

Copyright © 2015 Magnolia Press





http://dx.doi.org/10.11646/zootaxa.4019.1.22 http://zoobank.org/urn:lsid:zoobank.org:pub:88F2DB05-58C4-4726-89D5-99302FABB908

# Spionidae (Annelida) from Lizard Island, Great Barrier Reef, Australia: the genera *Aonides, Dipolydora, Polydorella, Prionospio, Pseudopolydora, Rhynchospio*, and *Tripolydora*

#### VASILY I. RADASHEVSKY

A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok 690041, Russia. E-mail: radashevsky@gmail.com

#### Abstract

Nineteen species in seven genera of spionid polychaetes are described and illustrated based on new material collected from the intertidal and shallow waters around the Lizard Island Group, northern Great Barrier Reef. Only one of these species had been previously reported from the Reef. Six species are described as new to science, and the taxonomy of seven species should be clarified in the future. *Prionospio sensu lato* is the most diverse group with 11 species identified in the present study. One species is identified in each of the genera *Dipolydora*, *Polydorella*, *Rhynchospio* and *Tripolydora*, and two species are identified in each of the genera *Aonides* and *Pseudopolydora*. The fauna of spionid polychaetes of the Great Barrier Reef seems to be more diverse than previously described and more species are expected to be found in the future. An identification key is provided to 16 genera of Spionidae reported from or likely to be found on the Great Barrier Reef.

Key words: Queensland, morphology, ecology, reproductive biology, polychaetes, key to genera

#### Introduction

Spionidae Grube, 1850 is one of the largest taxa of polychaetous annelids; its members are common in marine and estuarine communities all over the world. Adult spionids and their developing larvae are readily recognized by their general body morphology and the pair of elongate prehensile palps extending from the head (see Blake, 1996, 2006; Radashevsky 2012 for an overview of the morphology, biology and systematic treatments of the spionids). Previous inferences of phylogenetic hypotheses about relationships of the Spionidae with other polychaetes, and among spionid taxa, using morphological characters, have provided ambiguous results. Analyses using nucleotide data have been inconsistent regarding relationships among spiomorph polychaetes but all agree that Spionida Dales, 1962 is polyphyletic as currently defined, and that *Apistobranchus* Levinsen, 1883, *Chaetopterus* Cuvier, 1830, and *Magelona* F. Müller, 1858 are not closely related to Spionidae. They confirmed the close relationships between Spionidae, *Poecilochaetus* Claparède in Ehlers, 1875 and *Trochochaeta* Levinsen, 1883 but were not able to resolve these relationships (Radashevsky 2013).

The first spionids from Australia were reported by Haswell (1885) who was requested to examine oysters from the Hunter River beds in New South Wales, which appeared to be dying in large numbers owing to the attacks of some parasites. Haswell (1885) identified two *Polydora* Bosc, 1802 species one of which was abundant and, according to him, identical with the European *Polydora ciliata* (Johnston, 1838). The only anterior fragment of the other species Haswell (1885) recognized as a new *Polydora (Leucodore) polybranchia*. Ironically, briefly described and without deposited type material the latter species turned to be a type species of *Boccardia* first recognized by Carazzi (1893) as a subgenus of *Polydora* and later given a genus rank by Chamberlin (1919). Later attempts to find and re-describe *Polydora polybranchia* from the Hunter River by Blake & Kudenov (1978) and myself in 2013 were unsuccessful and *Boccardia polybranchia* remains one of the enigmatic and poorly defined species which has nevertheless been reported all over the world. It seems to be a destiny of old polychaete species to become cosmopolitans. Their original brief descriptions often provided not specific but general characters

shared also by individuals of other species in remote places; those individuals have often been misidentified and given old names, thus incorectly extending the distribution of the stem species.

After Haswell (1885), the Australian spionids were described in various studies of which major systematic treatments of the family and of certain genera are by Blake & Woodwick (1976), Blake & Kudenov (1978), Hartmann-Schröder (1979, 1980, 1981, 1983), Hutchings & Rainer (1979), Hutchings & Murray (1984), Hutchings & Turvey (1984), Wilson (1990), Wilson & Humphreys (2001), Meißner & Hutchings (2003), Sato-Okoshi *et al.* (2008), and Greaves *et al.* (2011). Most of these studies described the spionids from south-eastern part of Australia: New South Wales, Victoria and South Australia.

Spionids from the Great Barrier Reef remain poorly known despite numerous biological surveys in the region. From the material collected by the Great Barrier Reef Expedition of the British Museum of Natural History in 1928–1929, Monro (1931) reported *Scolelepis indica* Fauvel, 1928 (now included in the genus *Malacoceros* Quatrefages, 1843) from Low Isles. From Heron Island Reef, Hartmann-Schröder (1991) reported *Prionospio cirrifera*, Rose (1988) described fine structure of spermatozoa of *Prionospio* cf. *queenslandica* Blake & Kudenov, 1978 and *Tripolydora* sp. (*=Pseudopolydora* sp.), and Skilleter *et al.* (2005) reported *Polydorella prolifera* Augener, 1914 inhabiting sponge *Haliclona* sp.

From the Lizard Island Group located on the northern Great Barrier Reef, Ben-Eliahu *et al.* (1984) reported *Malacoceros indicus* (Fauvel, 1928) and Dauer & Ewing (1991) described the functional morphology and feeding behavior of these worms. Dauer (1985) described a new species, *Scolelepis hutchingsae*, and Hutchings (1981) and Hutchings *et al.* (1992) described the spatial and temporal patterns of recruitment and colonization by *Polydora* sp. to dead corals.

In August 2013, the Australian Museum in Sydney hosted the 11th International Polychaete Conference. Immediately after the meeting, a group of researchers attended a Taxonomic Workshop held at the Lizard Island Research Station, a facility of the Australian Museum on the Great Barrier Reef. The purpose of the Workshop was to document polychaete fauna of around Lizard Island Group. This paper is one of a series of papers describing polychaetes which are produced in this special issue of *Zootaxa*. Specifically this paper deals with seven selected genera of Spionidae. Other spionids collected during the Workshop are described in this volume by Meißner & Götting (2015).

#### Material and methods

Collections were made in August, 2013 from most types of habitats on the intertidal and in shallow waters around the Lizard Island Group using SCUBA equipment and grabs. Locality data are provided in Ribas & Hutchings (2015, Zootaxa 4019) together with maps showing sites (referred below in the text to as MI QLD numbers). Additional material was collected in Darwin and the vicinity, Northern Territory in September, 2013. Collected sediments were washed on a 500 µm mesh sieve and the polychaetes retained in the residue were removed and examined alive under light microscopes in the laboratory. After examination, spionids were fixed in 10% formaldehyde solution, rinsed in fresh water and then transferred to 70% ethanol. These formalin preserved specimens are deposited in the polychaete collections of the Australian Museum (AM), Sydney, Australia, the Museum and Art Gallery of the Northern Territory (NTM), Darwin, Australia, and the Museum of the A.V. Zhirmunsky Institute of Marine Biology (MIMB), Vladivostok, Russia. Some specimens (usually posterior fragments of worms) were preserved directly in 95% ethanol for molecular analyses. Complete information about formalin-preserved material deposited in the museums is given below, in the Material examined sections along with the description of species. The number of specimens in a sample is given in parentheses after the MI QLD number or the museum abbreviation and registration number. In the descriptions, groups of chaetae in noto- and neuropodia (anterior, posterior, superior and inferior) and other characters are referred to as they were defined by Radashevsky (2012).

Photographs were taken of living individuals using a microscope equipped with a digital camera in the laboratory on Lizard Island and also from fixed specimens in the laboratory in Vladivostok. Images of multiple layers of worms were stacked using Zerene Stacker 1.04 software. Images of parts of worms were stitched into panoramas using Kolor Autopano Pro 3.7.0 software. Final plates were prepared using CorelDRAW<sup>®</sup>X5 15.2.0.695 software.

#### **Taxonomic account**

#### List of species of Spionidae from around Lizard Island reported in this study

Aonides cf. nodosetosa Störch, 1966 Aonides orensanzi n. sp. Dipolydora armata (Langerhans, 1880) Polydorella prolifera Augener, 1914 Prionospio anneae n. sp. Prionospio aucklandica Augener, 1923 Prionospio cerastae n. sp. Prionospio cooki n. sp. Prionospio kulin Wilson, 1990 Prionospio lylei n. sp. Prionospio multicristata Hutchings & Rainer, 1979 Prionospio cf. paucipinnulata Blake & Kudenov, 1978 Prionospio cf. tatura Wilson, 1990 Prionospio cf. tetelensis Gibbs, 1971 Prionospio cf. tridentata Blake & Kudenov, 1978 Pseudopolydora cf. paucibranchiata (Okuda, 1937) Pseudopolydora cf. rosebelae Radashevsky & Migotto, 2009 Rhynchospio darwini n. sp. Tripolydora spinosa Woodwick, 1964

#### Key to genera of Spionidae reported from or likely to be found on the Great Barrier Reef

1.	Branchiae absent. Neuropodia of chaetiger 1 with large crook-like spines in addition to capillaries
-	Branchiae present (except some <i>Polydorella</i> ). Neuropodia of chaetiger 1 with only capillaries
2. (1)	Chaetiger 5 with only capillaries
-	Chaetiger 5 with heavy spines in addition to capillaries
3. (2)	Branchiae throughout most of body length
-	Branchiae limited to anterior half of body
4. (3)	Head anteriorly conical and distally pointed
-	Head anteriorly wide, truncate to conical but not distally pointed
5. (4)	Dorsal branchiae from chaetiger 1. Lateral branchiae on posterior face of notopodia. Chaetiger 1 notopodial capillaries much longer than on succeeding chaetigers. Posterior notopodia with only capillaries
_	Dorsal branchiae from chaetiger 2. Lateral branchiae absent. Chaetiger 1 notopodial capillaries same or shorter than on succeeding chaetigers. Posterior notopodia with hooks and capillaries
6. (4)	Prostomium greatly expanded anteriorly, T-shaped or with fronto-lateral horns. Pygidium with two or more pairs of cirri 7
_	Prostomium narrow to slightly expanded anteriorly, without fronto-lateral horns. Pygidium with two pairs of cirri8
7. (6)	Branchiae from chaetiger 1. Nuchal organs entire
-	Branchiae from chaetiger 2. Nuchal organs metameric
8. (6)	Branchiae from chaetiger 1. Nuchal segmental metamers double pairs each composed of two halves of an oval structure separated anteriorly and posteriorly by narrow gaps
_	Branchiae from chaetiger 2. Nuchal segmental metamers single pairs of crescents or straight bands on a segment
9. (3)	Occipital antenna present. Nuchal organs extending beyond chaetiger 4. Branchiae over most of anterior body Laonice
-	Occipital antenna present or absent. Nuchal organs over 1–4 anterior chaetigers or absent. Branchiae limited to first 20 chaetigers
10. (9)	Prostomium conical with narrow and rounded tip anteriorly. Occipital antenna present or absent. Nuchal organs absent
_	Prostomium broadly rounded to truncate anteriorly (fronto-lateral horns present in <i>P. cerastae</i> n. sp.). Occipital antenna absent. Nuchal organs U-shaped over 1–4 chaetigers
11. (2)	Living in silty tubes on sponge surface. Body short, with constant number of chaetigers, up to 16. Branchiae one or two
	pairs, or entirely absent. Asexual reproduction by paratomy
_	Living otherwise. Body long, with lifelong increasing number of chaetigers, more than 16. Branchiae more than two pairs. Asexual reproduction by architomy, if present

12. (11)	Hooks tridentate, in neuropodia from chaetiger 9 Tripolydora
-	Hooks bidentate, in neuropodia from chaetiger 7 or 8
13. (12)	Hooks in neuropodia from chaetiger 8; upper part of hook shaft with constriction, lower part of hook shaft bent at about
	right angle. Branchiae from chaetiger 7Pseudopolydora
-	Hooks in neuropodia from chaetiger 7; upper part of hook shaft with or without constriction, lower part of hook shaft
	slightly curved. Branchiae from chaetigers 2–10
14. (13)	Branchiae from chaetiger 2 (from chaetiger 7 in early juveniles)
-	Branchiae from chaetigers 7–10 in all-size individuals
15. (14)	Notopodia of chaetiger 5 with heavy falcate spines alternating with bilimbate-tipped companion chaetae Boccardiella
-	Notopodia of chaetiger 5 with heavy falcate spines and brush-topped spinesBoccardia
16. (14)	Chaetiger 1 with notochaetae. Branchiae from chaetigers 7-10. Hooks accompanied by inferior capillaries at least in ante-
	rior neuropodia; upper part of hook shaft without constriction
-	Chaetiger 1 without notochaetae. Branchiae from chaetiger 7. Hooks not accompanied by inferior capillaries; upper part of
	hook shaft with constriction

#### Aonides Claparède, 1864

*Aonides* Claparède, 1864: 505; Pettibone 1963: 90; Foster 1971: 65–66; Blake & Kudenov 1978: 189; Imajima 1989: 214; Blake 1996: 100; Brito *et al.* 2006: 60.

Type-species. Aonides auricularis Claparède, 1864 [=Nerine oxycephala Sars, 1862], by monotypy.

**Remarks.** *Aonides* Claparède, 1864 is a small group of spionid polychaetes currently comprising nine species. The oldest and the type species of the group, *A. oxycephala* (Sars, 1862) originally described from Norway, has been reported worldwide and considered cosmopolitan. These reports, however, likely comprise a series of similar or sibling species, thus more detailed morphological comparisons and molecular investigations are needed to clarify their taxonomy.

The first *Aonides* from Australia were identified by Blake & Kudenov (1978). The authors reported that worms from New South Wales and Victoria had at least 20 pairs of branchiae, bidentate hooks in the notopodia from about chaetiger 29 and in the neuropodia from about chaetiger 40. Hutchings & Turvey (1984) reported that the only anterior fragment of *Aonides* from South Australia had occipital antenna on the prostomium, branchiae on chaetigers 2–18, bidentate hooks in notopodia from chaetiger 22–24 and in neuropodia from chaetiger 22. Both Blake & Kudenov (1978) and Hutchings & Turvey (1984) concluded that their worms agreed well with the description of *A. oxycephala* by Ramos (1976) and identified them as such. However, originally described from Norway, *A. oxycephala* may not occur in Australia. The conspecificity of the Australian individuals and those from Norway should be confirmed in a molecular analysis.

#### Key to Aonides from around Lizard Island Group

#### Aonides cf. nodosetosa Störch, 1966

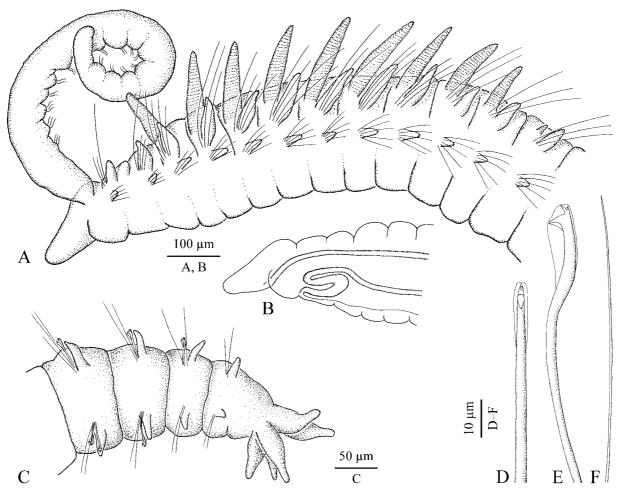
(Figs 1, 2)

Aonides nodosetosa Störch, 1966: 174-175, pl. 2, fig. 3a-d.

#### Material examined. Queensland: AM W.45224, MI QLD 2379 (2); MIMB 28110, MI QLD 2379 (2).

**Adult morphology.** Up to 5 mm long, 0.25 mm wide for 50 chaetigers; smallest examined individual 2.5 mm long for 31 chaetigers. Worms fragile, with thin cuticle easily destroyed during treatment and fixation. No

pigmentation on body and palps. Prostomium elongated, conical, anteriorly rounded, posteriorly blunt to rounded, not extending over chaetigers as a caruncle. Eyes and occipital antenna absent. Ciliary bands or patches of nuchal organs absent on posterior sides of prostomium. Peristomium reduced to a small ring around mouth. Palps as long as 5–10 chaetigers, with frontal longitudinal groove lined with fine cilia, and up to 15 short transverse ciliary bands regularly arranged on inner lateral surface; lateral bands fewer in small individuals; long cilia of bands beating towards distal end of palp (Fig. 1A).



**FIGURE 1.** *Aonides* cf. *nodosetosa*. AM W.45224. A. Anterior end of a 50-chaetiger individual in left lateral view with right palp missing; B. Same, optical section, showing ventral buccal bulb below anterior part of oesophagus; C. Posterior end of same individual in left lateral view; D–F. Chaetae from a middle neuropodium; D. Tridentate hooded hook in frontal view; E. Same in lateral view; F. Hair-like alimbate alternating capillary.

Chaetiger 1 with capillaries and small postchaetal lamellae in both rami. Postchaetal lamellae on succeeding chaetigers elongated in both rami (Fig. 1A). Dorsal crests, lateral pouches and ventral flaps absent.

Hooks in notopodia from chaetigers 9–13 (Fig. 2B), up to three in a series among capillaries. Hooks in neuropodia from chaetigers 8–13 (Fig. 2B), up to four in a series, accompanied by 1–5 alternating capillaries and 1–3 inferior capillaries throughout. Alternating capillaries alimbate, hair-like (Fig. 1F). Sabre chaetae absent. Hooks in both rami tridentate, with two upper teeth arranged vertically above main fang; upper part of shaft characteristically bent (Fig. 1D, E). Outer hood open distally; small membrane present below main fang, resembling inner subdistal hood (Fig. 1E).

Branchiae up to 10 pairs, from chaetiger 3 to chaetiger 12, fewer in small individuals (Figs 1A, 2A). Branchiae long on anterior chaetigers and gradually diminishing on 2–3 posterior chaetigers, up to 2.5 times as long as notopodial lamellae, free from lamellae, robust, flattened, with surfaces oriented perpendicular to body axis, with longitudinal bands of cilia along inner and outer edges. Afferent and efferent blood vessels of branchiae forming a loop and interconnected by radial capillaries giving branchiae annulate appearance.

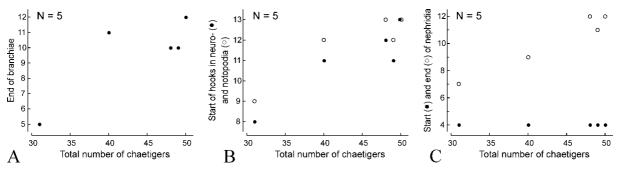
Dorso-lateral dense bands of short cilia from chaetiger 1 to chaetiger 11, fewer in small individuals. Bands short, extending between successive notopodia. Short nototrochs present on branchiate chaetigers, each composed by single row of short cilia.

Pygidium with five cirri of similar length, comprising one pair of ventral cirri, one pair of dorsal cirri and a midventral cirrus (Fig. 1C). Ventral cirri with weak yellow pigment.

Oesophagus extending through 9–10 anterior chaetigers. Ventral buccal bulb below oesophagus extending to middle of chaetiger 2 (Fig. 1B). Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Narrow heart body present in main dorsal vessel in anterior chaetigers. Blood red, without elements.

Nephridia from chaetiger 4 to chaetiger 12, fewer in small individuals (Fig. 2C).



**FIGURE 2.** Aonides cf. nodosetosa. A. Relationships between distribution of branchiae (referring to number of the last branchiate chaetiger) and total number of chaetigers in worm; B. Relationships between anterior position of hooks in neuroand notopodia (in chaetiger numbers) and total number of chaetigers in worm; C. Relationships between anterior and posterior position of excretory metanephridia (referring to number of the first and the last chaetigers bearing nephridiopores) and total number of chaetigers in worm.

**Reproduction.** All individuals of *A*. cf. *nodosetosa* collected in August 2013 were immature.

**Remarks.** *Aonides nodosetosa* was originally described from near Gaftun (Giftun) Island, El Ghardaqa (Hurghada) in the Red Sea by Storch (1966). Worms were collected from coarse sand with pebble in shallow water off wavy beach (die Grobsandzone des Brandungsstrandes in der Nähe der Insel Gaftun bei Ghardaqa). They were up to 5 mm long for 59 chaetigers and had a prostomium anteriorly rounded and posteriorly not extending as a caruncle, 8–9 pairs of branchiae beginning from chaetiger 3, pygidium with 2–3 pairs of short cirri, and tridentate hooks in noto- and neuropodia from chaetigers 11–12. Eyes and occipital antenna were absent. *Aonides nodosetosa* has never been redescribed or reported from a place other than type locality.

*Aonides* from Yonge Reef in Australia appear similar to *A. nodosetosa* from the Red Sea, Egypt in the shape of the prostomium, arrangement of branchiae and hooks and also shape and dentition of the hooks. Worms from the two localities slightly differ in number of cirri on the pygidium, 4–6 in *A. nodosetosa* and five in *Aonides* from Yonge Reef, but this may result from an individual variability and the small number of individuals examined in Australia. The Australian *Aonides* with branchiae from chaetiger 3 are tentatively referred to as *A. cf. nodosetosa*.

Aonides nodosetosa appears similar to other Aonides but differs from them in having branchiae from chaetiger 3 instead of chaetiger 2. Remarkably, the examined worms from Yonge Reef were small juveniles and it is likely that the Red Sea worms described by Storch (1966) were also juveniles. Mature individuals should be examined to verify if start of branchiae from chaetiger 3 is an adult or temporary juvenile condition prior to the development of definitive adult characters. Retarded development of branchiae on anterior chaetigers is characteristic for other spionids including *Boccardia, Boccardiella, Laonice, Malacoceros, Microspio, Prionospio, Spio* and can be misleading in identification of small individuals (Radashevsky 2012).

By having a pygidium with five cirri and tridentate hooks with upper teeth situated one above another *A. nodosetosa* appears similar to *A. selvagensis* Brito, Núñez & Riera, 2006 from Selvagens Islands in the Eastern Central Atlantic. Adults of both species also have no eyes and occipital antenna on the prostomium. They differ however in the beginning of branchiae, from chaetiger 2 in *A. selvagensis* and from chaetiger 3 in *A. nodosetosa*. The largest described specimen of *A. selvagensis* was 9.25 mm long with 52 chaetigers, i.e., by the number of chaetigers smaller than *A. nodosetosa*, but it had branchiae beginning from chaetiger 2.

**Habitat.** In this study, adult *Aonides* cf. *nodosetosa* were found on the outside of the Great Barrier Reef at about 10 m depth. Worms were likely crawling free in the coral sand.

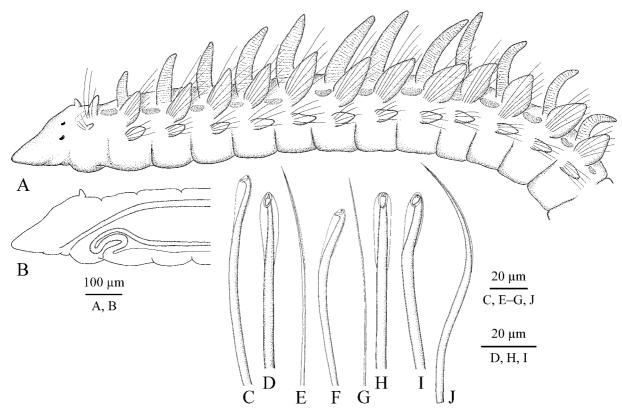
Distribution. Red Sea, Egypt; ? Queensland, Australia.

### Aonides orensanzi n. sp.

(Figs 3, 4)

**Type material. Queensland:** Holotype: AM W.45226, MI QLD 2415. Paratypes: AM W.45220, MI QLD 2330 (3), MIMB 28111, MI QLD 2330 (2); AM W.45221, MI QLD 2360 (1); AM W.45222, MI QLD 2363 (1); AM W.45223, MI QLD 2373 (4); MIMB 28112, MI QLD 2373 (3); AM W.45225, MI QLD 2410 (2); MIMB 28113, MI QLD 2415 (1); AM W.45505, MI QLD 2435 (2).

**Adult morphology.** Up to 12 mm long, 0.4 mm wide for 80 chaetigers; holotype a complete individual about 11 mm long for 77 chaetigers; smallest examined individual about 6 mm long for 50 chaetigers. No pigmentation on body and palps. Prostomium long, anteriorly sharply conical, posteriorly narrowed and pressed into chaetiger 1 but not extending over it as a caruncle. Small rounded knobs with short non-motile sensory cilia irregularly scattered on prostomium. Short finger-like antenna present on posterior most part of prostomium (Fig. 3A). Ciliary bands or patches of nuchal organs absent on posterior sides of prostomium. Two pairs of red eyes arranged almost in a straight transverse line; lateral eyes slightly larger than median eyes (Fig. 3A). Peristomium reduced to small ring around mouth. Palps as long as 5–15 chaetigers, with frontal longitudinal groove lined with fine cilia, and up to 25 short transverse ciliary bands regularly arranged on inner lateral surface; lateral bands fewer in small individuals; long cilia of bands beating towards distal end of palp.

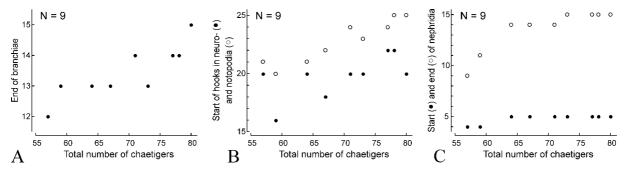


**FIGURE 3.** *Aonides orensanzi* n. sp. A, B—AM W.45222; C–H—AM W.45220; I, J—AM W.45226. A. Anterior end in left lateral view with palps missing; B. Same, optical section, showing ventral buccal bulb below anterior part of oesophagus; C–E. Chaetae from anterior neuropodium; C. Bidentate hooded hook in lateral view; D. Same in frontal view; E. Alternating capillary with narrow wing; F–J. Chaetae from posterior neuropodium; F. Tridentate hooded hook in lateral view; G. Same in frontal view; H. Quadridentate hook in fronto-lateral view; I. Hair-like alimbate alternating capillary; J. Inferior sabre chaeta.

Chaetiger 1 with capillaries and small postchaetal lamellae in both rami. Postchaetal lamellae on succeeding chaetigers elongated, leaf-like in both rami (Fig. 3A). Dorsal crests, lateral pouches and ventral flaps absent.

Hooks in notopodia from chaetigers 20–25 (Fig. 4B), up to six in a series among capillaries. Hooks in neuropodia from chaetigers 16–22 (Fig. 4B), up to six in a series, accompanied by 1–5 alternating capillaries and 1–3 inferior chaetae throughout. Alternating capillaries in anterior neuropodia with narrow limbation (Fig. 3E), in posterior neuropodia alimbate, hair-like (Fig. 3G). Inferior chaetae in anterior neuropodia capillaries, in posterior neuropodia of big mature individuals they gradually become larger and can be referred to as sabre chaetae (Fig. 3J). Hooks in both rami in anterior parapodia bidentate, with upper tooth situated at almost right angle to main fang (Fig. 3C, D). Hooks in posterior parapodia tridentate, with two small upper teeth situated side by side above main fang (Fig. 3F, H), and occasionally quadridentate, with an additional median superior tooth (Fig. 3I). Only outer hood present; no inner subdistal hood.

Branchiae up to 14 pairs, from chaetiger 2 to chaetiger 15, fewer in small individuals (Figs 3A, 4A). Branchiae longest on chaetigers 5–7, up to three times as long as notopodial lamellae, gradually diminishing in length on succeeding chaetigers, free from lamellae, robust, flattened, with surfaces oriented perpendicular to body axis, with longitudinal bands of cilia along inner and outer edges. Afferent and efferent blood vessels of branchiae forming a loop and interconnected by radial capillaries giving branchiae annulate appearance.



