173	–	85°18,10' N, 59°55,26' E	500–100
	ZMMU WS3650	MK559890	MK660172	–	85°18,10' N, 59°55,26' E	500–100
	ZMMU WS3651	MK559891	MK660171	MK660162	85°18,10' N, 59°55,26' E	500–100
	ZMMU WS4058	MK559897	–	–	86°00,43' N, 55°47,65' E	850–0
	ZMMU WS3662	MK559892	MK660168	MK660158	84°23,00' N, 29°46,50' E	3900–3000
<i>Bathypelagobia polaris</i> comb. nov.	ZMMU WS3663	MK559893	MK660167	MK660163	84°23,00' N, 29°46,50' E	3900–3000
	ZMMU WS3664	MK559894	MK660166	MK660157	84°23,00' N, 29°46,50' E	3900–3000
	ZMMU WS3665	MK559895	MK660165	MK660156	84°23,00' N, 29°46,50' E	3900–3000
	ZMMU WS3666	MK559896	MK660164	MK660154	84°23,00' N, 29°46,50' E	3900–3000
	ZMMU WS3673	MK559882	MK660182	MK660153	87°0'25" N 55°47'39" E	4000–4830
	ZMMU WS4057	MK559881	MK660181	MK660151	87°0'25" N 55°47'39" E	4000–4830
<i>Bathypolaria kondrashovi</i> sp. nov.	ZMMU WS3641	MK559898	MK660183	–	85°5,37' N, 139°40,83' E	3000–2000

*Reibisch, 1895* (now accepted as *Maupasia* Viguer, 1886) have prostomium and peristomium fused but three pairs of tentacular cirri on two segments. The genus *Mastigethus* Chamberlin, 1919 has large nuchal organs and first four pairs of parapodia modified, *Reibischia* Bergström, 1914 and *Hydrophanes* Claparède, 1870 (now accepted as *Lopadorrhynchus* Grube, 1855) have simple chaetae in parapodia of anterior segments and also three pairs of tentacular cirri on two segments.

**Etymology.** The generic name *Bathypelagobia* refers to the oceanic zone where the first representatives of the genus were found, and to the genus *Pelagobia*.

*Bathypelagobia polaris* (Buzhinskaja, 2017) comb. nov.

Type species: *Pedinosoma polaris* (Buzhinskaja, 2017).

**Material examined.** Three adult complete specimens ZMMU WS11198–11200 in 75% ethanol after 4% formalin (84°04,63' N, 164°13,43' W, PS78/239–7, September 06, 2011, 500–1000 m).

Six adult complete specimens in 96% ethanol ZMMU WS3667–3672 (84°23,00' N, 29°46,50' E, PS94/050, August 27, 2015, 3000–3800 m), 6 complete specimens in 75% ethanol after 4% formalin WS13795–13800 (86°55,52', N 055°58,20' E, PS 101/165, September 29, 2016, 200–2500 m). Material used for DNA extraction: ZMMU WS3662–3666.

**Description (based on all our material).** Worms small, without eyes, up to 3.2 mm long, with nine body segments, white, thick, non-transparent (Fig. 2A, 3 A–B). Pigmentation uniform white, both in life and after preservation (ethanol and formalin). Pair of pharyngeal jaws

(Fig. 2B). Prostomium short, rounded or slightly square-shaped, fused with peristomium (Figs. 2A, 3 A–B). Two pairs of thin filiform appendages (two palps and two antennae) on the front of peristomium (Figs. 2A, 3 A–B). One pair of ciliary pits on the dorsal side of prostomium (Fig. 2A). Tentacular segment with aciculae and fascicles of 2–6 thin short compound chaetae (Fig. 2A). Two pairs of thin filiform tentacular cirri, reaching the second to third segment (Fig. 3A and B). Lateral sensory organs bean-shaped, ciliar, in base of dorsal tentacular cirri (Fig. 2A). Parapodia uniramous, bilabiate; anterior labium rounded, posterior lobe conical, longer than anterior (Fig. 2D). First pair of parapodia lacking dorsal cirri, all following parapodia with dorsal and ventral cirri (Figs. 2A, 3 A–B). Dorsal cirri thick, short, reaching nearly end of parapodia; ventral cirri slightly shorter (Fig. 3B and C, 4 A–B). Parapodia stout, broadly-tapering, arranged with a tuft of 18–22 chaetae and single thick median acicula (Figs. 2D and 4A). Chaetae compound, with smooth heterogomph shaft and serrated blade (Fig. 2E). Pygidium with two very small rudimentary appendages (Figs. 2A, 3 A–B).

**Reproductive notes.** Specimens 3.0–3.2 mm long with eggs in the body cavity.

**Remarks.** *Bathypelagobia polaris* comb. nov. was initially described from the deep Makarov Basin as a late *Pedinosoma* larva. The placement of these worm within the *Pedinosoma* based on a short body, a short and broad prostomium with four appendages, prostomium fused with the peristomium, two pairs of tentacular cirri on one segment, all parapodia uniramous with dorsal and ventral cirri, all chaetae compound

**Table 3**  
GenBank sequences used for trees.

Name	Sequence number		
	18S	28S	16S
<b>Lopadorrhynchidae</b>			
<i>Pelagobia</i> cf. <i>longicirrata</i>	GU230894.1 GQ426581.1 GQ426582.1 JQ268610.1 JX104110.1 JX104108.1		
<i>Typhloscolecidae</i>			
<i>Typhloscolex</i> cf. <i>mulleri</i>	GU230895.1		
<i>Phyllodocidae</i>			
<i>Eulalia viridis</i>	AY340428.1	AY340392.1	AY340455.1
<i>Nereididae</i>			
<i>Nereis pelagica</i>	AY340438.1	AY340407.1	AY340470.1
<i>Polynoidae</i>			
<i>Abyssarya acus</i> Bonifácio and Menot, 2019	MH233230		MH233178
<i>Austropolaria magnicirrata</i> Neal. Barnich, Wiklund and Glover, 2012	MH233231 JX863895		MH233179 JX863896
<i>Bathyeliasona mariae</i> Bonifácio and Menot, 2019	MH233204		MH233149
<i>Bathyfauvelia glacigena</i> Bonifácio and Menot, 2019	MH233243 MH233208		MH233197 MH233162
<i>Bathyfauvelia ignigena</i> Bonifácio and Menot, 2019	MH233217 MH233218 MH233246		MH233163 MH233186 MH233196
<i>Bathykurila guaymasensis</i> Pettibone, 1989	MH233248		MH233203
<i>Bathymoorea lucasi</i> Bonifácio and Menot, 2019	MH233244		MH233166
<i>Bathypolaria</i> sp. 173	MH233223 MH233245 MH233206		MH233167 MH233151 MH233199
<i>Bathypolaria</i> sp. 608	MH233227 MH233228 MH233229 MH233241		MH233175 MH233176 MH233192 MH233193
<i>Hodor anduril</i> Bonifácio and Menot, 2019	MH233239		MH233190
<i>Hodor hodor</i> Bonifácio and Menot, 2019	MH233240 MH233238		MH233191 MH233189
<i>Pelagomacellcephala iliffei</i> Pettibone, 1985b	KY454409.1		KY454423.1
<i>Phloe baltica</i>	AY839573.1		JN852912.1
<i>Polaruschakov lamellae</i> Bonifácio and Menot, 2019	MH233205		MH233150
<i>Polaruschakov omnesae</i> Bonifácio and Menot, 2019	MH233226 MH233242 MH233213		MH233194 MH233174 MH233164

(Buzhinskaja, 2017). At the same time, the diagnosis of *Pedinosoma* implies the lack of chaetae on tentacular segment, and presence of dorsal cirrus on the first pair of parapodia (Reibisch, 1895). Also, jaws and serrated chaetal blades were never noted for *Pedinosoma* (Reibisch, 1895; Tebble, 1962; Day, 1967; Ushakov, 1972).

*Bathypelagobia polaris* comb. nov. has jaws and chaetae on tentacular segment, and lacks dorsal cirrus on the first pair of parapodia, that corresponds to the diagnosis of genus *Pelagobia* (Greiff, 1879). The main differences from *Pelagobia* are prostomium fused with peristomium and constant number of body segments. The 18S p-distances between *B. polaris* comb. nov. and *Pelagobia* cf. *longicirrata* from different localities are 7.2–7.5% (Arctic), 6–7.9% (Drake Passage), 7.9–8.2% (Shetland Islands) and 5.1–7.5% (Angola Basin).

Distribution. Type locality: Makarov Basin, depth layer 500–1000 m.

Nansen Basin, depth layer 3000–3800 m, Amundsen Basin, depth layer 200–2500 m.

DNA. Nuclear 18S, 28S and mitochondrial 16S sequence data of *Bathypelagobia* gen. nov. are available in GenBank under accession numbers given in Table 4. The analysis of species-level clusters for the 18S gene retrieved seven (Initial Partition with prior maximal distance  $P = 2.78e-03$ ) or six (Initial Partition with prior maximal distance  $P = 4.64e-03$ ) partitions, distance K80 Kimura MinSlope = 1.500000. In both cases, *Bathypelagobia* gen. nov. forms distinct separate group. The analysis of 28S using the same parameters retrieved two (Initial Partition with prior maximal distance  $P = 0.0010$ –0.0599) groups. The first one includes *Bathypelagobia* gen. nov. (MK660154, MK660156–660158, MK660163), the second one includes all remaining our species from the Arctic, *P. cf. longicirrata* (MK660162), *T. cf. muelleri* (MK660159–660160), *P. pictus borealis* (MK660155).

#### *Pelagobia* Greiff, 1879.

Type species: *Pelagobia longicirrata* Greiff, 1879.

Diagnosis. Prostomium with two antennae and two palps. Pharyngeal jaws present. Two pairs of tentacular cirri on one segment, chaetae and aciculae present on tentacular segment. Second segment without dorsal cirri; dorsal and ventral cirri digitiform, longer than parapodial lobes; all chaetae compound spinigers with serrated blades.

#### *Pelagobia* cf. *longicirrata* Greiff, 1879.

*Pelagobia longicirrata* Greiff, 1879 (Greiff, 1879; Viguer, 1886; Reibisch, 1895; Southern, 1909; Bergström, 1914; Ehlers, 1913; Fauvel, 1916, 1936; Okuda, 1937, 1938; Augener, 1929; Nolte, 1938; Stöp-Bowitz, 1948, 1949; Ushakov, 1957, 1972; Muus, 1953; Dales, 1957; Knox, 1959; Mileikovsky, 1962; Berkeley and Berkeley, 1964; Mileikovsky, 1970; Yingst, 1974a, b; Maurer and Reish, 1984; Hartmann-Schröeder and Rosenfeldt, 1992; Wilson, 2000; Bilbao et al., 2008; Sarda et al., 2009; Böggemann, 2009; Nygren and Pleijel, 2011; Isaychev et al., 2013; Isaychev, 2015)

*Pelagobia viguieri* Gravier, 1911 (Gravier, 1911; Chamberlin, 1919; Benham, 1921; Treadwell, 1943).

#### *Pelagobia erinensis* Nolte, 1938 (Nolte, 1938).

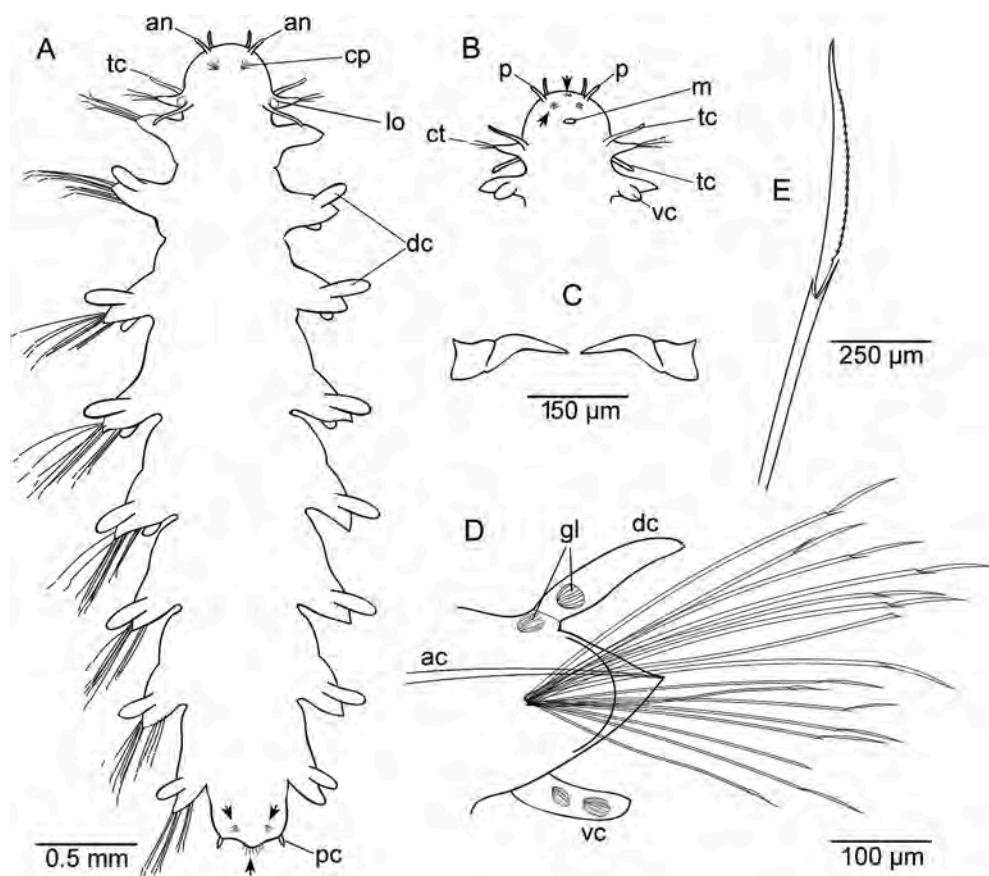
Material examined. 14 complete specimens and 4 specimens lacking posterior half of the body in 96% ethanol ( $85^{\circ}18,10' \text{ N}, 59^{\circ}55,26' \text{ E}$ , PS94/058, August 30, 2015, 100–500 m), and eight complete specimens in 75% ethanol after 4% formalin ( $86^{\circ}46,70' \text{ N}, 61^{\circ}30,05' \text{ E}$ , PS101/201, October 06, 2016, 0–750 m).

Description (based on all our material). Body length up to 5.0–8.0 mm, 14–18 segments. Live worms white-yellowish, semi-transparent, with yellow-orange lateral organs, orange spots on lateral side of each segment and on base of parapodial cirri. Preserved specimens white, without pigment patterns.

