

Research Article

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A new genus and three new species of tapeworms (Cestoda: Onchoproteocephalidea) in *Erythrolamprus* snakes (Colubridae: Dipsadinae) in South America

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Abstract: The species diversity of reptile parasites in the New World, including South America, remains poorly understood, and this also applies to tapeworms (Cestoda: Onchoproteocephalidea). Only 17 species of the non-monophyletic genus *Ophiotaenia* La Rue, 1911 have been recorded in reptiles in the Neotropical Region. In this paper, three new species are described from dipsadine snakes of the genus *Erythrolamprus* Boie (Colubridae) in Brazil and Paraguay, and a new genus, *Penetrocestus*, is proposed to accommodate these tapeworms that penetrate the intestinal wall of their hosts. The new genus differs from other proteocephalids parasitising snakes by the presence of a large apical glandular organ, which is larger than the suckers, and a large vaginal sphincter lined with a thick layer of chromophilic cells. *Penetrocestus* gen. n. is also characterised by a long and wide region ('metascolex') posterior to the scolex and a well-developed inner longitudinal musculature, which is weakly developed in most proteocephalids parasitising Neotropical snakes. *Ophiotaenia joanae* (de Chambrier et Paulino, 1997) from *Xenodon newwiedii* Günther (Colubridae) in Brazil is transferred to *Penetrocestus* as its type species and as a new combination. *Penetrocestus gorgonae* sp. n. from *Erythrolamprus aesculapii* (Linnaeus) in Brazil, *Penetrocestus jaegeri* sp. n. from *Erythrolamprus jaegeri* (Günther) in Paraguay, and *Penetrocestus tristani* sp. n. from *Erythrolamprus poecilogyrus* (Wied-Neuwied) in Paraguay differ from *Penetrocestus joanae* (de Chambrier et Paulino, 1997) comb. n. and from each other by the position of the metascolex, width of the scolex, morphology of the terminal (distal) portion of the vagina, and the number of testes, as summarised in the key to their identification. The phylogenetic relationships of the new species are unknown, as they were collected more than 35 years ago and no tissues were fixed in ethanol for genetic characterisation, but the new data support the assumption of strict host specificity of reptilian tapeworms in the Neotropical Region.

Key words: Biodiversity, *Penetrocestus* gen. n., Onchoproteocephalidea, new taxa, morphology, Ophidia, Colubridae, Neotropical Region

Parasites of reptiles remain insufficiently studied due to several factors. Many reptiles are now protected or difficult to capture, making specimen collection challenging and limiting opportunities to examine host species. Additionally, reptiles are underrepresented among parasitologists, further reducing the capacity to document their parasite fauna. Furthermore, the prevalence of infection with some parasite groups, such as tapeworms (Cestoda), can be very low (Ammann and de Chambrier 2008, de Chambrier et al. 2017), so examining only a few host animals may result in failing to detect infected individuals.

However, recent studies on reptile parasites have shown still unexplored species diversity and several new species of proteocephalid tapeworms have been described from snakes in North and South America (de Chambrier et al. 2023, 2024, de Chambrier and Scholz 2026).

de Chambrier et al. (2024) listed 21 species of proteocephalid tapeworms (all in the non-monophyletic *Ophiotaenia*

La Rue, 1911) from colubrid snakes (Ophidia) in the New World (five species in the USA, two species in Cuba and 14 species in South America), including three new species recently described by de Chambrier et al. (2023) from water snakes (*Nerodia*) in the USA and three new species from dipsadine snakes (Colubridae) in Ecuador (de Chambrier et al. 2024). So far, only 17 species of proteocephalid tapeworms have been found in snakes in South America, including nine species in Brazil (de Chambrier et al. 2024 – table 2).

In the present paper, three new species of proteocephalid tapeworms found in three species of snakes of the genus *Erythrolamprus* Boie (Colubridae: Dipsadinae) in Brazil and Paraguay are described, and a new genus is proposed to accommodate these new species that penetrate by their scoleces through the host's intestinal wall. The new species are described based on their morphology only as they were collected 35–40 years ago and no tissues fixed in ethanol for genetic characterisation are available.

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Zoobank number for article: [urn:lsid:zoobank.org:pub:16773691-3F36-4499-A6DA-9B7358377B0E](https://zoobank.org/pub:16773691-3F36-4499-A6DA-9B7358377B0E)

MATERIALS AND METHODS

The snakes were collected by members of the Natural History Museum Geneva (MHNG) expedition in Paraguay in 1979 and 1980, and at the Instituto Butantan, São Paulo, Brazil, as part of a collaboration with Fernando M. de Azevedo Correa and the MHNG in 1991. The snakes were captured in the field in Paraguay or were provided alive by the staff of the Butantan Institute (São Paulo). These snakes were immediately euthanised by injection of Nembutal (phenobarbital) or a solution of Dormicum (Midazolam 15 mg) into the heart region. Immediately after dissection, the cestodes were carefully isolated from the host's intestine, rinsed in saline solution, and fixed with a hot, almost boiling, 4% formaldehyde solution. After one or two weeks, the worms were transferred in 75% ethanol.

Later, in Geneva, the worms were processed by the first author (AdC), that is, stained with Mayer's hydrochloric carmine solution, dehydrated in an ethanol series, cleared with eugenol (clove oil) and mounted as permanent preparations in Canada balsam (Chervy 2024). For histological sections, pieces of the scolex and strobila were embedded in paraffin wax, sectioned at a thickness 12 µm, stained with Weigert's haematoxylin, and counterstained with 1% eosin B according to de Chambrier (2001). For scanning electron microscopic (SEM) observations, scolex of one tapeworm from *Erythrolamprus jaegeri* (Günther) (host code Py 162) was prepared following the standard procedure (Chervy 2024) and observed using a JEOL JSM-740 1F scanning electron microscope at the Institute of Parasitology in České Budějovice.

All measurements are given in micrometres unless stated otherwise. Abbreviations used in the descriptions: x = mean, n = number of measurements. Museum acronyms: IPCAS – Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic; MHNG-PLAT – Platyhelminthes collection, Natural History Museum, Geneva, Switzerland.

RESULTS

Penetrocestus gen. n.

ZooBank number for genus:

[urn:lsid:zoobank.org:act:3982B337-151D-4289-AAA4-B2A0786A1A03](https://zoobank.org/act:3982B337-151D-4289-AAA4-B2A0786A1A03)

Diagnosis. Onchoproteocephalidea, Proteocephalidae. Testes, ovary, vitellarium, and uterus medullary. Medium-sized worms. Strobila acraspedote, with immature and mature proglottids wider than long to longer than wide; pregravid proglottids wider than long to longer than wide; gravid proglottids often much longer than wide. Scolex followed by swollen elongated posterior part (= metascolex), bearing small uniloculate suckers. Apex of scolex with large glandular apical organ. Scolex penetrates through intestinal wall. Inner longitudinal musculature usually well-developed, formed by small bundles of muscle fibres. Ventral osmoregulatory canals in medulla, between vitelline follicles, laterally touching vitelline follicles. Dorsal canals often more median than ventral canals. Testes medullary, in one layer and two separate lateral fields, with some testes reaching posterior margin of proglottids, thus being posterior to ovary or even vitelline follicles. Testes degenerate in gravid proglottids. Vas deferens (internal sperm duct) coiled within

cirrus sac. Genital atrium narrow. Genital pores irregularly alternating, slightly pre-equatorial to equatorial. Vaginal canal anterior or posterior to cirrus sac. Pars copulatrix vaginae well developed. Terminal (distal) part of vagina with large sphincter, lined with thick layer of dense chromophilic cells. Ovary medullary, bilobed, with narrow ovarian isthmus. Vitelline follicles form two lateral bands, not reaching anterior or posterior margin of proglottids. Uterus ventral, with lateral digitate diverticula, with Type 1 of uterine development of de Chambrier et al. (2004). Parasites of Neotropical snakes (Colubridae: Dipsadinae).

Type species: *Penetrocestus joanae* (de Chambrier et Paulino, 1997) comb. n.

Additional species: *Penetrocestus gorgoniae* sp. n., *Penetrocestus jaegeri* sp. n., *Penetrocestus tristani* sp. n. (see below).

