



# Abysal fauna of polymetallic nodule exploration areas, eastern Clarion-Clipperton Zone, central Pacific Ocean: Annelida: Spionidae and Poecilochaetidae

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Received: 10 August 2021 / Revised: 21 March 2022 / Accepted: 29 March 2022 / Published online: 14 September 2022  
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## Abstract

This paper represents a continuation of taxonomic publications on the benthic fauna of polymetallic nodule fields in the eastern Clarion-Clipperton Zone (CCZ) using material collected during baseline environmental survey work targeting two exploration contract areas (“UK-1” and “OMS”) and one Area of Particular Environmental Interest, “APEI-6.” Families Poecilochaetidae Hannerz, 1956 and Spionidae Grube, 1850 of the annelid suborder Spioniformia were studied here. Taxonomic data are presented for 25 species from 98 records as identified by a combination of morphological and genetic approaches. Although sub-optimal morphological condition can prevent new species being formally described, it is essential that morphological, molecular, and voucher data are made available for future surveys. Descriptions of two new species—*Poecilochaetus brenkei* sp. nov. and *Laonice shulseeae* sp. nov.—increase the number of formally described new annelid species from the areas targeted in this study to 15 and CCZ-wide to 46. We also discuss the commonly reported “cosmopolitan” deep-sea spionid *Aurospio dibranchiata* Maciolek, 1981, which we show represents several genetically distinct species (three of these from CCZ area alone) but without reliable morphological characters to separate them. Molecular data provide evidence that 15 out of 25 species reported here have a wide distribution within the eastern CCZ and that *Aurospio* sp. “NHM\_2186” and the known species *Prionospio amarsupinata* Neal & Altamira in Paterson et al. 2016 may be cosmopolitan. Lastly, the molecular data provide insights into relationships within Spioniformia, suggesting that both Poecilochaetidae and Trochochaetidae belong within Spionidae.

**Keywords** CCZ · Deep-sea mining · Abyss · Spioniformia · Taxonomic novelty · Molecular phylogeny · Species distribution · 18S · 16S · COI

## Introduction

This publication presents results from an ongoing baseline survey of biodiversity in the Clarion-Clipperton Zone (CCZ)

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Communicated by T. Horton

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This article is a contribution to the Topical Collection *Biodiversity in Abyssal Polymetallic Nodule Areas*

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polymetallic nodule region. In recent decades, this vast area (~6 million km<sup>2</sup>) of the central abyssal Pacific has been targeted for exploration of deep-sea mineral resources (Gollner et al. 2017). Such exploration is managed through exploration licenses, regulated by the International Seabed Authority (ISA), which stipulates the need for baseline studies, environmental impact assessments and the establishment of area-based management tools such as preservation areas (Lodge et al. 2014). Here, we focus on areas in the eastern part of the CCZ—the UK Seabed Resources Ltd (UKSRL) exploration contract area “UK-1,” the Ocean Mineral Singapore exploration contract area “OMS,” and an Area of Particular Environmental Interest, “APEI-6.”

There is a particular interest in the knowledge of the biodiversity (including identity of species, abundance, and species richness) and distribution of benthic taxa found within areas of potential mining operations (e.g., Glover et al. 2018; Smith et al. 2011, 2021). Both biodiversity and species ranges in the deep sea remain poorly understood due to several factors, but mainly owing to under-sampling and the lack of comparable

datasets produced by different research groups and contractors (e.g., Smith et al. 2011, 2021). The latter factor is greatly confounded by the lack of formal description of the fauna given that most represent species new to science. Recent sampling and subsequent analytical efforts have finally started to produce some (but still limited) taxonomic and biodiversity data from CCZ on various benthic taxa, employing molecular (e.g., Janssen et al. 2015) or morphological approach (e.g., Blake 2016; Kersken et al. 2018, 2019) or a combination of both (e.g., Bonifácio and Menot 2019; Dahlgren et al. 2016; Glover et al. 2016a; Kaiser et al. 2018; Lim et al. 2017; Wiklund et al. 2017; Wiklund et al. 2019).

The lack of knowledge is particularly acute for sediment infauna, a benthic component of the fauna that cannot be captured by video or camera surveys. In general, polychaete worms dominate the abyssal sediment macrofauna, constituting 50–75% of macrofaunal abundance and species richness, and are therefore considered a key component of benthic biodiversity (e.g., Glover et al. 2002; Smith et al. 2008). Polychaetes also exhibit a broad range of feeding types and life-history strategies and are frequently used to evaluate anthropogenic disturbance in shallow-water habitats (Dean 2008). Thus, evaluation of the diversity and species ranges of polychaete worms is critical to predicting and managing the impacts of manganese nodule mining in the CCZ.

Our main objective has been to provide taxonomic and genetic data on macrofaunal polychaetes collected as part of the Abyssal Baseline (ABYSSLINE) environmental survey cruises “AB01” and “AB02” to the polymetallic nodule exploration contract areas “UK-1,” “OMS” as well as an Area of Particular Environmental Interest, “APEI-6.” These data build on previous taxonomic work on polychaete worms from UK-1 area (Wiklund et al. 2019) as well as wider CCZ area (Janssen et al. 2015; Bonifácio and Menot 2019; Blake 2016) and ultimately provide further insights into polychaete species distribution in the deep sea. Up to this date, 43 new polychaete species have been formally described from CCZ, with the focus on families Spionidae (Paterson et al. 2016), Polynoidae (Bonifácio and Menot 2019), Cirratulidae (Blake 2016) and Opheliidae, Scalibregmatidae, and Traviidae (Wiklund et al. 2019).

Spionidae Grube, 1850 represent one of the most species-rich annelid families with around 590 described species in 39 genera, although many taxa are in need of a revision (Blake et al. 2017). Spionidae are particularly abundant in soft-bottom environment from shallow waters to deep sea and are also commonly found in organically disturbed environments (e.g., Dean 2008). In the deep-sea sediments, Spionidae are well represented both in terms of abundance and species richness (e.g., Glover et al. 2002; Paterson et al. 2011), with species within the two closely related genera *Prionospio* Malmgren, 1867 and *Aurospio* Maciolek, 1981

particularly well represented (Paterson et al. 2016; Guggolz et al. 2019, 2020; Peixoto and Paiva 2019, 2020). On the other hand, the family Poecilochaetidae Hannerz, 1956 is rather species poor with 32 valid species confined to the single genus *Poecilochaetus* Claparède in Ehlers, 1875 and none known from the abyssal depths. Thus, targeting suborder Spioniformia in this study is likely to reveal a sizable and novel portion of benthic biodiversity within the areas samples in the CCZ.

## Materials and methods

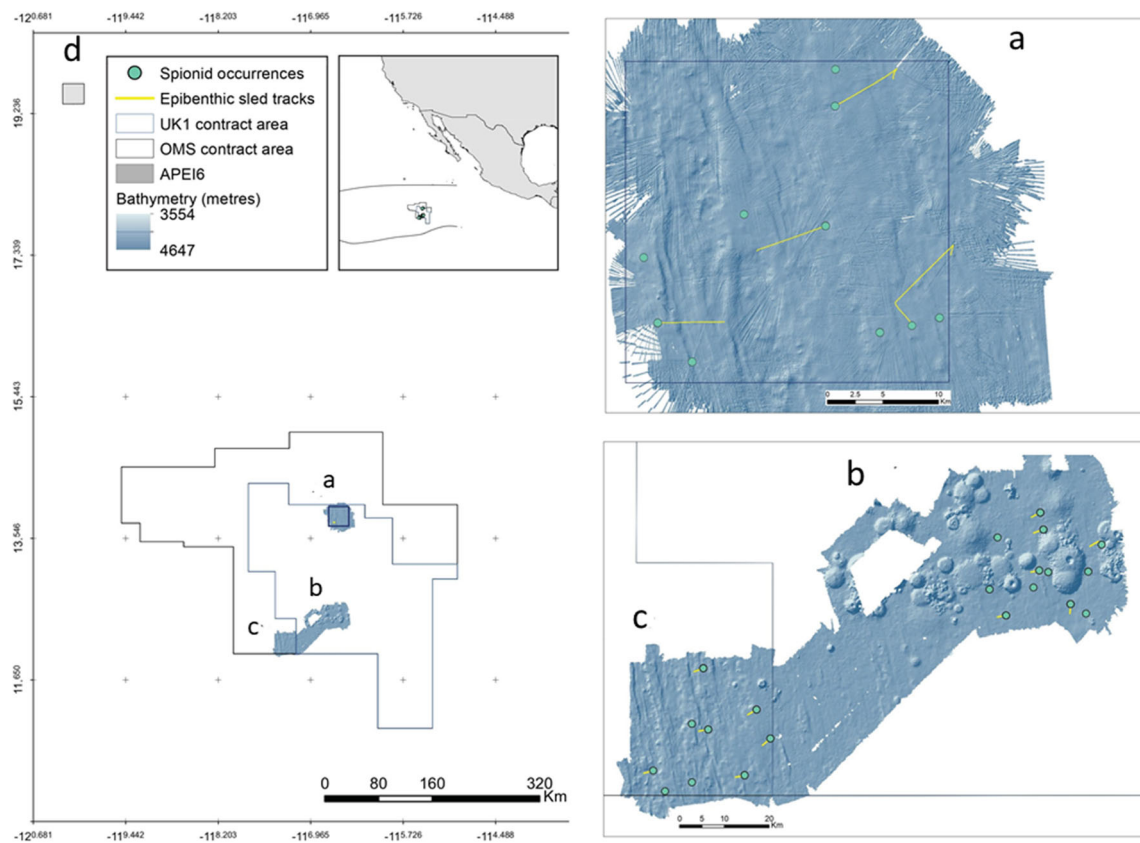
### Fieldwork

The first UKSR ABYSSLINE cruise (AB01) took place in October 2013 onboard the *RV Melville* and targeted the UK-1 exploration contract area (Fig. 1). The second cruise (AB02) took place in February–March 2015 onboard the *RV Thomas G. Thompson* and sampled a wider area (Fig. 1), including UK-1 (depth ~4200 m) and OMS (depth ~4200 m) exploration contract areas and APEI-6 (depth ~4050 m), an area zoned by the ISA as a potential conservation zone.

For a comprehensive description of the methodological pipeline, see Glover et al. (2016b). Briefly, specimens were collected using a range of benthic sampling gear including box corer and epibenthic sledges (EBS) (Brenke 2005). Geographic data from sampling activities were recorded on a central GIS database (Fig. 1). Live-sorting of specimen samples was carried out onboard both vessels in a “cold-chain” pipeline, with material maintained in chilled (2–4°C), filtered seawater. Specimens were assigned preliminarily identification and imaged live using stereo microscopes with attached digital cameras (Glover et al. 2016b). Specimens were then stored in individual microtube vials filled with aqueous solution of 80% non-denatured ethanol labeled appropriately and entered into a database. Samples were kept chilled throughout their transportation to the Natural History Museum, London, UK.

### Morphological laboratory work

In the laboratory, preserved specimens were re-examined using stereo and compound microscopes. They were identified to morphospecies and the best-preserved examples (voucher specimens) were then used to provide informal descriptions with key morphological features photographed with digital camera. Shirlastain A was used during the morphological examination on some specimens, in order to better observe certain characters. Scanning electron microscopy (SEM) using a SEM FEI Quanta 650 was conducted on selected specimens, following graded ethanol dehydration, critical point drying, and gold coating. Figures were assembled



**Fig. 1** Map over sampling sites. **a** UK-1 Stratum-A and **b** UK-1 Stratum-B study areas, both within the UK Seabed Resources UK-1 exploration contract area; **c** OMS Stratum-A study area, in the Ocean Mineral Singapore (OMS) polymetallic nodule exploration contract area; **d** Area of Particular Interest APEI-6. Inset map showing location of Clarion-

Clipperton Fracture Zone. Bathymetric survey and sample localities from the AB01 2013 RV Melville survey cruise and AB02 2015 Thomas G. Thompson survey cruise, data courtesy Craig R. Smith (University of Hawaii), UK Seabed Resources Ltd and Seafloor Investigations, LLC

using Adobe Photoshop CS6 software. In some instances, a fine line was used to outline and highlight particular morphological features where such features were unclear from images alone. Line drawings were made using camera lucida system.

### Molecular laboratory work

Extraction of DNA was done with DNeasy Blood and Tissue Kit (Qiagen) using a Hamilton Microlab STAR Robotic Workstation. Approximately 1800 bp of 18S were amplified using the primers 18SA 5'-AYCTGGTTGATCCTGCCAGT-3' (Medlin et al. 1988) and 18SB 5'-ACCTTGTTACGACTTTACTTCCTC-3' (Nygren and Sundberg 2003). Around 450 bp of 16S were amplified with the primers ann16Sf 5'-GCGGTATCCTGACCGTRCWAAGGTA-3' (Sjölin et al. 2005) and 16SbrH 5'-CCGGTCTGAACTCAGATCACGT-3' (Palumbi 1996), and around 650 bp of cytochrome *c* oxidase were amplified using LCO1490 5'-GGTC ACAAATCATAAAGATATTGG-3' (Folmer et al. 1994) and COI-E 5'-TATACTTCTGGGTGCCGAAGAATCA-3' (Bely and Wray 2004). PCR mixtures contained 1 µl of each primer (10 µM), 2 µl template DNA, and 21 µl of Red Taq

DNA Polymerase 1.1× MasterMix (VWR) in a mixture of total 25 µl. The PCR amplification profile for all gene fragments consisted of initial denaturation at 95°C for 5 min, 35 cycles of denaturation at 94°C for 45 s, annealing at 55°C for 45 s, extension at 72°C for 2 min, and a final extension at 72°C for 10 min. PCR products were purified using Millipore Multiscreen 96-well PCR Purification System, and sequencing was performed on an ABI 3730XL DNA Analyzer (Applied Biosystems) at The Natural History Museum Sequencing Facility, using the same primers as in the PCR reactions plus two internal primers for 18S, 620F 5'-TAAAGYTGTYGCAGTTAAA-3' (Nygren and Sundberg 2003) and 1324R 5'-CGGCCATGCACCACC-3' (Cohen et al. 1998). Overlapping sequence fragments were merged into consensus sequences using Geneious (Kearse et al. 2012) and aligned using MAFFT (Kato et al. 2002) for 18S and 16S, and MUSCLE (Edgar 2004) for COI, both programs used as plugins in Geneious, with default settings. The program jModelTest (Posada 2008) was used to assess the best model for each partition with BIC, which suggested the MrBayes possible GTR+I+G as the best model for both genes. The data was partitioned into two genes (18S and 16S), and

the evolutionary model mentioned above was applied to each partition. The parameters used for the partitions were unlinked. Bayesian phylogenetic analyses (BAs) were conducted with MrBayes ver. 3.2.6 (Ronquist et al. 2012). Analyses were run three times for 10,000,000 generations. Of these, the first 2,500,000 generations were discarded as burn-in. The tree files were interpreted with FigTree ver. 1.4.4 (available from <http://tree.bio.ed.ac.uk/software/figtree/>). Uncorrected “p” genetic distances within and between closely related species was calculated using Mesquite (Maddison and Maddison 2018).

### Taxonomic assignments

Here, we use a phylogenetic species concept *sensu* Donoghue (1985) with species determined by DNA-based phylogenetic analysis. Poor morphological preservation of some of the collected specimens and the subsequent lack of morphological data hindered formal species descriptions for most species found. For these, we provide the lowest-level taxonomic name possible aided by phylogenetic information. In these cases, we use an informal naming system where the voucher specimen number for one representative individual is used as the informal species name. Therefore, *Aurospio* sp. (NHM\_091) is the informal species name for all specimens that are the same species as the specimen number NHM\_091. This avoids confusion with the use of sp. A, sp. B, sp. C etc. where confusing false synonymy can easily arise. Newly formalized species recovered from ABYSSLINE cruises were named in honor of the scientists, technicians, and crew of the two vessels used, with the names being randomly selected from a list of all on board.

Type material, DNA specimen vouchers, and DNA extractions are deposited at the Natural History Museum, London. A full list of all taxa including Natural History Museum Accession Numbers (NHMUK), NHMUK Molecular Collection Facility (NHMUK-MCF), and NCBI GenBank accession numbers is provided in Table 1.

### Data handling

The field and laboratory work led to a series of databases and sample sets that were integrated into a “data-management pipeline.” This included the transfer and management of data and samples between a central collections database, a molecular collections database, and external repositories (GenBank, WoRMS, OBIS, GBIF, GGBN, ZooBank) through DarwinCore (in Supplementary material 1) archives and usage of the GGBN data standard (Droege et al. 2014). This provides a robust data framework to support DNA taxonomy, in which openly available data and voucher material are key to quality data standards. A further elaboration of the data pipeline is published in Glover et al. (2016b).

## Systematics section

### *Spioniformia sensu* Fauchald, 1977

#### *Poecilochaetidae* Hannerz, 1956

#### *Poecilochaetus* Claparède in Ehlers, 1875

Type species: *Poecilochaetus fulgoris* Claparède in Ehlers, 1875

**Diagnosis** (modified after Blake and Maciolek 2017). Prostomium small, rounded, two pairs of eyespots; prominent facial tubercle projecting from dorsal lip of mouth; one to three tentaculiform nuchal organs extending posteriorly or nuchal organs reduced to short lobes or knobs. Two long, grooved palps present. First parapodia directed anteriorly, bearing elongated postchaetal lobes, with long chaetae forming cephalic cage. Chaetigers 2 to 3 or 4 or 5 with thick, usually curved spines in neuropodia. Ampullaceous postchaetal lobes present on some anterior parapodia from chaetigers 7 to 10 or 17. Thin, filiform, or branched branchiae on posterior sides of some middle and posterior parapodia or branchiae entirely absent. Simple chaetae of numerous types in middle and posterior parapodia: plumose, hispid, and knobbed with arista either simple or plumose. Last 20 or so parapodia modified, with notopodial spines.

**Remarks.** The majority of ~30 currently known species of *Poecilochaetus* have been described from shallow tropical waters, although the type species of the genus, *Poecilochaetus fulgoris*, is a deep-sea species. It was described from fragments collected by the 1868 Lightning expedition at 1170 m depth in the north-east Atlantic, west of the Faroe Islands (Claparède in Ehlers, 1875). Subsequently collected deep-sea specimens also assigned to *P. fulgoris* were specimens from 1300 m on the Celtic Slope (Ehlers 1875), and specimens from off New England (1000–5000 m) and north-eastern South America (770–805 m) (Hartman 1965). Later, an additional three species were described from the deep sea: *Poecilochaetus bermudensis* Hartman, 1965 from 1000 m off Bermuda; hadal *Poecilochaetus vitjazi* Levenstein, 1962 from Tonga Trench, 10,415–10,687 m; and lastly *Poecilochaetus trachyderma* Read, 1986 from 477 to 515 m off South Island, New Zealand.

*Poecilochaetus fulgoris* was poorly defined by Claparède (in Ehlers, 1875) and based on fragmented material. The subsequent re-description by Pilato and Cantone (1976) was based on specimens originally examined by Hartman (1965), without the specifications of their collection locality and perhaps more importantly, collection depth. Given that Hartman (1965) examined specimens collected over vast geographical and bathymetrical ranges, we are cautious of possible misidentifications and as a result also of the definition of



**Table 1** (continued)

DNA taxonomy ID	NHMUK no.	GUID	NHMUK Reg no.	NHMUK MCF no.	GenBank AK no.
<i>Laonice shulseeae</i> sp. nov.	NHM_2098	374f46e7-3ac4-46c3-9aec-c4c9b52fd268	ANEA 2021.48	0109493214	MZ570377 MZ570290
<i>Laonice shulseeae</i> sp. nov.	NHM_2181	6509e7eb-575f-4c5a-b6e6-71725220f50e	ANEA 2021.49	0118302196	MZ570385
<i>Laonice shulseeae</i> sp. nov.	NHM_2182	b1c54d81-3077-4096-aa9b-76d98d2ab781	ANEA 2021.50	0109493200	MZ570386
	(holotype)				
<i>Prionospio</i> sp. (NHM_135)	NHM_783G	f3c63077-823b-4c9f-aa20-44846f154d51	ANEA 2019.10021	0118302233	MZ570329
<i>Prionospio</i> sp. (NHM_135)	NHM_701	16ada8e6-155f-4cf4-9574-5d94c550281d	ANEA 2019.10018	0118300516	MZ570323
<i>Prionospio</i> sp. (NHM_471)	NHM_471	4b863457-c4c7-488f-8d0c-dce0a29891d6	ANEA 2019.10011	0109493221	MZ570309 MZ570282
<i>Prionospio</i> sp. (NHM_471)	NHM_646	a4d416f6-4843-43c6-bd53-66243bf39d07	ANEA 2019.10016	0109493193	MZ562501 MZ570320
<i>Prionospio</i> sp. (NHM_471)	NHM_1930	c2399e87-2c50-4206-8440-62d443e468cc	ANEA 2019.10048	0118302208	MZ570372
<i>Prionospio</i> sp. (NHM_471)	NHM_698	dbf20c82-2b63-4a43-b702-6e6eff811cf6	ANEA 2019.10017	0109493195	MZ570322
<i>Prionospio</i> sp. (NHM_914)	NHM_914	740cb765-0221-4e99-b560-317baffa949	ANEA 2019.10024	0109493213	MZ562502 MZ570333 MZ570285
<i>Prionospio</i> sp. (NHM_914)	NHM_1002	ab7e36b0-a301-4d0c-8a94-438f0b779be0	ANEA 2019.10027	0109493211	MZ562504 MZ570337
<i>Prionospio</i> sp. (NHM_914)	NHM_1099	03e26933-52fa-4645-9b2b-16deb85c31d6	ANEA 2019.10030	0118302229	MZ570341
<i>Prionospio</i> sp. (NHM_914)	NHM_1545	e77f8d01-d276-4ebe-ba0a-0b892f0ac51d	ANEA 2019.10041	0109493209	MZ562506 MZ570358
<i>Prionospio</i> sp. (NHM_914)	NHM_1174A	a853d973-cdf3-49aa-9a31-745b4b4e1808	ANEA 2019.10031	0118302228	MZ570342
<i>Prionospio</i> sp. (NHM_914)	NHM_1600	47b121ba-a4e3-4be4-b3d1-6042fc4f93e2	ANEA 2021.42	0109493185	MZ570360
Spionidae sp. (NHM_564)	NHM_564	e3b3c05b-b22f-4352-9257-540c8b055142	ANEA 2019.10013	0109492899	MZ570314 MZ570283
Spionidae sp. (NHM_564)	NHM_1507	312c3120-0ff6-4ee1-b372-0a9d67ffid126	ANEA 2021.43	0118302226	MZ570355
Spionidae sp. (NHM_1415)	NHM_1415	90bf9f9d-c91d-422f-9b1f-274d9ba8ef3f	ANEA 2019.10039	0109493187	MZ570352
Spionidae sp. (NHM_1415)	NHM_520	90bf9f9d-c91d-422f-9b1f-274d9ba8ef3f	ANEA 2021.53	0109493191	MZ570311
Spionidae sp. (NHM_1415)	NHM_1544	3b669957-944d-448e-a28a-d8715394f8ae	ANEA 2019.10040	0109493186	MZ570357
Spionidae sp. (NHM_1415)	NHM_1025C	918f4936-4c71-4cba-88fc-8afb0e417c71	ANEA 2019.10029	0118302230	MZ570340
<i>Prionospio</i> sp. (NHM_266)	NHM_266	deef5795-5a5f-4278-99c8-0f9677320c29	ANEA 2019.10006	0109493226	MZ570304 MZ570281
<i>Prionospio</i> sp. (NHM_266)	NHM_227	30c5fb63-1ab9-4893-a3f8-cc7630d8a64c	ANEA 2019.10005	0109493239	MZ570303
<i>Prionospio</i> sp. (NHM_266)	NHM_301	2b298d74-bd08-4409-b50a-d39a82f73c85	ANEA 2019.10007	0109493225	MZ562497 MZ570305
<i>Prionospio</i> sp. (NHM_266)	NHM_302	b7e7fe38-7eb5-4442-94c7-84cc49a968d9	ANEA 2021.44	0109493224	MZ570306
<i>Prionospio</i> sp. (NHM_266)	NHM_582	dee43fe5-643f-4e48-a4dc-2811c59f8d18	ANEA 2019.10014	0109493204	MZ570316
<i>Prionospio</i> sp. (NHM_266)	NHM_1797F	39e48d77-5536-4747-b4c8-32aeda68856d	ANEA 2019.10046	0118302206	MZ570369
<i>Prionospio</i> sp. (NHM_266)	NHM_886	36a9ff16-fb53-4410-ab29-8ccf37082725	ANEA 2019.10023	0109492900	MZ570332
<i>Prionospio</i> sp. (NHM_266)	NHM_1343	01c661b7-a8a5-4315-9d17-7954519a8f90	ANEA 2019.10033	0118302217	MZ570345
<i>Prionospio</i> sp. (NHM_884)	NHM_884	53aa9a08-e363-4167-99cc-a2e8a938fad5	ANEA 2019.10022	0109493187	MZ570331
<i>Prionospio</i> sp. (NHM_884)	NHM_736	da7d9de9-7c2c-4af0-a22d-20186460c2da	ANEA 2019.10019	0118302237	MZ570325
<i>Prionospio</i> sp. (NHM_884)	NHM_943	baf64796-ee1c-4123-95d4-faba6208834e	ANEA 2019.10025	0109493215	MZ570334 MZ570286
Spionidae sp. (NHM_2123)	NHM_2123	894627d2-381f-4c42-bf94-8338ecb4bab8	ANEA 2021.45	0109493210	MZ562509 MZ570381 MZ570292
<i>Spiophanes</i> sp. (NHM_1897)	NHM_1897	fcbe5c24-c939-459f-b45a-748f3e991356	ANEA 2021.46	0109493189	MZ570371 MZ570289
<i>Spiophanes</i> sp. (NHM_1897)	NHM_3186	1ed33edf-3a9b-4000-9f61-2c77e1a333bc	ANEA 2021.47	0118302199	MZ562511 MZ570391

*P. fulgoris* provided by Pilato and Cantone (1976). Therefore, *P. fulgoris* remains a poorly defined species, which complicates the efforts of describing any new species. Nevertheless, with support from molecular characters, a new species *Poecilochaetus brenkei* sp. nov. is formalized here from eastern CCZ material, becoming the first species with the type locality in abyssal (rather than bathyal or hadal) depths and only a fifth species described from the deep sea.

#### *Poecilochaetus brenkei* sp. nov.

<http://zoobank.org/0713EA14-6C72-425F-A33B-4F82EE0C73DC>

Figs. 2a–h, 3a–e, 4a–f, 5a, 7a–b

**Material examined:** holotype NHM\_223, NHMUK ANEA.2021.1, coll. 15 Oct. 2013, collection method: Remotely Operated Vehicle, 13°57.7675, 116°33.0556, 4062 m.

**Additional material of *Poecilochaetus* sp. examined:** NHM\_2526, NHMUK ANEA.2021.2, coll. 03 Mar. 2015,

collection method: Brenke Epibenthic Sledge, 12°27.26N, 116°36.77W, 4137 m; NHM\_1797B, NHMUK ANEA.2021.3, coll. 11 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°10.43N, 117°11.57W, 4045 m; NHM\_1668A, NHMUK ANEA.2021.4, coll. 10 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°21.81N, 116°40.86W, 4233 m; NHM\_1948A, NHMUK ANEA.2021.5, coll. 13 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°02.49N, 117°13.03W, 4094 m; NHM\_2192, NHMUK ANEA.2021.6, coll. 26 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°06.93N, 117°09.87W, 4100 m.

Figs. 7c–h, 8a–d, 9a–d

**Description** (based on holotype, NHMUK ANEA.2021.1). Single specimen, represented by anterior fragment with 30 chaetigers, 7 mm long and 1.5 mm wide. Body, of near uniform width, covered with thin layer of sediment (Fig. 2a), when exposed pale yellow in ethanol.

Prostomium subquadrate anteriorly slightly widened and rounded with a shallow median notch (Fig. 2b). Eyes not observed. Nuchal lobes not observed. Facial tubercle dorsal to mouth, cirriform, short and smooth. Palps not observed. Dorsal chitinous plate on chaetiger 9 not observed. Interramal sensory papilla present, starting from chaetiger 1 and as large as in other anterior chaetigers; smaller from mid-body, distribution in the posterior part of the body uncertain. Branchiae absent. Interramal cirri absent.

Chaetiger 1 large, directed forward; neuropodial postchaetal lobes long, cirriform (Fig. 2c); notopodial postchaetal lobes absent. Postchaetal lobes present in both rami from chaetiger 2 (damaged in some chaetigers). On chaetiger 2 lobes short, robust with thickened base, relatively thick stalk and thickened distally (Fig. 2d); on chaetigers 3–6 resembling lobe of chaetiger 2 but getting progressively longer and more slender, approaching ampullaceous form; on chaetigers 7–11 lobes longest, thinnest, attaining distinct ampullaceous form, with globular base, long thin stalk, terminally enlarged (Fig. 2e). The size of postchaetal lobes on chaetiger 11 of unequal size with ventral lobe much shorter (Fig. 2f). In chaetigers 12 through to 18/19 both lobes short and thick, with distally enlarged tip (Fig. 2g); lobes getting thinner towards chaetigers 18/19. From around chaetiger 20, both lobes are thin, cirriform with base somewhat enlarged (Fig. 2h).

