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Reappraisal of *Goezeella* Fuhrmann, 1916 (Cestoda: Proteocephalidae), parasites of Neotropical catfishes (Siluriformes), with description of a new species from *Pimelodella cristata* (Heptapteridae)

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Abstract: The cestode genus *Goezeella* Fuhrmann, 1916 is reviewed on the basis of taxonomic evaluation of type and newly collected material from pimelodid and heptapterid catfishes (Siluriformes) in the Amazon River basin, South America, and its generic diagnosis is amended. The genus is typified by the exclusively ventral position of the cortical vitelline follicles, the inner longitudinal musculature formed by dense individual muscle fibres, rather than forming bundles as in other proteocephalids, a well-developed metascolex and biloculate suckers. The type species, *G. siluri* Fuhrmann, 1916, is redescribed based on its syntype from *Cetopsis coecutiens* (type-host) (Cetopsidae) and specimens from *Pinirampus pirinampu* (Pimelodidae). The validity of *G. danbrooksi* de Chambrier, Rego & Mariaux, 2004 from *Ageneiosus pardalis* (Auchenipteridae) is confirmed and some erroneous morphological traits are corrected based on examination of its holotype. A new species, *Goezeella mariae* sp. nov., is described from the heptapterid catfish *Pimelodella cristata* (Heptapteridae). The new species differs from congeners by its overall size (much smaller compared to *G. siluri*), morphology of the scolex (strongly wrinkled metascolex and weakly developed interlocular septum of suckers) and number of the testes. This is the third proteocephalid cestode described from a heptapterid catfish in South America and the first helminth parasite reported from *P. cristata*. *Goezeella* is unusual among other Neotropical proteocephalids by its occurrence in catfishes of as many as four families; all species of the genus are known only from the Amazon and Orinoco River basins. Molecular data on two of the three valid species and a key to their identification are provided.

Keywords: Morphology - taxonomy - tapeworms - Onchoproteocephalidea - systematics - host-associations - Neotropical Region - South America.

INTRODUCTION

South American catfishes (Siluriformes) are hosts of a vast diversity of tapeworms (Cestoda) of the recently erected order Onchoproteocephalidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014 (see Alves *et al*., 2017a; Scholz & Kuchta, 2017). This order includes the previously recognized order Proteocephalidea Mola, 1928 (all in one family, Proteocephalidae La Rue, 1911) and some members of the polyphyletic order 'Tetraphyllidea' Carus, 1863 (Caira *et al*., 2014). A total of 87 species of proteocephalids in 36 genera have been reported from South American catfishes (Alves *et al*., 2017a; de Chambrier *et al*., 2017), but new taxa are still being described and new genera erected (e.g. Alves *et al*., 2015, 2017b; Arredondo *et al*., 2017). Likewise, evaluation of type-specimens and newly collected material made it possible to elucidate the taxonomic status of some previously insufficiently known genera, such as *Brayela* Rego, 1984, *Megathylacus* Woodland, 1934 and *Chambriella* Rego, Chubb & Pavanelli, 1999 (de Chambrier *et al*., 2014; Alves *et al*., 2017b).

Goezeella Fuhrmann, 1916 was erected to accommodate *Goezeella siluri* Fuhrmann, 1916 from the blue whale

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catfish *Cetopsis coecutiens* (Lichtenstein) (Siluriformes: Cetopsidae) in the Amazon River basin (Fuhrmann, 1916). This author distinguished *Goezeella* from *Monticellia* La Rue, 1911, which has also the testes, ovary, vitelline follicles and uterus in the cortex, by its possession of a well-developed metascolex, formed by an enlargement of the neck (proliferation zone) and the posterior part of the scolex (Fuhrmann, 1916).

Woodland (1933a) confused tapeworms found in the pimelodid catfish *Brachyplatystoma vaillantii* (Valenciennes) (Pimelodidae) in the Brazilian Amazonia with *G. siluri*, even though they had eggs with polar projections, whereas *G. siluri* described by Fuhrmann (1916) possessed 'typical' eggs of proteocephalids, i.e. without polar projections. Woodland (1933a) apparently studied a mixture of *G. siluri* from *C. coecutiens* and the species later described as *Amphoteromorphus praeputialis* Rego, Santos & Silva, 1974 [now *Brooksiella praeputialis* (Rego, Santos & Silva, 1974) Rego, Chubb & Pavanelli, 1999]. For cestodes from *B. vaillantii*, which are devoid of polar projections on their eggs, Woodland (1933a) proposed a new species, *Goezeella piramutab* Woodland, 1933; this species was later synonymized with *G. siluri* by de Chambrier *et al*. (2004a).

Brooks & Deardorff (1980) reported *G. siluri* from the auchenipterid catfish *Ageneiosus caucanus* Steindachner (= syn. of *A. pardalis* Lütken) in Colombia, but these cestodes differed from *G. siluri* in several morphological traits, such as the arrangement of the vitelline follicles, number of the testes and relative position of the vaginal sphincter (de Chambrier *et al*., 2004a). Therefore, the latter authors proposed a new name, *G. danbrooksi* de Chambrier, Rego & Mariaux, 2004, to accommodate the specimens from *A. pardalis*, thus adding the second species to the genus.

As part of long-term studies on the diversity, host associations and interrelations of proteocephalid tapeworms in the Neotropical Region (e.g. de Chambrier & Vaucher, 1999; Alves *et al.*, 2015; de Chambrier *et al.*, 2015a), new material of *Goezeella* spp. from *Pinirampus pirinampu* (Spix & Agassiz) (Pimelodidae) and *Pimelodella cristata* (Müller & Troschel) (Heptapteridae) was collected. Evaluation of this new material, supplemented by examination of type-specimens of *G. siluri* and *G. danbrooksi*, made it possible to revise the genus including emendation of its diagnosis, to redescribe its type-species and to describe a new species from *P. cristata*. In addition, an identification key to the three species of the genus is provided.

MATERIAL AND METHODS

The present study is based on the evaluation of the syntypes of *Goezeella siluri* and the holotype of *G. danbrooksi* deposited at the Natural History Museum, Geneva and the National Museum of Natural History, Washington, D.C., respectively, and newly collected specimens from *Pimelodella cristata* and *Pinirampus pirinampu*.

The newly collected tapeworms were removed from the host's intestine and placed in 0.9% NaCl solution. Several posteriormost proglottids were excised and fixed in 96% molecular-grade ethanol for sequencing of the partial large subunit nuclear ribosomal RNA gene (*lsr*DNA gene; D1–D3 domains) (see Brabec *et al*., 2012 for methodology). The anterior parts (hologenophores *sensu* Pleijel *et al*., 2008) were placed in a small amount of saline and hot (almost boiling) 4% formaldehyde solution was immediately added to keep the worms straight; after two weeks they were transferred to 70% ethanol before further processing.

Specimens for morphological studies were stained with Mayer's hydrochloric carmine solution, dehydrated in an ethanol series, cleared with eugenol (clove oil) and mounted in Canada balsam. Eggs were drawn in distilled water. For histological sections, pieces of the strobila were embedded in paraffin wax, cross sectioned at 12-15 µm, stained with Weigert's haematoxylin and counterstained with 1% eosin B (acidified with five drops of pure acetic acid for 100 ml solution) following protocol outlined by de Chambrier (2001). For scanning electron microscopy (SEM) observations, scoleces of each species were dehydrated through a graded ethanol series, dried in hexamethyldisilazane, coated with gold and examined in a JEOL JSM-740 1F scanning electron microscope at the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences. Microthrix terminology follows Chervy (2009). All measurements are given in micrometres unless otherwise indicated; abbreviations used in descriptions are: x = mean; n = number of measurements. The fish names follow Froese & Pauly (2017).

Museum acronym abbreviations:

CHIOC	Helminthological Collection of the Instituto Oswaldo Cruz in Rio de Janeiro, Brazil
IPCAS	Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic
MHNG-PLAT	Platyhelminthes collection of the Natural History Museum of Geneva, Switzerland
USNM	National Museum of Natural History, Washington, D.C., USA

TAXONOMIC ACCOUNT

Goezeella Fuhrmann, 1916

Amended diagnosis: Onchoproteocephalidea, Proteocephalidae. Testes, ovary, vitelline follicles and uterus cortical. Small to medium-sized, robust worms, strobila acraspedote, with longitudinal and transverse grooves;

proglottids variable in shape and size. Scolex conical, with rounded to quadrangular apical part, without apical organ, wider than proliferative zone (neck); metascolex well-developed, wrinkled, formed by enlargement of neck. Suckers robust, biloculate; loculi variable in shape and size, interlocular septum conspicuous or not. Internal longitudinal musculature well-developed, with numerous individual fibres not forming bundles; fibres more abundant on lateral sides of proglottids. Testes in one irregular field, in one or two layers, dorsally overlapping cirrus-sac and vitelline follicles. Cirrus-sac elongated to pear-shaped, internal sperm duct thick-walled, strongly coiled in proximal half of cirrus-sac. Genital pores markedly pre-equatorial, irregularly alternating. Genital atrium present, deep. Ovary with medullary isthmus and 2 follicular (grape-like) lobes penetrating inner longitudinal musculature to dorsal cortex; lobes with numerous dorsal outgrowths. Vagina anterior to cirrus-sac, surrounded by numerous chromophilic cells in distal (terminal) part (*pars copulatrix vaginae*); vaginal sphincter present. Vitelline follicles only on ventral or ventrolateral side of cortex, arranged in two uninterrupted lateral bands, widened towards ovarian level. Uterine development type 2 according to de Chambrier *et al*. (2004b). Parasites of siluriform catfishes in the Neotropical Region.

Type species: *Goezeella siluri* Fuhrmann, 1916.

Additional species: *Goezeella danbrooksi* de Chambrier, Rego & Mariaux, 2004; *Goezeella mariae* sp. nov.

