



## New *Prionospio* and *Laubieriellus* (Annelida: Spionidae) species from Southeastern Brazil

ANTÔNIO JOÃO MALAFAIA PEIXOTO<sup>1,2,3</sup> & PAULO CESAR DE PAIVA<sup>1,2</sup>

<sup>1</sup>Laboratório de Polychaeta, Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, CCS, Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-902, Brazil.

<sup>2</sup>Programa de Biodiversidade e Biologia Evolutiva, Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, CCS, Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-902, Brazil.

<sup>3</sup>Corresponding author. E-mail: [antoniojmp@ufrj.br](mailto:antoniojmp@ufrj.br)

### Abstract

Two new *Prionospio* species—*Prionospio solisi* **sp. nov.** and *Prionospio nonatoi* **sp. nov.** and a new *Laubieriellus* species—*Laubieriellus decapitata* **sp. nov.** are described from Espírito Santo Basin, Southeast Brazil. For both *Prionospio* species, branchial pattern differed from the genus diagnosis, which is therefore emended. For *Laubieriellus*, a new species is described, and attention is drawn to the notch in the ventral crests, a structure that holds taxonomic value.

**Key words:** Taxonomy, Polychaeta, morphology, emended diagnosis

### Introduction

The annelid family Spionidae Grube, 1850 is one of the most diverse and abundant families, frequently dominating soft-bottom communities, particularly in disturbed environments. Worldwide, there are approximately 580 species distributed in 39 genera (Blake *et al.* 2017), although this number may be an underestimate since the family has a long history of taxonomic problems, with many well-documented species-complexes (Sato-Okoshi *et al.* 2016), as well as genera that have never been revised.

Around 90 nominal species distributed in 18 genera of the family have been recorded for the Brazilian coast (Amaral *et al.* 2013; Peixoto & Paiva 2017), although recent surveys and taxonomic efforts suggest these numbers are underestimates, as many species remain undescribed, particularly in the deep-sea (Paiva & Barroso 2010).

Spionid taxonomic studies in Brazil are still limited, as most of them are geographically restricted to the southern and southeastern coasts of Brazil and frequently limited to shallow coastal environments (except Paiva & Barroso 2010 and Peixoto & Paiva 2017). Only a few genera have been studied in detail, such as *Laonice* Malmgren, 1867 (Nonato *et al.* 1986; Radashevsky & Lana 2009), *Scolecopsis* Blainville, 1828 (Rocha *et al.* 2009; Rocha & Paiva 2012), *Pseudopolydora* Czerniavsky, 1881 (Radashevsky & Migotto 2009), *Dipolydora* Verrill, 1881 (Radashevsky & Nogueira 2003), *Polydora* Bosc, 1802 (Radashevsky *et al.* 2006), *Trochochaeta* Levinsen, 1884 (Radashevsky *et al.* 2018) and *Spiogalea* Aguirrezabalaga & Ceberio, 2005 (Peixoto & Paiva 2017). Large-scale studies are scarce, being restricted to Bolívar & Lana (1987) for the continental shelf of Paraná State, Southern Brazil, and Paiva & Barroso (2010) for the continental slope of Campos Basin, Rio de Janeiro State, Southeastern Brazil.

In Brazil, 14 *Prionospio* species have been recorded so far, mostly from shallow-water environments. *Prionospio malmgreni* Claparède, 1869, is also supposedly reported from Brazil, despite that it is considered as a *taxon inquirendum* and possibly represents more than one species (Maciolek 1985). It should be noted that most records should be used with caution, as these records include species described from distant locations and have never been confirmed, such as *Prionospio steenstrupi* Malmgren, 1867 (Iceland), *P. cirrifera* Wirén, 1883 (Russia),

*P. dubia* Day, 1961 (South Africa), *P. ehlersi* Fauvel, 1928 (Morocco), *P. pygmaeus* Hartman, 1961 (USA), *P. multibranchiata* Berkeley, 1927 (Canada) and *P. lighti* Maciolek, 1985 (USA) (see Amaral *et al.* 2013 for detailed Brazilian records). The veracity of these records will be addressed in a future work.

The *Prionospio* generic complex represents a diverse and rich assemblage of species among the spionids, being comprised of seven currently valid genera: *Apoprionospio* Foster, 1969, *Aurospio* Maciolek, 1981a, *Laubieriellus* Maciolek 1981b, *Orthoprionospio* Blake & Kudenov, 1978, *Paraprionospio* Caullery, 1914, *Prionospio* Malmgren, 1867, and *Streblospio* Webster, 1879 (Blake *et al.* 2017). Two additional taxa, *Minuspio* and *Aquilaspio*, were erected by Foster (1971) as subgenera of *Prionospio*, but were latter synonymized by Sigvaldadóttir (1998), due to the lack of support for its monophyletic condition, thus making *Prionospio* the largest spionid genus, with over 100 species (Blake *et al.* 2017). The current diagnosis of *Prionospio sensu lato* comprises considerable morphological diversity, especially in regards to the distribution and arrangement of smooth and pinnate branchiae.

The genus *Laubieriellus* Maciolek 1981b was erected to include species of the *Prionospio*-complex that lack notopodial hooks, possess four pairs of smooth branchiae on chaetigers 2–5, and ventral crests on several anterior chaetigers, a set of characters exclusive to the genus. Only three species have been described so far: *Laubieriellus salzi* (Laubier 1970), from the Coast of Israel, Mediterranean Sea, *L. grasslei* Maciolek 1981b from the Galápagos Rift, and *L. cacatua* Erickson & Wilson, 2018 from Western Australia.

In the present work, two unusual *Prionospio* species, *Prionospio nonatoi* **sp. nov.** and *P. solisi* **sp. nov.**, and a new *Laubieriellus* species, *L. decapitata* **sp. nov.**, are presented and described. The species were collected during the cruises of the “Marine Environmental Characterization of Espírito Santo Basin and Northern Portion of Campos Basin” (AMBES) Project, coordinated by CENPES/PETROBRAS (Research Center of the Brazilian Energy Company), focusing on the southeastern coast of Brazil.

## Materials and methods

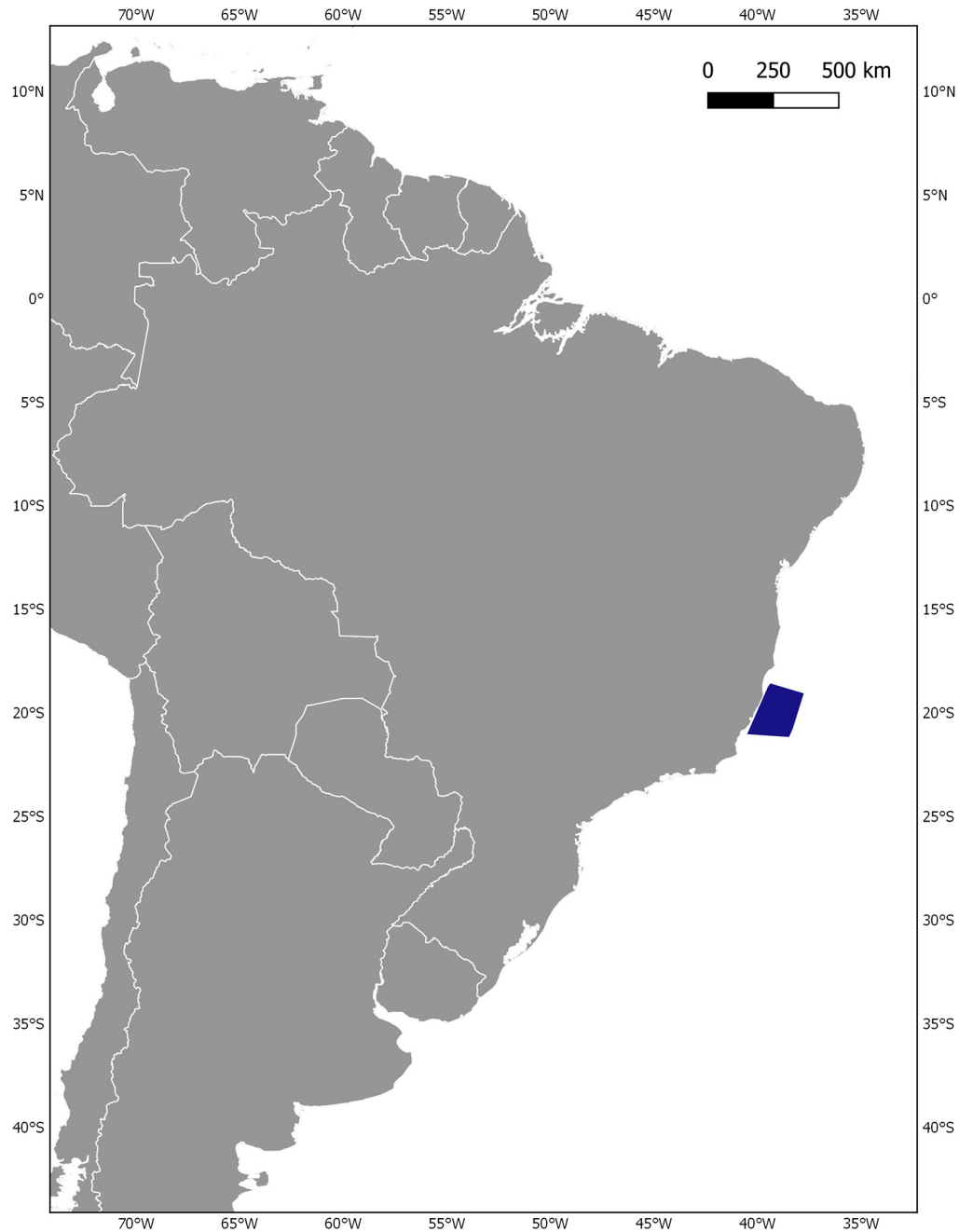
Sediment samples were collected on the continental shelf using a Van Veen Grab sampler and on the continental slope using a box corer during the summer (sample codes Amb1, Amb3, Amb4, Amb5, Amb6, and Amb7), and winter (sample codes Amb2, Amb11, Amb12, Amb13 and Amb14) cruises of the AMBES project (Figure 1). Sediment was fixed *in situ* in 10% formaldehyde in seawater solution. In the laboratory, sediment was washed on a 300- $\mu$ m-mesh sieve and transferred to 70% ethanol. Specimens were later sorted and examined under a Leica S8 APO stereomicroscope and Nikon Eclipse E200 microscope. Type material of *Laubieriellus grasslei* (USNM 65913 and USNM 65918) and *L. salzi* (USNM 42621) deposited in the Smithsonian National Museum of Natural History were also examined in this study and discrepancies found in described morphology were documented and illustrated.

Specimens were stained in an alcoholic solution of methyl green (1g/L in 70% EtOH) for 10 seconds and then transferred to distilled water, to examine the staining pattern. The stain Shirlastain A was used to enhance visualization of features such as branchial scars.

For SEM studies, specimens were dehydrated in a graded ethanol series, transferred to a graded HMDS (hexamethyldisilane) series, and subsequently dried in a fume hood. Afterwards, specimens were mounted on stubs, sputter coated with gold, and examined with a JEOL JSM-6390LV scanning electron microscope. The HMDS approach was used because regular CO<sub>2</sub> critical-point drying proved to be too destructive for *Laubieriellus decapitata* **sp. nov.** specimens. Two paratypes of *Laubieriellus grasslei* (USNM 65918) were dehydrated in a graded ethanol series, critical-point dried in CO<sub>2</sub>, mounted on stubs, sputter coated with carbon and gold-palladium and examined with a Philips XL-30 scanning electron microscope.

To examine hook morphology, prior to the treatment described above, posterior fragments were rinsed in distilled water and then sonicated in distilled water for a short time (between 15 to 40 sec) at 30 kHz to remove hoods from the hooks.

Type material was deposited in the Rio de Janeiro National Museum (MNRJP), Universidade Federal do Rio de Janeiro and the Museum of Zoology of the University of São Paulo (MZUSP), Universidade de São Paulo, both located in Brazil.