Neuropodial spines in chaetigers 2–5 (Fig. 3a); two spines on chaetigers 2–4 stout, distally curved (Fig. 3b–d); single spine on chaetiger 5 slender, only gently curved (Fig. 3e). Notopodial spines not observed in the posteriorly incomplete specimen. Capillary chaetae of 6 types present (Figs. 4a–f and 5a–i), differentiated by degree of ornamentation *sensu* Mackie (1990) as smooth (Figs. 4a and 5a), hirsute (Figs. 4b and 5b), plumose (Figs. 4c and 5d), spinose (Figs. 4d and 5f), and of mixed type (Figs. 4e–f and 5c, e, g, h, i); thickness of chaetal stems also variable (Fig. 5c).

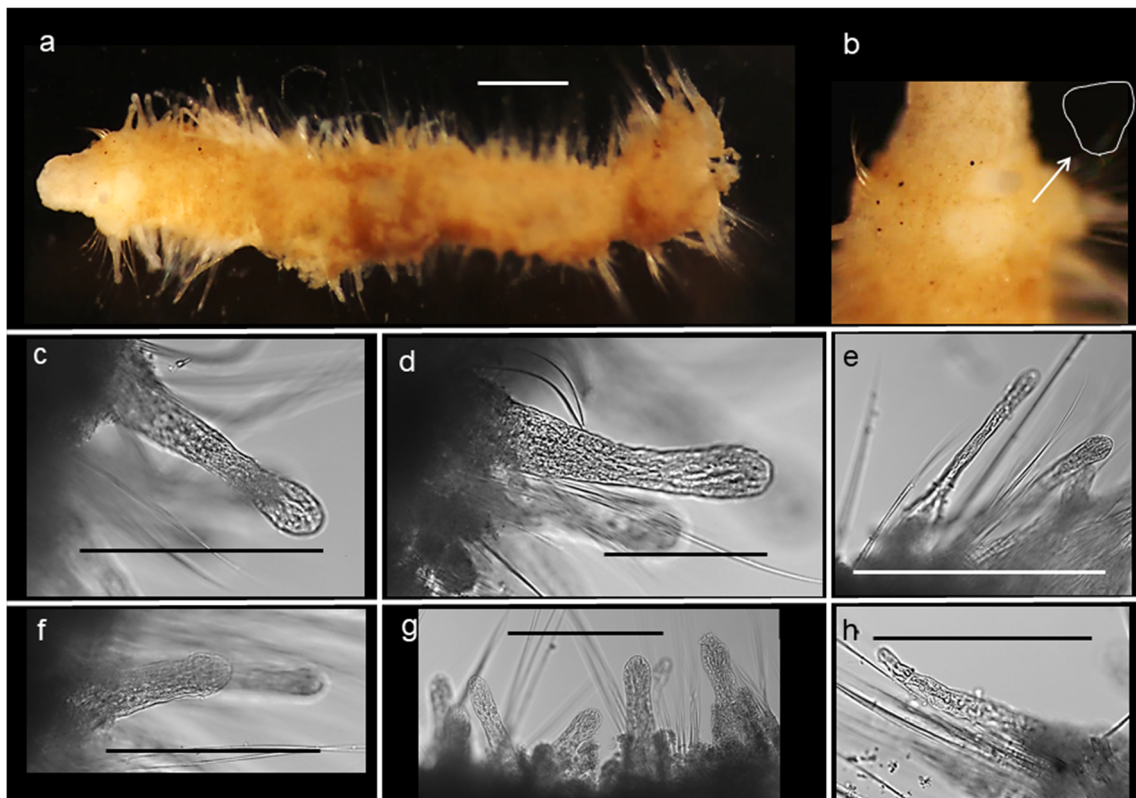
Capillaries of chaetiger 1 directed forward in fan-shape arrangement, forming a cephalic cage (Figs. 2a–b and 5a). Notochaetae of chaetiger 1 as 6 long capillaries; stems smooth with some hirsutation along the distal half (Fig. 5a). Neurochaetae of chaetiger 1 all short; lower neurochaetae composed of two thickened hirsute capillaries with ornamentation along most of the length of shaft and three short slender smooth capillaries; upper neurochaetae as two hirsute capillaries, longer with ornamentation limited to distal half. Additionally, 5 very short chaetae present between notopodia and neuropodia of chaetiger 1.

Notochaetae of chaetiger 2 as 7 capillaries—3 long hirsute in distal half, 2 short and 2 long smooth capillaries. Neurochaetae of chaetiger 2 composed of single short lower hirsute capillary, 2 thick curved hirsute spines (Fig. 3a–b) and 2 slightly longer upper hirsute capillaries. Chaetigers 3–4 with similar chaetal arrangement to

chaetiger 2, with capillaries longer than in chaetiger 2. Notochaetae of chaetiger 5 as five capillaries; short to long, proximal part of the shaft smooth, distal half hirsute. Neurochaetae of chaetiger 5 composed of single short lower hirsute capillary; single slender, almost straight hirsute spine (Fig. 3a, e); three shorter upper hirsute capillaries. Remaining parapodia composed of capillaries only. Until chaetiger 15 in notopodia and chaetiger 17 in neuropodia, capillaries mainly hirsute or spinose or smooth, differing in length and thickness of the shaft and the degree of ornamentation. Short, slender capillaries have ornamentation along most of the shaft, in longer and thicker capillaries ornamentation restricted to distal half of the chaeta. Plumose capillaries (Figs. 4c and 5d) appear from chaetiger 15 in notopodia and chaetiger 17 in neuropodia, becoming a prevalent type in the remaining parapodia, although combination of all capillaries continues till end of fragment. Posterior chaetigers and pygidium unknown.

**Molecular information.** The 16S sequence of *P. brenkei* sp. nov. matches two sequences from another area (BGR) in the eastern CCZ labeled as *Poecilochaetus* sp. 18 PB (Bonifácio et al. 2020, GenBank accession numbers MK970939, MK971102). The uncorrected (*p*) values among the sequences range between 0.0 and 0.017, while the uncorrected (*p*) distance to two other *Poecilochaetus* species is 0.24. The COI sequence from the holotype of *Poecilochaetus brenkei* sp. nov. is similar to five already published sequences on GenBank from another CCZ study labeled as *Poecilochaetus* sp. NB (Janssen et al. 2015, GenBank accession numbers KJ736555–KJ736559), but differs from these with an uncorrected (*p*) distance of 0.07. The uncorrected (*p*) distance among the five published GenBank sequences range from 0.0 to 0.007. In the phylogenetic tree, the new species is basal in a clade of other *Poecilochaetus* sequences obtained from GenBank, but support for the *Poecilochaetus* clade is low (Fig. 6). The *Poecilochaetus* clade falls within Spionidae, although its position within the family is unresolved (Fig. 6).

**Remarks.** Six ABYSSLINE specimens assigned to the genus *Poecilochaetus* were examined for their morphology (Figs. 7a–h and 8a–b). The 16S molecular data showed only limited variation (see “Molecular information” section above) suggesting that specimens belong to the same species, while morphological investigation showed variation in size, color/sediment covering of body, shape of prostomium, and development of parapodial lobes on chaetiger 11 (Fig. 7a–h). If these differences should be considered of inter- or intra-specific variability remains unresolved. In the case of paucity of morphological data, the evidence from more variable genes such as COI could provide further insight, but such data are

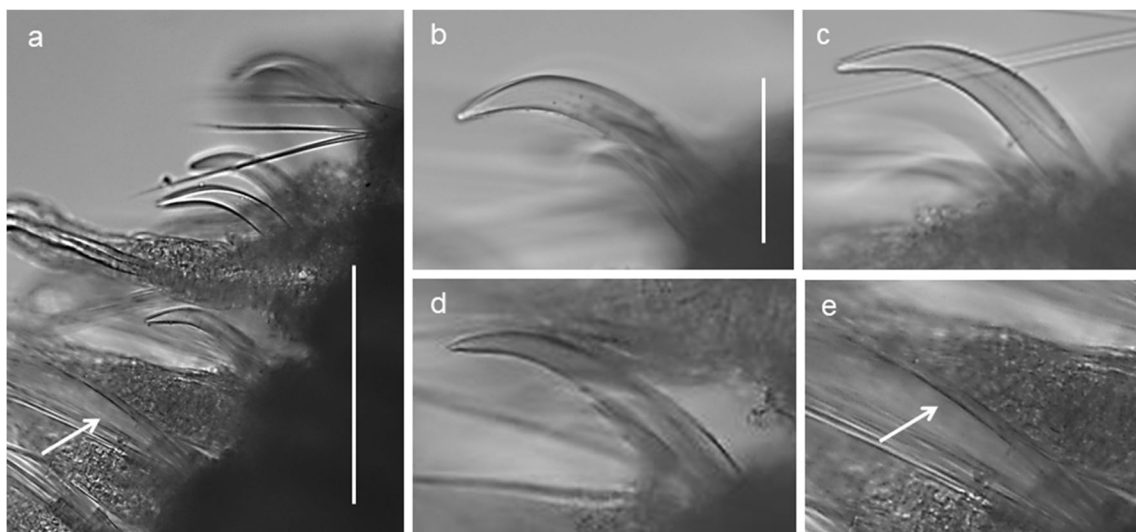


**Fig. 2** *Poecilochaetus brenkei* sp. nov., holotype NHMUK.ANEA.2021.1 **a** specimen in dorsal view; **b** detail of anterior end with prostomium highlighted by line drawing; **c** postchaetal lobe from chaetiger 1; **d** neuropodial postchaetal lobe from chaetiger 2; **e** ampullaceous

postchaetal lobes; **f** unequal postchaetal lobes in chaetiger 11; **g** postchaetal lobes from chaetigers 12–16; **h** postchaetal lobe from chaetiger 30. Scale bars: a 1000  $\mu$ m; c–h 250  $\mu$ m

currently unavailable for some of the specimens. Chaetae, a very diverse and important character in *Poecilochaetus* (Mackie 1990, Santos and Mackie 2008), need to be observed in great detail, throughout the series of parapodial

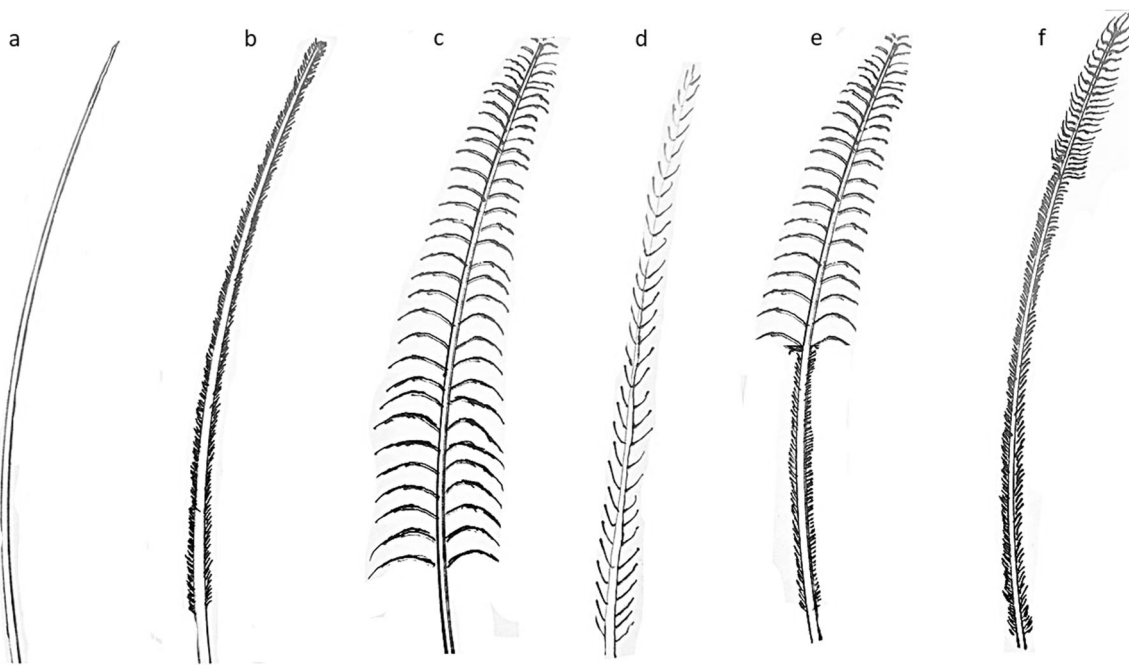
transections, leading to the destruction of the few fragile specimens available for this study, particularly as SEM observations may be necessary to fully understand the chaetal morphology. Additionally, some chaetae, such as notopodial



**Fig. 3** *Poecilochaetus brenkei* sp. nov., holotype NHMUK.ANEA.2021.1 **a** neuropodial spines in chaetiger 2-5, the slender spine on chaetiger 5 highlighted by arrow; **b** detail of spine from chaetiger 2; **c** detail of spine

from chaetiger 3; **d** detail of spine from chaetiger 4; **e** detail of spine from chaetiger 5 shown by arrow. Scale bars: 100  $\mu$ m





**Fig. 4** *Poecilochaetus brenkei* sp. nov., holotype NHMUK.ANEA.2021.1, line drawing representing the main types of capillaries **a** smooth; **b** hirsute (hairy); **c** plumose; **d** spinulose; **e** mixed hirsute-plumose, **f** mixed spinulose-plumose. Drawing not to scale

spines, are limited to the posterior region only (if at all present) in *Poecilochaetus* and all ABYSSLINE specimens are posteriorly incomplete.

Interestingly, all ABYSSLINE *Poecilochaetus* specimens share one important character, which sets them apart from all known *Poecilochaetus* species, the presence of spines in neuropodia of chaetigers 2–5 (Figs. 3a–e and 9a, c, d), while all known species have such distribution confined to chaetigers 2–3 or 2–4, although the spine in chaetiger 5 differs in morphology to those from chaetigers 2–4 by being slenderer and straighter rather than robust and curved. However, as mentioned above, some morphological differences were observed, and having only 16S sequences available for species delimitation we currently cannot determine with certainty if more than one species sharing the same spinal character are present in our samples. In order to avoid future taxonomic confusion, we prefer to base the formal description solely on specimen NHMUK ANEA.2021.1 (holotype of *P. brenkei* sp. nov.), for which both 16S and COI data are available. The rest of the material is discussed in this section as *Poecilochaetus* sp.

*Poecilochaetus* sp. (specimen NHM\_2192) is morphologically most aberrant as it is much bigger than the others (Fig. 7c, d). Thus, the observed morphological differences may be related to its size, given that this specimen shares the main character of *P. brenkei* sp. nov., the presence of spines in chaetigers 2–5. However, it also differs in the form of prostomium (Fig. 7d) and the size of lobes on chaetiger 11, which are equal, not unequal as in other specimens.

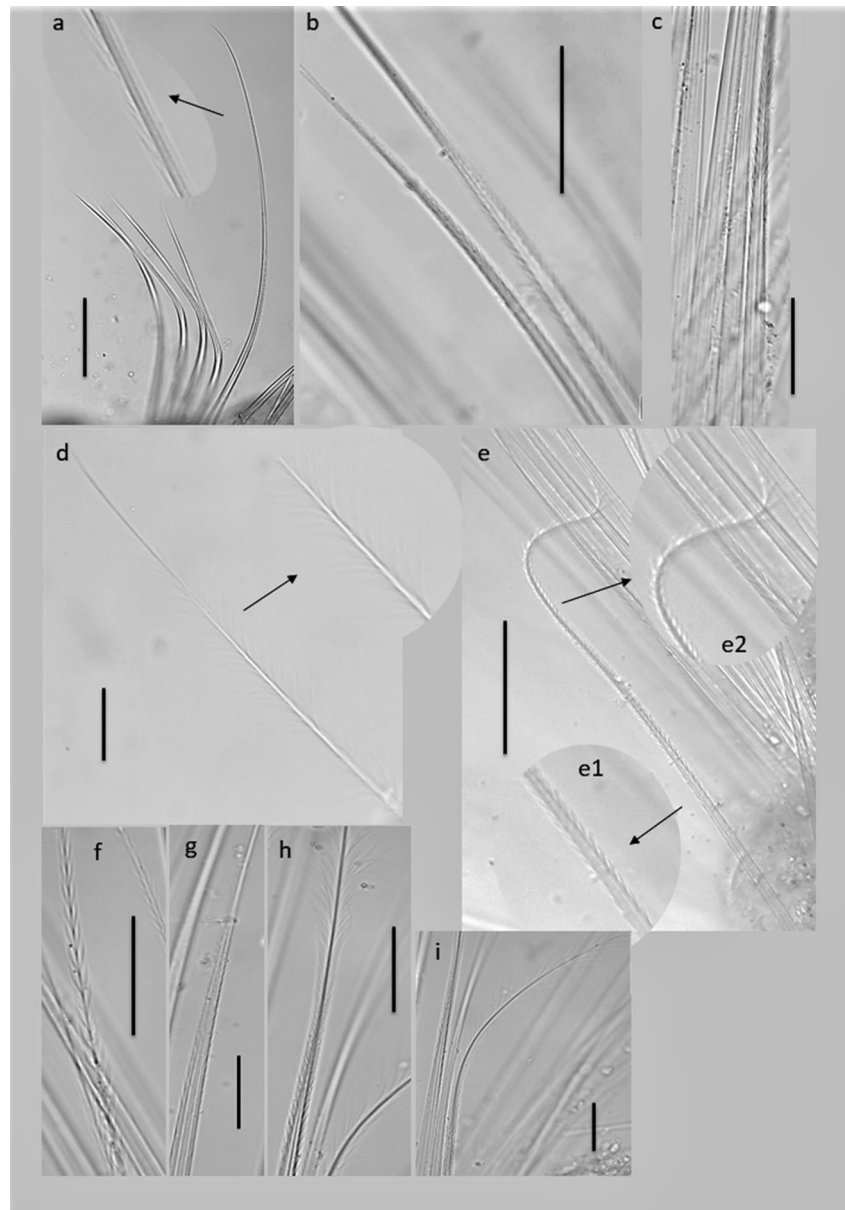
*Poecilochaetus* sp. (specimen NHM\_1948A) differs from all other specimens in not being covered by sediment and being white (Fig. 7f). This specimen was also imaged using SEM (Fig. 8a–b) and confirmed the presence of neuropodial spines in chaetigers 2–5 (Fig. 9c–d).

*Poecilochaetus* sp. (specimens NHM\_2526, NHM\_1668A, and NHM\_1797B) are most similar to *P. brenkei* sp. nov. morphologically (Fig. 7e, g, h) in terms of size, sediment coverage, prostomium shape, and the length of the lobes. The presence of neuropodial spines has also been confirmed. However, all anterior fragments are less than 15 chaetigers long and often too damaged for a meaningful comparison with specimen NHMUK.ANEA.2021.1, assigned to *P. brenkei* sp. nov.

Of the known species *Poecilochaetus brenkei* sp. nov. is closest in morphology to bathyal *P. fulgoris*, a poorly known species described from a single fragmented specimen (see also earlier Remarks under genus *Poecilochaetus*). The new species differs from *P. fulgoris* in the distribution of anterior neurochaetal spines found in chaetiger 2–5 rather than 2–4 as well as the form of spines, which are more strongly hooked in *P. fulgoris* (Fig. 9b).

**Distribution.** *Poecilochaetus brenkei* sp. nov. has been found in the UK-1 area in the eastern CCZ. Other specimens assigned to *Poecilochaetus* sp. were found in the UK-1 area and OMS area in the eastern CCZ. Barcode data indicate that the species occur in additional exploration contract areas in the eastern CCZ.

**Fig. 5** *Poecilochaetus brenkei* sp. nov., holotype NHMUK.ANEA.2021.1 **a** chaetae from chaetiger 1, with detail of ornamentation from the long chaetae of chaetiger 1; **b** example of hirsute chaetae; **c** bases on capillaries from chaetiger 3 showing a variable development of thickness and ornamentation from smooth to hirsute; **d** plumose chaeta from chaetiger 35; **e** mixed chaeta of basally spinose insert e1, distally plumose insert e2 type from chaetiger 35; **f** spinulose chaeta from chaetiger 35; **g** example of basally hirsute distally smooth chaeta; **h–i** mixed chaetae of basally hirsute and distally plumose type from chaetiger 35. Scale bars: **a** 100  $\mu$ m; **b, c, d, g, h, i** 25  $\mu$ m; **e** 50  $\mu$ m



**Etymology.** This species is named for Nils Brenke, who was responsible for deploying and recovering the epibenthic sledges on the first cruise (AB01) (see also Brenke 2005).

**Spionidae Grube, 1850**

**Spionidae sp. NHM\_017**

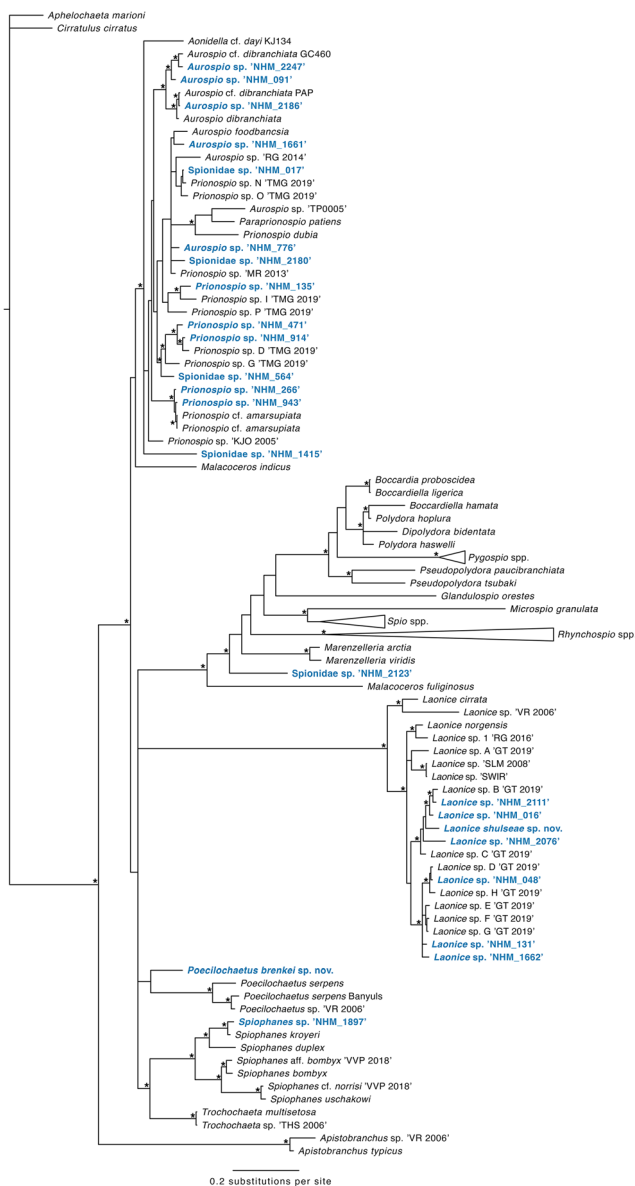
Fig. 10a–d

**Material examined:** NHM\_017, NHMUK ANEA.2021.7, coll. 9 Oct. 2013, collection method: Brenke Epibenthic Sledge, 13°50.232N, 116°33.506W, 4336 m.

**Description:** Single poorly preserved specimen, small and slender; now in two fragments—anterior fragment with 8 discernible chaetigers, 0.9 mm long and 0.25 mm wide and body fragment with about 7 discernible chaetigers. Color in alcohol pale yellow, without distinct pigmentation (Fig. 10a).

Prostomium anteriorly rounded, longer than wide, extending into blunt caruncle to beginning of chaetiger 2, without peaks. Eyes absent. Peristomium as narrow hood around prostomium, not forming lateral wings; dorsally not fused. Palps missing.

Parapodial lamellae and branchiae not observed, either missing or damaged.



**Fig. 6** Phylogenetic analysis of Spioniformia. 50% majority rule tree from the Bayesian analyses using 18S and 16S or COI, with significant posterior probability values on nodes marked by asterisks. Sixty-five taxa from GenBank were included (clades of the genera *Spio*, *Pygospio* and *Rhynchospio* collapsed) with Cirratulidae as outgroup

Chaetae of three types: capillaries, hooded hooks (Fig. 10b, c) and slender sabre chaetae (Fig. 10d). Eight chaetiger long anterior fragment with capillaries only. Long, limbate and rather slender sabre chaetae observed in neuropodia of body fragment; granulation not detected. Multidentate hooded hooks observed in neuropodia of body fragment; up to 6 per fascicle. Hooded hooks long and slender, with several small teeth above the main fang as observed under light microscopy (Fig. 10b, c); with inflated, rounded, anteriorly somewhat truncated hood and rudimentary secondary hood (Fig. 10b).

Notopodial hooded hooks not observed in available fragments. The rest of body and pygidium unknown.

**Molecular information:** The 16S sequence from this species does not match any sequences published on GenBank. In the phylogenetic tree (Fig. 6), this species falls in a low-support clade of mainly undescribed species assigned to *Aurospio* (including three morphospecies from this study) and *Prionospio*, and three known species—*Aurospio foodbancksia* Mincks, Dyal, Paterson, Smith & Glover, 2009 (in Mincks et al., 2009); *Prionospio dubia* Day, 1961; and *Paraprionospio patients* Yokoyama, 2007.

**Remarks:** The available fragment is in particularly poor morphological condition and cannot be morphologically compared with other species. Form of prostomium and the form and distribution of neuropodial hooded hooks suggest that this species may belong to *Prionospio*–*Aurospio* complex.

**Distribution:** This species is only known from UK-1 exploration area in the eastern CCZ.

**Spionidae sp. NHM\_564**

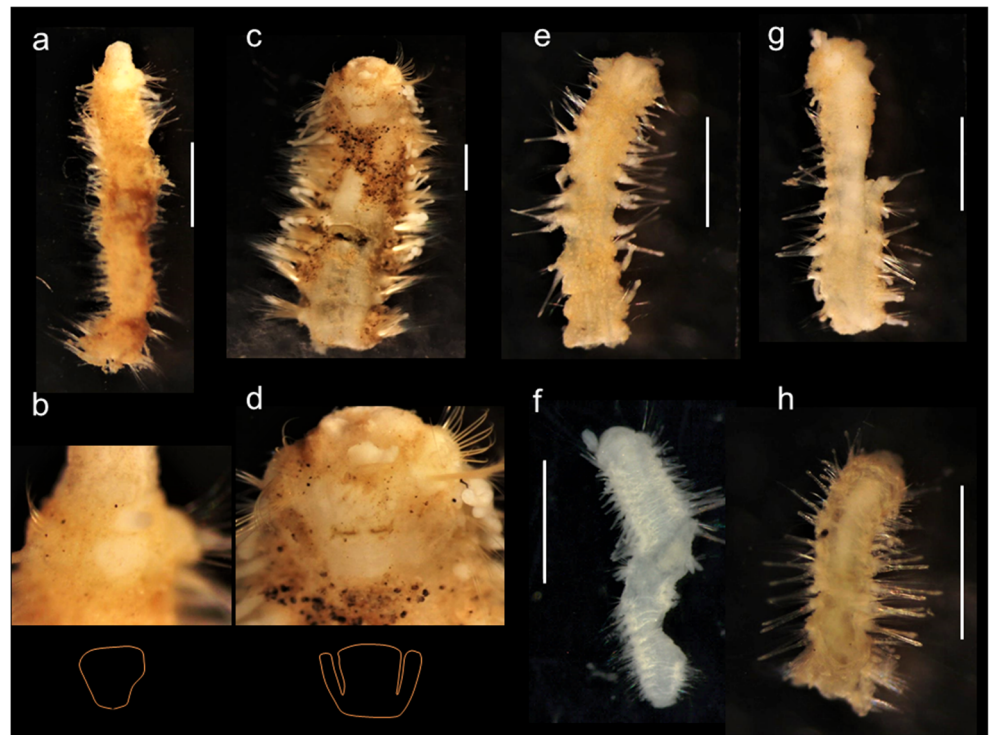
**Material examined:** NHM\_564, NHMUK ANEA.2019.10013, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_1507, NHMUK ANEA.2021.43, coll. 04 Mar. 2015, collection method: USNEL Box Core, 12°27.107N, 116°30.736W, 4196 m.

**Description:** Small, slender species represented by two very poorly preserved anterior fragments, consisting of anterior fragment with damaged prostomium and about 10 discernable damaged chaetigers; both fragments less than 1 mm in length.

**Molecular data.** The two 16S sequences from this species matches one sequence from another study labeled as Spionidae sp. 159-Ifr-0510 (Bonifácio et al. 2020, GenBank accession number MK970921), the uncorrected (*p*) distances among the three sequences are 0.0, extending this species distribution to the Ifremer exploration contract area in the eastern CCZ. This species falls into a well-supported clade of *Prionospio*, *Aurospio*, and *Paraprionospio* species (Fig. 6).

**Remarks.** Image of live specimen NHM\_564 (Fig. 11) shows a relatively well-preserved about 20 chaetiger long anterior fragment. However, only limited morphological details of taxonomic value can be observed from this image and the current state of both specimens renders them of no value for morphological observations. Therefore, this species is represented best by its molecular data.