Remarks: The validity of *Goezeella* has been questioned since its establishment, mainly due to different assumptions on the taxonomic usefulness of two morphological traits, i.e. the presence or absence of a metascolex and the distribution of the internal organs in relation to the internal longitudinal musculature. Woodland (1925) synonymized *Goezeella* with *Monticellia* because they share the cortical position of all internal organs, whereas Harwood (1933) synonymized it with *Corallobothrium* Fritsch, 1886 based on the presence of a metascolex in species of both genera (see Scholz *et al.*, 2011 for data on *Corallobothrium*). Based on a cladistic analysis inferred from morphological characters, Brooks (1995) synonymized *Choanoscolex* La Rue, 1911, *Goezeella*, *Jauella* Rego & Pavanelli, 1985 and *Peltidocotyle* Diesing, 1850 with *Spatulifer* Woodland, 1934, questioning validity of *Peltidocotyle*, which should have priority, because of the assumed similarity of the metascolex development shared by these genera (see Brooks & Rasmussen, 1984). However, this synonymy has never been accepted by most of the authors, including Rego *et al*. (1999), de Chambrier & Vaucher (1999) and de Chambrier *et al*. (2004a), who recognized *Goezeella* as a valid genus. Recent molecular data suggest that the above-mentioned features may not be useful to assess the interrelations among proteocephalids and a more natural classification, reflecting the evolutionary history of the group, should be proposed (de Chambrier *et al*., 2004b, 2015b; Scholz *et al*., 2013).

As a result, the subfamilial classification proposed by W. N. F. Woodland and widely used for proteocephalids (Rego, 1994; de Chambrier & Vaucher, 1999; Rego *et al*., 1999), based on the position of the testes, uterus and vitelline follicles in relation to the internal longitudinal musculature (see de Chambrier *et al*., 2009 and references therein) is not considered in the present account. Nevertheless, for practical reasons, we compared *Goezeella* with the 11 genera previously placed in the Monticelliinae (Table 1), which are typified by the cortical position of the testes, ovary, vitelline follicles and uterus (Rego, 1994).

Goezeella can be readily differentiated from all proteocephalid genera by the vitelline follicles present only in the ventral cortex, i.e. completely absent dorsally, with lateral bands widened at the ovarian level, and by the possession of the inner longitudinal musculature formed by individual muscle fibres rather than forming compact bundles.

Goezeella siluri Fuhrmann, 1916

Figs 3, 4, 10-19

Goezeella siluri Fuhrmann, 1916: 385.
Monticellia siluri. – Woodland, 1925: 714.
Corallobothrium siluri. – Harwood, 1933: 140.
Goezeella piramutab Woodland, 1933a: 488.
Monticellia piramutab. – Woodland, 1935: 222.
Spatulifer piramutab. – Brooks & Deardorff, 1980: 17.
Spatulifer siluri. – Brooks, 1995: 365.

Material examined

Syntype: MHNG-PLAT-36375, a whole-mounted specimen (2 slides) and 12 slides of serial cross-sections. *Additional specimens*: MHNG-PLAT-19858, a whole-mounted specimen (4 slides) and 6 slides of serial cross-sections, collected on 13.04.1992, host field no. Br 237a. – CHIOC 38858, a whole-mounted specimen (one slide) collected on 30.09.1995, host field no. Br 436. – MHNG-PLAT-21845, 21877, 2 uncomplete whole-mounted specimens (3 slides) and 3 slides of serial cross-sections collected on 02.09.1995, host field no. Br 472. – MHNG-PLAT-21879, CHIOC 38859, a whole-mounted specimen (4 slides) and 6 slides of serial cross-sections collected on 19.10.1995, host field No. Br 811; all specimens from *P. pirinampu* from Itacoatiara, State of Amazonas, Brazil (3°09’S, 58°26’W), collected by A. A. Rego and A. de Chambrier. – MHNG-PLAT-85161, a whole-mounted specimen (3 slides), collected on 07.10.2011, host field no. PI 819a; hologenophore; specimen from *P. pirinampu* from Iquitos, Region of Loreto, Peru (3°47’S, 73°20’W).

Table 1. Selected morphological traits of the genera previously placed in the Monticelliinae (Cestoda: Proteocephalidae), parasites of freshwater fishes in the Neotropical region.

Genus (number of species)	Scolex shape/ metascolex (development)	Suckers appearance/ number of loculi	ILM arrangement/ development	Cirrus-sac shape	Vagina in relation to cirrus-sac	Ovary arrangement	Vitelline follicles arrangement	References
Ageneiella de Chambrier & Vaucher, 1999 (1 sp.)	globose/absent	elongate/ biloculate	bundles of fibres/well developed	elongate	only anterior	isthmus medullary; crossing ILM	two lateral rows	de Chambrier & Vaucher (1999)
Chambriella Rego, Chubb & Pavanelli, 1999 (1 sp.)	conical/absent	large/biloculate	bundles of fibres/ weakly developed	subovate	anterior and/or posterior	only cortical	two lateral rows	Alves *et al*. (2017b)
Choanoscolex La Rue, 1911 (1 sp.)	conical/present (weakly developed)	large, elongate/ uniloculate	bundles of fibres/ weakly developed	pyriform	anterior or posterior	only cortical	two lateral rows	de Chambrier & Vaucher (1999); Rego *et al*. (1999)
Goezeella Fuhrmann, 1916 (3 spp.)	conical/present (well developed)	robust, elongate/ biloculate	individual fibres/well developed	elongate to pyriform	only anterior	isthmus medullary; crossing ILM	two ventral rows	present study
Manaosia Woodland, 1935 (1 sp.)	globose/absent	robust, hidden in scolex, horseshoe-shaped muscles/ uniloculate	bundles of fibres/well developed	pyriform	only anterior	isthmus medullary; crossing ILM	two lateral rows	de Chambrier (2003)
Monticellia La Rue, 1911 (8 spp.)	globose/ absent	usually rounded/ uniloculate	bundles of fibres/ variable	usually pyriform	variable in position	usually cortical	two lateral rows	Rego (1994); Arredondo & Gil de Pertierra (2010)
Regoella Arredondo, de Chambrier & Gil de Pertierra, 2013 (1 sp.)	quadrangular/ absent	inverted triangle-shaped/ uniloculate	bundles of fibres/ weakly developed	pyriform	usually posterior	only cortical	two lateral rows	Arredondo *et al.* (2013)
Riggenbachiella Alves, de Chambrier, Luque & Scholz, 2017 (2 spp.)	quadrilobed/ absent	large/ biloculate	bundles of fibres/ weakly developed	sigmoid, chambered	anterior, exceptionally posterior	only cortical	two lateral rows	Alves *et al*. (2017b)
Spasskyellina Freze, 1965 (3 spp.)	globose/absent	rounded, covered with conspicuous gladiate spinitriches/ uniloculate	bundles of fibres/ weakly developed	claviform	only posterior	only cortical	two lateral or slightly ventral rows	Pavanelli & Takemoto (1996); de Chambrier *et al.* (2015b)
Spatulifer Woodland, 1934 (3 spp.)	usually conical /present (well developed)	oval/ uniloculate	bundles of fibres/ weakly to well developed	elongate	only anterior or posterior	only cortical	two lateral or ventral rows	Woodland (1933b, 1935); Arredondo & Gil de Pertierra (2008)
Synbranchiella Arredondo, Alves & Gil de Pertierra, 2017 (1 sp.)	subspherical to quadrangular/ absent	robust, elongate/ biloculate	bundles of fibres/ weakly developed	elongate to pyriform	only anterior	only cortical	two lateral rows	Arredondo *et al.* (2017)

Abbreviation: ILM, internal longitudinal musculature

Type locality: Amazon River basin (specific locality unknown).

Other localities: Delta of the Orinoco River, Venezuela; Amazon River, Itacoatiara, State of Amazonas, Brazil; Amazon River, Iquitos, Region of Loreto, Peru.

Type host: Blue whale catfish *Cetopsis coecutiens* (Lichtenstein, 1819) (Siluriformes: Cetopsidae).

Other definitive hosts: *Cetopsis othonops* (Eigenmann) (Siluriformes: Cetopsidae) and *Brachyplatystoma vaillantii* (Valenciennes) (Siluriformes: Pimelodidae) (doubtful host – see remarks below); *Pinirampus pirinampu* (Spix & Agassiz) (Siluriformes: Pimelodidae).

Site of infection: Anterior intestine.

Prevalence of infection: Fuhrmann (1916) found 4 tapeworms in one *C. coecutiens*, but did not provide the total number of fish examined; 43 *P. pirinampu* examined/8 fish infected (19%) from Itacoatiara, Brazil.

Morphological description: Fuhrmann (1916), de Chambrier *et al*. (2004a), present study.

Representative DNA sequences: A fragment of 1491 bp long of the *lsr*DNA (D1–D3 domains) (GenBank MF370207). The newly generated sequence of an isolate of *G. siluri* from *P. pirinampu* is 483 bp longer than the sequence from the same host and river basin available in the GenBank (AJ388612).

Redescription (based on 6 whole worms, serial cross-sections of mature proglottids and 1 scolex studied using SEM from *P. pirinampu*; measurements taken from the syntype in brackets): Proteocephalidae. Testes, ovary, vitelline follicles and uterus cortical; medium-sized worms. Total body length 90-230 mm (n = 3), maximum width up to 3 mm (n = 3). Strobila acraspedote, anapolytic, with longitudinal and transverse grooves, consisting of about 335-360 proglottids: 195-200 immature (up to appearance of spermatozoa in vas deferens), 45-55 mature (up to appearance of eggs in uterus), 50-55 pregravid (up to appearance of hooks in oncospheres) and 45-50 gravid. Immature and mature proglottids much wider than long (length: width ratio 0.10-0.20), pregravid proglottids wider than long (length: width ratio 0.45-0.55), gravid proglottids wider than long to longer than wide (length: width ratio 0.80-1.93).

Scolex 1.18-1.60 × 1.45-1.94 mm (n = 5), much wider than neck (proliferation zone), 1.77-1.80 × 1.40-1.45 mm, bearing 4 robust suckers, biloculate, with loculi variable in size; anterior loculus 210-295 (x = 255; n = 5) in diameter, posterior loculus 205-255 (x = 217; n = 5) in diameter; conspicuous septum separating each loculus (Figs 11, 15). Metascolex present, uniformly wrinkled. Apex conical, lacking apical organ, with numerous gland-cells (Figs 3, 4, 11, 15). Apex of scolex and lumen of suckers covered with acicular filitriches, similar in density (not shown); surface between suckers, base of metascolex and neck covered with capilliform filitriches, similar in density (not shown); pregravid proglottids covered with acicular filitriches (Fig. 10).

Inner longitudinal musculature well-developed, composed by numerous, individual muscle fibres, concentrated on lateral sides of proglottids (Figs 13, 17). Osmoregulatory canals situated at same level, median to lateral-most testes and vitelline follicles, almost straight (Figs 16, 17); ventral osmoregulatory canal wider than dorsal one (Figs 16, 17).

