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Acanthostomum yahuarcaquense n. sp. (Digenea: Cryptogonimidae) infecting the intestine of an aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1817) (Serpentes: Elapidae) from the flooded rainforest habitat of the Yahuarcaca Lake System (Amazon River, Colombia) and phylogenetic analysis of Cryptogonimidae

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ABSTRACT

We herein describe *Acanthostomum yahuarcaquense* Cajiao-Mora and Bullard n. sp. (Digenea: Cryptogonimidae) based on specimens we collected from the intestine of an aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1817) (Serpentes: Elapidae) captured within the flooded rainforest habitat of the Yahuarcaca Lake System (Amazon River) Leticia, Amazonas, Colombia. We assign the new species to *Acanthostomum* Looss, 1899because it lacks a gonotyl and has an elongate body, spinose tegument, funnel-shaped oral sucker with circumoral spines, ceca each having a posterolateral and nearly terminal pore, and excretory vesicle arms reaching anteriad to the pharynx. The new species differs from its 19 accepted congeners by having 24–30 circumoral spines (vs. fewer than 20 or aspinose), a vitellarium extending from the anterior margin of the ovary to the posterior half of the body (vs. from testis or ovary but ending in anterior half of body), and paired elongate, symmetrical ceca each having an anal pore (vs. asymmetrical ceca, a single cecum, or lacking anal pores). Our *28S* phylogenetic analysis recovered a paraphyletic *Acanthostomum* (including *Neocladocystis* spp. and *Tanganyikatrema fusiforme* Kmentová, Georgieva, and Bray, 2020; both Cryptogonimidae) within a clade sister to other cryptogonimids. We discuss the implications of using nonugens and excessively short nucleotide sequences to compare species and to test phylogenetic relationships. Regarding advancing the systematics of the family, we discuss oral sucker shape and position, circumoral spine distribution, tegumental spine distribution, ceca symmetry, anal pore presence/absence and position, and gonotyl presence/absence and position as useful genus-level features. Many of these features remain indeterminate for several species. This is the first published study of a parasite infecting a tetrapod in the Yahuarcaca Lake System, first to record a parasite infecting a coral snake (*Micrurus* spp.) in Colombia, and only the second trematode species reported from the aquatic coral snake.

1. Introduction

Located in southern Colombia, the Yahuarcaca Lake System (YLS) comprises a series of interconnected freshwater lakes within the Amazon River floodplain (Urrea et al., 2019; Henao et al., 2020). It exhibits a dry and a wet season. The dry season comprises May through November, with the YLS typically having approximately 0.53 km^2 of wetland. The wet season comprises late November through April and more than doubles (1.19 km^2) the wetland area of the YLS (Urrea et al., 2019 ; Sánchez-López et al., 2024). During this period, a large portion of the

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YLS comprises flooded rainforest habitat, where the infected aquatic coral snake reported herein was captured.

The YLS is essential for local subsistence use by indigenous communities (Tikuna, Cocama, and Yagua ethnic groups) and serves as Leticia's primary water source. It also supports commercial fisheries, agriculture, and ecotourism (Henao et al., 2020; Sánchez-López et al., 2024). Portocarrero-Aya and Cowx (2016), Henao et al. (2020), and Sánchez-López et al. (2024) worked within the YLS and identified overfishing, changes in land use, and uncontrolled tourism as threats to the ecosystem. Few biotic surveys of the YLS exist, but Henao et al. (2020) emphasized the need for them for conservation. Previous biotic surveys there have focused on aquatic and terrestrial vegetation (Guisande et al., 2000; Diaz-Olarte and Duque, 2009; Andramunio-Acero and Caraballo, 2012; Donato-Rondon and Duque, 2023), phytoplankton (Duque et al., 1997; Salcedo-Hernández et al., 2012), zooplankton (Guisande et al., 2000), benthic macroinvertebrates (Guisande et al., 2000; Lobón-Cerviá et al., 2012), fishes (Mojica et al., 2005; Galvis et al., 2006; Prieto-Piraveque, 2012; Prieto-Piraveque et al., 2015), and frogs (Lynch, 2005). Yet, the parasites of the YLS remain clearly under sampled. KCM surveyed the YLS bat (Mammalia: Chiroptera) parasites and identified ectoparasites comprising 18 species in 3 families and endoparasites of 23 species in 8 families (Cajiao-Mora et al., 2023 [dataset; accessed Nov 05, 2024]). After a survey of the YLS by our team during 2023, Cajiao-Mora et al. (2024a) provided a supplemental description of an echinostomatoid [*Alobophora annulata* (Diesing, 1850) Cajiao-Mora and Bullard, 2024 (Digenea: Caballerotrematidae)] infecting an electric eel, *Electrophorus* cf. *varii* (Gymnotidae). To our knowledge, the present paper and Cajiao-Mora et al. (2024a) are the only published taxonomic studies of parasites in the YLS.

Coral snakes (*Micrurus* spp.), comprising 83 species (Uetz et al., 2024), are endemic to the Americas (Slowinski, 1995; Campbell and Lamar, 2004). The host species of interest to the present study, the aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1817) (Serpentes: Elapidae), is a venomous (neuromuscular venom) snake that ranges in the Amazon region of French Guiana, Guyana, Colombia, Ecuador, Peru, Brazil, and Bolivia (Vitt and Caldwell, 2013; Bucaretchi et al., 2016). In addition to being relatively unique in its wholly aquatic lifestyle (Nogueira et al., 2019), it is distinctive regarding functional anatomy because it has long temporal and quadrate bones and an accompanying wide gape (Silva et al., 2018; Almeida et al., 2024) that allow it to feed on large fish (including eels), lizards, and snakes (Silva-Haad, 1994; Pinto et al., 2011; Ávila et al., 2013; Tavares-Pinheiro et al., 2021). Its congeners, which lack this cranial adaptation, are specialists that feed on vermiform prey such as smaller species of snakes, amphibians, and caecilians (Almeida et al., 2016; Silva et al., 2018). This fundamental information is relevant to their parasites because the different diets could indicate/suggest the presence of distinct parasite communities, for example.

Little is known about the helminths infecting the aquatic coral snake throughout its range. In the only other study of aquatic coral snake parasites, Ávila et al. (2013) necropsied 4 preserved aquatic coral snake specimens (collected from Mato Grosso, Brazil) from the Vertebrate Collection of the Federal University of Mato Grosso. They recovered several nymphs of *Sebekia oxycephala* (Diesing, 1836) Sambon, 1922 (Pentastomida: Sebekidae), larval nematodes of *Physaloptera* sp. (Nematoda: Physalopteridae), and adults of *Opisthogonimus lecithonotus* Lühe, 1900 (Digenea: Opisthogonimidae). Many groups of parasites must be fixed or preserved following taxon-specific protocols, and, because of that, hosts that have been cold formalin-fixed and then stored in ethanol tend to yield poor helminth specimens. Hence, access to live parasite specimens can be critical in the taxonomy of a group because, in our opinion, heat-killed, formalin-fixed adult trematodes stain the best, elucidating the largest proportion of useful taxonomic features from the most specimens. That said, many examples of exciting discoveries from museum host specimens exist (Ávila et al., 2013; Orélis-Ribeiro and Bullard, 2015). The present study is the first to have access to live parasites from an aquatic coral snake.

While perusing the literature on coral snake parasites in general, we noted that most records comprise nematode, pentastomid, and protozoan infections (Lainson and Shaw, 1973; Lainson et al., 1991; Almeida et al., 2007; McAllister et al., 2010; Bursey and Brooks, 2011; Oliveira et al., 2018; de Luna et al., 2022), with relatively few comprising digenean infections (Table 1). Regarding non-digenean parasites of coral snakes, Pizzato and Madi (2002) reported cystacanths of *Oligacanthorhynchus spira* (Diesing, 1861) (Acanthocephala: Oligacanthorhynchidae) infecting the peritoneum of painted coral snake, *Micrurus corallinus* (Merrem, 1820) from São Paulo state, Brazil. Further, Dantas-Torres et al. (2010) and de Alcantara et al. (2018) reported the tick, *Amblyomma rotundatum* Koch, 1844 (Arachnida: Ixodida), infecting the skin of Caatinga coral snake, *Micrurus ibiboboca* (Merrem, 1820) and South American coral snake, *Micrurus lemniscatus* (Linnaeus, 1758) from Brazil. Hence, based on the few records of metazoan parasites, and especially trematodes, seemingly a great deal of new species discovery among coral snakes in the Americas is likely.

The aquatic coral snake has evidently rarely been examined for parasites; perhaps because it is elusive and infrequently encountered during field surveys. Various surveys and checklists of South American snake parasites lack a record from an aquatic coral snake: Almeida et al. (2007), Bursey and Brooks (2011), de Luna et al. (2022), Lacerda et al. (2023). A total of 32 coral snake species range in Colombia (Uetz et al., 2024); however, no parasite has been reported from a coral snake there. Aristizábal-Ángel et al. (2022) examined a redtail coral snake, *Micrurus mipartitus* (Duméril, Bibron, and Duméril, 1854) from Gorgona Island, Cauca, Colombia that was not infected. To our knowledge, Aristizábal-Ángel et al. (2022) and the present study are the only published records of any coral snake species being examined for parasites in Colombia.

Table 1
Records of adult digeneans infecting coral snakes (Serpentes: Elapidae: *Micrurus* spp.).

