



## New *Prionospio* and *Aurospio* Species from the Deep Sea (Annelida: Polychaeta)

GORDON L. J. PATERSON<sup>1,7</sup>, LENKA NEAL<sup>1</sup>, IRIS ALTAMIRA<sup>2</sup>, EULOGIO H. SOTO<sup>3</sup>, CRAIG R. SMITH<sup>2</sup>, LENAICK MENOT<sup>4</sup>, DAVID S.M. BILLETT<sup>5</sup>, MARINA R. CUNHA<sup>6</sup>, CLAIRE MARCHAIS-LAGUIONIE<sup>1,5</sup> & ADRIAN G. GLOVER<sup>1</sup>

<sup>1</sup>Life Sciences Department, The Natural History Museum, London, SW75BD, UK

<sup>2</sup>Oceanography Department, University of Hawaii, Honolulu USA

<sup>3</sup>Facultad de Ciencias del Mar y de Recursos Naturales, Universidad de Valparaíso, Avenida Borgoño 16344 Montemar, Reñaca, Viña del Mar, Chile

<sup>4</sup>Ifremer, Centre de Brest, REM/EEP/LEP, BP 70, 29280 Plouzané, France

<sup>5</sup>National Oceanography Centre, European Way, Southampton SO14 3ZH, UK

<sup>6</sup>Departamento de Biologia & CESAM, Universidade de Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal

<sup>7</sup>Corresponding author. E-mail: g.paterson@nhm.ac.uk

### Abstract

The number of records of the genus *Prionospio* Malmgren, 1867, from the deep sea (>2000 m) are relatively few and do not reflect the actual occurrence of species nor their potential ecological importance. In this paper we describe five new species of this genus (*Prionospio amarsupinata* **sp. nov.**, *P. vallensis* **sp. nov.**, *P. branchilucida* **sp. nov.**, *P. hermesia* **sp. nov.** and *P. kaplani* **sp. nov.**) all of which are abundant members of the deep-sea community. We also describe two new species of the genus *Aurospio* Maciolek, 1981 (*Aurospio abranchiata* **sp. nov.** and *A. tribranchiata* **sp. nov.**) again common elements of the abyssal fauna. Two of the new species have characters which question the generic distinctiveness of *Prionospio* and *Aurospio*. The problems in differentiating these two genera are discussed.

**Key words:** taxonomy, distribution, Pacific Ocean, Atlantic Ocean, *Prionospio*, *Aurospio*, *Prionospio amarsupinata* **sp. nov.**, *Prionospio vallensis* **sp. nov.**, *Prionospio branchilucida* **sp. nov.**, *Prionospio hermesia* **sp. nov.**, *Prionospio kaplani* **sp. nov.**, *Prionospio* Iberian Canyons sp. C, *Aurospio abranchiata* **sp. nov.**, *Aurospio tribranchiata* **sp. nov.**

### Introduction

The genus *Prionospio* Malmgren, 1867, is a widespread taxon of the Spionidae with species recorded from the Arctic to the Antarctic and ranging from the intertidal and shallow subtidal to the abyssal plain. A total of 113 nominal species have been recorded of which up to 81 are thought to be valid depending on the author consulted (e.g., K. Fauchald in WoRMS <http://www.marinespecies.org/>). Yet despite this widespread occurrence, the number of records of *Prionospio* species in the deep sea is rather limited. This is undoubtedly a major under-estimate, since many unpublished records exist within ecological studies and subsequent literature and species of the genus are among the major components of deep-sea polychaete assemblages within sediment systems (Glover, Paterson, Soto pers. observation; Glover 2000; Soto 2008).

The genus *Aurospio* Maciolek, 1981, has fewer species. Currently four species have been assigned to the genus: *A. banyulensis* (Laubier, 1968); *A. dibranchiata* Maciolek, 1981a; *A. foodbancsia* Mincks et al., 2008 and *A. pilkena* Wilson, 1990. Two of these species, *A. dibranchiata* and *A. foodbancsia*, are recorded from bathyal and abyssal depths. *A. dibranchiata* has a wide distribution being recorded from Atlantic, Southern and Pacific sites. *A. banyulensis* and *A. pilkena* were recorded from shelf depths and have a restricted geographic distribution.

In this study we present taxonomic descriptions of five new species of *Prionospio* and two of *Aurospio* from a range of deep-sea studies. The species were dominant members of the polychaete assemblages and were collected as part of intensive studies in the Pacific and Atlantic Oceans. Two of these species, *Aurospio abranchiata* **sp. nov.**

and *Prionospio kaplani* **sp. nov.**, highlight problems with the definition of *Prionospio*, particularly with regard to the boundaries of *Prionospio* and *Aurospio*. Currently *Prionospio* and its allies are defined using predominantly branchial characters such as the form of branchiae, arrangement, number, and particularly the chaetiger upon which the branchiae first arise. There has been debate as to the importance of this latter character with some authors using them to define subgenera (Foster 1971; Maciolek 1985; Blake & Kudenov 1978; Yokoyama 2007), while others consider these characters too variable and therefore such subgenera invalid (Wilson, 1990; Sigvaldadottir 1998). In this paper we review these arguments based on the characters the new species possess.

## Material and methods

### Study area and sampling programme (Table 1, Fig. 1).

1) **Central Pacific.** Clarion-Clipperton Fracture Zone (CCFZ): three sites within the manganese nodule areas were selected to study the ecology and distribution of species. The aim of the study was to provide baseline data relevant to the development of management plans in the event of commercial exploitation of the nodules. Study sites were selected across the CCFZ and also followed a gradient in surface primary productivity. Samples were taken in depths between 4900 m and 5035 m on three separate cruises. Samples were collected using a USNEL box core (area 0.25 m<sup>2</sup>) and sieved on a 0.3 mm mesh sieve.

2) **Equatorial Pacific** (EqPac). Sites from the EqPac Joint Global Ocean Fluxes Study (JGOFS) (Glover *et al.* 2002) were located along a longitudinal transect at 140° W and with stations at 0° N, 2° N, 5° N, and 9° N, at depths between 4300 m and 4900 m. The transect followed a decreasing productivity gradient northwards. Collecting methods and site descriptions are given in Smith *et al.* (1997) and Glover *et al.* (2002). All samples were collected using a USNEL box core and sieved on a 0.3 mm mesh sieve.

3) **Northeast Atlantic.** Abyssal sites on the Cap Verde Abyssal Plain, including the Eumeli Oligotrophic site (EOS), the Madeira Abyssal Plain (MAP), and the Porcupine Abyssal Plain (PAP). The depth of the sites varied from 4500 m to 5040 m. The site descriptions and collecting methods are given in Paterson *et al.* (1997) and Glover *et al.* (2001). The PAP site has been the locality of a long-term study (Billett & Rice 2001; Billett *et al.* 2001; Soto *et al.* 2010). All samples were collected using a USNEL box core. Cores were subsectioned into 0–1 cm, 1–3 cm, and 3–5 cm depth layers. Samples were sieved on 1.0 mm-mesh, 0.5 mm-mesh, and 0.3 mm-mesh sieves.

4) **Canyons of the Iberian Margin.** Samples were collected during an EU Framework 6 project called the Hotspot Ecosystem Research on the Margins of European Seas (HERMES; Tyler *et al.* 2007). Three canyons along the Western Iberian margin were studied: Nazaré, Cascais, and Setúbal canyons. These canyons cut through the continental shelf at water depths shallower than 50 m and reach down to the Tagus and Iberian abyssal plains to depths exceeding 5000 m (Lastras *et al.* 2009). Nazaré canyon lies between 39° and 40° N and it is one of Europe's largest canyon systems. The Setúbal canyon is located south of the Nazaré canyon and forms a more complex system connected to two major river basins, the Tagus and Sado. Cascais canyon lies in close geographical proximity to Setúbal-Lisbon canyon. A more detailed description of the Western Iberian Margin regional setting is given by Arzola *et al.* (2008) and Lastras *et al.* (2009). The polychaete ecology of the canyons is given in Paterson *et al.* (2011). Samples were taken either with an USNEL-type box corer or with a megacorer at approximately 3400 m and 4300 m depths. Samples were sieved with 1.0 mm-mesh and 0.5 mm-mesh sieves.

5) **Crozet.** Samples were collected at two abyssal plain sites close to the Crozet Archipelago in the Southern Indian Ocean. Two localities were sampled aboard RRS *Discovery* cruise D300, site M5 to the east of the Crozet Plateau (45°52.96' S, 56°23.78' E, depth 4186 m) and site M6 to the south (49°01.92' S 51° 13.88' E, depth 4192 m). The southern site (M6) lies within a High Nutrient Low Chlorophyll (HNLC) oceanic productivity regime and as such benthic biomass is reduced compared to M5, which lies in the eastern trail of the seasonal phytoplankton bloom that occurs around Crozet. This bloom is fuelled by natural iron fertilization from the Crozet Plateau (Wolff *et al.* 2011). The specimens from these sites were collected using a megacorer, sieved on a 0.3 mm-mesh screen and live-sorted on the ship with specimens preserved for both DNA and morphological study. DNA was extracted from the Crozet specimens and the 16S and 18S regions sequenced as described in Mincks *et al.* (2008) and deposited in GenBank under accession numbers EU340079, EU340081, EU340093, and EU340095.

**Taxonomic characters.** In describing the species found we have used characters set out in Sigvaldadottir (1998), particularly when describing shapes of features such as the prostomium. We have added detail as to the

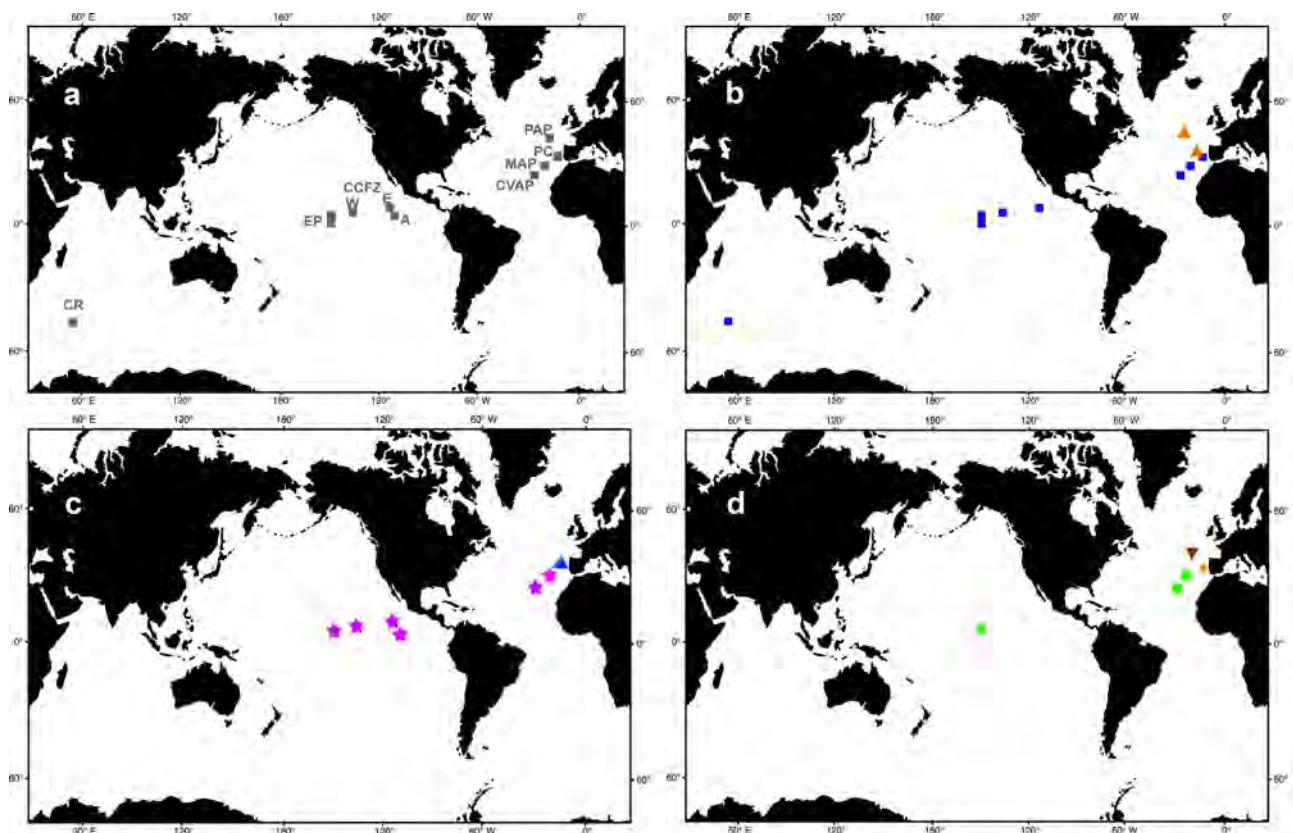
**TABLE 1.** Locality details of the material studied. See also Figure 1.

Locality	Latitude	Longitude	Depth (m)	Date	Ship	Programme Project
<b><i>Pacific</i></b>						
Clipperton Clarion Fracture Zone (Central site)	c. 14° 55' N	119° 2.0' W	4900–5035	February–March 2003	RV <i>New Horizon</i>	Kaplan
Clipperton Clarion Fracture Zone (West site)	c. 14° 2.0' N	130° 5 00' W	4900–5035	June 2004	RV <i>L'Atalante</i>	Nodinaut/Kaplan
Clipperton Clarion Fracture Zone (UK1 exploration area)	c. 13°43.00 N	116°40.00 W	4036–4171		RV <i>Melville</i>	ABYSSLINE
Equatorial Pacific	0°N, 2°N, 5°N, 9°N	140° W	4300–4900	November 1992	RV <i>Thomas Thompson</i>	EqPAC JGOFS
Crozet Site M5	45°52.96'S	56°23.78'E	4186	December 2005	RRS <i>Discovery</i>	Crozex
Crozet Site M6	49°01.92'S	51°13.88'E	4192	December 2005	RRS <i>Discovery</i>	Crozex
<b><i>Atlantic</i></b>						
Porcupine Abyssal Plain	48° 00' N	16° 00' W	4800	August 1989–September 1998,	Various	MAST I&II, BENGAL
Madeira Abyssal Plain	31° 00' N	21° 00' W	4900	August 1990	RRS <i>Discovery</i>	MAST I&II
Cap Verde Abyssal Plain	20° 00' N	30° 00' W	4600	October 1993	RRS <i>Discovery</i>	MAST I&II
Nazaré Canyon	c.39° 29' N	c.9° 55' W	3400	August 2005, May 2006	RRS <i>Discovery</i> , RRS <i>Charles Darwin</i>	HERMES
Setúbal Canyon	c.39° 35' N	c.10° 20' W	4300			
	c.38° 09' N	c.9° 36' W	3400	April–May 2006	RRS <i>Charles Darwin</i>	HERMES
	c.38° 06' N	c. 9° 59' W				
Cascais Canyon	c.38° 17' N	c.9° 47' W	4300	May 2006	RRS <i>Charles Darwin</i>	HERMES
	c.38°22' N	c.9° 53' W	4300			

relative sizes of features such as the branchiae to the adjacent dorsal lamellae, while appreciating that branchiae are often shed and may regenerate. One particular important feature is the shape of the anterior dorsal lamellae. This is a difficult character to describe in words so we have provided diagrams (Figures 2 and 11) which show the shape of the dorsal lamellae and how it changes in anterior chaetigers. The relative proportions of the dorsal lamellae and branchial length were measured from the SEM images. In this we are following the layout given by authors such as Maciolek (1985) Mackie (1984), Mackie & Hartley (1990), Sigvaldadottir & Mackie (1993).

**SEM.** Specimens of all species described were examined using an Phillips XL30 SEM. Specimens were dehydrated to 100% alcohol before being critically point dried, mounted on stubs, and coated with gold-vanadium using a sputter coater. Despite our best efforts it has not been possible to clean many specimens thoroughly. This was partly due to the methods used to separate specimens from the sediment, their small size, and that the individuals had often been archived for many years. Nevertheless, the individuals studied provide sufficient detail to supplement our observations made using light microscopes.

**Type material.** All holotypes were deposited in the Natural History Museum, London (NMHUK); paratype material was deposited in the NHMUK and Biological Research Collection of the University of Aveiro, Portugal (UA).



**FIGURE 1.** Maps showing location of collecting sites and distribution of species. a. Locations of the collection sites. CCFZ—Clarion—Clipperton Fracture Zone, W = west site, E = east site, A = UK concession area; CR—Crozet Island; CVAP Cap Verde Abyssal Plain; EP—Equatorial Pacific (EqPac); MAP—Madeira Abyssal Plain; PAP—Porcupine Abyssal Plain; PC—Portuguese Canyons. b. Distribution of *Prionospio amarsupiata* sp. nov. (blue squares), *Aurospio abranchiata* sp. nov. (orange triangles); c. Distributions of *Prionospio branchilucida* sp. nov. (purple stars), *P. vallensis* sp. nov. (blue triangle); d. Distributions of *Prionospio kaplani* sp. nov. (solid green hexagons); *P. hermesia* sp. nov. (yellow circle), *Aurospio tribranchiata* sp. nov. (inverted orange triangle)

## Species descriptions

### *Prionospio* Malmgren, 1867

***Prionospio amarsupiata* sp. nov. Neal & Altamira**

(Figures 1, 2.1, 3, 8e)

*Prionospio* sp D Paterson *et al.* 2011: 2453.

**Material examined.** 24 specimens examined.

**Holotype:** Setúbal canyon RRS *Charles Darwin* 179. April–May 2006, St. 56842#1, 38°06.45'N 9°59.94'W, 4482 m (NHMUK 2015:1042).

**Paratypes:** *Portuguese margin canyons:* Nazaré canyon RRS *Discovery* 297, August 2005, St. 15758#2, 39°34.94' N 10°19.00' W, 4332 m, 2 individuals; St. 15765#2, 39°35.00' N, 10°19.04' W, 4336 m, 1 individual.

RRS *Charles Darwin* 179, April–May 2006, St. 56861#1 39°35.57' N, 10°20.02' W, 4404 m, 1 individual. St. 56847#6 39°35.57'N 10°19.99'W 4403m, 1 individual.

Setúbal canyon RRS *Charles Darwin* 179. April–May 2006, St. 56804#5, 38°09.27'N 9°36.93'W, 3275m, 1 individual; St. 56804#6 38°09.26'N 9°36.94'W, 3275m, 3 individuals; St. 56806#1, 38°09.29'N 9°36.96'W, 3275m, 1 individual; St. 56838#2 38°06.50'N 9°59.98'W, 4482m, 1 individual; St. 56842#1, 38°06.45'N 9°59.94'W, 4482m, 3 individuals;

Cascais canyon RRS *Charles Darwin* 179. April–May 2006, St. 56837#8, 38°22.49'N 9°53.52'W, 4244 m, 1 individual; St. 56821#1, 38°17.96'N 9°46.87'W, 3219m, 1 individual; St. 56823#2, 38°18.01'N 9°47.02'W, 3218m, 1 individual; St. 56828#1, 38°18.02'N 9°46.98'W, 3199m, 1 individual.

**Other material studied:** *Crozet Island* RRS *Discovery* D300, December 2005–January 2006, site M6, 15773#31, 49°01.92'S 51°13.88'E, 4192 m, 1 individual. Site M5, 15773#18, 45°52.96' S, 56°23.78' E, 4186 m, 1 individual.

*Kaplan CCFZ Central Site (IFREMER Nodinaut campaign):* RV *L'Atalante*, May–June 2004 KAP3, CRS868/MTB9, 14°3.093'N, 130°4.7825'W, 5031m, individual KP397, 1 individual.