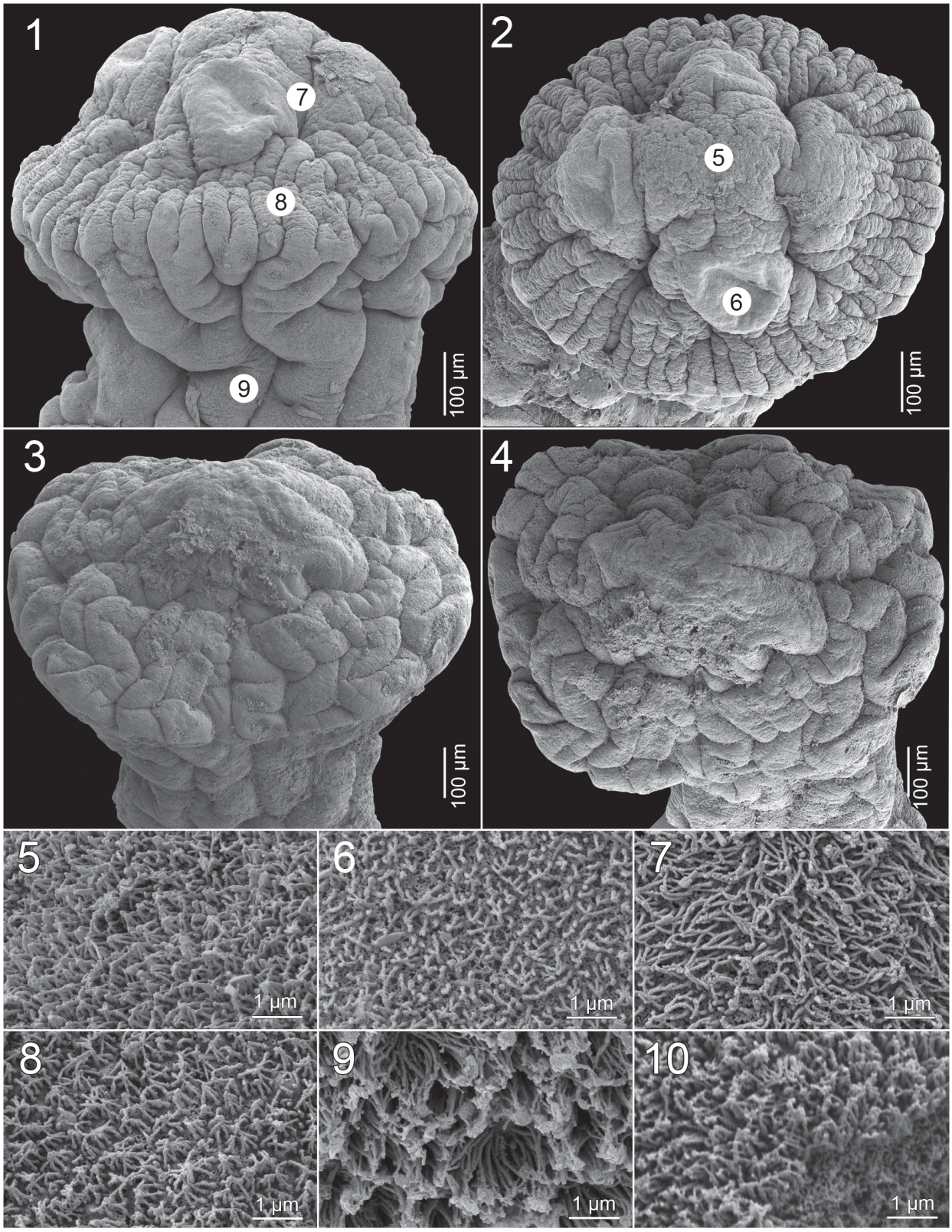
Testes numerous, spherical, small, 55-80 in diameter, in 1 or 2 irregular layers, 282-366 (x = 314; n = 13) [380-430] per mature proglottids (Figs 12, 16, 18). Testes form 1 irregular field on dorsal side, less numerous in median line of proglottids (uterine stem), usually surpassing osmoregulatory canals, dorsally overlapping cirrus-sac, vitelline follicles and sometimes ovary (Figs 12, 13, 16, 18). Testes present also in gravid proglottids.

Vas deferens coiled, with loops forming elongated field reaching to, but not crossing, median line of proglottid (Figs 12, 16, 18). Cirrus-sac pear-shaped, thin-walled, slightly widened towards distal (terminal) part (Figs 12, 13, 16, 18), 220-340 × 95-145 (n = 13) [250-300 × 80-110], its length representing 10-21% (x = 15; n = 13) [14-25%] of proglottid width. Sperm duct (internal vas deferens) sinuous. Cirrus muscular, reaching up to 82% (n = 13) [50%] of cirrus-sac length. Common genital atrium narrow, deep (Figs 12, 13, 16, 18). Genital pores alternating irregularly, markedly pre-equatorial, situated at 3-10% (x = 6; n = 13) [5-14%] of proglottid length from anterior margin (Figs 12, 16, 18).

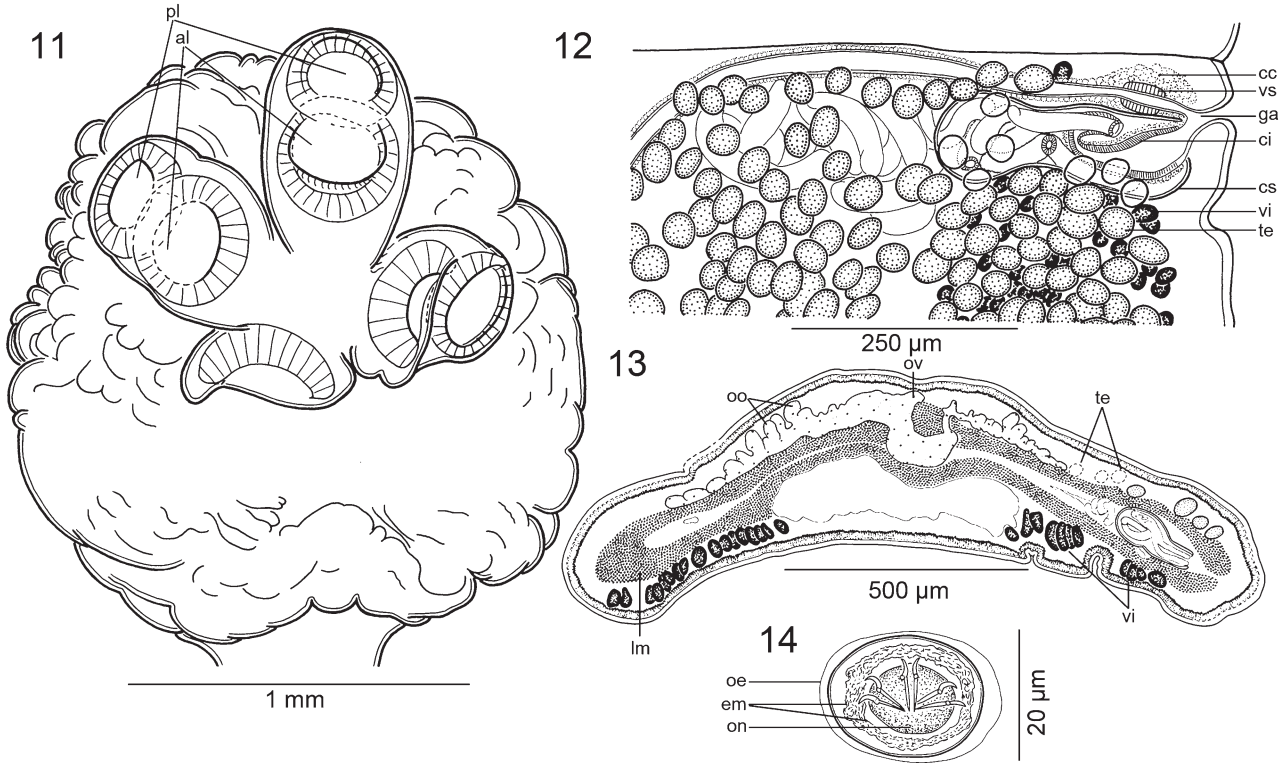
Ovary with wide isthmus in medulla and 2 follicular, grape-like lobes penetrating inner longitudinal musculature to dorsal cortex; numerous dorsal outgrowths present (Figs 13, 17). Length of ovary represents 27-37% (x = 30%; n = 13) [33-45%] of proglottid length, its width representing 57-76% (x = 68%; n = 13) [74-86%] of proglottid width (Figs 16, 17). Mehlis' gland about 110-165 in diameter, representing 7-20% of proglottid width (n = 13). Relative ovarian size, i.e., percentage of ovary surface to total surface of mature or pregravid proglottids (see de Chambrier *et al*., 2012), 11-16% (x = 13%; n = 10).

Vaginal canal slightly sinuous, surrounded by chromophilic cells, wider in terminal part (*pars copulatrix vaginae*), possessing a terminal vaginal sphincter (Figs 12, 16, 17). Vagina anterior to cirrus-sac (n = 35). Vitelline follicles cortical, ventral, forming 2 long uninterrupted bands, occupying large triangular field, widened and confluent posteriorly at ovary level (Figs 13, 16, 17). Length of bands represents 77-94% (x = 86%) [94-98%] and 84-98% (x = 90%; n = 13) [91-98%] of length of proglottid on poral and aporal side, respectively (Figs 12, 16).

Uterus cortical, with development of type 2 (see de Chambrier *et al*., 2004b, 2015b); uterine stem and



Figs 1-10. Scanning electron micrographs of *Goezeella* spp. (1, 2, 5-9) *Goezeella mariae* n. sp. ex *Pimelodella cristata* (IPCAS C-759). (1, 2) Scoleces, dorsoventral and apical views, respectively. (5-9) Microtriches on the apex of scolex, lumen of suckers, surface between suckers and base of metascolex and neck, respectively. (3, 4, 10) *Goezeella siluri* Fuhrmann, 1916 ex *Pinirampus pirinampu* (MHNG-PLAT-21908). (3, 4) Scoleces, dorsoventral and apical views, respectively. (10) Microtriches on the surface of pregravid proglottids. Note: small black numbers correspond to the figures showing higher magnification images of these surfaces.