**FIGURE 4.** Aonides orensanzi n. sp. A. Relationships between distribution of branchiae (referring to number of the last branchiate chaetiger) and total number of chaetigers in worm; B. Relationships between anterior position of hooks in neuroand notopodia (in chaetiger numbers) and total number of chaetigers in worm; C. Relationships between anterior and posterior position of excretory metanephridia (referring to number of the first and the last chaetigers bearing nephridiopores) and total number of chaetigers in worm; C. Relationships between anterior and posterior position of excretory metanephridia (referring to number of the first and the last chaetigers bearing nephridiopores) and total number of chaetigers in worm.

Dorso-lateral dense bands of short cilia from chaetiger 1 to chaetiger 14, fewer in small individuals. Each band of cilia extending between successive notopodia; bands short and straight to slightly curved on anterior chaetigers, becoming longer and horse-shoe shaped on posterior chaetigers, with lateral sides of horse-shoe directed to midline of body. Short nototrochs present on branchiate chaetigers, each composed by single row of short cilia.

Pygidium usually with five cirri, comprising one pair of ventral cirri, a midventral cirrus and one pair of slightly longer and thicker dorsal cirri; one individual (of seven examined complete individuals with pygidia) with four cirri, and one individual with six pygidial cirri.

Oesophagus extending through 13–15 anterior chaetigers. Ventral buccal bulb below oesophagus extending to middle of chaetiger 2 (Fig. 3B). Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Heart body up to 10  $\mu$ m in diameter inside main dorsal vessel extending from chaetigers 4–6 to chaetigers 13–15. Blood red, without elements.

Nephridia from chaetiger 4 in small individuals and from chaetiger 5 to chaetiger 15 in individuals with more than 60 chaetigers (Fig. 4C).

**Reproduction.** Aonides orensanzi n. sp. is gonochoristic. Both in females and males gametes develop from chaetigers 16–17 throughout most part of body. Oogenesis is intraovarian. Vitellogenesis occurs when oocytes grow attached to segmental blood vessels. Vitellogenic intraovarian oocytes are up to 130  $\mu$ m in diameter, with a germinal vesicle about 40  $\mu$ m and a single nucleolus 13  $\mu$ m in diameter. Oocyte envelope is 3–4  $\mu$ m thick, with honey-combed external surface and a circle of about 30 vesicles associated with inner surface; each vesicle is about 10  $\mu$ m in diameter. Sperm morphology and spermatogenesis are unknown.

**Remarks.** Adult *Aonides orensanzi* n. sp. appear similar to *A. californiensis*, *A. mayaguezensis*, *A. oxycephala* and *A. trifida* by the presence of an occipital antenna on the prostomium. The antenna was not described but was illustrated on the posterior edge of the prostomium in *A. californiensis* by Rioja (1947: fig. 11). *Aonides orensanzi* n. sp. differs from these species in having bi-, tri- and quadridentate hooks in same individual. Such variability of hook dentition is herein reported for the first time for *Aonides*.

Aonides orensanzi n. sp. collected off Lizard Island in August had intraovarian vitellogenic oocytes up to 130  $\mu$ m in diameter, each with a circle of about 30 vesicles associated with inner surface. Two circles of vesicles were described by Hannerz (1956), Sveshnikov (1967), and Lebsky (1970) in the oocytes and early larvae of *A. oxycephala* and *A. paucibranchiata*. One circle of vesicles instead of two in the oocytes of *A. orensanzi* n. sp. may be due to incomplete development of the oocytes.

Etymology. The species is named in honour of Jose Maria (Lobo) Orensanz, biologist, colleague and a great man.

**Habitat.** Adults of *A. orensanzi* n. sp. were found in coral sand on coral reefs at 5–16 m depth. Worms were likely crawling free in the coral sand.

**Distribution.** Great Barrier Reef, Australia.

#### Dipolydora Verrill, 1881

Dipolydora Verrill, 1881: 320; Blake 1996: 181, resurrected and redefined.

Type-species. Polydora concharum Verrill, 1879. Designated by Verrill (1881), by monotypy.

**Remarks.** *Dipolydora* Verrill, 1881 currently comprises about forty species of polydorin spionids (tribe Polydorini Benham, 1896 *sensu* Radashevsky, 2012) that occupy diverse habitats from the intertidal to deep water. The name *Dipolydora* was not in use after its designation by Verrill (1881) until Blake (1996) resurrected it and assigned to it a series of *Polydora* Bosc, 1802 species that, in contrast to species of *Polydora*, had notochaetae on chaetiger 1 and lacked a constriction or manubrium on the shaft of the hooded hooks.

Nine *Dipolydora* species were reported from Australian waters by Blake & Kudenov (1978) (as *Polydora* species), McDiarmid *et al.* (2004) and Sato-Okoshi *et al.* (2008).

#### Dipolydora armata (Langerhans, 1880)

(Fig. 5)

Polydora armata Langerhans, 1880: 93-94, pl. 4, fig. 5a-c; Blake & Kudenov 1978: 255-258, fig. 43a-e.

*Dipolydora armata.*—Blake 1996 (Part.): 196–198, fig. 4.36; Bick 2001: 178–186, figs. 1–7; Williams 2001: 438–442, figs 5, 6; Radashevsky & Nogueira 2003: 377–381, figs 1–7; Sato-Okoshi *et al.* 2008: 495–496, fig. 4.

Dipolydora cf. armata.-Radashevsky & Fauchald 2000: fig. 6F.

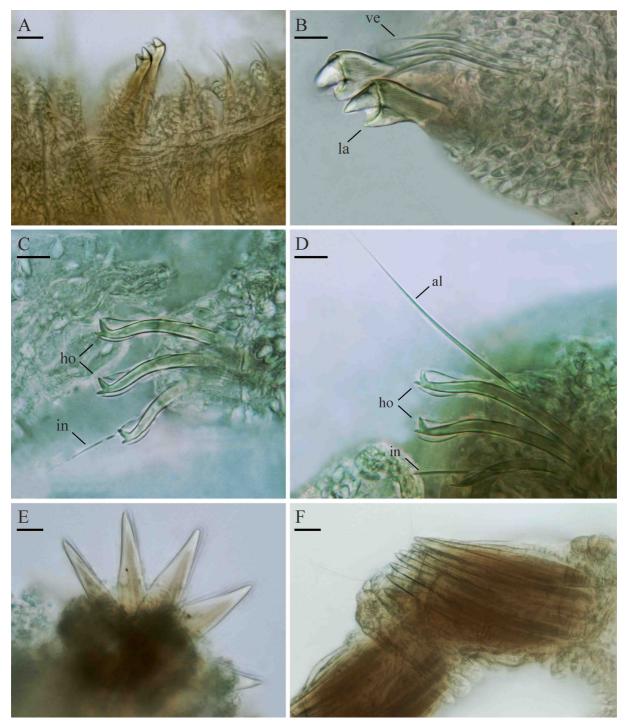
#### Material examined. Queensland: AM W.45506, MI QLD 2447 (20); MIMB 28114, MI QLD 2447 (7).

**Adult morphology.** Up to 2.5 mm long, 0.3 mm wide for 30 chaetigers. Body and palp pigmentation absent. Prostomium incised anteriorly, extending posteriorly to end of chaetiger 2 as a low caruncle. Occipital antenna and eyes absent.

Chaetiger 1 with capillaries and small postchaetal lamellae in both rami. Winged notopodial capillaries gradually becoming longer, thinner and less numerous along midbody chaetigers. Notopodia from chaetigers 18–24 onwards with up to three thin alimbate capillaries and 15 awl-like spines in a bundle (Fig. 5E, F).

Chaetiger 5 with up to three dorsal superior winged capillaries, two heavy falcate spines, and four ventral winged capillaries (Fig. 5A, B). Falcate spines with central main fang, large lateral tooth and apical structure appearing as wide cowling or third tooth on convex side of main fang; numerous fine bristles present on basis of teeth (Fig. 5B).

Hooks in neuropodia from chaetiger 7, up to three in a series, accompanied by 1-2 inferior capillaries throughout body and 1-3 alternating capillaries in 5-10 posterior chaetigers (Fig. 5C, D). Hooks bidentate; shaft slightly curved, without constriction (Fig. 5C, D).



**FIGURE 5.** *Dipolydora armata* AM W.45506. A. Left side of chaetigers 2–6 in ventral view; B. Right side of chaetiger 5 in ventral view; C. Bidentate hooded hooks and inferior capillary from a medium neuropodium, left side in rear view; D. Bidentate hooded hooks, alternating capillary and an inferior capillary from a posterior neuropodium, left side in rear view; E. Posterior chaetiger showing broken bundle of twisted awl-like spines; F. Posterior chaetiger showing intact notopodial bundle of awl-like spines occupying most of space of the chaetiger. Abbreviations: al—alternating capillary, ho—hooded hooks, in—ventral inferior capillary la—lateral tooth, ve—ventral capillary chaetae. Scale bars: A, E, F, 20  $\mu$ m; B–D–10  $\mu$ m.

Branchiae from chaetiger 7 to chaetiger 11, fewer in small individuals, flattened, with surfaces oriented parallel to body axis, basally fused to notopodial postchaetal lamellae.

Pygidium small, cup-shaped, with only narrow dorsal gap or bilobed, divided by dorsal gap and ventral incision into two rounded lateral lobes.

**Remarks.** *Dipolydora armata* was originally described from Madeira Island by Langerhans (1880) as a borer of calcareous algae and has since been reported world-wide. In Australia, *D. armata* was reported from Western Australia (Augener 1914; Hartmann-Schröder 1979; Sato-Okoshi *et al.* 2008), Victoria and South Australia (Blake & Kudenov 1978; Hartmann-Schröder 1987; McDiarmid *et al.* 2004). Worms from Lizard Island appear identical to *D. armata* described from California (Hartman 1941; Blake 1996), the Marshall Islands (Woodwick 1964), Mediterranean (Bick 2001), Philippines (Williams 2001), Brazil and other localities (Radashevsky & Nogueira 2003, type material re-examined).

*Dipolydora armata* has been considered cosmopolitan, widespread in tropical and subtropical waters, and rare in boreal and temperate waters. Such a wide distribution of the same species seems, however, suspicious taking into account small size of adults (usually 3–4 mm long for 30–35 chaetigers), low fecundity (up to 100 eggs per brood), adelphophagy (larvae feeding on the nurse eggs inside egg capsule), low larval production, and very short time that larvae swim in the water (see Lewis 1998 for details of larval development in the species). Molecular investigation is certainly needed to confirm the conspecificity of the remote populations.

**Habitat.** In this study, adult *D. armata* were found boring into the shell of a gastropod *Turbo* sp. at about 14 m depth.

**Distribution.** Widespread in tropical and subtropical waters. Intertidal to 100 m. The species is herein reported for the first time from Queensland and the Great Barrier Reef.

#### Polydorella Augener, 1914

Polydorella Augener, 1914: 16; Tzetlin & Britayev 1985: 177-178; Radashevsky 1996: 685; Williams 2004: 1342.

Type-species. *Polydorella prolifera* Augener, 1914, by monotypy.

**Remarks.** *Polydorella* Augener, 1914 is a small group of spionid polychaetes currently comprising five species, all symbionts of sponges in tropical and subtropical waters. Adults live in tiny silty tubes on sponge surfaces, reproduce asexually by paratomy and have limited number of body segments, no more than 16. Sexual reproduction and larval development are unknown.

Two species, *P. prolifera* Augener, 1914 and *P. stolonifera* (Blake & Kudenov, 1978, as *Pseudopolydora stolonifera*) were originally described from Australia. These are the only *Polydorella* species reported so far from the Australian waters.

#### Polydorella prolifera Augener, 1914

(Figs 6, 7)

*Polydorella prolifera* Augener, 1914: 16–20, pl. I, fig. 3, textfigs. 2a–d. *Pseudopolydora prolifera*.—Blake & Kudenov 1978: 271–273, fig. 50 k–n.

## **Material examined. Queensland:** AM W.45231, MI QLD 2435 (20); MIMB 28115, MI QLD 2435 (15); AM W.45512, MI QLD 2447 (30); MIMB 28116, MI QLD 2447 (20).

**Adult morphology.** Most individuals reproducing asexually by paratomy and appearing as chains of joined stocks and stolons at various stages of growth and regeneration. Single individuals up to 1.3 mm long, 0.25 mm wide for 14–15 chaetigers (15–16 segments). One female about 1.5 mm long for 16 segments. Paratomic growth zone situated in some worms between segments 10 and 11 and in others between segments 11 and 12 (Fig. 6A, B). Pigmentation greatly variable; dense fine net of black pigment present on dorsal and ventral sides of body in some individuals (Fig. 6A–C) while pigmentation weakly developed or absent in others.

Prostomium incised to bilobed anteriorly, extending posteriorly to end of segment 1 as a low caruncle. Nuchal organs short, wide ciliary bands, almost forming oval ciliary patches on sides of caruncle (Fig. 6C). Occipital antenna absent. One pair of white irregularly rounded eye-spots present in life, but not seen in preserved specimens. Palps as long as 10–15 segments, with longitudinal frontal groove lined with fine cilia, and short compound non-motile cilia arising directly from palp surface and scattered on fronto-lateral, lateral and abfrontal palp surfaces; fronto-lateral papillae absent.



**FIGURE 6.** *Polydorella prolifera*. A–C—AM W.45231. A. Entire stock individual in the beginning of asexual reproduction by paratomy, showing stolon developing between segments 11 and 12; B. Posterior end in dorsal view, showing newly developing stolon; C. Anterior end in left lateral view; D–F. Various sponges with worms in tubes on the surface. Abbreviations: br— branchium, nu—nuchal organ, pa—palp, py—pygidium, s1–s12—segments 1–12 of stock individual, s12'—newly regenerating segment 12 of stock individual. Scale bars: A—100 µm; B, C—50 µm; D–G—5 mm. Photo: E, F—Alexander Semenov.

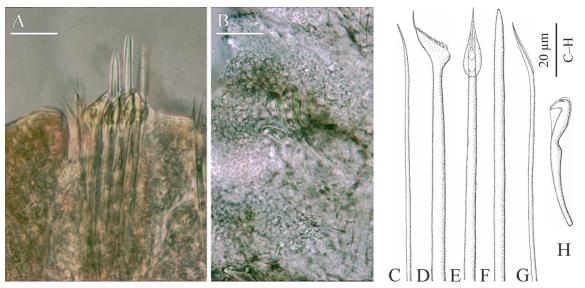
Segment 1 reduced, poorly demarcated from peristomium; chaetae and notopodial lamellae lacking; small neuropodial lamellae present (Fig. 6A). Segments 1–7 short as if compressed, while subsequent segments longer (Fig. 6A). Notopodia from segment 2 (chaetiger 1) onwards and neuropodia of segments 2–7 with fascicles of unilimbate capillaries. Posterior notopodia with only capillaries.

Segment 5 (chaetiger 4) similar in size to segments 4 and 6, with up to five dorsal superior winged capillaries shorter than those on segments 4 and 6 (Fig. 7C), two kinds of heavy notopodial spines (Fig. 7A), and six ventral winged capillaries same as those on segments 4 and 6 (Fig. 7G); notopodial postchaetal lamellae lacking but low neuropodial lamellae same as on segments 4 and 6. Anterior-row notopodial spines up to six in a series, distally enlarged and flat, with denticulate upper edge; lateral sides of flat distal part enveloped by thin sheath covered with tiny scales; one side of distal part with a pointed capillary extension (Fig. 7D, E). Posterior-row spines up to four in a series, simple acicular (Fig. 7F).

Hooks in neuropodia from segment 8 (chaetiger 7), up to four in a series, not accompanied by capillaries. Hooks bidentate; shaft slightly curved, with constriction in upper part and a low boss on concave side below constriction (Fig. 7B, H).

Single pair of branchiae present on segment 7 (chaetiger 6). Branchiae free from notopodial lamellae,

flattened, with surfaces oriented parallel to body axis, with longitudinal row of cilia along inner side (Fig. 6A). Nototrochs from segment 3 onwards, except segment 5, composed of single row of ciliated cells; longest nototroch cilia on segment 7 extending onto branchiae.



**FIGURE 7.** *Polydorella prolifera.* Morphology of chaetae. A–H—AM W.45231. A. Notopodial spines of segment 5 comprising anterior-row spines with denticulate upper edge, and posterior-row simple acicular spines; B. Bidentate hooded hooks from neuropodium of segment 8; C–G. Set of chaetae of segment 5; C. Dorsal superior alimbate capillary chaeta; D. Anterior-row notopodial spine in lateral view; E. Same in rear view; F. Posterior-row notopodial spine in lateral view; G. Ventral winged capillary chaeta; H. Bidentate hooded hook from neuropodium of segment 8. Scale bars: A, B—20 µm.

Pygidium elongated and rounded posteriorly, without appendages; anus terminal (Fig. 6A, B).

Glandular pouches in neuropodia from segment 1, largest in segments 6–7.

Oesophagus extending through 6–7 segments. Ventral buccal bulb and gizzard-like structure in digestive tract absent.

Main dorsal blood vessel without heart body. Blood red, without globules.

Nephridia from segment 4 (chaetiger 3) onwards.

**Reproduction.** Most *P. prolifera* examined in August 2013 were reproducing asexually by paratomy. One female had vitellogenic oocytes developing in segments 13–16; 2–3 oocytes were present in an ovary on each side of each fertile segment, with about 20 oocytes were present in total. The oocytes were up to 65  $\mu$ m in diameter with a germinal vesicle about 13  $\mu$ m and a single nucleolus 5  $\mu$ m in diameter. The oocyte envelope was thin and smooth, less than 1  $\mu$ m thick.

**Remarks.** *Polydorella prolifera* was originally described from Sharks Bay, South Passage, Western Australia by Augener (1914). Blake & Kudenov (1978) redescribed two syntypes of the species and also described *Pseudopolydora stolonifera* (=*Polydorella stolonifera*) from Victoria, Australia.

*Polydorella* from Lizard Island appear identical to *P. prolifera* and are referred to this species. The worms also appear very similar to *P. dawydoffi* originally described from Nhatrang Bay, South-China Sea, Vietnam, by Radashevsky (1999) and re-described based on material from Philippines and the Red Sea, Egypt, by Williams (2004). They differ, however, in that the posterior-row notopodial spines of segment 5 are simple acicular in *P. prolifera* and acicular with subdistal shelf on convex side in *P. dawydoffi*.

**Habitat.** Adult *P. prolifera* live in tiny silty tubes on the surface of various sponges (Fig. 6D–F). The worms capture food particles by elevating their paired palps into water currents produced by the sponges. The tubes are 160–220  $\mu$ m in diameter and 2.5–5.0 mm long. Two separate individuals often inhabit one tube looking out and feeding from opposite openings of the tube. Having occupied a sponge, worms live in colonies of tens of individuals per one square centimetre. Dense colonies are formed due to asexual reproduction of worms by paratomy.

Distribution. Western Australia and Queensland, Australia.

#### Prionospio Malmgren, 1867 sensu lato

Prionospio Malmgren, 1867: 201; Blake & Kudenov 1978: 211-212; Maciolek 1985: 329, 332; Wilson 1990: 245-246.

Type-species. Prionospio steenstrupi Malmgren, 1867, by monotypy.

**Remarks.** *Prionospio* Malmgren, 1867 and closely related spionids constitute the most diverse and complicated group within the Spionidae. The group currently comprises more than one hundred species occurring worldwide from the intertidal to deep sea. Historically treated together and referred to as a generic *Prionospio* complex, for a long time the genus was not explicitly defined and no single character or group of characters was suggested to support its monophyly. Systematic treatments of the complex were overviewed by Foster (1971), Blake & Kudenov (1978), Maciolek (1985), Wilson (1990), Blake (1996), and Sigvaldadóttir (1998). Different generic breakdowns of the complex were suggested by various authors based on different suits of external morphological characteristics of adults and ideas about their weight for taxonomy. All those groupings were considered artificial, convenient for identification purposes rather than reflecting phylogenetic relationships.

Sigvaldadóttir *et al.* (1997) and Sigvaldadóttir (1998) provided the first attempts to elucidate phylogenetic relationships within the *Prionospio* complex with explicit cladistic methodology. The analyses resulted in essentially different hypotheses and, as it was concluded by Sigvaldadóttir (1998: 185) herself, were based on "a too small number of characters to obtain reliable estimates". Preliminary phylogenies of spioniform polychaetes shown by Blake & Arnofsky (1999: fig. 13C) suggested *Prionospio* complex as a monophyletic group comprising *Prionospio*, *Paraprionospio* Caullery, 1914, and *Streblospio* Webster, 1879 but no single character was noted for its support.

The generic analysis by Sigvaldadóttir (1998) suggested monophyly of the group containing *Prionospio* Malmgren, 1867 *sensu stricto*, *Minuspio* Foster, 1971, *Aquilaspio* Foster, 1971, and *Apoprionospio* Foster, 1969. More than 80 valid species of these taxa were referred to *Prionospio* Malmgren, 1867 *sensu lato* which further generic division based on branchial form was suggested to be avoided. Ultimately, Sigvaldadóttir (1998: 185) concluded that future study of *Prionospio* "should endeavor to identifying natural groups rather than disputing Linnean ranking of taxa". Being in agreement with this conclusion, I suggest that in the absence of phylogenetic analyses of broader suits of diverse characters, it is useful to revise various groups of the *Prionospio* complex based at least on their superficial similarities, not necessarily following subgeneric categories established by Foster (1971) and subsequently modified by Maciolek (1985). Description of additional characters including internal anatomy and reproductive characteristics, and taxonomic revisions of certain groups of species with keys to their identification would clarify the diversity and composition of the complex in total. Good examples of those revisions are by Hylleberg & Nateewathana (1991) of the *Prionospio* with both pinnate and apinnate branchiae, and Delgado-Blas (2014, 2015) of the *Prionospio* with five pairs of branchiae, and *Prionospio* with both pinnate and apinnate branchiae on chaetigers 2–5 from the Grand Caribbean Region.

The two characters in support of *Prionospio sensu lato* in the analysis by Sigvaldadóttir (1998), the neuropodial lamellae of segment 2 pointed ventrally, and neuropodial hooks starting at segments 14–19, appear rather ambiguous. Nevertheless, this grouping is used in the present study, the subgenera are dispensed, and corresponding species from around the Lizard Island Group are referred to *Prionospio sensu lato*.

Foster (1971) clarified the terms "dorsal crest" and "dorsal fold" with regard to structures between notopodial postchaetal lamellae on the dorsal side of segments, and Maciolek (1985) clarified the terms used to describe branchial appearance (pinnate vs. apinnate) and shape of the pinnae (pinnules; digitiform vs. plate-like) on their surface. These terms are used in the present study.

Sigvaldadóttir & Mackie (1993) highlighted the importance of investigating size-related variability of *Prionospio* worms, and this importance is stressed again in the present study. Many crucial taxonomic characters, such as dentition of hooks, arrangement of hooks, sabre chaetae and branchiae, and the presence of pinnae on branchiae, are shown to modify during individual ontogenesis. Correct identification of certain stages is therefore problematic or even impossible without knowledge of the entire transformation series.

#### Key to Prionospio from around Lizard Island Group<sup>1</sup>

1.	Prostomium with two long pointed fronto-lateral horns. Median eyes small. Neuropodial postchaetal lamellae of chaetiger 1 with lower part elongated and directed ventrally. Branchiae smooth on chaetigers 2–4, pinnate on chaetiger 5. Hooded hooks in notopodia from chaetigers 12–30, in neuropodia from chaetigers 10–15. Ventral inferior chaetae capillaries
	throughout body; sabre chaetae absent. Dorsal crests absent
_	Prostomium anteriorly rounded, without horns. Neuropodial postchaetal lamellae of chaetiger 1 small, not elongated ven-
-	trally. Sabre chaetae present in neuropodia (absent in <i>P. anneae</i> n. sp.)
2. (1)	Three to four pairs of branchiae from chaetiger 2, at least one pair pinnate
2. (1) _	Up to 8 pairs of branchiae from chaetiger 2, all apinnate.
3. (2)	Three to four pairs of branchiae, all pinnate
_	Four pairs of pinnate and apinnate branchiae
4. (3)	Three pairs of pinnate branchiae on chaetigers $2-4^2$ . Caruncle to end of chaetiger 1. Median eyes small. Chaetiger 1 with-
(0)	out notochaetae. Dorsal crests absent. Hooks in notopodia from chaetigers 25–38, in neuropodia from chaetigers 16–21.
	Sabre chaetae from chaetiger 10
_	Four pairs of pinnate branchiae on chaetigers 2–5. Caruncle to end of chaetiger 3. Median eyes large. Chaetiger 1 with
	notochaetae. Dorsal crests present from chaetiger 6 at least on ten succeeding chaetigers. Sabre chaetae after chaetiger 10
5. (3)	Branchiae with pinnae on chaetigers 2 and 5, apinnate on chaetigers 3 and 4 Prionospio steenstrupi group-7
_	Pinnate and apinnate branchiae arranged otherwise
6. (5)	Sabre chaetae in neuropodia from chaetiger 11. Median eyes small. Branchiae apinnate on chaetigers 2-4, with many pin-
	nae on chaetiger 5. Caruncle to end of chaetiger 1. Dorsal crest on chaetiger 7. Hooks in neuropodia from chaetigers 19-20
	P. cf. tridentata
-	Sabre chaetae in neuropodia from chaetiger 10. Median eyes large. Branchiae with few pinnae on chaetigers $2-4^3$ , apinnate on chaetiger 5. Caruncle to end of chaetiger 4. Prominent semicircular dorsal crest on chaetiger 7; low crests from chaeti-
	ger 8 to chaetigers 16–31. Hooks in neuropodia from chaetigers 10–14 P. cf. paucipinnulata
7. (5)	Sabre chaetae absent in neuropodia. Hooks in neuropodia from chaetigers 8–9. Moderate dorsal crest present on chaetiger
	6 <i>P. anneae</i> n. sp.
-	Sabre chaetae in neuropodia from chaetiger 10. Hooks in neuropodia after chaetiger 9. Dorsal crest absent on chaetiger 68
8. (7)	Caruncle to end of chaetiger 1. Median eyes large. Dorsal crest on chaetiger 7, no on succeeding chaetigers. Hooks in neu-
	ropodia from chaetigers 11–12
-	Caruncle extending beyond chaetiger 1. Median eyes small or large. Dorsal crests from chaetiger 7 on a series of succeed-
	ing chaetigers
9. (8)	Median eyes small. Caruncle to end of chaetiger 4. Low dorsal crests from chaetiger 7 on a series of succeeding chaetigers.
	Hooks in neuropodia from chaetigers 12–14
-	Median eyes very large. Caruncle to end of chaetiger 2 or 3. Moderate dorsal crest on chaetiger 7 and low crests from chae-
10 (0)	tiger 8 on a series of succeeding chaetigers. Hooks in neuropodia from chaetigers 11–18
10. (9)	Eyes red in living and fixed specimens. Caruncle to end of chaetiger 2. Dorsal crests on chaetigers 7–24
_	Eyes red in living but black in formalin-fixed specimens. Caruncle to end of chaetiger 3. Dorsal crests on chaetigers 7–30
	P. multicristata

#### Prionospio anneae n. sp.

(Figs 8–10)

**Type material. Queensland:** Holotype: AM W.45273, MI QLD 2410. Paratypes: AM W.45271, MI QLD 2330 (1); AM W.45272, MI QLD 2363 (1); AM W.47870, MI QLD 2373 (1); AM W.47871, MI QLD 2410 (2); AM W.45274, MI QLD 2431 (3); MIMB 28109, MI QLD 2431 (1).