**Fig. 7** Images of preserved specimens of *Poecilochaetus* specimens examined from the ABYSSLINE collection, all specimens in dorsal view **a** holotype (NHMUK.ANEA.2021.1) of *Poecilochaetus brenkei* sp. nov.; **b** anterior end of holotype (NHMUK.ANEA.2021.1) of *Poecilochaetus brenkei* sp. nov., with line drawing of prostomium; **c** *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.6; **d** *Poecilochaetus* sp., anterior end of specimen NHMUK.ANEA.2021.6, with line drawing of prostomium; **e** *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.2; **f** *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.5; **g** *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.4; **h** *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.3. Scale bars: 1000  $\mu$ m



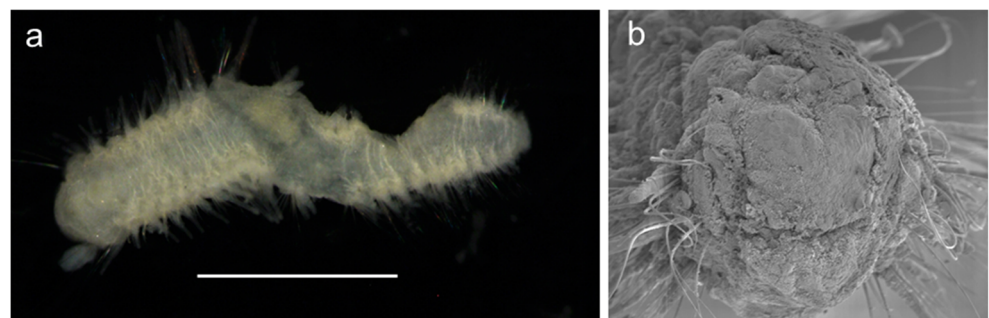
**Distribution:** This species is known from UK-1 and Ifremer exploration contract areas in the eastern CCZ.

#### *Spionidae* sp. NHM\_1415

Fig. 12a–c

**Material examined:** NHM\_520, NHMUK ANEA.2021.53, coll. 16 Feb. 2015, collection method: USNEL Box Core, 12°24.977N, 116°42.891W, 4127 m; NHM\_1544, NHMUK ANEA.2019.10040, coll. 06 Mar. 2015, collection method: USNEL Box Core, 12°30.382N, 116°29.073W, 4244 m; NHM\_1025C, NHMUK ANEA.2019.10029, coll. 24 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°08.02N, 117°17.52W, 4122 m; NHM\_1415, NHMUK ANEA.2019.10039, coll. 02 Mar. 2015, collection method: USNEL Box Core, 12°27.066N, 116°35.661W, 4130 m.

**Fig. 8** *Poecilochaetus* specimen NHMUK.ANEA.2021.5 **a** stereomicroscopy image, specimen in dorsal view; **b** SEM micrograph, anterior end with detail of prostomium. Scale bar: (a) 1000  $\mu$ m

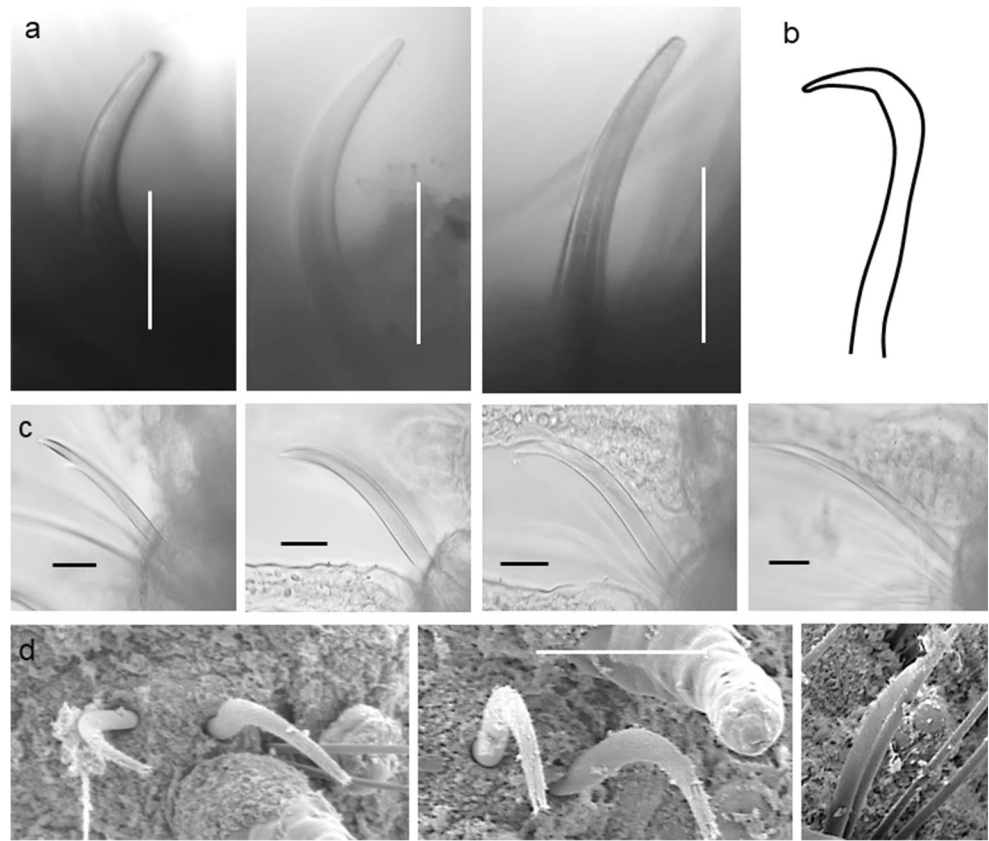


**Description:** Small, slender species represented by four poorly preserved, posteriorly incomplete specimens. The best example, specimen NHM\_1415, consisting of an anterior fragment with about 13 discernable chaetigers, 2.3 mm long and 0.25 mm wide and body fragment with about 10 chaetigers (Fig. 12a). Color in alcohol pale yellow.

Prostomium and peristomium not clearly observed. Parapodia mostly damaged or missing. Branchiae not observed, assumed missing.

Chaetae of three types: capillaries, hooded hooks (Fig. 12b), and sabre chaetae (Fig. 12c). The exact start of sabre chaetae and neuropodial hooded hooks unknown, first sabre chaeta observed in neuropodia of ca. chaetiger 15, first neuropodial hooks observed in neuropodia of ca. chaetiger 18. Sabre chaeta stout, curved, limbate. Hooded hooks, up to 5 per fascicle; long and slender, with large, blunt main fang and about 3 small teeth, observed under light microscopy (Fig. 12b); with rounded hood, secondary

**Fig. 9** Examples of neuropodial spines from *Poecilochaetus* sp. found in ABYSSLINE samples, unless stated otherwise **a** sequence of neuropodial spines from chaetigers 2–4 (spine on chaetiger 5 broken off, not imaged) of *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.6; **b** neuropodial spine characteristic of chaetigers 2–4 of *Poecilochaetus fulgoris* (after Claparède in Ehlers, 1875); **c** sequence of neuropodial spines from chaetigers 2–5 of *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.5; **d** SEM micrograph of sequence of neuropodial spines from chaetigers 2–5 of *Poecilochaetus* sp., specimen NHMUK.ANEA.2021.5. Scale bars: **a** 100 µm; **c** 25 µm; **d** 50 µm

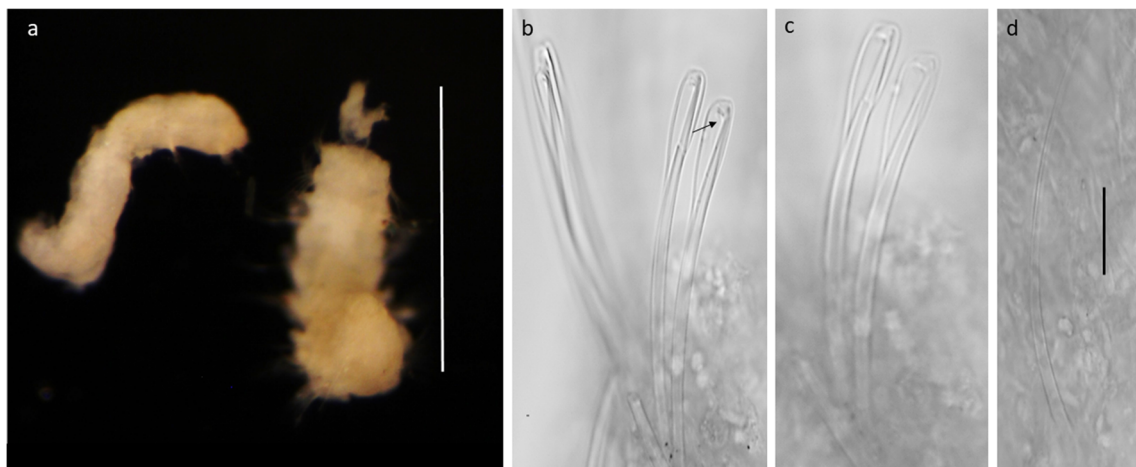


hood not observed (Fig. 12b). Notopodial hooded hooks not observed in available fragments. The rest of body and pygidium unknown.

**Molecular information:** The three 16S sequences from this species does not match any other sequences from the CCZ, the uncorrected (*p*) distances among the three sequences range

from 0.002 to 0.009. In the phylogenetic tree (Fig. 6) this species falls into a clade containing *Prionospio*, *Aurospio*, and *Paraprionospio* species.

**Remarks:** This poorly preserved species cannot be morphologically compared with other species and is therefore best represented by the molecular data.



**Fig. 10** Spionidae sp. NHM\_017, specimen NHMUK.ANEA.2021.7 **a** fragmented preserved specimen with body segments (left) and anterior fragment with prostomium in dorsal view (right); **b** fascicle of

neuropodial hooded hooks from body fragment, with secondary hood marked by arrow; **c** details of neuropodial hooded hooks; **d** slender neuropodial sabre chaeta. Scale bars: **a** 1000 µm; **b**, **d** 25 µm

**Distribution:** This species is only known from UK-1 claim area in the eastern CCZ and OMS-1 area.

### Spionidae sp. NHM\_2123

Fig. 13a, b

**Material examined:** NHM\_2123, NHMUK ANEA.2021.45, coll. 20 Mar. 2015, collection method: Brenke Epibenthic Sledge, 19 27.874 N, 120 01.525W, 4026 m.

**Description:** Poorly preserved single specimen represented by anterior fragment consisting of ca. 20 discernible chaetigers, 3.2 mm long and 1.9 mm wide at the widest part. Body very broad and dorsoventrally flattened anteriorly (Fig. 13a, b), color in ethanol pale yellow, anterior half of prostomium with distinct reddish pigmentation (Fig. 13b). Prostomium narrow, oval, with rounded anterior margin and posteriorly narrowing into caruncle. Pair of short, thick, grooved palps attached (Fig. 13b). Branchiae mostly missing or damaged. Only capillary chaetae observed in available fragment.

**Molecular information:** The COI and 16S sequences from this species do not match any other sequences from the CCZ. In the combined 18S and 16S tree (Fig. 6), it sits basally to a clade with several spionid genera, with no affiliation to any specific genus.

**Remarks:** Specimen is too poorly preserved for further identification or comparison. Within the ABYSSLINE spionid collection, this species can be morphologically distinguished by its very broad and flattened body.

**Distribution:** This species is only known from APEI-6, an area preliminary designated as a preservation area.

**Fig. 11** Live image of Spionidae sp. NHM\_564, specimen NHMUK.ANEA.2019.10013



### Spionidae sp. NHM\_2180

Fig. 14

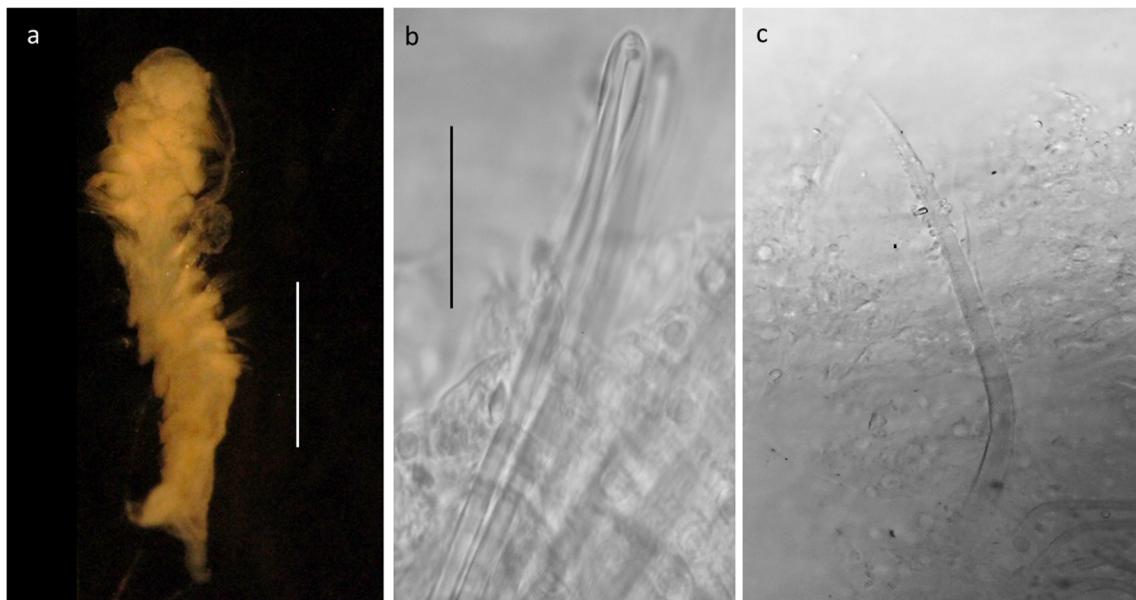
**Material examined:** NHM\_2180, NHMUK ANEA.2021.8, coll. 21 Mar. 2015, collection method: USNEL Box Core, 19 27.998N, 120 00.172W, 4141 m.

**Description:** Single poorly preserved specimen, small and slender, 1.6 mm long and 0.25 mm wide, anterior fragment with about 13 discernible chaetigers. Color in alcohol pale yellow, with faint gold-brown pigmentation around caruncle (Fig. 14a). Prostomium anteriorly rounded, longer than wide, extending into blunt caruncle to beginning of chaetiger 2, without peaks. Eyes absent. Peristomium as narrow hood around prostomium, not forming lateral wings; dorsally not fused. Palps missing. Parapodial lamellae often damaged or missing, all lamellae relatively small, but large subtriangular notopodial lamellae observed on chaetiger 3. Anterior neuropodial lamellae rounded, largest on chaetiger 3. Only capillary chaetae observed in the available fragment, chaetae particularly long in chaetiger 3. Multidentate hooded hooks in notopodia or neuropodia and sabre chaetae not observed in the available fragment. The rest of body and pygidium unknown.

**Molecular information:** The COI and 16S sequences from this species do not match anything published on GenBank. This species falls into a well-supported clade of *Prionospio*, *Aurospio*, and *Paraprionospio* species (Fig. 6).

**Remarks:** The available fragment is in particularly poor morphological condition and cannot be meaningfully compared with other species.

**Distribution:** This species is only known from APEI-6.



**Fig. 12** Spionidae sp. NHM\_1415, specimen NHMUK.ANEA.2019.10039 **a** preserved specimen in dorso-lateral view; **b** neuropodial hooded hooks from chaetiger 18; **c** neuropodial sabre chaeta from chaetiger 15. Scale bars: **a** 1 mm; **b** 25  $\mu$ m; **c** 50  $\mu$ m

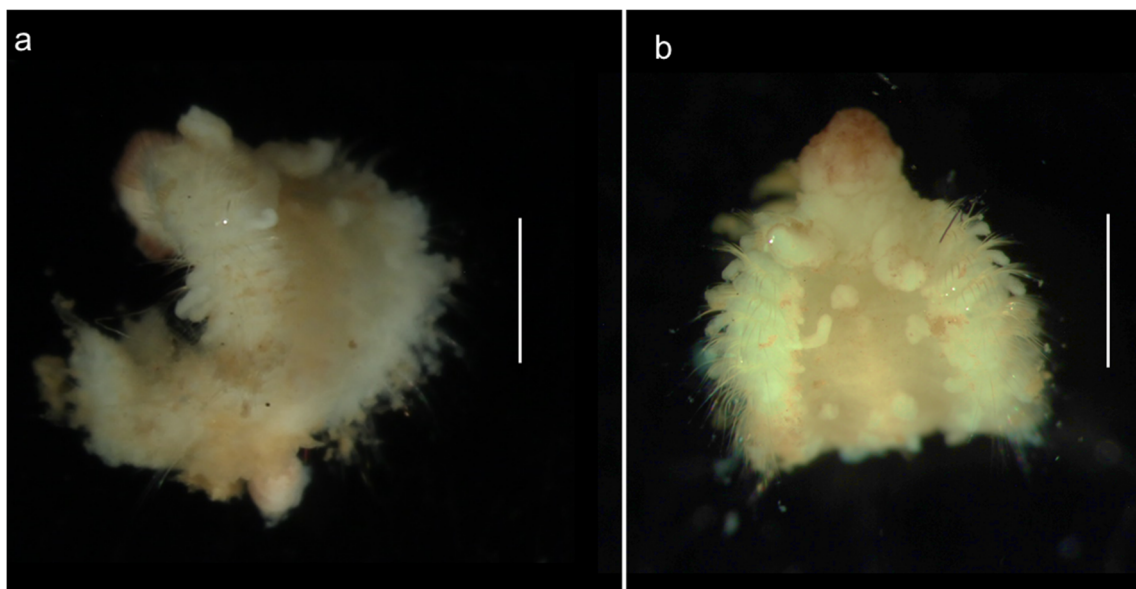
### *Aurospio* Maciolek, 1981

Type species: *Aurospio dibranchiata* Maciolek, 1981

**Definition:** Small and slender body. Prostomium anteriorly rounded, occipital antenna absent. Branchiae starting from chaetiger 3, small, maybe fused or free from notopodial lamellae or entirely absent. Neuropodial hooded hooks and sabre chaetae present.

**Remarks:** Definitions of *Aurospio* and closely related genus *Prionospio* are problematic and a matter of debate (e.g., Sigvaldadóttir 2002; Mincks et al. 2009; Paterson et al. 2016; Blake et al. 2017; Peixoto and Paiva 2019). It is generally agreed

upon that the taxonomic reliance on number, form, and distribution of branchiae is problematic, particularly given the recent discoveries of abranchiate species (Paterson et al. 2016, Peixoto and Paiva 2019). While the initial definition of *Aurospio* by Maciolek (1981) is too restrictive (almost equaling the specific definition), subsequent authors expanded the definition to include species in which branchiae start from chaetiger 3 instead of 2 as in *Prionospio* (Sigvaldadóttir 2002; Mincks et al. 2009; Paterson et al. 2016) or display the ultimate branchial reduction by becoming abranchiate, but with large quadrate notopodial lamellae (Paterson et al. 2016). The most recent attempt at



**Fig. 13** Preserved specimen NHMUK.ANEA.2021.45 of Spionidae sp. NHM\_2123 **a** specimen in dorsolateral view; **b** anterior end in dorsal view. Scale bar: 1 mm



**Fig. 14** Spionidae sp. NHM\_2180, preserved specimen NHMUK.ANEA.2021.8 in dorsal view. Scale bar: 500  $\mu$ m.

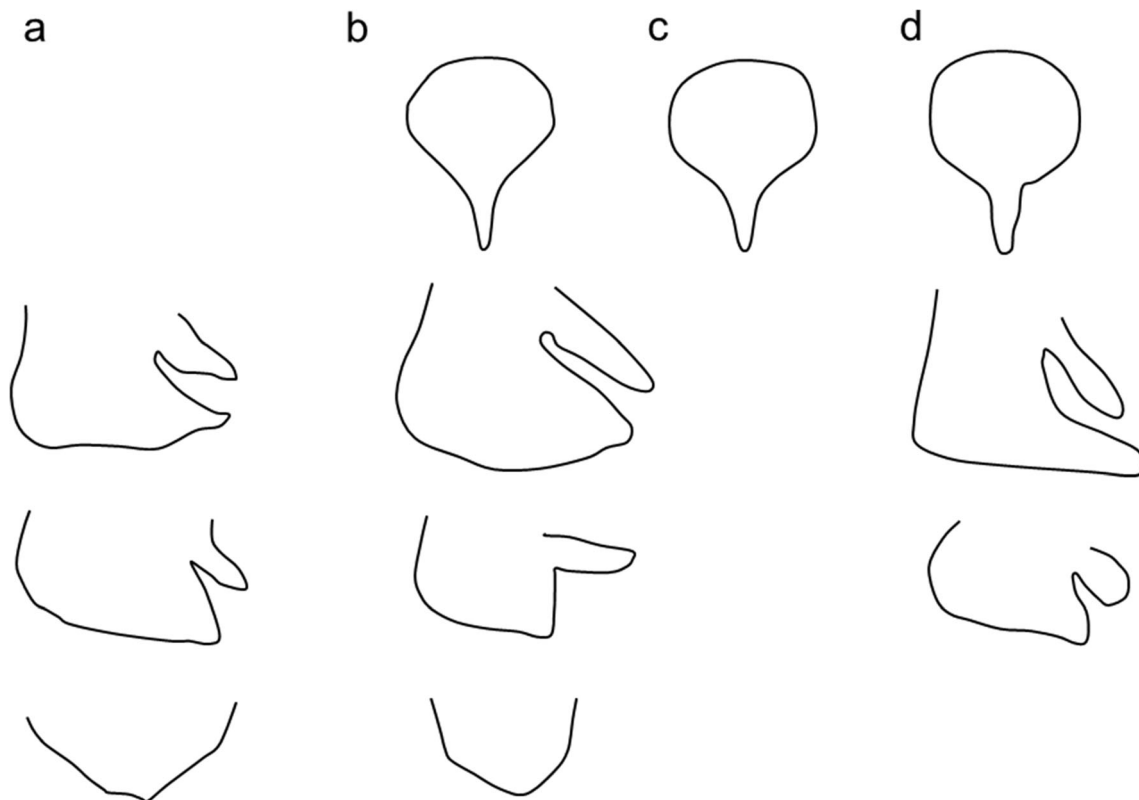
distinguishing *Aurospio* and *Prionospio* has been made by Blake et al. (2017), followed by Peixoto and Paiva (2019) who considered the fusion of branchiae to notopodial lamellae, the start of branchiae form chaetiger 3 and the absence of secondary hood in the hooks to be the defining characters of *Aurospio*. Currently there are six valid species of *Aurospio*, although Blake et al. (2017) argue that the genus is monotypic with *Aurospio dibranchiata*, its type species, the only valid species. Finally, the genetic data available so far suggest that there is no distinction between *Aurospio* and *Prionospio* (Fig. 6 this study; Guggolz et al. 2020), but currently no molecular data are available from the type localities, preventing firm conclusions.

*Aurospio dibranchiata*, the type species of genus *Aurospio*, is an often-reported deep-sea species. Although Maciolek (1981) designated the type specimens from Argentine Basin, SW Atlantic, depth range ca. 1600–2000 m, she considered the range of this species based on all material examined to be very large both geographically (pan-Atlantic) and bathymetrically (300–3600 m). Since the original publication this species has also been reported from the abyssal Pacific (e.g., Mincks et al. 2009) and Southern Oceans (e.g., Neal et al. 2018a). However, as our current (Fig. 6) and previously published (Neal et al. 2018b; Guggolz et al. 2020) molecular data

suggest, the specimens identified as *A. dibranchiata* in fact represent genetically distinct species. Three of those species, *Aurospio* sp. NHM\_091, *Aurospio* sp. NHM\_2186, and *Aurospio* sp. NHM\_2247, were collected from CCZ during ABYSSLINE cruises and will be further described in this publication.

Maciolek (1981) noted a remarkable consistency of taxonomic characters in *A. dibranchiata* over its wide geographic and bathymetric range. However, at the same time Maciolek (1981) reported some morphological variations, which were interpreted as within species, regional or preservation-related differences: the presence/absence of tiny prostomial peaks, the strength of pigmentation in the peristomium/first chaetiger, the variability in the start of neuropodial hooks over chaetigers 9–11, and the presence/absence of dorsal crests. While Maciolek (1981) elected the type specimens (those collected from Argentine Basin, SW Atlantic, depth range ca. 1600–2000 m), it appears that the original description is based on a collection of observations from all specimens in the material examined section, which may in fact belong to different species (for example, some specimens with 3 pairs of branchiae were considered an aberrant form of *A. dibranchiata*). This is further supported by our re-examination of *A. dibranchiata*





**Fig. 15** *Aurospio* sp. NHM\_091 (aff. *dibranchiata*). Line drawings of sequences (top to bottom) of intraspecific variation in prostomial shapes and notopodial lamellae (ntl) from chaetigers (ch) 3–5, drawings omitted where no clear observation was possible **a** sequence of specimen NHMUK.ANEA.2019.10001 (prostomium omitted, too damaged): ntl from ch 3, ntl from ch 4, ntl from ch 5; **b** sequence of specimen

NHMUK.ANEA.2019.10036: prostomium, ntl from ch 3, ntl from ch 4, ntl from ch 5; **c** prostomium of specimen NHMUK.ANEA.2019.10038, all ntl omitted; **d** sequence of specimen NHMUK.ANEA.2019.10049: prostomium, ntl from ch 3, ntl from ch 4, ntl from ch 5 omitted (not observed)

paratypes (BMNHUK.1981.82-91) deposited at NHMUK London (see details below) as part of this study. Therefore, until *A. dibranchiata* is re-defined more restrictively with molecular data from the type locality, the recognition and subsequent description of new species will be problematic (see also discussion in Paterson et al. 2016; Peixoto and Paiva 2019).

Having examined the newly collected CCZ material and Maciolek's paratypes (BMNH.1981.82-91), we investigated if variations reported by Maciolek (1981) as well as additionally observed characters could be considered of inter-specific importance. Based on our observations, the following characters were found to be variable within genetically defined species (comparative Fig. 15a–d) to the same degree as between genetically defined species (comparative Figs. 16a–d and 17a–d) and therefore cannot be considered as taxonomically informative. **Prostomium shape**, while generally best described as tear-shaped, differs in broadness and the abruptness of the narrowing into caruncle (Figs. 15a–d and 16a–d). **Branchial size**, although branchiae are always fused to notopodial lamellae and short (never longer than the corresponding notopodial lamellae), their size and the degree of fusion with the lamella can differ (Figs. 15a–d and 17a–d). The shape and

size of **parapodial lamellae** are considered taxonomically informative in closely related genus *Prionospio* (e.g., Sigvaldadóttir 1998; Paterson et al. 2016; Peixoto and Paiva 2019), but the observations so far have proved problematic in *A. dibranchiata* as the size and shape of lamellae can vary (Figs. 15a–d and, 17a–d), sometimes even the left and right lamellae of the same chaetiger can differ (Neal pers. obs.). The presence/absence and development of **dorsal crests** also appear to be variable.

No differences were observed in the distribution of **neuropodial hooks** (Fig. 18a–c) from Maciolek paratypes and these hooks were consistently found from chaetiger 10, a most commonly reported chaetiger by Maciolek (1981). However, the **secondary hood** of the hooks, which absence of was considered a genus-level character by Maciolek (1981) (Fig. 18b) and recently by Blake et al. (2017) and Peixoto and Paiva (2019), has been detected in the re-examined paratypes (BMNH. 1981.82-91) (Fig. 18c). Such observation suggests that this character was either previously overlooked or that it is variable, possibly strengthening our hypothesis that several species were in fact present in the material ascribed by Maciolek (1981) to *A. dibranchiata*. It certainly shows that it cannot be used to define the genus *Aurospio* as suggested by

Blake et al. (2017), further complicating the question: What is *Aurospio*?

One character that may warrant further investigation is the development of **peristomium**, which can dorsally form a tight narrow hood (UKSR-1 specimens, Fig. 16a–c, lower row) or flare into lateral wings (Fig. 16d, lower row) as observed in some (but not all) Maciolek's paratypes (BMNH.1981.82-91). The development of lateral wings in peristomium was neither reported, nor pictured by Maciolek (1981), although observed in this study of type material (Fig. 16d, lower row), further suggesting that the original description of *A. dibranchiata* may be problematic.

In the ABYSSLINE-collected material, three species similar to *Aurospio dibranchiata* in having tear-shaped prostomium and small branchiae fused to notopodial lamellae of chaetigers 3 and 4 were found. Further two species are assigned to genus *Aurospio* based on molecular and/or morphological similarity to *Aurospio foodbancsia* Mincks et al. (2009).

