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**Monograph**

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# Partial revision of northern European *Prionospio* Malmgren, 1867 (Annelida: Spionidae)

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**Abstract.** This study continues our revision of *Prionospio* Malmgren, 1867 from the Northeast Atlantic aiming to describe the morphology of the worms that we have previously examined using molecular methods. Nine species of *Prionospio* are described or redescribed and illustrated, including two new species, *P. fiordica* sp. nov. and *P. sigvaldadottirae* sp. nov. A neotype is designated for *P. plumosa* M. Sars, and *P. tripinnata* Maciolek, 1985 is considered a junior synonym of this species. We found no evidence to support the presence of *P. steenstrupi* Malmgren, 1867 in coastal or shelf waters of mainland Europe. *Prionospio* sp. 6 is distinguished but not formally described due to poor material available. An identification key for *Prionospio* from northern Europe is presented. Several species of *Prionospio* in this study demonstrate a broad geographic and bathymetric range.

**Keywords.** Polychaeta, taxonomy, *Prionospio*, Norway, Europe.

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## Introduction

Spionidae Grube, 1850 is one of the most specious polychaete families, currently comprising more than 600 species (Read & Fauchald 2025). *Prionospio* Malmgren, 1867 is the most species-rich genus of the family with more than 100 species (Blake *et al.* 2020). *Prionospio* worms are common globally from the intertidal to the deep sea and often form populations of high density. Some species are vital bioindicators in European waters (Borja *et al.* 2000; Borgersen *et al.* 2019), and thus of special interest to study.

The genus *Prionospio* was established to accommodate *P. steenstrupi* Malmgren, 1867 from northern Iceland. After Malmgren (1867), *Prionospio* from European waters were studied and described by many

authors (see reviews by Mackie 1984; Maciolek 1985; Sigvaldadóttir & Mackie 1993; Sigvaldadóttir 1998). Recent reviews and revisions recognize 17 species of *Prionospio* from the Northeast Atlantic (from the Barents Sea south to the Strait of Gibraltar). These include *P. aluta* Maciolek, 1985, *P. banyulensis* Laubier, 1966, *P. caspersi* Laubier, 1962, *P. cirrifera* Wirén, 1883, *P. cristaventralis* Delgado-Blas, Díaz-Díaz & Viéitez, 2018, *P. dubia* Day, 1961, *P. ehlersi* Fauvel, 1928, *P. fallax* Söderström, 1920, *P. malmgreni* Claparède, 1868, *P. multibranchiata* Berkeley 1927, *P. multisetosa* Delgado-Blas & Peraza, 2024 *P. parapari* Delgado-Blas, Díaz-Díaz & Viéitez, 2018, *P. plumosa* M. Sars in G.O. Sars, 1872, *P. pulchra* Imajima, 1990, *P. rikardoi* Martinez & Adarraga, 2019, *P. sanmartini* Delgado-Blas, Díaz-Díaz & Viéitez, 2019, and *P. steenstrupi.* It is, however, unlikely that either *P. dubia* or *P. multibranchiata* occur in the region based on recent studies (Delgado-Blas *et al.* 2019; Delgado-Blas & Peraza 2024; Hektoen *et al.* 2024). Thus, in northern Europe (Barents, Norwegian and North seas, and the British Channel), seven species are currently thought to occur: *P. banyulensis*, *P. cirrifera*, *P. fallax*, *P. multisetosa*, *P. plumosa*, *P. sanmartini*, and *P. steenstrupi*.

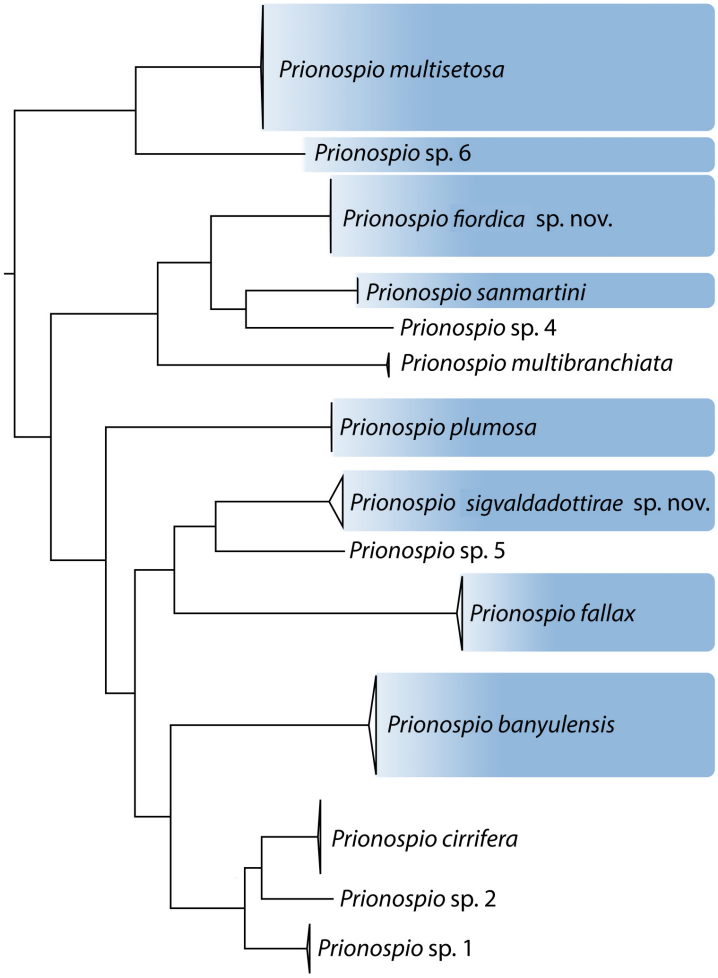


**Fig. 1.** Phylogram modified from Hektoen *et al.* (2024) based on all mitochondrial genes. The species considered in this study are marked in blue. In addition to the species marked in blue, *Prionospio cirrifera* Wiren, 1883 and *Prionospio* sp. 1 also occur in northern European waters but are not treated in this study. Species names are given in correspondence with results in this study: *Prionospio multisetosa* Delgado-Blas & Peraza, 2024 is *Prionospio* cf. *dubia* in Hektoen *et al.* (2024); *Prionospio fiordica* sp. nov. is *Prionospio* sp. 3; *Prionospio sanmartini* Delgado-Blas, Díaz-Díaz & Viéitez, 2019 is *Prionospio* cf. *sanmartini*; *Prionospio sigvaldadottirae* sp. nov. is *Prionospio* sp. 7.

Molecular data of *Prionospio* are scarce, and phylogenetic relationships have been studied mainly on Asian species (Abe & Sato-Okoshi 2021; Lee *et al.* 2023) or species from the deep sea (Guggolz *et al.* 2020; Neal *et al.* 2022). In northern Europe, short fragments of *COI* were obtained by Aylagas *et al.* (2016) for two individuals of *P. dubia* and four individuals of *P. ehlersi* from the Bay of Biscay, Spain. The first comprehensive molecular analysis of Northeast Atlantic *Prionospio* was performed by Hektoen *et al.* (2024). Ten species from the region were studied and four of them were suggested as new to science (*Prionospio* sp. 1, *Prionospio* sp. 3, *Prionospio* sp. 6, and *Prionospio* sp. 7.; Fig. 1). It was shown that worms earlier morphologically assigned to *P. multibranchiata* belong to two different species and *P. multibranchiata* is absent in East Atlantic waters. *Prionospio banyulensis* was found nested within *Prionospio* (where it was originally assigned) and therefore transferred from *Aurospio* Maciolek, 1981 where it was placed by some authors (e.g., Sigvaldadóttir 1998, 2002).

The purpose of the present study is to continue our revision of *Prionospio* from northern Europe and describe the morphology of the worms that we have previously examined using molecular methods. *Prionospio cirrifera* is not treated in this paper but will be discussed in an upcoming study.

## Material and methods

New material was obtained from biomonitoring surveys conducted by Åkerblå AS, STIM AS, and the Norwegian Institute of Water Research (NIVA) along the Norwegian coast. The samples were collected and treated in accordance with the International Standard ISO:16665; collected with a 0.1 $m^2$ Van Veen grab and washed on a 1 mm mesh sieve. The residues were fixed in 4% formaldehyde solution buffered with 10% borax and stained with rose bengal. The specimens of *Prionospio* were sorted and examined using a light microscope in the laboratory and transferred to 70% ethanol. Some material was conserved directly in 96% ethanol and was previously used for phylogenetics and the delimination of the species (Hektoen *et al.* 2024). After examination, the newly collected material was deposited in the collections of the Norwegian University of Science and Technology, NTNU University Museum (NTNU-VM) (Bakken *et al.* 2025). Museum collections, including specimens from outside of northern Europe, and existing types of most northern European species of *Prionospio*, were also studied. In total, approximately 2500 specimens of *Prionospio* spp. were examined.

In the Taxonomy section below, species are listed alphabetically, except for *Prionospio* cf. *sanmartini* which is discussed before *Prionospio fiordica* sp. nov., and *P. multisetosa* which is placed after *P. dubia*. In the Material examined section, specimens previously sequenced by Hektoen *et al.* (2024) are listed separately. A list of museums and their acronyms holding the samples which are reported in this study is given below.

**Institutional abbreviations**

LACM-AHF = Allan Hancock Foundation Polychaete Collection, Natural History Museum of Los Angeles County, USA
MNCN = National Museum of Natural History, Madrid, Spain
NHMO = Natural History Museum, University of Oslo, Oslo, Norway
NTNU-VM = NTNU University Museum, Trondheim, Norway
SMNH = Swedish Natural History Museum, Stockholm, Sweden
UPSZTY = Museum of Evolution, Uppsala, Sweden
USNM = National Museum of Natural History, Washington DC, USA
ZMBN = University Museum of Bergen, University of Bergen, Bergen, Norway

For morphology, specimens were stained with a water solution of Methylene Green, Zinc Chloride Double Salt (Chroma) to increase contrast, and then studied using a compound microscope equipped with a digital camera LEICA DMC5400. Twenty-five specimens were dehydrated using a critical point

dryer, mounted on stubs, sputter coated with gold-palladium and then examined using a Teneo Scanning Electron Microscope (SEM) at NTNU Cellular & Molecular Imaging Core Facility (CMIC). Due to the lack of complete specimens, for size estimates, we used the width of the specimens on the 10$^{th}$ chaetiger. Plates and line drawings were created and edited in Adobe Photoshop ver. 24.3.0. The morphological terminology used for the descriptions of the species follows that of Radashevsky (2012). A list of abbreviations used to mark morphological details on the figures is given below.

**Morphological abbreviations**

br = branchia
ca = caruncle
ch = chaetiger
ci = cilia
cr = dorsal crest
es = esophagus
fo = dorsal fold
lc = dorsolateral longitudinal ciliation
ls = lateral swelling
me = median eye
ne = neuropodial postchaetal lamella
no = notopodial postchaetal lamella
nu = nuchal organ
pa = palp
pe = peristomium
pe+ch1 = fold formed by fusion of posterior dorsolateral part of peristomium and notopodial postchaetal lamella of chaetiger 1
pr = prostomium
sa = sabre chaeta
sc = scar

## Results

### *Taxonomy*

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Family Spionidae Grube, 1850

Genus ***Prionospio*** Malmgren, 1867

*Prionospio* Malmgren, 1867: 201.

*Prionospio* – Blake & Kudenov 1978: 211–212. — Maciolek 1985: 325–283. — Blake *et al.* 2020: 61–62.

**Type species**

*Prionospio steenstrupi* Malmgren, 1867, by monotypy.

**Diagnosis**

Prostomium anteriorly rounded to truncate, with frontal margin entire to weakly incised, rarely with fronto-lateral horns; subtriangular, rectangular or oval in shape, extending posteriorly at least to end of chaetiger 1 as a low caruncle. Nuchal organs U-shaped lateral to caruncle. Red, rarely black eyes

present or absent. Occipital antenna absent. Peristomium at least partially fused with notopodial postchaetal lamellae of chaetiger 1, forming low wings to prominent ear-shaped structures on lateral sides of prostomium. Notopodial lamellae of chaetiger 1 small, usually fused with dorsal posterior parts of peristomium; neuropodia lamellae small. Noto- and neuropodial postchaetal lamellae largest on branchiate chaetigers, reduced thereafter. Notopodial lamellae on postbranchiate chaetigers often interconnected by dorsal transverse low ridges to high crests. Interparapodial pouches or membranous folds present or absent. Branchiae usually from chaetiger 2, rarely from chaetiger 3 or absent, limited to anterior part of body, cylindrical or flattened with surfaces perpendicular to body axis, free from notopodial lamellae, smooth, apinnate or with digitiform pinnules. Hooks bi-, tri-, quadri- or multidentate, with inner and / or rarely only outer hoods, present in noto- and neuropodia; shaft slightly curved, without constriction. Sabre chaetae usually present in neuropodia, rarely absent. Pygidium with one long middorsal cirrus and two shorter ventral cirri; rarely ventral cirri reduced.

**Remarks**

This diagnosis mainly follows that of Blake *et al.* (2020), with addition of characters described by Radashevsky (2012) and as required by accommodation of *Prionospio cerastae* Radashevsky, 2015 which has fronto-lateral horns on the prostomium.

***Prionospio banyulensis*** Laubier, 1966
Figs 2–3

*Prionospio banyulensis* Laubier, 1966: 258.
*Prionospio ockelmanni* Pleijel, 1985: 177–181, figs 1–3.

*Prionospio banyulensis* – Laubier 1968: 99–105, figs 10–15. — Sigvaldadóttir 1992: 210–217, figs 1–5, table 1. — Kirkegaard 1996: 79, fig. 35. — Hektoen *et al.* 2024: figs 1, 4.
*Prionospio* (*Minuspio*) *banyulensis* – Hartmann-Schröder 1996: 328–329.
*Aurospio banyulensis* – Sigvaldadóttir 1998: 186. — Sigvaldadóttir 2002: 210.

**Diagnosis**

Prostomium anteriorly rounded, posteriorly extending to end of chaetiger 1 as a short, thick caruncle. Median eyes large, crescentic. Three pairs of apinnate branchiae on chaetigers 3–5 similar in size to notopodial postchaetal lamellae. Neuropodial lamellae of chaetiger 2 quadrangular, upwards-turned, of chaetiger 3 subrectangular, upwards-turned. Sabre chaetae in neuropodia from chaetiger 10. Hooded hooks in neuropodia from chaetigers 11–14.

**Type material of *Prionospio banyulensis***

**Neotype**

FRANCE • Banyuls-sur-Mer, Cap d'Osne; 42°29.8′ N, 3°8.48′ E; depth 24 m; 9. Oct. 1991; stn Banyuls1991h; van Veen grab; designated by Sigvaldadóttir (1992); SMNH Type-4422.

**Type material of *Prionospio ockelmanni***

**Holotype**

SWEDEN • Öresund; depth 29 m; 11 Sep. 1976; Fredrik Pleijel leg.; stn Öresund1976; SMNH Type-3358.

**Paratypes**

SWEDEN • 3 specs; Öresund; depth 29 m; 11 Sep. 1976; Fredrik Pleijel leg.; stn Öresund1976; SMNH Type-3358.

**Other material examined**

FRANCE • 1 spec.; Banyuls-sur-Mer, Coralligene; 42°30.220′ N, 3°8.300′ E; depth 18 m; 14 Jan. 1991; stn Banyuls1991f; van Veen grab; SMNH 111890 • 1 spec.; Banyuls-sur-Mer; Arne Nygren leg.; stn 257; NTNU-VM 84125 • 3 specs; Banyuls-sur-Mer; Fredrik Pleijel leg.; 1 Oct. 1993; LACM-AHF Poly 4424.

NORWAY – **Møre og Romsdal** • 1 spec.; Smøla, Andholman; 63°28.017′ N, 7°51.455′ E; depth 22 m; 17 Dec. 2019; Åkerblå AS leg.; stn AND-7; van Veen grab; NTNU-VM 84030. – **Trøndelag** • 1 spec.; Hitra Singsholmen; 63°24.876′ N, 8°25.368′ E; depth 41 m; 18 Nov. 2020; Åkerblå AS leg.; stn SIN-2; van Veen grab; SEM stub; NTNU-VM 84148 • 1 spec.; same data as for preceding; NTNU-VM 84035 • 1 spec.; Frøya, Olaugsskjæret; 63°47.664′ N, 8°31.230′ E; depth 36 m; 6 Nov. 2019; Åkerblå AS leg.; stn OLA-1; van Veen grab; NTNU-VM 84026 • 4 specs; Bjugn Havsund; 63°48.073′ N, 9°26.799′ E; depth 22 m; 27 Aug. 2019; Åkerblå AS leg.; stn HAV-3; van Veen grab; NTNU-VM 84024 • 1 spec.; Frøya, Tennøya; 63°48.327′ N, 8°27.493′ E; depth 120 m; 13 Aug. 2020; Åkerblå AS leg.; stn TEN-4; van Veen grab; SEM stub; NTNU-VM 84147 • 7 specs; Steinskjær Tjuin; 64°4.367′ N, 11°14.203′ E; depth 25 m; 16 Jul. 2020; Åkerblå AS leg.; stn TJU-3; van Veen grab; NTNU-VM 84036 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 84149 • 1 spec.; Frøya, Kya; 63°46.216′ N, 8°19.535′ E; depth 41 m; 27 Jul. 2022; stn Kya-5; van Veen grab; NTNU-VM 84142. – **Nordland** • 3 specs; Herøy, Nordgåsvær; 66°4.639′ N, 12°4.353′ E; depth 75 m; 27 Sep. 2021; Åkerblå AS leg.; stn NGÅ-2; van Veen grab; NTNU-VM 84031. – **Troms** • 5 specs; Tranøy, Hallvarsøya; 69°9.284′ N, 16°54.531′ E; depth 60 m; 29 Oct. 2019; Åkerblå AS leg.; stn HAL-4; van Veen grab; NTNU-VM 84023 • 1 spec.; Senja, Ørnfjordbotn; 69°29.640′ N, 17°39.969′ E; depth 80 m; 14 Jul. 2021; Åkerblå AS leg.; stn ØRN-3; van Veen grab; NTNU-VM 84025 • 1 spec.; Karlsøy, Korsnes; 69°59.065′ N, 19°55.377′ E; depth 101 m; 18 Sep. 2019; Åkerblå AS leg.; stn KOR-1; van Veen grab; SEM stub; NTNU-VM 84150 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 84151 • 2 specs; Karlsøy, Karanes; 70°4.132′ N, 19°18.715′ E; depth 73 m; 11 Aug. 2021; Åkerblå AS leg.; stn KAR-4; van Veen grab; NTNU-VM 84068 • 1 spec.; Karlsøy, Mjønes; 70°6.477′ N, 19°35.958′ E; depth 216 m; 7 Dec. 2021; Åkerblå AS leg.; stn MJØ-3; van Veen grab; NTNU-VM 84072 • 4 specs; Tromsø, Nordnibba; 70°9.855′ N, 19°21.322′ E; depth 73 m; 11 Oct. 2021; Åkerblå AS leg.; stn NOR-REF; van Veen grab; NTNU-VM 84034 • 2 specs; Tromsø, Nordnibba; 70°9.993′ N, 19°22.469′ E; depth 67 m; 11 Oct. 2021; Åkerblå AS leg.; stn NOR-5; van Veen grab; NTNU-VM 84033. – **Finnmark** • 2 specs; Alta, Langnes; 70°6.537′ N, 23°0.061′ E; depth 26 m; 22 Jun. 2022; Åkerblå AS leg.; stn LAN-1; van Veen grab; NTNU-VM 84066 • 11 specs; Hammerfest, Bårdfjord; 70°25.701′ N, 22°51.086′ E; depth 61 m; 3 Nov. 2021; Åkerblå AS leg.; stn BÅR-REF; van Veen grab; NTNU-VM 84032.

SWEDEN – **Halland** • 1 spec.; Varberg, Värö; 57°10.000′ N, 12°5.000′ E; depth 20 m; 1980; stn Varö spring 1980 2; van Veen grab; SMNH 9556. – **Bohuslän** • 2 specs; Stora Fjädern; depth 35 m; stn St. Fjädern; SMNH 111891 • 1 spec.; Väderöarna, SE of Hamnerö; depth 22–30 m; 10 Jul 1984; SMNH 111892 • 1 spec.; Kostergrund; depth 40 m; 29 Jun 1990; stn Koster1991; SMNH 111894.

UNITED KINGDOM • 5 specs; Plymouth, Stoke point, Millbay channel; depth 35–40 m; 6 Jun. 1986; stn Ply1986i; SMNH 111878.

**Examined material with sequence data**

FRANCE • 1 spec.; Banyuls sur Mer; leg. Arne Nygren leg.; stn 256; NTNU-VM 84037.

NORWAY – **Viken** • 1 spec.; Drøbak; 59°38.694′ N, 10°36.702′ E; depth 125–130 m; 22 Oct. 2014; POLYSKAG exped.; stn POLYSKAG-2014/10-19; dredge; ZMBN 152614. — **Finnmark** • 1 spec.; Hammerfest Borvika; 70°44.517′ N, 23°25.965′ E; depth 49 m; 26 Aug. 2020; Åkerblå AS leg.; stn BOR-REF; van Veen grab; NTNU-VM 84027 • 1 spec.; same data as for preceding; NTNU-VM 84028

• 1 spec.; Hammerfest, Borvika; 70°45.454′ N, 23°26.833′ E; depth 46 m; 26 Aug. 2020; Åkerblå AS leg.; stn BOR-2; van Veen grab; NTNU-VM 84029.

**Description** (adults)

Neotype (SMNH Type-4422) complete, 7 mm long, 0.15 mm wide, with 47 chaetigers, laterally flattened, likely due to previously being mounted on slide. Other complete specimens up to 12.6 mm long, 0.4 mm wide, with up to 65 chaetigers. Color in alcohol pale white. Prostomium anteriorly broadly rounded, posteriorly extending to end of chaetiger 1 as a thick caruncle (Fig. 2A). Nuchal organs U-shaped ciliary bands lateral to caruncle. Two pairs of eyes arranged trapezoidally, bright red in alcohol, red to dark brown in formalin, color fading during storage in alcohol. Median eyes large, crescent- to oval-shaped; lateral eyes large round spots, situated anteriorly and set wider apart. Dorsolateral parts of peristomium fused with notopodial postchaetal lamellae of chaetiger 1, forming ear-shaped structures lateral to prostomium (Fig. 2A). Palps missing in neotype, in other specimens as long as 10–15 chaetigers.

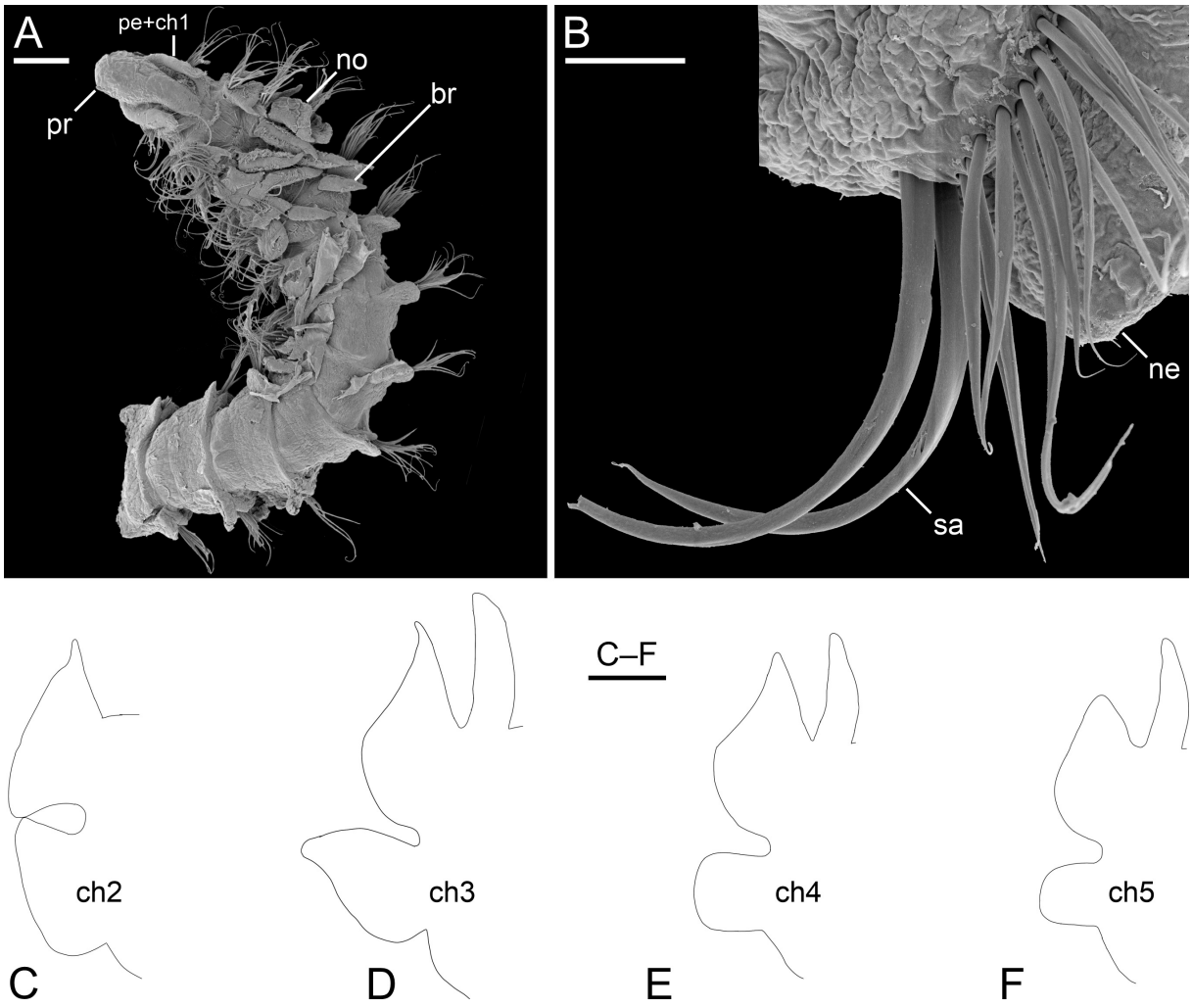


**Fig. 2.** Adult morphology of *Prionospio banyulensis* Laubier, 1966. **A–B**. SEM micrographs. **C–F**. Line drawings of parapodia. **A**. Anterior end, dorsal view (NTNU-VM 84148). **B**. Neuropodium of chaetiger 10, showing two vertical rows of capillary chaetae and two inferior sabre chaetae (NTNU-VM 84148). Scale bars: A = 100 μm; B = 20 μm; C–F = 100 μm.

Branchiae on chaetigers 3–5, apinnate, with dense ciliation on lateral edges, approximately equal in size, slightly longer than notopodial postchaetal lamellae (Fig. 2A, 3A). Nototrochs transverse ciliary bands on chaetiger 2 and between bases of branchiae of chaetigers 3 and 4. Dorsolateral longitudinal ciliation absent.

Notopodial prechaetal lamellae small, rounded on chaetigers 2 and 3, inconspicuous on succeeding chaetigers. Notopodial postchaetal lamellae of chaetiger 1 fused with dorsal posterior parts of peristomium; lamellae subrectangular on chaetiger 2, largest on chaetigers 3 and 4, sometimes with short tips on branchiate chaetigers (Figs 2A, C–D), smaller on postbranchiate chaetigers (Figs 2A, 3A), oval from chaetigers 7–8 onwards. Low dorsal crests present between notopodial lamellae from chaetigers 6–9 to chaetigers 10–15 (Figs 2A, 3A). Neuropodial prechaetal lamellae inconspicuous. Neuropodial postchaetal lamellae of chaetiger 1 small and oblong, of chaetiger 2 subtriangular, higher than long and slightly upwards-pointed (Fig. 2C), of chaetiger 3 triangular with upwards-pointed tip (Fig. 2D), rounded, small from chaetiger 4 onwards (Fig. 2E–F). Interneuropodial pouches absent.

Notopodial capillaries on anterior chaetigers arranged in two rows, unilimbate and slightly granulated. Anterior row shorter than posterior row. Notopodial capillaries in middle and posterior chaetigers alimbate, long, thin, sometimes coiled. Neuropodial capillaries arranged in two rows on anterior chaetigers unilimbate, granulated, anterior row shorter than posterior row. Sabre chaetae in neuropodia from chaetiger 10, with slight granulation on distal part, one or rarely two per fascicle (Fig. 2B). Hooded hooks in notopodia from chaetigers 23–43; in neuropodia from chaetigers 12–14, up to nine in a series, alternating with 1–3 capillary chaetae. Both noto- and neuropodial hooks with 4–5 pairs of upper teeth arranged in two vertical rows above main fang, with outer and inner hoods.

Pygidium with one long middorsal cirrus and one pair of short ventral cirri.

**Reproduction**

*Prionospio banyulensis* is dioecious. Of the 12 sexually mature individuals studied, seven were males and five were females. The smallest mature worms had about 45 chaetigers. In both females and males, gametes develop from chaetiger 10 to chaetigers 33–60. Spermatids were interconnected in tetrads; spermatozoa were ect-aquasperm with spherical nucleus about 2 µm in diameter. Largest oocytes were about 70 µm in diameter, with smooth envelope about 2 µm thick having single depression about 10 µm in diameter and 5-6 µm deep; nucleus was about 27 µm in diameter, with a single nucleolus about 8 µm in diameter. The mature individuals had notopodial capillaries essentially longer than capillaries in juveniles, indicating possible swimming and swarming during spawning event.

