# TWO NEW GENERA OF FISH BLOOD FLUKES (DIGENEA: APOROCOTYLIDAE) FROM CATFISHES IN THE PERUVIAN AMAZON

Raphael Orélis-Ribeiro and Stephen A. Bullard

Aquatic Parasitology Laboratory, School of Fisheries, Aquaculture and Aquatic Sciences, College of Agriculture, Auburn University, 203 Swingle Hall, Auburn, Alabama 36849. Correspondence should be sent to: ror0002@auburn.edu

ABSTRACT:    *Cladocaecum tomasscholzi* n. gen., n. sp. infects the heart (lumen of ventricle) of driftwood catfish, *Ageneiosus inermis* Linnaeus, 1766 (Siluriformes: Auchenipteridae) from the Nanay River (Amazon River Basin, near Iquitos, Peru). It differs from all other aporocotylid genera by having a highly branched intestine comprising a central cecum that terminates immediately anterior to the ovary and that has numerous laterally directed diverticula. *Kritsky platyrhynchi* (Guidelli, Isaac, and Pavanelli, 2002) n. gen., n. comb. (= *Plehniella p.*) is redescribed based on paratypes plus new specimens collected from the body cavity of the type host (porthole shovelnose catfish, *Hemisorubim platyrhynchos* Valenciennes, 1840) (Pimelodidae) from the nearby Itaya River. *Kritsky* differs from *Sanguinicola* Plehn, 1905, *Plehniella* Szidat, 1951, *Nomasanguinicola* Truong and Bullard, 2013, and *Cladocaecum* by the combination of having a spinous anterior sucker, an intestine comprising 6 asymmetrical ceca, a lanceolate body, a straight vas deferens, an ovary with finger-like lateral projections, a small and spheroid oötype, numerous, minute, spheroid uterine eggs, and separate genital pores. An updated list of hosts, tissues infected, and geographic localities for the catfish blood flukes (9 spp.; 5 genera) is provided. This is the first report of a fish blood fluke infecting a member of Auchenipteridae and first proposal of a new genus of blood fluke (Schistosomatoidea) from South America in 64 yr. It brings the total number of Amazonian fish blood flukes to a mere 4 species.

Catfishes (Siluriformes), comprising 3,695 species of 39 families, are among the most species-rich vertebrate taxa, totaling 1 in 9 fishes and 1 in 18 vertebrate species (Chapman, 2009; Eschmeyer and Fong, 2015). South America is a catfish biodiversity focus (Reis et al., 2003), including species that are highly prized by the aquarium pet trade (Mitchell and Tully, 2008), commercial and recreational fishing industries (Welcomme et al., 2014), and production aquaculture sector (Queiroz et al., 2002). Despite the regional economic importance of catfishes, as well as their ecological and phylogenetic diversity, few studies have explored their metazoan parasites, especially their fish blood flukes (Digenea: Aporocotylidae) (Szidat, 1951; Guidelli et al., 2002; Orélis-Ribeiro and Bullard, 2015). Catfishes worldwide host 8 aporocotylids (of 138 accepted aporocotylid species, 6%) currently assigned to *Plehniella* Szidat, 1951, *Nomasanguinicola* Truong and Bullard, 2013, and "*Sanguinicola* Plehn, 1905" (see Truong and Bullard, 2013; Orélis-Ribeiro and Bullard, 2015). Catfish blood flukes mature in the circulatory system (Woodland, 1923, 1924; Odhner, 1924; Paperna, 1964, 1996; Truong and Bullard, 2013) and the body cavity (Szidat, 1951; Guidelli et al., 2002; Orélis-Ribeiro and Bullard, 2015) of 10 catfishes of 6 genera and 4 families (Table I).

Herein we propose 2 new genera, describe a new species, and redescribe a nominal species of Aporocotylidae based on specimens that infect the heart and body cavity of catfishes in the Peruvian Amazon. This is the first proposal of a new genus of blood fluke (Schistosomatoidea) from South America since Szidat's (1951) proposal of *Plehniella*.