Figs 11-14. *Goezeella siluri* Fuhrmann, 1916 ex *Cetopsis coecutiens* (syntype MHNG-PLAT-36375). (11) Scolex, apical view. (12) Terminal genitalia, dorsal view. (13) Cross-section at ovary level. (14) Eggs drawn in distilled water. Abbreviations: al – anterior sucker loculus; cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; em – bilayered embryophore; ga – genital atrium; lm – internal longitudinal musculature; oe – outer envelope; on – oncosphere; oo – ovary outgrowths; ov – ovary; pl – posterior sucker loculus; te – testes; vi – vitelline follicles; vs – vaginal sphincter.

diverticula (lateral uterine branches) in mature and pregravid proglottids lined with numerous chromophilic cells, extended much beyond branches (Fig. 16). Uterus with 20-26 [17-22] lateral diverticula on each side (Fig. 16). Eggs oval, outer envelope 22-23 × 19-20, bilayered embryophore 17-18 × 12-14 [21-22 ×14-22], oncosphere 11-12 × 9-10 [10-11 × 7-8], embryonic hooks 6-7 long (Fig. 19).

Remarks: The original description of *Goezeella siluri* was detailed and contained basic measurements and illustrations (Fuhrmann, 1916). However, the only complete specimen preserved is slightly decomposed, contracted and twisted on the slide. Moreover, Fuhrmann (1916) overlooked an important feature of the scolex morphology, i.e. the presence of biloculate, rather than uniloculate, suckers (compare the same scolex drawn in his Fig. 2 and Fig. 11 of the present study). This characteristic was first reported by Rego (1975; see his fig. 8), but not by Woodland (1933a) as reported by Brooks & Deardorff (1980). In fact, morphology of the suckers may be difficult to observe, especially if the suckers are hidden within wrinkles of a contracted metascolex (see Fig. 3).

The specimens from *P. pirinampu* are considered conspecific with *G. siluri* even though they differ from those found in *C. coecutiens* described by Fuhrmann (1916) in the lower number of the testes (282-366 vs. 380-430), a longer cirrus (reaching up to 82% of the cirrus-sac length vs. reaching only up to 50%), and in the anterior extent of the bands of vitelline follicles on the poral side, which represents 77-94% of proglottids length vs. 94-98% in the syntype. These differences are considered to be accounted for by intraspecific variability, but poor quality of the type material of *G. siluri* should also be considered. Therefore, new material of *G. siluri* from its type host, *C. coecutiens*, is needed for confirmation of measurements taken from the type specimen.

Specimens from *Pseudocetopsis othonops* (syn. of *Cetopsis othonops*) in the Orinoco River, Venezuela, reported by Brooks & Rasmussen (1984) as *G. siluri*, possess the vagina anterior or posterior to the cirrus-sac, unlike the exclusively anterior position in all species of *Goezeella* including *G. siluri* and the newly described species (see below). This feature has been broadly used to differentiate species of proteocephalid cestodes (Arredondo & Gil de Pertierra, 2010; Gil de Pertierra & de Chambrier, 2013), but Alves *et al*. (2017b) described conspecific cestodes (genetically identical individuals based on the *lsr*DNA) with both the anterior and posterior vagina in relation to the cirrus-sac. Therefore, this

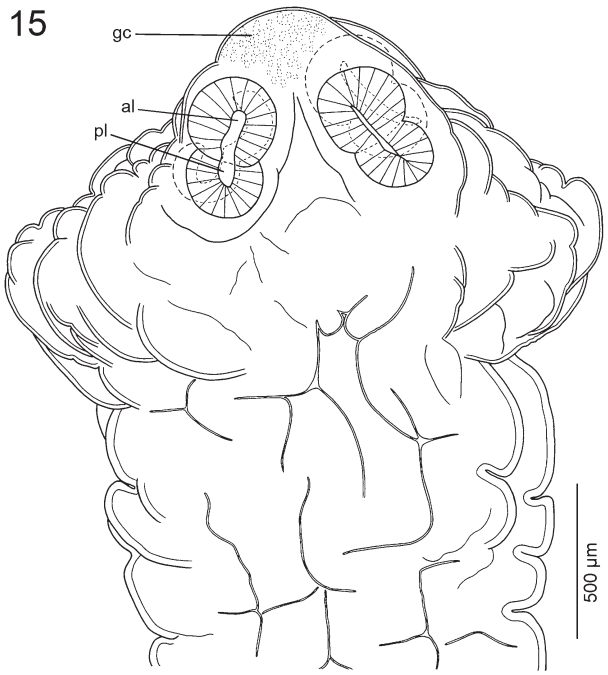


Fig. 15. *Goezeella siluri* Fuhrmann, 1916 ex *Pinirampus pirinampu* (MHNG-PLAT-21845). Scolex, dorso-ventral view. Abbreviations: al – anterior sucker loculus; gc – glandular cells; pl – posterior sucker loculus.

character should be considered with caution. Since all specimens from *P. othonops* were fixed in AFA (alcohol-formalin-acetic acid), they could not be used for DNA sequencing.

Brooks & Rasmussen (1984) also reported immature cestodes identified as *G. siluri* from *B. vaillantii*, but reliable identification of juvenile specimens is almost never possible because they lack key morphological traits that are present only in their mature forms. Two of the present authors (TS and AdC) have not found *G. siluri* in any of the 25 *B. vaillantii* examined (de Chambrier *et al*., 2015a); therefore, this record of *G. siluri* in a species of *Brachyplatystoma* Bleeker requires verification.

Goezeella danbrooksi de Chambrier, Rego & Mariaux, 2004

Figs 20, 21

Goezeella siluri. – Brooks & Deardorff, 1980: 15.

Holotype: USNM 1370061 (USNPC 74498), a whole-mounted specimen (2 slides) – USNM 1370107 (USNPC 74544), fragments on 19 slides of serial cross- and frontal sections.

Type and only known locality: Magdalena River near San Cristóbal, Province of Bolívar, Colombia.

Type and only known host: *Ageneiosus pardalis* Lütken (= *A. caucanus* Steindachner) (Siluriformes: Auchenipteridae).

Site of infection: Anterior intestine.

Prevalence of infection: Unknown.

Morphological description: Brooks & Deardorff (1980).

Remarks: The description of this species, which was originally identified as *G. siluri* by Brooks & Deardorff (1980), was based on a single specimen, which is partially decomposed. However, de Chambrier *et al*. (2004a) observed several morphological differences between this specimen and *G. siluri*, such as the position of the vitelline follicles, which are ventrolateral in *G. danbrooksi* (vs. only ventral in *G. siluri*), fewer testes (183-310 vs. 380-430), and the position of the vaginal sphincter (at a distance from the genital atrium in *G. danbrooksi* vs. terminal, i.e. close to the genital atrium in *G. siluri*). Based on these differences, de Chambrier *et al.* (2004a) proposed the new name, *G. danbrooksi*, for the tapeworm from *A. pardalis*.

Brooks & Deardorff (1980) reported the vitelline follicles to be present both in the ventral and dorsal cortex. However, the study of the holotype including its histological sections revealed that the follicles are only on the ventral side of the cortex, reaching only to its lateral margin (Figs 20, 21).

The study of the type material of *G. danbrooksi* also showed that some fibres of the inner longitudinal musculature are close together, thus somewhat resembling muscle bundles (Figs 20, 21). However, the tissue of histological sections is partially decomposed and thus a new, well fixed material of the species has to be examined to reveal the actual structure of the inner longitudinal muscles of *G. danbrooksi*.

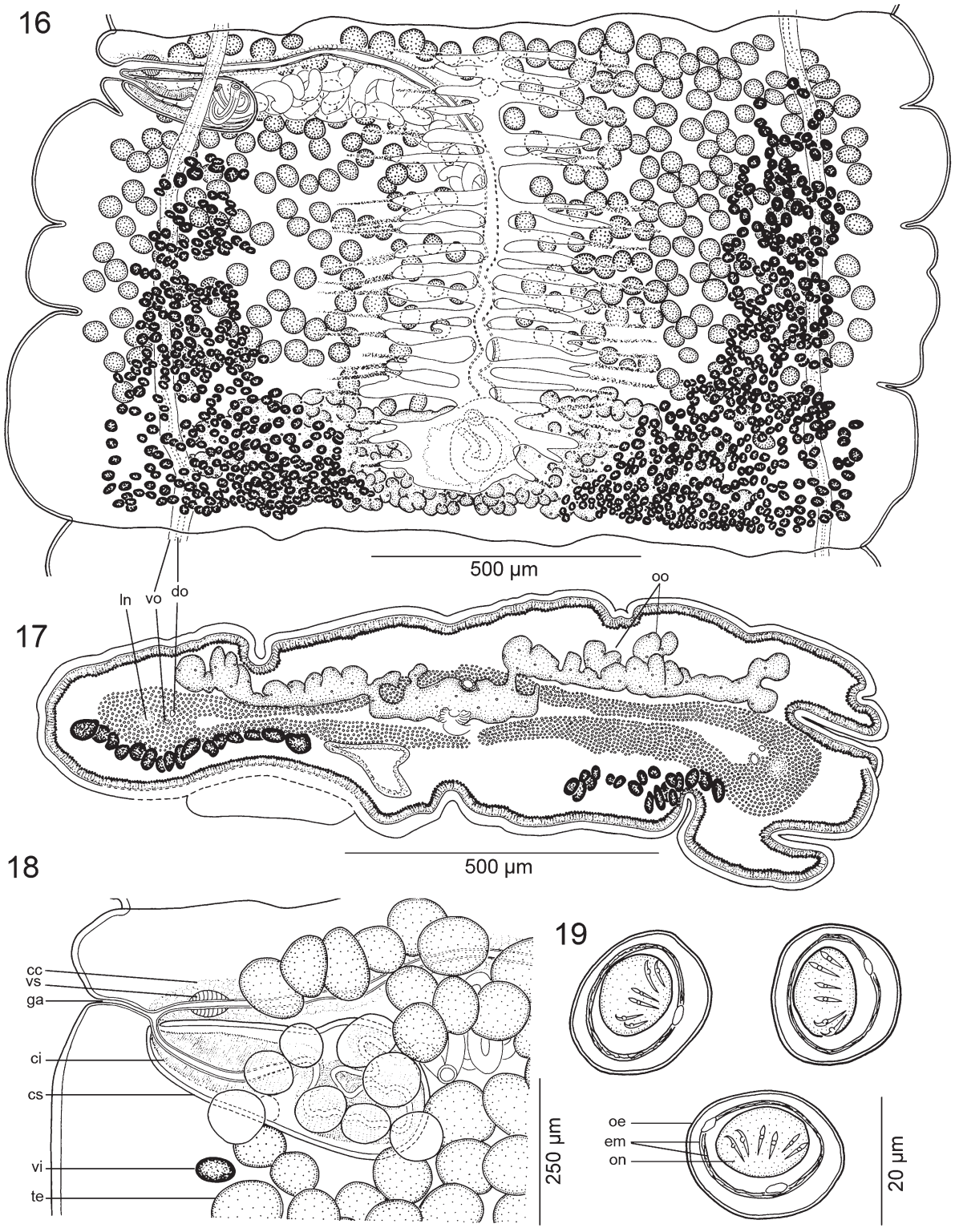
Goezeella mariae sp. nov.

