

# Three Species of Ribbon Worms (Nemertea) from Cebu, the Philippines

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Three species of nemerteans, *Balionemertes* cf. *australiensis* Sundberg, Gibson, and Olsson, 2003 (Palaeonemertea), *Prosadenoporus olympiae* sp. nov. (Hoplonemertea: Eumonostilifera), and *Coella gloriae* sp. nov. (Hoplonemertea: Polystilifera: Reptantia), are reported based on material collected intertidally at a rocky shore in Cebu Island, Republic of the Philippines. Cytochrome *c* oxidase subunit I (COI) barcode sequences of these species have earlier been published elsewhere. The Cebu specimen that is herein identified tentatively as *Balionemertes* cf. *australiensis* possesses *i*) small black dots on the ventral body surface, *ii*) a neurochord in the lateral nerve, *iii*) serial rhynchocoelic septa, and *iv*) nephrostomes, characters that were not mentioned in the original description of the species from Australia; the exact species identification requires barcode sequences from topotypes. *Prosadenoporus olympiae* can be differentiated morphologically from other congeners by having three accessory-stylet pouches; when alive, worms of this species showed negative hydrotaxis. *Coella gloriae* differs from all the reptant polystiliferans by having *i*) four rows of the eyes, *ii*) the cephalic furrows, *iii*) no dorsal marking, *iv*) separate mouth and proboscis openings, *v*) blind-ending extracerebral vessels, *vi*) non-forked fibre core in the dorsal ganglia, *vii*) the subdorsal nerves, and *viii*) the cerebral organs partly overlapping the brain.

**Key Words:** Carmen, intertidal, marine invertebrates, Pacific, Sulu Sea, taxonomy, Visayas.

## Introduction

To date, only four species of nemerteans have been reported from the Philippines: the decapod-egg predator *Carcinonemertes mitsukurii* Takakura, 1910 from a museum specimen of the crab *Charybdis miles* (de Haan, 1835) collected in 1908 from San Andreas Island (Humes 1942); the land nemertean *Geonemertes philippinensis* Gibson and Moore, 1998 from a cave in Quezon National Park, Luzon Island (Gibson and Moore 1998); the mud-dwelling palaeonemertean *Callinera emiliae* Kajihara, 2007 from a tidal flat in Dumaguete, Negros Island (Kajihara 2007); and the uniformly brown-coloured monostiliferous hoplonemertean *Diplomma serpentina* (Stimpson, 1855) found in an experimental tank at the Aquaculture Department, South-East Asian Fisheries Development Centre, Tigbauan, Iloilo, Panay Island (Kajihara *et al.* 2011). In the present paper, I report three species found in Cebu Island, which have been preliminarily reported based on the external features (Kajihara *et al.* 2007). Sequences of the cytochrome *c* oxidase subunit I (COI) gene as DNA barcodes for these species have been published by Sundberg *et al.* (2016).

## Materials and Methods

Sampling was made on 22 September 2006 at a rocky shore, 10°37'15"N, 124°1'40"E, Buente, Carmen, Cebu Is-

land, Republic of the Philippines (Fig. 1A, B). Nemerteans were anaesthetized in MgCl<sub>2</sub> solution isotonic with seawater. While the posterior fragment from each individual was fixed and preserved in 70% EtOH for DNA extraction, anterior fragments for histological observations were fixed in Bouin's fluid for 12 hr, and preserved in 70% EtOH, before dehydrated in 99% EtOH and cleared in xylene, embedded in 56–57°C m.p. paraffin wax and sectioned at 8 µm. Sections were subsequently stained by the Mallory trichrome method. Three-dimensional reconstruction from serial sections was performed by IMOD ver. 4.9 (Kremer *et al.* 1996; available at <http://bio3d.colorado.edu/imod/>). Type and voucher specimens are deposited in the Zoology Division, Philippine National Museum of Natural History (PNM), Manila. Digital photographs of the ribbon worms taken in life and photomicrographs of transverse sections are available at figshare (10.6084/m9.figshare.11363141.v1; 10.6084/m9.figshare.11363150; 10.6084/m9.figshare.11363165; 10.6084/m9.figshare.11363168; 10.6084/m9.figshare.11363180; 10.6084/m9.figshare.11363186; 10.6084/m9.figshare.11363213; 10.6084/m9.figshare.11363237; 10.6084/m9.figshare.11363288; 10.6084/m9.figshare.11363405; 10.6084/m9.figshare.11363438). DNA was extracted using a DNeasy Tissue Kit (QIAGEN K. K., Japan) and sent to Professor Per Sundberg (Gothenburg University) for COI sequencing.

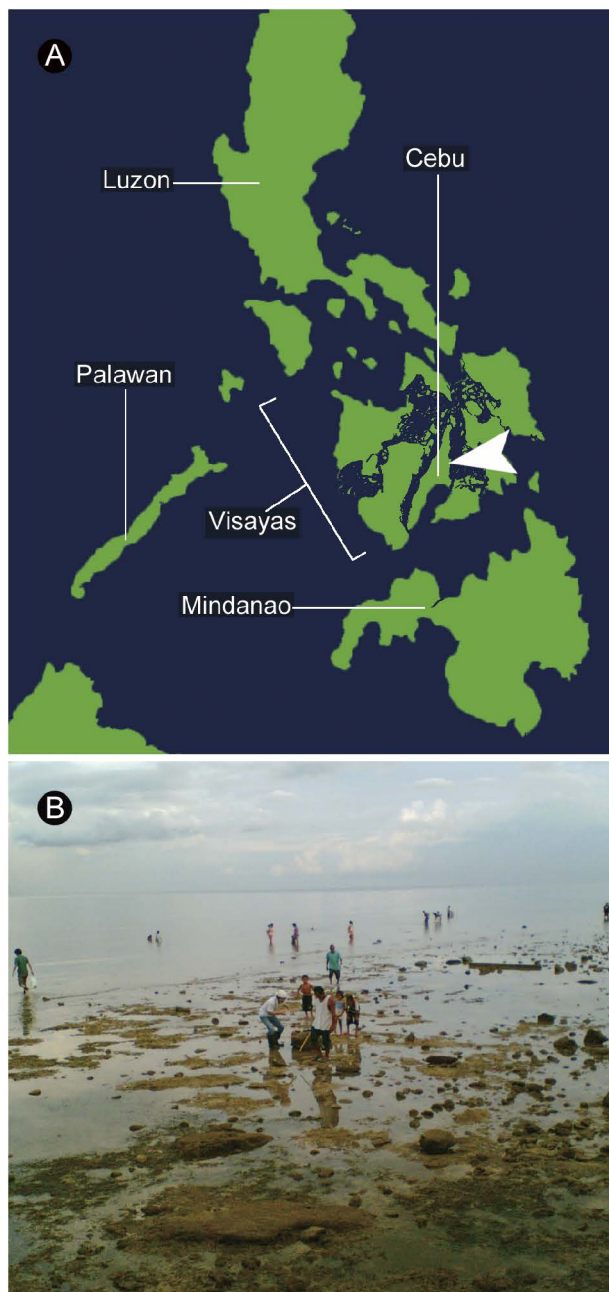


Fig. 1. A, Map of the Philippines, showing the sampling locality (indicated by arrowhead); B, scenery of the sampling locality, Buente, Cebu, photo courtesy of Dr Emilia S. Yap, taken on 22 September 2006.

## Results

Class **PALAEONEMERTEA**

Subclass **ARCHINEMERTEA**

Family **Cephalotrichellidae** Chernyshev, 2011a

Genus **Balionemertes** Sundberg, Gibson, and Olsson, 2003

**Balionemertes cf. australiensis** Sundberg, Gibson, and Olsson, 2003 (Figs 2–6; Table 1)

*Pilidiophora* [sic.] sp.: Kajihara *et al.* 2007: 125.

*Balionemertes australiensis*: Sundberg *et al.* 2016:

NemBar0830; Chernyshev and Kajihara 2019: 195–200, fig. 2A, B; Chernyshev *et al.* 2019: 520, table 2.

?*Balionemertes australiensis* Sundberg *et al.*, 2003: 285, figs 4–20.

**COI barcode.** KU840157 (513 bp; Sundberg *et al.* 2016).

**Material examined.** PNM 4644, female, serial transverse sections of the anterior portion of the body (3 slides), succeeding intestinal region (11 slides), and everted proboscis (25 slides).

**External features.** Single specimen obtained had lost its posterior end; anterior fragment measured 3 cm in length, 1 mm in width; head not demarcated from rest of body (Fig. 2A), provided with two groups (anterior and posterior) of ocelli on each side, without cephalic furrow; anterior group of ocelli further divided into dorsal and ventral sub-groups (Fig. 2B); basement body colour greyish white, covered with brown pigments (epidermis on dorsal side of body largely lost when collected); spots of unpigmented area more or less regularly distributed along body surface; small, black mottles irregularly arranged among brown pigments on ventral surface (Fig. 2C); minute white dots found in unpigmented spots, comprising rings arranged at more or less regular intervals along body; anterior-most white ring completely encircling head, succeeding rings discontinuous and incomplete (Fig. 2A). Swam by quick body undulation when irritated, seemingly without dorsoventral body flattening as found in some heteronemerteans in *Cerebratulus* and cratenemertid monostiliferous hoplonemerteans.

**Body wall and musculature.** Composed of ciliated epidermis, connective tissue basement membrane, body-wall diagonal muscle layer, outer circular muscle layer, and inner longitudinal muscle layer (Fig. 3A, B). Body-wall inner circular muscle layer poorly developed, evident only around ventral and ventrolateral sides of anterior portion of foregut (Fig. 3B); its continuation with dorso-lateral to distal sides of lateral blood vessel wall and rhynchocoel outer circular muscle layer not confirmed in light microscopy. Dorsoventral muscles not found. Longitudinal muscle plate present between rhynchocoel wall and alimentary canal (Fig. 3C), extending posteriorly to intestinal region. Extracellular matrix not well developed.

**Proboscis apparatus.** Proboscis pore opening subterminally (Fig. 4A). Rhynchodaeal wall unciliated, composed of cells with acidophilic cytoplasm (Fig. 4B, C). Rhynchodaeal sphincter present just in front of proboscis insertion (Fig. 4D). Proboscis insertion situated in front of ventral cerebral commissure; no precerebral septum developed; after leaving from body-wall longitudinal muscle layer behind brain region, longitudinal muscle fibres running anteriorly between extraganglionic tissue and brain leading into proboscis insertion. Rhynchocoel wall composed of outer circular and inner longitudinal muscle layers; degree of posterior extension of rhynchocoel indeterminable. Rhynchocoel appears to be antero-posteriorly compartmentalized by valves, or incomplete septa, into at least 14 chambers in foregut region; each valve innervated by lower mid-dorsal rhynchocoel nerve running immediately on rhynchocoel outer circular



Fig. 2. *Balionemertes* cf. *australiensis* Sundberg, Gibson, and Olsson, 2003, photographs taken in life, PNM 4644. A, Anterior portion, dorsal view; head twisted leftward; epidermis on dorsal side largely damaged and exfoliated; B, head, right lateral view; arrowhead showing ocellus in ventral sub-group of anterior eye group; C, anterior end of body, ventral view, showing distribution of black dots.

muscle layer (Fig. 5A–J).

Proboscis bilaterally symmetrical in cross section, consisting of partially glandular epithelium, outer circular muscle layer, and outer longitudinal muscle layer; crisscrossed diagonal layer between outer circular and outer longitudinal muscle layers (Chernyshev 2015; Chernyshev and Kajihara 2019) not confirmed in light microscopy; on each side, thick-walled glandular portion of epithelium basally possessing two bundles of outer longitudinal muscles and proboscis nerves on outer circular muscle layer; additional median outer longitudinal muscle bundle and proboscis nerve present between thin-walled non-glandular epithelium and outer circular muscle layer (Fig. 5K).

**Alimentary system.** Mouth ventrally opening behind brain; foregut anteriorly covered with circular muscles, mostly one or two fibre thick (Fig. 3B); intestine without lateral diverticula. Intestinal caecum absent.

**Blood system.** Pair of cephalic vessels meeting anteriorly above proboscis pore, leading backward between dorsal and ventral extraganglionic tissues (Fig. 4A–C); after passing through cerebral ring, these running posteriorly as lateral

vessels on lateral sides of rhynchocoel wall (Fig. 3A). Neither median vessel nor rhynchocoel vessels found.

