Oligodendrorhynchus hesperides gen. et sp. n. (Heteronemertea) from the Bellingshausen Sea

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Abstract: A new genus and species of heteronemertean from the Antarctic (Bellingshausen Sea), *Oligodendrorhynchus hesperides*, is described and illustrated. Some morphological features with major systematic significance are following: the mode of branching of the proboscis and its low number of terminal branches; the lack of horizontal lateral cephalic slits but in their place a pair of shallow epidermal depressions; a gelatinous amorphous connective stratum between the outer longitudinal and circular muscle layers; the presence of a rhynchocoelic nerve; isolated fibres of the rhynchocoel circular muscle layer interwoven with bundles of the adjacent body-wall inner longitudinal muscle fibres in the intestinal region. Other anatomical characters which can also be used to distinguish the new taxon from existing heteronemertean species that have a branched proboscis are also discussed.

Key words: Antarctic, Nemertea, branched proboscis, *Oligodendrorhynchus*.

Introduction

In the most recent revision of Antarctic marine benthic diversity by Clarke and Johnston (2003), the Nemertea are considered to be a relatively well-known group. However, in Gibson's (1985a) revision of heteronemerteans from Antarctic and Subantarctic waters south of latitude 50°S, none of the 15 heteronemertean genera were reported to have a branched proboscis. A recent publication on Antarctic nemertean biodiversity, based only on molecular techniques, suggests that this biodiversity is greatly underestimated (Mahon *et al.* 2010).

During the Spanish Antarctic Expedition (Bentart-03) nemerteans were collected from several locations, mainly in the Bellingshausen Sea and in surrounding areas at depths ranging from 10 to 2045 m. The Bellingshausen Sea, in the western sector of Antarctica, is one of the least explored Antarctic seas due to the preva-

lence of ice (Saíz *et al*. 2008); its benthic communities have been researched relatively poorly.

The collection includes hoplonemerteans (Uz *et al.* 2010) and heteronemerteans, and among the latter a single specimen with a branched proboscis was found. To date, four genera with a branched proboscis have been described (*Gorgonorhynchus* Dakin and Fordham, 1931; *Panorhynchus* Serna de Esteban and Moretto, 1969*; Polybrachiorhynchus* Gibson, 1977 and *Dendrorhynchus* Yin and Zeng, 1985). The most recent revision of heteronemerteans with a branched proboscis was made by Sun (2006), in which three species from China are synonymized in a single taxon – *Dendrorhynchus sinensis* Yin and Zeng, 1985 – and it was compared with the rest of the species of heteronemerteans with a branched proboscis.

The present paper describes a new species of Heteronemertea from the Bellingshausen Sea (the Antarctic). Although cladistic validity of Gibson's (1985b) family groupings has been challenged (Schwartz and Norenburg 2001, Sundberg *et al.* 2009), for practical purposes the species belongs to Gibson's (1985b) Group E, in having a branched proboscis; yet it possesses a combination of characters that excludes it from any of the genera within this group.

Material and methods

The material examined was obtained during the "Bentart-03" Spanish Antarctic expedition, in February 2003, from the Bellingshausen Sea (the Antarctic) – off Peter I Island – 68° 49.61'S 90°48.78'W (station 6), aboard the RV *Hespérides*. Peter I Island is an isolated oceanic island of volcanic origin (Kimura 1982) in the Antarctic sector corresponding to the Bellingshausen Sea (Fig. 1c).

The only specimen available was collected at 210 m depth with a Box-corer, from dark muddy-sand and gravel bed (73.25% silt, 26.40% sand, 0.36% gravel and 1.83% organic matter); redox (Eh) value 31.4.

The living animal was anaesthetised in 7.5% $MgCl_2$ in distilled water prior to fixation in Bouin's fluid. For internal morphological examination, the specimen was embedded in paraffin following the Peterfi method (Pantin 1968). It was sectioned at 7 μm and stained with Para-pak® (Meridian Biosciences, Inc., Cincinnati, Ohio) trichrome method.

Results and discussion

Oligodendrorhynchus gen. n.

Etymology: The generic name *Oligodendrorhynchus* refers to the presence of a branched proboscis with a small number of branches. It is derived from the Greek: *oligo* (a few), *dendron* (tree) and *rhynchos* (snout).
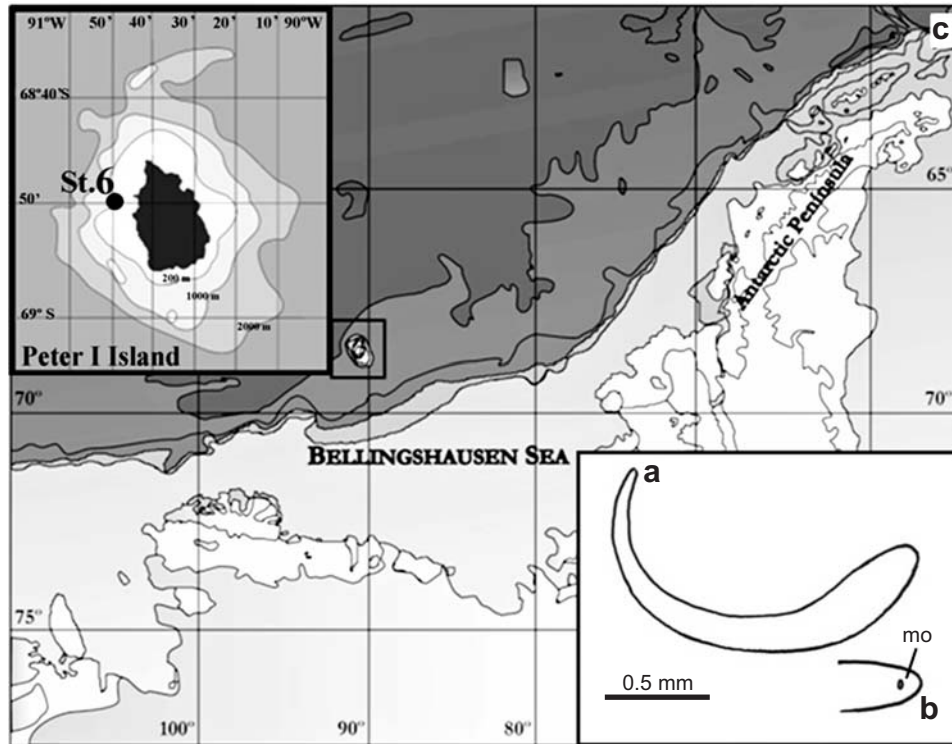
Fig. 1. *Oligodendrorhynchus hesperides* gen. et sp. nov. **a**. Sketch of the preserved specimen (holotype). **b**. Sketch of the anterior end from ventral surface. **c**. Map of Bentart-03 expedition with the location of station where *Olygodendrorhynchus hesperides* gen. et sp. nov. was found. mo, mouth.