*EqPac:* RV *Thomas Thompson*, November 1992, BC15, 5°N 140 W, 0-1cm, EP436 1 individual

*Madeira Abyssal Plain:* RRS *Discovery*, August 1990, 12174 3-5cm, 300µm: (MAST\_Polychaete Intercalibration Project number–map 55), 1 individual.

*Cape Verde Abyssal Plain:* RRS *Discovery*, October 1993, 12600#10 213.2'N 3111.0'W, 4543 m, MAST\_cv7, 1 individual.

**Diagnostic features.** Lack of interparapodial pouches, first branchial pair with only few pinnules at the base of branchiae.

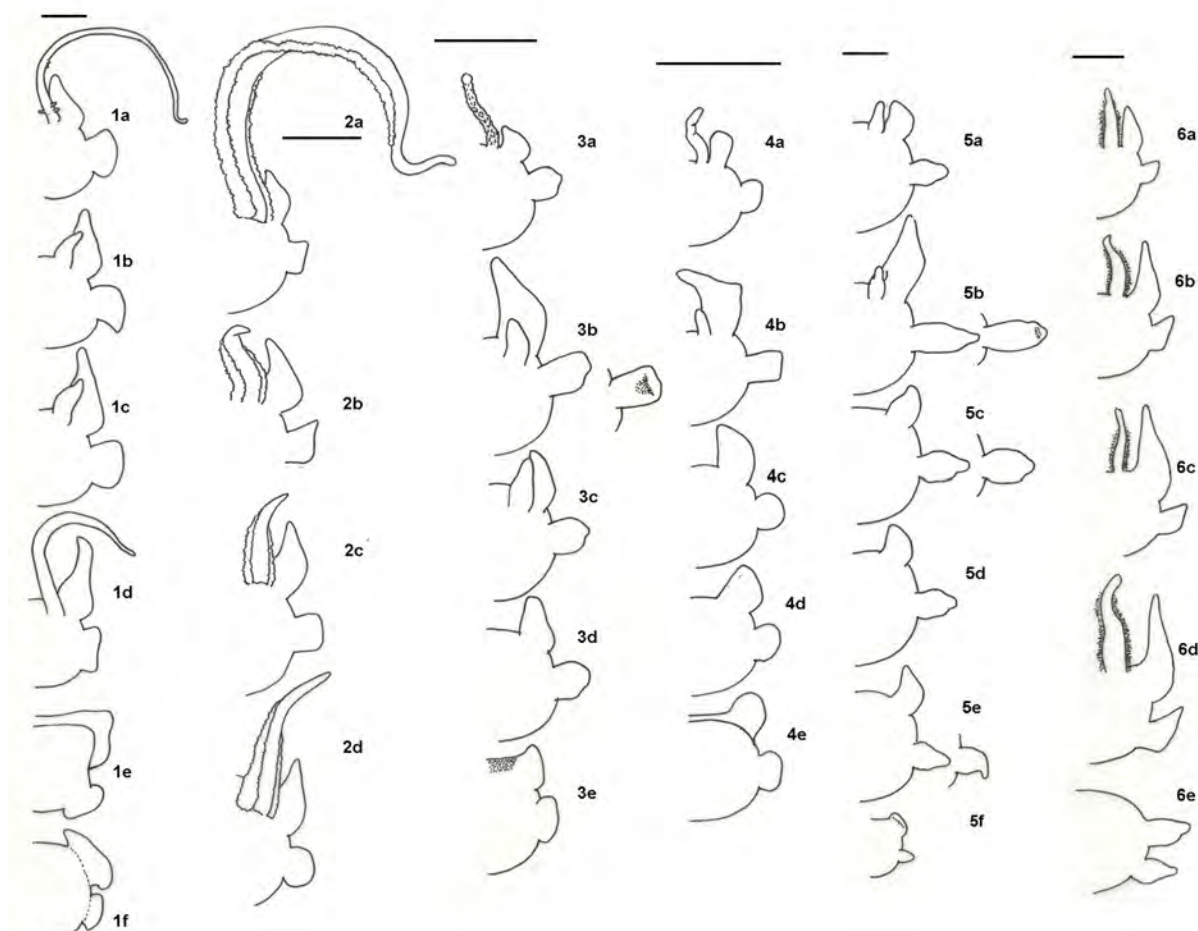
**Description.** Holotype incomplete with 42 segments, measuring 14.5 mm long for 42 chaetigers and 0.63 mm wide at chaetiger 1. Pale yellow colour in alcohol. Prostomium angular, bottle-shaped with broadly rounded anterior margin, prostomial peaks normally absent (but two small peaks observed in one of the CROZET specimens); slender caruncle extending to anterior margin of chaetiger 2 (Fig.3a); eyes not observed. Peristomium well developed, encircling prostomium closely like a collar, partially fused to chaetiger 1, forming low lateral wings (Fig3.a).

Four pairs of branchiae present on chaetigers 2–5. First pair longest, reaching to chaetiger 10, very slender and cylindrical, although slightly flattened near base and with slender, slightly curled tips; surface mostly smooth to slightly wrinkled (Fig.2.1a); very few (1–3) pinnules near base; fourth pair of branchiae similar to first pair but about half the length, apinnate, no rudimentary pinnules observed. Branchial pairs 2 and 3 short, fleshy, foliaceous, wider at base, tapering into somewhat swollen tip, laterally ciliated, both pairs slightly shorter than accompanying notopodial lamellae, in dorsal view both pairs covered by enlarged notopodial lamellae. All branchial pairs situated lateral and slightly posterior to notopodial lamellae.

Anterior notopodial lamellae from chaetiger 2–20 (holotype) generally enlarged, subtriangular, largest on branchial segments, particularly on chaetigers 3 and 4; more narrow on chaetiger 5; from chaetiger 6 increasing in width, becoming nearly square by chaetiger 10; after chaetiger 20 greatly reduced in size, becoming flattened assuming broadly ovoid shape with sharp pointed dorsal end and broad round posterior ventral end (Fig.2.1e chaetiger 22). Dorsal crests on chaetigers 5–20.

Neuropodial lamellae small on chaetiger 1, largest on branchial chaetigers, then gradually becoming reduced in size; lamellae on chaetiger 2 fan-shaped with rounded corners (Fig 2.1a); lamellae on chaetiger 3 also fan-like possessing well developed ventral tip (Fig. 2.1b); lamellae on chaetiger 4 rounded; lamellae on chaetiger 5 low,

rectangular (Fig. 2.1c); from chaetiger 6 more rounded ventrally, starting to assume broadly ovoid in shape with somewhat pointed ventral tip (Fig. 2e–f); similarly shaped through chaetiger 42, with lamellae becoming more flattened and pointed both dorsally and ventrally (Fig. 2.1f). Interparapodial pouches absent (Fig. 3b).



**FIGURE 2.** Profiles of anterior chaetigers of the *Prionospio* species described.

1) *Prionospio amarsupiata* sp. nov. a) Chaetiger 2; b) Chaetiger 3; c) Chaetiger 4; d) Chaetiger 5; e) Chaetiger 10; f) Chaetiger 22; scale bar = 100  $\mu$ m.

2) *Prionospio vallensis* sp. nov. a) Chaetiger 2; b) Chaetiger 3; c) Chaetiger 4; d) Chaetiger 5; scale bar = 200  $\mu$ m.

3) *Prionospio branchilucida* sp. nov. a) Chaetiger 2; b) Chaetiger 3, the ventral lamellae can often be folded over forming a hollow and making the edge of the lamellae appear square in profile; c) Chaetiger 4; d) Chaetiger 5; e) Chaetiger 14; scale bar = 200  $\mu$ m.

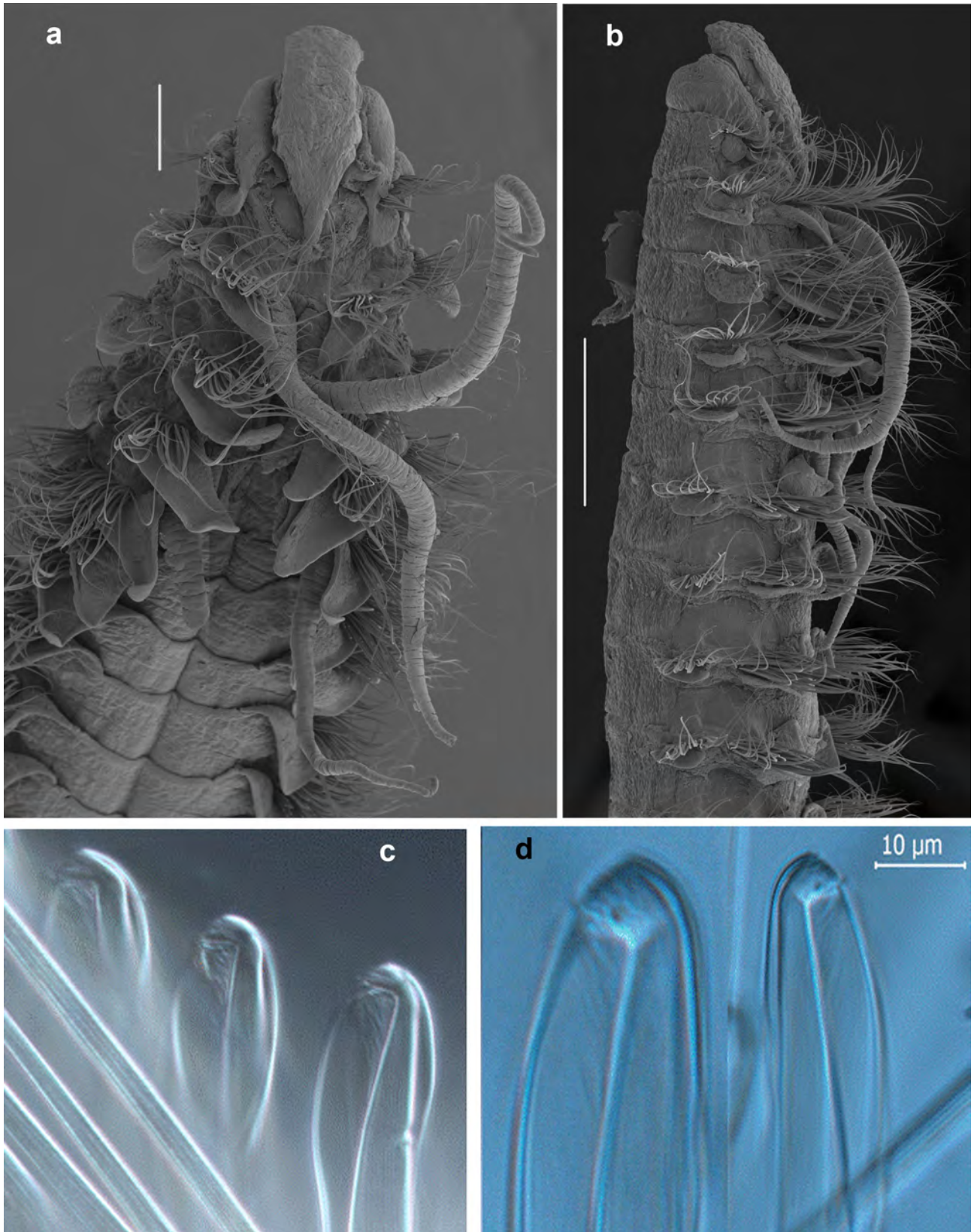
4) *Prionospio hermesia* sp. nov. a) Chaetiger 2; b) Chaetiger 3; c) Chaetiger 4; d) Chaetiger 5; e) Chaetiger 8; scale bar = 100  $\mu$ m.

5) *Prionospio kaplani* sp. nov. specimen 735 a) Chaetiger 2; b) Chaetiger 3 showing both shapes of ventral lamellae; c) Chaetiger 4 also showing two basic morphologies of ventral lamellae; d) Chaetiger 5; e) Chaetiger 8 also showing alternative morphology of ventral lamellae; f) Chaetiger 14; scale bar = 200  $\mu$ m.

6) *Prionospio* sp. C a) Chaetiger 2; b) Chaetiger 3; c) Chaetiger 4; d) Chaetiger 12; e) Chaetiger 20; scale bar = 100  $\mu$ m.

Notopodia in anterior region with four rows of dense, yellow-hued capillaries, anterior neuropodial capillaries arranged in two rows. Sabre chaetae and neuropodial hooks start on chaetiger 19 in holotype and other specimens of similar size, but on chaetiger 18 in smaller specimens. Sabre chaetae long, slender, gently curved, often broken; anterior half is lightly granulated; 1 to 2 per fascicle. Neuropodial hooks up to 10 per fascicle. Neuropodial hooks long, slender, with round, inflated primary hood and striated secondary hood; shaft very constricted just below multidentate head, with six pairs of small teeth above the main fang (Fig. 3c,d). Notopodial hooks not present in 42 chaetigers. Pygidium unknown.





**FIGURE 3.** *Prionospio amarsupiata* sp. nov. a) Dorsal view of anterior chaetigers; scale bar = 200 µm. b) Lateral view of anterior chaetigers; scale bar = 500 µm; c) Photomicrograph of a group of neuropodial hooded hooks. d) Photomicrograph close-up of neuropodial hooded hooks; scale bar = 10 µm, applies to c) and d).

**Methyl green pattern.** Prostomium, peristomium and the edge of notopodial and neuropodial lamellae on chaetiger 1–4 stained strongly, thereafter only edges of notopodial lamellae and dorsal crest with faint stain.

**Remarks.** This species closely resembles *Prionospio ehlersi* Fauvel, 1928 in the shape of the prostomium and peristomium and the chaetiger where the sabre chaetae and neuropodial hooks appear; neuropodial hooded hooks and sabre chaetae begin on chaetigers 18–19 in *P. amarsupiata* **sp. nov.**, which is within the range of their occurrence on chaetigers 18–22 in *P. ehlersi*. The major difference is in the small number of pinnules on first branchial pair and lack of pouches in *Prionospio amarsupiata* **sp. nov.** This feature has been encountered in specimens collected from Crozet as well as in Portuguese canyons, EqPac and PAP specimens. It seems likely, therefore, that reduction in number of pinnules is a real feature of this species rather than a loss of pinnules, damaged during the handling of the specimens

Interestingly, a species identified as *Prionospio* cf. *ehlersi* but lacking pouches was reported by Blake (1983) from the deep sea in the Antarctic and Chile. In a later publication Blake (1996) concluded that: “...these widely scattered deep-sea records of a *P. ehlersi*-like species that lack interparapodial pouches represent at least one, yet undescribed species.” It is likely that at least some of Blake’s specimens are *P. amarsupiata* **sp. nov.** In additional deep-sea material examined, Blake encountered a specimen that lacked pouches but had a full branchial set (first pair short and pinnate, pairs 2, 3, and 4 short, all the same length, thick, and apinnate). This particular specimen is clearly different from *P. amarsupiata* **sp. nov.** based on its branchial form.

Some specimens collected from HERMES canyons were reproductive with eggs, the largest of which were approximately 70 microns in diameter.

**Etymology.** *amarsupiata*, meaning “lacking pouches”; from the Latin *marsupium*, a pouch; reference is to the lack of interparapodial pouches in this species.

**Distribution.** This species is widespread in the deep sea; confirmed records indicate the species has been recorded from the Nazaré, Setúbal and Cascais canyons along the Portuguese margin (3199–4488 m), Crozet Island (3500 m), the Equatorial Pacific (EqPac), and the Northeast Atlantic (Cape Verde Abyssal Plain 4500 m, Madeira Abyssal Plain 4800 m).

### ***Prionospio vallensis* sp. nov. Neal & Paterson**

(Figures 1, 2.2, 4, 8g)

*Prionospio* sp G Curdia *et al.* 2004:

*Prionospio* sp A Paterson *et al.* 2011: 2453

**Material examined:** 1035 specimens examined.

**Holotype:** RRS *Charles Darwin*, cruise 179 April–May 2006, Setúbal canyon St. 56859#1, 39°35.58′N 10°20.00′W 4418m, megacore (NHMUK 2015:1040).

**Paratypes:** *Portuguese margin canyon: Nazaré canyon* RRS Discovery 297 August 2005, St.15755#1 39°30.62′N 09°56.19′W 3461m, 175 individuals; St.15760#1 39°30.02′N 09°56.17′W 3465m, 54 individuals; St.15762#1 39°30.02′N 09°56.22′W 3464m, 103 individuals; St.15758#2 39°34.94′N 10°19.00′W 4332m, 26 individuals; St. 15758#6 39°34.99′N 10°19.00′W 4335m, 65 individuals; St.15765#2 39°35.00′N 10°19.04′W 4336m, 39 individuals.

RRS *Charles Darwin* 179, April/May 2006, St. 56847#6 39°35.57′N 10°19.99′W 4403m, 33 individuals; St. 56847#7 39° 35.55′N 10° 20.06′W 4404m 33 individuals; St. 56851#1 39° 29.99′N 09° 55.97′W 3517m, 36 individuals; St. 56851#2 39°29.99′N 09°56.01′W 3517m, 76 individuals; St.56856#1 39° 29.95′N 09° 56.00′W 3519m, 40 individuals; St. 56856#2 39°30.00′N 09° 55.98′W 3522m 49 individuals; St. 56859#1 39°35.58′N 10°20.00′W 4418m, 37 individuals; St. 56861#1 39°35.57′N 10°20.02′W 4404m, 44 individuals.

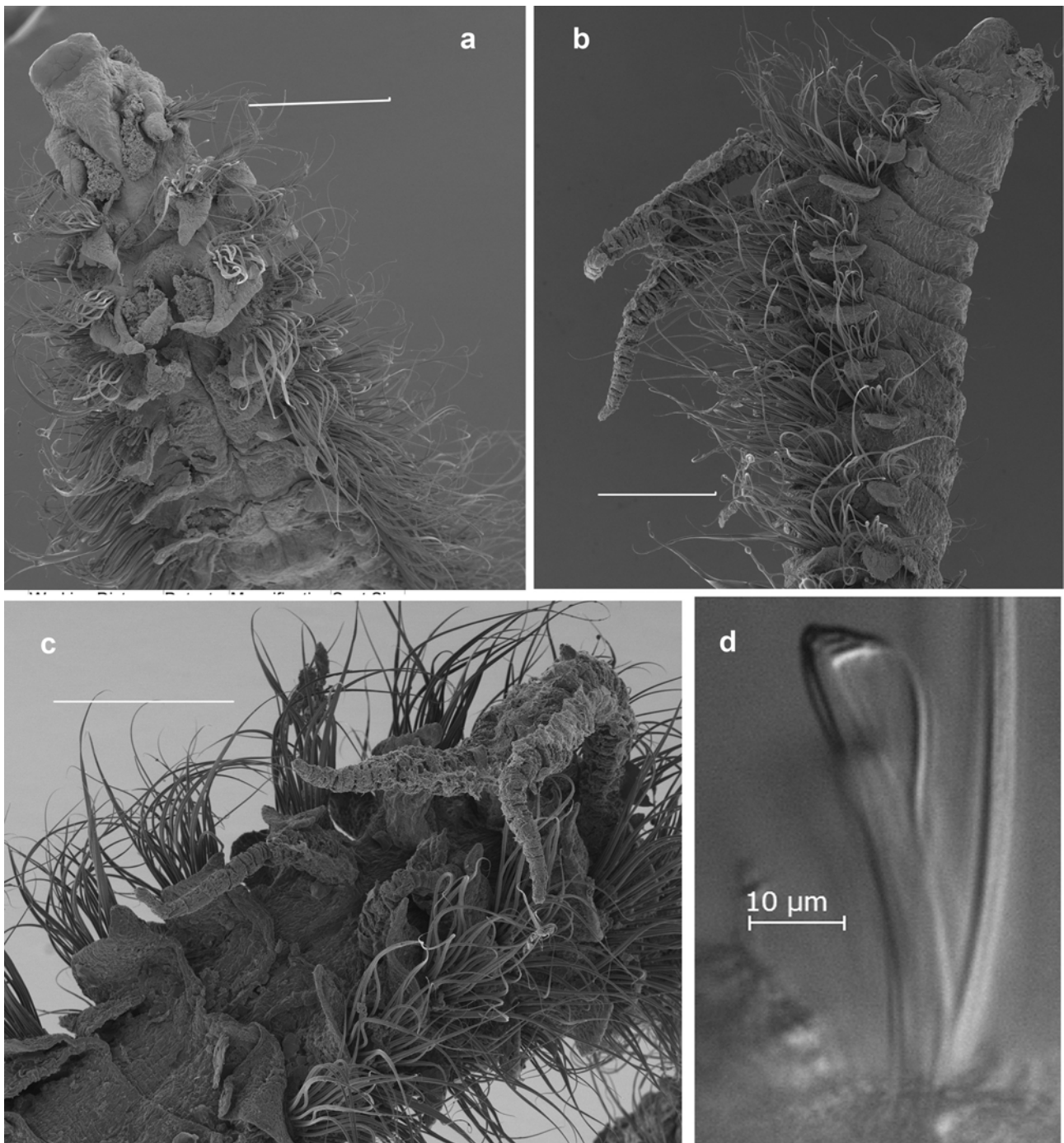
*Setúbal canyon:* RRS *Charles Darwin* 179 April/May 2006, St. 56804#5 38°09.27′N 09°36.93′W 3275m, 75 individuals; St. 56804#6 38°09.26′N 09°36.94′W 3275m, 48 individuals; St. 56806#1 38°09.29′N 09°36.96′W 3275m, 60 individuals; St. 56810#1 38°09.22′N 09°37.02′W 3224m, 23 individuals; St. 56816#1 38°09.27′N 09°36.94′W 3275m, 37 individuals.