## MATERIALS AND METHODS

Hosts were captured by seine or cast net near Iquitos, Peru (from 2005 to 2006) and examined with a dissecting microscope immediately after euthanasia. Flukes were pipetted onto a glass slide and heat-killed with an EtOH burner flame before being transferred to a vial of 5% neutral buffered formalin. Later, whole specimens were rinsed thoroughly with distilled water and cleaned with fine brushes to remove any debris, stained

overnight in Van Cleave's hematoxylin with several additional drops of Ehrlich's hematoxylin, made basic in 70% ethanol with lithium carbonate and butyl-amine, dehydrated, cleared in clove oil, and permanently mounted in Canada balsam. Illustrations of stained, whole-mounted specimens were made with the aid of a Leica DM-2500 camera (Leica, Wetzler, Germany) equipped with differential interference contrast optical components and a drawing tube. Measurements were obtained by using a calibrated ocular micrometer (as straight lines along the course of each duct) and are herein reported in micrometers (μm) followed by their mean and the number measured in parentheses. Morphometric data for the borrowed paratypes (Coleção Helmintológica do Instituto Oswaldo Cruz [CHIOC] collection nos. 34361a and 34361b) are reported in brackets following the measurements of the newly collected voucher specimens. Scientific names including taxonomic authorities and dates for fishes follow Eschmeyer (2015). Common names are taken from FishBase (Froese and Pauly, 2015). Higher level fish classification and nomenclature follows Nelson (2006). Nomenclature for Aporocotylidae follows Bullard et al. (2009). Brown (1956) was used to help construct the genus name and specific epithet. Type and voucher materials are deposited in the United States National Museum (USNM, Washington, D.C.) and Coleção Helmintológica do Instituto Oswaldo Cruz (CHIOC, Rio de Janeiro, Brazil).

## DESCRIPTIONS

### *Cladocaecum* n. gen.
(Figs. 1–4)

*Diagnosis:* Body of adult elongate, <6× longer than wide, strongly dorsoventrally flattened, ventrally concave, lacking posterolateral protuberance, anterior body end less tapered than posterior end, lacking tegumental body spines ("Marginalstacheln"), rods and bristles ("Stäbchen-Börstchen"), and rosethorn-shaped spines. Ventrolateral nerve cords indistinct. Dorsolateral nerve cords extending nearly entire body length (BL), with commissures anteriorly and posteriorly. Anterior sucker indistinct. Mouth medioventral. Pharynx a diminutive zone of muscle encircling anterior end of the esophagus immediately posterior to mouth. Esophagus medial, extending directly posteriad (not convoluted) approximately 1/3 of BL, connecting with ceca anteromedially, including subtle anterior and posterior esophageal swellings immediately anterior to nerve commissure and cecal ramification (respectively); anterior esophageal gland enveloping anterior esophageal swelling, between mouth and anterior nerve commissure; posterior esophageal gland enveloping posterior esophageal swelling, occupying space anterior to cecal ramification. Intestine comprising paired anterior ceca plus a medial cecum with numerous branches extending laterad, asymmetrical, lacking clearly discernible paired posterior ceca, penetrating into posterior body half. Testis single, medial, immediately anterior to ovary. Cirrus sac indistinct. Male genital pore slightly sinistral, post-gonadal, post-cecal, opening

TABLE I. Blood flukes (Digenea: Aporocotylidae) of catfishes (Siluriformes).