#### *Aurospio* sp. NHM\_091

Figs. 15a–d, 16a, 17a, 18a, 19a–d, 20a–d, 22c–d

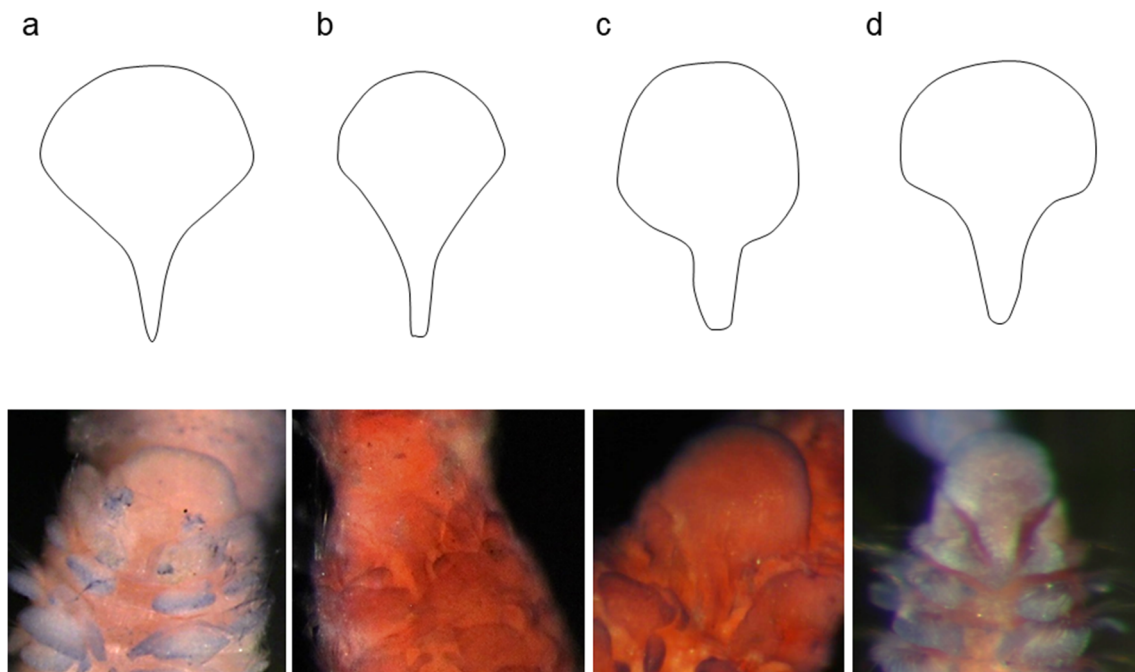
**Material examined:** NHM\_091, NHMUK ANEA.2019.10001, coll. 10 Oct. 2013, collection method: Multi Corer, 13°50.792N, 116°37.590W, 4079 m; NHM\_323, NHMUK ANEA.2019.10010, coll. 18 Oct. 2013, collection method: USNEL Box Core, 13°45.001N, 116°30.799W, 4036

m; NHM\_322, NHMUK ANEA.2019.10009, coll. 18 Oct. 2013, collection method: USNEL Box Core, 13°45.001N, 116°30.799W, 4036 m;

NHM\_134, NHMUK ANEA.2019.10002, coll. 11 Oct. 2013, collection method: Brenke Epibenthic Sledge 02, 13°45.500N, 116°41.911W, 4080 m; NHM\_957C, NHMUK ANEA.2019.10026, coll. 23 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°34.28N, 116°36.63W, 4198 m; NHM\_1668C, NHMUK ANEA.2019.10044, coll. 10 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°21.81N, 116°40.86W, 4233 m;

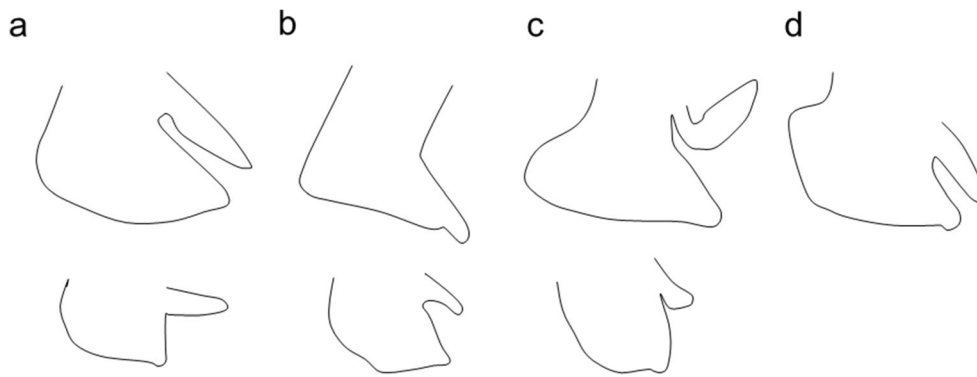
NHM\_1768, NHMUK ANEA.2019.10045, coll. 11 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°10.43N, 117°11.57W, 4045 m; NHM\_1025A, NHMUK ANEA.2019.10028, coll. 24 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°08.02N, 117°17.52W, 4122 m; NHM\_1351D, NHMUK ANEA.2019.10036, coll. 01 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°15.44N, 117°18.13W, 4302 m;

NHM\_1797J, NHMUK ANEA.2019.10047, coll. 11 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°10.43N, 117°11.57W, 4045 m; NHM\_1347G, NHMUK ANEA.2019.10035, coll. 01 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°15.44N, 117°18.13W, 4302 m; NHM\_1351F, NHMUK ANEA.2019.10037, coll. 01 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°15.44N, 117°18.13W, 4302 m; NHM\_1390A, NHMUK



**Fig. 16** Interspecific variation in prostomial shapes of ABYSSLINE *Aurospio dibranchiata*-like species presented as line drawings (top row) and stereomicroscopy images, all specimens stained with Shirlastain (bottom row) **a** ABYSSLINE species *Aurospio* sp. NHM\_91, specimen NHMUK. ANEA.2019.10036; **b** ABYSSLINE species

*Aurospio* sp. NHM\_2186, specimen NHMUK. ANEA.2019.10052; **c** ABYSSLINE species *Aurospio* sp. NHM\_2247, specimen NHMUK.ANEA.2021.9; **d** *Aurospio dibranchiata*, one of paratypes BMNH.1981.82-91



**Fig. 17** Interspecific variation in shapes of notopodial branchiae carrying lamellae of ABYSSLINE-collected *Aurospio dibranchiata*-like species presented as line drawings—chaetiger 3 (top row) and chaetiger 4 (bottom row) **a** ABYSSLINE species *Aurospio* sp. 91, specimen NHMUK.ANEA.2019.10036; **b** ABYSSLINE species *Aurospio* sp.

NHM\_2186, specimen NHMUK. ANEA.2019.10052; **c** ABYSSLINE species *Aurospio* sp. NHMUK\_2247, specimen NHMUK.ANEA.2021.9; **d** *Aurospio dibranchiata*, one of paratypes BMNH.1981.82-91, chaetiger 3 only

ANEA.2019.10038, coll. 02 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°08.695N, 117°19.526W, 4044 m; NHM\_2020, NHMUK ANEA.2019.10049, coll. 16 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°03.03N, 117°24.28W, 4235 m; NHM\_2151, NHMUK ANEA.2019.10050, coll. 20 Mar. 2015, collection method: Brenke Epibenthic Sledge, 19 27.874 N, 120 01.525W, 4026 m; NHM\_2152, NHMUK ANEA.2019.10051, coll. 20 Mar. 2015, collection method: Brenke Epibenthic Sledge, 19 27.874 N, 120 01.525W, 4026 m; NHM\_176, NHMUK ANEA.2019.10004, coll. 13 Oct. 2013, collection method: Brenke Epibenthic Sledge, 13°56.089N, 116°33.011W, 4082 m.

**Description** (based on specimens NHM\_091, NHM\_1390A, NHM\_2020 and NHM\_1351D [SEM specimen]) (Fig. 19a–d). Small slender species represented by 17 posteriorly incomplete specimens, measuring up to 2.8 mm long and up to 0.4 mm wide for max. of 15 discernible chaetigers (specimen NHM\_091 composed of three fragments: anterior fragment with 12 chaetigers and two body fragments of 8 and 10 chaetigers, respectively). Live specimens tanned with distinct orange gut from around chaetiger 10 (Fig. 20a); the color in alcohol pale yellow to tanned (Fig. 20b, c), with reddish pigmentation concentrated near the anterior margin of prostomium and peristomium (best observed in specimen NHM\_1390A (Fig. 20d), now blueish due to retention of Shirlastain, but pigmentation still visible).

Prostomium rounded, widest medially, broadly rounded anteriorly, posteriorly narrowing into caruncle to the end of chaetiger 1, with some variability observed to overall width, abruptness of narrowing into caruncle and robustness of caruncle (Figs. 15b–d and 20a–d). Eyes not observed. Peristomium forms a narrow hood around prostomium, not

forming lateral wings. Palps missing. Pharynx an eversible soft pouch (Fig. 20b).

Branchiae present on chaetigers 3–4 only; both short, smooth, cirriform and basally fused to the corresponding notopodial lamellae (Figs. 15a, b, d and 20a, b, d). Branchiae on chaetiger 3 longer, approaching the length of corresponding notopodial lamellae; branchiae on chaetiger 4 short, stubby, reaching max. 2/3 length of corresponding notopodial lamellae. Cilia not observed.

Parapodial lamellae morphologically plastic, particularly in anterior chaetigers in size and shape (see comparative Fig. 15a, b, d and Fig. 20a–d). In specimens NHM\_091 and NHM\_1351D anterior notopodial lamellae large, almost covering dorsum (Fig. 20a, b), in specimens NHM\_1390A and NHM\_2020 small, with dorsum well exposed (Fig. 20c, d). As a general trend, notopodium of chaetiger 1 reduced to a small rounded lamella. Notopodial lamellae best developed on chaetigers 2–4 (to chaetiger 7 in specimen NHM\_091), with those on chaetiger 3 largest and those on chaetigers 2 and 4 (or 4–7) smaller of similar size (Fig. 20a). Notopodial lamellae on chaetiger 2 subquadrate to broadly rounded (Fig. 20a). Notopodial lamellae on chaetiger 3 broad and foliaceous, with the medial edge prolonged over the dorsum, tip blunt or pronounced (Fig. 15a, b, d and Fig. 20a). Notopodial lamellae on chaetiger 4 broad to subquadrate with short blunt tip (Fig. 15a, b, d and Fig. 20a). Neuropodium of chaetiger 1 reduced to a small rounded lamella. On chaetiger 2, it is a small auricular lobe which becomes larger on chaetiger 3 and then again smaller on chaetiger 4. In general, from chaetiger 5, both noto- and neuropodial lamellae as broadly rounded lobes, getting progressively smaller and lower, with notolamellae being larger in anterior chaetigers (Fig. 20a). Dorsal crests not consistently detected, at best appearing low from chaetiger 5 or 6 but integument often damaged to some

degree. Form of parapodia not established past chaetiger 15 (end of the longest fragment).

Chaetae consist of 3 types: capillaries, ventral sabre chaetae (Fig. 18a), and multidentate hooded hooks (Figs. 18a and 22c–d). Anterior chaetae arranged in 2 rows of longer and shorter limbate capillaries; chaetae particularly long in neuropodia of chaetiger 2. A single heavily granulated and ventral sabre chaeta present from chaetiger 10 (Fig. 18a). Neuropodial hooded hooks first observed in chaetiger 10, with six hooks per fascicle accompanied by two capillaries (in body segments of specimen NHM\_091 up to 12 hooks per fascicle observed). Neuropodial hooks with squarish primary hood, secondary hood not observed; with four slender teeth of unequal size in lateral view (Figs. 18a and 22c–d). Notopodial hooks not observed in available fragments. Mid to posterior chaetigers and pygidium not observed.

**Molecular information.** Seventeen 16S sequences obtained for *Aurospio* sp. NHM\_091 form a well-supported clade (Fig. 6). The 16S sequences from specimens within this species match 15 sequences of *Aurospio* sp. ‘20 PB’ reported from other areas (GSR, Ifremer and IOM) in the eastern CCZ (Bonifácio et al. 2020). The uncorrected (*p*) values among all 32 sequences range between 0.0 and 0.01, while the lowest uncorrected (*p*) distance considered inter-specific (with *Aurospio* sp. NHM\_2247 being the closest species) is 0.08.

**Remarks.** *Aurospio* sp. NHM\_091 is the first of three CCZ collected species so far that correspond well to *Aurospio dibranchiata* based on following characters, the shape of prostomium, two pairs of small branchiae partially fused to notopodial lamellae of chaetigers 3 and 4 and neuropodial hooded hooks from chaetiger 10.

Differentiation of commonly encountered species similar to *Aurospio dibranchiata* is important in order not to overestimate the range of *A. dibranchiata* by lumping similar species together. This information is in turn crucial to the future conservation efforts. However, as already discussed earlier, the problematic definition of *A. dibranchiata* makes comparisons difficult. Such effort is further compounded by the lack of molecular data from the type locality, the plasticity of certain characters as observed in this study and paucity of well-preserved material from the CCZ and deep sea in general. Therefore, we assign these specimens to morphospecies only and identify it primarily by molecular data (Fig. 6). Two other morphologically similar but genetically distinct species have been found in ABYSSLINE samples (see Remarks under *Aurospio* sp. NHM\_2186 and *Aurospio* sp. NHM\_2247).

**Distribution.** Molecular evidence based on 16S suggests that *Aurospio* sp. NHM\_091 is a widely distributed species within the eastern CCZ as it was found in the UKSR-1, OMS-1, GSR, Ifremer, and IOM exploration areas and APEI-6 region.

### *Aurospio* sp. NHM\_2186

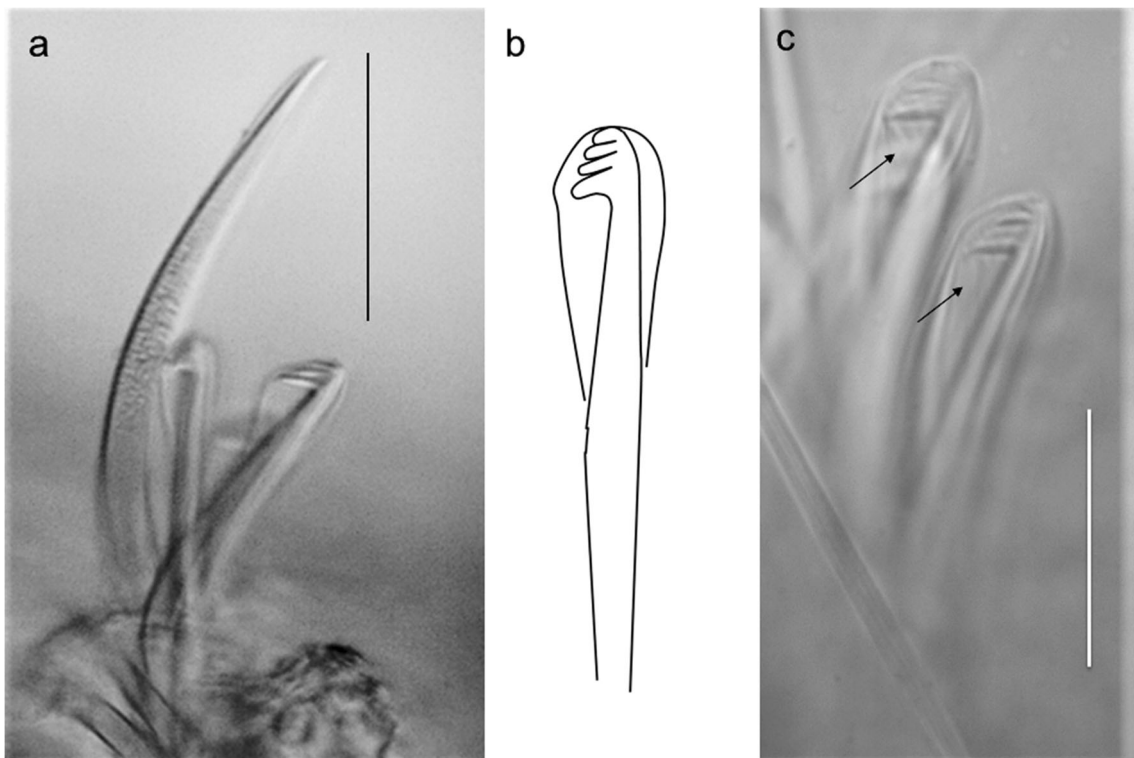
Figs. 16b, 18b, 21a–k, 22e, f

**Material examined:** NHM\_513, NHMUK ANEA.2019.10012, coll. 16 Feb. 2015, collection method: USNEL Box Core, 12°24.977N, 116°42.891W, 4127 m; NHM\_2186, NHMUK ANEA.2019.10052, coll. 22 Mar. 2015, collection method: USNEL Box Core, 19 28.342N, 120 11.495W, 4115 m.

**Description.** Small slender species represented by a posteriorly incomplete specimen (NHM\_2186), now split into anterior fragment 1.3 mm long and 0.3 mm wide for 10 discernible chaetigers and about 7 discernible chaetigers long body fragment; in addition, another example (NHM\_513) represented by around 10 discernible chaetigers long body fragment was observed. Live example observed as tanned body fragment with distinct orange gut (Fig. 21a), the color in alcohol pale yellow (Fig. 21b), pigmentation not observed.

Prostomium rounded, widest medially, broadly rounded anteriorly, posteriorly narrowing into slender caruncle to the end of chaetiger 1 (Figs. 16b and 21c, g). Two pairs of well separated tiny red eyes observed. Peristomium forms a narrow hood around prostomium, not forming lateral wings. Palps missing. Pharynx an eversible soft pouch.

Branchiae present on chaetigers 3–4 only; both short, smooth, cirriform and basally fused to the corresponding notopodial lamellae (Figs. 17b and 21i–j). Branchiae on chaetiger 3 longer, approaching the length of corresponding notopodial lamellae; branchiae on chaetiger 4 short, slender, reaching about 1/2 length of corresponding notopodial lamellae. Cilia not observed. Notopodium of chaetiger 1 rudimentary. Notopodial lamellae best developed on chaetigers 2–5 (Fig. 21d, h–k), with those on chaetiger 3 largest; almost meeting medially, leaving only a part of dorsum exposed. Notopodial lamellae on chaetiger 2 as broadly rounded to subquadrate lobe. Notopodial lamellae on chaetiger 3 broad subquadrate with the medial edge prolonged over the dorsum into elongated produced tip (Figs. 16b and 21i). Notopodial lamellae on chaetiger 4 either broadly conical not produced into short tip (L.H. side, Fig. 21j) or broadly rounded to subquadrate with short produced tip directed medially over dorsum (R.H. side, Fig. 21j). Neuropodium of chaetiger 1 rudimentary; on chaetiger 2 as a small broadly rounded lobe which becomes larger on chaetiger 3 and then again smaller on chaetiger 4. On chaetiger 5, notolamellae remain well developed, as broadly subtriangular lobes (Fig. 21k), with neuropodial lamellae as low broadly rounded lobes. From chaetiger 6, both noto- and neuropodial lamellae as broadly rounded lobes, getting progressively smaller and lower, with notolamellae being larger in anterior chaetigers. On chaetigers 6–7, a very low dorsal crest detected, becoming high and well developed in chaetigers 9–12.



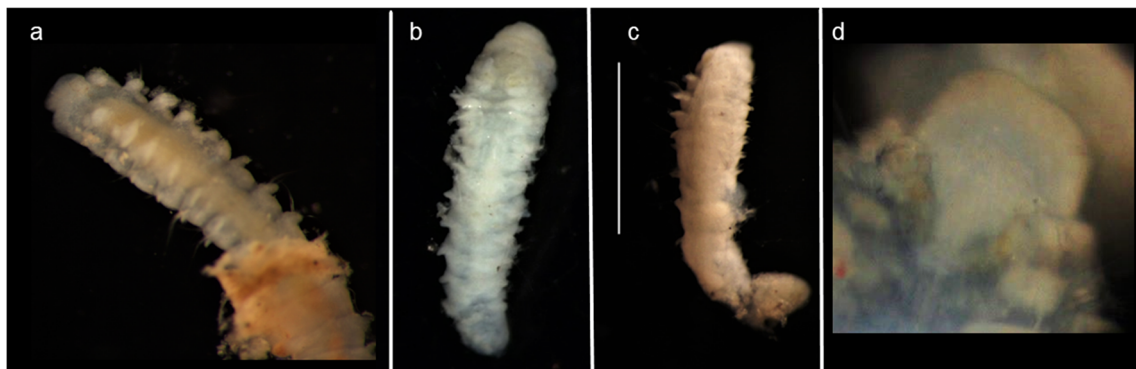
**Fig. 18** Comparison of neuropodial hooded hooks **a** neuro-podial hooded hooks and sabre chaeta from *Aurospio* sp. NHM\_091, specimen NHMUK.ANEA.2019.10001; **b** drawing of neuropodial hooded hook

of *Aurospio dibranchiata* (after Maciolek 1981), secondary hood absent; **c** hooks from paratypes of *Aurospio dibranchiata* BMNH.1981.82-91, with secondary hood present (arrow). Scale bars: **a**, **c** 25  $\mu$ m

Chaetae consist of 3 types: narrowly bilimbate capillaries, ventral sabre chaetae, and multidentate hooded hooks. Anterior chaetae arranged in 2 rows of longer and shorter limbate capillaries; chaetae particularly long in neuropodia of chaetiger 2. A single heavily granulated and ventral sabre chaeta present from chaetiger 10. Neuropodial hooded hooks first observed in chaetiger 10, with six hooks per fascicle accompanied by few capillaries. Neuropodial hooks with rounded primary hood and detectable secondary hood, with 3 teeth in lateral view (Figs. 21e–f and 22e–f). Notopodial

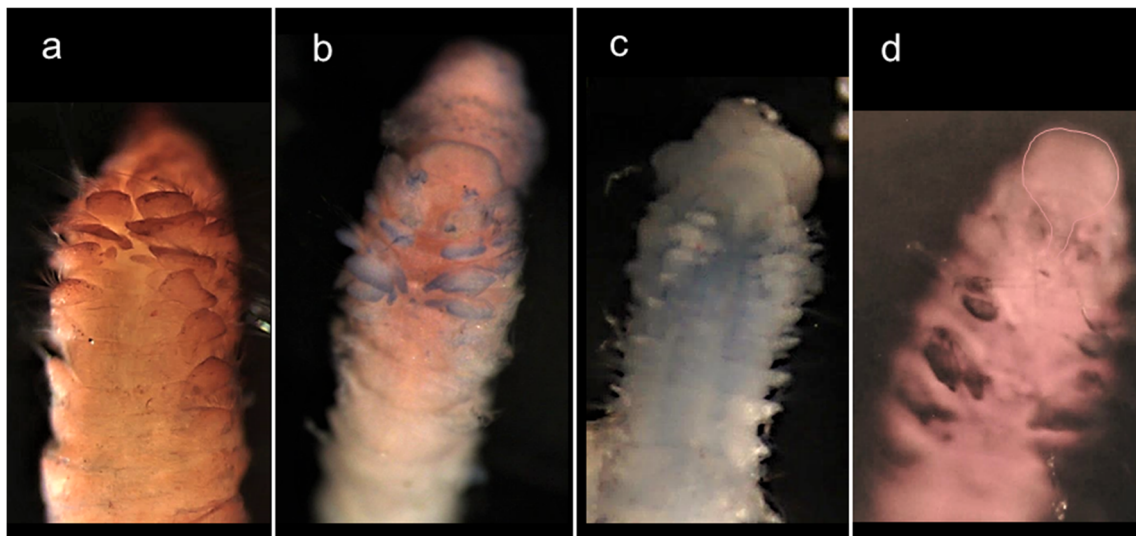
hooks not observed in available fragments. The rest of body and pygidium unknown.

**Molecular information.** The two 16S sequences from specimens of this species match with 14 published sequences of *Aurospio* sp. ‘249 PB’ from other eastern CCZ areas (GSR, Ifremer, IOM) (Bonifácio et al. 2020). The uncorrected (*p*) distances among the 16 sequences range between 0.0 and 0.017. It also matches an already published sequence labeled *Aurospio dibranchiata* KP342 with GenBank accession



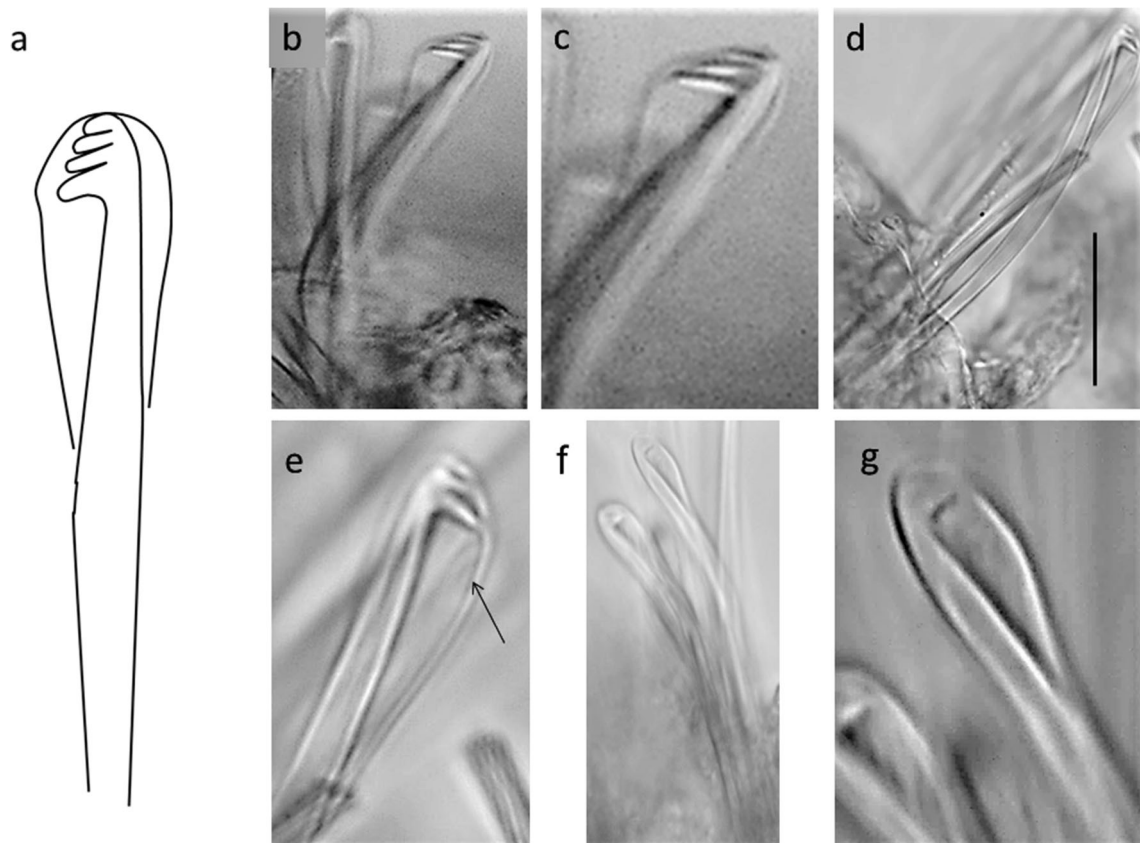
**Fig. 19** Selected examples of four specimens genetically identified as *Aurospio* sp. NHM\_091 **a** live specimen NHMUK.ANEA.2019.10045 in dorsolateral view; **b** preserved specimen NHMUK.ANEA.2019.10036 in dorsal view; **c** preserved specimen NHMUK.ANEA.2019.10049 in

dorsolateral view; **d** anterior end with prostomium of preserved specimen NHMUK.ANEA.2019.10038 in dorsal view. Scale bar: **c** 1000  $\mu$ m



**Fig. 20** Intraspecific variation in prostomial shapes and parapodial lamellae in *Aurospio* sp. NHM\_091, all specimens stained with Shirlastain **a** specimen NHMUK.ANEA.2019.10001 in dorsal view (prostomium not clearly

visible); **b** specimen NHMUK.ANEA.2019.10036 in dorsal view; **c** specimen NHMUK.ANEA.2019.10038 in dorsal view; **d** specimen NHMUK.ANEA.2019.10049 in dorso-lateral view



**Fig. 22** Comparison of neuropodial hooded hooks (from chaetiger 10–11) of ABBYSSLINE-collected *Aurospio dibranchiata*-like species as seen under light microscopy **a** line drawing of *Aurospio dibranchiata* with quadridentate hooks, without secondary hood after Maciolek (1981); **b** hooks from paratypes of *Aurospio dibranchiata* BMNH.1981.82-91, with secondary hood (arrow); **c-d** ABBYSSLINE

species *Aurospio* sp. NHM\_091 with quadridentate hooks, without discernible secondary hood; **e-f** ABBYSSLINE species *Aurospio* sp. NHM\_2186 with tridentate hooks, with secondary hood (marked by arrow); **g-h** ABBYSSLINE species *Aurospio* sp. NHM\_2247, hooks dentition not clearly observed, secondary hood may be present. Scale bar: 25  $\mu$ m

number EU340087 (Mincks et al. 2009) collected from the CCZ during the Kaplan project and another sequence labeled *Aurospio* cf. *dibranchiata* PAP with GenBank accession number MH379971 collected from the Porcupine Abyssal Plain, NE Atlantic (Neal et al. 2018b). The uncorrected ( $p$ ) distances to published sequences were 0.009 and 0.004, respectively.

**Remarks.** *Aurospio* sp. NHM\_2186 is the second of three CCZ collected species so far that corresponds well to *Aurospio dibranchiata* based on characters such as the shape of prostomium, two pairs of small branchiae partially fused to notopodial lamellae of chaetigers 3 and 4 and neuropodial hooded hooks from chaetiger 10. However, as already discussed, reliable taxonomic characters have not been found during the examination of the available material. This may change in the future, should better preserved material become available, but currently DNA identification appears to be the best tool available.