Digenean	Host	Locality	Reference
Haplometroides buccicola Odhner, 1910 (Plagiorchiidae)	painted coral snake, *Micrurus corallinus* (Merrem, 1820)	Botucatu, São Paulo, Brazil	Santos et al. (2008)
		Misiones, Argentina	Lunaschi and Drago (2010)
	short-tailed coral snake, *Micrurus frontalis* (Duméril, Bibron, and Duméril, 1854)	Misiones, Argentina	Poumarau (1968)
Haplometroides odhneri Ruiz and Perez, 1959 (Plagiorchiidae)	short-tailed coral snake	Botucatu, São Paulo, Brazil	Silva and Barrella (2002)
	South American coral snake, *Micrurus lemniscatus* (Lonnaeus, 1758)	Brazil	Ruiz and Perez (1959)
Opisthogonimus lecithonotus Lühe, 1900 (Opisthogonimidae)	Argentinian coral snake, *Micrurus pyrrhocryptus* (Cope, 1862)	Chaco, Argentina	Poumarau (1968)
Styphlodora condita Faria, 1911 (Plagiorchiidae)	aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1817)	Chaco, Argentina	Poumarau (1968)
		Mato Grosso, Brazil	Ávila et al. (2013)
Acanthostomum yahuarcaquense Cajiao-Mora and Bullard n. sp. (Cryptogonimidae)	aquatic coral snake	Yahuarcaca Lake System (Amazon River) Leticia, Amazonas, Colombia	Present study

We herein describe a new species of *Acanthostomum* Looss, 1899 (Digenea: Cryptogonimidae) infecting an aquatic coral snake from the YLS. We also provide new nucleotide-based phylogenetic information for the genus. The present study is first to report a parasite infecting an aquatic tetrapod in the YLS, documents only the second trematode known to mature in the aquatic coral snake, and is the first record of a parasite infecting a coral snake in Colombia.

2. Materials and methods

2.1. Specimen collection, preparation, and deposition

An adult male aquatic coral snake (102.3 cm total length, 89.5 cm snout–vent length, 12.8 cm tail length; Fig. 1) was collected by the authors from within the flooded rainforest habitat (4°11′36.7"S, 69°57′17"W; 70 m above sea level) of the YLS on April 23, 2023. We examined the intestinal mucosa using a Zeiss Stemi 305 stereo-dissecting microscope (Carl Zeiss Microscopy, White Plaines, NY). After necropsy, the snake specimen was deposited in the reptile collection at the Sinchi Institute under accession number SINCHI-R-4083. Fifteen trematode specimens were collected. Ten live trematode specimens intended for morphology were heat-killed and fixed in 10 % neutral buffered formalin (n.b.f.). Five specimens were preserved in 95 % non-denatured ethanol (EtOH) for DNA extraction. Seven fixed specimens were stained and mounted following Cajiao-Mora et al. (2024b). Three specimens were drawn using an Olympus BX51 compound microscope (Olympus, Tokyo, Japan) equipped with differential interference contrast optical components and a drawing tube (Figs. 2–4). Measurements and microphotographs were obtained using a Jenotipik Gryphax camera (Jenotipik AG, Jena, Germany) (Figs. 3 and 4). Measurements are reported in micrometers (μm) unless otherwise stated as the range followed by the mean, standard deviation, and sample size in parentheses. Nomenclature for Cryptogonimidae follows Miller and Cribb (2008) except that the terminology associated with the esophagus follows Truong et al. (2021; esophagus length comprises the esophagus from the posterior end of the oral sucker to the intestinal bifurcation). The holotype and three paratypes of the new species were deposited in the National Museum of Natural History's Invertebrate Zoology Collection (USNM, Smithsonian Institution, Washington, DC) under accession numbers USNM 1752126, 1752127, 1752128. Additional paratypes were deposited in Animal Parasitological Collection (APC, Agrarian Science Department, Universidad de Antioquia, Medellín, Antioquia, Colombia) under accession numbers 345, 346, 347-PA-FCA-UdeA.

Fig. 1. Adult male aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1876) (Serpentes: Elapidae) (102.3 cm total length, 89.5 cm snout–vent length, 12.8 cm tail length) collected from a site (4°11′36.7"S, 69°57′17"W; 70 m above sea level; floodable forest) at the Yahuarcaca Lake System (Amazon River) Leticia, Amazonas, Colombia. Whole body (voucher SINCHI-R-4083) at the reptile collection of the Instituto Amazónico de Investigaciones Científicas Sinchi (Leticia, Amazonas, Colombia).

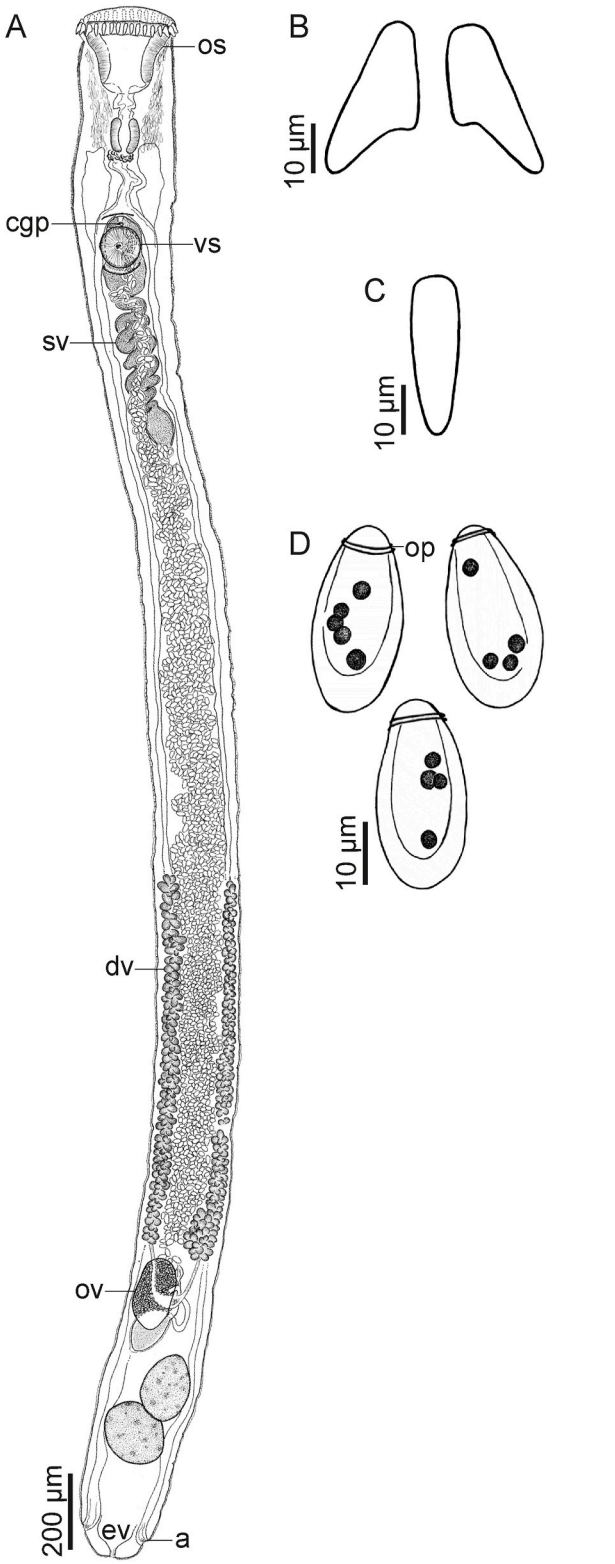

Fig. 2. *Acanthostomum yahuarcaquense* Cajiao-Mora and Bullard n. sp. (Digenea: Cryptogonimidae) (holotype USNM 1752126) infecting the intestine of an aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1876) (Serpentes: Elapidae) from the Yahuarcaca Lake System (Amazon River) Leticia, Amazonas, Colombia. Scale view beside bars. **A.** Whole body ventral view. **B.** Circumoral spines, lateral view. **C.** Circumoral spines, dorsal view. **D.** Eggs. Abbreviations: anal pore (a); common genital pore (cgp); dextral vitellarium (dv); excretory vesicle (ev); operculum (op); oral sucker (os); ovary (ov); seminal vesicle (sv); ventral sucker (vs.).