*Cascais canyon:* RRS *Charles Darwin* 179 April/May 2006, St. 56821#1 38°17.96′N 09°46.87′W 3219m, 1 individual; St. 56823#2 38°18.01′N 09°47.02′W 3218m, 2 individuals; St. 56823#3 38°17.99′N 09°47.07′W 3219m, 2 individual; St. 56828#1 38°18.02′N 09°46.98′W 3199m, 3 individuals; St. 56837#7 38.3748° -9.8920°, 4243 m, 3 individuals.



**Other material studied:** *Prionospio laciniosa* Maciolek, 1985; paratypes (USNM 67674-75).

**Diagnostic features.** Wrinkled branchiae on chaetigers 2 and 5, rectangular prostomium, dorsal crests from chaetiger 6 extending to beyond chaetiger 20, distal ends of proximal dorsal lamellae bent toward the mid-line and produced into slender tips.



**FIGURE 4.** *Prionospio vallensis* sp. nov. a) Dorsal view of anterior chaetigers; scale bar = 200 µm. b) Lateral view of anterior chaetigers; scale bar = 200 µm. c) Detail of branchial arrangement; scale bar = 200 µm. d) Photomicrograph of neuropodial hooded hooks; scale bar = 10 µm.

**Description.** A small and slender species, holotype complete with 65 chaetigers, measuring 12.4 mm long and 0.25 mm wide at chaetiger 1. Colour in alcohol pale yellow. Prostomium rectangular for about 2/3 of length, then tapering into caruncle reaching to anterior margin of chaetiger 2; posterior portion surrounded by heavily ciliated nuchal organs (Fig. 4a); anterior margin truncated (Fig.4), prostomial peaks absent; eyes absent (1 pair of

colourless eyes present in some specimens, positioned on prostomium just before caruncle, best observed on stained specimens). Peristomium well developed ventrally, forming distinct lateral wings; chaetiger 1 reduced, dorsally fused to peristomium.

Branchiae present on chaetigers 2–5, 4 pairs, all apinnate, but wrinkled (Fig. 4 b,c). First pair longest, reaching to the anterior margin of chaetiger 8, approximately six times longer than the corresponding notopodial lamellae, distinctly wrinkled with deep grooves, thickened at the base, then cylindrical, tapering into blunt tip (in some specimens the first pair rather slender, still wrinkled but without deep grooves, possibly regenerating), heavily ciliated; pair 4 similar to pair 1 but shorter, by a ratio of 1:4, approximately four times longer than the corresponding notopodial lamellae; pairs 2 and 3 short and heavily ciliated, only slightly longer than notopodial lamellae, with wrinkled surface, fleshy and triangular, wider at base and tapering distally, both pairs are partially covered by enlarged notopodial lamellae; all branchiae free from notopodial lamellae, positioned laterally and slightly posteriorly in relation to inner edge of notopodial lamellae (branchial pairs 1 and 4 easily lost and missing in majority of specimens).

Notopodial lamellae on chaetiger 1 well developed (Fig. 2.2a), rounded with very produced tip pointed dorsally; lamellae largest on branchial segments, particularly on chaetigers 3 and 4, subtriangular and somewhat bent, with tips pointing to the midline of dorsum (Fig. 2.2 b,c), notopodial lamellae on chaetiger 6 becoming smaller; from chaetiger 7 lamellae small, triangular, pointed distally, often bent, in mid-body segments becoming low, globular (Fig. 2.2d). Distinct dorsal crests present from chaetiger 6 and on subsequent chaetigers (Fig. 4a) to beyond chaetiger 20. Interparapodial pouches absent.

Neuropodial lamellae largest in branchial segments; small and rounded in chaetiger 1, neuropodia of chaetiger 2 square-shaped, similar in shape but with distinct tip pointing dorsally on chaetiger 3 (Fig. 2.2), in chaetigers 4 and 5 tip not protruded, lamellae square to slightly rounded in shape; from chaetiger 6 becoming small (low rising) and distinctly globular (Fig. 1.2d).

Anterior chaetae all capillaries, granulated, forming dense fascicles, arranged in two rows in both noto- and neuropodia, neuropodial capillaries become long in middle and posterior segments reaching over 4–5 chaetigers in length. Sabre chaetae first occur in neuropodia of chaetiger 10, up to two per fascicle, robust, curved, heavily granulated. Neuropodial hooks first occur on chaetiger 12 but occasionally start from chaetiger 13, up to eight per fascicle; primary hood inflated and somewhat rectangular in shape, secondary hood present and well developed; each hook with six pairs of smaller teeth sequentially reduced in size above the main fang. Notopodial hooks appear around segment 45 (holotype damaged in this section, all other specimens examined were incomplete and notopodial hooks not observed), two per fascicle, long and slender.

Pygidium conical, without any appendages, but these might have been lost.

**Methyl green pattern.** The borders of prostomium, including caruncle, peristomium, and dorsal crests on segments 12–20 stain strongly.

**Remarks.** *Prionospio vallensis* **sp. nov.** is characterised by wrinkled branchiae on segments 2 and 5. *Prionospio fauchaldi* and *P. laciniosa*, both described by Maciolek, 1985, also possess wrinkled branchiae. *Prionospio fauchaldi* is recorded from the West Atlantic, SE coast of Africa in 530–4950 m and in the western Pacific in approximately 2500 to 3000 m (Blake et al. 2009), and *P. laciniosa* is recorded from the west coast of Africa at 527–542m. *Prionospio vallensis* **sp. nov.** further resembles *P. fauchaldi* by having a similar shape of prostomium and peristomium, with sabre chaetae and neuropodial hooks starting in the same segments. The major differences are that in *P. fauchaldi* the first and fourth pair of branchiae are of the same length, while the first pair is longer than fourth in *P. vallensis* **sp. nov.**; sabre chaetae are slender in *P. fauchaldi* but robust in *P. vallensis* **sp. nov.**; and *P. fauchaldi* possesses extremely long capillaries on the third chaetiger, but these are lacking in *P. vallensis* **sp. nov.**

*Prionospio vallensis* **sp. nov.** is most similar to *P. laciniosa*, which also has the first wrinkled pair of branchiae longer than the fourth, but differs from *P. vallensis* **sp. nov.** in having a triangular rather than rectangular prostomium and presence of distinct dorsal flaps, which were not seen in *P. vallensis* **sp. nov.** The dorsal crests in *P. laciniosa* are present only on chaetigers 5–13 while in *P. vallensis* **sp. nov.** they start on chaetiger 6 and continue beyond chaetiger 20. The shape of notopodial lamellae of the branchial region is also different, whilst subtriangular in both species, the distal ends are bent and directed to the middle and extend into slender tips in *P. vallensis* **sp. nov.**, whereas in *P. laciniosa* this bend is less prominent and the tips are more robust. The sabre chaetae in *P. vallensis* **sp. nov.** are more robust and shorter than in *P. laciniosa*. The specimens of both species were of similar

size, therefore these differences, particularly presence/absence of dorsal flaps are unlikely to be of result of different developmental stages.

**Etymology.** *vallensis* from the Latin *valles*, meaning valley, the closest Latin expression for canyon.

**Ecology.** *P. vallensis* **sp. nov.** was previously recorded from Setúbal canyon at 3400 m during the RRS *Discovery* cruise 186 in 1989; although not formally described, it was recorded as Spionidae H. It was the second most abundant species in that study. Examination of photographs of polychaete specimens collected in 1999 during OMEX II from Nazaré canyon and reported by Curdia *et al.* (2004) as *Prionospio* sp. G is likely to be *Prionospio vallensis*. It was reported as the most abundant macrofaunal species at 3514 m and 4141 m.

*Prionospio vallensis* **sp. nov.** was the single most abundant polychaete in Portuguese canyons, achieving densities of 784 ind./m<sup>2</sup> in Setúbal canyon (3400 m) and up to 918 ind./m<sup>2</sup> in Nazaré canyon (3400 m) (Cunha *et al.* 2011; Paterson *et al.* 2011). The difference in the abundance between our study and previous ones may be a reflection of different sampling design used during RRS *Discovery* cruise 186, where macrofauna was sieved on 300-micron mesh. However, it was not present in Portuguese canyon samples collected at 1000 m or on the Tagus Abyssal Plain, which is adjacent to Setúbal and Cascais canyons. It is possible that this is a deep canyon “specialist” able to utilize the organically enriched sediments found within the canyon (compared to similar non-canyon depths) and/or rapidly occupy sediments following frequent disturbances, which occur within canyons. Data from previous studies in these canyons (Gage *et al.* 1995; Curdia *et al.* 2004) suggest that *P. vallensis* **sp. nov.** has been able to maintain high-density populations in Portuguese canyons on more than a decadal timescale (sampling in 1989, 1999, 2005, 2006).

**Distribution.** Nazaré, Setúbal, and Cascais canyons along the Portuguese margin, 3199–4419 m.

### ***Prionospio branchilucida* sp. nov. Altamira, Glover, & Paterson**

(Figure 1, 2.3, 5, 8a, Table 2)

**Material examined:** 41 specimens examined in total.

**Holotype:** Kaplan Clarion-Clipperton Fracture Zone East Site, RV *New Horizon*, February, March 2003, BC 830 14°55.85'N 119°2.97'W 4076 m. specimen KP77 (NHMUK 2015: 1118).

**Paratypes.** Kaplan Clipperton-Clarion Fracture Zone East Site: RV *New Horizon*, February–March 2003, BC 847 15°1.98'N 119°0.02'W 4078 m, 1 individual.

Kaplan CCFZ Central Site (IFREMER Nodinaut campaign): RV *L'Atalante*, May–June 2004, BC 876/KGS17 14°3.4024'N 130°5.5851'W 5012 m, 2 individuals (KP319, KP333; BC 877/KGS19 14°2.9823'N 130°5.6489'W 5027 m, 3 individuals (KP338, KP348), KP; BC 879/KGS26 14°3.3980'N 130°5.5828'W 5012 m, 1 individual (KP368); BC 880/KGS27 14°2.7524'N 130°5.4972'W 5041 m, 1 individuals (KP379); BC 878/KGS20 14°3.4687'N 130°5.5994'W 5012 m, 1 individual (KP443).

ABYSSLINE 01 CCFZ: RV *Melville* October 2013: Stn A, 1352.900 N 11628.0 W 4171 m, 1 individual (CRS 1493, BC\_03, in 2–5 cm fraction); Stn C, 1347.601 N 11642.185 W 4081 m, 1 individual (CRS 1504, BC\_05, in 0–2 cm fraction); Stn G, 1345.727 N 11627.824 W 4110 m, 2 individuals (CRS 1529, BC\_09, in 5–10 cm fraction); Stn I, 1345.001 N 11630.799 W 4036 m, 2 individuals (CRS 1532, BC\_10, in 0–2 cm fraction); Stn J, 1354.113 N 11635.442 W 4163 m, 2 individuals (CRS 1542, BC\_13, in 0–2 cm and 2–5 cm fractions); Stn L, 1343.597 N 11640.200 W 4160 m, 1 individual (CRS 1545, BC\_14, 0–2 cm sub-sample).

Equatorial Pacific (EqPac): RV *Thomas Thompson*: EqPac November 1992 BC15 5°N 140°W m. 4 individuals

Cap Verde Abyssal Plain: RSS *Discovery* 12600#10 September 1993, 0–1 cm, 21° 3.2' N 31° 11.0' W 4543 m, 4 individuals;

12600#28, October 1993, 0–1 cm, 21° 4.8' N 31° 11.1' W 4613 m, 1 individual;

12600#32, October 1993, 0–1 cm, 21° 3.6' N 31° 10.0' W 4545 m, 1 individual.

Madeira Abyssal Plain: RSS *Discovery* 12174 #11 August 1990, 1–3 cm, 31° 4.4' N 21° 10.3' W 4936 m, 1 individual; 12174#11 August 1990, 3–5 cm, 31° 4.4' N 21° 10.3' W 4936 m, 1 individual; 12174#16 August 1990, 0–1 cm, 31° 4.9' N 21° 9.4 W 4947 m, 1 individual; 12174#16 August 1990, 1–3cm, 31° 4.9' N 21° 9.4 W 4947 m, 1 individual; 12174#43 August 1990, 3–5 cm, 31° 5.3' N 21° 10.9' W 4947 m, 1 individual; 12174#53 August 1990, 3–5 cm 31° 5.2' N 21° 1.2' W 4942 m, 1 individual; 12174#60, August 1990, 0–1 cm 31° 6.0' N 21° 10.0'

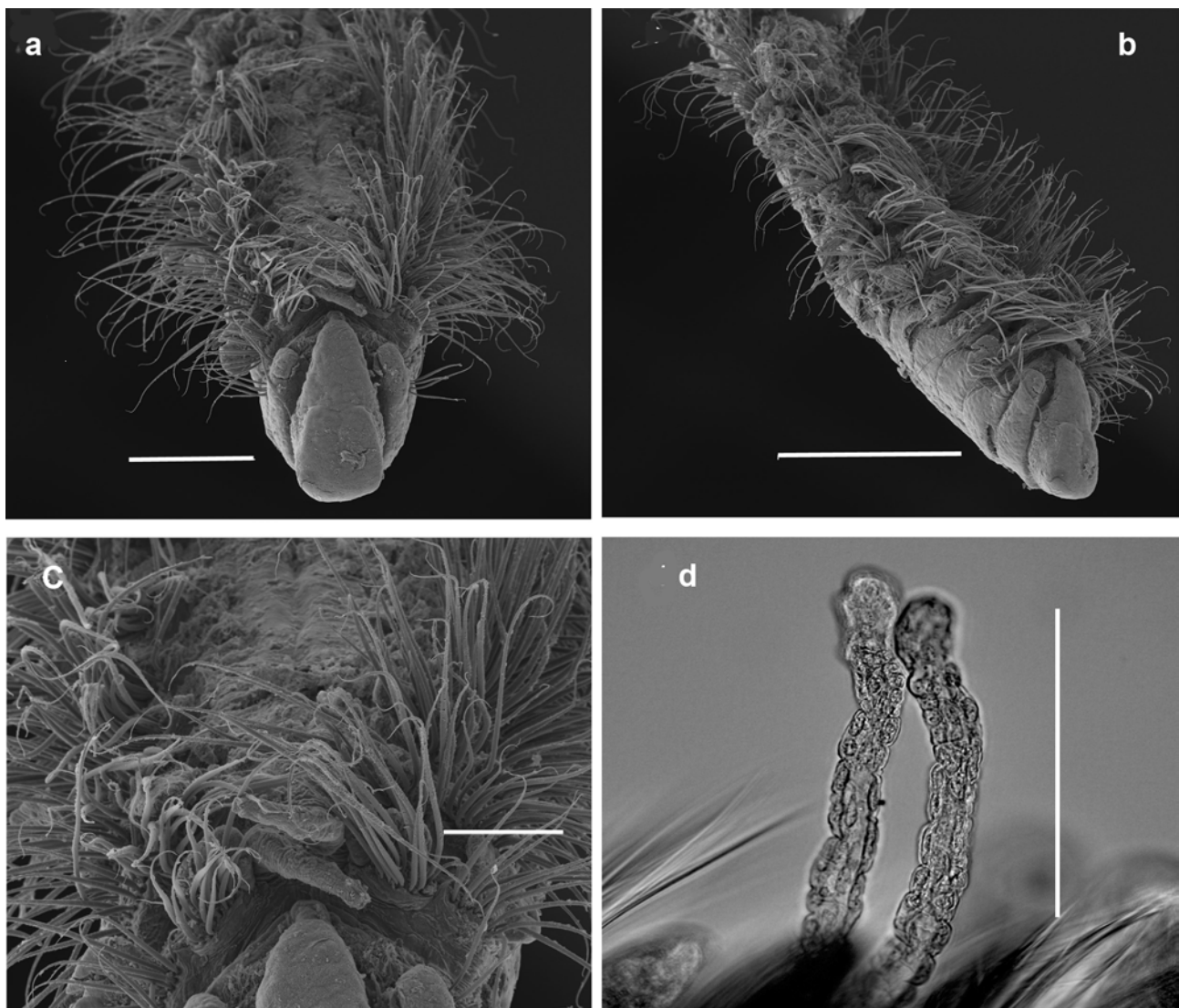
W 4947 m, 2 individuals; 12174#60, August 1990, 1–3 cm 31° 6.0' N 21° 10.0' W 4947 m, 1 individual; 12174#60, August 1990, 3–5 cm 31° 6.0' N 21° 10.0' W 4947 m, 2 individuals.

**Other material studied.** *Kaplan Clipperton-Clarion Fracture Zone East Site*: RV *New Horizon*, February–March 2003, BC 822 14°57.34N 119°1.18W 4038 m, 1 individual; BC 834 14°59.95N 118°58.07W 3982 m, 1 individual;

**Diagnostic features.** Two pairs of branchiae on chaetigers 2 and 3, sabre chaetae lacking, dorsal crests from chaetiger 7, neuropodial hooded hooks from chaetiger 11.

**Description.** Body cylindrical, narrow throughout; holotype 1.86 mm long for 20 chaetigers, (0.62 mm up to chaetiger 10); 0.08 mm wide at chaetiger 1. Prostomium rectangular with flat, entire anterior margin; one pair prostomial peaks present; caruncle short with rounded apex, extending to anterior margin of chaetiger 2. Eyes absent. Peristomium incomplete dorsally, not forming lateral wings, separate from chaetiger 1 (Fig.5a).