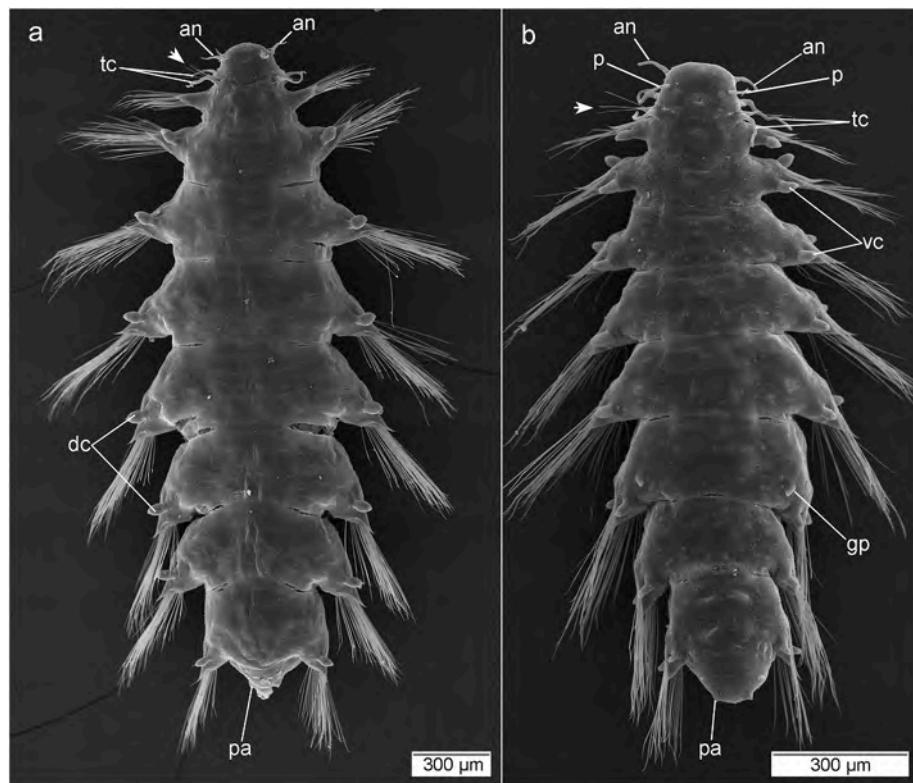
Prostomium pentagonal-rounded, with two pairs of thin filiform appendages (pair of palps and pair of antennae), of about 0.5–0.75 length of prostomium (Fig. 6A, 7 A–B). One pair of red eyes with lenses, well visible both in live and preserved specimens. Two large nuchal organs laterally on dorsal side of peristomium (Fig. 6A). Proboscis smooth, with pair of small jaws which are reported by Friedrich (1949), Ushakov (1972) and Sarda et al. (2009); each jaw consists of basal part and falcate proximal one (Fig. 6B).

Tentacular segment with fascicle of 3–4 compound chaetae and two pairs of large tentacular cirri of subequal length, reaching fourth to sixth segment. Acicular structures in tentacular cirri mentioned by Hartmann-Schröeder and Rosenfeldt (1992), Böggemann (2009) and Isaychev et al. (2013) absent. Parapodia of second segment without dorsal cirri, parapodia of following segments with dorsal and ventral cirri (Figs. 6A and 7A, C). Dorsal cirri attain nearly end of chaetae; ventral cirri slightly shorter (Fig. 6C). Each parapodium with tuft of 16–20 chaetae and one thick median acicula. Chaetae compound spinigers, with long smooth heterogomph shaft and serrated blade (Figs. 6D and 7D). Additional chaetae, mentioned by Tebble (1960) and Böggemann (2009) absent. Pygidium with two rudimentary appendages (Fig. 7C).

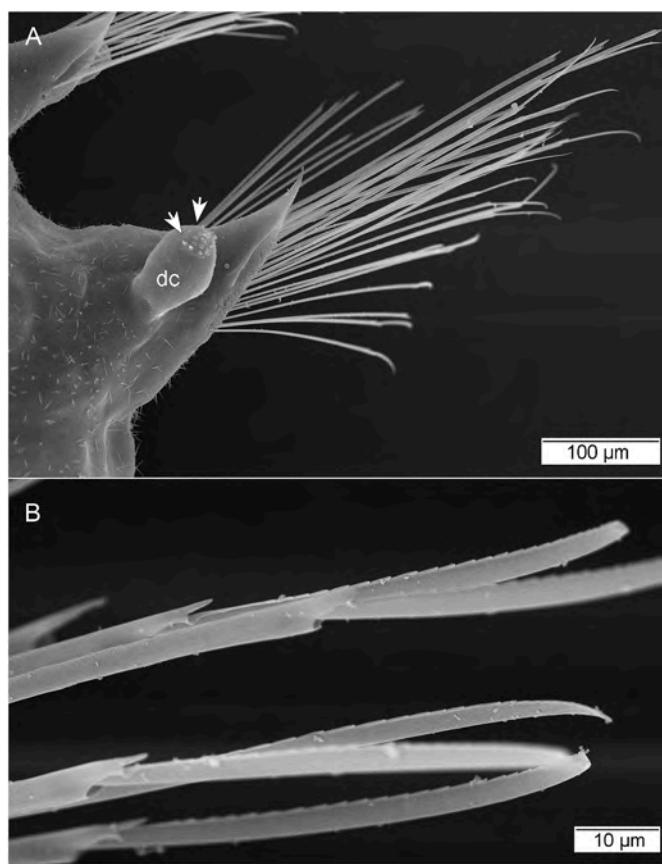
Reproductive notes. Some specimens 7.0–8.0 mm long with eggs in



**Fig. 2.** *Bathypelagobia polaris* gen. nov. comb. nov. (based on the specimen ZMMU WS11198). A, dorsal side of the entire specimen. B, anterior end, ventral view. C, jaws. D, parapodium of the third segment, frontal view. E, chaeta. Chaetae on the right side of the body are not shown. Abbreviations: ac – acicula, an – antennae, ct – compound chaetae of tentacular segment, dc – dorsal cirrus, lo – lateral ciliary organ, m – mouth, nr – neurochaetae, nt – notochaetae, gl – parapodial glands, p – palps, pc – pygidial cirri, tc – tentacular cirri, vc – ventral cirri. Arrows show ciliary pits.



**Fig. 3.** *Bathypelagobia polaris* gen. nov. comb. nov. SEM. A, dorsal view of entire specimen ZMMU WS13796. B, ventral view of entire specimen ZMMU WS13897. Abbreviations: an – antennae, cp – ciliary pits, dc – dorsal cirri of parapodia, gp – genital pore, p – palps, pc – pygidial cirri, tc – tentacular cirri, vc – ventral cirri of parapodia. Arrows show compound chaetae of tentacular segment.



**Fig. 4.** *Bathypelagobia polaris* gen. nov. comb. nov. SEM (specimen ZMMU WS13796). A, parapodium of the third segment, dorsal view. B, heterogomph compound chaetae with smooth shafts and serrated blades. Abbreviations: dc – dorsal cirrus. Arrows show glands.

**Table 4**

Minimum and maximum pairwise genetic distances (%) for *Bathypelagobia polaris* comb. nov. based on nuclear 18 S rDNA (alignment length 1199 bp), mitochondrial 16 S rDNA (220 bp) and nuclear 28 S rDNA (420 bp).

Name	Uncorrected	Corrected
	<i>Bathypelagobia polaris</i> comb. nov.	
<b>18S</b>		
<i>Pelagobia</i> cf. <i>longicirrata</i> Arctic (Nansen Basin)	7.3–7.5	7.2–7.5
<i>P. cf. longicirrata</i> Antarctic (Shetland Islands)	7.9–8.2	8.1
<i>P. cf. longicirrata</i> Antarctic (Drake Passage)	6–7.4	7.6–7.9
<i>P. cf. longicirrata</i> South Atlantic (Angola Basin)	5.1	7.5
<i>Phalacrophorus pictus borealis</i> Arctic (Nansen Basin)	9.1–9.4	9–9.3
<i>Typhloscolex</i> sp. Pacific (Monterey Bay)	8.8	8.8–9.1
<i>T. cf. muelleri</i> Arctic (Nansen Basin)	8.5–8.8	8.7–9
<b>16S</b>		
<i>P. cf. longicirrata</i> Arctic (Nansen Basin)	24.6	24.6
<i>P. pictus borealis</i> Arctic (Nansen Basin)	34.5	34
<b>28S</b>		
<i>P. cf. longicirrata</i> Arctic (Nansen Basin)	8.8	8.7
<i>P. pictus borealis</i> Arctic (Nansen Basin)	9.5	10–12
<i>T. cf. muelleri</i> Arctic (Nansen Basin)	11.4	10

the body cavity.

**Remarks.** Morphologically, *P. cf. longicirrata* from the Arctic Ocean corresponds well to descriptions by Friedrich (1949), Dales (1957), and Ushakov (1972). It also corresponds to the original description, but the third pair of tentacular cirri, mentioned for the type specimens (Greeff, 1879) is absent in our specimen. In contrast to the description of *P. cf.*

*longicirrata* from the Arctic by Yingst (1974a, b), in our specimens jaws are present, but acicular-like structures in tentacular cirri, described for this species from South Atlantic (Böggemann, 2009) and Antarctic (Hartmann-Schröeder and Rosenfeldt, 1992; Isaychev et al., 2013) are absent. The 18S p-distance between *P. cf. longicirrata* from the Arctic and *P. longicirrata* from the Drake Passage is 0.5–0.7%, and 1.7% for *P. cf. longicirrata* from the Angola Basin. The p-distances between *P. cf. longicirrata* from the Arctic and *P. cf. longicirrata* from Shetland Islands is 0.9%.

**Distribution.** Collected in the deep Nansen and Amundsen Basins of the Arctic Ocean, depths from 500 to 1000 m.

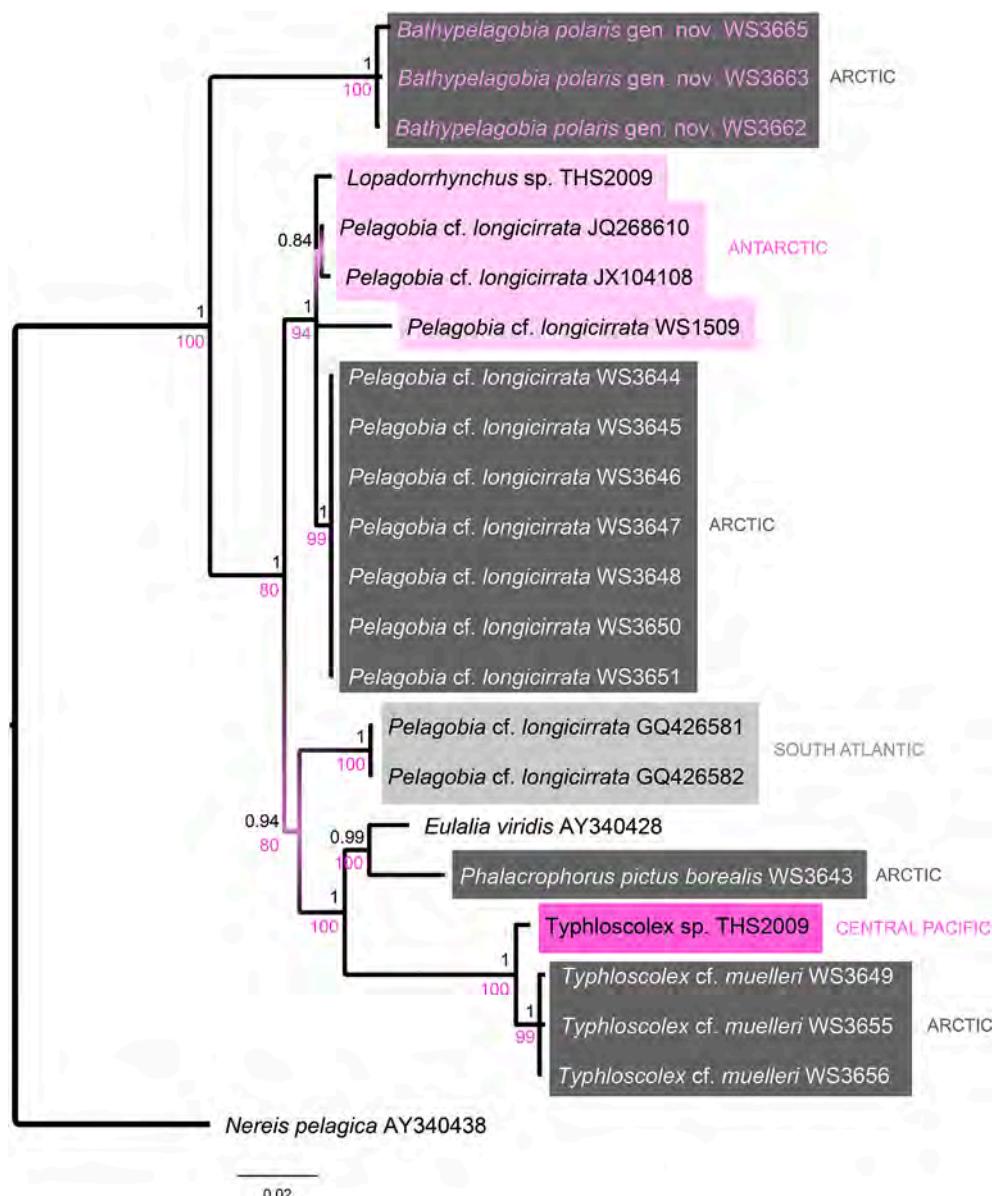
The type locality of *P. longicirrata* is the Tenerife Bay, Canarian Islands (Greeff, 1879). Also reported from the North Atlantic (Stöp-Bowitz, 1948; Muus, 1953), Norwegian Sea (Ushakov, 1974; Mileikovsky, 1962), Greenland (Reibisch, 1895; Nolte, 1938), Gulf-stream, East- and West-Greenland, Labrador and Florida streams, the Sargasso Sea, Bermudans (Reibisch, 1895), North-Equatorial, Guinea and South-Equatorial streams (Reibisch, 1895; Nolte, 1938), Dublin Bay (Southern, 1909), Azores (Nolte, 1938), the Mediterranean Sea (Reibisch, 1895; Sarda et al., 2009), Algerian Bay (Viguer, 1886), South Atlantic (Tebble, 1958, 1960), Angola, Cape and Guinea Basins (Böggemann, 2009), Antarctic (Ehlers, 1913; Benham, 1921, 1927; Stöp-Bowitz, 1948; Hartmann-Schröeder and Rosenfeldt, 1992), the Weddell Sea (Augener, 1929), Drake Passage (Isaychev et al., 2013; Isaychev, 2015), the Indian Ocean, Sumatra (Reibisch, 1895), South Pacific (Nolte, 1938), Boca del Guapo and Elefantes Channel (Bilbao et al., 2008), Galapagos, Easter, Paumotu Islands (Chamberlin, 1919), Peru (Berkeley and Berkeley, 1964), Central Pacific, the Monterey Bay (Dales, 1957; 1957), Northwestern Pacific (Mileikovsky, 1969), Japan (Okuda, 1937; 1938), Okhotsk Sea (Ushakov, 1972), Kurile-Kamchatka trench (Mileikovsky, 1970), North Pacific (Ushakov, 1972; 1974), the Barents Sea (Mileikovsky, 1962) and the Arctic Basin (Ushakov, 1972, 1974; Knox, 1959; Yingst, 1974a, b; Maurer and Reish, 1984).

**DNA.** Nuclear 18S, 28S and mitochondrial 16S sequence data of *P. cf. longicirrata* obtained in this study are available in GenBank under accession numbers given in Table 5.