Figs 1, 2, 5-9, 22-30

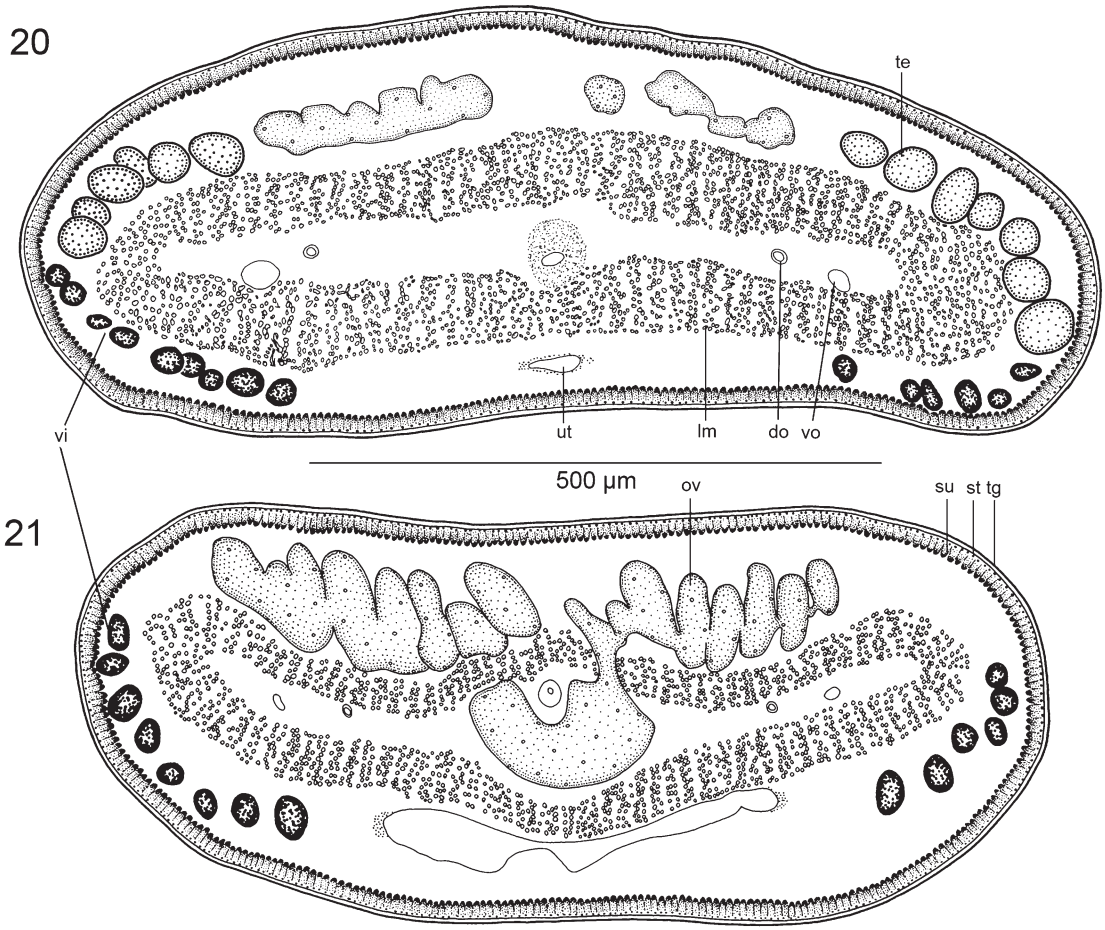
Holotype: CHIOC 38860a-f, a whole-mounted specimen (1 slide) and 5 slides of serial cross-sections, collected on 25.05.2013, host field no. BR AMP 46a. – MHNG-PLAT-97017 (2 slides of cross-sections).

Paratypes: IPCAS C-759, a whole-mounted specimen (1 slide; hologenophore), host field no. BR AMP 106b. – CHIOC 38861, IPCAS C-759, MHNG-PLAT-86883, a whole-mounted specimen (one slide), 6 slides of serial cross-sections and 2 slides of sagittal sections of scolex, host field No. BR AMP 109a. – MHNG-PLAT-97016, a whole-mounted specimen (one slide; SEM voucher), host field no. BR AMP 111b; all specimens collected on 25.05.2013.

Type and only known locality: Lowermost Amazon River near Macapá, State of Amapá, Brazil (00°01’N, 50°59’W).



Figs 16-19. *Goezeella siluri* Fuhrmann, 1916 ex *Pinirampus pirinampu*. (16) Pregravid proglottid, ventral view (MHNG-PLAT-21877). (17) Cross-section at ovary level (MHNG-PLAT-21879). (18) Terminal genitalia, dorsal view (MHNG-PLAT-21879). (19) Eggs drawn in distilled water (MHNG-PLAT-19858). Abbreviations: cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; do – dorsal osmoregulatory canal; em – bilayered embryophore; ga – genital atrium; ln – longitudinal nerve cord; oe – outer envelope; on – oncosphere; oo – ovary outgrowths; te – testes; vi – vitelline follicle; vo – ventral osmoregulatory canal; vs – vaginal sphincter.



Figs 20-21. *Goezeella danbrooksi* de Chambrier, Rego & Mariaux, 2004 ex *Ageneiosus pardalis* (holotype, USNM 1370061). (20) Cross-section at middle part of proglottid. (21) ovary level. Abbreviations: do – dorsal osmoregulatory canal; lm – internal longitudinal musculature; ov – ovary; st – subtegumental muscle fibres; su – subtegumental cells; te – testes; tg – tegument; ut – uterus; vi – vitelline follicles; vo – ventral osmoregulatory canal.

Type and only known host: *Pimelodella cristata* (Müller & Troschel) (Siluriformes: Heptapteridae).

Site of infection: Anterior intestine.

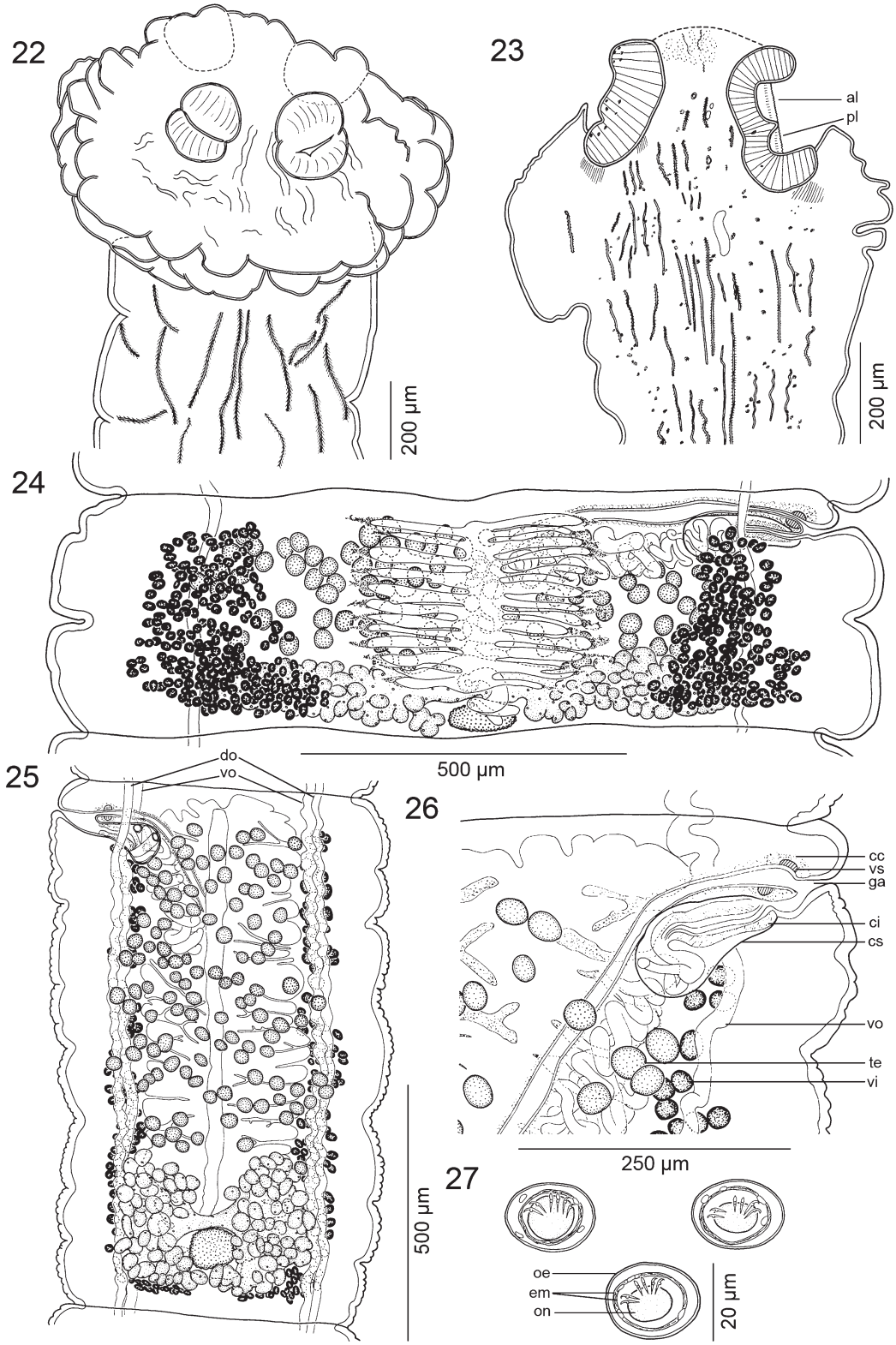
Prevalence: 7 fish examined/4 fish infected (57%).

Representative DNA sequences: A fragment 1491bp long of the *lsr*DNA (D1–D3 domains) (GenBank MF370208).

Etymology: The species is dedicated to the first author's mother, Maria Thereza Vieira Pinto Alves, for providing continuous support for his studies.