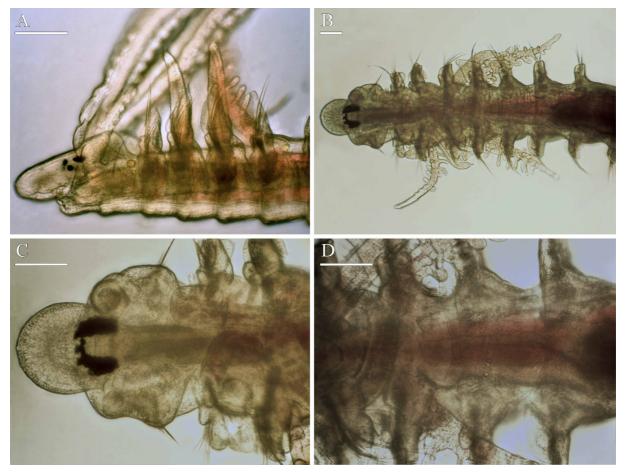
Adult morphology. Up to 14 mm long, 0.3 mm wide for about 90 chaetigers; holotype 12 mm long for 53 chaetigers. Pigmentation on body absent; some yellow indistinct spots present on branchiae in life. Prostomium narrow and rounded anteriorly, extending posteriorly to middle of chaetiger 2 as a prominent caruncle. Occipital

<sup>1.</sup> The identification key is based on characters appearing in completely developed adults. For example, median eyes enlarge in ontogenesis apparently in association with sexual maturation of an individual, caruncle elongates with age up to a certain species-specific limit, pinnae on branchiae (especially on posterior pairs) may appear in a while after development of the branchiae, thus smooth, apinnate branchiae are present in small and median-size individuals on chaetigers where pinnate branchiae are present in completely developed adults. Identification of those small and median-size individuals is therefore problematic, unless ontogenetic development and transformation of characters is taken into account.

<sup>2.</sup> Branchiae pinnate only on chaetiger 2 in small individuals, on chaetigers 2 and 3 in median-size individuals.

<sup>3.</sup> Branchiae pinnate only on chaetiger 2 in small individuals, on chaetigers 2 and 4 in median-size individuals.

antenna absent. Two pairs of red eyes arranged trapezoidally, comprising one pair of median eyes and one pair of lateral eyes situated anteriorly and set wider apart; median eyes small to moderately large in individuals with 40–60 chaetigers, very large in bigger individuals (Fig. 8A–C). Nuchal organs U-shaped ciliary bands on each side of caruncle. Posterior dorsal part of peristomium fused to notopodial lamellae of chaetiger 1 forming prominent rounded ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and narrow longitudinal band of cilia running on outer fronto-lateral side along frontal groove; cilia of transverse bands beating towards distal end of palp along palp axis, while cilia of longitudinal band beating towards frontal groove perpendicular to palp axis.



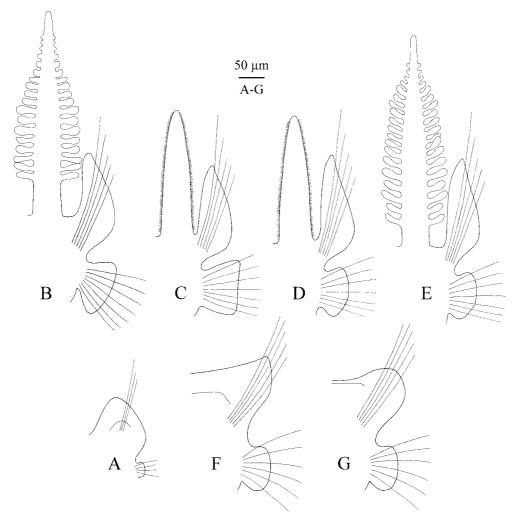
**FIGURE 8.** *Prionospio anneae* n. sp. A—AM W.45272; B–D—AM W.45273 (holotype). A. Anterior end, left lateral view; B, C. Anterior end, dorsal view; D. Chaetigers 5–8, dorsal view. Scale bars: A–D—100 μm.

Chaetiger 1 in individuals with less than about 50 chaetigers having only few capillaries in neuropodia; bigger individual with few short capillaries and postchaetal lamellae in both rami; notopodial lamellae large, flat, fused to posterior dorsal part of peristomium forming prominent ear-shaped structures (Figs 8A, 9A). Notopodial postchaetal lamellae largest on branchial chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 elongated and rounded ventrally (Fig. 9B). Neuropodial postchaetal lamellae trapezoidal on chaetiger 3, smaller and rounded on succeeding chaetigers (Fig. 9C–G).

Moderate dorsal crest present on chaetiger 6 (Fig. 9F); very low crests or folds present from chaetiger 7 (Fig. 9G) to chaetigers 15–21 (dorsal crest on chaetiger 6 and folds on chaetigers 7–20 in holotype). Lateral pouches and ventral flaps absent.

Hooks in notopodia from chaetigers 28–39 (39 in holotype), up to five in a series among capillaries. Hooks in neuropodia from chaetigers 8–9 (8 in holotype), up to eight in a series, accompanied by 1–2 inferior capillaries and 1–4 alternating capillaries throughout (Fig. 10B). Inferior capillaries as long as hooks, alternating capillaries about two times as long as hooks; both kinds of capillaries in anterior chaetigers slender, with narrow limbation, in

posterior chaetigers hair-like, alimbate. Hooks multidentate, with 4–6 pairs of thin, long upper teeth arranged in two vertical rows above main fang, with inner and outer hoods; shaft slightly bent. Sabre chaetae in neuropodia absent.



**FIGURE 9.** *Prionospio anneae* n. sp. AM W.45273 (holotype). A. Chaetiger 1, frontal view; B. Chaetiger 2, frontal view; C. Chaetiger 3, frontal view; D. Chaetiger 4, frontal view; E. Chaetiger 5, frontal view; F. Chaetiger 6, frontal view; G. Chaetiger 7, frontal view. Scale bars: A–G–50 µm.

Four pairs of branchiae on chaetigers 2–5 (Figs 8A, B, 9B–E); those on chaetigers 2 and 5 cylindrical, similar in length to each other, up to two times as long as notopodial lamellae, with numerous digitiform pinnae arranged along lateral and posterior sides along their length. Branchiae on chaetigers 3 and 4 up to 1.5 times as long as notopodial lamellae, apinnate, robust, flattened, with surface oriented perpendicular to body axis. An anterior fragment of a small individual about 0.15 mm wide with 2–3 pairs of small buds of pinnae on each of branchiae on chaetiger 2, and 7–8 pairs of well developed pinnae on each of branchiae on chaetiger 5. Longitudinal bands of cilia running on inner and outer edges on each branchia; ciliation heavier on branchiae on chaetigers 3 and 4. Afferent and efferent blood vessels interconnected by numerous radial capillaries forming loops inside individual pinnae.

Short nototrochs present on chaetigers 3 and 4, each composed by one transverse row of cilia. Dorso-lateral longitudinal ciliation present on chaetigers 3–5 as short bands of cilia extending between successive notopodia.

Pygidium with thin, long middorsal cirrus and one pair of short and thick ventral cirri (3–4 times as short as middorsal cirrus) (Fig. 10A).

Oesophagus extending through 6–9 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

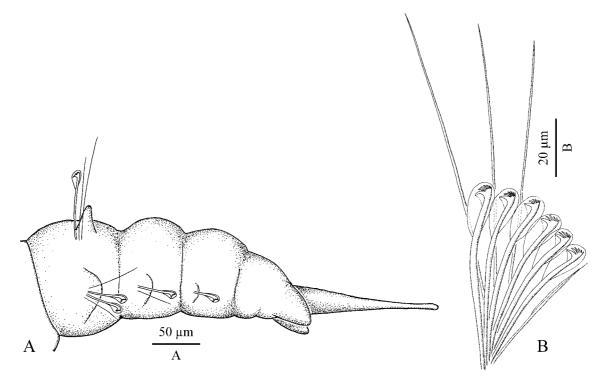


FIGURE 10. Prionospio anneae n. sp. AM W.45273 (holotype). A. Pygidium, left lateral view; B. Neurochaetae of chaetiger 8.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 13  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to chaetigers 10–13. Blood red, without globules or other elements.

#### Nephridia in chaetigers 4-6, greenish in life.

**Reproduction.** *Prionospio anneae* n. sp. is gonochoristic. Four females have oocytes from chaetiger 10 to chaetigers 45–48, and two males have spermatozoa from chaetiger 11 to chaetigers 50–60. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. Intraovarian oocytes were up to 75  $\mu$ m in diameter, with germinal vesicle about 30  $\mu$ m and single nucleolus 13  $\mu$ m in diameter. Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3  $\mu$ m in diameter, spherical mitochondria probably four in number, and a long flagellum.

**Remarks.** *Prionospio* with branchiae from segment 2, some apinnate and some with digitiform pinnules, have been treated as *Prionospio* Malmgren *sensu stricto* after Foster (1971) and Maciolek (1985). Those with four pairs of branchiae, pinnate on chaetigers 2 and 5, and apinnate on chaetigers 3 and 4, have conventionally been combined into the *P. steenstrupi* group of species named after *P. steenstrupi* described from northern Iceland by Malmgren (1867). Twelve species of this group occurring worldwide were summarized by Maciolek (1985: table 3, species 1–12). Imajima (1990a, b) described six new species from Japan. Hylleberg & Nateewathana (1991) recognized *Prionospio malayensis* Caullery, 1914, originally described as a subspecies, as a valid species, and also described eight new species, members of the *P. steenstrupi* group, from the Andaman Sea. Sigvaldadóttir & Mackie (1993) recognized *P. fallax* Söderström, 1920 as a distinct species. Blake (1996) described two new species, *P. jubata* and *P. marsupialia*, from California. Zhou & Li (2009) described a new species, *P. pacifica*, from the South-China Sea, and Delgado-Blas (2015) described four new species from the Grand Caribbean Region.

In Australia, Blake & Kudenov (1978) reported *P. steenstrupi* from New South Wales and Victoria, and described two new species, *P. australiensis* and *P. queenslandica*, from Queensland. Hutchings & Rainer (1979) described a new species, *P. multicristata*, from New South Wales, and Wilson (1990) described three new species, members of the group, *P. coorilla*, *P. kulin*, and *P. nirripa*, from south-eastern Australia. Three new species, *P. anneae* n. sp., *P. lylei* n. sp. and *P. cooki* n. sp., with the same arrangement of branchiae as in *P. steenstrupi* are described in the present paper, thus making total number of species in the group 41. No identification key for the whole group is provided.

*Prionospio anneae* n. sp. belongs to the *P. steenstrupi* group and is characterized by having large median eyes, dorsal crest on chaetiger 6, hooks in neuropodia from chaetigers 8–9 and in notopodia from chaetigers 28–39, and inferior capillaries present in hook-bearing neuropodia instead of sabre chaetae. A low dorsal crest on chaetiger 6 is also present in only one other member of the *P. steenstrupi* group, *P. marsupialia* Blake, 1996 which differs from most of those species by having inter-neuropodial pouches. Inferior capillaries but not sabre chaetae are also present in neuropodia of *P. perkinsi* Maciolek, 1985 and *P. cerastae* n. sp. described below. These two species are, however, not members of the *P. steenstrupi* group and have an arrangement of pinnate branchiae different from *P. anneae* n. sp.

**Etymology.** The species is named in honour of Dr Anne Hoggett, a co-director (with her husband Dr Lyle Vail) of the Lizard Island Research Station, an avid enthusiast of marine biology and coral reef protection.

Habitat. Adult P. anneae n. sp. were found in coral sand and rubble at 5-16 m depth.

Distribution. Australia, Queensland, Great Barrier Reef.

#### Prionospio aucklandica Augener, 1923

(Fig. 11)

Prionospio aucklandica Augener, 1923: 69–70, fig. 24; 1926: 158–159, fig. 1; Wilson 1990: 247. Prionospio (Aquilaspio) aucklandica.—Blake & Kudenov 1978: 221–222, fig. 25 b–g. Aquilaspio aucklandica.—Foster 1971 (Part.): 106; Hutchings & Turvey 1984: 8–9.

**Material examined. Queensland:** AM W.45236, MI QLD 2330a (1); MIMB 28117, MI QLD 2330a (1); AM W.47866, MI QLD 2373 (6); MIMB 28118, MI QLD 2373 (4); AM W.45237, MI QLD 2410 (1); AM W.45238, MI QLD 2431 (1); AM W.45509, MI QLD 2435 (1); AM W.47867, MI QLD 2447 (1).

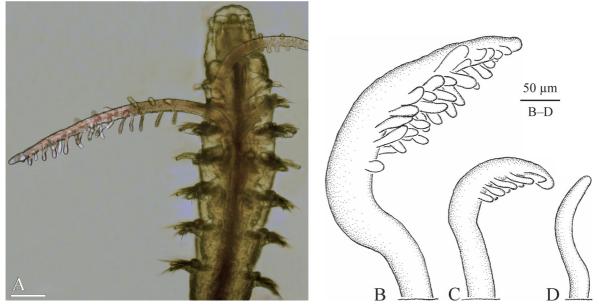
**Adult morphology.** Up to 16 mm long, 0.4 mm wide for 100 chaetigers. Pigmentation in life absent. Prostomium narrow, rounded anteriorly, extending posteriorly to end of chaetiger 1 as a prominent caruncle (Fig. 11A); posterior part of caruncle pressed into anterior part of chaetiger 2 towards level of nototroch, thus caruncle appearing as extending until middle of chaetiger 2. Small knobs with short non-motile cilia present on frontal and fronto-lateral edges of prostomium. Occipital antenna absent. Two pairs of small red eyes arranged trapezoidally; lateral eyes situated anteriorly and set wider apart, slightly larger than median eyes. Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming prominent ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and with narrow longitudinal band of cilia running on outer fronto-lateral side along frontal groove on distal half; cilia of inner transverse bands beating towards distal end of palp, while cilia of outer longitudinal band beating towards frontal groove.

Chaetiger 1 with short capillaries in neuropodia and postchaetal lamellae in both rami; notopodial postchaetal lamellae fused to posterior dorsal parts of peristomium forming ear-shaped structures; notochaetae absent. Notopodial lamellae of chaetigers 2–4 triangular, small on chaetiger 2, largest on chaetiger 4; lamellae smaller and rounded on succeeding chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 rounded to pointed and elongated ventrally. Dorsal crests, lateral pouches and ventral flaps absent.

Sabre chaetae in neuropodia from chaetiger 10, 1-2 in a tuft, with narrow wing and fine granulation on distal half of shaft.

Hooks in notopodia from chaetigers 23–38, 1–2 in a group among capillaries. Hooks in neuropodia from chaetigers 16–21, up to five in a series, accompanied by alternating capillaries and inferior sabre chaetae throughout. Hooks with three pairs of small upper teeth arranged in two vertical rows above main fang, with inner and outer hoods; shaft slightly curved.

Three pairs of pinnate branchiae on chaetigers 2–4 in adults; branchiae of chaetiger 2 up to three times longer than those of chaetiger 3; branchiae of chaetigers 4 1.5 times shorter than those on chaetiger 3; small individuals with two pairs of pinnate branchiae on chaetigers 2 and 3; median-sized individuals with three pairs of branchiae of which first and second pairs pinnate and third pair smooth, apinnate (Fig. 11B–D). All branchiae cylindrical, with longitudinal bands of cilia along inner and outer sides; flattened digitiform pinnae regularly arranged along lateral and posterior sides in 2–5 rows (Fig. 11A). Afferent and efferent branchial blood vessels interconnected by circular capillaries which forming loops inside branchial pinnae.



**FIGURE 11.** *Prionospio aucklandica*. A—AM W.45237; B–D—AM W.47866. A. Anterior end, dorsal view; B–D. Set of branchiae of a median-sized individual; B. Branchium of chaetiger 2, lateral view; C. Branchium of chaetiger 3, lateral view; D. Branchium of chaetiger 4, lateral view. Scale bar: A—100 μm.

Nototrochs with short cilia present between branchial bases on chaetigers 2 and 3. No other ciliation on chaetigers. Pygidium with thin, long middorsal cirrus and one pair of short and thick ventral cirri; all cirri bearing long non-motile sensory cilia.

Oesophagus extending through 6–8 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Heart body up to 20  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 through chaetigers 11–14. Blood red, without globules or other elements.

Nephridia in chaetigers 4–6, greenish in life.

**Reproduction.** All individuals of *P. aucklandica* collected around Lizard Island Group in August 2013 were immature.

**Remarks.** *Prionospio aucklandica* was originally described from Port Ross, Auckland Island, New Zealand by Augener (1923, 1926). The only two types of the species have never been re-described and were apparently lost. The most characteristic features of the species reported by Augener (1923, 1926) included three pairs of pinnate branchiae on chaetigers 2–4, sabre chaetae from chaetiger 10 and hooded hooks in neuropodia from chaetiger 19. Foster (1971) noticed that similar features were also present in *P. krusadensis* described from Krusadai Island, India by Fauvel (1929) and considered the latter species to be a junior synonym of *Aquilaspio aucklandica*<sup>1</sup>.

Blake & Kudenov (1978) identified *Prionospio (Aquilaspio) aucklandica* for the first time from Australia: New South Wales and Victoria. They reported that worms had notochaetae on chaetiger 1 and dorsal crest on chaetiger 7. Hutchings & Turvey (1984) reported *Aquilaspio aucklandica* from South Australia and noticed ventrally acuminate neuropodial lamellae of chaetiger 2, and absence of notochaetae on chaetiger 1 and dorsal crest on chaetiger 7. Wilson (1990) reported *Prionospio aucklandica* from Western Australia and noticed that his material agreed closely with the description by Hutchings & Turvey (1984). He also re-examined Blake & Kudenov's material and confirmed the absence of dorsal crests in those specimens.

Foster (1971) established a new genus Aquilaspio to encompass Prionospio members with two to four pairs of only pinnate branchiae beginning from chaetiger 2. The taxon was treated as genus or a subgenus by following authors but Wilson (1990) and Sigvaldadóttir (1998) placed those species back into Prionospio sensu lato (see above Remarks to the Prionospio sensu lato section). In the absence of a phylogenetic hypothesis about relationships of the Prionospio members and support of monophyly of Aquilaspio, it would be however practical to recognize non-taxonomic groups of species based on shared simple diagnostic characters. One of those groups may include Prionospio members with three pairs of only pinnate branchiae beginning from chaetiger 2 and be referred to as the Prionospio aucklandica group of species.

*Prionospio* with three pairs of pinnate branchiae from Lizard Island fit the descriptions of *P. aucklandica* by Hutchings & Turvey (1984) and Wilson (1990) and are referred to this species. They are characterized by two pairs of small eyes, three pairs of pinnate branchiae on chaetigers 2–4, sabre chaetae consistently starting from chaetiger 10, and by the absence of dorsal crests, folds and lateral pouches. Conspecificity of worms with three pairs of only pinnate branchiae from Auckland Island, New Zealand, Australia and Krusadai Island, India, should be verified in a future study.

Habitat. In this study, adult P. aucklandica were found in coral sand and rubble at 6–16 m depth.

**Distribution.** Auckland Island, New Zealand; possibly all around Australia. This is the first report of *P. aucklandica* from Queensland.

#### Prionospio cerastae n. sp.

(Figs 12-14)

**Type material. Queensland:** Holotype: AM W.47463, MI QLD 2379. Paratypes: AM W.45267, MI QLD 2365 (1); AM W.45268, MI QLD 2373 (4); AM W.45270, MI QLD 2410 (1); AM W.45269, MI QLD 2379 (3); MIMB 28119, MI QLD 2379 (2).

**Adult morphology.** Up to 7 mm long, 0.28 mm wide for 60 chaetigers. Cuticle and epithelium thin, worms extremely fragile and break easily during handling and fixation. Pigmentation in life absent. Prostomium with one pair of long, pointed fronto-lateral horns (Figs 12A, B, D, F, 14A), extending posteriorly to middle of chaetiger 1 as a low caruncle. Occipital antenna absent. Two pairs of small red eyes arranged trapezoidally (Fig. 12B). Nuchal organs U-shaped ciliary bands on sides of caruncle, posteriorly extending almost to end of chaetiger 1. Peristomium small, not forming dorso-lateral wings. Palps as long as 15–20 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and narrow longitudinal band of cilia running on outer fronto-lateral side along frontal groove on distal half; cilia of inner transverse bands beating towards distal end of palp, while cilia of outer longitudinal band beating towards frontal groove.

Chaetiger 1 with capillaries and postchaetal lamellae in both rami; notopodial lamellae large, flat, semicircular; neuropodial postchaetal lamellae with lower part rounded and directed ventrally (Fig. 14A). Notopodial postchaetal lamellae of chaetiger 2 and succeeding chaetigers leaf-like, large on branchiate chaetigers, gradually diminishing in size on succeeding chaetigers. Neuropodial postchaetal lamellae of chaetiger 2 and succeeding chaetigers semi-oval, elongated posteriorly (Fig. 14A). Notopodial lamellae of middle chaetigers with large glandular cells with granular content (Fig. 13A). Dorsal crests, folds, lateral pouches and ventral flaps absent.

Hooks in notopodia from chaetigers 12–30, up to three in a series among capillaries. Hooks in neuropodia from chaetigers 10–15, up to five in a series, accompanied by 1–2 inferior capillaries and 2–3 alternating capillaries throughout. Hooks with only outer hood, with main fang surmounted by five apical teeth comprising two pairs of small teeth situated in two vertical rows, and one smaller superior median tooth; upper part of shaft characteristically bent in middle (Fig. 14C–G). In lateral and frontal views, hooks appearing tridentate (Figs 13B, C, 14C, D). Sabre chaetae absent in neuropodia.

Four pairs of branchiae on chaetigers 2–5 (Figs 12A, C, 14A); those on chaetigers 2–4 apinnate, flattened, with surfaces oriented perpendicular to body axis, similar in length, up to two times as long as notopodial lamellae. Branchiae on chaetiger 5 slightly flattened to cylindrical, slightly longer than branchiae on previous chaetigers, each with up to 15 pairs of digitiform pinnules arranged on inner lateral and posterior sides; short apinnate branchiae on this chaetiger in some large individuals probably resulted from regenerating after occasional lost. Each branchia with longitudinal bands of cilia along inner and outer edges. Afferent and efferent branchial blood vessels interconnected by numerous radial capillaries giving branchiae annulate appearance; radial capillaries forming loops inside pinnae in fourth pair of branchiae.

Short nototrochs present on chaetigers 2–5, each composed of one transverse row of 4–6 ciliated cells. Transverse and longitudinal intersegmental ciliation absent.

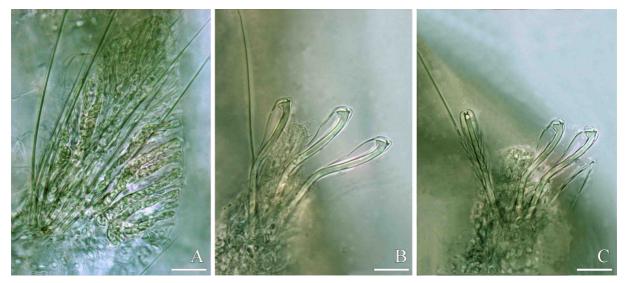
Pygidium with one thin middorsal cirrus and one pair of short fleshy ventral cirri or lappets, all bearing numerous non-motile sensory cirri up to 35  $\mu$ m long (Fig. 14B). Middorsal cirrus often broken during handling and fixation (Fig. 12F).



**FIGURE 12.** *Prionospio cerastae* n. sp. A–F—AM W.45269. A. Anterior end in dorsal view, showing branchiae on chaetigers 2–5; B. Anterior end in dorsal view, showing eyes and fronto-lateral horns on prostomium; C. Chaetigers 3–6 in dorsal view, showing pinnate branchiae on chaetiger 5; D. Anterior end in dorsal view; E. Anterior end in ventral view; F. Posterior end in dorsal view, showing two short ventral bulbs, middorsal cirrus missing. Scale bars: A–C, E, F—50 µm. D—100 µm.

Oesophagus extending through 6–7 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 11  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to chaetigers 9–10. Blood red, without globules or other elements.



**FIGURE 13.** *Prionospio cerastae* n. sp. A–C—AM W.45267. A. Notopodium of chaetiger 11, showing long glandular cells with granular content in postchaetal lamella; B. Left notopodium from middle chaetiger in lateral view; C. Left neuropodium from posterior chaetiger in lateral view. Scale bars: A–C—100 µm.

Nephridia in chaetigers 4-6, greenish in life.

**Reproduction.** *Prionospio cerastae* n. sp. is gonochoristic. Both in females and males gametes develop from chaetigers 12–13 to chaetigers 36–40. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. Intraovarian oocytes were up to 110  $\mu$ m in diameter, with germinal vesicle about 50  $\mu$ m and single nucleolus 17  $\mu$ m in diameter. Oocyte envelope is about 1  $\mu$ m thick. Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3  $\mu$ m in diameter, spherical mitochondria probably four in number, and a long flagellum.

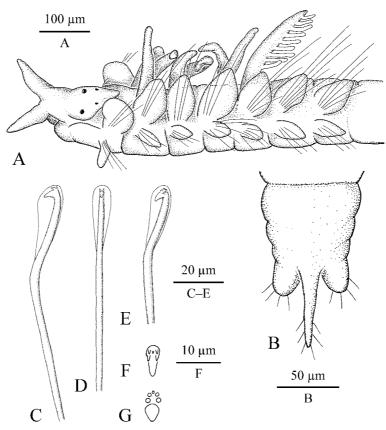
**Remarks.** Adult *P. cerastae* n. sp. are characterized by the pair of long fronto-lateral horns on the prostomium, two pairs of small eyes, chaetiger 1 with large semicircular notopodial postchaetal lamellae and elongated ventrally directed semi-oval neuropodial postchaetal lamellae, apinnate branchiae on chaetigers 2–4 and pinnate branchiae on chaetiger 5, large glandular cells with granular content in notopodial lamellae of middle chaetigers, hooks with main fang surmounted by five apical teeth, inferior capillaries instead of sabre chaetae in hook-bearing neuropodia, and three pairs of excretory nephridia in chaetigers 4–6. They share short U-shaped nuchal organs, four pairs of pinnate and apinnate branchiae on anterior chaetigers, hooks in both rami in parapodia, and three-cirrate pygidium with members of *Prionospio sensu lato* and are therefore referred to this group.

Adult *P. cerastae* n. sp. are unique among *Prionospio* in having long fronto-lateral horns on the prostomium. Two rounded fronto-lateral "horns", actually short extensions, are present on the prostomium in *P. cornuta* Hylleberg & Nateewathana, 1991 from the Andaman Sea. Adults of the latter species differ from *P. cerastae* n. sp. in having pinnate branchiae on chaetigers 2 and 5, and smooth, robust flattened branchiae on chaetigers 3 and 4, dorsal membranous folds on chaetigers 10–37, multidentate hooks, and sabre chaetae in neuropodia from chaetiger 12 onwards.

By the characteristically bent shaft in hooded hooks, and the presence of glandular cells in postchaetal lamellae, adult *P. cerastae* n. sp. appear similar to adults of *Aonides*.

**Etymology.** The species name refers to one of the characteristic features of adults, the presence of long and pointed fronto-lateral horns on the prostomium. The Latin word *cerastes* (horned) is derived from the Greek word keras, κέρας (horn).

**Habitat.** Adult *Prionospio cerastae* n. sp. were found in fine coral sand at 5–10 m depth. **Distribution.** Australia, Queensland, Great Barrier Reef.