**FIGURE 1.** Map showing sampling area of the AMBES project (blue polygon).

## Results

### Taxonomy

#### *Prionospio* Malmgren, 1867

Type species: *Prionospio steenstrupi* Malmgren, 1867

**Diagnosis** (emended from Blake *et al.* 2017): Prostomium anteriorly rounded or truncate, sometimes weakly incised, often with peaks, without frontal horns; subtriangular, rectangular or oval in shape, caruncle extending at

least to chaetiger 1; eyespots present or absent; occipital antenna absent. Peristomium at least partially fused with chaetiger 1, often surrounding prostomium with free, flattened lateral wings. Parapodia of chaetiger 1 reduced; noto- and neuropodial lamellae largest in branchial region, reduced thereafter; notopodial lamellae often connected by low to high dorsal ridges or crests. **Branchiae from chaetiger 2, chaetiger 3 or rarely absent. Branchiae limited to anterior chaetigers, 0–15 pairs**, rarely more; branchiae all apinnate, all pinnate, or various combinations of both; pinnate branchiae with pinnules digitiform, not platelike; each branchia entirely free from dorsal lamella. Interparapodial pouches present or absent. Anterior chaetae limbate capillaries; posterior noto- and neuropodial hooded hooks present, bi-, tri-, or multidentate, with secondary hood. Neuropodial sabre chaetae present or absent. Pygidium with one long dorsomedial cirrus and two shorter ventrolateral lobes, all three sometimes fused.

**Remarks:** Blake *et al.*'s (2017) diagnosis was amended to include *Prionospio solisi* **sp. nov.** and *Prionospio nonato* **sp. nov.**, which either lack branchiae or have only two pairs (see description and remarks for each species below). Changes in Blake *et al.*'s (2017) diagnosis have been highlighted in bold.

The *Prionospio*-complex represents one of the most morphologically diverse groups within the Spionidae and even within *Prionospio sensu stricto*, exhibiting remarkable branchial diversity, with many different arrangements. These different branchial arrangements were used in the past to erect other genera or subgenera within *Prionospio* (Foster 1971), such as *Aquilaspio* and *Minuspio* which are no longer considered as valid (e.g., Sigvaldadóttir 1998) by some authors and thus were synonymized with *Prionospio*, although such synonymy is not fully accepted and some researchers still consider *Aquilaspio* (Zhou & Li 2009; Dagli & Çinar 2009; Dagli & Çinar 2011) and *Minuspio* (Aguirrezabalaga & Ceberio 2005; Zhou & Li 2009; Dagli & Çinar 2009; Dagli & Çinar 2011; Dagli *et al.* 2011; Dagli 2013; Delgado-Blas & Díaz-Díaz 2013) as valid.

As for the species described in this work, despite bearing a branchial pattern (or lack of branchiae) that is similar to *Aurospio*, neither species could be placed in *Aurospio*, based on the lack of fusion of the branchiae to the notopodial lamellae (in *Prionospio solisi* **sp. nov.**) and the presence of a secondary hood on the hooded hooks.. Blake *et al.* (2017) noted that, over the past few years, several *Prionospio* species have been erroneously attributed to *Aurospio*. As further discussed in the Remarks section of each species, both species are morphologically similar to *Prionospio*. The placement of these species in *Prionospio*, however, should be treated as conservative, as we consider that the different branchial arrangements observed in both species do not justify the erection of a new taxon, neither within the *Prionospio*-complex nor within *Prionospio sensu stricto*.

### ***Prionospio solisi* sp. nov.**

(Figures 2–5)

**Type material.** Brazil. Espírito Santo Basin. **Holotype:** Amb6 D4R1, 19° 45' 55.39" S 39° 30' 25.74" W, 12/2011 to 02/2012, 149m, **MZUSP 3390.** **Paratypes:** Amb6 D4R1, 19° 45' 55.39" S 39° 30' 25.74" W, 12/2011 to 02/2012, 149m, MNRJP 1826 (6 ind), MZUSP 3391 (3 ind); Amb6 D4R2, 19° 45' 54.88" S 39° 30' 26.22" W, 12/2011 to 02/2012, 142m, MNRJP 1825 (2 ind); Amb6 D4R3, 19° 45' 54.96" S 39° 30' 26.46" W, 12/2011 to 02/2012, 144m, MNRJP 1827 (1 ind).

**Additional material examined.** Brazil. Espírito Santo Basin. Amb 3 CAND4, 19° 31' 51.66" S 39° 3' 4.04" W, 171m (114 ind); Amb 3 CAND7, 19° 42' 18.42" S 39° 5' 52.41" W, 1307m (1 ind); Amb4 B8, 20° 41' 33.45" S 39° 35' 14.76" W, 1914m (1 ind); Amb5 C7, 20° 17' 41.07" S 39° 42' 38.02" W, 1358m (1 ind); Amb6 D4, 19° 45' 55.39" S 39° 30' 25.74" W, 149m (56 ind); Amb6 E4, 19° 36' 5.17" S 39° 10' 32.93" W, 153m (1 ind); Amb11 A5, 21° 4' 4.67" S 40° 13' 6.06" W, 415m (1 ind); Amb11 C7, 20° 17' 37.38" S 39° 42' 36.72" W, 1355m (1 ind); Amb11 E8, 20° 15' 55.44" S 38° 40' 48.23" W, 1892m, (1 ind); Amb11 F8, 20° 16' 38.17" S 38° 27' 26.52" W, 1904m (3 ind); Amb12 CAND4, 19° 31' 51.68" S 39° 3' 4.79" W, 171m (40 ind); Amb12 CAND6, 19° 37' 45.14" S 39° 3' 58.75" W, 1050m (12 ind).

**Diagnostic features:** Branchiae only on chaetigers 3–4, apinnate; dark yellow pigment present on anterior region.

**Description.** A small-sized spionid, largest individual about 7.5 mm long, 0.25 mm wide for 81 chaetigers, holotype 7.3 mm long, 0.23 mm wide for 65 chaetigers. Body cylindrical, slightly dorsoventrally compressed after branchial region and tapered towards the pygidium. Body color whitish in alcohol with conspicuous dark yellow

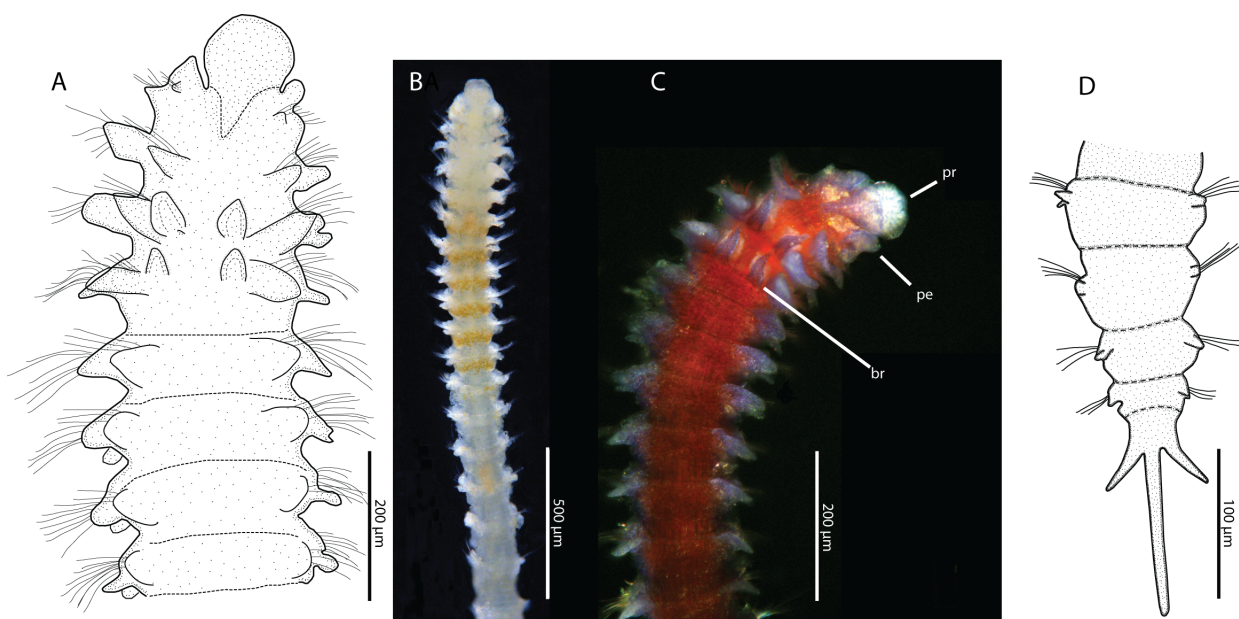
pigment inclusions present on dorsal and ventral sides from chaetiger 4 or 5 to chaetigers 8–12 (strongest on chaetigers 8–10), including parapodia (Fig 2A–C).

Prostomium anteriorly rounded, extending posteriorly as a narrow keel to the posterior margin of chaetiger 1 (Figs 2A–C; 3A; 4A–B). Two pairs of black eyes in trapezoidal arrangement (posterior pair faded in alcohol) present or eyes absent. Prostomial peaks absent. Peristomium surrounding prostomium and partially fused to the first chaetiger, lacking lateral wings. Grooved palps reaching up to chaetiger 8, lost in most individuals.

Chaetiger 1 with only a few short chaetae in both rami. Postchaetal lamellae rounded, reduced. Prechaetal lamellae absent.

Notopodial postchaetal lamellae triangular on chaetigers 2–4, largest on chaetigers 3 and 4, rounded with a pointed tip on chaetiger 5, rounded on chaetiger 6, and reduced to a low flap from chaetiger 7 onwards (Figs 2A–C; 3A; 4A–B). Dorsal crests absent. Prechaetal lamellae absent throughout.

Neuropodial postchaetal lamellae triangular with rounded corners on chaetiger 2, rounded on chaetigers 3 and 4 and flaplike from chaetiger 5, drastically reduced in size from chaetiger 7 onwards (Figs 2A–B; 3B; 4A); lamellae slightly more developed in both rami on last 4–7 chaetigers. Prechaetal lamellae absent throughout.



**FIGURE 2.** *Prionospio solisi* sp. nov., dorsal view (MZUSP 3391, paratypes). A. Anterior chaetigers. B. Anterior chaetigers and mid-body, showing characteristic pigmentation in ethanol. C. Anterior chaetigers stained with Shirlastain A. D. Posterior chaetigers and pygidium. Abbreviations: br, branchia; pe, peristomium; pr, prostomium.

Chaetae organized in two rows of unilimbate and sparsely granulated capillaries (Fig. 5A). In anterior notopodia, capillaries of posterior rows up to 1.3 times longer than capillaries in anterior row (Fig. 5B). Towards the posterior region, capillaries progressively become elongate, non-limbate, thin and less numerous (Fig. 5C).

Hooks in notopodia from chaetigers 48–61, up to two per fascicle, accompanied by 1–4 short non-limbate capillaries. Hooks in neuropodia from chaetigers 9–14, up to eight per fascicle, accompanied by 3–6 non-limbate capillaries. Neuropodial hooks slightly curved near the tip. Hooks multidentate, with 8–10 secondary teeth arranged in two rows above main tooth (Figs 3C; 5E). Small secondary hood present (Fig. 5E). Hooks accompanied by 3–10 short non-limbate capillaries.

Sabre chaetae with light granulations along the shaft, from chaetiger 9–11 (usually chaetiger 10) (Figs 3B; 5D).