**Nervous system.** Brain situated inside body-wall inner longitudinal muscle layer, composed of dorsal and ventral ganglia (Figs 4E, F, 6A–C), latter posteriorly divided into superior and inferior lobes (Figs 4G, 6B–D); giant nervous cell present on each side behind ventral cerebral commissure, situated medially to fibrous tissue of inferior lobe of ventral ganglion, embedded among neuronal tissue. In addition to main, anterior dorsal commissure connecting dorsal ganglia (Fig. 6B), posterior dorsal commissure present (Fig. 6A), connecting fibrous core of ventral ganglion on each side. Mid-dorsal nerve running both anteriorly and posteriorly from anterior dorsal commissure (Fig. 6A, B); posteriorly bifurcating into upper and lower mid-dorsal nerves (Fig. 3C). In addition to main, ventral commissure connecting ventral ganglia, at least three additional ventral commissures present, connecting inferior lobe of ventral ganglion on each side (Fig. 6D, E). Inner neurilemma present, separating fibrous and neuronal tissues in brain; outer neurilemma also present, separating neuronal tissue of brain from extraganglionic



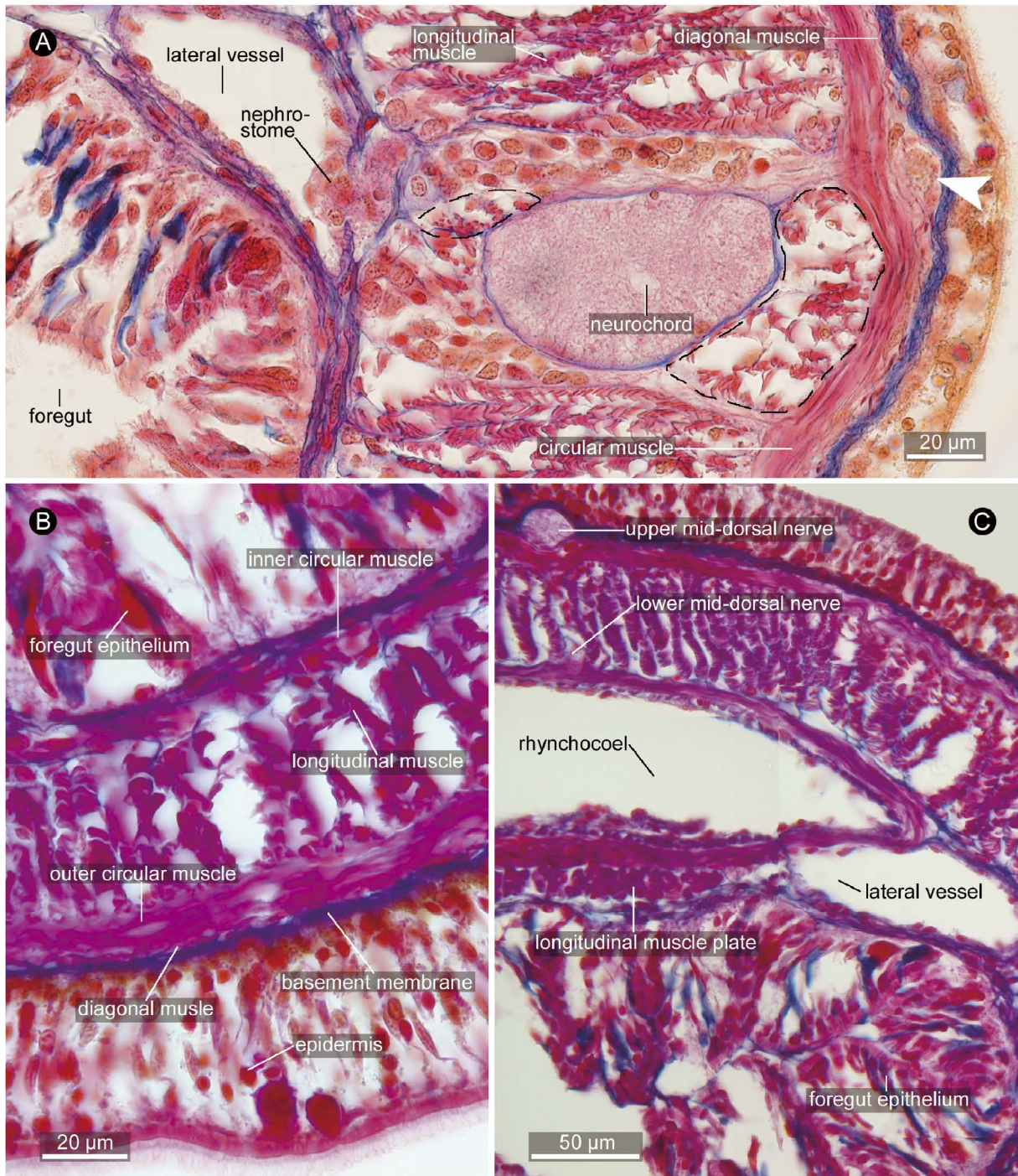


Fig. 3. *Balionemertes* cf. *australiensis* Sundberg, Gibson, and Olsson, 2003, photomicrographs of transverse sections, PNM 4644. A, Posterior foregut region through nephrostome; dotted lines indicate longitudinal muscles associated with lateral nerve cord; arrowhead indicates cells of unknown function; B, anterior foregut region showing inner circular muscles; C, foregut region showing mid-dorsal nerves and longitudinal muscle plate between rhynchocoel and foregut.

tissue and body-wall longitudinal muscle layer.

From posterior-most additional ventral commissure, pair of nerve trunks leading antero-ventrally to form buccal nerve ganglion (Fig. 6A, E), from which pair of buccal nerves emerge posteriorly (Fig. 6C), passing on either side of buccal region, post-orally meeting medially to form post-oral commissure.

Dorsal and ventral extraganglionic tissues present on each side beneath body-wall inner longitudinal muscle layer

covering brain, extending from near tip of head to brain region (Fig. 4A–F).

Inferior lobe of ventral ganglion turning laterally at right angle, then directing posteriorly again at right angle to lead to lateral nerve cord (Fig. 6B, C). Lateral nerve cord situated lateral to alimentary canal, completely dividing body-wall longitudinal muscle layer into dorsal and ventral halves; longitudinal muscles present in area enclosed by fibrous core, nervous cells, and body-wall outer circular muscle layer;



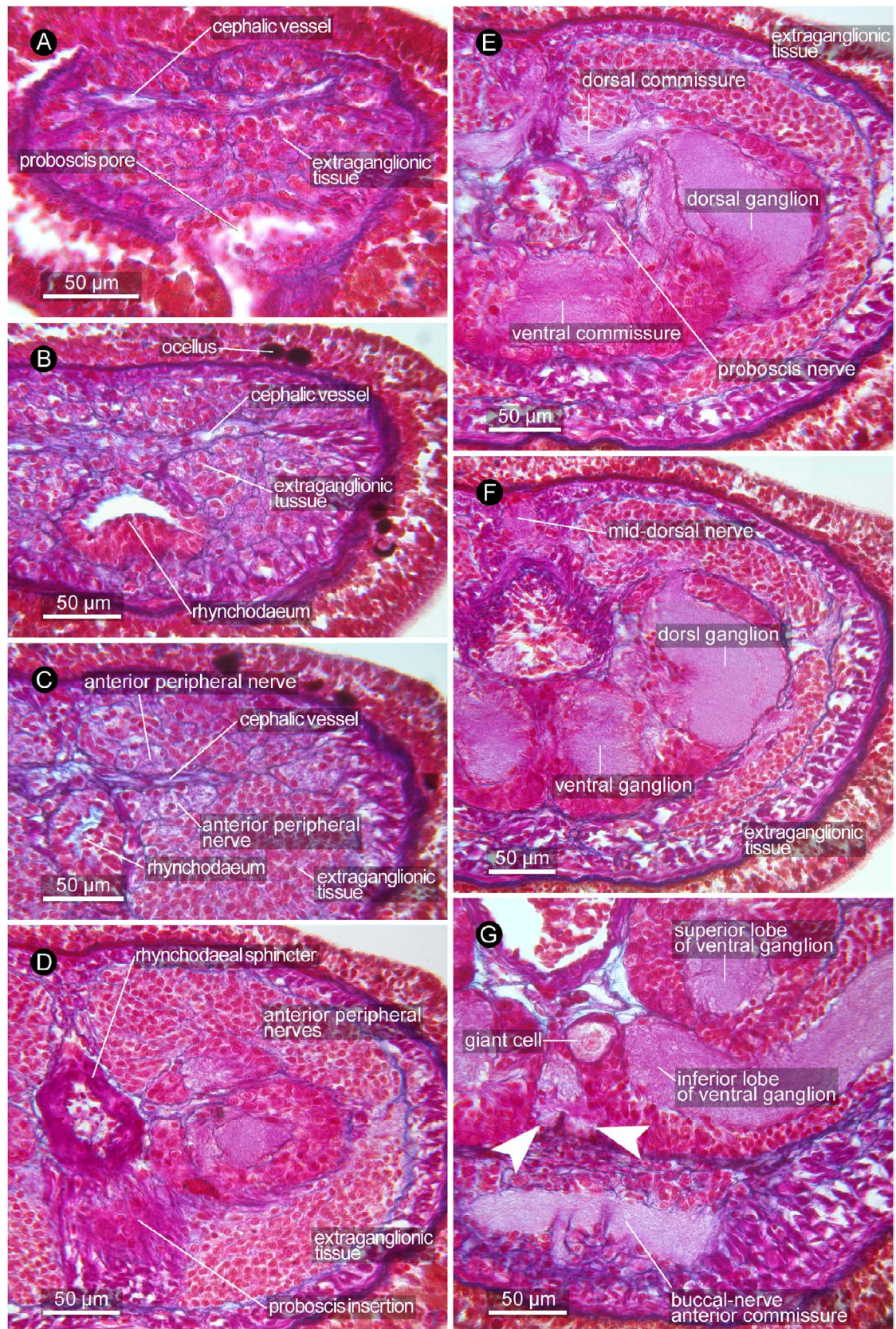


Fig. 4. *Balionemertes* cf. *australiensis* Sundberg, Gibson, and Olsson, 2003, photomicrographs of transverse sections, PNM 4644. A–C, Precerebral regions; D, proboscis insertion; E, anterior brain region; F, middle brain region just before ventral ganglion bifurcates into superior and inferior lobes; G, posterior brain region; arrowheads indicating nerve fibres leading to buccal nerves sent out antero-ventrally from a commissure between inferior lobes of ventral ganglia.



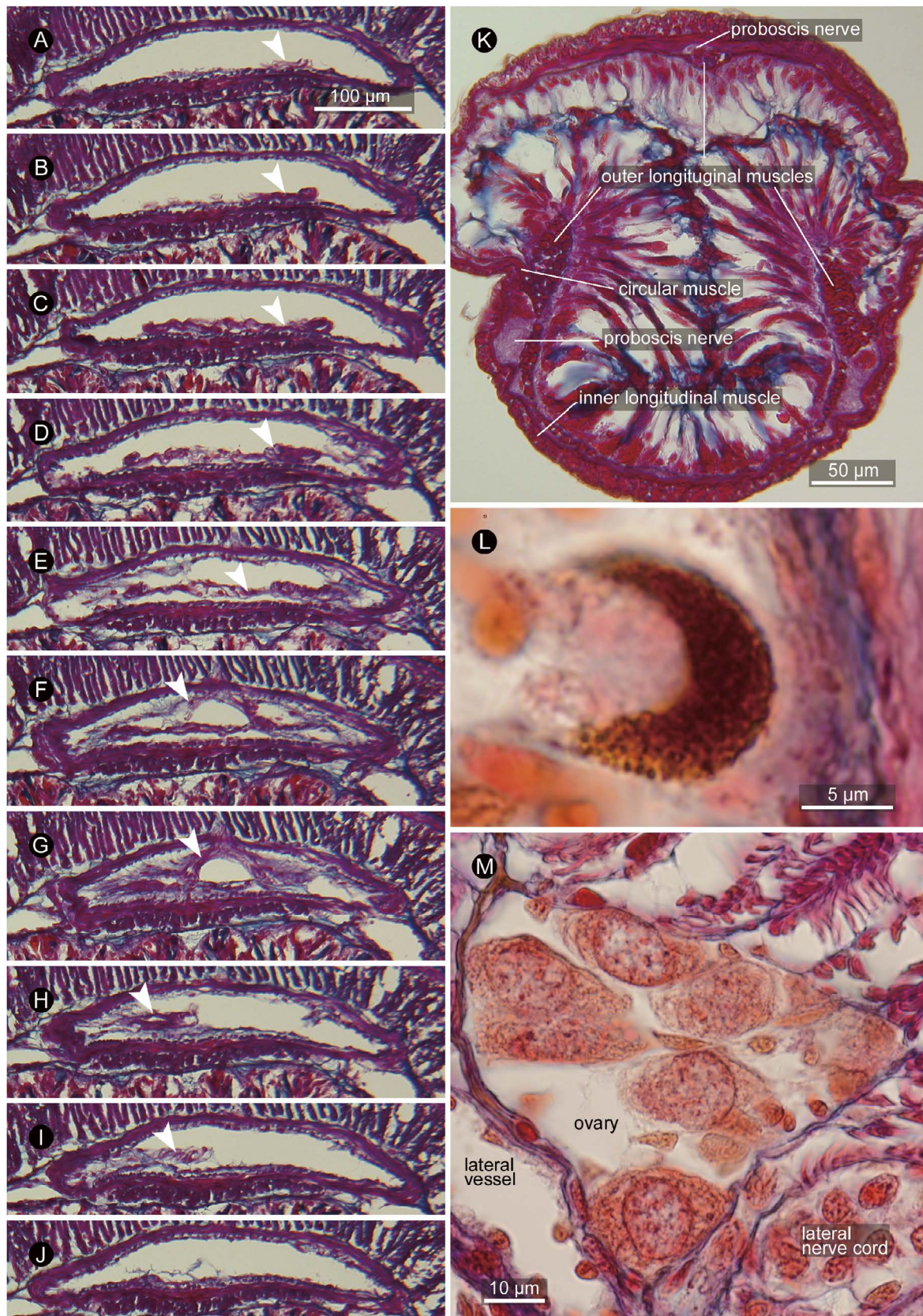


Fig. 5. *Balionemertes cf. australiensis* Sundberg, Gibson, and Olsson, 2003, photomicrographs of transverse sections, PNM 4644. A–J, Serial images showing rhynchocoelic valves (indicated by arrowhead) in foregut region; K, proboscis; L, ocellus; M, ovary.