The analysis of species-level clusters for the 18S retrieved seven (Initial Partition with prior maximal distance  $P = 2.78e-03$ ) or six (Initial Partition with prior maximal distance  $P = 4.64e-03$ ) partitions, distance K80 Kimura MinSlope = 1.500000. In both cases, *Pelagobia* forms three groups. The first one includes *P. cf. longicirrata* from the South Atlantic (GQ426581.1 and GQ426582.1). The second one includes all our specimens from the Arctic (MK660174–660178), specimen from the Monterey Bay (GU230894.1), and two specimens from the Antarctic (JQ268610.1 and JX104108.1). The third specimen from the Antarctic (JX104110.1) forms separate group. For the 28S the analysis of species-level clusters retrieved two (Initial Partition with prior maximal distance  $P = 0.0010–0.0599$ ) groups. Due to very few number of samples, *P. cf. longicirrata* from the Arctic (MK660162) belongs to the group including *T. cf. muelleri* (MK660159–660160) and *P. pictus borealis* (MK660155); *Bathypelagobia* (MK660154, MK660156–660158, MK660163) forms the second group.

**Key to genera of Lopadorrhynchidae (modified from Fauchald, 1977).**

- Two acicular chaetae ..... *Nans* Chamberlin, 1919.
- One acicular chaetae ..... 2.
- 2 Fascicle of chaetae at the base of the tentacular cirri present ..... 3.
- Fascicle of chaetae at the base of the tentacular cirri absent ..... 5.
- 3 Prostomium and peristomium separated, two pairs of tentacular cirri on one segment, jaws present ..... *Pelagobia* Greeff, 1879.
- Prostomium and peristomium fused .....



**Fig. 5.** Bayesian (BI) phylogenetic tree based on 18S gene of *Pelagobia* cf. *longicirrata*, *Bathypelagobia polaris* gen. nov. comb. nov. *Phalacrophorus pictus borealis* and *Typhloscolex* cf. *muelleri*. Black numbers above branches indicate posterior probabilities from BI; purple numbers below—bootstrap values from ML. Where available, GenBank sequences of other pelagic annelids were included in the analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

- ..... 4.
- 4 Two pairs of tentacular cirri on one segment, jaws present ..... *Bathypelagobia* gen. nov.
- Three pairs of tentacular cirri on two segments, jaws absent ..... *Maupasia Viguer, 1886*.
- 5 All parapodia similar, chaetae compound ..... *Pedinosoma Reibisch, 1895*.
- Parapodia of the first two or three segments modified and bearing simple chaetae ..... *Lopadorrhynchus Grube, 1855*

### 3.2. *Iospididae* Bergström, 1914

*Phalacrophorus* Greeff, 1879.

Type species: *Phalacrophorus pictus* Greeff, 1879.

**Diagnosis.** Prostomium without antennae, one pair of palps. Eyes absent, pharyngeal jaws present. First segment without appendages, second segment with pair of dorsal tentacular cirri and reduced parapodia, third and fourth segments with reduced parapodia without cirri.

Following parapodia uniramous, acicular; dorsal and ventral cirri two times shorter than parapodial lobes; all chaetae very thin compound spinigers. Pygidium without appendages.

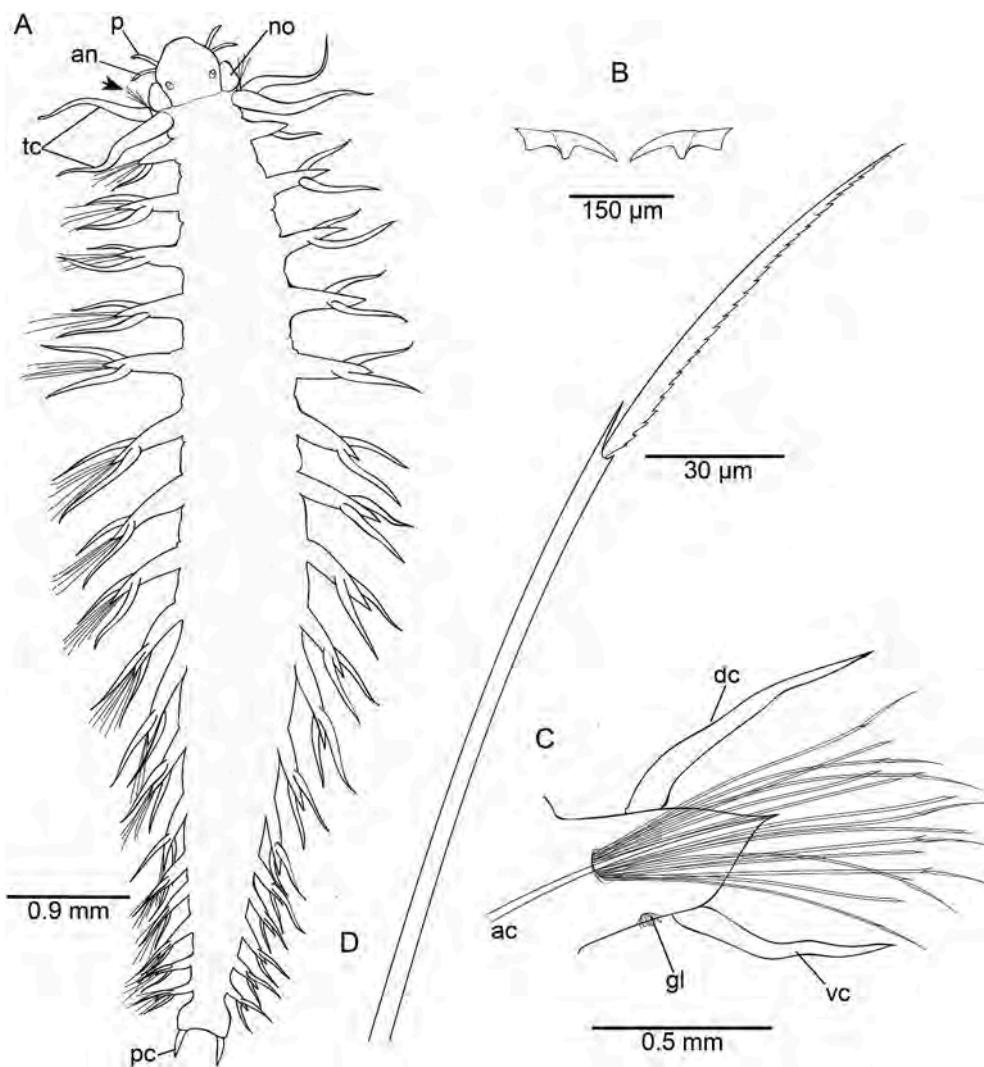
*Phalacrophorus pictus borealis* Reibisch, 1895.

*Phalacrophorus borealis* Reibisch, 1895 (Reibisch, 1895; Ditlevsen, 1914; Ushakov, 1957, 1972; Maurer and Reish, 1984; Druzhkov et al., 2000).

*Phalacrophorus pictus borealis* Reibisch, 1895 (Dales, 1957; Tebble, 1962; Dales and Peter, 1972; Jirkov, 2001).

Material examined. One specimen lacking the posterior end in 96% ethanol (89°0,62' N, 61°26,15' E, PS94/081, September 06, 2015, 0–4300 m) and two complete specimens in 75% ethanol after 4% formalin (82°10,27' N, 60°0,88' E, PS78/188, August 09, 2011, 50–100 m).

Description (based on all our material). Body 1.9–2.7 mm long, with 12–14 segments, yellow or yellow-white; pigmentation absent in preserved specimens. Prostomium with two thin palps (Fig. 8A and B, 9A). Eyes absent, as it was mentioned by Reibisch (1895), Ushakov (1972) and Druzhkov et al. (2000). Large muscular pharynx armored with two gently curved, chitinous jaws (Fig. 8C). First segment without parapodia



**Fig. 6.** *Pelagobia* cf. *longicirrata* (based on specimens ZMMU WS3648 and ZMMU WS3650). A, dorsal view of entire specimen. B, jaws. C, parapodium, frontal view. D, chaeta. Chaetae on the right side of the body are not shown. Abbreviations: ac – acicula, an – antennae, dc – dorsal cirrus, no – nuchal organ, gl – parapodial glands, pc – pygidial cirri, tc – tentacular cirri, vc – ventral cirri.

and cirri; parapodia of segments 2–4 reduced to fascicles of 2–3 thin short compound chaetae (Fig. 8A and B, 9A). Segment two with pair of filiform dorsal cirri (Fig. 8A and B, 9A). Parapodia of all following segments uniramous, conical, with thick acicula and bundle of compound chaetae (Fig. 8D and E, 9 B–C). Chaetae very thin spinigers, with long smooth shaft and long, narrow distal part (Fig. 8D and E, 9 B–C). Dorsal parapodial cirri broadly-rounded, two times shorter than parapodial lobes, ventral parapodial cirri oval, three times shorter than parapodial lobes (Figs. 8D and 9C). Pygidium without appendages, small, slightly bilobed, deeply wedged between the posteriomost parapodia pair (Fig. 8A).

**Reproductive notes.** Body cavity contains numerous large eggs, 120–150 µm in diameter, and gregarine parasites.

**Distribution.** Collected in the deep Nansen and Amundsen Basins of the Arctic Ocean from the depth layer 0–700 m. Type locality is the Irminger Sea (Reibisch, 1895). Other localities: Labrador stream (Reibisch, 1895), the Greenland Sea, East Greenland (Ditlevsen, 1914; Druzhkov et al., 2000), continental slopes and deep-water troughs of the Barents and Kara Seas (Druzhkov et al., 2000), the central Arctic Basin (Ushakov, 1957, 1972; Maurer and Reish, 1984; Druzhkov et al., 2000).

**DNA.** Nuclear 18S, 28S and mitochondrial 16S sequence data of *P. pictus borealis* obtained in this study are available in GenBank under accession numbers given in Table 2.

### 3.3. *Typhloscolecidae* Uljanin, 1878

#### *Typhloscolex* Busch, 1851.

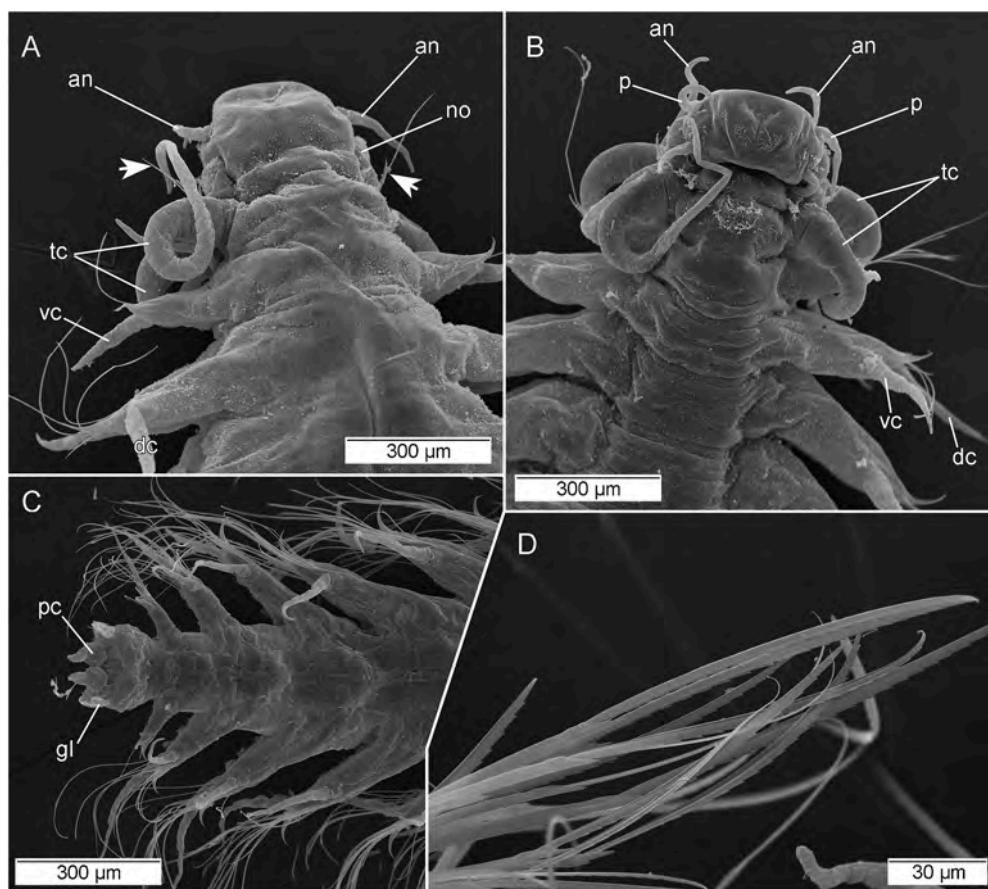
Type species: *Typhloscolex muelleri* Busch, 1851.

**Diagnosis.** Prostomium with a palpodium; nuchal organs as large, ciliated flaps dorsally and ventrally on prostomium, with additional pair of dorso-lateral lobes. Parapodia uniramous, acicular, with two simple stout chaetae; dorsal and ventral cirri large, flattened. Pygidium with two flattened appendages.

#### *Typhloscolex* cf. *muelleri* Busch, 1851.

**Material examined.** Ten complete specimens in 96% ethanol (84°23,00' N, 29°46,50'E, PS94/050, August 27, 2015, 0–500 m) and five complete specimens lacking most of cirri in 75% ethanol after 4% formalin (84°04,63' N, 164°13,43' W, PS78/239, September 06, 2011, 500–1000 m).

**Description** (based on all our material). Body length 2.1–5.1 mm, with 16–25 segments, fusiform, with anterior region relatively wide and posterior region tapered; segments separate indistinctly (Fig. 10A and B). Live worms white or pinky-white, preserved specimens white, without pigment patterns. Prostomium with dorsal and ventral preoral lobes about the same width as body; each lobe with marginal ciliar belts of long thick cilia (Fig. 10A and B, 11 A–B). Dorsal lobe with a pair of large dorsolateral nuchal organs (Figs. 10B and 11A). Prostomium with



**Fig. 7.** *Pelagobia* cf. *longicirrata*, SEM. A, anterior end, dorsal view. B, anterior end, ventral view. C, posterior end, ventral view. D, chaetae. Abbreviations: an – antennae, dc – dorsal cirri of parapodia, gl – glands, no – nuchal organs, p – palps, pc – pygidial cirri, tc – tentacular cirri, vc – ventral cirri of parapodia. Arrows show compound chaetae of tentacular segment.

**Table 5**

Minimum and maximum pairwise genetic distances (%) for investigated specimens of *Pelagobia* cf. *longicirrata* and *Typhloscolex* cf. *muelleri* based on 18S rDNA (alignment length 1199 bp).

Name	Uncorrected	Corrected
<i>P. cf. longicirrata</i> Arctic (Nansen Basin)		
<i>Pelagobia</i> cf. <i>longicirrata</i> Antarctic (Shetland Islands)	0.9	0.9
<i>P. cf. longicirrata</i> Antarctic (Drake Passage)	0.5–0.7	0.5–0.7
<i>P. cf. longicirrata</i> South Atlantic (Angola Basin)	1.7	1.7
<i>T. cf. muelleri</i> Arctic		
<i>Typhloscolex</i> cf. <i>muelleri</i> Pacific (Monterey Bay)	0.1	0.12

a palpodium anteriorly, consisting of cylindrical basal part and a thin distal one (Fig. 10A and B). Proboscis retracted, not observed.