Etymology: The new genus is named according to the ability of its species to penetrate through the wall of the intestine of the host and suffix “-cestus”, which means a tapeworm. The name is treated as masculine.

Differential diagnosis. The new genus has testes, ovary, vitellarium, and uterus medullary and its species occur in snakes. It differs from *Ophiotaenia* by the penetration of the scolex through the host's intestinal wall and by the presence of a metascolex, a large glandular apical organ, and a well-developed vaginal sphincter lined with a thick layer of chromophilic cells. It also differs from other proteocephalids parasitising snakes by the presence of a large apical glandular organ, which is larger than the suckers, and a long, swollen, elongated region posterior to the scolex or neck, here considered the metascolex. Two of its three species have well-developed inner longitudinal musculature, whereas most proteocephalids parasitising Neotropical snakes have a weakly developed inner longitudinal musculature.

Remarks

Three newly described species from *Erythrolamprus* are able to penetrate the host's intestinal wall (see below), which is rare among proteocephalid tapeworms, including those parasitising Neotropical reptiles. The only proteocephalid species from reptiles, in which the scolex penetrates the host's intestinal wall, is *Ophiotaenia joanae* (de Chambrier et Paulino, 1997), a parasite of Neuwied's false fer-de-lance, *Xenodon neuwiedi* Günther (Colubridae: Dipsadinae), in Brazil (de Chambrier and Paulino 1997). Because of the morphological similarity between this species and the three new taxa found in snakes of the same subfamily (Dipsadinae), *O. joanae* is transferred to the new genus as its type species.

The only fish proteocephalid that also penetrates the host's intestinal wall is *Jauella glandicephalus* Rego et Pavanelli, 1985, a parasite of the pimelodid catfish *Zungaro zungaro* (Humboldt) in South America (Rego and Pavanelli 1985). However, this species possesses testes and a vitellarium situated in the cortex, whereas species of the new genus have medullary testes and vitelline follicles. The cortical or medullary position of different organs was the diagnostic character for the classification of subfamilies within the Proteocephalidae (Woodland 1925, Rego 1995).

Phylogenetic relationships of species of the new genus are not known because no molecular data are available on any of its four species.

***Penetrocestus gorgonae* gen. n. et sp. n.** Figs. 1, 2

ZooBank number for species:

[urn:lsid:zoobank.org:act:902586D6-810C-4895-95C4-ADD2A59935AD](https://zoobank.org/act:902586D6-810C-4895-95C4-ADD2A59935AD)

Description (based on holotype): Proteocephalidae. Relatively large, wide worms, 183 mm long and up to 1.7 mm wide, flattened dorsoventrally, with proglottids square to elongated, up to 3.25 long. Strobila acraspedote, anapolytic. Immature and mature proglottids wider than long to longer than wide (length: width ratio 0.13–1.58 and 0.88–1.30, respectively), pregravid proglottids longer than wide (length: width ratio 1.03–1.70), gravid proglottids longer than wide (length: width ratio 1.10–2.49). Tegument thick, about 20 in thickness.

Scolex very large, with metascolex, aspinose, much wider than neck, 1,265 long and 1,330 wide, with four uniloculate, subspherical suckers 245–320 wide, directed anterolaterally (Fig. 1A). Apical organ present, 415 long and 315 wide (Fig. 1A). Neck up to 780 wide; unsegmented zone posterior to scolex to first recognisable proglottids very long (13 mm).

Inner longitudinal musculature well-developed, formed by bundles of muscle fibres (Fig. 2C–F). Osmoregulatory canals median to vitelline follicles and lateral to testicular fields, crossing or not lateral margin of ovarian wings. Ventral canals thin-walled, 50–80 in diameter, between vitelline follicles and testes, often touching or even overlapping vitelline follicles; dorsal canals thick-walled, about 10–17 in diameter, median to ventral canals, situated between vitelline follicles and testes. Genital ducts situated between osmoregulatory canals.

Testes oval to subspherical, 40–60 long and 45–65 wide, in one layer and in two compact longitudinal bands between vitelline follicles and uterine stem, well separated from each other anteriorly and posteriorly (Figs. 1A, B, 2C, E); testes 217–251 (mean = 228, $n = 7$) in number. Poral band of testes divided by cirrus sac to preporal and postporal groups (Fig. 1B). Testicular fields situated at 23–26% of proglottid width from lateral margin, i.e., more lateral in relation to mid-line of proglottids (Fig. 1B), not separated by osmoregulatory canals. Testicular bands may reach anterior margin of proglottids anteriorly, but do not reach anterior margin of ovary posteriorly, occupying about 78–81% of proglottid length and 15–22% of proglottid width. Testes degenerate progressively. Vas deferens strongly coiled, occupying round area reaching mid-line of proglottid (Fig. 1B).

Cirrus sac pyriform, thin-walled, 240–330 long and 115–160 wide (Fig. 2A, B); cirrus sac length/width ratio 41–55%. Cirrus sac relatively short, its length representing only 16–23% of proglottid width (Fig. 2A). Cirrus large, occupies 60–79% of length of cirrus sac (Fig. 2A). Genital atrium narrow and deep. Genital pores irregularly alternating, pre-equatorial, at 34–40% ($x = 39\%$; $n = 11$) of proglottid length (Fig. 1B, C)

Ovary relatively small, bilobed, with rounded lobes with short and narrow isthmus. Total width of ovary (in horizontal line) 720–875, representing 54–60% ($x = 56\%$; $n = 13$) of proglottid width; ovary length (in vertical line) represents 12–17% of proglottid length (Fig. 1B, C). Relative ovarian size, i.e., ratio of surface of ovary to surface of proglottid (see de Chambrier et al. 2012) 1.9–2.3% (Fig. 1B, C).

Vaginal canal narrow, thick-walled, enlarged in proximal portion dorsal to ovarian isthmus to small, pyriform seminal receptacle. Distal region of vaginal canal dilated and surrounded by layer of hair-like (digitiform), 30–75 long projections, and with vaginal sphincter (Fig. 2A, B). Mehlis' gland spherical, 55–120 in diameter, representing 6.1–8.7% of proglottid width (Fig. 1B, C).

Vitelline follicles arranged in two longitudinal bands on lateral sides of proglottid, occupying 92–95% and 92–97% of proglottid length on poral and aporal sides, respectively, not reaching anterior or posterior margin of proglottids (Fig. 1B, C). Follicles absent at level of terminal genitalia (cirrus sac and vagina) on both ventral and dorsal sides.

Primordium of uterine stem ventral (Fig. 1B). Type 1 formation of uterus according to de Chambrier et al. (2004). Uterus with 41–55 lateral diverticula on each side. Uterus between anterior part of proglottid and ovarian isthmus, occupying up to 96% of length and 51% of width of gravid proglottids.

Eggs measured in whole-mounted slides; embryophore 22–25 in diameter; oncosphere 10–11 in diameter.

Type and only known host: False coral snake *Erythrolamprus aesculapii* (Linnaeus) (Colubridae: Dipsadinae) (host code Bib 516), collected on 18 June 1991.

Site of infection: Intestine.

Type and only known locality: Itapecará da Serra, São Paulo State, Brazil (−23.746287; −46.858523).

Holotype: Complete, whole-mounted specimen collected by A. de Chambrier (MHNG-PLAT-0018644), 1 cross-section (IPCAS C-1054).

Infection rate: One tapeworm was found in a single host examined.

Etymology: The new species is named for the distinctive shape of the terminal (distal) portion of the vagina, whose external lining resembles the head of the Gorgons, female creatures in Greek mythology with snake-like hair.

Differential diagnosis. *Penetrocestus gorgonae* sp. n. is unique by the morphology of the distal region of vaginal canal, which is dilated and surrounded by a layer of hair-like (digitiform), 30–75 long projections (Fig. 2A, B). The new species also differs from the type species of the genus, *P. joanae* comb. n., by its larger scolex (width 1,330 μ m versus 480–790 μ m in *P. joanae*) and the number of testes (114–144 versus 147–210).