**Remarks**

*Prionospio banyulensis* was originally described from Banyuls-sur-Mer, Mediterranean Sea, France. Laubier (1966) first provided brief notes about the ecology of *P. banyulensis* and then described the morphology of this species (Laubier 1968) but never designated type specimens. Sigvaldadóttir (1992) redescribed *P. banyulensis*, designated a neotype, and for the first time reported the species from northern Europe. Moreover, Sigvaldadóttir (1992) treated *Prionospio ockelmanni* Pleijel, 1985, described from Öresund, Sweden, as a junior synonym of *P. banyulensis*. Based on the results of a phylogenetic analysis of morphological characters of the species of the *Prionospio*-complex, where *P. banyulensis* formed a monophyletic group with *Aurospio dibranchiata*, Sigvaldadóttir (1998) transferred *P. banyulensis* to *Aurospio*. Blake *et al.* (2020: 59) noted that some species of *Prionospio* have erroneously been assigned to *Aurospio* "based almost entirely on the first occurrence of branchiae from chaetiger 3 instead of chaetiger 2". They proposed that several species listed among *Aurospio* should be referred to *Prionospio* but did not act at that time. Hektoen *et al.* (2024) moved *banyulensis* back to *Prionospio* according to the results of a phylogenetic analysis of molecular data and noted that the remaining species of *Aurospio*

should be further studied. Our re-examination of the types of *P. banyulensis* and *P. ockelmanni* supports their conspecificity. The neotype of *P. banyulensis* is not imaged here as camera-equipped microscopes were not available at SMNH.

Sigvaldadóttir (1992) found specimens of *P. banyulensis* with two and three pairs of branchiae from chaetiger 3. We examined a greater number of specimens than in previous studies, some of larger sizes than previously reported. We found specimens with a greater variation in branchial configuration that potentially belongs to *P. banyulensis*. In addition to dibranchiate (two pairs) and tribranchiate (three pairs) specimens, worms with four (Fig. 3B, D) and five pairs of branchiae occurred. All worms with more than three pairs of branchiae were found from Norwegian coastal waters, while specimens with two and three pairs of branchiae occurred in both Norway and the type locality of Banyuls. No other differences in morphological characters were apparent, and the specimens with 4 and 5 pairs of branchiae were always found together with *P. banyulensis* with three pairs of branchiae, and were generally larger in size, indicating the number of branchiae could be a size related character. In dibranchiate specimens,

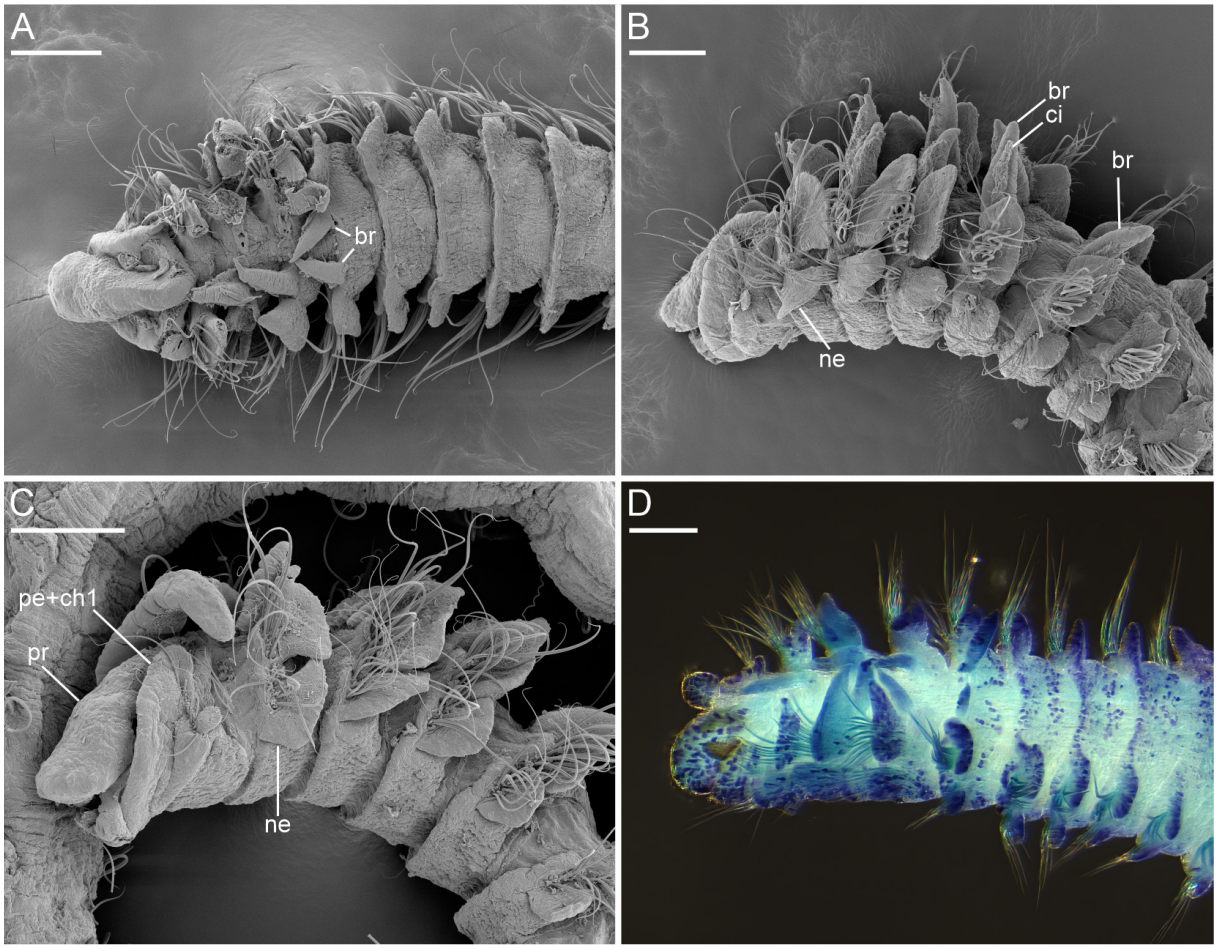


**Fig. 3.** Adult morphology of *Prionospio banyulensis* Laubier, 1966. **A–C**. SEM micrographs. **D**. Light microscope image. **A**. Anterior end, dorsal view, showing three pairs of branchiae from chaetiger 3 (NTNU-VM 84151). **B**. Anterior end, left lateral view, showing four pairs of branchiae from chaetiger 2 (NTNU-VM 84147). **C**. Anterior end, left lateral view, showing three pairs of branchiae from chaetiger 2 (NTNU-VM 84150). **D**. Anterior end stained with methylene green, left dorsolateral view, showing four pairs of branchiae from chaetiger 2 (NTNU-VM 84023). Abbreviations: see Material and methods. Scale bars = 100 µm.

the branchiae were present on chaetigers 3 and 4, while tribranchiate specimens had branchiae on chaetigers 3–5. Specimens with four pairs of branchiae had them on chaetigers 2–5 (NTNU-VM 84023, 94142), and specimens with five pairs had branchiae on chaetigers 2–6 (NTNU-VM 84024). However, there were two exceptions: one specimen had three pairs of branchiae starting from chaetiger 2 (NTNU-VM 84150; Fig. 3C), and another had four pairs starting from chaetiger 3 (NTNU-VM 84147; Fig. 3B).

All specimens of *P. banyulensis* sequenced by Hektoen *et al.* (2024) were studied here. This material was collected from Banyuls, the Oslofjord, and Finnmark. The individual from the type locality (NTNU-VM 84037) had two pairs of branchiae, while the remaining worms (ZMBN 152614, NTNU-VM 84027-84029) had three pairs of branchiae. This molecular evidence supports a single, widely distributed species with some intraspecific variation in branchial number. However, Hektoen *et al.* (2024) did not include any specimens with more than three pairs of branchiae in their analysis, and only six such specimens were found in total. Thus, we cannot yet determine whether this broader variation represents intraspecific variation. At present, we treat all observed forms as *P. banyulensis* sensu lato, but the conspecificity of specimens with more than three pairs of branchiae must be confirmed by integrative taxonomic approaches.

**Habitats and distribution**

Mediterranean France, South England, Iceland, and along Swedish West and Norwegian coasts north to the Barents Sea. Found at depths of 18–216 m, mainly in coarse sand and shell hash.

### ***Prionospio dubia*** Day, 1961
Figs 4–5; Table 1

*Prionospio malmgreni* var. *dubia* Day, 1961: 489–490, fig. 3j–n.

*Prionospio steenstrupi* – Day 1963: 418. — Day 1967: 489, fig. 18.9o–r.
*Prionospio dubia* – Wilson 1990: 243–274, figs 9–15 (partim). — Sigvaldadóttir & Mackie 1993: 211–215, figs 6–8 (partim).

Non *Prionospio* cf. *dubia* – Hektoen *et al.* 2024: figs 1, 4.

**Diagnosis**

Prostomium narrow, anteriorly rounded, posteriorly extending to end of chaetiger 1 as a narrow caruncle. Eyes present or absent. Four pairs of branchiae on chaetigers 2–5; those of chaetiger 2 up to 5 × as long as other pairs; branchiae of chaetigers 2 and 5 with many long, digitiform pinnules almost to tip of branchiae. Dorsal crests absent. Neuropodial postchaetal lamellae of chaetiger 3 upwards pointing. Sabre chaetae in neuropodia from chaetigers 16–21. Hooded hooks in neuropodia from chaetigers 18–22.

**Material examined**

SOUTH AFRICA • 13 specs (mix from nine different stations); 1960; J. Day leg.; BMNH 1961.19.635/662.

**Description** (based on adults from South Africa)

Largest anterior fragment 25 mm long, 0.7 mm wide, with 50 chaetigers. Color in alcohol pale to brownish. Prostomium narrow, anteriorly rounded, posteriorly extending to end of chaetiger 1 as a narrow caruncle. Nuchal organs U-shaped ciliary bands lateral to caruncle. Median eyes faint spots in one specimen (Fig. 4A), absent in others (Fig. 4B); lateral eyes present in one specimen. Both specimens

with eyes of approximately 0.6 mm width. Peristomium fused with notopodial postchaetal lamellae of chaetiger 1, forming ear-shaped structures lateral to prostomium. Palps missing in all specimens.

Branchiae on chaetigers 2–5. Branchiae of chaetiger 2 elongated, cylindrical, up to 5 × as long as of remaining branchiae, with digitiform pinnules on posterior side, with short apinnate tip. Branchiae of chaetiger 5 cylindrical, similar in length to notopodial postchaetal lamellae on same chaetiger, with pinnules on outer lateral sides, leaving short distal tip apinnate (Figs 4A–B, 5A–C). Branchiae of chaetigers 3 and 4 triangular, flat, with surface perpendicular to body axis, apinnate, with dense lateral ciliation, similar in length to notopodial postchaetal lamellae of same chaetigers. Nototrochs transverse ciliary bands between branchial bases on chaetigers 3 and 4. Dorsolateral longitudinal ciliation absent.

Notopodial prechaetal lamellae small, rounded in anterior chaetigers. Notopodial postchaetal lamellae of chaetiger 1 broadly rounded, fused with peristomium, of chaetigers 2–5 large and subtriangular, largest on chaetiger 3. Lamellae rapidly diminishing in size in postbranchial chaetigers, becoming lower, assuming low oval shape from chaetigers 12–15. Dorsal crests absent, but notopodial postchaetal lamellae extending slightly onto dorsum between chaetigers 10–16 (Fig. 5A–B). Dorsolateral longitudinal ciliation absent. Neuropodial prechaetal lamellae inconspicuous. Neuropodial postchaetal lamellae of chaetiger 1 small, oblong and rounded; of chaetiger 2 trapezoidal, with rounded edges, not elongated downwards;

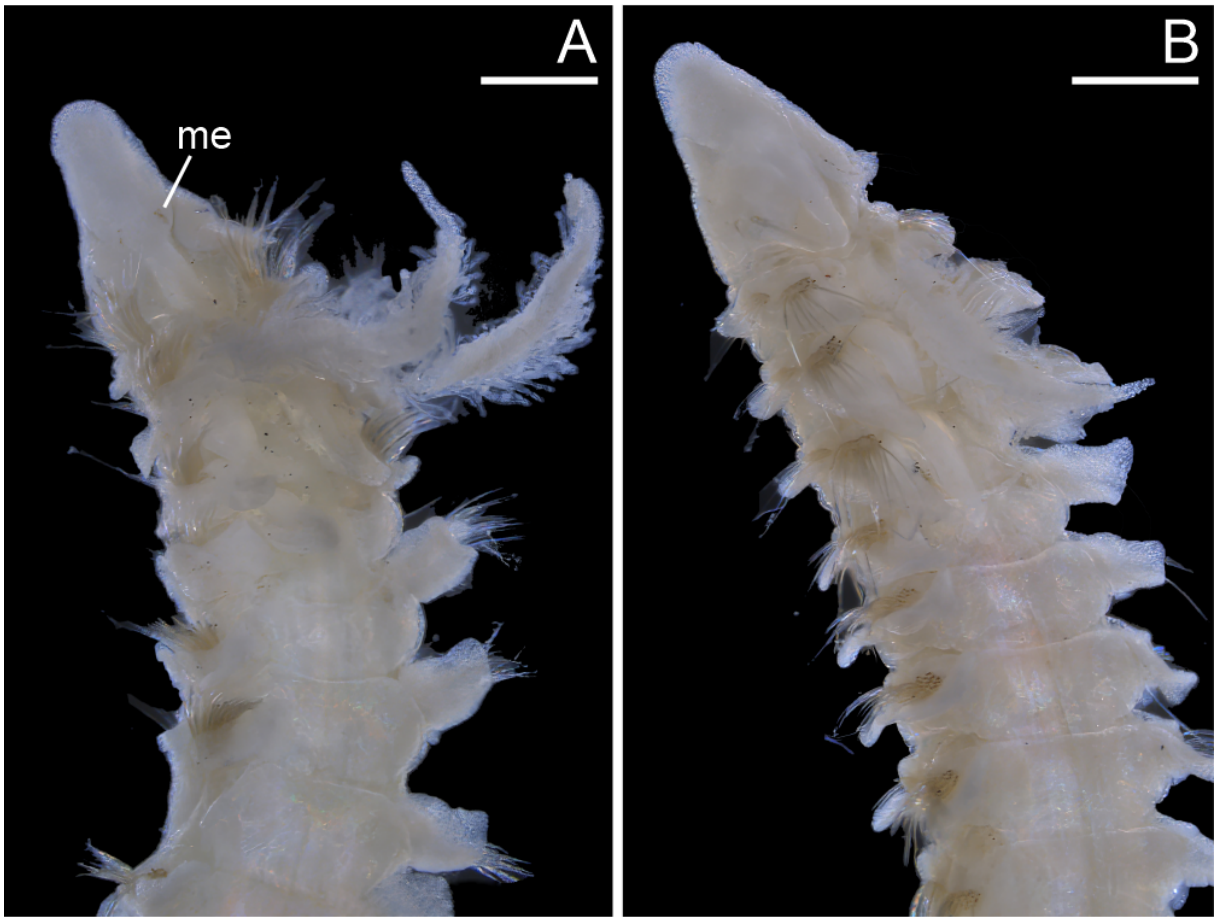


**Fig. 4.** Adult morphology of *Prionospio dubia* Day, 1961 (BMNH ZK.1961.19.635/662, South Africa). Anterior ends in left dorsolateral view. **A**. Individual with median eyes. **B**. Individual without eyes. Abbreviation: see Material and methods. Scale bars = 300 µm.

of chaetiger 3 subrectangular, often with dorsally projecting tip; of chaetiger 4 quadrangular. Lamellae on subsequent chaetigers more evenly rounded, low and oval by chaetiger 10 (Fig. 5C). Interneuropodial pouches absent.

Notopodial capillaries on anterior chaetigers arranged in up to five rows, unilimbate and granulated. Anterior row shorter than posterior row. Notopodial capillaries alimbate, long, thin, sometimes from approximately chaetiger 20. Neuropodial capillaries arranged in two rows on anterior chaetigers,

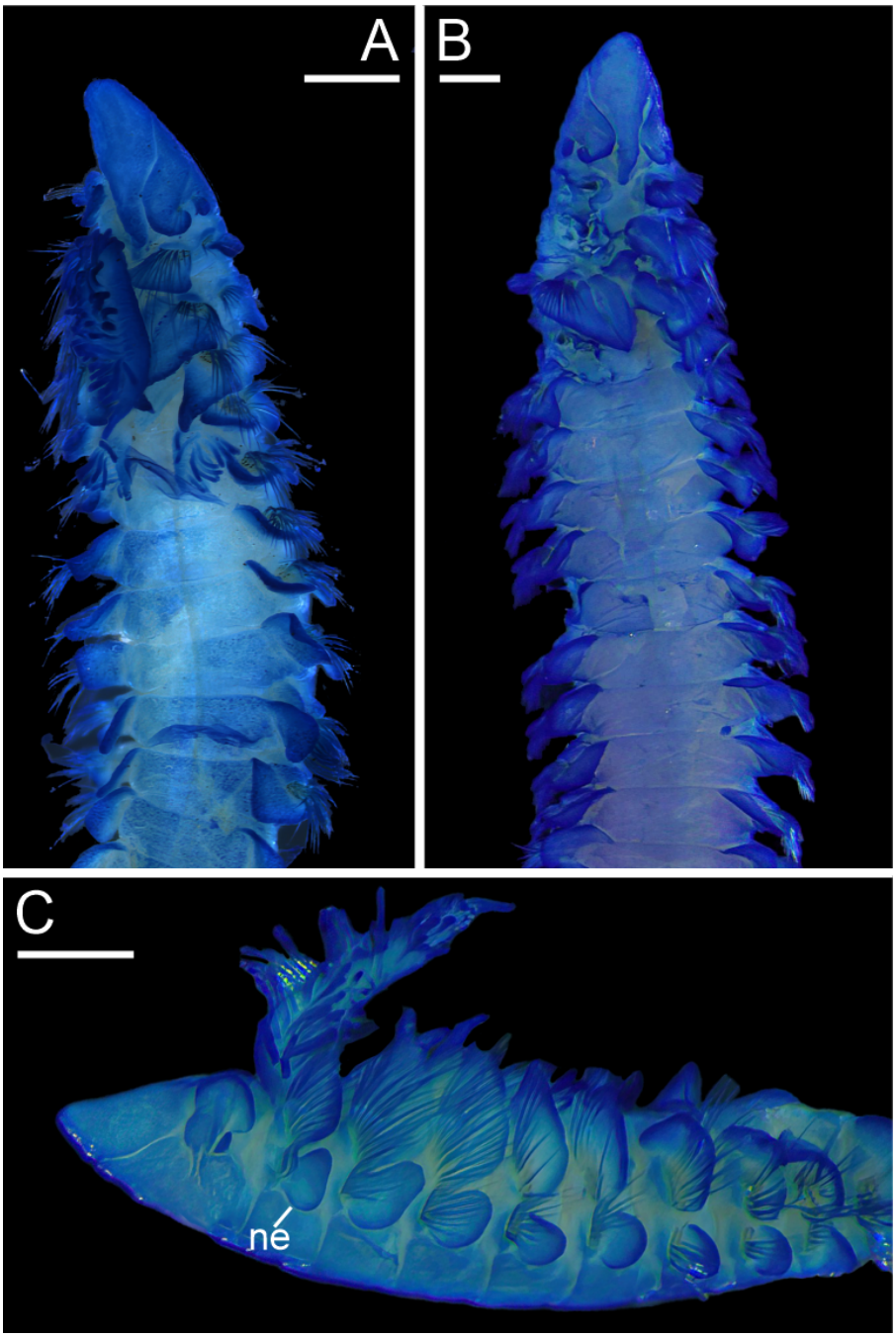


**Fig. 5.** Adult morphology of *Prionospio dubia* Day, 1961 (BMNH ZK.1961.19.635/662, South Africa). Anterior ends stained with methylene green. **A**–**B**. Dorsal view. **C**. Left lateral view. Abbreviation: see Material and methods. Scale bars = 300 µm.

**Table 1.** Morphological characters of adult specimens from different geographical regions referred to *Prionospio dubia* Day, 1961. *a complete description of Australian specimens was not provided, but it was noted that they matched the South African worms in every regard; **re-examination of specimens collected in South Africa in 1960.

| Reference | Region | Width at 10th chaetiger | Eyes | Neuropodial lamellae of chaetiger 3 shape | Sabre chaetae start chaetiger | Neuropodial hooded hooks start chaetiger |
|---|---|---|---|---|---|---|
| Day 1961, 1963, 1967 | South Africa | – | present or absent | rounded | 18 | 18–19 |
| Maciolek 1985 | West Atlantic | up to 0.75 mm | present or absent | squarish | 13–16 | 15–19 |
| Imajima 1990 | Japan | up to 0.8 mm | present | subrectangular, upwards-turned | 13–14 | 15–16 |
| Wilson 1990* | Australia | 0.25–0.6 mmm | present or absent | asymmetrical ovoid lobe | 17–20 | 18–19 |
| Sigvaldadóttir & Mackie 1993 | North East Atlantic | 0.3–0.7 mm | absent | subrectangular, upwards-turned | 16–22 | 17–22 |
| Blake 1996 | California | up to 0.6 mm | present or absent | squarish | 13–16 | 13–16 |
| Wilson 1990, Sigvaldadóttir & Mackie 1993, present study** | South Africa | 0.4–0.7 mm | present or absent | subrectangular, upwards-turned | 16–21 | 18–22 |

unilimbate, granulated, anterior row shorter than posterior row. Sabre chaetae in neuropodia from chaetigers 17–21, one to two per fascicle, with heavy granulation on distal part. Hooded hooks in notopodia not present in any examined specimen. Hooded hooks in neuropodia from chaetigers 18–22, up to 9 in a series, alternating with capillary chaetae; alternating capillaries limbate in anterior neuropodia, alimbate in posterior chaetigers; hooks with 3–4 pairs of upper teeth arranged in two vertical rows above main fang, with only outer hood, secondary inner hood absent. Chaetae in all ways similar to those of *P. multisetosa* (Fig. 7G–H).

Pygidium missing in all examined specimens.

### Remarks

*Prionospio dubia* was originally described as a variety of *P. malmgreni* from a shelf area off the southern coast of South Africa by Day (1961). Later, Day (1963, 1967) considered it as a junior synonym of *P. steenstrupi*, a species described from Iceland. Maciolek (1985) recognized *P. dubia* as a valid species.

Day (1961) described *P. dubia* as having indistinct eyes but later noted that eyes were likely only visible in juveniles, and disappeared with age (Day 1963, 1967). Faint eyespots were observed in two of 13 specimens examined in the present study: one specimen with the lateral pair and another with the median pair of eyes; both specimens relatively large, 0.6 mm wide at chaetiger 10, excluding parapodia. Like Sigvaldadóttir & Mackie (1993), we found no essential morphological differences other than the presence of eyes in some specimens between South African *P. dubia* and specimens from the Northeast Atlantic now assigned to *P. multisetosa*. Additional material from the type locality is needed to clarify the morphological variation and obtain genetic characteristics of the species. However, *P. dubia* has not been

found in South African waters since 1961 (Carol Simon pers. comm.). No molecular data is available for the species, as the *Prionospio* cf. *dubia* in Hektoen *et al.* (2024) is here identified as *P. multisetosa*.

Outside of South Africa, *P. dubia* has been reported from both sides of the north Atlantic (Maciolek 1985; Sigvaldadóttir & Mackie 1993), Japan (Imajima 1990), Australia (Wilson 1990), and the East Pacific (Blake 1996). All reports noted characters slightly different from those of specimens from South Africa, especially regarding the presence / absence of eyes and distribution of sabre chaetae and hooded hooks in neuropodia. Blake (1996) noted that these differences were likely due to different sizes of studied worms, as many morphological characters are size dependent. However, considering quite similar size ranges reported by these authors, this assertion seems unlikely. It is more likely that these reports include more than one cryptic species. An overview of the main morphological characteristics of worms referred by different authors to *P. dubia* is given in Table 1. The worms from Australia studied by Wilson (1990) are most similar to South African *P. dubia*, with no apparent morphological differences between them.

**Habitat and distribution**

Pending further study of additional specimens from the type locality and a comprehensive revision of the data obtained from outside, it can be confirmed that *P. dubia* is found only in the waters of South Africa, at depths of 84–183 m.

***Prionospio multisetosa*** Delgado-Blas & Peraza, 2024
Figs 6–7

*Prionospio multisetosa* Delgado-Blas & Peraza, 2024: 69–82, figs 4a–t, 5a–b.

*Prionospio steenstrupi* – Söderström 1920: 232–233, figs 136–140 (partim).
*Prionospio dubia* – Sigvaldadóttir & Mackie 1993: 211–215, figs 6–8. — Sigvaldadóttir 2002: 210–211.
*Prionospio* cf. *dubia* – Hektoen *et al.* 2024: figs 1, 4.
*Prionospio* (*Prionospio*) *steenstrupi* – Hartmann-Schröder 1996: 327–328 (partim).
*Prionospio* (*Prionospio*) *dubia* – Dagli & Cinar 2009: 6.

Non *Prionospio* (*Prionospio*) *dubia* – Maciolek 1985: 336–339, figs 2–3. — Imajima 1990: 118–120, figs 8–9. — Blake 1996: 130–133, fig. 4.12.

**Diagnosis**

Prostomium narrow, anteriorly rounded, posteriorly extending to end of chaetiger 1 as a narrow caruncle. Eyes absent. Four pairs of branchiae on chaetigers 2–5; branchiae of chaetiger 2 up to 5 × as long as other pairs. Branchiae on chaetigers 2 and 5 densely pinnate almost to tip, on chaetigers 3 and 4 apinnate; pinnules long and digitiform. Dorsal crests absent. Neuropodial postchaetal lamellae of chaetiger 3 upwards pointing. Sabre chaetae in neuropodia from chaetigers 17–22. Hooded hooks in neuropodia from chaetigers 18–22.

**Material examined**

FRANCE • 10 specs; Bay of Biscay; 43°43.200′ N, 3°47.802′ W; depth 641 m; 19 Jul. 1967; H. Sanders leg.; stn 56; epibenthic sled; USNM 65931 • 2 specs; Bay of Biscay; 43°46.698′ N, 3°37.800′ W; depth 2379 m; 18 Jul. 1967; H. Sanders leg.; stn 50; epibenthic sled; USNM 65930.

MAURITANIA • 1 spec.; 16°22.698′ N, 16°51.972′ W; depth 509 m; 8 Nov. 2011; CCLME exped.; stn 2011410-GR10; van Veen grab; ZMBN 152650 • 7 specs; same data as for preceding; ZMBN 152604**.**

MOROCCO • 2 specs; 28°52.026′ N, 12°34.176′ W; depth 495 m; 6 Jun. 2011; CCLME exped.; stn 2011410-GR35; van Veen grab; ZMBN 112312 • 1 spec.; 33°46.164′ N, 7°41.424′ W; depth 99 m; 15 Nov. 2011; CCLME exped.; stn 2011410-GR55; van Veen grab; ZMBN 152578.