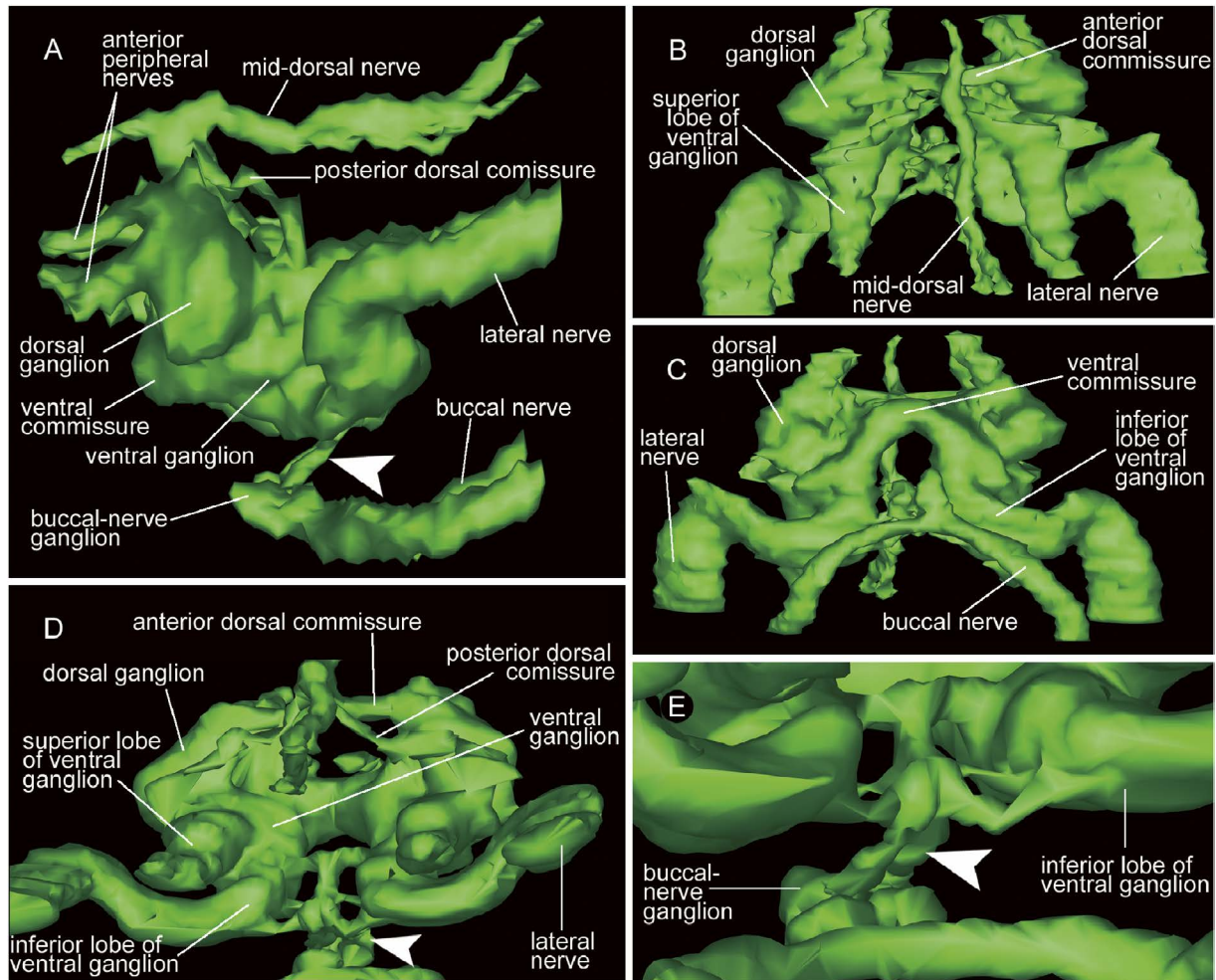


Fig. 6. *Balionemertes* cf. *australiensis* Sundberg, Gibson, and Olsson, 2003, three-dimensional reconstructions of medullary fibrous tissue of the nervous system in brain region (i.e., cortical neuronal tissue is omitted); arrowheads indicating nerve fibres leading to buccal nerves sent out antero-ventrally from a commissure between inferior lobes of ventral ganglia. A, Left lateral view; B, dorsal view; C, ventral view; D, right rear view; E, magnification of commissures between inferior lobes of ventral ganglia, left rear view.

Table 1. Genetic distances between four GenBank entries for *Balionemertes* spp. in terms of K2P (above diagonal) and uncorrected *p*-distance (below diagonal) based on 513 bp partial sequences of the mitochondrial COI gene.

Accession number	Locality	Taxon				References
		<i>Balionemertes</i> cf. <i>australiensis</i>		<i>Balionemertes</i> sp.		
		KU840157	MK307892	KU840275	KP270866	
KU840157	Philippines	—	0.005	0.130	0.122	Sundberg <i>et al.</i> (2016); present study
MK307892	Guam	0.005	—	0.125	0.110	Chernyshev <i>et al.</i> (2019)
KU840275	Vietnam	0.118	0.115	—	0.005	Chernyshev (2011b, 2016); Sundberg <i>et al.</i> (2016)
KP270866	Vietnam	0.113	0.102	0.005	—	Kvist <i>et al.</i> (2015); Chernyshev (2016)

inner and outer neurilemmas present; neurochord present, appearing as clear circle in cross section in fibrous core (Fig. 3A), but its origin not traced. Putative neuronal cells occasionally present lateral to lateral nerve cord between basement membrane and body-wall diagonal (or circular) muscle layer in foregut region (Fig. 3A).

Mid-dorsal nerve emerging posteriorly from anterior dorsal cerebral commissure (Figs 4E, F, 5A), divided into upper and lower nerves in mouth-opening region; upper mid-dorsal nerve running between connective tissue dermis

and body-wall outer circular muscle layer, lower mid-dorsal nerve situated directly above rhynchocoel wall (Fig. 3C).

**Glandular system.** No frontal organ and cephalic glands.

**Sensory system.** Eyes situated in epidermis abutting on basement membrane (Figs 4B, C, 5L). Neither cerebral organs nor lateral sensory organs present.

**Excretory system.** At least three pairs of nephrostomes present in foregut region, protruded into lateral blood vessel (Fig. 3A); anterior-most one situated just posterior to level of mouth-opening. Neither collecting tubules nor nephrid-

iopores confirmed.

**Reproductive system.** The single specimen was immature female; ovaries arranged in single dorsolateral row on each side, situated above lateral nerve cord (Fig. 5M), each containing up to about eight oocytes. Gonopores not found.

**Remarks.** The peculiar proboscis muscular arrangement in the present specimen, with five (one unpaired plus four paired) outer ('inner' in the retracted state) longitudinal muscle strands (Fig. 5K) (*cf.* Chernyshev 2015; Chernyshev and Kajihara 2019), undoubtedly places the form in *Balionemertes*, which is currently monospecific. The present Cebu form possessed black dots on its ventral side (Fig. 2B, C), a neurochord in the lateral nerve chord (Fig. 3A), the nephrostomes protruding into the lateral vessel (Fig. 3A), and serial rhynchocoelic septa (Fig. 5A–J), all of which were not mentioned in the original description of *B. australiensis* from the Great Barrier Reef, Australia (Sundberg *et al.* 2003). At present, however, whether or not these characters represent species difference cannot be ascertained. The exact identity of the present Cebu material should thus remain tentative until COI barcodes become available from reliably identified topotypes from Australia, although the present form has been mentioned as *Balionemertes australiensis* (without "*cf.*" before the specific name) in some literature (Sundberg *et al.* 2016; Chernyshev and Kajihara 2019; Chernyshev *et al.* 2019).

Although the genus is currently monospecific, there are at least two distinct species distributed in warmer West Pacific, including the present form tentatively identified as *B. cf. australiensis* from the Philippines (present study) and Guam (Chernyshev *et al.* 2019), as well as an unidentified form from Vietnam (Chernyshev 2011b; Kvist *et al.* 2015; Chernyshev 2016; Sundberg *et al.* 2016). These two forms differ by 0.102–0.118 in terms of uncorrected *p*-distance and 0.110–0.130 in terms of K2P (Table 1).

Among Archinemertea, serial rhynchocoelic septa have been reported for *Cephalothrix 'linearis'* (Rathke, 1799) [possibly *C. rufifrons* (Örsted, 1843)] (McIntosh 1873–1874), *Cephalothrix mediterranea* Gerner, 1969 (Gerner 1969), and *Cephalothrix filiformis* (Johnston, 1828) *sensu* Iwata (1954) [as *Cephalothrix cf. spiralis* Coe, 1930 in Chernyshev and Magarlamov (2013); see Chernyshev and Kajihara (2019)]. Taking into account currently recognised character distribution and archinemertean tree topology (*cf.* Chernyshev and Kajihara 2019), the serial rhynchocoelic septa—and the serial nerve rings as well (Chernyshev *et al.* 2019)—may represent another synapomorphy for Archinemertea in addition to the body-wall outer diagonal muscle layer. These septa may prevent the rhynchocoelic fluid from flowing antero-posteriorly when the chamber contracts to expel the proboscis by increased hydrostatic pressure. A comparable structure would be the rhynchocoel posterior chamber in palaeonemertean species of *Callinera* Bergendal, 1900 and *Tubulanus borealis* Friedrich, 1936 (*cf.* Friedrich 1936; Kajihara 2007). The wall protruded into the rhynchocoel lumen from the portion between the anterior and posterior chambers in *Callinera* and *T. borealis* may functionally be equivalent to the rhynchocoelic valves in archinemerteans. Such septa have also been reported in het-

eronemerteans with a branched proboscis (Sun 2006).

The nephrostomes (Fig. 3A) in the present specimen represent the first confirmation of the excretory system in the Cephalotrichellidae.

#### Class HOPLONEMERTEA

#### Order MONOSTILIFERA

#### Suborder EUMONOSTILIFERA

#### Family Prosorhochmidae Bürger, 1895

#### Genus *Prosadenoporus* Bürger, 1890

#### *Prosadenoporus olympiae* sp. nov. (Figs 7–10; Tables 2, 3)

Prosorhochmidae sp.: Kajihara *et al.* 2007: 126; Sundberg *et al.* 2016: NemBar0832, 0833.

**Etymology.** The specific name is dedicated to Dr Minerva Olympia (University of the Philippines), a Filipino food scientist who supported my collecting trip in Cebu.

**COI barcodes.** KU840159 (513 bp) from the holotype; KU840160 (513 bp) from one of the paratypes (PNM 4646) (Sundberg *et al.* 2016).

**Material examined.** Holotype, PNM 4645, female, serial transverse sections of anterior end of body (24 slides), intestinal region (28 slides), posterior end of body (21 slides), and proboscis (16 slides), total 89 slides. Paratypes: PNM 4646, female, serial longitudinal section of anterior end of body (14 slides) and transverse sections of intestinal region and proboscis (28 slides), total 42 slides; PNM 4647, male, serial transverse sections, total 50 slides.

**External features.** Body pale brown dorsally (Fig. 7A), cream-white ventrally, without obvious marking; transition of dorso-ventral coloration indistinct; about 6–9 cm long in fully stretched state, 1 mm wide. Head spatula-shaped (Fig. 7B), wider than succeeding body region, with median depression on anterior margin from above (Fig. 7B, C); anterior horizontal cephalic furrow ["prosorhochmid smile" of Maslakova *et al.* (2005) and Maslakova and Norenburg (2008)] present (Fig. 7D); posterior cephalic furrow completely encircling head, mid-dorsally forming V-shape pointing backward; two pairs of eyes anterior to posterior cephalic furrow, anterior pairs are larger than the posterior pairs. Brown cephalic patch on dorsal surface of head, posteriorly continuous with dorsal body coloration, mid-dorsally paler (Fig. 7A), lateral edges distinct (Fig. 7D), giving an impression that there is a pair of longitudinal dorsal stripes on head, depending on direction of view. Tail slightly pointed.