Diagnosis. — Heteronemertean with head bearing lateral shallow epidermal depressions (not cephalic slits); branched proboscis having an undivided main axis from which some primary branches emerge alternately; proboscis axis contains three muscle layers (outer and inner longitudinal, middle circular) and one muscle cross; isolated fibres of the rhynchocoelomic circular muscle laterally and ventrally interwoven with bundles of adjacent body-wall inner longitudinal muscle in intestinal region; dermis separated from outer longitudinal muscle fibres by fibrous connective tissue layer; outer longitudinal and body-wall circular muscle separated by gelatinous, amorphous connective stratum; intestine with distinct coating of circular and longitudinal muscle fibres; fibrous core of dorsal brain lobe not forked posteriorly; neurochords in lateral nerve cords; rhynchocoelic nerve and mid-dorsal nerve present; frontal organ with three separate pits; blood system in foregut region developed into a vascular plexus.

Oligodendrorhynchus hesperides sp. n.

Type specimen: Holotype female, 23 mm long and 2 mm maximum width; 26 slides of serial transverse sections through the anterior portion of the body including the head, foregut re-

gion and anterior intestinal region. The specimen has been deposited in the Museo Nacional de Ciencias Naturales, Madrid (MNCN.5.01/15).

Type locality: West of Peter I Island, Bellingshausen Sea (68°49.61'S 90°48.78'W), 210 m depth, muddy-sand and gravel bed, February 2003.

Etymology: The specific name *hesperides* refers to the specimen being collected from the RV *Hespérides*.

Diagnosis. — Body cylindrical anteriorly, intestinal region dorsoventrally compressed; uniform pale pink colour; head rounded, not distinctly demarcated from remainder of body; lacking eyes; proboscis with maximum number of six terminal branches; caudal cirrus is absent.

Description. — *External features*: The anaesthetized living specimen measured 23 mm long and 2 mm in width. The body anterior region is rounded, while the posterior region is dorsoventrally compressed (Figs 1a, b, 2a, b). Overall body colour is a pale pink.

The head is not well delimited, without eyes, and, as seen in transverse sections, bears a single pair of horizontal lateral shallow epidermal depressions (Figs 2a, 4b). At the rear of the head a small mouth is situated ventrally (Fig. 1b). The posterior end of the body presents a slightly pointed tip that appears intact and lacks a caudal cirrus.

Body-wall, musculature and parenchyma: The epidermis, 50–57 μm thick, is composed of ciliated columnar cells and by numerous oval red-stained serous gland-cells and some mucous glands. The basement layer is up to 6 μm thick; the dermis is 85–140 mm thick. The outermost dermal zone is predominantly fibrous and the innermost region presents packets of subepithelial glands, as well as muscle fibres of the outer longitudinal muscle stratum (Fig. 2c). The body wall possesses the characteristic heteronemertean arrangement but has a gelatinous amorphous connective stratum, 20–29 mm thick, between the outer longitudinal and main circular musculature. The fibrous nerve sheath encircling the body between the circular and outer longitudinal muscle zone forms a layer inside the amorphous stratum.The amorphous stratum appears in the foregut region and extends along the body (Fig. 2d).