Remarks

Only one specimen was available, which would not normally allow us to propose a new species because its intraspecific variations cannot be described. We are well aware of this limitation, but *P. gorgonae* sp. n. has two peculiar mor-

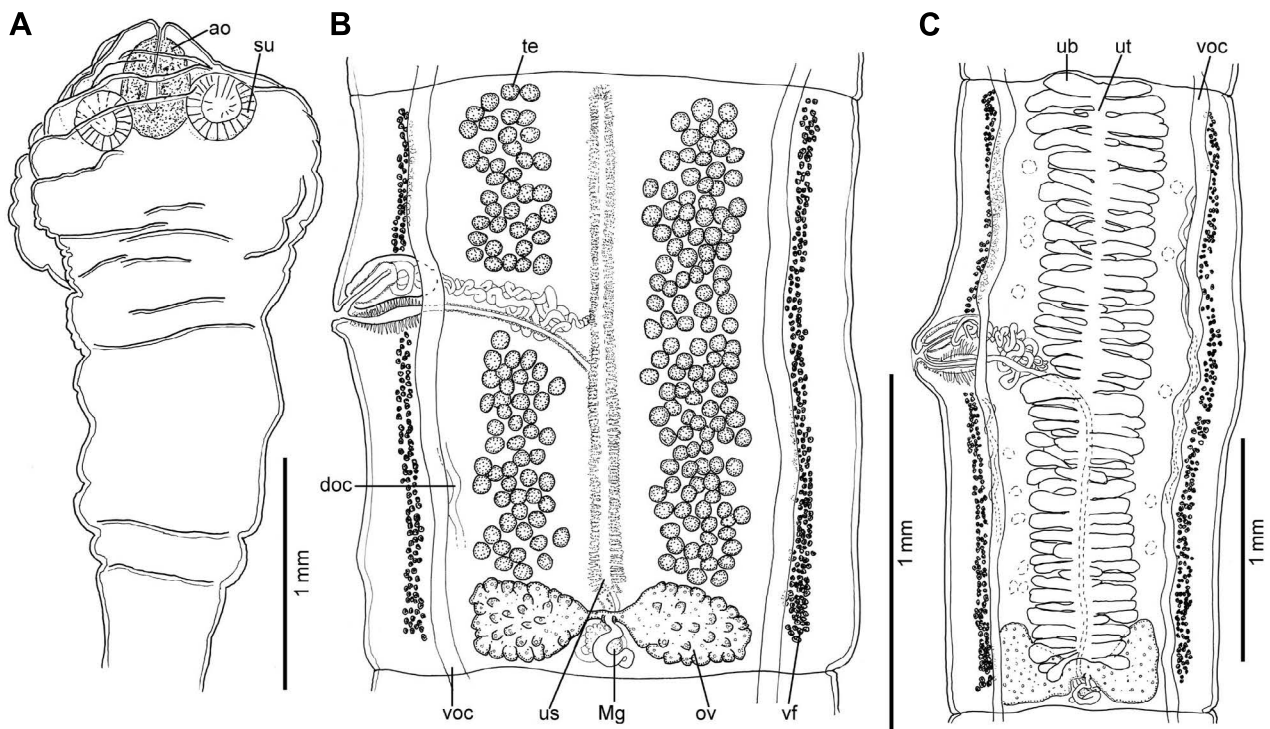


Fig. 1. *Penetrocestus gorgonae* gen. n. et sp. n. from *Erythrolamprus aesculapii* (Linnaeus) (host No. Bib 516), Brazil. **A** – scolex; **B** – mature proglottid, ventral view; **C** – pregravid proglottid, ventral view (note degeneration of testes). **Abbreviations:** ao – apical organ; doc – dorsal osmoregulatory canal; Mg – Mehlis' glands; ov – ovary; su – sucker; te – testes; ub – uterine branches (lateral diverticula); us – uterine stem; ut – uterus; vf – vitelline follicles; voc – ventral osmoregulatory canal.

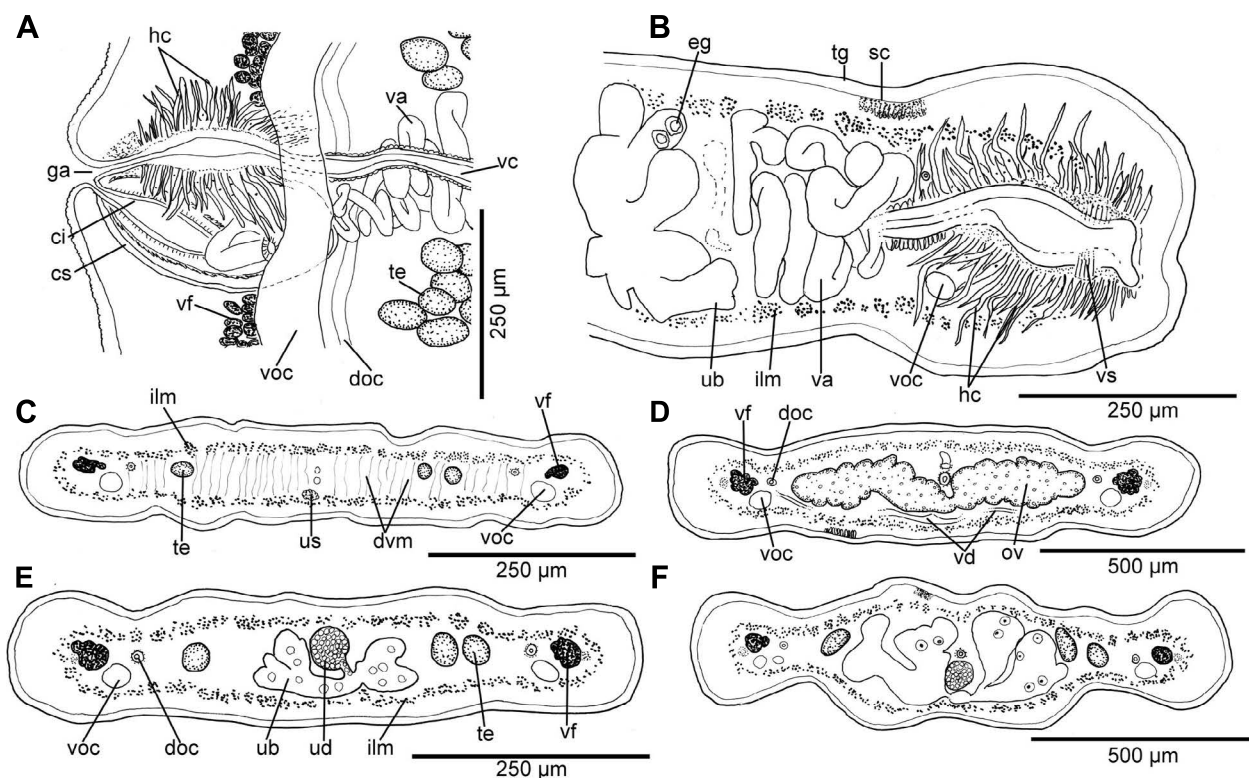


Fig. 2. *Penetrocestus gorgonae* gen. n. et sp. n. from *Erythrolamprus aesculapii* (Linnaeus) (host No. Bib 516), Brazil. **A** – terminal genitalia, ventrally; **B** – cross section of terminal (distal) portion of vagina; **C**, **D** – cross sections at level of testes and ovary, respectively; **E**, **F** – cross sections at level of uterus. **Abbreviations:** ci – cirrus; cs – cirrus sac; doc – dorsal osmoregulatory canal; dvm – dorsoventral muscles fibres; eg – egg; hc – hair-like (digitiform) projections; ga – genital atrium; ilm – inner longitudinal musculature; ov – ovary; sc – subtegumental cells; te – testes; tg – tegument; ub – uterine branches (lateral diverticula); ud – uteroduct; us – uterine stem; va – vas deferens; vc – vaginal canal; vd – vitelloduct; vf – vitelline follicles; voc – ventral osmoregulatory canal; vs – vaginal sphincter.

phological characteristics, which are unique or rare among proteocephalids: (i) a distinctive vagina, with its distal (terminal) portion invested by numerous hair-like cells (Fig. 2A, B); and (ii) a very large scolex (width 1.3 mm; Fig. 1A) bearing a massive apical organ, apparently related to penetration of the host's intestinal wall.