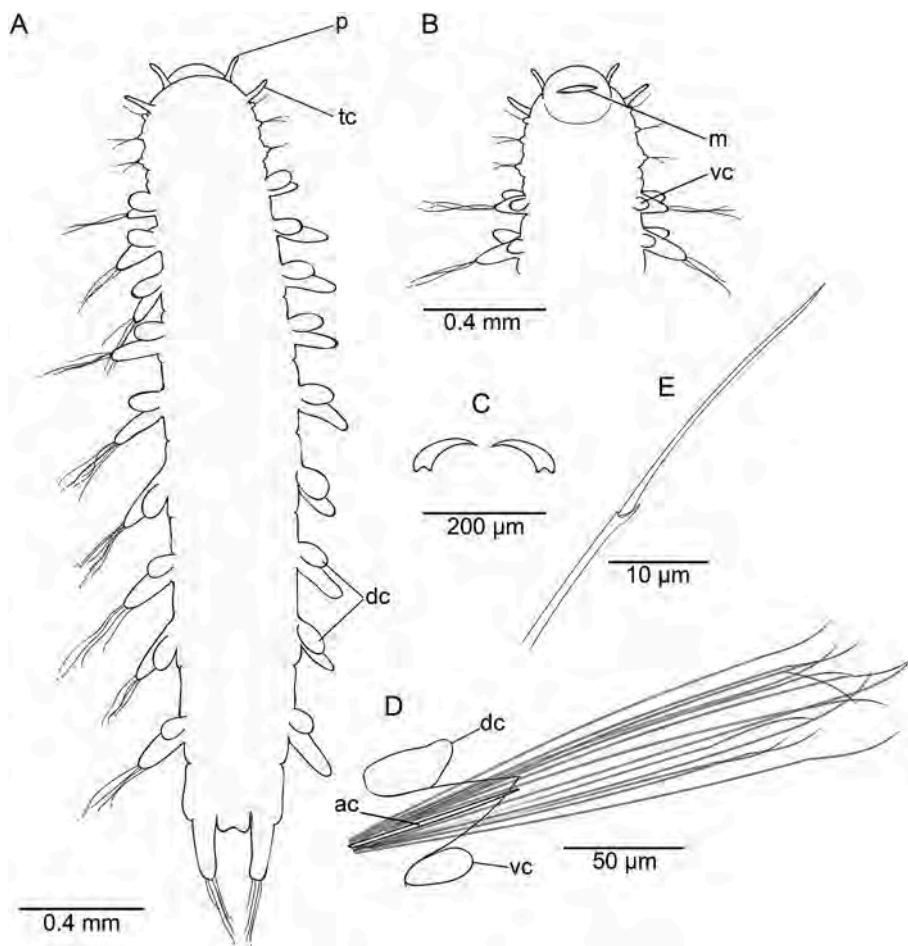
The first three segments lack parapodia and ventral cirri; dorsal cirri enlarged and enfold the prostomium (Fig. 10A and B). All following segments with small, conical, uniramous parapodia, each with two simple recurved capillary chaetae, and one thick acicula, the tip of acicula penetrates epidermis (Fig. 10C). Parapodial cirri modified to large flattened lobes, the external surface of cirri with numerous knob-like glandular clusters (Figs. 10C and 11A). The first three pair of cirri bend anteriorly and cover the head region (Fig. 10A and B, 11 A–B). Dorsal cirri roundish-cordiform in mid-region, oval-shaped in posterior; the largest ones in the second third of the body (Fig. 10A and B, 11 A–B). Ventral cirri smaller, then dorsal, oval-shaped (Fig. 10A and B, 11 A–B). Pygidial cirri narrow, elongated (Figs. 10A and 11 A–B).

Reproductive notes. Specimens 3.5–5.0 mm long with eggs in the

#### body cavity.

**Distribution.** Collected in the deep Nansen and Makarov Basins of the Arctic Ocean from the depth layer 400–500 m. Type locality: Adriatic Sea, Triest (Busch, 1851). Other localities: Mediterranean Sea, Isola d'Elba (Bonifazi et al., 2016), northern Adriatic Sea, the Tyrrhenian Sea, Gulf of Naples (Lo Bianco, 1904), Monaco, Gulf of Marseilles (Peres, 1954), North Atlantic (Stop-Bowitz, 1948), Vancouver Island (Berkeley and Berkeley, 1957, 1964), Gulf of Tehuantepec (Fernández-Álamo, 2004), equatorial Atlantic (Treadwell, 1943), Guinea Basin (Böggemann, 2009), South Atlantic (Treadwell, 1943; Tebble, 1960; Day, 1967), Antarctic waters (Ehlers, 1913; Fauvel, 1936; Stop-Bowitz, 1948; Berkeley and Berkeley, 1957, 1964; Dales, 1962; Tebble, 1958, 1962; Reish, 1968; Ushakov, 1974; Fernández-Álamo, 2004; Fernández-Álamo, 2004; Fernández-Álamo and Sanvicente-Añorve, 2005), Weddell Sea (Augener, 1929), Bellingshausen Sea, west of Alexander I Island (Fauvel, 1936; Treadwell, 1943), southwestern Indian Ocean (Day, 1967), Boca del Guapo and Elefantes Channel (Bilbao et al., 2008), tropical and subtropical Pacific (Treadwell, 1943; Tebble, 1962), Gilbert Islands (Chamberlin, 1919), eastern tropical Pacific (Fernández-Álamo, 2000, 2004), Peru (Berkeley and Berkeley, 1964), Baja California peninsula (Rioja, 1962; Fernández-Álamo, 1996), Gulf of California (Reish, 1968; Fernández-Álamo, 1996), Monterey Bay, California Current (Dales, 1957), subarctic North Pacific (Tebble, 1962), Japan (Imajima and Hartman, 1964), Sea of Okhotsk, Bering Sea, southeastern Kamchatka (Ushakov, 1957; 1972), Barents Sea (Ushakov, 1972), Artic (Maurer and Reish, 1984; Gagayev and Kosobokova, 2012).

**DNA.** The 18S uncorrected pairwise distances between *T. cf. muelleri* from the Arctic and the only available sequence of *Typhloscolex* sp. from the Monterey Bay is 0.1%, the distance corrected by Kimura-2-



**Fig. 8.** *Phalacrophorus pictus borealis* (based on specimens ZMMU WS11169 and ZMMU WS11170). A, dorsal view of entire specimen. B, anterior end, ventral view. C, jaws, dorsal view. D, right parapodium of the 10th segment, frontal view. E, chaeta. Chaetae on the left side of the body are not shown. Abbreviations: ac – acicula, dc – dorsal cirrus, m – mouth, p – palps, tc – tentacular cirri, vc – ventral cirrus.

parameter is 0.12% (Table 5).

The analysis of species-level clusters for the 18S gene retrieved seven (Initial Partition with prior maximal distance  $P = 2.78\text{e-}03$ ) or six (Initial Partition with prior maximal distance  $P = 4.64\text{e-}03$ ) partitions, distance K80 Kimura MinSlope = 1.500000. In the first case, the *Typhloscolex* sp. GU230895.1 from the Monterey Bay forms the separate group from our *Typhloscolex* specimens, due to few of samples available for the analysis. Nuclear 18S and 28S sequence data of *T. cf. muelleri* obtained in this study are available in GenBank under accession numbers given in Table 2.

#### 3.4. Polynoidae Kinberg, 1856

Macellicecephalinae Hartmann-Schröder, 1971.

*Bathypolaria* Levenstein, 1981.

*Austropolaria* Neal, Barnich, Wiklund and Glover, 2012.

Type species: *Bathypolaria carinata* Levenstein, 1981.

**Diagnosis (emended):** Short body, 13–20 segments. Prostomium bilobed. Frontal filaments absent. Eyes absent. Median antenna present, lateral antennae absent. Facial tubercle absent. Tentaculophores without chaetae. Pharynx with two pairs of jaws, small secondary tooth in margin; with seven pairs of pharyngeal papillae. Dorsal tubercles absent. Elytrophores small, up to 9 pairs (on segments 2, 4, 5, 7, 9, 11, 13, 15, and 17). Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae flattened, with spines on convex side, smooth on straight side, stout; notochaetae

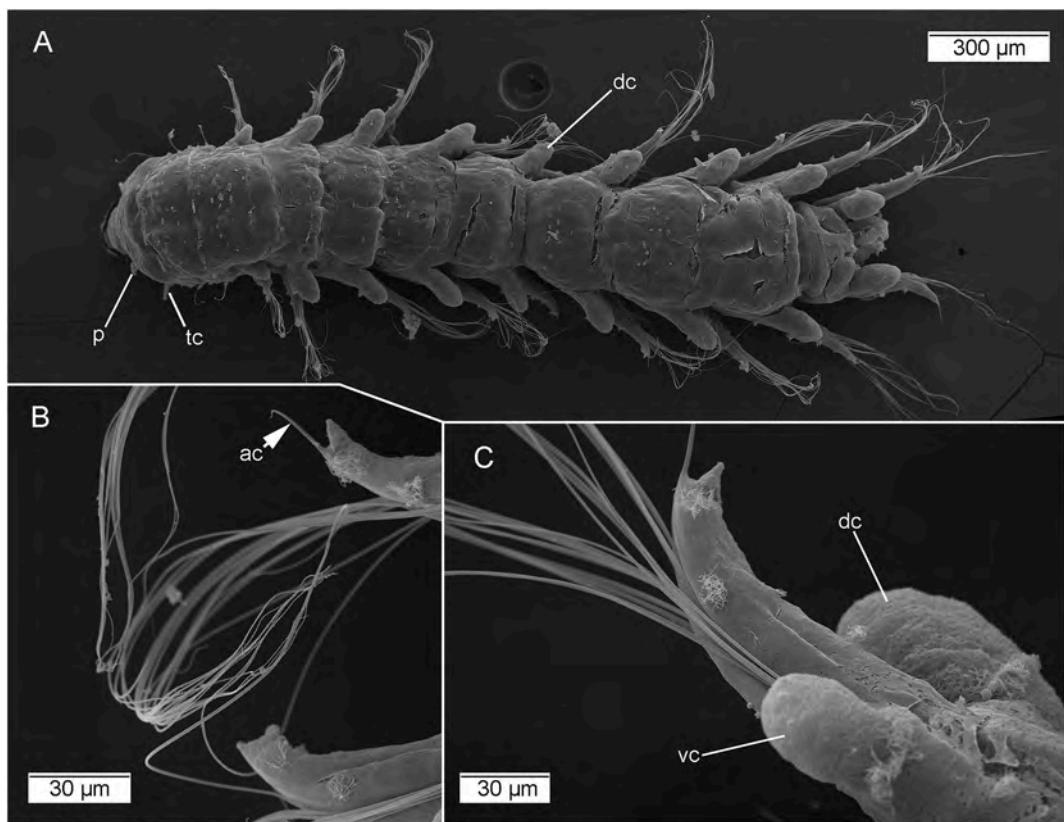
stouter than neurochaetae. Neurochaetae distally flattened to concave, serrated along both margins. From segment 3, ventral cirri inserted subdistally on neuropodia. Pygidium with longitudinal keel that may extend to ventral side of last segments.

**Remarks.** The combined 16S, 18S and COI genes analysis shows that *Austropolaria* should be synonymized with *Bathypolaria* (Bonifácio and Menot, 2019). Based on *A. magnicirrata* description (Neal et al., 2012), and on results of the present study, we extended the range of segments in the diagnosis from 15 to 13–20, and, the number of elytrophores from 7 to 9, respectively. The posterior keel in *B. kondrashovi* sp. nov. is short and does not reach the ventral side of the body.

*Bathypolaria kondrashovi* sp. nov. Kolbasova, 2020.

**Material examined.** Holotype ZMMU WS11184 (86°00'43" N, 55°47'65" E, PS101/183, October 04, 2016, 4400–2800 m) in 75% ethanol after fixation in Bouin's solution. Adult male with 14 segments, body length 6 mm, maximum width 1.2 mm, parapodia 1.3 mm, chaetae 2 mm. Six pairs of elytrophores on segments 2, 4, 5, 7, 9, 11, and 13. All prostomial antennae and parapodial cirri are lost. Nephridial papillae on segments 6–12. On the right body side third parapodium damaged, fourth parapodium absent. All elytra and most dorsal podial cirri are missing. One pair of anal cirriophores, styles missing. Extended pharynx with 9 pairs of papillae. Segments 6–14 are full of sperm.

**Paratypes:** ZMMU WS11183 (86°00'43" N, 55°47'65" E, PS101/183, October 04, 2016, 4400–2800 m) in 75% ethanol after fixation in Bouin's solution, male 3.2 mm long, 1.0 mm wide, pharynx inverted. ZMMU WS11185 (86°00'43" N, 55°47'65" E, PS101/183, October 04, 2016, 4400–2800 m) in 75% ethanol after fixation in Bouin's solution,



**Fig. 9.** *Phalacrophorus pictus borealis*, SEM. A, dorsal view of entire specimen. B, chaetae of the left parapodium of the 6th segment. C, left parapodium of the 6th segment, ventral view. Abbreviations: ac – acicula, dc – dorsal cirrus, p – palps, tc – tentacular cirri, vc – ventral cirrus.

male 8.0 mm long, 2.5 mm wide, pharynx inverted. Both of specimens have sperm in the body cavity and lost elytra and most of dorsal podial cirri. Parapodia 1.0–2.5 mm long, completely lacking chaetae.

Material used for DNA extraction: three anterior fragments of adults specimens in 96% ethanol ZMMU WS3641, ZMMU WS3673 and ZMMU WS4057 (86°00'43'' N, 55°47'65'' E, PS101/183, October 04, 2016, 4000–4830 m).

Other material: 7 complete specimens (one adult female with 14 segments WS11186, adult male with 13 segments WS11187) (86°00'43'' N, 55°47'65'' E, PS101/183, October 04, 2016, 4400–2800 m). Two complete three juveniles and two larvae dried and mounted on aluminium stubs for SEM after the Bouine fixation. One juvenile (84°23'00'' N, 29°46'50'' E, PS94/050–9, August 27, 2015, 3800–3000 m), four adults (86°00'43'' N, 55°47'65'' E, PS101/183, October 04, 2016, 4400–2800 m) in formalin 10%.