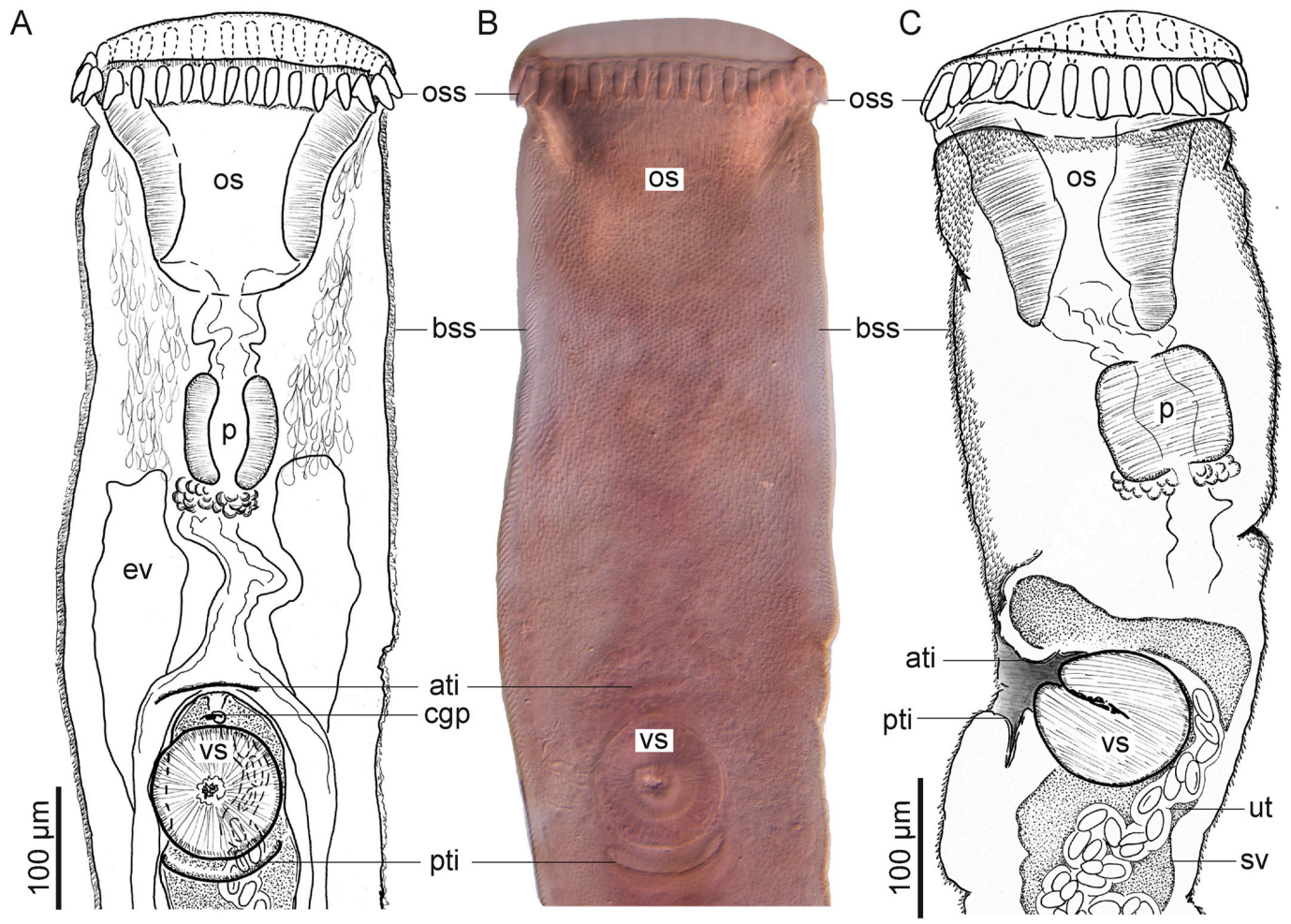

Fig. 3. *Acanthostomum yahuarcaquense* Cajiao-Mora and Bullard n. sp. (Digenea: Cryptogonimidae) infecting the intestine of an aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1876) (Serpentes: Elapidae) from the Yahuarcaca Lake System (Amazon River) Leticia, Amazonas, Colombia. Scale view beside bars. **A.** Holotype USNM 1752126, anterior end, ventral view. **B.** Holotype USNM 1752126, microphotography of anterior end, ventral view. **C.** Paratype 345-PA-FCA-UdeA, anterior end, lateral view. Abbreviations: anterior tegumental infolding (ati); body surface spines (bss); excretory vesicle (ev); oral sucker (os); oral sucker spines (oss); pharynx (p); posterior tegumental infolding (pti); seminal vesicle (sv); uterus (ut); ventral sucker (vs.).

2.2. DNA extraction

One EtOH-preserved specimen was used for DNA extraction and sequencing. Extraction was performed using the DNeasy™ Blood and Tissue kit (Qiagen) following the manufacturer's protocol, except that the proteinase-K incubation period was extended overnight. Once extracted, DNA concentration was measured using a NanoDrop-One Microvolume Spectrophotometer (Thermo Fisher Scientific), diluted to 50 ng/µL, and stored at −20 °C. Segments of the *28S* and *ITS2* genes were amplified using primers outlined in Cajiao-Mora et al. (2024a). PCR reactions were performed following Truong et al. (2021). DNA amplification was verified with a 1 % agarose gel stained with ethidium bromide. PCR products were purified using the QIAquick PCR Purification Kit (Qiagen) according to the manufacturer's protocol, except that the last elution step was performed with autoclaved nanopure water. DNA sequencing was performed by Genewiz (South Plainfield, New Jersey). Sequence assembly and analysis of chromatograms were performed with Geneious prime version 2023.2.1. Forward and reverse sequences were aligned using MAFFT tool (Katoh and Standley, 2013) and low-quality read-ends were trimmed resulting in sequences of 1624 base pairs (bp) of the *28S* gene and 404 bp of the *ITS2*. All sequence data were deposited in GenBank under accession numbers PV210949, PV210950 (*28S*), PV210951 (*ITS2*).

2.3. Phylogenetic analysis

We performed a maximum likelihood (ML) analysis using *28S* and *ITS2* sequences. However, the *ITS2* phylogeny did not show enough resolution, perhaps because of low taxon sampling, and therefore is not shown herein. The ingroup taxa of the *28S* analysis comprised our newly generated sequences and those ascribed to Cryptogonimidae following Kmentová et al. (2020) and Yong et al. (2023) but excluding those sequences shorter than 1000 bp. The *Acanthostomum* and *Caimanicola* Teixeira de Freitas and Lent, 1938 sequences in Martínez-Aquino et al. (2017) and Palumbo et al. (2024) were not used in the present phylogenetic analysis due to their short length (<900 bp). The outgroup follows Yong et al. (2023). Sequences were aligned using the multiple alignment using fast Fourier transform (MAFFT) tool (Katoh and Standley, 2013), and the alignment was trimmed to the shortest sequence. The phylogeny was inferred using IQTREE v.1.16.12 (Nguyen et al., 2015). Substitution model testing was done with ModelFinder (Kalyaanamoorthy et al., 2017) as implemented in IQTREE. After model testing, tree inference was done using best-fitting substitution models (Chernomor et al., 2016). Default tree search parameters were used, except perturbation strength was set to 0.2 and 500 iterations had to be unsuccessful to stop the tree search. Tree inference was done 20 times with only the tree with the best log-likelihood score reported. Support for relationships was measured with 1000 ultrafast bootstrap replicates

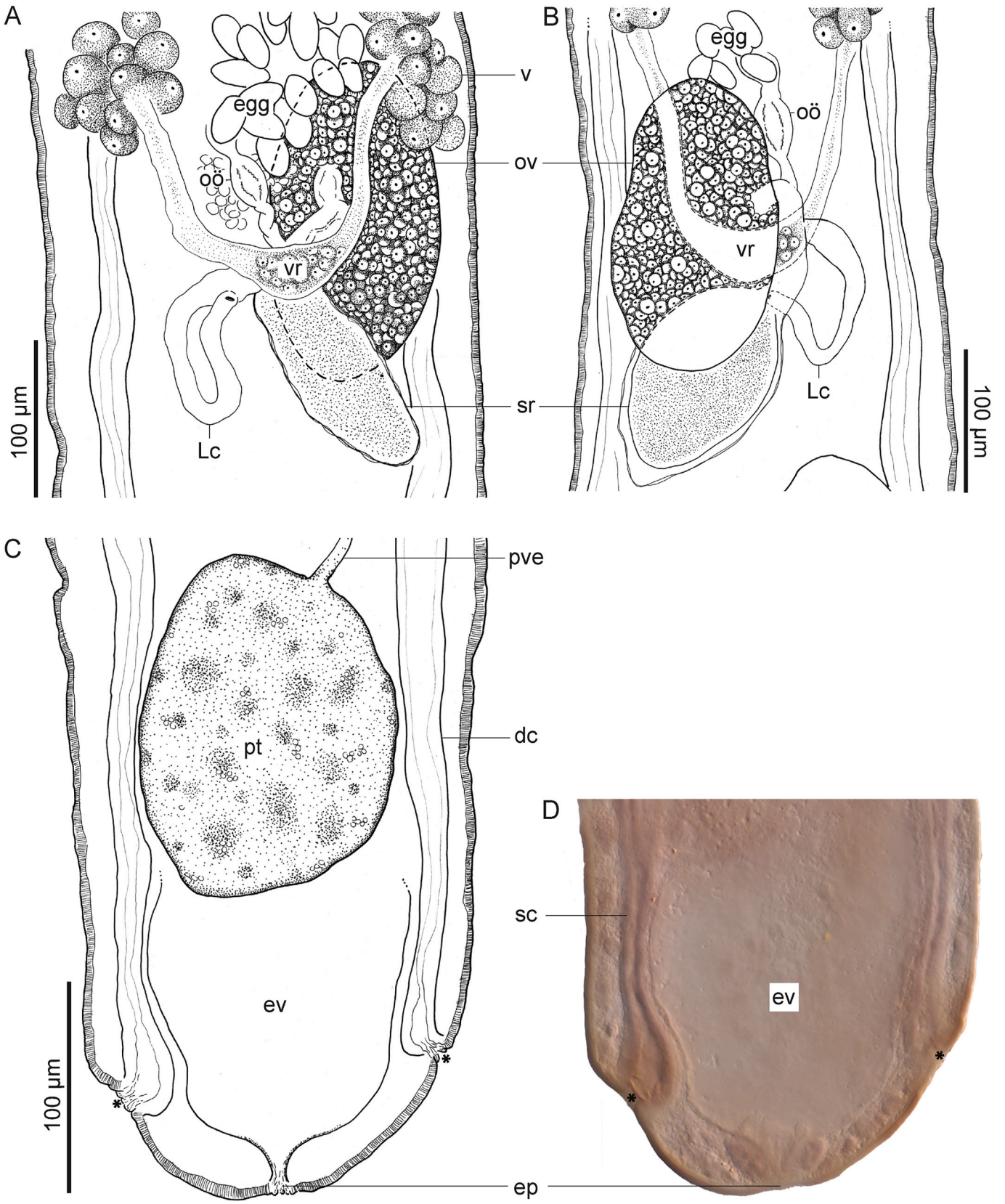

Fig. 4. *Acanthostomum yahuarcaquense* Cajiao-Mora and Bullard n. sp. (Digenea: Cryptogonimidae) infecting the intestine of an aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1876) (Serpentes: Elapidae) from the Yahuarcaca Lake System (Amazon River) Leticia, Amazonas, Colombia. Scale view beside bars. **A.** Paratype USNM 1752127, female genitalia, dorsal view. **B.** Holotype USNM 1752126, female genitalia, ventral view. **C.** Paratype USNM 1752127, posterior end, dorsal view. **D.** Paratype USNM 1752127, microphotography of posterior end, dorsal view. Abbreviations: anal pores (*); dextral cecum (dc); eggs (egg); excretory pore (ep); excretory vesicle (ev); Laurer's cannal (Lc); oötype (oö); ovary (ov); posterior testis (pt); posterior vas efferent (pve); seminal receptacle (sr); sinistral cecum (sc); vitellarium (v); vitelline reservoir (vr).