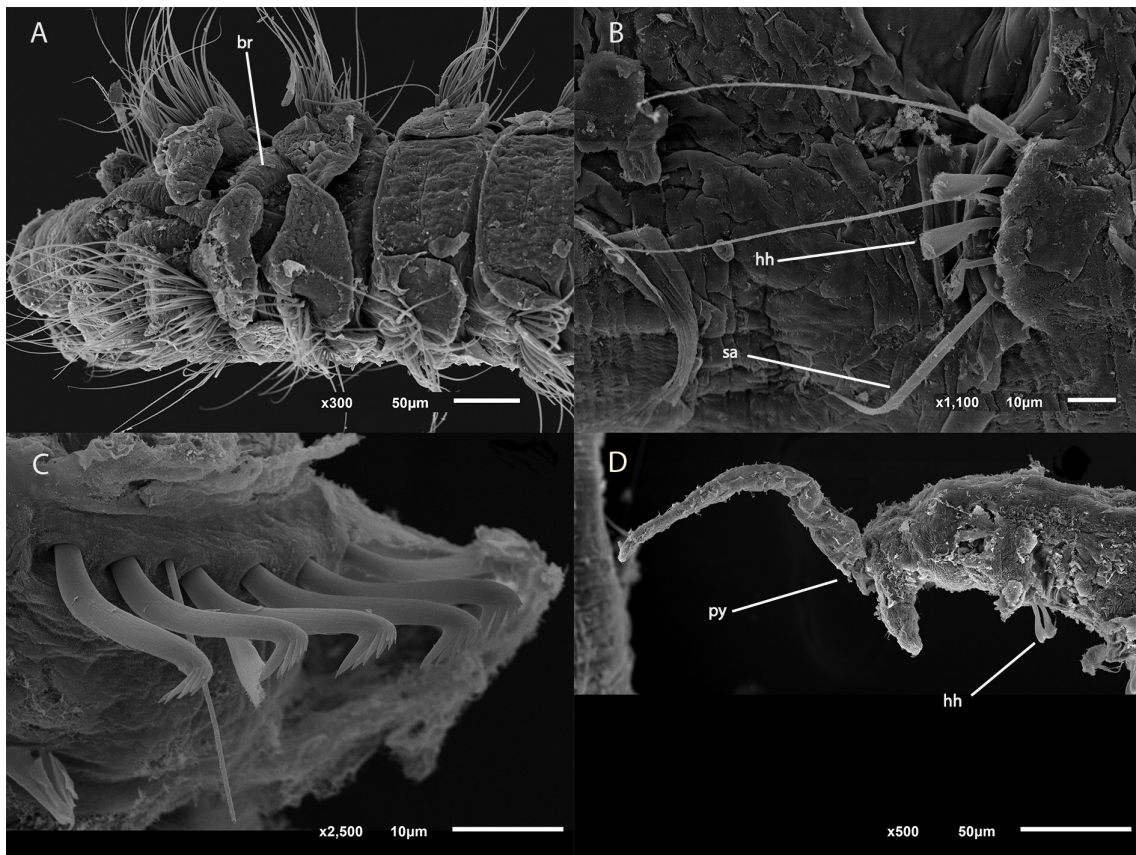
Two pairs of branchiae on chaetigers 3 and 4, of the same length or slightly longer than notopodial postchaetal lamellae (longer on chaetiger 3), completely free from notopodial lamellae. Branchiae triangular, flattened and densely ciliated (Figs 2A, C; 3A; 4A–B). Branchiae absent on chaetigers 2 and 5 (Figs 2A, C; 3A; 4A–B).

Pygidium with one long mid-dorsal cirrus and a pair of shorter ventral cirri (Figs 2D; 3D).

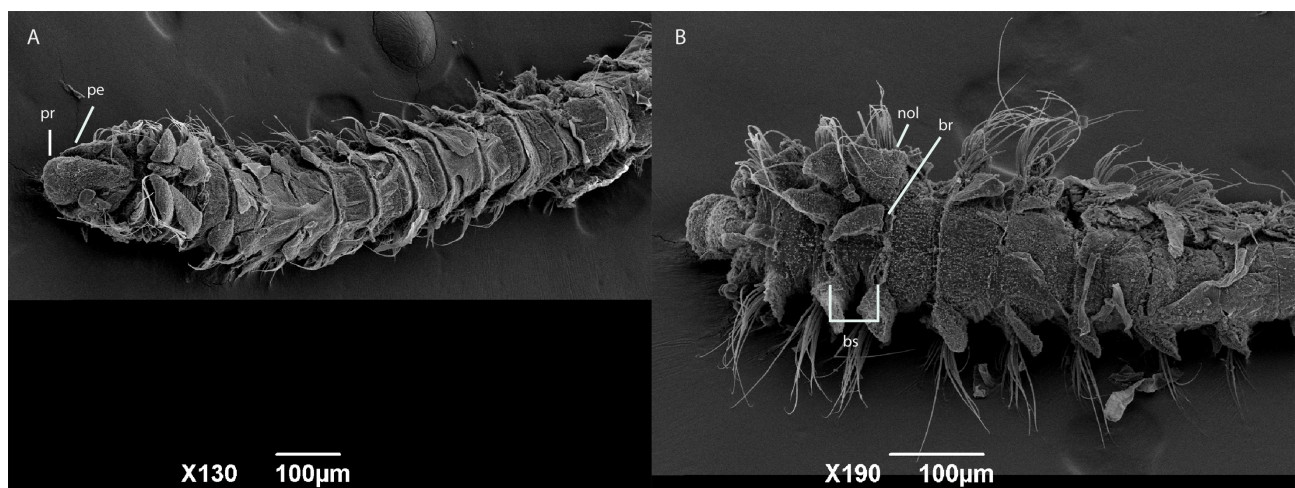
Oocytes from chaetigers 11–14, measuring up to 100 µm.

**Methyl green pattern:** Intense staining on prostomium, dorsal side of peristomium, dorsum of chaetigers 8–16 and lateral sides of chaetigers 8–20.

**Remarks:** The placement of this species in any current genus is problematic since, based on branchiae starting on chaetiger 3 and pigmentation of the anterior chaetigers, it resembles *Aurospio* species. However, the branchiae are morphologically similar to the apinnate branchiae observed in chaetigers 3 and 4 of *Prionospio sensu stricto* (i.e., robust, flattened, densely ciliated, and free from the notopodial postchaetal lamellae), as well as the presence of a secondary hood on the hooded hooks, places the species closer to the genus *Prionospio*.



**FIGURE 3.** SEM of *Prionospio solisi* sp. nov. A. Anterior chaetigers, dorso-lateral view. B. Mid-body neuropodium, lateral view. C. Posterior neuropodium, dorso-lateral view. D. Pygidium, dorso-lateral view. Abbreviations: br, branchia; hh, hooded hook; py, pygidium, sa, sabre chaeta.

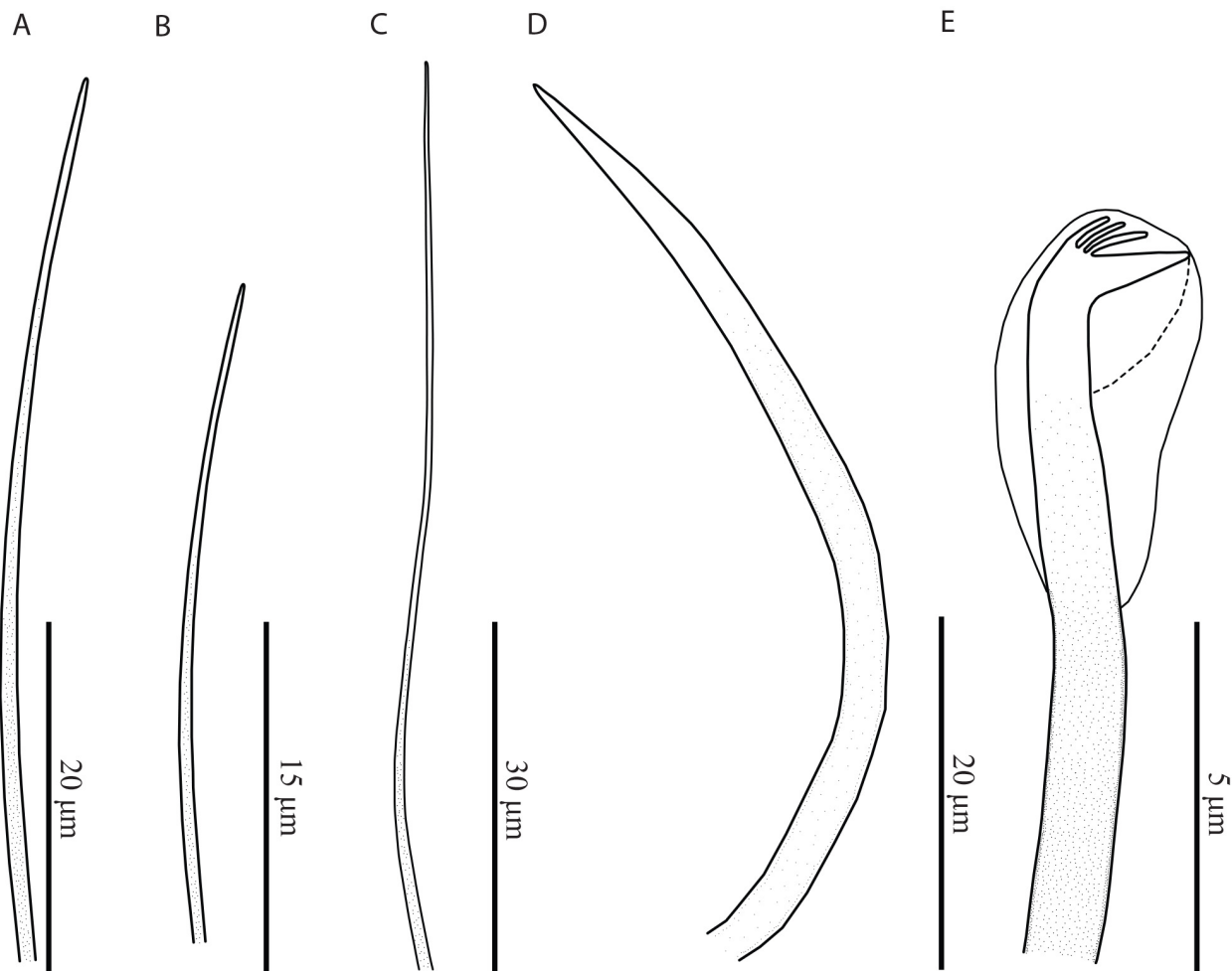


**FIGURE 4.** SEM of *Prionospio solisi* sp. nov., dorsal view. A. Anterior chaetigers and mid-body. B. Anterior chaetigers. Abbreviations: br, branchia; bs, branchial scars; nol, notopodial lamella; pe, peristomium; pr, prostomium.

Boundaries between both genera are still discussed, although, according to Blake *et al.* (2017), in the last years, several *Prionospio* species have been erroneously attributed to *Aurospio* (Sigvaldadóttir 2002; Mincks *et al.* 2009; Patterson *et al.* 2016). According to the current valid diagnosis, only species bearing branchiae starting from chaetiger 3 and partially fused to the notopodial postchaetal lamellae and lacking a secondary hood on the hooded hooks should be included in *Aurospio*, a view also followed in this work. *Aurospio pilkena* (Wilson, 1990), a species with a similar branchial arrangement and morphology, was described as *Prionospio pilkena* Wilson 1990 and placed in *Aurospio* by Sigvaldadóttir (1998), although Dagli & Çinar (2011) treat it as *Prionospio (Minuspio) pilkena*.

An amended diagnosis of the genus *Prionospio* is proposed in this work to include species with branchiae starting from chaetiger 3 and not fused to the notopodial lamellae, rather than erecting a new taxon within the *Prionospio*-complex, which is beyond the scope of this work as it would require a review of all related taxa.

*Prionospio solisi* **sp. nov.** differs from the remaining *Prionospio* species by the presence of conspicuous dark yellow pigment inclusions on the anterior region and the presence of only two pairs of branchiae, on chaetigers 3 and 4. According to Radashkevsky (2012), late development of branchiae on anterior chaetigers is common in *Prionospio*, which could suggest that the species represents a juvenile stage. However, the same branchial pattern was observed in all individuals, regardless of size or sexual maturity.



**FIGURE 5.** *Prionospio solisi* **sp. nov.** A. Anterior capillary chaeta from posterior row. B. Anterior capillary chaeta from anterior row. C. Posterior capillary chaeta. D. Sabre chaeta. E. Hooded hook (as seen in light microscopy).