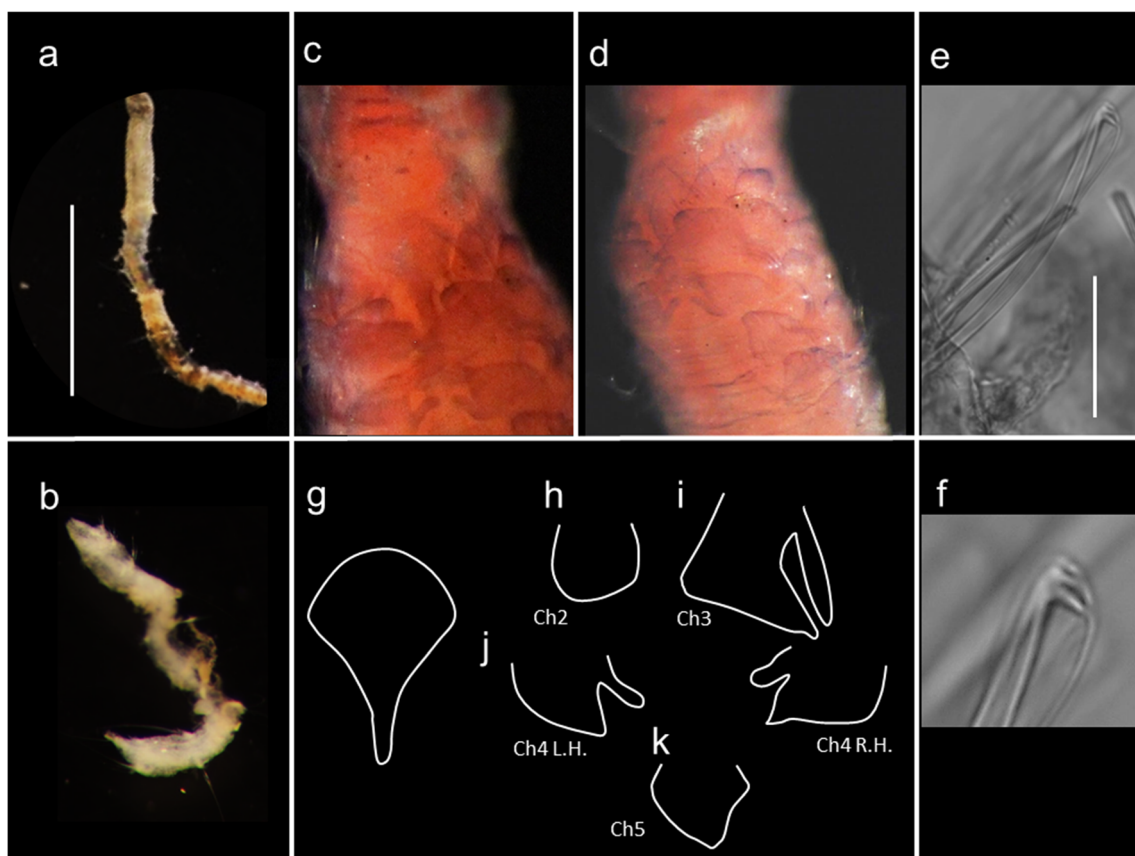
One character of note in the case of *Aurospio* sp. NHM\_2186 is the **form of neuropodial hooks** (see

comparative Fig. 22a–h). These differ from both Maciolek type material (BMNH.1981.82-91) and *Aurospio* sp. NHM\_091 in being tridentate (Fig. 22f), rather than quadridentate (Fig. 22a–d). Also, the hooks are overall more slender and higher magnification is necessary to achieve a similar detailed view to *Aurospio* sp. NHM\_091. Form of neuropodial hooks in the third ABYSSLINE species—*Aurospio* sp. NHM\_2247—cannot be established with certainty, as these hooks have proved particularly difficult to observe with necessary detail (Fig. 22g, h).

**Distribution.** Molecular evidence based on 16S suggests that *Aurospio* sp. NHM\_2186 is a widely distributed species as it was found in the UKSR-1, GSR, Ifremer, and IOM exploration areas in the eastern CCZ, Kaplan site CCZ, and Porcupine Abyssal Plain in NE Atlantic (Neal et al. 2018b).

#### *Aurospio* sp. NHM\_2247

Figs. 16c, 17c, 22g–h, 23a–f, 24a–e



**Fig. 21** *Aurospio* sp. NHM\_2186 **a** live; and **b** preserved body fragments genetically identified as *Aurospio* sp. NHM\_2186; **c** anterior end in dorsal view, specimen NHMUK. ANEA.2019.10052 stained with Shirlastain; **d** dorsolateral view of anterior parapodial lamellae, specimen stained with Shirlastain; **e** neuropodial hooded hooks; **f** close-up of neuropodial

hooded hook. Images **g–k** all line drawings of specimen NHMUK. ANEA.2019.10052 (**g**) prostomium; **h** notopodial lamella from chaetiger 2; **i** notopodial lamella from chaetiger 3; **j** notopodial lamellae from chaetiger 4, left (L.H.) and right-hand side (R.H.); **k** notopodial lamella from chaetiger 5. Scale bars: **a** 500 µm; **e** 25 µm

**Material examined:** NHM\_2247, NHMUK ANEA.2021.9, coll. 01 Mar. 2015, collection code: EB06, 12°15.44N, 117°18.13W, 4302 m.

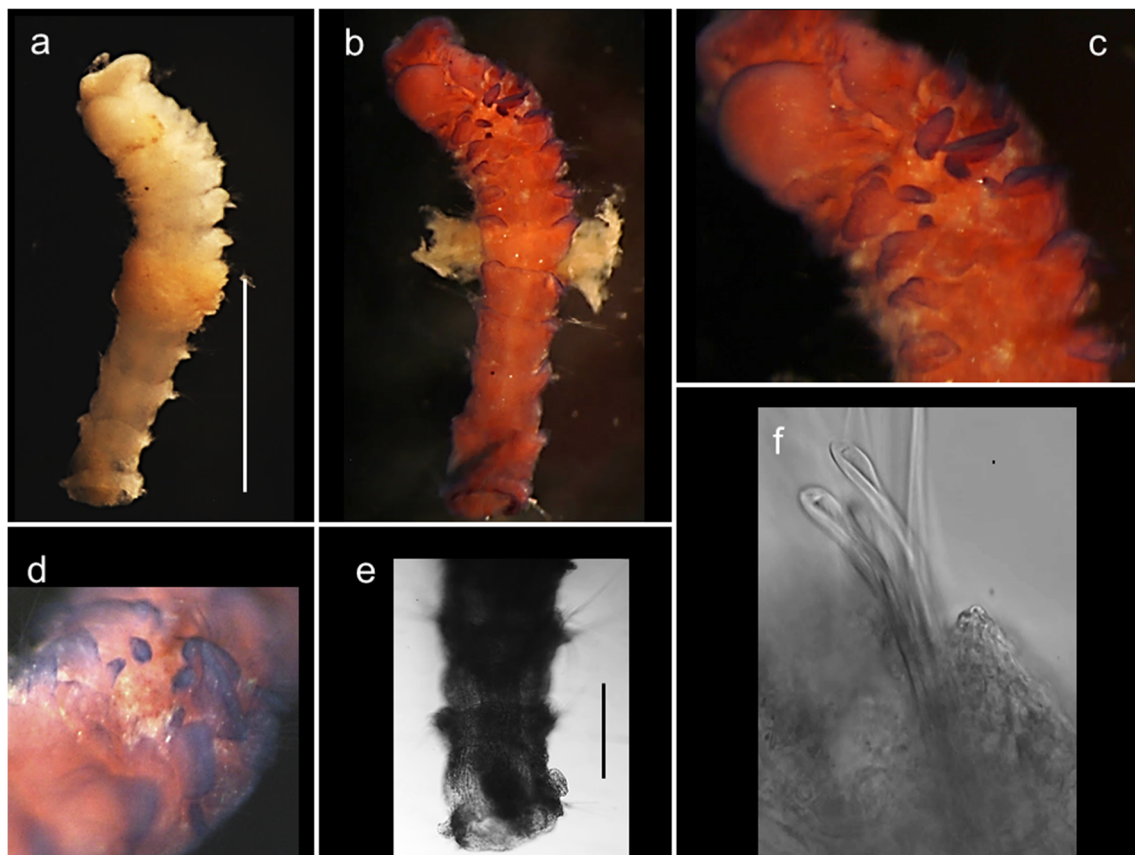
**Description.** Small slender species represented by a single posteriorly incomplete specimen, 2.1 mm long and 0.4 mm wide for 12 discernible chaetigers (Fig. 23a–b). Live specimens not observed; the color in alcohol tanned with very strong reddish pigmentation dorsally on peristomium (Fig. 23a).

Prostomium rounded, posteriorly narrowing into relatively thick caruncle to the end of chaetiger 1 (Figs. 16c, 23c, 24a). Eyes not observed. Peristomium forms a narrow hood around prostomium, not forming lateral wings (Fig. 23c). Palps missing.

Branchiae present on chaetigers 3–4 only; both short, smooth, cirriform, and basally fused to the corresponding notopodial lamellae (Figs. 17c, 23c–d, 24b–c). Branchiae on chaetiger 3 longer, approaching the length of corresponding notopodial lamellae; branchiae on chaetiger 4 very short, stubby, only reaching about 1/3 length of corresponding notopodial lamellae.

Notopodium of chaetiger 1 rudimentary. Notopodial lamellae best developed on chaetigers 2–6, with those on chaetiger 3 largest; not meeting medially, leaving part of dorsum exposed (Fig. 23c). Notopodial lamellae on chaetiger 2 approaching rhomboid shape. Notopodial lamellae on chaetiger 3 broad, subquadrate with the medial edge prolonged over the dorsum into blunt tip (Figs. 17c and 24b). Notopodial lamellae on chaetiger 4 broadly subquadrate with short blunt tip (Figs. 17c and 24c). Neuropodium of chaetiger 1 rudimentary; on chaetiger 2 as a small broadly rounded lobe which becomes larger on chaetiger 3 and then again smaller on chaetiger 4. From chaetiger 5, both noto- and neuropodial lamellae as broadly rounded lobes, getting progressively smaller and lower, with notolamellae being larger in anterior chaetigers (Fig. 24d–e). On chaetigers 6–7, a low dorsal crest detected, becoming very high and well developed in chaetigers 9–12 (end of the fragment) (Fig. 23e). Form of parapodia not established past chaetiger 12 (end of the longest fragment).

Chaetae consist of 3 types: capillaries, ventral sabre chaetae and multidentate hooded hooks. Anterior chaetae arranged in 2 rows of longer and shorter limbate capillaries; chaetae

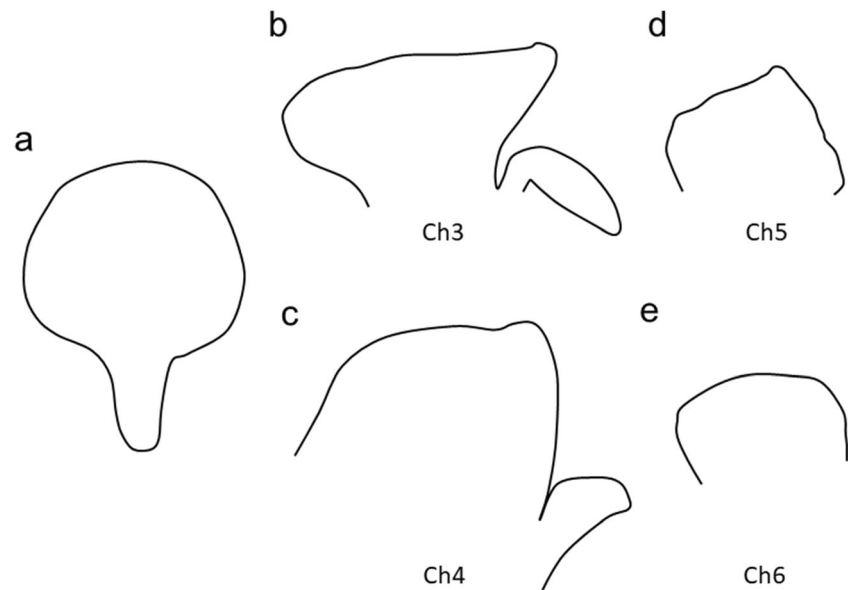


**Fig. 23** *Aurospio* sp. NHM\_2247 **a** preserved specimen NHMUK.ANEA.2021.9 in dorsal view, with peristomial pigmentation visible; **b** specimen in dorsal view stained with Shirlastain, with dorsal crests visible; **c** detail of anterior end in dorsal view, specimen stained

with Shirlastain; **d** detail of branchial chaetigers 3 and 4, specimen stained with Shirlastain; **e** close-up image of dorsal crests; **f** neuropodial hooded hooks. Scale bars: **a** 1000  $\mu$ m; **e** 250  $\mu$ m; **f** 25  $\mu$ m



**Fig. 24** Line drawings of *Aurospio* sp. NHM\_2247, specimen NHMUK.ANEA.2021.9 **a** prostomium; **b** notopodial lamella from chaetiger 3 (ch3); **c** notopodial lamella from chaetiger 4 (ch4); **d** notopodial lamella from chaetiger 5 (ch5); **e** notopodial lamella from chaetiger 6 (ch6)



particularly long in neuropodia of chaetiger 2. A single heavily granulated and ventral sabre chaeta present from chaetiger 10, but mostly broken off. Neuropodial hooded hooks first observed in chaetiger 10, with six hooks per fascicle accompanied by few capillaries. Neuropodial hooks with squarish primary hood, secondary hood not confirmed, with several minute teeth in lateral view (Figs. 22g–h and 23f). Notopodial hooks not observed in available fragments. The rest of body and pygidium unknown.

**Molecular information.** The 16S sequence from this species matches four sequences from *Aurospio* sp. ‘80 PB’ (Bonifácio et al. 2020), with the uncorrected (*p*) distances ranging from 0.0 to 0.005 among the five sequences. Interestingly, *Aurospio* sp. NHM\_2247 falls out as sister taxon to species found in bathyal (1000–1600 m) East and West Atlantic rather than CCZ abyssal species (Fig. 6).

**Remarks.** This is the third species morphologically consistent with *Aurospio dibranchiata* found in the ABYSSLINE material. It is of interest to report that *Aurospio* sp. NHM\_2247 has the best developed dorsal lamellae of any ABYSSLINE-collected specimens, but often this character cannot be established with certainty due to integument damage and *Aurospio* sp. NHM\_2247 is represented by a single specimen only.

**Distribution.** This species has been found in OMS-1, GSR, and Ifremer exploration areas.

#### *Aurospio* sp. NHM\_776

**Material examined:** NHM\_776, NHMUK ANEA.2019.10020, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m.

**Description:** Single poorly preserved specimen, small and slender, 2.5 mm long and 0.25 mm wide, anterior fragment with about 14 discernible chaetigers. Color in alcohol pale yellow, without distinct pigmentation (Fig. 25).

Prostomium anteriorly rounded, longer than wide, extending into blunt caruncle to beginning of chaetiger 2, without peaks. Eyes absent. Peristomium as narrow hood around prostomium, not forming lateral wings; dorsally not fused. Palps missing.

Parapodial lamellae often damaged or missing, but large foliaceous to subtriangular notopodial lamellae observed on chaetiger 3, these arch medially over dorsum. Single pair of branchiae only on chaetiger 3, other branchiae absent; smooth and cirriform branchial pair, about the same length as notopodial lamellae on chaetiger 3. Neuropodial lamellae on chaetiger 3 also greatly enlarged, rounded.

Only capillary chaetae observed in the available fragment, chaetae particularly long in chaetiger 3. Multidentate hooded hooks in notopodia or neuropodia and sabre chaetae not observed in the available fragment. The rest of body and pygidium unknown.

**Molecular information:** The 16S sequence from this species matches one spionid sequence from another study (Bonifácio et al. 2020) with collection locality in Ifremer exploration



**Fig. 25** Preserved specimen NHMUK.ANEA.2019.10020 of *Aurospio* sp. NHM\_776. Scale bar: 1000  $\mu$ m

contract area and accession number MK971061, the uncorrected ( $p$ ) distance between the two sequences is 0.005.

**Remarks:** Although this single specimen is in rather poor condition, the shape of prostomium and the presence of single branchial pair on chaetiger 3, accompanied by greatly enlarged notopodial lamellae suggest similarities to *Aurospio foodbancsia* Mincks et al., 2009. This species was described from the Bellingshausen Sea, the Southern Ocean, depths of around 500 m, where it was particularly abundant (Mincks et al. 2009). Due to poor preservation of the ABYSSLINE specimen, meaningful comparison is difficult. It appears that no sabre chaetae or hooded hooks are present in *Aurospio* sp. NHM\_776 in first 14 chaetigers, while these were detected from chaetiger 10 and 11, respectively, in the known species. However, it is not currently clear if this is a true absence of hooks and sabre chaetae, or true posterior distribution or absence. Another species collected from ABYSSLINE samples also share these characters (see Remarks under *Aurospio* sp. 1661).

**Distribution:** This species is known from UK-1 and Ifremer exploration contract areas in the eastern CCZ.

#### *Aurospio* sp. NHM\_1661

Fig. 26a–c

**Material examined:** NHM\_1661, NHMUK ANEA.2019.10043, coll. 10 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°21.81N, 116°40.86W, 4233 m.

**Description:** Single poorly preserved specimen, small and slender, 1.9 mm long and 0.25 mm wide, anterior fragment with 15 chaetigers (Fig. 26a).

Prostomium anteriorly rounded, longer than wide, extending into blunt caruncle to beginning of chaetiger 2, without peaks. Eyes absent. Peristomium as narrow hood around prostomium, not forming lateral wings; dorsally not fused. Palps missing.

Parapodial lamellae relatively small, rudimentary on chaetiger 1; notopodial lamellae enlarged and foliaceous on chaetiger 3. Single pair of branchiae only on chaetiger 3, other branchiae absent; smooth and cirriform branchial pair, slightly longer than notopodial lamellae on chaetiger 3. Neuropodial lamellae on chaetiger 3 also enlarged, rounded.

Chaetae of three types: capillaries, hooded hooks (Fig. 26b) and sabre chaetae (Fig. 26c). First 9 chaetigers with capillaries only. Stout, curved, limbate and distally granulated sabre chaeta from chaetiger 10. Multidentate hooded hooks observed in neuropodia from chaetiger 11 where

4 per fascicle, up to 6 per fascicle in subsequent chaetigers. Hooded hooks long and slender, with several about 4 small teeth above main fang as observed under light microscopy (Fig. 26b); with inflated, rounded hood; secondary hood not observed. Notopodial hooded hooks not observed in available fragments. The rest of body and pygidium unknown.

**Molecular information:** The 16S sequence from this species matches five sequences from another CCZ study labeled as Spionidae sp. (Bonifácio et al. 2020, GenBank accession numbers MK970880, MK970987, MK971006, MK971016, MK971114), with the uncorrected ( $p$ ) distances ranging from 0.0 to 0.005 among the six sequences. The COI sequence from this species has a 100% match with a polychaete sequence from the Belgian (GSR) contract area in CCZ submitted to GenBank by Janssen et al. (2015) and labeled as Polychaeta sp. NB-Po304, accession number KJ736487.1. Interestingly, in the phylogenetic tree (Fig. 6), the sister taxon of *Aurospio* sp. NHM\_1661 is the Southern Ocean species *A. foodbanesia*, with which it also shares morphological similarities.

**Remarks:** This species corresponds well to *Aurospio foodbanesia* from the Southern Ocean as already discussed in Remarks of *Aurospio* sp. NHM\_776. It agrees in the shape of prostomium, form and distribution of branchiae and lamellae on chaetiger 3 as well as distribution of sabre chaetae and neuropodial multidentate hooks on chaetigers 10 and 11, respectively. However, the single incomplete specimen cannot be meaningfully differentiated from the known species beyond observation that parapodial lamellae are rather small.

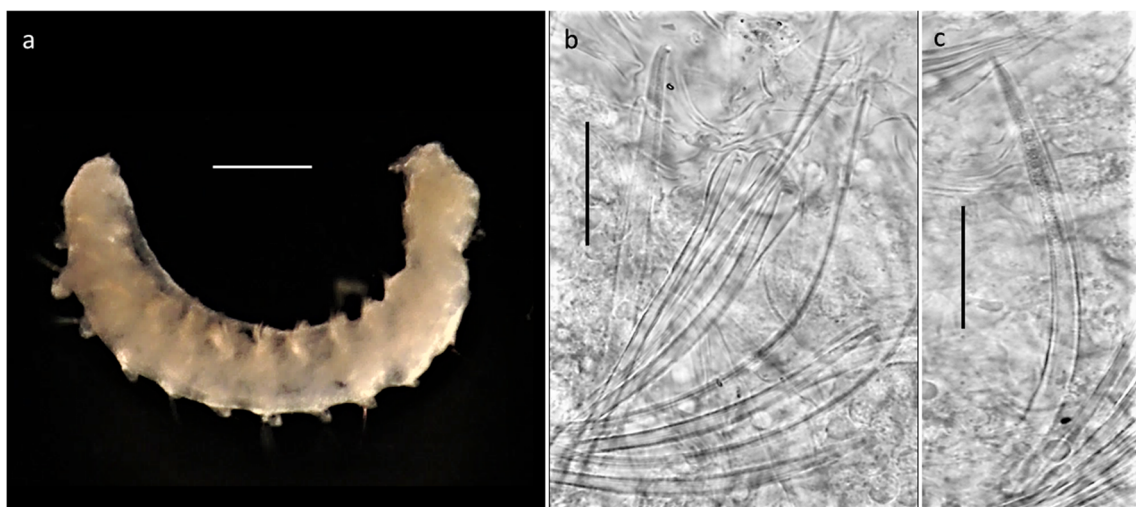
**Distribution:** This species is known from UK-1, GSR, and IOM exploration areas in the eastern CCZ.

***Laonice* Malmgren, 1867**

Type species: *Laonice cirrata* Malmgren, 1867

**Diagnosis:** Prostomium anteriorly rounded or T-shaped, maybe free from peristomium or dorsally or completely fused with peristomium. Occipital tentacle present or absent. Caruncle followed by nuchal organs on dorsal surface along several anterior chaetigers. Palps without sheath at base. Peristomium not fused to chaetiger 1. Branchiae present from chaetiger 2. Neuropodial inferior fascicles with sabre chaetae and usually bidentate (in lateral view) hooded hooks starting in the anterior part of the body. Genital pouches present. Pygidium terminal, with two small ventral papilliform cirri and several pairs of comparatively long dorsal cirri.

**Remarks:** Genus *Laonice* consists of 38 described species with many more not formalized especially from deep sea environments, in part reflecting the problematic taxonomy of this group (e.g., Sikorski et al. 2017; Bogantes et al. 2018). *Laonice* has recently been divided into four subgenera: *Laonice*, *Sarsiana*, *Appelloefia*, and *Norgensia* by Sikorski et al. (2017), based on characters such as fusion of prostomium and peristomium, development of nuchal organs, presence of notopodial hooks, number of rows of capillaries in anterior chaetigers, and the distribution of branchiae and genital pouches. This division has not been based on a phylogenetic approach and is not followed here also due to the fact that



**Fig. 26** *Aurospio* sp. NHM\_1661 **a** preserved specimen NHMUK.ANEA.2019.10043 in lateral view; **b** fascicle of neuropodial hooded hooks; **c** neuropodial sabre chaeta. Scale bars: a 250  $\mu$ m; b-c 25  $\mu$ m

necessary diagnostic characters could not be observed in the ABYSSLINE specimens owing to their poor preservation.

Although *Laonice* is commonly encountered in deep-sea samples (Guggolz et al. 2019), currently only 11 species of *Laonice* have been described from waters deeper than 400 m (Sikorski et al. 2017; Sikorski et al. 2021). In ABYSSLINE material, seven species of *Laonice* have been recognized based on morphology and molecular data. Six species are represented by poorly preserved specimens. The other species, although represented by incomplete specimens possesses unique “easy to recognize” characters that distinguish them from all know *Laonice* and thus decision has been made to formally described it as new species—*Laonice shulseeae* sp. nov.

Our phylogenetic analysis recovered the species assigned to *Laonice* in a well-supported clade (Fig. 6), although its position within Spionidae was unresolved.

#### *Laonice* sp. NHM\_2111

**Material examined:** NHM\_2111, NHMUK ANEA.2021.10, coll. 20 Mar. 2015, collection method: Brenke Epibenthic Sledge, 19 27.874 N, 120 01.525W, 4026 m.

**Description:** Poorly preserved single specimen consisting of damaged prostomium and about 10 discernable chaetigers long anterior fragment, about 0.9 mm long.

**Molecular information:** The 16S sequence from this species does not match any other available sequences from the CCZ, but it falls into a well-supported *Laonice* clade (Fig. 6).

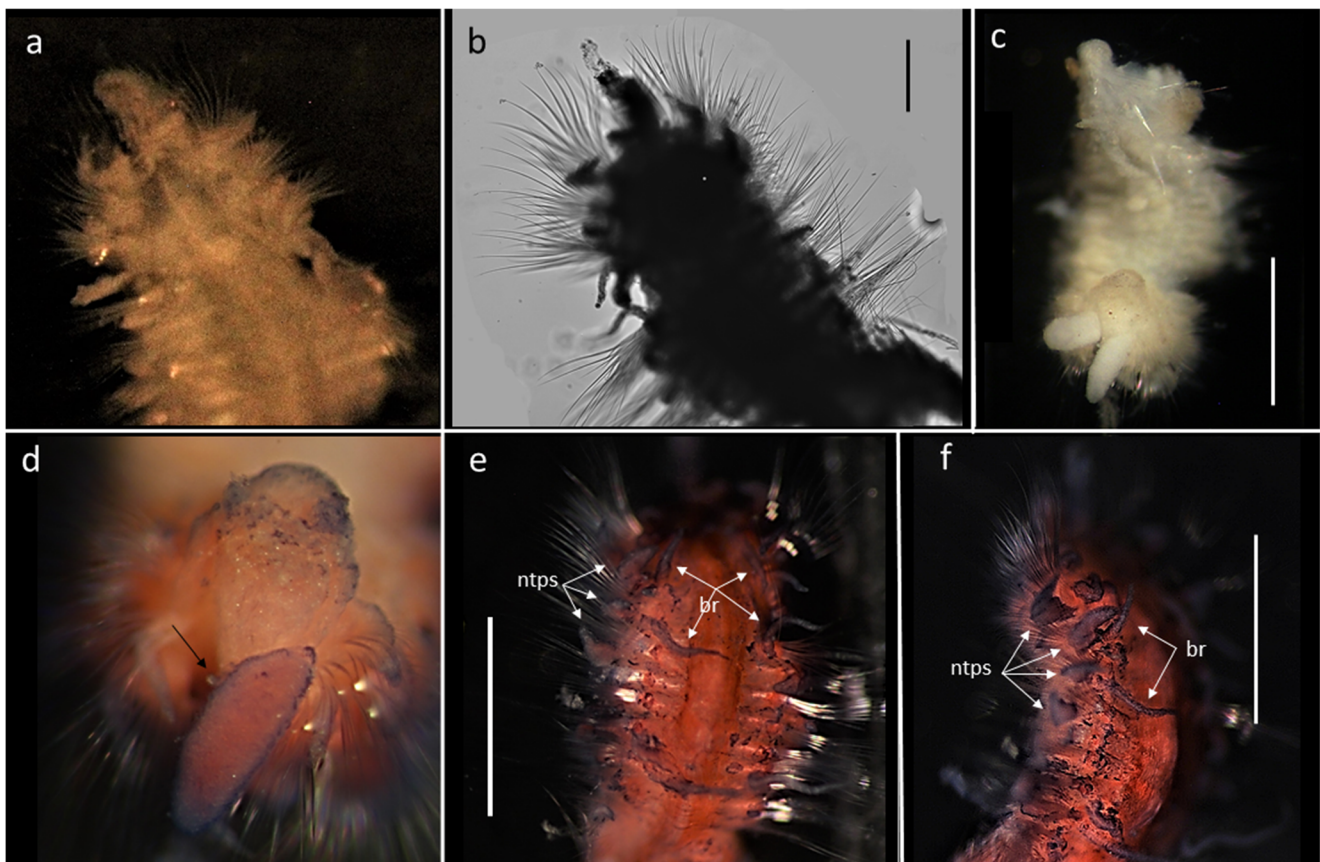
**Remarks:** The available anterior fragment is in particularly poor morphological condition and cannot be meaningfully compared with other species.

**Distribution:** This species is only known from APEI-6.

#### *Laonice* sp. NHM\_1662.

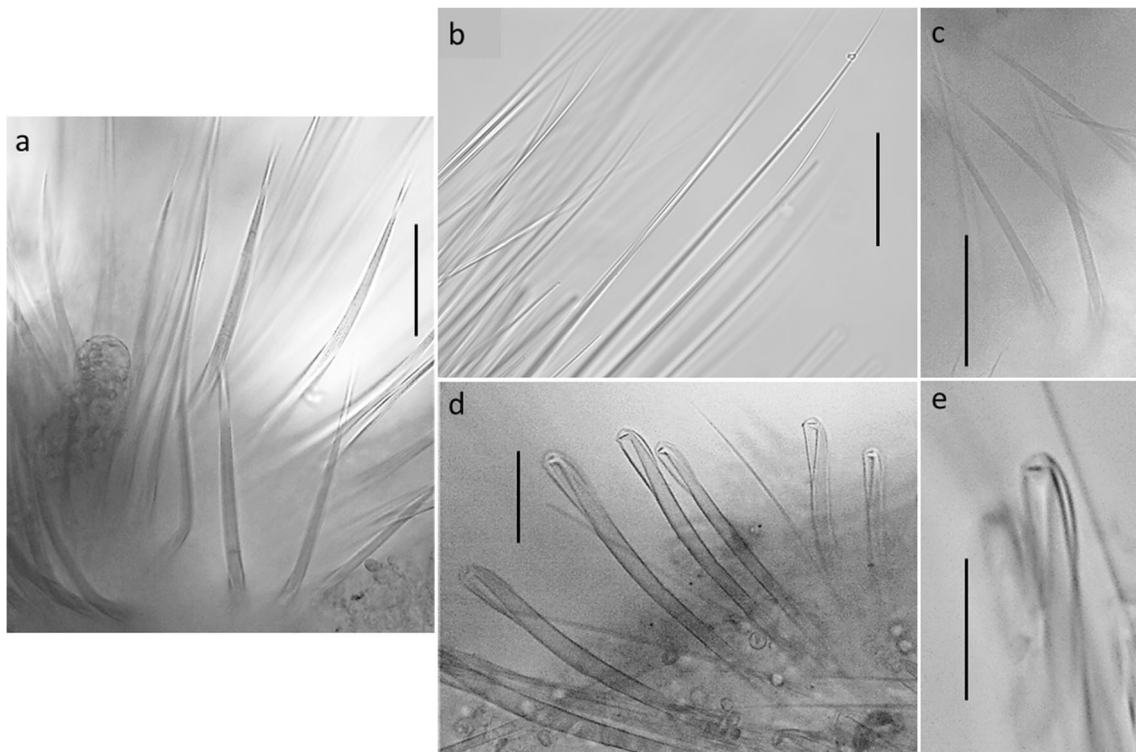
Figs. 27a–f and 28a–e

**Material examined:** NHM\_1662, NHMUK ANEA.2021.11, coll. 10 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°21.81N, 116°40.86W, 4233 m.