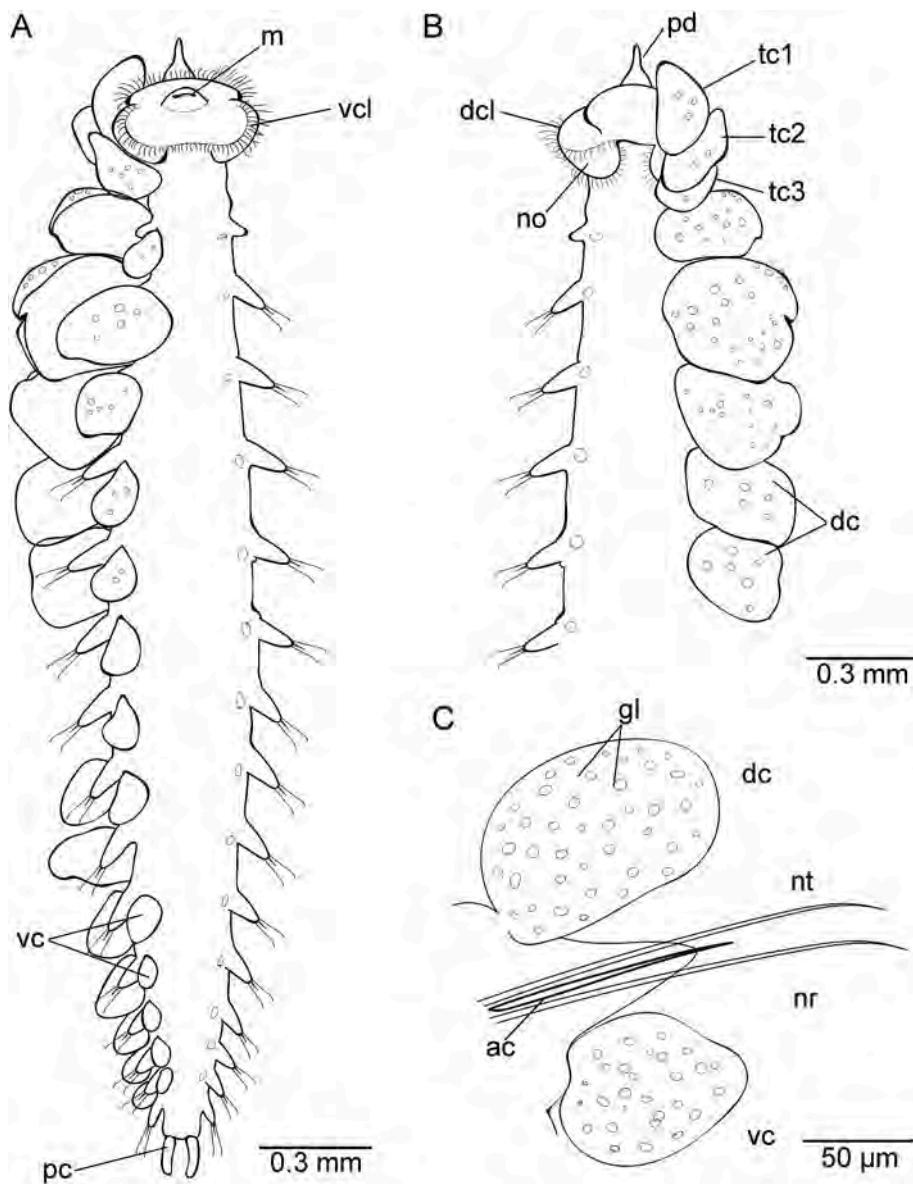
**Diagnosis.** Body with 13–14 (including tentacular) segments. Eyes absent. 7 pairs of pharyngeal papillae, two pairs of jaws. Prostomium bilobed, median antennae present, frontal filaments and lateral antennae absent. Palps smooth, tapered, as long as the body. Two pairs of tentacular cirri. Segment 1 without chaetae. Segment 2 with buccal (ventral) cirri attached to the basal part of parapodia, remaining parapodia with subdistal ventral cirri. Parapodia subbiramous. Notopodia shorter than neuropodia. Notopodia tapering into acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia rectangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Elytrophores on segments 2, 4, 5, 7, 9, 11, and 13. Cirrophores on segments 3, 6, 8, 10, 12, 14. Nephridial papillae imperceptible, round, on segments 6–11. Pygidium between reduced parapodia of the last segment. Anus dorsal. Pygidial keel short, does not reach the ventral side of the last segment.

**Description (based on all our material).** Body short, with up to 14 (including tentacular) segments, 3.2–8.0 mm long, 1.0–2.5 mm wide,

slightly flattened (Fig. 12A–D, 13 A–D). Live and formalin-fixed specimens white, semi-transparent; prostomium, cirrophores, and pygidial keel pink (Fig. 14A and B). Anterior part of the body translucent, making visible protruded red muscular pharynx and dorsal blood vessel. Posterior part of the body often full of yellow (male) or pink (female) gametes. Eyes absent. Prostomium bilobed, wider than long, with deep median notch between prostomial lobes; lobes slightly pronounced, anteriorly rounded, without frontal filaments (Figs. 12A and 15B). Median antenna with small ceratophore attached to middle of prostomium; style tapered, long, smooth, 2–3 times shorter than palps (Figs. 12A and 15B). Tentacular segment fused to prostomium (Figs. 12A and 15B). Two pairs of tentacular cirri, with cylindrical tentaculophores and thin, tapering, smooth styles. Dorsal pair of tentaculophores three times smaller than ventral pair, dorsal tentacular style reaches segment 2, ventral style reaches segment 3 (Fig. 12A). Palps smooth, tapered, long (equal to body length in preserved specimens) (Figs. 12A and 15A).

Lips in a bulbous projection when pharynx not everted, extruded pharynx long, muscular, with seven pairs of conical papillae (Fig. 12B). In fixed specimens two pairs of short, rounded bulbs may present on lateral side of pharynx (Fig. 12B). Two pairs of jaws each one with one main fang, outer margin with a very small pointed or blunt secondary tooth (Fig. 12C).

Seven pairs of small elytrophores on segments 2, 4, 5, 7, 9, 11, and 13. All elytrophores are missing. Four pairs of large cylindrical cirrofore on segments 3, 6, 8, 10, 12, and 14. Parapodia subbiramous, acicular (Figs. 12A and 13 A–B). Notopodia approximately 1.5 times shorter than neuropodia. Both noto- and neuroacicula are not penetrating the epidermis (Fig. 13A and B). Dorsal cirri with cylindrical cirrophores 1/2–1/3 shorter than notopodia; styles are missed (Fig. 15A and B). Neuropodia subretangular, with projecting prechaetal acicular lobe (Fig. 13A). Ventral cirri small, thin, tapering. Segment two with ventral cirri basally inserted, subsequent parapodia with subdistal ventral cirri



**Fig. 10.** *Typhloscolex* cf. *muelleri* (based on specimens ZMMU WS11179–WS11181). A, ventral side of the entire specimen. B, anterior end, dorsal view. C, parapodium, frontal view. Parapodial cirri on the left side of the body are not shown. Abbreviations: ac – acicula, dc – dorsal cirrus, dcl – dorsal ciliar lobe, m – mouth, no – nuchal organ, nr – neurochaetae, nt – notochaetae, gl – glands, pc – pygidial cirri, pd – palpodium, tc – tentacular cirri, vc – ventral cirrus, vcl – ventral ciliar lobe.

(Figs. 13A and 15A). Notochaetae distinctly more stout than neurochaetae, flattened (scalpel-like), as long as neuropodia, numerous, forming fan-shaped bundles, with spines (15–19) on convex side, smooth on straight side, with pointed tips. (Fig. 13C and D).

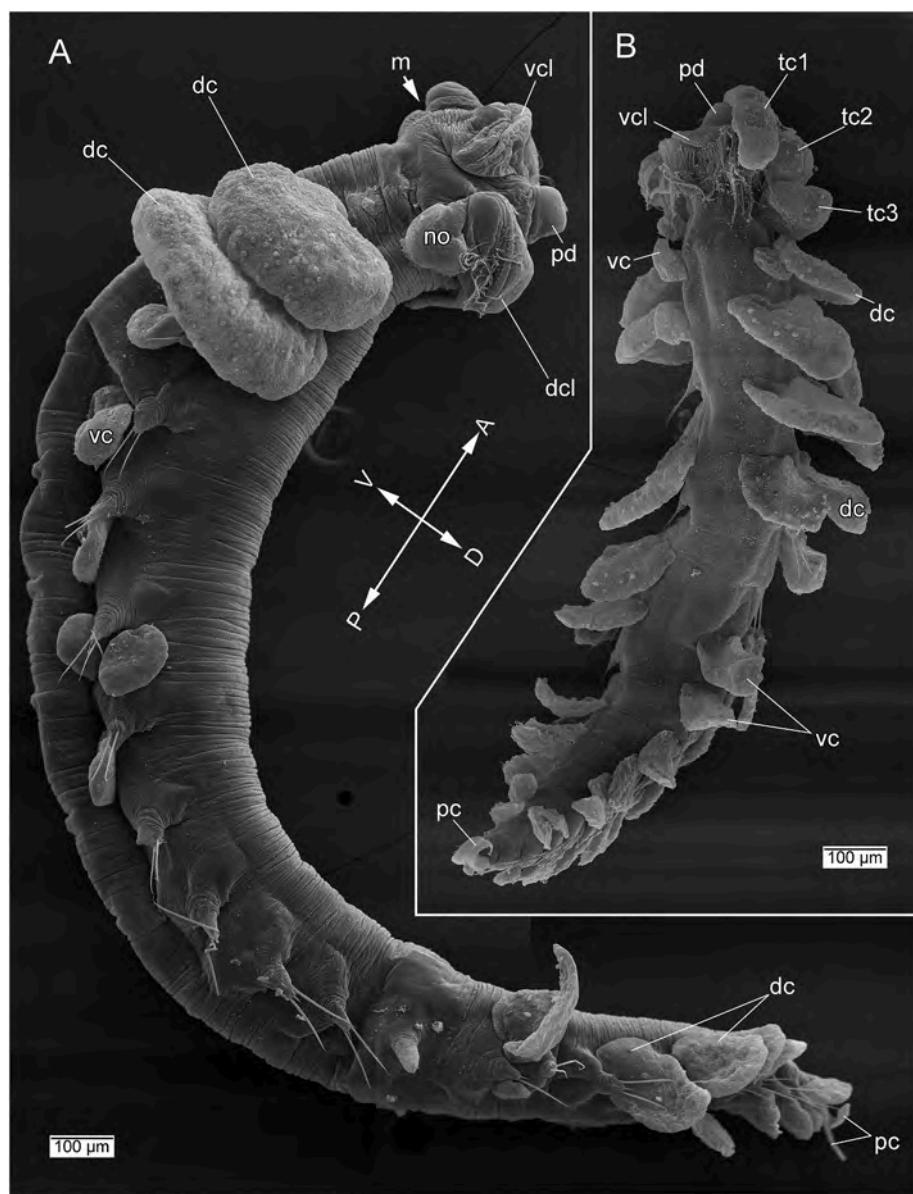
Neurochaetae as long as notochaetae, gently, slender, with distal part flattened and serrated along lateral margins, tip unidentate (Fig. 13A, C). Nephridial papillae poorly visible, on segments 6–11; papillae on 8 and 9 two times larger than other ones. Pygidium keel short, pink, perpendicular to the body axis, does not reach the ventral side of the last segment, wedged between reduced parapodia of the last segment, with pair of anal cirrophores; styles of anal cirri are missed (Figs. 12C and 14 A–B, 15 B). Anus dorsal, with two pink ciliar glands (Fig. 14A).

**Ontogenetic variation.** Late juveniles are 1.5–1.8 mm long; with long palps, antenna and parapodia of adult type, the number of segments is 11, pygidial keel is absent (Fig. 15A). Early juvenile has well differentiated head, with pro- and peristomium, short palps, medial antennae and two pairs of rudimentary tentacular styles (Fig. 17C and D). The body length is 1.5 mm and the specimen still has 10 segments with chaetae

like in adults (Fig. 16A and B, 17E). Larvae are about 800 μm long; a half of the length is the head region, the remaining half is the body trunk (Fig. 17A). The head region of trochophore consists of epi- and hyposphere with mouth and prototroch. The body trunk consists of 10 segments with parapodia, each bearing 1 notopodial chaeta; neuropodial chaetae show only tips (Fig. 16A and B, 17A). Both dorsal and ventral cirri are poorly developed (Fig. 17A).

**Remarks.** The main difference of *Bathypolaria kondrashovi* sp. nov. from other *Bathypolaria* species is a short pygidial keel, that does not reach the last body segment. In *B. carinata*, *Bathypolaria* sp. 173 and *Bathypolaria* sp. 608 ventral keel is present on several last segments (Levenstein, 1982; Bonifácio and Menot, 2019). In *A. magnicirrata* ventral keel also reaches up to 17th body segment (Neal et al., 2012).

The genetic p-distances for 18S and 16S between *B. kondrashovi* sp. nov and *Bathypolaria* sp. 173 are 0.8% and 9.6–10.5%, respectively. The p-distances between *B. kondrashovi* sp. nov and *Bathypolaria* sp. 608 is 0.6% for the 18S, and 3.3–3.7% for the 16S. The p-distances between *B. kondrashovi* sp. nov and *A. magnicirrata* is 0.9% for the 18S, and 9–9.8% for the 16S (Table 6).



**Fig. 11.** *Typhloscolex cf. muelleri*, SEM. A, lateral view of the entire specimen. B, ventral view of the entire specimen. Abbreviations: dc – dorsal cirrus, dcl – dorsal ciliar lobe, m – mouth, no – nuchal organ, pc – pygidial cirri, pd – palpodium, tc – tentacular cirri, vc – ventral cirrus, vcl – ventral ciliar lobe. A – anterior, P – posterior, D – dorsal, V – ventral.

**Etymology.** The species name is given after Professor Alexey Kondrashov (University of Michigan, Department of Ecology and Evolutionary Biology) for his inexhaustible and inspiring contributions to molecular investigations of marine fauna at White Sea Biological Station (Moscow State University).

**Distribution.** Type locality: Amundsen Basin, depth layer 2800–4400 m (bottom depth 4830 m). Other localities: the Nansen Basin, depth layer 3000–3800 m (bottom depth 3929 m).

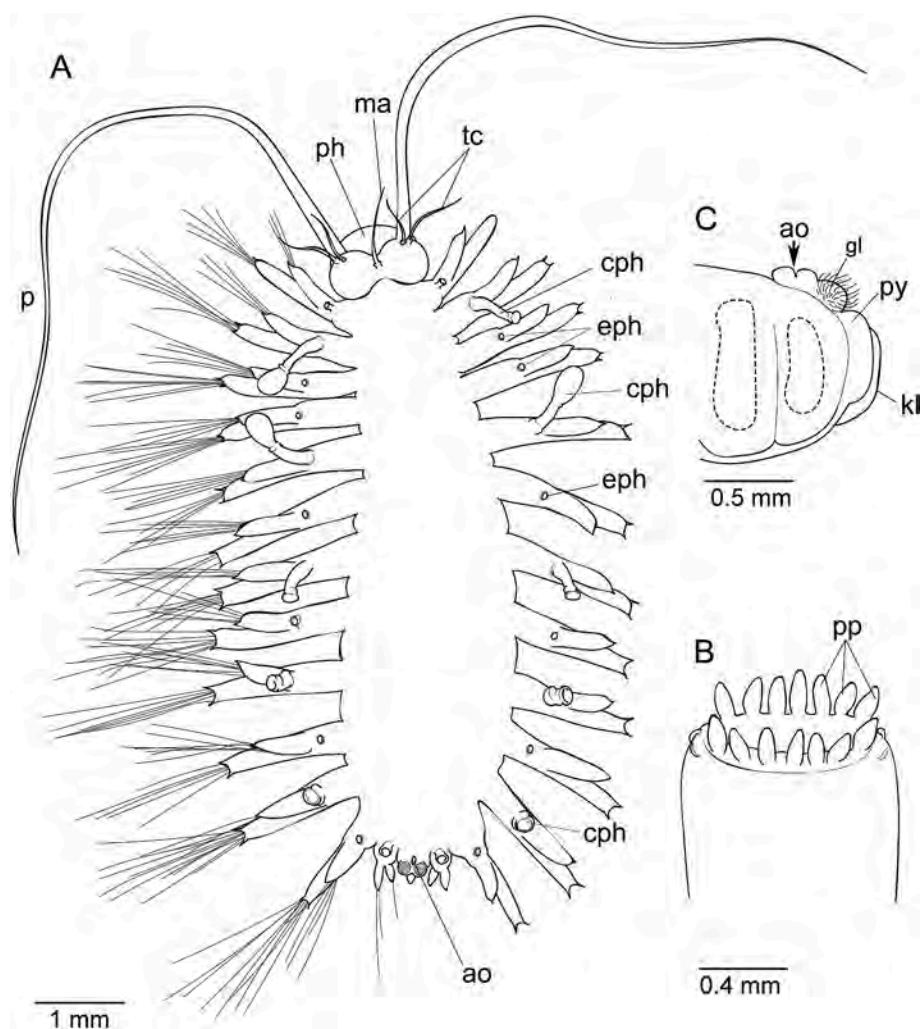
**DNA.** The analysis of species-level clusters for the 18S gene of all available *Bathypolaria* and *A. magnicirrata* samples retrieved four (Initial Partition with prior maximal distance  $P = 4.64e-03$ ) partitions, distance K80 Kimura MinSlope = 1.500000. The first one includes *Bathypolaria* sp. 173 from the Equatorial Pacific (MH233245.1, MH233206.1), the second one includes *Bathypolaria* sp. 608 from the Equatorial Pacific (MH233227.1, MH233228.1, MH233229.1, and MH233241.1). The third partition includes *A. magnicirrata* (JX863895-1), the fourth one includes our specimens of *B. kendirashovi* sp. nov. from the Arctic (MK660183.1 and MK660181.1).