**Body wall and musculature.** Composed of ciliated epidermis, connective tissue basement membrane, outer circular muscle layer, diagonal muscle layer, and inner longitudinal muscle layer (Fig. 8A, B). From anterior foregut region forward, body-wall longitudinal muscle layer internally sending fibres; these separated from main longitudinal layer by thin connective tissue membrane, as well as by posterior extension of cephalic glands where they present (mainly in dorsal and dorso-lateral portions); most of these fibres contributing to proboscis insertion (Fig. 8C); circular muscles developed around oesophagus-foregut junction (Fig. 8C);



precerebrally, rhynchodaeum and oesophagus surrounded by longitudinal fibres (Fig. 8E). Dorsoventral muscles present in posterior foregut and intestinal regions. Extracellular matrix not well developed, found around brain and in intestinal region below rhynchocoel.

**Proboscis apparatus.** Proboscis pore subterminal. Rhynchodaeal wall unciliated, composed of cells with acidophilic cytoplasm (Fig. 8E). Rhynchodaeal sphincter present just in front of proboscis insertion. Rhynchocoel extending almost to hind end of body, its wall consisting of inner longitudinal and outer circular muscle layers. Anterior proboscis composed of inner glandular epithelium, inner circular, middle longitudinal, and outer circular muscle layers; proboscis nerves 18 in holotype (15 and 19 in paratypes). Central stylet length (S) 170  $\mu$ m in holotype (150  $\mu$ m and 140  $\mu$ m in paratypes), basis length (B) 220  $\mu$ m in holotype (210  $\mu$ m and 220  $\mu$ m in paratypes), S/B ratio 0.78 in holotype (0.66 and 0.67 in paratypes); three accessory stylet pouches, each containing two to three accessory stylets (Fig. 9A).

**Alimentary system.** Oesophagus opening to ventral wall of rhynchodaeum, its wall composed of ciliated cells con-

taining acidophilic cytoplasm, basally associated with longitudinal muscle fibres (Fig. 8E). Stomach with folded epithelium containing both acidophilic and basophilic glandular cells (Fig. 8C, I); pylorus less glandular, but containing both acidophilic and basophilic glandular cells, opening to dorsal wall of intestine; intestinal caecum anteriorly forked under pylorus, each branch possessing antero-lateral diverticula (Fig. 8I), reaching almost to brain; intestine with well developed lateral diverticula (Fig. 9B, C).

**Blood system.** Pair of cephalic vessels mid-dorsally meeting in front of brain at level of posterior ocelli, running forward latero-distally among cephalic glands, then curving posteriad at level of anterior ocelli, running beside rhynchodaeum; after passing through cerebral ring, left lateral vessel giving off single mid-dorsal vessel, that penetrates into rhynchocoel to form single vascular plug (Fig. 9D); no pseudometameric transverse connectives between mid-dorsal and lateral vessels.

**Nervous system.** Brain with outer neurilemma (Fig. 8C), but without inner neurilemma; neurochord cell abutting on medial side of fibrous core of ventral ganglion on each

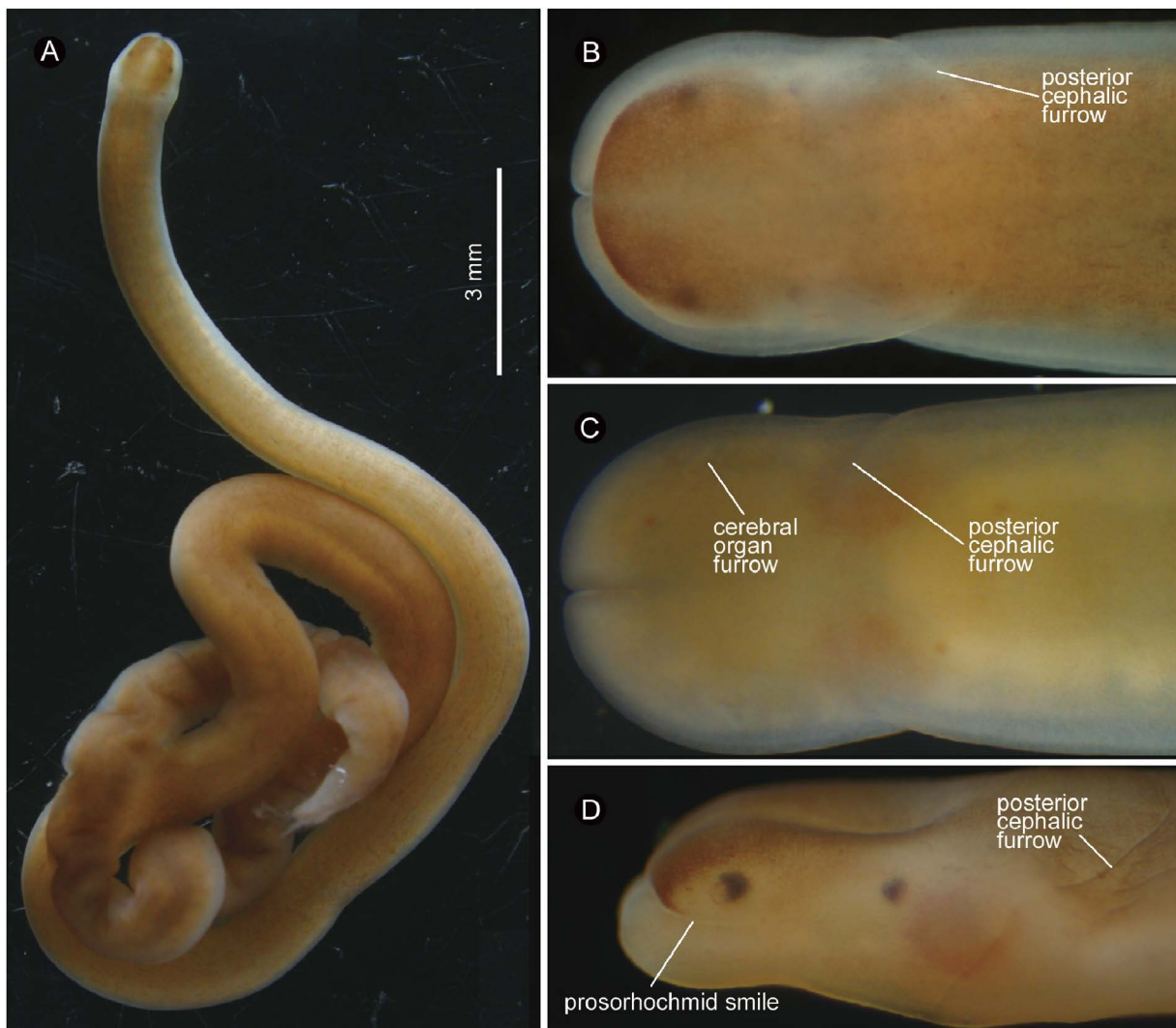


Fig. 7. *Prosadenoporus olympiae* sp. nov., photographs taken in life. A–C, Holotype, PNM 4645; D, paratype, PNM 4646. A, Entire body; B, head, dorsal view; C, head, ventral view; D, head, left lateral view.



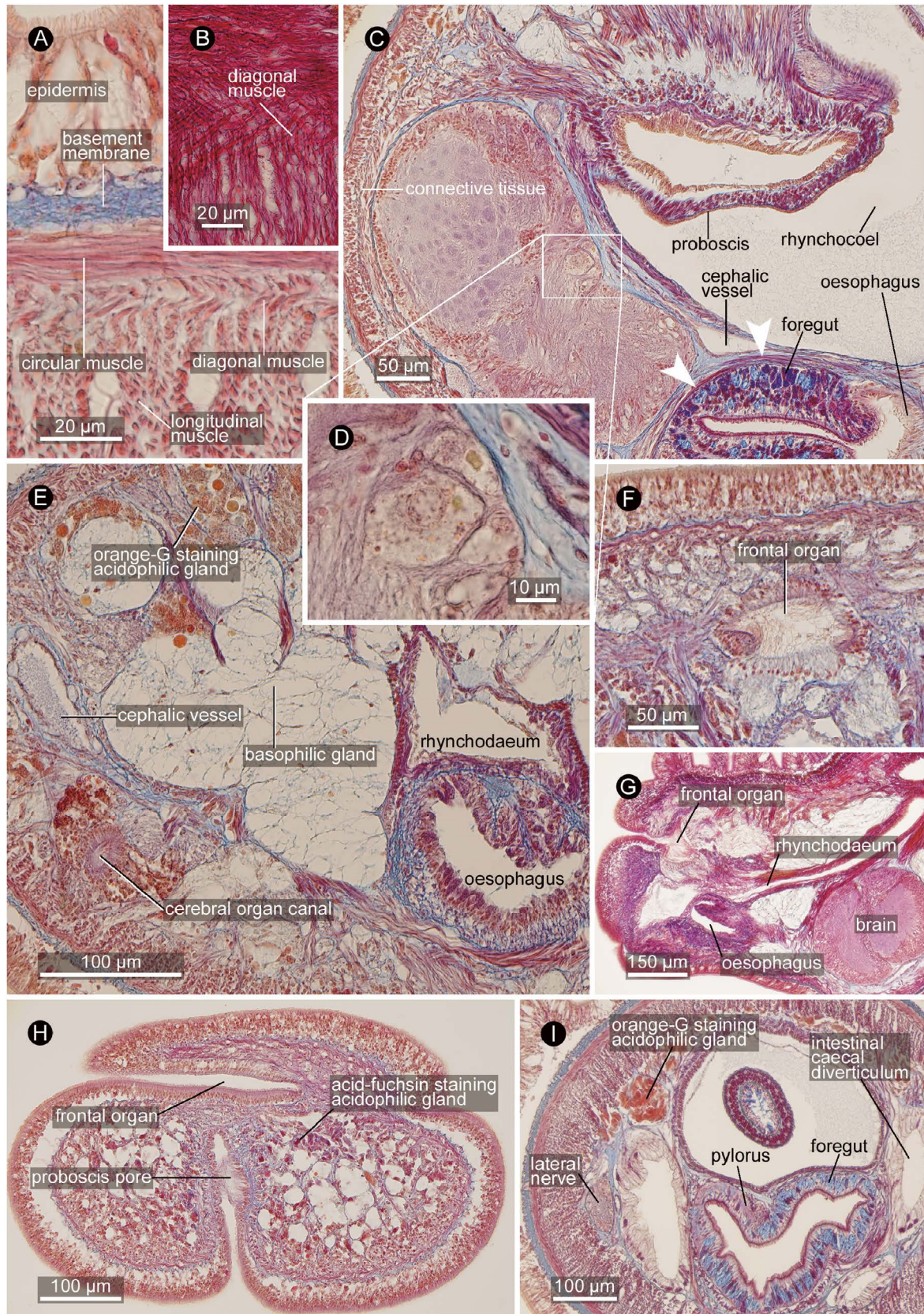


Fig. 8. *Prosadenoporus olympiae* sp. nov., A, C–F, H–I, photomicrographs of transverse sections, holotype, PNM 4645; B, G, photomicrographs of longitudinal sections, paratype, PNM 4646. A, Body wall in foregut region; B, body wall in intestinal region; C, proboscis insertion (indicated by arrowheads); D, enlargement of neurochord cell; E, precerebral region, showing cerebral organ and cephalic glands; F, G, precerebral regions through frontal organ; H, near anterior tip through openings of frontal organ and rhynchodaeum; I, foregut–pylorus junction.