Fig. 2. *Oligodendrorhynchus hesperides*. **a**. Transverse section through the cerebral region. **b**. Transverse section through the posterior portion of intestinal region showing the arrangement of the various body structures, including the ovaries. **c**. Transverse section through a part of the body wall, showing the basement layer. **d**. Transverse section at the level of the foregut region showing the amorphous intercellular stratum, white arrowheads points to the circular fibres of splanchnic musculature. **e**. Transverse section through the foregut region, showing a detail of the foregut and rhynchocoel close to a nephridial duct (arrowhead).**f**. Transverse section through the foregut region to show a sagittal section of the nephridial efferent canal and nephridiopore (arrowhead). **g**. Transverse section through the posterior intestinal region, white arrowheads to the dorso-ventral muscles, the arrows points to the circular muscle fibres around the mid-dorsal vessel. ais, amorphous intercellular stratum; cd, connective tissue layer of dermis; cl, cephalic lacunae; cm, circular muscle layer; ep, epidermis; fg, foregut; gd, glandular layer of dermis; ilm, inner longitudinal muscle layer; in, intestine; lbv, lateral blood vessel; lnc, lateral nerve cord; mbv, mid-dorsal blood vessel; ns, neural sheath; oc, opening of cerebral organ; olm, outer longitudinal muscle layer; ov, ovary; rc, rhynchocoel. a–b: scale bar = 500 μm; c–g: scale bar = 100 μm.
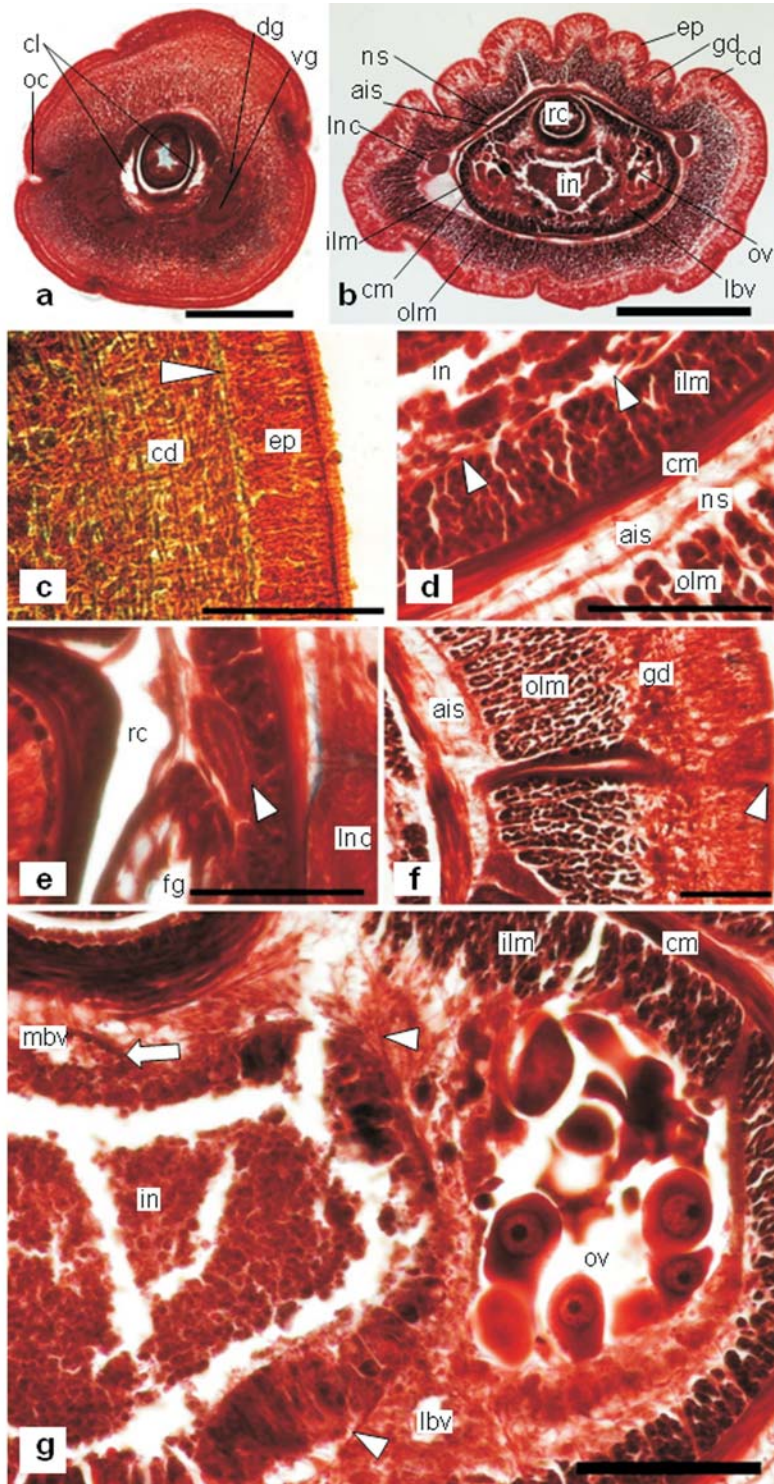
In *Amorphonemertes kubergensis*, a heteronemertean from Tromsø area (Northern Norway), Cantell (1998) reported a special basement membrane, with amorphous intercellular substance containing few cells and a lot of fibres, which resembles the dermis composed of hyaline connective tissue in paleonemerteans; this amorphous stratum was also observed in a specimen of heteronemertean collected in the benthos off Livingston Island (South Shetland Islands) (N. Anadón unpublished observation). Yet, the novelty for the present specimen of heteronemertean is a similar amorphous stratum situated inward, between the outer longitudinal and circular muscle layers.

The thickness of the three muscle layers is variable, according to the contraction state of the body. The inner longitudinal muscle layer is thinner in the dorsal region than in the ventral region. It is particularly thin in the foregut region, where the rhynchocoel becomes more spacious and contains some branches of the proboscis or the folded proboscis. The maximum thickness of these body-wall layers are: outer longitudinal muscle layer, ~160 μm; neural sheath, ~15 μm; gelatinous layer, ~60 μm; circular muscle layer, ~30 μm; inner longitudinal muscle layer, ~60 μm. The longitudinal muscle layers are irregularly penetrated by radial connective fibres that extend to the epidermis (Fig. 2f).

Posteriorly, in the intestinal region, a parenchymatous extracellular matrix, with some circular and longitudinal muscle fibres, is well-developed between the inner longitudinal muscle layer and the intestine, and also around the gonads. However, in the foregut the parenchyma is weakly formed.

In the foregut region, there is no horizontal longitudinal muscle plate between the dorsal wall and the rhynchocoel, unlike other genera with a branched proboscis – *Gorgonorhynchus*, *Polybrachiorhynchus* and *Dendrorhynchus* – Sun (2006) (Table 1).

Similarly to *Panorhynchus* (Serna de Esteban and Moretto 1969; Gibson 1977), the dorsoventral muscles are scarce and confined to the gonadal region (Fig. 2g). By contrast, *Polybrachiorhynchus* has well-developed ones that extend along the body (Gibson 1977).

In the rhynchodeal region radial fibres from all parts of the inner longitudinal muscle layer form the proboscideal insertion muscle, a closed pre-cerebral septum.

Rhynchodaeum: The proboscis pore opens subterminally and ventrally (~35 μm diameter) and leads into a short thin-walled rhynchodaeum lined by a ciliated but non-glandular epithelium (~20 μm thick) in the anterior region. The rhynchodaeum is elliptical in its transverse section and is enclosed in its posterior portion by some circular muscle fibres that, in turn, are situated between the incipient inner longitudinal muscle layer of the body wall and precerebral blood lacunae (Fig. 3a). At its posterior, the rhynchodeal epithelium presents some acidophilic cells.

Rhynchocoel: The rhynchocoel extends through the whole length of the body and the area of its transverse section is very variable depending on the number of

Table 1

Comparison of the five heteronemertean genera with a branched proboscis. Based on Gibson (1977), Sun (2006) and the present study.