The analysis of species-level clusters for the 18S gene of the same species also retrieved four (Initial Partition with prior maximal distance  $P = 1.67e-03$ ) partitions, distance K80 Kimura MinSlope = 1.500000. The first one includes *Bathypolaria* sp. 173 from the Equatorial Pacific (MH233151.1, MH233154.1, and MH233199.1), the second one includes *Bathypolaria* sp. 608 from the Equatorial Pacific (MH233175.1, MH233176.1, MH233192.1, and MH233193.1). The third partition includes *A. magnicirrata* (JX863896-1), the fourth one includes our specimens of *B. kendirashovi* sp. nov. from the Arctic (MK559881.1 and MK559882.1).

18S and 16S sequence data of *B. kendirashovi* sp. nov. are available in GenBank under accession numbers given in Table 2.

#### 4. Discussion

Pelagic polychaetes represent a common component of zooplankton, but their diversity, taxonomy, and biology are still poorly documented (Dales, 1962; Day, 1967; Dales and Peter, 1972; Ushakov, 1972, 1974; Yingst, 1974a, b; Hartman, 1991; Stöp-Bowitz, 1991, 1992; Halanych



**Fig. 12.** *Bathypolaria kondrashovi* sp. nov. (based on holotype ZMMU WS11184). A, dorsal view of entire specimen. B, extended pharynx, ventral view. C, posterior end, lateral view; parapodia omitted, dorsal and anal cirri missing. Chaetae on the right side of the body are not shown. Abbreviations: ao – anal opening, cph – cirrophore, eph – elytrophore, gl – pygidial ciliary glands, kl – keel, lb – lateral bulb, ma – medial antennae, p – palps, ph – pharynx, pp – pharyngeal papillae, py – pygidium, tc – tentacular cirri.

et al., 2007; Struck and Halanych, 2010). To date, about 140 species from seven holopelagic families (Alciopidae Ehlers, 1864, Lopadorrhynchidae, Iospiidae, Pontodoridae, Tomopteridae Grube, 1850, Typhloscolecidae, Yndolaciidae Stöp-Bowitz, 1987), and 15 holopelagic species from benthic families (Acrocirridae Banse, 1969, Chaetopteridae Audouin and Milne Edwards, 1833 and Flabelligeridae Saint-Joseph, 1894) are known.

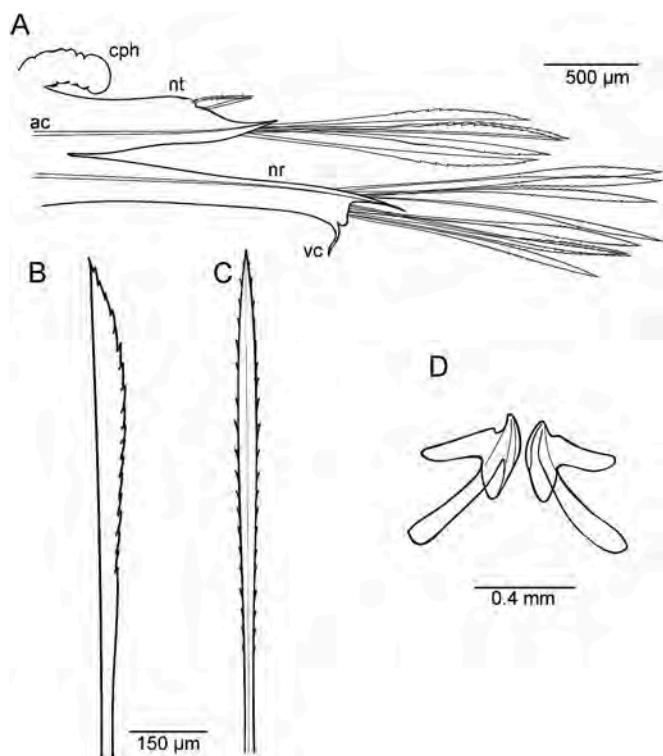
Most holoplanktonic polychaetes are bathypelagic, occurring between 1000 and 3000 m water depth, and rarely gather in large clusters (Ushakov, 1972; Gagaev and Kosobokova, 2012). The standard gears for zooplankton collection and usual methods for zooplankton preservation are intended mostly for pelagic crustaceans, and not suitable for fragile pelagic polychaetes. Without separating sampling and preservation techniques, polychaete specimens collected are in poor condition and cannot be identified by morphological examination. The molecular methods could be used to identify polychaetes in alcohol-preserved zooplankton samples, but DNA sequence reference libraries for barcode gene regions for zooplankton taxa in the Arctic, and for polychaetes in particular, are largely incomplete (Bucklin et al., 2010). It is necessary first to obtain DNA sequences from accurately identified specimens, which can then be used to identify unknown, morphologically unidentifiable or incorrectly identified specimens.

In the present study, we combined morphological examination of pelagic polychaetes from the Arctic Ocean along with molecular analysis for the same specimens and analyzed our results in comparison with morphological descriptions and taxonomic conclusions of other authors, as well as DNA sequences data available from GenBank. Our approach

allowed us to elevate new genus, to describe one new species, and to suggest to reconsider status of three well-known species, till now considered as cosmopolitan (noted from the Arctic, Antarctic, Pacific and Atlantic).

The new genus described here, *Bathypelagobia* gen. nov. was initially described as *Pedinosoma* species (Buzhinskaja, 2017). *Bathypelagobia* gen. nov. and *Pedinosoma* belong to the holopelagic family Lopadorrhynchidae and have typical lopadorrhynchid external appearance. Compared to representatives of other holopelagic polychaetes families, often having long appendages, large eyes or bright coloration, Lopadorrhynchidae are small and imperceptible. Most of Lopadorrhynchidae genera were described in the XIX century and currently five of them are valid: *Lopadorrhynchus*, *Maupasia*, *Nans*, *Pedinosoma* and *Pelagobia*. Four other genera, *Hydrophanes*, *Mastigethus*, *Halyplaniella* and *Halyplanes*, are now synonymized with *Lopadorrhynchys* (*Hydrophanes* and *Mastigethus*) and *Maupasia* (*Halyplaniella* and *Halyplanes*). The main characters, used for the genus separation include the shape of prostomium and peristomium, the number of tentacular segments and tentacular cirri, and the presence or absence of eyes, jaws and simple chaetae.

*Lopadorrhynchus* is a biggest genus of the family, it includes ten species with non-fused prostomium and peristomium, three pairs of tentacular cirri on two segments, and simple chaetae in anterior in parapodia. *Maupasia* includes six of five species, which are also characterized by three pairs of tentacular cirri on two segments, but have prostomium fused with peristomium. Simple chaetae may be present in some *Maupasia* species. The genus *Nans* stands out among all Lopadorrhynchidae genera. It is a monotypic genus, containing one species

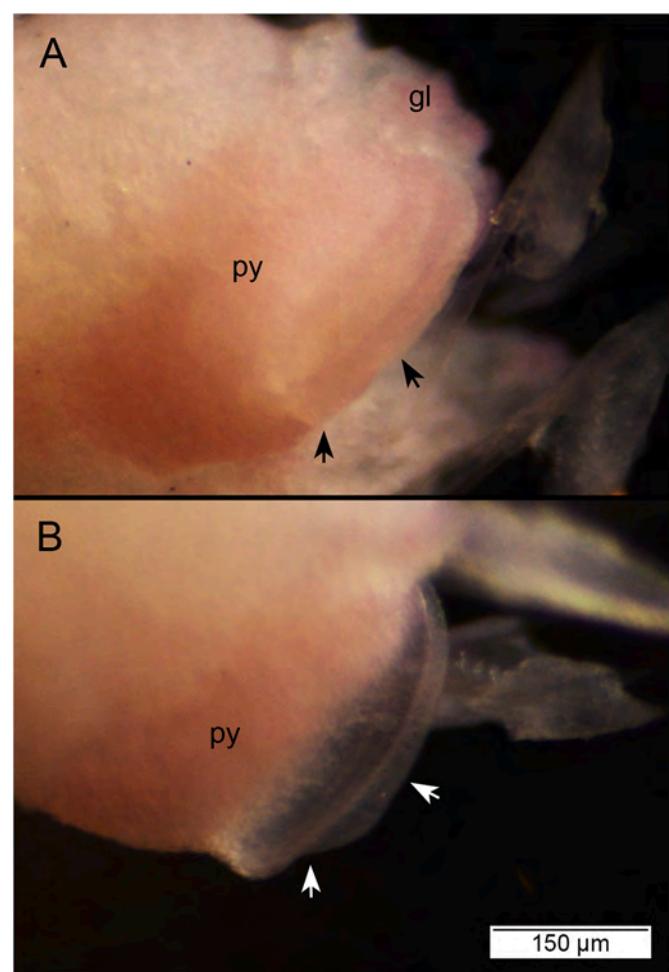


**Fig. 13.** *Bathypolaria kondrashovi* sp. nov. A, parapodia of segment 6 (specimen ZMMU WS3641), frontal view, cirrus missing. B, notochaetae in frontal view (paratype ZMMU WS11186). C, neurochaetae in frontal view (paratype ZMMU WS11186). D, inner view of half side of dissected jaws of non-type specimen ZMMU WS11186. Abbreviations: ac – acicula, cph – cirrophore, nt – notopodium, nr – neuropodium, vc – ventral cirrus.

*N. simplex* Chamberlin, 1919, having prostomium and peristomium non-fused, two pairs of tentacular cirri on one segment, biramous parapodia with two aciculae and simple chaetae. Such a shape of parapodia are unusual for Lopadorrhynchidae, and it will be very interesting to clarify phylogenetic relationships between *Nans* and other polychaetes families using molecular methods.

*Pedinosoma* and *Pelagobia* have two pairs of tentacular cirri on one segment and the only compound chaetae. The type species of *Pedinosoma* is *P. curtum* Reibisch, 1895. It was described from the Atlantic Ocean (Reibisch, 1895), and some variability between specimens from different localities is present (Tebble, 1962; Day, 1967; Ushakov, 1972; Buzhinskaja, 2017). For example, in the original description, the antennae and palps are equal in length and cirrophores are present (Reibisch, 1895), whereas specimens from the North-West Pacific also have cirrophores, but their antennae are longer than palps (Buzhinskaja, 2017). Specimens from North-East Pacific have no cirrophores and have antennae shorter than the palps (Bergström, 1914; Tebble, 1958, 1962; Day, 1967). The number of segments in *P. curtum* is nine-twelve (Reibisch, 1895; Tebble, 1962; Day, 1967; Ushakov, 1972; Buzhinskaja, 2017).

Originally *Bathypelagobia polaris* gen. nov. comb. nov. was described as a late larva of *P. polaris* (Buzhinskaja, 2017). The main reasons to place these worms to *Pedinosoma* were few number of segments and prostomium fused with peristomium (Buzhinskaja, 2017). Jaws and serrated chaetal blades were not detected during the original description, whereas the presence of chaetae on tentacular segment and first pair of parapodia lacking dorsal cirri were considered as juvenile characters and to be unimportant (Buzhinskaja, 2017). At the first glance, *Bathypelagobia* gen. nov. looks similar with *Pedinosoma*, mainly because of the short, thick body, but by the combination of key characters it is closer to *Pelagobia* (Ushakov, 1972; Fauchald, 1977; Dales, 1957).



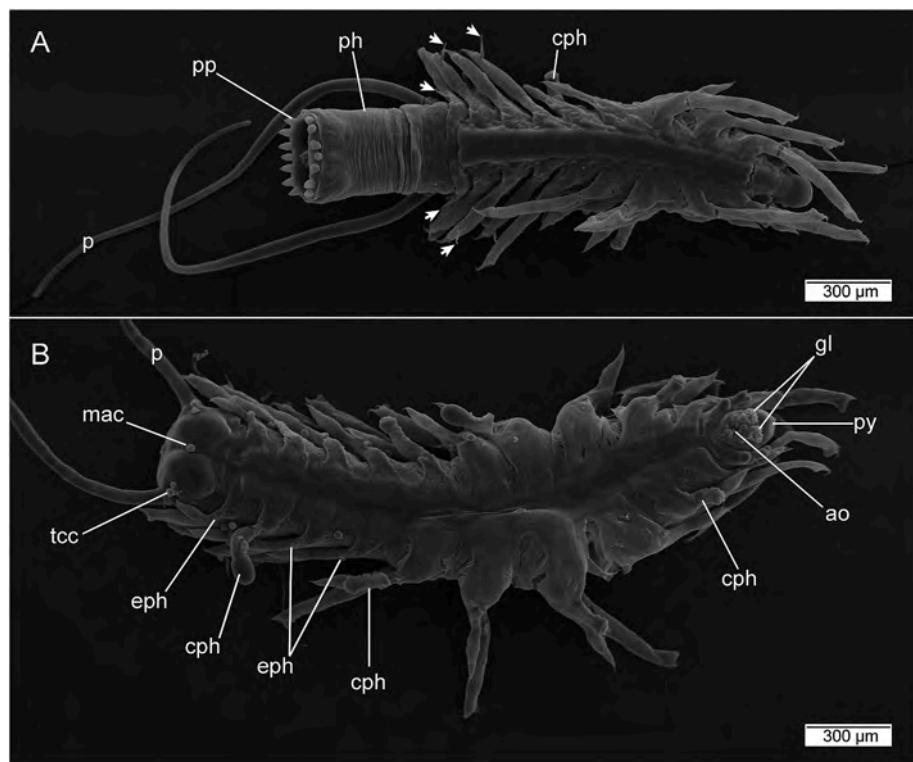
**Fig. 14.** *Bathypolaria kondrashovi* sp. nov. (ZMMU WS11186). A, posterior end, dorsolateral view. B, posterior end, lateral view. Abbreviations: gl – glands, py – pygidium. Arrows show the pygidial keel.

Specimens from our samples have gametes within the body cavity, and their morphological characters are not juvenile. Therefore, we believe the amendment to the *Pedinosoma* diagnosis by Buzhinskaja (2017) is unjustified.

