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Phylogenetic analyses elucidate the identity and distribution of two early-described species of Arctic Cirratulidae (Annelida, Sedentaria)

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Abstract. Recent expeditions to the North-East Atlantic and the Arctic Ocean yielded an abundance of specimens resembling two species of polychaetes of the family Cirratulidae Ryckholt, 1851 originally described in 1879 and tentatively placed within the genus *Cirratulus* Lamarck, 1818. In this study, we set out to confirm their identity, assess the potential presence of cryptic species, determine their correct generic placement, and gain insights into their distributions. Our approach involved comprehensive analyses using four molecular markers (COI, 16S, 28S, and 18S) through Bayesian inference, maximum likelihood analyses, and haplotype networks. Additionally, we conducted detailed morphological examinations of the specimens using both light and electron microscopy techniques. Notably, this study provides the first DNA sequences for a species within the genus *Chaetocirratulus* Blake, 2018. By integrating molecular phylogenetic analyses with morphological assessments, we establish the revised taxonomic placements of these two species as *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov. and *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov. Phylogenetic analyses also recover a close relationship between *Chaetocirratulus*, *Cirratulus* and *Cirriformia*. Furthermore, our research reveals the wide distribution of these species in the North-East Atlantic and Arctic waters, marking the first report of *Chaetocirratulus* in this region. We present re-descriptions of these species according to contemporary taxonomic standards, complemented by extensive illustrations. A lectotype is selected for *Chaetocirratulus abranchiatus* and a neotype is selected for *Aphelochaeta abyssorum*.

Keywords. Deep-sea, North-East Atlantic, polychaetes, barcoding, museum.

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Introduction

The exploration of marine biodiversity in the North Atlantic has a long history, and a large number of polychaete species were described from the area in the early period of zoological studies in the 18th and 19th centuries (Oug *et al.* 2014). However, the species descriptions and illustrations of these early described species were often general and superficial with limited information about morphological details, and still today identity and status of some of these species remain unclear.

During the Norwegian North-Atlantic Expedition (1876–78), two species of Cirratulidae Ryckholt, 1851 were described from the continental shelf slope in the Norwegian Sea (Hansen 1879, 1882). These species were placed in the genus *Cirratulus* Lamarck, 1818, albeit tentatively in one case: *Cirratulus abyssorum* Hansen, 1879 and *Cirratulus* (?) *abranchiatus* Hansen, 1879. When specimens matching the original descriptions were collected in large numbers not only from close to the type localities for the two species but also widely across the North-East Atlantic and the Arctic, it became possible to review them in depth. Indeed, in light of the modern classifications with the family Cirratulidae, the generic placement of these species had to be revised. In addition, cryptic and pseudo-cryptic diversity is frequent in annelids (Nygren 2014), and the presence of species complexes in the North-Eat Atlantic is well documented (Nygren *et al.* 2018; Grosse *et al.* 2020; Teixeira *et al.* 2023). DNA analyses such as phylogenetic analyses and haplotype network are useful tools in that regard as they allow to investigate relationships between species, specimens and their distributions (Nygren *et al.* 2018).

In this paper, we (i) provide updated descriptions and illustrations for both species; (ii) test for the presence of cryptic species by investigating whether one or several species were present at the type locality then more globally; (iii) confirm the generic placement of each species.

Material and methods

Study area and cruises

This study includes material from the Nordic Seas (Greenland-Iceland-Norwegian Seas, Oug *et al.* 2017) as well as from the Denmark Strait and the Arctic Ocean. The IceAGE project, 2011–2013 (Brix *et al.* 2014) has provided specimens from the Denmark Strait and the Norwegian Sea, and the Expeditions PS106/1 and 2 of the R/V *POLARSTERN* in 2017 (Macke & Flores 2018) has provided specimens from the Arctic Ocean. These specimens are kept at the Senckenberg Museum Frankfurt (SMF). The MAREANO project (https://www.mareano.no/en) has provided specimens from the Arctic Ocean, the Fram Strait, the Barents Sea and the Norwegian Sea. The Hausgarten project (Soltwedel *et al.* 2005) has provided specimens from the Fram Fram Strait. Specimens from a series of cruises with R/V "*Håkon Mosby*", University of Bergen, headed by Torleiv Brattegard, between 1981 to 1987, have also been included. These specimens as well as type material of *Cirratulus abyssorum* are kept at the University Museum of Bergen (ZMBN). Due to the mounting system, several specimens used for SEM could not be recovered and are referred to in the paper by their DNA code. For these specimens, a high-resolution picture is available from the BOLD database and serves as a digital voucher. All specimen data is included in Supp. file 1. Maps were created with QGIS ver. 3.22.4 (http://qgis.osgeo.org).

DNA sequencing

Most specimens were processed at Tjärnö Marine Laboratory for DNA sequencing according to the following protocol. A few tentacles and/or branchiae, parapodia, middle or posterior segments were

taken for molecular analyses. Tissues were placed in 50 µL of QuickExtract (Lucigen) and incubated at 65°C for one to five hours followed by 95°C for five minutes. PCR mixes contained 10 µL of RedTaq 1.1x MasterMix 2.0 mM MgCl2 (VWR), 0.30 µL of each primer and 1.4 µL of DNA template for a final reaction volume of 12 µL. COI was amplified using the primer pair jgLCO/jgHCO (Geller *et al.* 2013) or polyLCO/polyHCO (Carr *et al.* 2011), 16S was amplified using the primer pair 16Sarl/16SbrH (Palumbi *et al.* 1996), the D1-D2 region of 28S was amplified using the primer pair 28SC1/28SD2 (Le *et al.* 1993) and 18S was amplified using the primer pairs 18S1F/18S1R and 18S2F/18S2R (Medlin *et al.* 1998; Nygren & Sundberg 2003). PCR protocols are available in Supp. file 2. PCR products were run on a 1% agarose gel to check reaction success. Successful PCR products were purified and sequenced on both strands by Eurofins Genomics (Germany). Forward and reverse reads were merged into consensus sequences using Geneious Pro ver. 5.4.6 (https://geneious.com). Three specimens were processed at the University of Bergen for DNA sequencing according to the following protocol: DNA was extracted as above. PCR reactions contained 2.5 µL CoralLoad buffer (QIAGEN), 1 µL MgCl (QIAGEN, 25 mM), 2 µL dNTP (TaKaRa, 2.5 mM of each dNTP), 1 µL of each of the primers, 0.15 mL TaKaRa HS Taq, 1 or 2 µL DNA extraction and ddH2O to a total reaction volume of 25 µL. COI was amplified using the primer pair LCO1490/HCO2198 (Folmer 1994). 28S was amplified using the primer pair 28F5/Po28R4 (Passamaneck *et al.* 2004; Struck *et al.* 2006). PCR products were checked on a 1% agarose gel. Successful PCR products were prepared with BigDye ver. 3.1 (Life Technologies) and run on an Automatic Sequencer 3730XL at the sequencing facility of the Department of Biological Sciences, University of Bergen. Tissues of two specimens were sent to the Canadian Centre for DNA Barcoding (CCDB) at Guelph. DNA extraction, amplification and sequencing was performed following protocols and procedures of the BOLD system with the primers polyLCO/polyHCO (Ratnasingham & Hebert 2007).

Phylogenetic analyses

Eight different datasets were assembled (Supp. file 3). Three single gene datasets combined sequences of *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov. and *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov. with additional sequences of other Cirratulidae for inference of gene trees for COI, 28S and 18S. Two COI datasets were assembled for haplotype networks containing all sequences each of *Chaetocirratulus abranchiatus* and *Aphelochaeta abyssorum* only. One 16S dataset was assembled containing only sequences of *A. abyssorum* for inference of a haplotype network. No 16S sequence of *C. abranchiatus* could be obtained. One concatenated dataset was assembled from the COI, 28S and 18S alignments containing all available sequences for maximum likelihood inference (ML). A second concatenated dataset for Bayesian inference (BI) was created by removing some duplicate sequences and specimens for which only one marker was available from the concatenated dataset, when it was possible to do so without removing any taxa (Table 1).

Additional sequences of Cirratulidae were selected to represent the diversity of the family and to test the generic placement of the target species. Sequences were either downloaded from GenBank or sequenced for this study. Sequences from GenBank (*Raricirrus jennae* Magalhães, Linse & Wiklund, 2017, *Chaetozone barentsensis* Grosse, Capa & Bakken, 2021 and *Cirriformia tentaculata* (Montagu, 1808) were selected as they were produced recently and there is good knowledge of their morphology. The specimens sequenced for this study were carefully examined with light microscopy and sometimes scanning electron microscopy to confirm their generic placement.

COI sequences were aligned using MUSCLE (Edgard 2004) implemented in Aliview ver. 1.25 (Larson 2014). 16S, 28S and 18S sequences were aligned using MAFFT 7 online version (Katoh *et al.* 2017). Alignments were concatenated in Geneious Pro ver. 5.4.6.

Table 1. Specimens included in the Bayesian analysis with GenBank accession numbers. Sequences obtained for this study are underlined.

Species	Voucher number	GenBank Accession Numbers		
		COI	28S	18S
Chaetocirratulus abranchiatus	ZMBN136914	PV356806	PV356801	–
Chaetocirratulus abranchiatus	ZMBN162354	PV278000	PV277996	–
Chaetocirratulus abranchiatus	MGCIR487-22	PV216403	–	PV174042
Chaetocirratulus abranchiatus	SMF32846	PV216354	PV217053	PV174037
Chaetocirratulus abranchiatus	SMF32847	PV216335	PV217034	PV174033
Chaetocirratulus abranchiatus	SMF32803	PV216408	PV217098	–
Cirriformia tentaculata	NTNUVM74559	MT065953	MT365644	PV174032
Cirratulus cirratus	NTNUVM74558	MT065952	MT365643	PV174041
Cirratulus cirratus	NTNUVM72311	MT065951	MT365642	–
Aphelochaeta spB	ZMBN138604	PV074765	PV074798	PV081143
Aphelochaeta spN	NTNUVM76400	PV074775	PV074809	PV081144
Aphelochaeta abyssorum	SMF32853	PV216366	PV217063	–
Aphelochaeta abyssorum	MGCIR516-22	PV216404	PV217095	–
Aphelochaeta abyssorum	MGCIR309-22	PV216331	PV217027	PV174030
Aphelochaeta abyssorum	SMF32849	PV216334	PV217033	–
Aphelochaeta abyssorum	SMF32810	PV216391	PV217084	–
Aphelochaeta abyssorum	SMF32816	PV216382	PV217076	–
Aphelochaeta abyssorum	SMF32856	PV216357	PV217055	–
Tharyx killariensis	NTNUVM76398	PV216363	PV217061	PV174038
Tharyx robustus	ZMBN162358	PV216336	–	PV174034
Tharyx robustus	ZMBN162337	PV074783	PV074814	–
Caulleriella sp18	ZMBN162338	PV074764	PV074797	–
Caulleriella sp18	ZMBN162339	PV074784	–	–
Caulleriella sp43	MGCIR619-22	PV074771	PV074806	–
Caulleriella jormungandri	MGCIR678-22	PV074770	PV074803	–
Caulleriella jormungandri	SMF32880	PV074777	PV074810	–
Caulleriella jormungandri	SMF32878	PV074789	PV074820	–
Chaetozone quinta	SMF32890	PV074776	PV130174	PV081145
Chaetozone barentsensis	NTNUVM74493	MT066007	PV217028	PV174031
Chaetozone sp14	ZMBN129603	MT065937	MT365628	PV174036
Dodecaceria concharum	NTNUVM76405	PV074790	PV130175	PV081147
Raricirrus beryli	SMF32995	PV074786	–	–
Raricirrus beryli	NTNUVM76390	PV216377	–	PV174040
Raricirrus beryli	SMF32996	–	PV074817	–
Raricirrus jennae	NHMUK-2017-105	MF414724	–	–
Diplocirrus glaucus	ZMBN162345	PV074779	PV074812	–
Pherusa plumosa	ZMBN162347	PV074769	PV074802	PV174035

ML analyses were performed with IQ-TREE 2 (Minh *et al.* 2020) using ModelFinder for model selection (Kalyaanamoorthy *et al.* 2017) with 10 000 ultrafast bootstraps (BS) (Hoang *et al.* 2018). For the concatenated datasets, the TESTMERGE option was used, and partitions were allowed to have different speeds. BI analysis was performed in BEAST ver. 2.7.3 (Bouckaert *et al.* 2019) using the StarBEAST ver. 3 package (Douglas *et al.* 2022). Taxon sets followed species names. Substitution models were set following the results of ModelFinder in IQ-TREE 2, choosing the best model compatible with BEAUti: substitution model for COI and 28S was GTR model with four Γ category counts and empirical base frequencies; substitution model for 18S was TN93 model with four Γ category counts and equal base frequencies. A relaxed clock was used for the species tree. A Birth-Death model was used as species-tree prior. All other priors were left as default. Chain length was of 100 000 000 and sampled every 50 000. Convergence was visualised in Tracer ver. 1.7 (Rambaut *et al.* 2018) and a maximum clade credibility tree was created in TreeAnnotator ver. 2.7.3 (Bouckaert *et al.* 2019). ML and BI analyses were run on CIPRES Science Gateway (Miller *et al.* 2010).