Branchiae from chaetiger 2, two pairs, very small. Branchiae on chaetiger 2 digitiform, blunt-tipped, inserted lateral and slightly posterior to dorsal lamellae (Fig. 5c,d); branchiae approximately one-half chaetiger long, subequal to notopodial lamellae; branchiae on chaetiger 3 conical, inserted posterior to dorsal lamellae and obscured by them, one quarter the length of lamellae (Fig. 2.3b)



**FIGURE 5.** *Prionospio branchilucida* sp. nov. a) Dorsal view of anterior segment; scale bar = 100 µm. b) Lateral view of anterior chaetigers; scale bar = 200 µm. c) Detail dorsal view of anterior chaetigers showing the branchiae; scale bar = 50 µm. d) Photomicrograph showing the first pair of branchiae; bar scale = 50 µm.

Notopodial lamellae start on chaetiger 2, sub-quadrangular, slightly angled toward dorsal midline; largest on chaetiger 3, sub-quadrangular with slightly produced tips overlapping dorsal midline, three times as long as lamellae of chaetiger 2; thereafter, notopodial lamellae decrease in size, becoming low and subtriangular by chaetiger 7 (Fig. 2.3f). Dorsal crests present from chaetigers 7 to chaetiger 17.

Neuropodial lamellae start on chaetiger 1, papilliform, length equal to one-fifth chaetiger length; neuropodial lamellae on chaetigers 2–5 leaf-like, narrow with short tips; neuropodial lamellae largest on chaetiger 3, length equal to chaetiger length and nearly twice that of chaetiger 2, neuropodial lamellae thereafter decreasing in length and increasing in width, becoming broadly ovoid by chaetiger 9. Interparapodial pouches absent.

Notochaetae limbate capillaries, long, inserted in two densely packed rows from chaetigers 2–8 with up to 12 chaetae per row; thereafter, notochaetae reduced in number and density; all notochaetae angle forward on chaetigers 1–8 and anterior row always with shorter. Neurochaetae limbate capillaries, inserted in two distinct rows to chaetiger 8, up to eight chaetae per row, anterior row always shorter; thereafter, number of chaetae decrease, rows become indistinct. Neuropodial sabre chaetae not observed through 20 chaetigers (all specimens incomplete, the longest fragment comprises 30 chaetigers). Neuropodial hooded hooks present from chaetiger 11; shaft narrow with slender main fang, surmounted by two to three fine small teeth in one row, up to six chaetae per fascicle, inner hood absent; notopodial hooded hooks not observed. Pygidium not observed.

**Methyl green pattern.** Banding on subdistal portion of prostomium and distal portion of peristomium; partial banding on anterior chaetigers, beginning at bases of notopodial lamellae, and encircling venter

**Remarks.** This species is characterised by the small translucent digitiform branchiae on chaetiger 2, having only three pairs of branchiae and by the lack of sabre chaetae.

Few species of *Prionospio* have only three pairs of branchiae, a character more commonly found in the genus *Paraprionospio*. Only *P. aucklandica* Augener, 1923 has been recorded with three pairs but in that species the branchiae are all pinnate, dorsal crests occur only on chaetiger 7, and sabre chaetae are present from chaetiger 10. *P. branchilucida* **sp. nov.** resembles *P. hermesia* **sp. nov.** in apinnate branchiae and double rows of anterior chaetae; the two species differ in the number of branchiae, the form of the first pair of branchiae, extent of caruncle, and relative size of branchiae and notolamellae (see Table 2).

**TABLE 2.** Comparison of *Prionospio branchilucida* **sp. nov.**, *P. hermesia* **sp. nov.** and *P. kaplani* **sp. nov.**. Abbreviations: Br=branchiae Ch=chaetiger; Ch2: 0.5XDL = branchiae on chaetiger two are half the size of the dorsal lamellae (DL); HH = hooded hooks.

Species	No of branchiae	Shape of prostomium	Extent of caruncle	Br length in relation to DL	Largest DL	Dorsal crests	Neuropodial HH
<i>P. branchilucida</i>	3	Rounded	Anterior margin Ch2	Ch2: 3-4XDL CH3: 0.3XDL CH4: 0.5XDL	Ch 3	Ch10(12)–13(16)	Ch11
<i>P. hermesia</i>	2	Rounded, oval	Anterior margin Ch1	Ch2: 2XDL; Ch3: 0.5XDL	Ch 3	Ch8	Ch13–14
<i>P. kaplani</i>	2	Rectangular	Anterior margin Ch2	Ch2: 0.5XDL Ch3: 0.3XDL	Ch3	Ch7–17	Ch14–17

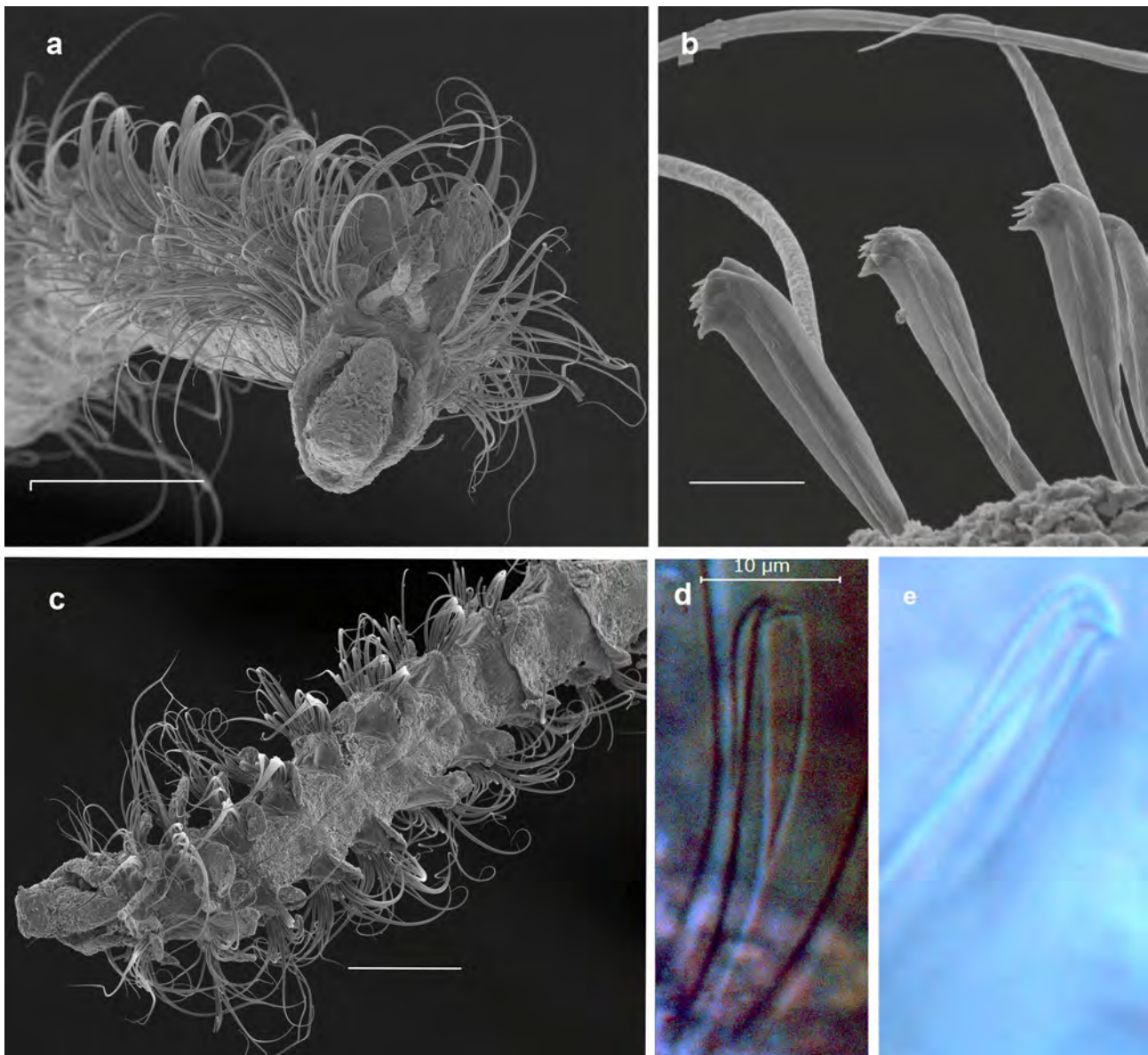
**Etymology.** *branchia*—a gill and *lucida*—meaning clear, referring to the transparency of the first pair of branchiae.

**Distribution.** This species has been recorded from the Central Pacific, the Equatorial Pacific (EqPac), and the Madeira and Cap Verde Abyssal Plains in the Northeast Atlantic. Bathymetric distribution ranges from 4800 m to 5041 m.

***Prionospio hermesia* sp. nov. Neal & Paterson**  
(Figures 1, 2.4, 6, 8f, Table 2)

**Material examined:** 9 specimens examined in total.





**FIGURE 6.** *Prionospio hermesia* sp. nov. a) Frontal view showing the first pair of branchiae; scale bar = 100 µm. b) Neuropodial multidentate hooded hooks; scale bar = 5 µm. c) Dorsal view of anterior chaetigers; scale bar = 100 µm. d) Photomicrograph of bidentate hook; scale bar = 10 µm. e) Photomicrograph of multidentate hook (x1000).

**Holotype:** Setúbal canyon, RSS *Charles Darwin* 179, April–May 2006, St. 56804#6, 38°09.26 N, 9°36.94 W, 3275 m (NHMUK 2015:1041).

**Paratypes.** *Nazaré canyon*, RSS *Discovery* 297, August 2005, St. 15760#1, 39°30.02 N, 09°56.17 W, 3465 m, 2 individuals; St. 15762#1, 39°30.02 N, 09°56.22 W, 3464 m, 1 individual ; St. 15758#2, 39°34.94 N, 10°19.00 W, 4332 m, 1 individual.

*Nazaré canyon*, RSS *Charles Darwin* 179, April/May 2006, St. 56851#1, 39°29.99' N, 9°55.97' W, 3517m, 2 individuals.

*Setúbal canyon*, RSS *Charles Darwin* 179, April/May 2006, St. 56816#1, 38°09.27' N, 9.36.94'W, 3275m, 1 individual.

*Cascais canyon*, RSS *Charles Darwin* 179, April/May 2006, St.56821#2, 38°17.97' N, 9°46.89' W, 3214m, 1 individual.

**Diagnostic features.** Two pairs of branchiae; lack of sabre chaetae; hooded hooks bi- or tridentate.

**Description.** Very small and slender species, holotype incomplete with 53 chaetigers, measuring 5.65 mm long and 0.08 mm wide at chaetiger 1. Colour in alcohol pale yellow. Body narrow and cylindrical, of uniform width

throughout. Prostomium oval, anteriorly slightly rounded, prostomial margin entire, prostomial peaks absent, posteriorly elongated into short blunt caruncle, extending to anterior of chaetiger 1 (Fig. 6a–b); eyes not observed. Peristomium well developed, ventrally and laterally distinct, dorsally partially fused to chaetiger 1, forming a collar around prostomium, without forming distinct lateral wings.

Branchiae 2 pairs, on chaetigers 2 and 3, both pairs apinnate with surface smooth to slightly wrinkled (Fig. 6a,b); first pair longest, very slender, cylindrical, at least twice the length of corresponding notopodial lamellae, inserted laterally to the base of notopodial lamellae, but not connected to it (Fig 6a); second pair short, about half the length of corresponding notopodial lamellae and one-third the length of first branchial pair, attached near the base of notopodial lamellae (Fig. 2.4b).

Notopodial lamellae on chaetiger 1 not developed; lamellae small, subquadrangular on chaetiger 2; lamellae greatly enlarged on chaetiger 3, subtriangular, the distal tip bent and pointed to the midline of the dorsum (Fig. 2.4b), in subsequent chaetigers notopodial lamellae reducing in size, becoming rounded. Dorsal crests from chaetiger 8 (Fig. 6c) to approximately chaetiger 25.

Neuropodial lamellae on chaetiger 1 not developed, thereafter well developed if small and rounded on all segments, with the exception of chaetiger 3, on which they are shifted dorsally (Fig. 2.4), enlarged (at least twice the size of neuropodial lamellae on other segments), oar-shaped, sometimes extending from body horizontally.

Capillary chaetae particularly dense in anterior region, arranged in two rows in both noto- and neuropodia, capillaries in anterior row very long capillaries in posterior row shorter, all lightly granulated, limbate. Sabre chaetae absent. Neuropodial hooded hooks present from chaetiger 13 in holotype, from chaetiger 14 in other specimens, often only single hooks present at first but up to seven hooks per fascicle in subsequent chaetigers; primary hood rounded, tightly follows the head of the hooks, secondary hood present and well developed; some hooks bidentate with large main fang and smaller secondary tooth, others appear to be multidentate (at least tridentate) with main fang and at least two smaller teeth above, arranged in a single row. Notopodial hooks present singly from chaetiger 48. Pygidium unknown.

**Methyl green pattern:** The anterior half of prostomium and peristomium stain strongly, the margins of the notopodial and neuropodial lamellae on chaetigers 4–14 stain less intensely.

**Remarks.** The distinguishing feature of this species is that it has only two pairs of branchiae. This species has affinities with *Prionospio branchilucida* **sp. nov.** and *P. kaplani* **sp. nov.** from abyssal plains. Lack of sabre chaetae is unusual, but was encountered in all three species (*P. hermesia* **sp. nov.**, *P. branchilucida* **sp. nov.**, and *P. kaplani* **sp. nov.**). Further similarity with *Prionospio kaplani* **sp. nov.** is that it also possesses a combination of bidentate and multidentate hooks (1+3 combination), and these hooks also appear to be flattened in SEM images (unlike the chunky, more inflated style of hooks in other *Prionospio* species). In both species dorsal crests begin on segment 8, but only a single pair of very short branchiae on the second chaetiger was found in *P. kaplani* **sp. nov.** compared with in *P. hermesia* **sp. nov.** *Prionospio branchilucida* **sp. nov.** has a prostomium similar to that of *P. hermesia* **sp. nov.** and has similar branchiae on the second chaetiger, but at least three pairs of branchiae were confirmed to be present in *P. branchilucida* **sp. nov.**, hooks appear to be more like the usual shape found in *Prionospio* in SEM images, and the dorsal crests begin after chaetiger 8.

**Etymology.** *P. hermesia* **sp. nov.** named after the research programme HERMES.

**Distribution.** *P. hermesia* **sp. nov.** has been recorded from the Nazaré, Setúbal and Cascais canyons of the Portuguese margin at depths of 3214–4364 m.

### ***Prionospio kaplani* sp. nov. Altamira, Glover, & Paterson**

(Figure 1, 2.5, 7, 8b, Table 2)

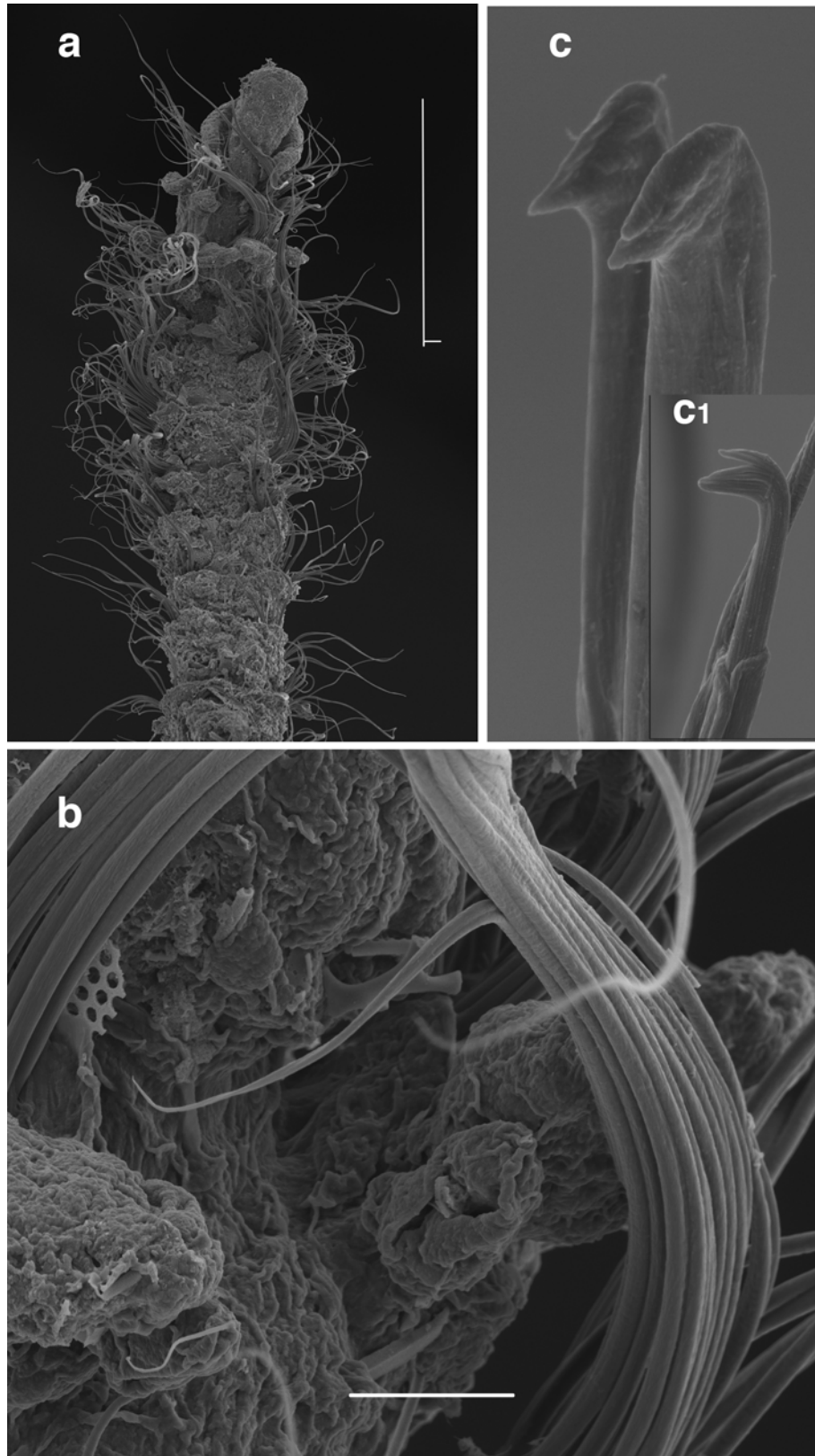
**Material examined:** 12 specimens examined.