**Fig. 27** *Laonice* sp. NHM\_1662 NHMUK ANEA.2021.11, in images d–e specimen stained with Shirlastain **a–b** anterior end in dorsal view showing the stout chaetae; **c** specimen in ventral view with prostomium and palps in antero-dorsal view; **d** detail of prostomium in antero-dorsal view

with one remaining palp attached and small antenna (arrow); **e–f** remaining notopodial lamellae and branchiae on chaetigers 3–6 marked by arrows, ntps—notopodial lamellae, br—branchiae. Scale bars: b 250  $\mu$ m; c, e, f 1 mm



**Fig. 28** *Laonice* sp. NHM\_1662, NHMUK ANEA.2021.11 **a** capillaries from anterior chaetigers; **b** capillaries from chaetiger 9; **c** sabre chaetae d neuropodial hooded hooks; **e** detail of dentition of neuropodial hooks. Scale bars: **a, b, c** 50  $\mu$ m; **e** 25  $\mu$ m; **d** 20  $\mu$ m

**Description:** Single specimen consisting of 16 chaetigers long anterior fragment, 1.5 mm long and 0.4 mm wide. Preserved specimens pale yellow in ethanol (Fig. 27a, c), with some reddish pigmentation near the anterior margin of prostomium. Body narrow and cylindrical, not anteriorly expanded. Anterior chaetae very well developed, stout and long, almost forming a cephalic cage (Fig. 27b).

Prostomium narrow, anteriorly rounded (Fig. 27c–d); dorsally free from peristomium; no eyes observed; with very slender cirriform antenna (Fig. 27d). Pair of short, thick grooved palps attached (one lost during the examination) reaching to chaetiger 3 (Fig. 27c–d). Caruncle not clearly detected. Branchiae often missing, but still attached in some chaetigers, including chaetiger 2, branchiae very slender and cirriform, long (about twice the length of corresponding notopodial lamellae) (Fig. 27e–f).

Parapodial lamellae of chaetiger 1 well developed, but smaller than those on subsequent chaetigers; notopodial lamellae, slender elongated conical; neuropodial lamellae foliaceous, widened basally, distally produce into rounded tip. Parapodial lamellae of chaetiger 2 similar to those in chaetiger 1, but larger. Notopodial lamellae largest on chaetigers 3–5 with those in chaetiger 3 largest; foliaceous with their produced tips bent medially towards dorsum (Fig. 27e–f). Neuropodial lamellae of chaetigers 3–6 wide rounded lobes. Parapodial lamellae past chaetiger 7 mostly

missing/damaged. Genital pouches not observed in 16 chaetiger long fragment.

Notochaetae capillaries, arranged in two rows, in first 12 chaetigers notochaetae shorter and very stout (Fig. 28a) than those in subsequent chaetigers, which are very long, silky in appearance, very slender and narrowly bilimbate (Fig. 28b). Neurochaetae in first 12 chaetigers very stout, shorter than notochaetae. Sabre chaetae first observed on chaetiger 9, two per fascicle, relatively slender, granulated and non-limbate (Fig. 28c). Neuropodial hooded hooks first clearly observed on chaetiger 13, up to 8 per fascicle (Fig. 28d), accompanied by few thin capillaries; all hooks bidentate, with main fang and slender secondary tooth well separated (Fig. 28e); with tight fitting, somewhat anteriorly truncated hood. The rest of the body unknown.

**Molecular information.** The 16S sequence from this species matches one sequence from another study (Bonifácio et al. 2020) with collection locality in GSR exploration area labeled as *Laonice* sp. 381 PB and GenBank accession number MK971107; the uncorrected (*p*) distance between the two sequences is 0.002. The sequence from the CCZ specimen falls into a well-supported *Laonice* clade (Fig. 6).

**Remarks.** Although the description is based on a single, incomplete specimen and not all characters could have been

observed, the following combination of the characters is unique to this specimen, suggesting it belongs to a new species: the narrow form of prostomium, the anterior start of neuropodial hooks (chaetiger 13) and the marked change in the form of capillary chaetae throughout the body, with anterior chaetae creating an effect of “cephalic cage.” However, as the species cannot be meaningfully compared with other species due to poor preservation we ascribe this specimen to morphospecies only.

**Distribution.** This species is known from UK-1 and GSR exploration areas in the eastern CCZ.

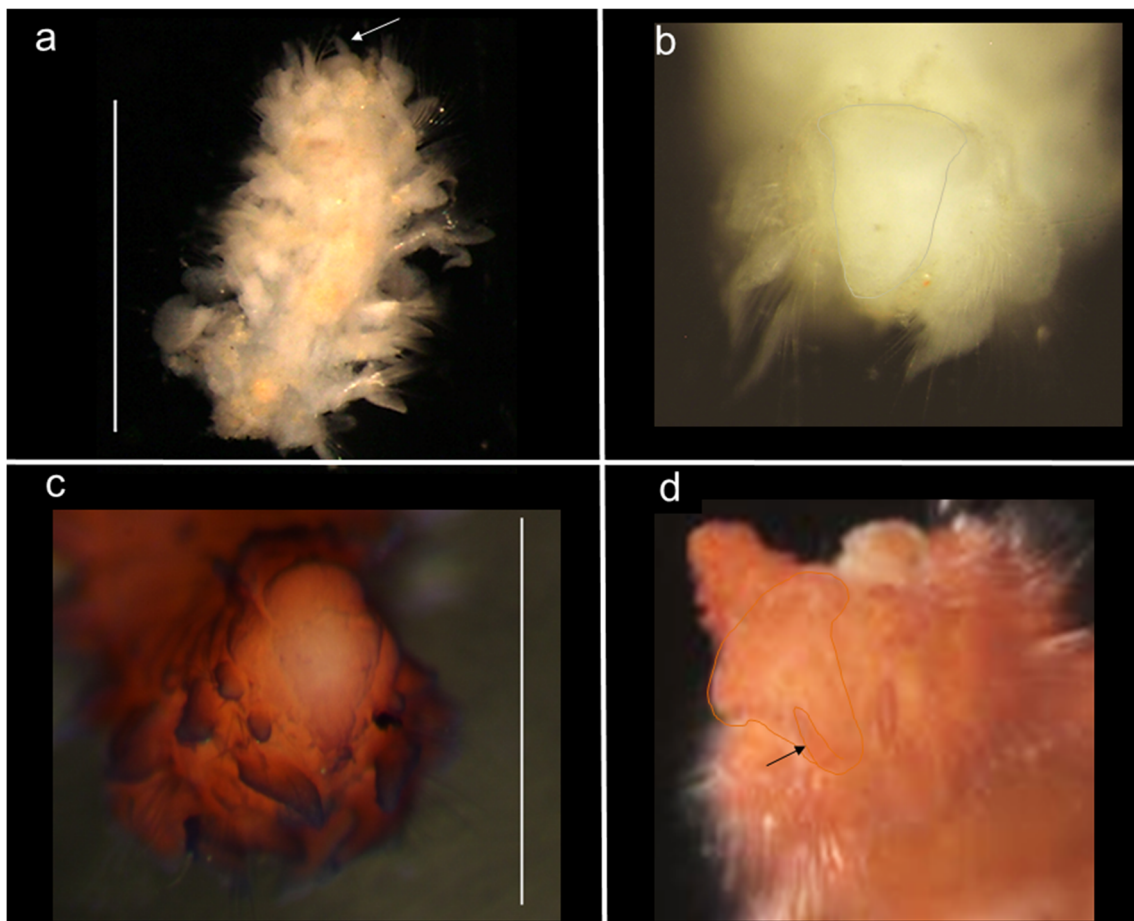
***Laonice* sp. NHM\_131**

Fig. 29a–b

**Material examined:** NHM\_131, NHMUK ANEA.2021.17, coll. 11 Oct. 2013, collection method: Brenke Epibenthic Sledge, 13°45.500N, 116°41.911W, 4080 m; NHM\_577,

NHMUK ANEA.2021.18, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_586, NHMUK ANEA.2021.19, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_1510, NHMUK ANEA.2021.20, coll. 05 Mar. 2015, collection method: Multi Corer, 12°27.125N, 116°30.736W, 4199 m; NHM\_2117, NHMUK ANEA.2021.21, coll. 20 Mar. 2015, collection method: Brenke Epibenthic Sledge, 19 27.874 N, 120 01.525W, 4026 m; NHM\_1581, NHMUK ANEA.2021.22, coll. 07 Mar. 2015, collection method: USNEL Box Core, 12°25.195N, 116°37.477W, 4136 m.

**Description:** Six poorly preserved specimens, consisting of body fragments or short anterior fragments only. Preserved specimens pale yellow in ethanol. The best-preserved specimen (NHM\_2117) 1.2 mm long and 0.4 mm wide for 8 chaetigers (Fig. 29a). Prostomium anteriorly somewhat truncated, only slightly expanded without obvious lateral horns;



**Fig. 29** *Laonice* species from the ABYSSLINE samples **a** live image of *Laonice* sp. NHM\_131 in dorsal view, prostomium not visible except for small antenna (arrow) showing enlarged parapodial lamellae; **b** preserved specimen of *Laonice* sp. NHM\_131 in anterior-dorsal view showing prostomium and parapodial lamellae of chaetiger 1; **c** *Laonice* sp. 016

specimen NHMUK.ANEA.2021.15 in in antero-dorsal view, showing prostomium and parapodial lamellae of chaetigers 1–3, specimen stained with Shirlastain; **d** *Laonice* sp. 048 with prostomium in dorsal view, showing antenna (arrow), specimen stained with Shirlastain. All scale bars: 1 mm

dorsally free from peristomium (Fig. 29b); no eyes observed; with large triangular antenna (Fig. 29a). Caruncle not detected. Branchiae mostly missing, but still attached in few chaetigers, including chaetiger 2 (Fig. 29b), slightly longer than corresponding notopodial lamellae.

First notopodial and neuropodial lamellae well developed only slightly smaller than in subsequent chaetigers. Notopodial lamellae on chaetiger 1 elongated (Fig. 29b), similar in anterior most chaetigers, soon becoming very large rounded (Fig. 29a) and remaining as such till end of fragment. Neuropodial lamellae on chaetiger 1 auricular to rounded (Fig. 29b), getting progressively larger on chaetigers 2–4 and then remaining well developed, rounded till end of the fragment (Fig. 29a). Neuropodial genital pouches not detected in the available fragments. Capillary chaetae in first chaetiger stouter and shorter and granulated, in subsequent chaetiger capillaries more slender and longer, neurochaetae with some granulation, notochaetae smooth and narrowly bi-limbate. Sabre chaetae and hooded hooks not observed in the available fragments. The rest of the body unknown.

**Remarks.** This species appears to have particularly large and rounded parapodial lamellae in comparison to other UKSR-1 species.

**Molecular information.** The 16S sequences from the specimens within this species group matches sequences from *Laonice* sp. '349 PB' from other areas in the eastern CCZ (Bonifácio et al. 2020), extending its distribution from the UK1 area to BGR, GSR and Ifremer exploration contract areas in the Eastern part of CCZ. The uncorrected (*p*) distances among the in total 15 sequences range between 0.0 and 0.013.

**Distribution:** This species is known from UK-1, BGR, GSR, and Ifremer exploration contract areas in the eastern CCZ.

#### *Laonice* sp. NHM\_016

Fig. 29c

**Material examined:** NHM\_016, NHMUK ANEA.2021.12, coll. 9 Oct. 2013, collection method: Brenke Epibenthic Sledge, 13°50.232N, 116°33.506W, 4336 m; NHM\_685, NHMUK ANEA.2021.13, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m; NHM\_882, NHMUK ANEA.2021.14, coll. 23 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°34.28N, 116°36.63W, 4198 m; NHM\_1243, NHMUK ANEA.2021.15, coll. 01 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°15.44N, 117°18.13W, 4302 m; NHM\_1425, NHMUK ANEA.2021.16, coll. 03 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°27.26N, 116°36.77W, 4137 m.

**Description:** Five poorly preserved specimens, consisting of 12–18 chaetigers long anterior fragments, 1.5–2.3 mm long and 0.7–1 mm wide. Preserved specimens pale yellow in ethanol. Prostomium narrow, anteriorly only slightly expanded and rounded; dorsally fused to peristomium; with a pair of tiny faint red eyes positioned medially; with very small triangular antenna (maybe scar?) observed in specimens NHM\_882 and NHM\_1243 upon staining with Shirlastain (Fig. 29c). Caruncle not detected. Branchiae all missing. Notopodial lamellae very small on chaetiger 1 where broadly conical (Fig. 29c), becoming larger and more elongated in chaetiger 2 and largest over chaetiger 3 where tips bent medially over dorsum; then remaining well developed till chaetiger 18 (the last observed chaetiger). Neuropodial lamellae very small on chaetiger 1, round to auricular (Fig. 29c), then getting larger and elongated on chaetiger 2 and becoming best developed on chaetigers 3–5, then getting progressively smaller, but remaining well developed. Neuropodial genital pouches present, first observed between chaetigers 14 to 15, then detected till rest of the fragment. Capillary chaetae in anterior chaetigers stouter, shorter and granulated, becoming very long, smooth and threadlike towards the end of the fragment. Sabre chaetae and hooded hooks not observed in 18 chaetigers long fragment. The rest of the body unknown.

**Molecular information:** The five 16S sequences from this species does not match any other sequences on GenBank, the uncorrected (*p*) distances within the species range between 0.0 and 0.009. The COI sequence matches six sequences from CCZ submitted to GenBank by Janssen et al. (2015) and labeled as *Polychaeta* sp. (accession numbers KJ736571–KJ736576); the uncorrected (*p*) distances among these seven sequences range between 0.004 and 0.02.

**Remarks.** As with other species of *Laonice* collected from UK-1, several taxonomically informative characters cannot be observed due to poor preservation. This species is therefore assigned to morphospecies only, accompanied by DNA sequences.

**Distribution:** This species is known from UK-1 and BGR claim areas in the eastern CCZ.

#### *Laonice* sp. NHM\_048

**Material examined:** NHM\_048, NHMUK ANEA.2021.23, coll. 9 Oct. 2013, collection method: Brenke Epibenthic Sledge, 13°50.232N, 116°33.506W, 4336 m; NHM\_538, NHMUK ANEA.2021.24, coll. 17 Feb. 2015, collection method: USNEL Box Core, 12°22.020N, 116°31.017W, 4158 m; NHM\_563, NHMUK ANEA.2021.25, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_591,

NHMUK ANEA.2021.26, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_592, NHMUK ANEA.2021.27, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_706, NHMUK ANEA.2021.28, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m; NHM\_741, NHMUK ANEA.2021.29, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m; NHM\_944, NHMUK ANEA.2021.30, coll. 23 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°34.28N, 116°36.63W, 4198 m; NHM\_781, NHMUK ANEA.2021.31, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m; NHM\_1676, NHMUK ANEA.2021.32, coll. 10 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°21.81N, 116°40.86W, 4233 m; NHM\_1335, NHMUK ANEA.2021.33, coll. 01 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°15.44N, 117°18.13W, 4302 m; NHM\_1451, NHMUK ANEA.2021.34, coll. 03 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°27.26N, 116°36.77W, 4137 m; NHM\_1663, NHMUK ANEA.2021.35, coll. 10 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°21.81N, 116°40.86W, 4233 m; NHM\_1992, NHMUK ANEA.2021.36, coll. 15 Mar. 2015, collection method: USNEL Box Core, 12°00.559N, 117°22.818W, 4141 m; NHM\_2120, NHMUK ANEA.2021.37, coll. 20 Mar. 2015, collection method: Brenke Epibenthic Sledge, 19 27.874 N, 120 01.525W, 4026 m; NHM\_1018, NHMUK ANEA.2021.38X, coll. 24 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°08.02N, 117°17.52W, 4122 m.

**Description:** Sixteen poorly preserved specimens, consisting of very short anterior fragments. Preserved specimens pale yellow in ethanol. The best-preserved specimen (NHMUK\_048) anterior fragment with 12 chaetigers, 2 mm long and 0.85 mm wide. Prostomium anteriorly somewhat truncated, expanded into short, but distinct rounded lateral horns (Fig. 29d); dorsally free from peristomium; no eyes observed; with large triangular antenna (Fig. 29d). Caruncle not detected. Branchiae all missing. First notopodial and neuropodial lamellae well developed only slightly smaller than in chaetiger 2; notopodial lamellae elongated, conical; neuropodial lamellae broad, somewhat triangular; the rest of parapodial lamellae missing or damaged (12 chaetiger long fragment). Neuropodial genital pouches in the available fragments. Capillary chaetae in anterior chaetigers stouter, shorter, and granulated, becoming long and smooth towards the end of the fragment. Sabre chaetae first detected in neuropodia of chaetiger 10, up to per fascicle, slender, heavily granulated and uni-limbate. Hooded hooks not detected in the available fragments. The rest of the body unknown.

**Molecular information.** The 16S sequences from this species matches seven sequences from *Laonice* sp. ‘361 PB’ (Bonifácio et al. 2020), the uncorrected (*p*) distances among the sequences range between 0.0 and 0.007, extending this species distribution to the BGR, GSR, and Ifremer exploration contract areas in the Eastern CCZ. The COI sequences matches four sequences from CCZ submitted to GenBank by Janssen et al. (2015) and labeled as *Laonice* sp. with accession numbers KJ736564, KJ736566, KJ736567, and KJ736570, and three sequences from another study (Bonifácio unpubl. data), the uncorrected (*p*) distances among these 13 sequences range between 0.0 and 0.009.

**Remarks.** Due to poor preservation of available material this species is assigned to morphospecies only, accompanied by DNA sequences.

**Distribution:** This species is known from UK-1, BGR, GSR, and Ifremer exploration contract areas in the eastern CCZ.

#### *Laonice* sp. NHM\_2076

Fig. 30a–d

**Material examined:** NHM\_2076, NHMUK ANEA.2021.39, coll. 17 Mar. 2015, collection method: USNEL Box Core, 12°01.643N, 117°19.512W, 4139 m.

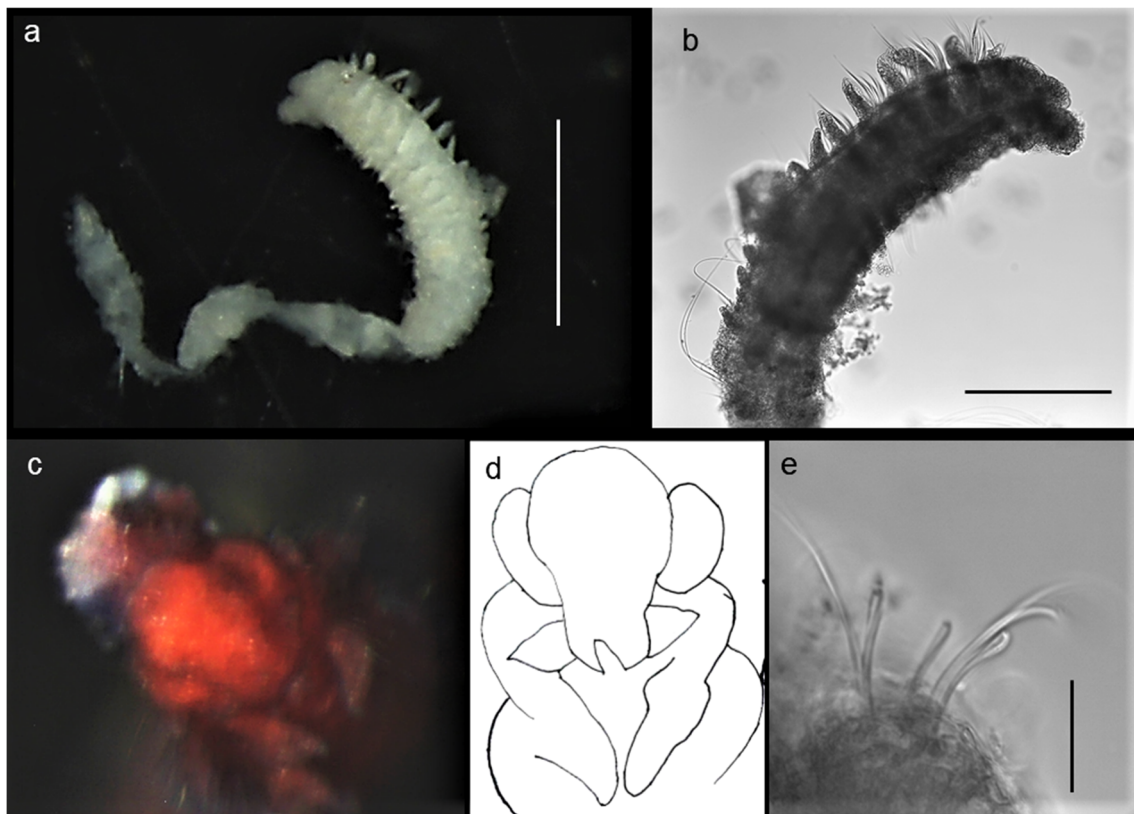
**Description:** Anterior fragment of specimen consisting of ca. 20 discernable chaetigers (ca. 0.8 mm long) and damaged body region. Body narrow and cylindrical. Preserved specimen white in ethanol (Fig. 30a, b).

Prostomium anteriorly rounded, appearing free from peristomium (Fig. 30c, d); no eyes observed; antenna not confirmed. Branchiae mostly missing or damaged. Parapodial lamellae overall small, best developed over the first 5 chaetigers. Genital pouches not confirmed likely due to poor preservation. Observed capillaries slender and lightly granulated. Sabre chaetae not detected. Neuropodial hooded hooks observed from chaetiger 18 (Fig. 30e), hooks very slender and sigmoid, with 2 small teeth in profile and narrow primary hood. The rest of the body unknown.

**Molecular Information.** The 16S sequence from this species matches three sequences from *Laonice* sp. ‘334 PB’ (Bonifácio et al. 2020), the uncorrected (*p*) distances among the four sequences are 0.0, extending this species distribution to the GSR, Ifremer, and IOM exploration contract areas in the eastern CCZ.

**Remarks.** This single anterior fragment appears atypical of *Laonice* species in having rather narrow cylindrical body and small parapodial lamellae.





**Fig. 30** *Laonice* sp. NHM\_2076, specimen NHMUK.ANEA.2021.39 **a–b** preserved specimen in lateral view, **c** anterior end in antero-dorsal view, specimen stained with Shirlastain; **d** diagrammatic line drawing of

prostomium and anterior dorsal lamellae; **e** neuropodial hooded hooks from chaetiger 18. Scale bars: **a** 500  $\mu$ m; **b** 250  $\mu$ m; **e** 25  $\mu$ m

**Distribution:** This species is known from OMS-1, GSR, Ifremer, and IOM exploration contract areas.

***Laonice shulseae* sp. nov.**

<http://zoobank.org/02AF55D7-4F41-44FB-B9A4-49E34F99715E>

Figs 31a–e, 32a–i

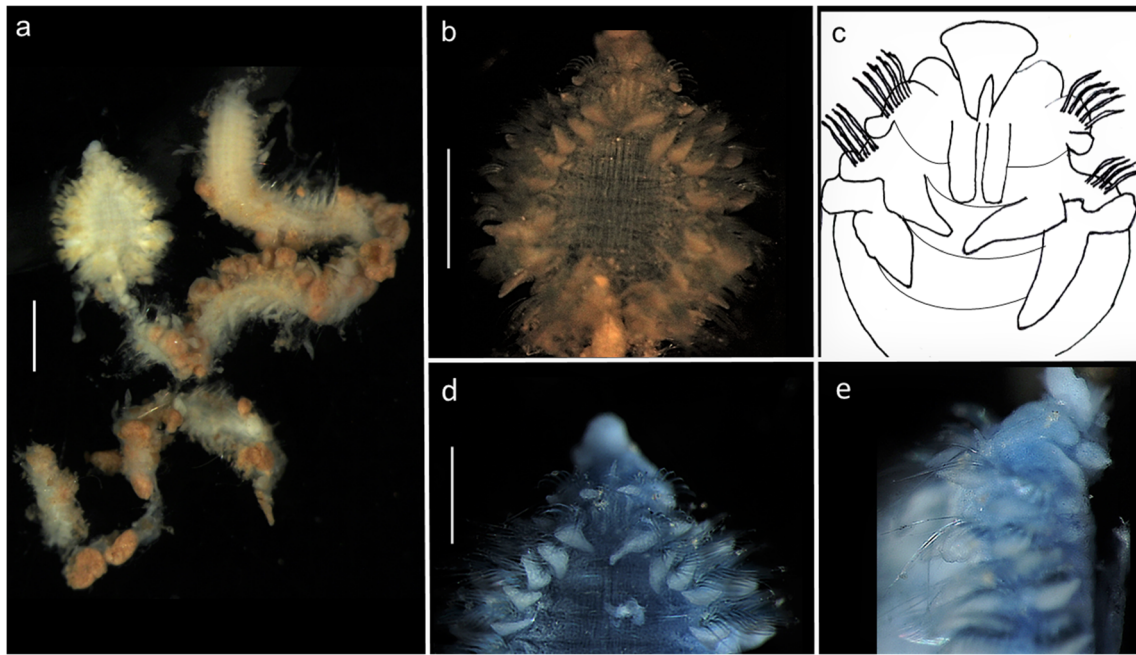
**Material examined:** holotype NHM\_2182, NHMUK ANEA.2021.50, coll. 21 Mar. 2015, collection method: USNEL Box Core, 19 27.998N, 120 00.172W, 4141 m; NHM\_2098, NHMUK ANEA.2021.48, coll. 20 Mar. 2015, collection method: Brenke Epibenthic Sledge, 19 27.874 N, 120 01.525 W, 4026 m; NHM\_2181, NHMUK ANEA.2021.49, coll. 21 Mar. 2015, collection method: USNEL Box Core, 19 27.998N, 120 00.172W, 4141 m.

**Description:** Three posteriorly incomplete specimens; the best-preserved specimen (holotype NHM\_2182) now in two fragments, anterior fragment 11.5 mm long for ca. 100 chaetigers and 1.25 mm at the widest region and body fragment with ca. 40 chaetigers (Fig. 31a). Anterior 10 chaetigers widest, flattened dorso-ventrally; following chaetiger gradually narrowing (Fig. 31a–d). Body pale yellow in alcohol (Fig. 31a).

Prostomium bell-shaped (Fig. 31b, c), anterior margin with shallow median incision, with slender cirriform occipital antenna present at the anterior end of the caruncle (Fig. 31c–e). Eyes absent. Peristomium moderately developed and appearing separated from the prostomium dorsally and laterally (Fig. 31e). Palps missing. Nuchal organ as pair of thick short loops extending past the anterior margin of chaetiger 2 (Fig. 31b–d), with light brown pigmentation.

Notopodial postchaetal lamellae overall well developed, smallest in chaetiger 1; large, fleshy and triangular (Fig. 31b–d) in the widest anterior part of the body (chaetigers 2–10); damaged or missing in the rest of the body but occasionally elongated triangular lamellae with blunt distal tip observed. Neuropodial postchaetal lamellae similar in development, with the smallest lamella in chaetiger 1 and largest lamellae in chaetigers 2–10; all lamellae broadly oval (Fig. 31e). Neuropodial pouches could not be confirmed. Branchiae missing.