Characters	Gorgonorhynchus	Panorhynchus	Polybrachiorhynchus	Dendrorhynchus	Oligodendrorhynchus
Caudal cirrus	present	absent	present	absent	absent
Branching mode of proboscis	regularly dichotomous	alternate from main axis	alternate from main axis	alternate from main axis	alternate from main axis
Plane of proboscis branching	successive branches at right angles to each other	open spiral	single plane	single plane	unknown
Maximum number of terminal branches of proboscis	64[1]	22[1]	96[1]	110[2]	6[2]
Valves in axils of proboscis branches	present	absent	absent	absent	absent
Number of muscle layers in main portion of unbranched proboscis axis	2	3	3	3	3
Number of muscle layers in terminal branches of proboscis	3	2	2	2	3
Number of muscle crosses in main proboscis axis	0	1	2	2	1
Number of muscle crosses in terminal branches of proboscis	2	0	0	0	1
Body-wall subepidermical gland zone separated from outer longitudinal muscles by distinct connective tissue stratum	absent	present	present	present	present
Fibrous core of dorsal cerebral lobe posteriorly forked or not	forked	not forked	not forked	forked	not forked
Horizontal muscle plate of longitudinal muscle fibres	present	absent	present	present	absent
Muscles around foregut	absent	spiral	circular	circular+longitudinal	circular+longitudinal
Foregut subepithelial gland layer	present	absent	present	present	present
Longitudinal splanchnic muscles around intestine	absent	absent	present	present	absent
Intestine with differential distribution of lateral diverticula and gland cells	absent	absent	present	present	absent
Cephalic lacunar network of blood system	absent	present	present	present	present
Foregut vascular plexus	absent	present	present	present	present
Main longitudinal vessels with distinct muscular walls	mid-dorsal vessel only	mid-dorsal vessel only	mid-dorsal and lateral vessels	mid-dorsal vessel and lateral vessels	mid-dorsal and lateral vessels
Number of circular muscle layers around rhynchodaeum	2	1	1	1	1
Frontal organ	trifoliate, opening *via* a common pore	unknown	three pits, opening separately	three pits, opening separately	three pits, opening separately
Rhynchocoelic nerve	unknown	unknown	unknown	present	present

[1] Theoretical number. [2] Observed number.

branches and folds of the proboscis (Fig. 3b); at the anterior part of the intestinal region it is very spacious and contains up to nine sections of the proboscis axis and the proboscis branches (Fig. 3g–h).

The rhynchocoel wall consists of an outer circular and inner longitudinal muscle layer and a lining endothelium. The thickness of these layers changes hugely according to the extension of the cavity. In the rhynchocoelic ventral part, at the level of the intestinal region, several fibres of the circular muscle layer are entwined with the internal longitudinal muscle layer of the body wall, as if it was an anchorage (Fig. 3c). This feature was also observed by Sun (2006) in *Dendrorhynchus* and four other genera of heteronemerteans: *Micrurides*, *Micrurinella*, *Craticulineus* and *Paramicrurinella* (Gibson 1984, 1985b; Cantell 1988).

Among nemerteans with a branched proboscis it appears to be common that the anterior region of the rhynchocoel is divided into a series of chambers by folds of its wall (Sun 2006), as was observed by Dakin and Fordham (1936) in *Gorgonorhynchus,* by Gibson (1977) in *Polybrachiorhynchus* and by Sun (2006) in *Dendrorhynchus*. However, this condition is not present in *Oligodendrorhynchus*.

Proboscis apparatus: The proboscis is of a typical heteronemertean structure but it is branched, with a branching pattern that differs from all other heteronemerteans. It consists of a single long main axis and five primary branches that arise alternately along the main axis (Fig. 3f). One of them is secondarily branched, and only once. The plane of proboscis branches is unknown, because the only specimen found has the proboscis withdrawn.

The thickness of the proboscis axis and the branches are similar, unlike the condition in *Gorgonorhynchus, Panorhynchus*, *Polybrachiorhyncus* and *Dendrorhynchus*, where the branches are distinctly thinner than the axial portion.

The maximum number of primary branches of the proboscis is lower (5) than in the other genera and species with a branched proboscis that have been described. The main proboscis axis and its branches possess the same recognisable layers: an outer glandular epithelium up to 50–60 μm, an outer longitudinal muscle layer about 15 μm thick, a neural sheath not developed into distinct nerves, a circular

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Fig. 3. *Oligodendrorhynchus hesperides*. **a**. Transverse section through the rhynchodaeal region, →
showing circular muscle fibres around the rhynchodaeum. **b**. Transverse section through the rhynchocoel and the proboscis at the level of the intestinal region. **c**. Transverse section to show the rhynchocoel wall organisation at the intestinal region, the black arrowhead points to the muscular fibres of rhynchocoel circular muscle layer interwoven with the inner muscular layer. **d**. Transverse section through the foregut region of a branch of proboscis, showing the structure of the proboscis wall. **e**. Transverse section through the proboscis wall, white arrowhead points to a muscle cross. **f**. Schematic reconstruction showing the branching of the proboscis apparatus inside of the rhynchocoel, from 538 transverse sections, 1–5 primary branches. **g–h**. Transverse section of the rhynchocoel at A – level and B – level, anterior-to-posterior, of the reconstruction of the proboscis; en, endothelium; ma, main axis; pcm, circular muscles; pe, proboscidial epithelium; pilm, proboscidial inner longitudinal muscles; pns, proboscidial neural sheath; polm, proboscidial outer longitudinal muscles; sb, secondary branches. a–f, h: scale bar = 100 μm; g: scale bar = 500 μm.
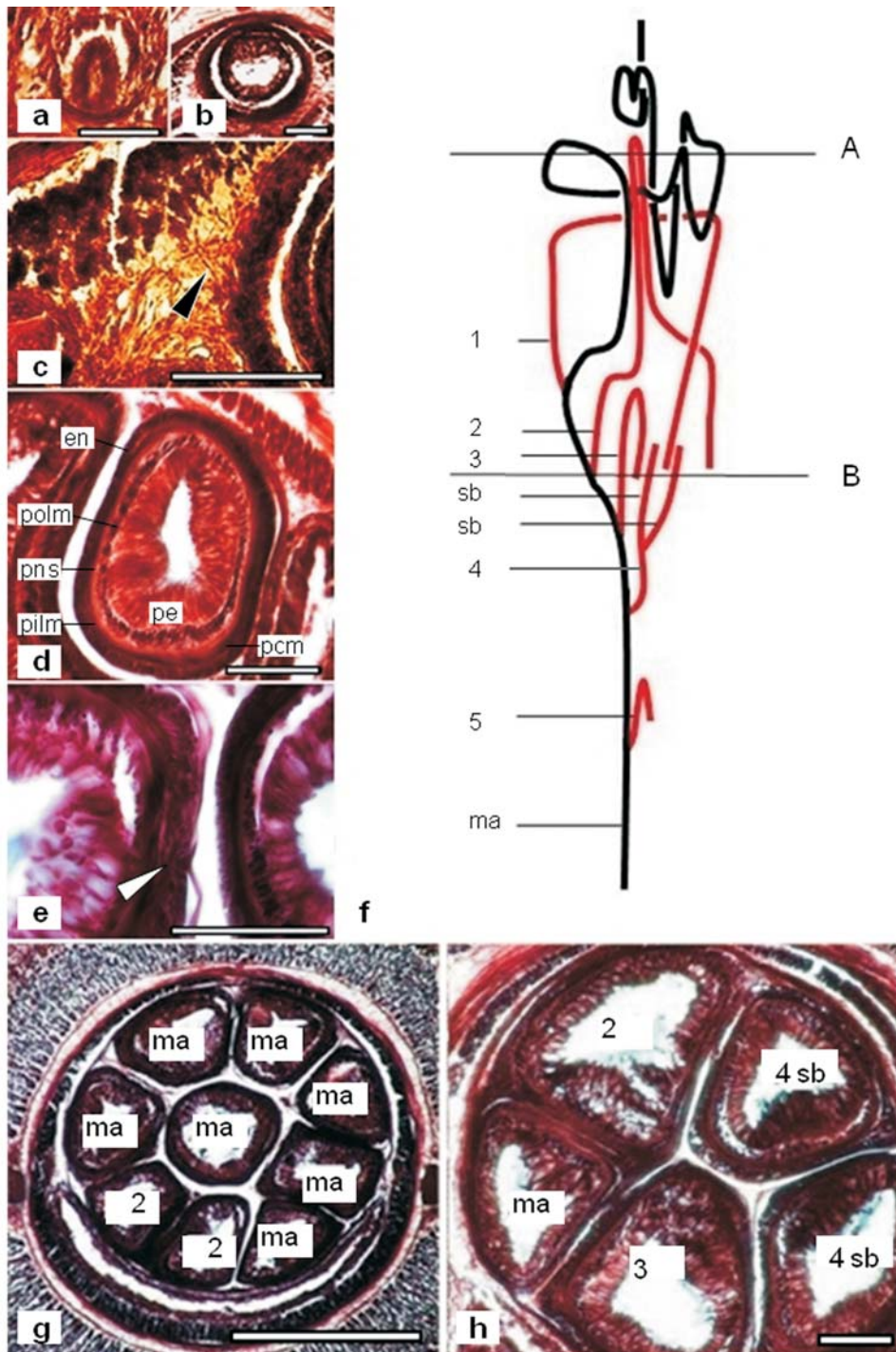
muscle layer about 10 μm thick, an inner longitudinal muscle layer 15 μm thick and a flattened endothelium (Fig. 3d). Below the flat endothelium is a thin inner circular muscle layer. The epithelium of the proboscis is dominated by cells producing mucus and rhabditoids (Fig. 3e).