| Aporocotylid | Host | Site | Locality | Reference(s) |
|---|---|---|---|---|
| *Cladocaecum tomasscholzi* n. gen., n. sp. | *Ageneiosus inermis* Linnaeus, 1766 (Auchenipteridae) | Ventricle in heart | Nanay River, Peru | Present study |
| *Kritsky platyrhynchi* (Guidelli, Isaac, and Pavanelli, 2002) n. gen., n. comb. (originally as *Sanguinicola*) | *Hemisorubim platyrhynchos* Valenciennes, 1840 (Pimelodidae) | Body cavity | Baía River, Brazil | Guidelli et al., 2002, 2003 (as *Plehniella* in Truong and Bullard, 2013) |
| | | Body cavity | Itaya River, Peru | Present study |
| *Nomasanguinicola canthoensis* Truong and Bullard, 2013 | *Clarias macrocephalus* Günther, 1864 (Clariidae) | Branchial vessels | Can Tho fish market, Vietnam (Mekong River) | Truong and Bullard, 2013 |
| *Plehniella armbrusteri* Orélis-Ribeiro and Bullard, 2015 | *Pimelodus blochii* Valenciennes, 1840 (Pimelodidae) | Body cavity | Lake Tumi Chucua, Bolivia | Orélis-Ribeiro and Bullard, 2015 |
| *Plehniella coelomicola* Szidat, 1951 | *Iheringichthys labrosus* Lütken, 1874 (Pimelodidae) | Body cavity | La Plata River, Argentina | Szidat, 1951 |
| | *Pimelodus albicans* Valenciennes, 1840 (Pimelodidae) | Body cavity | La Plata River, Argentina | Lunaschi, 1985; Avendaño de Mac Intosh and Ostrowski de Núñez, 1998 |
| | *Pimelodus maculatus* Lacépède, 1803 (Pimelodidae) (as *P. clarias*) | Body cavity | La Plata River, Argentina | Lunaschi, 1985 |
| | | Body cavity | La Plata River, Argentina | Avendaño de Mac Intosh and Ostrowski de Núñez, 1998 |
| | | Body cavity | Paraná River Basin, Brazil | Brasil-Sato and Pavanelli, 2004; Takemoto et al., 2009 |
| | | Body cavity | São Francisco River Basin, Brazil | Brasil-Sato, 2003; Brasil-Sato and Pavanelli, 2004 |
| *Plehniella dentata* Paperna, 1964 *incertae sedis* (likely a species of *Nomasanguinicola*) | *Clarias gariepinus* Burchell, 1822 (Clariidae) (as *C. lazera*) | "Intestine" (probably mesenteric vessels) | Lake Tiberias and Hule Nature Reserve, Israel | Paperna, 1964; Truong and Bullard, 2013 |
| *Plehniella sabajperezi* Orélis-Ribeiro and Bullard, 2015 | *Pimelodus albofasciatus* Mees, 1974 (Pimelodidae) | Body cavity | Demerara River, Guyana | Orélis-Ribeiro and Bullard, 2015 |
| | | Body cavity | Rupununi River, Guyana | Orélis-Ribeiro and Bullard, 2015 |
| | *Pimelodus blochii* Valenciennes, 1840 (Pimelodidae) | Body cavity | Lago Tumi Chucua, Bolivia | Orélis-Ribeiro and Bullard, 2015 |
| | | Body cavity | Napo River, Peru | Orélis-Ribeiro and Bullard, 2015 |
| *Plehniella* sp. | *Pimelodus grosskopfii* Steindachner, 1879 (Pimelodidae) | Body cavity | Cienega de Jobo and Canal del Dique, Colombia | Orélis-Ribeiro and Bullard, 2015 |
| *Sanguinicola chalmersi* Odhner, 1924 | *Auchenoglanis occidentalis* Valenciennes, 1840 (Claroteidae) | Blood, heart | Sudan, Africa | Woodland, 1923; Odhner, 1924; Khalil, 1969, 1971; Paperna, 1996 |
| | *Synodontis schall* Block and Schneider, 1801 (Mochoidae) | Mesenteric and branchial blood vessels | Cairo and Giza fish markets, Egypt | Woodland, 1923; Imam et al., 1984 |
| *Sanguinicola clarias* Imam, Marzouk, Hassan, and Itman, 1984 *incertae sedis* (likely a species of *Nomasanguinicola*) | *Clarias gariepinus* Burchell, 1822 (Clariidae) (as *C. lazera*) | "Mesenteric and other blood vessels" | Cairo and Giza fish markets, Egypt | Imam et al., 1984; Truong and Bullard, 2013 |
| | | Not specified | Beni-Suef fish market, Egypt | Imam and El-Askalany, 1990 |

approximately 1/12 of BL from posterior body end. Ovary medial, post-cecal, immediately post-testicular, as wide as testis, occupying posterior 1/4 of body. Oviduct extending posteriad from posteromedial surface of ovary, connecting with vitelline duct near level of male genital pore; oviducal seminal receptacle present, immediately post-ovarian. Ovo-vitelline duct short, connecting with oötype dextrally; oötype spheroid, thick-walled, enveloping large gland cells, post-cecal, post-gonadal, posterior to genital pores. Laurer's canal absent. Uterus post-cecal, primarily post-gonadal, with straight (not convoluted) ascending and descending segments; uterine seminal receptacle lacking; uterine eggs spheroid, lacking appendages or filaments. Metraterm indistinct. Female genital pore dorsal, anteromedial to male genital pore. Excretory vesicle indistinct. Adults in the heart of "driftwood catfishes" (Siluriformes: Auchenipteridae).

*Differential diagnosis:* Ventrolateral tegumental body spines absent. Anterior sucker indistinct. Pharynx present. Esophagus approximately 1/3 of BL, with anterior and posterior esophageal swellings enveloped by respective esophageal gland. Intestine comprising paired anterior ceca plus a medial cecum with numerous branches extending laterad, asymmetrical, lacking clearly discernible paired posterior ceca, penetrating into posterior body half. Testis single, pre-ovarian. Proximal portion of oviduct comprising an oviducal seminal receptacle. Oötype spheroid, thick-walled, enveloping large gland cells. Laurer's canal absent. Uterus with straight ascending and descending segments. Metraterm indistinct. Genital pores separate.