Chaetal types undergoing marked change between chaetigers 2 and 3 and then 8 and 9. Chaetigers 1 and 2 with eight stout spine-like chaetae in a fan-shaped arrangement (Fig. 31a–d), spines abruptly curved, extending into very long slender tip and covered with fine hair when observed under high magnification (Fig. 32a); few slender, smooth narrowly

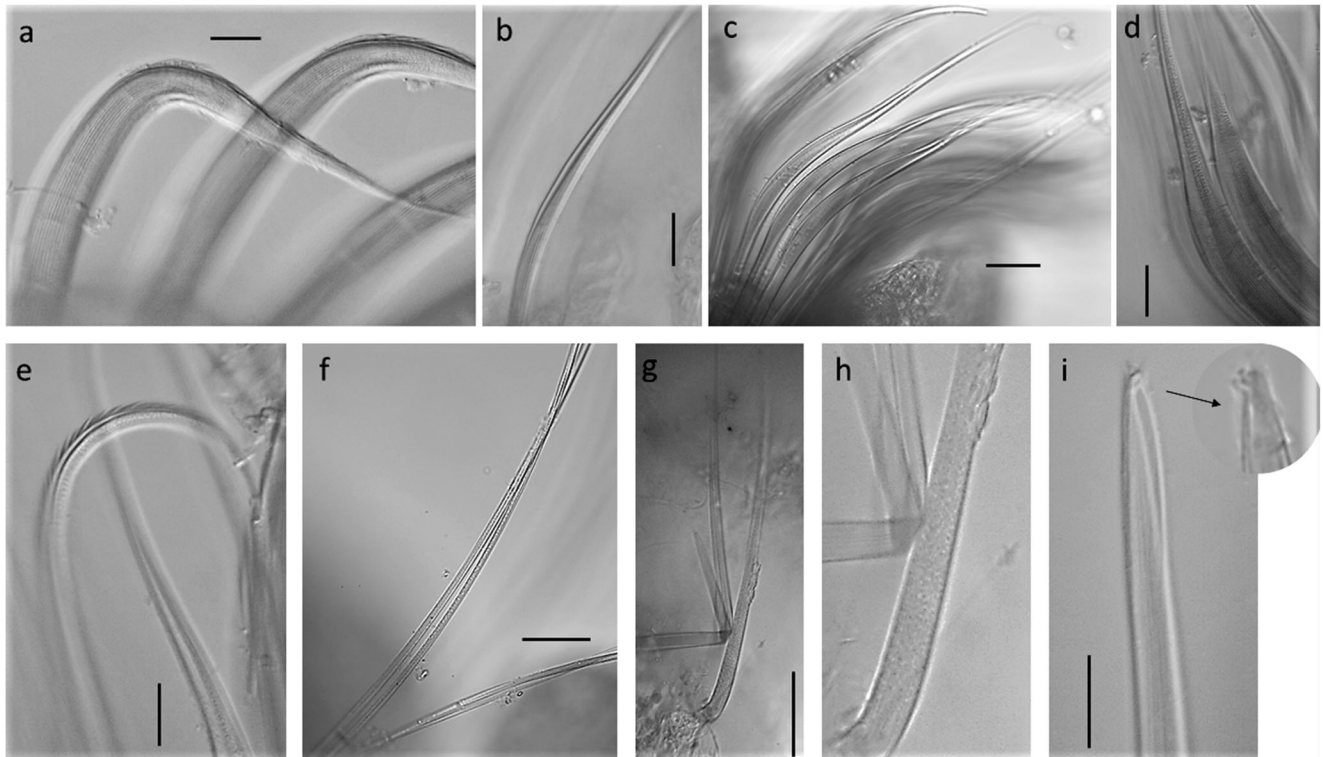


**Fig. 31** *Laonice shulseeae* sp. nov., holotype NHMUK.ANEA.2021.50, in images **d–e** specimen with retained Shirlastain **a** preserved specimen in dorsal view; **b–d** anterior part in dorsal view, with image **c** anterior end

in dorsal view represented as diagrammatic line drawing; **d** anterior end in lateral view, showing separation of prostomium and peristomium. Scale bars: **a** 1000  $\mu$ m; **b, d** 500  $\mu$ m

bi-limbate capillaries also present (Fig. 32b). In chaetigers 3–8, chaetae arrange in four rows, chaetae broadly limbate capillaries (Fig. 32c), broadest in the middle (Fig. 32d), and

abruptly extending into long slender tips, covered with fine hair when observed under high magnification (Fig. 32e). From chaetiger 9 capillaries long and slender, narrowly bi-limbate



**Fig. 32** *Laonice shulseeae* sp. nov., holotype NHMUK.ANEA.2021.50 **a** spines from chaetiger 1; **b** capillary chaetae from chaetiger 1; **c** capillary chaetae from ch 7 (typical for chaetigers 4–8); **d** detail of capillary chaetae

from ch 4 (typical for chaetigers 4–7); **e** hairy tips from chaetiger 7; **f** capillaries from chaetiger 9; **g** sabre chaeta; **h** detail of sabre chaeta; **i** neuropodial hooks. Scale bars: **a, b, d, e, i** 10  $\mu$ m; **c, f, g** 25  $\mu$ m

without granulations and hair (Fig. 32f). Sabre chaetae first detected from chaetiger 9, one or two per neuropodium, long, stout, and granulated (Fig. 32g, h). Neuropodial hooded hooks present (Fig. 32i), their start uncertain due to damage (~chaetiger 25); hooks very long and slender, about three per fascicle; bidentate in lateral view, both teeth minute without obvious main fang, with very short and narrow hood and appearing aristate under high magnification. Most of the body past chaetiger 10 too damaged, pygidium unknown.

**Molecular information.** In our phylogenetic analysis (Fig. 6), *Laonice shulseeae* sp. nov. has been recovered within a well-supported clade containing other species in the genus *Laonice*. The three 16S sequences from this species did not match any other sequences from the CCZ, the uncorrected (*p*) distances between the sequences range between 0.0 and 0.005.

**Remarks.** *Laonice shulseeae* sp. nov. possess an unusual character among known *Laonice* species—the spines in chaetigers 1 and 2 (Fig. 32a). Only one recently described species from the bathyal Atlantic, *Laonice plumisetosa* Bogantes, Halanych and Meißner, 2018 possesses similar chaetae that Bogantes et al. (2018) described as “stout capillaries with plush-like texture.” However, *L. shulseeae* sp. nov. can be easily distinguished from the known species by the following characters. New species has a different body shape, with the anterior chaetigers distinctly broadened (Fig. 31a, b, c). Although both species share the looped nuchal organs (also rare in *Laonice*), these are much shorter in the known species, not exceeding chaetiger 1, while they surpass the anterior margin of chaetiger 2 in *L. shulseeae* sp. nov. (Fig. 31b, c). Furthermore, the two species can be differentiated based on the morphology of hooded hooks, which are tri-dentate with distinct main fang in the known species, but in *L. shulseeae* sp. nov. they have a very small bidentate distal dentition, without obvious main fang (Fig. 3i).

While it is clear that ABYSSLINE specimens represent a new species, many other characters of taxonomic importance among species of *Laonice* cannot be ascertained due to poor morphological preservation (e.g., missing branchiae). Nevertheless, we formalize new species *Laonice shulseeae* sp. nov. despite limitations of the material as unique morphological and molecular characters are available and allow for easy identification (see also Bogantes et al. 2018). Should better preserved specimens be found in the future, the current morphological description can be amended.

**Distribution:** This species has only been found in CCZ APEI-6, an area assigned for preservation.

**Etymology.** This species is named for Dr. Christine Shulse, a scientist that participated in the first ABYSSLINE cruise in 2013.

*Prionospio* Malmgren, 1867

Type species: *Prionospio steenstrupi* Malmgren, 1867

**Diagnosis (emended from Peixoto and Paiva, 2019).** Prostomium without occipital antenna. Peristomium at least partially fused with chaetiger 1. Parapodia of chaetiger 1 reduced. Noto- and neuropodial lamellae largest in branchial region. Branchiae from chaetiger 2 or rarely absent. Branchiae limited to anterior chaetigers, can be all apinnate, all pinnate, or various combinations of both; free from dorsal lamellae. Dorsal crests present or absent. Interparapodial pouches present or absent. Anterior chaetae limbate capillaries; posterior noto- and neuropodial hooded hooks present, bi-, tri-, or multidentate, with secondary hood. Neuropodial sabre chaetae present or absent. Pygidium with long dorsomedial cirrus and two shorter ventrolateral cirri, all sometimes fused.

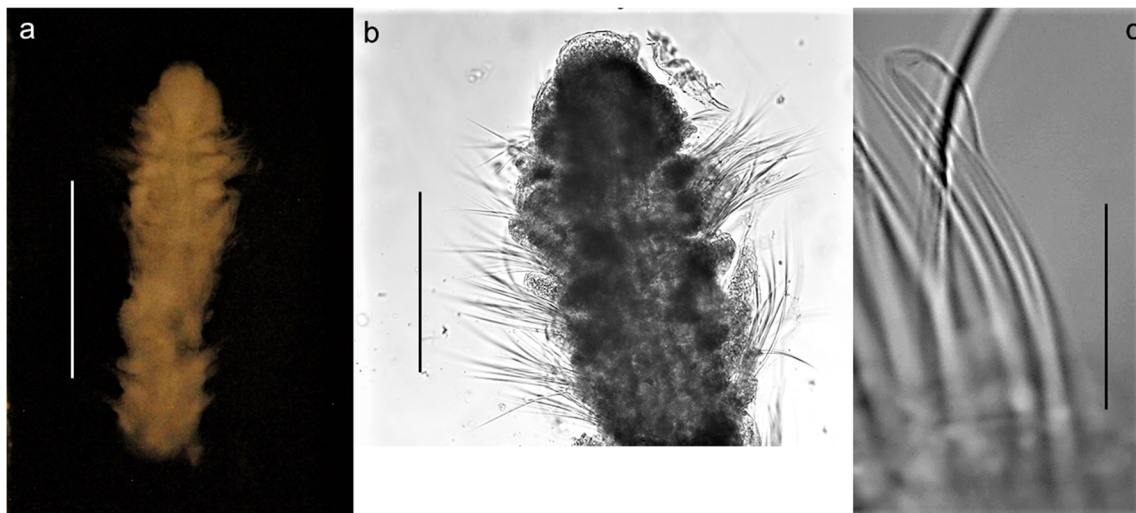
**Remarks.** The *Prionospio*-complex represents one of the most morphologically diverse and species rich groups within the Spionidae, although it is currently poorly defined. The arrangements of branchial diversity were used in the past to inform systematics of *Prionospio* (e.g., Foster 1971; Sigvaldadóttir 1998), a problem highlighted by recent discoveries of abranchiate species (Paterson et al. 2016; Peixoto and Paiva 2019). Our phylogenetic analyses (Fig. 6) recovered species assigned to *Prionospio* in a clade with strong support, but this clade also contain species assigned to *Aurospio* and *Paraprionospio*.

*Prionospio* sp. NHM\_135

Fig. 33a–c

**Material examined:** NHM\_135, NHMUK ANEA.2021.40, coll. 11 Oct. 2013, collection method: Brenke Epibenthic Sledge, 13°45.500N, 116°41.911W, 4080 m; NHM\_1413, NHMUK ANEA.2021.41, coll. 02 Mar. 2015, collection method: USNEL Box Core, 12°27.066N, 116°35.661W, 4130 m; NHM\_1347B, NHMUK ANEA.2019.10034, coll. 01 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°15.44N, 117°18.13W, 4302 m; NHM\_783G, NHMUK ANEA.2019.10021, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m; NHM\_701, NHMUK ANEA.2019.10018, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m.

**Description:** This small and slender species is represented by five poorly preserved specimens; the best example is specimen NHMUK\_135, an anterior fragment 0.95 mm long and



**Fig. 33** *Prionospio* sp. NHM\_135 **a** preserved specimen in dorsal view; **b** anterior end in dorsal view; **c** neuropodial hooded hooks from chaetiger 11. Scale bar: **a** 500  $\mu$ m; **b** 250  $\mu$ m; **c** 25  $\mu$ m

0.22 mm wide for about 11 discernible chaetigers. Color in alcohol pale yellow (Fig. 33a).

Prostomium anteriorly rounded, posteriorly elongated into slender caruncle reaching the anterior margin of chaetiger 2. Eyes absent. Peristomium forming a narrow hood around prostomium, not pronounced into distinct lateral wings (Fig. 33a, b).

Parapodial lamellae mostly missing or damaged. Branchiae not observed, assumed missing.

Chaetae of three types: capillaries, hooded hooks and sabre chaetae. First 9 chaetigers with capillaries only, which are granulated and narrowly bi-limbate. Sabre chaeta in neuropodia from chaetiger 10; stout, curved, limbate. Single multidentate hooded hook observed in neuropodia of chaetiger 11 (the last available chaetiger). Hooded hook long and slender, multidentate observed under light microscopy; with inflated, rounded hood; secondary hood not observed (Fig. 33c). Notopodial hooded hooks not observed in available fragments.

The rest of body and pygidium unknown.

**Molecular Information:** The 16S sequences from this species matches four sequences from *Prionospio* sp. ‘73 PB’ (Bonifácio et al. 2020), the uncorrected ( $p$ ) distances among the sequences range between 0.0 and 0.01, extending this species distribution to the BGR, GSR, Ifremer, and IOM exploration contract areas in the Eastern CCZ.

**Remarks:** Due to poor preservation (the loss of branchiae in particular), this species cannot be meaningfully compared with either known *Prionospio* species or other *Prionospio* species found in the ABYSSLINE samples.

**Distribution:** This species is only known from the eastern CCZ: UK-1, OMS-1, BGR, GSR, Ifremer and IOM exploration contract areas.

### *Prionospio* sp. NHM\_471

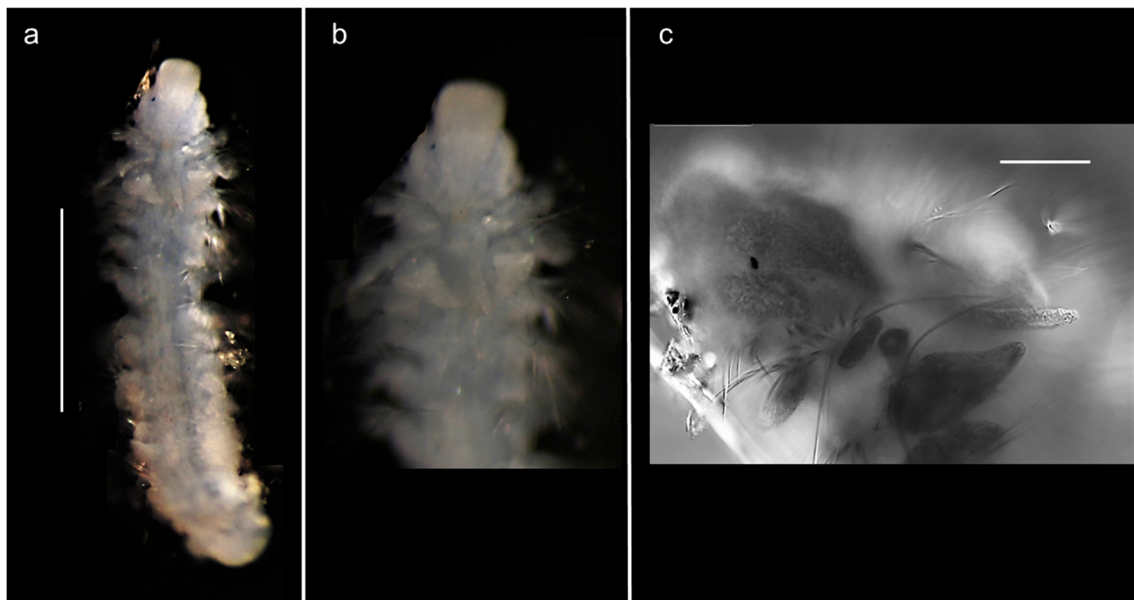
Fig. 34a–c

**Material examined:** NHM\_471, NHMUK ANEA.2019.10011, coll. 22 Oct. 2013, collection method: USNEL Box Core, 13°43.597N, 116°40.200W, 4160 m; NHM\_646, NHMUK ANEA.2019.10016, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_1930, NHMUK ANEA.2019.10048, coll. 13 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°02.49N, 117°13.03W, 4094 m; NHM\_698, NHMUK ANEA.2019.10017, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°32.23N, 116°36.25W, 4425 m.

**Description:** Small, slender species represented by four posteriorly incomplete specimens. The best example, specimen NHM\_471, an anterior fragment with 16 discernible chaetigers, 1.5 mm long and 0.25 mm wide (Fig. 34a). Preserved specimen whitish in color (Fig. 34a).

Prostomium anteriorly truncated, with anterior margin lightly pigmented (Fig. 34b), longer than wide, extending into slender caruncle to beginning of chaetiger 2, without peaks. Eyes absent. Peristomium not developed into lateral wings (Fig. 34b); dorsally not fused. Palps missing.

Parapodial lamellae rudimentary on chaetiger 1, best developed on branchial chaetigers, then getting smaller in postbranchial chaetigers. Notopodial lamellae largest on chaetiger 3, foliaceous to subtriangular with blunt rounded tip, arching medially over dorsum (Fig. 34c); notopodial lamellae on chaetiger 2 about half the size and similar in shape to those in chaetiger 3; notopodial lamellae on chaetiger 4 smaller and much more slender than those on chaetiger 3. Neuropodial lamellae largest on chaetigers 2–4; particularly



**Fig. 34** *Prionospio* sp. NHM\_471 **a** preserved specimen in dorsal view, faint Shirlastain still retained, anterior prostomial pigmentation visible; **b** anterior end in dorso-lateral view, showing notopodial lamellae and

branchiae of chaetiger 2; **c** prostomium with caruncle and peristomium in dorsolateral view. Scale bars: **a** 1000  $\mu$ m; **c** 100  $\mu$ m

large on chaetiger 3, blunt and oval. Three pairs of branchiae observed on chaetigers 2–4; all smooth, slender cirriform; first pair of branchiae (= chaetiger 2) longest, surpassing the length of corresponding notopodial lamellae (Fig. 34c); the second pair of branchiae very small, about half the size of corresponding notopodial lamellae; the third pair of branchiae extremely small, stubby. Dorsal ridge not confirmed.

Capillary chaetae only observed in 16 chaetiger long fragment. The presence and distribution of sabre chaetae, noto- and neuropodial hooded hooks unknown. The rest of body unknown.

**Molecular information:** The four 16S sequences from this species match five sequences from *Prionospio* sp. ‘268 PB’ (Bonifácio et al. 2020), the uncorrected ( $p$ ) distances among the nine sequences range between 0.0 and 0.01, extending this species distribution to the BGR, GSR and IOM exploration contract areas in the Eastern CCZ. The COI sequences match three sequences from CCZ submitted to GenBank by Janssen et al. (2015) and labeled as *Prionospio* sp. with accession numbers KJ736506, KJ736507 and KJ736509.

**Remarks:** Although this species could not be described in great detailed with characters such as hooded hooks missing, it appears that this species belongs to a group of deep-sea *Prionospio* species with reduced number of branchiae (Paterson et al. 2016) and relatively posterior start of neuropodial hooks. The fact that hooded hooks were not observed in the 16 chaetiger long anterior fragment of *Prionospio* sp. NHM\_471 suggests their more posterior distribution. Three pairs of branchiae of similar form were also recorded

in the species *Prionospio* sp. NHM\_914 and previously in *Prionospio branchilucida* Altamira, Glover & Paterson in Paterson et al. (2016) also described from CCZ (see Paterson et al. 2016 for details). Further comparison with known species is hampered by poor preservation of ABYSSLINE-collected specimens.

**Distribution:** This species is only known from CCZ: UK-1, OMS-1, BGR, GSR, and IOM exploration contract areas in the eastern CCZ.

#### *Prionospio* sp. NHM\_914

Figs 35a–e, 36a–d

**Material examined:** NHM\_914, NHMUK ANEA.2019.10024, coll. 23 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°34.28N, 116°36.63W, 4198 m; NHM\_1002, NHMUK ANEA.2019.10027, coll. 24 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°08.02N, 117°17.52W, 4122 m; NHM\_1099, NHMUK ANEA.2019.10030, coll. 26 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°06.93N, 117°09.87W, 4100 m; NHM\_1545, NHMUK ANEA.2019.10041, coll. 06 Mar. 2015, collection method: USNEL Box Core, 12°30.382N, 116°29.073W, 4244 m; NHM\_1174A, NHMUK ANEA.2019.10031, coll. 26 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°06.93N, 117°09.87W, 4100 m; NHM\_1600, NHMUK ANEA.2021.42, coll. 08 Mar. 2015, collection method: USNEL Box Core, 12°31.273N, 116°41.889W, 4237 m.



**Fig. 35** *Prionospio* sp. NHM\_914 **a** preserved specimen in lateral view and **b** specimen stained with Shirlastain; **c** preserved specimen in dorsal view; **d** specimen stained with Shirlastain; **e**

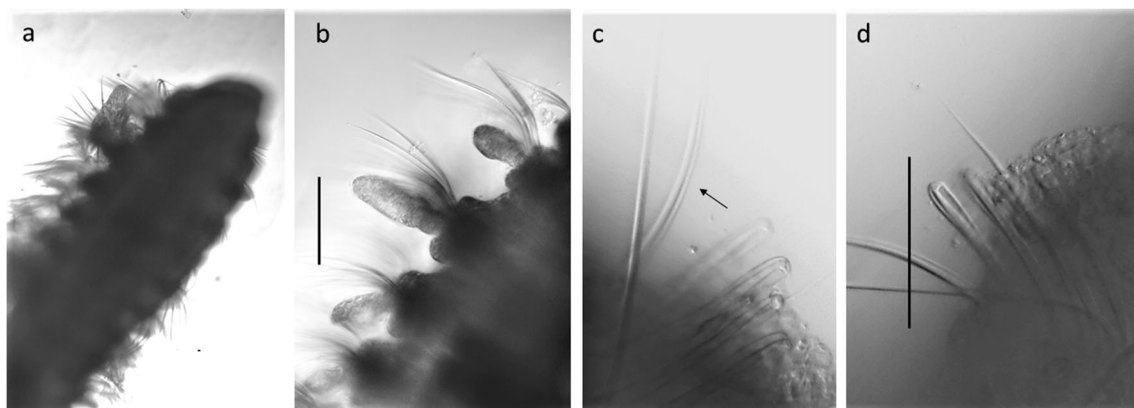
antero-dorsal view, showing prostomium and peristomium, first pair of branchiae and enlarged notopodial lamellae of chaetiger 3. Scale bars: 1000  $\mu$ m

**Description:** Small, slender species represented by six posteriorly incomplete specimens. The best example, specimen NHM\_914, an anterior fragment with 19 discernible chaetigers, 2.6 mm long and 0.35 mm wide (Fig. 35a–d). Preserved specimen pale yellow (Fig. 35a, c).

Prostomium anteriorly truncated, longer than wide, extending into slender caruncle to beginning of chaetiger 2, without peaks (Fig. 35e). Eyes absent. Peristomium forming slightly developed lateral wings (Fig. 35e). Palps missing.

Parapodial lamellae rudimentary on chaetiger 1, best developed on branchial chaetigers, then getting smaller in

postbranchial chaetigers. Notopodial lamellae largest on chaetiger 3, foliaceous to subtriangular with blunt rounded tip, arching medially over dorsum (Figs 34e, 35a); notopodial lamellae on chaetiger 2 about half the size and similar in shape to those in chaetiger 3, notopodial lamellae on chaetiger 4 smaller and much more slender than those on chaetiger 3, approaching bottle-shape. Neuropodial lamellae largest on chaetigers 2–4; particularly large, blunt and oval on chaetiger 3 (Fig. 36b); on chaetiger 2 about half the size of those on chaetiger 3, squarish to rounded; on chaetiger 4 smaller than those on chaetiger 3, rounded.



**Fig. 36** *Prionospio* sp. NHM\_914 **a** detail of enlarged notopodial lamellae; **b** neuropodial lamellae of chaetigers 2–4; **c** neuropodial sabre chaeta (arrow) from chaetiger 19; **d** neuropodial hooded hooks from chaetiger 19. Scale bars: **a** 250  $\mu$ m; **b** 100  $\mu$ m; **d** 50  $\mu$ m

Three pairs of branchiae observed on chaetigers 2–4; all smooth and cirriform; first pair of branchiae (= chaetiger 2) longest, surpassing the length of corresponding notopodial lamellae (Fig. 35e); the second and third pairs of branchiae extremely small, stubby. Dorsal ridges not confirmed.

Chaetae of three types: capillaries hooded hooks and sabre chaetae. Capillaries slender, narrowly bi-limbate and lightly granulated. The exact start of sabre chaetae uncertain, with first sabre chaeta observed in neuropodia of chaetiger 19; relatively slender with aristate tip, curved, limbate, granulation not observed (Fig. 36c). Hooded hooks singly from chaetiger 18; with 5 per fascicle in chaetiger 19; hooks with main fang and several small teeth, observed under light microscopy (Fig. 36d); with tight-fitting rounded hood and rudimentary secondary hood (Fig. 36d). Notopodial hooded hooks not observed in available fragments.

The rest of body and pygidium unknown.

**Molecular information:** Six 16S sequences from this species match five sequences from *Prionospio* sp. ‘29 PB’ (Bonifácio et al. 2020), the uncorrected (*p*) distances among the 11 sequences range between 0.0 and 0.002, thus extending this species distribution to the GSR, Ifremer and IOM exploration areas in the Eastern CCZ. COI sequences match eight sequences from CCZ submitted to GenBank by Janssen et al. (2015) and labeled as *Prionospio* sp. with accession numbers KJ736496-KJ736500 and KJ736502-KJ736504.

**Remarks:** Although this species cannot be described in great detail and the consistency of the characters reported above is currently uncertain, it appears that this species belong to group of deep-sea *Prionospio* species with reduced number of branchiae (Paterson et al. 2016) and relatively posterior start of neuropodial hooks. Three pairs of branchiae of similar form were also recorded in ABYSSLINE species *Prionospio* sp. NHM\_471 and in *Prionospio branchilucida* Altamira, Glover & Paterson in Paterson et al. (2016) previously described from CCZ and collected during Kaplan project. See also Remarks under *Prionospio* sp. NHM\_471.

**Distribution:** This species is known from UK-1, OMS-1, GSR, Ifremer, and IOM exploration contract areas in the eastern CCZ.

#### *Prionospio* sp. NHM\_266

Fig. 37a–e

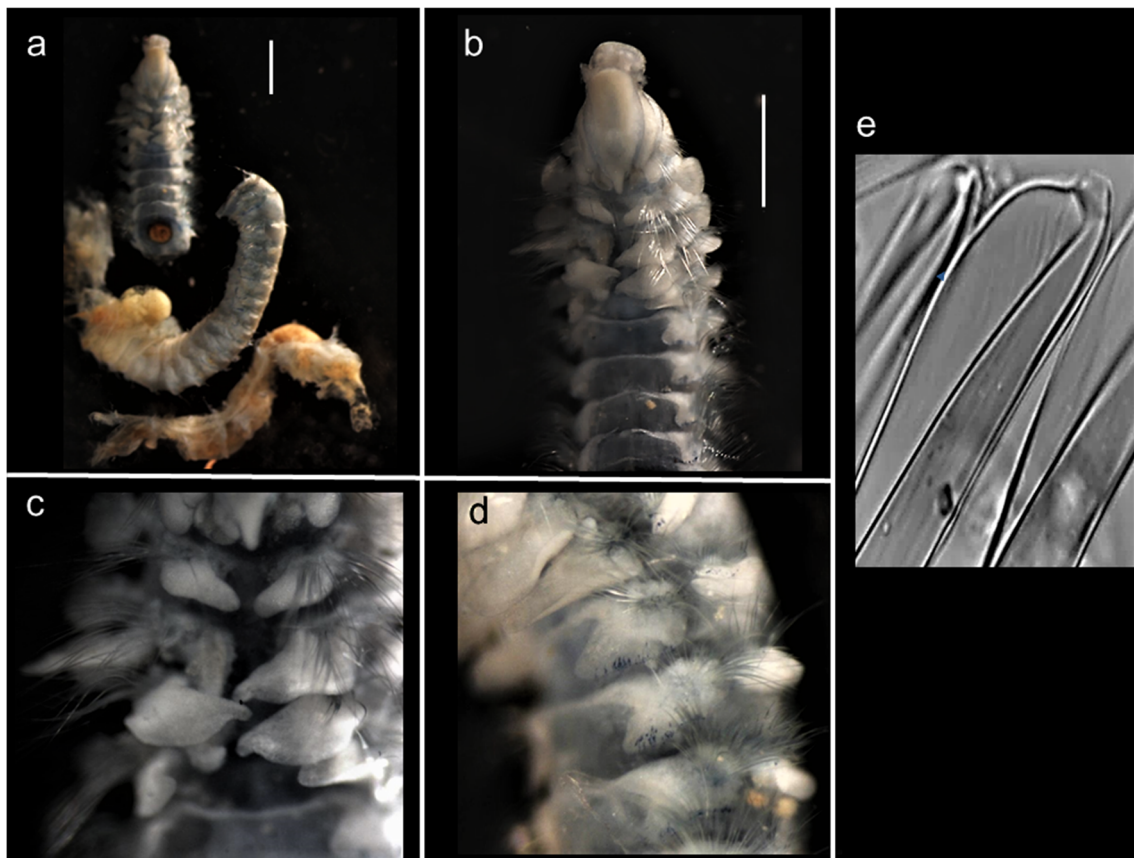
**Material examined:** NHM\_227, NHMUK ANEA.2019.10005, coll. 15 Oct. 2013, collection method: Remotely Operated Vehicle, 13°57.880N, 116°32.993W, 4072 m; NHM\_301, NHMUK ANEA.2019.10007, coll. 17 Oct. 2013, collection method: USNEL Box Core, 13°45.726N, 116°27.825W, 4110

m; NHM\_302, NHMUK ANEA.2021.44, coll. 17 Oct. 2013, collection method: USNEL Box Core, 13°45.726N, 116°27.825W, 4110 m; NHM\_266, NHMUK ANEA.2019.10006, coll. 17 Oct. 2013, collection method: Brenke Epibenthic Sledge, 13°45.21N, 116°29.12W, 4128 m; NHM\_582, NHMUK ANEA.2019.10014, coll. 17 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°23.17456N, 116°32.92021W, 4202 m; NHM\_1797F, NHMUK ANEA.2019.10046, coll. 11 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°10.43N, 117°11.57W, 4045 m; NHM\_886, NHMUK ANEA.2019.10023, coll. 23 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°34.28N, 116°36.63W, 4198 m; NHM\_1343, NHMUK ANEA.2019.10033, coll. 01 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°15.44N, 117°18.13W, 4302 m.