Trees were visualised on Interactive Tree of Life (iTOL) ver. 6.7 (Leutunic & Bork 2021).

Haplotypes networks based on COI sequences for *Chaetocirratulus abranchiatus* comb. nov. and COI and 16S sequences for *Aphelochaeta abyssorum* comb. nov. were created and visualised in PopART (Leigh & Bryant 2015) using the TCS approach (Clement *et al.* 2002).

Abbreviations

br1 = first branchia
br2 = second branchia
ch1 = first chaetiger
ch2 = second chaetiger
dCr = dorsal crest
dT = dorsal tentacle
mo = mouth
nuO = nuchal organ
per = peristomium
pr = prostomium
pyg = pygidium
vR = ventral ridge

N.N.H.E = Norske Nordhavs-expedition (Norwegian North Atlantic expedition)

Morphological observations

All specimens were examined with a Leica M165 C or M125 stereo microscope and photographed with a Canon EOS 5D Mark II camera equipped with a 65 mm macro lens. Detailed pictures were taken with the camera mounted on the stereo microscope. Stacks of images were assembled with Zerene Stacker ver. 1.04 (https://www.zerenesystems.com). Some specimens were stained with a solution of methylene blue to reveal potential staining patterns and/or a Shirlastain A to increase contrast. Parapodia of some specimens were mounted on slides in glycerol, observed with an Olympus BX51 microscope equipped with DIC and photographed with a Canon EOS 600D Camera. Two specimens were examined and imaged with a HITACHI S-3400N scanning electron microscope. Four specimens were examined and imaged with a Zeiss SUPRA 55VP scanning electron microscope. Specimens were first dehydrated in a series of baths from pure ethanol to pure HMDS, air dried, and then sputter-coated with gold or gold/palladium. Line drawings were made by hand. Images and plates were edited with Gimp ver. 2.10.30 (https://www.gimp.org) and Inkscape ver. 1.2.1 (https://www.inkscape.org).

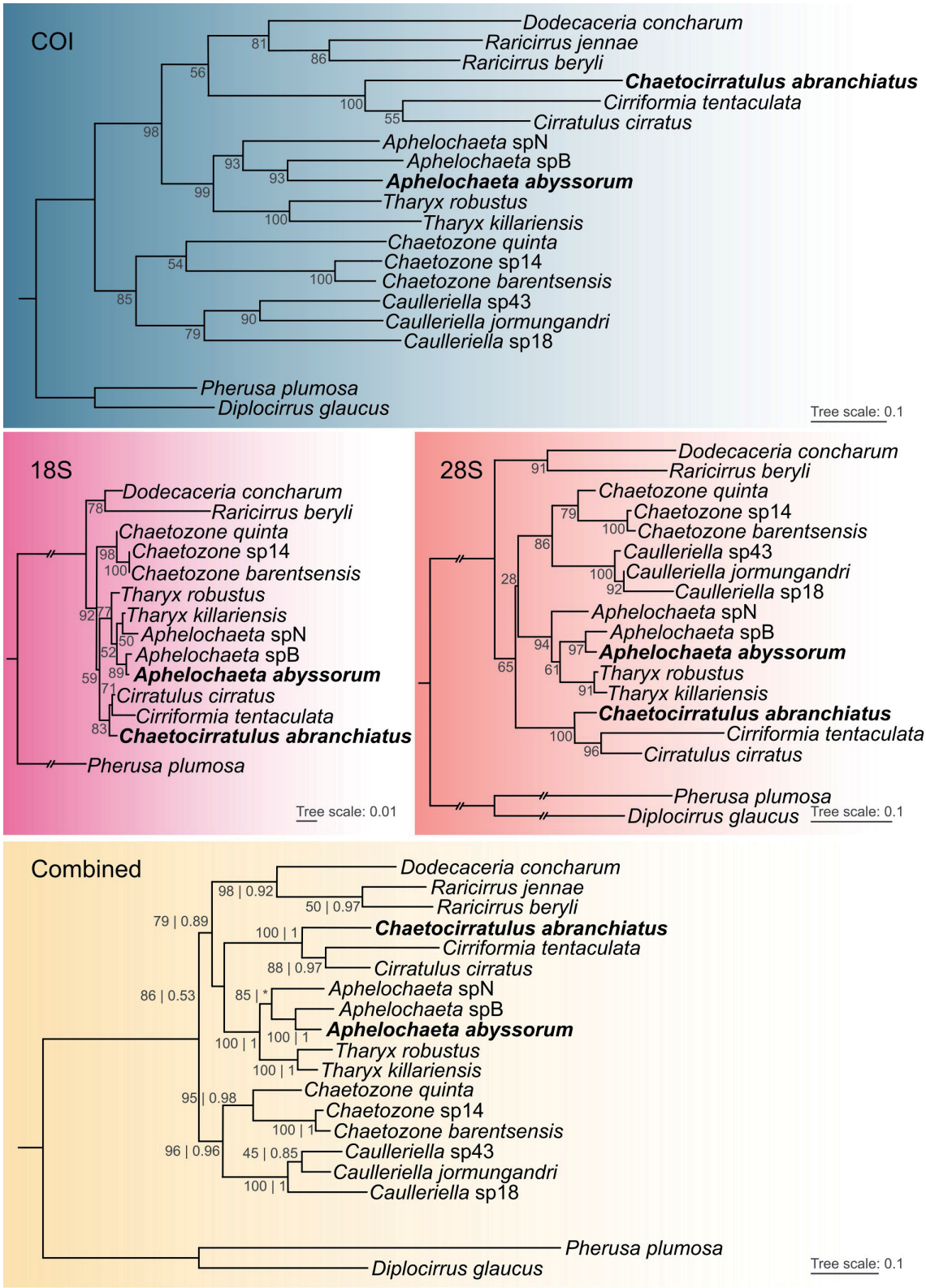

Fig. 1. Phylogenetic trees. The three gene trees and the species tree based on the combined dataset are the result of ML analysis. Bootstrap values (BS) are indicated under or above branches. On the combined tree, posterior probability values (PP) from BI analysis are indicated under or above branches. * indicates a clade that was not recovered in the BI analysis.

Results

Phylogeny

A total of 17 species in nine genera (excluding outgroup) were included in the phylogenetic analyses. The concatenated matrix for the ML analyses consisted of 2615 positions with 885 variable and 616 parsimony informative sites. All trees are available in Supp. file 4.

The first sequences for a species of *Chaetocirratulus* Blake, 2018 were obtained for this study (COI, 28S and 18S). *Chaetocirratulus abranchiatus* comb. nov. is consistently recovered as a single species and sister taxa to a clade formed by *Cirratulus cirratus* (O.F. Müller, 1776) and *Cirriformia tentaculata* both in the gene trees and the combined analyses (BS 100; PP 1) (Fig. 1). *Aphelochaeta abyssorum* comb. nov. is consistently recovered as a single species and as sister taxa to *Aphelochaeta* sp. B.

Haplotype networks showed little variation within COI (for both species) and 16S (for *A. abyssorum* comb. nov.), with no particular geographic structure (Fig. 2), suggesting gene flow and the lack of strong population structure. Intraspecific COI distances (HKY) ranged between 0 and 0.5% for *C. abranchiatus* comb. nov. (26 sequences) and between 0 and 1.7% for *A. abyssorum* comb. nov. (55 sequences). Intraspecific 28S distances (HKY) ranged between 0 and 0.2% for *C. abranchiatus* comb. nov. (20 sequences) and between 0 and 0.3% for *A. abyssorum* (55 sequences). No intraspecific variation was observed in 18S for *C. abranchiatus*, and only a single 18S sequence was available for *A. abyssorum* which did not allow to investigate intraspecific variation. Intraspecific 16S distances (HKY) for *A. abyssorum* ranged between 0 and 1.1% (55 sequences). These confirm the absence of cryptic species, both when looking at the type locality and when looking at the broader North-East Atlantic and Arctic.

Taxonomy

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Subclass Sedentaria Lamarck, 1818
Superorder Canalipalpata Rouse & Fauchald, 1997
Order Cirratulida Dales, 1962
Family Cirratulidae Ryckholdt 1851

Genus ***Chaetocirratulus*** Blake, 2018

Chaetocirratulus Blake, 2018: 56.

Type species

Heterocirrus andersenensis Augener, 1932. Original designation by Blake (2018).

Diagnosis (after Blake 2018)

Prostomium broadly rounded anteriorly or wedge-shaped; eyespots absent; with a pair of small nuchal organs as slits or depressions at posterior edge. Peristomium with a single pair of grooved dorsal tentacles arising from posterior margin or interface with chaetiger 1. First pair of branchiae arising from posterior margin of peristomium, an achaetous segment, or chaetiger 1. Body typically thick and fusiform over many segments, rarely with middle or posterior body segments beaded or moniliform; individual segments short, numerous. Setae include capillaries on most chaetigers and thick, pointed spines in neuropodium and a few in notopodium or spines in neuropodium only; spines few, often small and inconspicuous, not forming cinctures. Individual spines straight to weakly sigmoid. Pygidium a simple ventral lobe.

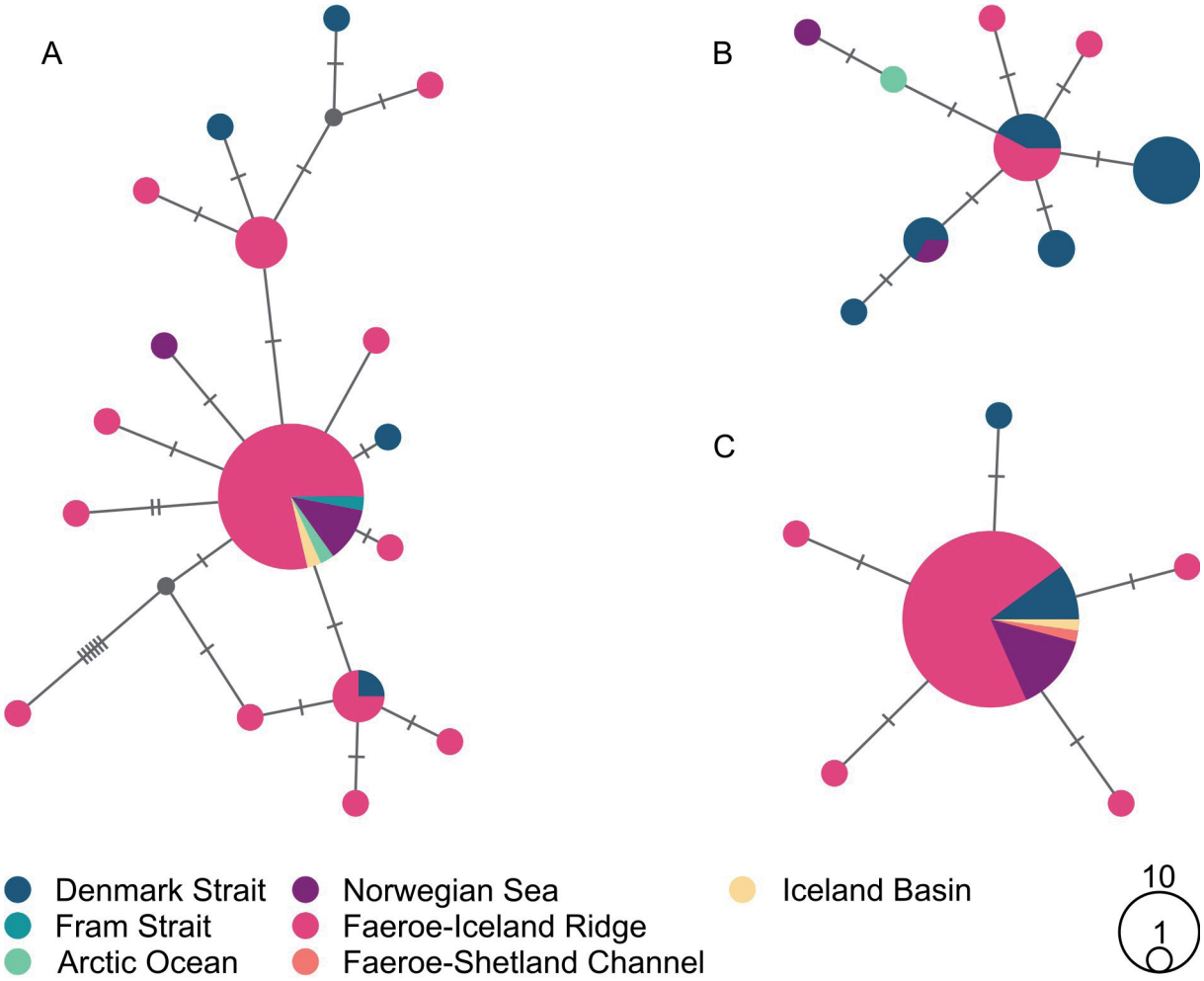

Fig. 2. Haplotype networks. **A**. Haplotype network of COI for *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov. **B**. Haplotype network of COI for *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov. **C**. Haplotype network of 16S for *Aphelochaeta abyssorum* (Hansen, 1879).