*Type and only known species: Cladocaecum tomasscholzi* n. sp.

*Etymology:* The genus name is for the highly branched (clados) gut of the type species.

## Remarks

*Cladocaecum* differs from all other aporocotylid genera by having a highly branched intestine comprising a central cecum that terminates immediately anterior to the ovary and that has numerous laterally directed diverticula. It is most similar to several other aporocotylid genera (*Sanguinicola* Plehn, 1905; *Plehniella* Szidat, 1951; *Nomasanguinicola* Truong and Bullard, 2013) accommodating blood flukes that mature in primary division freshwater fishes.

*Sanguinicola* Plehn, 1905, the aporocotylid genus that has historically accommodated the vast majority of freshwater fish blood flukes, needs systematic revision. No type materials exist for the type species *Sanguinicola armata* Plehn, 1905 but Ejsmont's (1926) treatment of that species is most taxonomically informative. Because *Sanguinicola* includes several species of doubtful identity and uncertain systematic position, we base our generic comparisons on Ejsmont's (1926) description of *S. armata*. The new genus resembles *Sanguinicola* by having an esophagus that is 1/3 of BL, a pre-ovarian testis, an oötype that is posterior to all other segments of the male and female genitalia, a post-ovarian uterus, and separate genital pores as well as by lacking a Laurer's canal. The oötype of these genera is thick-walled and highly glandular, so much so that it may appear muscular in some whole mounts (Schell, 1974). This type of oötype differs from that of *Cardicola* spp. (Bullard and Overstreet, 2004), which have an ovoid, thin-walled oötype surrounded by an obvious Mehlis' gland. The new genus is most easily differentiated from *Plehniella* also by the shape of the intestine. *Cladocaecum* resembles *Nomasanguinicola*, the other genus of catfish blood fluke, by lacking ventrolateral tegumental spines, rods, and bristles and a Laurer's canal and by having a post-testicular ovary, a post-ovarian uterus with ascending and descending segments, and separate genital pores. The new genus is most easily distinguished from the closely related *Sanguinicola* and *Nomasanguinicola* by lacking lateral tegumental body spines and by having a highly branched intestine that extends to the ovary. *Sanguinicola* and *Nomasanguinicola* have a compact, multi-lobed intestine that does not extend into the posterior half of the body. In addition to that feature, *Sanguinicola* has a column of lateral tegumental body spines, whereas *Nomasanguinicola* has an anterior sucker with denticles forming a column per each side of mouth.
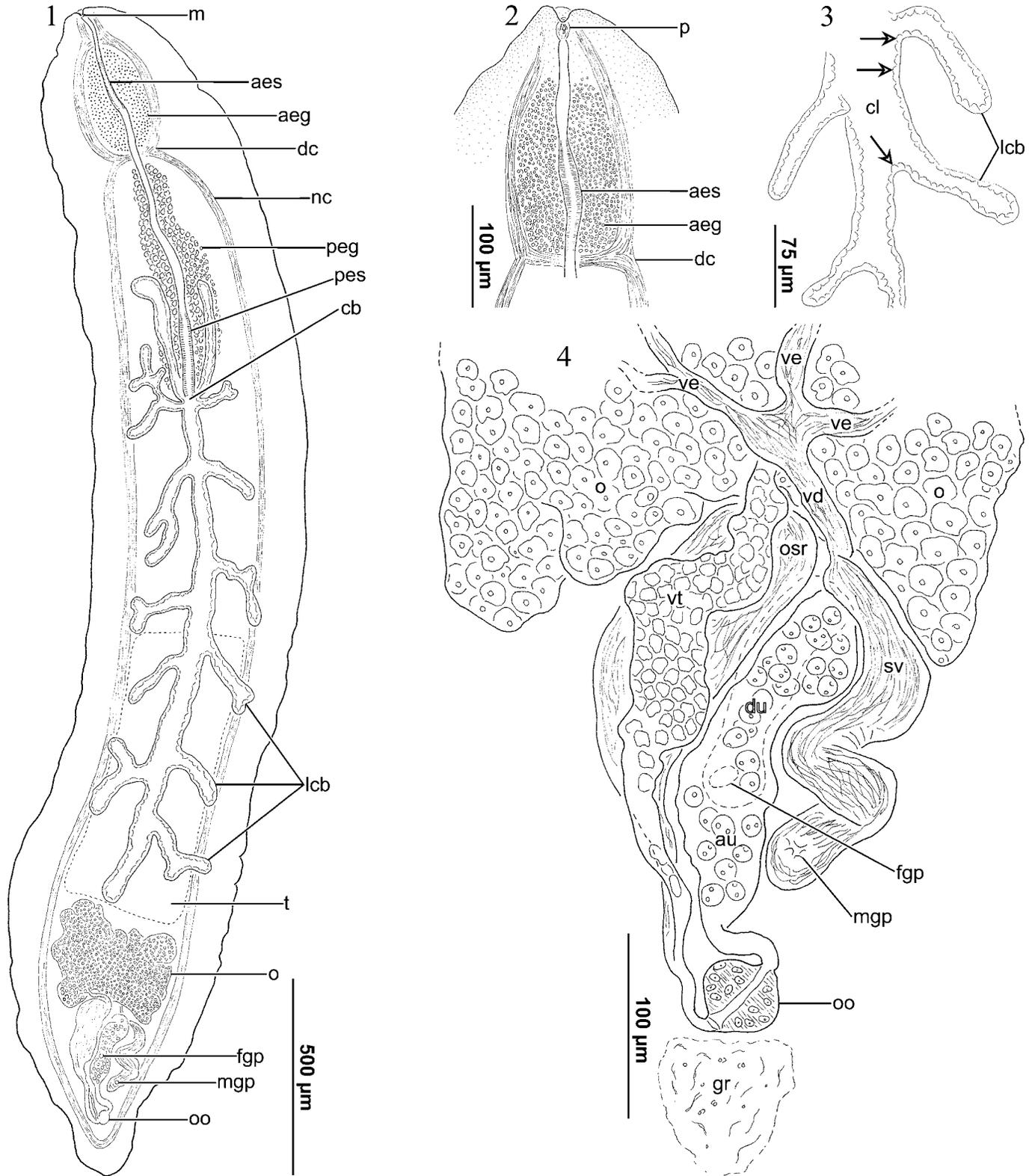
### *Cladocaecum tomasscholzi* n. sp.
(Figs. 1–4)