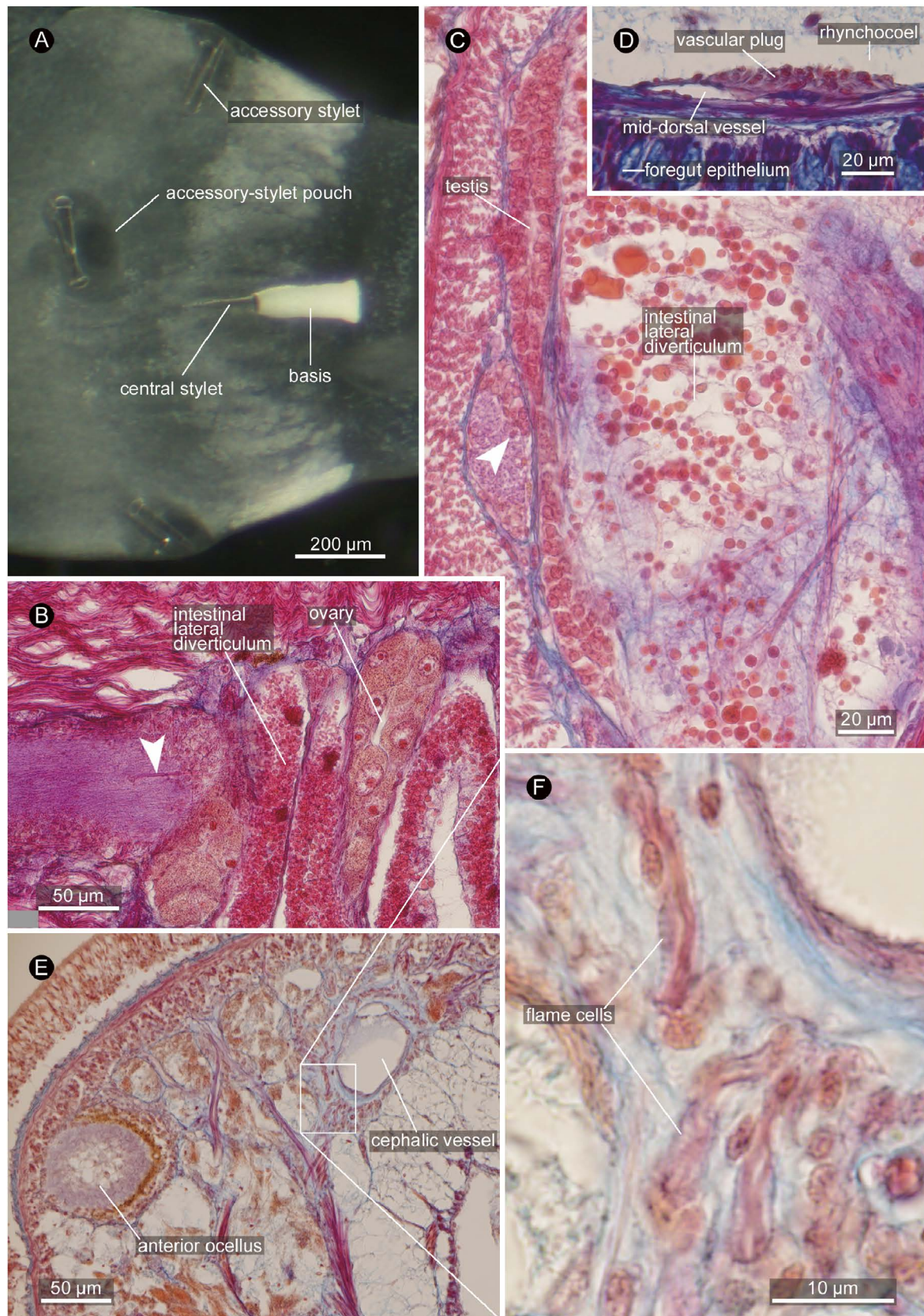


Fig. 9. *Prosadenoporus olympiae* sp. nov., A, D–F, holotype, PNM 4645; B, paratype, PNM 4646; C, paratype, PNM 4647. A, Photograph of stylet apparatus taken from live proboscis under cover slip; B, C, intestinal regions; arrowhead indicates muscle fibre in lateral nerve; D, foregut region showing mid-dorsal vascular plug; E, precerebral region; F, magnification of flame cells.



side (Fig. 8D). Lateral nerve cord without accessory lateral nerve; containing muscle bundle on medio-dorsal side with-in fibrous core (Fig. 8B, C).

**Glandular system.** Frontal organ about 200  $\mu\text{m}$  long, its wall anteriorly composed of cells with acidophilic cytoplasm, laterally differentiated into strongly acidophilic epithelium (Fig. 8G, H); posterior wall composed of cells with neutrophilic cytoplasm, from where basophilic cephalic glands discharge (Fig. 8F). Cephalic glands voluminous, containing both acidophilic glandular mass and basophilic lobes (Fig. 8E); orange-G staining acidophilic glandular mass located dorsally and dorso-laterally, extending posteriorly to pyloric region (Fig. 8I); basophilic glandular lobes extending posteriorly to foregut region.

**Sensory system.** Anterior and posterior eyes about 100  $\mu\text{m}$  and 90  $\mu\text{m}$  in diameter, respectively (Fig. 8E). Cerebral sensory organ, about 100  $\mu\text{m}$  in diameter, situated in front of brain (Fig. 8E); cerebral organ canal opening ventro-laterally shortly behind anterior eyes.

**Excretory system.** Thin-walled collecting tubules, about 6  $\mu\text{m}$  in diameter, only confirmed in precerebral region, embedded in extracellular matrix around cephalic vessels (Fig. 10A, D), opening into frontal organ from each side (Fig. 10A–C). Flame cells binucleate, 14  $\mu\text{m}$  long and 4–5  $\mu\text{m}$  wide, with 7–8 transverse support bars (Fig. 9E, F).

**Reproductive system.** Sexes separate. Gonads arranged in single row on each side, alternating with intestinal lateral diverticula (Fig. 9B, C). Each ovary containing up to 10 oocytes. Of the three specimens examined, only one of the paratypes was male, which did not contain fully developed spermatozoa (Fig. 9C).

**Remarks.** Among the characters observed in the present Cebu specimens, the following features are characteristic for *Prosadenoporus*: i) the ‘prosorhochmid smile,’ ii) the well-developed, long frontal organ with laterally differentiated epithelium, iii) well-developed cephalic glands including orange-G staining acidophilic glands, iv) recurved cephalic vascular loop, and v) excretory system with binucleate terminal flame cells reinforced by transverse support bars (Moore and Gibson 1988; Maslakova and Norenburg 2008).

In addition to nine species considered as valid in Maslakova and Norenburg’s (2008) taxonomic revision of *Prosadenoporus*, there are four nominal species that were earlier deemed to be invalid by Moore and Gibson (1988) (Table 2). *Prosadenoporus olympiae* can be differentiated from all the 13 congeners by the characters listed in Table 2 except *P. buergeri* Punnett, 1903 from Laccadive, for which some diagnostic morphological characters—such as the presence or absence of the neurochord cell and the number of accessory-stylet pouches—are unknown. Furthermore, the number of the proboscis nerves reported for *P. buergeri*, being 19 (Punnett 1903), is the same as that observed in one of the paratypes (PNM 4646) of *P. olympiae*. However, these two are different in the body colour in life, which is pinkish white in *P. buergeri* but dorsally pale brown and ventrally cream white in *P. olympiae*.

*Prosadenoporus olympiae* showed 0.012 intraspecific variation between two specimens sequenced (holotype and one

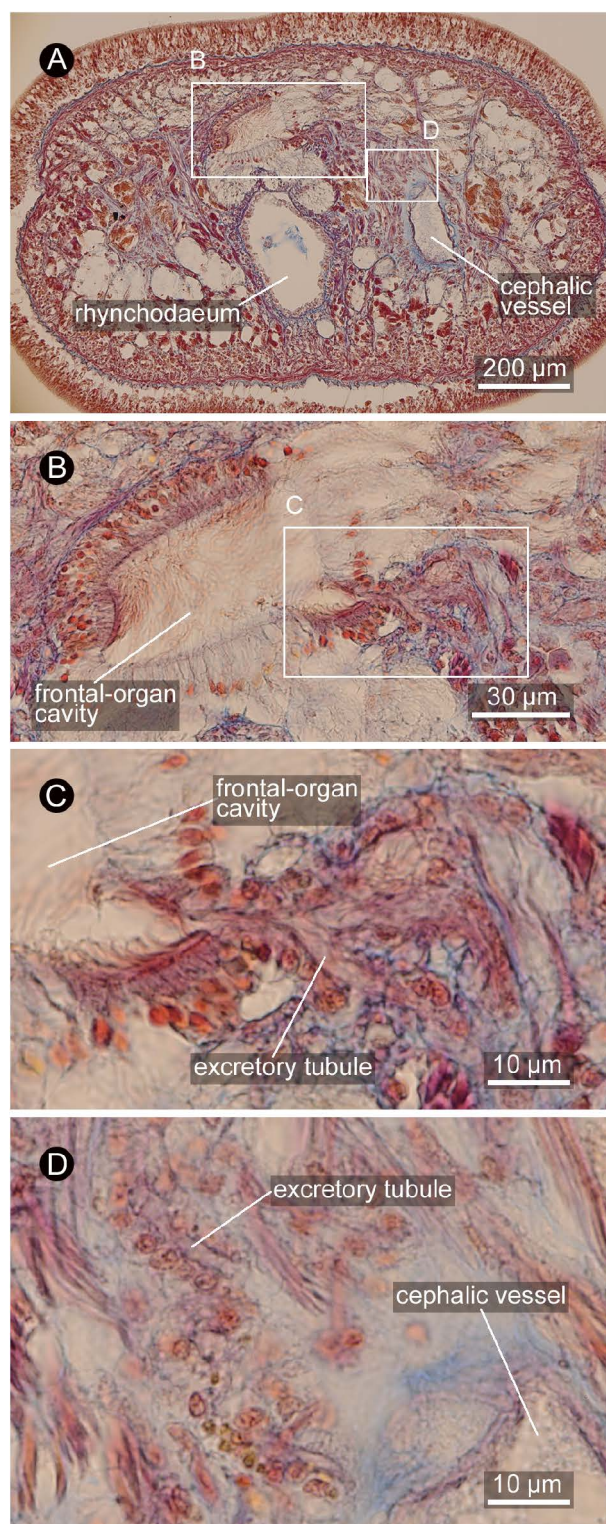


Fig. 10. *Prosadenoporus olympiae* sp. nov., photomicrographs of transverse sections, holotype, PNM 4645. A, Precerebral region through frontal organ; B, magnification of a rectangle above rhynchodaeum on A, showing excretory tubules opening into frontal organ; C, magnification of rectangle on B, showing excretory tubules; D, magnification of a rectangle above cephalic vessel on A, showing excretory tubules.



Table 2. Type locality, habitat, mode of sex, presence or absence of neurochord cells, number of accessory-stylet pouches, and number of proboscis nerves in 14 species of *Prosadenophorus*.

Species	Type locality	Habitat	Sex (H, hermaphroditic; D, dioecious)	Neurochord cells present (+) or absent (-)	Number of accessory- stylet pouches	Number of proboscis nerves	References
<i>Prosadenophorus agricola</i> (Willemoes-Suhm, 1874)	Bermuda	terrestrial	H	+	2	12–15	Willemoes-Suhm (1874); Coe (1904); Maslakova and Norenburg (2008)
<i>Prosadenophorus arenarius</i> Bürger, 1890	Indonesia	intertidal	H	+	2	12	Bürger (1890)
<i>Prosadenophorus badiovagatus</i> Bürger, 1890*	Indonesia	intertidal	H	+	4	15	Bürger (1890)
<i>Prosadenophorus buergeri</i> Punnett, 1903*	Laccadive	intertidal?	?	?	?	19	Punnett (1903)
<i>Prosadenophorus enalios</i> (Moore and Gibson, 1981)	Australia	intertidal	D	-	?	14–16	Moore and Gibson (1981); Maslakova and Norenburg (2008)
<i>Prosadenophorus floridensis</i> Maslakova and Norenburg, 2008	Florida	semi-terrestrial	D	+	2	11–14	Maslakova and Norenburg (2008)
<i>Prosadenophorus fujianensis</i> (Sun, 2001)	China	semi-terrestrial	D	+	5	19–20	Sun (2001); Maslakova and Norenburg (2008)
<i>Prosadenophorus janthinus</i> Bürger, 1890*	Indonesia	intertidal	H	+	2?	?	Bürger (1890)
<i>Prosadenophorus mooreae</i> (Gibson, 1982)	Australia	intertidal	D	-	2	15–16	Gibson (1982); Maslakova and Norenburg (2008)
<i>Prosadenophorus mortoni</i> (Gibson, 1990)	China	intertidal	D	-	?	14	Gibson (1990); Maslakova and Norenburg (2008)
<i>Prosadenophorus oleaginus</i> Bürger, 1890*	Indonesia	intertidal	H?	+	2	?	Bürger (1890)
<i>Prosadenophorus olympiae</i> sp. nov.	Philippines	intertidal	D	+	3	15–19	present study
<i>Prosadenophorus spectaculus</i> (Yamaoka, 1940)	Japan	semi-terrestrial	?	+	2	18–22	Yamaoka (1940); Gibson (1990); Maslakova and Norenburg (2008)
<i>Prosadenophorus winsoni</i> (Moore and Gibson, 1981)	Australia	semi-terrestrial	D	+	6–9	22–24	Moore and Gibson (1981); Maslakova and Norenburg (2008)

\*Considered as invalid by Moore and Gibson (1988).

Table 3. Genetic distances between six species of *Prosadenoporus* in terms of K2P (above diagonal) and uncorrected *p*-distance (below diagonal) based on 513 bp partial sequences of the mitochondrial COI gene along with their locality and accession number.

Species	1	2	3	4	5	6	Locality	Accession number	Reference
1 <i>Prosadenoporus floridensis</i> Maslakova and Norenburg, 2008	—	0.112	0.117	0.105– 0.114	0.103	0.124	Florida, USA	EF157596	Maslakova and Norenburg (2008)
2 <i>Prosadenoporus mooreae</i> (Gibson, 1982)	0.103	—	0.051	0.146– 0.153	0.133	0.119	Magnetic Island, Australia	EF157595	Maslakova and Norenburg (2008)
3 <i>Prosadenoporus mortoni</i> (Gibson, 1990)	0.107	0.049	—	0.134– 0.143	0.133	0.126	Fujian, China	EF157593	Maslakova and Norenburg (2008)
4 <i>Prosadenoporus olympiae</i> sp. nov.	0.097– 0.105	0.131– 0.136	0.121– 0.129	—	0.122– 0.134	0.118– 0.127	Cebu, Philippines	KU840159, KU840160	Sundberg <i>et al.</i> (2016); present study
5 <i>Prosadenoporus spectaculus</i> (Yamaoka, 1940)	0.096	0.121	0.121	0.111– 0.121	—	0.119	Guangdong, China	KC710981	Sun and Sun (2014)
6 <i>Prosadenoporus winsori</i> (Moore and Gibson, 1981)	0.133	0.109	0.115	0.107– 0.129	0.109	—	Townsville, Australia	EF157594	Maslakova and Norenburg (2008)



Fig. 11. *Coella gloriae* sp. nov., photographs taken in life, holotype, PNM 4648. A, Entire body in contracted state, dorsal view; B, magnification of head, dorsal view.



of the paratypes) in terms of both uncorrected *p*-distance and K2P based on 513-bp COI sequences. Among the five species for which COI barcodes are available in public databases, *P. olympiae* is most closely related to *P. floridensis* Maslakova and Norenburg, 2008, differing by 0.097–0.105 in *p*-distance and 0.122–0.134 in K2P distance (Table 3).