**Description.** Medium-sized species represented by four posteriorly incomplete specimens and several body fragments. The best example is specimen NHM\_301, now in three fragments (Fig. 37a): anterior fragment with 10 chaetigers measuring 3.7 mm long, 0.9 wide (at chaetiger 1) and two body fragments with 20 and approximately 10 discernable chaetigers respectively. Preserved specimens whitish in alcohol, with faint brown pigmentation around prostomial caruncle (Fig. 37b). Prostomium long, bottle-shaped with broadly rounded anterior margin (Fig. 37b); slender caruncle extending to anterior margin of chaetiger 2. Eyes not observed. Peristomium well developed, encircling prostomium closely like a collar, partially fused to chaetiger 1, forming low lateral wings (Fig. 37b).

Four pairs of branchiae present on chaetigers 2–5, with first and fourth pair lost in all available specimens. Branchial pairs 2 and 3 short, fleshy, triangular and laterally ciliated; both pairs slightly shorter than accompanying notopodial lamellae, in dorsal view both pairs covered by enlarged notopodial lamellae (Fig. 37c).

Anterior notopodial lamellae well developed, particularly enlarged in branchial chaetigers and largest on chaetigers 3 and 4 (Fig. 37c); triangular and elongated; from chaetiger 6 increasingly smaller and wider (Fig. 37d), becoming subquadrate with somewhat produced dorsal tip; in the available 20 chaetiger long body fragment notopodial lamellae low, flattened. Low dorsal crests from chaetiger 5 (Fig. 37b, c), till end of anterior fragment and also observed on most chaetigers of the 20 chaetiger long body fragment. Neuropodial lamellae small on chaetiger 1, largest on branchial chaetigers, then gradually becoming reduced in size; lamellae on chaetigers 2–4 fan-shaped (rhomboid) with rounded corners to slightly developed blunt ventral tip; then becoming progressively smaller and low (form not known from around chaetiger 30 due to damage of specimen). Interparapodial pouches absent.



**Fig. 37** *Prionospio* sp. NHM\_266, specimen NHMUK.ANEA.2019.10007. **a** Fragmented preserved specimen, anterior fragment in dorsal view, specimen retaining faint Shirilastain; **b** anterior end in dorsal view; **c** detail of notopodial lamellae on chaetigers 2–5, with short branchiae on chaetigers

3–4 and dorsal crest on chaetiger 5 visible; **d** specimen in lateral view, showing parapodial lamellae of chaetigers 5–7; **e** neuropodial hooded hooks. Scale bars: **a**, **b** 1 mm

Both notopodia and neuropodia in anterior region with capillaries arranged in three to four irregular rows. Capillaries slender, smooth and narrowly bi-limbate. Sabre chaetae and neuropodial hooks start around chaetiger 18 (observed on body fragments only, none found in 10 chaetiger long anterior fragment). Sabre chaetae long, slender, gently curved, with distal half lightly granulated, up to 2 per fascicle. Neuropodial hooks up to 8 per fascicle; long, slender, with angular, inflated primary hood and striated secondary hood; shaft very constricted just below multidentate “head”, with several small teeth, without particularly pronounced main fang (Fig. 37e). Notopodial hooks not present in available fragments. The mid body, posterior chaetigers and pygidium unknown.

**Molecular information.** Ten 16S sequences from this species match four sequences from *Prionospio* sp. ‘14 PB’ (Bonifácio et al. 2020), the uncorrected ( $p$ ) distances among the 14 sequences range between 0.0 and 0.006. This group of sequences is very similar to its sister taxon (Fig. 6), *Prionospio* sp. NHM\_884, with uncorrected ( $p$ ) distances in 16S ranging between 0.028 and 0.03. In the phylogenetic tree (Fig. 6), the clade with these two taxa also contains

*Prionospio* cf. *amarsupiata*, and the uncorrected ( $p$ ) distance to this taxon is equally low, 0.028.

Molecular data suggest close relationship of ABYSSLINE collected specimens to *Prionospio* cf. *amarsupiata*. It is important to note that the published sequences linked to *P. amarsupiata* by Paterson et al. (2016) were obtained from Crozet Island (abyssal South Atlantic) specimens and not from type locality (Setubal Canyon, NE Atlantic, 4482 m). Thus, we suggest here that Crozet Island specimens are assigned to *Prionospio* cf. *amarsupiata* rather than *Prionospio amarsupiata*. However, as supported by both molecular (this study; Guggolz et al. 2020) and morphological observations (this study, Paterson et al. 2016), *P. cf. amarsupiata* appears to be widely distributed in the abyss.

**Remarks.** Specimens collected from CCZ during Kaplan project were morphologically considered to belong to *P. amarsupiata* by Neal & Altamira in Paterson et al. (2016). ABYSSLINE specimens correspond well to *P. amarsupiata* in shape of prostomium, form of anterior parapodial lamellae, relatively late start of hooded hooks and their form, the presence of low dorsal crest from chaetiger 5 and lack of neuropodial genital pouches (see also discussion of



*P. amarsupiata* in Paterson et al. 2016). However, one of the main diagnostic characters – the form of branchiae, cannot be compared as first and fourth pairs of branchiae have been lost in all ABYSSLINE-collected specimens. Therefore, as a precaution we assigned these specimens to *Prionospio*. cf. *amarsupiata* till better preserved specimens become available (see also Molecular information).

In addition, another ABYSSLINE collected species—*Prionospio* sp. NHM\_884—has shown both morphological and molecular affinities to *P. amarsupiata*. For further details, see Remarks section of *Prionospio* sp. NHM\_884.

**Distribution:** This species has here been recorded from the eastern CCZ (UK-1, OMS-1, GSR and Ifremer areas). Previously this species has been reported from wider CCZ (Kaplan project).

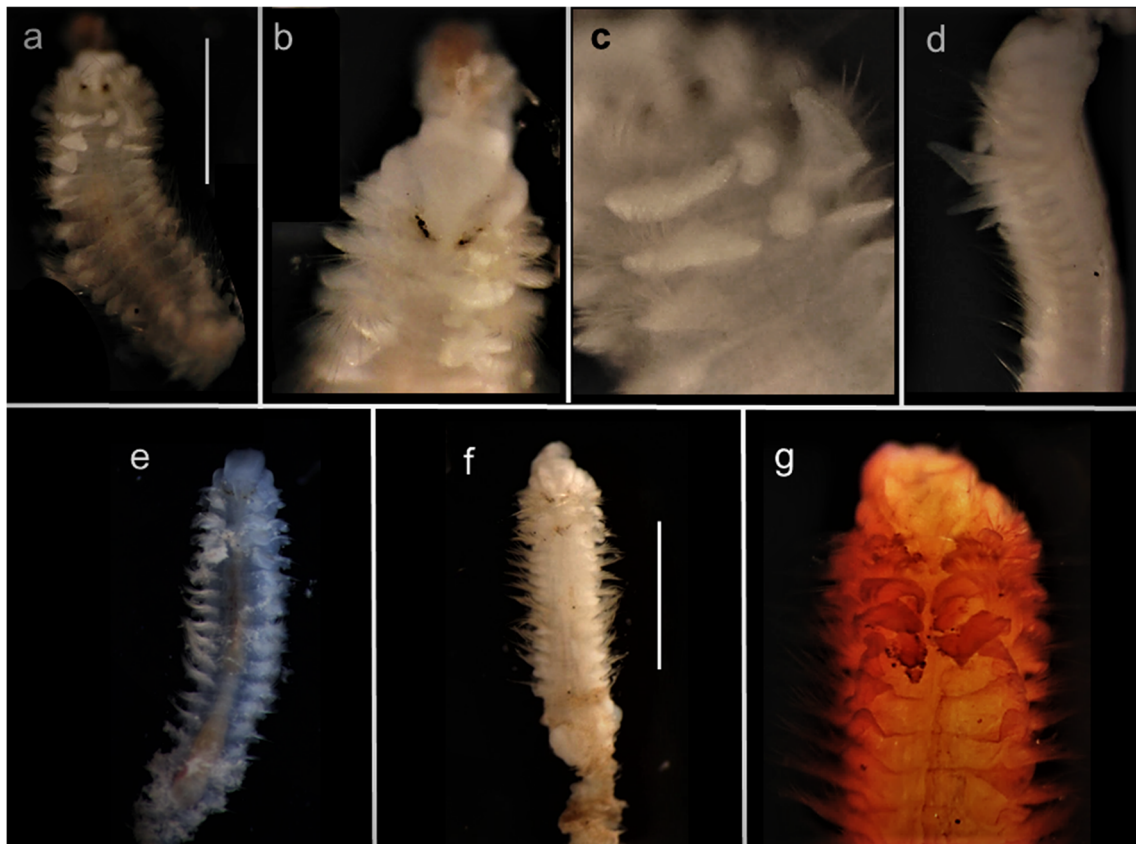
#### *Prionospio* sp. NHM\_884

Figs. 38a–g, 39a, c

**Material examined:** NHM\_736, NHMUK ANEA.2019.10019, coll. 20 Feb. 2015, collection method: Brenke Epibenthic Sledge,

12°32.23N, 116°36.25W, 4425 m; NHM\_884, NHMUK ANEA.2019.10022, coll. 23 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°34.28N, 116°36.63W, 4198 m; NHM\_943, NHMUK ANEA.2019.10025, coll. 23 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°34.28N, 116°36.63W, 4198 m.

**Description:** small species represented by three posteriorly incomplete specimens. The best example is specimen NHM\_844, measuring 2.2 mm long, 0.7 mm wide (at chaetiger 1) for 17 chaetigers (Fig. 38a–c). Live specimens (NHM\_736) observed, 3.1 mm long, 0.5 mm wide for about 20 discernable chaetigers) translucent, with pale blue hues, distinct rusty pigmentation around prostomial caruncle, with orange to brown gut (Fig. 38e); preserved specimens pale yellow in alcohol, with distinct dark rusty pigmentation around prostomial caruncle (Fig. 38a, b, f). Prostomium angular, anteriorly truncated (Fig. 38b), with slender caruncle extending to anterior margin of chaetiger 2. Eyes not observed. Peristomium well developed, encircling prostomium closely like a collar, partially fused to chaetiger 1, forming low lateral wings (Fig. 38b).



**Fig. 38** *Prionospio* sp. NHM\_884, showing specimen NHMUK.ANEA.2019.10022 unless stated otherwise **a** preserved specimen in dorsal view; **b** detail of anterior end, showing the

pigmentation; **e–g** live, preserved and stained with Shirlastain specimen NHMUK.ANEA.2019.10019 in dorsal view. Scale bars: 1 mm

Four pairs of branchiae present on chaetigers 2–5, with first and fourth pair lost in all specimens. Branchial pairs 2 and 3 short, somewhat stubby, cirriform (Fig. 38c, g).

Anterior notopodial lamellae well-developed in all observed chaetigers, but particularly enlarged in branchial chaetigers and largest on chaetigers 3 and 4 (Fig. 38c, d, g); triangular and elongated, from chaetiger 6 increasingly smaller, wider, conical with broadly rounded tip. Low dorsal crests from chaetiger 6 (Fig. 38g), till end of the fragment. Neuropodial lamellae small on chaetiger 1, largest on branchial chaetigers, then gradually becoming reduced in size; lamellae on chaetiger 2–4 fan shaped with rounded corners to slightly developed blunt ventral tip; then becoming rounded and smaller, particularly low past chaetiger 15. Interparapodial pouches absent.

Both notopodia and neuropodia in anterior region with capillaries arranged in two rows of longer and short chaetae. Capillaries slender, smooth and narrowly bi-limbate. Sabre chaetae and neuropodial hooks start on chaetiger 17. Sabre chaetae stout, gently curved and heavily granulated, up to 2 per fascicle (Fig. 39c). Neuropodial hooks long, slender, with angular, primary hood (Fig. 39a); the presence of secondary hood uncertain; shaft very constricted just below very small multidentate “head” (difficult to observe even under high magnification), with several very small teeth, no main fang detected (Fig. 38a); five per fascicle observed. Notopodial hooks not present in available anterior fragments. The mid body, posterior chaetigers, and pygidium unknown.

**Molecular information.** Three 16S sequences obtained from this species do not match any other sequences, the uncorrected (*p*) distance among the three sequences range from 0.0 to 0.002. However, this group of sequences is very similar to its sister taxa in the tree (Fig. 6), *Prionospio* sp. NHM\_266, with uncorrected (*p*) distances in 16S ranging between 0.028 and 0.03. In the tree (Fig. 6), the clade with these two taxa also

contains *Prionospio* cf. *amarsupiata*, and the uncorrected (*p*) distance to this taxon is equally low, 0.028.

**Remarks.** Molecular data suggest close relationship of *Prionospio* sp. NHM\_884 with *Prionospio amarsupiata* as well as another ABYSSLINE collected specimens assigned to *Prionospio* sp. NHM\_266 (= cf. *amarsupiata*) (Fig. 6). Morphologically, these species are similar in the shape of anterior parapodial lamellae, relatively posterior start of hooded hooks and their form (Figs 36e, 38a, b), the presence of low dorsal crest and lack of neuropodial genital pouches (see also discussion of *P. amarsupiata* in Paterson et al. 2016). The main differences observed are the shape of prostomium, which is anteriorly rounded and bottle shaped in *P. amarsupiata* and *Prionospio* sp. NHM\_226 (Fig. 37b) but distinctly truncated in *Prionospio* sp. NHM\_884 (Fig. 38b) and possession of four, not two rows of capillaries in anterior notopodia in *P. amarsupiata*. However, the main diagnostic characters—the form of branchiae, cannot be compared as first and fourth pairs of branchiae have been lost in all ABYSSLINE specimens.

**Distribution.** This species is only known from UK-1 exploration contract area in the eastern CCZ.

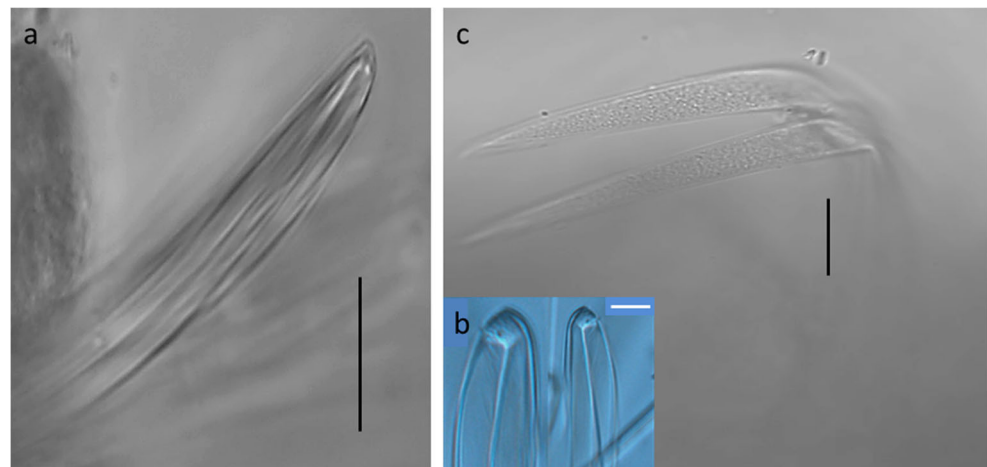
*Spiophanes* Grube, 1860

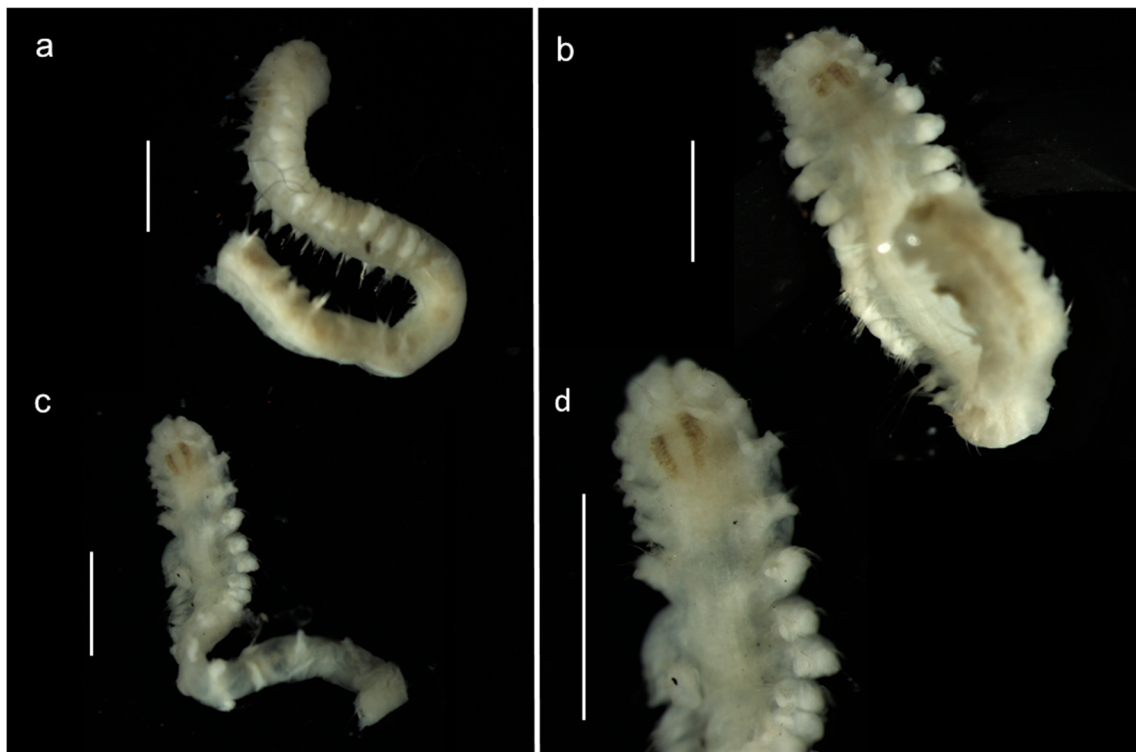
*Spiophanes* sp. NHM\_1897

Fig. 40a–d

**Material examined:** NHM\_1897, NHMUK ANEA.2021.46, coll. 13 Mar. 2015, collection method: Brenke Epibenthic Sledge, 12°02.49N, 117°13.03W, 4094 m; NHM\_3186, NHMUK ANEA.2021.47, coll. 24 Feb. 2015, collection method: Brenke Epibenthic Sledge, 12°08.02N, 117°17.52W, 4122 m.

**Fig. 39** Comparison of neuropodial hooded hooks **a** neuropodial hooded hooks of *Prionospio* sp. NHM\_884; **b** neuropodial hooded hooks of *Prionospio amarsupiata* from Paterson et al. (2016); **c** neuropodial sabre chaetae of *Prionospio* sp. NHM\_884. Scale bars: **a**, **c** 25  $\mu$ m; **b** 10  $\mu$ m





**Fig. 40** Preserved specimens of *Spiophanes* sp. NHM\_1897, specimen NHMUK. ANEA.2021.46 in **a** lateral view and **b** dorsal view; **c–d** specimen NHMUK.ANEA.2021.47 in dorsal view. Scale bars: 1000  $\mu$ m

**Description:** This species is represented by two anterior fragments (Fig. 40a–d), consistent with genus *Spiophanes* due to presence of modified hooks in chaetiger 1 and absence of branchiae.

**Molecular information:** The 16S sequences from this species did not match any other available sequences. The COI sequence from this species matched five previously published sequences from the CCZ and labeled as *Spiophanes* sp. (Janssen et al. 2015, GenBank accession numbers KJ736657–KJ736661), with uncorrected ( $p$ ) values ranging from 0.0 to 0.02. The COI sequence also matches a recently described species from the Adriatic Sea, *Spiophanes adriaticus*, D'Alessandro, Castriota, et al. (2020) (GenBank accession number MT177912) with uncorrected ( $p$ ) value between the species of 0.017.

**Remarks:** This species is currently studied by Karin Meissner (Meissner pers. comm.). Therefore, we only report this species as present in ABYSSLINE material for the completeness of Spioniformia species checklist.

**Distribution:** This species is known from the eastern CCZ and was found in the OMS-1 contract area and previously also in the BGR contract area (Janssen et al. 2015).

## Discussion

This study has added 25 annelid species, two of those formalized, and 98 records to the knowledge of the benthic annelid macrofauna of the CCZ, bringing a published record from the ABYSSLINE (UK-1 and OMS) investigated areas to 48 polychaete species, with 15 formalized (see also Wiklund et al. 2019; Drennan et al. 2021). Additional studies to either provide taxonomic data for or to formalize remaining ABYSSLINE polychaetes are currently underway by the authors.

It is well known that Spionidae are well represented in sediment infauna, both in terms of abundance and species richness in shallow water and deep sea, including the CCZ area (e.g., Glover et al. 2002; Paterson et al. 2011, 2016). Although Spionidae represent a species rich group within Annelida, interestingly, its ca. 40 genera tend to be reduced to only four, commonly encountered in the deep-sea samples—*Aurospio*, *Prionospio*, *Laonice*, and *Spiophanes* (Neal pers. obs.)—as also mirrored in this study. Of those, *Prionospio* and the allied *Aurospio* tend to be particularly abundant and species rich in the deep sea (e.g., Paterson et al. 2016; Guggolz et al. 2020; Peixoto and Paiva 2020). Unfortunately, the discovery and description of this great diversity tends to be compromised by two problems, a poor

definition of *Prionospio* and related taxa and the poor preservation and easy fragmentation of available specimens. Such issues were also encountered here preventing a formal description of several new species. Furthermore, as already observed by Paterson et al. (2016) the main diagnostic character of *Prionospio*—the branchiae not only tend to be lost due to damage in deep-sea specimens, but even if observed, they tend to have reduced morphology compared to shallow waters species (i.e., <4 branchial pairs or even absence of branchiae is commonly seen, pinnules are often absent etc.). Therefore, the search for characters that would reliably identify deep-sea *Prionospio* is greatly dependent on specimens in pristine condition, which are currently lacking.

Owing to the paucity and unreliability of morphological characters, molecular data gain even more importance for species identification and estimation of species ranges. Molecular data on Spionidae mimic the now well-established pattern of molecular data revealing the presence of more species than what can be established based on morphology alone, commonly known as cryptic diversity (Knowlton 1993). The diversity is not necessarily 100% cryptic, but careful examination of new material is needed to establish the presence of new and previously overlooked characters. We have highlighted some of these issues in the Remarks section of certain taxa, particularly *Auropsio dibranchiata*—long considered a deep-sea “cosmopolitan” species, a view now challenged by molecular data.

Studies of annelid species’ ranges in the deep sea in general and CCZ in particular as estimated from molecular data are still in their infancy. At present, many of abyssal annelid taxa, including those from CCZ appear to have a restricted distribution. Bonifácio et al. (2020) showed that 49% of CCZ polychaete species had their distribution limited to the single investigated area, a pattern also observed for CCZ tanaid crustaceans (Błazewicz et al. 2019). Nevertheless, such patterns may change with the increased future sampling and analytical efforts from other CCZ areas as well as other deep-sea regions. Only nine out of 25 species in this study have been found in a single area only and these were usually represented by singletons. Fifteen out of 25 species reported here have been found distributed across at least the eastern CCZ. Interestingly, two spionid species, *Prionospio* cf. *amarsupiata* and *Auropsio* sp. NHM\_2186 (one of *A. dibranchiata*-like species), may truly be considered cosmopolitan, although more data is needed. Guggolz et al. (2020) analyzed a relatively large deep-sea molecular *Prionospio* and *Auropsio* dataset and reported that seven out of 21 lineages had pan-oceanic distributions, suggesting that high dispersal abilities may be due to free-swimming long-lived planktonic larval stages. Such findings are not unique to Spionidae though, with several other annelid taxa reported to have a wide distribution as supported by molecular data (Ahrens et al., 2013; Eilertsen et al. 2018; Georgieva et al. 2015; Neal et al. 2018). In fact, a

recent review of genetic studies of deep-sea taxa revealed a general pattern of greater connectivity over long distances at similar depths, rather than across depth (Taylor and Roterman 2017). Contrary to this pattern, we found *Spiophanes* COI sequences from the CCZ matching a shallow water species from the Mediterranean (*Spiophanes adriaticus*). Such a result is difficult to explain, particularly as the two species are not morphologically similar and the validity of the Mediterranean species has been recently questioned (Jourde et al. 2020). Thus, distribution results based on single gene analyses must be scrutinized carefully. In our *Spiophanes* case, nine single base mutations among 593 bp resulted in five amino acids differences between the two species. This is an important result as it shows that using only COI sequences, as is common in, e.g., metabarcoding studies, could be potentially misleading.

Lastly, the molecular data presented here enable us to comment on phylogenetic relationships within Spioniformia (Fig. 6). Although both Poecilochaetidae and Trochochaetidae are currently considered valid (Read and Fauchald 2018, 2019), these spioniform monogeneric families have a confused history and their status is yet to be resolved. Their close relationship to Spionidae has long been recognized, even though Mesnil (1897) formed a separate family Disomidae to accommodate *Disoma mulisetosum* described by Örsted (1844). Problematic systematics of *Disoma multisetosum* (now *Trochochaeta multisetosa*) achieved some stabilization following the decision of Pettibone (1963) to establish the new family Trochochaetidae (see Radashevsky et al. 2018 for details). The family Poecilochaetidae was established by Hannerz (1956) for *Poecilochaetus* species due to larval differences, as it was argued that divergences in the formation of the prostomium and the peristomium and the prototroch differentiate *Poecilochaetus* from *Disoma*.

In recent decades, most works treated Poecilochaetidae and Trochochaetidae as two valid monogeneric families, although there were exceptions (Rouse and Pleijel 2006; Radashevsky et al. 2018). The phylogenetic approach to this question has so far been limited. Cladistic analysis of Blake and Arnofsky (1999) based on morphological and reproductive data suggested that the status of Trochochaetidae and Poecilochaetidae should be re-considered as these were recovered within Spionidae. Similarly, the inclusion of Trochochaetidae and Poecilochaetidae within Spionidae has been supported by Hausen (2007), due to presence and structure of light-sensitive organs within the prostomium. Eiby-Jacobsen’s (2005) cladistic analysis concentrated solely on the relationships within Poecilochaetidae, using Trochochaetidae and Apistobranchidae (but not Spionidae) as an outgroup. Molecular approaches that included Poecilochaetidae and Trochochaetidae to date have been of limited value, as these were higher level phylogenies, often including only one representative per family (e.g., Struck et al. 2007; Zrzavý et al.

2009) or family specific. Very recently, while investigating relationships of horned *Spiophanes* species, Radashevsky et al. (2020) recovered *Trochochaeta* as a sister group to *Spiophanes*. Our molecular results based on Bayesian analysis of 102 spioniform taxa and three genes (CO1, 16S, 18S) (Fig. 6, Table 1, Supplementary materials 1 and 2) are in agreement with those of Radashevsky et al. (2020). Therefore, our molecular data provide further support for the inclusion of both Poecilochaetidae and Trochochaetidae within Spionidae, although the position of *Poecilochaetus* within Spionidae was unresolved.

To summarize, despite the recent efforts, there are still few DNA sequences for benthic faunal groups from the CCZ available on GenBank, mainly restricted to echinoderms (Glover et al. 2016a), cnidarians (Dahlgren et al. 2016), molluscs (Wiklund et al. 2017), annelids (Bonifácio and Menot 2019; Janssen et al. 2015; Wiklund et al. 2019; Guggolz et al. 2020), Porifera (Lim et al. 2017), and crustaceans (Janssen et al. 2015). Although the morphological data presented here are limited for most species due to their poor condition, it is our hope that the accompanying molecular data may ease identification in future surveys and better-preserved specimens may become available with further sampling. The information presented here therefore represents a further step in improving our understanding of benthic fauna from the CCZ area, which in turn is essential for informing conservation efforts, as well as providing future practical identification guides to the fauna of this region.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s12526-022-01277-1>.

**Acknowledgments** We thank the masters, crew, and technical staff on the *RV Melville* and *RV Thomas G Thompson* for their outstanding support. We acknowledge the expert leadership of the research cruises and ABYSSLINE project by Prof Craig R Smith, University of Hawaii. We acknowledge the continued support from the NHMUK Consultancy team (Harry Rousham, Robyn Fryer, Kate Rowland). We received help sorting and sieving samples at sea from Magdalena Georgieva and Madeleine Brasier, and the entire ABYSSLINE science team in successful deep-sea coring operations. Finally, we would like to thank to two anonymous reviewers who helped to improve this publication.

**Funding** This study was funded by UK Seabed Resources Ltd, Contract No. SRD100200 (NHM) & Contract No. SRD100500 (NORCE) and Norwegian Research Council (JPIO MiningImpact2, Grant #290931).

## Declarations

**Conflict of interest** AGG and TGD have received research grants from UK Seabed Resources Ltd, the Metals Company, NOAA and the Moore Foundation. AGG has received research grants from the Pew Foundation.

**Ethical approval** All applicable international, national, and/or institutional guidelines for use of animals were followed by 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 and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

**Data availability** All data generated or analyzed during this study are included in this published article and its supplementary information files.

**Author contribution** The first author, LN, led the morphological investigation of the specimens used in this study and led the publication. HW collected the specimens and was responsible for the molecular study of the specimens. MR collected the specimens and compiled the DarwinCore database. TGD and AGG conceptualized the research and collected the specimens. All authors contributed to the writing of the manuscript.

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