*Diagnosis of adult (measurements and illustrations based on light microscopy of 1 whole-mounted specimen):* Body 2,925 long, 553 wide, maximum width at level of ovary, 5.4× longer than wide (Fig. 1). Ventral

and dorsal sensory papillae not evident with light microscopy. Dorsolateral nerve cords difficult to trace for most of BL; 10 wide near mid-body at widest level; 110 or 20% of body width from body margin at mid-body, paired, contiguous anteriorly and posteriorly, becoming confluent with paired cord 40 or 1% of BL from posterior body end; commissure 375 or 13% of BL from anterior body end, 125 or 23% of body width across width of worm, 13 wide, perpendicular to long axis of body, coursing dorsal to posterior end of esophageal anterior swelling (Fig. 1). Mouth 5 in diameter, 13 long or 0.4% of BL from anterior body end (Figs. 1, 2); pharynx ovoid, 25 or 3% of esophagus length, 20 wide or 1.3× longer than wide, with muscular wall 8 thick. Esophagus 943 long or 34% of BL, including (i) a distal portion, (ii) an anterior esophageal swelling portion, (iii) an elongated narrow portion, and (iv) a posterior swelling portion; distal portion dilating to 25 after pharynx and extending directly posteriad for 133 or 14% of esophagus total length, with wall 3 thick, narrowing to 10 wide before connecting with anterior esophageal swelling; anterior esophageal swelling 175 long or 19% of esophagus total length, 30 wide or 5% of maximum body width, with wall 13 thick, 171 or 6% of BL from anterior body end; elongated narrow portion 15 wide, with wall 5 thick, extending directly posteriad 435 before connecting with posterior esophageal swelling; posterior esophageal swelling delineated anteriorly from narrow region of esophagus by slight bend, 200 long or 21% of esophagus length, 43 wide or 1.4× maximum esophagus width, with wall 13 thick, posterior portion immediately anterior to cecal ramification, connecting with intestine anteromedially (Figs. 1, 2). Anterior esophageal gland 200 long or 21% of esophagus length, 170 wide or 5.7× maximum width of anterior esophageal swelling (Figs. 1, 2); posterior esophageal gland 593 long or 63% of esophagus length or 3× length of anterior portion of esophageal gland, 150 in maximum width or 3.5× maximum width of posterior esophageal swelling (Fig. 1). Intestine thick-walled, with crenulated luminal surface (Fig. 3); ceca bifurcation 980 or 34% of BL from anterior body end; anterior ceca extending approximately in parallel with body margin and esophagus, not extending laterad beyond dorsolateral nerve cord; anterodextral cecum 318 long or 11% of BL, 80 wide; anterosinistral cecum 286 long or 10% of BL, 32 wide; medial branch of posterior cecum extending directly posteriad along midline 1,303 or 45% of BL, approximately 4× length of either anterior cecum, 80 wide or approximately as wide as either anterior cecum; secondary cecal branches 159–318 (n = 11) long, approximately 80 wide, not extending laterad far beyond dorsolateral nerve cord (Fig. 1).