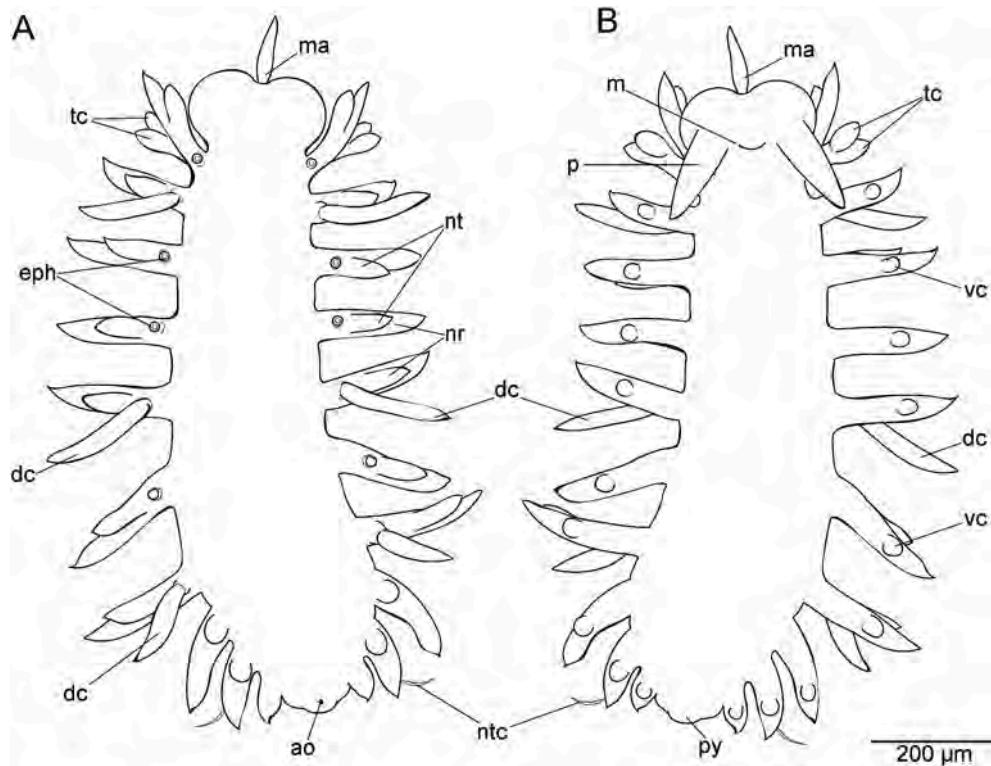
At present, the genus *Pelagobia* includes two valid species, *P. serrata* Southern, 1990 and *P. longicirrata*. By some features *Bathypelagobia* gen. nov. resembles a figure of the anterior part of *P. serrata* (Southern, 1909). The former was described from Ireland (Southern, 1909; Read and Fauchald, 2018), and currently has unclear status (Tebble, 1960). Except for the original description, there is no other data on occurrence or morphology of *P. serrata*, and the holotype in the Natural History Museum, London, is in poor condition, making re-examination of the species morphology almost impossible (Dr. A.N. Isaychev, pers. comm.). Unfortunately, number of segments for *P. serrata* was not noted in the species description. We infer that *P. serrata* may be closer to *Bathypelagobia* gen. nov. than to *Pelagobia*, but representative material for both species is needed to better clarify the relationship among *P. cf. longicirrata*, *P. serrata* and *Bathypelagobia* gen. nov.

The genetic distances between *Bathypelagobia* gen. nov. and *Pelagobia* are large, the p-distances between *Bathypelagobia* gen. nov and *Pelagobia* cf. *longicirrata* from different localities are 5.1–8.2% for the 18S gene, 24.6% for the 16S gene, and 8.7–8.8% for the 28S gene (Table 4). The molecular data, as well as morphological features, indicate that the former belongs to a new genus within the family Lopadorrhynchidae (Fig. 5).

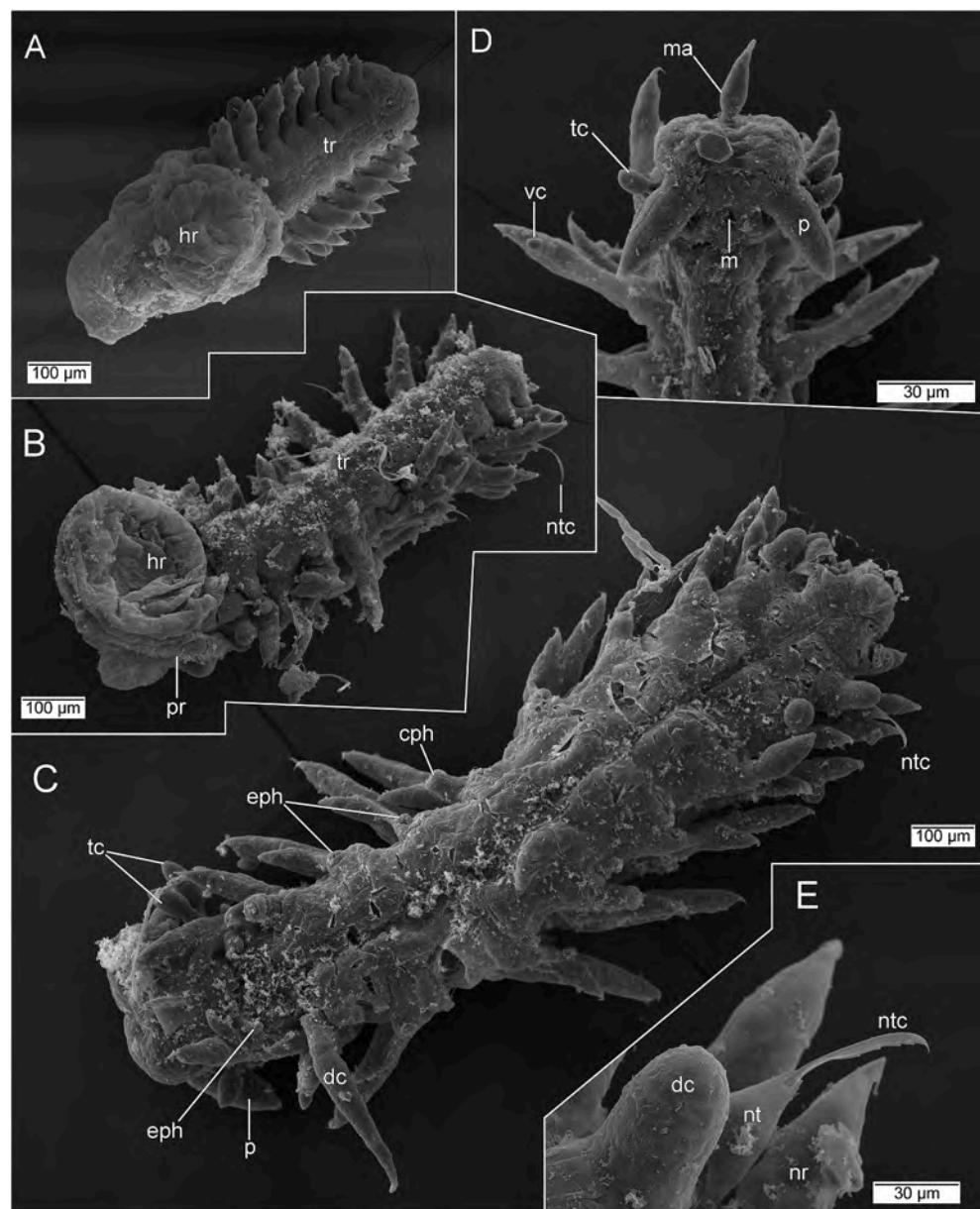
*Pelagobia longicirrata* was described from Canary Islands (Greiff,



**Fig. 15.** *Bathypolaria kondrashovi* sp. nov. juvenile, SEM. A, ventral view. B, dorsal view. Abbreviations: ao – anal opening, cph – cirrophore, eph – elytrophore, mac – cirrophore of the medial antenna, gl – ciliary glands, tcc – cirrophore of tentacular cirrus, p – palps, ph – pharynx, pp – pharyngeal papillae, py – pygidium. Arrows show ventral neuropodial cirri.



**Fig. 16.** *Bathypolaria kondrashovi* sp. nov. juvenile. A, dorsal view of entire specimen. B, ventral view of entire specimen. Abbreviations: ao – anal opening, dc – dorsal cirri, eph – elytrophore, ma – medial antennae, nr – neuropodia, nt – notopodia, ntc – notopodial chaetae, p – palps, tc – tentacular cirri, vc – ventral cirri.



**Fig. 17.** *Bathypolaria kondrashovi* sp. nov. developmental stages, SEM. A, trochophore, ventral view. B, metatrochophore, ventral view. C, early juvenile, dorsal view. D, early juvenile, anterior end, ventral view. E, early juvenile parapodium, dorsal view. Abbreviations: cph – cirrophore, dc – dorsal cirrus, eph – elytrophore, hr – head region, m – mouth, ma – medial antenna, nt – notopodium, ntc – notochaetae, nr – neuropodium, tr – body trunk, p – palp, pr – prototroch, tc – tentacular cirri, vc – ventral cirrus of parapodia.

**Table 6**

Minimum and maximum pairwise genetic distances (%) for *Bathypolaria kondrashovi* sp. nov. based on nuclear 18S rDNA (alignment length 1810 bp) and mitochondrial 16S rDNA (404 bp).

Name	Uncorrected	Corrected
<i>Bathypolaria kondrashovi</i> sp. nov.		
18S		
<i>Bathypolaria</i> sp. 173	0.8	0.8
<i>Bathypolaria</i> sp. 608	0.6	0.6
<i>Austropolaria magnicirrata</i>	0.9	0.9
16S		
<i>Bathypolaria</i> sp. 173	9.6	10.5
<i>Bathypolaria</i> sp. 608	3.3–3.6	3.4–3.7
<i>A. magnicirrata</i>	9	9.8

1879) and is currently considered cosmopolitan. Two other *Pelagobia* species, *P. viguieri* (Gravier, 1911) from Antarctic and *P. erinensis* (Nolte, 1938) from North Atlantic are currently not considered valid.

Description of *P. erinensis* based on larval and juvenile stages is incomplete, whereas description of *P. viguieri* does not show the novelty of the described species. Therefore, both of them were synonymized with *P. longicirrata* (Gravier, 1911; Augener, 1929; Nolte, 1938; Dales, 1957; Dales and Peter, 1972).

It must be emphasized that descriptions of *P. longicirrata* from different localities vary considerably (Gravier, 1911; Benham, 1921; Augener, 1929; Yingst, 1974a; Hartmann-Schröeder and Rosenfeldt, 1992; Wilson, 2000; Böggemann, 2009; Nygren and Pleijel, 2011; Isaychev et al., 2013; Isaychev, 2015). Thus, Friedrich (1949), Ushakov (1972) and Sarda et al. (2009) described pharyngeal jaws in *P. longicirrata*, while Stöp-Bowitz (1992) does not mention jaws, and Yingst (1974a) and Böggemann (2009) stated the absence of jaws. Benham (1921), Hartmann-Schröeder and Rosenfeldt (1992), Böggemann (2009) and Isaychev et al. (2013, 2015) noted chitinous acicular structures within the tentacular cirri, which were not mentioned in the original description by Greeff (1879). Body size and number of segments also vary in descriptions of specimens from different ocean regions, with up to 12 mm body length and up to 30

segments in the Antarctic specimens (Fauvel, 1916; Böggemann, 2009; Ushakov, 1972) in contrast to 4–5 mm body length and 12–16 segments for specimens from the tropics (Bergström, 1914; Fauvel, 1916).

The morphological examination of our *P. cf. longicirrata* from the Arctic Ocean corresponds well to the original description by Greeff (1879) and later descriptions by Friedrich (1949), Dales (1957) and Ushakov (1972). The only exception is the absence of third pair of tentacular cirri, mentioned by Greeff for type specimens (Greeff, 1879), but such tentacular cirri were never noted by other researchers. At the same time, acicular-like structures in cirri of the first segment, described for *P. cf. longicirrata* from South Atlantic (Böggemann, 2009) and Antarctic (Hartmann-Schröder and Rosenfeldt, 1992; Isaychev et al., 2013), are absent in our specimens, while jaws are present, in contrast to the description by Yingst (1974a).

Genetically, *P. cf. longicirrata* was not recovered as monophyletic (Fig. 5). The p-distance for 18S between *P. cf. longicirrata* from the South Atlantic and *Pelagobia* from the Arctic and Antarctic is 1.7% that compared with inter-species distances (Table 5). This, as well as the presence of acicular structures in tentacular cirri, allow us to consider the Böggemann's *Pelagobia* a separate species. Our specimens from the Arctic form a well-supported clade inside the *Pelagobia*, whereas *Pelagobia* cf. *longicirrata* specimens from the Antarctic (Isaychev et al., 2013) occurs inside the *Pelagobia* but show genetic variability, which may indicate either genetic polymorphism of this group, or the presence of a species complex. In the 18S tree it shows possible four different species, currently assigned to *P. cf. longicirrata* (Fig. 5). Additional investigations and revision of *Pelagobia* may lead to re-description of antarctic *P. viguieri* or description of a new species (Isaychev et al., 2013).

The status of *Typhloscolex* cf. *muelleri* seems to be similar, but data available is not sufficient to declare it as a species complex. According to Tebble (1962) "*Typhloscolex muelleri* is a cosmopolitan species that has been reported from all explored water masses". Initially, *T. muelleri* was described from Mediterranean, and later recorded both in the Pacific and Atlantic Oceans, from the tropic zone to polar waters (Greeff, 1879; Chamberlin, 1919; Augener, 1929; Fauvel, 1936; Friedrich, 1949; Tebble, 1960; Dales, 1957; Dales and Peter, 1972; Ushakov, 1972; Maurer and Reish, 1984; Pleijel and Dales, 1991; Fernández-Álamo, 1991; Fernández-Álamo and Thuesen, 1999; Wilson, 2000; Fernández-Álamo and Sanvicente-Añorve, 2005; Bilbao et al., 2008; Böggemann, 2009; Struck and Halanych, 2010). Morphological characters used for *Typhloscolex* species identification include the shape of prostomium, ciliar lobes and nuchal organs that may depend on fixation of specimens (Ushakov, 1972). Thus, Tebble (1960) and Dales and Peter (1972) have suggested *T. leuckarti* Reibisch, 1895, *T. phylloides* Reibisch, 1895, *T. reibisci* Friedrich, 1950, and *T. robusta* Friedrich, 1950 to be variations of *T. muelleri*, but molecular investigations of these species are necessary to clarify their status. To the existing knowledge on *T. muelleri* we may add that our *T. muelleri* specimens from the deep Arctic basins are morphologically similar to the original description by Busch (1851) and to subsequent descriptions by Reibisch (1895) and Ushakov (1972). Genetically, however, they form a sister clade to *Typhloscolex* sp. from the Monterey Bay (Struck and Halanych, 2010). The genetic distance between these species for the 18S rDNA gene corresponds to inter-species distance (1.7%) that allows us to suppose two different species (Table 5). Our results once again raise a question regarding status of *Typhloscolex* cf. *muelleri* and true diversity of the genus *Typhloscolex*, but these questions are challenging to answer without additional molecular studies.

The genus *Phalacrophorus* currently includes two valid species, *P. pictus* Greeff, 1879 and *P. uniformis* Reibisch, 1895. *Phalacrophorus niger* (Treadwell, 1943) was moved to genus *Iosipilus* and accepted as the synonym of *I. phalacroides* Viguer, 1886 (Dales and Peter, 1972). *Phalacrophorus attenuatus* (Treadwell, 1943) and *P. maculatus* (Treadwell, 1943) were synonymised with *P. uniformis* and *P. pictus*, respectively (Dales, 1957; Dales and Peter, 1972). According to Dales, Treadwell's *P. maculatus*, collected during the Carnegie expedition in Ecuador is

"certainly conspecific with *P. pictus*" having type locality in Canary Islands, whereas type specimen of *P. attenuatus* collected from Marshall Islands "is identical with *P. uniformis*", having type locality in tropical Atlantic (Dales, 1957).