In the field, the specimens were found between crevices of exposed rocks during ebb tide. When placed in a plastic case half filled with seawater, they crawled upward escaping from the seawater. These observations suggest *P. olympiae* prefers upper intertidal zone, if not semi-terrestrial as in some congeners.

#### Order POLYSTILIFERA

##### Suborder REPTANTIA

##### Infraorder EUREPTANTIA

Family **Coellidae** Stiasny-Wijnhoff, 1936

Genus **Coella** Stiasny-Wijnhoff, 1936

*Coella glorieae* sp. nov. (Figs 11–15; Table 4)

Reptantia sp.: Kajihara *et al.* 2007: 127.

Polystilifera sp.: Sundberg *et al.* 2016: Nembar0831.

**Etymology.** The specific name is dedicated to Dr Gloria Gomez-Delan (Cebu Technological University), a Filipino fisheries scientist, who helped my sampling trip in Cebu.

**COI barcode.** KU840158 (513 bp; Sundberg *et al.* 2016) from the holotype.

**Material examined.** Holotype, PNM 4648, male, 6 series of serial transverse sections (99 slides in total): anterior end of body (13 slides), foregut region (19 slides), anterior intestinal region (22 slides), posterior intestinal region (13 slides), posterior end of body (7 slides), proboscis (25 slides). The specimen everted its proboscis during anaesthetization and was not completely relaxed while fixation, causing contraction to a certain degree.

**External features.** Body about 5 cm long, 3.5 mm wide, with thin lateral margins, posteriorly rounded; pale orange in colour except cephalic region and body margins being more or less transparent (Fig. 11A). Head not wider than succeeding region of body, possessing mid-dorsal ridge; edges of ridge anteriorly connected at near tip of head, posteriorly curving latero-ventrally along body surface before turning forward on latero-ventral surface (Fig. 11B). Brain seen as pair of red antero-posteriorly elongated ellipses, situated in front of region where edges of mid-dorsal ridge starting to curve. Eyes arranged precerebrally in two rows on each side, median rows situated in mid-dorsal cephalic ridge; peripheral rows outside ridge. Cephalic furrows comprising primary and secondary furrows; primary, transverse furrow beginning from lateral portion at level near cerebral commissures running obliquely postero-medial to mid-dorsal ridge; numerous (~10 in number), secondary cephalic furrows running anteriorly or dorsally from primary furrows, not exceeding frontal end of brain. Cerebral sensory organs visible as dark hue immediately posterior to brain.

**Body wall and musculature.** In foregut region, ciliated epidermis 40–60 µm thick, connective tissue basement

membrane 10–20 µm thick, body-wall outer circular muscle layer 4–6 fibres thick, diagonal muscle layer, and body-wall longitudinal muscle layer (Fig. 12A). Dorsoventral muscles present, running both medial and lateral sides of lateral nerve cord (Fig. 12B); in foregut region, medial ones appearing as if comprising incomplete inner circular muscle 'layer' (Fig. 12C).

Just in front of brain, fibres from body-wall longitudinal muscle layer partially turning inward to form proboscis insertion (Fig. 12D); rest of fibres running further anteriorly around rhynchodaeum as peri-rhynchodaeal longitudinal muscle layer (Fig. 12E), eventually diffusing near extreme tip of head. Anterior to proboscis insertion, precerebral radial muscles present, comprised of numerous bundles of fibres from body-wall longitudinal muscle layer cross-sectionally giving out from one side of body to another in various angles, medially abutting peri-rhynchodaeal longitudinal muscle layer (Fig. 12E).

**Proboscis apparatus.** Proboscis detached from body during fixation. Proboscis pore situated subterminally, independent from mouth opening (Fig. 12F). Rhynchodaeal wall unciliated except its extreme anterior end, composed of cells with acidophilic cytoplasm. Proboscis insertion just in front of brain (Fig. 12D). Rhynchocoel composed of interwoven longitudinal and circular muscle fibres, extending to posterior end of body, with thin-walled lateral diverticula (Fig. 12B, G) arranged pseudometamerically; anterior-most diverticula found just posterior to brain near cerebral organ (Fig. 12G). Proboscis anterior chamber composed of inner glandular epithelium, inner circular, middle longitudinal, and outer circular muscle layers; proboscis nerves anteriorly 19, posteriorly 25 (mostly 24) in number, embedded in longitudinal muscle layer (Fig. 12H, I). Middle chamber with sickle-shaped basis spanning for 43 serial sections (=344 µm) in length, about 100 µm in maximum width (Fig. 13A); central stylets up to 15 µm long (Fig. 13B); at least 10 central stylets confirmed from serial sections, arranged along median line of basis; 10 accessory-stylet pouches on each side of middle chamber, each pouch containing about eight accessory stylets (Fig. 13D). Posterior chamber composed of outer longitudinal and inner circular muscle layers, filled with basophilic contents.

**Alimentary system.** Mouth opening ventrally (Fig. 12E), 400 µm posterior to proboscis pore, about 300 µm ahead of dorsal cerebral commissure, leading to oesophagus, about 100 µm in diameter, passing below ventral cerebral commissure to connect to stomach. Anterior stomach wall acidophilic, posterior basophilic; in holotype, anterior stomach pushed forward into brain ring, possibly as a result of contraction during fixation (Fig. 13G). Pylorus opening to dorsal wall of intestinal caecum. Intestine, as well as intestinal caecum, possessing numerous lateral diverticula.

**Blood system.** Pair of cephalic vessels mid-ventrally meeting above rhynchodaeum, posteriorly running between precerebral radial muscles. Each cephalic vessel bifurcating into medial and lateral branches at level of proboscis insertion; lateral branch posteriorly continues as extracerebral vessel between brain and body-wall longitudinal muscle



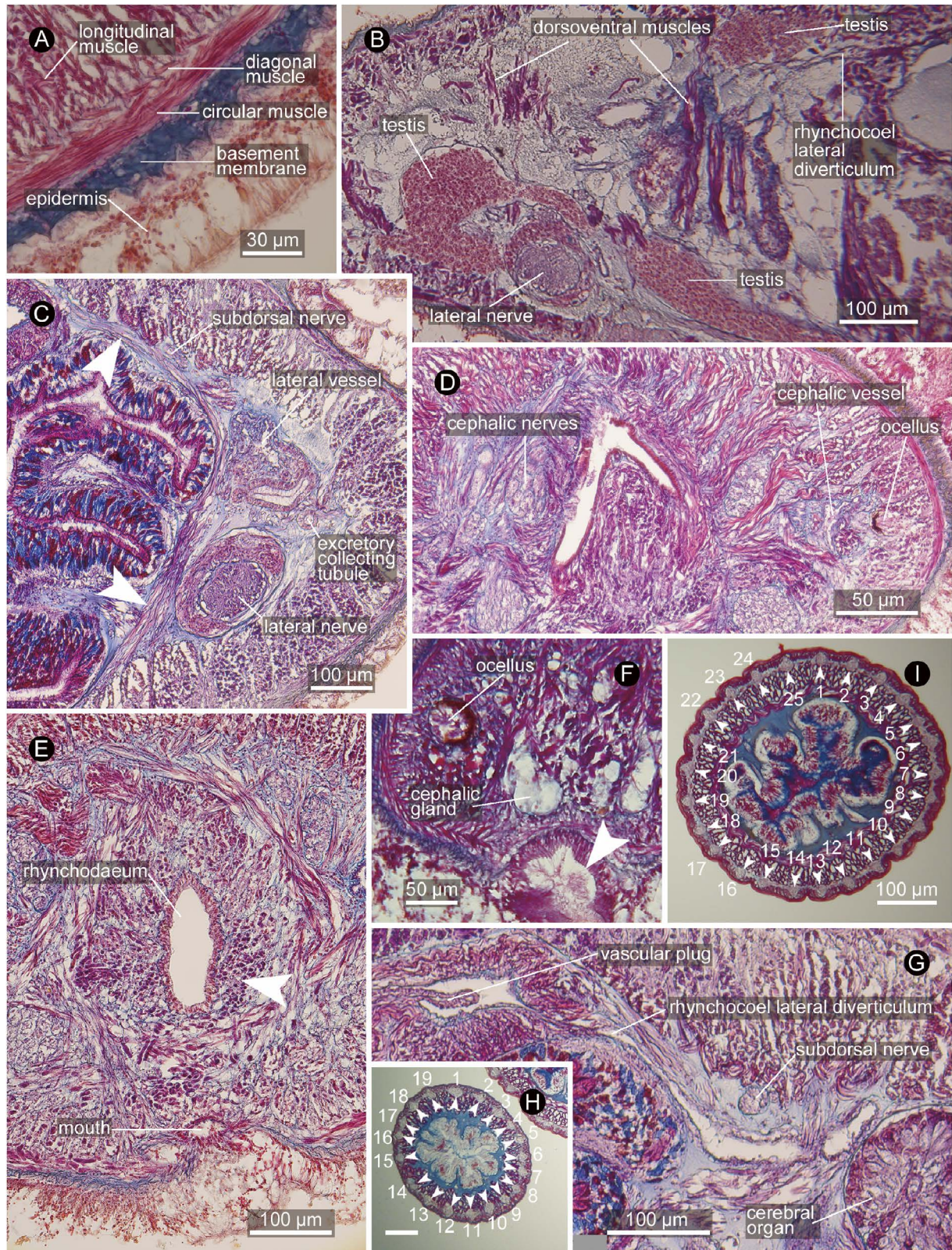


Fig. 12. *Coella glorieae* sp. nov., photomicrographs of transverse sections, holotype, PNM 4648. A, Body wall in foregut region; B, intestinal region showing dorsoventral muscles, testes, and rhynchocoel lateral diverticulum; C, foregut region showing well-developed circular muscles (indicated by arrowheads); D, proboscis insertion; E, precerebral region near mouth opening (indicated by arrowheads); F, precerebral region through proboscis pore (indicated by arrowhead); G, anterior-most rhynchocoel lateral diverticulum; H, I, proboscis anterior chamber; arrowheads indicating proboscis nerves differing in number by position. Scale bar for H: 50  $\mu$ m.