***Penetrocestus jaegeri* gen. n. et sp. n.**

Figs. 3–5

ZooBank number for species:

[urn:lsid:zoobank.org:act:EAA72A7D-11EF-4F2F-9C50-2F0B68A6D75A](https://zoobank.org/act:EAA72A7D-11EF-4F2F-9C50-2F0B68A6D75A)

Description (based on holotype and a voucher used for SEM): Proteocephalidae. Relatively large, wide worms, 72 cm long, up to 1.7 mm wide, flattened dorsoventrally, with proglottids square to elongated, up to 4 mm long. Strobila acraspedote, anapolytic. Immature proglottids wider than long to longer than wide (length: width ratio 0.12–1.52), mature proglottids longer than wide (1.35–2.61), pregravid proglottids longer than wide (2.35–2.75), gravid proglottids from almost quadrate to much longer than wide (1.05–6.64). Tegument thick, about 10–15 in thickness.

Scolex globular, aspinose, much wider than neck, 340–660 long and 450–705 wide, with four uniloculate, spherical suckers 120–195 wide, directed anterolaterally (Figs. 3A–D, 4A–C). Apical organ present, large, 175–260 long and 175–230 wide (Fig. 3A). Neck up to 210 wide; unsegmented zone posterior to scolex to first recognisable proglottids long (14–16 mm).

Inner longitudinal musculature, consisting of isolated muscle fibres (Fig. 5C, D). Osmoregulatory canals median to vitelline follicles and lateral to testicular fields, not crossing lateral margin of ovarian wings. Ventral canals thin-walled, 35–65 in diameter, situated between vitelline follicles and testes, often overlapping vitelline follicles; dorsal canals thick-walled, about 20–35 in diameter, median to ventral canals (Fig. 5A, B). Genital ducts run between osmoregulatory canals.

Testes oval to subspherical, 85–115 long and 55–80 wide, in one layer and in two dispersed longitudinal bands between vitelline follicles and uterine stem, well separated from each other anteriorly and posteriorly (Fig. 5A, B). Poral band of testes divided by cirrus sac to preporal and postporal groups (Fig. 5A). Testes 114–144 (mean = 121, n = 8) in number; each testicular field situated at 19–25% of proglottid width from lateral margin, i.e., more lateral in relation to mid-line of proglottids (Fig. 5A), overlapped by osmoregulatory canals. Testicular bands may reach anterior margin of proglottids anteriorly, and anterior margin of ovary posteriorly, occupying about 87–93% of proglottid length and 20–26% of proglottid width. Testes degenerate progressively (Fig. 5B). Vas deferens coiled, occupying elongate area, reaching mid-line of proglottid (Fig. 5A, B).

Cirrus sac pyriform, thin-walled, 215–355 long and 65–130 wide (Fig. 5E); cirrus sac length/width ratio 43–57%. Cirrus sac relatively short, its length representing only 14–19% of proglottid width (Fig. 5E). Cirrus large, occupies up to 88% of length of cirrus sac (Fig. 5E). Genital atrium narrow and deep. Genital pores irregularly alternating, more or

less equatorial, at 40–53% (x = 46%; n = 11) of proglottid length (Fig. 5A, B).

Ovary bilobed, with folliculate narrow lateral wings connected by a short and narrow isthmus. Total width of ovary (in horizontal line) 700–1,000, representing 47–53% (x = 51%; n = 11) of proglottid width; ovary length (in vertical line) represents 5–9% of proglottid length. Relative ovarian size, i.e., ratio of surface of ovary to surface of proglottid (see de Chambrier et al. 2012), 5.0–5.6% (Fig. 5A).

Vaginal canal narrow, thick-walled, enlarged in proximal portion dorsal to ovarian isthmus to small, pyriform seminal receptacle. Terminal (distal) part of vagina with spherical sphincter (Fig. 5E), lined with thick layer of numerous, dense chromophilic cells (Fig. 5E). Mehlis' gland spherical, 60–100 in diameter, representing 3.8–5.7% of proglottid width.

Vitelline follicles arranged in two longitudinal bands on lateral sides of proglottid occupying 89–93% and 87–94% of proglottid length on poral and aporal sides, respectively, not reaching anterior or posterior margin of proglottids (Fig. 5A, B). Follicles absent at level of terminal genitalia (cirrus sac and vagina) on both ventral and dorsal sides.

Primordium of uterine stem ventral (Fig. 5A, C). Type 1 formation of uterus according to de Chambrier et al. (2004). Uterus with 38–50 lateral diverticula on each side. Uterus between anterior part of proglottid and ovarian isthmus, occupying up to 91–97% of gravid proglottids width.

Eggs with outer envelope, collapsed in permanent preparations (whole-mounts). Inner envelope consists of bilayered embryophore, with thick external layer, 28–33 in diameter; and nucleated envelope, 16–17 in diameter. Oncospheres spherical, 11–12 in diameter.

Type and only known host: False coral snake *Erythrolamprus jaegeri* (Günther) (Colubridae: Dipsadinae) (host code Py 162), collected on 15 October 1979.

Site of infection: Intestine.

Infection rate: Three adults and eight immature tapeworms were found in a single host examined.

Type and only known locality: Estancia Estrellas, Río Apa, San Lazaro, Paraguay (-22.16667, -57.7).

Type specimens: Holotype: complete, whole-mounted specimen collected by the members of the expedition of the Museum in Paraguay (MHNG-PLAT-0018182); paratypes: (IPCAS C-1049); MHNG-PLAT-0160654; 0160655.

Etymology: This new species refers to the name of the host species, *E. jaegeri*.

Differential diagnosis. The present species is assigned to the genus *Penetrocestus* because of its unarmed, simple scolex (embedded in the intestinal wall) with uniloculate suckers and a large apical organ. The new species differs from the two other *Penetrocestus* species in the position of the 'metascolex' (the elongate, swollen anterior part posterior to the scolex) and the neck region where the host intestinal wall is located: in *P. jaegeri*, the 'metascolex' is posterior to the neck region (Fig. 3B, D), meaning it lies inside the host's intestinal lumen and only the scolex penetrates the host's intestinal wall (Figs. 3C, 4A). In contrast, in *P. joanae* and *P. gorgonae*, the 'metascolex' is situated immediately

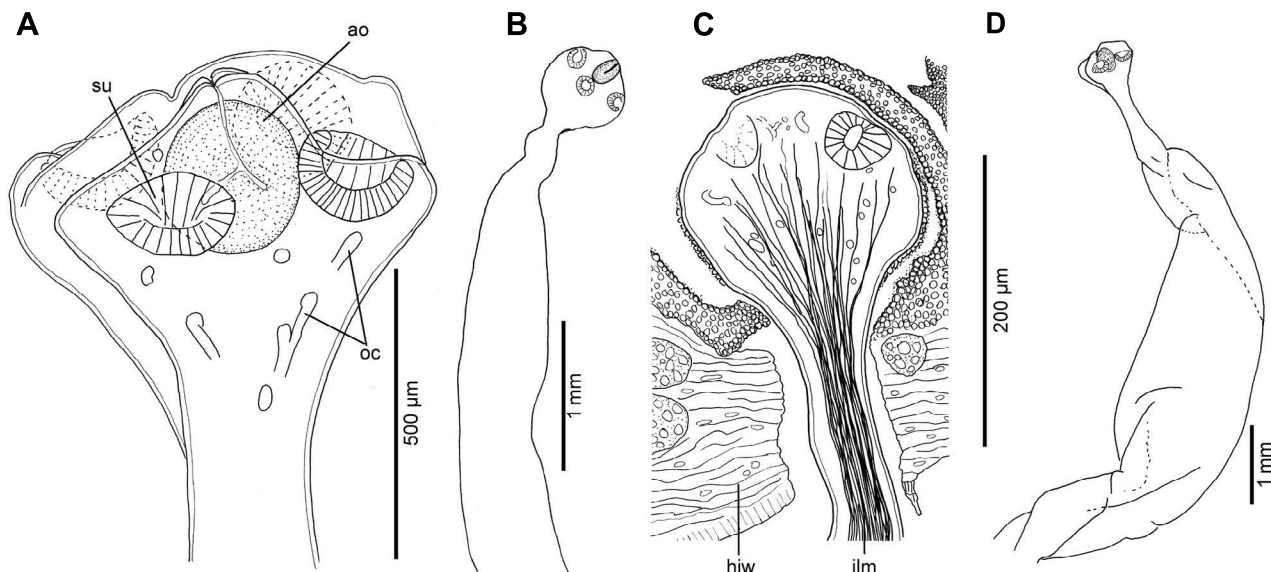


Fig. 3. *Penetrocestus jaegeri* gen. n. et sp. n. from *Erythrolamprus jaegeri* (Wied) (host No. Py 162), Paraguay. **A** – scolex; note large glandular apical organ; **B**, **D** – anterior part of body (scolex with ‘metascolex’); **C** – sagittal section of the scolex pierced in the host’s intestinal wall. **Abbreviations:** ao – apical organ; oc – osmoregulatory canals; hiw – host intestinal wall; ilm – inner longitudinal musculature; su – sucker.