In several sections of the main axis and branches one muscle cross extends from the circular muscle layer through the longitudinal muscle fibres to the flat endothelium (Fig. 3e). The main axis and the branches do not show histological differences.

Gorgonorhynchus differs by having two muscle crosses in branches and not having one in the main axis. The other genera do not have a muscle cross in primary branches, but *Panorhynchus* has only one in the main axis and *Polybrachiorhynchus* and *Dendrorhynchus* have two in the unbranched region (Sun 2006) (Table 1).

Digestive system: The mouth is small and oval and opens ventrally immediately behind the ventral cerebral ganglia. The mouth and buccal cavity are surrounded by a densely ciliated epithelium and glandular cells with mucous or acidophilic secretion. Also, in the buccal cavity and in the foregut there is a subepithelial stratum with glands distributed in the parenchyma about 100 μm thick. The foregut epithelium in the ventral foregut wall is deeply folded, 60–70 μm thick and it is surrounded by a subepithelial gland zone, which is in turn enclosed by a thin covering, up to 4 μm thick, of circular and longitudinal splanchnic musculature (Fig. 2d). The dorsal part of the foregut has a thin epithelium and there is no somatic muscle plate between this part of the gut and the rhynchocoel. In contrast, *Polybrachiorhynchus dayi* has a delicate layer of circular fibres around the foregut and a horizontal muscle plate between the rhynchocoel and dorsal foregut wall (Gibson 1977). In *Gorgonorhynchus* spp. definitive splanchnic muscle is lacking and in *Panorhynchus* it is apparently formed by spiral fibres. Sun (2006) observed in *Dendrorhynchus* that the circular muscles are intermingled with longitudinal muscle fibres along the dorsal margin of the foregut, thereby forming a weakly developed muscle plate.

The anterior region of intestine is flattened dorsoventrally under the spacious rhynchocoel and the intestine lacks lateral diverticula. Posteriorly, the intestine is not compressed and lacks lateral pouches (Fig. 2b). The intestinal lining is composed of ciliated columnar and acidophilic gland cells filled with numerous small spherical globules. Immediately beneath the epithelium, some circular and longitudinal muscle fibres can be observed, but this does not constitute a conspicuous splanchnic muscle layer. This is the same as in *Gorgonorhynchus* and *Panorhynchus* but contrasts with *Polybrachiorhynchus dayi* (Gibson 1977).

Blood system: A single thin-walled cephalic blood lacuna begins near the cephalic tip, in front of the proboscis pore, and extends posteriorly and ventrally beside the rhynchodaeum, where it is subdivided by muscle strands and surrounded by the inner longitudinal muscle fibres of the cephalic muscle cylinder, near the proboscis insertion. The cerebral lacunae run internal to the brain lobes and give rise to the

two crescent-like lacunae flanking the rhynchocoel (Fig. 2a). Posteriorly, the two lacunae meet medially to form a flattened lacuna beneath the anterior rhynchocoel; this gives rise posteriorly to the mid-dorsal blood vessel. Near the front of the mouth the lacuna splits to form the origin of the foregut vascular plexus. There is no rhynchocoelic villus.

In the foregut and the anterior intestinal region there are two vascular plexus: between the inner longitudinal muscle layer and the gut; and between the gut and the rhynchocoel. In the foregut region lateral vessels are associated with the nephrotubules (Fig. 2e).

Panorhynchus, *Polybrachiorhynchus* and *Dendrorhynchus* coincide with the present species in having a foregut with vascular plexus (Table 1). However, it can be distinguished from *Gorgonorhynchus*, *Polybrachiorhynchus* and *Dendrorhynchus* by absence of a rhynchocoel villus (Gibson 1974, 1977; Sun 2006).