NORWAY – **Norwegian Sea** • 2 specs; 61°13.050′ N, 2°16.677′ E; depth 218 m; 28 May 2014; stn GFC-30; van Veen grab; ZMBN 152582 • 1 spec.; 61°22.622′ N, 2°6.729′ E, depth 280 m; 31 May 2014; stn VTG-32; van Veen grab; ZMBN 152591 • 6 specs; same data as for preceding; ZMBN 152590 • 6 specs; 61°22.629′ N, 2°6.581′ E; depth 284 m; 28 May 2011; stn VGPT2-10_2011; van Veen grab; ZMBN 152593. – **Akershus** • 3 specs; Drøbak; 59°38.664′ N, 10°37.152′ E; depth 100–106 m; 20 Oct. 2014; POLYSKAG leg.; stn POLYSKAG2014/10-4; sledge; ZMBN 152580 • 1 spec.; Drøbak, Stormberget; 6 Mar. 1953; M.E.H-B.C leg.; dredge; NHMO • 2 specs; Asker, Håøyfjorden; 59°40.812′ N, 10°33.156′ E; depth 57 m; 4 Aug. 2021; NIVA leg.; stn STZ-4+3; van Veen grab; NTNU-VM 84022. – **Vestfold** • 1 spec.; Larvik, Larviksfjorden; 59°2.667′ N, 10°1.537′ E; depth 43 m; 2020; NIVA leg.; stn lar-S27; van Veen grab; NTNU-VM 84020. – **Rogaland** • 1 spec.; Stavanger, Boknafjorden; 59°12.833′ N, 5°46.519′ E; depth 168 m; 10 Jun. 2014; Bergen University Museum leg.; stn HM2014/06-56; van Veen grab; ZMBN 152584 • 1 spec.; Sandnes Strand; 58°56.913′ N, 5°59.179′ E; depth 250–251 m; 10 Jun. 2014; Bergen University Museum leg.; stn HM2014/06-43; sledge; ZMBN 152589. – **Vestland** • 1 spec.; Øygarden Nautnes; 60°37.544′ N, 4°39.917′ E; depth 253 m; 1 May 2017; Bergen University Museum leg.; stn KB-66; van Veen grab; ZMBN 152601 • 1 spec.; Øygarden, Sund; 60°11.061′ N, 5°11.737′ E; depth 665 m; 26 Apr. 2017; Bergen University Museum leg.; stn KB-03; van Veen grab; ZMBN 152599 • 1 spec.; Aurland Aurlandsvangen; 60°54.233′ N, 7°10.088′ E; depth 115 m; 17 Nov. 2012; Bergen University Museum leg.; stn HM2012-11-12; van Veen grab; ZMBN 152597 • 16 specs; Bjørnafjord, Sævareidfjorden; 60°8.813′ N, 5°40.206′ E; depth 235 m; 26 May 2021; Åkerblå AS leg.; stn MJÅ-REF; van Veen grab; NTNU-VM 84009 • 4 specs; Bjørnafjord, Sævareidfjorden; 60°10.436′ N, 5°42.816′ E; depth 253 m; 26 May 2021; Åkerblå AS leg.; stn MJÅ-2.2; van Veen grab; NTNU-VM 84007 • 4 specs; Bjørnafjord Sævareidfjorden; 60°10.551′ N, 5°43.070′ E; depth 237 m; 26 May 2021; Åkerblå AS leg.; stn MJÅ-3.2; van Veen grab; NTNU-VM 84008 • 2 specs; Bjørnafjord Sævareidfjorden; 60°10.581′ N, 5°43.153′ E; depth 235 m; 26 May 2021; Åkerblå AS leg.; stn MJÅ-1; van Veen grab; NTNU-VM 84006 • 2 specs; Bjørnafjord, Sævareidfjorden; 60°10.778′ N, 5°43.676′ E; depth 166 m; 26 May 2021; Åkerblå AS leg.; stn MJÅ-4; van Veen grab; NTNU-VM 84010 • 2 specs; Hardbakkeneset; 61°1.035′ N, 4°56.645′ E; depth 110 m; 19 Sep. 2019; Åkerblå AS leg.; stn HAR-3; van Veen grab; NTNU-VM 84015 • 1 spec.; Fjaler, Hegnes; 61°21.470′ N, 5°17.110′ E; depth 243 m; 4 Dec. 2019; Åkerblå AS; HEG-1; van Veen grab; NTNU-VM 84062 • 17 specs; Selje, Beitveit; 62°8.171′ N, 5°19.906′ E; depth 138 m; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-3; van Veen grab; SEM stub; NTNU-VM 83988 • 20 specs; Selje, Beitveit; 62°8.551′ N, 5°20.113′ E; depth 129 m; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-5; NTNU-VM 84141. – **Møre og Romsdal** • 3 specs; Rauma, Skarbukta; 62°35.870′ N, 7°22.444′ E; depth 414 m; 28 Oct. 2021; Åkerblå AS leg.; stn SKA-4; van Veen grab; NTNU-VM 84019 • 2 specs; Midsund Stabben; 62°40.170′ N, 6°33.357′ E; depth 119 m; 5 Sep. 2019; Åkerblå AS leg.; stn STA-2; van Veen grab; NTNU-VM 84016 • 1 spec.; Molde, Setevika; 62°44.123′ N, 6°56.613′ E; depth 292 m; 29 Jun. 2021; Åkerblå AS leg.; stn SET-2.1; van Veen grab; NTNU-VM 84021 • 19 specs; Aukra, Sandholmane; 62°47.266′ N, 6°40.379′ E; depth 105 m; 18 Jul. 2021; Åkerblå AS leg.; stn SAN-REF; van Veen grab; NTNU-VM 84005 • 4 specs; Aukra, Sandholmane; 62°47.780′ N, 6°40.894′ E; depth 153 m; 18 Jul. 2021; Åkerblå AS leg.; stn SAN-3; van Veen grab; NTNU-VM 84002 • 1 spec.; Sandøy, Sandholmane; 62°47.780′ N, 6°40.894′ E; depth 153 m; 4 Sep. 2019; Åkerblå AS leg.; SAN-4; van Veen grab; SEM stub; NTNU-VM 84156 • 1; same data as for preceding; NTNU-VM 84041 • 17 specs; Aukra, Sandholmane; 62°48.042′ N, 6°40.451′ E; depth 150 m; 18 Jul. 2021; Åkerblå AS leg.; stn SAN-4; van Veen grab; NTNU-VM 84003 • 15 specs; same data as for preceding; NTNU-VM 84001 • 18 specs; Aukra, Sandholmane; 62°48.068′ N, 6°39.863′ E; depth 102 m; 18 Jul. 2021; Åkerblå AS leg.; stn SAN-5.2; van Veen grab; NTNU-VM 84004 • 7 specs; Aukra Fausken; 62°53.858′ N 6°43.390′ E; depth 130 m; 17 Jun. 2021; Åkerblå AS leg.; stn FAU-4; van Veen grab; NTNU-VM 84000 • 6 specs; Gjemnes,

Slettnes Vest; 62°57.660′ N, 7°50.739′ E; depth 135 m; 27 May 2021; Åkerblå AS leg.; stn SLE-REF; van Veen grab; NTNU-VM 84014 • 5 specs; Gjemnes, Slettnes Vest; 62°57.670′ N, 7°51.966′ E; depth 163 m; 27 May 2021; Åkerblå AS leg.; stn SLE-5; van Veen grab; NTNU-VM 84013 • 1 spec.; Tingvoll, Halsbukta; 63°4.952′ N, 8°8.815′ E; depth 343 m; 2 Jun. 2021; Åkerblå AS leg.; stn hal-3; van Veen grab; NTNU-VM 84011 • 1 spec.; Tingvoll, Halsbukta; 63°4.219′ N, 8°8.888′ E; depth 304 m; 2 Jun. 2021; Åkerblå AS leg.; stn hal-4; van Veen grab; SEM stub; NTNU-VM 84153 • 1 spec.; same data as for preceding; NTNU-VM 84012 • 9 specs; Averøy, Skjellingen; 63°8.698′ N, 7°33.211′ E; depth 111 m; 5 Jul. 2021; Åkerblå AS leg.; stn SKJ-1.4; van Veen grab; NTNU-VM 84017 • 1 spec.; Aure Hagahammaren; 63°8.027′ N, 8°1.332′ E; depth 207 m; 22 May 2019; Åkerblå AS leg.; stn HAG-2; van Veen grab; SEM stub; NTNU-VM 84155 • 1 spec.; same data as for preceding; NTNU-VM 83992 • 5 specs; Aure, Hagahammaren; 63°8.187′ N, 8°2.185′ E; depth 213 m; 22 May 5 2019; Åkerblå AS leg.; stn HAG-5; van Veen grab; NTNU-VM 83991. – **Trøndelag** • 1 spec.; Hitra, Værøya; 63°24.700′ N, 8°28.885′ E; depth 205 m; 21 May 2021; Åkerblå AS leg.; stn VÆR-REF; van Veen grab; SEM stub; NTNU-VM 84154 • 4 specs; same data as for preceding; NTNU-VM 84018 • 6 specs; Indre Fosen, Frengåsen; 63°42.106′ N, 9°52.857′ E; depth 91 m; 23 Jun. 2021; Åkerblå AS leg.; stn FRE-2; van Veen grab; NTNU-VM 83994 • 1 spec.; Indre Fosen, Frengåsen; 63°42.157′ N, 9°53.129′ E; depth 98 m; 23 Jun. 2021; Åkerblå AS leg.; stn FRE-3.2; van Veen grab; NTNU-VM 83995 • 4 specs; Indre Fosen, Frengåsen; 63°42.210′ N, 9°53.399′ E; depth 120 m; 23 Jun. 2021; Åkerblå AS leg.; stn FRE-1; van Veen grab; NTNU-VM 83993 • 2 specs; Indre Fosen, Frengåsen; 63°42.334′ N, 9°53.802′ E; depth 162 m; 23 Jun. 2021; Åkerblå AS leg.; stn FRE-4; van Veen grab; NTNU-VM 83996 • 1 spec.; Indre Fosen, Frengåsen; 63°42.436′ N, 9°53.802′ E; depth 196 m; 23 Jun. 2021; Åkerblå AS leg.; stn FRE-5.1; van Veen grab; NTNU-VM 83997 • 1 spec.; Skjoldryggen; 65°30.034′ N, 6°16.109′ E; depth 397 m; 23 Jun. 2013; MAREANO leg.; stn R1119-67; van Veen grab; ZMBN 152585. – **Troms** • 1 spec.; Tranøy, Gjervika; 69°2.628′ N. 16°51.239′ E; depth 160 m; 30 Oct. 2019; Åkerblå AS leg.; stn GJE-REF; van Veen grab; NTNU-VM 83999 • 1 spec.; Tranøy Gjervika; 69°2.796′ N, 16°53.047′ E; depth 250 m; 30 Oct. 2019; Åkerblå AS leg.; stn GJE-4.1; van Veen grab; SEM stub; NTNU-VM 84152 • 4 specs; same data as for preceding; NTNU-VM 83998.

SENEGAL • 3 specs; 14°27.576′ N, 17°36.624′ W; depth 489 m; 5 Nov. 2011; CCLME exped.; stn 2011410-GR08; van Veen grab; ZMBN 152596 • 3 specs; 15°28.812′ N, 17°13.566′ W; depth 504 m; 7 Nov. 2011; CCLME exped.; stn 2011410-GR09; van Veen grab; ZMBN 152588.

SWEDEN • 1 spec.; Varberg, Värö; 57°10′ N, 12°1′ E; depth 47 m; 1981; stn VÄRH81#3; van Veen grab; SMNH 11281 • 1 spec.; same data as for preceding; 1978; stn VÄRH78#3; van Veen grab; SMNH 8105 • 1 spec.; same data as for preceding; SMNH 6450 • 1 spec.; same data as for preceding; 1979; stn VÄRV79#3; van Veen grab; SMNH 9009 • 1 spec.; same data as for preceding; SMNH 8716 • 2 specs; same data as for preceding; 1980; VÄRV80#3; van Veen grab; SMNH 9667 • 3 specs; same data as for preceding; 1984; VÄRV84#3; van Veen grab; SMNH 53676.

WESTERN SAHARA • 1 spec.; 25°3.900′ N, 16°18.612′ W; depth 568 m; 25 Nov. 2011; CCLME exped.; stn 2011410-GR20; van Veen grab; ZMBN 152587 • 19 specs; 26°27.402′ N, 14°30.612′ W; depth 435 m; 29 Nov. 2011; CCLME exped.; stn 2011410-GR24; van Veen grab; ZMBN 152595.

**Examined material with sequence data**

GUINEA • 1 spec.; 9°38.724′ N, 16°40.002′ W; depth 509 m; 15 May 2012; CCLME exped.; stn 2012404-GR03; van Veen grab; ZMBN 152594.

MAURITANIA • 1 spec.; 16°22.698′ N, 16°51.972′ W; depth 509 m; 8 Nov. 2011; CCLME exped.; stn 2011410-GR10; van Veen grab; ZMBN 152602 • 1 spec.; 17°20.538′ N, 16°46.590′ W; depth 572 m; 1 Jun. 2012; CCLME exped.; stn 2012404-GR28; van Veen grab; ZMBN 114671.

MOROCCO • 1 spec.; 28°52.026′ N, 12°34.176′ W; depth 495 m; 6 Jun. 2011; CCLME exped.; stn 2011410-GR35; van Veen grab; ZMBN 152581 • 1 spec.; 33°46.164′ N, 7°41.424′ W; depth 99 m; 15 Nov. 2011; CCLME exped.; stn 2011410-GR55; van Veen grab; ZMBN 152759.

NORWAY – **Norwegian Sea** • 1 spec.; 61°13.050′ N, 2°16.677′ E; depth 218 m; 28 May 2014; stn GFC-30; van Veen grab; ZMBN 152598 • 1 spec.; 61°22.629′ N, 2°6.581′ E; depth 284 m; 28 May 2011; stn VGPT2-10_2011; van Veen grab; ZMBN 152583. – **Akershus** • 1 spec.; Drøbak; 59°38.664′ N, 10°37.152′ E; depth 100–106 m; 20 Oct. 2014; POLYSKAG leg.; stn POLYSKAG2014/10-4; sledge; ZMBN 152603. – **Rogaland** • 1 spec.; Stavanger, Boknafjorden; 59°12.833′ N, 5°46.519′ E; depth 168 m; 10 Jun. 2014; Bergen University Museum leg.; stn HM2014/06-56; van Veen grab; ZMBN 152584 • 1 spec.; Sandnes Strand; 58°56.913′ N, 5°59.179′ E; depth 250–251 m; 10 Jun. 2014; Bergen University Museum leg.; stn HM2014/06-43; sledge; ZMBN 152589. – **Vestland** • 1 spec.; Øygarden Nautnes; 60°37.544′ N, 4°39.917′ E; depth 253 m; 1 May 2017; Bergen University Museum leg.; stn KB-66; van Veen grab; ZMBN 152601 • 1 spec.; Øygarden, Sund; 60°11.061′ N, 5°11.737′ E; depth 665 m; 26 Apr. 2017; Bergen University Museum leg.; stn KB-03; van Veen grab; ZMBN 152599 • 1 spec.; Aurland Aurlandsvangen; 60°54.233′ N, 7°10.088′ E; depth 115 m; 17 Nov. 2012; Bergen University Museum leg.; stn HM2012-11-12; van Veen grab; ZMBN 152597 • 1 spec.; Selje, Beitveit; 62°8.171′ N, 5°19.906′ E; depth 138 m; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-3; van Veen grab; SEM stub; NTNU-VM 83989. – **Trøndelag** • 1 spec.; Ørland, Brekstad; 63°39.444′ N, 9°38.025′ E; depth 260–278 m; 24 Oct. 2016; stn 2016041; sledge; ZMBN 114364 • 1 spec.; Haltenbanken; 64°8.214′ N, 8°43.170′ E; depth 233 m; 5 Oct. 2013; MAREANO leg.; stn R890-105; van Veen grab; ZMBN 152600 – **Troms** • 1 spec.; Tranøy, Gjervika; 69°2.628′ N. 16°51.239′ E; depth 250 m; 30 Oct. 2019; Åkerblå AS leg.; stn GJE-4; van Veen grab; NTNU-VM 83990.

REPUBLIC OF THE CONGO • 1 spec. 4°29.616′ S, 10°55.878′ E; depth 202 m; 12 May 2008; GCLME exped.; stn 8CR-01; van Veen grab; ZMBN 114799.

SENEGAL • 1 spec.; 15°28.812′ N, 17°13.566′ W; depth 504 m; 7 Nov. 2011; CCLME exped.; stn 2011410-GR09; van Veen grab.

WESTERN SAHARA • 1 spec.; 26°27.402′ N, 14°30.612′ W; depth 435 m; 29 Nov. 2011; CCLME exped.; stn 2011410-GR24; van Veen grab; ZMBN 152592.

**Comparative material**

***Prionospio gayheadia*** Delgado-Blas & Peraza, 2024

UNITED STATES – **Massachusetts** • >25 specs; 40°1.248′ N, 70°55.086′ W; depth 250 m; 4 May 1985; Battelle-New England Marine Lab For BLM/ MMS leg.; USNM 1002841 • >25 specs;same data as for preceding; USNM 1002842 • >25 specs; 40°1.302′ N, 70°55.098′ W; depth 250 m; 4 May 1985; Battelle-New England Marine Lab For BLM/ MMS leg.; USNM 1002843 • 2 specs; Georges Bank, Lydonia Canyon; 40°27.468′ N, 67°40.266′ W; depth 556 m; 6 Jul. 1985; Battelle-New England Marine Lab For BLM/ MMS leg.; USNM 1002845 • 1 spec.; 39°48.252′ N, 70°54.948′ W; depth 1273 m; 30 Jul. 1986; Battelle-New England Marine Lab For BLM/ MMS leg.; USNM 1002854 • 1 spec.; 30°3.420′ N, 88°38.080′ W; depth 20 m; 20 Aug. 1988; D. Harper leg.; box corer; USNM 1573961 • 2 specs; 29°4.932′ N, 88°45.516′ W; depth 150 m; 11 Mar. 1988; D. Harper leg.; box corer; USNM 1573962 • 1 spec.; 29°16.302′ N, 88°6.498′ W; depth 150 m; 21 Aug. 1988; D. Harper leg.; box corer; USNM 1573963 • 1 spec.; 29°16.302′ N, 88°6.498′ W; depth 150 m; 16 Mar. 1988; D. Harper leg.; box corer; USNM 1573964 • 3 specs; 29°42.084′ N, 87°20.166′ W; depth 100 m; 13 Mar. 1988; D. Harper leg.; box corer; USNM 1573965. – **Florida** • 1 spec.; 29°40.500′ N, 89°16.002′ W; depth 200 m; 23 Aug. 1988; D. Harper leg.; box corer; USNM 1573982 • 2 specs; 29°42.084′ N, 87°20.166′ W; depth 100 m; 16 Mar. 1988; D. Harper leg.; box corer; USNM 1573983 • 2 specs; same data as for

preceding; USNM 1573987 • 1 spec.; 30°2.118′ N, 88°38.082′ W; depth 20 m; 19 Aug. 1988; D. Harper leg.; box corer; USNM 1573984 • 1 spec.; 30°2.118′ N, 88°38.082′ W; depth 20 m; 12 Mar. 1988; D. Harper leg.; box corer; USNM 1573985 • 1 spec.; same data as for preceding; USNM 1573986 • 1 spec.; 29°24.000′ N, 88°7.002′ W; depth 100 m; 17 Mar. 1988; D. Harper leg.; box corer; USNM 1573988 • 1 spec.; 29°42.084′ N, 87°20.166′ W; depth 100 m; 22 Aug. 1988; D. Harper leg.; box

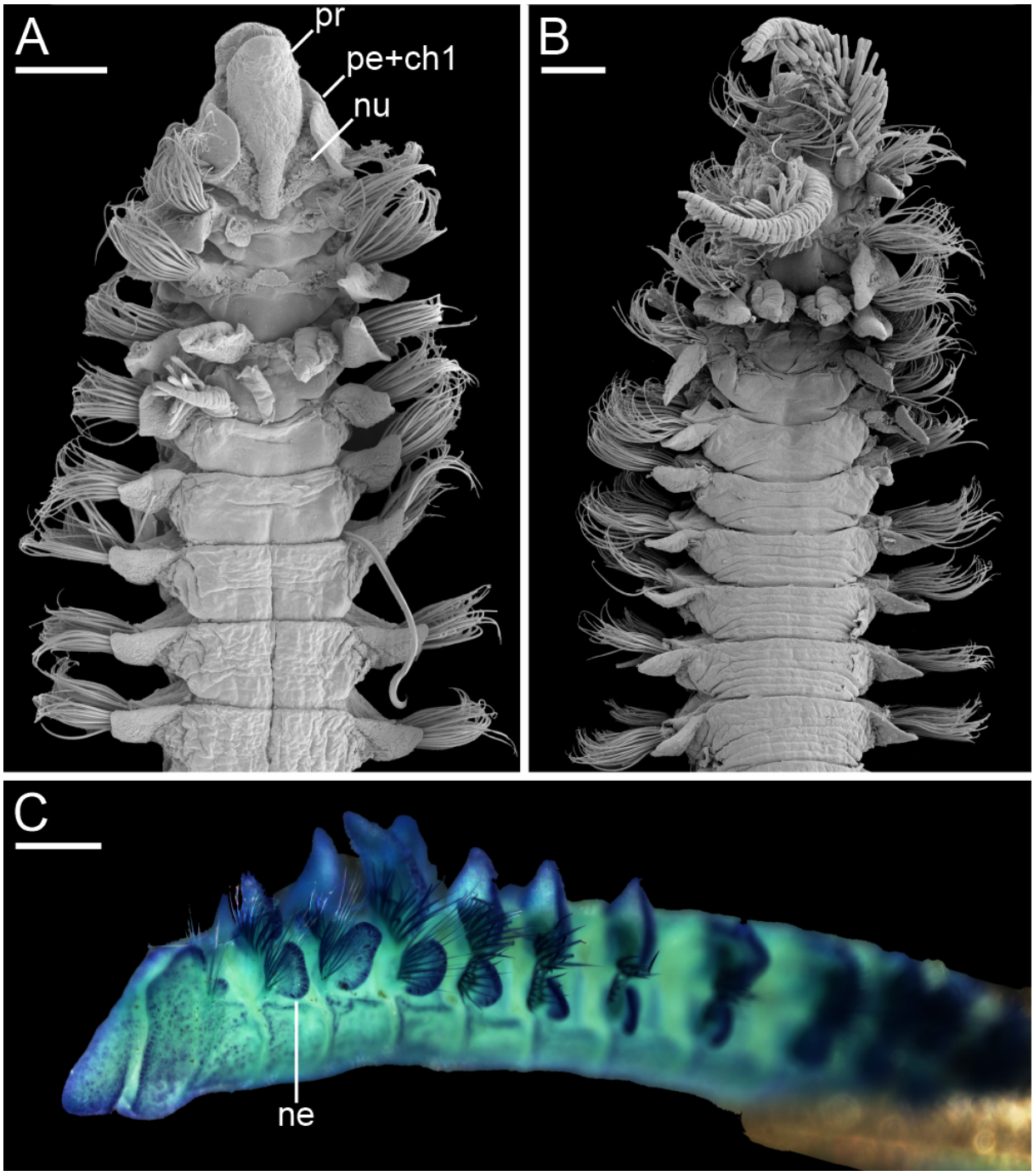


**Fig. 6.** Adult morphology of *Prionospio multisetosa* Delgado-Blas & Peraza, 2024. **A–B**. SEM micrographs. **C**. Light microscope image. **A**. Anterior end, dorsal view (NTNU-VM 84156). **B**. Anterior end, dorsal view (NTNU-VM 84152). **C**. Anterior end stained with methylene green, left lateral view (NTNU-VM 84000). Abbreviations: see Material and methods. Scale bars = 200 µm.

corer; USNM 1573989 • 3 spec.; 29°24.000′ N, 88°7.002′ W; depth 100 m; 20 Aug. 1988; D. Harper leg.; box corer; USNM 1573990 • 3 specs; same data as for preceding; USNM 1573991 • 2 specs; 29°42.084′ N, 87°20.166′ W; depth 100 m; 16 Mar. 1988; D. Harper leg.; box corer; USNM 1573992 • 3 specs; 29°40.500′ N, 89°16.002′ W; depth 200 m; 23 Aug. 1988; D. Harper leg.; box corer; USNM 1573993 • 1 spec.; 29°48.000′ N, 87°22.800′ W; depth 40 m; 16 Mar. 1988; D. Harper leg.; box corer; USNM 1573994 • 1 spec.; 29°24.000′ N, 88°7.002′ W; depth 100 m; 20 Aug. 1988; D. Harper leg.; box corer; USNM 1573995 • 2 specs; 29°14.898′ N, 88°7.284′ W; depth 200 m; 20 Aug. 1988; D. Harper leg.; box corer; USNM 1573996.

**Remarks**

*Prionospio multisetosa* was described by Delgado-Blas & Peraza (2024) during the preparation of the present manuscript. We were not able to examine the type material, and given the thorough and detailed original description, we did not find it necessary to provide a full redescription here. Instead, we present additional observations based on a larger number of specimens from a broader geographic and bathymetric range, contributing further information on the intraspecific variability and distribution of the species.

Delgado-Blas & Peraza (2024) based the description of *P. multisetosa* on 15 specimens from the west coast of Sweden, which they compared with the descriptions (not specimens) of *P. dubia* from South Africa provided by Day (1961) and Wilson (1990). Earlier, *Prionospio* with same characteristics from northern Europe were referred by various authors to *P. dubia* (Sigvaldadóttir & Mackie 1993; Sigvaldadóttir 2002). Delgado-Blas & Peraza (2024: table 1) noticed that the described South African

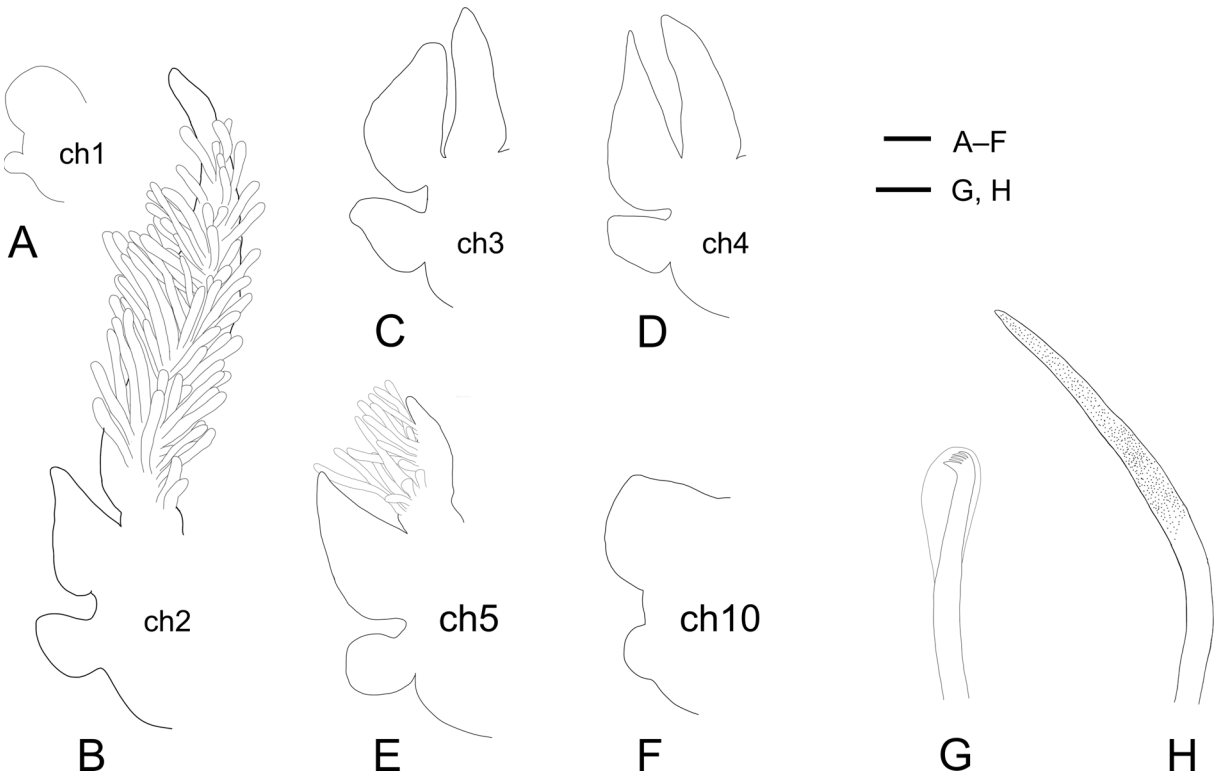


**Fig. 7.** Parapodia and chaetal morphology of *Prionospio multisetosa* Delgado-Blas & Peraza, 2024 (NTNU-VM 84022). **A**–**F**. Posteriorly facing parapodia of chaetigers 1–5 and 10. **G**. Hooded hook from neuropodium of chaetiger 20. **H**. Sabre chaeta from neuropodium of chaetiger 20. Abbreviations: see Material and methods. Scale bars: A–F = 100 μm; G–H = 10 μm.

specimens of *P. dubia* had 26–50 chaetigers while Swedish specimens, which they described as *P. multisetosa*, had 60–98 chaetigers, despite that all worms from South Africa were anterior fragments. They noted a series of morphological characters to distinguish *P. multisetosa* and *P. dubia*: presence or absence of eyes, size of the branchiae, position of the pinnules on the branchiae of chaetiger 5, whether the notopodial postchaetal lamellae extend slightly onto the dorsum or not, size of the notopodial prechaetal lamellae, shape of the notopodial postchaetal lamellae of chaetiger 3, shape of the neuropodial capillaries of chaetigers 2–5, the appearance and shape of sabre chaetae and the notopodial and neuropodial hooded hooks.

In this study, we examined 313 specimens previously identified as *P. dubia* from northern Norway south to the Republic of the Congo and could not find any morphological differences between Nordic and West African worms. We provide more insight into the intraspecific variation in *P. multisetosa*, and new images of anterior morphology (Fig. 6A–C) and drawings of parapodia and chaetae (Fig. 7A–H) of this species. We found some specimens with branchiae of chaetiger 2 extending to chaetiger 9, rather than to chaetiger 5, as reported by Delgado-Blas & Peraza (2024) for North Atlantic specimens, and that the branchiae of chaetigers 3 and 4 are similar in length to the notopodial postchaetal lamellae on the same chaetiger rather than shorter (Fig. 7C–D). While it was common for the notopodial postchaetal lamellae of chaetiger 2 to have a short ventral edge, not all worms had lamellae shaped like this. The neuropodial lamellae of chaetiger 3 were dorsally pointed in most worms (Fig. 8C), which was not clearly expressed or illustrated in the original description of *P. multisetosa* by Delgado-Blas & Peraza (2024). We also found slightly larger ranges of the first appearance of hooded hooks and sabre chaetae in neuropodia. The smallest juveniles (0.1 mm wide) had hooded hooks in neuropodia from chaetiger 14 and sabre chaetae from chaetiger 13. In comparison, Delgado-Blas & Peraza (2024) reported the first appearance of hooded hooks and sabre chaetae in neuropodia from chaetigers 16 and 14, respectively, likely due to their studying slightly larger specimens (0.2 mm wide).

The studied material includes all specimens sequenced by Hektoen *et al.* (2024), which came from the same broad geographic range, from northern Norway to the Republic of the Congo, and depths from 106 m to 665 m. Their molecular analysis confirmed their conspecificity.

To summarize, we observed a wide range of ontogenetic variability of specimens with diagnostic characters of *P. dubia* but could not find distinct morphological differences between them to assume the presence of more than one species. Our previous molecular analysis confirmed the conspecificity of worms collected from northern Norway south to the Republic of the Congo (Hektoen *et al.* 2024). This wide distribution range combined with the minute morphological differences between *P. dubia* and *P. multisetosa* may indicate that *P. multisetosa* is a junior synonym of *P. dubia*. However, this will likely only be resolved once new material of *P. dubia* from South Africa is collected and sequenced.