Regarding species recorded in Brazil, *Prionospio solisi* **sp. nov.** shares the absence of dorsal crests with *P. dubia*, *P. lighti*, *P. perkinsi* Maciolek, 1985 and *P. pygmaeus*. *Prionospio solisi* **sp. nov.** differs from *P. lighti* and *P. perkinsi* by the lack of prostomial peaks, lack of lateral wings, starting chaetiger of notopodial hooded hooks and number of branchial pairs, up to 12 pairs in *P. lighti* and 10 pairs in *P. perkinsi*, starting chaetiger of sabre chaetae

(in *P. lighti*) and absence of sabre chaetae (in *P. perkinsi*) (Maciolek, 1985). *Prionospio solisi* **sp. nov.** differs from *P. pygmaeus* by the prostomial shape, branchial pattern and starting chaetiger of notopodial and neuropodial hooded hooks. The species is most similar to *P. dubia*, sharing a similar prostomium shape, lack of prostomial peaks and lateral wings, but the species can be distinguished by branchial pattern, the starting chaetiger of neuropodial hooded hooks, and sabre chaetae.

*Prionospio solisi* **sp. nov.** is similar to *Aurospio dibranchiata* Maciolek 1981a and some individuals of *A. banyulensis* Laubier, 1966 due to the presence of only two pairs of branchiae, on chaetigers 3 and 4. However, *P. solisi* **sp. nov.** can be distinguished from *A. dibranchiata* by the morphology of branchiae—robust and completely free from the notopodial postchaetal lamellae, by the absence of dorsal crests, starting chaetiger of notopodial and neuropodial hooded hooks and presence of a secondary hood on the hooded hooks. *Prionospio solisi* **sp. nov.** can be distinguished from *A. banyulensis* by the starting chaetiger of notopodial and neuropodial hooded hooks, the shape of postchaetal neuropodial lamellae on anterior chaetigers and absence of dorsal crests.

**Etymology:** The species name, *solisi*, refers to the dark yellow to orange pigment observed on anterior chaetigers (*solis*, Latin for sun).

**Habitat:** muddy sand to mud, 142–1914 m depth.

**Distribution:** Northeastern Brazil (Alagoas and Sergipe states) and Southeastern Brazil (Espírito Santo and Campos basins).

### ***Prionospio nonatoi* sp. nov.**

(Figures 6–9)

**Type material.** Brazil. Espírito Santo Basin. **Holotype:** Amb7 D4, 19° 45' 54.56" S 39° 30' 25.23" W, 12/2011 to 02/2012, 144m, MZUSP 3387. **Paratypes:** Amb7 B4R1, 20° 35' 25.16" S 39° 54' 58.31" W, 12/2011 to 02/2012, 157m, MNRJP 1828 (3 ind), MZUSP 3388 (2 ind), MZUSP 3389 (2 ind).

**Additional material:** Amb7 B4, 20° 35' 25.16" S 39° 54' 58.31" W, 157m (47 ind); Amb7 D4, 19° 45' 54.56" S 39° 30' 25.23" W, 144m (15 ind); Amb7 E4, 19° 36' 4.32" S 39° 10' 34.07" W, 147m (6 ind).

**Diagnostic feature:** Branchiae absent.

**Description:** A small-sized spionid, largest individual about 4.8 mm long, 0.18 mm wide for 65 chaetigers, holotype 4.6 mm long, 0.18 mm wide for 62 chaetigers. Body cylindrical, slightly dorsoventrally compressed throughout body, tapered towards the pygidium (Fig. 6A–D; 8A). Color in alcohol white. Pigmentation absent.

Prostomium narrow, slightly widened towards the anterior margin, rounded anteriorly, extending posteriorly as a narrow keel to the posterior margin of chaetiger 1 (Figs 6A–D; 7A; 8A–B). Eyes absent. Prostomial peaks not observed. Prostomium and peristomium well-delimited by a deep incision (Figs 6A–D; 8A–B). Peristomium short, surrounding prostomium and partially fused to chaetiger 1, lacking lateral wings. Palps lost in all individuals.

Chaetiger 1 with few and short chaetae on both rami. Postchaetal lamellae auricular, reduced. Prechaetal lamellae absent.

Notopodial postchaetal lamellae foliaceous on chaetigers 2–5, largest on chaetiger 3 (Figs 6A–D; 7A; 8A–B) and smaller on chaetigers 4 and 5. Lamellae rounded from chaetiger 6 to chaetiger 11–14 and reduced to a low flap afterwards. Notopodial prechaetal lamella absent throughout. Dorsal crests low, from chaetiger 8 to chaetiger 10–15 (Fig. 8A).

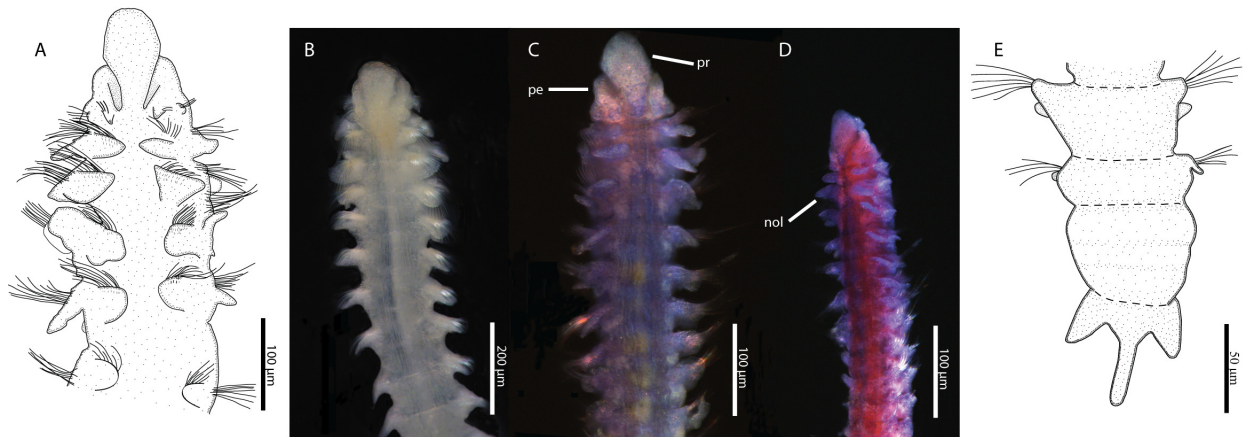
Neuropodial postchaetal lamellae of chaetiger 2 well-developed, triangular and elongated ventrally, triangular and not elongated ventrally on chaetiger 3, rounded on chaetigers 4–11 and reduced to a low flap afterwards (Fig. 6D; 8A). Neuropodial prechaetal lamellae absent throughout.

Chaetae organized in two rows of sparsely granulated non-limbate capillaries (Fig. 9A). Towards the posterior region, capillaries progressively become elongate, thinner and less numerous (Fig. 9B).

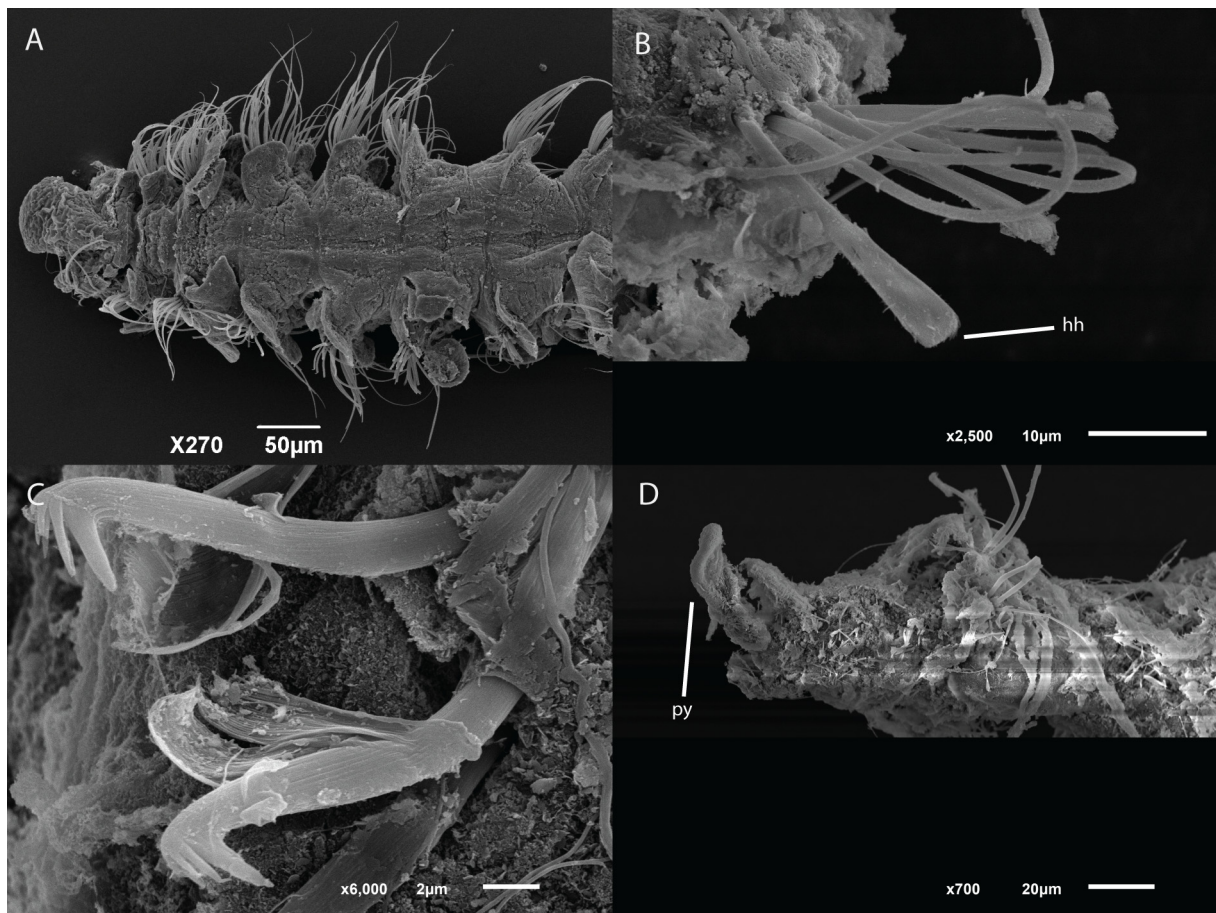
Hooks in notopodia from chaetigers 32–44, up to three per fascicle, accompanied by 1–4 short, non-limbate capillaries. Hooks in neuropodia from chaetigers 11–12, up to seven per fascicle, accompanied by 1–4 non-limbate capillaries. Hooks multidentate, with 8 secondary teeth arranged in two rows above the main tooth (appearing as a single row of 4 secondary teeth in light microscopy) (Figs 7A–B; 9D). Small secondary hood present (Fig. 9D). Hooks accompanied by 3–10 short non-limbate capillaries.

Non-limbate and sparsely granulated sabre chaetae consistently from chaetiger 10 (Fig. 9C).





**FIGURE 6.** *Prionospio nonatoi* sp. nov. (MNRJP 1828, paratypes). A. Anterior chaetigers, dorsal view. B. Anterior chaetigers and mid-body, dorsal view. C. Anterior chaetigers and mid-body stained with Shirlastain A, dorsal view. D. Anterior chaetigers and mid-body stained with Shirlastain A, dorso-lateral view. E. Pygidium, dorsal view. Abbreviations: nol, notopodial lamella; pe, peristomium; pr, prostomium.



**FIGURE 7.** SEM of *Prionospio nonatoi* sp. nov. A. Anterior chaetigers, dorsal view. B. Hooded hooks, dorso-lateral view. C. Hooks (hoods removed), lateral view. D. Pygidium, lateral view. Abbreviations: hh, hooded hooks; py, pygidium.

Branchiae absent in all individuals (Figs 6A–D; 7A; 8A–B). Pygidium with a pair of short rounded ventral cirri and a slightly longer mid-dorsal cirrus (Figs 6E; 7D).

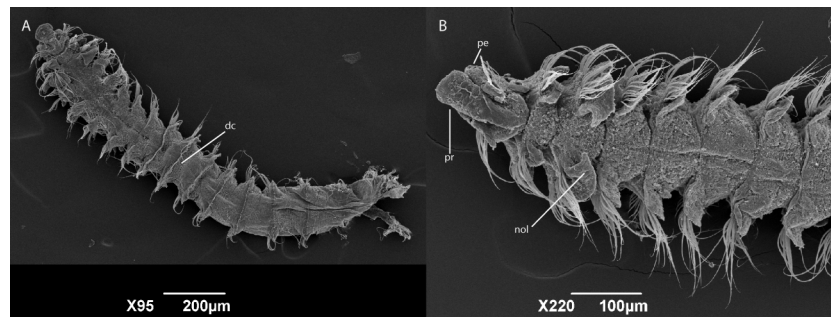
Oocytes from chaetigers 10–11, measuring up to 80  $\mu$ m.