**Holotype:** *CVAP:* RSS *Discovery* October 1993, 12600#45 October 1993, 21°3.4'N 31°9.8' W, 4524 m, 1 individual (NHMUK 2015:1190)

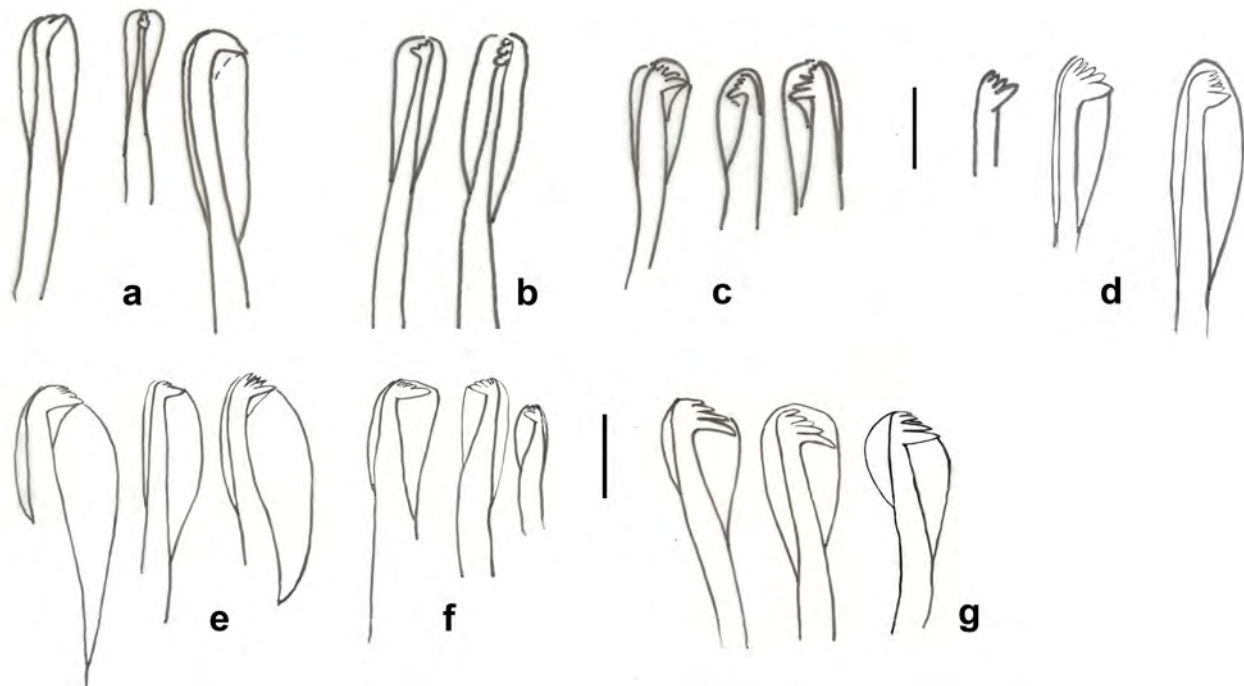
**Paratypes:** *Equatorial Pacific:* 2°N 140°W, 4300 m, 4 individuals (EP410, EP425, EP427, EP444); 5°N 140°W 4300 m, 3 individuals (EP 431, 432, 473); 9°N 140°W, 4900 m, 1 individual (EP414).

**MAP:** RSS *Discovery* August 1990, 12174#53, 31 5.2' N 21 1.2' W, 4942 m, 1 individual.

**Other material examined:** *CVAP:* RSS *Discovery* October 1993, 12600#28, 21° 4.8' N 31° 11.1' W, 4613 m, 1 individual.



**FIGURE 7.** *Prionospio kaplani* sp. nov. (EqPac specimen 888). a) Dorsal view of anterior segments; scale bar = 200  $\mu$ m. b) Close up of chaetiger 2 show very small branchia (Br) to left of dorsal lamella (DL); scale bar = 10  $\mu$ m. c) Electron micrograph of hooded hooks; scale bar = 2  $\mu$ m; c1) electron micrograph of hooded hook showing bidentate condition (scale as in (c)).



**FIGURE 8.** Drawings of hooded hooks of a) *Prionospio branchilucida* **sp. nov.**; b) *Prionospio kaplani* **sp. nov.**; c) *Aurospio abbranchiata* **sp. nov.**; d) *Aurospio tribranchiata* **sp. nov.** (left hook shown without hood). Bar scale=0.001 mm (a–d). e) *Prionospio amarsupiata* **sp. nov.**; f) *Prionospio hermesia* **sp. nov.** g) *Prionospio vallensis* **sp. nov.** Bar scale=0.001 mm (e–g).

*Equatorial Pacific*: EqPac 0°N 140°W, 4300 m, 1 individual (EP488).

**Diagnostic features.** Two pairs of branchiae on chaetigers 2 and 3, sabre chaetae lacking, dorsal crests from chaetiger 7, neuropodial hooded hooks from chaetiger 11.

**Description.** Body cylindrical, narrow throughout; holotype 1.86 mm long for 20 chaetigers, (0.62 mm up to chaetiger 10); 0.08 mm wide at chaetiger 1. Prostomium rectangular with flat, entire anterior margin; one pair prostomial peaks present; caruncle short with rounded apex, extending to anterior margin of chaetiger 2. Eyes absent. Peristomium incomplete dorsally, not forming lateral wings, separate from chaetiger 1 (Fig 7a).

Branchiae from chaetiger 2, two pairs, very small. Branchiae on chaetiger 2 digitiform, blunt-tipped, inserted lateral and slightly posterior to dorsal lamellae; branchiae approximately one-half chaetiger long, subequal to notopodial lamellae; branchiae on chaetiger 3 conical, inserted posterior to dorsal lamellae and obscured by them, one quarter the length of lamellae (Fig.2.5).

Notopodial lamellae start on chaetiger 2, sub-quadrangular, slightly angled toward dorsal midline (Fig 2.5a); largest on chaetiger 3, sub-quadrangular with slightly produced tips overlapping dorsal midline, three times as long as lamellae of chaetiger 2 (Fig 2.5b); thereafter, notopodial lamellae decrease in size, becoming low and subtriangular by chaetiger 7. Dorsal crests present from chaetigers 7 to chaetiger 17 (Fig. 2.5f chaetiger 14).

Neuropodial lamellae start on chaetiger 1, papilliform, length equal to one-fifth chaetiger length; neuropodial lamellae on chaetigers 2–5 leaf-like, narrow with short tips; neuropodial lamellae largest on chaetiger 3, length equal to chaetiger length and nearly twice that of chaetiger 2, neuropodial lamellae thereafter decreasing in length and increasing in width, becoming broadly ovoid by chaetiger 9. Interparapodial pouches absent.

Notochaetae limbate capillaries, long, inserted in two densely packed rows from chaetigers 2–8 with up to 12 chaetae per row; thereafter, notochaetae reduced in number and density; all notochaetae angle forward on chaetigers 1–8 and anterior row always with shorter. Neurochaetae smooth and limbate capillaries, inserted in two distinct rows to chaetiger 8, up to eight chaetae per row, anterior row always shorter; thereafter, number of chaetae decrease, rows become indistinct. Neuropodial sabre chaetae not observed through 20 chaetigers (all specimens incomplete). Neuropodial hooded hooks present from chaetiger 11; shaft narrow with slender main fang, surmounted by two to three fine small teeth in one row, up to six chaetae per fascicle, inner hood absent; notopodial hooded hooks not observed. Pygidium not observed.

**Methyl green pattern.** Not observed.

**Remarks.** The key feature of this species is the presence of only two pairs of branchiae, the apparent absence of sabre chaetae, dorsal crests occurring from chaetigers 7 to 17, and the hooded hooks starting on chaetiger 11. Two other species of *Prionospio* have only two pairs of branchiae: *P. sexoculata* Augener, 1923 and *P. hermesia* **sp. nov.** *Prionospio kaplani* **sp. nov.** differs from *P. sexoculata* because in the latter species all the branchiae are pinnate while in *P. kaplani* **sp. nov.** all are apinnate. *P. hermesia* **sp. nov.** is similar to *P. kaplani* **sp. nov.**, but differs in the shape of the prostomium in particular, having a flat anterior margin as opposed to a rounded one as in *P. hermesia* **sp. nov.** (Fig.7); the caruncle extends to anterior boundary of chaetiger 1 in *P. hermesia*, while in *P. kaplani* **sp. nov.** it extends to anterior boundary of chaetiger 2; the neuropodial lamellae in *P. kaplani* **sp. nov.** are rounded with extended tips while in *P. hermesia* **sp. nov.** they are merely rounded. *Prionospio kaplani* **sp. nov.** also resembles *P. branchilucida* **sp. nov.** in having similarly shaped branchiae, a similarly shaped prostomium, and the peristomium being separated from chaetiger 1. They differ in the number of pairs of branchiae, two in *P. kaplani* **sp. nov.** but three in *P. branchilucida* **sp. nov.**; the dorsal crests start on chaetiger 7 rather than 10; and the neuropodial hooded hooks start on chaetiger 11 rather than chaetigers 14–17 as in *P. branchilucida* **sp. nov.**

**Etymology.** This species is named in honour of the Kaplan Foundation in grateful acknowledgement of their support.

**Distribution.** *Prionospio kaplani* **sp. nov.** has been recorded from the central Pacific and NE Atlantic Oceans from depths of 4300–4942 m (Fig. 1).

### ***Prionospio* Iberian Canyons sp. C** (Figures 2.7, 9)

**Material examined:** 23 specimens examined.

**Voucher specimens:** *Portuguese margin* Nazaré canyon: St. 15765#2 39°35.00'N 10°19.04'W, 4336 m; 5 individuals.

**Other material examined:** *Nazaré canyon:* RSS *Discovery* 2005, St. 15758#2 39°34.94'N 10°19.00'W, 4332m, 8 individuals; St. 15758#6 39°34.99'N, 10°19.00'W 4335 m, 8 individuals;

RSS *Charles Darwin* 179 April/May 2006, St. 56847#7 39°35.55'N 10°20.06'W, 4404 m, 2 individuals.

**Diagnostic features.** Eleven pairs apinnate branchiae, neuropodial hooded hooks and sabre chaetae not present in the first 31 chaetigers.

**Description.** Voucher specimen incomplete with 31 segments, measuring 1.6 mm long (length to chaetiger 10) and 0.22mm wide (at chaetiger 1). Body wide and somewhat flattened; appears divided into two parts: branchial region plus four following segments with enlarged notopodial lamellae and dense capillaries and postbranchial region, with abruptly smaller notopodial lamellae and less dense capillaries. Colour pale yellow colour in alcohol. Prostomium nearly oval, with anterior margin somewhat truncated, prostomial peaks absent; distinct caruncle not formed, posterior margin of prostomium reaching to chaetiger 1 (Fig. 10a); eyes not observed. Peristomium well developed, closely surrounding prostomium, ventrally distinct, dorsally incomplete; partially fused to chaetiger 1; lateral wings not formed. Palps missing.

Eleven pairs of branchiae present on chaetigers 2–12; branchiae only slightly longer than accompanying notopodial lamellae, all of similar shape and size throughout, but with last two pairs shorter; all apinnate, but heavily ciliated on both sides, except for the tip; branchiae rather narrow but somewhat flattened–strap-like, wider at the base and tapering into somewhat swollen tip (Fig. 10a,b).

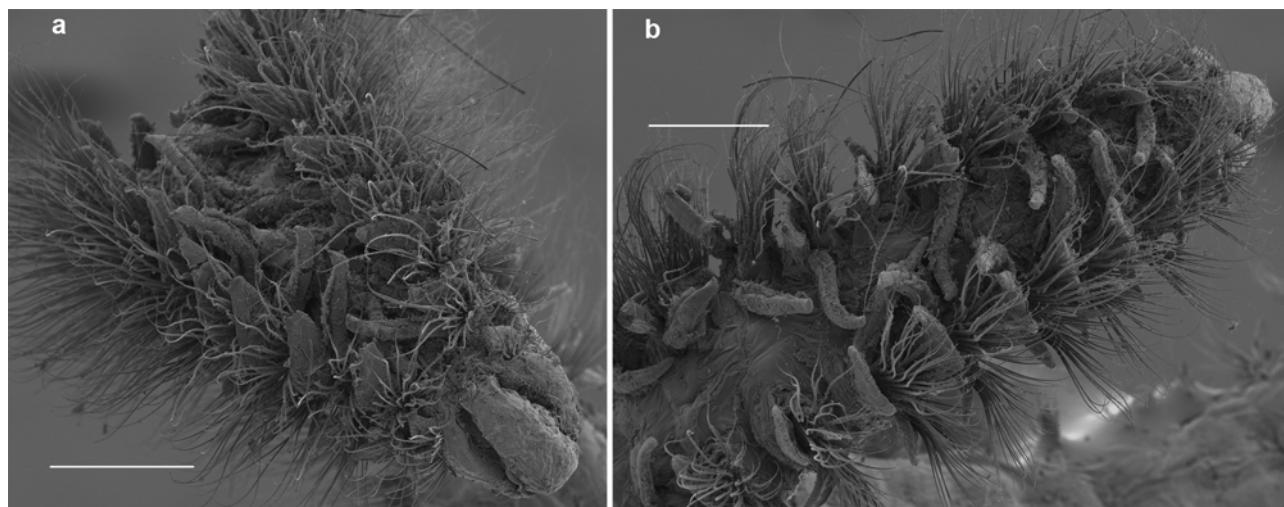
Notopodial postchaetal lamellae enlarged in branchial region (chaetigers 2–12) (Fig. 2.7a–d), about three times longer than neuropodial postchaetal lamellae, reduced in size in chaetigers 13–16, then abruptly smaller from chaetiger 17 (Fig.2.7e), similar in size to neuropodial postchaetal lamellae; notopodial postchaetal lamellae subtriangular in branchial segments, becoming more small, oval, somewhat produced into blunt tip in postbranchial segments. No dorsal crests in 31 segments. Interparapodial pouches absent.

Neuropodial postchaetal lamellae on chaetiger 2 small, oval with blunt distal tip; in other branchial segments enlarged, subquadrangular with produced tip dorsally; gradually becoming smaller and more oval assuming shape similar to the one on chaetiger 2 in postbranchial segments.

Only capillary chaetae present in incomplete 31chaetiger-long holotype. Capillaries long and dense in



branchial region; straw-coloured, arranged in four rows: two rows of shorter and two rows of longer capillaries; capillaries in postbranchial segments less dense, arranged in single row. Neuropodial hooded hooks, sabre chaetae and notopodial hooded hooks absent in 31 segments. Pygidium unknown.



**FIGURE 9.** *Prionospio* sp. C a) Dorsal view of anterior chaetigers; scale bar = 200  $\mu$ m. b) Dorsal view showing arrangement of branchiae; scale bar = 200  $\mu$ m.

**Methyl green pattern:** Prostomium and peristomium stain strongly, the margins of notopodial and neuropodial lamellae in branchial regions also stained, more intensively in anteriormost segments.

**Remarks.** Given that in the voucher specimen all branchiae are apinnate, this species is similar to species grouped by many authors into *Minuspio*. *Minuspio* was erected by Foster (1971) to include all species with only apinnate branchiae. Maciolek (1985) in her revision of *Prionospio* suggested that *Minuspio* was only a sub-genus. Subsequent authors have been similarly divided in their designations and *Minuspio* has been used as a genus and subgenus. Many of the species designated to this taxon have more than four pairs of branchiae. Eleven pairs of branchiae are present on chaetigers 2–12 in the voucher of *Prionospio* spC, but branchiae are missing in all other specimens and their number may be variable. The absence of neuropodial sabre chaetae and neuropodial hooded hooks in 31 segments (the largest fragment) appears to be a unique feature of this species. In other species of *Prionospio* described to date, the neuropodial hooks usually start around segment 20 at the latest and sabre chaetae are usually present before this. However, given that the largest specimen available for examination was only 31 chaetigers long, it is possible that sabre chaetae/neuropodial hooks may start later in body. Given that no described species of *Prionospio* have the either neuropodial hooks or sabre chaetae starting so far back on the body, we consider that this is a distinct species but we are reluctant to formally classify it until we have more complete specimens. We therefore choose to describe but not name the species to enable future workers to identify it with the hope that complete specimens will be discovered and allow a more comprehensive description.

**Distribution.** Nazaré canyon (Portuguese margin) at 4364–4404 m.

### *Aurospio* Maciolek, 1981a

#### *Aurospio tribranchiata* sp. nov. Paterson & Soto

(Figure 1, 8d, 10, 11, 12, Table 3)

*Minuspio* sp4 Soto 2008: 89.

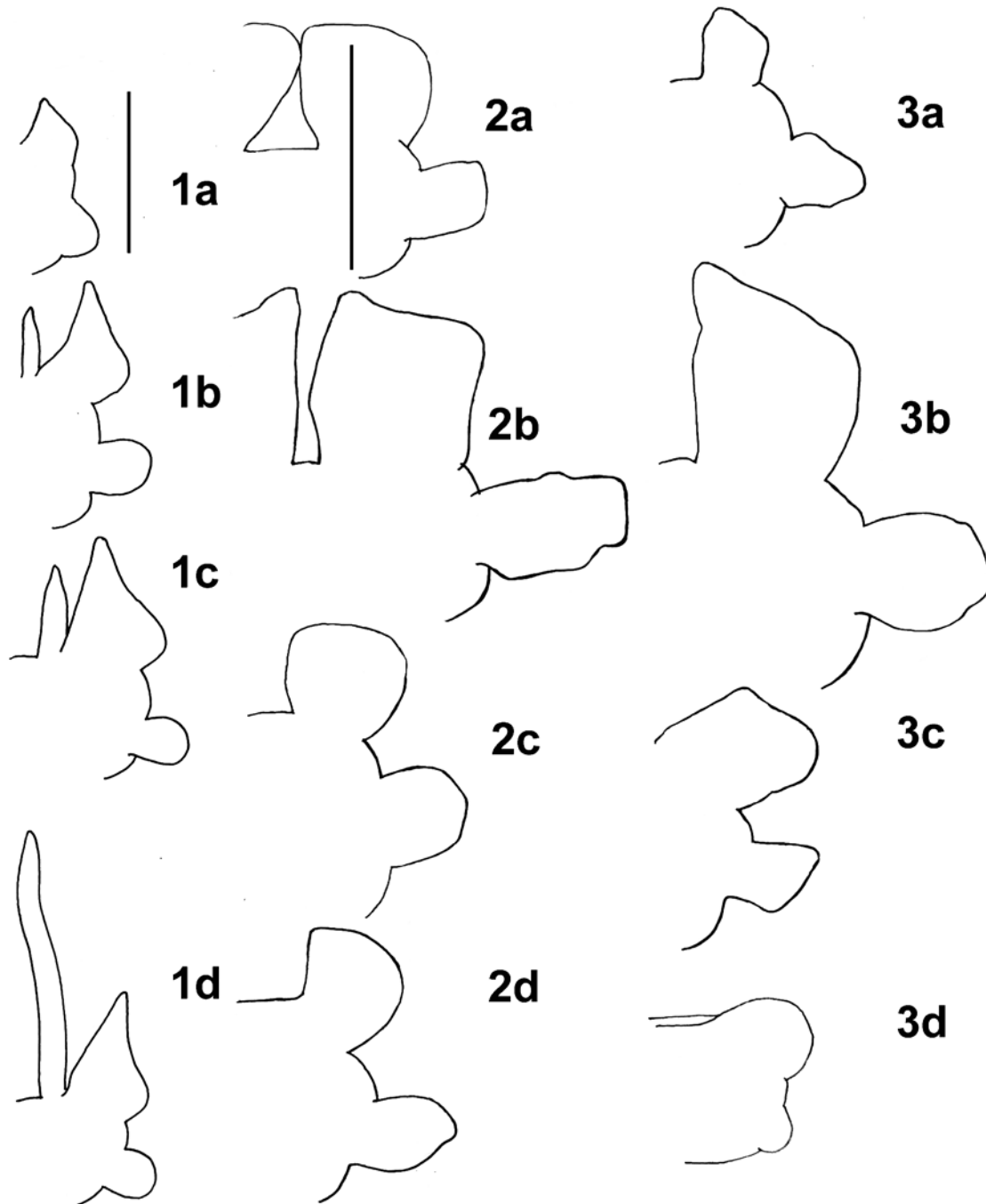
**Material examined:** 33 specimens examined in total.

**Holotype:** *Porcupine Abyssal Plain*, RRS *Discovery* D229, July 1997, 13200#20, 48°49.8' N, 16°29.62' W, 4844 m, 1–3 cm, 0.3 mm (NHMUK 2015:1199).

**Paratypes:** *Porcupine Abyssal Plain*, RRS *Challenger* 79, May 1991, 52701#9, 48°51.6' N, 16°27.4' W, 4842

m, 2 individual ; 52701#25, 48°50.4' N, 16°29.6' W, 4844 m, 3 individuals; 52701#47, 48°50.6' N, 16°29.9' W 4841 m, 1 individual.