Chaetocirratulus abranchiatus (Hansen, 1879) comb. nov.
Figs 3–9

Cirratulus (?) *abranchiatus* Hansen, 1879: 10, pl. VII figs 3–7.

Chaetozone abranchiata – Hartman 1959: 401.

Diagnosis

In adults, short anterior region distinctively narrower than following segments; prostomium broadly triangular, three rings visible dorsally, two ventrally, dorsal crest absent; wide ventral ridge.

Type material

Neotype (here designated)
NORWEGIAN SEA • 64.10522° N, 5.72433° E; depth 636 m; 27 Jun. 2007; collected with RP sledge; MAREANO sample R932-75, RP; fixed in 96% ethanol; ZMBN 136930.

Other material examined

ARCTIC OCEAN • 4 specs; 81.60734° N, 33.40031° E; depth 518 m; 27 Jun. 2022; collected with grab; MAREANO sample R2915-55, GR; fixed in 96% ethanol; DNA voucher: MG1126; ZMBN 149490 • 1 spec.; 81.34727° N, 21.99029° E; depth 458 m; 2 Jul. 2022; collected with grab; MAREANO sample R2963-79, GR; fixed in 96% ethanol; ZMBN 149491 • 1 spec.; 81.41596° N, 21.67928° E; depth 704 m; 5 Jul. 2022; collected with grab; MAREANO sample R2983-90, GR; fixed in 96% ethanol; ZMBN 149492.

BARENTS SEA • 1 spec.; 71.92061° N, 20.38130° E; depth 349 m; 1 Jun. 2019; MetaMon project; collected with grab; sample GE-09; fixed in 96% ethanol; ZMBN 136914.

GREENLAND SEA – **Denmark Strait** • 4 specs; 67.86783° N, 23.69633° W; depth 1281 m; 15 Sep. 2011; collected with RP sledge; IceAGE sample M85-3 1144; fixed in 96% ethanol; SMF 32846, 32847, 32832, 32833 • 1 spec.; same data as for preceding; DNA voucher: MG810; no repository (specimen used for SEM) • 2 specs; 67.21383° N, 26.22516° W; depth 700 m; 14 Sep. 2011; collected with CliSAP sledge; IceAGE sample M85-3 1119; fixed in 96% ethanol; SMF 32876, 32877 • 2 specs; 67.837° N, 23.702° W; depth 1241 m; 15 Sep. 2011; collected with box corer; IceAGE sample M85-3 1142; fixed in 96% ethanol; SMF 32809, 32863 • 1 spec.; same data as for preceding; DNA voucher: MG978; no repository (specimen used for SEM) • 3 specs; 67.8465° N, 23.696° W; depth 1249 m; 15 Sep. 2011; collected with epibenthic sledge; IceAGE sample M85-3 1148; fixed in 96% ethanol; SMF 32864 to 32866 • 1 spec.; same data as for preceding; DNA voucher: MG984; no repository (specimen used for SEM) • 2 specs; 67.84° N, 23.696° W; depth 1250 m; 15 Sep. 2011; collected with epibenthic sledge; sample IceAGE M85-3 1148; fixed in 96% ethanol; SMF 32884, 32885 • 1 spec.; 67.86783° N, 23.69616° W; depth 1270 m; 15 Sep. 2011; collected with epibenthic sledge; IceAGE sample M85-3 1144; fixed in 96% ethanol; SMF 32886 • 1 spec.; 67.21383° N, 26.2075° W; depth 716 m; 14 Sep. 2011; collected with RP sledge; IceAGE sample M85-3 1123; fixed in 96% ethanol; SMF 32834. – **Fram Strait** • 1 spec.; 79.03412° N, 7.26576° E; depth 1275 m; 27 Oct. 2019; collected with grab; MAREANO sample R2099-2155, GR; fixed in 96% ethanol; ZMBN 136920 • 1 spec.; 79.1385° N, 6.08217° E; depth 1282 m; 10 Jul. 2017; Hausgarten project; collected with UNSEL box corer; fixed in 96% ethanol; ZMBN 144610 • 1 spec.; 78.9888° N, 5.432° E; depth 995 m; 2 Jul. 2016; Hausgarten project; fixed in 96% ethanol; ZMBN 130912 • 1 spec.; 79.08467° N, 6.45138° E; depth 1235 m; 29 Sep. 2019; collected with grab; MAREANO sample R2107-2163, GR; fixed in 96% ethanol; ZMBN 144613 • 1 spec.; 79.10622° N, 6.15371° E; depth 1235 m; 29 Sep. 2019; collected with grab; MAREANO sample R2108-115, GR; fixed in 96% ethanol; mounted on SEM-stub; ZMBN 144614 • 12 specs; 79.11608° N, 6.15363° E; depth 1229 m; 29 Sep. 2019; collected with beam trawl; MAREANO sample R2108-18, BT; fixed in 96% ethanol; ZMBN 144615 • 5 specs; 79.10649° N, 6.15297° E; depth 1262 m; 29 Sep. 2019; collected with RP sledge; MAREANO sample R2108-21, RP; fixed in 96% ethanol; DNA vouchers: MG1173, MG1174; ZMBN 144616 • 1 spec.; same data as for preceding; mounted on SEM-stub; ZMBN 144616-SEM • 12 specs; 79.10189° N, 6.15166° E; depth 1238 m; 30 Sep. 2019; collected with RP sledge; MAREANO sample R2108-22, RP; fixed in 96% ethanol; ZMBN 144617 • 8 specs; 79.10372° N, 6.15409° E; depth 1236 m; 30 Sep. 2019; collected with RP sledge; MAREANO sample R2108-23, RP; fixed in 96% ethanol; DNA voucher: MG1172; ZMBN 144618, 144619 • 1 spec.; same data as for preceding; mounted on SEM-stub; ZMBN 144618-SEM • 1 spec.; 78.98620° N, 7.24162° E; depth 1232 m; 30 Sep. 2019; collected with grab; MAREANO sample R2114-2170, GR; fixed in 96% ethanol; ZMBN 144620.

NORWEGIAN SEA • 3 specs; 63.41033° N, 8.187° W; depth 687 m; 31 Jul. 2913; collected with epibenthic sledge; IceAGE 2 sample POS456 880; fixed in 96% ethanol; SMF 32868 to 32870 • 5 specs; 63.09366° N, 8.572° W; depth 500 m; 31 Jul. 2013; collected with epibenthic sledge; IceAGE 2 sample POS456 879; fixed in 96% ethanol; SMF 32881 to 32883, 32862, 32811 • 1 spec.; 63.57766° N,

7.7115° W; depth 1044 m; 1 Aug. 2013; collected with brenke sledge; IceAGE 2 POS456 881; fixed in 96% ethanol; SMF 32803 • 1 spec.; 66.84333° N, 7.8945° E; depth 735 m; 2 Sep. 2015; collected with RP sledge; IceAGE 2 sample R1569-179, RP; fixed in 96% ethanol; ZMBN 120504 • 1 spec.; 64.10311° N, 5.73214° E; depth 626 m; 27 Jun. 2013; collected with beam trawl; MAREANO sample R932-454, BT; fixed in 96% ethanol; ZMBN 144621 • 4 specs; 62.553° N, 0.981° E; depth 800 m; 16 Aug. 1981; R/V "*H. Mosby*" sample HM81.08.16.7; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144594 • 3 specs; 62.491° N, 1.721° E; depth 604 m; 21 Jan. 1982; R/V "*H. Mosby*" sample HM82.01.21.2; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144595 • 4 specs; 62.56° N, 0.981° E; depth 804 m; 21 Jan. 1982; R/V "*H. Mosby*" sample HM82.01.21.4; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144596 • 2 specs; 62.198° N, 0.003° W; depth 708 m; 2 Jun. 1983; R/V "*H. Mosby*" sample HM83.06.02.1; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144597 • 10 specs; 61.343° N, 3.185° W; depth 1338 m; 3 Jun. 1983; R/V "*H. Mosby*" sample HM83.06.03.1; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144598 • 1 spec.; 65.168° N, 9.493° W; depth 784 m; 8 Jun. 1983; R/V "*H. Mosby*" sample HM83.06.08.1; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144599 • 11 specs; 62.593° N, 1.233° E; depth 781 m; 17 Jun. 1983; R/V "*H. Mosby*" sample HM83.06.17.3; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144600 • 2 specs; 62.585° N, 1.793° E; depth 656 m; 23 May 1984; R/V "*H. Mosby*" sample HM84.05.23.1; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144601 • 20 specs; 62.508° N, 1.851° E; depth 576 m; 23 May 1984; R/V "*H. Mosby*" collected with RP sledge; sample HM84.05.23.3; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144602 • 5 specs; 62.603° N, 2.233° E; depth 576 m; 23 May 1984; Brattegards exped.; collected with RP sledge; sample HM84.05.23.5; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144603 • 1 spec.; 62.553° N, 1.82° E; depth 652 m; 21 Nov. 1984; R/V "*H. Mosby*" collected with RP sledge; sample HM84.11.21.2; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144604 • 3 specs; 62.706° N, 1.186° E; depth 897 m; 8 Nov. 1885; R/V "*H. Mosby*" collected with RP sledge; sample HM85.01.08.2; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144605 • 2 specs; 63.045° N, 7.028° W; depth 1022 m; 13 Jun. 1986; R/V "*H. Mosby*" collected with RP sledge; sample HM86.06.13.4; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144606 • 9 specs; 62.948° N, 7.002° W; depth 748 m; 13 Jun. 1986; R/V "*H. Mosby*" collected with D sledge; sample HM86.06.13.5; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144607 • 1 spec.; 62.855° N, 5.698° W; depth 750 m; 16 Jun. 1986; R/V "*H. Mosby*" collected with D sledge; sample HM86.06.16.1; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144608 • 2 specs; 62.61° N, 1.573° E; depth 654 m; 15 Jun. 1986; R/V "*H. Mosby*" collected with RP sledge; sample HM86.08.15.5; fixed in formaldehyde and transferred to 75% ethanol; ZMBN 144609 • 1 spec.; 63.59067° N, 5.57533° E; depth 763 m; 20 Jun. 2014; collected with beam trawl; MAREANO sample R1349-274, BT; fixed in 96% ethanol; ZMBN 144611 • 1 spec.; 66.84067° N, 7.88867° E; depth 734 m; 2 Sep. 2015; collected with beam trawl; MAREANO sample R1569-553, BT; fixed in 96% ethanol; ZMBN 144612 • 1 spec.; 63.59067° N, 5.57533° E; depth 763 m; 20 Jun. 2014; collected with beam trawl; MAREANO sample R1349-274, BT; fixed in 96% ethanol; ZMBN 162355 • 1 spec.; 68.28796° N, 10.70476° E; depth 689 m; 28 Apr. 2012; collected with beam trawl; MAREANO sample R763-001; fixed in 96% ethanol; ZMBN 162356 • 1 spec.; 67.59864° N, 9.31061° E; depth 918 m; 5 May 2012; collected with RP sledge; MAREANO sample R818-9, RP; fixed in 96% ethanol; ZMBN 162357 • 4 specs; 62.42324° N, 1.20725° E; depth 654 m; 2 May 2021; collected with grab; MAREANO sample R2531-101, GR; fixed in 96% ethanol; DNA voucher: BeMG457; ZMBN 162348 • 2 specs; 64.74521° N, 5.19276° E; depth 707 m; 9 May 2021; collected with grab; MAREANO sample R2574-216, GR; fixed in 96% ethanol; DNA voucher: BeMG460; ZMBN 162349 • 1 spec.; 64.73235° N, 5.41943° E; depth 631 m; 9 May 2021; collected with grab; MAREANO sample R2577-220, GR; fixed in 96% ethanol; DNA voucher: BeMG458; ZMBN 162350.