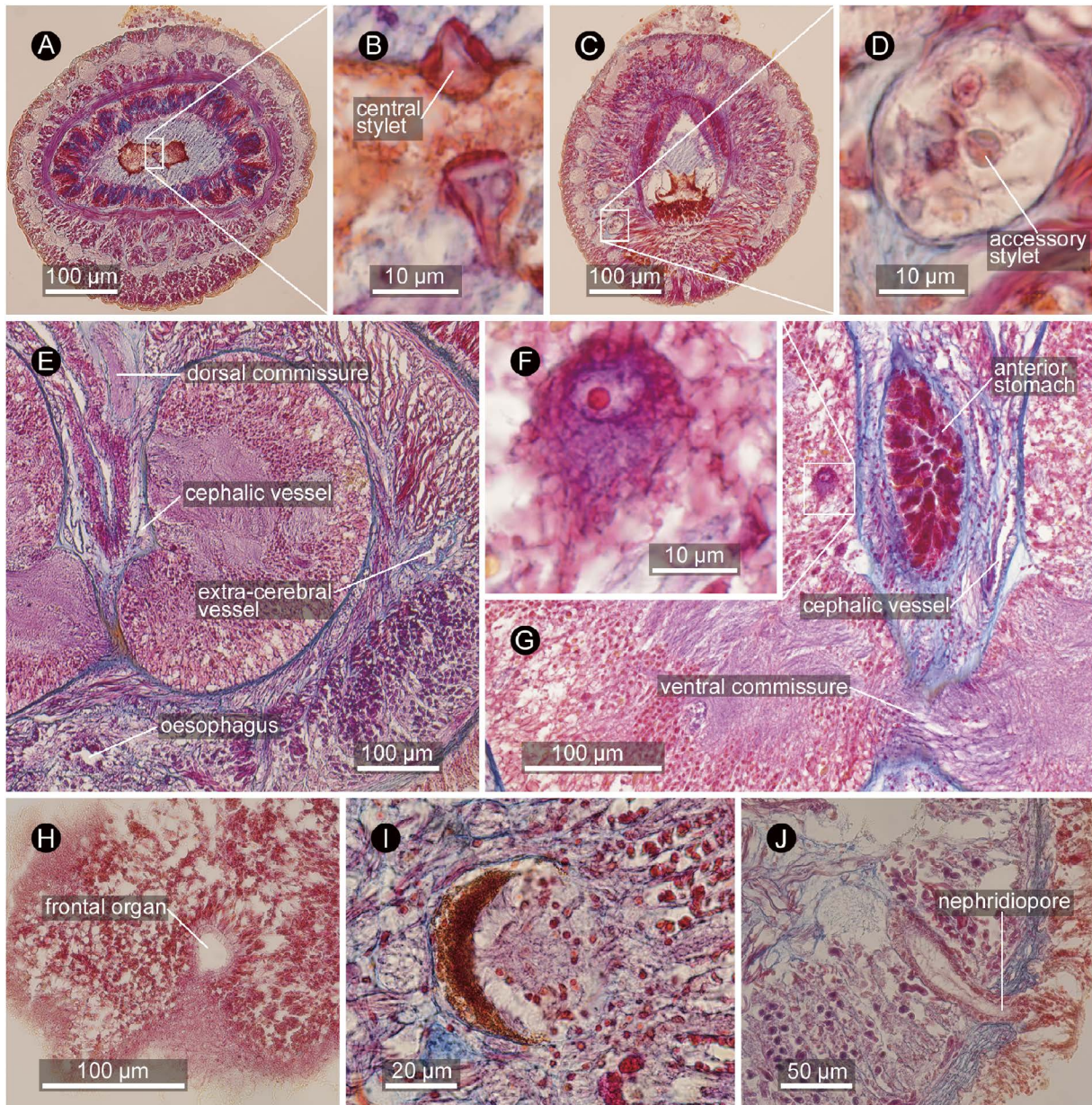


Fig. 13. *Coella gloriae* sp. nov., photomicrographs of transverse sections, holotype, PNM 4648. A, Proboscis anterior chamber near its posterior end, showing stylet basis; B, magnification of central stylets; C, proboscis middle chamber; D, magnification of accessory stylet pouch; E, brain region; F, magnification of neurochord cell; G, brain region; stomach was pushed forward due to contraction during anesthetization/fixation; H, cephalic tip showing frontal organ; I, pigment-cup ocellus; J, excretory pore in foregut region.

layer (Fig. 13E) before eventually ending blindly at level of cerebral-organ-canal opening; medial branch on both sides meeting medially above ventral cerebral commissure below rhynchocoel, from where three post-cerebral vessels (one mid-dorsal and two lateral vessels) leading posteriorly. Soon after its origin, mid-dorsal vessel penetrating rhynchocoel to form vascular plug (Fig. 12G), exposed to rhynchocoel lumen to run backward for 600 µm before descending below rhynchocoel wall above alimentary canal to extend for the rest of body. Lateral vessel tangling with excretory collecting tubules above lateral nerve cord in anterior stomach region. Pseudometameric transverse connectives between lateral and mid-dorsal vessels present in intestinal region. Blood corpuscles not found.

**Nervous system.** Brain comprised of dorsal and ventral ganglia on each side, covered with outer neurilemma, but no inner neurilemma separating outer neuronal layer and inner fibrous core; dorsal ganglion not forked posteriorly; single neurochord cell present on each side, about 20 µm in diameter, situated medially to posterior end of dorsal cerebral fibrous core (Fig. 13F). Ventral ganglion bending laterally at right angle, then curving posteriorly at right angle again to lead to lateral nerve (Fig. 14A, B). Lateral nerve with inner and outer neurilemma (Fig. 12C); longitudinal muscle bundles arranged just inside inner neurilemma. Single mid-dorsal nerve originating from dorsal commissure, situated between basement membrane and body-wall outer circular muscle layer. Pair of subdorsal nerves originating from me-



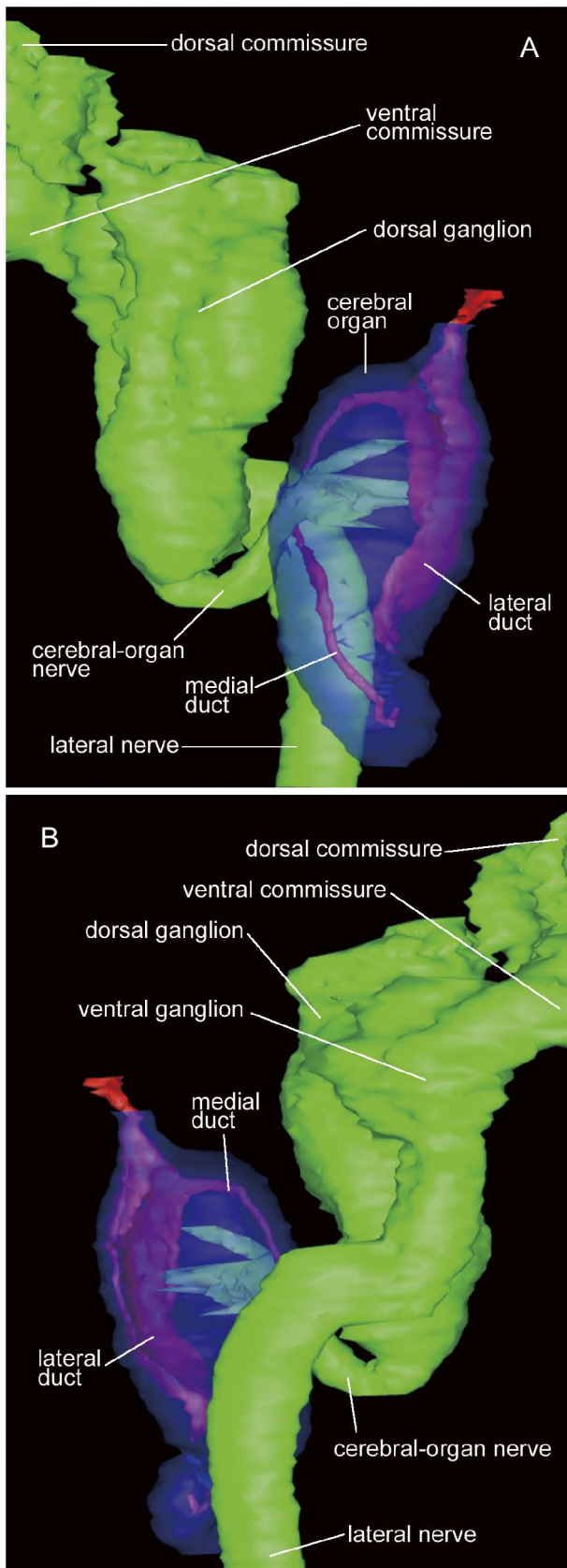


Fig. 14. *Coella gloriæ* sp. nov., three-dimensional reconstructions of brain and cerebral organ based on holotype, PNM 4648. A, Dorsal view; B, ventral view.

dial sides of dorsal ganglia and moving dorsolaterally along dorsal ganglia, then running posteriorly just beneath body-wall inner longitudinal muscle layer dorsolaterally to foregut (Fig. 12C, G).

**Glandular system.** Single frontal organ about  $30\mu\text{m}$  in diameter,  $40\mu\text{m}$  in length, situated subterminally (Fig. 13H), from which basophilic cephalic glands discharge. Cephalic glands poorly developed (Fig. 12F), situated inside body-wall longitudinal muscle layer anterior to level of mouth opening: basophilic lobules  $\sim 30\mu\text{m}$  diameter extend posteriorly to level of mouth opening; acidophilic glandular masses situated latero-ventrally near proboscis pore.

**Sensory system.** Pigment-cup ocelli (Fig. 13I) up to  $50\mu\text{m}$  in diameter, arranged precerebrally in four rows (15–18 lateral and 5–6 dorsolateral on each side; about 40 in total), all restricted anterior to proboscis insertion, embedded just below body-wall longitudinal muscle layer.

Cerebral organ comprised of *i*) canal, *ii*) neuronal component, and *iii*) glandular component. Canal opening dorso-laterally at primary transverse cephalic furrow (almost equivalent to level of ventral cerebral commissure), leading medio-posteriorly (Fig. 15A–D) to fuse with neuronal component, where it bifurcates into lateral and medial ducts (Fig. 15E, F); lateral duct wider than medial one; initially, lateral duct medially associated with 'sensory furrow' *sensu* Kirsteuer (1973) [thus the organ is of Aequifurcata *sensu* Stiasny-Wijnhoff (1926, 1936), as opposed to Inaequifurcata, where the lateral duct is not surrounded by sensory cells in any place and directly leads to sack] and laterally comprised of 'sack' *sensu* Kirsteuer (1973) lined with ciliated epithelium (Fig. 15F–I), posteriorly comprised entirely of sack-type epithelium (Fig. 15J–M), ending blindly without bifurcation; medial duct anteriorly lined with sensory cells (Fig. 15F–I), posteriorly bending upward after passing below insertion of cerebral-organ nerve (Fig. 15J) and fused with glandular component (Fig. 15K), slightly twisted (Fig. 15O, P) before terminating blindly. Neuronal and glandular components both antero-posteriorly accounting for about 60% of entire length of organ, overlapping for about 20%, where glandular component situated medio-dorsally, while neuronal component ventrally (Fig. 15H–L). Neuronal component innervated by single bundle ( $50\mu\text{m}$  thick) of nerve fibres sent antero-laterally from posterior end of dorsal cerebral fibre core (Figs 14A, B, 15H–K). Glandular component posteriorly tapered (Figs 14A, B, 15N–S), in close contact with blood vessel and excretory collecting tubules (Fig. 15R).

**Excretory system.** Excretory collecting tubules ramified and convoluted, embedded in extracellular matrix around lateral blood vessels (Fig. 12C), distributed from rear end of cerebral sensory organ to anterior portion of intestinal caecum. Single pair of excretory ducts leading laterally above lateral nerve cord to single nephridiopore, opening at foregut region (Fig. 13J).

**Reproductive system.** The single specimen was immature male; testes arranged in single lateral row on each side. Each testis comprised of single dorsal and single ventral branches, each above and below intestinal lateral diverticu-



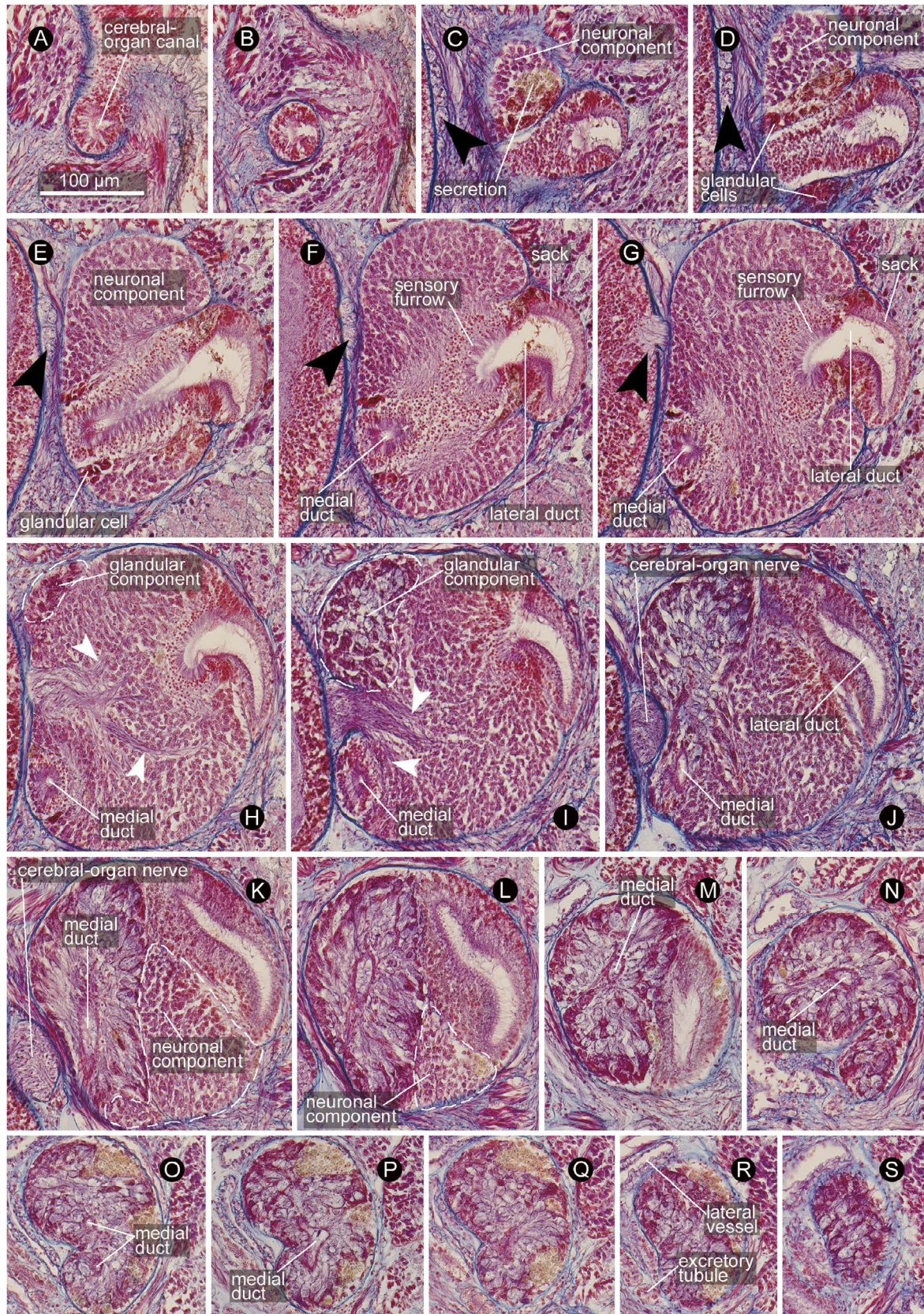


Fig. 15. *Coella gloriae* sp. nov., photomicrographs of transverse sections through cerebral organ, holotype, PNM 4648. A–D, Canal leading medio-posteriorly to fuse with neuronal component; E–I, canal bifurcating into lateral and medial ducts; J–P, medial canal surrounded by sensory cells; Q–S, glandular component posteriorly in close contact with blood vessel and excretory collecting tubules; black arrowheads (C–G) indicating anterior nerve from brain, not innervating cerebral organ; white arrowheads (H, I) indicating cerebral-organ nerve fibres.