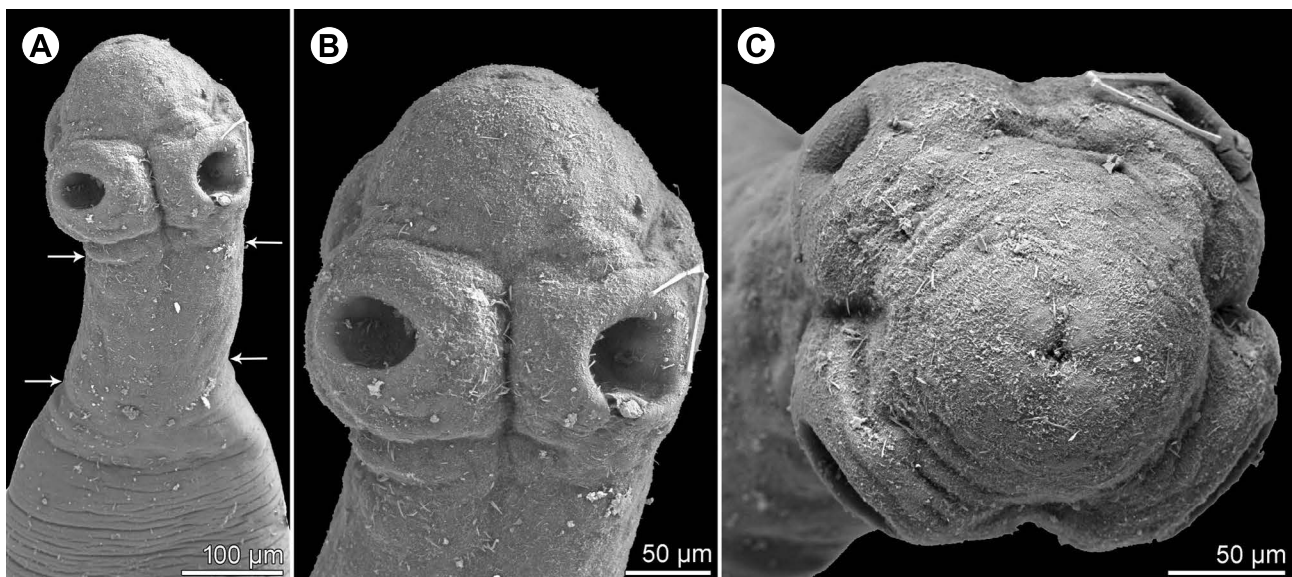


Fig. 4. *Penetrocestus jaegeri* gen. n. et sp. n. from *Erythrolamprus jaegeri* (Wied) (host No. Py 162), Paraguay. Scanning electron micrographs. **A** – anterior part with the scolex and neck region; **B**, **C** – frontal and apical view of the scolex; note the orifice of an apical organ in **C**. Arrows indicate position of the host’s intestinal wall.

posterior to the scolex, that is, anterior to the neck region surrounded by the host’s intestinal wall (Fig. 1; fig. 3 in de Chambrier and Paulino 1997). This means that the scolex and metascolex are located outside the host’s intestine within the body cavity (Fig. 1A; fig. 14 in de Chambrier and Paulino 1997). The new species is also characterised by a lower number of testes (114–144; mean = 121) compared to *P. joanae* (217–251) and *P. gorgonae* sp. n. (147–210) and differs from *P. gorgonae* sp. n. in the morphology of the terminal (distal) portion of the vaginal canal (compare Fig. 5E with Fig. 2A, B). Other distinguishing characteristics are summarised in Table 1.

Remarks

Although the new species differs markedly from congeners in the position of the ‘metascolex’, it is placed in the new genus because it shares several morphological characteristics typical of *Penetrocestus*, particularly the peculiar morphology of the distal portion of the vaginal canal, which has a large vaginal sphincter and a thick layer of numerous chromophilic cells. However, the generic assignment of *P. jaegeri* should be confirmed by molecular data, which are not available for any of the four species currently placed in this new genus.