*Porcupine Abyssal Plain*, RRS *Discovery* D222, August 1996, 12930#14, 48°50.92'N, 16°30.24'W, 4837 m, 1 individual; 12930#44, 48°49.95'N, 16°30.2'W, 4839 m, 1 individual; 12930#59, 48°50.45'N, 16°30.58'W, 4837 m, 1 individual; 12930#68, 48°49.92'N, 16°29.76'W, 4840 m, 2 individual; 12930#73, 48°50.08'N, 16°29.69'W 4839 m, 2 individuals.

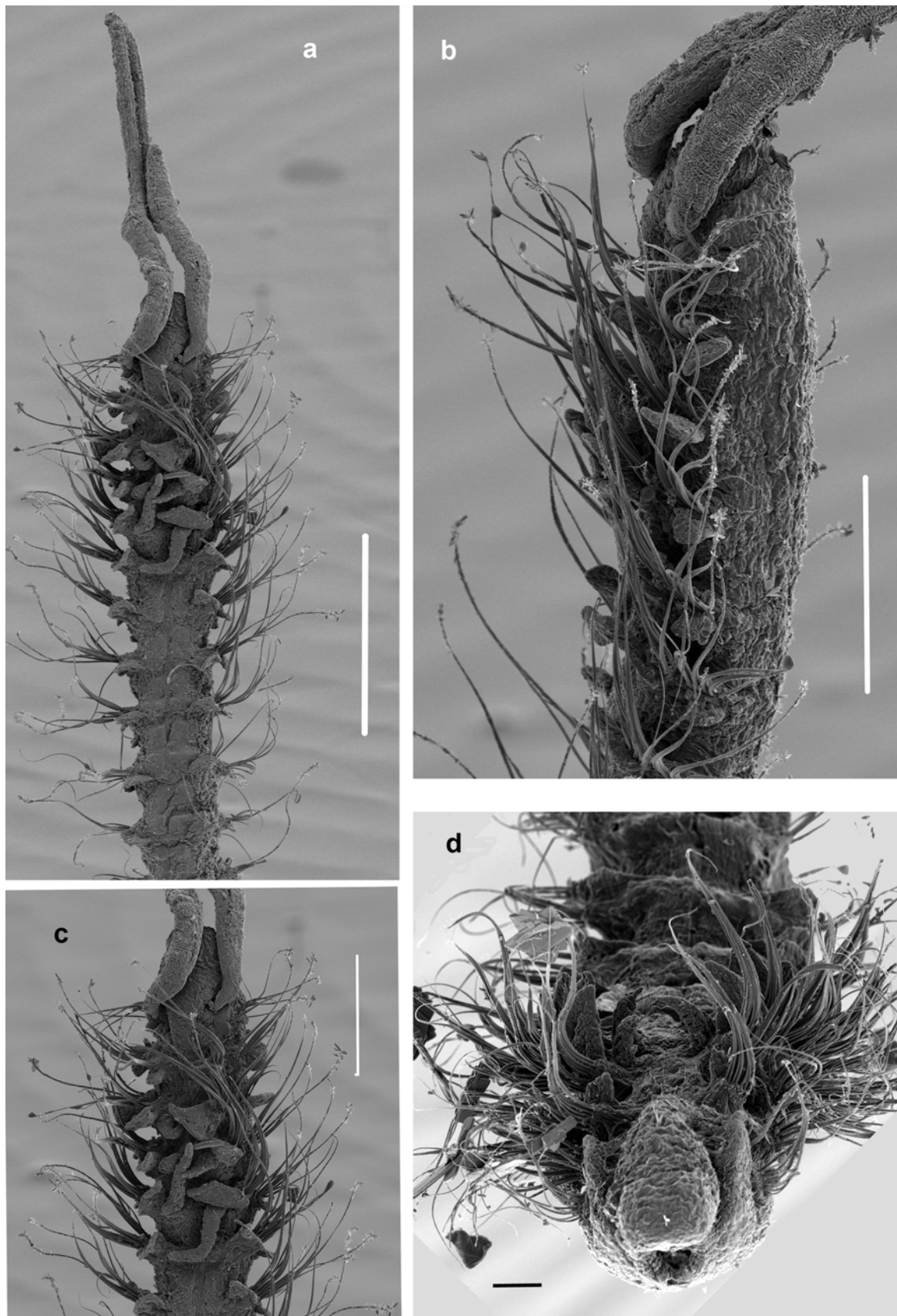


**FIGURE 10.** Profiles of anterior chaetigers of the *Aurospio* species described.

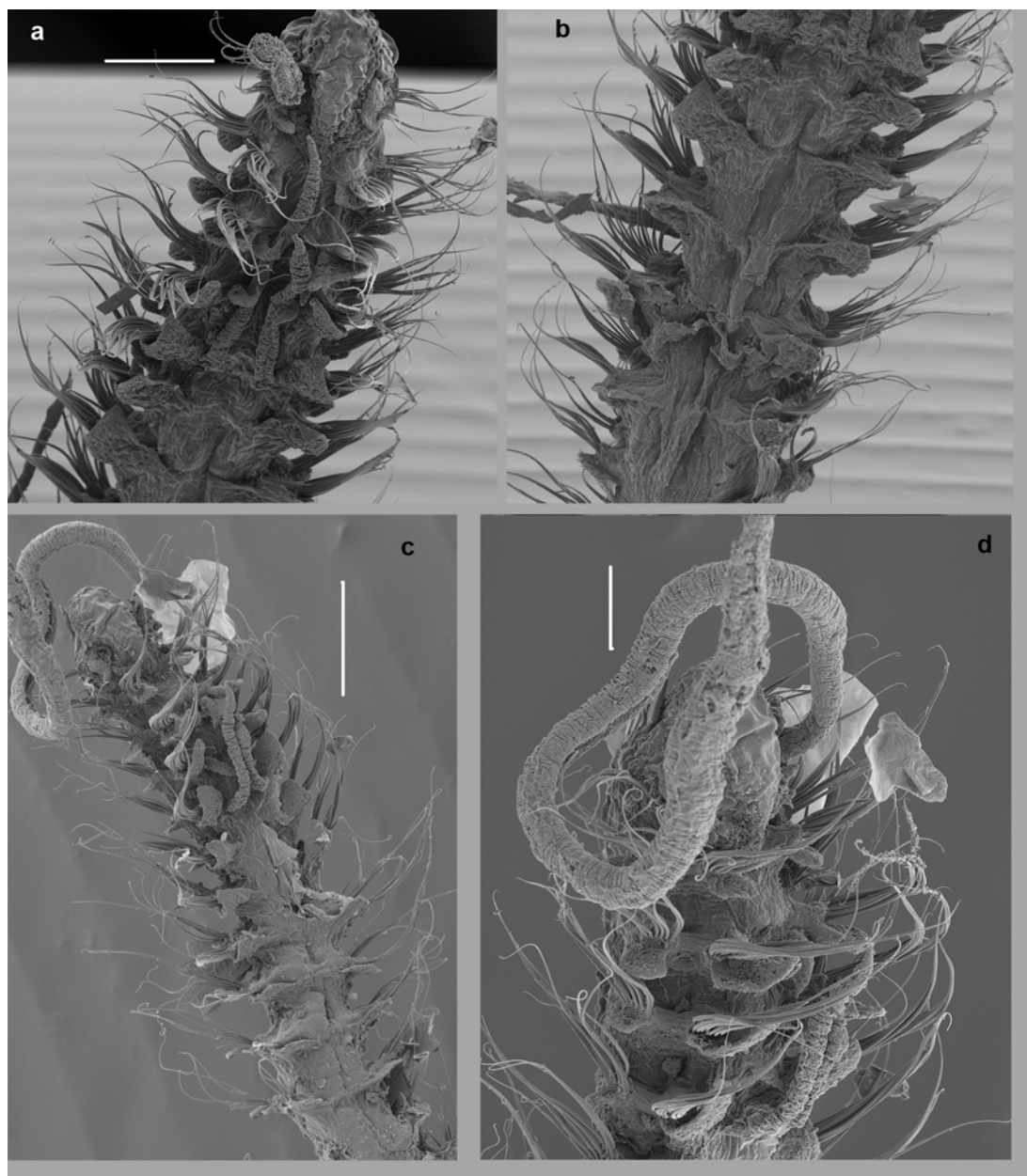
1) *Aurospio tribranchiata* **sp. nov.** a) Chaetiger 2; b) Chaetiger 3; c) Chaetiger 4; d) Chaetiger 5; scale bar = 100  $\mu$ m.

2) *Aurospio abranchiata* **sp. nov.** from PAP a) Chaetiger 2; b) Chaetiger 3; c) Chaetiger 4; d) Chaetiger 5; e) Chaetiger 8; scale bar = 100  $\mu$ m.

3) *Aurospio abranchiata* **sp. nov.** from canyons a) Chaetiger 2; b) Chaetiger 3; c) Chaetiger 4; Chaetiger 5; scale bar =  $\mu$ m.



**FIGURE 11.** *Aurospio tribranchiata* sp. nov. (Bengal5 D231 13368#25). a) Dorsal view of anterior chaetigers; scale bar = 200 µm. b) Detail of the anterior chaetigers; scale bars = 100 µm. c) Lateral view of anterior chaetigers; scale bars = 100 µm. d) Second specimen (D222\_12390#59) showing anterior chaetigers, the third pair of branchiae are missing; scale bar = 50 µm.



**FIGURE 12.** *Aurospio tribranchiata* sp. nov. (Bengall D222 12390#59). a) Dorsal view of anterior chaetigers, showing regenerating palp on left side; scale bar = 100 µm. b) Mid body region show dorsal folds; scale bar = 100 µm. c) Second specimen dorsal view of anterior chaetigers; scale bars = 100 µm. d) Detail of anterior chaetigers of second specimen, showing detail of palp and long third branchiae; scale bar = 50 µm.

*Porcupine Abyssal Plain*, RRS *Discovery* D226, March 1998, 13077#19, 4850°N, 1630.05°W, 4846 m, 4 individual; 13077#23, 4849.28°N, 1630.56°W, 4844 m, 1 individual; 13077#59, 48 49.98N, 16 29.96W, 4845 m, 1 individual; 13078#13, 48°50.00°N, 16°30.0°W, 4843 m, 1 individual.

*Porcupine Abyssal Plain*, RRS *Discovery* D229, July 1997, 13200#17, 4849.67°N, 1628.72°W, 4843 m, 2 individuals; 13200#20, 48°49.8° N, 16°29.62° W, 4844 m, 3 individuals; 13200#47, 4839.29°N, 1630.27°W, 4844 m, 1 individual; 13200#52, 48°49.84°N, 16°29.84°W, 4844 m, 2 individuals.

*Porcupine Abyssal Plain*, RRS *Discovery* D231, March 1998, 48 50.51°N 16 29.43°W, 4842 m, 1 individual; 13368#25, 48° 50.51°N, 16° 29.43°W, 3 individuals.

*Porcupine Abyssal Plain*, RRS *Discovery* D237 September 1998, 13627#17, 4849.9°N, 16 49.9°W, 4837 m 2 individuals.

**Diagnostic features:** three pairs of branchiae, first pair starting on chaetiger 3 and the last pair being much longer than the other two.

**Description.** Small slender species with thorax widening posteriorly then staying the same width; holotype fragment with 20 chaetigers, 3.00 mm long; 0.18 mm wide at chaetiger 1 (not including the chaetae). Colour cream to pale yellow.

Prostomium rounded to rectangular; caruncle long extending to anterior edge of chaetiger 2, well developed, then appearing to extend weakly beyond segment boundary. No eyes. Peristomium separated ventrally and laterally from chaetiger 1, fused dorsally forming a distinct rounded collar. Palps simple up to 5 chaetigers in length, no basal sheath.

Branchiae present on chaetigers 3 to 5; all apinnate, cylindrical, tapering gradually to a rounded point; branchiae on chaetigers 3 and 4 short, about the same length as the accompanying dorsal lamellae; branchiae on chaetiger 5 long, up to five chaetigers in length and two to three times the length of the accompanying dorsal lamellae (Fig. 11.1d; 12 a,c, 13a,c).

Chaetiger 1 with small rounded notopodial lamellae. Notopodial lamellae increase in size with the largest on chaetigers 4 and 5; lamellae triangular on chaetigers 2 and 3, becoming wider and more rounded on chaetigers 5 and 6. Notopodial lamellae in mid-body low and rounded. Dorsal crests low difficult to see but occur on chaetigers 9 to 12.

Neuropodial lamellae on chaetiger 1 small rounded, increasing over chaetigers 2 to 9; lamellae largest on chaetiger 3 (Fig 12 b).

Capillaries arranged on two rows on notopodia and neuropodia, capillaries bilimbate with those in the lower row slightly granulated. Sabre chaetae robust, curved, limbate, slightly or non-granulated, starting on chaetiger 10 or 11; one per fascicle. Neuropodia hooded hooks start on chaetiger 12, up to six per fascicle; two to three pairs of small teeth above the main fang (specimens small difficult to see the exact arrangement), no inner hood; Notopodial hooded hooks not observed. Pygidium unknown.

**Methyl green pattern.** Band of stain across middle of prostomium or across whole prostomium, diffuse over body.

**Remarks.** *A. tribranchiata* **sp. nov.** is assigned to *Aurospio* because the branchiae start on chaetiger 3. All specimens of *A. tribranchiata*, were carefully examined stained with Shirlastain A (SDL international. A textile fibre identification stain - very useful in revealing features, such as scars) and were not able to detect the presence of scars on any of our specimens. As further supporting evidence there was no branchial pair on chaetiger 2 or evidence of their scars even on otherwise complete specimens which had very long branchiae of chaetiger 4 (which could be easily lost) and palps (almost always lost in spionids) still attached. Based on current evidence we have assigned this species to *Aurospio* until proven otherwise. Other characters such as the shape of the prostomium, lack of an internal secondary hood in the hooded hooks also are common to species in this genus (but see Remarks in the previous species for a discussion on the problems of defining this genus).

*A. tribranchiata* **sp. nov.** is similar to *A. pilkena* Wilson, 1990 and *A. banyulensis* (Laubier, 1963), in particular the form of the prostomium, having three pairs of branchiae (see Table 4). *A. banyulensis* also has dorsal crests starting on chaetiger 8, hooded hooks starting on chaetiger 12 and sabre chaetae on chaetiger 10. *A. tribranchiata* **sp. nov.** differs in the arrangement of the third pair branchiae which are long whereas on *A. pilkena* and *A. banyulensis* they are all the same size. *A. longibranchiata* differs from *A. pilkena* in the starting positions of the sabre chaetae and hooded hooks and having dorsal crests (see Table 4).

**TABLE 3.** Comparison of species of *Aurospio*. Abbreviations: Ch—Chaetiger, HH—hooded hooks. Characters taken from original descriptions.

Species	No of pairs branchiae	Size of branchiae	Sabre chaetae	Start of HH	Dorsal crests
<i>A. abbranchiata</i> <b>sp. nov.</b>	absent	n/a	Ch10	Ch11–12	Ch8
<i>A. dibbranchiata</i>	2	Ch3>Ch4	Ch9–11	Ch9–11	Ch5–10*
<i>A. banyulensis</i>	3	All equal	Ch10	Ch12–13	Ch7–8
<i>A. pilkena</i>	3	All equal	Ch15–16	Ch18–19	absent
<i>A. tribranchiata</i> <b>sp. nov.</b>	3	Ch3<<Ch5	Ch10/11	Ch12	Ch8
<i>A. foodbancsia</i>	1	n/a	Ch10	Ch11	Ch9

\*absent in some specimens



**Etymology.** *tribranchiata* refers to the three pairs of branchiae found on this species.

**Ecology.** *A. tribranchiata* sp. nov. is one of the dominant species of spionids found on the Porcupine Abyssal Plain, found in densities of between 4 and 24 individuals per m<sup>2</sup>. This species was found within the sediment at depths between 0–5 cm.

**Distribution.** This species has only been recorded from the Porcupine Abyssal Plain 48°N, 16° W (Northeast Atlantic Ocean) and from a depth of 4800 m.

***Aurospio abranchiata* sp. nov. Neal, Paterson & Soto**

(Figures 8c, 10, 13, 14, Table 3)

*Prionospio* sp B: Paterson *et al.*, 2011

**Material examined:** 97 specimens examined in total.

**Holotype:** Cascais canyon: RRS *Charles Darwin*, cruise 179, April–May 2006, St. 56823#2 2006.04.27, 38°18.01' N, 09°47.02' W, 3218 m, megacore (NHMUK 2015:1043).

**Paratypes:** *Portuguese margin:* Nazaré canyon RSS *Discovery* 297 August 2005, St. 15755#1 39°30.62' N, 09°56.19' W, 3461 m, 3 individuals; St. 15760#1, 39°30.02' N, 09°56.17' W 3465 m, 5 individuals; St. 15762#1, 39°30.02' N, 09°56.22' W, 3464 m, 2 individuals; St. 15758#6, 39°34.99' N, 10°19.00' W, 4335 m, 5 individuals; St. 15765#2, 39°35.00' N, 10°19.04' W, 4336 m 4 individuals.

RSS *Charles Darwin* cruise 179 April–May 2006, St. 56851#1, 39°29.99' N, 09°55.97' W, 3517 m, 2 individuals; St. 56851#2, 39°29.99' N, 09°56.01' W, 3517 m, 2 individuals.

*Setúbal canyon:* RSS *Charles Darwin* cruise 179 April–May 2006, St. 56804#5 2006.04.21 38° 09.27'N 09° 36.93'W 3275m 8 individuals; St. 56804#6 2006.04.21 38° 09.26'N 09° 36.94'W 3275m, 10 individuals; St. 56806#1 2006.04.21 38° 09.29'N 09° 36.96'W 3275m, 10 individuals; St. 56810#1 2006.04.23 38° 09.22'N 09° 37.02'W 3224m, 1 individual; St. 56816#1 2006.04.25 38° 09.27'N 09° 36.94'W 3275m, 14 individuals; St. 56842#1 2006.05.05 38° 06.45'N 09° 59.94'W 4482m, 2 individuals.

*Cascais canyon:* RSS *Charles Darwin* cruise 179 April–May 2006, St. 56823#2 2006.04.27 38° 18.01'N 09° 47.02'W 3218m, 9 individuals; St. 56828#1 18.02'N 09° 46.98'W 3199m, 1 individual.

*PAP:* RRS *Challenger II* 79 May 1991: 52701#5 48°51.0'N 16°30.0'W, 4840 m, 1 individual.

RRS *Discovery* D222 September 1996: 12930#39 48°49.95' N, 16°29.4' W, 4840 m, 1 individual.

RRS *Discovery* D226 March 1998: 13077#23, 48°49.28' N, 16°30.56' W, 4844 m, 2 individuals.