**FIGURE 14.** *Prionospio cerastae* n. sp. A, C–F—AM W.45267; B—AM W.45269. A. Anterior end, left lateral view; B. Posterior end, dorsal view; C–G. Hooded hook morphology; C. Hook in lateral view with only two upper teeth visible above main fang; D. Hook in frontal view with only two upper teeth visible above main fang; E. Hook in fronto-lateral view, showing one pair of upper teeth and three superior teeth above main fang; F. Same from above; G. Schematic presentation of hook dentition.

## *Prionospio cooki* n. sp. (Fig. 15)

**Type material. Queensland:** Holotype: AM W.45275, MI QLD 2379. Paratypes: AM W.45276, MI QLD 2385 (3). Adult morphology. Largest individual intact holotype about 20 mm long, 0.5 mm wide for 80 chaetigers with caruncle extending to end of chaetiger 4 (Fig. 15A) (16 anterior chaetigers of the holotype deposited as AM W.45275, while the posterior chaetigers fixed in ethanol to be used in molecular analysis). There paratypes (AM W.45276) comprising 22-chaetiger anterior fragment of a big worm 0.7 mm wide with caruncle extending to end of chaetiger 4 (Fig. 15B), 60-chaetiger complete individual 0.35 mm wide with caruncle to end of chaetiger 3, and 16-chaetiger anterior fragment of a small worm about 0.3 mm wide with caruncle to end of chaetiger 3. All paratypes with branchiae missing but branchial scars present on chaetigers 2–5.

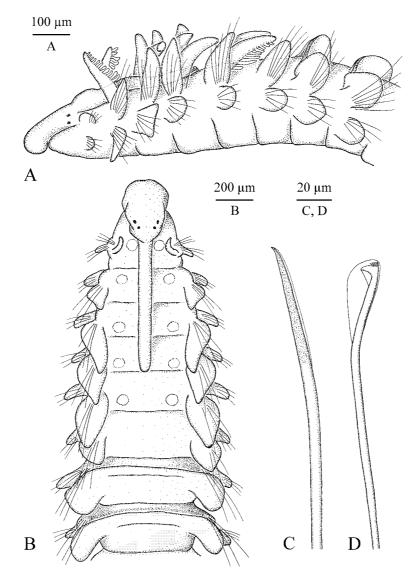
Pigmentation in life absent. Prostomium broadly-rounded anteriorly, extending posteriorly to end of chaetiger 4 as a distinct caruncle, shorter in small individuals. Small knobs with short non-motile cilia present on frontal and fronto-lateral edges of prostomium. Occipital antenna absent. Two pairs of small red eyes present (Fig. 15A, B). Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and short compound motile cilia on fronto-lateral surfaces along frontal groove; cilia of transverse bands beating towards distal end of palp, while compound fronto-lateral cilia beating perpendicular palp axis towards frontal groove.

Chaetiger 1 with capillaries and lamellae in both rami; notopodial postchaetal lamellae fused to posterior

dorsal parts of peristomium forming ear-shaped structures. Notopodial lamellae of chaetigers 2–5 largest, triangular, gradually becoming smaller and rounded on following chaetigers. Capillaries thick, with fine granulation in 10–15 anterior chaetigers, becoming thinner and smooth on succeeding chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 acuminate and elongated ventrally. Neuropodial lamellae of chaetiger 3 trapezoidal, from chaetiger 4 onwards rounded, semicircular, diminishing in size on succeeding chaetigers.

Low dorsal crests present from chaetiger 7 on a series of succeeding chaetigers (Fig. 15B), at least to chaetiger 22, gradually diminishing in height posteriorly. Lateral pouches and ventral flaps absent.

Sabre chaetae in neuropodia from chaetiger 10, one in a group, with narrow limbation and fine dense granulation on distal end of shaft (Fig. 15C). Sabre chaetae large in chaetiger 12, gradually diminishing in size in succeeding chaetigers.



**FIGURE 15.** *Prionospio cooki* n. sp. A, C, D—AM W.45249 (holotype); B—AM W.45276. A. Anterior end, left lateral view; B. Anterior end, dorsal view; C, D. Neurochaetae from chaetiger 16; C. Inferior sabre chaeta; D. Multidentate hooded hook.

Hooks in notopodia from about chaetiger 30, up to five in a series among capillaries. Hooks in neuropodia from chaetigers 12–14 (in holotype three hooks present in chaetiger 14 and seven hooks in each of chaetigers 15 and 16), up to eight in a series, accompanied by inferior sabre chaetae and alternating capillaries throughout. Alternating capillaries thin, with narrow wing in anterior neuropodia, gradually becoming alimbate in posterior chaetigers, 2–3 times as long as hooks. Hooks with outer and small inner hoods, multidentate, with 4–6 pairs of small upper teeth arranged in two vertical rows above main fang; shaft slightly bent (Fig. 15D).

Four pairs of branchiae on chaetigers 2–5 almost equal in length and slightly longer than notopodial postchaetal lamellae; those on chaetigers 2 and 5 cylindrical, with numerous pinnae regularly arranged along lateral and posterior sides all along stem. Branchiae on chaetigers 3 and 4 apinnate, robust, flattened, with surfaces oriented perpendicular to body axis. Longitudinal bands of cilia running along inner and outer edges on each branchia; ciliation heavier on branchiae on chaetigers 3 and 4. Afferent and efferent branchial blood vessels interconnected by numerous radial capillaries which forming loops inside pinnae.

Nototrochs present between branchial bases on chaetigers 3–5. Dorso-lateral longitudinal ciliation present on chaetigers 3–6 as short bands of dense cilia extending between successive notopodia.

Pygidium with one long middorsal cirrus and a pair of short ventral cirri; all cirri bearing non-motile sensory cilia.

Oesophagus extending through 6–10 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 20  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to chaetigers 9–13. Blood red, without globules or other elements.

Nephridia in chaetigers 4-6, greenish in life.

**Reproduction**. *Prionospio cooki* n. sp. is gonochoristic. In a female (holotype) and a male (paratype) gametes are present from chaetiger 13 onwards. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. Intraovarian oocytes were up to 115  $\mu$ m in diameter, with germinal vesicle about 50  $\mu$ m and single nucleolus 20  $\mu$ m in diameter. Oocyte envelope is 2–3  $\mu$ m thick. Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3  $\mu$ m in diameter, spherical mitochondria probably four in number, and a long flagellum.

**Remarks.** *Prionospio cooki* n. sp. belongs to the *P. steenstrupi* group (see above Remarks for *P. anneae* n. sp.) and is characterized by small red eyes, long caruncle extending to end of chaetiger 4, sabre chaetae in neuropodia from chaetiger 10, multidentate hooks in notopodia from around chaetiger 30 and in neuropodia from chaetigers 12–14, and gametes developing from chaetiger 13 onwards. Of the species of *Prionospio* occurring in Australian waters, the only other species with a caruncle extending over chaetiger 4 is *P. paucipinnulata* originally described from Port Phillip Bay, Victoria by Blake & Kudenov (1978). This species however has large median eyes, large dorsal crest on chaetiger 7, and different arrangement of pinnate branchiae (see below comments on this species).

Adult *P. cooki* n. sp. appear similar to *P. kulin* and *P. multicristata* in the shape of branchiae and neuropodial postchaetal lamellae on anterior chaetigers (with elongated acuminate lower part in chaetiger 2, trapezoidal in chaetiger 3, and rounded, semicircular from chaetiger 4 onwards), moderate dorsal crest on chaetiger 7 and lower crests on a series of succeeding chaetigers, arrangement of sabre chaetae and hooks, and hook dentition. They differ, however, in that *P. cooki* n. sp. has small eyes, caruncle extending to end of chaetiger 4, and gametes develop from chaetiger 13, whereas *P. multicristata* and *P. kulin* have large crescent-shaped eyes, gametes from chaetiger 12, and caruncle over chaetiger 3 and chaetiger 2 respectively.

**Etymology.** The species is named in honour of James Cook, a British explorer, navigator, cartographer, and captain in the Royal Navy who made three voyages to the Pacific Ocean. During the first voyage (1768–71) on the HMS *Endeavour*, on August 11, 1770, Cook climbed an island's summit to find a way through the maze of reefs in the Great Barrier Reef (Beaglehole 1968; Banks 2008). The only land animals on the island were lizards and Cook named the island Lizard Island. The opening through the reef was found and is now called Cook's Passage, and the Lizard Island's summit has since been called Cook's Look. The Cook's Passage (14.517°S, 145.567°E, the HMS *Endeavour* entered the Pacific Ocean through the Passage on August 13, 1770) is located north, next to the Yonge Reef, the type locality of *P. cooki* n. sp. (collected on the reef by diving on August 17, 2013).

**Habitat.** Adult *P. cooki* n. sp. were found off Yonge Reef, at the edge of the Great Barrier Reef in coral sand at 3–10 m depth.

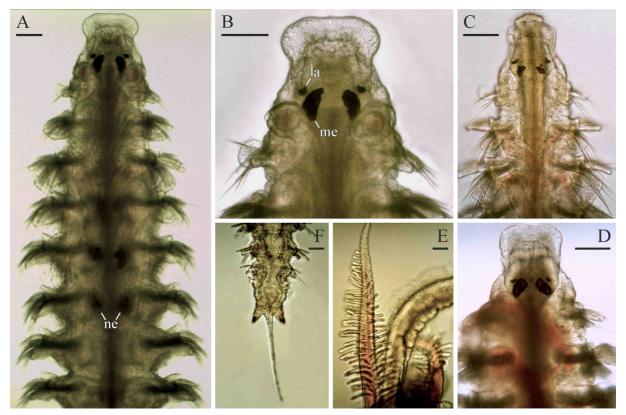
Distribution. Australia: Queensland, Great Barrier Reef.

#### Prionospio kulin Wilson, 1990

(Figs 16, 17)

Prionospio kulin Wilson, 1990: 253-256, figs 24-33.

**Material examined. Queensland:** AM W.45248, MI QLD 2330b (2); AM W.45249, MI QLD 2360; MIMB 28120, MI QLD 2360 (1); AM W.47865, MI QLD 2373 (12); MIMB 28121, MI QLD 2373 (7); AM W.45250, MI QLD 2374 (2); AM W.45254, MI QLD 2410 (2); MIMB 28122, MI QLD 2410 (2); AM W.45255, MI QLD 2410 (4); MIMB 28123, MI QLD 2410 (4); AM W.47461, MI QLD 2391 (1); AM W.45233, MI QLD 2405 (1); AM W.45257, MI QLD 2439 (1); AM W.45258, MI QLD 2440 (1); MIMB 28124, MI QLD 2440 (1); AM W.45507, MI QLD 2447 (2); AM W.45511, MI QLD 2447 (1); AM W.45252, MI QLD 2382 (1). Northern Territory: AM W.47462 (4), MIMB 28125 (3), Bullocky Point, Fannie Bay, Darwin, 12.4356°S, 130.8323°E, muddy sand intertidal, 3 Sep 2013; MIMB 28126 (1), same locality, 5 Sep 2013.



**FIGURE 16.** *Prionospio kulin.* A, B—AM W.45248; C—AM W.45250; D–F—MIMB 28125. A–D. Anterior ends, dorsal view, showing various shapes of prostomium and eyes; E. Branchia of chaetiger 2; F. Posterior end with pygidium, dorsal view. Abbreviations: la—lateral eyes, me—median eyes, ne—nephridia. Scale bars: A–C—100 µm; D–F—50 µm.

**Adult morphology.** Up to 32 mm long, 0.5 mm wide for 100 chaetigers. Pigmentation in life absent. Prostomium bell-shaped, wide anteriorly, extending posteriorly to end of chaetiger 2 as a distinct caruncle (Fig. 16A). Seven small knobs with short non-motile sensory cilia present on frontal and fronto-lateral edges of prostomium. Occipital antenna absent. Two pairs of eyes arranged trapezoidally; lateral eyes small, situated anteriorly and set wider apart; median eyes small in individuals up to 0.2 mm wide, large, crescent-shaped in larger worms (Fig. 16B–D); eyes red in living and fixed specimens. Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming moderate ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and short compound motile cilia on fronto-lateral surfaces along frontal groove (Fig. 17A, B); cilia of transverse bands beating towards distal end of palp, while compound fronto-lateral cilia beating perpendicular palp axis towards frontal groove. Longitudinal band of cilia not observed on outer fronto-lateral side along frontal groove.



**FIGURE 17.** *Prionospio kulin.* A, B, D–F–MIMB 28125; C–AM W.45255; G–I–AM W.45249. A. Left palp, inner side, with short transverse ciliary bands; B. Same, frontal side, showing longitudinal ciliated groove; C. Chaetigers 6–9, dorsal view, showing soft heart body inside main dorsal blood vessel; D, E. Heart body inside main dorsal blood vessel; D. Main dorsal blood vessel partly contracted; E. Main dorsal blood vessel open; F. Chaetigers 7–14, dorsal view, showing prominent transverse crest on chaetiger 7 and lower crests on succeeding chaetigers; G. Inferior sabre chaeta from a median neuropodium; H. Multidentate hooded hooks from a posterior neuropodium; I. Developed coelomic oocyte with soft envelope. Abbreviations: cb–ciliary bands, dc–dorsal crests, dv–main dorsal blood vessel, gv–germinal vesicle, hb–heart body, nl–nucleolus, ve–vesicles, depressions in oocyte envelope. Scale bars: A, F–200 μm; B–E–50 μm; G–I–20 μm.

Chaetiger 1 with short capillaries and small postchaetal lamellae in both rami; notopodial lamellae fused to posterior dorsal parts of peristomium forming moderate ear-shaped structures. Notopodial lamellae of chaetigers 3–5 largest, triangular, gradually becoming smaller and rounded on succeeding chaetigers. Capillaries thick, with fine granulation in 10–15 anterior chaetigers, becoming thinner and smooth in succeeding chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 acuminate and elongated ventrally. Neuropodial lamellae of chaetiger 3 trapezoidal, from chaetiger 4 onwards rounded, semicircular, diminishing in size on posterior chaetigers.

Moderate dorsal crest present on chaetiger 7 and low crests present from chaetiger 8 to chaetigers 15–24, gradually diminishing in height on posterior chaetigers (Fig. 17F). Lateral pouches and ventral flaps absent.

Sabre chaetae in neuropodia from chaetiger 10, usually one, occasionally two in a group in first two-three chaetigers; large in chaetiger 10, gradually diminishing in size in succeeding chaetigers. Sabre chaetae with narrow limbation and fine dense granulation on distal end of shaft (Fig. 17G).

Hooks in notopodia from chaetigers 24–51, up to six in a series among capillaries. Hooks in neuropodia from chaetigers 11–18, up to 11 in a series, accompanied by inferior sabre chaetae and alternating capillaries throughout. Alternating capillaries thin, with narrow wing in anterior neuropodia, gradually becoming alimbate in posterior chaetigers, 2–3 times as long as hooks. Hooks with outer and small inner hoods, multidentate, with 2–6 pairs of small upper teeth situated in two vertical rows above main fang; shaft slightly bent (Fig. 17H). Hooks in anterior neuropodia of small individuals with 2–3 pairs of small upper teeth above main fang; hooks in large individuals with 4–6 pairs of upper teeth.

Four pairs of branchiae on chaetigers 2–5; those on chaetigers 2 and 5 cylindrical, with numerous long digitiform pinnae regularly arranged on lateral and posterior sides; those on chaetigers 3 and 4 apinnate, stout flattened triangles, with surfaces oriented perpendicular to body axis, similar in length to notopodial lamellae. Branchiae on chaetiger 2 up to two times as long as those on chaetigers 3 and 4, with pinnae arranged all along stem or leaving 1/5–1/6 distal tip free (Fig. 16E). Branchiae on chaetiger 5 longest, up to three times as long as those on chaetigers 3 and 4, in large individuals extending posteriorly to end of chaetiger 9, with 1/3–1/4 distal tip free from pinnae. Longitudinal bands of cilia running on inner and outer edges on each branchia; ciliation heavier on branchiae on chaetigers 3 and 4. Afferent and efferent branchial blood vessels interconnected by numerous radial capillaries which forming loops inside pinnae.

Nototrochs present between branchial bases on chaetigers 3 and 4. Short transverse curved band of short cilia present between chaetigers 3 and 4. Dorso-lateral longitudinal ciliation present on chaetigers 3–6 as short bands of dense cilia extending between successive notopodia.

Pygidium with one long middorsal cirrus and a pair of short ventral cirri; all cirri bearing non-motile sensory cilia (Fig. 16F).

Oesophagus extending through 6–10 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 22  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to chaetigers 9–13 (Fig. 17C–E). Blood red, without globules or other elements.

Nephridia in chaetigers 4–6, greenish in life (Fig. 16A).

**Reproduction.** *Prionospio kulin* is gonochoristic. Both in female and males gametes develop from chaetiger 12 to chaetigers 41–72. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. One female (AM W.45249) had intraovarian oocytes up to 100  $\mu$ m in diameter, with germinal vesicle about 50  $\mu$ m and single nucleolus 30  $\mu$ m in diameter (Fig. 171). Oocyte envelope is 2–3  $\mu$ m thick, with rugose external surface and about 10 depressions (vesicles) arranged in a circle; each vesicle is about 10  $\mu$ m in diameter and 8–9  $\mu$ m deep, with external opening about 5  $\mu$ m in diameter. Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3  $\mu$ m in diameter, spherical mitochondria probably four in number, and a long flagellum.

**Remarks.** *Prionospio kulin* was originally described from Eastern Bass Strait by Wilson (1990). Worms were numerous and widespread in Bass Strait on a variety of sediments at 16–137 m depth, and a single record was off North Head, Sydney at 32 m. The species has not been reported since. The species was characterized by the caruncle extending back to end of chaetiger 2, large red median eyes, chaetiger 1 with capillaries in both rami, chaetiger 2 with prominent acuminate neuropodial lamellae elongated ventrally, pinnate branchiae on chaetigers 2 and 5, smooth branchiae on chaetigers 3 and 4, prominent dorsal crest on chaetiger 7 and low crests from chaetiger 8 to chaetigers 17–21, sabre chaetae in neuropodia from chaetiger 10, and hooded hooks with 4–5 pairs of upper teeth in notopodia from chaetigers 21–39 and in neuropodia from chaetigers 13–21.

*Prionospio* from around Lizard Island and Darwin appear similar to *P. kulin* and are herein referred to this species. Change of the dentition of hooks in ontogenesis, and oocytes with rugose vesiculate envelope are reported for the first time for *Prionospio*.

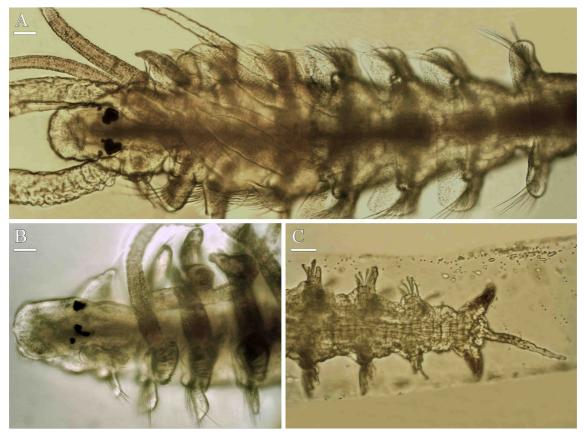
Habitat. In this study, adult *P. kulin* were found in fine coral sand and rubbles from intertidal to 21 m depth.

**Distribution.** Australia: Bass Strait, New South Wales, Queensland, Northern Territory. This is the first report of *P. kulin* from Queensland and Northern Territory.

*Prionospio lylei* n. sp. (Figs 18, 19)

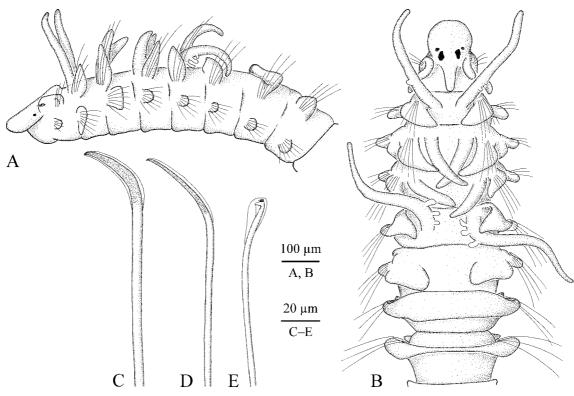
**Type material. Queensland:** Holotype: AM W.45260, MI QLD 2365. Paratypes: AM W.45263, MI QLD 2410 (1); AM W.45264, MI QLD 2440 (1); AM W.45261, MI QLD 2379 (2); AM W.45262, MI QLD 2382 (1).

**Adult morphology.** Largest complete individual, holotype, 14 mm long, 0.25 mm wide for 60 chaetigers. Pigmentation in life absent. Prostomium round anteriorly, extending posteriorly to end of chaetiger 1 as a prominent caruncle. Three small knobs with short non-motile sensory cilia present on frontal and fronto-lateral edges of prostomium. Occipital antenna absent. Two pairs of red eyes arranged trapezoidally comprising one pair of median eyes and one pair of lateral eyes situated anteriorly and set wider apart; median eyes small in small worms and very large, crescent-shaped in large individuals (Figs 18A, B, 19A, B). Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming moderate elevated ear-shaped structures. Palps as long as 5–10 chaetigers, with longitudinal frontal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and narrow longitudinal band of cilia running on outer fronto-lateral side along frontal groove on distal half of palp; cilia of transverse bands beating towards the distal end of palp, while cilia of longitudinal band beating towards frontal groove.



**FIGURE 18.** *Prionospio lylei* n. sp. A, C—AM W.45261; B—AM W.45262. A. Anterior end, dorsal view; B. Anterior end, dorso-lateral view; C. Posterior end, dorsal view. Scale bars: A–C—50 µm.

Chaetiger 1 with short capillaries and small postchaetal lamellae in both rami; notopodial lamellae fused to posterior dorsal parts of peristomium forming elevated ear-shaped structures; neuropodial postchaetal lamellae oval. Notopodial lamellae of chaetigers 3–5 largest, triangular, gradually becoming smaller and rounded on succeeding chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 acuminate and elongated ventrally. Neuropodial lamellae of chaetiger 3 trapezoidal, from chaetiger 4 onwards rounded, semicircular, diminishing in size on succeeding chaetigers (Fig. 19A).



**FIGURE 19.** *Prionospio lylei* n. sp. A—AM W.45263 (paratype); B–E—AM W.45260 (holotype). A. Anterior end, left lateral view; B. Anterior end, dorsal view; C. Sabre chaeta from neuropodium of chaetiger 10; D. Sabre chaeta from neuropodium of chaetiger 16; E. Multidentate hooded hook from neuropodium of chaetiger 10.

Dorsal crest on chaetiger 7 high (Figs 18A, 19A, B); notopodial postchaetal lamellae on succeeding chaetigers extended towards dorsal midline but not joined to form crests; low dorsal folds present from chaetiger 8 on 4–6 succeeding chaetigers in some individuals (on chaetiger 8 in holotype). Lateral pouches and ventral flaps absent.

Sabre chaetae in neuropodia from chaetiger 10, usually one, occasionally two in a group in first two-three neuropodia, thick, robust, with narrow limbation and fine granulation on distal end of shaft; chaetae largest in chaetiger 10, gradually diminishing in size on succeeding chaetigers towards midbody (Fig. 19C, D), then gradually increasing again.

Hooks in notopodia from chaetigers 22–38, up to five in a series among capillaries. Hooks in neuropodia from chaetigers 11–12, up to nine in a series, accompanied by inferior sabre chaetae and alternating capillaries throughout. Alternating capillaries 2–2.5 times as long as hooks, in anterior chaetigers slender, with narrow limbation, in posterior chaetigers hair-like, alimbate. Hooks multidentate, with 4–5 pairs of thin upper teeth arranged in two vertical rows above main fang, with inner and outer hoods; shaft slightly bent (Fig. 19E).

Four pairs of branchiae on chaetigers 2–5 (Figs 18A, 19A, B). Branchiae on chaetigers 2 and 5 cylindrical, similar in length to each other or chaetiger 5 pair longer, up to three times as long as notopodial lamellae. Branchiae of chaetiger 2 with 1–2 pairs of short pinnae (1 pair in holotype), apinnate in some individuals; branchiae of chaetiger 5 with 1–4 pairs of digitiform pinnae on low part (three pairs in holotype). Branchiae on chaetigers 3 and 4 apinnate, robust, flattened, with surface oriented perpendicular to body axis, similar in length or slightly longer than notopodial lamellae. Longitudinal bands of cilia running on inner and outer edges on each branchia; ciliation heavier on branchiae on chaetigers 3 and 4. Afferent and efferent blood vessels interconnected by numerous radial capillaries making also loops inside pinnules.

Nototrochs on chaetigers 2–5. Dorso-lateral longitudinal ciliation present on chaetigers 3–6 as short bands of dense cilia extending between successive notopodia.

Pygidium with long thin, transparent middorsal cirrus and one pair of short, thick and yellowish ventral cirri (Fig. 18C).

Oesophagus extending through 6–7 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Main dorsal vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 40  $\mu$ m in diameter present in main dorsal vessel from level of chaetigers 3–4 to chaetigers 8–9. Blood red, without globules or other elements.

Nephridia in chaetigers 4–6, greenish in life.

**Reproduction.** *Prionospio lylei* n. sp. is gonochoristic. Both in females and males gametes develop from chaetiger 11 to chaetigers 50–55. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3 µm in diameter, spherical mitochondria probably four in number, and a long flagellum.

Remarks. Prionospio lylei n. sp. belongs to the P. steenstrupi group (see above Remarks for P. anneae n. sp.) and is characterized by short caruncle extending to the end of chaetiger 1, large median eyes, dorsal crest only on chaetiger 7, hooks beginning in neuropodia from chaetigers 11–12 and in notopodia from chaetigers 22–38, and sabre chaetae in neuropodia invariably from chaetiger 10. Most members of the group have the caruncle extending to the end of chaetiger 2 or longer. Short caruncles extend to the end of chaetiger 1 in P. fallax Söderström, 1920, P. dubia Day, 1961, P. anuncata Fauchald, 1972, P. membranacea Imajima, 1990, P. oshimensis Imajima, 1990, P. variegata Imajima, 1990, and P. phuketensis Hylleberg & Nateewathana, 1991. Of these, only P. fallax and P. membranacea have single prominent dorsal crest on chaetiger 7. These two species also have large median eyes, ventrally pointed and elongated neuropodial lamellae on chaetiger 2, and sabre chaetae in neuropodia from chaetiger 10. Prionospio lylei n. sp. differs from P. membranacea in that adults of the latter species have numerous pinnae on the pinnate branchiae, and hooks beginning in neuropodia from chaetigers 13-16 and in notopodia from chaetigers 49-51. Prionospio lylei n. sp. appears most similar to P. fallax where adults have hooks beginning in neuropodia from chaetigers 10-13 and in notopodia from chaetigers 18-45. It differs, however, from the latter by having fewer numbers of pinnae on the branchiae. Remarkably, *P. fallax* was originally described from Sweden by Söderström (1920) (redescribed by Sigvaldadóttir & Mackie 1993) and later reported from Australia by Day & Hutchings (1979), Hartmann-Schröder (1979), and Hutchings & Rainer (1979). These records should be verified to confirm the presence of the species in the Australian waters.

**Etymology.** The species is named in honour of Dr Lyle Vail, a co-director (with his wife Dr Anne Hoggett) of the Lizard Island Research Station, an avid enthusiast of marine biology and coral reef protection.

Habitat. Adults of *P. lylei* n. sp. were found in coral sand and rubble at 6–21 m depth.

Distribution. Australia, Queensland, Great Barrier Reef.