Testis 675 long or 14% of BL, 500 wide or 93% of body width, rectangular, poorly delineated from surrounding parenchyma (Fig. 1); post-testicular space 783 or 27% of BL. Vas deferens extending slightly diagonally toward sinistral body margin before connecting with seminal vesicle; seminal vesicle S-shaped, 239 long, containing sperm for entire length (Figs. 1, 4). Male genital pore 225 or 8% of BL from posterior body end, 100 from sinistral body margin, 200 from dextral body margin (Fig. 4).

Ovary 330 long or 11% of BL, 350 wide or 63% of body width, dorsal to vas deferens, having an irregular margin (Figs. 1, 4); post-ovarian space 300 long or 10% of BL. Oviduct curving sinistrad immediately posterior to ovary and lateral to vas deferens, 408 long, 68 in maximum width, comprising (i) abbreviated proximal duct, (ii) dilated portion (=oviducal seminal receptacle), and (iii) distal portion; proximal duct extending 75 toward sinistral body margin, 8 wide, curving posteromediad to connect with oviducal seminal receptacle; oviducal seminal receptacle filled with sperm, 215 long or 53% of total oviduct length, 68 wide or 6× longer than wide; distal portion of oviduct narrow, 10 wide or 15% of oviducal seminal vesicle maximum width, continuing posteriad approximately in parallel with dextral body margin before uniting with vitelline duct (Fig. 4). Primary vitelline collecting duct indistinct in region anterior to ovary, passing ventral to ovary before extending ventrally 335 along oviducal seminal receptacle to unite with distal portion of oviduct immediately proximal to oötype. Oötype 50 in diameter, 125 or 4% of BL from posterior body end; oötype wall 20 thick, enveloping clearly delineated spheroid cells (Figs. 1, 4). Mehlis' gland indistinct but perhaps an amorphous glandular region primarily concentrating immediately posterior to oötype (Fig. 4). Uterus medial, flanked by primary vitelline duct and seminal vesicle; ascending portion of uterus extending 238 anteriad from oötype, curving dorsally immediately posterior to posterior margin of ovary, 78 in maximum width; descending uterus extending 140 posteriad from posterior margin of ovary, 0.6× length of ascending uterus, 38 in maximum width or approximately 1/2 width of ascending

FIGURES 1–4.    *Cladocaecum tomasscholzi* n. gen., n. sp. (Digenea: Aporocotylidae) from the heart of the driftwood catfish *Ageneiosus inermis* Linnaeus, 1766 (Siluriformes: Auchenipteridae), from the Nanay River, Peru. Ventral view. Holotype USNM Coll. No. 1254657. Scale values beside each bar. (**1**) Body of adult showing mouth (m), anterior esophageal swelling (aes), anterior esophageal gland (aeg), anterior commissure of dorsolateral nerve cord (dc), dorsolateral nerve cord (nc), posterior esophageal gland (peg), posterior esophageal swelling (pes), esophagus (e), cecal bifurcation (cb), lateral cecal branches (lcb), putative testis (t, dashed), ovary (o), female genital pore (fgp), male genital pore (mgp), oötype (oo). (**2**) Anterior end showing mouth residing within anterior concavity and minute, weakly muscular pharynx (p) enveloping extreme distal end of esophagus. (**3**) Laterally

uterus, lacking muscular wall; uterine eggs thin-shelled, spheroid, 15 (15; 63) in diameter. Female pore 10 in diameter.

Excretory system indistinct.

*Type and only known host:* Driftwood catfish, *Ageneiosus inermis* Linnaeus, 1766 (Siluriformes: Auchenipteridae).

*Site in host:* Heart, ventricle lumen.

*Type locality and collection date:* Nanay River (3°43′12″S, 73°16′50″W), Amazon River Basin, near Iquitos, Peru, August 2005.