Description: (based on 4 whole-mounted worms; 13 slides with serial cross-sections of mature proglottids and 2 slides with sagittal sections of 1 scolex; 1 scolex studied using SEM). Proteocephalidae. Testes, ovary, vitelline follicles and uterus cortical; small-sized worm. Total body length 14-38 mm (n = 3), maximum width up to 1.3 mm (n = 3). Strobila acraspedote, anapolytic, with longitudinal and transverse grooves, consisting of about 40-90 proglottids: 27-32 immature, 4-8 mature, 10-15 pregravid and 23-39 gravid. Immature and mature proglottids much wider than long (length: width ratio 0.17-0.35), pregravid proglottids markedly wider than long (length: width ratio 0.40-0.76) and gravid proglottids slightly wider than long to much longer than wide (length: width ratio 0.80-2.60).

Scolex 0.68-0.83 × 0.91-1.15 mm (n = 3), much wider than neck (proliferation zone), 0.83-1.20 × 0.75-0.81 mm, bearing 4 biloculate suckers, with loculi unequal in size; anterior loculus 158-161 (x = 160; n = 3) in diameter, posterior loculus 123-126 (x = 125; n = 3) in diameter; loculi separated by inconspicuous interlocular septum (Figs 1, 2, 22, 23). Metascolex present, more wrinkled than neck (Figs 1, 2, 22). Apex rounded, lacking apical organ, with few gland cells (Figs 1, 2, 22, 23). Apex of scolex, lumen of suckers, surface between suckers and base of metascolex covered with acicular filitriches, less dense on lumen of suckers (Figs 5-8); neck covered with capilliform filitriches (Fig. 9).



Figs 22-27. *Goezeella mariae* sp. nov. ex *Pimelodella cristata*. (22) Scolex, dorsoventral view (holotype, CHIOC 38860a). (23) Scolex, sagittal section (paratype, CHIOC 38861). (24) Pregravid proglottid, ventral view (paratype MHNG-PLAT-97016). (25) Gravid proglottid, dorsal view (holotype, CHIOC 38860a). (26) Terminal genitalia, dorsal view (holotype, CHIOC 38860a). (27) Eggs drawn in distilled water (paratype IPCAS C-759). Abbreviations: al – anterior sucker loculus; cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; do – dorsal osmoregulatory canal; em – bilayered embryophore; ga – genital atrium; oe – outer envelope; on – oncosphere; pl – posterior sucker loculus; te – testes; vi – vitelline follicles; vo – ventral osmoregulatory canal; vs – vaginal sphincter.

Inner longitudinal musculature well-developed, formed by numerous, individual muscle fibres not forming compact bundles, more concentrated laterally (Figs 28-30). Osmoregulatory canals situated at same level of lateral-most testes, median to vitelline follicles, markedly sinuous (Figs 24-26, 28-30); ventral osmoregulatory canal wider than dorsal one (Fig. 30).

Testes numerous, spherical to oval, small, 34-46 in diameter, in 1 irregular layer, 103-167 (x = 134; n = 13) per mature proglottid (Figs 24, 25). Testes form 1 irregular field on dorsal side, less numerous alongside median line of proglottids (uterine stem), usually reaching laterally to osmoregulatory canals, dorsally overlapping cirrus-sac, vitelline follicles and sometimes ovary (Figs 24-26, 28-30). Testes present also in gravid proglottids.

Vas deferens coiled, with loops forming elongate field reaching to, but not crossing, median line of proglottid (Figs 24-26). Cirrus-sac elongated to pear-shaped, thin-walled (Figs 24-26, 28), 130-213 × 59-85 (n = 13), its length representing 11-24% (x = 17; n = 13) of proglottid width. Sperm duct (internal vas deferens) sinuous (Figs 24-26, 28). Cirrus muscular, reaching up to 64% (n = 13) of cirrus-sac length. Common genital atrium narrow, deep (Figs 24-26, 28). Genital pores alternating irregularly, markedly pre-equatorial, situated at 7-17% (x = 11; n = 13) of proglottid length from anterior margin (Figs 24-26).

Ovary with wide isthmus in medulla and two follicular, grape-like lobes penetrating to dorsal cortex; numerous dorsal outgrowths present (Figs 24, 25, 30). Length of ovary represents 21-31% (x = 26%; n = 13) of proglottid length, its width representing 57-77% (x = 66%; n = 13) of proglottid width (Figs 24, 25). Mehlis' gland about 60-138 in diameter, representing 8-11% of proglottid width (n = 13). Relative ovarian size, i.e., percentage of ovary surface to total surface of mature or pregravid proglottids (see de Chambrier *et al*., 2012), 10-15% (x = 12%; n = 13).

Vaginal canal slightly sinuous, surrounded by chromophilic cells, wider in terminal part (*pars copulatrix vaginae*); terminal vaginal sphincter present (Figs 24-26). Vagina anterior to cirrus-sac (n = 32). Vitelline follicles cortical, ventral, forming 2 long uninterrupted bands, occupying large triangular field, widened and confluent posteriorly at ovary level; lateral to lateral-most testes (Figs 24-26, 29). Length of bands represents 73-91% (x = 83%) and 72-91% (x = 83%) of length of proglottid on poral and aporal side, respectively (n = 13) (Figs 24, 25). Uterus cortical, with development of type 2 (see de Chambrier *et al*., 2004b, 2015b); uterine stem and diverticula (lateral uterine branches) in mature and pregravid proglottids lined with numerous chromophilic cells, extended much beyond branches (Fig. 24). Uterus with 14-25 lateral diverticula on each side (Figs 24, 25). Eggs oval, outer envelope 21-25 × 18-19, bilayered embryophore 19-20 × 13-15, oncosphere 9-10 × 11-12, embryonic hooks 5-6 long (Fig. 27).

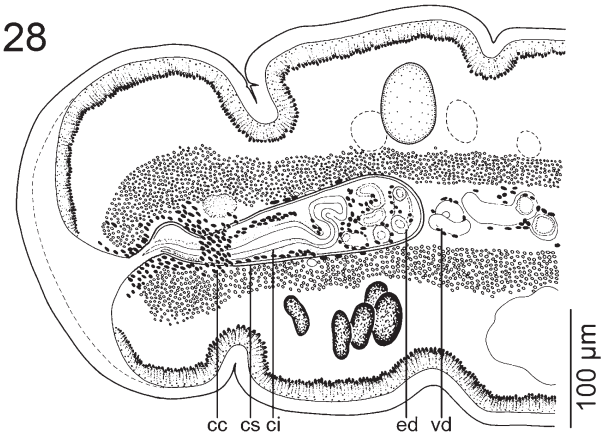
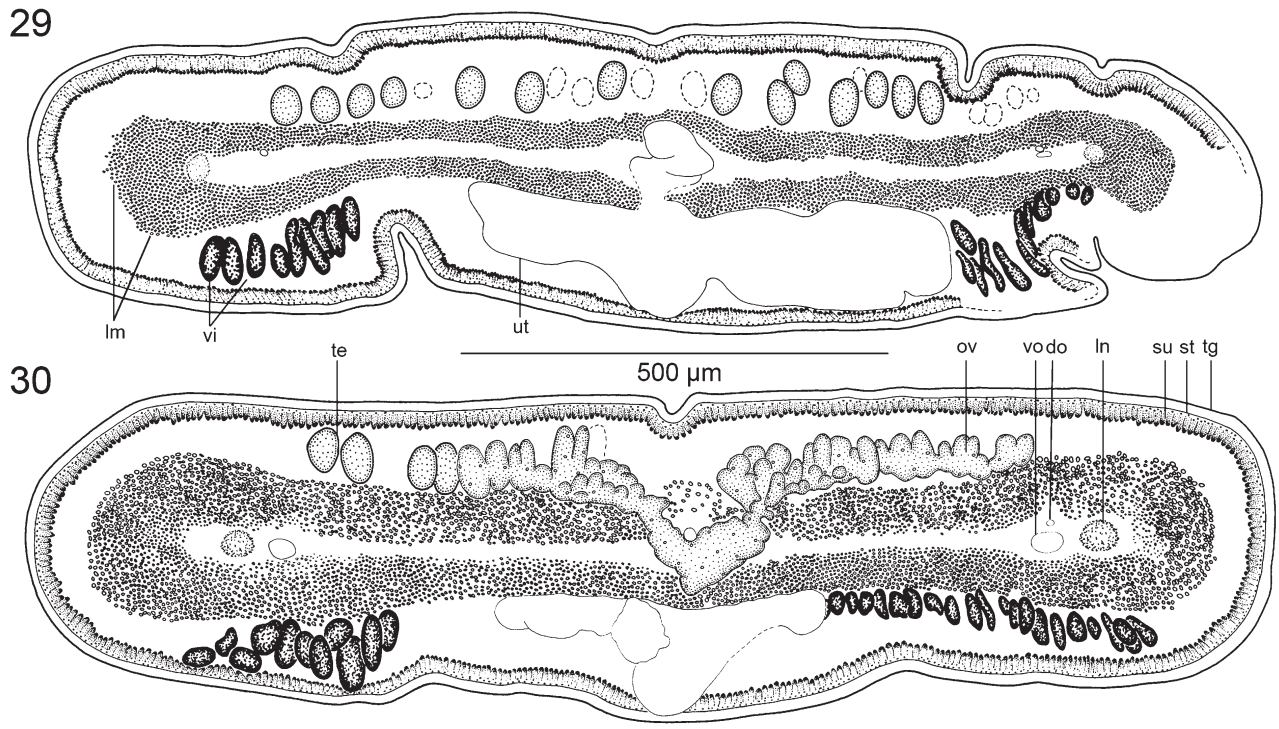


Fig. 28. *Goezeella mariae* sp. nov. ex *Pimelodella cristata*. Cross-section at the cirrus-sac level (holotype, CHIOC 38860d). Abbreviations: cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; ed – ejaculatory duct; va – vas deferens.

Remarks: *Goezeella mariae* sp. nov. differs from *G. siluri* and *G. danbrooksi* in having fewer testes (103-167 vs. 183-310 and 282-366 in *G. danbrooksi* and *G. siluri*, respectively) and inconspicuous interlocular septum (not obvious in SEM images; see Figs 1, 2), rather than the septum conspicuous as in the two other species. The new taxon can be further distinguished from *G. siluri* by its smaller dimensions, such as the total body length (14-38 mm vs. 90-230 mm), scolex width (0.91-1.15 mm vs. 1.45-1.94 mm) and the length of the cirrus-sac (130-213 µm vs. 220-340 µm) as well as the appearance of the metascolex, which is more wrinkled in *G. mariae* sp. nov. compared to that of *G. siluri*; compare Figs 1, 2 with Figs 3, 4. Moreover, *G. mariae* sp. nov. possesses a terminal, rather than markedly subterminal, vaginal sphincter as it is in *G. danbrooksi*.