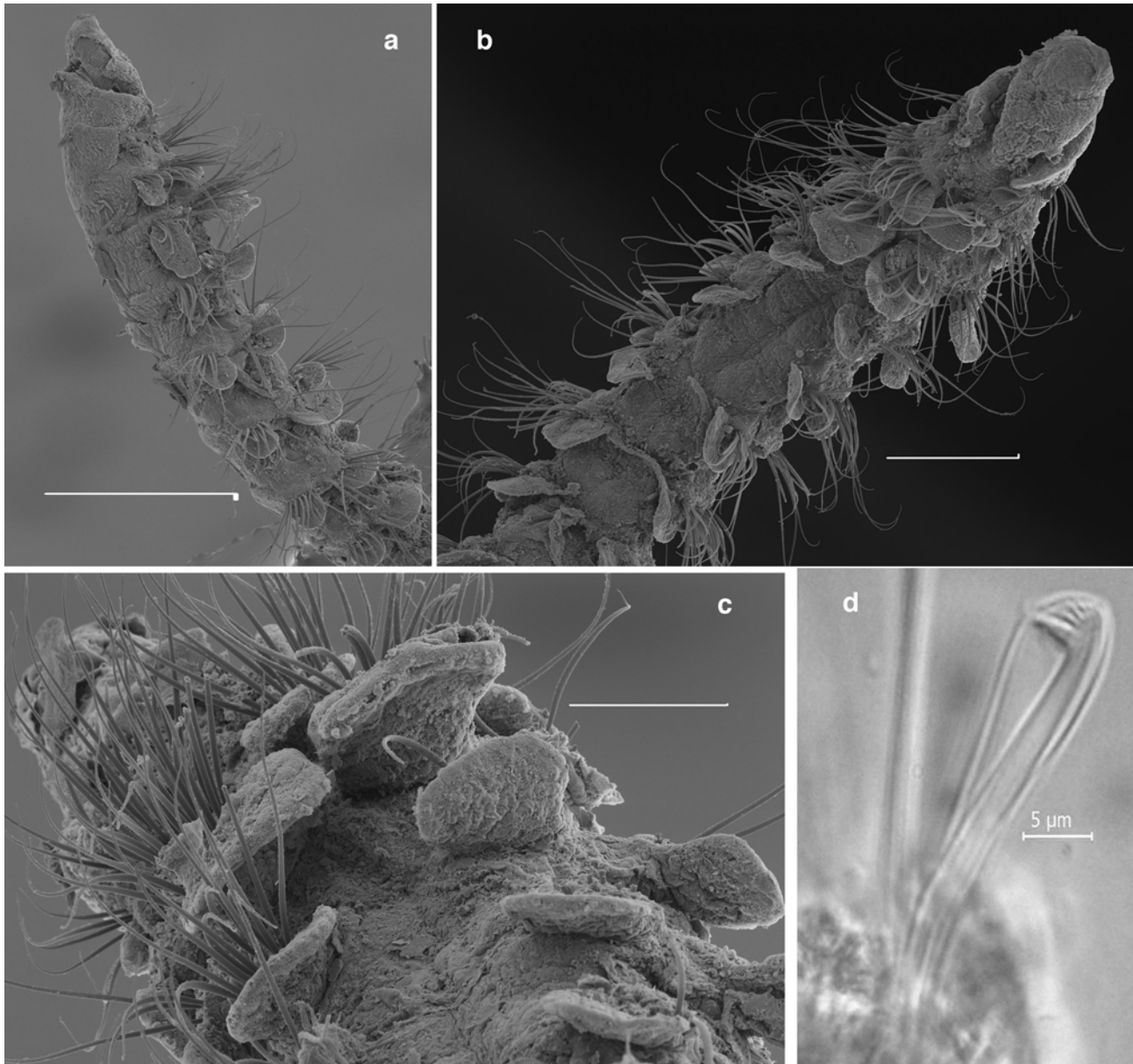
RRS *Discovery* D229 July 1997: 13200#20, 48°49.8' N, 16°29.62' W, 4844 m, 2 individuals; 13200#47 48°39.29' N, 16°30.27' W, 4844 m, 1 individual.

RRS *Discovery* D231 March 1998: 13368#36, 48°49.78' N, 16°30.17' W, 4845 m, 2 individuals; 13368#42, 48°50.08' N, 16°29.88' W, 4844 m, 1 individual; 13368#44, 48° 49.7' N, 16°30.12' W, 4844 m, 1 individual.

**Diagnostic features.** Lack of branchiae, enlarged square-shaped notopodial lamellae on third segment; neuropodial lamellae largest on chaetiger 3 forming long, rectangular with rounded edges, wing-like structure which sometimes extends horizontally away from body.

**Description.** Small and slender species, holotype incomplete with 45 segments, measuring 5.65 mm long for 45 segments and 0.2 mm wide (width at chaetiger 1). Colour in alcohol pale yellow. Body narrow and cylindrical, of uniform width throughout. Prostomium rounded, anterior margin entire, broadly rounded, prostomial peaks absent; short blunt caruncle, extending to anterior of chaetiger 1; eyes not observed. Peristomium well developed, ventrally and laterally distinct, dorsally partially fused to chaetiger 1, forming a collar around prostomium, without forming distinct lateral wings.

Branchiae absent. Notopodial and neuropodial postchaetal lamellae reduced in chaetiger 1; notopodial lamellae on chaetiger 2 nearly square-shaped, meeting at midline and covering the dorsum in larger specimens but more widely separated in smaller ones (Fig. 11.2a,3a); largest on chaetiger 3; lamellae large, nearly square, almost meeting at the midline, covering the entire dorsal surface of the segment in large specimens but not in smaller ones (Fig. 11.2b,3b). Notopodial postchaetal lamellae on chaetigers 4–5 smaller, about half the size of those on chaetiger 3, changing from square to rounded shape from chaetiger 6 onwards, all well separated, not covering the dorsum (Fig. 11.2c,2d,3c,3d). Distinct dorsal crests from chaetiger 8–12. Interparapodial pouches absent.



**FIGURE 13.** *Aurospio abranchiata* sp. nov. Portuguese Canyons a) Lateral view of anterior chaetigers; scale bar = 200 µm. b) dorsal view of anterior chaetigers; scale bar = 100 µm. c) Detail of anterior chaetiger, note absence of branchiae; scale bar = 50 µm. d) Photomicrograph of ventral hooded hook; scale bar = 5 µm.

Neuropodial lamellae on chaetiger 2 square-shaped with rounded corners; on chaetiger 3 very large, rectangular with rounded edges (somewhat indented on outer rim), wing-like structure which sometimes extends horizontally away from body. The neuropodial postchaetal lamellae in other segments becoming more rounded and of similar size.

Capillaries in two rows in both notopodia and neuropodia. Sabre chaetae present singly from chaetiger 10 in neuropodia; stout, strongly curved, no granulation. Neuropodial hooded hooks present from chaetiger 11–12, up to 4–5 par fascicle; at least five pairs of small teeth above the main fang; square-shaped primary hood, secondary hood present, rudimentary. Notopodial hooks present singly from chaetiger 38. Pygidium unknown.

**Methyl green pattern.** Strong stain remains on sides of segments 5–17, even six months after staining.

**Remarks.** The absence of branchiae together with the shape and size of both notopodial and neuropodial lamellae on third segment are diagnostic characteristics of this species. The absence of branchiae poses a difficulty in assigning this species to a genus with certainty. Within the Spionidae the genera *Spiophanes* Grube, 1860 and *Spiogalea* Aguirrezabalaga and Cebrio, 2005, are characterised by a lack of branchiae. However, the specimens

described here do not belong to these genera because they lack modified, hook-like setae in the neuropodia of chaetiger 1, which are found in *Spiophanes* and the two chitinous plates surrounding the peristomium, which are characteristic of *Spiogalea*. The specimens also lack the characteristic arrangement of neuropodial chaetae found in the mid-chaetigers of *Spiophanes* described by Meißner & Hutchings (2003) and Meißner (2005).

In overall appearance this species bears close resemblance to species belonging to the *Prionospio* complex. Our species does not seem to belong to either *Paraprionospio* or *Orthoprionospio* based on the first segment having chaetae and the first chaetiger not being completely separated from peristomium usually found in *Paraprionospio* and *Orthoprionospio*. The genus *Streblospio* can be eliminated because our specimens lack a ridge across chaetiger 1 and a prominent hood or collar across the dorsum of chaetiger 2; the form of the neuropodial multidentate hooks is also different.

The problem of generic assignment arises when trying to determine whether the species belongs to the genus *Aurospio* or *Prionospio*. *Aurospio* was separated from *Prionospio* primarily on branchiae starting from third chaetiger, their shape, and that they are partially fused at their base to the notopodia. An additional character cited by Maciolek (1981) is the absence of a secondary hood in the hooks of *Aurospio*. Sigvaldadottir (1998) emphasised a lack of prostomial peaks, a short caruncle reaching to the anterior margin of chaetiger 1; pointed dorsal lamellae in mid-body segments, the absence of dorsal crests, and sabre chaetae starting on chaetiger 10 or earlier in her analyses of *Prionospio*.

However, *A. banyulensis* (Laubier, 1966) and *A. pilkensis* (Wilson, 1990) do not have the branchiae fused to the base of the notopodia. Also, many species of *Prionospio* do not have secondary hoods in the neuropodial hooded hooks (Wilson 1990). Many of the characters highlighted by the cladistic analyses of Sigvaldadottir (1998) are actually also found in species of *Prionospio*. For example, short caruncles can be found in *P. coorilla* Wilson, 1990; *P. pulchra* Imajima, 1990; *P. somaliensis* Cognetti-Varriale, 1988; and *P. varigata* Imajima, 1990. Such overlap blurs the distinction between the genera and so we are left with the characters of the branchiae. Our species lacks these key characters. Thus it becomes difficult to place this new species into a genus. We do not believe that the absence of branchiae justifies erection of a new genus or subgenus within *Prionospio*-complex, but provides further support for view of Wilson (1990) and Sigvaldadottir (1998) that the differentiation of genera/subgenera based primarily on branchial arrangement is not justified. Therefore, based on the overall body shape, shape of the prostomium and shape of the dorsal lamellae, particularly the pair associated with chaetiger 3, this new species most closely resembles the characters displayed by species of *Aurospio*.

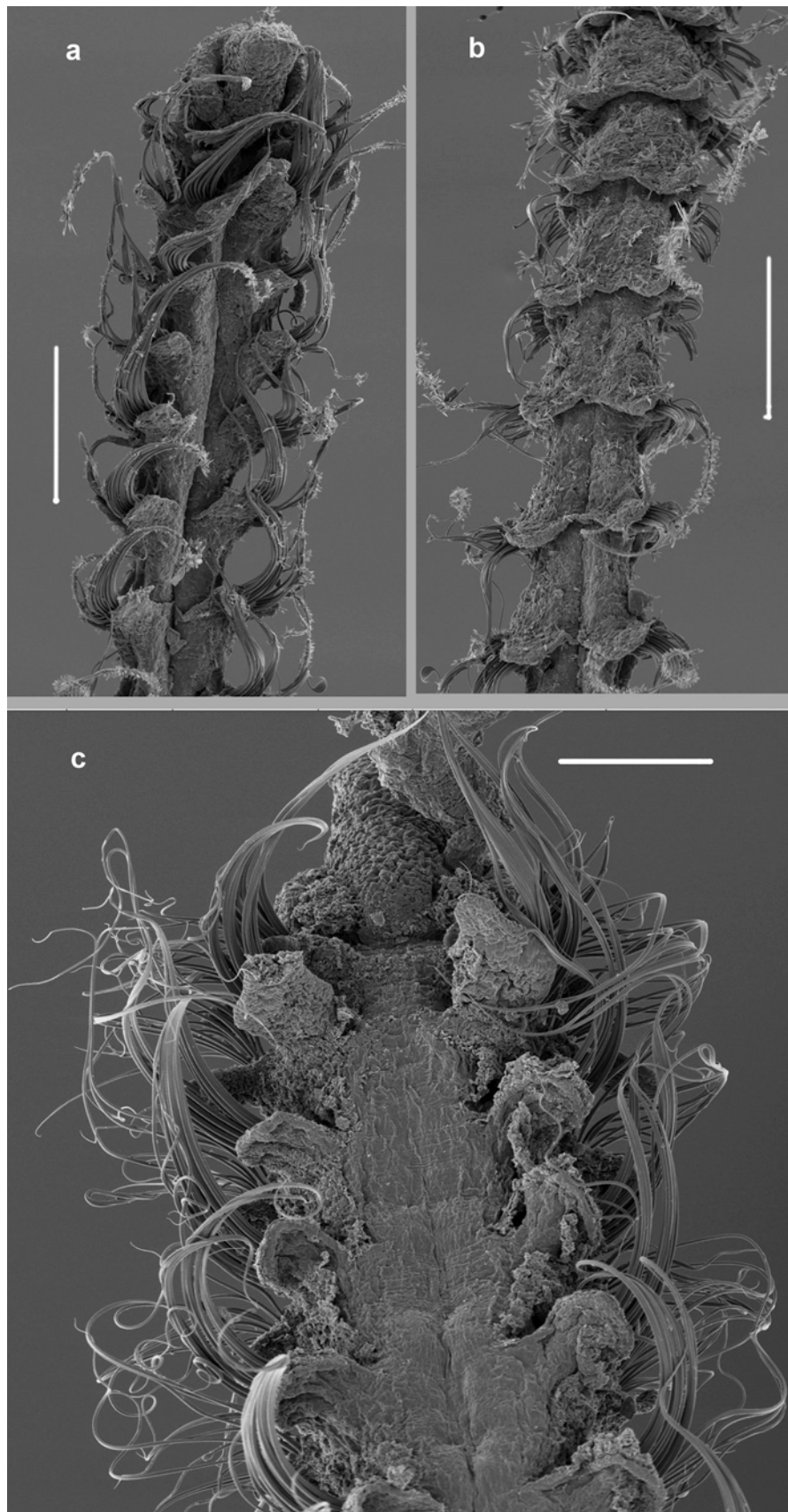
*Aurospio dibranchiata*, *A. foodbancsia* Mincks *et al.*, 2008, and *A. banyulensis* appear to have large rectangular-shaped dorsal lamellae on chaetiger three, often orientated towards the mid-line. By contrast the dorsal lamellae of chaetiger 3 in *Prionospio* are usually described as foliose or auricular and pointed with a rounded tip. *A. pilkena* is an exception to this rule, having been placed in *Aurospio* presumably because the branchiae start on chaetiger 3.

However, such characters have not been completely assessed by comparison with all other species of *Prionospio* and the assignment to *Aurospio* is principally by the general impression of the specimens, in particular the rounded shape of the prostomium. This is not a satisfactory conclusion. A major review of the generic boundaries, using molecular as well as morphological characters, will be needed to resolve this problem.

**Etymology.** *abbranchiata*—refers to the absence of branchiae.

**Ecology.** *A. abbranchiata* **sp. nov.** was the second most abundant spionid species found in the canyons of the Iberian margin by the HERMES programme. However, it achieved higher densities in mid-depth canyons (around 3400 m) than in deep-water canyons with highest densities found in Cascais canyon, where it replaced *P. vallensis* **sp. nov.** as the most dominant spionid species. Cascais canyon is considered to be the most quiescent of the three canyons studied along the Portuguese margin. Cascais canyon also had the lowest abundance, but highest diversity and evenness, of polychaete assemblages. *Aurospio abbranchiata* **sp. nov.** was also found in Setúbal canyon at 3400 m during RRS *Discovery* cruise 186 in 1989, where it was highly dominant, contributing nearly 30% of the total polychaete abundance. The increased density during D186 compared with densities recorded during the HERMES program is difficult to interpret as different mesh-sized sieves were used. *A. abbranchiata* **sp. nov.** is a very slender species and larger numbers could have been caught in the 0.3-mm mesh used during D186 than in 0.5-mm and 1-mm mesh used during the HERMES sampling program.

The species is also quite numerous in the sediment samples from the Porcupine Abyssal Plain where it reaches abundances of 40 individuals per metre<sup>2</sup>.



**FIGURE 14.** *Aurospio abranchiata* **sp. nov.** Porcupine Abyssal Plain (Bengal5\_D231\_13368#20 sp81). a) Dorsal view of anterior chaetigers; scale bar = 100 µm. b) Mid-body chaetigers showing dorsal folds; scale bar = 100 µm. c) Detail of anterior chaetigers scale bar = 100 µm.

The absence of branchiae provides an interesting insight into evolutionary adaptations in these deep-sea spionids. The deep-sea species of *Aurospio*—*A. dibranchiata*, *A. foodbancsia*, and *A. abbranchiata* **sp. nov.** show a reduction both in the size of branchiae and also in the number. *A. dibranchiata* has two pairs of small branchiae, *A. foodbancsia* has one pair while *A. abbranchiata* **sp. nov.** has no branchiae. The absence of branchiae in *A. abbranchiata* **sp. nov.** could be compensated by extremely large notopodial lamellae, which are also a diagnostic feature of this species.

**Distribution.** Porcupine Abyssal Plain at 4800 m, Nazaré, Setúbal and Cascais canyons along Portuguese margin at 3199–4485 m.

## Discussion

**What is *Prionospio*?** The reason for posing this question arises as a result of our description of *Aurospio abbranchiata* **sp. nov.** The lack of branchiae results in an inability to accurately place the species within a genus and in particular highlights problems with the current definitions of *Prionospio* and *Aurospio*. This lack of defining characters, other than the branchial arrangement and chaetiger of branchial initiation, is also highlighted in the available molecular data which indicated that there was not a clear separation of species belonging to these two genera, using 18S rRNA markers (Mincks *et al.* 2008); although this result needs to be confirmed with greater gene and taxon sampling. A review of the definitions of the genus *Prionospio* did not provide any greater clarity. For example, Wilson's (1990) definition widely encompasses many of the putative subgenera and overlaps with other accepted genera such as *Apoprionospio*: “peristomium reduced, with or without lateral wings; chaetiger 1 reduced, fused to peristomium; branchiae commence chaetiger 2 or 3 [our emphasis], 3–40 pairs apinnate or digitiform pinnae or both; dorsal crests may be present on some post branchial chaetigers; hooded hooks present in notopodia and neuropodia, secondary hood small; pygidium 1 long dorsomedial cirrus and 2 lateral lappets”. In a subsequent analyses of *Prionospio*, Sigvaldadottir (1998) refined the definition to exclude species where the branchiae started on chaetiger three, transferring such species to *Aurospio*.

So the characters used to define the members of the *Prionospio* complex are subtle. *Laubieriellus* Maciolek, 1981 can be distinguished because there are no notopodial hooks. The difference between *Prionospio* and other genera, such as *Apoprionospio* and *Aurospio*, is often down to one particular feature which may fall within the range of characters currently found in species assigned to *Prionospio*. For example *Apoprionospio* differs in having either no dorsal crests or a prominent crest on chaetiger 7, the presence of plate-like pinnules on the branchiae and a small secondary hood in the hooded hooks. However these characters also appear in species of *Prionospio sensu stricto*: for example, *P. auckandica* Augener, 1923 (referred to *P. (Aquilospio)* by Foster 1971 and Blake & Kudenov 1989), *P. caspersi* Laubier, 1962, *P. fallax* Söderström 1920, and *P. membranacea* Imajima, 1990 have dorsal crests only on chaetiger 7. Sigvaldadottir (1998) considered that *Apoprionospio* was a congener of *Prionospio*.

One distinguishing feature of *Aurospio* is where the branchiae first arise. The only new interpretation of existing characters is that in *Prionospio* species the anterior notopodial lamellae are more foliose with gradually tapering edges to a rounded, sometimes produced point; whereas in *Aurospio* the anterior lamellae, particularly those associated with the branchiae, have a more truncated, less gradual taper and are more angular in profile.

It is not that the branchial arrangement is unimportant nor that these characters do not work for the majority of the species and in distinguishing genera, it is merely that they highlight how limited the characters are that are being used to distinguish and establish genera and their phylogenetic relationships. Even then there has been considerable debate as to whether the arrangement and form of the branchiae are important in the definition of the genera/ subgenera within these spionids as detailed in the Remarks under *A. abbranchiata* **sp. nov.** This debate is still not settled. In a cladistic analysis carried out by Yokoyama (2007), *Prionospio (Aquilospio)* was considered a valid clade distinguished by having a basal sheath on the palp (a character shared with *Paraprionospio*) and with the branchial arrangement of pinnules on all branchiae with found within this subgenus, therefore, a valid character set. The problem will only be resolved when well-supported phylogenetic reconstructions based on molecular data are available for the majority of the *Prionospio/Aurospio* taxa.