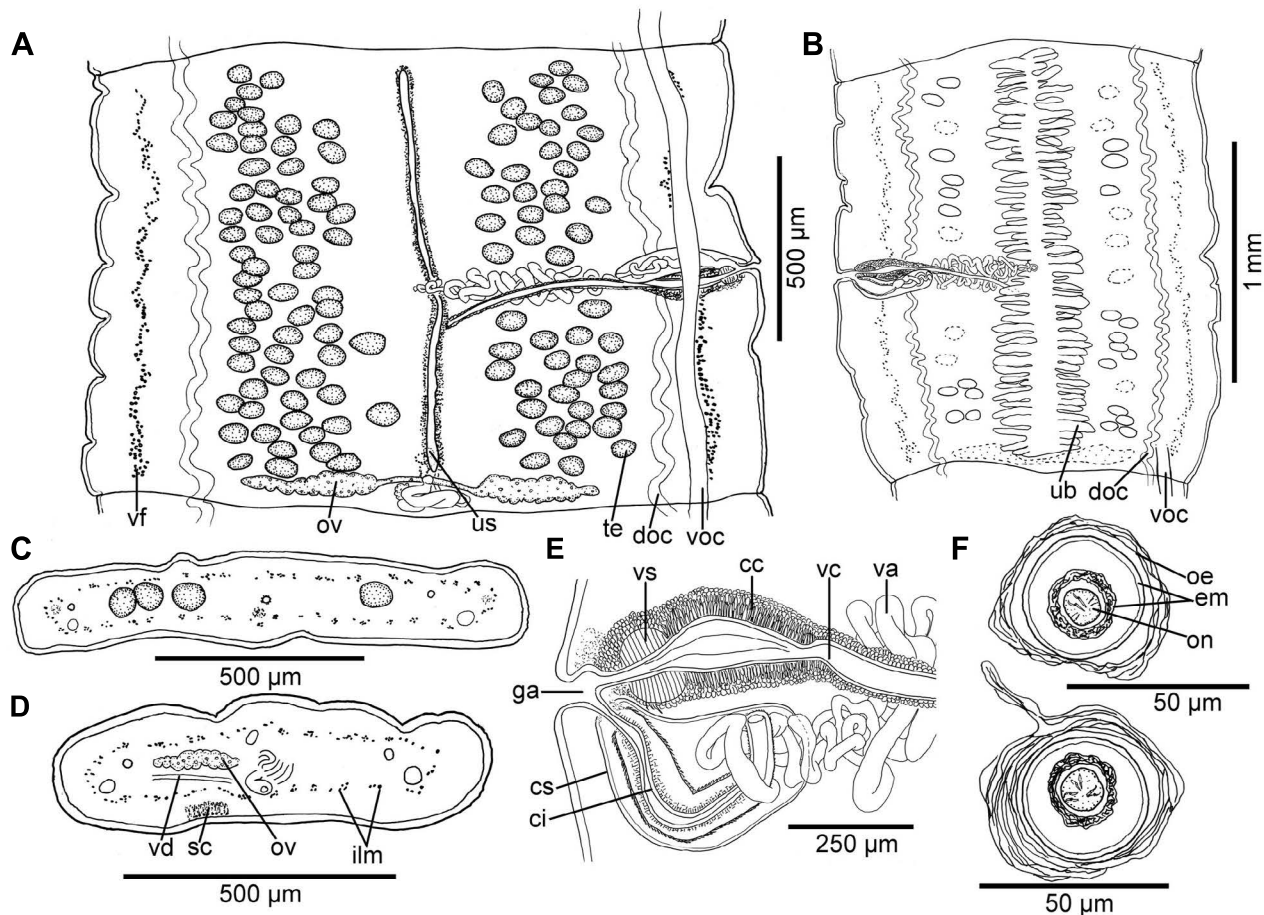


Fig. 5. *Penetrocestus jaegeri* gen. n. et sp. n. from *Erythrolamprus jaegeri* (Wied) (host No. Py 162), Paraguay. **A** – mature proglottid, ventral view; **B** – gravid proglottid, ventral view (note the degeneration of testes, vitelline follicles and ovary); **C**, **D** – cross sections at level of testes and ovary, respectively; **E** – terminal genitalia; note a ring-like vaginal sphincter and wide region consisting of numerous chromophilic cells; **F** – eggs. **Abbreviations:** cc – chromophilic cells; ci – cirrus; cs – cirrus sac; doc – dorsal osmoregulatory canal; em – bilayered embryophore; ga – genital atrium; ilm – inner longitudinal musculature; oe – outer envelope; on – oncosphere; ov – ovary; sc – subtegumental cells; te – testes; ub – uterine branches (lateral diverticula); us – uterine stem; va – vas deferens; vc – vaginal canal; vd – vitelloduct; vf – vitelline follicles; voc – ventral osmoregulatory canal; vs – vaginal sphincter.

Penetrocestus tristani gen. n. et sp. n.

Fig. 6

ZooBank number for species:

[urn:lsid:zoobank.org:act:6805FA88-4459-4B31-BC85-8292BD1AB63C](https://zoobank.org/act:6805FA88-4459-4B31-BC85-8292BD1AB63C)

Description (based on holotype and two paratypes): Proteocephalidae. Relatively large, wide worms, up to 303 cm long, up to 3.2 mm wide, flattened dorsoventrally, with proglottids square to elongated, up to 3.9 long. Strobila acraspedote, anapolytic. Immature, mature, pregravid and gravid proglottids wider than long to longer than wide (length: width ratio 0.11–1.26, 0.33–2.42, 0.35–1.18 and 0.53–6.64 respectively). Tegument thick, about 20 in thickness.

Scolex (holotype) very large, with metascolex, aspinose, much wider than neck, 920 long and 945 wide, with four uniloculate, subspherical suckers 255–290 wide, directed anterolaterally (Fig. 6A). Apical organ present, 490 long and 345 wide (Fig. 6A). Neck up to 1065 wide; unsegmented zone posterior to scolex to first recognisable proglottids very long (17 mm).

Inner longitudinal musculature well-developed, formed by bundles of muscle fibres (Fig. 6D, E). Osmoregulatory

canals median to vitelline follicles and lateral to testicular fields, not crossing lateral margin of ovarian wings. Ventral canals thin-walled, broad, 30–115 in diameter, between vitelline follicles and testes, sometimes overlapping vitelline follicles; dorsal canals thick-walled, about 15–40 in diameter, median to ventral canals, situated between vitelline follicles and testes. Genital ducts run between osmoregulatory canals.

Testes numerous, dense, oval to subspherical, 55–90 long and 40–65 wide, in one layer and in two compact longitudinal bands between vitelline follicles and uterine stem, well separated from each other anteriorly and posteriorly (Fig. 6B). Poral band of testes divided by cirrus sac to preporal and postporal groups (Fig. 6B). Testes 215–279 (mean = 250, $n = 13$) in number; each testicular fields situated at 13–19% of proglottid width from lateral margin, i.e., more lateral in relation to mid-line of proglottids (Fig. 6B), not separated by osmoregulatory canals. Testicular bands may reach anterior margin of proglottids anteriorly, and reach anterior margin of ovary posteriorly, occupying about 87–89% of proglottid length each band occupies 23–26% of proglottid width. Testes degenerate progressively. Vas deferens strongly coiled,

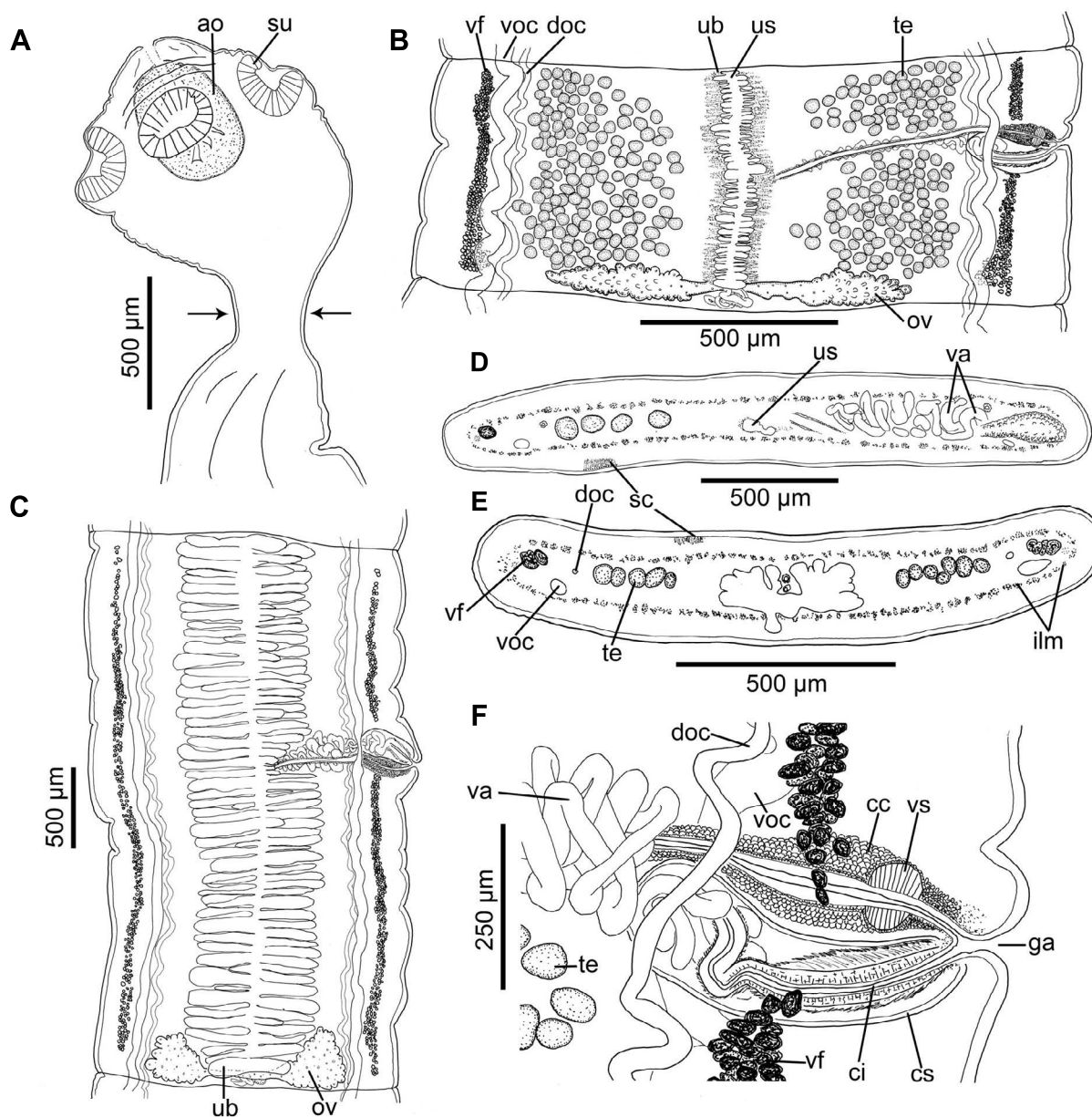


Fig. 6. *Penetrocestus tristani* gen. n. et sp. n. from *Erythrolamprus poecilogyrus* (Wied-Neuwied) (host No. Py 4720), Paraguay. **A** – scolex; arrows indicate position of the host’s intestinal wall; **B** – mature proglottid, ventral view; **C** – gravid proglottid, ventral view; note the absence of testes; **D** – cross-section at level of testes; **E** – cross-section at level of uterus; **F** – terminal genitalia, dorsal view. *Abbreviations:* ao – apical organ; cc – chromophilic cells; ci – cirrus; cs – cirrus sac; doc – dorsal osmoregulatory canals; ga – genital atrium; ilm – inner longitudinal musculature; ov – ovary; sc – subtegumental cells; su – sucker; te – testes; ub – uterine branch (lateral diverticula); us – uterine stem; va – vas deferens; vf – vitelline follicles; voc – ventral osmoregulatory canals; vs – vaginal sphincter.

forming elongated mass, reaching mid-line of proglottid but not overlapping it (Fig. 6B, C).