**Habitats and distribution**

Originally, *P. multisetosa* was reported from the west coast of Sweden. Here, we provide additional records of this species from East Atlantic waters, from northern Norway south to the Republic of the Congo, from depths of 47–665 m. Adults mainly occur in fine silt and muddy sediments.

***Prionospio fallax*** Söderström, 1920
Fig. 8

*Prionospio fallax* Söderström, 1920: 235–237, figs 135, 144–145.

*Prionospio malmgreni* – Eliason 1920: 51, fig. 13a–b. — Fauvel 1927: 61–62, fig. 21a–c. — Hannerz 1956: 40–46, figs 12–13.

*Prionospio fallax* – Sigvaldadóttir & Mackie 1993: 207–211, figs 3–5. — Kirkegaard 1996: 82–83, fig. 37 — Hektoen *et al.* 2024: figs 1, 4.

**Diagnosis**

Prostomium anteriorly truncate, posteriorly extending to end of chaetiger 1 as a thick caruncle. Two pairs of dark red eyes (appear black when fixed in ethanol or formalin); median eyes small single spots to large patches; lateral eyes single spots. Four pairs of branchiae on chaetigers 2–5; branchiae of chaetigers 2 and 5 long, pinnate, with pinnules arranged in single lateral rows; branchiae of chaetigers 3 and 4 apinnate, similar in size to notopodial postchaetal lamellae. Dorsolateral longitudinal ciliation present between successive notopodia on chaetigers 4–7. High dorsal crest on chaetiger 7 only. Neuropodial postchaetal lamellae of chaetiger 2 elongated ventrally. Sabre chaetae in neuropodia from chaetiger 10. Hooded hooks in neuropodia from chaetigers 12–13.

**Type material**

**Lectotype**

SWEDEN • Bohuslän, Lysekil, Islandsberg; 1891; A. Wirén leg.; designated by Sigvaldadóttir & Mackie (1993); UPSZTY 2255.

**Paralectotypes**

SWEDEN • 11 specs; Bohuslän, Lysekil, Islandsberg; 1891; A. Wirén leg.; designated by Sigvaldadóttir & Mackie (1993); UPSZTY 2255.

**Other material examined**

FRANCE • 14 specs; Banyuls-sur-Mer; 42°29.000′ N, 3°9.000′ E; depth 32 m; 1991; F. Pleijel leg.; Banyuls2; van Veen grab; SMNH 111902 • 9 specs; Banyuls-sur-Mer; 42°30.000′ N, 3°9.000′ E; depth 4 m; 1991; F. Pleijel leg.; van Veen grab; SMNH 111900 • 18 specs; Banyuls-sur-Mer; 42°30.102′ N, 3°9.288′ E; depth 40 m; 7 Oct. 1991; F. Pleijel leg.; stn Banyuls1991c; van Veen grab; SMNH 180570.

ITALY • 17 specs; Siracusa, Brucoli; 37°16.300′ N, 15°11.500′ E; depth 60 m; 23 May 1990; F. Pleijel leg.; stn Sicily7; van Veen grab; SMNH 180568 • 10 specs; Catania; 37°35.500′ N, 15°11.800′ E; depth 140 m; 18 May 1990; F. Pleijel leg.; stn Acitrezza7; van Veen grab; SMNH 180567.

NORWAY – **Skagerrak** • 8 specs; Oslofjorden; 28 Mar. 1952; van Veen grab; NHMO. – **Østfold** • 10 specs; Halden, Sponvika; 59°5.500′ N, 11°11.000′ E; depth 85 m; 23 Sep. 1992; stn Singlefjord 1992; van Veen grab; SMNH 111896 • 1 spec.; Halden, Sponvika; depth 25 m; 16 Sep. 1984; stn Sponvika2; van Veen grab; SMNH 111883. – **Akershus** • 1 spec.; Frogn, Drøbak; 59°38.682′ N, 10°37.302′ E; depth 10–45 m; 22 Oct. 2014; stn POLYSKAG 2014/10-18; van Veen grab; ZMBN 152633. – **Vestfold** • 1 spec.; Larvik; 59°2.667′ N, 10°1.537′ E; depth 43 m; 2020; NIVA leg.; stn lar-S27; van Veen grab; NTNU-VM 84043 • 4 specs; Holmestrand, Sande; 59°32.952′ N, 10°16.932′ E; depth 20–29 m; 30 May 2011; ZMBN leg; stn TR6; van Veen grab; ZMBN 152631 • 14 specs; 58°49.716′ N, 10°34.626′ E; depth 127–148 m; 17 May 2009; ZMBN leg.; stn BS48-82; sledge; ZMBN 152630. – **Telemark** • 1 spec.; Brevik, 59°3.620′ N, 9°41.891′ E; depth 10 m; 26 Aug. 2019; T. Bakken leg.; stn 2019091; van Veen grab; NTNU VM 77612. – **Agder** • 3 specs; Kristiansand, Skoltebukta; 58°7.503′ N, 7°58.788′ E; depth 31 m; 2020; NIVA leg.; stn K17; van Veen grab; NTNU-VM 84115 • 1 spec.; Tvedestrand, Sandvika; 58°34.080′ N, 9°1.860′ E; depth 22 m; 27 May 2011; NIVA leg.; stn GR3; van Veen grab; ZMBN 152616. – **Vestland** • 2 specs; Alver, Jibbersholmen; 60°45.052′ N, 4°53.330′ E; depth 80 m; 18 Dec. 2019; Åkerblå AS leg.; stn JIB-4; van Veen grab; NTNU-VM 84095 • 3 specs; Alver, Jibbersholmen; 60°45.169′ N, 4°53.273′ E; depth 115 m; 18 Dec. 2019; Åkerblå AS leg.; stn JIB-1; van Veen grab; NTNU-VM 84063 • 5 specs; Gulen, Hardbakkeneset; 61°1.035′ N, 4°56.645′ E; depth 110 m; 19 Sep. 2019; Åkerblå AS leg.; stn HAR-3; van Veen grab; NTNU-VM 84067 • 1 spec.;

Fjaler, Hegnes; 61°21.470′ N, 5°17.110′ E; depth 243 m; 4 Dec. 2019; Åkerblå AS leg.; stn HEG-1; van Veen grab; SEM stub; NTNU-VM 84157 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 84158 • 1 spec.; Fjaler, Hegnes; 61°21.579′ N, 5°17.270′ E; depth 244 m; 4 Dec. 2019; Åkerblå AS leg.; stn Heg-2; van Veen grab; NTNU-VM 84050 • 17 specs; same data as for preceding; NTNU-VM 84051 • 15+ specs; Bremanger Gulestø; 61°45.701′ N, 5°4.096′ E; depth 146 m; 8 Oct. 2019; Åkerblå AS leg.; stn GUL-3; van Veen grab; NTNU-VM 84059 • 11 specs; Bremanger Gulestø; 61°45.868′ N, 5°4.050′ E; depth 170 m; 8 Oct. 2019; Åkerblå AS leg.; stn GUL-2; van Veen grab; NTNU-VM 84057 • 10 specs; Sogndal, Beitveit; 62°8.171′ N, 5°19.906′ E; depth 138 m; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-3; van Veen grab; NTNU-VM 84097 • 20 specs; Sogndal, Beitveit; 62°8.551′ N, 5°20.113′ E; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-5; van Veen grab; NTNU-VM 84040 • 1 spec.; Bergen, Mortholmosen; 60°12.864′ N, 5°20.736′ E; depth 42–60 m; 9 Feb. 2006; ZMBN leg.; stn HB2006.02.09-2; sledge; ZMBN 152620 • 17 specs; Øygarden, Sund; 60°10.080′ N, 5°0.420′ E; depth 17 m; 23 Apr. 2014; ZMBN leg.; stn HB2014.04.24-3; van Veen grab; ZMBN 152627 • 1 spec.; Øygarden, Sund; 60°10.380′ N, 5°0.180′ E; depth 6 m; 23 Apr. 2014; ZMBN leg.; stn HB2014.04.24-4; van Veen grab; ZMBN 152626 • 50+ specs; Øygarden, Sund; 60°12.000′ N, 5°2.460′ E; depth 60 m; 23 Apr. 2014; ZMBN leg.; stn HB2014.04.24-5; van Veen grab; ZMBN 152623 • 35 specs; Øygarden, Sund; 60°12.046′ N, 5°2.305′ E; depth 30–60 m; 7 Sep. 2016; ZMBN leg.; stn HB2016.09.07-2; sledge; ZMBN 152621 • 7 specs; Bergen, Flesland; 60°17.052′ N, 5°12.087′ E; depth 72 m; 2 Sep. 2014; ZMBN leg.; stn HB2014.09.02-1; van Veen grab; ZMBN 152625 • 37 specs; Alver, Håøysundet; 60°32.984′ N, 5°13.738′ E; depth 37 m; 20 Apr. 2017; ZMBN leg.; stn HB2017.04.20-2; van Veen grab; ZMBN 152632 • 3 specs; Alver, Radfjorden; 60°36.009′ N, 5°9.262′ E; depth 106m; 6 Mar. 2017; ZMBN leg.; stn HB2017.03.06-5; van Veen grab; ZMBN 152624. – **Møre og Romsdal** • 10 specs; Rauma, Lybergsvika; 62°38.678′ N, 7°26.648′ E; depth 104 m; 18 Jul. 2019; Åkerblå AS leg.; stn LYB-5; van Veen grab; NTNU-VM 84058 • 5 specs; Rauma, Lybergsvika; 62°38.777′ N, 7°27.359′ E; depth 95 m; 18 Jul. 2019; Åkerblå AS leg.; stn LYB-6; van Veen grab; NTNU-VM 84056 • 1 spec.; Kristiansund, Or; 63°2.087′ N, 7°50.760′ E; depth 60 m; 13 Nov. 2019; Åkerblå AS leg.; stn OR-2; van Veen grab; NTNU-VM 84159 • 2 specs; same data as for preceding; NTNU-VM 84047 • 4 specs; Kristiansund, Or; 63°2.527′ N, 7°51.402′ E; depth 56 m; 13 Nov. 2019; Åkerblå AS leg.; stn OR-4; van Veen grab; NTNU-VM 84046 • 1 spec.; Smøla, Andholmane; 63°28.525′ N, 7°51.111′ E; depth 53 m; 17 Dec. 2019; Åkerblå AS leg.; stn AND-8; van Veen grab; NTNU-VM 84042 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 85853. – **Trøndelag** • 1 spec.; Trondheim, Grillstad; 63°26.340′ N, 10°30.329′ E; depth 3 m; 4 Sep. 2018; M. Capa *et al.* leg.; stn 2018033; van Veen grab; NTNU-VM 76719 • 1 spec.; Hitra, Reitholmen; 63°37.339′ N, 9°7.762′ E; depth 38 m; 27 Jan. 2022; Åkerblå AS leg.; stn REI-3; van Veen grab; NTNU-VM 84044 • 5 specs; Ørland, Havsund; 63°47.870′ N, 9°26.236′ E; depth 35 m; 30 Oct. 2019; Åkerblå AS leg.; stn HAV-5; van Veen grab; NTNU-VM 84055 • 1 spec.; Ørland, Havsund; 63°48.073′ N, 9°26.799′ E; depth 22 m; 30 Oct. 2019; Åkerblå AS leg; stn HAV-3; van Veen grab; NTNU-VM 84053 • 6 specs; Ørland, Havsund; 63°48.091′ N, 9°26.385′ E; depth 26 m; 30 Oct. 2019; Åkerblå AS leg.; stn HAV-4; van Veen grab; NTNU-VM 84054. – **Nordland** • 1 spec.; Bodø, Brønnøyskjæran; 67°25.242′ N, 13°54.936′ E; depth 15 m; 25 Nov. 2021; Åkerblå AS leg.; stn BRØ-REF; van Veen grab; NTNU-VM 84045. – **Troms** • 2 specs; Gratangen, Follesøy; 68°41.586′ N, 17°25.972′ E; depth 34 m; 28 Jan. 2022; Åkerblå AS leg.; stn FOL-2; van Veen grab; NTNU-VM 84065 • 4 specs; Hamarøy, Jøvik; 69°8.155′ N, 17°19.840′ E; depth 20 m; 21 Oct. 2020; Åkerblå AS leg.; stn JØV-1; van Veen grab; NTNU-VM 84060 • 1 spec.; Hamarøy, Hallarøy; 69°8.820′ N, 16°51.778′ E; depth 97 m; 29 Oct. 2019; Åkerblå AS leg.; stn HAL-REF; van Veen grab; NTNU-VM 84061 • 1 spec.; Tromsø; 69°46.362′ N 19°13.869′ E; 29 Mar. 2021; Åkerblå AS leg.; stn R1-4; van Veen grab; NTNU-VM 84052 • 2 specs; Karlsøy, Dåvøy; 70°3.313′ N, 19°18.781′ E; depth 72 m; 11 Nov. 2021; Åkerblå AS leg; stn DÅV-REF; van Veen grab; NTNU-VM 84069 • 5 specs; Karlsøy, Karaneset; 70°3.586′ N, 19°18.296′ E; depth 63 m; 11 Aug. 2021; Åkerblå AS leg.; stn KAR-2; van Veen grab; NTNU-VM 84070 • 9 specs; Karlsøy, Karaneset; 70°3.734′ N, 19°18.379′ E; depth 97 m; 11 Aug. 2021; Åkerblå AS leg.; stn KAR-3; van Veen grab; NTNU-VM 84071 • 1 spec.; Karlsøy Karaneset; 70°4.132′ N, 19°18.715′ E; depth 73 m; 11 Aug.

2021; Åkerblå AS leg.; stn KAR-4; van Veen grab; NTNU-VM 84064 • 2 specs; Karlsøy, Karaneset; 70°6.109′ N, 19°35.191′ E; depth 134 m; 11 Aug. 2021; Åkerblå AS leg.; stn KAR-5; van Veen grab; NTNU-VM 84073 • 5 specs; Karlsøy, Nordnibba; 70°9.855′ N, 19°21.322′ E; depth 73 m; 11 Oct. 2021; Åkerblå AS leg.; stn NOR-REF; van Veen grab; NTNU-VM 84038 • 1 spec.; Karlsøy, Nordnibba; 70°9.993′ N, 19°22.469′ E; depth 67 m; 11 Oct. 2021; Åkerblå AS leg.; stn NOR-5; van Veen grab; NTNU-VM 84039.

SWEDEN • 1 spec.; depth 10–20 m; 1991; stn Krugglö91; sledge; SMNH 111893. – **Halland** • 7 specs; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1984; stn VÄRV84#3; van Veen grab; SMNH 53678 • 88 specs; Varberg, Värö; 57°10.000′ N, 12°5.000′ E; depth 20 m; 1980; stn Varö spring 1980 2; van Veen grab; SMNH 9554 • 50 specs; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1978; stn Varö spring 1980 3; van Veen grab; SMNH 6453 • 30 specs; Varberg Värö; 57°10.000′ N, 12°5.000′ E; depth 20 m; 1984; stn VÄRH84#2; van Veen grab; SMNH 52794 • 100 specs; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1979; stn VÄRV79#3; van Veen grab; SMNH 8710 • 20 specs; Varberg, Värö; 57°13.000′ N, 12°1.000′ E; depth 39 m; 1984; stn VÄRH84#4; van Veen grab; SMNH 53565 • 20 specs; Varberg, Värö; 57°13.000′ N, 12°4.000′ E; depth 21 m; 1987; stn VÄRV87#1; van Veen grab; SMNH, 54728 • 50 specs; Varberg, Värö; 57°13.000′ N, 12°4.000′ E; depth 21 m; 1984; stn VÄRH84#1; van Veen grab; SMNH 52763 • 13 specs; Varberg, Värö; 57°16.000′ N, 12°5.000′ E; depth 19 m; 1981; stn VÄRH81#7; van Veen grab; SMNH, 11431 • 150 specs; Varberg, Värö; 57°16.000′ N, 12°5.000′ E; depth 19 m; 1984; stn VÄRV84#7; van Veen grab; SMNH 53617.

UNITED KINGDOM • 10 specs; Loch Creran; 56.523511 N, 5.355115 W; depth 25 m; 31 May 1905; stn Loch Creran4; van Veen grab; SMNH 180569.

**Examined material with sequence data**

NORWAY – **Akershus** • 2 specs; Asker, Sætre; 59°39.372′ N, 10°36.486′ E; depth 18–45 m; 20 Oct. 2014; stn POLYSKAG 2014/10-3; van Veen grab; ZMBN 152617. – **Oslo** • 1 spec.; Oslo; 59°54.434′ N, 10°44.013′ E; depth 13 m; 18 Sep. 2018; M. Capa leg; stn 2018188; van Veen grab; NTNU-VM 76527. – **Vestfold** • 1 spec.; 58°49.716′ N, 10°34.626′ E; depth 127–148 m; 17 May 2009; ZMBN leg.; stn BS48-82; sledge; ZMBN 152618. – **Agder** • 1 spec.; Kristiansand, Skoltebukta; 58°9.026′ N, 8°2.060′ E; depth 8 m; 23 Aug. 2019; T. Bakken leg.; etsn. 2019060; van Veen grab; NTNU-VM 77485.

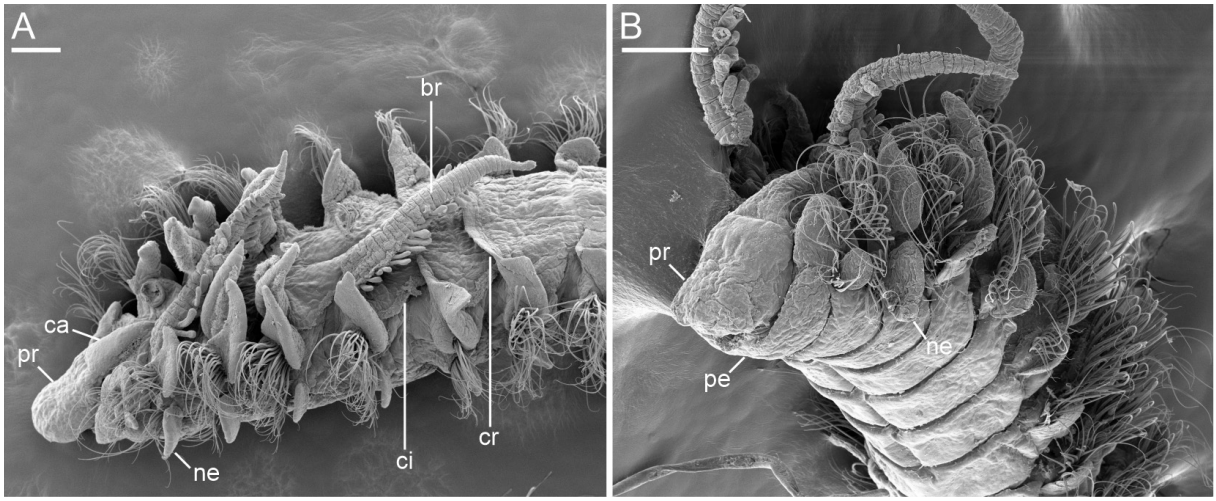


**Fig. 8.** Adult morphology of *Prionospio fallax* Söderström, 1920. SEM micrographs. **A**. Anterior end, left dorsolateral view (NTNU-VM 85853). **B**. Anterior end, left ventro-lateral view (NTNU-VM 84159). Abbreviations: see Material and methods. Scale bars = 100 μm.

– **Vestland** • 12 specs; Bergen, Bergsvika; 60°19.133′ N, 5°15.317′ E; depth 48 m; 12 Sep. 2019; M. Capa leg.; stn SØR D1; van Veen grab; NTNU-VM 76741 • 1 spec.; Alver, Jibbersholmen; 60°45.052′ N, 4°53.330′ E; depth 80 m; 18 Dec. 2019; Åkerblå AS leg.; stn JIB-4; van Veen grab; NTNU-VM 84096 • 1 spec.; Fjaler, Hegnes; 61°21.470′ N, 5°17.110′ E; depth 243 m; 4 Dec. 2019; Åkerblå AS leg.; stn HEG-1; van Veen grab; NTNU-VM 84049 • 1 spec.; Sogndal, Beitveit; 62°8.171′ N, 5°19.906′ E; depth 138 m; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-3; van Veen grab; NTNU-VM 84098 • 1 spec.; Øygarden, Fjell; 60°19.591′ N, 5°8.451′ E; depth 75 m; 2 Sep. 2014; ZMBN leg.; stn HB2014.09.02-2; van Veen grab; ZMBN 152629 • 1 spec.; Øygarden, Sund; 60°10.080′ N, 5°0.420′ E; depth 17 m; 23 Apr. 2014; ZMBN leg.; stn HB2014.04.24-3; van Veen grab; ZMBN 152615 • 1 spec.; Øygarden, Sund; 60°12.046′ N, 5°2.305′ E; depth 30–60 m; 7 Sep. 2016; ZMBN leg.; stn HB2016.09.07-2; sledge; ZMBN 152628 • 1 spec.; Bergen, Flesland; 60°17.052′ N, 5°12.087′ E; depth 72 m; 2 Sep. 2014; ZMBN leg.; stn HB2014.09.02-1; van Veen grab; ZMBN 152619 • 1 spec.; Alver, Håøysundet; 60°32.984′ N, 5°13.738′ E; depth 37 m; 20 Apr. 2017; ZMBN leg.; stn HB2017.04.20-2; van Veen grab; ZMBN 152622 • 1 spec.; Alver, Radfjorden; 60°36.009′ N, 5°9.262′ E; depth 106m; 6 Mar. 2017; ZMBN leg.; stn HB2017.03.06-5; van Veen grab; ZMBN 152634. – **Møre og Romsdal** • 1 spec.; Kristiansund, Or; 63°2.087′ N, 7°50.760′ E; depth 60 m; 13 Nov. 2019; Åkerblå AS leg.; stn OR-2; van Veen grab; NTNU-VM 84048. – **Trøndelag** • 1 spec.; Trondheim; 63°26.308′ N, 10°23.940′ E; depth 6 m; 5 Sep. 2018; M. Capa *et al.* leg.; stn 2018044; van Veen grab; NTNU-VM 75547.

**Remarks**

The new material agrees well with the type specimens and original and later descriptions of *P. fallax* (Söderström 1920; Sigvaldadóttir & Mackie 1993). Among Northeast Atlantic species of *Prionospio*, *P. fallax* is uniquely distinguished by the presence of a prominent single dorsal crest on chaetiger 7. Although the type material was made available for examination at UPSZTY, the microscopy facilities on site were inadequate for detailed morphological study or for obtaining diagnostic photographs. Additionally, the types were not available for loan. Due to these limitations, we did not attempt a full redescription or imaging of the type material.

Some morphological features not previously described for *P. fallax* were observed in the present study in the non-type material. Some large individuals had pinnules present almost to the tip of branchiae (Fig. 8A), rather than absent on long distal part of branchiae (Fig. 8B), as described by Söderström (1920) and Sigvaldadóttir & Mackie (1993). Large specimens had notopodial postchaetal lamellae of chaetiger 6 and/or chaetiger 8 basally extending halfway across the dorsum; however, these extensions never met middorsally to form transverse crests (Fig. 8A). Dorsolateral longitudinal ciliation between chaetigers 4–7 is documented here for *P. fallax* for the first time. *Prionospio fallax* has been reported from Norway, Sweden, Scotland, and the Mediterranean Sea (Sigvaldadóttir & Mackie 1993). We found no morphological differences between populations from northern Europe and the Mediterranean. However, it should be noted that molecular data are currently only available for specimens from Norwegian waters. Broader sampling and genetic analysis might be needed to confirm the identity of the Mediterranean populations.

**Habitats and distribution**

*Prionospio fallax* is known from Norway, Sweden, Scotland and the western Mediterranean Sea between 4 and 244 m depth.

***Prionospio sanmartini*** Delgado-Blas, Díaz-Díaz & Viéitez, 2019
Figs 9–11

*Prionospio* (*Minuspio*) *sanmartini* Delgado-Blas, Díaz-Díaz & Viéitez, 2019: 568–573, fig. 3, table 1.

*Prionospio* (*Minuspio*) *multibranchiata* – Mackie 1984: 40–42, fig. 3, table 2.
*Prionospio multibranchiata* – Kirkegaard 1996: 84–85, fig. 38.
*Prionospio* (*Minuspio*) *cirrifera* – Hartmann-Schröder 1996: 329–330 (partim).
*Prionospio* cf. *sanmartini* – Hektoen *et al.* 2024: figs 1, 4.

**Diagnosis**

Prostomium narrow, anteriorly rounded, posteriorly extending to middle of chaetiger 2 as a narrow caruncle. Two pairs of eyes present; median eyes single or multiple spots sometimes fused together. Eight to 13 pairs of apinnate branchiae from chaetiger 2. Low dorsal crests from chaetigers 12–14. Neuropodial postchaetal lamellae of chaetiger 2 not elongated ventrally. Sabre chaetae in neuropodia from chaetigers 12–17. Hooded hooks in notopodia from chaetigers 35–41, in neuropodia from chaetigers 13–19.

**Type material**

**Paratypes**

SPAIN • 9 specs; Galicia, Ría de Foz; 43°33′ N, 7°15′ W; J. Junoy leg.; stn CC1. XII.85; MNCN 16.01/18448.

**Other material examined**

FRANCE • 20 specs; Banyuls sur Mer; 42°30.000′ N, 3°9.000′ E; depth 4 m; F. Pleijel leg.; stn Banyuls1; van Veen grab; SMNH 111901 • 3 specs; Banyuls sur Mer; 42°29.000′ N, 3°9.000′ E; depth 32 m; F. Pleijel leg.; stn Banyuls2; van Veen grab; SMNH 111903.

ITALY • 11 specs; Sicily, Brucoli; 37°17.000′ N, 15°11.000′ E; depth 40 m; 1990; Mission Sicile Orientale 1990 leg.; stn Sicily1 1990; van Veen grab; SMNH 111895.

NORWAY – **Vestfold** • 3 specs; Larvik, Larviksfjorden; 59°2.667′ N, 10°1.537′ E; depth 43 m; 2020; NIVA leg.; stn LAR-S27; van Veen grab; NTNU-VM 84121 • 1 spec.; Sandefjord; 59°0.786′ N, 10°22.301′ E; depth 57 m; 2019; NIVA leg.; stn A05/BT40; van Veen grab; NTNU-VM 84118 • 8 specs; Larvik, Stavern; 58°59.815′ N, 10°2.710′ E; depth 13 m; 2020; NIVA leg.; stn STA-1; van Veen grab; NTNU-VM 84119. – **Telemark** • 7 specs; Porsgrunn; 59°3.220′ N, 9°45.069′ E; depth 31 m; 2018; NIVA leg.; stn F04-C; van Veen grab; NTNU-VM 84122. – **Agder** • 6 specs; Kristiansand, Skoltebukta; 58°7.503′ N, 7°58.788′ E; depth 31 m; 2020; NIVA leg.; stn K17; van Veen grab; NTNU-VM 84116 • 18 specs; Kristiansand, Skoltebukta; 58°7.465′ N, 7°58.472′ E; depth 20 m; 2020; NIVA leg.; stn EC1; van Veen grab; NTNU-VM 84117 • 3 specs; Kristiansand, Skoltebukta; 58°7.161′ N, 7°58.661′ E; depth 17 m; 2020; NIVA leg.; stn KH03; van Veen grab; NTNU-VM. 84120.

SWEDEN – **Bohuslän** • 1 spec.; Strömstad, Tjärnö; 58°52.860′ N, 11°6.480′ E; 2019; A. Nygren leg.; stn KAU-02; van Veen grab; NTNU-VM 84124 • 5 specs; Tanum, Väderöarna; depth 118 m; 1985; stn Väderöarna2; van Veen grab; SMNH 111879 • 4 specs; Tanum, Väderöarna; depth 40 m; 1984; van Veen grab; SMNH 111880. – **Halland** • 2; Varberg, Värö; 57°10.000′ N, 12°5.000′ E; depth 20 m; 1978; stn VÄRV78#2; van Veen grab; SMNH 6442 • 50 specs; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1978; stn VÄRV78#3; van Veen grab; SMNH 6452 • 100 specs; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1979; stn VÄRV79#3; van Veen grab; SMNH 8706 • 50 specs.; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1980; stn VÄRV80#3; van Veen grab; SMNH 9630 • 50 specs; Varberg, Värö; 57°16.000′ N, 12°5.000′ E; depth 19 m; 1980; stn VÄRV80#7; van Veen grab; SMNH 10104 • 2 specs; Varberg, Värö; 57°13.000′ N, 12°4.000′ E; depth 21 m; 1984; stn VÄRH84#1; van Veen grab; SMNH 52762 • 4 specs; Varberg, Värö; 57°16.000′ N, 12°5.000′ E; depth 19 m; 1984; stn VÄRV84#7; van Veen grab; SMNH 53618 • 12 specs; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1984; stn VÄRV84#3; van Veen grab; SMNH 53677 • 5 specs; Varberg, Värö; 57°13.000′ N, 12°1.000′ E; depth 39 m; 1984; stn VÄRH84#4; van Veen grab; SMNH 53565 • 5 specs; Varberg, Värö;

57°13.000′ N, 12°4.000′ E; depth 21 m; 1987; stn VÄRV87#1; van Veen grab; SMNH 54729 • 5 specs; Varberg, Värö; 57°8.000′ N, 12°6.000′ E; depth 22 m; 1984; stn VÄRV84#8; van Veen grab; SMNH 53644 • 1 spec.; Varberg, Värö; 57°16.000′ N, 12°5.000′ E; depth 19 m; 1981; stn VÄRH81#7; van Veen grab; SMNH 11433 • 25 specs; Varberg, Värö; 57°10.000′ N, 12°1.000′ E; depth 47 m; 1987; stn VÄRV87#3; van Veen grab; SMNH 67943.