Description

Neotype incomplete, 12 mm long, 2.5 mm wide, 50 segments (Fig. 3). Other complete specimens range from 3 to 21 mm long, 0.5 to 5 mm wide and 34 to 59 segments (Fig. 4A–N). Colour in ethanol light tan to light grey, old formalin fixed specimens with light pink colour. Body short and stout, of uniform width and height abruptly tapering at both extremities or with a distinct enlarged anterior half and posterior tail; anterior up to twice as wide as posterior, tapering towards pygidium (Fig. 4A–N). In larger specimens, first 6–8 segments not enlarged, slightly wider than pre-chaetiger area, and approximately as wide as tall. Smaller specimens often round in cross section, larger specimen oval to dorso-ventrally flattened. Specimens fixed in tubes with much thinner shape, with constant width (Fig. 4M). Dorsal groove or ridge nearly always absent, rarely a thin dorsal groove anteriorly. A wide ventral ridge made from segmental pads along entire body.

Prostomium half as long as peristomium, broadly triangular, without rings; eyespots absent; nuchal organs simple slits at posterior lateral margin (Figs 5A–E, 6A–C). Peristomium as long as four anterior chaetigers, with three distinct rings, anterior one longer with prominent rounded dorsum slightly overlapping prostomium anteriorly, anterior and middle rings fused ventrally with, middle and posterior rings each slightly wider and as long as anterior chaetigers (Figs 5A–E, 6A–C). Dorsal tentacles arising between last peristomial ring and chaetiger 1, well separated (Figs 5A–B, D–E, 6A–C). First pair of branchiae arising between last peristomial ring and chaetiger 1, lateral to tentacles (Figs 5A–B, D–E, 6A–C). Second pair of branchiae arising from chaetiger 1, dorsal and slightly posterior to parapodia. Subsequent branchiae similarly placed, branchiae or branchial stubs present on all chaetiger on enlarged anterior half (Fig. 6A, D), absent from posterior region (Figs 6E, 7A).

Parapodia biramous, low mounds or ridges distinct in larger specimens. Capillary chaetae 4–6 per neuropodium; 5–10 per notopodium, arranged in two rows; 2–4 capillary chaetae per neuropodium and notopodium are longer than body width in anterior region, each finely serrated along one edge (Fig. 7C–E). Short capillary chaetae progressively transition to thicker chaetae to 2–3 straight spines per neuropodium and notopodium in posterior half, with 2–4 alternating capillary chaetae, long, straight and slender (Fig. 7F).

Pygidium with terminal anus and short, rounded ventral lobe (Fig. 7A–B).

Fig. 3. *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov., neotype (ZMBN 136930). Scale bar = 1 mm.

Fig. 4. *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov., complete specimens. **A**. SMF 32883 **B**. SMF 32866. **C**. SMF 32864. **D**. SMF 32847. **E**. SMF 32863. **F**. SMF 32884. **G**. DNA voucher MG810 (no repository, specimen used for SEM). **H**. SMF 32885. **I**. SMF 32832. **J**. DNA voucher MG984 (no repository, specimen used for SEM). **K**. SMF 32833. **L**. SMF 32865. **M**. DNA voucher MG978 (no repository, specimen used for SEM). **N**. SMF 32846. Scale bar = 1 mm.

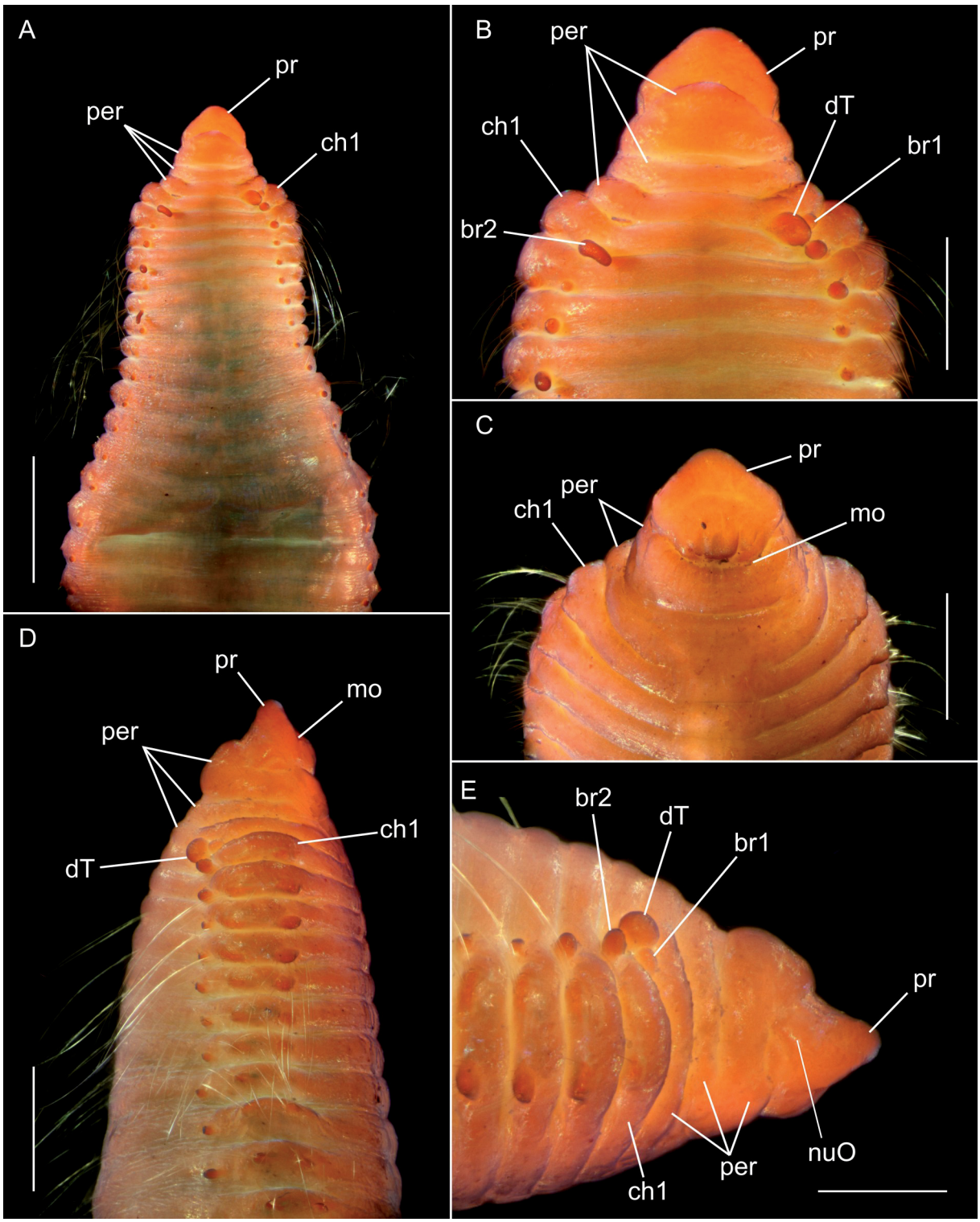

Fig. 5. *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov., anterior morphology. **A–E**. SMF 32846, stained with Shirlastain A. **A–B**. Dorsal view. **C**. Ventral view. **D–E**. Lateral view. Abbreviations: br1 = first branchiae; br2 = second branchiae; ch1 = first chaetiger; dT = dorsal tentacles; mo = mouth; nuO = nuchal organ; per = peristomium; pr = prostomium. Scale bars: A = 1 mm; B–C = 50 µm; D = 60 µm; E = 40 µm.

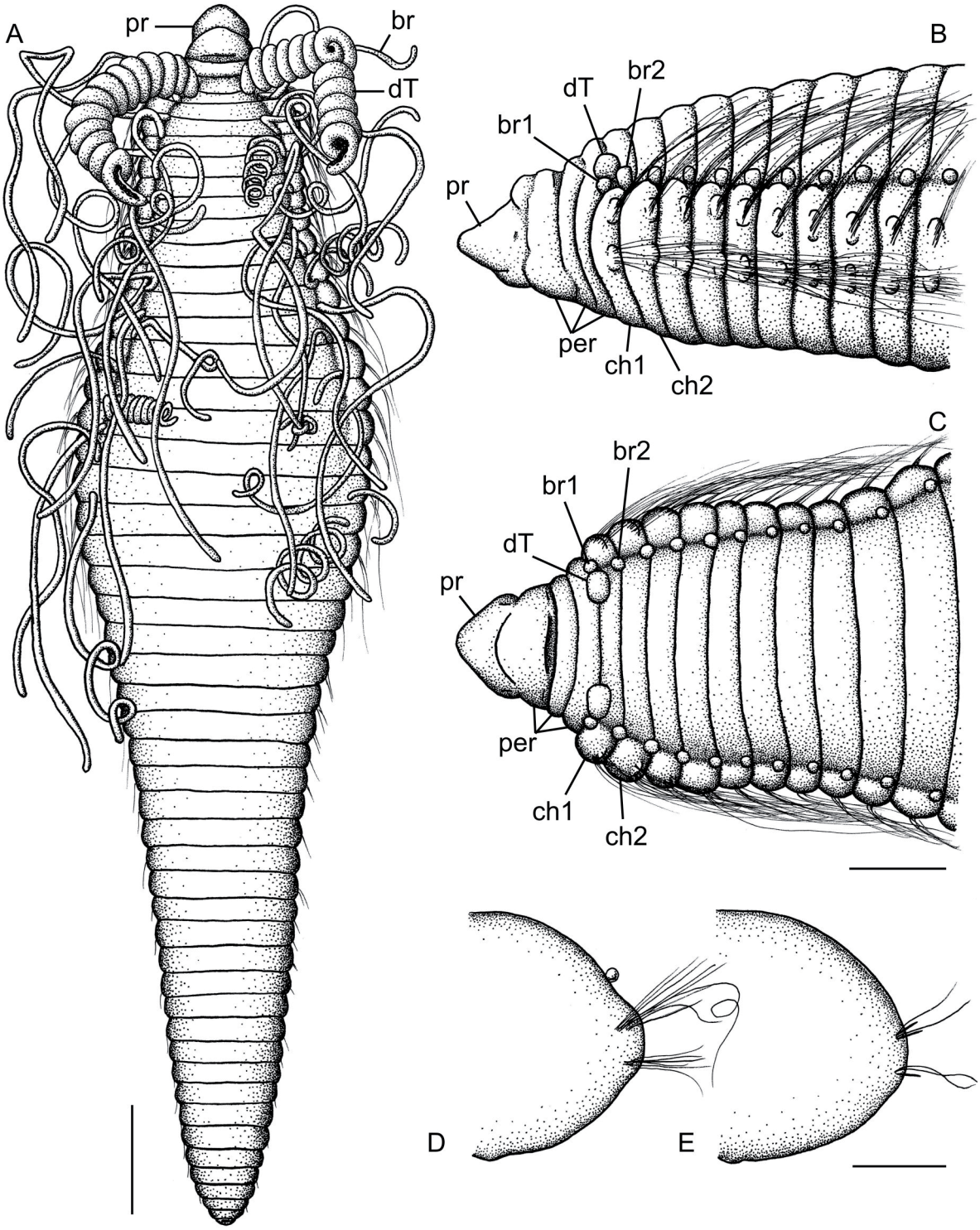

Fig. 6. *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov., schematic representation. **A**. Complete specimen in dorsal view. **B**. Anterior end in lateral view. **C**. Anterior end in dorsal view. **D**. Cross section of anterior segment. **E**. Cross section of posterior segment. Abbreviations: br1 = first branchiae; br2 = second branchiae; ch1 = first chaetiger; ch2 = second chaetiger; dT = dorsal tentacles; per = peristomium; pr = prostomium. Scale bars: A = 1 mm; B–C = 50 µm; D–E = 200 µm.