(UFBoot) (Hoang et al., 2018). The inferred phylogenetic tree was visualized using FigTree v1.4.4 (Rambaut et al., 2018) and further edited for visualization purposes with Adobe Illustrator (Adobe Systems) (Fig. 5).

3. Results

3.1. Taxonomic summary

***Acanthostomum yahuarcaquense* Cajiao-Mora and Bullard n. sp.** (Figs. 2–4)

Type host: Aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1817) (Serpentes: Elapidae).

Type locality: Yahuarcaca Lake System (4°11′36.7"S, 69°57′17"W), Amazon River (Leticia, Amazonas, Colombia).

Site of infection: Intestine.

Prevalence and intensity: 1 of 1 *M. surinamensis* was infected with 15 adult specimens of *A. yahuarcaquense* n. sp.

Type specimens: Holotype USNM 1752126; paratypes USNM 1752127, USNM 1752128, 345-PA-FCA-UdeA, 346-PA-FCA-Udea, 347-PA-FCA-UdeA.

ZooBank registration: urn:lsid:zoobank.org:act: A3EAD0FB-F40E-4762-886E-44C5940F4A24.

Representative DNA sequences: *28S* GenBank accession No. PV210949, PV210950; *ITS2* GenBank accession No. PV210951.

Etimology: The specific epithet "*yahuarcaquense*" refers to the collection site, the Yahuarcaca Lake System.

3.1.1. Description

Based on 7 heat-killed, stained, and permanently whole-mounted adults: Body elongate, rounded posterior end, 3.1–4.0 mm (3.4 mm ± 0.56 mm; 3) total length, 256–278 (264 ± 12; 3) maximum width at level of pharynx, 12–15 × (13 ± 2; 3) longer than wide, 246–269 (257 ± 11; 3) width at level of intestinal bifurcation, 178–224 (207 ± 26; 3) width at level of ovary, 152–253 (204 ± 51; 3) width at level of anterior testis, 92–157 (133 ± 36; 3) width at level of anal pores (Fig. 2A). Forebody 509–589 (552 ± 40; 3) long, or 14–18 % (16 % ± 2 %; 3) of total body length (Fig. 2A). Hindbody 2.4–3.4 mm (2.8 mm ± 0.55 mm; 3) long, or 79–84 % (81 % ± 3 %; 3) of total body length (Fig. 2A). Tegument thick, containing body surface spines and 2 tegumental infoldings ("pits") (Fig. 2A and 3A–C); tegumental infoldings anterior and posterior to ventral sucker (Fig. 3A–C); body surface spines densely arranged in forebody, becoming smaller and fewer posteriad, extending to near posterior end of body, 10 (10 ± 0; 3) long at level of pharynx, 6–8 (7 ± 1; 3) long at level of ventral sucker, 4–5 (4 ± 1; 3) long at level of anterior end of vitellarium, becoming minute posterior to vitellarium. Ventral sucker spherical, in first quarter of body (Fig. 2A), protractile (Figs. 3C), 106–119 (110 ± 8; 3) long, 106–121 (113 ± 8; 3) wide.

Oral sucker terminal, funnel shaped, 205–257 (226 ± 27; 3) long, 208–244 (228 ± 19; 3) maximum width, 136–144 (140 ± 4; 3) base width, having circumoral spines; oral sucker spines forming a collar-like structure (Fig. 2A and 3A–C), 24 (n = 1), 27 (n = 5), or 30 (n = 1; holotype) in number; triangular with blunt corners in lateral view, having the ventral-most side slightly concave (Fig. 2B); bullet shaped in ventral view, tapering posteriad (Figs. 2C), 33–40 (36 ± 2; 6) length in ventral view, 9–12 (10 ± 1; 6) proximal width in ventral view, 4–6 (5 ± 1; 6) distal width in ventral view. Esophagus medial, 305–308 (307 ± 2; 2) total length, or 8–10 % (9 % ± 2 %; 2) of total body length, 48 (n = 1) maximum width, extending from posterior margin of oral sucker to anterior tegumental infolding, comprising pre-pharyngeal and post-pharyngeal parts (Fig. 2A, 3A and 3C). Pre-pharyngeal esophagus sinuous, thick walled, 52–78 (65 ± 18; 2) long or 17–25 % (21 % ± 6 %; 2) of total esophagus length. Pharynx quadrate, with blunt corners (Fig. 2A, 3A and 3C), surrounding anterior portion of esophagus, 79–100 (92 ± 11; 3) long or 26–31 % (29 % ± 4 %; 2) of total esophagus length. Post-pharyngeal esophagus slightly sinuous, thick walled, surrounded anteriorly by clusters of glandular cells (Fig. 2A, 3A and 3C), 120–168 (142 ± 24; 3) long or 45–55 % (50 % ± 7 %; 2) of esophagus total length. Intestinal bifurcation at level of anterior tegumental infolding, anterior to common genital pore and ventral sucker (Figs. 3A), 470–532 (507 ± 33; 3) from anterior body end or 13–17 % (15 % ± 2 %; 3) of body length. Ceca slender, extending posteriad parallel to lateral body margins, 2.4–3.4 mm (2.8 mm ± 535 mm; 3) long or 79–84 % (82 % ± 3 %; 3) of body length, equal in width (sinistral cecum 4 × wider than dextral cecum in 1 specimen), having posterolateral anal pores at posterior body end, flanking excretory pore (Fig. 2A and 4C–D).

Testes 2, in last quarter of body, post-ovarian, rounded or ovoid in outline (Fig. 4C), tandem and separated or oblique and contiguous, in midline of body (Fig. 2A); anterior testis 114–179 (139 ± 35; 3) long, 81–126 (105 ± 23; 3) wide; posterior testis 118–181 (153 ± 32; 3) long, 85–143 (115 ± 29; 3) wide; pre-testicular space 2.7–3.5 mm (3 mm ± 0.5 mm; 3) or 86–91 % (88 % ± 3 %; 3) of total body length; post-testicular space 101–244 (162 ± 74; 3) or 3–6 % (5 % ± 1 %; 3) of total body length. Vasa efferentia only visible emerging from testes (Fig. 4C), obscured by dense mass of eggs through its length. Seminal vesicle long, occupying 106–119 (110 ± 8; 2) or 15–19 % (17 % ± 2 %; 2) of total body length, extending from anterior tegumental infolding to end of first quarter of body far posterior to ventral sucker (Fig. 2A), having convoluted proximal portion (Fig. 2A), having distal portion straight, enlarged, sac-like (Fig. 2A, 3A and 3C). Prostatic duct and cirrus not observed. Lacking a gonotyl. Genital pore median, immediately anterior to ventral sucker, in anterior tegumental infolding (Fig. 2A, 3A and 3C).

Ovary oblong, 137–182 (161 ± 23; 3) long, 74–96 (86 ± 11; 3) wide, ventral, dextral, in posterior quarter of body (Fig. 1A and 3A–B); pre-ovarian space 2.4–3.3 mm (2.8 mm ± 0.4 mm; 3) or 78–86 % (82 % ± 4 %; 3) of total body length; post-ovarian space 357–608 (501 ± 130; 3) or 12–17 % (15 % ± 3 %; 3) of total body length. Oviduct emerging dorsally from ovary (Fig. 4A). Oviducal seminal receptacle oblong, thick-walled, 96–134 (115 ± 27; 2) long, 51–86 (68 ± 25; 2) wide, postero-dorsal to ovary (Fig. 4A and B); oviducal seminal receptacle wall 6–8 (7 ± 1; 2) thick. Laurer's canal elongate, sinistral, extending posteriad then curving anteriad, opening on dorsal body surface (Fig. 4A and B). Oötype ovoid in outline, sinistro-dorsal to ovary (Fig. 4A and B), 27–42 (33 ± 8; 3) long, 19–20 (20 ± 1; 3) wide, continued by uterus. Mehlis' gland indistinct. Uterus coiling anteriorly between ceca, extending from oötype to common genital pore, having a highly convoluted proximal portion, having a sinuous to straight distal portion (Figs. 2A and 3C), having numerous eggs (Fig. 2A), extending 1.9–2.7 mm (2.2 mm ± 0.4 mm; 3) or 63–68 % (66 % ± 3 %; 3) of total body length; distal portion ventral to seminal vesicle; metraterm indistinct. Eggs ovoid, operculate (Figs. 2D), 5–26 (26 ± 1; 3) long, 13–14 (14 ± 1; 3) wide. Vitellarium follicular, distributing in 2 bilaterally symmetrical fields, post-equatorial, extending from anterior margin of ovary to a point midway third quarter of body, enveloping ceca (Figs. 2A), 380–992 (674 ± 307; 3) long, or 12–24 % (19 % ± 6 %; 3) of total body length; pre-vitellarium space 1.8–2.3 mm (2.1 mm ± 0.2 mm; 3) or 56–74 % (63 % ± 10 %; 3) of total body length; post-vitellarium space 480–814 (650 ± 167; 3) or 16–21 % (19 % ± 3 %; 3) of total body length. Vitelline ducts emanating from posterior end of vitellarium, extending posteriad, 100–147 (123 ± 34; 2) long, 9 (9 ± 0; 2) wide, forming a vitelline reservoir (Fig. 2A and 4A–B); vitelline reservoir dorsal to ovary and oviduct, connecting with oviduct (Fig. 4A and B).