#### Prionospio multicristata Hutchings & Rainer, 1979

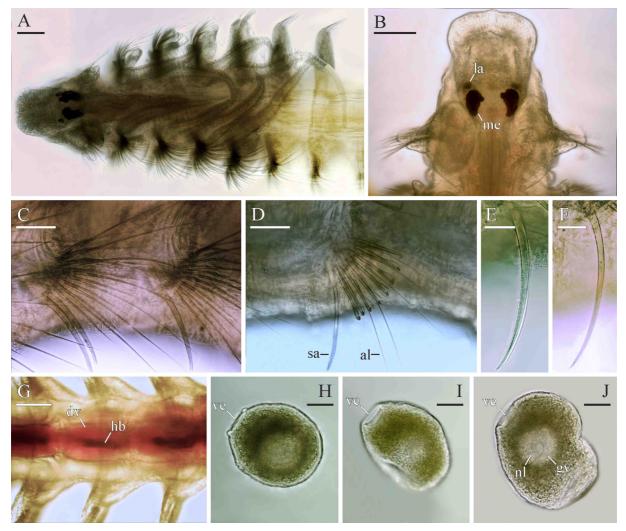
(Figs 20, 21)

*Prionospio multicristata* Hutchings & Rainer, 1979: 768–771, fig. 5; Hutchings & Turvey 1984: 11–12; Hutchings & Murray 1984: 60–61; Hartmann-Schröder 1982: 86–87, 1984: 36; Wilson 1990: 256.

**Material examined. Queensland:** AM W.45251, MI QLD 2391 (1); AM W.45256, MI QLD 2433 (2); MIMB 28127, MI QLD 2433 (1); AM W.45253, MI QLD 2408 (1); MIMB 28128, MI QLD 2408 (1); AM W.45234, MI QLD 2431 (11). Northern Territory: MIMB 28129 (1), Lake Alexander, Darwin, 12.41272°S, 130.83192°E, intertidal, muddy sand, 11 Sep 2013.

Adult morphology. Up to 20 mm long, 0.5 mm wide for 80 chaetigers. Pigmentation in life absent. Prostomium broadly-rounded anteriorly, extending posteriorly to end of chaetiger 3 as a distinct caruncle (Fig. 20A), shorter in small individuals. Small knobs with short non-motile sensory cilia present on frontal and frontolateral edges of prostomium. Occipital antenna absent. Two pairs of eyes arranged trapezoidally; lateral eyes small, set anteriorly and wider apart; median eyes each comprising small cup and a large, crescent-shaped spot composed of many spherical pigment globules (Figs 20B, 21A); eyes red in life but appearing black in formalin-fixed specimens. Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and short compound motile cilia on fronto-lateral surfaces along frontal groove; cilia of transverse bands beating towards distal end of palp, while compound fronto-lateral cilia beating perpendicular to palp axis towards frontal groove.

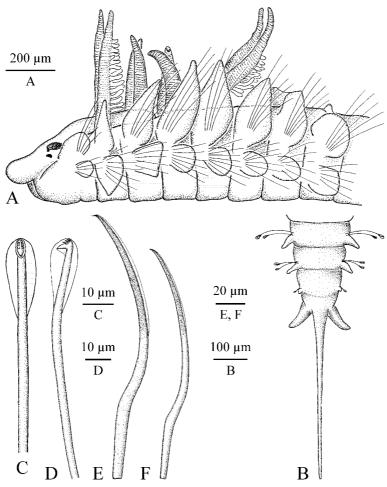
Chaetiger 1 with capillaries and small lamellae in both rami; notopodial postchaetal lamellae fused to posterior dorsal parts of peristomium forming ear-shaped structures. Notopodial lamellae of chaetigers 2–5 largest, triangular, gradually becoming smaller and rounded on succeeding chaetigers. Small prechaetal lamellae present in both rami of 10–15 anterior chaetigers. Capillaries thick, with fine granulation in 10–15 anterior chaetigers, becoming thinner and smooth on succeeding chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 acuminate and elongated ventrally (Fig. 21A). Neuropodial lamellae of chaetigers. The chaetiger 4 onwards lamellae rounded, semicircular, diminishing in size on posterior chaetigers.



**FIGURE 20.** *Prionospio multicristata.* A, C–G—AM W.45256; B—AM W.45251; H–J—MIMB 28129. A, B. Anterior end, dorsal view; C. Neuropodia of chaetigers 11 and 12, left lateral view; D. Neuropodium of chaetiger 21, left lateral view; E. Sabre chaeta from neuropodium of chaetiger 10; F. Sabre chaeta from neuropodium of chaetiger 15; G. Chaetigers 8–10 in dorsal view, showing soft heart body inside main dorsal blood vessel; H–J. Developed coelomic oocytes with soft envelope. Abbreviations: al—hair-like alimbate capillaries alternating with hooded hooks, dv—main dorsal blood vessel, gv—germinal vesicle, hb—heart body, la—lateral eye, me—median eye, nl—nucleolus, sa—sabre chaetae, ve—vesicles, depressions in oocyte envelope. Scale bars: A, B, G—100 μm; C, D—50 μm; E, F—20 μm; H–J—30 μm.

Moderate dorsal crest present on chaetiger 7; low dorsal crests present from chaetiger 8 to about chaetiger 30 (Fig. 21A); gradually diminishing in height posteriorly. Lateral pouches and ventral flaps absent.

Sabre chaetae in neuropodia consistently from chaetiger 10, one, occasionally two in a group, with narrow limbation and fine dense granulation on distal end of shaft. Sabre chaetae large in chaetiger 10, gradually diminishing in size in succeeding chaetigers (Figs 20C–F, 21E, F).



**FIGURE 21.** *Prionospio multicristata*. A–F—AM W.45256. A. Anterior end, left lateral view; B. Posterior end, dorsal view; C. Hooded hook from neuropodium of chaetiger 20, frontal view; D. Same, lateral view; E. Sabre chaeta from neuropodium of chaetiger 10; F. Sabre chaeta from neuropodium of chaetiger 15.

Hooks in notopodia from chaetigers 32–44, up to five in a series among capillaries. Hooks in neuropodia from chaetigers 14–16, up to ten in a series, accompanied by inferior sabre chaetae and alternating capillaries throughout (Fig. 20D). Alternating capillaries thin, about two times as long as hooks, with narrow limbation in anterior neuropodia, gradually becoming alimbate on posterior chaetigers. Hooks with outer and small inner hoods, multidentate, with 4–6 pairs of small upper teeth arranged in two vertical rows above main fang; shaft slightly bent (Fig. 21C, D). Younger hooks situated in lower parts of hook series in anterior neuropodia of small individuals with 2–3 pairs of small upper teeth above main fang.

Four pairs of branchiae on chaetigers 2–5; with those on chaetigers 2 and 5 cylindrical, almost equal in length or on chaetiger 5 slightly longer than on chaetiger 2, each as long as two-three chaetigers; pinnae regularly arranged along lateral and posterior sides leaving 1/4–1/3 distal tip free. Branchiae on chaetigers 3 and 4 apinnate, about 2/3 of length of pinnate branchiae, as long as 1.5–2 chaetigers, robust, flattened, with surfaces oriented perpendicular to body axis. Longitudinal bands of cilia running on inner and outer edges on each branchia; ciliation heavier on branchiae on chaetigers 3 and 4. Afferent and efferent branchial blood vessels interconnected by numerous radial capillaries which forming loops inside pinnae.

Nototrochs present between branchial bases on chaetigers 3 and 4. Short transverse curved band of short cilia present between chaetigers 3 and 4. Dorso-lateral longitudinal ciliation present on chaetigers 3–6 as short bands of dense cilia extending between successive notopodia.

Pygidium with one long middorsal cirrus and a pair of short ventral cirri, all bearing short non-motile sensory cilia (Fig. 21B).

Oesophagus extending through 6–11 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 20  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to chaetigers 9–12 (Fig. 20G). Blood red, without globules or other elements.

Nephridia in chaetigers 4–6, greenish in life.

**Reproduction.** *Prionospio multicristata* is gonochoristic. Both in females and males from around Lizard Island the gametes develop from chaetiger 12 to chaetigers 50–62. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. Intraovarian oocytes were up to 110  $\mu$ m in diameter, with germinal vesicle about 60  $\mu$ m and single nucleolus 20  $\mu$ m in diameter. Oocyte envelope is 2–3  $\mu$ m thick, with rugose external surface. One mature female off Darwin (MIMB 28129) has all morphological features same as specimens from Lizard Island but oocytes from chaetiger 15 onwards; the oocyte envelope has single semi-spherical depression 25–30  $\mu$ m in diameter and 15–20  $\mu$ m deep (Fig. 20H–J). Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3  $\mu$ m in diameter, spherical mitochondria probably four in number, and a long flagellum.

**Remarks.** *Prionospio multicristata* belongs to the *P. steenstrupi* group (see above Remarks for *P. anneae* n. sp.). It was originally described from Careel Bay, New South Wales, Australia by Hutchings & Rainer (1979). The species was characterized by the prostomium broadly-rounded anteriorly, black eyes in fixed specimens, with median eyes large, comma-shaped, caruncle extending to end of chaetiger 3, chaetiger 1 with capillaries in both rami, chaetiger 2 with prominent acuminate neuropodial lamellae elongated ventrally, moderate dorsal crest on chaetiger 7 and lower crests from chaetiger 8 to chaetigers 25–30, sabre chaetae in neuropodia from chaetiger 10, and hooded hooks with 5–6 pairs of upper teeth in notopodia from chaetigers 40–50 and in neuropodia from chaetiger 17. Hutchings & Turvey (1984) reported the species from South Australia. They did not describe the color of eyes but mentioned that the only specimen had caruncle to end of chaetiger 4. This caruncle appears longer than originally described in specimens from Careel Bay and also observed in specimens from Queensland. The record from South Australia should be verified.

*Prionospio* with black eyes from Lizard Island and Darwin appear identical to the original description of *P. multicristata* and are herein referred to this species. These worms also appear very similar to *P. kulin* in the shape of branchiae and neuropodial postchaetal lamellae on anterior chaetigers (with elongated acuminate lower part in chaetiger 2, trapezoidal in chaetiger 3, and rounded, semicircular from chaetiger 4 onwards), moderate dorsal crest on chaetiger 7 and lower crests on a series of succeeding chaetigers, arrangement of sabre chaetae and hooks, hook dentition and gametes starting from chaetiger 12. The two species occur together in some localities. Fixed adults of these species can be distinguished by the color of eyes, black in *P. multicristata* and red in *P. kulin*, and length of the caruncle, to the end of chaetiger 3 in *P. multicristata* and to the end of chaetiger 2 in *P. kulin*. Living small individuals of the two species have red eyes and short caruncles and appear similar to each other.

**Habitat.** In this study, adults of *P. multicristata* were found in fine coral sand from intertidal to 16 m depth. **Distribution.** Australia: New South Wales, Queensland, Northern Territory.

#### Prionospio cf. paucipinnulata Blake & Kudenov, 1978

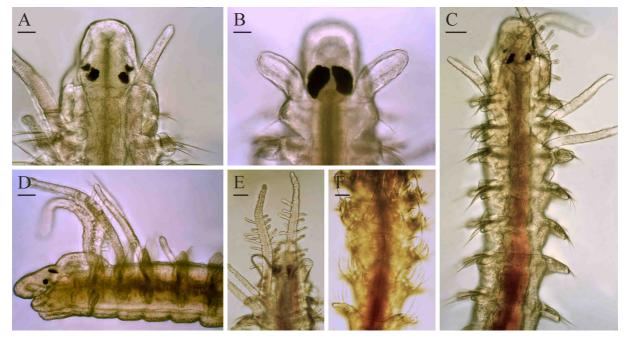
(Figs 22–24)

*Prionospio (Prionospio) paucipinnulata* Blake & Kudenov, 1978: 217–219, fig. 22. *Prionospio paucipinnulata.*—Hutchings & Murray, 1984: 61.

**Material examined. Queensland:** AM W.45239, MI QLD 2330a (12); AM W.45240, MI QLD 2357 (1); AM W.45241, MI QLD 2360 (1); AM W.45242, MI QLD 2365 (2); AM W.45243, MI QLD 2373 (6); AM W.45377, MI QLD 2391 (1); AM W.45244, MI QLD 2410 (2); AM W.45245, MI QLD 2410 (4); AM W.45246, MI QLD 2431 (1); AM W.45378, MI QLD 2440 (4); MIMB 28108, MI QLD 2440 (2).

**Adult morphology.** Up to 13 mm long, 0.3 mm wide for 60 chaetigers; smallest examined individual with 30 chaetigers. Pigmentation in life absent. Prostomium narrow, rounded anteriorly (Fig. 22A–C), extending posteriorly to end of chaetiger 4 as a low caruncle, shorter in small individuals (Fig. 23B). Five small knobs with short non-motile cilia present on frontal and fronto-lateral edges of prostomium. Occipital antenna absent. Two

pairs of eyes present, comprising one pair of small lateral eyes and one pair of median eyes; median eyes small to moderately large in 30–45-chaetiger immature individuals (Fig. 22A, D); in larger mature individuals, median eyes very large, overlapping lateral eyes (Fig. 22B); eyes red in life, appearing black in many formalin-fixed specimens. Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming moderate ear-shaped structures (Fig. 24A). Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and narrow longitudinal band of cilia running on outer fronto-lateral side along frontal groove on distal half of palp; cilia of inner transverse bands beating towards distal end of palp, while cilia of outer longitudinal band beating towards frontal groove.

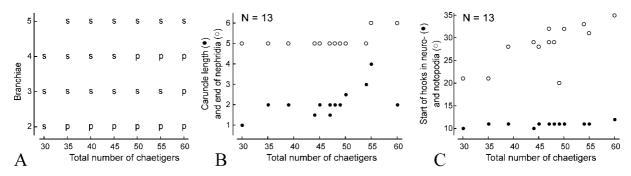


**FIGURE 22.** *Prionospio* cf. *paucipinnulata*. A, B—AM W.45239; C, D—AM W.45243; E, F—AM W.45247. A–C. Anterior ends, dorsal view, showing eyes of various shapes; D. Anterior end, left lateral view; E, Anterior end, dorsal view, showing branchiae with few pinnae on chaetiger 2 and apinnate branchiae on chaetigers 3 and 4; F. Chaetigers 4-8, dorsal view, showing apinnate branchiae on chaetiger 5 and prominent dorsal crest on chaetiger 7 overlapping chaetiger 6. Scale bars: A, B, D–F—50 µm; C—100 µm.

Chaetiger 1 with short capillaries and small postchaetal lamellae in both rami; notopodial postchaetal lamellae fused to posterior dorsal parts of peristomium forming moderate ear-shaped structures. Notopodial lamellae of chaetigers 3–5 largest, triangular; lamellae getting gradually smaller and rounded on succeeding chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 acuminate and elongated ventrally (Fig. 24A). Neuropodial lamellae of chaetiger 3 trapezoidal, from chaetiger 4 onwards lamellae rounded, semicircular, diminishing in size on posterior chaetigers (Fig. 24A).

Prominent semi-circular dorsal crest joining notopodial lamellae of chaetiger 7 (Fig. 24A), when oriented forward, crest overlapping chaetiger 6 and posterior half of chaetiger 5. Low dorsal crests present from chaetiger 8 to chaetigers 16–31 gradually diminishing in size on posterior chaetigers. Lateral pouches and ventral flaps absent. Sabre chaetae in neuropodia from chaetiger 10, one, occasionally two in a group; chaetae with narrow limbation and fine granulation on distal end (Fig. 24E).

Hooks in notopodia from chaetigers 20–35 (Fig. 23C), up to six in a series among capillaries. Hooks in neuropodia from chaetigers 10–14 (Fig. 23C), up to eight in a series, accompanied by inferior sabre chaetae and alternating capillaries throughout. Alternating capillaries thin, with narrow wing in anterior neuropodia, alimbate in posterior chaetigers, 2–3 times as long as hooks. Hooks with outer and small inner hoods, multidentate, with 4–5 pairs of small upper teeth arranged in two vertical rows above main fang; shaft slightly bent (Fig. 24D).



**FIGURE 23.** *Prionospio* cf. *paucipinnulata*. A. Relationships between shape of branchiae (smooth (s) or pinnate (p)) on a particular chaetiger (chaetigers 2–5) and total number of chaetigers in worm; B. Relationships between caruncle length (in chaetiger numbers) and total number of chaetigers in worm, and posterior position of excretory metanephridia (referring to number of the last chaetigers bearing nephridiopores) and total number of chaetigers in worm; C. Relationships between anterior position of hooks in neuro- and notopodia (in chaetiger numbers) and total number of chaetigers in worm.

Smallest 30-chaetiger individual with three pairs of smooth apinnate branchiae on chaetigers 2–4; individuals up to 45–50-chaetiger stage with pinnate branchiae on chaetiger 2 and smooth branchiae on chaetigers 3–5 (Fig. 24B); individuals with 50–55 chaetigers usually with 7–9 pairs of pinnae on each branchia of chaetiger 2, 4–6 pairs of pinnae on each branchia of chaetiger 4, and smooth branchiae on chaetigers 3 and 5 (Fig. 24A, C); larger individuals with up to 12 pairs of pinnae on each branchia of chaetiger 4; branchiae on chaetiger 2, 2–4 pairs on each branchia of chaetiger 3, and 5–7 pairs on each branchia of chaetiger 4; branchiae on chaetiger 5 smooth, apinnate (Fig. 23A). In large individuals, branchiae on chaetiger 2 longest, 3–5 times as long as notopodial lamellae; branchiae on chaetiger 3, about half of length of those on chaetiger 2; branchiae on chaetiger 4 up to 2/3 of length of those on chaetiger 2, and branchiae on chaetiger 5 equal or slightly shorter than those on chaetiger 3. All branchiae cylindrical to slightly flattened antero-posteriorly, with longitudinal bands of cilia running along inner and outer edges. Pinnae short, regularly arranged in two rows on postero-lateral sides of branchiae leaving basal parts about 1/5 and distal parts 1/4 free from pinnules. Afferent and efferent blood vessels interconnected by numerous radial blood capillaries giving branchiae annulate appearance; radial capillaries making loops inside pinnae.

Nototrochs present between branchial bases, each composed of one row of short cilia. Dorso-lateral longitudinal ciliation present on chaetigers 3–6 as short bands of dense cilia extending between successive notopodia.

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

Oesophagus extending through 5–7 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

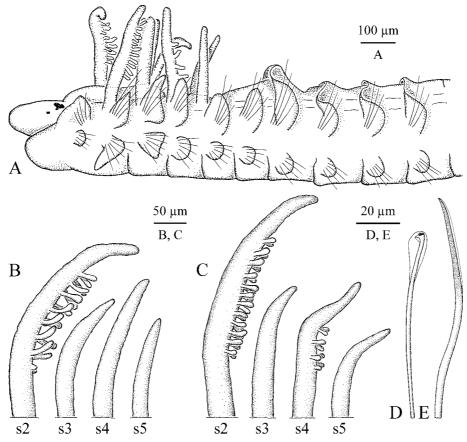
Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 20  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to chaetigers 9–11. Blood red, without globules or other elements.

Nephridia in small individuals in chaetigers 4–5, in large individuals in chaetigers 4–6 (Fig. 23B), large and greenish in chaetiger 4, smaller and less pigmented to transparent in chaetiger(s) 5 (6).

**Reproduction.** *Prionospio* cf. *paucipinnulata* is gonochoristic. Both in female and males gametes develop from chaetiger 10 through most part of body. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. Intraovarian oocytes were up to 100  $\mu$ m in diameter, with germinal vesicle about 45  $\mu$ m and single nucleolus 17  $\mu$ m in diameter. Oocyte envelope is 1.5–2  $\mu$ m thick, smooth, with single depression about 13  $\mu$ m in diameter and 10–13  $\mu$ m deep. Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3  $\mu$ m in diameter, spherical mitochondria probably four in number, and a long flagellum.

**Remarks.** *Prionospio* from Lizard Island with 30–60 chaetigers having sabre chaetae from chaetiger 10, prominent dorsal crest on chaetiger 7 and low crests on succeeding chaetigers showed significant variation of other taxonomic morphological characters as it described above. This variation is herein explained by transformation of characters during ontogenesis. It is suggested that median eyes enlarge greatly at 45–50-chaetiger stage apparently

in association with sexual maturation of an individual. Branchiae develop successively from chaetiger 2 to chaetiger 5, and pinnae appear first on the first pair of branchiae when only two or three pairs of branchiae are developed. After development of the fourth pair of branchiae on chaetiger 5, pinnae begin to appear on the third pair of branchiae and later on the second pair. As growth proceeds, hooks are gradually lost from neuropodia until chaetiger 14 and from notopodia until chaetiger 35. Sabre chaetae retain their anterior position on chaetiger 10 during entire life span.



**FIGURE 24.** *Prionospio* cf. *paucipinnulata*. A, D, E—AM W.45377; B, C—AM W.45243. A. Anterior end, left lateral view; B. Set of branchiae on chaetigers 2–5 of a 45-chaetiger individual; C. Set of branchiae on chaetigers 2–5 of a 50-chaetiger individual; D, E. Neurochaetae from a middle chaetiger; D. Multidentate hooded hook; E. Inferior sabre chaeta.

Mid-size, 45-55-chaetiger Prionospio from Lizard Island appear similar to P. paucipinnulata Blake & Kudenov, 1978 which was originally described from Port Phillip Bay, Victoria, Australia. Blake & Kudenov (1978) noticed small size of adults, up to 7 mm long for 53 chaetigers, and described them as having caruncle extending to end of chaetiger 4, large red median eyes, chaetiger 1 with capillaries in both rami, chaetiger 2 with small rounded neuropodial lamellae, pinnate branchiae on chaetigers 2 and 4, smooth branchiae on chaetigers 3 and 5, prominent dorsal crest on chaetiger 7 and low crest on chaetiger 8, sabre chaetae in neuropodia from chaetiger 10, and hooded hooks with 3-4 pairs of upper teeth, beginning in notopodia from chaetigers 34-35 and in neuropodia from chaetiger 13. Large Prionospio from Lizard Island have pinnae on the first three pairs of branchiae and thus differ from the original description of *P. paucipinnulata*. It may be, however, that Blake & Kudenov (1978) described an intermediate stage of the development of P. paucipinnulata, and in larger worms from Victoria pinnae develop on the second pair of branchiae (on chaetiger 3) same as in large worms (with 55-60 chaetigers) from Queensland. The number of branchial pinnae and the arrangement of hooks in noto- and neuropodia in *P. paucipinnulata* is within the range of those characters in *Prionospio* from Lizard Island. Two characters, neuropodial lamellae of chaetiger 2 and dorsal crests (as they were described by Blake & Kudenov 1978) are, however, different in the two groups of worms. According to the original description, P. paucipinnulata has small rounded neuropodial lamellae on chaetiger 2, and a low crest only on chaetiger 8, whereas Prionospio from Lizard Island have acuminate and ventrally elongated neuropodial lamellae on chaetiger 2, and low crests from chaetiger 8 to 20-30th chaetigers.

After Blake & Kudenov (1978), Hutchings & Murray (1984) reported *P. paucipinnulata* from New South Wales, and Dagli & Çinar (2010) suggested introduction of the species to the Aegean and Levantine coasts of Turkey with ballast waters of ships. The latter authors described worms 5.9 mm long for 45 chaetigers and having pinnate branchiae on chaetigers 2 and 4 and apinnate branchiae on chaetigers 3 and 5. They also noticed small rounded neuropodial lamellae on chaetiger 2, but in addition to the prominent dorsal crest on chaetiger 7 described low crests arranged from chaetiger 8 to chaetiger 16.

Completely developed 55-60-chaetiger Prionospio from Lizard Island appear similar to P. ergeni originally described from the Levantine Sea by Dagli & Çinar (2009). Worms in both groups are unique among Prionospio in having three pairs of pinnate branchia on chaetigers 2-4 and one pair of apinnate branchiae on chaetiger 5. Only incomplete specimens were available for the original description of *P. ergeni*, thus it is impossible to estimate the size of the complete worms. Remarkably, however, adult P. ergeni appear quite similar to adult P. paucipinnulata from Turkey decsribed by Dagli & Çinar (2010). Worms in both groups have large median eyes, small rounded neuropodial lamellae on chaetiger 2, sabre chaetae in neuropodia from chaetiger 10, and hooded hooks with 4-5 pairs of small upper teeth above main fang. They differ from each other mainly in the presence of pinnate branchiae on chaetiger 2 in worms of the former group and apinnate branchiae in the latter. More posterior start of hooks in neuropodia in P. ergeni (from chaetigers 16-18) than in P. paucipinnulata from Turkey (from chaetiger 13) may indicate larger size of the former worms (hooks gradually lost in neuropodia with age in many Prionospio species), while earlier start of hooks in notopodia in *P. ergeni* (from chaetiger 30) than in *P. paucipinnulata* from Turkey (from chaetigers 32–33) may result from limited observations by the authors (arrangement of hooks in notopodia in Prionospio worms is always size-dependent and usually variable even among same-size individuals). Comparison of caruncle length in P. ergeni and P. paucipinnulata from Turkey is also confusing. Dagli & Çinar (2009: 7) noticed that in P. ergeni "caruncle extending to chaetiger 2" (meaning end of chaetiger 1-VIR) but depicted caruncle to middle of chaetiger 3 (Dagli & Çinar 2009: fig. 3B) and SEM illustrated caruncle extending apparently to end of chaetiger 3 (Dagli & Çinar 2009: fig. 4).

Taking into account succession of the development of pinnae on branchiae in *Prionospio* from Lizard Island (first on the first pair of branchiae, then on third and ultimately on second pair of branchiae) and loss of hooks in parapodia with age in *Prionospio*, differences described by Dagli & Çinar (2009, 2010) between *P. ergeni* and *P. paucipinnulata* from Turkey may be explained by ontogeny and the two groups of worms may belong to the same species. This species may actually be different from *P. paucipinnulata* from Victoria, Australia in the shape of neuropodial lamellae on chaetiger 2, if small rounded lamellae will not be confirmed in the Australian specimens. If *P. paucipinnulata* from Victoria do have small rounded neuropodial lamellae on chaetiger 2, *Prionospio* from Lizard Island described herein should be referred to a new species because these worms have lamellae on chaetiger 2 with lower part acuminate and elongated ventrally.

Further examination of *P. paucipinnulata* from Victoria, Australia is needed to clarify the morphology of branchiae and neuropodial lamellae of chaetiger 2 in completely developed individuals. Pending such examination, worms from Lizard Island are herein referred to as *P.* cf. *paucipinnulata*.

**Habitat.** In this study, adults of *P*. cf. *paucipinnulata* were found in fine sand on the intertidal and at 14 m depth.

Distribution. Australia: Victoria, New South Wales, ? Queensland.

Prionospio cf. tatura Wilson, 1990

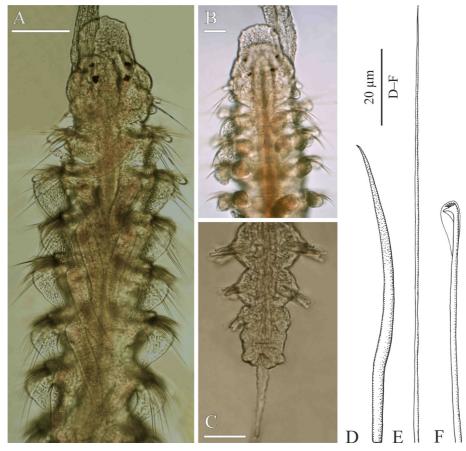
(Fig. 25)

Prionospio tatura Wilson, 1990: 260-263, figs 48-56.

Material examined. Queensland: AM W.45265, MI QLD 2330 (1); AM W.45266, MI QLD 2440 (1).