**Methyl green pattern:** Intense staining on prostomium and peristomium.

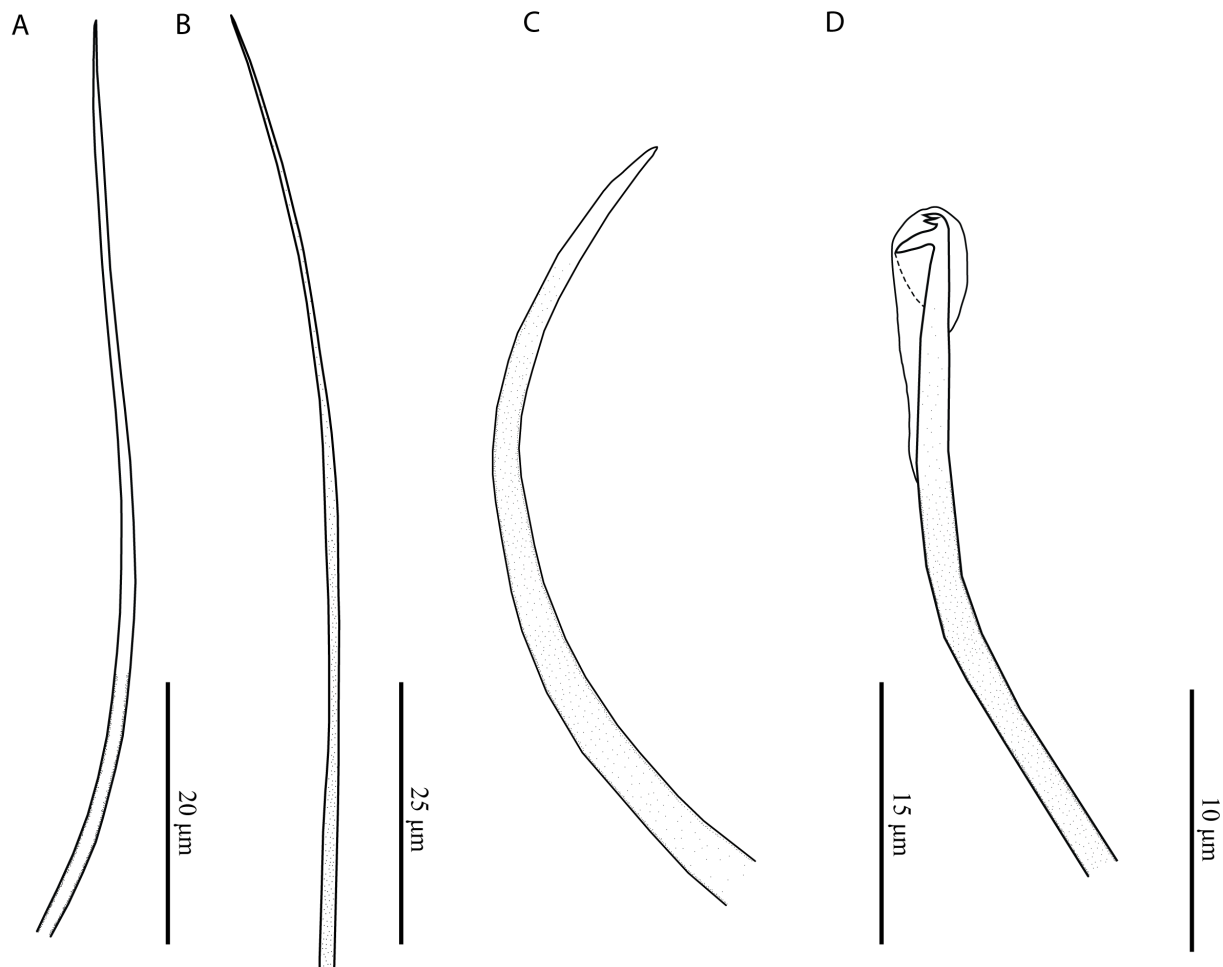
**Remarks:** According to Radashevsky (2012), the late development of branchiae on anterior chaetigers is

common in *Prionospio*, which could lead to the assumption that the species represents a juvenile stage. However, the complete absence of branchiae was observed in all 76 individuals, regardless of size (from 2.5 to 4.8 mm long; from 39 to 65 chaetigers) or sexual maturity.

Owing to the lack of branchiae, the placement of this species in any current genus is problematic, since branchial morphology and distribution are characters of great significance for spionid taxonomy (Foster 1969, 1971; Blake & Kudenov 1978; Johnson 1984; Maciolek 1985; Blake 1996; Bick 2005; Delgado-Blas 2009; Radashevsky 2012; Blake *et al.* 2017). For the *Prionospio*-complex, lack of branchiae is unusual, shared only with *Aurospio abranchiata* Neal, Paterson & Soto in Paterson *et al.*, 2016, although its placement in *Aurospio* is questioned by Blake *et al.* (2017), stating that, recently, several *Prionospio* species have been erroneously attributed to *Aurospio*.



**FIGURE 8.** *Prionospio nonatoi* sp. nov., dorsal view. A. Anterior segments and mid-body. B. Anterior segments. Abbreviations: dc, dorsal crest; nol, notopodial lamella; pe, peristomium; pr, prostomium.



**FIGURE 9.** *Prionospio nonatoi* sp. nov. A. Anterior capillary chaeta. B. Posterior capillary chaeta. C. Sabre chaetae. D. Hooded hooks (as seen in light microscopy).

Among Brazilian species, *Prionospio nonatoi* **sp. nov.** is similar to *P. cirrifera*, *P. delta* Hartman, 1965, *P. fauchaldi* Maciolek, 1985 and *P. multibranchiata* in having only low dorsal crests and significant overlapping in starting chaetiger of notopodial and neuropodial hooded hooks. However, not only do these species possess branchiae, but *P. cirrifera*, *P. delta*, and *P. multibranchiata* present multiple pairs of smooth apinnate branchiae, while *P. fauchaldi* presents distinctly wrinkled branchiae on chaetigers 2–5. Even if branchiae are completely lost in these species, they can still be separated from *P. nonatoi* **sp. nov.** by prostomial shape.

As for *Aurospio abbranchiata*, both species are similar in having an enlarged notopodial postchaetal lamellae on chaetiger 3, distribution of dorsal crests, lack of branchiae, starting chaetiger of sabre chaetae and hooded hooks and presence of a secondary hood on the hooks. However, they can be separated based on the shape of notopodial postchaetal lamellae from chaetigers 2–5, the shape of neuropodial postchaetal lamellae from chaetigers 2–4 and by bathymetrical distribution.

**Etymology:** The species name, *nonatoi*, is a tribute to Edmundo Ferraz Nonato (1920–2014), who dedicated his life to the study of marine worms and is considered the “father” of Brazilian polychaetology.

**Habitat:** Fine sand to muddy sand, at 144–153 m depth.

**Distribution:** Southeast Brazil (Espírito Santos and Campos Basins), and only found during the summer.

### Genus *Laubieriellus* Maciolek, 1981b

Type-species: *Laubieriellus grasslei* Maciolek, 1981b

**Diagnosis** (emended from Erickson & Wilson, 2018): Prostomium anteriorly rounded, or with slight medial incision, extended posteriorly as a caruncle, occipital tentacle absent. Peristomium distinct from chaetiger 1, partly fused to prostomium. Four pairs of branchiae from chaetiger 2; branchiae elongate, cylindrical, smooth and distinct from notopodial lamellae. **Neuropodial lamellae connected by ventral crests from chaetiger 2, rarely 1.** Post-branchial notopodial lamellae connected in dorsal crests. Anterior chaetae all capillaries, multidentate hooded hooks present in posterior neuropodia. Notopodial hooks absent. Pygidium with two short ventrolateral lobes or cirri and one dorsomedial cirrus, or three subequal lobes or an undifferentiated ring.

**Remarks:** Maciolek (1981b) described *Laubieriellus* based on deep-sea specimens found on the Galápagos Rift and also placed *Prionospio salzi* Laubier, 1970 in *Laubieriellus*. Laubier (1970) considered his specimens as late-stage larvae, despite an adult morphology, as noted by Maciolek (1981b). The reexamination of the holotype (USNM 42621) also revealed the presence of oocytes from chaetiger 9–10.

Blake *et al.* (2017) considered *Laubieriellus* as part of the *Prionospio*-complex, as although morphologically similar to *Prionospio*, *Laubieriellus* species lack notopodial hooks and present ventral crests on several anterior chaetigers. The ventral crest, however, is not exclusive to *Laubieriellus* and has been observed in *Prionospio rugosa* Sigvaldadóttir, 1997 and *Prionospio cristaventralis*, Delgado-Blas *et al.* 2018. The genus diagnosis was emended to include a ventral crest on chaetiger 1, as observed in *Laubieriellus grasslei* (Fig. 10).



**FIGURE 10.** SEM of *Laubieriellus grasslei* (USNM 65918, paratypes). A. Anterior and median chaetigers, dorsal view. B. Anterior and median chaetigers, ventral view. C. Close-up of the ventral crests, ventral view. Abbreviations: br, branchia; cha1, chaetiger 1; cn, complete notch; dc, dorsal crests; pe, peristomium; pr, prostomium; vc, ventral crests.

The notch on the ventral crests, a character generally neglected, is present in *Laubieriellus grasslei* (Maciolek 1981b: Fig. 4A), *L. cacatua* Erickson & Wilson, 2018, *L. decapitata* sp. nov. (Fig. 11B; 12C) and *L. salzi* (Laubier 1970; Dagli 2013: Fig. 3A), as indicated in Laubier's (1970) description: "Enfin, en avant du neuropode une crête fine se prolonge ventralement presque jusqu'à la ligne médioventrale." (*Finally, in front of the neuropodium, a fine crest extends ventrally almost to the medioventral line*). This notch can be shallow and incomplete, as seen in *L. cacatua* and *L. decapitata* sp. nov., or a complete notch, as in *L. salzi* and *L. grasslei* (Fig 10B–C).

***Laubieriellus decapitata* sp. nov.**

(Figures 11–13)

**Type material.** Brazil. Espírito Santo Basin. **Holotype:** Amb1 Foz 14R3, 19° 42' 34.9" S 39° 39' 3.42" W, 12/11–19/2010, 39m, **MZUSP 3383.** **Paratypes:** Amb6 D4R2, 19° 45' 54.88" S 39° 30' 26.22" W, 12/2011 to 02/2012, 142m, MNRJP 1830 (2 ind), MZUSP 3386 (2 ind); Amb6 E4R3, 19° 36' 5.08" S 39° 10' 32.85" W, 12/2011 to 02/2012, 149m, MNRJP 1829 (1 ind), MZUSP 3384 (1 ind), MZUSP 3385 (1 ind); Amb7 E3R3, 19° 26' 4.07" S 39° 17' 38.2" W, 12/2011 to 02/2012, 50m, MNRJP 1831 (5 ind).