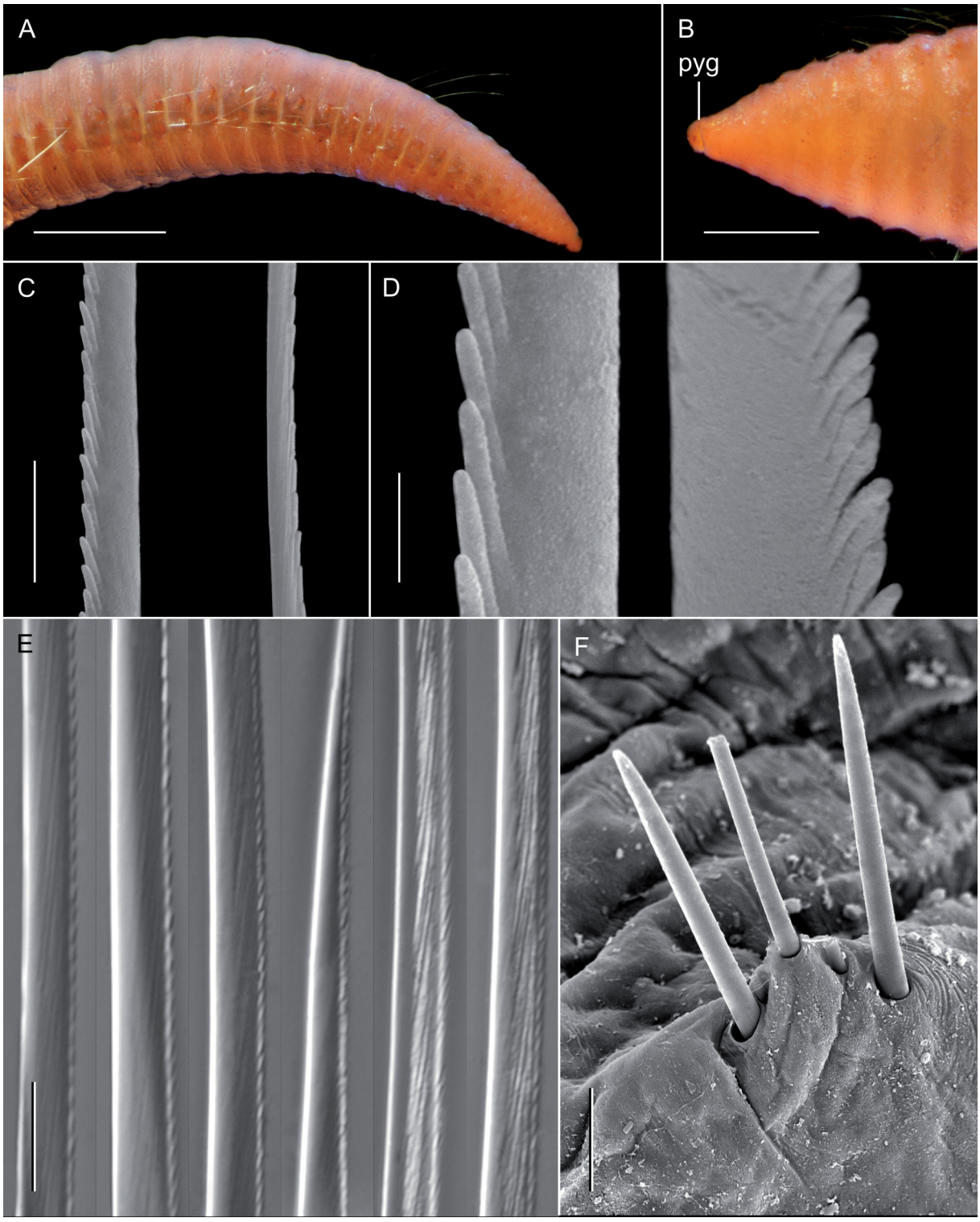

Fig. 7. *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov., posterior morphology and chaetae morphology. **A–B**. SMF 32846, stained with Shirlastain A. **C–D**. DNA voucher MG984 (no repository, specimen used for SEM). **E**. SMF 32881. **F**. DNA voucher MG978 (no repository, specimen used for SEM). **A**. Posterior end in lateral view. **B**. Pygidium in dorsal view. **C–E**. Details of capillary chaetae. **F**. Spines. Abbreviation: pyg = pygidium. Scale bars: A = 60 µm; B = 50 µm; C = 5 µm; D = 1.5 µm; E = 20 µm; F = 25 µm.

Methylene blue

Use of methylene blue results in variable patterns. All specimens retain a uniform light blue colour, branchiae retain a dark colour usually accompanied by dark blue spots spread at least over the proximal half. On some specimens sparse to very dense dark blue spots can be observed on the prechaetigerous area as well as on the first 5–6 parapodia.

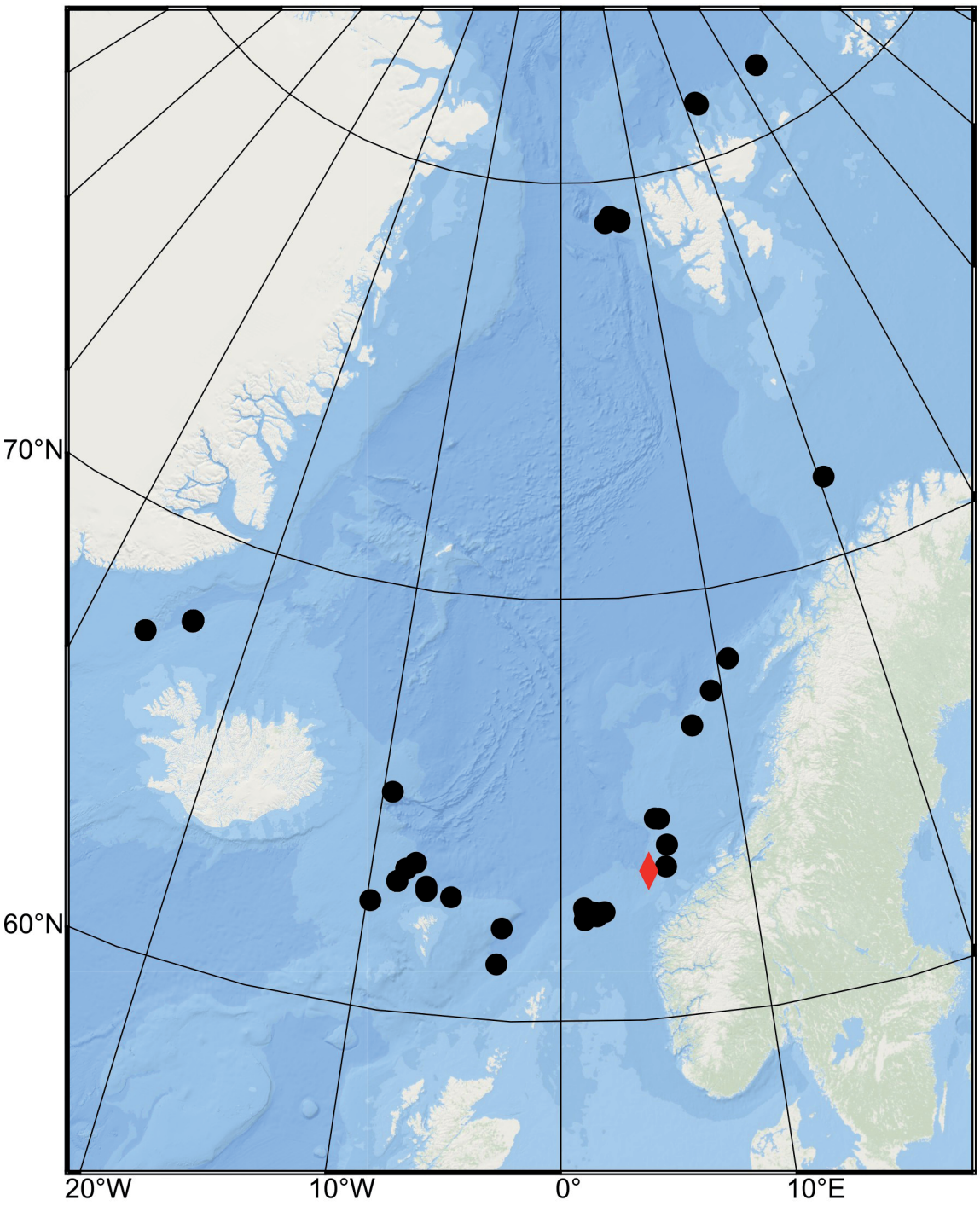

Fig. 8. *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov., distribution. Red diamond indicates type locality. Black circles indicate sampling locations.

Biology

Some specimens have been observed partially inside sandy tubes (Fig. 4). This phenomenon has previously been observed in *Chaetocirratulus gayheadius* (Hartman, 1965) where the tubes were assumed to be made by *C. gayheadius* which was considered unusual among cirratulids where tubes, when present, are usually muddy (Blake 2022). However, when examining bulk samples, such tubes were found in various sizes and occupied by a variety of animals and seem more likely to be made by some other organism such as Foraminifera d'Orbigny, 1826 and opportunistically occupied or temporarily crawled through by *C. abranchiatus* comb. nov.

A few of the larger specimens were found with eggs in the body cavity. While numerous examples of asexual reproduction and budding were found in *C. gayheadius* (Blake 2022), none was observed in the material examined for *C. abranchiatus* comb. nov.

Distribution

This species is distributed all around the North-East Atlantic on continental shelves and slopes (Fig. 8).

Comparative remarks

So far, *Chaetocirratulus abranchiatus* comb. nov. is the only member of its genus recorded from the North-East Atlantic. There are several other species occurring in the North-West Atlantic. Among them,

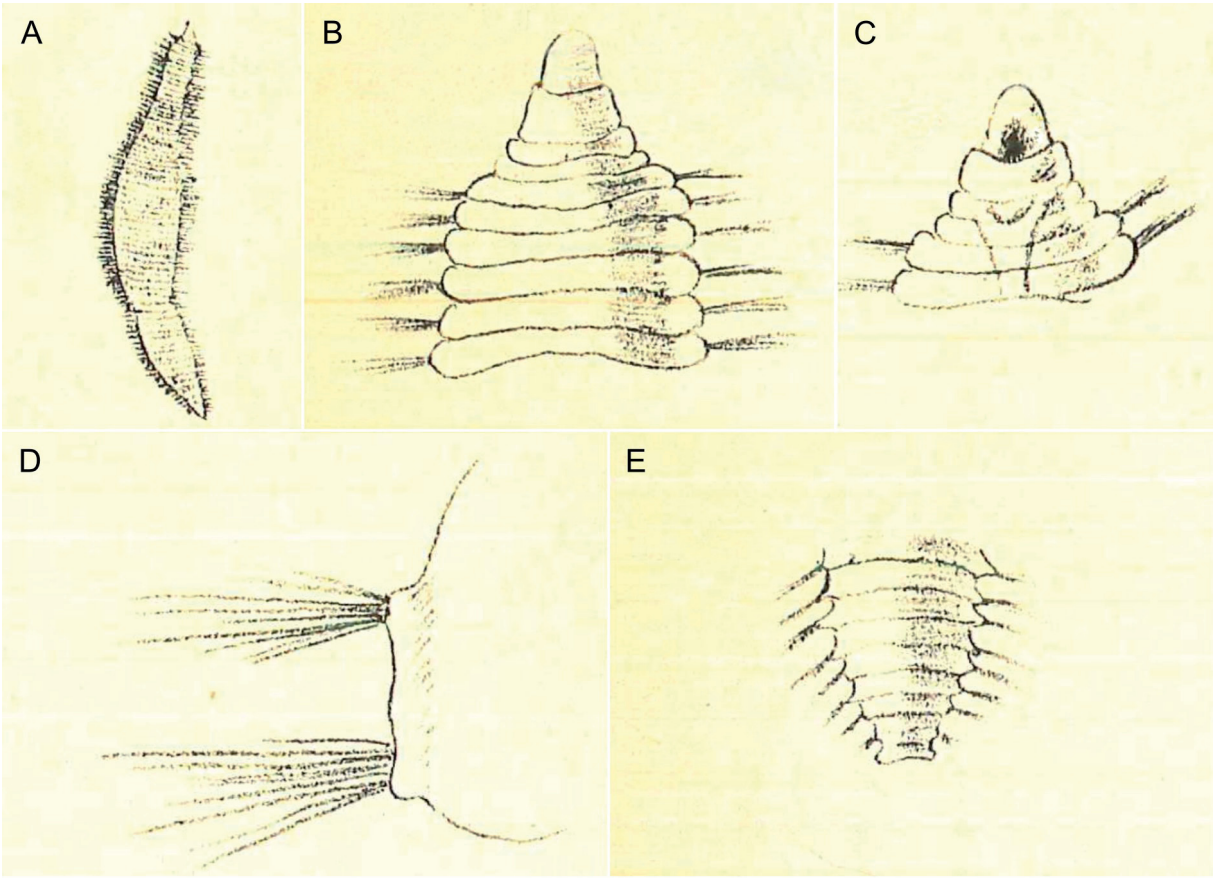

Fig. 9. *Chaetocirratulus abranchiatus* (Hansen, 1879) comb. nov., original illustrations by Hansen. **A–E**. Modified from Hansen (1979). **A**. Entire specimen in dorsal view. **B**. Anterior region in dorsal view. **C**. Anterior region in ventral view. **D**. Parapodium. **E**. Pygidium in dorsal view.