**Adult morphology.** Up to 10 mm long, 0.2 mm wide for 55 chaetigers. Pigmentation in life absent. Prostomium narrow, rounded anteriorly, extending posteriorly to end of chaetiger 1 as a low caruncle (Fig. 25A, B). Seven small knobs with short non-motile sensory cilia present on frontal and fronto-lateral edges of prostomium. Occipital antenna absent. Two pairs of small red eyes arranged trapezoidally comprising one pair of median eyes and one pair of lateral eyes situated anteriorly and set wider apart. Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming small

ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and narrow longitudinal band of cilia running on outer fronto-lateral side along frontal groove on distal half of palp; cilia of inner transverse bands beating towards distal end of palp, while cilia of outer longitudinal band beating towards frontal groove.



**FIGURE 25.** *Prionospio* cf. *tatura*. A, C, D–F—AM W.45266; B—AM W.45265. A, B. Anterior ends, dorsal view; C. Posterior end, dorsal view; D–F. Neurochaetae from median chaetiger; D. Sabre chaeta; E. Alternating capillary; F. Multidentate hooded hook. Scale bars: A–C—50 μm.

Chaetiger 1 with short capillaries and small postchaetal lamellae in both rami; notopodial lamellae fused to posterior dorsal parts of peristomium forming small ear-shaped structures. Notopodial lamellae of chaetigers 3 and 4 subtriangular, slightly larger than on other chaetigers; lamellae gradually becoming smaller and rounded on succeeding chaetigers. Neuropodial postchaetal lamellae of chaetiger 2 rounded, not elongated ventrally.

Low single dorsal folds present from chaetigers 10–12 to chaetigers 13–23. Prominent dorsal crests, lateral pouches and ventral flaps absent.

Sabre chaetae in neuropodia from chaetigers 11–12, usually one, occasionally two in a group, very thin on first chaetiger, full-sized from chaetigers 12–13, alimbate, with fine granulation on distal part (Fig. 25D).

Hooks in notopodia from chaetigers 25–28, 1–3 in a tuft among capillaries. Hooks in neuropodia from chaetigers 13–15, up to seven in a series, accompanied by inferior sabre chaetae and 1–4 alternating capillaries throughout. Alternating capillaries up to 2.5 times as long as hooks, in anterior neuropodia with narrow limbation, in posterior neuropodia thin, alimbate (Fig. 25E). Hooks multidentate, with 3–4 pairs of very thin upper teeth arranged in two vertical rows above main fang, with inner and outer hoods; shaft slightly bent (Fig. 25F).

Up to eight pairs of branchiae on chaetigers 2–9, fewer in small individuals, all apinnate, robust, flattened, with surfaces oriented perpendicular to body axis, longitudinal bands of cilia running along inner and outer edges (Fig. 25A). Branchiae full-sized on chaetiger 3, up to two times as long as notopodial lamellae, and then gradually becoming shorter on succeeding chaetigers. Afferent and efferent blood vessels interconnected by numerous radial capillaries giving branchiae annulate appearance.

Nototrochs present on branchiate chaetigers.

Pygidium with long and thin middorsal cirrus and one pair of very short ventral cirri or knobs (Fig. 25C).

Oesophagus extending through chaetigers 7–9. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 20  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to chaetigers 10–11. Blood red, without globules or other elements.

Nephridia in chaetigers 4–6, greenish in life.

Reproduction. The only two individuals collected, in August 2013, were immature.

**Remarks.** *Prionospio* with only apinnate branchiae<sup>1</sup> from around Australia were referred to *P. cirrifera* Wirén, 1883 by Blake & Kudenov (1978), Hutchings & Rainer (1979), Hutchings & Murray (1984), and Hartmann-Schröder (1985, 1989, 1990, 1991). Wilson (1990) reassessed all southern Australian records of this species and referred them to three new species, *P. tatura*, *P. wambiri* and *P. yuriel*. He also concluded that additional species might be expected to occur in northern Australia, and *P. cirrifera* is unlikely to occur in Australian waters.

*Prionospio tatura* was originally described from estuarine localities in Port Phillip Bay, Victoria, and also recorded from Paynesville, Victoria, and Nornalup, Western Australia, by Wilson (1990). Adults were characterized by the prostomium broadly-rounded anteriorly, two pairs of small red eyes, caruncle extending to end of chaetiger 1, chaetiger 1 with capillaries in both rami, chaetiger 2 with rounded neuropodial lamellae not elongated ventrally, up to 11 pairs of apinnate branchiae from chaetiger 2, branchiae on chaetiger 2 two-three times as long as notopodial lamellae, sabre chaetae in neuropodia from chaetigers 9–12, and hooded hooks with four pairs of upper teeth beginning in notopodia from chaetigers 23–38 and in neuropodia from chaetigers 13–17. Adult *P. tatura* appear very similar to those of *P. wambiri* and *P. yuriel* and differ from them in the shape of prostomium, length of branchiae and arrangement of sabre chaetae and hooks in neuropodia (Wilson 1990: Table 2).

Adult *Prionospio* from Lizard Island with only apinnate branchiae fit the original description of *P. tatura*. They slightly differ, however, in that worms from Lizard Island have shorter branchiae, up to two times as long as notopodial lamellae, while those from Victoria have branchiae up to three times as long as notopodial lamellae. Moreover, coral reef conditions around Lizard Island differ significantly from estuarine conditions in the type locality of *P. tatura*. At this point, however, no character was found to distinguish the Lizard material as a separate species. It is therefore herein referred to as *P. cf. tatura*.

**Habitat.** In this study, adults of *P*. cf. *tatura* were found in coral sand at 14–15 m depth. **Distribution.** Australia: Victoria, Western Australia, ? Queensland.

## Prionospio cf. tetelensis Gibbs, 1971

(Fig. 26)

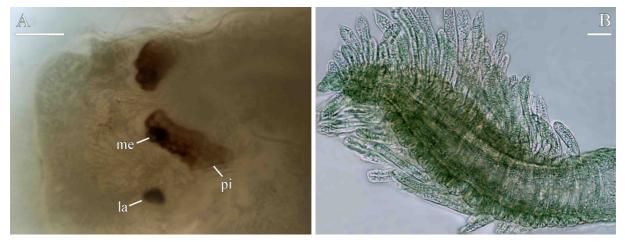
*Prionospio tetelensis* Gibbs, 1971: 171–173, fig. 13. *Prionospio (Aquilaspio) tetelensis.*—Maciolek 1985: 331.

#### Material examined. Queensland: AM W.45510, MI QLD 2440 (1).

Adult morphology. Single 17-chaetiger anterior fragment 4.5 mm long, 1.25 mm wide (body without parapodia 0.75 mm wide). Pigmentation in life absent. Prostomium wide and rounded anteriorly, extending posteriorly almost to end of chaetiger 3 as an undulating caruncle. Occipital antenna absent. Two pairs of red eyes arranged trapezoidally, comprising one pair of small lateral eyes situated anteriorly and set wider apart, and one pair of large median eyes, each composed of a small rounded cup and a large wide pigment band oriented

<sup>1.</sup> Foster (1971) established a new genus *Minuspio* to encompass *Prionospio* members with only apinnate branchiae beginning from chaetiger 2. The taxon was treated as genus or a subgenus by following authors but Wilson (1990) and Sigvaldadóttir (1998) placed back those species into *Prionospio sensu lato* (see above Remarks to the *Prionospio sensu lato* section). In the absence of a phylogenetic hypothesis about relationships of the *Prionospio* members and support of monophyly of *Minuspio*, it would be however practical to recognize non-taxonomic groups of species based on shared simple diagnostic characters. One of those groups may include *Prionospio* members with only apinnate branchiae beginning from chaetiger 2 and be referred to as the *Prionospio cirrifera* group of species. Because of great number of species in this group (recently reviewed by Dagli & Çinar 2011), it can further be subdivided into smaller groups to facilitate their revisions and identification of species.

transversally (Fig. 26A). Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming prominent ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia and transverse bands of cilia regularly arranged on inner surface; cilia of inner transverse bands beating towards distal end of palp.



**FIGURE 26.** *Prionospio* cf. *tetelensis*. A, B—AM W.45510. A, Prostomium, dorso-left lateral view, showing lateral eyes (la), median eyes (me) and associated transverse bands of red pigment (pi); B. Branchium of chaetiger 3 in frontal view, showing numerous pinnae arranged on lateral and rear sides. Scale bars: A, B—50 µm.

Chaetiger 1 with well developed capillaries and postchaetal lamellae in both rami; notopodial postchaetal lamellae fused to dorsal posterior parts of peristomium forming ear-shaped structures. Notopodial lamellae of chaetigers 2–4 triangular, small on chaetiger 2, largest on chaetiger 4; lamellae smaller and rounded on following chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 rounded, slightly elongated ventrally.

Distinct low dorsal crests present from chaetiger 6 to end of fragment.

Sabre chaetae and hooks absent in fragment.

Three pairs of pinnate branchiae present on chaetigers 3–5 and a pair of scars present on chaetiger 2; branchiae gradually shorter on posterior chaetigers. All branchiae cylindrical, rounded in cross section, with longitudinal bands of cilia running along inner and outer sides; pinnae regularly arranged along lateral and posterior sides (Fig. 26B). Afferent and efferent blood vessels interconnected by circular capillaries which form loops inside branchial pinnae.

Oesophagus extending through 6–8 anterior chaetigers. Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Heart body about 30  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 to almost end of fragment. Blood red, without globules or other elements.

**Reproduction.** The single individual of *P*. cf. *tetelensis* is a mature male with sperm present from chaetiger 13 to end of the fragment. Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus  $2-3 \mu m$  in diameter, spherical mitochondria probably four in number, and a long flagellum.

**Remarks.** The single individual from Lizard Island has three pairs of pinnate branchiae on chaetigers 3–5, but has branchial scars on chaetiger 2 meaning that the first pair of branchiae on chaetiger 2 was lost. There is no described spionid with the first apinnate pair of branchia on chaetiger 2 and three more pairs of pinnate branchiae on succeeding chaetigers (see Maciolek 1985; Blake 1996; Sigvaldadóttir 1998), but four pairs of pinnate branchiae on chaetigers 2–5 are present in four *Prionospio* species: *P. peruana* Hartmann-Schröder, 1962 originally described from Peru, *P. tetelensis* Gibbs, 1971 from Tetel Island of Solomon Islands, *P. multipinnulata* Blake & Kudenov, 1978 from New South Wales and Victoria, Australia, and *P. pyramidalis* (Hutchings & Turvey, 1984) from South Australia. By having large median eyes, caruncle extending to end of chaetiger 3, dorsal crests arranged from chaetiger 6 on a series of succeeding chaetigers, and possible start of sabre chaetae and hooks after chaetiger 17, the specimen from Lizard Island appears very similar to *P. tetelensis* and is tentatively referred to this species.

The five type specimens of *P. tetelensis* have never been re-described and the species has never been reported from outside of the type locality. The single individual from Lizard Island differs, however, in having capillary notochaetae on chaetiger 1, which, according to Gibbs (1971), were absent in *P. tetelensis*. This may indicate the presence of a new species in the Australian waters that should be described when more material becomes available.

Habitat. A single individual of *P*. cf. *tetelensis* was found in fine coral sand at 14 m depth.

Distribution. Solomon Islands; ? Queensland, Australia.

# Prionospio cf. tridentata Blake & Kudenov, 1978

(Figs 27-29)

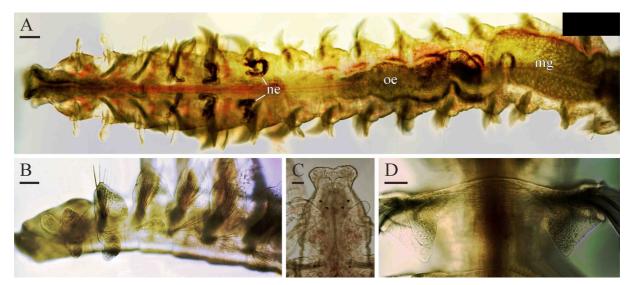
*Prionospio (Prionospio) tridentata* Blake & Kudenov, 1978: 219, fig. 23. *Prionospio tridentata.*—Hutchings & Murray 1984: 61; Wilson 1990: 246.

**Material examined. Queensland:** AM W.45259, MI QLD 2330b (1); AM W.45379, MI QLD 2440 (2); AM W.47869, MI QLD 2431 (2). **Northern Territory**: AM W.47868 (5), NTM W025903 (4), MIMB 28130 (3), Dudley Point, Fanny Bay, Darwin, 12.435600°S, 130.832300°E, muddy sand intertidal, 5 Sep 2013.

**Adult morphology.** Up to 14 mm long, 0.55 mm wide for 62 chaetigers. Pigmentation in life absent. Prostomium bell-shaped, anteriorly wide, blunt to concave, extending posteriorly to end of chaetiger 1 as a prominent caruncle (Fig. 27C). Five small knobs with short non-motile sensory cilia present on frontal and fronto-lateral edges of prostomium. Occipital antenna absent. Two pairs of small red eyes arranged trapezoidally. Nuchal organs U-shaped ciliary bands on lateral sides of caruncle. Posterior dorsal parts of peristomium fused to notopodial lamellae of chaetiger 1 forming prominent ear-shaped structures. Palps as long as 10–15 chaetigers, with frontal longitudinal groove lined with fine cilia, short transverse bands of cilia regularly arranged on inner surface, and short compound motile cilia on fronto-lateral surfaces along frontal groove; cilia of inner transverse bands beating towards distal end of palp, while compound fronto-lateral cilia beating perpendicular palp axis towards frontal groove. Longitudinal band of cilia absent on outer fronto-lateral side along frontal groove.

Chaetiger 1 with capillaries and postchaetal lamellae in both rami; notopodial lamellae fused to posterior dorsal parts of peristomium forming prominent ear-shaped structures. Notopodial lamellae of chaetigers 2–6 largest, triangular; lamellae becoming gradually smaller and rounded on following chaetigers. Lower part of neuropodial postchaetal lamellae of chaetiger 2 rounded to pointed, elongated ventrally (Fig. 27A).

Prominent dorsal crest with straight upper edge joining notopodial postchaetal lamellae of chaetiger 7 (Fig. 27D); no crests or folds on other chaetigers. Lateral pouches and ventral flaps absent.



**FIGURE 27.** *Prionospio* cf. *tridentata.* A, D—MIMB 28130; B—AM W.45259; C—AM W.45379. A. Anterior end, ventral view, showing oesophagus, anterior part of midgut and three pairs of nephridia in chaetigers 4–6; B. Anterior end, left lateral view, showing shape of postchaetal lamellae; C. Head, dorsal view, showing bell-shaped prostomium and two pairs of small eyes; D. Chaetiger 7, dorsal view, showing prominent transverse crest joining notopodial postchaetal lamellae. Abbreviations: mg—midgut, ne—nephridia, oe—oesophagus. Scale bars: A, B—100 µm; C, D—50 µm.

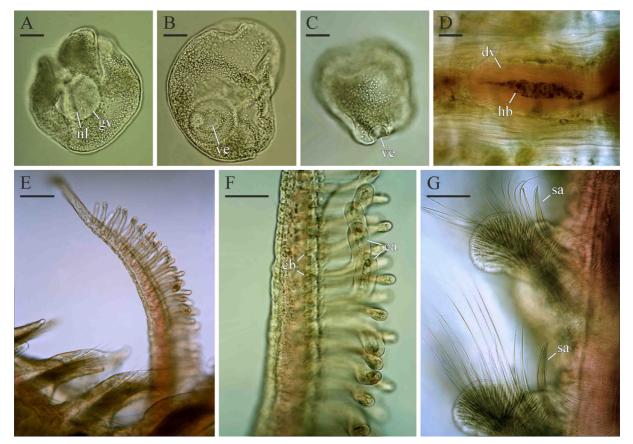
Sabre chaetae in neuropodia from chaetiger 11, thick, robust, with narrow limbation and fine granulation on distal end of shaft (Fig. 28G); chaetae largest in chaetiger 11 (Fig. 29C) and gradually diminishing in size on succeeding chaetigers (Fig. 29D) towards midbody, then gradually increasing again.

Hooks in notopodia from chaetigers 33–41, up to six in a series among capillaries. Hooks in neuropodia from chaetigers 19–26, up to ten in a series, accompanied by inferior sabre chaetae and alternating capillaries throughout. Alternating capillaries thin, alimbate, about twice as long as hooks. Hooks bidentate, with small median upper tooth above main fang, with outer and inner hoods; shaft slightly curved (Fig. 29A, B).

Four pairs of branchiae on chaetigers 2–5. Branchiae on chaetiger 2 shortest, as long as notopodial lamellae; branchiae on chaetigers 3 and 4 slightly longer than notopodial lamellae; all three pairs apinnate, robust, flattened, with surfaces oriented perpendicular to body axis. Branchiae on chaetiger 5 longest, extending posteriorly to end of chaetiger 9 (shorter in small individuals), cylindrical, with digitiform pinnae regularly arranged along lateral and posterior sides (Fig. 28E). All branchiae with longitudinal bands of cilia running along inner and outer sides; afferent and efferent blood vessels interconnected by numerous circular blood capillaries giving branchiae annulate appearance; circular capillaries forming loops inside pinnae on chaetiger 5 branchiae (Fig. 28F).

Short nototrochs present between branchial bases on chaetigers 2–4, each composed of one row of short cilia. Dorso-lateral longitudinal ciliation present on chaetigers 3–6 as short bands of cilia extending between successive notopodia. Intersegmental transverse ciliation absent.

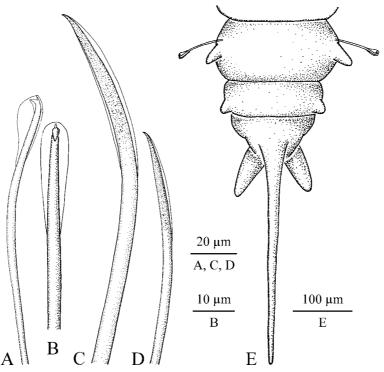
Pygidium with one long middorsal cirrus and a pair of shorter and thicker ventral cirri; middorsal cirrus 3–4 times as long as ventral cirri (Fig. 29E).



**FIGURE 28.** *Prionospio* cf. *tridentata*. A–G—MIMB 28130. A–C. Developed coelomic oocytes with soft envelope; D. Chaetigers 7 and 8, dorsal view, showing soft heart body inside main dorsal vessel; E. Pinnate branchia of chaetiger 5; F. Fragment of pinnate branchia, showing longitudinal ciliary band on lateral side, and blood capillaries forming a loop inside each pinna; G. Right neuropodia of chaetigers 11 and 12, ventral view. Abbreviations: ca—blood capillaries; cb—ciliary bands, dv—main dorsal blood vessel, gv—germinal vesicle, hb—heart body, nl—nucleolus, sa—sabre chaetae, ve—vesicles, depressions in oocyte envelope. Scale bars: A–D—30 µm. E—100 µm; F, G—50 µm.

Oesophagus extending through 7–13 anterior chaetigers (Fig. 27A). Ventral buccal bulb below oesophagus extending to end of chaetiger 1. Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Soft heart body up to 35  $\mu$ m in diameter extending inside main dorsal vessel from level of chaetigers 3–4 through chaetigers 11–12 (Fig. 28D). Nephridia in chaetigers 4–6, greenish in life (Fig. 27A).



**FIGURE 29.** *Prionospio* cf. *tridentata*. MIMB 28130. A. Bidentate hooded hook from anterior neuropodium, lateral view; B. Same in frontal view; C. Sabre chaeta from neuropodium of chaetiger 11; D. Same individual, sabre chaeta from neuropodium of chaetiger 16; E. Posterior end, dorsal view.

**Reproduction.** *Prionospio* cf. *tridentata* is gonochoristic. Both in female and males gametes develop from chaetiger 17 to chaetigers 50–55. Oogenesis is intraovarian. Vitellogenic oocytes develop in ovaries attached to segmental blood vessels. Intraovarian oocytes were up to 90  $\mu$ m in diameter, with germinal vesicle about 50  $\mu$ m and single nucleolus 18  $\mu$ m in diameter. Oocyte envelope is 2–3  $\mu$ m thick, with smooth external surface. Developed coelomic oocytes were about 140  $\mu$ m in diameter, with germinal vesicle about 60  $\mu$ m and single nucleolus 20  $\mu$ m in diameter (Fig. 28A–C). The oocyte envelope has single semi-spherical depression about 20  $\mu$ m in diameter and 15  $\mu$ m deep (Fig. 28B, C). Spermatogonia proliferate in testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with small acrosome, spherical nucleus 2–3  $\mu$ m in diameter, spherical mitochondria probably four in number, and a long flagellum.

**Remarks.** *Prionospio tridentata* was originally described based on two individuals collected from Burwood Beach, Newcastle, New South Wales, Australia, by Blake & Kudenov (1978). Two individuals from Botany Bay, New South Wales were also mentioned in the original description but not designated as types of the species. The species was characterized by the bell-shaped prostomium, two pairs of small red eyes, short and smooth branchiae on chaetiger 2, thick and smooth branchiae on chaetigers 3 and 4, and long pinnate branchiae on chaetiger 5, prominent dorsal crest on chaetiger 7, sabre chaetae in neuropodia from chaetiger 11, and tridentate hooks in notopodia from chaetiger 28 and in neuropodia from chaetiger 19.

Imajima (1990b) reported *P. tridentata* from the Ryukyu Islands, Japan. This record may, however, be misidentification of *Prionospio nova* Annenkova, 1938 originally described from the Russian part of the Sea of Japan.

Prionospio from Lizard Island and Darwin fit major diagnostic characteristics of P. tridentata but differ from

the description of the species in having bidentate instead of tridentate hooks. Blake & Kudenov (1978: 219, fig. 23d) described and illustrated two upper teeth situated in line above main fang. Tridentate hooks with teeth arranged in a vertical line are unusual for *Prionospio* where adults usually have multidentate hooks with paired upper teeth arranged in two vertical rows above main fang. Bidentate hooks are present in *Prionospio caspersi* Laubier, 1962 originally described from Venice, Mediterranean, Italy, and *Prionospio saldanha* Day, 1961 originally described from Saldanha Bay, South Africa<sup>1</sup>. Adult *Prionospio* cf. *tridentata* from Lizard Island and Darwin differ from those of *P. saldanha* by having sabre chaetae in neuropodia from chaetiger 11 instead of chaetiger 12. They also differ from *P. caspersi* by more posterior start of hooks in neuropodia, from chaetigers 19–26 instead of chaetigers 18–19. If the tridentate dentition of hooks will be confirmed in *P. tridentata* from New South Wales, *Prionospio* from Queensland and Northern Territory should be recognized as a new species.

**Habitat.** In this study, adults of *Prionospio* cf. *tridentata* were found in fine coral sand or muddy sand from intertidal to 16 m depth.

Distribution. Australia: New South Wales, ? Queensland, Northern Territory. ? Ryukyu Islands, Japan.

## Pseudopolydora Czerniavsky, 1881

*Pseudopolydora* Czerniavsky, 1881: 362; Blake & Kudenov 1978: 267; Blake 1996: 202. *Polydora* (*Carazzia*).—Fauvel 1927: 48. *Polydora* (*Pseudopolydora*).—Hartmann-Schröder 1971: 317; 1996: 322.

Type-species. Polydora antennata Claparède, 1868, by monotypy.

**Remarks.** *Pseudopolydora* Czerniavsky, 1881 currently comprises 18 species of polydorin spionids that usually inhabit tubes on the intertidal and in shallow water in estuarine environments.

Four *Pseudopolydora* species were reported from the Australian waters, comprising *P. antennata* (Claparède, 1868), *P. paucibranchiata* (Okuda, 1937), *Pseudopolydora kempi* (Southern, 1921), and *Pseudopolydora glandulosa* Blake & Kudenov, 1978 (Blake & Kudenov 1978<sup>2</sup>; Hutchings & Rainer 1979; Hartmann-Schröder 1981, 1983; Hutchings & Murray 1984; Hutchings & Turvey 1984; Hewitt *et al.* 2004). *Pseudopolydora glandulosa* was originally described from Victoria, Australia, and also reported from Queensland and New South Wales (Blake & Kudenov 1978; Hutchings & Murray 1984). The other three species were originally described from Italy, Japan, and India, respectively.

# Key to Pseudopolydora from around Lizard Island Group

Foster (1971) established a new genus Apoprionospio to encompass Prionospio members with apinnate branchiae on chaetigers 2–4 and pinnate branchiae on chaetiger 5. The taxon was treated as genus or a subgenus by following authors, re-defined by Maciolek (1985), but Wilson (1990) and Sigvaldadóttir (1998) placed back those species into Prionospio sensu lato (see above Remarks to the Prionospio sensu lato section). In the absence of a phylogenetic hypothesis about relationships of the Prionospio members and support of monophyly of Apoprionospio, it would be however practical to recognize non-taxonomic groups of species based on shared simple diagnostic characters. One of those groups may include Apoprionospio sensu Foster, 1971 with plate-like pinnae on chaetiger 5 (Apoprionospio sensu Maciolek, 1985) and be referred to as the Prionospio pygmaea group of species. Another group was already distinguished by Wilson (1990) as Prionospio caspersi group of species to include Apoprionospio sensu Foster, 1971 with digitiform pinnae on chaetiger 5.

<sup>2.</sup> *Pseudopolydora prolifera* and *Pseudopolydora stolonifera* described from Australia by Blake & Kudenov (1978) are currently referred to *Polydorella* (see above).

# Pseudopolydora cf. paucibranchiata (Okuda, 1937)

(Fig. 30)

Polydora (Carazzia) paucibranchiata Okuda, 1937: 231–233, figs. 11, 12.

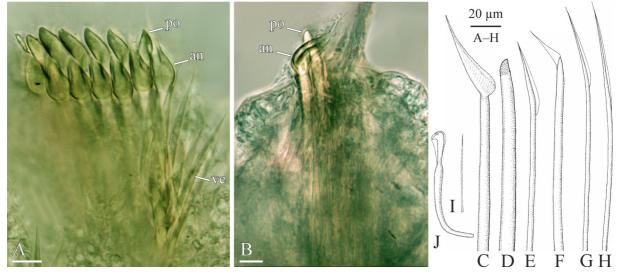
Pseudopolydora paucibranchiata.—Hartman 1959: 387; Blake & Kudenov 1978: 268; Hutchings & Murray 1984: 61–62; Hutchings & Turvey 1984: 17, fig. 7.

## Material examined. Queensland: AM W.45380, MI QLD 2440 (1).

Adult morphology. Single 12-chaetiger anterior fragment 1.5 mm long, 0.25 mm wide. Pigmentation on body absent. Anterior margin of prostomium and occipital antenna slightly damaged and unclear (apparently prostomium rounded and occipital antenna present). Caruncle extending to end of chaetiger 3. Nuchal organs ciliary bands on lateral sides of caruncle. Two pairs of small black eyes arranged trapezoidally. Palps in life with eight branching yellow chromatophores; chromatophores invisible after fixation.

Chaetiger 1 fused to peristomium ventrally and weakly separated from it dorsally, with few very short capillaries in neuropodia, small notopodial postchaetal lamellae and well-developed neuropodial lamellae; notochaetae absent. Notochaetae of chaetigers 2–4 and 6 slender capillaries with narrow wing (Fig. 30E). Anterior-row notopodial capillaries from chaetiger 7 to end of fragment with triangular pennon-like wing (Fig. 30F), 3–5 in a series; superior and posterior-row notochaetae in these chaetigers slender capillaries with narrow wing; superior capillaries longer than posterior-row capillaries, with longer wing (Fig. 30G, H).