Throughout most of the intestinal region the blood system is reduced to a pair of lateral vessels and a mid-dorsal vessel lined by a thin endothelium. The main longitudinal vessels bear inner circular and outer longitudinal muscle fibres only in the posterior intestinal region (Fig. 2g).

Excretory system: The excretory collecting tubules are located in the foregut region and adjacent to the lateral blood vessels and the foregut vascular plexus. They extend from about 0.5 mm behind the mouth to about 1 mm back. The main nephridial canals are branched asymmetrically, at most into three ducts. The cuboidal nephridial epithelium is about 10 μm thick (Fig. 2e).

Two symmetrical efferent tubules enter the body wall and discharge to the exterior by a single pair of nephridiopores positioned on the dorsolateral body surface. The efferent duct is about 20 μm in diameter (Fig. 2f).

The nephridial arrangements show quite distinctive differences in genera with a branched proboscis: in *Gorgonorhynchus* the number of nephridiopores is variable from one to four, but only two main longitudinal tubes are distinguishable (Dakin and Fordham 1936; Gibson 1974); in *Polybrachiorhynchus* the tubules are profusely branched alongside the ventrolateral margins of the foregut but with two efferent ducts open to the dorsolateral surface (Gibson 1977); in *Panorhynchus* there are several main collecting tubules (Gibson 1977); in *Dendrorhynchus*, Sun (2006) observed a similar pattern to that of *Polybrachiorhynchus*.

Nervous system: The brain consists of two ventral and two dorsal ganglia, situated anteriad of the mouth (Fig. 4c, d). All the brain mass is surrounded by longitudinal muscle fibres of the cephalic body wall.

The dorsal and ventral ganglia are joined by dorsal and ventral commissures, situated above and below the rhynchocoel respectively. The dorsal cerebral commissure is at the front edge of the dorsal ganglia (Fig. 4b), about 40 μm thick, and the ventral commissure is broader, about 75 μm thick. The dorsal ganglia are approximately 2.5 times larger than the ventral ganglia. The brain is enclosed by a

delicate outer neurilemma and an evident inner neurilemma (Fig. 4c, d). Around the fibrous cores of the dorsal and ventral cerebral lobes, there is ganglionic tissue with numerous cells about 5–7 μm in diameter surrounding the central core of the dorsal and ventral ganglia and, as well, several cells 12–14 μm in diameter, close to the inner neurilemma of the ventral ganglia. The dorsal fibre cores are not posteriorly forked as reported for *Gorgonorhynchus* and *Dendrorhynchus*. No neurochord cells were observed in the ganglionic layer.

In the posterior region of each dorsal lobe there is a transition zone with the cerebral organs (Fig. 4d). The ventral ganglia on either side extend into the main two lateral nerve cords at the posterior end of the cerebral organs, in the normal heteronemertean position. Single neurochord cells were observed asymmetrically distributed in the fibrous core of the lateral nerve cords. Neurochords were reported for the lateral nerve cords of *Panorhynchus* and in *Polybrachiorhynchus* (Serna de Esteban and Moretto 1969; Gibson 1974).

Several other distinct nerves are found. A mid-dorsal nerve is present outside the middle circular muscle layer and is connected with a rhynchocoelic nerve that is in contact with the rhynchocoelic musculature. Such a rhynchocoelic nerve was found by Sun (2006) in *Dendrorhynchus*. External to the outer circular muscle layer, the lateral and mid-dorsal nerves are connected by a peripheral network (Fig. 4g).

A pair of buccal nerves arises from the two ventral cerebral lobes, but these nerves are not observed posteriad of the mouth, where a distinct nerve plexus is present (Fig. 4d).

The proboscis nerve supply is simple. In the main axis of the proboscis and in the branches, a neural sheath within the proboscis wall is formed between the outer longitudinal and circular muscle layers (Fig. 3d).

Sense organs: The precerebral part of the body possesses mucus-secreting cephalic glands that discharge through the three separate pits of the frontal organ (Fig. 4a). Each pit is ~45 μm deep and extends inward as a canal about ~75 μm long, lined by columnar ciliated epithelium without gland cells.