UNITED KINGDOM • 5 specs; Loch Creran; depth 25 m; 1978; A. Mackie leg.; stn Loch Creran2; van Veen grab; SMNH 178632 • 5 specs; same data as for preceding; USNM; 80865.

**Examined material with sequence data**

SWEDEN – **Bohuslän** • 1 spec.; Strömstad, Tjärnö; 58°52.860′ N, 11°6.480′ E; 2019; A. Nygren leg.; stn KAU-02; van Veen grab; NTNU-VM 84123 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 84140.

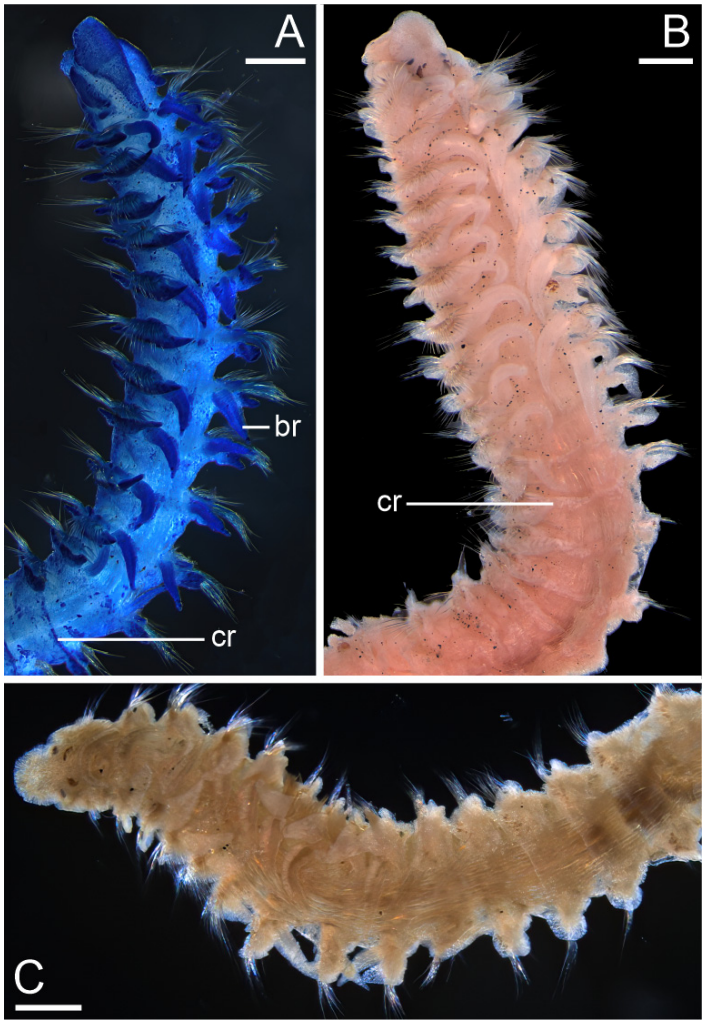


**Fig. 9.** Adult morphology of *Prionospio sanmartini* Delgado-Blas, Díaz-Díaz & Viéitez, 2019. **A**. Anterior end stained with methylene green, left dorsolateral view (NTNU-VM 84118). **B**. Anterior end, left dorsolateral view stained with rose bengal (NTNU-VM 84117). **C**. Anterior end, dorsal view (MNCN 16.01/18448, paratype). Abbreviations: see Material and methods. Scale bars = 200 µm.

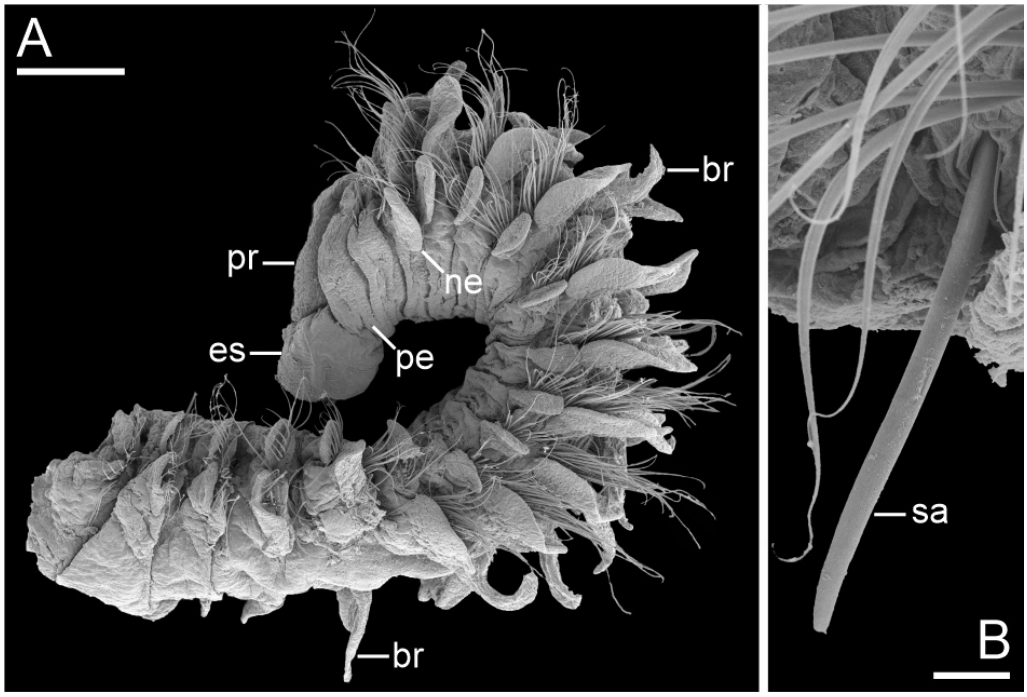


**Fig. 10.** Adult morphology of *Prionospio sanmartini* Delgado-Blas, Díaz-Díaz & Viéitez, 2019, SEM micrograps (NTNU-VM 84140). **A**. Anterior end, left lateral view. **B**. Neurochaeta of chaetiger 15. Abbreviations: see Material and methods. Scale bars: A = 200 μm; B = 10 μm.

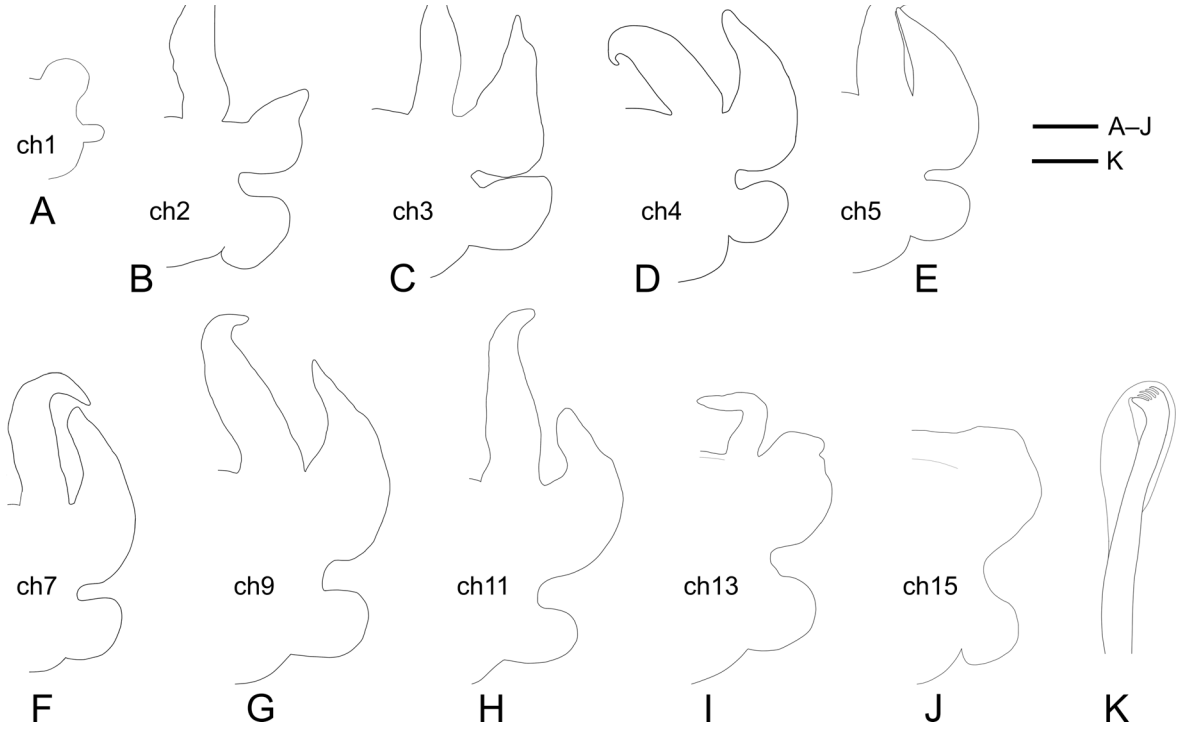


**Fig. 11.** Morphology of parapodia and chaetae of *Prionospio sanmartini* Delgado-Blas, Díaz-Díaz & Viéitez, 2019 (NTNU-VM 84117). **A–J**. Chaetigers 1–5, 7, 9, 11, 13, 15. **K**. Hooded hook from neuropodium of chaetiger 18. Abbreviations: see Material and methods. Scale bars: A–J = 100 μm; K = 10 μm.

**Description** (adults)

Largest complete specimen 35 mm long, 0.4 mm wide for 72 chaetigers; largest anterior fragment 0.5 mm wide. Color in alcohol brownish to pale white. Prostomium narrow, widest in front of lateral eyes (Fig. 9A–C), anteriorly rounded, posteriorly extending to middle of chaetiger 2 as narrow caruncle. Nuchal organs U-shaped ciliary bands lateral to caruncle (Fig. 9A). Most specimens with two pairs of eyes arranged trapezoidally; median eyes multiple small spots, often fused together forming crescent; lateral eyes single round spots (Fig. 9B). Posterior dorsolateral parts of peristomium fused with notopodial postchaetal lamellae of chaetiger 1 forming ear-shaped structures lateral to prostomium. Palps missing in all specimens.

Branchiae from chaetiger 2 to chaetigers 9–14 (usually to chaetigers 10–14) (Figs 9A–C, 10A), cirriform, apinnate with lateral ciliation. First pair of branchiae usually longest, up to 2 × as long as notopodial lamellae; last pair usually shortest; remaining branchiae similar to each other and equal to or slightly longer than notopodial postchaetal lamellae (Figs 9A–C, 10A, 11B–I). Nototrochs transverse ciliary bands between branchial bases. Dorsolateral longitudinal ciliation absent.

Notopodial prechaetal lamellae small, rounded in anterior region, reduced in posterior part of body. Notopodial postchaetal lamellae of chaetiger 1 broadly rounded, fused with peristomium (Fig. 11A). Lamellae of chaetigers 2–12 subtriangular, largest on chaetigers 3–10 (Fig. 11B–H), lower and rounded on postbranchial chaetigers (Fig. 11I–J). Notopodial postchaetal lamellae joined across dorsum forming low transverse crests from chaetigers 12–14 to chaetigers 27–34 (Figs 9–10). Neuropodial prechaetal lamellae inconspicuous. Neuropodial postchaetal lamellae of chaetiger 1 small, oblong, rounded; lamellae of chaetiger 2 rectangular, wider than long, not pointing ventrally; on chaetiger 3 longer than wide; from chaetiger 4, lamellae evenly rounded, almost circular by chaetiger 15 (Fig. 11A–J), reduced on succeeding chaetigers. Interneuropodial pouches absent.

Notopodial capillaries on anterior and middle chaetigers arranged in two rows, unilimbate, slightly granulated; anterior row shorter than posterior row. Notopodial capillaries on posterior chaetigers alimbate, long, thin. Neuropodial capillaries arranged in two rows on anterior chaetigers, unilimbate, slightly granulated, anterior row shorter than posterior row. Sabre chaetae in neuropodia from chaetigers 12–17, with granulation on distal part of shaft, up to two per fascicle (Fig. 10B). Hooded hooks in notopodia from chaetigers 35–41. Hooks in neuropodia from chaetigers 13–19, up to eight per ramus, alternating with capillary chaetae. Both noto- and neuropodial hooded hooks with 4–5 pairs of upper teeth arranged in two vertical rows above main fang, with outer and small inner hoods (Fig. 11K).

Pygidium with one long middorsal cirrus and a pair of short ventral cirri.

**Remarks**

*Prionospio* with more than six pairs of smooth apinnate branchiae from the Northeast Atlantic have historically been attributed to *P. multibranchiata* (e.g., Mackie 1984). In the last 15 years, such worms from the Levantine Sea (Turkey) were described as *P. maciolekae* Dagli & Çinar, 2011, and worms from the Atlantic coast of Spain were described as *P. sanmartini* Delgado-Blas, Díaz-Díaz & Viéitez, 2019. Delgado-Blas *et al.* (2019) provided an updated description of *P. multibranchiata* based on specimens from Vancouver (British Columbia, Canada), but did not study the type material of this species. The authors distinguished *P. sanmartini* from the description of northern European specimens previously described and identified as *P. multibranchiata* by Mackie (1984); however, they did not study material described by Mackie (1984). *Prionospio sanmartini* and *P. multibranchiata* sensu Mackie (1984) were distinguished based on the shape of the prostomium, size and shape of the eyes, and shape of the neuropodial postchaetal lamellae of chaetiger 2 (Delgado-Blas *et al.* 2019). However, our study of new material from Skagerrak, specimens from Scotland examined and described by Mackie (1984), as well

as other specimens identified by Mackie and present in the Swedish Natural History Museum from Italy, France, and Sweden, and paratypes of *P. sanmartini*, showed that differences between them can be interpreted as either individual or ontogenetic variability of one species. The prostomium is rounded both in paratypes of *P. sanmartini* and the other specimens (Fig. 9A–C). Both paratypes of *P. sanmartini* and the other specimens have eyes of varying sizes and shapes (from single points to crescentic). Similarly, there was no significant difference between the shape of the neuropodial postchaetal lamellae of chaetiger 2. Hektoen *et al.* (2024) showed that specimens from the Swedish west coast were genetically similar to one specimen from northern Spain, close to the type locality of *P. sanmartini*, indicating the existence of an extended population of one species, rather than geographically separated two species. Thus, we consider *P. sanmartini* to also occur in Skagerrak waters in Norway and Sweden.

We found some differences between the paratypes of *P. sanmartini* and northern European specimens of similar sizes: the number of branchiae (10 pairs in the *P. sanmartini* paratypes and usually 10–13 pairs in specimens of similarly size from northern Europe), distribution of dorsal crests (on chaetigers 12–18 in *P. sanmartini* and from chaetigers 13–14 on more than 15 succeeding chaetigers in northern European specimens), and start of sabre chaetae (from chaetigers 12–16 in *P. sanmartini* and 14–17 in northern European specimens). However, we do not find this evidence sufficient to separate northern and southern European populations and consider them conspecific, especially considering the genetic evidence for an extended geographical distribution of one species. The holotype of *P. sanmartini* was not available for this study.

**Habitats and distribution**

*Prionospio sanmartini* is known from fine-grained sediments between 4 and 118 m depth in southern Norway, the West coast of Sweden, Scotland, France, Spain, and Italy.

***Prionospio fiordica*** sp. nov.
urn:lsid:zoobank.org:act:6A2054E0-DCE1-47DC-9C65-8572FB18FAFC
Figs 12–14

*Prionospio* sp. 3 – Hektoen *et al.* 2024: figs 1, 4.

**Diagnosis**

Prostomium triangular, anteriorly wide, truncate, posteriorly extending to end of chaetiger 1 as a short caruncle. Two pairs of small eyes present. Branchiae from chaetiger 2 to chaetigers 10–14, cirriform, apinnate, longest on the first chaetiger and then gradually diminishing in size. Dorsal crests low, on chaetigers 12–16. Neuropodial postchaetal lamellae of chaetiger 2 not elongated ventrally, large and rectangular on chaetigers 3–4. Sabre chaetae in neuropodia from chaetigers 16–17. Hooded hooks in notopodia from chaetiger 34, in neuropodia from chaetigers 17–18.

**Etymology**

The name '*fiordica*' refers to the type locality and common occurrence of the species in the Norwegian fjords.

**Type material**

**Holotype**

NORWAY • Vestland, Stad, Midthjell; 61°55.306′ N, 5°32.774′ E; depth 576 m; 20 Apr. 2022; STIM AS leg.; stn C5.2; van Veen grab; NTNU-VM 84107.

**Paratypes**

NORWAY • 2 specs; Vestland, Stad, Midthjell; 61°55.232′ N, 5°31.303′ E; depth 580 m; 20 Apr. 2022; STIM AS leg.; stn C3.1; van Veen grab; NTNU-VM 84111 • 4 specs; Møre og Romsdal, Volda, Voldsfjorden; 62°6.058′ N, 6°7.302′ E; depth 462 m; 14 Dec. 2021; STIM AS leg.; stn LOK C-REF; van Veen grab; NTNU-VM 84110 • 3 specs; Stad, Juvika B; 61°53.747′ N, 5°39.023′ E; depth 559 m; 9 Dec. 2021; Åkerblå AS leg.; stn JUV-2; van Veen grab; NTNU-VM 84114.

**Paratypes with sequence data**

NORWAY • 1 spec.; Stranda, Opshaugvik; 62°17.350′ N, 6°59.630′ E; depth 376 m; 31 Mar. 2020; Åkerblå AS leg.; stn OPS-3.1; van Veen Grab; NTNU-VM 84105 • 1 spec.; Alver, Trollholmen; 60°30.978′ N, 5°10.434′ E; depth 367 m; 13 Aug. 2019; Rådgivende Biologer AS leg.; stn C1; van Veen grab; NTNU-VM 84101.

**Other material examined**

NORWAY – **Møre og Romsdal** • 1 spec.; Kinn, Brunsvik; 61°54.238′ N, 5°17.256′ E; depth 389 m; 14 Dec. 2020; Åkerblå AS leg.; stn BRU-6.1; van Veen Grab; NTNU-VM 84112 • 3 specs; Hareid, Uravika; 62°24.006′ N, 6°1.933′ E; depth 435 m; 23 Oct. 2021; Åkerblå AS leg.; stn URA-4; van Veen grab; NTNU-VM 84108 • 2 specs; Tingvoll, Halsbukta; 63°4.952′ N, 8°8.815′ E; depth 343 m; 4 Mar. 2021; Åkerblå AS leg; stn HAL-3.2; van Veen grab; NTNU-VM 84106 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 85854 • 1 spec.; Rauma, Skarbukta; 62°35.870′ N, 7°22.444′ E; depth 414 m; 28 Oct. 2021; Åkerblå AS leg.; stn SKA-4; van Veen grab; NTNU-VM 84109 • 1 spec.; Hareid, Uravika; 62°23.610′ N, 6°2.911′ E; depth 446 m; 23 Oct. 2021; Åkerblå AS leg.; stn URA-6; van Veen grab; NTNU-VM 84113. – **Vestland** • 1 spec.; Masfjorden, Laberget; 60°44.922′ N, 5°17.400′ E; depth 450 m; 13 May 2019; Rådgivende Biologer AS leg.; stn C2B; van Veen grab; NTNU-VM 84099 • 2 specs; same data as for preceding; NTNU-VM 84100 • 1 spec.; Øygarden, Sund; 60°11.061′ N, 5°11.737′ E; depth 665 m; 26 Apr. 2017; Bergen University Museum leg.; stn KB-03; van Veen grab; ZMBN 152607 • 1 spec.; Kvinnherad Hondskår; 60°6.282′ N, 5°56.262′ E; depth 378 m; 3 May 2018; Rådgivende Biologer AS leg.; stn C3B; van Veen grab; NTNU-VM 84103 • 2 specs; same data as for preceding; NTNU-VM 84104 • 4 specs; Masfjorden, Laberget; 60°44.922′ N, 5°17.400′ E; depth 450 m; 13.05.2019; Rådgivende Biologer AS leg.; stn C2B; van Veen grab; NTNU-VM 84102 • 2 specs; Hyllestad Sognefjorden; 61°3.0072′ N, 5°24.034′ E; depth 1236 m; 3 May 2017; Bergen University Museum leg.; stn KB2017-05-02; van Veen grab; ZMBN 152609 • 3 specs; Øygarden, Sund; 60°11.061′ N, 5°11.737′ E; depth 665 m; 26 Apr. 2017; Bergen University Museum leg.; kb-03; van Veen grab; ZMBN 152611.

**Examined material with sequence data**

NORWAY – **Vestland** • 1 spec.; Øygarden, Sund; 60°11.061′ N, 5°11.737′ E; depth 665 m; 26 Apr. 2017; Bergen University Museum leg.; stn KB-02; van Veen grab; ZMBN 152612 • 1 spec.; Lustrafjorden; 61°22.136′ N, 7°23.070′ E; depth 374 m; 5 May 2017; Bergen University Museum leg.; stn kb2017-05-25AG; van Veen grab; ZMBN 152608 • 1 spec.; Bømlo; 59°34.331′ N, 5°13.813′ E; depth 340 m; 28 Apr. 2017; Bergen University Museum leg.; stn KB-22; van Veen grab; SEM stub; ZMBN 152647 • 1 spec.; Hyllestad Sognefjorden; 61°3.0072′ N, 5°24.034′ E; depth 1236 m; 3 May 2017; Bergen University Museum leg.; stn KB2017-05-02; van Veen grab; ZMBN 152613 • 1 spec.; Hyllestad, Åfjorden; 61°12.784′ N, 5°2.285′ E; depth 379 m; 14 Jul. 2015; Bergen University Museum leg.; stn HM2015-07-15GR; van Veen grab; ZMBN 117450 • 1 spec.; Øygarden, Sund; 60°11.061′ N, 5°11.737′ E; depth 665 m; 26 Apr. 2017; Bergen University Museum leg.; kb-03; van Veen grab; ZMBN 152606 • 1 spec.; Austevoll, Bakkasund; 60°9.105′ N, 5°5.913′ E; depth 616 m; 26 Apr. 2017; Bergen University Museum leg.; stn KB-06; van Veen grab; ZMBN 152610 • 1 spec.; Bømlo; 59°34.037′ N, 5°12.941′ E; depth 328 m; 28 Apr. 2017; Bergen University Museum leg.; stn KB-20; van Veen grab; ZMBN 152605.

**Description** (adults)

Holotype (NTNU-VM 84107), anterior fragment, 8 mm long, 0.3 mm wide, with 40 chaetigers (Fig. 12). Paratypes and other anterior fragments of specimens with fewer segments, some lost branchiae and lamellae during fixation and handling. Color in alcohol pale white. Prostomium triangular, anteriorly truncate, posteriorly extending to end of chaetiger 1 as short, thick caruncle (Figs 12, 13A). Nuchal organs U-shaped ciliary bands lateral to caruncle. Two pairs of small eyes arranged trapezoidally (Fig. 12). Eyespots faint or become invisible after fixation in formalin; bright red spots when preserved directly in ethanol. Peristomium fused with notopodial lamellae of chaetiger 1, enclosing prostomium laterally. Palps missing in all specimens.

Branchiae from chaetiger 2 to chaetigers 9–13 (on chaetigers 2–11 in holotype), cirriform, apinnate, with lateral ciliation. First pair of branchiae usually longest, about 2.5–3 × as long as length of the notopodial postchaetal lamellae; branchiae gradually diminishing in size on following chaetigers (Figs 13A–B, 14B–H). Branchiae of chaetigers 3–6 slightly longer than notopodial postchaetal lamellae, twice as long as notopodial postchaetal lamellae by chaetiger 10. Nototrochs transverse ciliary bands between branchial bases. Dorsolateral longitudinal ciliation absent.

Notopodial prechaetal lamellae small, rounded in anterior chaetigers. Notopodial postchaetal lamellae of chaetiger 1 broadly rounded, fused with peristomium; lamellae subtriangular on chaetigers 2–9, largest, often with slender tips on chaetigers 3–5. Lamellae decreasing in size and becoming rounder on chaetigers 10–12 (Fig. 14A–I). On chaetigers 12–16, notopodial postchaetal lamellae extending middorsally and joining in the middle forming low crests. Neuropodial prechaetal lamellae inconspicuous. Interneuropodial pouches absent. Neuropodial postchaetal lamellae of chaetiger 1 small, oblong (Fig. 14A); lamellae of chaetiger 2 large and trapezoidal with rounded edges, not elongated

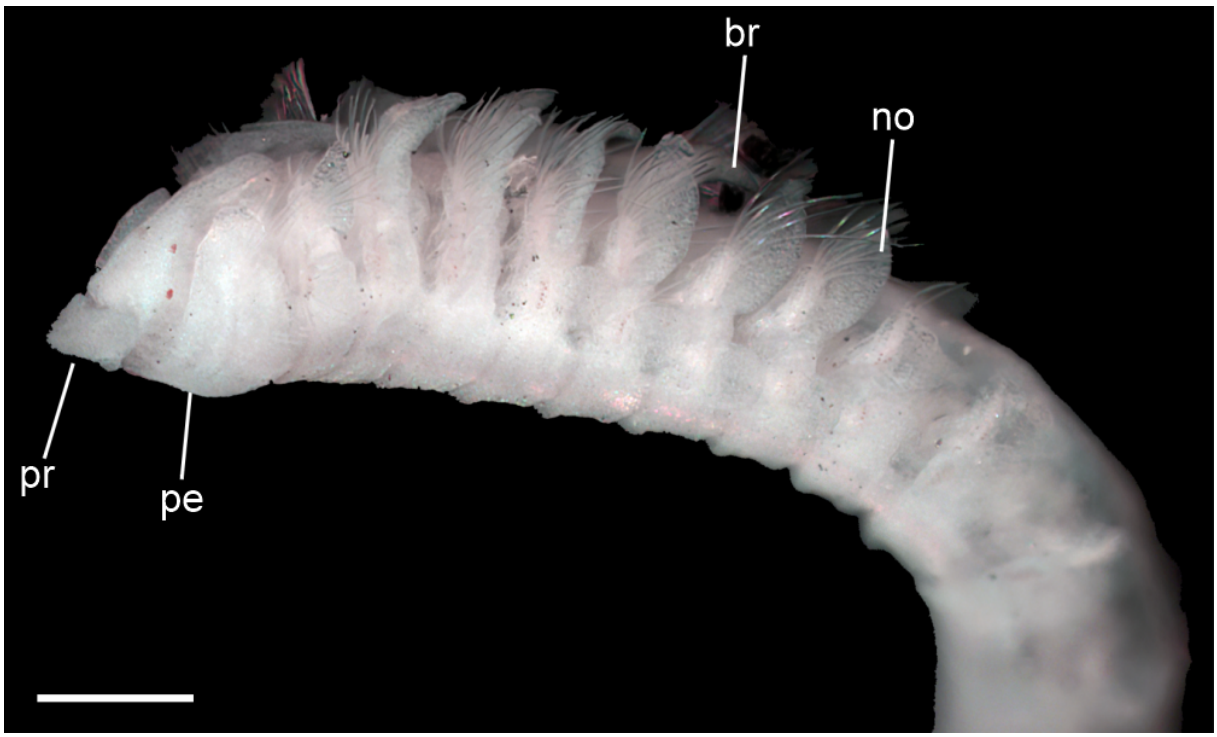


**Fig. 12.** Holotype of *Prionospio fiordica* sp. nov. (NTNU-VM 84107). Lateral view of anterior end. Abbreviations: see Material and methods. Scale bar = 200 μm.

ventrally (Fig. 14B), subrectangular on chaetigers 3 and 4 (Fig. 14C–D), from chaetiger 5 evenly rounded (Fig. 14E–I), from chaetiger 13 low and oval.

Notopodial capillaries on anterior and middle chaetigers arranged in two rows, unilimbate and granulated. Neuropodial capillaries arranged in two rows in anterior chaetigers, unilimbate and granulated; anterior row shorter than posterior row in both rami. Chaetae on posterior chaetigers not observed. Sabre chaetae in neuropodia from chaetigers 16–17 (chaetiger 17 in holotype), up to two per fascicle, with granulation on distal part of shaft (Fig. 14K). Hooded hooks in notopodia present only in holotype, from chaetiger 34 onwards (other specimens are shorter anterior fragments). Hooded hooks first appearing in neuropodia from chaetigers 17–18 (chaetiger 18 in holotype), alternating with capillary chaetae. Neuropodial hooded hooks usually appear in next chaetiger after the first sabre chaetae, up to eight in series. Both noto- and neuropodial hooks with 4–5 pairs of small upper teeth arranged in two vertical rows above main fang (Fig. 14J), with outer and a small inner hoods.