Chaetiger 5 same size as chaetigers 4 and 6, with four dorsal superior winged capillaries, two kinds of notopodial spines arranged in a double J-shaped series, and eight ventral winged capillaries; notopodial postchaetal lamellae lacking but neuropodial lamellae well developed. Dorsal superior capillaries slightly shorter and fewer than those capillaries on chaetigers 4 and 6. Ventral capillaries same as those on chaetiger 4 or 6. Anterior-row notochaetae enlarged pennon spines with curved tip and weak constriction between tip and shaft (Fig. 30A, B, C), eight in a series; posterior-row notochaetae simple falcate spines, with fine scales on distal end, seven in a series (Fig. 30A, B, D).



**FIGURE 30.** *Pseudopolydora* cf. *paucibranchiata*. A–J—AM W.45380. A, B. Right parapodia of chaetiger 5, ventral view. C, D. Notopodial spines of chaetiger 5; C. Anterior-row enlarged pennon spine with curved tip and weak constriction between tip and shaft; D. Posterior-row simple falcate spine with fine scales on distal end; E. Anterior-row notopodial capillary chaeta of chaetiger 6; F–H. Notopodial capillary chaetae of chaetiger 7; F. Anterior-row capillary chaeta with triangular pennon-like wing; G. Posterior-row slender capillary chaeta; H. Dorsal superior slender capillary chaeta; I, J. Neurochaetae of chaetiger 8; I. Hair-like alternating capillary chaeta; J. Bidentate hooded hook. Abbreviations: an—anterior-row notopodial spines, po—posterior-row notopodial spines, ve—ventral capillary chaetae. Scale bars: A, B—10 µm.

Hooks in neuropodia from chaetiger 8, up to seven in a series, accompanied by 1–3 hair-like alternating capillaries until chaetigers 10–11 (Fig. 30I); alternating capillaries situated between upper hooks in a row, very short, mostly embedded into body wall and slightly protruding above surface. Hooks bidentate, with upper tooth

closely applied to main fang; upper part of shaft with constriction, lower part of shaft bent at right angle (Fig. 30J). Branchiae from chaetiger 7 to end of fragment, free from notopodial postchaetal lamellae.

**Remarks.** *Pseudopolydora paucibranchiata* was originally described from the Inland Sea, Japan by Okuda (1937). The species is common in tidal flats and estuaries in the temperate northern Pacific along the Asian and American coasts (Radashevsky 1993; Blake 1996). It was likely introduced to eastern Mediterranean (Dagli & Çinar 2008) and Brazil (Junqueira *et al.* 2009). In Australia, *P. paucibranchiata* was reported from New South Wales, Victoria and South Australia (Blake & Kudenov 1978; Poore & Kudenov 1978a, b; Hutchings & Rainer 1979; Hutchings & Murray 1984; Hutchings & Turvey 1984).

The only anterior fragment from Lizard Island and other worms collected by the author from Victoria and Northern Territory and examined alive appear morphologically identical to worms from the northern Pacific. However, preliminary molecular analysis of 28S rDNA showed more than 3% difference between specimens from Australia and the Sea of Japan and 2.4% difference between specimens from Victoria and Northern Territory (Radashevsky unpublished). It is possible that two or more sibling species are actually present. Further molecular analysis is needed to clarify their taxonomy.

**Habitat.** In this study, a single individual of *P*. cf. *paucibranchiata* was found in fine coral sand at 14 m depth. **Distribution.** Native in northern Pacific; introduced to the Mediterranean and Brazil. ? Australia.

# Pseudopolydora cf. rosebelae Radashevsky & Migotto, 2009

(Figs 31, 32)

Pseudopolydora rosebelae Radashevsky & Migotto, 2009: 462–467, figs 1–6 (adult and larval morphology).

## Material examined. Queensland: AM W.45381, MI QLD 2347 (1).

Adult morphology. Single 25-chaetiger anterior fragment about 6 mm long and 1 mm wide (Fig. 31). Irregular black spots present on dorso-lateral sides of chaetigers 1 and 3. White pigment diffused on prostomium and 6–8 anterior chaetigers in life, not visible after fixation. Prostomium anteriorly bifid, extending posteriorly to end of chaetiger 1 as a low caruncle. Nuchal organs ciliary bands on sides of caruncle. Short occipital antenna present on caruncle. Three small black eyes present, comprising two median eyes and right lateral eye. Palps missing.

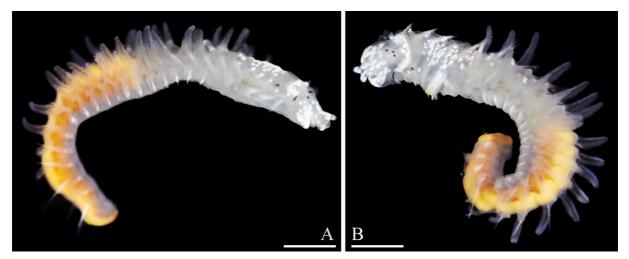


FIGURE 31. *Pseudopolydora* cf. *rosebelae*. A, B—AM W.45381. A. Anterior end, right lateral view; B. Same, left lateral view. Scale bars: A, B—1 mm. Photo: A, B—Alexander Semenov.

Chaetiger 1 weakly separated from peristomium, with short capillaries in neuropodia and small postchaetal lamellae in both rami; notochaetae lacking. Chaetigers 2–4 and 6 with slender capillaries in both rami. From chaetiger 7 onwards notochaetae smooth slender capillaries with narrow limbation.

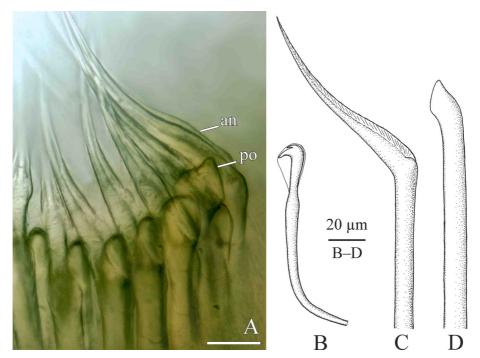
Thin transparent hood, an extension of epithelium, arising from dorsal anterior edge of chaetiger 3. Hood oriented forward and upward at an angle of  $30-45^{\circ}$  to body surface and forming a prominent pouch above chaetiger

2. Lateral sides of hood curved anteriorly and laterally situated near notopodial postchaetal lamellae of chaetiger 2, but not joined to these.

Chaetiger 5 same in size as chaetigers 4 and 6, with six dorsal superior winged capillaries, two kinds of notopodial spines arranged in a double J-shaped series, and about 20 ventral winged capillaries; notopodial postchaetal lamellae lacking but neuropodial lamellae well developed. Dorsal superior capillaries slightly shorter and fewer than those capillaries on chaetigers 4 and 6. Ventral capillaries same as those on chaetigers 4 and 6. Anterior-row notochaetae enlarged pennon spines with long sharply pointed tip (Fig. 32A, C), 12 in a series; posterior-row notochaetae simple falcate spines, 10 in a series (Fig. 32A, D).

Hooks in neuropodia from chaetiger 8, up to 14 in a series, not accompanied by capillaries. Hooks bidentate, with upper tooth closely applied to main fang; upper part of shaft with constriction, lower part of shaft bent at right angle (Fig. 32B).

Branchiae on chaetigers 7–22, full-sized from chaetigers 8–9, free from notopodial postchaetal lamellae. Nototrochs from chaetiger 7 onwards, each composed of one row of cilia extending onto branchiae.



**FIGURE 32.** *Pseudopolydora* cf. *rosebelae*. A–D—AM W.45381. A. Notopodial spines of chaetiger 5. B. Bidentate hooded hook from neuropodium of chaetiger 8; C, D. Notopodial spines of chaetiger 5; C. Anterior-row pennon spine with long sharply pointed tip; D. Posterior-row simple falcate spine. Abbreviations: an—anterior-row notopodial spines, po—posterior-row notopodial spines. Scale bar: 20 µm.

Narrow transparent oesophagus extending to end of chaetiger 12. Ventral buccal bulb and gizzard-like structure in digestive tract absent.

Main dorsal blood vessel without heart body. Blood transparent, without elements and colored respiratory pigment.

Nephridia from chaetiger 4 onwards.

**Remarks.** *Pseudopolydora rosebelae* was originally described from the states of São Paulo and Rio de Janeiro by Radashevsky & Migotto (2009). Since then, the species had not been reported outside of Brazil. Adults are unique among spionids in their pigmentation pattern (intense black and white pigment on dorsal side of head and anterior chaetigers), dorsal pouch over chaetiger 2, and transparent blood without coloured respiratory pigment. The only anterior fragment from Lizard Island has white pigment on the dorsal side of anterior chaetigers and a dorsal pouch over chaetiger 2 similar to that in the Brazilian worms. It also has a similarly shaped prostomium, a caruncle of the same length and heavy spines of chaetiger 5 of a similar morphology as the worms from Brazil. It slightly differs however in having less intense black pigmentation on anterior chaetigers. It is preliminary identifed as *P. cf. rosebelae* pending confirmation with a molecular analysis.

**Habitat.** In this study, a single individual of *P*. cf. *rosebelae* was found in coral sand at 10 m depth. **Distribution.** Brazil; ? Australia.

# Rhynchospio Hartman, 1936

*Rhynchospio* Hartman, 1936: 51; Fauchald 1977: 25; Blake & Kudenov 1978: 198–199; Radashevsky 2007: 996. *Malacoceros (Rhynchospio).*—Pettibone 1963: 98–99; Foster 1971: 48.

Type-species. *Rhynchospio arenincola* Hartman, 1936, by monotypy.

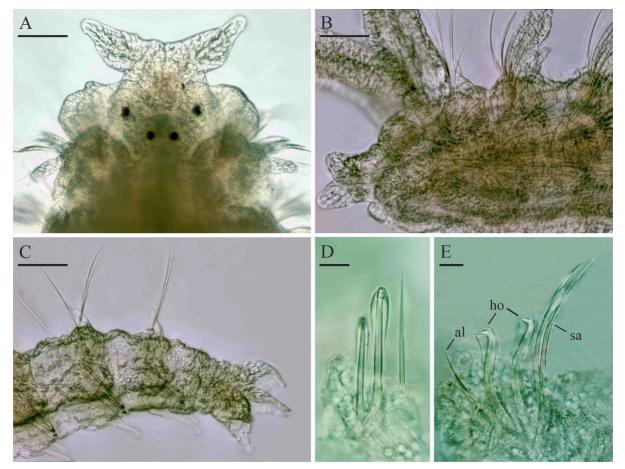
**Remarks.** *Rhynchospio* Hartman, 1936 is a small group of spionid polychaetes currently comprising ten species. The species were recently reviewed and a key to their identification was provided by Radashevsky *et al.* (2014).

First *Rhynchospio* from Australia were reported by Blake & Kudenov (1978) who described two new species, *R. glycera* from Burwood Beach, New South Wales, and *R. australiana* from Perth, West Australia. Both species were described based on single individuals, never re-described and not reported from other localities.

# Rhynchospio darwini n. sp.

(Figs 33, 34)

**Type material.** Holotype: NTM W025648, **Northern Territory,** Fannie Bay, Darwin, Bullocky Point, 12.4356°S, 130.8323°E, intertidal, muddy sand, coll. V.I. Radashevsky, 3 Sep 2013. Paratypes: MIMB 28105 (1), same details as holotype; AM W.45506 (1), **Queensland**, Lizard Island, MI QLD 2408.



**FIGURE 33.** *Rhynchospio darwini* n. sp. A—MIMB 28105; B–E—AM W.45382. A. Anterior end with palps missing, dorsal view; B. Anterior end, left lateral view; C. Posterior end, left lateral view; D, E. Bidentate hooded hooks from median neuropodia; D. Hooks in frontal view; E. Hooks in lateral view. Abbreviations: al—alternating capillary, ho—hooded hooks, sa—ventral inferior sabre chaetae. Scale bars: A–C—50 µm; D, E–10 µm.

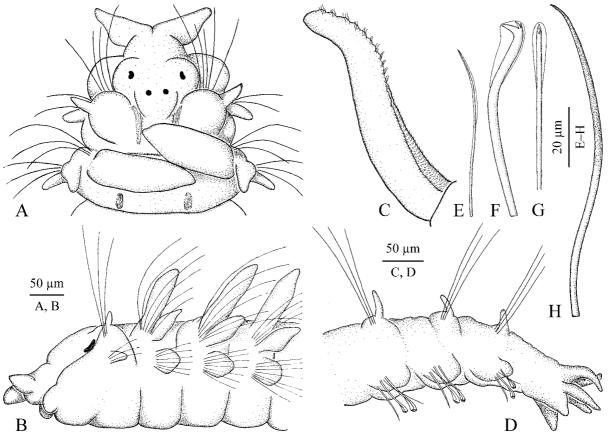
**Adult morphology.** Largest intact individual holotype 5 mm long, 0.3 mm wide for 60 chaetigers (21 anterior chaetigers of the holotype deposited at the NTM W025648, while the posterior chaetigers fixed in ethanol for a molecular analysis); smallest individual 2.5 mm long, 0.2 mm wide for 33 chaetigers (AM W.45506). Pigmentation absent on body and palps; yellow pigment present on ventral pair of pygidial cirri. Prostomium with two conical fronto-lateral horns (Figs 33A, B, 34A, B), bearing small knobs with short non-motile cilia. Caruncle low, indistinct, levelled in end of chaetiger 1. Occipital antenna absent. Two pairs of small red eyes arranged trapezoidally. Nuchal organs metameric; first pair of metamers on chaetiger 1 as curved ciliary bands on lateral sides of low caruncle; successive metamers as one pair of ciliary bands on posterior half of each chaetiger ending on at least chaetiger 15. Palps as long as 5–10 chaetigers, with frontal longitudinal groove lined with fine cilia, fronto-lateral compound cilia situated on sides of groove and beating towards the groove, and short transverse bands of long cilia regularly arranged on inner lateral side on distal half of each palp.

Chaetiger 1 with long capillaries and small postchaetal lamellae in both rami. Posterior notopodia with only capillaries. Prechaetal lamellae not developed. Notopodial postchaetal lamellae elongated; neuropodial lamellae short and rounded.

Sabre chaetae in neuropodia from chaetigers 11–12, 1–3 in a tuft, alimbate, with fine granulation on distal half of shaft (Figs 33E, 34H).

Hooks in neuropodia from chaetigers 11–12, up to four in a series, accompanied by 1–4 alternating capillaries and inferior sabre chaetae throughout. Alternating capillaries with narrow wing in anterior hook-bearing neuropodia (Fig. 34E), alimbate, hair-like in posterior neuropodia. Hooks with only outer hood, tridentate, with two small upper teeth arranged in line above main fang (Figs 33D, E, 34F, G); uppermost tooth tiny in hooks in anterior neuropodia, prominent in hooks in posterior neuropodia.

Branchiae from chaetiger 2 through most part of body, free from notopodial postchaetal lamellae, flattened, with surfaces orientated parallel to body axis, each with two rows of short cilia running along inner surface. Afferent and efferent branchial blood vessels forming a loop and not interconnected by radial capillaries.



**FIGURE 34.** *Rhynchospio darwini* n. sp. A—NTM W025648; B–H—AM W.45382. A. Anterior end in dorsal view with palps missing; B. Anterior end in left lateral view with palps missing; C. Left palp, inner lateral view; D. Posterior end, left lateral view; E–H. Neurochaetae from middle chaetiger; E. Alternating capillary chaeta with narrow wing; F. Tridentate hooded hook in lateral view; G. Same in frontal view; H. Inferior sabre chaeta.

Nototrochs from chaetiger 1 onwards, each composed of two rows of cilia, separated from branchial ciliation by narrow gap. Nototroch on chaetiger 1 interrupted middorsally by caruncle; nototrochs on succeeding chaetigers complete transverse rows. Intersegmental transverse ciliation absent. Intersegmental longitudinal ciliation from chaetiger 2 onwards, as short bands of short cilia on dorso-lateral edges of chaetigers, extending from one chaetiger onto anterior part of successive chaetiger.

Pygidium with one pair of ventral cirri and two pairs of thinner, slightly longer dorsal cirri in all three type specimens (Figs 33C, 34D).

Glandular pouches in neuropodia from chaetigers 7–8.

Narrow oesophagus extending through 8–12 anterior chaetigers. Ventral buccal bulb below oesophagus extending to almost end of chaetiger 2. Gizzard-like structure in digestive tract absent.

Main dorsal blood vessel transformed into gut sinus in anterior part of midgut. Heart body absent inside main dorsal vessel. Blood red, without globules or other elements.

Nephridia from chaetiger 4 onwards.

**Reproduction.** *Rhynchospio darwini* n. sp. is hermaphroditic. The holotype has sperm in chaetigers 11–14 and small developing oocytes in paired ovaries in chaetigers 15–30. The oocytes are up to 65  $\mu$ m in diameter, with thin and smooth membrane less than 1  $\mu$ m thick, with germinal vesicle about 30  $\mu$ m, and single nucleolus about 10  $\mu$ m in diameter. The paratype MIMB 28105 has sperm in chaetigers 11–14 and small oocytes up to 25  $\mu$ m in diameter developing in ovaries from chaetiger 15.

**Remarks.** *Rhynchospio darwini* n. sp. appears similar to *Rhynchospio nhatrangi* Radashevsky, 2007 originally described from Nhatrang Bay, Vietnam, in having up to three pairs of cirri on the pygidium, sperm developing in chaetigers 11–14 and oocytes from chaetiger 15 onwards. The two species differ however in that adults of *R. nhatrangi* have falcate unidentate hooks in neuropodia of chaetigers 11–14 and tridentate hooks from chaetiger 15 onwards, whereas adults of *R. darwini* n. sp. have only tridentate hooks in neuropodia from chaetigers 11–12.

*Rhynchospio darwini* n. sp. differs from two other Australian species, *R. australiana* and *R. glycera*, by the shape of prostomium, and from *R. glycera* also by the presence of tridentate hooks in neuropodia from chaetigers 11–12 instead of quadridentate hooks from chaetiger 27. *Rhynchospio australiana* has tridentate hooks in neuropodia from chaetiger 8 but has no notochaetae in chaetiger 1 which are present in *Rhynchospio darwini* n. sp.

**Etymology.** The species is named after its type locality, Darwin, the capital and chief port of Northern Territory, Australia, and thus is in honour of the British naturalist Charles Darwin. On 9 September 1839, HMS *Beagle* sailed into Darwin harbour during its surveying of the northern Australia. The ship's captain, Commander John Clements Wickham named the region "Port Darwin" in honour of his former shipmate Charles Darwin, who had sailed on the earlier second expedition of the Beagle which had ended in October 1836.

Habitat. Adults of Rhynchospio darwini n. sp. were found on sandy intertidal.

Distribution. Australia: Northern Territory and Queensland.

#### Tripolydora Woodwick, 1964

Tripolydora Woodwick, 1964: 155.

Type-species. Tripolydora spinosa Woodwick, 1964, by monotypy.

**Remarks.** *Tripolydora* Woodwick, 1964 is a monotypic genus containing *T. spinosa*. With heavy modified spines on chaetiger 5 in adults, *T. spinosa* has been considered as a polydorin, member of the *Polydora*-complex (currently defined as a tribe Polydorini Benham, 1896 *sensu* Radashevsky, 2012). Based on general appearance of the worms and of the fifth chaetiger, Woodwick (1964) suggested closer affinities of *Tripolydora* with *Pseudopolydora* than with other polydorins. Blake & Woodwick (1981) examined adults using both the light and scanning electron microscopy (SEM) and proposed close relationship of *T. spinosa* to a non-polydorin genus *Microspio* Mesnil, 1896. This hypothesis was not however supported in a phylogenetic analysis of the spioniform polychaetes provided by Blake & Arnofsky (1999). The analysis of a very limited suit of morphological and reproductive characters resulted in *Tripolydora* nested among polydorin taxa which relationships remained entirely unresolved (Blake & Arnofsky 1999: fig. 13).

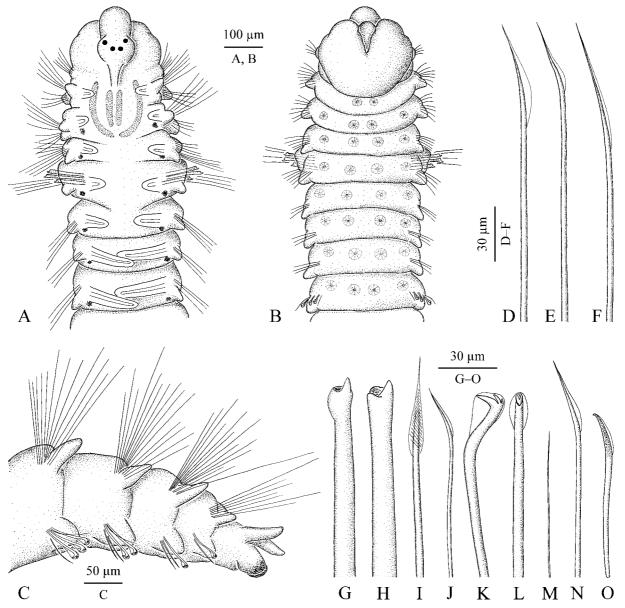
In Australia, Tripolydora was not reported so far in any taxonomic or ecological survey, but Rouse (1988)

described fine structure of spermatozoa of *Tripolydora* sp. from Heron Island. The specimens studied by Rouse (1988; AM W 200627) were examined and referred to *Pseudopolydora* sp. (Radashevsky unpublished).

# Tripolydora spinosa Woodwick, 1964

(Fig. 35)

*Tripolydora spinosa* Woodwick, 1964: 155–156, fig. 4 (6–9); Reish 1968: 222; Kohn & Lloyd 1973: 700; Blake & Woodwick 1981: 352–362, figs 1–5; Ward 1981: 730; 1987: 368–369, fig. 3.II.148; Hartmann-Schröder 1992: 70–71, figs 72–75; Williams 2001: 457–459, fig. 15.



**FIGURE 35.** *Tripolydora spinosa*. A–H—AM W.47872. A. Anterior end in dorsal view with palps missing; B. Same in ventral view; C. Posterior end, left lateral view; D–F. Notochaetae of chaetiger 4; D. Anterior-row capillary chaeta; E. Posterior-row capillary chaeta; F. Superior-group capillary chaeta; G, H. Notopodial anterior-row heavy aciculate spines of chaetiger 5; I. Posterior-row capillary notochaeta of chaetiger 7; J–N. Neurochaetae of chaetiger 7; J. Anterior-row winged capillary chaeta; K. Tridentate hooded hook in lateral view; L. Same in frontal view; M. Alimbate hair-like alternating capillary chaeta; N. Inferior winged capillary chaeta; O. Inferior sabre chaeta from a neuropodium of a posterior chaetiger.

#### Material examined. Queensland: AM W.47872, MI QLD 2379 (1).

Adult morphology. Single specimen in two fragments, comprising 16 anterior chaetigers 1.75 mm long, 0.3 mm wide and 15 posterior chaetigers about 1.5 mm long. Dark paired spots (possibly remains of larval melanophores) present on dorso-lateral sides from chaetiger 3 to end of anterior fragment; ochre pigment present in distal part of ventral pygidial cirri. Prostomium rounded anteriorly, extending posteriorly to end of chaetiger 3 as a low indistinct caruncle. Two pairs of dark eyes (appearing dark reddish in formalin-fixed specimen) arranged trapezoidally. Occipital antenna absent. Nuchal organs two pairs of wide ciliary bands comprising inner pair of almost straight longitudinal bands situated on sides of low indistinct caruncle, and longer outer pair with anterior part oriented longitudinally and posterior part curved inwards (Fig. 35A). Palps missing.

Chaetiger 1 with short capillaries and low postchaetal lamellae in neuropodia; notopodia lacking. Chaetigers 2 and 3 with slender capillaries in both rami. Chaetigers 4 and 6 with dorsal superior and posterior-row notochaetae and neurochaetae slender capillaries (Fig. 35E, F). Chaetiger 4 anterior-row notochaetae capillaries with swollen wing (Fig. 35D); similar capillaries with less swollen wing also present in anterior row in notopodia on chaetiger 6. Posterior-row capillary notochaetae on chaetigers 7 and 8 with ribbed structures oriented obliquely on wing surface (Fig. 35I). Notopodia on middle chaetigers with 5–10 slender capillaries and small postchaetal lamellae; notopodia on posterior chaetigers with bundles of 15–20 separate long needle-like spines and small postchaetal lamellae (Fig. 35C).

Chaetiger 5 slightly larger than chaetigers 4 and 6, with noto- and neuropodial postchaetal lamellae same as those on chaetigers 4 and 6. Notochaetae comprising 2–3 long dorsal superior capillaries, four shorter posterior-row capillaries, both kinds of chaetae same but fewer than those on chaetigers 4 and 6, and four anterior-row heavy acicular spines with terminal tooth flanked on one side by two wide knobs (Fig. 35G, H). Neurochaetae comprising two vertical rows of capillaries (four capillaries in each row) and two shorter inferior capillary chaetae, all capillaries same as those on chaetigers 4 and 6.

Hooks in neuropodia from chaetiger 9, up to five in a series, accompanied by 2–4 short winged capillaries arranged in a vertical row in front of hook row (Fig. 35J), 1–4 hair-like capillaries alternating with hooks (Fig. 35M), and 1–2 inferior chaetae situated below hook row. Inferior chaetae in anterior hook-bearing segments winged capillaries (Fig. 35N), on chaetigers 14–15 gradually transformed into sabre chaetae with narrow wing and fine granulation on distal part (Fig. 35O). Hooks tridentate, with two upper teeth arranged in line above main fang, with only outer hood, shaft slightly curved, without constriction (Fig. 35K, L).

Branchiae from chaetiger 2 to almost end of body, short on anterior chaetigers, full-sized from chaetiger 7 (Fig. 35A). Branchiae free from notopodial postchaetal lamellae, flattened, with surfaces oriented parallel to body axis, with longitudinal ciliation on inner surface. Afferent and efferent arms of branchial blood loop not interconnected by radial capillaries.

Pygidium small, with one pair of thin dorsal cirri and one pair of thicker and shorter ventral bulbs (Fig. 35C). Paired glandular organs arranged in transverse lines on ventral side of anterior chaetigers (Fig. 35B). Apparently one pair of organs present on each of chaetigers 2 and 3; two pairs of organs present on each chaetiger from chaetiger 4 to about chaetiger 10; organs indistinct on succeeding chaetigers. Each organ appearing as a round pore about 3  $\mu$ m in diameter, sided by 10–15 cells forming a rosette-like structure up to 25  $\mu$ m in diameter.

Glandular pouches in neuropodia from chaetiger 1, very small in anterior chaetigers.

Digestive tract without gizzard-like structure.

Main dorsal blood vessel without heart body.

Nephridia from chaetiger 4 onwards.

Reproduction. Unknown.

**Remarks.** *Tripolydora spinosa* was originally described from the rocky intertidal on Eniwetok Atoll in the Marshall Islands by Woodwick (1964). It was later recorded from the tropical Pacific and western Indian Ocean (Reish 1968; Kohn & Lloyd 1973; Ward 1981; 1987; Hartmann-Schröder 1992; Williams 2001). Blake & Woodwick (1981) recorded material from the Cook Islands and for the first time described the unique ribbed capillaries in the notopodia of chaetigers 7–10 and established homology of the modified chaetae of chaetigers 4 and 5 with corresponding groups of chaetae on chaetigers 2–3 and 6–10. Williams (2001) examined a single living specimen from the Philippines and described black pigmentation on the palps, prostomium, and dorsal side of the anterior and posterior chaetigers. He noted that this pigmentation disappeared after fixation. This is probably why this kind of pigmentation was not reported by other authors and also not observed in the present study. Reproductive biology and larval development of *T. spinosa* remain unknown.