**Additional material:** Amb1 Foz6, 19° 54' 56.16" S 39° 56' 40.83" W, 34m (1 ind); Amb1 Foz11, 19° 57' 32.89" S 39° 53' 30.69" W, 47m (1 ind); Amb1 Foz14, 19° 42' 32.21" S 39° 38' 57.36" W, 42m (4 ind); Amb1 Foz15, 19° 37' 48.27" S 39° 35' 25.83" W, 42m (15 ind); Amb1 Foz16, 20° 1' 3.73" S 39° 50' 13.76" W, 52m (5 ind); Amb1 Foz17, 19° 55' 44.66" S 39° 45' 38.7" W, 52m (3 ind); Amb2 Foz11, 19° 57' 32.36" S 39° 53' 33.01" W, 47m (2 ind); Amb2 Foz16, 20° 1' 2.6" S 39° 50' 18.72" W, 51m (1 ind); Amb2 Foz17, 19° 55' 45.59" S 39° 45' 41.35" W, 51m (3 ind); Amb2 Foz19, 19° 46' 10.69" S 39° 34' 55.84" W, 50m (1 ind); Amb2 Foz20b, 19° 41' 29.14" S 39° 31' 18.18" W, 53m (1 ind); Amb6 D4, 19° 45' 55.39" S 39° 30' 25.74" W, 132m (79 ind); Amb6 E4, 19° 36' 5.17" S 39° 10' 32.93" W, 153m (10 ind); Amb6 CAND4, 19° 31' 51.68" S 39° 3' 4.79" W, 171m (2 ind); Amb6 CANWN4, 19° 49' 7.27" S 39° 36' 8.52" W, 158m (2 ind); Amb7 A2, 21° 2' 47.31" S 40° 32' 28.94" W, 40m (1 ind); Amb7 A3, 21° 4' 1.29" S 40° 18' 50.11" W, 50m (2 ind); Amb7 B3, 20° 34' 53.42" S 40° 6' 27.43" W, 50 m (13 ind); Amb7 B4, 20° 35' 25.16" S 39° 54' 58.31" W, 157m (2 ind); Amb7 C2, 20° 11' 25.35" S 40° 2' 16.02" W, 39m (5 ind); Amb7 C3, 20° 12' 20.26" S 39° 57' 59.7" W, 50m (4 ind); Amb7 D1, 19° 35' 37.21" S 39° 41' 19.68" W, 26m (1 ind); Amb7 D2, 19° 40' 26.04" S 39° 36' 19.65" W, 40m, (4 ind); Amb7 D3, 19° 43' 14.34" S 39° 33' 34.86" W, 50m (6 ind); Amb7 D4, 19° 45' 54.56" S 39° 30' 25.23" W, 145m (6 ind); Amb7 E2, 19° 18' 5.9" S 39° 23' 23.3" W, 39m (3 ind); Amb7 E3, 19° 26' 5" S 39° 17' 38.92" W, 50m (33 ind); Amb7 E4, 19° 36' 4.32" S 39° 10' 34.07" W, 147m (2 ind); Amb7 F2, 18° 52' 32.61" S 39° 8' 42.82" W, 39m (10 ind); Amb7 F3, 18° 53' 29.72" S 39° 6' 23.3" W, 52m (2 ind); Amb7 F4, 19° 33' 2.92" S 38° 42' 52.26" W, 152m (1 ind); Amb7 G2, 18° 36' 31.68" S 39° 9' 33" W, 39m (5 ind); Amb7 G3, 18° 40' 55.3" S 38° 55' 41.48" W, 55m (11 ind); Amb12 D4 P300, 19° 45' 53.43" S 39° 30' 25.97" W, 146m (1 ind); Amb12 D4, 19° 45' 53.43" S 39° 30' 25.97" W, 146m (3 ind); Amb12 D4 T300, 19° 45' 53.43" S 39° 30' 25.97" W, 144m (1 ind); Amb12 E4, 19° 36' 3.57" S 39° 10' 33.64" W, 152m (3 ind); Amb14 A2, 21° 3' 31.13" S 40° 22' 59.88" W, 40m (1 ind); Amb14 E2, 19° 18' 6.12" S 39° 23' 23.35" W, 38m (1 ind); Amb 14 F3, 18° 53' 31.97" S 39° 6' 21.78" W, 51m (13 ind); Amb13 G2, 18° 36' 32.45" S 39° 9' 32.83" W, 40m (9 ind); Amb13 G3, 18° 40' 57.41" S 38° 55' 39.92" W, 53m (30 ind).

**Diagnostic features:** Large auricular notopodial prechaetal and postchaetal lamellae on chaetiger 1; prostomium often obscured by peristomium.

**Description:** A small-sized spionid, largest individual about 5 mm long, 0.3 mm wide for 45 chaetigers, holotype 3.5 mm long, 0.28 mm wide for 37 chaetigers. Body translucent and fragile, dorsoventrally flattened throughout. Pigmentation absent.

Prostomium truncate, weakly incised anteriorly, eyes absent. Caruncle extending posteriorly to end of chaetiger 3. Prostomial peaks absent. Peristomium encircling the prostomium and partially fused with chaetiger 1, lateral wings absent (Figs 11; 12A–B). Grooved palps extending up to chaetiger 8, lost in most specimens.

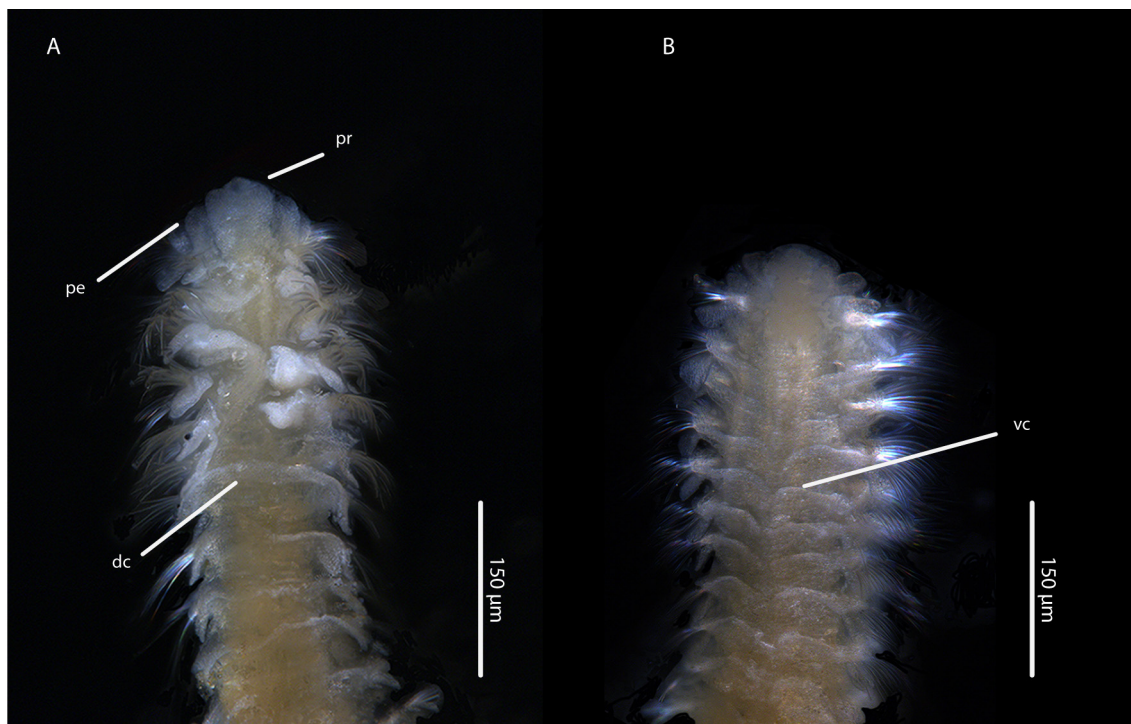
Chaetiger 1 with short chaetae on both rami. Notopodial and neuropodial postchaetal lamellae large, auricular-shaped, well-developed in adults, although smaller than those on following chaetigers (Figs 11; 12A–C). Notopodial prechaetal lamellae large and auricular-shaped.

Notopodial postchaetal lamellae foliaceous and largest on chaetigers 2–5, extending to mid-dorsum (Figs 11A; 12A–B; 13A–D). Postchaetal lamellae round on chaetigers 6–7, progressively smaller on chaetigers 8–9 and

reduced from chaetiger 10 onwards. Prechaetal lamellae absent. Dorsal crests high from chaetiger 7 to 9 and low crest from chaetiger 10 to chaetigers 11–12 (Figs 11A; 12A–B).

Neuropodial postchaetal lamellae rounded from chaetigers 2–9, broad in the branchial region, largest on chaetiger 3 and reduced from chaetiger 10 onwards. Prechaetal lamellae absent. Ventral crests with median notch from chaetiger 2 to chaetigers 9–11, shallow on chaetigers 2 and 3 (Figs 11B; 12C).

Chaetae organized in two rows of non-limbate and lightly granulated capillaries. In anterior notopodia, capillaries of the posterior rows up to two times longer than capillaries from the anterior row (Fig. 13F–G). Towards the posterior region, capillaries progressively become elongate, thin and less numerous.



**FIGURE 11.** *Laubieriellus decapitata* sp. nov. (MNRJP 1831, paratypes). A. Anterior chaetigers, dorsal view. B. Anterior chaetigers, ventral view. Abbreviations: dc, dorsal crest; pe, peristomium; pr, prostomium; vc, ventral crest.

Neuropodial hooded hooks from chaetiger 9–10, up to eight per fascicle. Notopodial hooks absent. Hooks multidentate, with 6–8 secondary teeth arranged in two rows above main tooth (Figs 12D; 13H). Small secondary hood present. Hooks accompanied by 3–10 short non-limbate capillaries. Granulated sabre chaetae from chaetiger 10 (Fig. 13I).

Branchiae on chaetigers 2–5, longer than postchaetal notopodial lamellae. Branchiae apinnate, cirriform on chaetigers 2 and 5 and robust, flattened and densely ciliated on chaetigers 3 and 4, all pairs narrowing abruptly at tips (Figs 11A; 12A–B; 13A–D).

Pygidium with one long mid-dorsal cirrus and a pair of shorter ventral cirri (Fig. 13E).

Oocytes from chaetigers 9–12, measuring up to 120 μm.

**Variation:** Around 20% of all specimens presented two sabre chaetae per rami on chaetigers 10 and 11.

**Methyl green pattern:** Diffused throughout the body. Margins of lamellae slightly more stained from chaetiger 1 to chaetiger 10.

**Remarks:** The genus *Laubieriellus* was erected by Maciolek (1981b) to include species of the *Prionospio*-complex that bear ventral crests on anterior chaetigers, have cylindrical apinnate branchiae, and lack notopodial hooded hooks.

Only three *Laubieriellus* species are known: *L. grasslei*, from hydrothermal vents on the Galápagos Islands (Ecuador), *L. salzi*, from the coast of Israel, Mediterranean Sea, and *L. cacatua*, from Western Australia.

*Laubieriellus* species present remarkable character overlapping. Thus, characters such as caruncle length, first chaetiger with hooded hooks and sabre chaetae may not be helpful to distinguish species (Table 1).