Excretory vesicle Y-shaped, extending from posterior body end to posterior margin of pharynx (Fig. 2A, 3A and 4C), point of bifurcation not observed; excretory pore terminal (Fig. 4C and D) surrounded by gland cells (Fig. 4D).

3.1.2. Taxonomic remarks

The new species is assigned to *Acanthostomum* (see Table 2 for species list) because it has an elongate body (body length: width 1:12–13), spinose tegument (Fig. 3B), funnel-shaped and terminal oral sucker with

Table 2
Acanthostomum spp. with associated type host, type locality, and museum type series.

Acanthostomum spp.	Type host	Type locality	Type series	Reference
Acanthostomum spiniceps (Looss, 1896) Looss, 1899 (type)	bayad, *Bagrus bajad* (Fabricius, 1775) (Siluriformes: Bagridae)	Nile River, Cairo, Egypt	–	Looss (1896, 1899)
Acanthostomum burminis (Bhalerao, 1926) Bhalerao, 1936	asiatic water snake, *Fowlea piscator* (Schneider, 1799) (Serpentes: Colubridae)	Kamayut, Myanmar	–	Bhalerao (1926, 1936)
Acanthostomum floridense (McCoy, 1928) Price, 1940	Unknown	Florida, US	–	McCoy (1929)
Acanthostomum minimum Stunkard, 1938	pale catfish, *Rhamdia guatemalensis* (Günther, 1864) (Siluriformes: Heptapteridae)	Yucatan, Mexico	AMNH 268, holotype; AMNH 852, paratype	Stunkard (1938)
Acanthostomum indicum Sinha, 1942	"crocodile"	Tehri River, India	–	Sinha (1942)
Acanthostomum absconditum (Looss, 1901) Poche, 1926	semutundu, *Bagrus docmak* (Fabricius, 1775) (Siluriformes: Bagridae)	Cairo, Egypt	–	Looss (1901); Moravec (1976); Brooks (1980)
Acanthostomum simhai Khalil, 1963	asiatic water snake	Hyderabad, India	Museum of the Zoology Department, Osmania University, Hyderabad, India	Simha (1958; as *Athropocaecum indicum*); Khalil (1963)
Acanthostomum acuti Caballero y Caballero and Brenes-Madrigal, 1958	American crocodile, *Crocodylus acutus* Cuvier, 1807 (Crocodilia: Crocodylidae)	Los Chiles de Grecia, Costa Rica	Universidad Nacional Autónoma de México, "Caballero Collection" No. 216–6, holotype	Caballero y Caballero and Brenes-Madrigal (1958); Brooks (1980)
Acanthostomum marinum (Coil and Kuntz, 1960)	Chinese seasnake, *Laticauda semifasciata* (Reinwardt, 1837) (Serpentes: Elapidae)	Orchid (Lan Yü) Island, Taiwan	USNM 1339867, holotype	Coil and Kuntz (1960)
Acanthostomum cerberi (Fischthal and Kuntz, 1965)	South Asian bockadam, *Cerberus rynchops* (Schneider, 1799) (Serpentes: Homalopsidae)	Ranau, North Borneo, Malaysia	USNM 1356677, holotype; USNM 1363679, syntype	Fischthal and Kuntz (1965)
Acanthostomum proctophorum (Dwivedi, 1966) Yamaguti, 1971	asiatic water snake	India	–	Dwivedi (1966)
Acanthostomum cherysdrusi (Chattopadhyaya, 1970)	little filesnake, *Acrochordus granulatus* (Schneider, 1799) (Serpentes: Achrocoridae)	Arabian sea, Mumbai coast, India	–	Chattopadhyaya (1970)
Acanthostomum madanmohani (Chattopadhyaya, 1970)	common sea snake, *Hydrophis schistosus* Daudin, 1803 (Serpentes: Elapidae)	Arabian sea, Mumbai coast, India	–	Chattopadhyaya (1970)
Acanthostomum astorquii Watson, 1976	Nicaraguan catfish. *Rhamdia nicaraguensis* (Günther, 1864) (Siluriformes: Heptapteridae)	Fish market, Granada, Nicaragua	USNM 1357053, holotype	Watson (1976)
Acanthostomum slusarskii Kalyankar, 1977	mugger crocodile, *Crocodylus palustris* Lesson, 1831	Nanded, Maharashtra, India	–	Kalyankar (1977)
Acanthostomum lobacetabulare (Brooks and Caira, 1982)	common sea snake	Penang, Malaysia	USNM 1372659, holotype; USNM 1372660–62, paratypes	Brooks and Caira (1982)
Acanthostomum saoudi Hassan, Khidr and Abu Samak, 1990	European seabass, *Dicentrarchus labrax* (Linnaeus, 1758) (Teleostei: Moronidae)	Mediterranean Sea, Egypt	Helminthological collection, Department of Zoology, University of Ain Shams, Egypt	Hassan et al. (1990)
Acanthostomum americanum (Pérez-Vigueras, 1956) Herber, 1961	American crocodile	Ciénaga de Zapata, Matanzas, Cuba	–	Pérez-Vigueras (1956); Brooks (1980); Moravec (2001)
Acanthostomum gnerii Szidat, 1954	South American catfish, *Rhamdia quelen* (Quoy and Gaimard, 1824) (Siluriformes: Heptapteridae)	Rio Paraná, Rosario, Argentina	–	Szidat (1954)
Acanthostomum megacetabulum Thatcher, 1963	Texas indigo snake, *Drymarchon melanurus* (Duméril, Bibron and Duméril, 1854) (Serpentes: Colubridae)	Tabasco, Mexico	USNM 1356083, holotype; Paratypes in CNHE and Dept. of Zoology, LSU	Thatcher (1963)
Acanthostomum yahuarcaquense Cajiao-Mora and Bullard n. sp.	aquatic coral snake, *Micrurus surinamensis* (Cuvier, 1817) (Serpentes: Elapidae)	Yahuarcaca Lake System (Amazon River), Leticia, Amazonas, Colombia.	USNM 1752126 holotype; USNM 1752127, 1752128 paratypes; 345, 346, 347-PA-FCA-UdeA, paratypes	Present study

Abbreviations: American Museum of Natural History, Division of Invertebrate Zoology, New York, US (AMNH); Animal Parasitological Collection, Agrarian Science Department, Universidad de Antioquia, Medellín, Antioquia, Colombia (PA-FCA-UdeA); Colección Nacional de Helmintos del Instituto de Biología, México D.F. (CNHE); Louisiana State University (LSU); Natural History Museum, London, UK (NHMUK); Smithsonian National Museum of Natural History, Washington DC (USNM).

circumoral spines (Fig. 3A–C), anal pores located near the posterior body end (Fig. 4C and D), and excretory vesicle arms that reach anteriad to the level of the pharynx (Fig. 2A and 3A). The new species differs from its 19 accepted congeners by having 24–30 circumoral spines (vs. fewer than 20 or aspinose), a vitellarium extending from the anterior margin of the ovary to the posterior half of the body (vs. from testis or ovary but ending in anterior half of body), and paired elongate, symmetrical ceca each having an anal pore (vs. asymmetrical ceca, a single cecum, or lacking anal pores).

Our specimens most closely resemble the type species of *Acanthostomum*, *Acanthostomum spiniceps* (Looss, 1896) Looss, 1899, *Acanthostomum absconditum* (Looss, 1901) Poche, 1926, *Acanthostomum acuti* Caballero y Caballero and Brenes-Madrigal, 1958, and *Acanthostomum slusarskii* Kalyankar (1977). Like the new species, each of these congeners has an elongate body, spinose tegument, funnel-shaped and terminal oral sucker with circumoral spines, testes and ovary in the