The new species differs in its sequence of the partial *lsr*DNA gene (D1–D3 domains) from that of *G. siluri* from *P. pirinampu* in 14 nucleotides, i.e. genetic divergence 0.9%. A phylogenetic analysis (data not shown) revealed both taxa clustered in a clade comprising also both known species of *Gibsoniela* Rego, 1984, i.e. *G. mandube* (Woodland, 1935) and *G. meursaulti* de Chambrier & Vaucher, 1999, parasites of the auchenipterid catfish *Ageneiosus inermis* (Linnaeus, 1766) in the Neotropical Region, but interrelations within this lineage remain unresolved. Close relationship of species of *Goezeella* with those of the genus *Gibsoniela* is not evident based on their morphology, because they differ in the position of the internal organs in relation to the inner longitudinal musculature (previously used to distinguish individual subfamilies – see Rego, 1994), but also by the morphology of the scolex (no metascolex in the latter genus) and their suckers (biloculate in *Goezeella* vs.



Figs 29-30. *Goezeella mariae* sp. nov. ex *Pimelodella cristata*. (29) Cross-section at middle part of proglottid (holotype, CHIOC 38860d). (30) Cross-sections at ovary level (paratype MHNG-PLAT-86883). Abbreviations: do – dorsal osmoregulatory canal; lm – internal longitudinal musculature; ln – longitudinal nerve cord; ov – ovary; st – subtegumental muscle fibres; su – subtegumental cells; te – testes; tg – tegument; ut – uterus; vi – vitelline follicles; vo – ventral osmoregulatory canal.

triloculate in *Gibsoniela*) (Rego, 1984; de Chambrier & Vaucher, 1999).

To the best of our knowledge, this is the first parasite found in *Pimelodella cristata*. This heptapterid catfish was described from a tributary of the Branco River, Guyana (Bockmann & Guazzelli, 2003) and is distributed throughout the Amazon River basin, inhabiting the sand bottom of creeks and rivers (Reis & Lima, 2009). *Proteocephalus bagri* Holcman-Spector & Mañé-Garzón, 1988 and *P. rhamdiae* Holcman-Spector & Mañé-Garzón, 1988, both from *Rhamdia sapo* (Valenciennes) [syn. of *Rhamdia quelen* (Quoy & Gaimard)] in Uruguay, are the only other proteocephalids known from heptapterids in South America (Holcman-Spector & Mañé-Garzón, 1988). In addition, *Proteocephalus brooksi* García-Prieto, Rodríguez & Pérez-Ponce de León, 1996 was described from *Rhamdia guatemalensis* (Günther) in Mexico by García-Prieto *et al.* (1996).

DISCUSSION

The present study provides a new insight into the taxonomy, species composition and host associations of *Goezeella*, one of insufficiently known genera of Neotropical proteocephalid cestodes. An important feature newly added into an amended generic diagnosis is the unique arrangement of the inner longitudinal musculature, which does not form compact bundles as usually in proteocephalids (Rego, 1994). In contrast, the musculature in species of *Goezeella* is formed by numerous individual muscle fibres not forming such bundles. The exclusively ventral or ventrolateral position of the vitelline follicles and the possession of a metascolex with numerous, largely longitudinal wrinkles and biloculate suckers, represent other typical characteristics of this genus.

Species of *Rudolphiella* Fuhrmann, 1916 and *Ephedrocephalus* Diesing, 1850 also have the vitelline follicles restricted to the ventral cortex (not in the dorsal field as given in the key of de Chambrier *et al*., 2009; see Rego *et al*., 1999 and Gil de Pertierra & de Chambrier, 2000). However, they differ markedly from *Goezeella* by their topography of the genital organs in relation to the inner longitudinal musculature (see Rego, 1994) and possess the uniloculate, rather than biloculate, suckers (Mola, 1906; Gil de Pertierra & de Chambrier, 2000). *Spatulifer maringaensis* Pavanelli & Rego, 1989, which also shares the same distribution of the internal organs in relation to the inner musculature with *Goezeella* (both were previously placed in the Monticelliinae), and possesses a metascolex and the vitelline follicles limited to the

Identification key to the species of *Goezeella* Fuhrmann, 1916

1A Vaginal sphincter at a distance from genital atrium; vitelline follicles ventrolateral. In auchenipterids (*Ageneiosus pardalis*) ..... *G. danbrooksi*

1B Vaginal sphincter near genital atrium (terminal); vitelline follicles only on ventral side of cortex, missing laterally 2

2A Much more than 200 testes per proglottid. In cetopsids (*Cetopsis*) and pimelodids (*Pinirampus*) .....*G. siluri*

2B Much fewer than 200 testes per proglottid. In heptapterids (*Pimelodella cristata*) ..... *G. mariae* sp. nov.

ventral cortex (Arredondo & Gil de Pertierra, 2008), bears only uniloculate suckers, rather than biloculate as in species of *Goezeella*.

Species of *Goezeella* including *G. mariae* sp. nov. have been found in the Amazon and Orinoco River basins, whereas no published record exists from the Paraná River basin. The spectrum of definitive hosts of this genus, i.e. fishes of four siluriform families (Auchenipteridae, Cetopsidae, Heptapteridae and Pimelodidae) is markedly wider than typical for comparably species-rich genera of Neotropical proteocephalids, which are usually specific to only a single fish family (Rego *et al*., 1999; de Chambrier *et al*., 2015a).

Several attempts have been made to assess the phylogenetic relationships of the species-rich fauna of Neotropical proteocephalids, but their actual interrelations remain unclear (Zehnder & Mariaux, 1999; de Chambrier *et al*., 2004b; Hypša *et al*., 2005; de Chambrier *et al*., 2015a). Neither the addition of terminal taxa, nor the use of new molecular markers seem to have improved the phylogenetic signal of the large polytomy of the 'Neotropical superclade' (de Chambrier *et al*., 2015a), where *G. siluri* ex *P. pirinampu* appears together with 37 taxa (including 29 taxa from Neotropical fishes). This lack of phylogenetic resolution was also observed in the recent published studies by Alves *et al*. (2017b) and Arredondo *et al*. (2017). Therefore, no tree is presented in this paper. Addition of a new sequence (a representative of *G. mariae* n. sp.) also did not increase resolution of this clade, but revealed this new taxon within a small clade comprising *G. siluri* and both species of *Gibsoniela*. In contrast, molecular data on *G. danbrooksi* are not available to assess its interrelations to the remaining congeners and thus new material should be collected, similarly as specimens of *G. siluri* from the type host. All attempts of the present authors, who examined seven *C. coecutiens* between 1992 and 1995, to find this cestode in this fish host have failed.

Caira *et al*. (2014) proposed a new order, Onchoproteocephalidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014, to group together phylogenetically closely related, but morphologically and ecologically conspicuously dissimilar hook-bearing parasites of elasmobranchs, placed previously in the 'tetraphyllidean' family Onchobothriidae Braun, 1900, with parasites of freshwater bony fishes, amphibians and reptiles of the former order Proteocephalidea Mola, 1926. The authors speculated that the allegedly synapomorphy of both distinct groups could be the presence of gladiate spinitriches on the strobila. However, these spinitriches were observed neither in *G. siluri* nor *G. mariae* sp. nov., similarly as they are absent in other proteocephalids studied using SEM (e.g. Arredondo *et al*., 2017). Therefore, identification of morphological synapomorphies for members of this newly erected, conspicuously heterogeneous order is still pending (Arredondo *et al*., 2014).

To help identify the species of *Goezeella*, a simple morphology-based key is presented above.

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REFERENCES

Alves P.V., de Chambrier A., Scholz T., Luque J.L. 2015. A new genus and species of proteocephalidean tapeworm (Cestoda), first parasite found in the driftwood catfish *Tocantinsia piresi* (Siluriformes: Auchenipteridae) from Brazil. *Folia Parasitologica* 62: 006.

Alves P.V., de Chambrier A., Scholz T., Luque J.L. 2017a. Annotated checklist of fish cestodes from South America. *ZooKeys* 650: 1-205.

Alves P.V., de Chambrier A., Luque J.L., Scholz T. 2017b. Untangling convoluted taxonomy of *Chambriella* Rego, Chubb & Pavanelli, 1999 (Cestoda: Proteocephalidae), with erection of *Riggenbachiella* n. g. and description of a new species from pimelodid catfishes in the Neotropical Region. *Systematic Parasitology* 94: 367-389.

Arredondo N.J., Gil de Pertierra A.A. 2008. The taxonomic status of *Spatulifer* cf. *maringaensis* Pavanelli & Rego, 1989 (Eucestoda: Proteocephalidea) from *Sorubim lima* (Bloch & Schneider) (Pisces: Siluriformes), and the use of the microthrix pattern in the discrimination of *Spatulifer* spp. *Systematic Parasitology* 70: 223-236.

Arredondo N.J., Gil de Pertierra A.A. 2010. *Monticellia santafesina* n. sp. (Cestoda: Proteocephalidea), a parasite of *Megalonema platanum* (Günther) (Siluriformes: Pimelodidae) in the Paraná River basin, Argentina. *Systematic Parasitology* 76: 103-110.

Arredondo N.J., de Chambrier A., Gil de Pertierra A.A. 2013. A new genus and species of the Monticelliinae (Eucestoda: Proteocephalidea), a parasite of *Pseudoplatystoma fasciatum* (Pisces: Siluriformes) from the Paraná River basin (Argentina), with comments on microtriches of proteocephalideans. *Folia Parasitologica* 60: 248-256.

Arredondo N.J., Gil de Pertierra A.A., de Chambrier A. 2014. A new species of *Pseudocrepidobothrium* (Cestoda: Proteocephalidea) from *Pseudoplatystoma fasciatum* (Pisces: Siluriformes) in the Paraná River basin (Argentina). *Folia Parasitologica* 61: 462-472.

Arredondo N.J., Alves P.V., Gil de Pertierra A.A. 2017. A new genus of proteocephalid tapeworm (Cestoda) from the marbled swamp eel *Synbranchus marmoratus* Bloch (Synbranchiformes: Synbranchidae) in the River Paraná basin, Argentina. *Folia Parasitologica* 64: 015.

Bockmann F.A., Guazzelli G.M. 2003. Family Heptapteridae (pp. 406–431). *In:* Reis, R.E., Kullander, S.O., Ferraris C.J. (Eds), Checklist of the freshwater fishes of South and Central America. *Editora da Pontifícia Universidade Católica do Rio Grande do Sul – EDIPUCRS, Porto Alegre*, 729 pp.