Table 4. Morphological comparison between eight species of Reptantia that possess extracerebral vessels terminating blindly. Character compilation and coding based on Härlin and Sundberg (1995) and Härlin and Härlin (2001).

Species	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Coella gloriae</i> sp. nov.	2	2	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
<i>Coella tiurensis</i> Stiasny-Wijnhoff, 1936	2	0	0	0	0	0	1	0	1	1	0	1	1	0	1	?	1	1	1	0
<i>Drepanophorina guineensis</i> Stiasny-Wijnhoff, 1936	2	2	0	1	1	0	0	0	0	1	0	1	1	0	1	?	1	1	1	1
<i>Drepanophorina savuensis</i> Stiasny-Wijnhoff, 1936	2	2	0	1	1	1	0	0	1	1	0	1	1	0	1	?	1	1	1	1
<i>Drepanophoringia waingapuensis</i> Stiasny-Wijnhoff, 1936	2	?	?	?	0	1	0	0	1	1	?	1	1	0	1	1	1	1	0	1
<i>Punnettia micrommata</i> Stiasny-Wijnhoff, 1936	2	2	0	0	0	0	0	0	0	1	0	1	1	0	1*	?	1	1	1	0
<i>Punnettia maldivensis</i> Stiasny-Wijnhoff, 1936	2	2	0	0	0	0	0	0	1	1	0	?	1	0	1	?	1	1	1	0
<i>Xenonemertes rhamphocephalus</i> Gibson, 1983	1	2	0	0	1	0	1	0	1	1	0	1	1	0	1	0	1	1	0	0

\*Coded as “?” in Härlin and Sundberg (1995) and Härlin and Härlin (2001), but Stiasny-Wijnhoff (1936: 143) stated that extracerebral vessels were present in *Punnettia micrommata*.

1. Eyes: absent (0), two rows (1), four rows (2), four groups (3)
2. Cephalic furrows: absent (0), present (1), with secondary grooves (2)
3. Position of mouth: anterior to brain (0), below brain (1)
4. Longitudinal dorsal stripes: absent (0), present (1)
5. Longitudinal head furrows: absent (0), present (1)
6. Mouth and proboscis openings: separate (0), united as an atrium (1)
7. Tubular stomach projections: absent (0), present (1)
8. Intestinal diverticula: not branched (0), branched (1)
9. Inner circular muscle layer: absent (0), present (1)
10. Dorsoventral muscles: absent (0), present (1)
11. Muscle layers in rhynchodaeum: absent (0), present (1)
12. Oesophagus musculature: absent (0), present (1)
13. Muscular septum at proboscis insertion: absent (0), present (1)
14. Neuromuscular fibrils: absent (0), present (1)
15. Cerebral vessels: absent (0), blind ending (1), looped (2)
16. Blood loops around nephridia: absent (0), present (1)
17. Transverse blood vessels: absent (0), present (1)
18. Rhynchocoel vessels: absent (0), present (1)
19. Rhynchocoel diverticula: branched (0), not branched (1)
20. Neurochord cells: absent (0), present (1)

lum, extending laterally to merge above lateral nerve cord, further extending laterally (Fig. 12B); testes thus assuming 90°-rotated Y-shape. Gonopore not found, but probably opening ventrolaterally.

**Remarks.** The benthic body form (Fig. 11A, B) and the minute central stylets mounted on a sickle-shaped basis (Fig. 13A, B) in the present Cebu specimen undoubtedly affiliate the species in the Reptantia within the Polystilifera. However, its generic placement had to be admittedly arbitrary because no synapomorphy is apparent as to all the currently known ~15 genera in Reptantia (Härlin and Sundberg 1995; Härlin and Härlin 2001). At the moment, the reptantian systematics is not based on molecular data. Of the reptantian sequences currently available in public databases, those that are tagged to species names pertain to only two species in two genera: *Drepanophorus spectabilis* (Quatrefages, 1846) and *Paradrepanophorus crassus* (Quatrefages, 1846) (Andrade *et al.* 2012; Beckers *et al.* unpubl.); others are left unidentified, such as “Reptant nemertean sp.” (Thollessen and Norenburg 2003), “Polystilifera sp.” (Andrade *et al.* 2012; Sundberg *et al.* 2016), and “Reptantia sp.” (Kvist *et al.* 2014).

I included the present Cebu species in the genus *Coella*

on the basis of an *a priori* assumption that vascular-system morphology would have greater phylogenetic significance than some other characters; needless to say, however, this assumption should be tested in future studies. In addition to *Coella gloriae*, seven other species of Reptantia are reported to possess extracerebral vessels that branch off from the cephalic vessels and run backward outside the cerebral ring before terminating blindly without turning forward or making a loop: these are *Coella tiurensis* Stiasny-Wijnhoff, 1936; *Drepanophorina guineensis* Stiasny-Wijnhoff, 1936; *Drepanophorina savuensis* Stiasny-Wijnhoff, 1936; *Drepanophoringia waingapuensis* Stiasny-Wijnhoff, 1936; *Punnettia maldivensis* Stiasny-Wijnhoff, 1936; *Punnettia micrommata* Stiasny-Wijnhoff, 1936; and *Xenonemertes rhamphocephalus* Gibson, 1983 (Stiasny-Wijnhoff 1936: text-fig. 75b, c; Gibson 1983: fig. 12B). Of these seven species, *Coella tiurensis*, *Drepanophorina savuensis*, and *Drepanophoringia waingapuensis* are the type species of the respective genera. Of these three, *Coella gloriae* shares with *Coella tiurensis* the greatest number—25 out of 40—of morphological characters that were utilized in a cladistic analysis by Härlin and Härlin (2001); it shares 23 with *Drepanophorina savuensis* and 18 with *Drepanophoringia waingapuensis* (Table



Table 4. Continued.

Species	Characters																				Number of characters shared with <i>Coella gloriae</i>
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
<i>Coella gloriae</i> sp. nov.	1	1	0	0	1	1	0	1	0	1	1	0	2	1	0	1	1	4	?	0	—
<i>Coella tiurensis</i> Stiasny-Wijnhoff, 1936	0*	1	1	1	1	1	0	0	0	0	0	0	2	1	0	0	1	?	?	0	25
<i>Drepanophorina guineensis</i> Stiasny-Wijnhoff, 1936	0	1	0	0	1	0	1	2	0	1	0	1	1	1	0	1	1	1	?	0	25
<i>Drepanophorina savuensis</i> Stiasny-Wijnhoff, 1936	0	1	0	0	0	0	1	2	0	1	0	1	0	1	0	2	1	3	2	0	23
<i>Drepanophoringia waingapuensis</i> Stiasny-Wijnhoff, 1936	1	1	?	1	1	0	1	1	?	0	?	1	0	1	1	0	1	1	2	0	18
<i>Punnettia micrommata</i> Stiasny-Wijnhoff, 1936	1	1	0	1	1	0	1	1	0	1	0	1	0	1	0	2	1	1	?	0	24
<i>Punnettia maldivensis</i> Stiasny-Wijnhoff, 1936	0	1	0	1	0	0	1	1	1	1	0	1	1	1	0	1	1	4	2	0	23
<i>Xenonemertes rhamphocephalus</i> Gibson, 1983	1	1	0	1	1	0	0	2	0	0	0	1	2	1	0	0	1	?	?	0	24

\*Although Stiasny-Wijnhoff (1936: 75) stated “Der laterale Kern gabelt sich nicht...” [The lateral core (of the dorsal ganglion) does not fork], this character was coded as ‘forked’ by Härlin and Sundberg (1995) and Härlin and Härlin (2001).

21. Fibre core in dorsal ganglia: forked (0), simple (1)  
 22. Dorsal and ventral brain lobes: in horizontal plane (0), not (1)  
 23. Size of brain lobes: dorsal > ventral (0), equal size (1)  
 24. Ventral ganglia below ventral commissure: yes (0), no (1)  
 25. Subdorsal nerve: absent (0), present (1)  
 26. Dorsal nerve: absent (0), present (1)  
 27. Inner neurilemma: absent (0), present (1)  
 28. Lateral nerve: prolonged ventral lobe (0), emerge laterally with free tips (1), emerge laterally without free tips (2)  
 29. Cerebral canal enter cerebral organs: anterior (0), posterior (1)  
 30. Glandular appendage in cerebral organ: absent (0), present (1)  
 31. Cerebral organ sac: on dorsal branch (0), lateral (1), ventral (2), outgroup (3)  
 32. Neurilemma in cerebral organ: absent (0), present (1)  
 33. Position of cerebral organs: lateral to brain (0), behind brain (1), partly overlapping (2)  
 34. Glands at cerebral canal fork: absent (0), present (1), outgroup (2)  
 35. Cerebral organ canal (s): forked equal (0), forked unequal (1), not forked (2)  
 36. Cerebral pore: lateral (0), ventral (1), dorsal (2)  
 37. Precerebral region: absent (0), present (1)  
 38. Type of gonads: sack-like (0), V-shaped (1), sack with projections (2), W-shaped (3), Y-shaped (4)  
 39. Gonopores: dorsal (0), lateral (1), ventral (2)  
 40. Blood vessels run: through brain ring (0), below ventral commissure (1)

4). Along with *Coella tiurensis*, *Coella gloriae* may also be equally similar to *Drepanophorina guineensis* by sharing the same number of characters (Table 4). Therefore, *Coella gloriae* could have been placed in *Drepanophorina* Gibson, 1995 if the latter was a distinct genus from *Coella*. Should the two genera turn out to be synonymous, that genus must be referred to as *Coella* because it has nomenclatural precedence over *Drepanophorina*. *Drepanophorina* was established by Stiasny-Wijnhoff (1936: 60) for four nominal species—*Drepanophorina argus* Stiasny-Wijnhoff, 1936; *Drepanophorina guineensis*; *Drepanophorina savuensis*; and *Drepanophorus latus* Bürger, 1890—without type-species fixation. The name *Drepanophorina* became nomenclaturally available when Gibson (1995: 357) fixed *Drepanophorina savuensis* as the type species.

Apart from the characters listed in Table 4, *Coella gloriae* also differs from the seven species by the following characteristics: from *Coella tiurensis* by the rhynchodaeal sphincter

(present in *C. gloriae*; absent in *C. tiurensis*); from *Drepanophorina guineensis* by the direction of the innervation into the cerebral organ (laterally in *C. gloriae*; from anterior backward in *D. guineensis*); from *Drepanophorina savuensis* by the pigments in the outer portion of the epithelium (absent in *C. gloriae*; present in *D. savuensis*); from *Drepanophoringia waingapuensis* by the number of the eyes (~40 in *C. gloriae*; ~100 in *D. waingapuensis*) and by the innervation from the lateral nerve to the cerebral organ (absent in *C. gloriae*; present in *D. waingapuensis*); from *Punnettia maldivensis* by the number of the proboscis nerves (19–25 in *C. gloriae*; 14 in *P. maldivensis*); from *Punnettia micrommata* by the length of the cerebral organ relative to the ventral ganglion (longer in *C. gloriae*; shorter in *P. micrommata*) (Stiasny-Wijnhoff 1936); and from *Xenonemertes rhamphocephalus* by the blood corpuscles (absent in *C. gloriae*; present in *X. rhamphocephalus*) (Gibson 1983). Indeed, *Coella gloriae* is morphologically unique among all the known rep-

tantians in that it has *i*) four rows of eyes, *ii*) the cephalic furrows, *iii*) no dorsal marking, *iv*) separate mouth and proboscis openings, *v*) blind-ending extracerebral vessels, *vi*) non-forked fibre core in the dorsal ganglia, *vii*) the sub-dorsal nerve, and *viii*) cerebral organs partly overlapping the brain (Härlin and Sundberg 1995; Härlin and Härlin 2001).

“Reptant nemertean sp. 500” of Thollessen and Norenburg (2003) from Shirahama, Japan, would be congeneric with *Coella gloriae*, between which it shows 7.6% uncorrected *p*-distance in terms of 513-bp COI sequence.

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