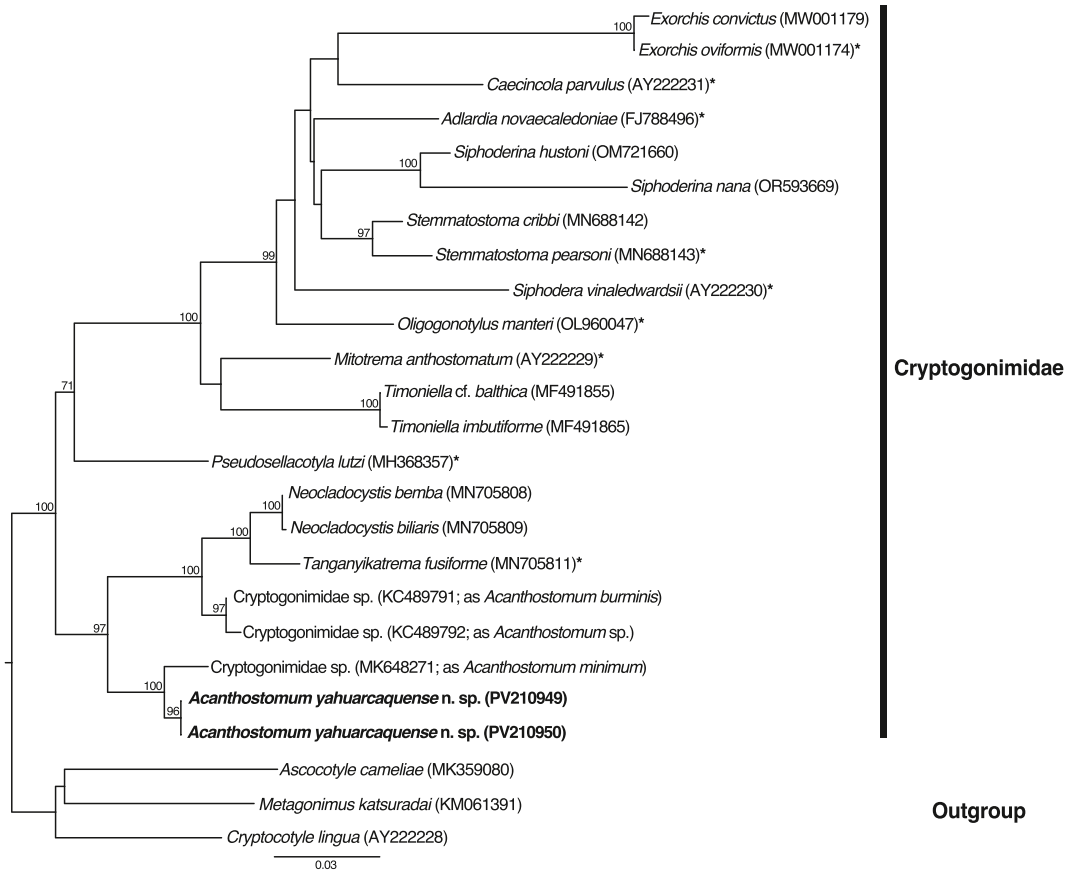

Fig. 5. *28S* maximum likelihood phylogenetic analysis inferred tree. Values aside nodes are bootstrap percentage. Only bootstrap percentage >70 are shown. Scalebar is in substitutions per site. GenBank accession numbers are in parenthesis following each taxon. Type species are indicated by asterisk (*). The newly generated sequences of *Acanthostomum yahuarcaquense* Cajiao-Mora and Bullard n. sp. (Digenea: Cryptogonimidae) are bolded.

posterior quarter of the body, and anal pores located at the posterior body end. The new species differs from these species by the combination of having a vitellarium that extends from the anterior margin of the ovary posteriad to the middle of the third quarter of body (posterior half of body) (Fig. 1A) (occupying 12–24 % [19 % ± 6 %; 3] of the total body length). This contrasts with congeners that have a vitellarium extending more anteriad (middle of the body or anterior half of body) to the ovary (*A. acuti*, *A. slusarskii*) or anterior testis (*A. absconditum*, *A. spiniceps*) (occupying >50 % of total body length in *A. slusarskii*) (Fig. 1 in Kalyankar, 1977). The new species further differs from *A. spiniceps* and *A. slusarskii* by having a relatively short body that is 3.1–4.0 mm (3.4 mm ± 0.56 mm; 3) vs. 7 mm (*A. spiniceps*) and 8.5 mm (*A. slusarskii*; Fig. 1 in Kalyankar, 1977). The new species differs from *A. absconditum* and *A. slusarskii* by having 24–30 circumoral spines (vs. 19 in *A. absconditum*, 18–19 in *A. slusarskii*) and by having large spines approximately 33–40 (36 ± 2; 6) long (vs. 100 in *A. spiniceps* and reportedly 54–63 in *A. absconditum*). The new species differs from *A. acuti* by having a forebody:hindbody ratio of 1:6 (vs. 1:2.2; see Figs. 4 and 5 in Caballero y Caballero and Brenes-Madrigal, 1958) and by having an intestinal bifurcation immediately anterior to the genital pore (Fig. 3A) (vs. more anterior, immediately posterior to the pharynx (see Figs. 4–5 in Caballero y Caballero and Brenes-Madrigal, 1958).

Acanthostomum yahuarcaquense differs from *Acanthostomum marinum* (Coil and Kuntz, 1960), *Acanthostomum cerberi* (Fischthal and Kuntz, 1965), *Acanthosomum madanmohani* (Chattopadhyaya, 1971), and *Acanthostomum cherysdrusi* (Chattopadhyaya, 1971) by having a terminal, funnel-shaped oral sucker with circumoral spines (Fig. 3A–C) and a vitellarium that extends from the anterior margin of the ovary posteriad to the middle of third quarter of the body (Fig. 2A) vs. oral sucker ovoid, sub-terminal, aspinose (*A. marinum, A. cerberi, A. madanmohani*) and vitellarium reaching seminal vesicle in *A. cerberi*, *A. madanmohani* and *A. cherysdrusi* (see Coil and Kuntz, 1960; Fischthal and Kuntz, 1965; Chattopadhyaya, 1971).

Acanthostomum yahuarcaquense differs from *Acanthostomum burminis* (Bhalerao, 1926) Bhalerao, 1936, *Acanthostomum indicum* Sinha, 1942, and *Acanthostomum saoudi* Hassan, Khidr, and Abu-Samak, 1990 by having anal pores (Fig. 4C and D) (vs. lacking anal pores). It further differs from *A. saoudi* by having an entirely pre-ovarian uterus (Fig. 2A) (vs. uterus reaching posterior body end) and operculate eggs (Fig. 2D) (vs. non-operculate eggs). However, *A. burminis* needs redescription because Bhalerao (1926, 1936, 1940) reassigned it from *Acanthoschasmus* to *Acanthostomum* and then to *Athropocaecum* (as type species) before ultimately reassigning it to *Acanthostomum* again. Within that range of publications, Bhalerao has stated that *A. burminis* has both blind ending symmetrical ceca (Bhalerao, 1926, 1936) and asymmetrical ceca with anal pores (Bhalerao, 1940). Additional records of *A. burminis* are based on cercariae and metacercariae from Sri Lanka and India, respectively (Jayawardena et al., 2017; Jithila and Prasadan, 2022). The experimental life cycle of *A. burminis* was described by Roopa and Janardanan (1998). Two additional trematode species infect Asiatic water snake, i.e. *Acanthostomum simhai* Khalil, 1963 (as *Athropecaecum indicum* Simha, 1958) and *Acanthostomum proctophorum* (Dwivedi, 1966) Yamaguti, 1971. Because several congeners reportedly infect the same snake species, workers should be careful to morphologically identify all specimens and select a molecular voucher. Also important is that resulting specimens should be compared to existing types of

nominal congeners whenever possible.

Acanthostomum simhai, *Acanthostomum astorquii* Watson, 1976, and *Acanthostomum lobacetabulare* (Brooks and Caira, 1982), reportedly have anal pores and asymmetrical ceca. One of our 7 specimens had the sinistral cecum 4 × wider than the dextral cecum, whereas all remaining specimens had symmetrical (equal in total length and width) ceca. The descriptions of *A. astorquii*, *A. simhai*, and *A. lobacetabulare* were based on 3, an undefined number of specimens collected during various seasons, and 34 specimens, respectively (Watson, 1976; Simha, 1958; Brooks and Caira, 1982). The new species can be further differentiated from *A. astorquii* by having an elongate body (vs. ovoid), a pre-pharyngeal and post-pharyngeal esophagus (vs. lacking them), and 24–30 (vs. 20) circumoral spines. It differs from *A. simhai* by the extent of the vitellarium (see above) and from *A. simhai* and *A. lobacetabulare* by having anal pores located near the posterior body end (vs. having one anal pore at level of the anterior margin of the posterior testis and another anal pore at level of the seminal receptacle) (see Figs. 1–4 in Brooks and Caira, 1982). The new species differs from *A. proctophorum*, by having two ceca each with an anal pore (vs. having a single cecum with an anal pore).

Acanthostomum asymmetricum (Simha, 1958) Khalil, 1963 was described infecting Malayan green whipsnake, *Ahaetulla mycterizans* (Serpentes: Colubridae) from India. It was originally designated as the type species for *Haplocaecum* Simha, 1958 because it had a single blind-ending cecum. Simha (1958; p 188) mentioned that the ventral sucker is sinistral (not medial). The drawing (see Fig. 15 in Simha, 1958) is based on a rolled specimen that came to rest in lateral view. Rather than having a single cecum and sinistral ventral sucker, we suspect that the oral sucker is simply viewed from a lateral perspective and that paired ceca are aligned such that one obstructs the view of the other in lateral view. The figure legend is erroneous in stating that the specimen is in dorsal view. The types for this species are reportedly housed in the Museum of the Zoology Department, Osmania University, Hyderabad, India. As is the case with all other type materials curated in museums in India, we have no hope of ever borrowing this specimen. Therefore, because the description is erroneous and we cannot borrow the types, we consider *A. asymmtericum* a *species inquirenda* until someone re-collects and redescribes it from the type host and locality and/or until types are restudied.

A marine species, *Acanthostomum floridense* (McCoy, 1928) Price, 1940, was described based upon cercariae shed from the sea snail, *Cerithium litteratum* (Born, 1778) (Gastropoda: Cerithiidae) and metacercaria from experimentally infected small reef fishes from Tortugas, Florida, United States (see p 31 in McCoy, 1929 for a list of the infected fishes). The metacercaria developed 27 circumoral spines. To our knowledge, no description of the adult has been provided. *Acanthostomum minimum* Stunkard, 1938 was described infecting the pale catfish, *Rhamdia guatemalensis* (Günther, 1864) (Siluriformes: Bagridae) from Yucatan, Mexico. The description was based on 1 highly contracted specimen (see Fig. 2 in Stunkard, 1938) and another specimen that was serially sectioned. Stunkard (1938) reported that this species had 18–20 circumoral spines, differentiating it from *A. yahuarcaquense* with 24–30 spines.