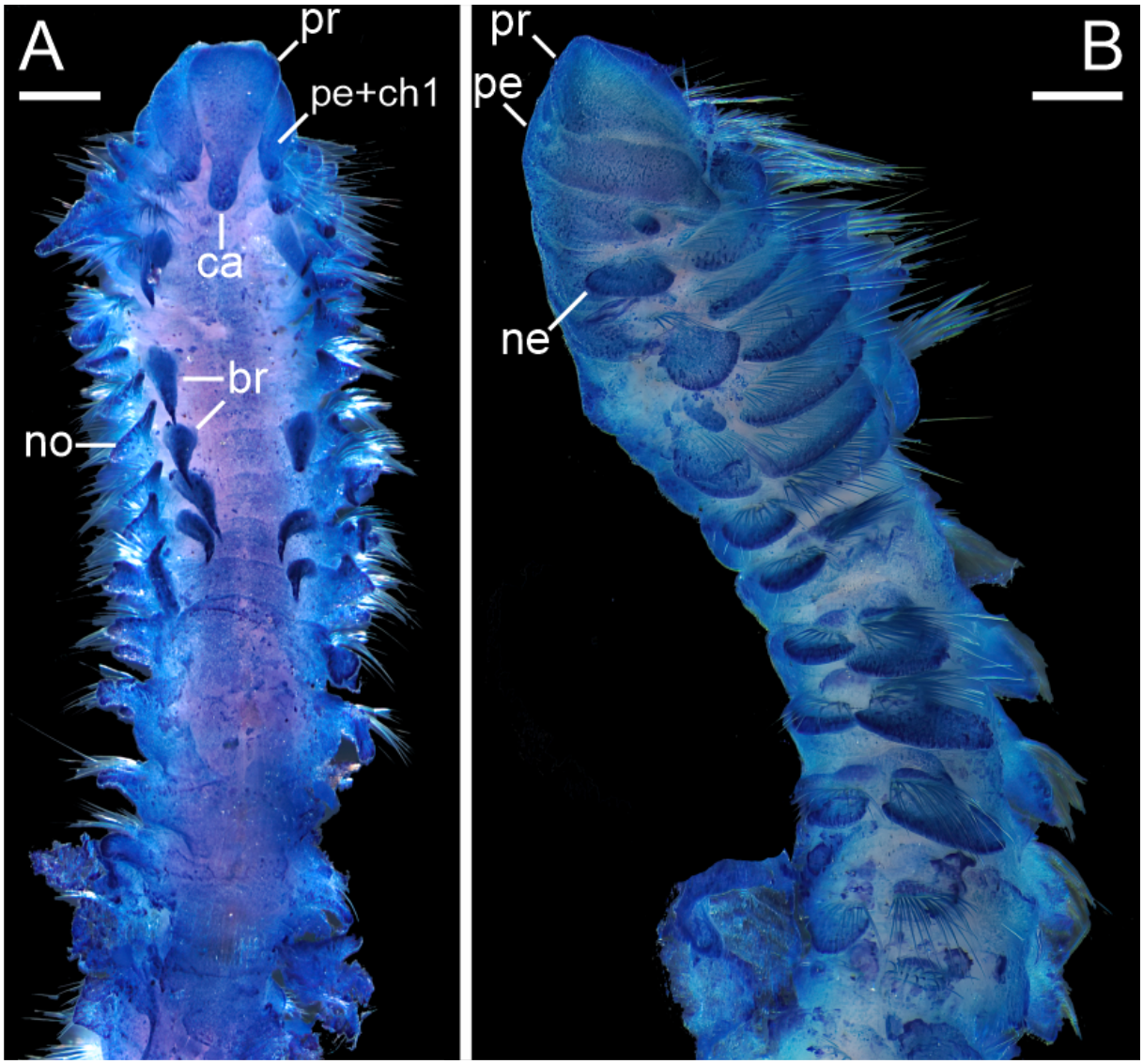


**Fig. 13.** Adult morphology of *Prionospio fiordica* sp. nov. Anterior ends stained with methylene green. **A**. Paratype (NTNU-VM 84110 ), dorsal view. **B**. Paratype (NTNU-VM 84114), left lateral view. Abbreviations: see Material and methods. Scale bars = 200 µm.

Pygidium missing in all specimens.

**Remarks**

Fixed specimens of *Prionospio fiordica* sp. nov. are fragile, making detailed study challenging. All specimens were anterior fragments, often damaged, lacking notopodial postchaetal lamellae and branchiae. Only the holotype had more than 30 chaetigers and was the only specimen with hooded hooks in notopodia. The species was sequenced by Hektoen *et al.* (2024) and was found to be genetically different from all other species studied.

*Prionospio fiordica* sp. nov. can be distinguished from *P. multibranchiata* (based on the redescription by Delgado-Blas *et al.* 2018) primarily by the dorsal crests (present in *P. fiordica* sp. nov. and absent in *P. multibranchiata*). Other differences include the shape of the eyes (small and represented by single eyespots in the former and large and conspicuous in the latter). It can be distinguished from *P. maciolekae* (based on the description by Dagli & Çinar, 2011) by the shape of prostomium (triangular, anteriorly truncate in *P. fiordica* and subrectangular, anteriorly rounded in *P. maciolekae*), the shape of the neuropodial postchaetal lamellae of chaetiger 3 (broadly rounded in the former and narrowly rounded, becoming finger-like in the latter).

*Prionospio fiordica* sp. nov. can be distinguished from *P. sanmartini* primarily by the shape of prostomium (triangular and truncate anteriorly with a short thick caruncle in the former, and anteriorly

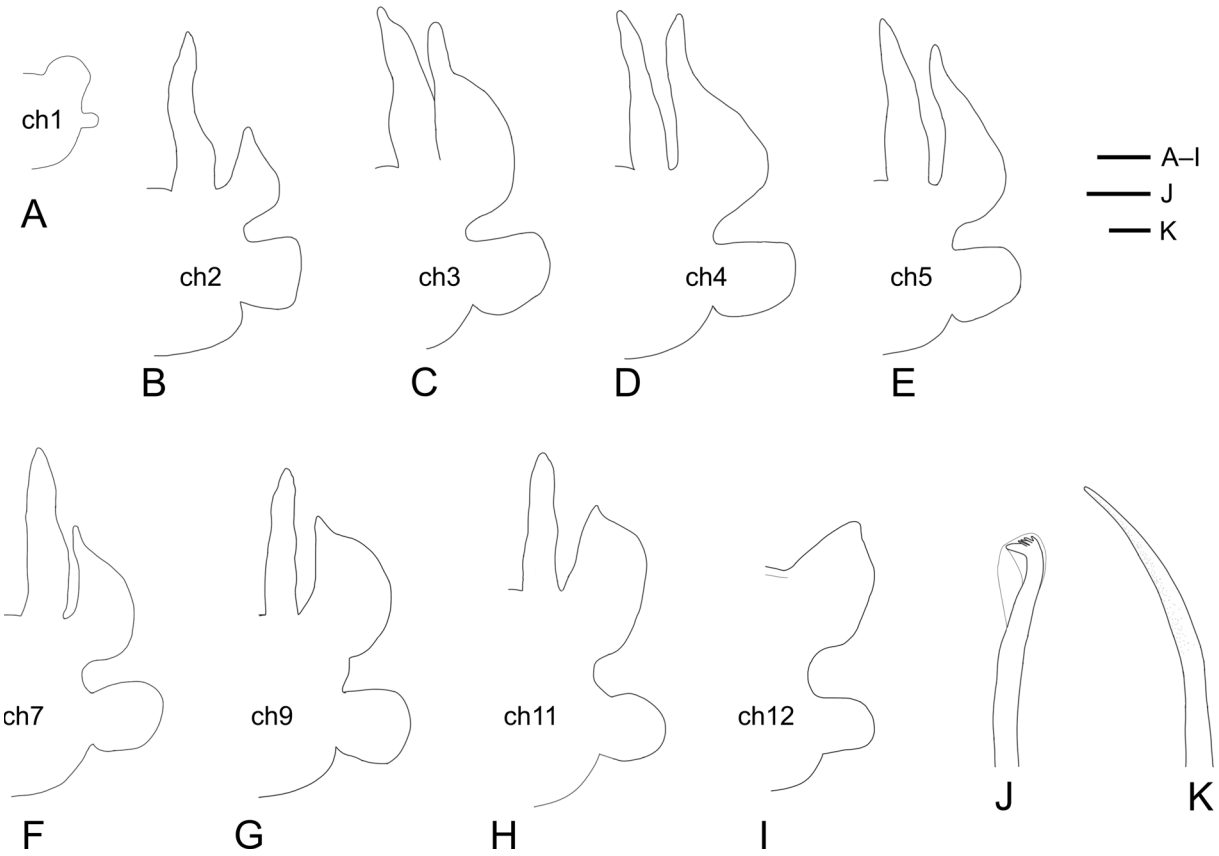


**Fig. 14.** Morphology of parapodia and chaetae of *Prionospio fiordica* sp. nov. (ZMBN 152606). **A–I**. Chaetigers 1–5, 7, 9, 11, 12. **J**. Hooded hook from neuropodium of chaetiger 15. **K**. Sabre chaeta from neuropodium of chaetiger 20. Abbreviations: see Material and methods. Scale bars: A–I = 100 µm; J–K = 10 µm.

rounded, widest just before the lateral eyes, with a narrow caruncle in the latter), and the shape of the peristomium (more developed in *P. fiordica*). Other differences include the shape of eyes (always indistinct small single spots in the former, and larger in the latter), and sabre chaetae and hooded hooks in neuropodia, generally starting later in *P. fiordica* (from chaetigers 16–17 and 17–18, respectively) than in *P. sanmartini* (from chaetigers 12–17 and 13–18).

*Prionospio fiordica* sp. nov. was referred in the molecular study by Hektoen *et. al.* (2024) as *Prionospio* sp. 3. The species is genetically distinct from multibranchiate *Prionospio* from Skagerrak and southern Europe (*Prionospio* cf. *sanmartini* in Hektoen *et al.* 2024, assigned here to *P. sanmartini*), and from the Eastern and Western Pacific (referred in Hektoen *et al.* 2024 as *P. multibranchiata*). Based on the current data, there seems to be a geographic and bathymetric separation between *P. fiordica* and *P. sanmartini*, where *P. sanmartini* has not yet been recorded from Western Norway, and not deeper than 118 m, while *P. fiordica* has exclusively been found in fjords and offshore western Norway deeper than 328 m.

**Habitats and distribution**

Adults of *P. fiordica* sp. nov. were collected from the northern part of the North Sea and southern part of the Norwegian Sea, both offshore and in fjords in Vestland and Møre og Romsdal counties of Norway. They were found in fine silt and muddy sediments at depts of 328–1236 m. The conspecificity of individuals from such a wide bathymetric range was confirmed with molecular analysis by Hektoen *et al.* (2024).

### ***Prionospio plumosa*** M. Sars in G.O. Sars, 1872
Figs 15–17

*Prionospio plumosus* M. Sars in G.O. Sars, 1872: 410–411.
*Prionospio* (*Prionospio*) *tripinnata* Maciolek, 1985: 343–345, fig. 6. **Syn. nov.**

*Prionospio plumosus* – Sars 1873: 263–268, figs 13–29. — Bidenkap 1894: 94.
*Prionospio steenstrupi* – Bidenkap 1894: 93.
*Prionospio plumosa* – Söderström 1920: 233–234, fig. 141. — Kirkegaard 1996: 86, fig. 39. — Hektoen *et al.* 2024: figs 1, 4.
*Prionospio* (*Prionospio*) *plumosa* – Hartmann-Schröder 1996: 326–327.
*Prionospio* sp. – Gaudron *et al.* 2010: 5 (genetic data). — Rubin-Blum *et al.* 2014 (genetic data).

**Diagnosis**

Prostomium triangular, anteriorly truncate, posteriorly extending to end of chaetiger 1 as a short caruncle. Eyes absent in adults. Four pairs of branchiae on chaetigers 2–5; those of chaetigers 2, 3 and 5 with digitiform pinnules, branchiae of chaetiger 4 apinnate. Branchiae of chaetigers 2 and 5 long, with naked distal tips, on chaetigers 3 and 4 short and stout. Neuropodial postchaetal lamellae of chaetiger 2 not elongated ventrally. Dorsal crests from chaetiger 6 or 7. Sabre chaetae in neuropodia from chaetigers 10–12, with heavily granulated distal part. Hooded hooks in notopodia from chaetigers 26–43, in neuropodia from chaetigers 12–14.

**Type material of *Prionospio plumosa***

**Neotype** (designated here)
NORWAY • Filtvedt, Brændtangen, Drøbaksundet; 18 Aug. 1910; Hvitfisken Kristianiafjorden leg.; van Veen grab; NHMO C7075.

**Type material of *Prionospio tripinnata***

**Holotype**

LIBYA • 33°57.000′ N, 15°8.202′ E; depth 500–509 m; 2 Sep. 1970; Atlantis II R/V 59 leg.; stn 211; USNM 67678.

**Other material examined**

SWEDEN – **Bohuslän** • 5 specs; Väderön; depth 109 m; 29 Jun. 1869; stn VädOls6; SMNH 120288.

NORWAY – **Rogaland** • 1 spec.; Sauda; depth 38 m; 6 May 1981; stn7; NTNU-VM 25670 • 10 specs; Bokn, Lådeskjera; 59°11.893′ N, 5°28.880′ E; depth 102 m; 4 Apr. 2021; Åkerblå AS leg.; stn LÅD-1; van Veen grab; NTNU-VM 84075. – **Vestland** • 2 specs.; Ullensvang, Hessvik; 0°07.754′ N, 6°09.062′ E; depth 66 m; 1 Jul. 2010; SAM leg.; stn HES 1-1; van Veen grab; SMNH 129904 • 1 spec.; Bergen, Lyreneset; 60°23.692′ N, 5°16.214′ E; depth 34 m; 6 Jun. 1999; SAM leg.; stn Lyr2-1, van Veen grab; SMNH 129905 • 20 specs; Gulen, Hardbakkeneset; 61°01.003′ N, 4°57.039′ E; depth 80 m; 19 Sep. 2019; Åkerblå AS leg.; stn HAR-1; van Veen grab; NTNU-VM 84082 • 15 specs; Fjaler, Hegnes; 61°21.470′ N, 5°17.110′ E; depth 244 m; 4 Dec. 2019; Åkerblå AS leg.; stn HEG-1; van Veen grab; NTNU-VM 84079 • 2 specs; Flora, Vågsøya; 61°29.177′ N, 5°01.489′ E; depth 71 m; 31 Oct. 2019; Åkerblå AS leg.; stn VÅG-1; van Veen grab; NTNU-VM 84080 • 30 specs; Bremanger Gulestø; 61°45.515′ N, 5°04.437′ E; depth 145 m; 8 Oct. 2019; Åkerblå AS leg.; stn GUL-1; van Veen grab; NTNU-VM 84078 • 2 specs; same data as for preceding; SEM stub; NTNU-VM 85856 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 85855 • 2 specs; Selje, Beitveit; 62°08.325′ N, 5°19.764′ E; depth 117 m; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-1; van Veen grab; NTNU-VM 84091 • 20 specs; Alver, Jibbersholman; 60°45.052′ N, 4°53.330′ E; depth 80 m; 18 Dec. 2019; Åkerblå AS leg; stn JIB-4; van Veen grab; NTNU-VM 84076 • 5 specs; Gulen, Lyngholmen; 61°00.924′ N, 5°00.550′ E; depth 112 m; 20 Apr. 2021; Åkerblå AS leg.; stn LYN-1; van Veen grab; NTNU-VM 84084 • 10 specs; Fjaler, Kyravika; 61°19.115′ N, 5°09.559′ E; depth 400 m; 14 Dec. 2021; Åkerblå AS leg.; stn KYR-1; van Veen grab; NTNU-VM 84081 • 20 specs; Bremanger, Juvika B; 61°53.805′ N, 5°38.062′ E; depth 186 m; 9 Dec. 2021; Åkerblå AS leg.; stn JUV-1; van Veen grab; NTNU-VM 84088 • 2 specs; Bergen, Brettesnes; depth 36–55 m; M. Sars leg.; van Veen grab; NHMO C7022. – **Møre og Romsdal** • 25 specs; Stranda, Opshaugvik; 62°17.350′ N, 6°59.630′ E; depth 376 m; 31 Mar. 2020; Åkerblå AS leg.; stn OPS-3; van Veen grab; NTNU-VM 84093 • 17 specs; Fræna, Storvika; 62°48.113′ N, 6°58.539′ E; depth 182 m; 24 Sep. 2019; Åkerblå AS leg.; stn STO-1; van Veen grab; NTNU-VM 84074 • 1 spec.; Gjemnes, Høybuvika; 62°57.443′ N, 8°03.334′ E; depth 285 m; 14 Dec. 2021; Åkerblå AS leg.; stn HØY-3; van Veen grab; NTNU-VM 84077 • 20 specs; Høybuvika; 62°57.545′ N, 8°03.082′ E; depth 281 m; 14 Dec. 2021; Åkerblå AS leg.; stn HØY-1; van Veen grab; NTNU-VM 84086 • 15+ specs; Ørsta, Sagelva; 62°20.277′ N, 6°23.084′ E; depth 186 m; 7 Oct. 2020; Åkerblå AS leg.; stn SAG-1; van Veen grab; NTNU-VM 84085 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 85857 • 1 spec.; same data as for preceding; SEM stub; NTNU-VM 85858 • 10 specs; Kristiansund, Endreset; 63°01.893′ N, 7°42.726′ E; depth 203 m; 10 Sep. 2019; Åkerblå AS leg.; stn END-4; van Veen grab; NTNU-VM 84087. – **Trøndelag** • 5+ specs; Heim, Vullum; 63°02.888′ N, 8°12.819′ E; depth 282 m; 3 Aug. 2021; Åkerblå AS leg.; stn VUL-1; van Veen grab; NTNU-VM 84090 • 13 specs; Fiborgtangen; 63.7165° N, 11.1457°; depth 30 m; 1983; stn 13; van Veen grab; NTNU-VM 25391 • 3 specs; same data as for preceding; NTNU-VM 25389 • 5 specs; same data as for preceding; NTNU-VM 25390 • 1 spec.; Ørland, Storforsna, Vågen; 63.6541° N, 9.4069° E; depth 80–120 m; 1951; E. Sivertsen leg.; NTNU-VM 25797. – **Troms** • 5 specs; Tromsø, Tromsø; depth 273 m; 30 Jun. 2010; van Veen grab; SMNH 129903.

**Examined material with sequence data**

NORWAY – **Vestland** • 1 spec.; Fjaler, Hegnes; 61°21.470′ N, 5°17.110′ E; depth 244 m; 4 Dec. 2019; Åkerblå AS leg.; stn HEG-1; van Veen grab; NTNU-VM 84089 • 1 spec.; Selje, Beitveit; 62°08.325′ N,

5°19.764′ E; depth 117 m; 10 Oct. 2019; Åkerblå AS leg.; stn BEI-1; van Veen grab; NTNU-VM 84092 • 1 spec.; Alver, Jibbersholman; 60°45.052′ N, 4°53.330′ E; depth 80 m; 18 Dec. 2019; Åkerblå AS leg.; stn JIB-4; van Veen grab; NTNU-VM 84094 • 1 spec.; Bergen, Flesland; 60°17.052′ N, 5°12.087′ E; depth 72 m; 2 Sep. 2014; Bergen University Museum leg.; stn HB2014.09.02-1; van Veen grab; ZMBN 152635. – **Nordland** • 1 spec.; Alstahaug, Skorpa; 66°01.900′ N, 12°28.864′ E; depth 107 m; 22 Nov. 2019; Åkerblå AS leg.; stn NSK-1; van Veen grab; NTNU-VM 84083.

**Description** (adults)

Neotype (NHMO C7075) anterior fragment, 18 mm long, 1.7 mm wide, with 30 chaetigers, too damaged for close morphological examination after chaetiger 20. Color in alcohol pale brown to white. Prostomium triangular, anteriorly truncate, posteriorly extending to end of chaetiger 1 as a short, narrow caruncle. Nuchal organs U-shaped ciliary bands lateral to caruncle (Fig. 15A). Neotype without eyes, some small specimens with faint lateral eyespots (NTNU-VM 84077, 84085; Fig. 15B–C). Posterior dorsolateral parts of peristomium fused with notopodial postchaetal lamellae of chaetiger 1, forming ear-shaped structures lateral to prostomium. Palps missing in all specimens.

Branchiae on chaetigers 2–5; those of chaetigers 2, 3 and 5 with digitiform pinnules on anterior sides; branchiae of chaetiger 4 apinnate. Branchiae of chaetigers 2 and 5 long, rounded in cross section, those of chaetigers 3 and 4 shorter, triangular in cross section (Fig. 15A) with dense lateral ciliation, distally flattened, foliaceous (Figs 15C–D, 16C–D). Branchiae of chaetiger 2 with apinnate basal part, densely pinnate on anterior side three-fourths up the branchiae, ending in apinnate tip (Fig. 16B). Branchiae of chaetiger 3 sparsely pinnate on anterior side halfway to two-thirds up branchiae (Fig. 16C). Branchiae of chaetiger 4 apinnate, with raised edge running up the branchia (Figs 15A, 16D); branchiae of chaetiger 5 densely pinnate on anterior side along almost entire length, with short slender apinnate tip (Fig. 16E). Nototrochs transverse ciliary bands between branchial bases on chaetigers 2–5. Dorsolateral longitudinal ciliation present between chaetigers 4–6.

Notopodial prechaetal lamellae small, rounded on anterior chaetigers, reduced in posterior chaetigers. Notopodial postchaetal lamellae of chaetiger 1 triangular (Figs 16A, 17A), fused with peristomium, on chaetigers 2–5 large and subtriangular, largest on chaetiger 3 (Figs 16B–E, 17A). Lamellae rapidly diminishing in size, lower and rounded in postbranchial chaetigers, assuming low oval shape from chaetigers 8–9 (Fig. 16F–H). Notopodial postchaetal lamellae joined across dorsum forming transverse crests from chaetiger 6 to chaetigers 10–15, crest highest on chaetiger 7 (Figs 15A, C–D, 16F–H). Crest not visible at all on chaetiger 6 in some smaller specimens. Neuropodial prechaetal lamellae inconspicuous. Neuropodial postchaetal lamellae of chaetiger 1 broadly rounded, about one third to half the size of lamellae on subsequent chaetigers (Figs 16A, 17A); lamellae of chaetiger 2 subrectangular, higher than broad with rounded edges (Figs 16B, 17A); lamellae of chaetiger 3 oval, broad (Figs 16C, 17A); lamellae of chaetiger 4 quadrangular with rounded edges (Figs 16D, 17A); lamellae of subsequent chaetigers rounded, low and oval by chaetiger 12 (Fig. 16E–H), reduced on succeeding chaetigers. Interneuropodial pouches absent.

Notopodial capillaries on anterior chaetigers arranged in numerous rows (7+), unilimbate and slightly granulated. Notopodial capillaries on middle chaetigers in two rows, unilimbate and slightly granulated. Neuropodial capillaries arranged in two rows in anterior chaetigers, unilimbate, granulated, anterior row shorter than posterior row. Posterior chaetae not observed in neotype, but notopodial capillaries in posterior chaetigers long, thin, alimbate and granulated in other specimens (NTNU-VM 85856). Sabre chaetae in neuropodia from chaetigers 10–12 (chaetiger 10 in neotype) with strong granulation on median and distal parts of shaft, up to 10 per fascicle in neotype, up to three in smaller specimens (Fig. 17B). Hooded hooks in notopodia not present in neotype, from chaetigers 26–47 in other specimens (NTNU-VM 84090), up to six per ramus. Hooded hooks in neuropodia from chaetiger 12–14 (14 in neotype), up

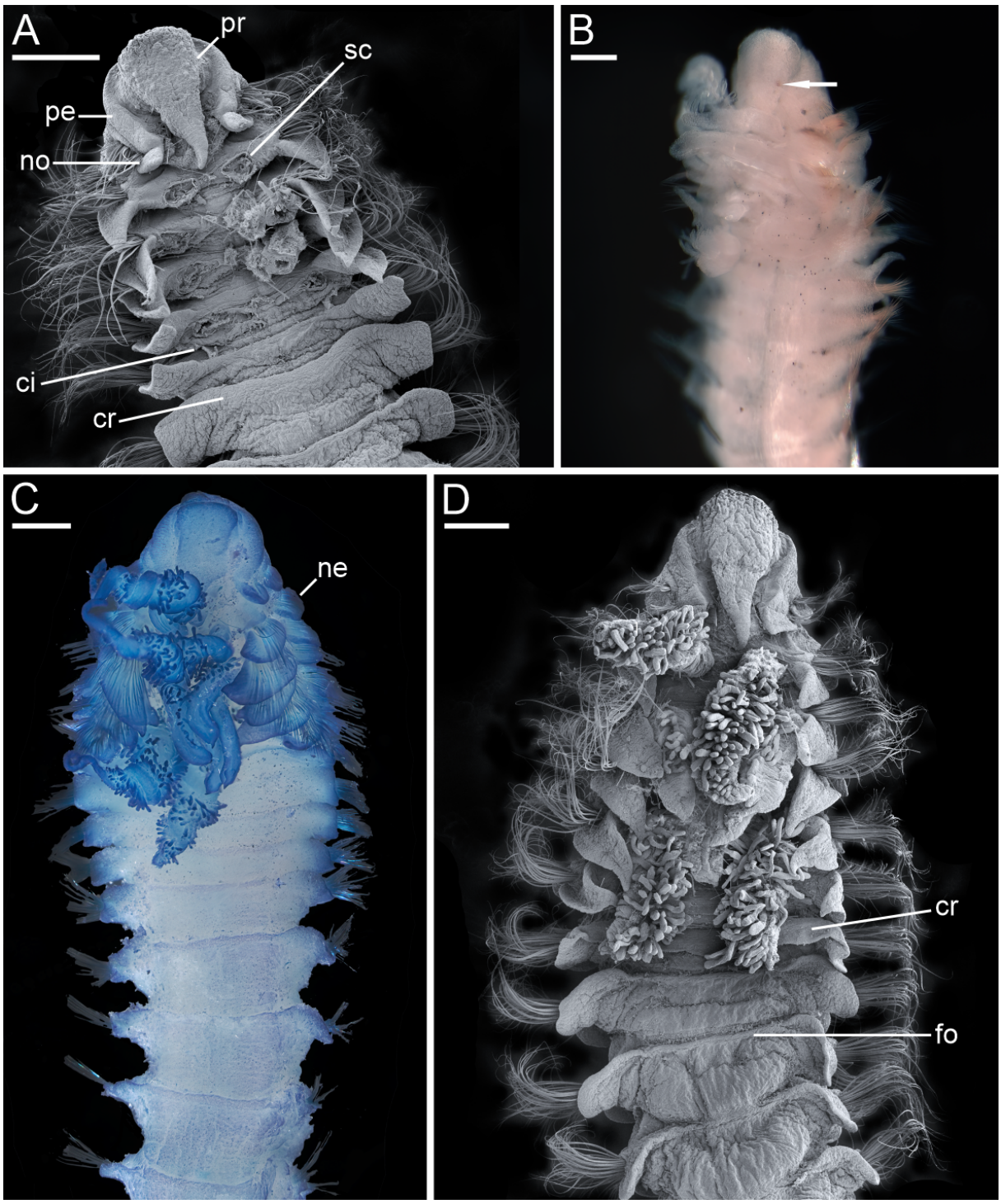


**Fig. 15.** Adult morphology of *Prionospio plumosa* M. Sars in G.O. Sars, 1872. **A, D**. SEM micrographs. **B–C**. Light microscope images. **A–D**. Anterior ends, dorsal view. **A**. NTNU-VM 85856. **B**. NTNU-VM 84085 (arrow pointing to small red eye). **C**. Neotype (NHMO C7075) stained with methylene green. **D**. NTNU-VM 84085. Abbreviations: see Material and method. Scale bars: A–B, D = 200 µm; C = 500 µm.

to eight per ramus. Both notopodial and neuropodial hooks with 3–4 pairs of upper teeth arranged in two vertical tows above main fang, with only outer hood, secondary inner hood absent (Fig. 17C).

Pygidium with one long middorsal cirrus and one pair of short ventral cirri (NTNU-VM 84084, 84086, 84093), missing in neotype.

**Remarks**

A brief original description of *Prionospio plumosus* by Michael Sars was published after his death (22 October 1869) by his son, a Norwegian marine and freshwater biologist and professional illustrator Georg Ossian Sars (1872). The original description was based on an unknown number of specimens from the Drøbak sound, southern Norway. Later, Sars (1873) provided a detailed description and illustrations of this species. The type material was likely originally stored in the Natural History Museum, Oslo, but was not located by us or the curator of the NHMO (Ann-Helén Rønning pers.