The single specimen from Yonge Reef examined in the present study after fixation appears similar to T. spinosa described by Woodwick (1964) and other authors, and is referred to this species. Glandular pouches in neuropodia, ventral glands on anterior chaetigers, and nephridia are described herein for the first time for this spionid. The nuchal organs described in the present study, however, differ from those described by previous authors. Remarkably, fine epithelium of fragile worms is easy to destroy and dorsal ciliation of worms often appears indistinct, especially after fixation. Woodwick (1964) noted the caruncle extending to end of chaetiger 3 and did not provide any comment on the morphology of the nuchal organs. Blake & Woodwick (1981: fig. 1A) did not illustrate nuchal organs with SEM but depicted them as a pair of longitudinal bands of cilia on the sides of a wide caruncle extending to middle (until nototroch) of chaetiger 3. Williams (2001: 457) noted broad caruncle reaching end of chaetiger 2 but depicted nuchal organs as a pair of longitudinal bands of cilia on sides of caruncle extending to end of chaetiger 3 or even middle of chaetiger 4 (Williams 2001: fig. 15A). This kind of nuchal organs is typical for polydorins and might have been in mind of the authors during interpretation of an indistinct structure. Nuchal organs as two pairs of wide ciliary bands comprising inner pair of almost straight longitudinal bands situated on sides of low and narrow indistinct caruncle, and a longer outer pair with anterior part oriented longitudinally and posterior part curved inwards are described in T. spinosa for the first time in the present study (Fig. 35A). Same organs were also observed in other specimens of *T. spinosa* from other regions (Radashevsky unpublished). These nuchal organs appear similar to J-shaped organs typical for adult Microspio and Spio (see Jelsing 2002: fig. 2A, 2003: 2G; Bick et al. 2010: fig. 9; Radashevsky 2012: figs 2E, 4B).

Adult *T. spinosa* are unusual among polydorins in having tridentate instead of bidentate hooks, anterior-row capillaries and alternating capillaries accompanying hooks, and sabre chaetae in neuropodia. The heavy acicular spines of chaetiger 5 positioned in the anterior row in notopodia of *T. spinosa* are not homologs of the falcate spines positioned in the posterior-row in notopodia of Polydorini members (see Radashevsky & Fauchald 2000: fig. 4; Radashevsky 2012). The nuchal organs and ventral glands described herein for *T. spinosa* are typical for *Microspio* and *Spio* (for ventral glands see Rößger *et al.* 2015). All these characters support the hypothesis of closer relationship of *T. spinosa* to *Microspio* and *Spio* than to polydorins. This hypothesis will be estimated in a phylogenetic analysis of spiomorph polychaetes elsewhere.

**Habitat.** In this study, a single individual of *T. spinosa* was found in coral sand at 10 m depth. **Distribution.** Tropical Pacific. This is the first record of the species for the Great Barrier Reef and Australia.

#### Acknowledgements

My sincere thanks are to Pat Hutchings and Elena K. Kupriyanova, both from the Australian Museum, and Anne Hoggett and Lyle Vail, co-directors of the Lizard Island Research Station, for organizing the Taxonomic Workshop at the Station. Anne Hoggett and Lyle Vail provided instant help and assistance during this Workshop. My sincere gratitude is also to buddy divers for their underwater company on the Reef, Alexander Semenov for taking photos, and Mika Simboura for discussion of etymology and Greek origin of some names. James A. Blake and Robin S. Wilson provided important comments and editing during reviewing the manuscript. The workshop was funded by the Lizard Island Reef Research Foundation.

#### References

Augener, H. (1914) Polychaeta II, Sedentaria. Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwestaustralischen Forschungsreise 1905 herausgegeben von Prof. Dr. W. Michaelsen und Dr. R. Hartmeyer, 5, 1–172.

Augener, H. (1923) Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. XIV. Polychaeta I. Polychaeten von den Auckland- und Campbell-Inseln. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, 75, 1–115.

- Augener, H. (1926) Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. XXXIV. Polychaeta III. Polychaeten von Neuseeland. II. Sedentaria. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, 81, 157–294.
- Banks, J. (2008) *The Endeavour journal of Joseph Banks: 1768–1771. Vol. 2.* New Zealand Electronic Text Centre, Wellington, 80 pp. [pp. 276–355]

Beaglehole, J.C. (1968) The Journals of Captain James Cook on His Voyages of Discovery, vol. I: The Voyage of the Endeavour 1768–1771. Cambridge University Press, Cambridge, 696 pp.

Ben-Eliahu, M.N., Hutchings, P.A. & Glasby, C.J. (1984) Ceratonereis lizardensis n. sp. (Polychaeta; Nereididae) and

*Malacoceros indicus* (Spionidae), from a mangrove habitat at Lizard Island, North Queensland. *In:* Hutchings, P.A. (Ed.), *Proceedings of the First International Polychaete Conference, Sydney, Australia, July 1983*. The Linnean Society of New South Wales, Sydney, pp. 91–97.

Bick, A. (2001) The morphology and ecology of *Dipolydora armata* (Polychaeta, Spionidae) from the western Mediterranean Sea. *Acta Zoologica*, 82, 177–187. [Stockholm]

http://dx.doi.org/10.1046/j.1463-6395.2001.00078.x

- Bick, A., Otte, K. & Meißner, K. (2010) A contribution to the taxonomy of *Spio* (Spionidae, Polychaeta, Annelida) occurring in the North and Baltic Seas, with a key to species recorded in this area. *Marine Biodiversity*, 40, 161–180. http://dx.doi.org/10.1007/s12526-010-0040-5
- 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. *In:* Blake, J.A., Hilbig, B. & Scott, P.H. (Eds.), *Taxonomic Atlas of the Benthic Fauna* of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. The Annelida Part 3 - Polychaeta: Orbiniidae to Cossuridae. Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 81–223.
- Blake, J.A. (2006) Spionida. In: Rouse, G. & Pleijel, F. (Eds.), Reproductive Biology and Phylogeny of Annelida. Vol. 4. Series: Reproductive Biology and Phylogeny. Science Publisher, Enfield, NH, pp. 565–638.
- Blake, J.A. & Arnofsky, P.L. (1999) Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Hydrobiologia*, 402, 57–106. http://dx.doi.org/10.1023/A:1003784324125
- 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.
- Blake, J.A. & Woodwick, K.H. (1976) A new species of *Boccardia* (Polychaeta: Spionidae) from two freshwater lakes in southeastern Australia. *Records of the Australian Museum*, 30, 123–128. http://dx.doi.org/10.3853/j.0067-1975.30.1976.397
- Blake, J.A. & Woodwick, K.H. (1981) The morphology of *Tripolydora spinosa* Woodwick (Polychaeta: Spionidae): an application of the scanning electron microscope to polychaete systematics. *Proceedings of the Biological Society of Washington*, 94, 352–362.
- Brito, M.C., Núñez, J. & Riera, R. (2006) A new species of the genus *Aonides* Claparede, 1864 (Polychaeta: Spionidae) from the Macaronesian region (Eastern Central Atlantic). *Scientia Marina*, 70, 59–64.
- Carazzi, D. (1893) Revisione del genere *Polydora* Bosc e cenni su due specie che vivono sulle ostriche. *Mittheilungen aus der zoologischen Station zu Neapel*, 11, 4–45.
- Chamberlin, R.V. (1919) The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 48, 1–514.
- Claparède, E. (1864) Glanures zootomiques parmi les Annélides de Port-Vendres (Pyrénées Orientales). *Mémoires de la Société de Physique et d'Histoire naturelle de Genève*, 17, 463–600.
- Czerniavsky, V. (1881) Materialia ad zoographiam Ponticam comparatam. Fasc. III. Vermes. *Bulletin de la Société impériale des naturalistes de Moscou*, 56, 338–420.
- Dagli, E. & Çinar, M.E. (2008) Invasion of polluted soft substratum of Izmir Bay (Aegean Sea, eastern Mediterranean) by the spionid polychaete worm, *Pseudopolydora paucibranchiata* (Polychaeta: Spionidae). *Cahiers de Biologie Marine*, 49, 87– 96.
- Dagli, E. & Çinar, 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. & Çinar, M.E. (2010) Presence of the Australian spionid species, *Prionospio paucipinnulata* (Polychaeta: Spionidae), in the Mediterranean Sea. *Cahiers de Biologie Marine*, 51, 311–317.
- Dagli, E. & Çinar, 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.
- Dauer, D.M. (1985) A new species of *Scolelepis* (Polychaeta: Spionidae) from Lizard Island, Australia. *Proceedings of the Biological Society of Washington*, 98, 678–681.
- Dauer, D.M. & Ewing, R.M. (1991) Functional morphology and feeding behavior of *Malacoceros indicus* (Polychaeta: Spionidae). *Bulletin of Marine Science*, 48, 395–400.
- Day, J.H. & Hutchings, P.A. (1979) An annotated check-list of Australian and New Zealand Polychaeta, Archiannelida and Myzostomida. *Records of the Australian Museum*, 32, 80–161. http://dx.doi.org/10.3853/j.0067-1975.32.1979.203
- Delgado-Blas, V.H. (2014) Redescriptions and reestablishments of some species belonging to the genus *Prionospio* (Polychaeta, Spionidae) and descriptions of three new species. *Helgoland Marine Research*, 68, 113–132. http://dx.doi.org/10.1007/s10152-013-0372-1
- Delgado-Blas, V.H. (2015) *Prionospio* (Polychaeta, Spionidae) from the Grand Caribbean Region, with the descriptions of five new species and a key to species recorded in the area. *Zootaxa*, 3905 (1), 69–90. http://dx.doi.org/10.11646/zootaxa.3905.1.4
- Fauchald, K. (1977) The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series*, 28, 1–188.

Fauvel, P. (1927) Polychètes sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. Faune de France, 16, 1–494.

Fauvel, P. (1929) Polychètes nouvelles du Golfe de Manaar (Inde). Bulletin de la Société zoologique de France, 54, 180–186.

- 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.
- Gibbs, P.E. (1971) The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum (Natural History) Zoology*, 21, 101–211.
- Greaves, E., Meißner, K. & Wilson, R. (2011) New *Laonice* species (Polychaeta: Spionidae) from western and northern Australia. *Zootaxa*, 2903, 1–20.
- Hannerz, L. (1956) Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden). *Zoologiska Bidrag, Uppsala*, 31, 1–204.
- Hartman, O. (1936) New species of Spionidae (Annelida Polychaeta) from the coast of California. University of California Publications in Zoology, 41, 45–52.
- Hartman, O. (1941) Some contributions to the biology and life history of Spionidae from California. With keys to species and genera and descriptions of two new forms. *Allan Hancock Pacific Expeditions*, 7, 289–323.
- Hartman, O. (1959) Catalogue of the Polychaetous Annelids of the World. Allan Hancock Foundation Publications, Occasional Papers, 23, 1–628.
- Hartmann-Schröder, G. (1971) Annelida, Borstenwürmer, Polychaeta. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise, 58, 1–594.
- Hartmann-Schröder, G. (1979) Teil 2. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby im Norden und Port Hedland im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 76, 77–218.
- Hartmann-Schröder, G. (1980) Teil 4. Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Port Samson im Norden und Exmouth im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 77, 42–110.
- Hartmann-Schröder, G. (1981) Teil 6. Die Polychaeten der tropisch-subtropischen Westküste Australiens (zwischen Exmouth im Norden und Cervantes im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 78, 19–96.
- Hartmann-Schröder, G. (1982) Teil 8. Die Polychaeten der subtropisch-antiborealen Westküste Australiens (zwischen Cervantes im Norden und Cape Naturaliste im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 79, 51–118.
- Hartmann-Schröder, G. (1983) Teil 9. Die Polychaeten der antiborealen Südwestküste Australiens (zwischen Dunsborough im Norden und Denmark im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 80, 123–167.
- Hartmann-Schröder, G. (1984) Teil 10. Die Polychaeten der antiborealen Südküste Australiens (zwischen Albany im Westen und Ceduna im Osten). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 81, 7–62.
- Hartmann-Schröder, G. (1985) Teil 11. Die Polychaeten der antiborealen Südküste Australiens (zwischen Port Lincoln im Westen und Port Augusta im Osten). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 82, 61–99.
- Hartmann-Schröder, G. (1987) Teil 13. Die Polychaeten der antiborealen Küste von Victoria (Australien) (zwischen Warrnambool im Western und Port Welshpool im Osten). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 84, 27–66.
- Hartmann-Schröder, G. (1989) Teil 14. Die Polychaeten der antiborealen und subtropisch-tropischen Küste Südost-Australiens zwischen Lakes Entrance (Victoria) im Süden und Maclean (New South Wales) im Norden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 86, 11–63.
- Hartmann-Schröder, G. (1990) Teil 15. Die Polychaeten der subtropisch-tropischen und tropischen Ostküste Australiens zwischen Lake Macquarie (New South Wales) im Süden und Gladstone (Queensland) im Norden. *In*: Hartmann-Schröder, G. (Ed.), Zur Kenntnis des eulitorals der australischen Küsten unter besonderer Berücksichtigung des Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 87, pp. 41–87.
- Hartmann-Schröder, G. (1991) Teil 16. Die Polychaeten der subtropisch-tropischen bis tropischen Ostküste Australiens zwischen Maclean (New South Wales) und Gladstone (Queensland) sowie von Heron Island (Grobes Barriere-Riff). In: Hartmann-Schröder, G. und G. Hartmann. Zur Kenntnis des eulitorals der australischen Küsten unter besonderer Berücksichtigung des Polychaeten und Ostracoden. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut, 88, 17–71.
- Hartmann-Schröder, G. (1992) Zur Polychaetenfauna der Polynesischen Inseln Huahiné (Gesellschaftsinseln) und Rangiroa (Tuamotu-Inseln). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 89, 49–84.
- Hartmann-Schröder, G. (1996) Annelida, Borstenwürmer, Polychaeta. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise, 58, 1–645.
- Haswell, W.A. (1885) On a destructive parasite of the rock oyster. *Proceedings of the Linnean Society of New South Wales*, 10, 273–275.
- Hewitt, C.L., Campbell, M.L., Thresher, R.E., Martin, R.B., Boyd, S., Cohen, B.F., Currie, D.R., Gomon, M.F., Keough, M.J., Lewis, J.A., Lockett, M.M., Mays, N., McArthur, M.A., O'Hara, T.D., Poore, G.C.B., Ross, D.J., Storey, M.J., Watson, J.E. & Wilson, R.S. (2004) Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Marine Biology*, 144, 183–202.
  - http://dx.doi.org/10.1007/s00227-003-1173-x

Hutchings, P. & Murray, A. (1984) Taxonomy of polychaetes from the Hawkesbury River and the southern estuaries of New

South Wales, Australia. *Records of the Australian Museum, Supplement*, 3, 1–118. http://dx.doi.org/10.3853/j.0812-7387.3.1984.101

- Hutchings, P. & Rainer, S. (1979) The polychaete fauna of Careel Bay, Pittwater, New South Wales, Australia. *Journal of Natural History, London*, 13, 745–796.
  - http://dx.doi.org/10.1080/00222937900770561
- Hutchings, P.A. (1981) Polychaete recruitment onto dead coral substrates at Lizard Island, Great Barrier Reef, Australia. Bulletin of Marine Science, 31, 410–423.
- Hutchings, P.A., Kiene, W.E., Cunningham, R.B. & Donnelly, C. (1992) Spatial and temporal patterns of non-colonial boring organisms (polychaetes, sipunculans and bivalve molluscs) in *Porites* at Lizard Island, Great Barrier Reef. *Coral Reefs*, 11, 23–31.

http://dx.doi.org/10.1007/BF00291931

- Hutchings, P.A. & Turvey, S.P. (1984) The Spionidae of South Australia (Annelida: Polychaeta). *Transactions of the Royal* Society of South Australia, 108, 1–20.
- Hylleberg, J. & Nateewathana, A. (1991) Polychaetes of Thailand. Spionidae (Part 1); *Prionospio* of the *steenstrupi* group with description of eight new species from the Andaman Sea. *Phuket Marine Biological Center Research Bulletin*, 55, 1–32.
- Imajima, M. (1989) Spionidae (Annelida, Polychaeta) from Japan. I. The genera *Aonides* and *Apoprionospio*. *Bulletin of the National Science Museum*, Series A (Zoology), 15, 213–222. [Tokyo]
- Imajima, M. (1990a) Spionidae (Annelida, Polychaeta) from Japan. IV. The genus Prionospio (Prionospio). Bulletin of the National Science Museum, Series A (Zoology), 16, 105–140. [Tokyo]
- Imajima, M. (1990b) Spionids (Annelida, Polychaeta) obtained by dredging from Oshima Strait and Yakiuchi Bay, Amami-Oshima of the Ryukyu Islands. *Memoirs of the National Science Museum*, 23, 93–99. [Tokyo]
- Jelsing, J. (2002) Ultrastructural investigations on the cephalic and metameric nuchal organs of *Spio* cf. *filicornis* (Polychaeta, Spionidae). *Zoomorphology*, 121, 213–220.

http://dx.doi.org/10.1007/s00435-002-0060-1

Jelsing, J. (2003) Ultrastructural studies of dorsal ciliated organs in Spionidae (Annelida: Polychaeta). *Hydrobiologia*, 496, 241–251.

http://dx.doi.org/10.1023/A:1026105200983

- Junqueira, A.O.R., Tavares, M.D.S., Schaeffer-Novelli, Y., Radashevsky, V.I., Cirelli, J.O., Julio, L.M., Romagnoli, F.C., dos Santos, K.C. & Ferreira-Silva, M.A.G. (2009) Capítulo 6 - Zoobentos. *In:* R.M. Lopes (Ed.), *Informe sobre as espécies exóticas invasoras marinhas no Brasil.* MMA/SBF, Brasília, pp. 145–371.
- Kohn, A.J. & Lloyd, M.C. (1973) Marine polychaete annelids of Easter Island. Internationale Revue der Gesamten Hydrobiologie, 58, 691–712.

http://dx.doi.org/10.1002/iroh.19730580508

- Langerhans, P. (1880) Die Wurmfauna von Madeira. III. Zeitschrift für wissenschaftliche Zoologie, 34, 87-143.
- Lebsky, V.K. (1970) Development of *Glycera capitata* Ørsted and *Aonides paucibranchiata* Southern (Annelides, Polychaeta). *Biology of the White Sea*, 3, 91–97.
- Lewis, J.B. (1998) Reproduction, larval development and functional relationships of the burrowing, spionid polychaete Dipolydora armata with the calcareous hydrozoan Millepora complanata. Marine Biology, 130, 651–662. [Berlin] http://dx.doi.org/10.1007/s002270050287
- 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, 325–383. http://dx.doi.org/10.1111/j.1096-3642.1985.tb01804.x
- Malmgren, A.J. (1867) Annulata polychæta Spetsbergiæ, Grönlandiæ, Islandiæ et Scandinaviæ hactenus cognita. Öfversigt af Kongl. Vetenskaps-akademiens forhandlingar Stockholm, 24, 127–235.
- McDiarmid, H., Day, R. & Wilson, R. (2004) The ecology of polychaetes that infest abalone shells in Victoria, Australia. Journal of Shellfish Research, 23, 1179–1188.
- Meißner, K. & Götting, M. (2015) Spionidae (Annelida: 'Polychaeta': Canalipalpata) from Lizard Island, Great Barrier Reef, Australia: the genera *Malacoceros, Scolelepis, Spio, Microspio*, and *Spiophanes. Zootaxa*, 4019 (1), 378–413. http://dx.doi.org/10.11646/zootaxa.4019.1.15
- Meißner, K. & Hutchings, P.A. (2003) Spiophanes species (Polychaeta: Spionidae) from Eastern Australia with description 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
- Monro, C.C.A. (1931) Polychaeta, Oligochaeta, Echiuroidea and Sipunculoidea. Great Barrier Reef Expedition 1928–29. Scientific Reports of the Great Barrier Reef Expedition British Museum Natural History, 4, 1–37.
- Okuda, S. (1937) Spioniform polychaetes from Japan. *Journal of the Faculty of Science, Hokkaido Imperial University*, Series VI (Zoology), 5, 217–254.
- Pettibone, M.H. (1963) Revision of some genera of polychaete worms of the family Spionidae, including the description of a new species of *Scolelepis*. *Proceedings of the Biological Society of Washington*, 76, 89–104.
- Poore, G.C.B. & Kudenov, J.D. (1978a) Benthos of the Port of Melbourne: the Yarra River and Hobson Bay, Victoria. Australian Journal of Marine and Freshwater Research, 29, 141–155.

http://dx.doi.org/10.1071/MF9780141

- Poore, G.C.B. & Kudenov, J.D. (1978b) Benthos around an outfall of the Werribee sewage-treatment farm, Port Phillip Bay, Victoria. Australian Journal of Marine and Freshwater Research, 29, 157–167. http://dx.doi.org/10.1071/MF9780157
- Radashevsky, V.I. (1993) Revision of the genus *Polydora* and related genera from the North West Pacific (Polychaeta: Spionidae). *Publications of the Seto Marine Biological Laboratory*, 36, 1–60.
- Radashevsky, V.I. (1996) Morphology, ecology and asexual reproduction of a new *Polydorella* species (Polychaeta: Spionidae) from the South China Sea. *Bulletin of Marine Science*, 58, 684–693.
- Radashevsky, V.I. (2007) Morphology and biology of a new *Rhynchospio* species (Polychaeta: Spionidae) from the South China Sea, Vietnam, with the review of *Rhynchospio* taxa. *Journal of Natural History, London*, 41, 985–997. http://dx.doi.org/10.1080/00222930701376717
- 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.
- Radashevsky, V.I. (2013) The Origin and Evolution of Spionidae (Annelida). In: Program and Abstract Book. 11th International Polychaete Conference - Sydney, Australia 4–9 August 2013. Sydney, Australia, pp. 106.
- Radashevsky, V.I. & Fauchald, K. (2000) Chaetal arrangement and homology in spionids (Polychaeta: Spionidae). *Bulletin of Marine Science*, 67, 13–23.
- 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. http://dx.doi.org/10.1017/S002531540800177X
- Radashevsky, V.I., Neretina, T.V., Pankova, V.V., Tzetlin, A.B. & Choi, J.-W. (2014) Molecular identity, morphology and taxonomy of the *Rhynchospio glutaea* complex with a key to *Rhynchospio* species (Annelida, Spionidae). *Systematics and Biodiversity*, 12, 424–433.
  - http://dx.doi.org/10.1080/14772000.2014.941039
- 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. http://dx.doi.org/10.1017/S0025315403007227h
- Ramos, J.M. (1976) Aonides oxycephala (Sars, 1862) remarques taxonomiques. Vie et Milieu, Série A, 26, 11-20.
- Reish, D.J. (1968) The polychaetous annelids of the Marshall Islands. Pacific Science, 22, 208-231.
- Ribas, J. & Hutchings, P. (2015) Lizard Island Polychaete Workshop: sampling sites and a checklist of polychaetes. *Zootaxa*, 4019 (1), 7–34.

http://dx.doi.org/10.11646/zootaxa.4019.1.4

- Rioja, E. (1947) Estudios anelidologicos. XVII. Contribucion al conocimiento de los anelidos poliquetos de Baja California y Mar de Cortes. *Anales del Instituto de Biología*, 18, 197–224. [México]
- Rößger, A., Meißner, K., Bick, A. & Müller, C.H.G. (2015) Histological and ultrastructural reconstruction of ventral epidermal glands of *Spio* (Polychaeta, Spionidae, Annelida). *Zoomorphology*. [published online] http://dx.doi.org/10.1007/s00435-015-0264-9
- Rouse, G.W. (1988) An ultrastructural study of the spermatozoa from *Prionospio* cf. *queenslandica* and *Tripolydora* sp.: Two spionid polychaetes with different reproductive methods. *Acta Zoologica (Stockholm)*, 69, 205–216. http://dx.doi.org/10.1111/j.1463-6395.1988.tb00917.x
- Sato-Okoshi, W., Okoshi, K. & Shaw, J. (2008) Polydorid species (Polychaeta: Spionidae) in south-western Australian waters with special reference to *Polydora uncinata* and *Boccardia knoxi*. *Journal of the Marine Biological Association of the United Kingdom*, 88, 491–501.

http://dx.doi.org/10.1017/S0025315408000842

- Sigvaldadóttir, E. (1997) A new species of *Prionospio* (Polychaeta: Spionidae) from the Cape d'Aguilar Marine Reserve, Hong Kong. *In:* B. Morton (Ed.), 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.

http://dx.doi.org/10.1111/j.1463-6409.1998.tb00435.x

- Sigvaldadóttir, E. & Mackie, A.S.Y. (1993) *Prionospio steenstrupi*, *P. fallax* and *P. dubia* (Polychaeta, Spionidae): reevaluation of identity and status. *Sarsia*, 78, 203–219.
- Sigvaldadóttir, 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
- Skilleter, G.A., Russel, B.D., Degnan, B.M. & Garson, M.J. (2005) Living in a potentially toxic environment: comparison of endofauna in two congeneric sponges from the Great Barrier Reef. *Marine Ecology Progress Series*, 304, 67–75. http://dx.doi.org/10.3354/meps304067

Storch, V. (1966) Drei neue Polychaeten aus dem Litoral des Roten Meeres. Kieler Meeresforschungen, 22, 171–175.

Sveshnikov, V.A. (1967) Larvae of Archiannelids and Polychaets of the Possjet Bay (the Sea of Japan). *Explorations of the Fauna of Seas*, 5, 125–159.

Tzetlin, A.B. & Britayev, T.A. (1985) A new species of the Spionidae (Polychaeta) with asexual reproduction associated with

sponges. Zoologica Scripta, 14, 177–181.

http://dx.doi.org/10.1111/j.1463-6409.1985.tb00188.x

- 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.
- Walker, L.M. (2011) A review of the current status of the *Polydora*-complex (Polychaeta: Spionidae) in Australia and a checklist of recorded species. *Zootaxa*, 2751, 40–62.
- Ward, L.A. (1981) Spionidae (Polychaeta: Annelida) from Hawaii, with descriptions of five new species. *Proceedings of the Biological Society of Washington*, 94, 713–730.
- Ward, L.A. (1987) Family Spionidae. [*In*: J.H. Bailey-Brock: Phylum Annelida.] *In*: D.M. Devaney & L.G. Eldredge (Eds.), Bishop Museum Press, Honolulu, pp. 340–369.
- Williams, J.D. (2001) Polydora and related genera associated with hermit crabs from the Indo-West Pacific (Polydora: Spionidae), with descriptions of two new species and a second polydorid egg predator of hermit crabs. Pacific Science, 55, 429–565.

http://dx.doi.org/10.1353/psc.2001.0037

- Williams, J.D. (2004) Reproduction and morphology of *Polydorella* (Polychaeta: Spionidae), including the description of a new species from the Philippines. *Journal of Natural History, London*, 38, 1339–1458.
- Wilson, R.S. (1990) Prionospio and Paraprionospio (Polychaeta: Spionidae) from Southern Australia. Memoirs of Museum Victoria, 50, 243–274.
- Wilson, R.S. & Humphreys, W.F. (2001) *Prionospio thalanji* sp. nov. (Polychaeta: Spionidae) from an anchialine cave, Cape Range, north-west Western Australia. *Records of the Western Australian Museum Supplement*, 64, 105–113.
- Woodwick, K.H. (1964) *Polydora* and related genera (Annelida, Polychaeta) from Eniwetok, Majuro, and Bikini Atolls, Marshall Islands. *Pacific Science*, 18, 146–159.
- Zhou, J. & Li, X.Z. (2009) Report of *Prionospio* complex (Annelida: Polychaeta: Spionidae) from China's waters, with description of a new species. *Acta Oceanologica Sinica*, 28, 116–127.