**Distribution patterns in deep-sea spionids.** The species described in this paper showed a range of geographic distributions. As these distributions are based on morphological taxonomy, they should be treated with caution.



However, we believe it is essential to start getting species descriptions for putative abyssal species available in the literature so we can start to address these questions of connectivity within and between ocean basins. Morphological consistency across ocean basins may, or may not, imply gene-flow. This can be tested only with molecular evidence from a large number of individuals from each site, something we are currently not able to do owing to sampling limitations in the abyss. But it does provide both a hypothesis to test and evidence of (at the very least) close connections at evolutionary scales.

*Prionospio amarsupialis* **sp. nov.**, *P. branchilucida* **sp. nov.**, and *P. kaplani* **sp. nov.** have wide geographic ranges, being recorded from the North Atlantic, Southern Ocean, and central Pacific, all at abyssal depths. *Aurospio abranchiata* **sp. nov.**, while more restricted, appears to be widespread in the northeast Atlantic being found in both canyon and abyssal plain sites. By contrast *P. vallensis* **sp. nov.**, *P. hermesia* **sp. nov.**, *P. canyons* **sp. nov.**, and *Aurospio tribranchiata* **sp. nov.** have only been recorded from one locality, albeit with the proviso that these species can occur in large densities in the localities within which they were found.

The widespread distributions of some of our new abyssal morphospecies is a phenomenon that has also been observed in, for example, abyssal ophiuroids (Belyaev & Litvinova 1972; Paterson 1985) and foraminifera (Cornelius *et al.* 2004). Where widespread distributions have been tested with molecular methods, the results are not consistent. For example, studies in foraminifera and nematodes have confirmed broad distributions (Pawlowski *et al.* 2007; Bik *et al.* 2010), whilst cryptic speciation has been detected in other groups such as hydroids and limpits (e.g., Moura *et al.* 2008, 2011; Johnson *et al.* 2008). These may be related to the type of habitat, and unfortunately there are rather few molecular studies of non-vent/seep deep-sea taxa. Although it is difficult to generalise based on these few studies, it is likely that abyssal soft-sediment taxa are quite broadly distributed and our morphological species concepts may not necessarily be refuted by future molecular evidence.

**Author contributions:** Taxonomic sections and species descriptions: Gordon Paterson (lead author), Iris Altamira, Adrian Glover, Lenka Neal, and Eulogio Soto.

Ecological context, project and cruise PI, access to material and editorial input: David Billett (Crozet Archipelago: CROZEX; PAP: BENGAL; Iberian Canyons: HERMES), Marina Cunha (Iberian Canyons: HERMES), and Lenaick Menot (CCFZ: NODINAUT Central Pacific, EUMELI CVAP), Craig Smith (CCFZ: KAPLAN Central Pacific; Equatorial Pacific: EqPac).

Claire Marchais-Laguionie undertook the SEM preparation and imaging of the PAP species.

## Acknowledgements

We would like to thank the officers, crew, and scientific parties of RSS *Discovery*, RRS *Challenger II*, RRS *Charles Darwin*, RRS *James Cook*, RV *Thomas Thompson*, RV *New Horizon*, RV *Melville* and RV *l'Atalante*.

We thank the staff of the NHM Imaging and Analyses Unit for advice, support, and access to the SEM facilities, and the late Dr Kristian Fauchald and the collections management staff at USNM for the loan of type material.

We gratefully acknowledge funding support from the Kaplan Foundation, EC MAST I & II (EC contract number MAST2-CT920033), EC MAST III BENGAL (EC Contract number MAS3-CT950018); *Deepsets* Responsive Mode Project within the Marine Biodiversity Ecosystem and Function (MarBEF) Network of Excellence (EC Contract number GOCE-CT-2003-505446); HERMES (EC contract number GOCE-CT-511234) under the European Commission's Framework Six Programme, the United Kingdom's Natural Environment Research Council Research Grant NER/A/S/2003/00573 (Benthic Crozet), International Seabed Authority, Mecsup UVA0205 Project from Universidad de Valparaíso; and samples provided by the ABYSSLINE consortium (funder: UK Seabed Resources Ltd).

The manuscript benefited from the constructive remarks and suggestions made by Drs Nancy Maciolek and Robin Wilson. Their insight is gratefully appreciated.

## References

- Aguirrezabalaga, F. & Ceberio, A. (2005) Spionidae (Annelida: Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with descriptions of a new genus and three new species. *Marine Biology Research*, 1, 267–280.

<http://dx.doi.org/10.1080/17451000500262066>

- Augener, H. (1923) Polychaeten von Westpatagonien. *Göteborgs Kungl. Vetenskaps och Vitterhets Samhälles Handlingar F. 4*, 27, 1–5.
- Arzola, R.G., Wynn, R.B., Lastras, G., Masson, D.G. & Weaver, P.P.E. (2008) Sedimentary features and processes in the Nazaré and Setúbal submarine canyons, west Iberian margin. *Marine Geology*, 250, 64–88.  
<http://dx.doi.org/10.1016/j.margeo.2007.12.006>
- Belyaev, G.M. & Litvinova, N.M. (1972) New genera and species of deep-sea Ophiuroidea. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody Otdel Geologicheskii*, 3, 5–20.
- Bik, H., Thomas, W.K., Lunt, D.H. & Lamshead, P.J.D. (2010) Low endemism, continued deep-shallow interchanges, and evidence for cosmopolitan distributions in free-living marine nematodes (order Enoplida). *BMC Evolutionary Biology*, 10, 389.  
<http://dx.doi.org/10.1186/1471-2148-10-389>
- Billett, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.H., Galeron, J., Sibuet, M. & Wolff, G.A. (2001) Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Progress in Oceanography*, 50, 325–348.  
[http://dx.doi.org/10.1016/S0079-6611\(01\)00060-X](http://dx.doi.org/10.1016/S0079-6611(01)00060-X)
- Billett, D.S.M. & Rice, A.L. (2001) The BENGAL Programme: Overview and Introduction. *Progress in Oceanography*, 50, 13–25.  
[http://dx.doi.org/10.1016/S0079-6611\(01\)00046-5](http://dx.doi.org/10.1016/S0079-6611(01)00046-5)
- Blake, J.A. (1983) Biology of the Antarctic seas 14. Polychaetes of the family Spionidae from South America, Antarctica, and adjacent seas and islands. *Antarctic Research Series*, 39, 205–288.
- Blake, J.A. (1996) Family Spionidae Grube, 1850. Including a review of the genera and species from California and a revision of the genus *Polydora* Bosc, 1802. *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the western Santa Barbara Channel. Volume 6 - the Annelida Part 3 - Polychaeta: Orbiniidae to Cossuridae*, 81–223.
- Blake, J.A. & Kudenov, J.D. (1978) The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. *Memoirs of the National Museum of Victoria, Supplement*, 39, 171–280.
- Blake, J. A., Maciolek, N. J., Ota, A. Y. & Williams, I. P. (2009) Long-term benthic infaunal monitoring at a deep-ocean dredged material disposal site off northern California. *Deep-Sea Research Part II Topical Studies in Oceanography*, 56, 1775–1803.
- Böggemann, M. (2009) Polychaetes (Annelida) of the abyssal SE Atlantic. *Organisms Diversity & Evolution*, 9 (4–5), 252–428.
- Cornelius, N. & Gooday, A. J. (2004) ‘Live’ (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends in abundance, diversity and taxonomic composition along a depth transect. *Deep-sea Research II*, 51, 1571–1603.  
<http://dx.doi.org/10.1016/j.dsr2.2004.06.024>
- Cognetti Varriale, A.M. (1987) *Prionospio somaliensis* (Annelida Polychaeta), un nuovo spionide delle coste della Somalia. *Atti della Società Toscana di Scienze Naturali Residente in Pisa Memorie, Serie B*, 94, 369–372.
- Cunha, M.R., Paterson, G.L.J., Amaro, T., Blackbird, S., de Stigter, H.C., Ferreira, C., Glover, A., Hilário, A., Kiriakoulakis, K., Neal, L., Ravara, A., Rodrigues, C.F., Tiago, A. & Billett, D.S.M. (2011) Biodiversity of macrofaunal assemblages from three Portuguese submarine canyons (NE Atlantic). *Deep-Sea Research II*, 58, 2433–2447.  
<http://dx.doi.org/10.1016/j.dsr2.2011.04.007>
- Curdia, J., Carvalho, S., Ravara, A., Gage, J.D., Rodrigues, A.M. & Quintino V. (2004) Deep macrobenthic communities from Nazaré Submarine Canyon (NW Portugal). *Scientia Marina*, 68, 171–180.
- Foster, N.M. (1971) Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. (Studies on the Fauna of Curaçao and other Caribbean Islands: No. 129). *Uitgaven Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen*, No. 63, 1–183.
- Gage, J.D., Lamont, P.A. & Tyler, P.A. (1995) Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary results: 1. Introduction and diversity comparisons. *Internationale Revue der Gesamten Hydrobiologie*, 80, 235–250.  
<http://dx.doi.org/10.1002/iroh.19950800211>
- Glover, A.G. (2000) *Abyssal polychaete assemblages along latitudinal gradients of productivity in the Equatorial Pacific and North Atlantic Ocean*. PhD Thesis University of Southampton. 202 pp
- Glover, A., Paterson, G., Bett, B., Gage, J., Sibuet, M., & Shearer, M. (2001) Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic. *Deep-Sea Research Part I*, 48, 217–236.  
[http://dx.doi.org/10.1016/S0967-0637\(00\)00053-4](http://dx.doi.org/10.1016/S0967-0637(00)00053-4)
- Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L. & Shearer, M. (2002) Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. *Marine Ecology Progress Series*, 240, 157–170.  
<http://dx.doi.org/10.3354/meps240157>
- Hartman, O. (1961) Polychetous annelids from California. *Allan Hancock Pacific Expeditions*, 25, 1–226.
- Hartmann-Schröder, G. (1962) Die Polychaeten des Eulitorals. in Hartmann-Schröder, G. & Hartmann, G. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut./Hamburg*, 60, 57–167.
- Imajima, M. (1990) Spionidae (Annelida, Polychaeta) from Japan 4. The genus *Prionospio* (*Prionospio*). *Bulletin of the*

National Science Museum, Series A (Zoology), 16, 105–140.

- Johnson, S.B., Waren, A. & Vrijenhoek, R.C. (2008) DNA barcoding of *Lepetodrilus* limpets reveals cryptic species. *Journal of Shellfish Research*, 27, 43–51.  
[http://dx.doi.org/10.2983/0730-8000\(2008\)27\[43:DBOLLR\]2.0.CO;2](http://dx.doi.org/10.2983/0730-8000(2008)27[43:DBOLLR]2.0.CO;2)
- Lamont, P.A., Gage, J.D. & Tyler, P.A. (1995) Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary results: 2. Spatial dispersion. *Internationale Revue der Gesamten Hydrobiologie*, 80, 251–265.  
<http://dx.doi.org/10.1002/iroh.19950800212>
- Lastras, G., Arzola, R.G., Masson, D.G., Wynn, R.B., Huvenne, V.A.I., Huhnerbach, V. & Canals, M. (2009) Geomorphology and sedimentary features in the Central Portuguese submarine canyons, Western Iberian margin. *Geomorphology*, 103, 310–329.  
<http://dx.doi.org/10.1016/j.geomorph.2008.06.013>
- Laubier, L. (1962) Quelques Annelides Polychetes de la lagune de Venise. Description de *Prionospio caspersi* n. sp. *Vie et Milieu*, 13, 123–159.
- Laubier, L. (1966) Le coralligene des Alberes; monographie biocenotique. *Annales de l'Institut Oceanographique Monaco N S*, 43, 137–316.
- Laubier, L. (1968) Contribution a la faunistique du coralligene 7. A propos de quelques annelides polychetes rases au nouvelles (Chrysopetalidae, Syllidae et Spionidae). *Annales de l'Institut de Oceanographie. Monaco*, 46, 80–107.
- Maciolek, N.J. (1981a) A new genus and species of Spionidae (Annelida: Polychaeta) from the north and south Atlantic. *Proceedings of the Biological Society of Washington*, 94, 228–239.
- Maciolek, N.J. (1981b) Spionidae (Annelida: Polychaeta) from the Galapagos Rift geothermal vents. *Proceedings of the Biological Society of Washington*, 94, 826–837.
- Maciolek, N.J. (1985) A revision of the genus *Prionospio* Malmgren, with special emphasis on species from the Atlantic Ocean, and new records of species belonging to the genera *Apoprionospio* Foster and *Paraprionospio* Caullery (Polychaeta, Annelida, Spionidae). *Zoological Journal of the Linnean Society*, 84, 325–385.  
<http://dx.doi.org/10.1111/j.1096-3642.1985.tb01804.x>
- Mackie, A.S.Y. (1984) On the identity and zoogeography of *Prionospio cirrifera* Wiren, 1883 and *Prionospio multibranchiata* Berkeley, 1927 (Polychaeta; Spionidae). *Proceedings of the First International Polychaete Conference, Sydney, Australia*, July 1983, 35–47.
- Mackie, A.S.Y. & Hartley, J.P. (1990) *Prionospio saccifera* sp. nov. (Polychaeta: Spionidae) from Hong Kong and the Red Sea, with a redescription of *Prionospio ehlersi* Fauvel, 1928. *The Marine Flora and Fauna of Hong Kong and Southern China*, 2 (1), 363–375.
- Meißner, K. (2005) Revision of the genus *Spiophanes* (Polychaeta, Spionidae); with new synonymies, new records and descriptions of new species. *Mitteilungen aus dem Museum fuer Naturkunde in Berlin Zoologische Reihe*, 81, 3–65.  
<http://dx.doi.org/10.1002/mmzn.200310001>
- Meißner, K. & Hutchings, P.A. (2003) *Spiophanes* species (Polychaeta: Spionidae) from eastern Australia: with descriptions of new species, new records and an emended generic diagnosis. *Records of the Australian Museum*, 55, 117–140.  
<http://dx.doi.org/10.3853/j.0067-1975.55.2003.1379>
- Mincks, S.L., Dyal, P.L., Paterson, G.L.J., Smith, C.R. & Glover, A.G. (2009) A new species of *Aurospio* (Polychaeta, Spionidae) from the Antarctic shelf, with analysis of its ecology, reproductive biology and evolutionary history. *Marine Ecology*, 30, 181–197.
- Moura, C.J., Harris, D.J., Cunha, M.R. & Rogers, A.D. (2008) DNA barcoding reveals cryptic diversity in marine hydroids (Cnidaria, Hydrozoa) from coastal and deep-sea environments. *Zoologica Scripta*, 37 (1), 93–108.
- Paterson, G.L.J. (1985) The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History). Zoology*, 49 (1), 1–162.
- Paterson, G.L.J., Glover, A.G., Cunha, M.R., Neal, L., de Stigter, H., Kiriakoulakis, K., Billett, D.S.M., Wolff, G., Tiago, A., Ravara, A., Lamont, P. & Tyler, P.A. (2011) Disturbance, productivity and diversity in deep-sea canyons: a worm's eye view. *Deep-Sea Research II*, 58, 2448–2460.  
<http://dx.doi.org/10.1016/j.dsr2.2011.04.008>
- Paterson, G.L.J., Wilson, G.D.F., Cosson, N. & Lamont, P.A. (1998) Hessler and Jumars (1974) revisited: abyssal polychaete assemblages from the Atlantic and Pacific. *Deep-Sea Research Part II Topical Studies in Oceanography*, 45, 225–251.  
[http://dx.doi.org/10.1016/S0967-0645\(97\)00084-2](http://dx.doi.org/10.1016/S0967-0645(97)00084-2)
- Pawlowski, J., Fahrni, J., Lecroq, B., Longet, D., Cornelius, N., Excoffier, L., Cedhagen, T. & Gooday, A.J. (2007) Bipolar gene flow in deep-sea benthic foraminifera. *Molecular Ecology*, 16, 4089–4096.  
<http://dx.doi.org/10.1111/j.1365-294X.2007.03465.x>
- Sigvaldadottir, E. (1998) Cladistic analysis and classification of *Prionospio* and related general genera (Polychaeta, Spionidae). *Zoologica Scripta*, 27, 175–187.  
<http://dx.doi.org/10.1111/j.1463-6409.1998.tb00435.x>
- Sigvaldadottir, E. & Mackie, A.S.Y. (1993) *Prionospio steenstrupi*, *P. fallax* and *P. dubia* (Polychaeta, Spionidae): re-evaluation of identity and status. *Sarsia*, 78, 203–219.
- Sigvaldadottir, E., Mackie, A.S.Y. & Pleijel, F. (1997) Generic interrelationships within the Spionidae (Annelida: Polychaeta). *Zoological Journal of the Linnean Society*, 119, 473–500.

<http://dx.doi.org/10.1111/j.1096-3642.1997.tb00144.x>

- Smith, C.R., Berelson, W., Demaster, D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Pope, R.H. & Stephens, M. (1997) Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Research Part II*, 44, 2295–2317.  
[http://dx.doi.org/10.1016/S0967-0645\(97\)00022-2](http://dx.doi.org/10.1016/S0967-0645(97)00022-2)
- Söderstrom, A. (1920) *Studien uber die Polychaetenfamilie Spionidae*. Dissertaion, Uppsala, Almqvist and Wiksells, 266 pp.
- Soto, E.H. (2008) *Taxonomy and biology of dee-sea polychaetes: temporal variability in polychaete assemblages of rhe abyssal NE Atlantic Ocean*. PhD Thesis, University of Southampton, Southampton, 262 pp.
- Soto, E.H., Paterson, G.L.J., Billett, D.S.M., Hawkins, L.E., Galéron, J. & Sibuet, M. (2010) Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean. *Deep Sea Research Part II*, 57 (15), 1396–1405.  
<http://dx.doi.org/10.1016/j.dsr2.2009.02.003>
- Tyler, P., Amaro, T., Arzola, R., Cunha, M.R., de Stigter, H., Gooday, A., Huvenne, V., Ingels, J., Kiriakoulakis, K., Lastras, G., Masson, D., Oliveira, A., Pattenden, A., Vanreusel, A., van Weering, T., Vitorino, J., Witte, U. & Wolff, G. (2009) Europe's Grand Canyon. Nazaré Submarine Canyon. *Oceanography*, 22, 46–57.  
<http://dx.doi.org/10.5670/oceanog.2009.05>
- Wolff, G.A., Billett, D.S.M., Bett, B.J., Holtvoeth, J., FitzGeorge-Balfour, T., Fisher, E.H., Cross, I., Shannon, R., Salter, I., Boorman, B., King, N.J., Jamieson, A. & Chaillan, F. (2011) The effects of natural iron fertilisation on deep-sea ecology. *PLoS One*, 6 (6), 1–9. [e20697]
- Wilson, R.S. (1990) *Prionospio* and *Paraprionospio* (Polychaeta: Spionidae) from southern Australia. *Memoirs of Museum Victoria*, 50, 243–274.
- Wiren, A. (1884) *Chaetopoder fran Sibiriska Ishafvet och Berings Haf imamlade under Vega-Expeditionen 1878-79. Vol. II. Vega-Expeditionens Vetenskapliga Iakttagelser*, Stockholm, pp. 383–428.
- Yokoyama, H. (2007) A revision of the genus *Paraprionospio* Caullery (Polychaeta: Spionidae). *Zoological Journal of the Linnean Society*, 151, 253–284.  
<http://dx.doi.org/10.1111/j.1096-3642.2007.00323.x>