Chaetocirratulus gayheadius is, as far as we can tell, closely related to *C. abranchiatus*. The North-East Atlantic species agree well with the description of the West Atlantic species (Blake 2022), except for the methyl green/methylene blue staining pattern. Indeed, while some specimens examined in this study show the same pattern as described for the North American species, this pattern is variable as not all specimens retain a dark stain. This variation in staining pattern is seen among specimens collected together in the same sample, which partially excludes collection, fixation or preservation artefacts and could be due instead to intraspecific variability, specimen maturity or sexual dimorphism.

However, cryptic diversity is common in Cirratulidae (Grosse *et al.* 2020), and the known distribution of the two species is restricted to different biogeographical regions (Costello *et al.* 2017). In addition, asexual reproduction and budding are well documented for *C. gayheadius* (Blake 2022), but not observed in *C. abranchiatus* comb. nov. (this study). Therefore, we do not at this stage propose to synonymize the two species until genetic information can be obtained from specimens identified as *C. gayheadius*.

Remarks on the original description and illustrations and on the neotype

No type material could be found for this species and no mention is made of type specimens in the original description. All the existing material from the N.N.H.E. expeditions is kept at the Bergen University Natural History Museum and the Natural History Museum in Oslo. However, no specimens of *Chaetocirratulus abranchiatus* comb. nov. was found in either collection, and there are no records of it in the archives and the protocols of the museums. Therefore, we conclude that the original specimens were never deposited in any collection and a neotype has to be designated. The specimen designated as neotype in this study was chosen as it was collected the closest to the type locality, about 135 km, and sequences were available for it. While it is incomplete (part of the posterior region is missing), none of the specimens in better condition were collected so close to the type locality.

The original description was short, as was often the case in those times. It was however informative enough with regards to the body shape, the shape of the prechaetiger area and the shape of the parapodia in particular. One point of disagreement between the original description and our observations is on the capillary chaetae that were described as perfectly smooth. This can be explained by the techniques available at the time as the characteristic serrations present on the capillary chaetae of *Chaetocirratulus abranchiatus* comb. nov., while easily observed with SEM, are difficult to see even with modern light microscopy (Fig. 7E). Compared to the description, the original illustrations were particularly informative, as they show very well the distinctive body shape and anterior morphology of this species (Fig. 9). In addition to the fact that some specimens studied in this work were collected close to the type locality, this leaves no doubt about the fact that the specimens examined by Hansen for his description and the specimens examined for this study belong to the same species.

Genus ***Aphelochaeta*** Blake, 1991

Aphelochaeta Blake, 1991: 28.

Type species

Aphelochaeta monilaris Hartman, 1960. Original designation by Blake (1991).

Diagnosis (after Blake 2018)

Prostomium conical to rounded; peristomium elongate with pair of grooved dorsal tentacles arising either on or anterior to chaetiger 1. Anterior segments often expanded, crowded or uncrowded; abdominal segments sometimes beaded or moniliform in appearance; chaetae simple capillaries lacking distinct serration using light microscopy but distinct fibrils may be visible using SEM; posterior end frequently expanded tapering to a simple pygidial lobe.

Aphelochaeta abyssorum (Hansen, 1879) comb. nov.
Figs 10–16

Cirratulus (?) *abyssorum* Hansen, 1879: 10, pl. VII fig. 1.

Cirratulus abyssorum – Hartman 1959: 402.

Diagnosis

Body long and slender, segments never beaded, anterior dorso-ventrally flattened; three peristomial rings, dorsal crest present, pigmentation absent; latero-ventral bands anteriorly with MB.

Type material

Lectotype

NORWEGIAN SEA • anterior fragment; Vøringen; 64.2° N, 5.35° E; depth 911 m; 1876–1878; N.N.H.E. stn 87; clay; ZMBN 1970.

Paralectotypes

NORWEGIAN SEA • 7 intermediate fragments; same data as for lectotype; ZMBN 1970.

Other material examined

ARCTIC OCEAN • 1 spec.; 81.89659° N, 9.85533° E; depth 834 m; 8 Jun. 2017; collected with box corer; R/V *Polarstern* sample PS 106-1; fixed in 96% ethanol; DNA voucher: MG751; no repository (specimen used for SEM).

GREENLAND SEA • 1 spec.; 67.63266° N, 26.76650° W; depth 316 m; 14 Sep. 2011; collected with CliSAP sledge; IceAGE sample M 85-3 1136; fixed in 96% ethanol; SMF 32821 • 1 spec.; 67.21383° N, 26.22516° W; depth 697 m; 14 Sep. 2011; collected with CliSAP sledge; sample IceAGE M85-3 1119; fixed in 96% ethanol; SMF 32810, 32856 • 1 spec.; 67.83700° N, 23.70200° W; depth 1241 m; 15 Sep. 2011; collected with box corer; IceAGE sample M85-3 1142; fixed in 96% ethanol; SMF 32857 • 3 specs; 67.63800° N, 26.75466° W; depth 318 m; 14 Sep. 2011; collected with epibenthic sledge; IceAGE sample M85-3 1132; fixed in 96% ethanol; SMF 32871, 32872, 32808.

NORTH ATLANTIC • 1 spec.; 63.33333° N, 23.16666° W; depth 305 m; 4 Sep. 2011; collected with box corer; sample IceAGE M85-3 1031; fixed in 96% ethanol; SMF 32839.

NORWEGIAN SEA • 1 spec.; 63.38933° N, 8.157° W; depth 687 m; 31 Jul. 2013; collected with brenke sledge; IceAGE 2 sample POS456 880; fixed in 96% ethanol; DNA voucher: MG597; no repository (specimen used for SEM) • 1 spec.; 61.77600° N, 3.87333° W; depth 834 m; 28 Jul. 2013; collected with grab; IceAGE 2 sample POS456 880; fixed in 96% ethanol; SMF 32822 • 2 specs; 62.75533° N, 0.89900° W; depth 1571 m; 26 Jul. 2013; collected with grab; sample IceAGE 2 POS456 871; fixed in 96% ethanol; SMF 32829, 32835 • 1 spec.; 66.30100° N, 12.37333° W; depth 732 m; 22 Sep. 2011; collected with box corer; IceAGE sample M85-3 1217; fixed in 96% ethanol; SMF 32836 • 1 spec.; 62.20866° N, 0.26200° E; depth 669 m; 25 Jul. 2013; collected with box corer; IceAGE sample POS456 868; fixed in 96% ethanol; DNA voucher: MG779; no repository (specimen used for SEM) • 1 spec.; 66.53816° N, 12.86483° W; depth 316 m; 22 Sep. 2011; collected with RP sledge; IceAGE sample M85-3 1209; fixed in 96% ethanol; SMF 32837 • 1 spec.; 67.07866° N, 13.06383° W; depth 1575 m; 21 Sep. 2011; IceAGE sample M85-3 1191; fixed in 96% ethanol; SMF 32838 • 1 spec.; 63.57766° N, 7.74650° W; depth 1043 m; 1 Aug. 2013; collected with epibenthic sledge; IceAGE 2 sample POS456 881; fixed in 96% ethanol; SMF 32867 • 12 specs; 63.09366° N, 8.57200° W; depth 511 m; 31 Jul. 2013; DZMB exped; collected with epibenthic sledge; IceAGE 2 sample POS456 879; fixed in 96% ethanol;

SMF 32823, 32806, 32873, 32874, 32887, 32848 to 32854 • 1 spec.; same data as for preceding; DNA voucher: MG1055; no repository (specimen used for SEM) • 26 specs; 63.41733° N, 10.96633° W; depth 441 m; 2 Aug. 2013; collected with epibenthic sledge; IceAGE 2 sample POS456 882; fixed in 96% ethanol; SMF 32855, 32812, 32840 to 32845, 32814 to 32820, 32824 to 32828, 32875, 32830, 32831, 32858 to 32860 • 1 spec.; same data as for preceding; DNA voucher: MG738; no repository (specimen used for SEM) • 1 spec.; same data as for preceding; DNA voucher: MG839; no repository (specimen used for SEM) • 1 spec.; same data as for preceding; DNA voucher: MG950; no repository (specimen used for SEM) • 1 spec.; same data as for preceding; DNA voucher: MG953; no repository (specimen used for SEM) • 1 spec.; same data as for preceding; DNA voucher: MG765; no repository (specimen used for SEM) • 1 spec.; 63,64533° N, 7,7858°3 W; depth 1080 m; 1 Aug. 2013; collected with grab; sample IceAGE 2 sample POS456 881; fixed in 96% ethanol; SMF 32861.

Description

Mostly based on lectotype and 10 newly collected complete specimens. Lectotype ovigerous female in eight fragments including anterior and posterior end for about 30 mm, up to 1 mm wide (Fig. 10). Ten complete specimens 13 to 20 mm long, 0.5 to 0.9 mm wide for 87 to 139 segments (Fig. 11A–F). Colour in ethanol light tan or cream to light grey, venter often lighter than dorsum. Body elongate; short anterior

Fig. 10. *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov., lectotype (anterior fragment) and paralectotypes (ZMBN 1970). Scale bar = 1 mm.

region distinct, flattened, nearly twice as wide as midbody; midbody segments cylindrical, never longer than wide or high, never beaded; short posterior region enlarged, tapering towards pygidium. Anterior 22–27 segments 12–14 times as wide as and 4–9 times as high as long, oval in cross section. Midbody

Fig. 11. *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov., complete specimens. **A**. SMF 32828. **B**. SMF 32815. **C**. SMF 32818. **D**. SMF 32826. **E**. SMF 32827. Scale bar = 1 mm.