*Phalacrophorus borealis* is also invalidated; Dales (1957) supposed it "may well be merely a young *P. pictus*" and Tebble (1962) considered the absence of eyes in *P. borealis* as not significant and that *P. pictus* and *P. borealis* are synonyms. At present, the species name *P. borealis* is not valid, but some researchers believe *P. borealis* is either a separate species or a geographically isolated *P. pictus* subspecies (Ushakov, 1972; Druzhkov et al., 2000; Jirkov, 2001). Specimens of *Phalacrophorus* from our material fit well to the *P. borealis* type description by Reibisch (1895) and differ from the *P. pictus* description by smaller body size, less pronounced pigmentation and absence of eyes (Reibisch, 1895; Greeff, 1879). A noteworthy feature is the presence of gametes in their body cavity, which was also noted by Reibisch for his specimens (Reibisch, 1895). For this reason, it seems unlikely Reibisch's and our specimens to be a *P. pictus* juvenile form. The presence or absence of eyes also seems to be important morphological character, as well as more northern distribution of *P. borealis* compared to *P. pictus* (Reibisch, 1895; Tebble, 1960, Ushakov, 1972; Druzhkov et al., 2000; Bilbao et al., 2008). *P. borealis* was originally described from Greenland, and was later described from the Arctic Basin, Kara and Barents Seas, East Greenland and Labrador stream, whereas *P. pictus* is abundant in the North Atlantic and North Pacific, and has not been recorded north of the Norwegian and Barents Seas (Reibisch, 1895; Tebble, 1960; Ushakov, 1972; Druzhkov et al., 2000). According to the original description by Greeff (1879), *P. pictus* has sharply curved jaws, eyes with lenses, 20–30 segments and yellow-brown pigmentation (Greeff, 1879; Tebble, 1960; Ushakov, 1972; Druzhkov et al., 2000). In all our specimens we note slightly curved jaws, less than 20 segments and no eyes. The pigmentation pattern, with brown-yellow spots in the base of each parapodia, which gave the species name of *P. pictus* (Greeff, 1879) is also absent in our specimens. All live worms are uniform yellowish-white and white in the preservation. Taking into account differences in morphology between our specimens and *P. pictus*, as well as differences in their geographical distributions, we agree with Ushakov (1972) and Druzhkov et al. (2000) and conclude that *P. borealis* should be re-instated as a valid species. Given the current problems of cryptic biodiversity, the underestimation of morphological characters such as absence of eyes, pigmentation, or body shape may be of importance, but in all cases, the genetic analysis of specimens from the different geographic populations is needed to clarify the *P. borealis* validity.

Amongst the holopelagic species, noted above, *Bathypolaria kondrashovi* sp. nov. takes a special place. Polynoidae are mostly benthic worms, however some pelagic species are known, such as *Drieschia pelagica* Michaelsen, 1892, *Natopolynoe kensmithi* Pettibone, 1985b and *Podarmus ploa* Chamberlin, 1919 (Pettibone, 1966, 1985b; Gonzalez et al., 2018). The deep-water species *Bathytrichia filamentosa* (Moore, 1910), *Bathyfauvelia affinis* (Fauvel, 1914), *Hesperonoe complanata* (Johnson, 1901), are possible bathypelagic (Muus, 1953; Pettibone, 1966, 1976, 1985a, b, 1989, 1993; Hartmann-Schröder, 1974), but some of them occur in the trawl material (Levenstein, 1971, 1975; 1978, 1982; Schüller and Ebbe, 2007; Neal et al., 2018; Bonifácio and Menot, 2019). Perhaps, they exhibit semi-pelagic lifestyle, or can rise up by swimming, as was described for the benthic *Bylgides sarsi* (Kinberg in Malmgren, 1866) (Sarvala, 1971; Pettibone, 1993). Some other deep-water polynoids, *Lepidasthenia grimaldii* (Marenzeller, 1892) and *Lagisca hubrechti* (McIntosh, 1900), are benthic, but have young bathypelagic stage (Stop-Bowitz, 1948).

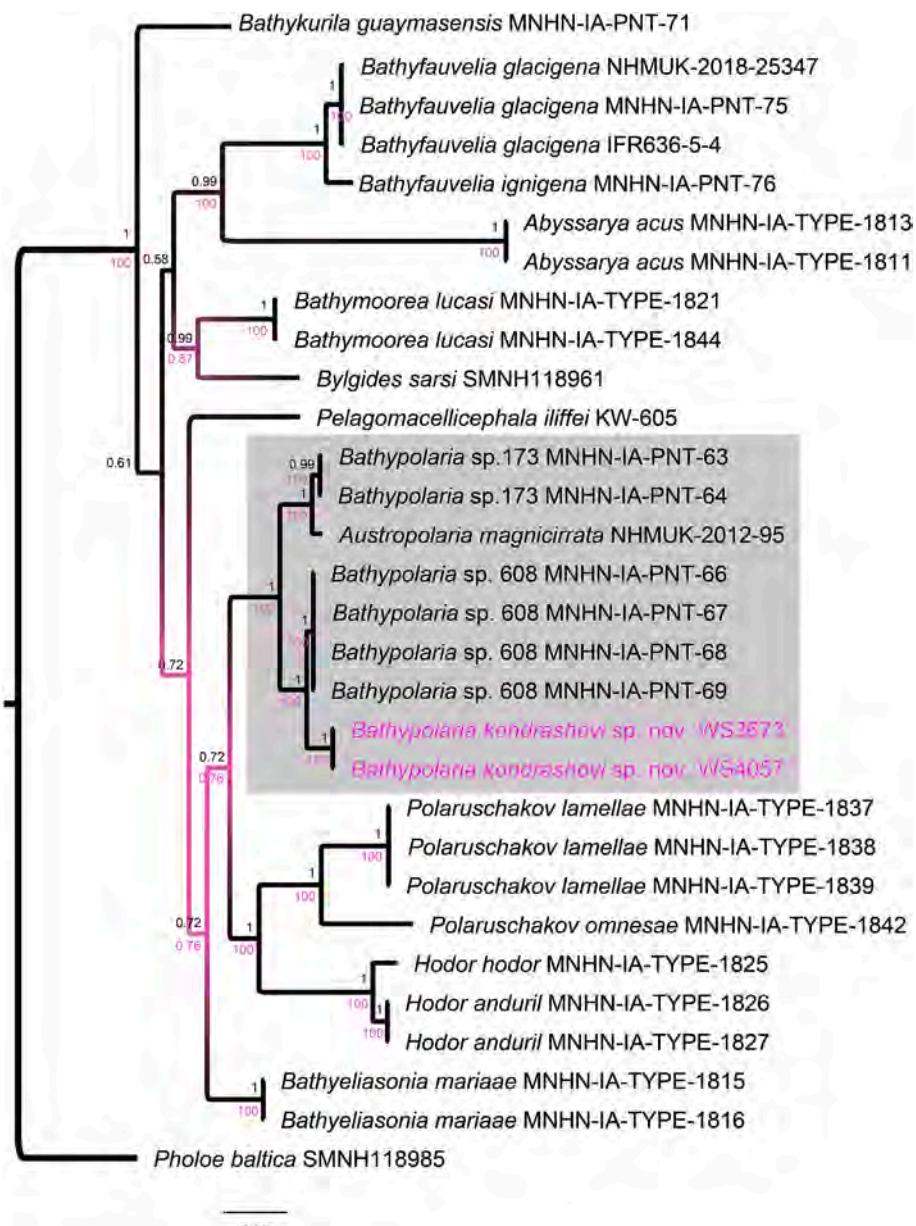
All *B. kondrashovi* sp. nov. specimens examined in the present study were sampled in the water column, from depths 430–1000 m above the seabed. Mature adults, juveniles and larvae of different developmental stages occurred together in the same samples. It may mean that these worms spend significant time in the pelagic, at least during the spawning and larval development period (August–October, according to

our material). This inference is supported by our record of an unusual larvae of *B. kondrashovi* sp. nov. which has a large spherical head region, measuring up to 2 mm in diameter, and a rudiment of the adult body with 10 segments (Fig. 17A and B). A similar type of giant larva with a combination of larval and adult features has been described earlier for the Phyllodocidae (Tzetlin, 1998). Such an unusual pattern of development of the adult body may be an adaptation for a long pelagic life and a rapid settlement (Tzetlin, 1998).

Morphologically, *Bathypolaria kondrashovi* sp. nov. is very similar with the descriptions of *B. carinata* (Levenstein, 1982), and with two *Bathypolaria* species from the abyssal Equatorial Pacific (Bonifácio and Menot, 2019), except for the shape of pygidial keel and the number of segments. The 15 body segments was considered a genus character of *Bathypolaria* (Levenstein, 1982), and three from five currently known *Bathypolaria* species have 15 body segments (Levenstein, 1982; Bonifácio and Menot, 2019). In our samples mature specimens both with 13 and 14 segments are present, thus, we suppose the number of

segments may slightly vary with the specimen's age. The type material of *B. carinata* is unfortunately lost, but we examined additional material of R.Y. Levenstein from the type locality (trawl samples from the expedition of the Russian drifting station North Pole-22, 1976–1977, stored at IORAS). In these samples, there are specimens with 13, 14 and 15 segments. As this material is formalin-preserved and is in a poor condition, both further morphological and molecular-genetics analyses are challenging.

Genetically, *B. kondrashovi* sp. nov. is close to *Austropolaria magnicirrata* and two undescribed *Bathypolaria* species from the abyssal Equatorial Pacific (Fig. 18). In a combined 18S and 16S genes analysis it forms separate clade inside the *Bathypolaria-Austropolaria* group with robust support (Fig. 18). The phylogeny for combined 18S and 16S genes places *A. magnicirrata* inside the *Bathypolaria* clade (Fig. 18). The same grouping based on combined 16S, 18S and COI genes analysis was shown by Bonifácio and Menot (2019). As their study was focused on the evaluation of the monophyly of Macellicephalinae and inter-subfamily



**Fig. 18.** Bayesian (BI) phylogenetic tree based on the concatenated 18S and 16S genes dataset representing relationships between *Bathypolaria kondrashovi* sp. nov. and other Macellicephalinae members (sequences from GenBank), black numbers above branches indicate posterior probabilities from BI, purple numbers below—bootstrap values from ML. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

relationships, they did not make statement about the position of *Austropolaria* (Bonifácio and Menot, 2019). However, according to results of Bonifácio and Menot (2019), and the result of the present investigation, *Austropolaria* should be synonymized with *Bathypolaria*. Based on data Neal et al. (2012), Bonifácio and Menot (2019) and on our data, we emended the diagnosis of *Bathypolaria*, that originally stated 15 body segments, and elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, and 17 (Levenstein, 1982; Bonifácio and Menot, 2019). *Austropolaria magnicirrata* has up to 20 (18–20) segments and elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, and 17 (Neal et al., 2012), whereas *B. kondrashovi* sp. nov. has 13–15 segments and elytrophores on segments 2, 4, 5, 7, 9, 11, 13, and 15. Thus, we extended the range of segments and elytrophores in the diagnosis (13–20 segments, and, 8 or 9 elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, and 17). The shape of the posterior keel, that gave the name of the type species, *B. carinata*, (from latin “carina” meaning “keel”) also differs in the new species. In *B. kondrashovi* sp. nov. posterior keel is very short, it is present only on the pygidium and does not reach the ventral side of the posteriomost segment, whereas in *B. carinata*, *B. sp. 173*, *B. sp. 608*, and *A. magnicirrata* it is present on the ventral side of three last segments of the body.

## 5. Conclusions

We examined five polychaetes species from families Polynoidae, Lopadorrhynchidae, Typhloscolecidae and Iospiidae collected in the deep basins of the Arctic Ocean. Polynoidae is one of the three largest polychaetes families, and the number of polynoid species increases every year (Read and Fauchald, 2020). Here we described one more new pelagic (or semi-pelagic) polynoid species, *Bathypolaria kondrashovi* sp. nov. Based on results of our molecular examinations and recent data from Bonifácio and Menot (2019), we also emended the diagnosis of genus *Bathypolaria* that turned to have wider range of morphological characters than it was considered previously (Levenstein, 1982).

Holopelagic polychaetes families, even taken together, are not as species rich as Polynoidae, but their true diversity seems to be higher than we currently believe. Based on morphological and molecular data, we elevate a new genus of Lopadorrhynchidae, *Bathypelagobia* gen. nov. with a re-description of *Pedinosoma polaris* (Buzhinskaja, 2017). Our morphological and molecular results also raised questions regarding status of three well-known holopelagic species, the lopadorrhynchid *Pelagobia cf. longicirrata*, the typhloscolecid *Typhloscolex cf. muelleri* and the iospidid *Phalacrophorus pictus*, till now considered cosmopolitan. We believe, none of them is cosmopolitan, but represents species complexes. True diversity of these three genera cannot be assessed without examination of samples from type localities. As type material is lost, newly collected topotypes should be carefully compared with the original descriptions and also sequenced (Nygren, 2014; Nygren and Pleijel, 2011). Thus, further comparative molecular studies on material from different regions of the world are required to clarify their taxonomic status.

## Funding

The ship time during the PS101 expedition was funded by AWI Grant No. AWI\_PS101\_01. This study was performed in the framework of the state assignment of IO RAS (theme No. 0149–2019–0008), and partially supported by Russian Science Foundation grant № 16–14–10173 and by Russian Foundation for Basic Research grants 18–05–60158, 19–04–00501 and 19–04–00955.

## Ethical approval

This article does not contain any studies with animals performed by any of the authors.

## Sampling and field studies

All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

## Data availability

All data generated or analyzed during this study are included in this published article.

## Declaration of competing interest

The authors declare that they have no conflict of interest.

## Acknowledgements

We would like to thank Captain S. Schwarze, his crew of the RV “Polarstern” and the chief scientists Dr. Ursula Schauer and Dr. Antje Boetius for their efforts and support during PS78, PS94 and PS101 expeditions; Drs. Nicole Hildebrandt, Barbara Niehoff and Hans-Jürgen Hirche (AWI) for their contribution to organization and implementation of the zooplankton sampling during these expeditions. We acknowledge support of Scientific Committee on Oceanic Research (SCOR) and its Working Group 157 MetaZooGene. Thanks to Dr. Ann Bucklin (University of California at Berkeley) and Dr. Dieter Fiege (Senckenberg Research Institute and Natural History Museum Frankfurt) for their helpful comments during the manuscript preparation; Dr. Ilya Artukhov and Dr. Alexandra Stupnikova ([Shirshov Institute of Oceanology](#)) for the aid with molecular data analysis, and George N. Davidovich and Anatoly G. Bogdanov (Laboratory of Electron Microscopy, MSU) for the technical support.

Finally, we would sincerely thank Msc. Lenka Neal (*Department of Life Sciences, Natural History Museum, London*), Dr. Paulo Bonifácio (*Pat Hutchings's Lab, Australian Museum Research Institute, Sydney*) and Dr. Tina Molodtsova ([Shirshov Institute of Oceanology](#)) for their inestimable help and advices during our work.

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