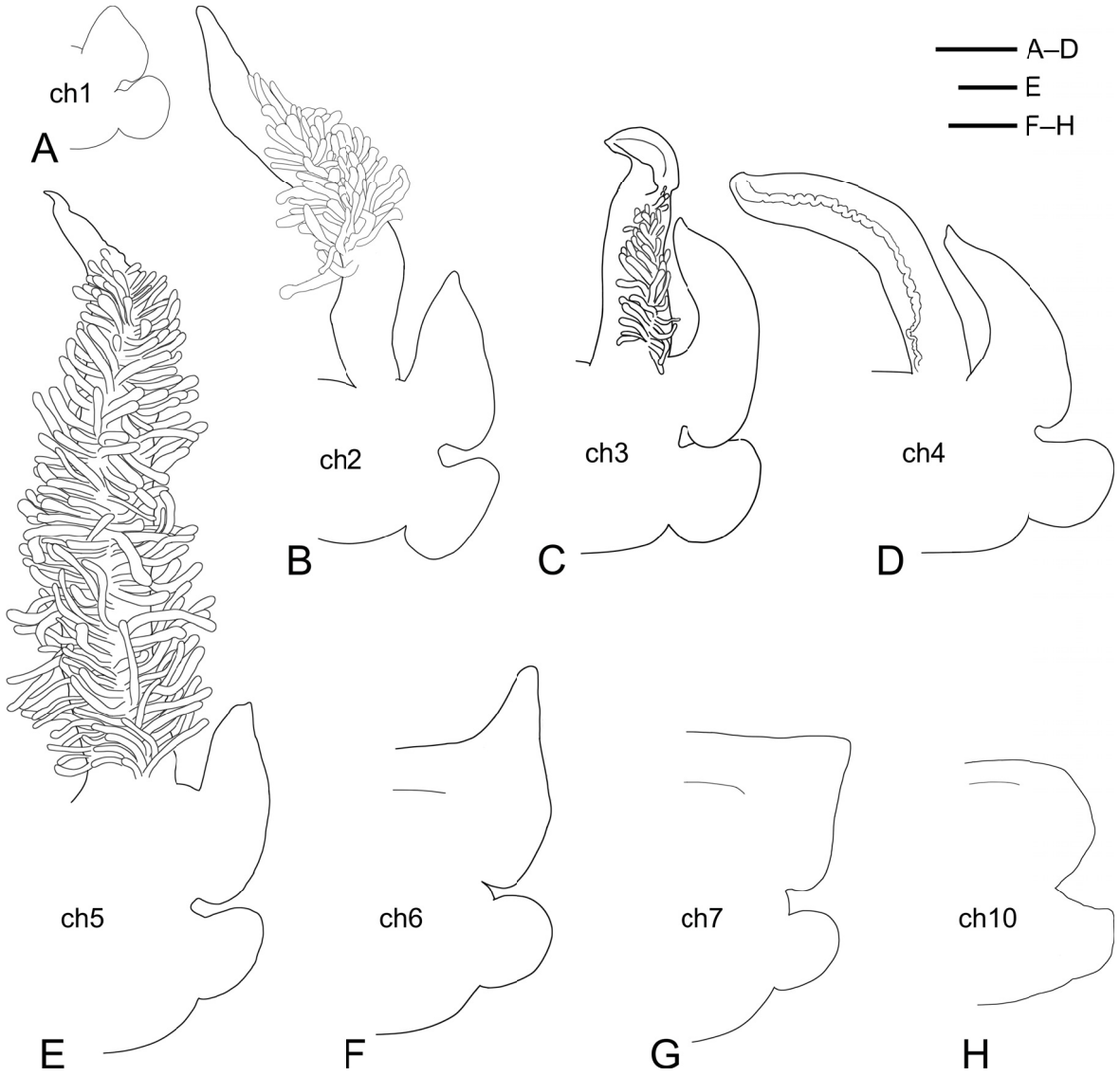


**Fig. 16.** Morphology of anteriorly facing parapodia of *Prionospio plumosa* M. Sars in G.O. Sars, 1872 (NTNU-VM 84088). **A–G**. Chaetigers 1–7. **H**. Chaetiger 10. Abbreviations: see Material and methods. Scale bars = 200 µm.

comm.). Sigvaldadóttir (1998) listed the type material of *P. plumosa* as deposited in the polychaete collection of the Smithsonian Institution, Washington D.C. (USNM 32698). However, neither the authors or curators were able to locate this material in the museum and the noted catalogue number is currently assigned to the holotype of *Prionospio ornata* Berkeley & Berkeley, 1961 from Peru (http://n2t.net/ark:/65665/308a8bc18-4af6-4154-8d3b-e822fb633267). Therefore, we consider the types of *P. plumosa* to be lost. To ensure nomenclatural stability, we designate here a neotype (NHMO C7075). The specimen was collected in 1910 between Filtvet and Brenntangen in the Oslofjord, which is a narrow stretch of approximately 1.5 km long and depth up to 200 m. No further information is given on the label. The noted location is about 10 km south of the original type locality at Drøbak (Sars 1872; Oug *et al.* 2014). *Prionospio plumosa* is rare, if still occurring, in the Oslofjord. The species has not been reported in the region in over a century, despite targeted sampling of Sars' type localities in the past decade (Oug *et al.* 2015).

*Prionospio tripinnata* Maciolek, 1985 was described based on a single specimen from a depth of 500 m in the Mediterranean Sea (Maciolek 1985). The species was differentiated from *P. plumosa* by the branchiae of chaetigers 3 and 4 being shorter and stouter than those on chaetigers 2 and 5, and the branchiae of chaetiger 3 having only a basal patch of pinnules instead of having pinnules along ⅔ of the length. Sars (1873) noted regarding the length of the branchiae that "3$^{die}$ og 2$^{det}$ Par omtrent ligestore og kun halvt saa lange som første og sidste Par" (the 3$^{rd}$ and 2$^{nd}$ pairs are approximately equal in size, and ½ as long as the first and last pairs). This is also apparent in the provided illustrations (Sars 1873: pl. xvii figs 13–14). Regarding the differences in the distribution of the pinnules on the branchiae of chaetiger 3, it can be considered due to worms studied being of different sizes. Sars (1873) described a specimen that was 30 mm long and 1.5 mm wide, while the only specimen of *P. tripinnata* was 12 mm long and 0.75 mm wide. Upon examination of the holotype of *P. tripinnata*, we found it similar to smaller specimens of *P. plumosa* from Norway and Sweden. *Prionospio tripinnata* is accordingly considered

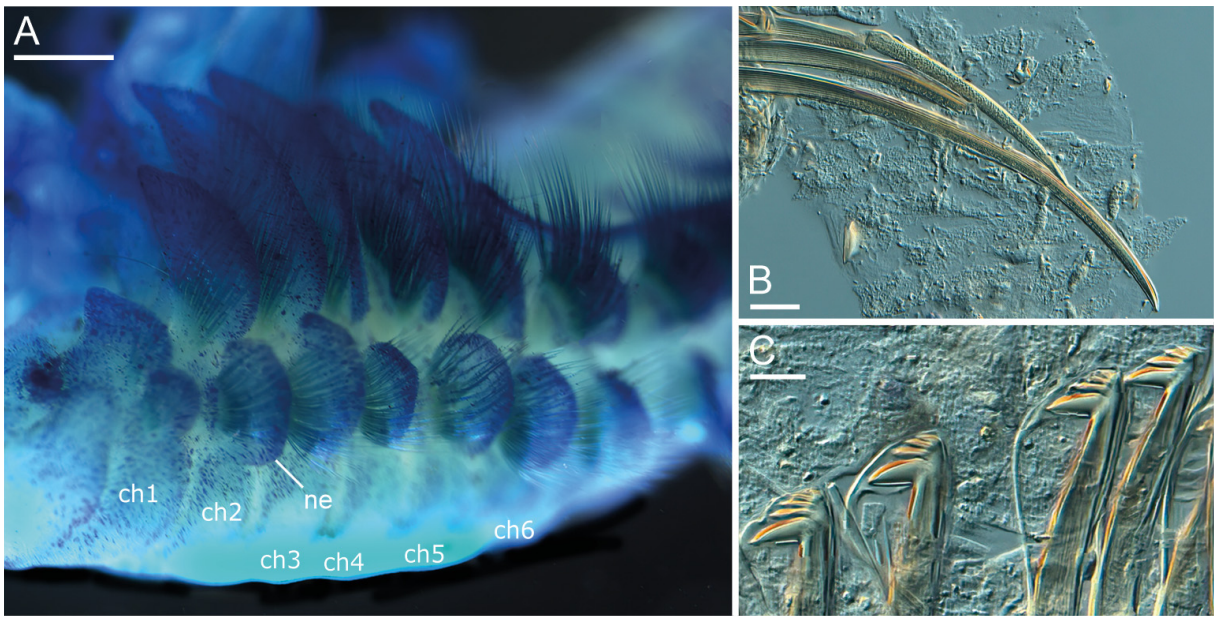


**Fig. 17.** Adult and chaetal morphology of *Prionospio plumosa* M. Sars in G.O. Sars, 1872, neoptype (NHMO C7075). **A**. Anterior end stained with methylene green, left lateral view. **B**. Sabre chaetae from neuropodium of chaetiger 30. **C**. Hooded hooks from neuropodium of chaetiger 30. Abbreviations: see Material and methods. Scale bars: A = 50 µm; B = 10 µm; C = 5 µm.

a junior synonym of *P. plumosa*. The molecular analysis by Hektoen *et. al.* (2024) also indicated that *P. plumosa* is present in deep waters in the Eastern Mediterranean.

*Prionospio plumosa* can be distinguished from all other *Prionospio* by the presence of digitiform pinnules on the branchiae of chaetigers 2, 3 and 5. To our knowledge, it is the only species, together with *Prionospio kirrae* Wilson, 1990, with pinnules covering the anterior side of the branchiae (the branchiae of chaetiger 5 in *P. kirrae*) rather than the posterior and/or lateral sides. Dorsal crests in the examined specimens of *P. plumosa* were present from either chaetiger 6 or 7. The worms sequenced by Hektoen *et al.* (2024) included specimens with dorsal crests both from chaetiger 6 and 7, indicating that the absence of crest on chaetiger 6 is either intraspecific variation or a preservation artifact.

*Prionospio plumosa* has been noted as rare in taxonomic literature (Sars 1872; Bidenkap 1894; Söderström 1920; Kirkegaard 1996), with sparse records in the 20th century. However, in the last decade, *P. plumosa* has been frequently reported in ecological surveys near aquaculture sites in Norway. The species was originally described from dead algal fragments (Sars 1873), indicating that the type locality was an area where organic matter accumulated, perhaps mirroring conditions close to modern day finfish farms. Through the examination of unidentified material in various museum collections, additional specimens collected in the 20th century were discovered, amending the spotty records, including the 1910 neotype (NHMO C7075) and specimens from the Trondheimsfjord (Norway) collected in 1951 (NTNU-VM 25797) and the 1980s (NTNU-VM 25389–25391).

**Habitats and distribution**

*Prionospio plumosa* is common along the Norwegian coast, most often in muddy and silty sediments affected by high organic load at depths of 34–500 m. It has also been recorded from the Mediterranean Sea at depths of 500–1000 m.

***Prionospio sigvaldadottirae*** sp. nov.
urn:lsid:zoobank.org:act:72F6B797-4133-4B15-937A-C30AF6215151
Figs 18–20; Table 2

*Prionospio* sp. 7 – Hektoen *et al.* 2024: figs 1, 4.

**Diagnosis**

Prostomium anteriorly truncate, posteriorly extending to end of chaetiger 2 as a narrow caruncle. Four pairs of branchiae on chaetigers 2–5; those on chaetiger 2 long, with lateral pinnules, on chaetiger 5 long or shorter, with lateral pinnules, on chaetigers 3 and 4 shorter, apinnate. Dorsal crests from chaetiger 7 to chaetigers 20–22, highest on chaetiger 7. Neuropodial postchaetal lamellae of chaetiger 2 pointed and elongated ventrally. Sabre chaetiger in neuropodia from chaetiger 10. Hooded hooks in notopodia from chaetigers 43–58, in neuropodia from chaetigers 15–17.

**Etymology**

The species is named in honor of Dr Elin Sigvaldadóttir, an Icelandic zoologist who made a great contribution to the study of the Northeastern Atlantic *Prionospio*.

**Type material**

**Holotype**

NORWAY • Norwegian Sea, Vigdis D oil field; 61°21.000′ N 2°4.200′ E; depth 246 m; Aug.–Sep. 2020; STIM AS leg.; stn VTD-10; van Veen grab; NTNU-VM 84143.

**Paratypes**

NORWAY • 6 specs; Norwegian Sea, Vigdis D oil field; 61°22.009′ N, 2°2.079′ E; depth 246 m; 31 May 2014; STIM AS leg.; stn VTD-R; van Veen grab; NTNU-VM 84145 • 2 specs; Norwegian Sea, Vigdis D oil field; 61°21.000′ N, 2°4.200′ E; depth 246 m; Aug.–Sep. 2020; STIM AS leg.; stn VTD-10; van Veen grab; NTNU-VM 84144 • 6 specs; Norwegian Sea, Vigdis D oil field; 61°20.923′ N, 2°4.176′ E; depth 248 m; Aug.–Sep. 2020; STIM AS leg.; stn VTD-12; van Veen grab; NTNU-VM 84146 • 1 spec.; Vigdis D oil field; 61°20.923′ N, 2°4.176′ E; depth 248 m; Aug.–Sep. 2020; STIM AS leg.; stn VTD-12; van Veen grab; SEM stub; NTNU-VM 85860.

**Other material examined**

NORWAY – **Norwegian Sea** • 1 spec.; Vigdis D oil field; 61°20.923′ N, 2°4.176′ E; depth 250 m; 31 May 2014; STIM AS leg.; stn VTD12_14; van Veen grab; ZMBN 105363 • 1 spec.; Vigdis D oil field; 61°21.000′ N, 2°4.200′ E; depth 246 m; Aug.–Sep. 2020; STIM AS leg.; stn VTD-10; van Veen grab; SEM stub; NTNU-VM 85859.– **North Sea** • 1 spec.; Oseberg oil field; 60°27′ N, 2°43′ E; depth 104 m; 14 Apr. 1983; stn A10.5; van Veen grab; NTNU-VM 25276 • 1 spec.; Oseberg oil field; 60°27′ N, 2°43′ E; depth 104 m; 5 Jul 1983; stn b7.4; van Veen grab; NTNU-VM 25285 • 1 spec.; Oseberg oil field; 60°27′ N, 2°43′ E; depth 104 m; 5 Jul. 983; stn b5.7; van Veen grab; NTNU-VM 25287 • 1 spec.; Oseberg oil field; 60°27′ N, 2°43′ E; depth 104 m; 5 Jul. 1983; stn b1.gr1; van Veen grab; NTNU-VM 25286 • 1 spec.; Oseberg oil field; 23 Feb. 1984; van Veen grab; NTNU-VM 25275 • 1 spec.; Oseberg oil field; 17 Feb. 1984; van Veen grab; NTNU-VM 25217.

**Examined material with sequence data**

NORWAY – **Norwegian Sea** • 1 spec.; Vigdis D oil field; 61°20.923′ N, 2°4.176′ E; depth 250 m; 31 May 2014; STIM AS leg.; stn VTD12_14; van Veen grab; ZMBN 152646.


**Fig 18.** *Prionospio sigvaldadottirae* sp. nov., holotype (NTNU-VM 84143), lateral view of anterior end, black spots are sediment rests stuck to the animal. Abbreviations: see Material and methods. Scale bar = 200 μm.

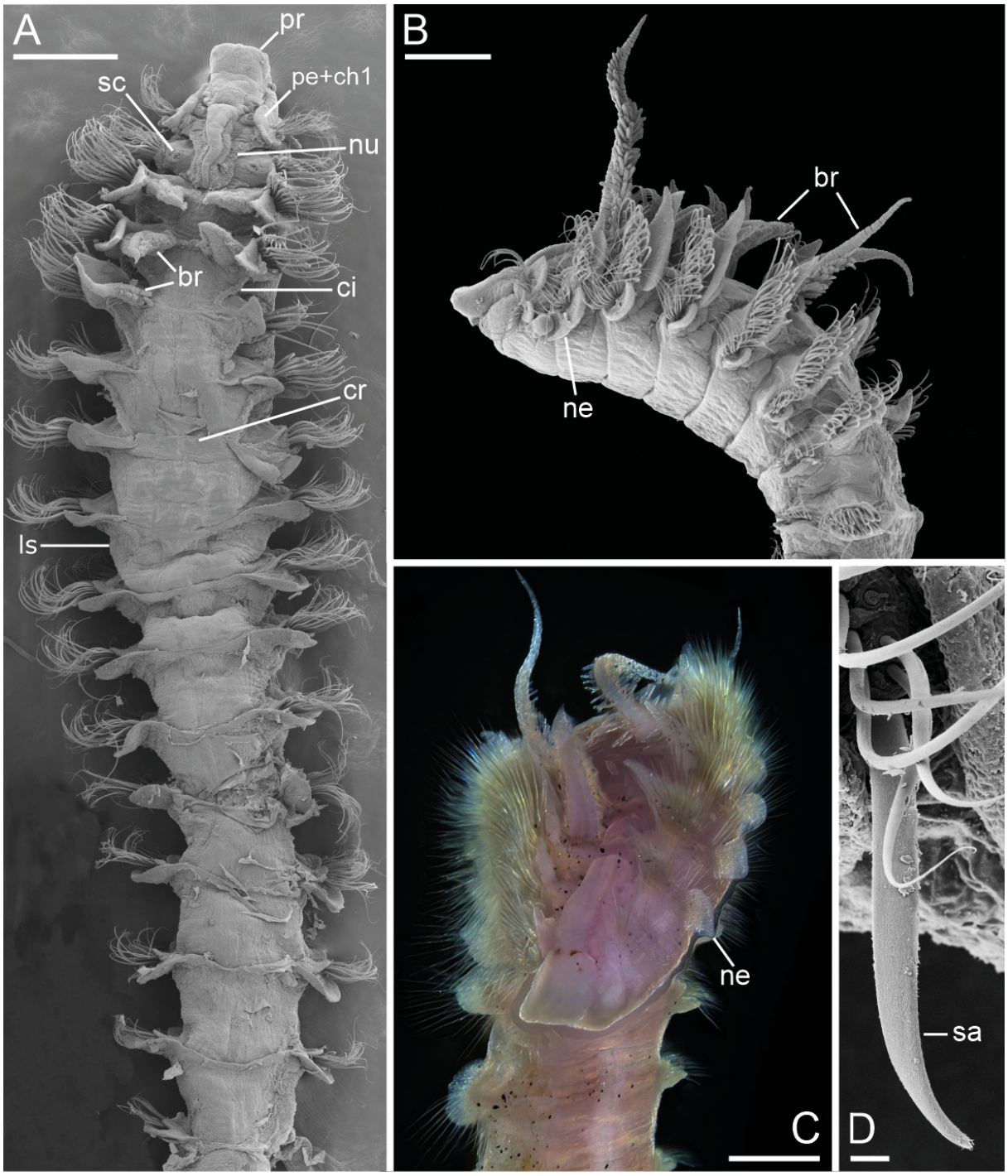


**Fig 19.** Adult and chaetal morphology of *Prionospio sigvaldadottirae* sp. nov. **A–B, D**. SEM micrographs. **C**. Light microscope image. **A**. Anterior end, dorsal view (NTNU-VM 85859). **B**. Paratype (NTNU-VM 85860), anterior end, left lateral view. **C**. Paratype (NTNU-VM 84146), anterior end, frontal view. **D**. Paratype (NTNU-VM 85860), neurochaetae of chaetiger 13. Abbreviations: see Material and methods. Scale bars: A–C = 300 μm; D = 10 μm.

SENEGAL • 1 spec.; 14°27.576′ N, 17°36.624′ W; depth 489 m; 5 Nov. 2011; CCLME leg.; stn 2011410-GR08; van Veen grab; ZMBN 152649.

WESTERN SAHARA • 1 spec.; 25°5.100′ N, 16°18.612′ W; depth 568 m; 25 Nov. 2011; CCLME leg.; stn 2011410-GR20; van Veen grab; ZMBN 152648.

**Description** (adults)

Holotype (NTNU-VM 84143) anterior fragment, 12 mm long, 0.8 mm wide, with 37 chaetigers (Fig. 18). Longest complete specimen 16 mm long with 55 chaetigers; smallest specimen 0.3 mm wide. Color in alcohol pale white. Prostomium rectangular, anteriorly truncate, with small ciliated tubercles on frontal edge, posteriorly extending to end of chaetiger 2 as long narrow caruncle (Fig. 19A). Nuchal

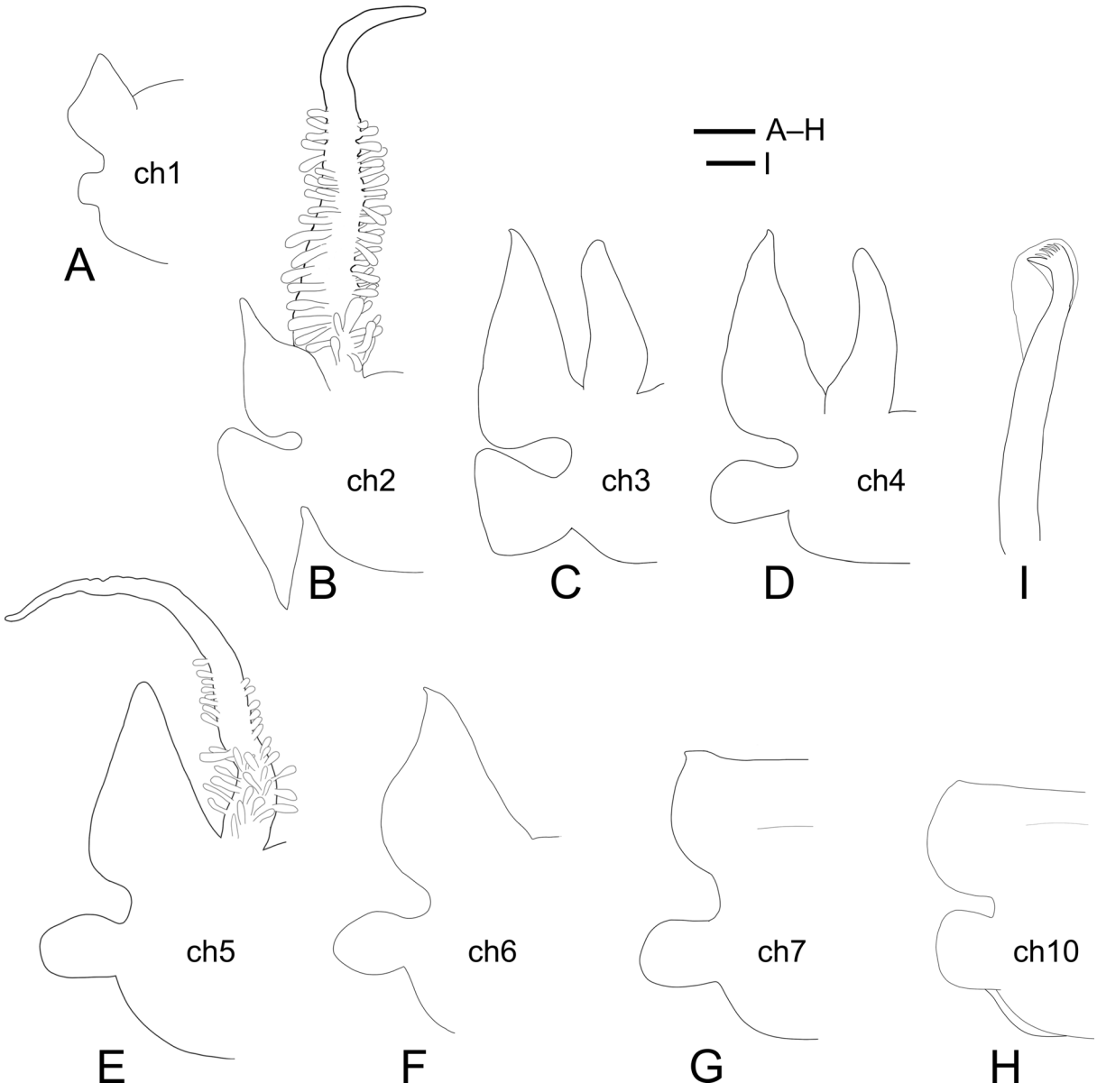


**Fig. 20.** Morphology of posteriorly facing parapodia and hooded hook of *Prionospio sigvaldadottirae* sp. nov. (NTNU-VM 84145). **A–G**. Chaetigers 1–7. **H**. Chaetiger 10. **I**. Hooded hook from neuropodium of chaetiger 20. Scale bars: A–H = 100 μm; I = 10 μm.

organs prominent V-shaped ciliary bands lateral to caruncle. Two pairs of red-brown eyes arranged trapezoidally; median eyes large, often crescent-shaped (Fig. 19C), sometimes as single or multiple small spots; lateral eyes single round spots. Posterior dorsolateral parts of peristomium fused with notopodial postchaetal lamellae of chaetiger 1 forming ear-shaped structures lateral to prostomium. Palps missing in all specimens.

Branchiae on chaetigers 2–5 (Figs 18, 19A–C, 20B–E); those on chaetiger 2 long, cylindrical, with digitiform pinnules; pinnules approximately two thirds to three fourths up branchiae, arranged in lateral rows except for the base where often present also on posterior side (Fig. 20B, E). Branchiae of chaetiger 5 in holotype half the length of branchiae on chaetiger 2, in other specimens varying from half length to similar in length to branchiae on chaetiger 2 (Figs 18, 19B–C); pinnules about halfway to two thirds up branchiae; otherwise similar to branchiae on chaetiger 2. Branchiae of chaetigers 3 and 4 apinnate, similar in lengths to notopodial postchaetal lamellae, flat, with surface perpendicular to body axis, with dense lateral ciliation. Nototrochs transverse ciliary bands between branchial bases on chaetigers 3 and 4. Dorsolateral longitudinal ciliation between chaetigers 3–7 (Fig. 19A).

Notopodial prechaetal lamellae large and oval, conspicuous on anterior chaetigers (Fig. 19A) until about chaetiger 25, gradually reduced on posterior chaetigers. Notopodial postchaetal lamellae of chaetiger 1 triangular, fused with peristomium (Fig. 20A); lamellae of chaetigers 2–5 large and subtriangular, largest on chaetiger 3 (Fig. 20B–E); diminishing in size on postbranchial chaetigers, low and rounded from chaetiger 8 onwards. Notopodial postchaetal lamellae extending middorsally and forming low transverse crests from chaetiger 7 to chaetigers 20–22 (21 in holotype); crest significantly higher on chaetiger 7 than on subsequent chaetigers (Fig. 20G–H). Dorsolateral membranous folds absent. Lateral swelling between anterior postbranchial chaetigers sometimes present (Fig. 19A). Neuropodial prechaetal lamellae large and rounded, conspicuous to approximately chaetiger 20. Neuropodial prechaetal lamellae extending slightly onto ventral side from chaetigers 8–10 to 16–24 (9–20 in holotype) (Fig. 20H). Neuropodial postchaetal lamellae of chaetiger 1 small, broadly rounded (Fig. 20A); lamellae of chaetiger 2 subtriangular, with acute ventral point (Fig. 20B); lamellae of chaetiger 3 trapezoid, with rounded edges (Fig. 20C). Lamellae of subsequent chaetigers evenly rounded (Fig. 20D–H). Neuropodial postchaetal lamellae largest on chaetigers 2 and 3, diminishing in size posteriorly, lower and broader from chaetiger 8. Interneuropodial pouches absent.

Notopodial capillaries on anterior and middle chaetigers arranged in three rows, unilimbate and smooth. Neuropodial capillaries arranged in two rows in anterior chaetigers, unilimbate and smooth. In both rami, anterior row of capillaries shorter than those in posterior rows. Capillary chaetae in posterior chaetigers not observed. Sabre chaetae in neuropodia from chaetiger 10, with slight granulation on median and distal parts of shaft, usually one, occasionally two per fascicle (Fig. 19D). Hooks in notopodia from chaetigers 36–47 (NTNU-VM 84145), not present in holotype. Hooks in neuropodia from chaetigers 16–18 (chaetiger 17 in holotype), up to eight in a series, alternating with capillary chaetae. Both noto- and neuropodial hooks with 4–6 pairs of upper teeth arranged in two vertical rows above main fang, with outer and a small inner hoods.

Pygidium missing in all specimens.

**Remarks**

*Prionospio sigvaldadottirae* sp. nov. belongs to the large *Prionospio steenstrupi* group, comprising more than 40 species. The group is characterized by having pinnate branchiae on chaetigers 2 and 5 and apinnate branchiae on chaetigers 3 and 4. Twelve species of this group have dorsal crests starting from, but not limited to, chaetiger 7, like in *P. sigvaldadottirae* sp. nov. (see Table 2). *Prionospio sigvaldadottirae* is most similar to *Prionospio depauperata* Imajima, 1990 from Japan in having

an anteriorly truncate prostomium extending back to end of chaetiger 2, dorsal crests starting from chaetiger 7, and sabre chaetae from chaetiger 10. *Prionospio sigvaldadottirae* can be distinguished from *P. depauperata* by having pinnules up half the length of the branchiae on chaetiger 5 or more (rather than the basal third), hooded hooks in neuropodia from chaetigers 16–18 (rather than 15–16), and dorsal crests always extending at least to chaetiger 20 (rather than to chaetiger 13).

Adults of *P. sigvaldadottirae* sp. nov. were previously misidentified as *P. steenstrupi* in environmental monitoring surveys in Norway (lead author personal observation). *Prionospio sigvaldadottirae* sp. nov. can be readily distinguished from *P. steenstrupi* by having dorsal crests from chaetiger 7 rather than from chaetiger 6, the dorsal crest being significantly higher on chaetiger 7 than on subsequent chaetigers, and by lacking membranous folds between anterior notopodia. Based on our study of Icelandic material, these dorsolateral folds were present in all Icelandic *P. steenstrupi*, regardless of size. Some specimens of *P. sigvaldadottirae* have lateral swellings between parapodia of postbranchial chaetigers (Fig. 19A). These swellings might be similar to what Blake (1996) described for Californian specimens identified by him as *P. steenstrupi*. However, since Blake (1996) did not illustrate these swellings, their similarity in Californian and Norwegian specimens remains uncertain. They are either way clearly different from the dorsolateral membranous folds of Icelandic *P. steenstrupi* (see remarks for *P. steenstrupi* below). Like Blake (1996), we are not sure if these swellings are a preservation artifact, thus the examination of live specimens is needed to clarify this.

Our previous study (Hektoen *et al.* 2024) confirmed the conspecificity of specimens (referred as *Prionospio* sp. 7) from Norway, Western Sahara and Senegal collected from 248–568 m depth. Additional formalin-fixed specimens reported here were all from offshore Norway, some from the same exact location as the sequenced specimen.

**Habitats and distribution**

*Prionospio sigvaldadottirae* sp. nov. is known from offshore Norway, Western Sahara and Senegal, from 104–568 m depth.

***Prionospio steenstrupi*** Malmgren, 1867
Fig. 21; Table 2

*Prionospio steenstrupi* Malmgren, 1867: 201–202, pl. 10 fig. 55.

*Prionospio steenstrupi* – Wesenberg-Lund 1951: 70. — Sigvaldadóttir & Mackie 1993: 204–207, figs 1–2. — Sigvaldadóttir 2002: 213–214.
*Prionospio* (*Prionospio*) *steenstrupi* – Maciolek 1985: 332 (partim).