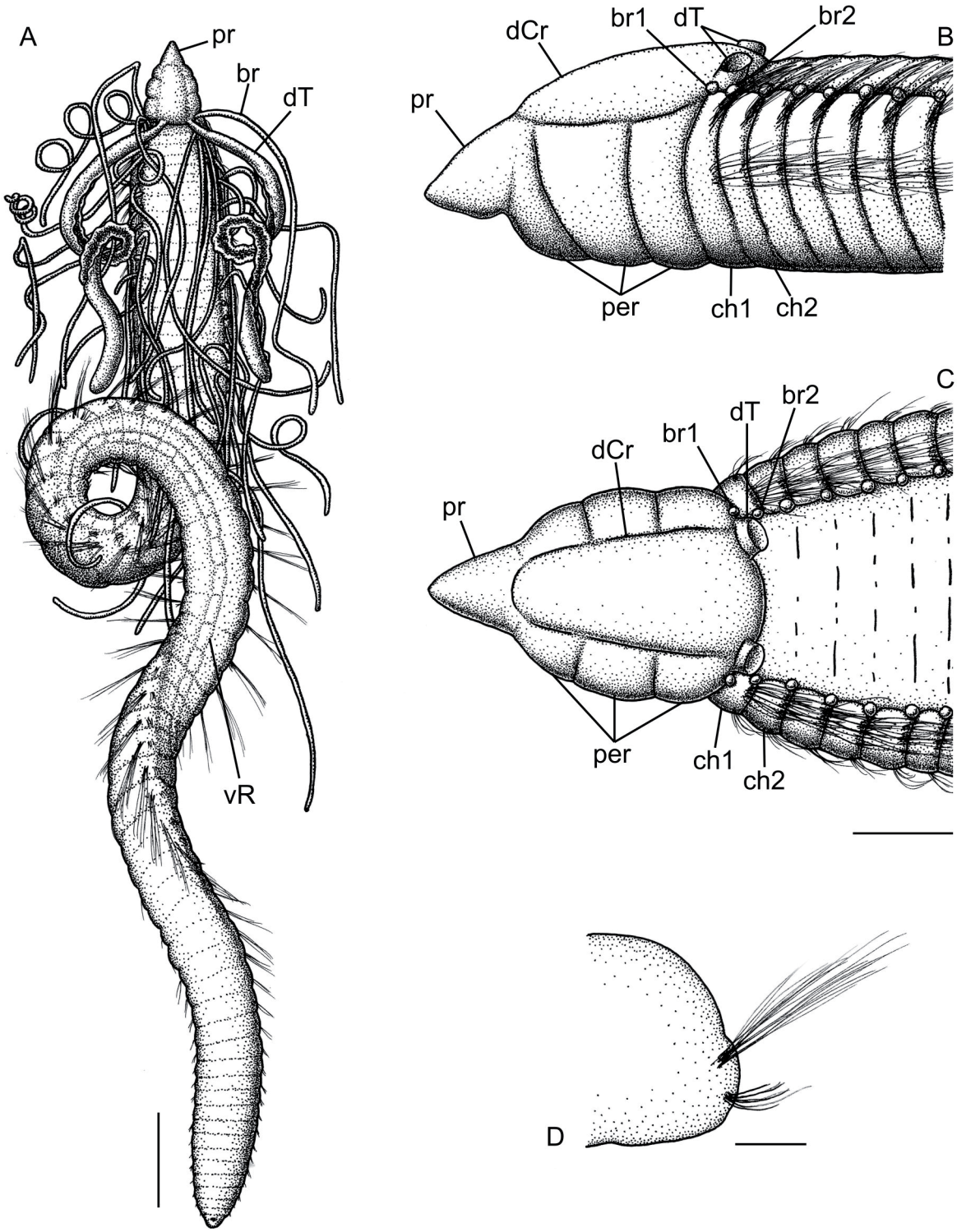

Fig. 12. *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov., schematic representation. **A**. Complete specimen, dorsal view. **B**. Anterior end, lateral view. **C**. Anterior end, dorsal view. **D**. Cross section of middle segment. Abbreviations: br1 = first branchiae; br2 = second branchiae; ch1 = first chaetiger; ch2 = second chaetiger; dCr = dorsal crest; dT = dorsal tentacles; per = peristomium; pr = prostomium; vR = ventral ridge. Scale bars: A = 1 mm; B–D = 200 μm.

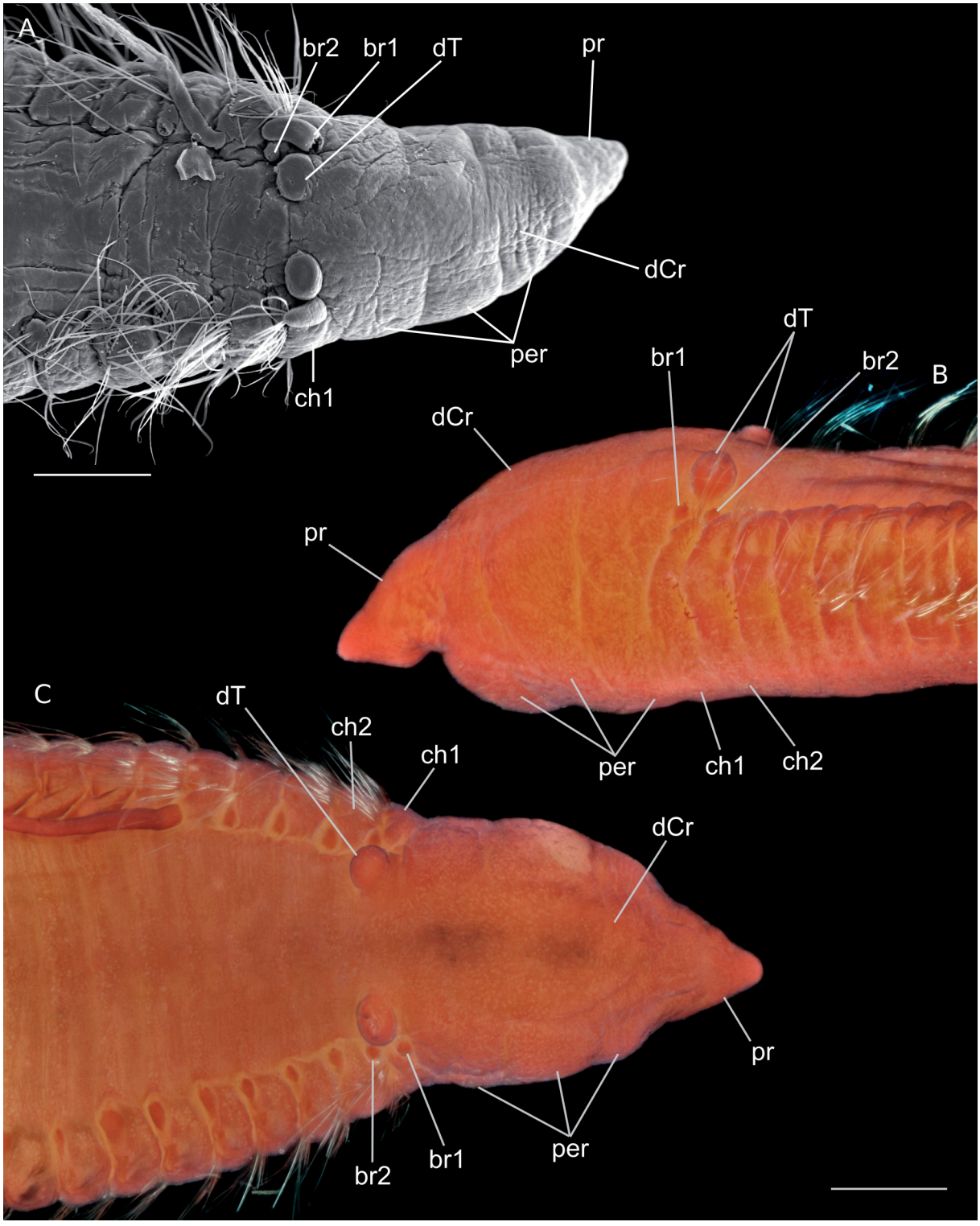

Fig. 13. *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov., anterior morphology. **A**. DNA voucher MG765 (no repository, specimen used for SEM). **B–C**. SMF 32825, stained with Shirlastain A. **A, C**. Anterior end in dorsal view. **B**. Anterior end in lateral view. Abbreviations: br1 = first branchiae; br2 = second branchiae; ch1 = first chaetiger; ch2 = second chaetiger; dCr = dorsal crest; dT = dorsal tentacles; per = peristomium; pr = prostomium. Scale bars: A = 150 μm; B–C = 200 μm.

segments progressively lengthening to 2–3 times as wide and high as long, round in cross section, with distinct, thin and shallow transversal intersegmental grooves, never beaded or moniliform. Posterior 20–50 segments 5–8 times as wide as and 3–6 times as high as long, oval to flattened in cross section, sometimes distinctly enlarged over anteriormost segments and tapering towards pygidium. A thin, shallow dorsal groove sometimes present over posterior enlarged region. A wide, low ventral ridge present along entire body (Figs 12A, 15D).

Prostomium one third to half as long as peristomium, broad, conical, without rings; eyespots absent; nuchal organs simple slits on posterolateral margins (Figs 12A–C, 13A–C). Peristomium as long as 6–7

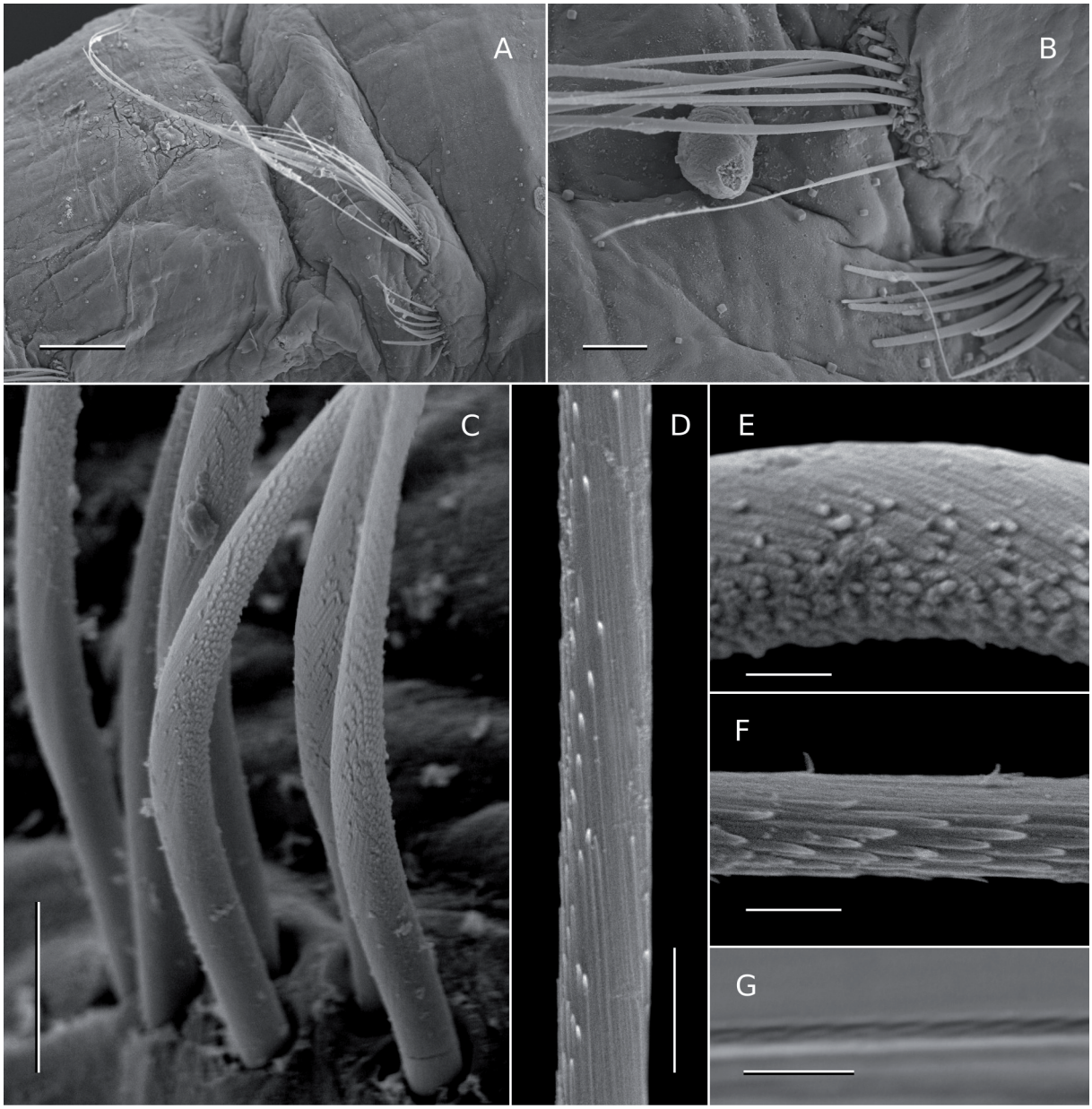

Fig. 14. *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov., chaetae morphology. **A–E**. DNA voucher MG738 (no repository, specimen used for SEM). **G**. SMF 32845. **A–B**. Midbody parapodium. **C**. Detail of midbody neuropodium. **D, F–G**. Detail of notochaetae. **E**. Detail of neurochaeta. Scale bars: A = 100 μm; B = 25 μm; C = 10 μm; D, G = 5 μm; E = 1.5 μm; F = 2.5 μm.

anterior segments, generally longer than wide, with three distinct rings visible laterally and ventrally, incomplete over dorsum due to broad, elongate dorsal crest, overlapping chaetiger 1 between dorsal tentacles, often higher than first 2–4 chaetigers (Figs 12A–C, 13A–C). Dorsal tentacles arising from posterior margin of peristomium, medial to parapodium of chaetiger 1, well separated. First pair of branchiae arising lateral to dorsal tentacles on anterior margin of chaetiger 1 (Figs 12A–C, 13A–C). Second pair of branchiae arising from chaetiger 1, directly above and slightly posterior to parapodia (Figs 12B–C, 13A–C). Subsequent branchiae similarly placed, present on nearly all anterior chaetigers, occasionally along first half of body, and rarely along posterior half.