*Specimen deposited:* Holotype USNM Coll. No. 1254657.

*Prevalence of infection:* :1 of 5 (20%) *A. inermis* was infected by 1 fluke.

*Etymology:* The specific name *tomasscholzi* honors Professor Tomáš Scholz (Institute of Parasitology Biology Centre, ASCR, Helminthology, Czech Republic) in recognition of his significant contributions to fish parasitology.

### *Kritsky* n. gen.
(Figs. 5–9)

*Diagnosis:* Body of adult lanceolate, 6× longer than wide, strongly dorsoventrally flattened, ventrally concave, lacking posterolateral protuberance, more rounded posteriorly than anteriorly, lacking tegumental body spines ("Marginalstacheln"), rods and bristles ("Stäbchen-Börstchen"), and rosethorn-shaped spines. Ventrolateral nerve cords indistinct. Dorsolateral nerve cords present, extending nearly entire BL, with commissures anteriorly and posteriorly. Anterior sucker with concentric spine rows anterior to mouth and ornamenting anterior aspect of sucker, demarcated from body by posterior constriction of tegument, comprising an obvious proboscis accommodating mouth, lacking lateral denticles. Mouth medioventral. Pharynx diminutive, with tri-radiate lumen, in anterior portion of esophagus. Esophagus medial, extending directly posteriad (not convoluted) >1/4 of BL, connecting with ceca anteromedially, including anterior and posterior esophageal swellings enveloped by respective esophageal glands. Intestine restricted to anterior half of body, having glandular wall, comprising 6 ceca; ceca asymmetrical, saccular, each approximately 1/9 of esophagus length, smooth (lacking diverticula). Testis single, medial, post-cecal, pre-ovarian, >1/3 of BL, 4× longer than wide, diffuse, extensively lobed, extending laterad beyond nerve cords. Vasa efferentia extensive, having secondary ducts extending from lateral margins of testicular lobes and coalescing ventrally along midline; vas deferens predominantly straight, lacking sinistral or dextral loops. Cirrus sac present, sinistral, post-gonadal, enclosing seminal vesicle and cirrus; inverted cirrus having a transverse pore; everted cirrus having a proximal base circular, everting dorsally near midline; male genital pore post-gonadal, post-cecal, 1/12 of BL from posterior body end. Ovary medial or slightly dextral, post-testicular, occupying posterior 1/4 of body, a loose aggregation of spheroid ova bound by a thin membrane, with finger-like laterally directed lobes and narrow middle portion (hourglass- or butterfly-shaped), dorsal to vas deferens, extending lateral to dorsolateral nerve cords, as wide as testis. Vitellarium follicular, occupying space from middle of esophagus to posterior end of testis. Oviduct emanating from posteromedial dorsal surface of ovary, connecting with vitelline duct near level of male genital pore; oviducal seminal receptacle present, immediately post-ovarian. Ovo-vitelline duct short, connecting with oötype dextrally; oötype longer than wide, post-cecal, post-gonadal, at level of or posterior to genital pores. Laurer's canal absent. Uterus inverse J-shaped, post-cecal, post-gonadal; ascending portion longer than descending portion; ascending portion straight or slightly convoluted; uterine seminal receptacle lacking; uterine eggs spheroid, lacking appendages or filaments. Metraterm indistinct. Female genital pore transverse, anteromedial to male genital pore. Excretory vesicle indistinct. Adults in body cavity of South American pimelodids.

*Differential diagnosis:* Ventrolateral tegumental body spines absent. Spinous anterior sucker with concentric spine rows present in adult. Pharynx present. Esophagus > 1/4 of BL, with anterior and posterior esophageal swellings enveloped by respective esophageal glands. Intestine comprising 6 asymmetrical, saccular ceca. Testis single, >1/3 of BL, diffuse, with many lobes extending laterad beyond nerve cords. Vas deferens straight, lacking sinistral or dextral loops. Cirrus sac present;

inverted cirrus having a transverse pore. Male genital pore post-gonadal, post-cecal, 1/12 of BL from posterior body end. Ovary with finger-like laterally directed lobes and narrow middle portion. Proximal portion of oviduct comprising an oviducal seminal receptacle. Oötype occupying space at level of or posterior to genital pores. Laurer's canal absent. Uterus inverse J-shaped. Genital pores separate, transverse.

*Type and only known species: Kritsky platyrhynchi* (Guidelli, Isaac, and Pavanelli, 2002) n. gen., n. comb.