Non *Prionospio steenstrupi* – Söderström 1920: 232–233, figs 136–140. — Day 1963: 418; 1967: 489, fig. 18.9o–j. — Blake & Kudenov 1978: 213, fig. 20a.
Non *Prionospio* (*Prionospio*) *steenstrupi* – Blake 1996: 123–125, fig. 9. — Dagli & Çinar 2009: 12–13.

**Diagnosis**

Prostomium anteriorly truncate, posteriorly extending to end of chaetiger 2 as a narrow caruncle. Four pairs of branchiae on chaetigers 2–5; those of chaetigers 2 and 5 long, pinnate, branchiae of chaetigers 3 and 4 short, apinnate. Dorsal crests from chaetiger 6 to chaetigers 16–18, slightly higher on chaetiger 7. Membranous folds between notopodia on chaetigers 4–13. Neuropodial postchaetal lamellae of chaetiger 2 subrectangular with acute ventral point. Sabre chaetae in neuropodia from chaetiger 10. Hooded hooks in notopodia from chaetigers 43–58, in neuropodia from chaetigers 15–17.

**Type material**

**Lectotype**

ICELAND • Skagafjördur, Hofsås; 65°54.000′ N, 19°25.000′ W; depth 73 m; stn IcelandMalm; designated by Sigvaldadóttir & Mackie (1993); SMNH Type-3170.

**Paralectotypes**

ICELAND • 4 specs. Skagafjördur, Hofsås; 65°54.000′ N, 19°25.000′ W; depth 73 m; stn IcelandMalm; designated by Sigvaldadóttir & Mackie (1993); SMNH Type-3170.

**Other material examined**

ICELAND • 13 specs; Eyiafjordur, Akureyri; 21 Mar. 1972; S. Ingvarsson leg.; stn akureypollur 1972; SMNH 174654 • 30 specs; Reydarfjördur; 66°22.000′ N, 13°57.000′ W; depth 127 m; 13 Jul. 1980; J. Svavarsson det.; stn R-2; SMNH 174656 • 10 specs; Reydarfjördur; 66°1.000′ N, 14°9.083′ W; depth 87 m; 13 Jul. 1980; J. Svavarsson leg.; stn R-1; SMNH 174655 • 20 specs; Reydarfjördur; 64°59.117′ N, 13°50.117′ W; depth 160 m; 13 Jul. 1980; stn R-3; SMNH 174657.

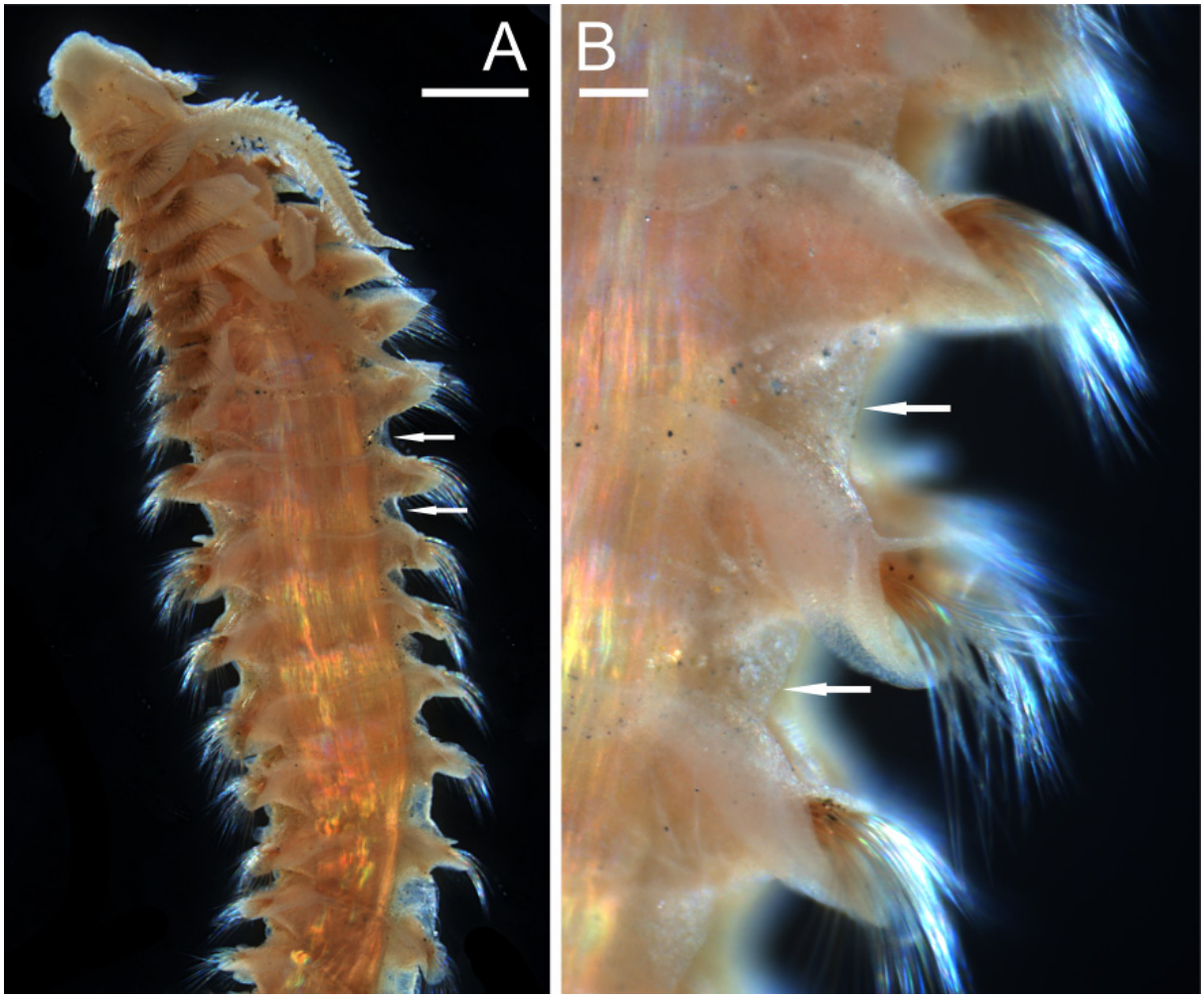


**Fig. 21.** Adult morphology of *Prionospio steenstrupi* Malmgren, 1867 (SMNH 174654). **A**. Anterior end, left dorsolateral view. **B**. Chaetigers 7–10 of same specimen, dorsal view of lateral side. Arrows pointing to thin membranous folds between notopodia. Scale bars: A = 500 µm; B = 100 µm.

**Comparative material**

***Prionospio* cf. *steenstrupi***

UNITED STATES – **Massachusetts** • 5 specs; Cape Cod Bay, between Combination Buoy and Ellisville; depth 20 m; 17 Jun. 1954; M. Pettibone leg; USNM 34200 • 7 specs; same data as for preceding; USNM 34203 • 2 specs; Cape Cod Bay, 0.5 mile E and 2 mile N of Combination Buoy; depth 20–22 m; 9 Aug. 1954; M. Pettibone leg.; USNM 34193 • 1 spec.; 0.75 mile South Vineyard Sound Lightship; depth 29 m; 4 Aug. 1953; M. Pettibone leg.; USNM 34204.

CANADA – **Quebec** • 27 specs; Gaspe Peninsula, Gaspe Bay, NW of Gaspe Harbor; depth 13 m; 14 Jul. 1959; P. Brunel leg.; USNM 34194 • 15 specs; Gaspe Bay, Mouth of Gaspe Bay, SE of Gape Gaspe; depth 102 m; 15 Jul. 1959; P. Brunel leg.; USNM 34197 • 10 specs; Gaspe Peninsula, Bay of Chaleur, Miscou Bank; 48°44′ N, 64°11′ W; depth 60 m; 30 Aug. 1953; P. Brunel leg.; stn HEC 216; USNM 34198 • 5 specs; same data as for preceding; USNM 34199. – **New Brunswick** • 5 specs; Bay of Chaleur, Nipissiquit Bay; depth 37 m; 20 Jul. 1956; P. Brunel leg.; USNM 34201 • 5 specs; same data as for preceding; USNM 34195.

**Remarks**

The original description of *P. steenstrupi* from Iceland by Malmgren (1867) was brief and imprecise. Since then, the species has been reported from the Pacific and Atlantic coasts of the United States (e.g., Foster 1971), South Africa (Day 1967), Australia (Blake & Kudenov 1978), the Sea of Japan (Uschakov 1955), Brazil (Bolivar & Lana 1987), and Chile (Blake 1983). However, the conspecificity of the distant populations has never been verified by molecular data and such data from Icelandic specimens are absent.

In the Northeast Atlantic, species of the *P. steenstrupi* group were weakly delineated until the end of the 20th century. Sigvaldadóttir & Mackie (1993) re-examined the type specimens, designated a lectotype and clarified the morphology of *P. steenstrupi* using additional material from Iceland. They noted that *P. steenstrupi* could only be proven to occur around Iceland, and all other records of this species require re-evaluation.

We examined the type and additional material of *P. steenstrupi* from Iceland reported by Sigvaldadóttir & Mackie (1993). The redescription provided by the authors is detailed and comprehensive, and we found no significant deviations from their findings. As such, a full redescription was deemed unnecessary. Thus, we only provide additional notes on the species. The dorsolateral membranous folds between notopodia (Fig. 21B) were present in all specimens studied, at the very least visible as remnants. These folds have not been reported for any other species of *Prionospio* (see comments below on *P. steenstrupi* from Turkey reported by Dagli & Çinar 2009). We also examined specimens from the Atlantic and Pacific coasts of the US identified as *P. steenstrupi* and stored in the Smithsonian National Museum of National History, Washington, D.C. Most of these specimens morphologically differed from Icelandic specimens. However, one series of lots identified by Marian Pettibone from the Northeast US coast and East Canadian coast (USNM 34193–34205) contained specimens with dorsolateral membranous folds like *P. steenstrupi*. The only difference between these and the Icelandic specimens was that some West Atlantic specimens had sabre chaetae in neuropodia from chaetiger 11 rather than chaetiger 10 as in all Icelandic specimens. The conspecificity of these specimens requires further study.

*Prionospio steenstrupi* has been predominantly reported in Iceland since its morphology was clarified by Sigvaldadóttir & Mackie (1993), with no peer-reviewed reports corroborating its presence in European Atlantic waters outside of Iceland. However, ecological surveys over the last two decades reported common occurrences of this species in Norwegian waters (https://www.artsdatabanken.no accessed 20 Aug. 2023). Our examination of specimens collected in these surveys showed a great number of misidentifications. Worms identified as *P. steenstrupi* from Norwegian coastal waters actually belonged

**Table 2** (continued on next page). Morphological characteristics of species of the *Prionospio steenstrupi* Malmgren, 1867 group with dorsal crests on chaetiger 7 and a series of subsequent chaetigers.

| Species | Eye number, shape and size | Prostomium shape | Caruncle length |
|---|---|---|---|
| *P. cooki* Radashevsky, 2015 | two pairs; single spots | anteriorly broadly rounded | end of chaetiger 4 |
| *P. atrovitta* Gopal *et al.*, 2020 | no eyes | narrow, anteriorly rounded | end of chaetiger 1 |
| *P. cristata* Foster, 1971 | two pairs; lateral single spot, median comma-shaped | anteriorly blunt or rounded | end of chaetiger 1 |
| *P. depauperata* Imajima, 1990 | two pairs; lateral single spot, median comma-shaped | anteriorly truncate | end of chaetiger 2 |
| *P. komaeti* Hylleberg & Nateewathana, 1991 | two pairs; lateral single spot, median larger irregular in shape composed of multiple ocelli | anteriorly truncate | end of chaetiger 2 |
| *P. kulin* Wilson, 1990 | 0-2 pairs; large comma-shaped | anteriorly truncate | end of chaetiger 2 |
| *P. multicristata* Hutchings & Rainer, 1979 | two pairs; median comma-shaped | anteriorly broadly rounded | end of chaetiger 3 |
| *P. oligopinnulata* Delgado-Blas, 2015 | two pairs; both cup-shaped | anteriorly truncate | end of chaetiger 1 |
| *P. orensanzi* Blake, 1983 | two pairs; lateral single spot, median larger irregular in shape composed of multiple ocelli | anteriorly broadly rounded | Middle of chaetiger 2 |
| *P. parapari* Delgado-Blas, Díaz-Díaz & Viéitez, 2018 | two pairs; lateral pair small, median large crescent | anteriorly truncate | end of chaetiger 1 |
| *P. runei* Hylleberg & Nateewathana 1991 | one pair, small | narrow, anteriorly rounded | end of chaetiger 2 |
| *P. sigvaldadottirae* sp. nov. | two pairs; lateral single spot, median weakly crescentic or spots | anteriorly truncate | end of chaetiger 2 |
| *P. steenstrupi* sensu Dagli & Çinar, 2009 | two pairs of small indistinct subdermal eyes | anteriorly truncate | end of chaetiger 1 |
| *P. variegata* Imajima, 1990 | two pairs; lateral single spot, median comma-shaped | widest anteriorly, rounded | end of chaetiger 1 |

either to *P. fallax* or *P. plumosa*, while the offshore worms are here referred to *P. sigvaldadottirae* sp. nov. (see remarks on *P. sigvaldadottirae* above). No evidence has been found to support the presence of *P. steenstrupi* in the coastal or shelf waters of mainland Europe, suggesting that the species, if present, is rare in this region.

Dagli & Çinar (2009) reported *P. steenstrupi* from the Eastern Mediterranean, Turkey, with dorsolateral membranous folds as in the Icelandic specimens. However, the Turkish specimens had dorsal crests from chaetiger 7 (rather than from chaetiger 6) and caruncle reaching the end of chaetiger 1 (rather than the end of chaetiger 2) and might represent a yet undescribed species.

**Table 2** (continued).

| Species | Sabre chaetae start [chaetiger] | Neuropodial hooks start [chaetiger] | Lower part of neuropodial lamellae of chaetiger 2 | Dorsal crest size | Dorsal crest end [chaetiger] | Region |
|---|---|---|---|---|---|---|
| *P. cooki* Radashevsky, 2015 | 10 | 12–14 | ventrally pointed | all low | 22 | Australia |
| *P. atrovitta* Gopal *et al.*, 2020 | 15–16 | 16–18 | rounded | all low | 17 | North Indian Ocean |
| *P. cristata* Foster, 1971 | 10 | 11–12 | ventrally rounded | 7 and 9 high, rest low | 12 | West Atlantic |
| *P. depauperata* Imajima, 1990 | 10 | 15–16 | ventrally pointed | 7 high, rest low | 13 | Japan |
| *P. komaeti* Hylleberg & Nateewathana, 1991 | 10 | 12–18 | ventrally pointed | 7 high, rest low | 11 | Thailand |
| *P. kulin* Wilson, 1990 | 10 | 13–21 | ventrally pointed | 7 high, rest low | 17–21 | Australia |
| *P. multicristata* Hutchings & Rainer, 1979 | 10 | 14–18 | ventrally pointed | All low | 25–30 | Australia |
| *P. oligopinnulata* Delgado-Blas, 2015 | 10 | 12–14 | ventrally pointed | 7 high, rest low | 14 | Gulf of Mexico |
| *P. orensanzi* Blake, 1983 | 10 | 20 | rounded | ? | 19 | Argentina |
| *P. parapari* Delgado-Blas, Díaz-Díaz & Viéitez, 2018 | 10–13 | 11–15 | ventrally pointed | 7 high, rest low | 9 | Spain |
| *P. runei* Hylleberg & Nateewathana, 1991 | 10 | 8–12 | rounded | all low | 9 | Thailand |
| *P. sigvaldadottirae* sp. nov. | 10 | 16–18 | ventrally pointed | 7 high, rest low | 20–22 | East Atlantic |
| *P. steenstrupi* sensu Dagli & Çinar, 2009 | 10 | 14–16 | ventrally pointed | 7 high, rest low | 18 | Eastern Mediterranean |
| *P. variegata* Imajima, 1990 | 10 | 11 | rounded | all low | 14 | Japan |

### Habitats and distribution

*Prionospio steenstrupi* is only known from Iceland, between 73 and 160 m depth.

***Prionospio*** sp. 6
Fig. 22; Table 3

*Prionospio* sp. 6 – Hektoen *et al.* 2024: figs 1, 4.

**Diagnosis**

Prostomium narrow, anteriorly rounded, posteriorly extending to middle of chaetiger 1 as a short caruncle. Eyes absent. One pair of apinnate branchiae on chaetiger 3. Notopodial postchaetal lamellae of chaetiger 3 largest, rounded, of chaetigers 2 and 4 triangular. Dorsal crests absent. Neuropodial postchaetal lamellae oblong. Sabre chaetae in neuropodia from chaetiger 10. Hooded hooks in neuropodia from chaetigers 10–11.

**Material examined**

NORWAY – **Vestland** • 1 spec.; Høyanger, Torvund; 61.13583° N, 5.75473° E; depth 1255 m; 3 May 2017; Bergen University Museum leg.; stn KB2017-05-05GR; van Veen grab; SEM stub; ZMBN 152561 • 1 spec.; Bømlo, Sveio; 59.56729° N, 5.21568° E; depth 328 m; 28 Apr. 2017; Bergen University Museum leg.; stn KB-20; van Veen grab; ZMBN 152636.

**Examined material with sequence data**

NORWAY – **Vestland** • 1 spec; Sognefjorden; 61.05012° N, 5.40056° E; depth 1236 m; 3 May 2017; Bergen University Museum leg.; stn kb2017-05-02; van Veen grab; ZMBN 152637.

**Description**

Three specimens examined, all 0.1 mm wide or smaller. One specimen likely complete, but damaged posteriorly, in three fragments totaling 40 chaetigers. Color in alcohol pale white. Prostomium narrow, anteriorly rounded (Fig. 22A–B), extending to middle of chaetiger 1 as a short caruncle. Eyes absent. Posterior dorsolateral parts of peristomium fused with notopodial postchaetal lamellae of chaetiger 1 forming ear-shaped structures lateral to prostomium. Palps in one specimen, broken, as long as four chaetigers (Fig. 22A).

One pair of branchiae on chaetiger 3 in all three specimens, with no scars visible on other chaetigers. Branchiae apinnate, with lateral ciliation, triangular, shorter than notopodial postchaetal lamellae on the same chaetiger (Fig. 22A). Nototrochs transverse ciliary bands between branchial bases. Dorsolateral longitudinal ciliation absent.

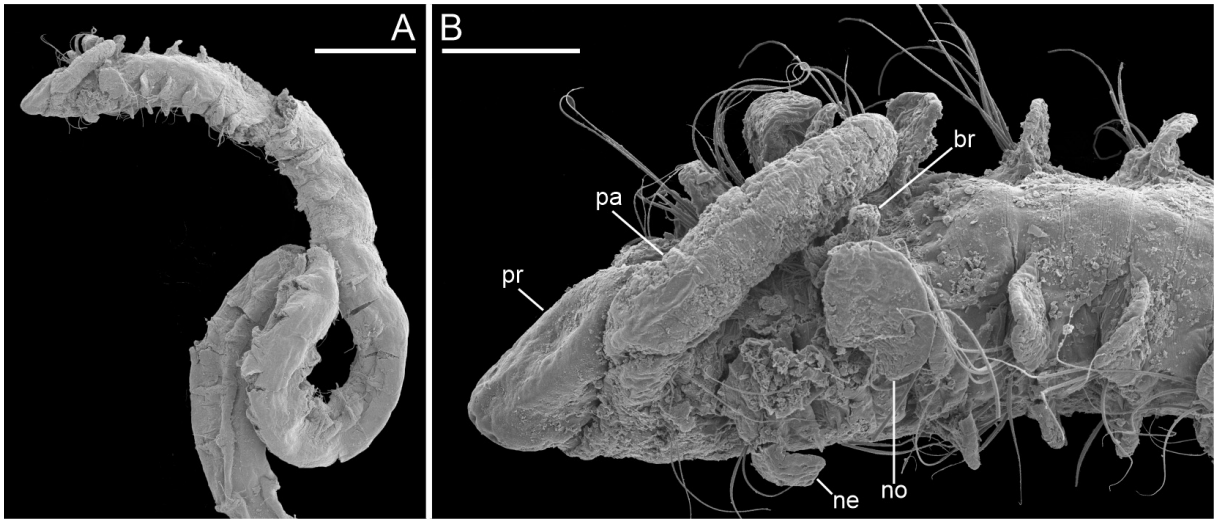


**Fig. 22.** Morphology of *Prionospio* sp. 6 (ZMBN 152561), SEM micrographs. **A**. Anterior end, left dorsolateral view. **B**. Closeup of same specimen. Abbreviations: see Material and methods. Scale bars: A = 200 μm; B = 50 μm.

**Table 3.** Morphological characters of species of *Prionospio* Malmgren, 1867 and *Aurospio* Maciolek 1981 with less than three pairs of branchiae.

| Species | No. of chaetigers with branchiae | Branchae from [chaetiger] | Dorsal crests | Sabre chaetae start [chaetiger] | Neuropodial hooded hooks start [chaetiger] | Distribution | Width (mm) |
|---|---|---|---|---|---|---|---|
| *A. abranchiata* Neal, Paterson & Soto, 2016 | 0 | – | present | 10 | 11–12 | Porcupine abyssal plain | 0.2 |
| *A. dibranchiata* Maciolek, 1981 | 2 | 3 | present or absent | 9–11 | 10 | Atlantic Ocean | 0.2 |
| *A. foodbancsia* Mincks, Dyal, Paterson, Smith & Glover, 2009 | 1 | 3 | present | 10 | 11 | Antarctica | 0.2 |
| *P. alexandrae* Peixoto & Paiva, 2020 | 2 | 2 | absent | absent | 10–20 | Brazil | 0.25 |
| *P. branchilucida* Altamira, Glover & Paterson, 2016 | 2 | 2 | present | absent | 11 | Brazil | 0.08 |
| *P. hermesia* Neal & Paterson, 2016 | 2 | 2 | present | absent | 13–14 | Portugal, deep sea | 0.08 |
| *P. kaplani* Altamira, Glover & Paterson, 2016 | 2 | 2 | present | absent | 11 | Atlantic and Pacific deep sea | 0.08 |
| *P. nonatoi* Peixoto & Paiva, 2019 | 0 | – | present | 10 | 11–12 | Brazil | 0.18 |
| *P. solisi* Peixoto & Paiva, 2019 | 2 | 3 | absent | 9–11 | 9–14 | Brazil | 0.25 |
| *P.* sp. 6 | 1 | 3 | absent | 10 | 10–11 | Norwegian coast | 0.1 |

Notopodial prechaetal lamellae inconspicuous. Notopodial postchaetal lamellae of chaetiger 1 rounded, fused with peristomium. Lamellae of chaetiger 2 triangular; lamellae of chaetiger 3 greatly enlarged, rounded, with a small, elongated tip; lamellae triangular on chaetiger 4, rounded on chaetiger 5, lower and oval-shaped on succeeding chaetigers. Dorsal crests absent. Neuropodial prechaetal lamellae inconspicuous. Neuropodial postchaetal lamellae of chaetiger 1 small and oblong; lamellae of chaetigers 2–7 rectangular, broader than high; lamellae lower and rounded on succeeding chaetigers (Fig. 22A–B). Interneuropodial pouches absent.

Capillary chaetae in single rows in all chaetigers, alimbate and smooth. Sabre chaetae in neuropodia from chaetiger 10. Hooded hooks in notopodia not observed. Hooded hooks in neuropodia from chaetigers 10–11.

Pygidium missing in all specimens.

**Remarks**

*Prionospio* sp. 6 is represented only by three small incomplete specimens which could be juveniles with not yet fully developed features. Although molecular data of one of these specimens distinguished it from other *Prionospio* (Hektoen *et al.* 2024: figs 1, 4), we do not formally name it pending examination of additional specimens.

The species does bear resemblance to other small-sized species of *Prionospio* and *Aurospio* but can be distinguished morphologically from all such species (Table 3).

**Habitats and distribution**

*Prionospio* sp. 6 was collected from Norwegian fjords in the northern part of the North Sea and southern part of the Norwegian Sea. Worms were found in silty and muddy sediments at depths of 328–1255 m.

### *Identification key to the species of adult Prionospio Malmgren, 1867 in Northern Europe*

1. At least some branchiae with pinnules ..... 2
– All branchiae apinnate ..... 6

2. Pinnate branchiae on chaetigers 2, 3 and 5, pinnules on branchiae of chaetiger 3 may only be present basally ..... ***Prionospio plumosa*** M. Sars in G.O. Sars, 1872
– Pinnate branchiae otherwise ..... 3

3. Dorsal crests absent ..... ***Prionospio multisetosa*** Delgado-Blas & Peraza, 2024
– Dorsal crests present ..... 4

4. High dorsal crest present on chaetiger 7 only ..... ***Prionospio fallax*** Söderström, 1920
– Dorsal crests present on more than one chaetiger ..... 5

5. Dorsal crests from chaetiger 6, membranous folds between successive notopodia on some chaetigers between chaetigers 4 and 17 ..... ***Prionospio steenstrupi*** Malmgren, 1867
– Dorsal crests from chaetiger 7, membranous folds between successive notopodia absent ..... ***Prionospio sigvaldadottirae*** sp. nov.

6. One pair of branchiae on chaetiger 3 ..... ***Prionospio*** sp. 6
– More than one pair of branchiae ..... 7

7. 2–5 pairs of branchiae from chaetiger 2 or 3 (usually three pairs of branchiae from chaetiger 3). Low dorsal crests from chaetiger 6–9 ..... ***Prionospio banyulensis*** Laubier, 1966
– At least five pairs of branchiae from chaetiger 2. Dorsal crests from chaetiger 10 or later ..... 8

8. Up to six pairs of branchiae. Prostomium extending to end of chaetiger 2. Lower part of neuropodial postchaetal lamellae of chaetiger 2 elongated and pointed downwards ..... ***Prionospio cirrifera*** Wirén, 1883 agg.
– Up to 13 pairs of branchiae. Prostomium extending at the most to the middle of chaetiger 2. Lower part of neuropodial postchaetal lamellae of chaetiger 2 rounded ..... 9

9. Prostomium anteriorly rounded, narrow caruncle extending to middle of chaetiger 2. Median eyes small or large ..... ***Prionospio sanmartini*** Delgado-Blas, Díaz-Díaz & Viéitez, 2019
– Prostomium triangular, anteriorly truncate, thick caruncle extending to end of chaetiger 1. Eyes indistinct in all individuals ..... ***Prionospio fiordica*** sp. nov.

## Discussion

A commonality between many contemporary studies on polychaete diversity is that species have less intraspecific morphological variation and more limited geographical distribution than previously estimated (e.g., Hutchings & Kupriyanova 2018; Nygren *et al.* 2018; Grosse *et al.* 2020). Species of *Prionospio* seem to be at least partly an exception to this. Molecular studies have shown that species of *Prionospio* can be widely distributed in both the deep sea (Guggolz *et al.* 2020; Neal *et al.* 2022) and coastal waters (Hektoen *et al.* 2024). In addition to what was already found by Hektoen *et al.* (2024) we here found no morphological distinctions between East and West Atlantic specimens of *P. steenstrupi*, or Norwegian and West African specimens of *P. multisetosa* and *P. sigvaldadottirae* sp. nov. In addition to their broad geographic ranges, several species of *Prionospio* in our study also displayed substantial bathymetric distributions. The most notable examples include *P. fiordica*, recorded from depths between 328 and 1236 meters, and *P. multisetosa*, found between 47 and 665 meters. These depth ranges were largely confirmed by molecular species delimitation (Hektoen *et al.* 2024). However, it is important to note that many of the deeper records originate from Norwegian fjords. These fjord systems, while deep, are enclosed and exhibit oceanographic conditions that differ markedly from those of the open deep sea (Oug *et al.* 2010). As such, the ecological barriers associated with depth in these environments may not be as pronounced as in non-coastal ecosystems.

With this review, we have identified ten species of *Prionospio* in samples from northern European waters, up from seven reported previously. The diversity of *Prionospio* is much better understood than in previous centuries; however, there is still much to be studied and understood. For example, *Prionospio* sp. 6 was left unresolved here. More specimens are needed to describe and name this species. The small size of available specimens and their morphology could indicate that we dealt with juveniles. These specimens are morphologically similar to species of *Prionospio* and *Aurospio* described from the deep sea (Paterson *et al.* 2016; João *et al.* 2019; Peixoto & Paiva 2019) or the Antarctic shelf (Mincks *et al.* 2009), such as very small size, greatly enlarged notopodial postchaetal lamellae and reduced number of branchiae. *Prionospio sanmartini* also require further revision. Additional specimens of *P. sanmartini* of different sizes are needed to better understand the morphological variability of this species and taxonomic relationships between the Spanish and Nordic populations. The molecular study of Hektoen *et al.* (2024) also indicated that *P. cirrifera* likely comprises two or three species in Northeast Atlantic and Arctic waters. This species complex will be treated separately in an upcoming study.

We decided not to designate a neotype and redescribe *P. dubia* based on the 13 available specimens from South Africa. Since these specimens were a mix from nine different stations, it was impossible to know the sampling locality of a potential neotype. The type of *P. dubia* may also still exist under a different name, as it was first described as a variety of *P. malmgreni* and later referred to *P. steenstrupi*. It is even unclear whether the 13 studied specimens are conspecific or comprise more than one species as some of them have eyes while others lack. It becomes clear that more specimens from South Africa should be collected and studied to elucidate the specific morphological and molecular characteristics of *P. dubia*.

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