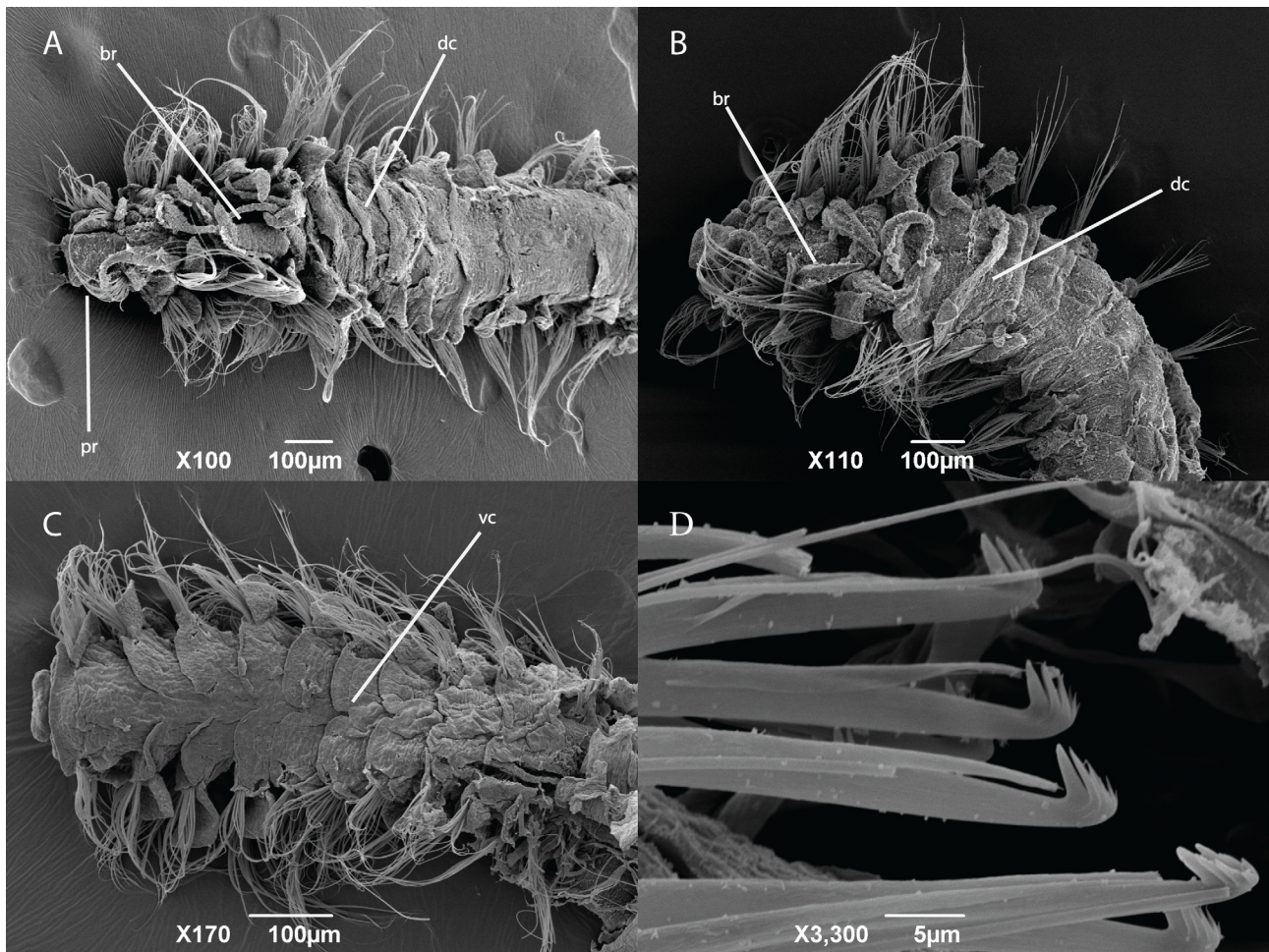
**TABLE 1.** Comparison among *Laubieriellus* species. Data marked with “\*\*” refers to Dagi’s (2013) description, based on material from the Marmara Sea (Turkey).

Species	Prostomium shape	Caruncle length	Notopodial lamellae on chaetiger 1	Dorsal crests distribution	Ventral crests distribution	Notch on ventral crests
<i>Laubieriellus salzi</i>	Reduced, truncate with median incision	Up to chaetiger 3 (4)*	absent	8–10 (7–?)*	2–9	Complete
<i>Laubieriellus grasslei</i>	Rounded, with slight median incision	Up to chaetiger 3	Present	7–9 (high) to 10–14 (low)	1–11	Complete
<i>Laubieriellus cacatua</i>	Rounded with anterior margin slightly indented	Up to chaetiger 2	Present	6–7 to 9–11	2 to 6–12	Incomplete; notch reduced posteriorly
<i>Laubieriellus decapitata</i> <b>sp. nov.</b>	Truncate with slight median incision	Up to chaetiger 3	Present	7–9 (high) to 10–12 (low)	2–11	Incomplete, notch slightly reduced posteriorly

continued.

Species	Neuropodial hooded hooks from chaetiger	Number of secondary teeth on hooded hooks	Sabre chaetae from chaetiger	Number of sabre chaetae per neuropodium	Pygidial dorsal cirrus	Pygidial ventral cirri
<i>Laubieriellus salzi</i>	10	4–6 (8)*	10 (10–11)*	1	Present; short cirrus	Absent
<i>Laubieriellus grasslei</i>	10	7	10–11	Usually 2	Present; thin and short cirrus	Present; short rounded lobes
<i>Laubieriellus cacatua</i>	10	4 (possibly 6)	10–11	Usually 1	Absent	Absent
<i>Laubieriellus decapitata</i> <b>sp. nov.</b>	9–10	6–8	10	Usually 1	Present, long cirrus	Present; short cirri

*Laubieriellus decapitata* **sp. nov.** is similar to *L. cacatua* in the distribution of dorsal and ventral crests, but these species can be distinguished by prostomial shape, shape of postchaetal neuropodial lamellae (especially on chaetiger 1), arrangement and number of secondary teeth on the hooded hooks, and pygidial shape. *Laubieriellus decapitata* **sp. nov.** can be readily distinguished from *L. grasslei* by prostomial shape, distribution of dorsal and ventral crests, notch morphology, pygidial shape, and bathymetry.



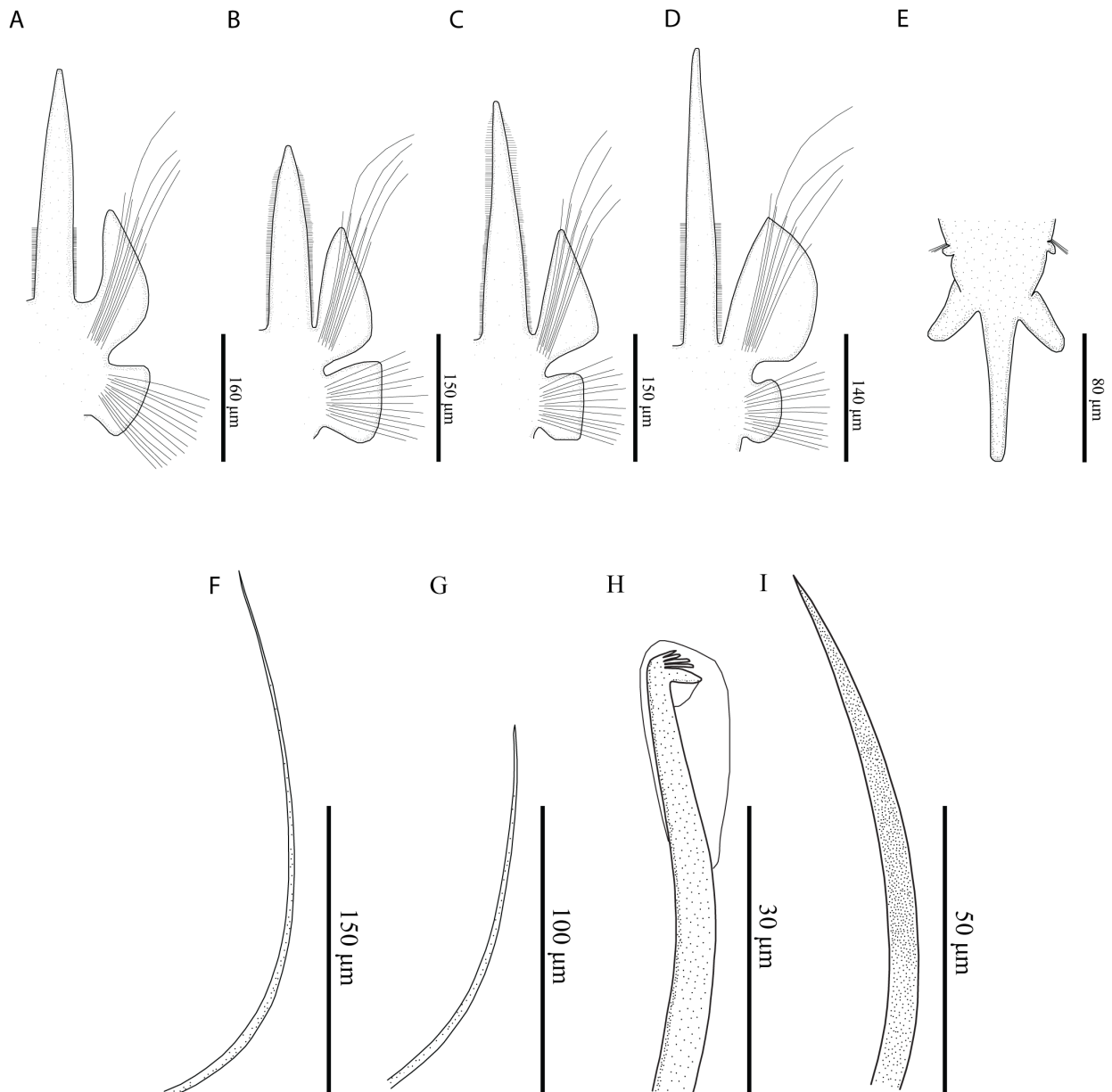
**FIGURE 12.** SEM of *Laubieriellus decapitata* **sp. nov.** A. Anterior chaetigers, dorsal view. B. Anterior chaetigers, dorso-lateral view. C. Anterior chaetigers, ventral view. D. Hooks (hoods removed), lateral view. Abbreviations: br, branchia; dc, dorsal crest; pr, prostomium; vc, ventral crest.

*Laubieriellus decapitata* **sp. nov.** is most similar to *L. salzi* in prostomial shape, but the two species can be distinguished by the distribution of dorsal and ventral crests, shape of parapodial lamellae on chaetiger 1, shape of notopodial lamellae after chaetiger 10 (reduced in *L. decapitata* and digitiform in *L. salzi*) and number of secondary teeth on the hooded hooks.

**Etymology:** The epithet *decapitata* (Latin for beheaded) refers to the prostomium, which is difficult to distinguish as it is translucent and does not stand out from the surrounding structures, and is also encircled by the peristomium for the most part. This led many students to consider specimens as fragments with the prostomium absent.

**Habitat:** Coarse to fine sand.

**Distribution:** Espírito Santo and Campos basins, 25–150 m deep. The present record expands the geographic range of the genus to the Southern Atlantic Ocean.



**FIGURE 13.** *Laubieriellus decapitata* sp. nov. A. Parapodium from chaetiger 2. B. Parapodium from chaetiger 3. C. Parapodium from chaetiger 4. D. Parapodium from chaetiger 5. E. Pygidium. F. Anterior capillary chaetae from posterior row. G. Anterior capillary chaeta from anterior row. H. Hooded hooks (as seen in light microscopy). I. Sabre chaeta.

### Acknowledgments

We are grateful to CENPES/PETROBRAS for the opportunity and access to this material and to Benthos Ambiental and its staff for initially sorting out the specimens. Thanks are due to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) for providing laboratory financial support. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001, granted to AJMP. AJMP was awarded a fellowship provided by the National Museum of Natural History, Smithsonian Institution, U.S.A. (Kenneth Jay Boss Fellowship in Invertebrate Zoology, 2018). PCP also has a research fellowship from CNPq. Finally, we would also like to thank Nancy J. Maciolek and an anonymous referee, whose insightful comments greatly improved the quality of this paper.