Fig. 4. *Oligodendrorhynchus hesperides*. **a**. Transverse section through the precerebral region show- →
ing the three areas of cephalic glands (black arrowheads) and one frontal pit (white arrowheads). **b**. Transverse section through the anterior cerebral region, black arrowhead points to the dorsal commisure, white arrowhead points to the precerebral septum. **c**. Transverse section through the region of the dorsal and ventral ganglia, white arrowhead points to inner neurilemna. **d**. Transverse section through the posterior cerebral region to show the ventral ganglion and cerebral sensory organ, the buccal nerve is arrowed, black arrowhead points to outer neurilemma, white arrowhead to inner neurilemma. **e**. Transverse section through cephalic region showing the horizontal lateral shallow epidermal depression (arrowhead). **f**. Transverse section at the level of the posterior cerebral region, showing the canal of cerebral organ (black arrowhead) with its opening to external medium (white arrowhead). **g**. Transverse section through the intestinal region showing the mid-dorsal nerve (black arrowhead) and the rhynchocoelic nerve (white arrowhead). co, cerebral organ; dg, dorsal cerebral ganglion, vg, ventral cerebral ganglion. b: scale bar = 500 μm, a, c–g: scale bar = 100 μm.
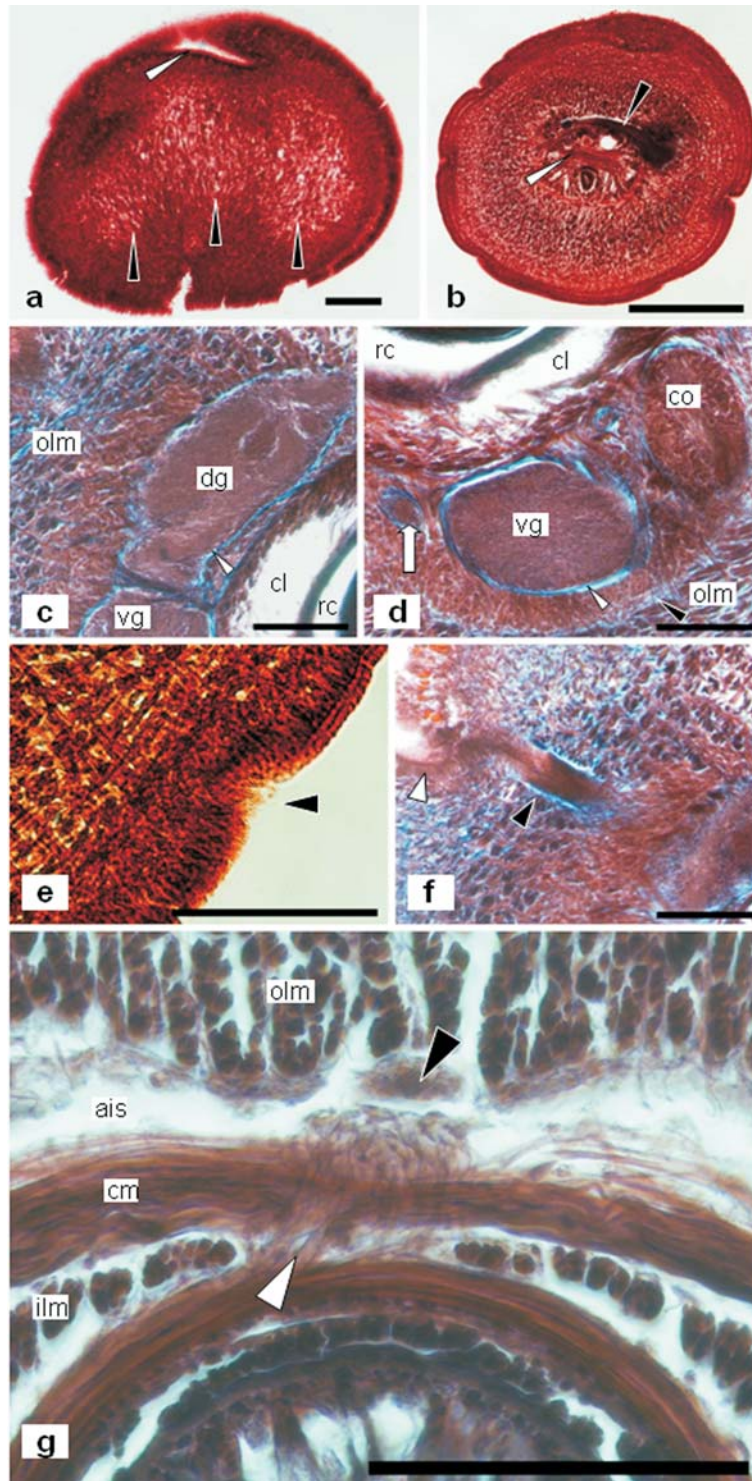
Polybrachiorhynchus and *Dendrorhynchus* have a similar frontal organ that consists of three separate pits opening independently (Gibson 1977; Sun 2006). There is a single apical pit in *Gorgonorhynchus* (Gibson 1974). The presence or nature of this structure is unknown for *Panorhynchus* (Table 1).

A pair of cerebral sense organs extends behind the dorsal cerebral ganglia; they form an ovoid structure, about 160 μm long and 100 μm broad (Fig. 4d). The ciliated cerebral canals, about 15 μm broad, turn by up to 90° before terminating near the posterior of the neuroglandular organ. These organs are not bathed by any cerebral lacuna, as they are in *Dendrorhynchus* (Sun 2006).

Instead of horizontal lateral cephalic slits there is a pair of shallow epidermal depressions (Fig. 4e). In the epidermis of the depression the cilia are longer than the adjacent epithelium. The lateral depressions are invaginated posteriorly, up to 93 μm, precisely at the opening of the ciliated cerebral canals (Fig. 4f). Similar lateral depressions were reported by Iwata (1993) from *Paralineopsis taki*. The cephalic slits in *Polybrachiorhynchus* and *Dendrorhynchus* are deeper, typical of heteronemerteans (Gibson 1977; Sun 2006).

The eyes are absent. This is characteristic of all species that have a branched proboscis.

Reproductive system: The single specimen was a nearly sexually mature female collected in February (austral summer). The ovaries are confined to the intestinal region. There is one gonadal sac in a lateral position on each side of the body between the intestine and body-wall longitudinal muscle layer (Fig. 2b). The number of oocytes varies but generally 10–16 oocytes in slightly different stages of maturity may be counted in a section of a single ovary (Fig. 2g); the oocytes are 30–50 μm in diameter.

Conclusions

This heteronemertean is described as a new genus and new species, *Oligodendrorhyncus hesperides*. Its branched proboscis is a feature shared with only four genera: *Gorgonorhynchus*, *Panorhynchus*, *Polybrachiorhynchus* and *Dendrorhynchus*. Gibson (1985b) placed those known at the time, the first three, in his Group E, and proposed for each a family: Gorgonorhynchidae, Panorhynchidae and Polybrachiorhynchidae. The phylogenetic validity of Gibson's (1985b) heteronemertean families has been challenged (Schwartz and Norenburg 2001, Thollesson and Norenburg 2003, Sundberg *et al.* 2009), and has not been widely adopted. *Dendrorhynchus*, the most recently described heteronemertean with a branched proboscis (Yin and Zen 1985) was recently revised, along with discussion of the three other genera, by Sun (2006).

The principal morphological features of *Oligodendrorhynchus hesperides* compared with those of *Gorgonorhynchus*, *Panorhynchus*, *Polybrachiorhynchus* and *Dendrorhynchus,* are summarized in Table 1.

The branching mode of the proboscis and the plane of branching are two of the major taxonomic characters for distinguishing among these genera (Dakin and Fordham 1936; Serna de Esteban and Moretto 1969; Gibson 1977; Sun 2006). In *Oligodendrorhynchus* the branches emerge alternately from the main axis as in *Panorhynchus*, *Polybrachiorhynchus* and *Dendrorhynchus,* in contrast to the regularly dichotomous branching in *Gorgonorhynchus.* Unfortunately, it was not possible to establish the plane of proboscis branching in *Oligodendrorhynchus*.

In contrast to the other genera with a branched proboscis, *Oligodendrorhynchus* bears only five primary branches and one of them with a single secondary branch (Fig. 3f). In *Panorhynchus*, the maximum number of primary branches is 11 and they never bifurcate more than once; the three other genera show much higher degrees of ramification (Table 1), with primary, secondary, tertiary and even quaternary branches.