Parapodia biramous, low mounds to inconspicuous, placed high over anterior region forming distinct shoulders (Figs 12B–C, 13A–C), shifting to a medium position in midbody (Fig. 14A–B) and a ventral position along posterior enlarged region (Fig. 12D). Chaetae all capillaries 7–10 per neuropodium, 16–19 per notopodium, typically arranged on two rows; neurochaetae short, 1–2 per neuropodium as long as notochaetae in midbody, basally strongly curved upwards in anterior segments, gradually straightening but retaining a light curvature throughout, covered in fine, short, dense scales on concave side made by

Fig. 15. *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov., morphological details and methylene blue pattern. **A–B**. Lectotype (ZMBN1970), stained with methylene blue. **C**. SMF 32822, stained with methylene blue. **A**. Anterior end in ventral view. **B–C**. Anterior end in lateral view. **D**. Detail of ventral ridge, stained with Shirlastain A. **E**. Pygidium in lateral view, stained with Shirlastain A. Scale bars: A, C = 1 mm; B = 500 µm; D–E = 200 µm.

protruding fibrils; notochaetae 1–2 times as long as body width in anterior and midbody, directed nearly upwards anteriorly, shifting laterally in midbody, covered in long, pointy, flat scales along one side (Fig. 14C–F); posterior neuro- and notochaetae short.

Pygidium with terminal anus, reduced with large rounded ventral lobe and 5 small dorsal lobes (Fig. 15E).

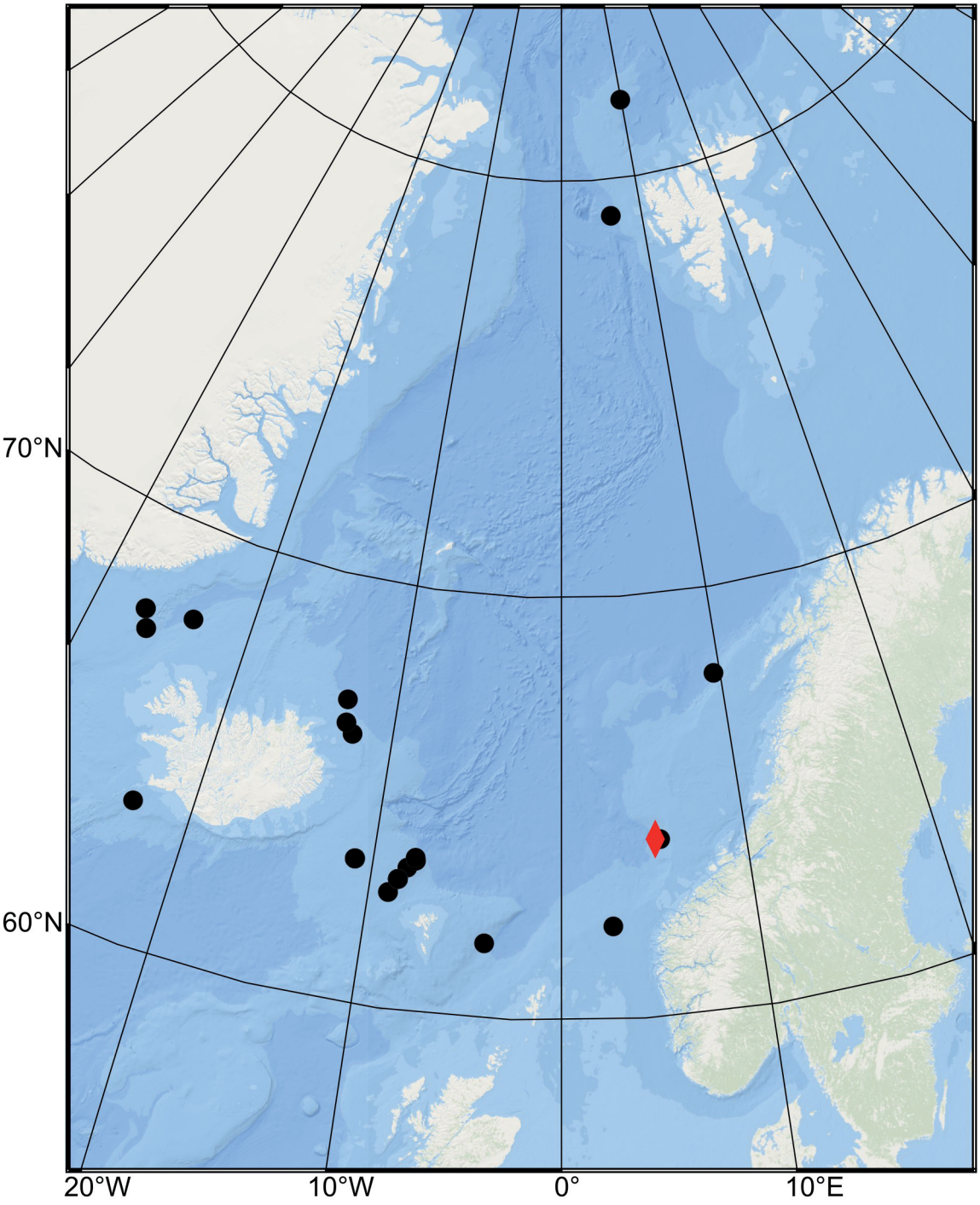

Fig. 16. *Aphelochaeta abyssorum* (Hansen, 1879) comb. nov., distribution. Red diamond indicates type locality. Black circles indicate sampling locations.

Methylene blue

Prostomium and peristomium retain a light stain without any particular pattern, although the dorsal crest is generally of a lighter colour and some longitudinal lines stay unstained. Distinct latero-ventral bands are present from segment 10–13 and fade in midbody where only faint lines of dark dots remain. More anterior segments retain a light stain laterally and ventrally over the posterior half of each segment. Bands of dark dots can be present dorsally over anterior segments (Fig. 15A–C).

Distribution and habitat

Aphelochaeta abyssorum comb. nov. is widely distributed at shelf and slope depths (300–1500 m deep) from the Arctic Ocean around Svalbard to the Norwegian Sea and Denmark Strait (Fig, 16).

Remarks

Hansen (1879) reported 3 specimens from the same station (N.N.H.E stn 87) in the original description of *C. abyssorum*. The type material for this taxon (ZMBN 1970) has been located in the collections of the University Museum of Bergen (Oug *et al*. 2014). However, the sample ZMBN 1870 includes only a single anterior fragment and 7 midbody fragments. The anterior fragment is in close agreement with the original description given by Hansen (1879, 1882) and is here designated the lectotype. The remaining midbody fragments may belong to other specimens and are considered paralectotypes.

In some specimens, the posterior end is not particularly enlarged. In smaller specimens, the anterior part is not always much wider, but nearly always flatter and with the notopodium forming distinct shoulders. In the smallest fragments (possibly juveniles) the prostomium is as long as the peristomium, the peristomial rings are not as distinct and the prechaetiger area is overall more elongated and cylindrical.

The genus *Aphelochaeta* is one of the least studied genera among the bitentaculate Cirratulidae. Some species have been studied in the Pacific (Blake 1991, 2018, 2019; Dean & Blake 2016), the Southern Ocean (Blake 2023) and to a small extent the West Atlantic (Elías & Rivero 2009; Blake & Dean 2019). However, these studies mostly concern species living in coastal waters or abyssal depths and very little is known about species living at shelf and slope depths. In the North-East Atlantic, very little is known about the genus in general. Only a few species have been described, all from coastal waters. In addition, as was the case in the present study, most of these descriptions are old, inadequate and need to be updated. Therefore, diversity of the genus *Aphelochaeta* in the area has never been properly surveyed and assessed. A revision of the genus in Europe is necessary to both properly re-describe known species and identify potential new species.

Discussion

DNA data to study species delimitation and distribution

With the understanding of species as independently evolving groups of organisms that are genetically and phenotypically distinct from other such groups (Barraclough 2019), DNA barcoding (Hebert *et al*. 2003a, 2003b) has become an increasingly used tool to study biodiversity. DNA barcoding is an easy and fast way to gain information about these lineages and perform accurate species delimitation (Hebert *et al*. 2003a, 2003b). In many organisms, including annelids (Nygren 2014) and in particular Cirratulidae (Grosse *et al.* 2020), such techniques have been keys to facilitate and accelerate diversity discovery. They can in particular reveal the presence of cryptic species (understood here as distinct but morphologically indistinguishable species). Therefore, in the presence of a large amount of seemingly identical specimens from a wide geographic area, as was the case in this study, it is necessary to use DNA data to assess the possible presence of cryptic species. This allows us to confirm the presence of a single, widely distributed species rather than a complex of morphologically similar species. Although previous studies have found such species complexes in Cirratulidae (Grosse *et al.* 2020), it has been proposed that

deep-sea species are more widely distributed. Such species have been found in Cirratulidae (Magalhães *et al.* 2017) as well as other polychaetes (Guggolz *et al.* 2020; Meissner *et al.* 2023). The same pattern is observed here for *Chaetocirratulus abranchiatus* comb. nov. and *Aphelochaeta abyssorum* comb. nov.

Phylogeny of Cirratulidae

In this study, DNA sequences of the genus *Chaetocirratulus* are analysed for the first time. This genus was erected to accommodate species that presented some morphological characteristics of *Chaetozone* Malmgren, 1867 (large paired dorsal tentacles) and some morphological characteristics of *Cirratulus* (few spines not arranged in cinctures and a broad to wedge-shaped prostomium) as well as a distinct, stout body shape with short, wide segments (Blake 2018). Each of the three genes analysed show that *Chaetocirratulus* forms a clade with *Cirriformia* and *Cirratulus*. *Chaetocirratulus* is recovered as sister taxa to the other two when analysing 28S and 18S, but this topology is unsupported by COI where the relationship between the tree genera is unresolved (Fig. 1). It is however recovered with strong support in analyses of the combined dataset.

The phylogenetic trees included in this paper present similar hypotheses to previous inferences (Grosse *et al.* 2020). Taxon sampling at the generic level is more comprehensive than previous studies, with the addition of sequences of *Tharyx* Webster & Benedict, 1887, *Caulleriella* Chamberlin, 1919 and *Chaetocirratulus*. In addition to a group containing *Chaetocirratulus*, *Cirratulus* and *Cirriformia* a group containing *Chaetozone* and *Caulleriella* is also recovered as monophyletic, as are *Dodecaceria* Örsted, 1843 with *Raricirrus* Hartman, 1961, and *Aphelochaeta* with *Tharyx* (Fig. 1). However, while *Tharyx* is recovered as monophyletic in all analyses, it is not the case for *Aphelochaeta* (Fig. 1).

Yet, this dataset is still incomplete, as DNA sequences are still unavailable for several genera, and more species with a broader range of morphological characteristics are required to fully investigate the systematics and the evolution of this family. While more complete and detailed analyses are beyond the scope of this paper, the gene and species trees presented here show that more extensive taxon and gene sampling will be needed in the future. This will be necessary to resolve conflicting topologies between gene trees and to assess generic monophyly.

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Supplementary files

Supp. file 1. List of specimens used in this study with collection data and accession numbers for molecular data. https://doi.org/10.5852/ejt.2025.987.2869.13029

Supp. file 2. PCR primers and cycles used in this study. https://doi.org/10.5852/ejt.2025.987.2869.13031

Supp. file 3. DNA alignments in fasta and nexus format.
https://doi.org/10.5852/ejt.2025.987.2869.13033

Supp. file 4. Phylogenetic trees in Newick format. https://doi.org/10.5852/ejt.2025.987.2869.13035