Brabec J., Scholz T., Králová-Hromadová I., Bazsalovicsová E., Olson P.D. 2012. Substitution saturation and nuclear paralogs of commonly employed phylogenetic markers in the Caryophyllidea, an unusual group of non-segmented tapeworms (Platyhelminthes). *International Journal for Parasitology* 42: 259-267.

Brooks D.R. 1995. Phylogenetic hypothesis, cladistic diagnoses, and classification of the Monticelliidae (Eucestoda: Proteocephaliformes). *Revista Brasileira de Biologia* 55: 359-367.

Brooks D.R., Deardorff T.L. 1980. Three proteocephalid cestodes from Columbian siluriform fishes, including *Nomimoscolex alovarius* sp. n. (Monticellidae: Zygobothriinae). *Proceedings of the Helminthological Society of Washington* 47: 15-21.

Brooks D.R., Rasmussen G. 1984. Proteocephalidean cestodes from Venezuelan siluriform fishes, with a revised classification of the Monticelliidae. *Proceedings of the Biological Society of Washington* 97: 748-760.

Caira J.N., Jensen K., Waeschenbach A., Olson P.D., Littlewood D.T.J. 2014. Orders out of chaos – molecular phylogenetics reveals the complexity of shark and stingray tapeworm relationships. *International Journal for Parasitology* 44: 55-73.

de Chambrier A. 2001. A new tapeworm from the Amazon, *Amazotaenia yvettae* gen. n., sp. n., (Eucestoda: Proteocephalidea) from the siluriform fishes *Brachyplatystoma filamentosum* and *B. vaillanti* (Pimelodidae). *Revue suisse de Zoologie* 108: 303-316.

de Chambrier A. 2003. Systematic status of *Manaosia bracodemoca* Woodland, 1935 and *Paramonticellia itaipuensis* Pavanelli et Rego, 1991 (Eucestoda: Proteocephalidea), parasites of *Sorubim lima* (Siluriformes: Pimelodidae) from South America. *Folia Parasitologica* 50: 121-127.

de Chambrier A., Vaucher C. 1999. Proteocephalidae et Monticelliidae (Eucestoda: Proteocephalidea) parasites de poissons d'eau douce au Paraguay, avec descriptions d'un genre nouveau et de dix espèces nouvelles. *Revue suisse de Zoologie* 106: 165-240.

de Chambrier A., Rego A.A., Mariaux J. 2004a. Redescription of *Brooksiella praeputialis* and *Goezeella siluri* (Eucestoda: Proteocephalidea), parasites of *Cetopsis coecutiens* (Siluriformes) from the Amazon and proposition of *Goezeella danbrooksi* sp. n. *Revue suisse de Zoologie* 111: 111-120.

de Chambrier A., Zehnder M., Vaucher C., Mariaux J. 2004b. The evolution of the Proteocephalidea (Platyhelminthes, Eucestoda) based on an enlarged molecular phylogeny, with comments on their uterine development. *Systematic Parasitology* 57: 159-171.

de Chambrier A., Coquille S.C., Mariaux J., Tkach V. 2009. Redescription of *Testudotaenia testudo* (Magath, 1924) (Eucestoda: Proteocephalidea), a parasite of *Apalone spinifera* (Le Sueur) (Reptilia: Trionychidae) and *Amia calva* L. (Pisces: Amiidae) in North America and erection of the Testudotaeniinae n. subfam. *Systematic Parasitology* 73: 49-64.

de Chambrier A., Binh T.T., Scholz T. 2012. *Ophiotaenia bungari* n. sp. (Cestoda), a parasite of *Bungarus fasciatus* (Schneider) (Ophidia: Elapidae) from Vietnam, with comments on relative ovarian size as a new and potentially useful diagnostic character for proteocephalidean tapeworms. *Systematic Parasitology* 81: 39-50.

de Chambrier A., Scholz, T., Kuchta R. 2014. Taxonomic status of Woodland's enigmatic tapeworms (Cestoda: Proteocephalidea) from Amazonian catfishes: back to museum collections. *Systematic Parasitology* 87: 1-19.

de Chambrier A., Kuchta R., Scholz T. 2015a. Tapeworms (Cestoda: Proteocephalidea) of teleost fishes from the Amazon River in Peru: additional records as an evidence of

unexplored species diversity. *Revue suisse de Zoologie* 122: 149-163.

de Chambrier A., Scholz T., Mariaux J., Kuchta R. 2017. Onchoproteocephalidea I Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014 [251-257]. *In:* Caira J.N., Jensen K. (Eds), Planetary Biodiversity Inventory (2008–2016): Tapeworms from vertebrate bowels of the earth. *University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence*.

de Chambrier A., Waeschenbach A., Fisseha M., Scholz T., Mariaux J. 2015b. A large 28S rDNA-based phylogeny confirms the limitations of established morphological characters for classification of proteocephalidean tapeworms (Platyhelminthes, Cestoda). *ZooKeys* 500: 25-59.

Chervy L. 2009. Unified terminology for cestode microtriches: a proposal from the International Workshops on Cestode Systematics in 2002–2008. *Folia Parasitologica* 56: 199-230.

Froese R., Pauly D. (Eds) 2017. FishBase. World Wide Web electronic publication. Accessed at http://www.fishbase.org, version (10/2016).

Fuhrmann O. 1916. Eigentümliche Fischcestoden. *Zoologischer Anzeiger* 46: 385-398.

García-Prieto L., Rodríguez L.M., Pérez-Ponce de León G. 1996. *Proteocephalus brooksi* n. sp. (Cestoda: Proteocephalidae) in the Neotropical freshwater fish *Rhamdia guatemalensis* (Siluriformes: Pimelodidae) from Lake Catemaco, Veracruz, Mexico. *Journal of Parasitology* 82: 992-997.

Gil de Pertierra A.A., de Chambrier A. 2000. *Rudolphiella szidati* sp. n. (Proteocephalidea: Monticelliidae, Rudolphiellinae) parasite of *Luciopimelodus pati* (Valenciennes, 1840) (Pisces: Pimelodidae) from Argentina with new observations on *Rudolphiella lobosa* (Riggenbach, 1895). *Revue suisse de Zoologie* 107: 81-95.

Gil de Pertierra A.A., de Chambrier A. 2013. *Harriscolex nathaliae* n. sp. (Cestoda: Proteocephalidea), from *Pseudoplatystoma corruscans* (Siluriformes, Pimelodidae) in the Paraná River basin, Argentina. *Journal of Parasitology* 99: 480-486.

Harwood P.D. 1933. The helminths parasitic in a water moccasin (snake) with a discussion of the characters of the Proteocephalidae. *Parasitology* 25: 130-142.

Holcman-Spector B., Mañé-Garzón F. 1988. Two new species of the genus *Proteocephalus* Weinland, 1858 (Proteocephalidea, Eucestoda) of freshwater fishes *Rhamdia sapo* (Valenciennes, 1840), from Uruguay. *Parasitología al Día* 12: 148-154.

Hypša V., Škeříková A., Scholz T. 2005. Phylogeny, evolution and host–parasite relationships of the order Proteocephalidea (Eucestoda) as revealed by combined analysis and secondary structure characters. *Parasitology* 130: 359-371.

Mola P. 1906. Di alcune specie poco studiate o mal note di Cestodi. *Annuario del Museo Zoologico della R Università di Napoli* 2: 1-12.

Pavanelli G.C., Takemoto R.M. 1996. *Spasskyellina mandi* n. sp. (Proteocephalidea: Monticelliidae), parasite of *Pimelodus ornatus* Kner, 1857 (Pisces: Pimelodidae) of the Paraná River, Paraná, Brazil. *Memórias do Instituto Oswaldo Cruz* 91: 723-726.

Pleijel F., Jondelius U., Norlinder E., Nygren A., Oxelman B., Schander C., Sundberg P., Thollesson M. 2008. Phylogenies without roots? A plea for the use of vouchers in molecular phylogenetic studies. *Molecular Phylogenetics and Evolution* 48: 369-371.

Rego A.A. 1975. Estudos de cestoides de peixes do Brasil. 2ª Nota: revisão do gênero Monticellia La Rue, 1911 (Cestoda, Proteocephalidae). *Revista Brasileira de Biologia* 35: 567-586.

Rego A.A. 1984. Proteocephalidea from Amazonian freshwater fishes: new systematic arrangement for the species described by Woodland as *Anthobothrium* (Tetraphyllidea). *Acta Amazonica* 14: 86-94.

Rego A.A. 1994. Order Proteocephalidea Mola, 1928 (pp. 257-293). *In:* Khalil L.F., Jones A., Bray R.A. (Eds), Keys to the Cestode Parasites of Vertebrates. *CAB International, Wallingford*, 751 pp.

Rego A.A., Chubb J.C., Pavanelli G.C. 1999. Cestodes in South American freshwater teleost fishes: keys to genera and brief description of species. *Revista Brasileira de Zoologia* 16: 299-367.

Reis R., Lima F. 2009. *Pimelodella cristata*. The IUCN Red List of Threatened Species accessed at http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T167812A6387343.en

Scholz T., de Chambrier A., Kuchta R., Littlewood D.T.J., Waeschenbach A. 2013. *Macrobothriotaenia ficta* (Cestoda: Proteocephalidea), a parasite of sunbeam snake (*Xenopeltis unicolor*): example of convergent evolution. *Zootaxa* 3640: 485-499.

Scholz T., de Chambrier A., Mariaux J., Kuchta R. 2011. Redescription of *Corallobothrium solidum* (Cestoda: Proteocephalidea) and erection of a new genus, *Essexiella*, for tapeworms from channel catfish (Ictaluridae). *Journal of Parasitology* 97: 1142-1151.

Scholz T., Kuchta R. 2017. A digest of fish tapeworms. *Vie et Milieu* 67(2) (in press).

Woodland W.N.F. 1925. On some remarkable new *Monticellia*-like and other cestodes from Sudanese siluroids. *Journal of Cell Science* 69: 703-729.

Woodland W.N.F. 1933a. On two new cestodes from the Amazon siluroid fish *Brachyplatystoma vaillanti* Cuv. and Val. *Parasitology* 25: 485-490.

Woodland W.N.F. 1933b. On the anatomy of some fish cestodes described by Diesing from the Amazon. *Quarterly Journal of Microscopical Science* 76: 175-208.

Woodland W.N.F. 1935. Some more remarkable cestodes from Amazon siluroid fish. *Parasitology* 27: 207-225.

Zehnder M.P., Mariaux J. 1999. Molecular systematic analysis of the order Proteocephalidea (Eucestoda) based on mitochondrial and nuclear rDNA sequences. *International Journal for Parasitology* 29: 1841-1852.