With respect to the characteristics of the proboscis, *Oligodendrorhynchus* possesses more features in common with *Panorhynchus* (low maximum number of primary branches, three muscle layers in the main proboscis axis, one muscle cross in the main proboscis axis) than with *Gorgonorhynchus*, *Polybrachiorhynchus* and *Dendrorhynchus*. Nevertheless, *Oligodendrorhynchus* has a very low number of primary branches and only one of them is bifurcated.

The low number of branches could be explained by the small size of the specimen. Sun (2006) reports that larger specimens of *Dendrorhynchus* tend to bear more branches at each branching level.

Two characters not listed by Sun (2006) (Table 2) are quite different in *Oligodendrorhynchus* compared with the other genera: (1) a pair of shallow epidermal depressions instead of typical horizontal lateral cephalic slits, and (2) a gelatinous amorphous connective stratum between the outer longitudinal and circular muscle layers. Three characters are shared only with the genus *Dendrorhynchus*: (1) the presence of a rhynchocoelic nerve, (2) several fibres of the rhynchocoelic circular muscle layer, at the level of the intestinal region, are interwoven with the internal longitudinal muscle layer of the body wall and (3) the foregut splanchnic musculature with distinct circular and longitudinal muscle fibres.

Among the heteronemerteans with a branched proboscis, *Oligodendrorhynchus* shared with *Polybrachiorhynchus* and *Dendrorhynchus* (Gibson 1977; Sun 2006) another feature related to the frontal organ: a frontal organ opening *via* three pits. By contrast, the frontal organ of *Gorgonorhynchus* species is described as a single trifoliate pit (Gibson 1974).

In addition, apart from *Gorgonorhynchus*, all the genera with a branched proboscis, including the present nemertean, contain three muscle layers in the unbranched proboscis axis, while only *Oligodendrorhynchus* and *Panorhynchus* share the presence of a single muscle cross in the main proboscis axis.

Table 2

A summary of the morphological features, discussed in the text and used to distinguish between the various heteronemerteans with a branched proboscis. Based on Gibson (1985), Sun (2006) and the present study.

	I	II	III	IV	V	VI	VII	VIII
Group E								
Proboscis branched								
Gorgonorhynchus [a]	0–2[b]	–	–	–	+	+	–	–
Panorhynchus [c]	1–0?[b]	+	–	s	+	–	–	+
Polybrachiorhynchus [d]	2–0[b]	+	–	c	+	+	+	+
Dendrorhynchus [e]	2–0[b]	+	+	c + l	+	–	+	+
Oligodendrorhynchus [f]	1–1[b]	+	+	c + l	+	–	+	+

I: Number of muscle crosses in proboscis.
II: Dermis with (+) or without (–) connective tissue layer between gland cells and body wall outer longitudinal musculature.
III: Rhynchocoel wall circular muscles interwowen with adjacent body wall inner longitudinal muscle fibres (+) or quite separate (–).
IV: Nature of foregut splanchnic musculature: –, absent; c, circular; l, longitudinal; s, spiral.
V: Presence (+) or absence (–) of neurochord cells in nervous system.
VI: Presence (+) or absence (–) of caudal cirrus.
VII: Foregut with (+) or without (–) subepithelial gland cell layer.
VIII: Blood system in foregut region developed into vascular plexus (+) or consisting of two lateral/ventrolateral vessels only (–).
[a] In *Gorgonorhynchus* the proboscis branches in a regularly dichotomous manner, successive branches being at right angles to each other (Gibson 1977).
[b] The number of muscle crosses respectively in the proximal unbranched portion of the proboscis and the terminal branches.
[c] In *Panorhynchus* the mode of proboscis branching is alternately from a main axis, with successive branches forming an open spiral (Gibson 1977).
[d] In *Polybrachiorhynchus* the proboscis branches arise alternately from a main axis within a single plane, but terminal branches are formed by axial bifurcation (Gibson 1977).
[e] In *Dendrorhynchus* the mode of proboscis branching is alternately from a main axis, in a single plane.
[f] In O*ligodendrorhynchus* the proboscis branches arise alternately from a main axis in an unknown plane.

We conclude that the specimen constitutes a new species and propose for it a new genus, because the combination of characters, especially the structure of the cephalic fissures, does not allow for sensible placement in an existing genus.

In addition to the singularities in morphological features, remarkable differences in the type of habitat and geographic distribution can also be emphasized (Table 3). The other four previous genera were never found in the Antarctic. The genus with the widest occurrence is *Gorgonorhynchus*, with a distribution in tropical and warmer temperate seas. Furthermore, all previously described species with a branched proboscis live in shallow waters, littorally, sublittorally (at 15–25 cm depth), in salt marshes and muddy to sandy sediments, under stones, among algae, etc. In contrast, the specimen of *Oligodendrorhynchus* was collected at 210 m

Table 3

Comparison of the habitats of the heteronemertean species with branched proboscis.

Species	Geographical distribution	Habitat	Depth	Reference
Gorgonorhynchus repens Dakin and Fordham, 1936	New South Wales (Australia) Indo-Pacific Bikini Atoll	on the shore, under small stones	mid-littoral level	Dakin and Fordham 1936 Gibson 1981
Gorgonorhynchus bermudensis Wheeler, 1940	St Georges Island (Bermuda) Atlantic coast of Florida (USA)	under stone Beneath rocks, among algae	low littoral upper littoral	Wheeler 1940 Gibson 1974
Panorhynchus argentinensis Serna de Esteban and Moretto, 1969	Mar del Plata (Argentina)	lagoon, brackish-water in sandy-muddy substrate	15–25 cm	Serna de Esteban and Moretto 1969
Polybrachiorhynchus dayi Gibson, 1977	Breede River mouth (South Africa)	*Upogebia* beds, from mud in *Zostera* zone sand bank, near river mouth	littoral	Gibson 1977
Dendrorhynchus zhanjiangensis Yin and Zen,1984	Xiashan beach Park, Zhanjiang(China)	mud banks and sand	littoral	Sun 2006
Oligodendrorhynchus hesperida gen. et sp. n	Off Peter I Island (Antarctica)	dark muddy-sand and boulders	210 m	current

depth in dark muddy-sand and gravel substrate, with low content of total organic matter (1.83%) and low redox value Eh (31.4).

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