Cirrus sac pyriform, thick-walled, 215–515 long and 140–215 wide (Fig. 6F); cirrus sac length/width ratio 24–57%. Cirrus sac relatively short, its length representing only 13–24% of proglottid width (Fig. 6F). Cirrus large, occupies up to 80% of length of cirrus sac (Fig. 6F). Genital atrium narrow and deep. Genital pores irregularly alternating, pre-equatorial, at 34–46% ($\bar{x}$ = 39%; n = 20) of proglottid length (Fig. 6B, C).

Ovary relatively small, bilobed, with rounded lobes and short and narrow isthmus. Total width of ovary (in horizontal line) 540–1840, representing 51–66% ($\bar{x}$ = 58%; n = 27) of proglottid width; ovary length (in vertical line) represents

9–17% of proglottid length (Fig. 6B, C). Relative ovarian size, i.e., ratio of surface of ovary to surface of proglottid (see de Chambrier et al. 2012) 3.0–5.1%, $\bar{x}$ = 4.0%, n = 2 (Fig. 6B, C).

Vaginal canal narrow, thick-walled, enlarged in proximal portion dorsal to ovarian isthmus to small, pyriform seminal receptacle. Terminal (distal) part of vagina large, its length represents 60 to 75% of cirrus-sac length, lined with thick layer of small rounded chromophil cells surrounding large vaginal sphincter, 40–65 long and 80–90 wide (Fig. 6F). Mehlis’ gland, spherical, 70–215 in diameter, representing 3.7–9.5% of proglottid width (Fig. 6B).

Vitelline follicles arranged in two dense longitudinal bands on lateral sides of proglottid occupying 85–94% and

Table 1. Comparative measurements of species of *Penetrocestus* gen. n. (Cestoda: Proteocephalidae), parasites of dipsadine snakes (Colubridae) in South America. Measurements in micrometres unless otherwise stated.

<i>Penetrocestus jouanae</i> (de Chambrier et Paulino, 1997) comb. n.		<i>Penetrocestus gorgoniae</i> sp. n.		<i>Penetrocestus jaegeri</i> sp. n.		<i>Penetrocestus tristanti</i> sp. n.	
Host species	<i>Xenodon newiedi</i> Günther	<i>Erythrolamprus aesculapii aesculapii</i> (Linnaeus)	<i>Erythrolamprus jaegeri</i> (Günther)	<i>Erythrolamprus poecilogyrus</i> (Girard, 1858)			
Host code	Bib 92/77	Bib 516	Py 162	Py 4587, 4720			
Collection No.	MHNG-PLAT-0022030-31	MHNG-PLAT-0018644	MHNG-PLAT-0018182, IPCAS (C-1049)	MHNG-PLAT-0018200, 0018201; IPCAS (C-1050)			
Locality	Pariquera-açu, São Paulo, Brazil	Itapecará da Serra, São Paulo, Brazil	Estancia Estrellas, Río Apa, Concepción, Paraguay	Paraguay, several localities			
Date of collecting	10 August 1992	18 June 1991	15 October 1979	27 October, 8 November 1985			
Total length (mm)	140–250	183	720	107–303			
Maximum width (mm)	3.3	1.7	1.7	1.2–3.2			
Immature proglottids length × width (mm)	N/A	0.20–1.45 × 0.77–1.43	0.19–1.77 × 0.78–1.20	0.240–1.62 × 1.16–2.54			
Immature proglottid (L : W ratio)	N/A	0.13–1.58	0.12–1.52	0.35–1.26			
Mature proglottids length × width	N/A	1.45–1.91 × 1.38–1.73	2.04–2.39 × 0.47–1.50	0.99–2.68 × 1.11–3.21			
Mature proglottids (L : W ratio)	N/A	0.88–1.30	1.36–2.61	0.33–2.42			
Pregavid proglottids length × width	N/A	1.58–2.18 × 1.28–1.54	1.00–1.19 × 2.76–2.80	1.09–2.42 × 2.05–3.16			
Pregavid proglottids (L : W ratio)	N/A	1.03–1.70	2.35–2.75	0.35–1.18			
Gravid proglottids length × width (mm)	1.28–4.80 × 0.29–1.09	2.19–3.24 × 1.11–1.50	1.51–4.03 × 0.61–1.63	1.66–6.44 × 0.97–3.22			
Gravid proglottids (L : W ratio)	1.18–1.5	1.47–2.49	1.05–6.64	0.53–6.64			
Length of scolex	370	1265	340–660	920			
Width of scolex	480–790	1330	450–705	945			
Scolex width/neck width ratio	1.04	1.69	2.88–3.40	3.5			
Diameter of suckers	150–230	245–320	120–195	255–290			
Apical organ: length × width	250–325	415 × 315	175–260 × 175–230	490 × 345			
Width of neck (µm)	425	790	155–210	270–1065			
Dorsal osmoregulatory canals: width	15–25	10–17	20–35	15–40			
Ventral osmoregulatory canals: width	30–80	50–80	35–65	30–115			
Number of testes	147–210, x = 174, n = 32	217–251, x = 228, n = 7	114–144, x = 121, n = 8	215–279, x = 250, n = 13			
Length × width of testes	95 × 50	45–65 × 40–60	85–115 × 55–80	55–90 × 40–65			
Position of gonopore (%)	28–56%, x = 44%, n = 45	34–40%, x = 38%, n = 10	40–53%, x = 46%, n = 11	34–46%, x = 39%, n = 20			
Length × width of cirrus sac	240–470	240–330 × 115–160	215–355 × 65–130	215–515 × 140–215			
Relative length of cirrus sac (%)	14–25%, x = 19%, n = 38	16–23%, x = 19%, n = 14	14–19%, x = 16%, n = 10	13–24%, x = 17, n = 25			
Cirrus sac width/length	N/A	41–55%, x = 49%, n = 9	43–57%, x = 47%, n = 5	24–57%, x = 35%, n = 17			
Length of cirrus/length of cirrus sac	up to 65%	up to 79%	up to 88%	up to 80%			
Ovary width	550–1150	720–875	700–1000	540–1840			
Ovary length	45–90	140–295	60–175	105–335			
Relative width of ovary (%)	39–56%, x = 47%, n = 40	54–60%, x = 56%, n = 13	47–53%, x = 51%, n = 11	51–66%, x = 58%, n = 27			
Relative surface of ovary (%)*	2.8–3.5%, x = 3.1%, n = 2	1.9–2.3%, x = 2.0%, n = 3	5.0–5.6%, x = 5.4%, n = 4	3.0–5.1%, x = 4%, n = 2			
Mehlis' gland width	75–140	85–120	60–95	70–215			
Mehlis' gland width/proglottid width	4–8%	6.1–8.7%	3.8–5.7%	3.7–9.5%			
Position of vagina	anterior 32%, posterior 68%	anterior 11%, posterior 89%	anterior 39%, posterior 61%	anterior, posterior			
Vaginal sphincter: length × width	70 × 60	25–40 × 85–95	50–55 × 65–80	40–65 × 80–90			
Length pars copulatrix vaginae/length cirrus sac	60%	68–87% (x = 77, n = 10)	75–105%, x = 86%, n = 5	60–75%			
Apical vitelline follicles – relative length	79–88%	92–97%, x = 94%, n = 9	87–93%, x = 89%, n = 6	87–96%			
Post vitelline follicles – relative length	75–88%	92–95%, x = 94%, n = 10	89–93%, x = 91%, n = 6	85–94%			
Number of uterine diverticula	26–49	41–55	38–50	29–60			
Diameter of embryophore	26–30	22–25**	30–33	25–29			
Diameter of oncosphere	10–12	10–11**	10–13	14–15			
Type of uterine formation [†]	Type 1	Type 1	Type 1	Type 1			

* relative size of the ovary (percentage of the ovarian size in relation to that of the entire proglottid – see p. 40 in de Chambrier et al. 2012 for methods of measuring);
** measurements in whole-mounted slides; # according to de Chambrier et al. (2004).