3.2. Phylogenetic results

Our *28S* and *ITS2* sequences representing *A. yahuarcaquense* comprised 1624 bp and 404 bp, respectively (GenBank accession Nos. PV210949, PV210950 [*28S*]; PV210951 [*ITS2*]). Both sequences were similar to corresponding sequences from *Caimanicola brauni* (Mañé-Garzón and Gil, 1961) Brooks, 1980 (GenBank accession No. OR137955, 950 bp [28S]; GenBank accession No. OR135713, 389 bp [*ITS2*]) infecting a Hilaire's side-necked turtle, *Phrynops hilarii* (Dumeril and Birbon, 1835) (Testudines: Chelidae) from Argentina (Palumbo et al., 2024). The *28S* sequence of *C. brauni* is short (950 bp) but was identical to our aligned sequence of the new species (100 % similarity, 57 % sequence coverage). The *ITS2* sequence of *C. brauni* differed from that of the new species by 6 bp (98.5 % similarity, 96 % sequence coverage). The sequence representing *Caimanicola brauni* (OR137955; Palumbo et al., 2024) is unaccompanied by a morphological diagnosis but a voucher (MLP-He 8084) was deposited in the Museo of La Plata, Argentina; which cannot currently loan specimens internationally. *Acanthostomum yahuarcaquense* differs from *C. brauni* as described by Mañé-Garzón and Gil (1961; as *A. brauni*) by having a short (3.1–4.0 mm vs. 4.13–5.22 mm) and narrow (256–278 vs. 450–470) body; a small oral sucker (205–257 long, 208–244 wide vs. 310–390 long, 330–430 wide), more numerous circumoral spines (24–30 vs. 23–24); a smaller pharynx (79–100 long, 81–89 wide vs. 183 long, 144 wide); a post-pharyngeal esophagus (vs. lacking); an intestinal bifurcation immediately anteriad to the genital pore (Fig. 2A; vs. being immediately after the pharynx); a long forebody (14–18 % of total body length vs. 3.12 % of total body length); and a vitellarium extending from the ovary to the middle of the posterior quarter of the body (far posterior to seminal vesicle; Fig. 2A; vs. reaching seminal vesicle). Apparently, *C. brauni* does not have tegumental infoldings anterior or posterior to the ventral sucker. Mañé-Garzón and Gil (1961) described the tegumental spines of *C. brauni* as "robust", however, they did not provide measurements.

Similar to that of Martínez-Aquino et al. (2017), our *28S* analysis (Fig. 5) recovered a paraphyletic *Acanthostomum* with our sequence of *A. yahuarcaquense* sister to that of *A. minimum* (GenBank accession no. MK648271). That clade was recovered sister to a clade comprising *Acanthostomum* sp. (KC489792), *A. burminis* (KC489791), *Tanganyikatrema fusiforme* Kmentová, Georgieva and Bray, 2020 (MN705811), *Neocladocystis biliaris* Kmentová, Georgieva and Bray, 2020 (MN705809), and *Neocladocystis bemba* Kmentová, Georgieva and Bray, 2020 (MN705808). The sequences identified as *Acanthostomum* sp. (derived from cercariae shed from *Mieniplotia scabra* [Müller, 1774] [Gastropoda: Thiatidae; as *Thiara scabra*] from Sri Lanka) and *A. burminis* (derived from an adult infecting an Asiatic coral snake from Thailand) are nonugens because they are unaccompanied by a morphological diagnosis or museum-curated voucher (Jayawardena et al., 2013; Roberts et al., 2018). Hence, the identity of these sequences cannot be confirmed without collecting them again. Until then, we provisionally identify those sequences as "Cryptogonimidae sp." because we have no means of knowing what species they represent. Further casting doubt on the identity of these sequences is that three species of *Acanthostomum* infect the Asiatic water snake (*A. burminis*, *A. simhai*, *A. proctophorum*). Moreover, the phylogenetic position of KC489791 ("*A. burminis*") and the cercarial sequence KC489792 ("*Acanthostomum* sp.") suggest that they do not belong in *Acanthostomum*. Any crytogonimid collected from this host would have to be carefully morphologically diagnosed based on a study of stained whole-mounted specimens and studied using a compound dissecting microscope to identify the specimens (and therefore the sequences) to species level.

4. Discussion

The systematics of Cryptogonimidae (including the Acanthostominae [not accepted in Miller and Cribb, 2008]: *Acanthostomum*; *Proctocaecum* Baugh, 1957; *Caimanicola*; *Gymnatrema* Morozov, 1955; *Timoniella* Rebecq, 1960) has included the synonymy of several genera and species as well as the proposal of several sub-families (Yamaguti, 1971; Nasir, 1974; Moravec, 1976; Brooks, 1980; Brooks and Caira, 1982; Lamothe-Argumedo and Ponciano-Rodriguez, 1986; Brooks and Holcman, 1993; Moravec, 2001; Tkach and Snyder, 2003; Brooks, 2004). Based on our assessment of the cyptogonimid taxonomic literature, we think that oral sucker shape, position, circumoral spines shape and distribution, tegumental spine shape and distribution, ceca shape and symmetry, anal pore presence/absence and position, and gonotyl presence/absence position comprise potentially useful genus-level diagnostic features. Problematic is that these character states are

indeterminate for numerous cryptogonimid taxa. Below we provide several specific examples.

Ceca size and shape, symmetry, and presence/absence of anal pores effectively differentiate *Acanthostomum* spp. *Acanthostomum burminis*, *A. astorquii*, *A. simhai*, and *A. lobacetabulare* have asymmetrical ceca, which is a diagnostic feature of *Atrophecaecum* Bhalerao, 1940 (*Atrophecaecum* lacks a gonotyl and has anal pores and a funnel-shaped oral sucker with circumoral spines). However, 1 of our 7 specimens had an asymmetrical cecum. Hence, numerous specimens should be studied before deciding if ceca symmetry is a reliable feature. Furthermore, the nonugen KC489791 ("*A. burminis*") was recovered sister to our new species. Of particular interest regarding generic features for *Acanthostomum* would be to know if the specimen that was sequenced had symmetrical or asymmetrical ceca, among other critical features. *Acanthostomum proctophorum* and *Acanthostomum gnerii* Szidat, 1954 have a single cecum. Ostrowski de Núñez and Gil de Pertierra (1991) described the life cycle of *A. gnerii* showing the development of the single cecum. In our opinion, those two species could provide evidence to emend *Haplocaecum* (its type species *A. asymmetricum* is a *species inquirenda*). Further workers should provide morphological and nucleotide evidence to prove that ceca size, shape, and symmetry is a useful genus level character.

The presence of circumoral spines is currently used to differentiate species within *Acanthostomum*. *Acanthostomum marinum*, *A. cherysdrusi*, *A. madanmohani*, and *A. cerberi* lack circumoral spines and have a subterminal broadly rounded oral sucker. *Acanthostomum marinum* was described as the type species of *Ateuchocephala* (see Coil and Kuntz, 1960), and *A. cerberi* was described as the type species of *Paracanthostomum* (see Fischthal and Kuntz, 1965). Both genera were differentiated from *Acanthostomum* by lacking circumoral spines. *Paracanthostomum* was differentiated from *Ateuchocephala* by having shorth excretory vesicle arms (Fischthal and Kuntz, 1965). Chattopadhyaya (1969) synonymized *Paracanthostomum* with *Ateuchocephala* based on the length of the excretory vesicle arms, interpreting the character state as diagnostic for the species rather than for the genus. Yamaguti (1971) considered *Paracanthostomum* a subgenus of *Acanthostomum* and accepted *Ateuchocephala* as the type and only genus of Ateuchocephalinae Yamaguti, 1971. Brooks and Caira (1982) synonymized *Paracanthostomum* and *Ateuchocephala* with *Atrophecaecum* (later synonymized with *Acanthostomum*) based on a cladistic analysis. The absence of spines and the shape of the oral sucker are strong characters for diagnosing genera. We refrain from emending *Ateuchocephala* because a redescription of the types (*A. marinum* museum accession No. USNM 39414; *A. cerberi* museum accession No. USNM 60943) and molecular based phylogenetic analyses are needed.

The presence of a muscular gonotyl in the terminal genitalia differentiate *Proctocaecum* and *Gymnatrema* from *Acanthostomum*, and *Caimanicola*. Lamothe-Argumedo and Ponciano-Rodríguez (1986) did not recognize this character and reassigned several species without a gonotyl and having anal pores to *Proctocaecum* (including *Acanthostomum* type species, *A. spiniceps*, in contravention of the International Code of Zoological Nomenclature). This confusion of genera delimitation within acanthostomids began when Looss (1899) proposed *Acanthostomum* for *A. spiniceps* (type species). The original diagnosis of Looss (1899) excluded the presence of anal pores and erroneously described the ceca as blind ending. Khalil (1963) and Moravec (1976, 2001) noted that Looss (1896, 1899) overlooked the presence of anal pores and confirmed their presence in *A. spiniceps*. At the time *Proctocaecum* Baugh, 1957 was proposed, it was differentiated from *Acanthostomum* by having anal pores (because at that time *Acanthostomum* was accepted as lacking anal pores). In fact, the type species of *Acanthostomum* (*A. spiniceps*) and several other species have anal pores. Later, the presence of a muscular gonotyl was found to be a more suitable character to differentiate *Proctocaecum* from *Acanthostomum* (see Brooks, 1980). Brooks and Holcman (1993) stated that the presence of a gonotyl was homoplasy, and a new diagnostic feature (excretory bladder stem length) was for *Acanthostomum* and *Proctocaecum*. Brooks and Holcman (1993) also proposed 4 *Acanthostomum* subgenera, which only increased the taxonomic confusion for acanthostomid genera. Subsequent workers have ignored it (Tkach and Snyder, 2003). Later Miller and Cribb (2008) rejected subgenera and subfamilies for *Acanthostomum* and Cryptogonimidae, respectively. They differentiated *Acanthostomum* from *Proctocaecum* based on the absence of a gonotyl.