## 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, 267–289.  
<https://doi.org/10.1080/17451000500262066>
- Amaral, A.C.Z., Nallin, S.A.H., Steiner, T.M., Forrone, T.O. & Filho, D.G. (2013) *Catálogo das espécies de Annelida Polychaeta do Brasil*. UNICAMP, Campinas, 141 pp. Available from: [http://www.ib.unicamp.br/museu\\_zoologia/files/lab\\_museu\\_zoologia/Catalogo\\_Polychaeta\\_Amaral\\_et\\_al\\_2012.pdf](http://www.ib.unicamp.br/museu_zoologia/files/lab_museu_zoologia/Catalogo_Polychaeta_Amaral_et_al_2012.pdf) (accessed 7 September 2018)
- Berkeley, E. (1927) Polychaetous annelids from the Nanaimo district. Part 3. Leodicidae to Spionidae. *Contributions to Canadian Biology and Fisheries*, 3, 407–422.
- Bick, A. (2005) A new polychaete genus and species of the Kongsfjorden, Spitsbergen, Svalbard. *Journal of Natural History*, 39, 2987–2996.  
<https://doi.org/10.1080/00222930500239843>
- Blainville, H. (1828) Mollusques, Vers et Zoophytes. In: Levrault, F.G. (Ed.), *Dictionnaire des Sciences Naturelles, Strasbourg & Paris*, 57, pp. 492–493.
- Blake, J.A. (1996) Chapter 4. Family Spionidae Grube, 1850, including a review of the genera and species from California and a revision of the genus *Polydora* Bosc, 1802. In: Blake, J. A., Hilbig, B. & Scott, P.H. (Eds.), *Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. Annelida Part 3. Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History, Santa Barbara, pp. 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*, 39, 171–280.  
<https://doi.org/10.24199/j.mmv.1978.39.11>
- Blake, J.A., Maciolek, N.J. & Meißner, K. (2017) Spionidae, Grube 1850. In: Westheide, W. & Purschke, G. (Eds.), *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. Annelida: Polychaetes*. De Gruyter, Berlin. [published online]
- Bolívar, G.A. & Lana, P.C. (1987) Spionidae (Annelida: Polychaeta) do litoral do Estado do Paraná. *Nerítica*, 2, 107–148.
- Bosc, L.A.G. (1802) *Histoire naturelle des vers contenant leur description et leurs moeurs, avec figures dessinées d'après nature. Tome Première*. De l'imprimerie de Guilleminet, Paris, 4 pp. [pp. 150–153]  
<https://doi.org/10.5962/bhl.title.64025>
- Caullery, M. (1914) Sur les polychètes du genre *Prionospio* Malmgr. *Bulletin de la Société Zoologique de France*, 39, 355–361.  
<https://doi.org/10.5962/bhl.part.24557>
- Claparède, E. (1869) Les Annélides Chétopodes du Golfe de Naples. Seconde partie. Annelides sédentaires. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, 20, 1–225.
- Czerniavsky, V. (1881) Materialia ad zoographiam Ponticam comparatam. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 56, 338–420.
- Dagli, E. (2013) Two new records for the Polychaeta fauna of the Sea of Marmara: *Laubieriellus salzi* and *Spiophanes afer* (Polychaeta: Spionidae). *Turkish Journal of Zoology*, 37, 376–379.
- Dagli, E. & Çınar, M.E. (2009) Species of the subgenera *Aquilaspio* and *Prionospio* (Polychaeta: Spionidae: *Prionospio*) from the southern coast of Turkey (Levantine Sea, eastern Mediterranean), with description of a new species and two new reports for the Mediterranean fauna. *Zootaxa*, 2275, 1–20.
- Dagli, E. & Çınar, M.E. (2011) Species of the subgenus *Minuspio* (Polychaeta: Spionidae: *Prionospio*) from the southern coast of Turkey (Levantine Sea, eastern Mediterranean), with the description of two new species. *Zootaxa*, 3043, 35–53.  
<http://dx.doi.org/10.11646/zootaxa.3043.1.4>
- Dagli, E., Çınar, M.E. & Ergen, Z. (2011) Spionidae (Annelida: Polychaeta) from the Aegean Sea (eastern Mediterranean). *Italian Journal of Zoology*, 78, 49–64.  
<https://doi.org/10.1080/11250003.2011.567828>
- Day, J.H. (1961) The Polychaet Fauna of South Africa. Part 6. Sedentary species dredged off Cape coasts with a few new records from the shore. *Journal of the Linnean Society of London*, 44, 463–560.  
<https://doi.org/10.1111/j.1096-3642.1961.tb01623.x>
- Delgado-Blas, V.H. (2009) Spionidae Grube, 1850. In: de León- González, J.A., Bastida-Zavala, J.R., Carrera-Parra, L.F., García-Garza, M.E., Peña-Rivera, A., Salazar-Vallejo, S.I. & Solís-Weiss, V. (Eds.), *Poliquetos (Annelida: Polychaeta) de México y América Tropical. Vol. 3*. Universidad Autónoma de Nuevo León, Monterrey, pp. 589–614.
- Delgado-Blas, V.H. & Díaz-Díaz, O. (2013) *Malacoceros longiseta*, a new species of Spionidae (Annelida: Polychaeta) from Venezuela. *Marine Biodiversity*, 43, 181–187.  
<https://doi.org/10.1007/s12526-013-0144-9>
- Delgado-Blas, V.H., Díaz-Díaz, O. & Viéitez, J.M. (2018) *Prionospio* from the coast of the Iberian Peninsula, with the description of two new species (Annelida, Spionidae). *ZooKeys*, 810, 1–18.  
<https://doi.org/10.3897/zookeys.810.26910>
- Erickson, R. & Wilson, R.S. (2018) A new *Laubieriellus* species (Annelida, Spionidae) from Western Australia. *Zootaxa*, 4461, 261–268.  
<https://doi.org/10.11646/zootaxa.4461.2.7>

- Fauvel, P. (1928) Annélides Polychètes nouvelles du Maroc. *Bulletin de la Société Zoologique de France*, 53, 9–13.
- Foster, N.M. (1969) New species of spionids (Polychaeta) from the Gulf of Mexico and Caribbean Sea with a partial revision of the Genus *Prionospio*. *Proceedings of the Biological Society of Washington*, 82, 381–400.
- 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*, 36, 1–183.
- Grube, A.E. (1850) Die Familien der Anneliden. *Archiv für Naturgeschichte*, 16, 249–364.
- Hartman, O. (1961) *Allan Hancock Pacific Expeditions. Vol. 25. Polychaetous annelids from California*. University of Southern California Press, Los Angeles, 226 pp.
- Hartman, O. (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Occasional Papers of the Allan Hancock Foundation*, 28, 1–384.
- Johnson, P.G. (1984) Family Spionidae Grube, 1850. In: Uebelacker, J.M. & Johnson, P.G. (Eds.), *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico. Vol. II*. Barry A. Vittor & Associates, Alabama, pp. 6.1–6.69.
- Laubier, L. (1966) Le coralligène des Albères. Monographie biocénotique. *Annales de l'Institut Océanographique, Monaco, Nouvelle Série*, 43, 137–316.
- Laubier, L. (1970) *Prionospio salzi* sp. nov., un spionidien (annélide polychète) des côtes Méditerranéennes d'Israël. *Israel Journal of Zoology*, 19, 183–190.
- Levinsen, G.M.R. (1884) Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjøbenhavn*, 45, 92–350.
- 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 Linnaean Society*, 84, 325–383.  
<https://doi.org/10.1111/j.1096-3642.1985.tb01804.x>
- Malmgren, A.J. (1867) *Annulata Polychaeta Spetsbergiae, Grønlandiae, Islandiae et Scandinaviae. Hactenus Cognita*. Ex Officina Frenckelliana, Helsingforslæ, 127 pp.  
<https://doi.org/10.5962/bhl.title.13358>
- 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.  
<https://doi.org/10.1111/j.1439-0485.2008.00265.x>
- Nonato, E.F., Bolívar, G.A. & Lana, P.C. (1986) *Laonice branchiata*, a new species of Spionidae (Annelida; Polychaeta) from the southeastern Brazilian coast. *Nerítica*, 1, 21–25.  
<https://doi.org/10.5380/rn.v1i3.41193>
- Paiva, P.C. & Barroso, R. (2010) Polychaeta. In: Lavrado, H.P. & Brasil, A.C.S. (Eds.), *Biodiversidade da Região Oceânica Profunda da Bacia de Campos: Macrofauna*. SAG Serv, Rio de Janeiro, pp. 97–172.
- Paterson, G.L., Neal, L., Altamira, I., Soto, E.H., Smith, C.R., Menot, L., Billett, D.S.M., Cunha, M.R., Marchais-Laguionie, C. & Glover, A.G. (2016) New *Prionospio* and *Aurospio* species from the deep sea (Annelida: Polychaeta). *Zootaxa*, 4092 (1), 1–32.  
<https://doi.org/10.11646/zootaxa.4092.1.1>
- Peixoto, A.J.M. & Paiva, P.C. (2017) A new species of *Spiogalea* (Polychaeta: Spionidae) from Brazil, with an amended diagnosis of the genus. *Journal of the Marine Biological Association of the United Kingdom*, 97, 955–960.  
<https://doi.org/10.1017/S0025315417000509>
- Radashevsky, V.I. (2012) Spionidae (Annelida) from shallow waters around the British Islands: an identification guide for the NMBAQC Scheme with an overview of spionid morphology and biology. *Zootaxa*, 3152, 1–35.  
<http://dx.doi.org/10.11646/zootaxa.3152.1.1>
- Radashevsky, V.I. & Lana, P.C. (2009) *Laonice* (Annelida: Spionidae) from South and Central America. *Zoosymposia*, 2, 265–295.  
<http://dx.doi.org/10.11646/zoosymposia.2.1.19>
- Radashevsky, V.I., Lana, P.C. & Nalesso, R.C. (2006) Morphology and biology of *Polydora* species (Polychaeta: Spionidae) boring into oyster shells in South America, with the description of a new species. *Zootaxa*, 1353, 1–37.  
<http://dx.doi.org/10.11646/zootaxa.1353.1.1>
- Radashevsky, V.I. & Migotto, A.E. (2009) Morphology and biology of a new *Pseudopolydora* (Annelida: Spionidae) species from Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 89, 461–468.  
<https://doi.org/10.1017/S002531540800177X>
- Radashevsky, V.I. & Nogueira, J.M.M. (2003) Life history, morphology and distribution of *Dipolydora armata* (Polychaeta: Spionidae). *Journal of the Marine Biological Association of the United Kingdom*, 83, 375–384.  
<https://doi.org/10.1017/S0025315403007227h>
- Radashevsky, V.I., Rizzo, A.E. & Peixoto, A.J.M. (2018) First record of *Trochochaeta japonica* (Annelida: Spionidae) in Brazil

- with identification key to species of the genus. *Zootaxa*, 4462 (4), 566–578.  
<https://doi.org/10.11646/zootaxa.4462.4.8>
- Rocha, M.B. & Paiva, P.C. (2012) *Scolelepis* (Polychaeta: Spionidae) from the Brazilian coast with a diagnosis of the genus. *Zoologia*, 29, 385–393.  
<https://doi.org/10.1590/S1984-46702012000400011>
- Rocha, M.B., Radashevsky, V. & Paiva, P.C. (2009) Espécies de *Scolelepis* (Polychaeta, Spionidae) de praias do Estado do Rio de Janeiro, Brasil. *Biota Neotropica*, 9, 101–108.  
<https://doi.org/10.1590/S1676-06032009000400012>
- Sato-Okochi, W., Abe, H., Nishitani, G. & Simon, C. (2016) And then there was one: *Polydora uncinata* and *Polydora hoplura* (Annelida: Spionidae), the problematic polydorid pest species represent a single species. *Journal of the Marine Biological Association of the United Kingdom*, 97, 1675–1684.  
<https://doi.org/10.1017/S002531541600093X>
- Sigvaldadóttir, E. (1997) A new species of *Prionospio* (Polychaeta: Spionidae) from the Cape d'Aguilar marine reserve, Hong Kong. In: Morton, B. (Ed.), *The Marine Flora and Fauna of Hong Kong and Southern China. Vol. IV*. Hong Kong University Press, Hong Kong, pp. 53–61.
- Sigvaldadóttir, E. (1998) Cladistic analysis and classification of *Prionospio* and related genera (Polychaeta, Spionidae). *Zoologica Scripta*, 27, 175–187.  
<https://doi.org/10.1111/j.1463-6409.1998.tb00435.x>
- Sigvaldadóttir, E. (2002) Polychaetes of the genera *Prionospio* and *Aurospio* (Spionidae, Polychaeta) from Icelandic waters. *Sarsia*, 87, 207–215.  
<https://doi.org/10.1080/00364820260294842>
- Verrill, A.E. (1881) New England Annelida. Part I. Historical sketch, with annotated lists of the species hitherto recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 4, 285–324.
- Webster, H.E. (1879) The Annelida Chaetopoda of New Jersey. *Annual Report of the New York State Museum of Natural History*, 32, 101–128.
- Wilson, R.S. (1990) *Prionospio* and *Paraprionospio* (Polychaeta: Spionidae) from Southern Australia. *Memoirs of the Museum of Victoria*, 50, 243–274.  
<https://doi.org/10.24199/j.mmv.1990.50.02>
- Wirén, A. (1883) *Chaetopoder från Sibiriska Ishafvet och Berings Haf Insamlade under Vega-Expeditionen 1878–1879*. In: *Vega-Expeditionens Vetenskapliga Iakttagelser bearbetade af deltagare i resan och andra forskare. Vol. 2*. F&G Beijers Förlag, Stockholm, pp. 383–428.
- Zhou, J. & Li, X. (2009) Report of *Prionospio complex* (Annelida: Polychaeta: Spionidae) from China's waters, with description of new species. *Acta Oceanologica Sinica*, 1, 116–127.