87–96% of proglottid length on poral and aporal sides, respectively, not reaching anterior or posterior margin of proglottids (Fig. 6B, C). Follicles rarely present at level of terminal genitalia (cirrus sac and vagina) on dorsal side.

Primordium of uterine stem ventral (Fig. 6D, E). Type 1 formation of uterus according to de Chambrier et al. (2004). Uterus with 29–60 lateral diverticula on each side. Uterus between anterior part of proglottid and ovarian isthmus, occupying up to 96% of gravid proglottids length and 51% of proglottids width.

Eggs measured in whole-mounted slides, embryophore 25–29 in diameter, oncosphere 14–15 in diameter.

Type and only known host: False coral snake *Erythrolamprus poecilogyrus* (Wied-Neuwied) (Colubridae: Dipsadinae) (host code Py 4720), collected on 8 November 1985.

Site of infection: Intestine

Infection rate: Three tapeworms were found in two hosts examined.

Type and only known locality: Km 293, Trans-Chaco, P. Hayes, Paraguay (-23.2066833, -59.2037).

Type specimens: Holotype: complete, whole-mounted specimen collected by A. de Chambrier (MH-NG-PLAT-0018201); paratypes: One specimen, including cross-sections (IPCAS C-1050); two specimens, including cross-sections (MHNG-PLAT-0018200, 0018184)

Etymology: The new species is named in honour of Tristan Le Lay, our friend and a renowned, but humble and extraordinary winemaker.

Differential diagnosis

The new species differs from *P. joanae* and *P. jaegeri* sp. n. by the number of testes (215–279 versus 147–210 and 114–144, respectively). Furthermore, it differs from *P. jaegeri* by the well-developed inner longitudinal musculature (versus weakly developed in *P. jaegeri*) (Table 1). *Penetrocestus tristani* sp. n. differs from *P. gorgonae* sp. n. by the absence of digitate cells on the pars copulatrix vaginae, by a smaller scolex (width 945 µm versus 1,330 µm) and by the last proglottid width/length ratio (1 : 6.64 versus 1 : 2.49) (Table 1).

To facilitate differentiation of the species of the new genus, a key to their identification is provided.

Key to the species of *Penetrocestus* gen. n.

- 1a. Testes fewer than 145; inner longitudinal musculature weakly developed; ovary relatively large, with the relative size of the ovary (ratio of its surface area to the surface area of the proglottid) greater than 5%; in *Erythrolamprus jaegeri* *P. jaegeri* sp. n.
- 1b. Testes more than 145; inner longitudinal musculature well developed; ovary relatively small, with the relative size of the ovary (ratio of its surface to surface of proglottid) smaller than 3% 2
- 2a. Scolex wider than 1.3 mm; distal (terminal) region of the vaginal surrounded by a layer of hair-like (digitiform) projections; in *Erythrolamprus aesculapii* *P. gorgonae* sp. n.
- 2b. Scolex narrower than 1 mm; vagina without hair-like (digitiform) projections 3

- 3a. Testes fewer than 210; metascolex close to the scolex; ‘neck’ where the host’s intestinal wall surrounds the worm lies posterior to the metascolex; apical organ spherical; in *Xenodon neuwiedi* *P. joanae* comb. n.
- 3b. Testes more than 215; metascolex separated from the scolex by the neck where the host’s intestinal wall surrounds the worm; apical organ ovoid; in *Erythrolamprus poecilogyrus* *P. tristani* sp. n.

DISCUSSION

All three new species of proteocephalid tapeworms described in this article were found in dipsadine snakes of the genus *Erythrolamprus*, which is a group native to Central America, the Caribbean, and South America (Uetz et al. 2026). These include the false coral snakes, which belong to the subfamily Dipsadinae (sometimes referred to as the family Dipsadidae) within the family Colubridae. *Erythrolamprus* previously contained only six species; however, molecular studies determined that *Erythrolamprus* was not monophyletic, so most snakes from the genera *Liophis* Wagler, *Leimadophis* Fitzinger, and *Umbrivaga* Roze were placed into *Erythrolamprus*, increasing the number of species up to 50 (Murphy et al. 2019).

Erythrolamprus snakes are usually less than 1.6 m in length. They are ground-dwelling snakes, with lifestyles ranging from fossorial (burrowing) and terrestrial to semi-aquatic, and inhabit from rainforests and savannas to the mountainous páramo, up to 3,500 m above sea level (Uetz et al. 2026). Information about helminth parasites of these snakes is scarce, including that on their tapeworms. In addition to the three new species described in this paper, two other species of *Ophiotaenia* are known to occur in *Erythrolamprus miliaris* (Linnaeus) in Brazil, namely *Ophiotaenia arandasi* (dos Santos et Tayt-Son Rolas, 1973) and *O. karipuna* Trindade, Rebêlo et Melo, 2024 (de Chambrier et al. 2024).

Together with *Jauella glandicephalus*, a parasite of the pimelodid catfish *Zungaro zungaro*, species of the new genus are unique among proteocephalid tapeworms in their ability to penetrate the intestinal wall of their hosts, a feature reflected in the genus name. However, the ability for deep penetration is also present, though rarely, in other cestodes parasitising poikilothermic vertebrates, especially teleosts. *Penetrocephalus ganapattii* (Rao, 1954) (Bothriocephalidae) parasitises *Saurida* fish in the Indian Ocean and penetrates the intestinal wall of its fish hosts with a long, narrow scolex (Kuchta et al. 2009).

Several species of caryophyllidean tapeworms, parasites of suckers (Cypriniformes: Catostomidae) in North America, are deeply embedded in the host’s intestinal wall, forming a pit or cyst-like structure at the site of attachment. This deep penetration into the host’s intestinal wall is associated with a conspicuous pathological condition of the host intestinal wall (Mackiewicz and McCrae 1962, Mackiewicz et al. 1972). Another caryophyllidean, *Djombangia penetrans* Bovien, 1926, penetrates the intestinal wall of its host, the catfish *Clarias batrachus* (Linnaeus), in the Oriental region (Ash et al. 2011).

All species of the new genus possess an enlarged part posterior to the scolex (‘metascolex’), but they differ in the extent to which their scoleces intrude into the body cavity of

their hosts. Two species, *Penetrocestus joanae* and *P. gorgonae*, have the metascolex immediately posterior to the scolex and this part of the body is located within the host's body cavity. In contrast, the 'metascolex' of the two remaining species, *P. jaegeri* and *P. tristani*, is posterior to the neck, i.e., the region surrounded by the host's intestinal wall. Despite this difference, all four species are assigned to the new genus, but molecular data are lacking to confirm this generic placement because all described species were collected in the pre-molecular era.

Given the shortage of data on these parasites and the increasingly difficult accessibility of herptiles in South America, it is important to characterise and formally describe putative new species based on museum specimens. Future research should focus on collecting new material of these parasites, which will be suitable for genetic analyses, thus clarifying the phylogenetic relationships of individual taxa and enabling the proposal of a more natural classification of proteocephalids parasitising herptiles.

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Received 1 April 2026

Accepted 3 July 2026

Published online 26 August 2026

Cite this article as: de Chambrier A., Scholz T. 2026: A new genus and three new species of tapeworms (Cestoda: Onchoproteocephalidea) in *Erythrolamprus* snakes (Colubridae: Dipsadinae) in South America. *Folia Parasitol.* 73: 008.