Several critical genus-level features still need to be assessed in species of *Caimanicola* and *Acanthostomum*, i.e., anal pores presence/absence and location; seminal vesicle presence/absence and distribution; and tegumental spine size and distribution. Although authors working on cryptogonimids typically report the presence/absence of spines and mention the general distribution of tegumental spines, the spines are not routinely described in detail for all species that would enable meaningful comparisons. Tkach and Snyder (2003) used SEM to study the tegument of *Proctocaecum macroclemidis* (Tkach and Snyder, 2003) Brooks, 2004, but no comparable study exists for the tegument of any species of *Acanthostomum* or *Caimanicola*, for example.

The taxonomic status of *Caimanicola* as an accepted genus or as a junior subjective synonym of *Acanthostomum* is indeterminate. This is mainly because the type specimens of the type species of *Caimanicola*, *Caimanicola marajoara* Teixeira de Freitas and Lent, 1938, have not been examined and the original description by these authors was incomplete. Further confusion was promulgated by an error cascade related to tegumental spine interpretation (see below). The description of *C. marajoara* makes no mention of anal pores but specifically indicated that the tegumental spines are small, scale-like, and distribute to the anterior third quarter of the uterus: "*cuticula provida de pequenos espinhos escamiformes … até o terço anterior da zona uterina*" (Teixeira de Freitas and Lent, 1938; p 55). Significantly, Teixeira de Freitas and Lent (1938) did not draw the spines; however, they drew, measured, and described the eggs in their adult specimens. *Caimanicola* was still monotypic when Price (1940) synonymized it with *Acanthostomum* without justification. Carter and Etges (1972) provided a supplemental description of *C. marajoara* based on both juvenile and adult specimens that they collected from the spectacled caiman, *Caiman crocodilus* (Linnaeus, 1758) (Crocodylia: Alligatoridae) in Colombia. The specimens described by Carter and Etges (1972) were small (~0.30 mm vs 1.18–1.24 mm; see Fig. 2 in Carter and Etges, 1972) and lacked eggs. Without studying the type specimens of *C. marajoara*, Carter and Etges (1972) asserted that Teixeira de Freitas and Lent (1938) types of *C. marajoara* were juveniles because the juvenile specimens of Carter and Etges (1972) had the same general body outline as the drawing of the adult *C. marajoara* by Teixeira de Freitas and Lent (1938). This argument is wholly unconvincing because there is no evidence that dorsoventral body outline diagnoses juvenile and adult cryptogonimids. That Teixeira de Freitas and Lent (1938) types of *C. marajoara* were juveniles is (quite obviously) further refuted by the fact that Teixeira de Freitas and Lent (1938) described eggs in their specimens (see above). Further, Carter and Etges (1972; p 235) described their specimens as having a "*tegument finely spined to level of posterior testis.*" Yet, Carter and Etges (1972) nevertheless stated that *C. marajoara* was probably conspecific with *A. acuti*.

Brooks (1980) studied the holotype and several vouchers of *A. acuti* (including the vouchers from Carter and Etges [1972]). Although none of these specimens of *A. acuti* matched the original description of *C. marajoara* by Teixeira de Freitas and Lent (1938), Brooks (1980) synonymized *A. acuti* with *C. marajoara*. To defend this decision, Brooks (1980) in part used the erroneous arguments in Carter and Etges (1972) combined with his own observations. Then, Brooks (1980) erroneously used the holotype of *A. acuti* as a voucher of *C. marajoara*. In doing so, Brooks (1980) dismissed and replaced Teixeira de Freitas and Lent (1938) original observation of the tegumental spines (small scale-like spines) with his observations of the spines ("*unusually robust in mid--forebody* ") in a different species, respectively. Hence, Brooks' (1980) diagnosis of *Caimanicola* (and therefore of its type species *C. marajoara*) became "*tegumental spines unusually robust in mid-forebody*," which is

objectively an error since that character state has not been confirmed in *Caimanicola*. Without studying the extant types of *C. marajoara* and given that the original description of *C. marajoara* indicates small spines (not large spines), we think this decision by Brooks (1980) regarding *A. acuti* and *C. marajoara* is baseless and that he was indeed describing specimens of *A. acuti*, not *C. marajoara*.

Erroneously assuming that the type species of *Caimanicola* had unusually robust spines in the mid-forebody, and thereby promulgating an error cascade, Brooks (1980) resurrected *Caimanicola* to include other congeners he interpreted as having large spines in the mid-forebody [i.e. *C. brauni*; *Caimanicola caballeroi* (Peláez and Cruz, 1953) Brooks, 1980; and *Caimanicola pavidus* (Brooks and Overstreet, 1977) Brooks, 1980]. However, only *C. brauni* and *C. pavidus* were described with "robust" spines; no measurement to objectively compare it with another specimen was provided. Peláez and Cruz (1953; p 273) described the tegumental spines of *C. caballeroi* as small and cone-shaped: "*pequeñas espinas de forma cónica con punta aguda*" measuring 0.0098 × 0.0033 mm (this the only description that includes measurements of the tegumental spines). And, as stated above, *C. marajoara* was described with small spines by Teixeira de Freitas and Lent (1938) and Carter and Etges (1972). Moravec (2001) stated that Brooks' (1980) characters were bogus and stated that *Caimanicola* had been synonymized with *Acanthostomum*. Miller and Cribb (2008) accepted *Caimanicola* as having robust spines.

We mention these issues pertaining to spine characteristics so that future workers can ensure to specifically describe tegumental spine shape, distribution and measurements in cryptogonimid descriptions. These features are important to the taxonomy of the group. Overall and quite simply, *C. marajoara* needs to be redescribed using the types and additional fresh specimens. Those observations will help solidify the generic diagnosis for *Caimanicola*, determine if the reassignment of the species *sensu* Brooks (1980) is warranted (it is currently baseless and justified by an erroneous argument), and establish a morphological framework with which to sensibly assess extant nucleotide sequences and phylogenetic analyses.

The nucleotide sequences of *A. yahuarcaquense* are the first sequences of *Acanthostomum* to be published with an accompanying morphological diagnosis. The paraphyly of *Acanthostomum* indicates that additional nucleotide sequences of species of *Acanthostomum*, *Proctocaecum, Gymnatrema,* and *Caimanicola* are needed to further resolve the Acanthostominae. We suggest that each sequence should be linked to a taxonomic description, a morphological diagnosis, a photograph, a drawing, or voucher(s) or type(s) deposited in a museum that will loan specimens. Any one of these defends the taxonomic identity of the sequence. Without any such evidence, the identity of the sequence cannot be confirmed without recollecting the parasite. Remarkably, we also noted that no (0 of 16) sequence of *Acanthostomum* was attached to an accompanying morphological diagnosis or voucher specimen and some were unpublished. This means that all 16 previous sequences of *Acanthostomum* are objectively taxonomically baseless sequences (nonugens [Roberts et al., 2018]) whose identities cannot be confirmed without recollecting the specimens. We are not calling into question the taxonomic knowledge or expertise of those who labeled those sequences and deposited them in GenBank. However, in taxonomy, no author is permitted to name a species without a proper justification and morphological diagnosis. This is a fundamental requirement. Submitting a holotype and or paratypes for a new species description or a voucher specimen for a new host or locality record is also a minimal but critical requirement. Reciprocally, a reputable museum will not accept a holotype or paratype without being presented evidence that the new name (new species) has been accepted for publication by a peer-reviewed journal and will be in print. Hence, given how PCR, nucleotide sequences, and phylogenetic evidence have become integral to taxonomy and systematics, we should enforce the same scientific methodological standard for the quality of data upon which we base our conclusions. Sequences, like species names, should be accompanied by a morphological diagnosis and (or) museum-curated vouchers as a justification for the species-level identification.

We also note the pervasive use of short nucleotide sequences in cryptogonomid systematics. We observed that >80 % (13 of 16; 81 %) of the *28S* nucleotide sequences for species of *Acanthostomum* in GenBank are short (640–880 bp) relative to other trematode *28S* nucleotide sequences (usually around 1200–2000 bp). Short sequences could omit useful diagnostic regions of the gene. This would lead the parasitologist who relies upon nucleotide-based phylogenetic results (i.e., phylogenetic bar coding) more so than morphology for species identification to erroneously lump/synonymize morphologically and genetically distinct cryptogonimids as a single species. We have noted that several works labeled as 'integrative taxonomy' question the validity/distinctiveness of clearly morphologically distinct species because the only representative sequence is short and lacks much variation. That is, the tree results show the morphologically distinct species as genetically indistinct from another (other) congener(s) simply because the gene region being compared is short and conserved/non-variable. The literature holds many examples of self-defined 'integrative taxonomists' basing their decisions wholly on an analysis of short, relatively non-variable nucleotide sequences (and lumping morphologically distinct species) rather than based upon a detailed morphological study that uses detailed illustrations of types and vouchers to diagnose taxa, assess genera, and revise the systematics of the group.

CRediT authorship contribution statement

Kamila Cajiao-Mora: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **John H. Brule:** Writing – review & editing, Methodology, Investigation. **Haley R. Dutton:** Writing – review & editing, Methodology. **José Rancés Caicedo-Portilla:** Writing – review & editing, Resources. **Stephen A. Bullard:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

Ethics statement

All applicable institutional, national, and international guidelines for the care and use of animals were followed.

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Declaration of competing interest

The authors declare no conflict of interest.

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