*Etymology:* The generic epithet honors Professor Delane Kritsky (Idaho State University, Pocatello) for his many contributions to the study of helminth biodiversity in South American freshwater fishes.

### Remarks

*Kritsky* n. gen., *Nomasanguinicola* Truong and Bullard, 2013, *Plehniella* Szidat, 1951, and *Sanguinicola* Plehn, 1905, are the only aporocotylid genera that lack a Laurer's canal and have the combination of an esophagus that extends at least 1/3 of the BL, an extensively lobed testis that occupies the space between the ceca and ovary, an approximately butterfly wing-shaped ovary, an oötype post-gonadal, and a post-ovarian uterus (Plehn, 1905; Ejsmont, 1926; Szidat, 1951; Truong and Bullard, 2013; Orélis-Ribeiro and Bullard, 2015, present study). The new genus resembles *Plehniella* by having that combination of features plus a body that lacks lateral tegumental spines as well as having a minute pharynx, anterior and posterior esophageal glands corresponding to esophageal swellings, an intestine comprising 6 asymmetrical and saccular ceca, and a prominent cirrus sac. Members of both genera mature in the body cavity of pimelodid catfishes from South America (Szidat, 1951; Orélis-Ribeiro and Bullard, 2015, present study). *Nomasanguinicola* can be easily differentiated from these genera by the presence of an anterior sucker with denticles directing posteroventrally, forming a column per each side of mouth (Truong and Bullard, 2013). *Sanguinicola armata,* and therefore *Sanguinicola sensu lato*, differs from these genera by the combination of having lateral tegumental body spines arranged in a single lateral column, 4–5 but not 6 ceca, and a large, tetrahedral egg in the oötype (Ejsmont, 1926; Kirk and Lewis, 1993).

Monotypic *Kritsky* differs from *Plehniella* by a combination of morphological features associated with body shape, anterior sucker, male genitalia, female genitalia, genital pores, and eggs. The adult body in the new genus is lanceolate, approximately 6× longer than wide, and more rounded posteriorly than anteriorly (Fig. 5). In *Plehniella*, the adult body is elongate or oblong (approximately 2–4× longer than wide) with a slight sinistral indentation at level of genitalia or not and anterior and posterior ends tapering equally or having a broadly rounded posterior end (Szidat, 1951; Orélis-Ribeiro and Bullard, 2015). Regarding the anterior sucker, *Kritsky* has a demarcated anterior sucker with concentric spine rows in large adult specimens, whereas a spinous anterior sucker has only been reported from small, putatively young, adult specimens of *Plehniella* spp. but never from large adult specimens (Orélis-Ribeiro and Bullard, 2015). *Kritsky* has a vas deferens that is predominantly straight, lacking sinistral or dextral loops (Fig. 5). *Plehniella* has a vas deferens that is strongly sinuous, forming obvious sinistral and dextral loops (Szidat, 1951; Orélis-Ribeiro and Bullard, 2015). The ovary of *Kritsky* has finger-like lateral extensions, whereas that of *Plehniella* comprises an extensively lobed mass (Szidat, 1951; Orélis-Ribeiro and Bullard, 2015). The oötype of the new genus is a small, spheroid chamber (Figs. 5, 8, 9), whereas that of *Plehniella* is an elongate chamber that exceeds the length of the ascending uterus (i.e., the ascending uterus is >3× oötype length in *K. platyrhynchi* vs. 1–2× oötype length in *Plehniella* spp.) (Szidat, 1951; Orélis-Ribeiro and Bullard, 2015). The new genus has numerous, minute, spheroid uterine eggs (Fig. 8), whereas *Plehniella* spp. typically have a single, large, ovoid uterine egg (Szidat, 1951; Orélis-Ribeiro and Bullard, 2015). *Kritsky* has separate, relatively anteromedial genital pores (Figs. 5, 8, 9), whereas *Plehniella* has a common atrium and pore that is circular, lateral, and opens near the posterior body extremity, appearing almost terminal (Szidat, 1951; Orélis-Ribeiro and Bullard, 2015).

The new genus differs from the blood flukes that infect chondrichthyans by lacking robust, C-shaped lateral tegumental spines and a

---

← 

extending cecal branches (lcb) showing mononucleate cells (arrows) lining the inner walls of the cecal lumen (cl). (**4**) Genitalia showing vasa efferentia (ve), seminal vesicle (sv), male genital pore (mgp), ovary (o), vitelline duct (vt), oviducal seminal receptacle (osr), oötype (oo), glandular region (gr), ascending uterus (au), descending uterus (du, dashed), and female genital pore (fgp).
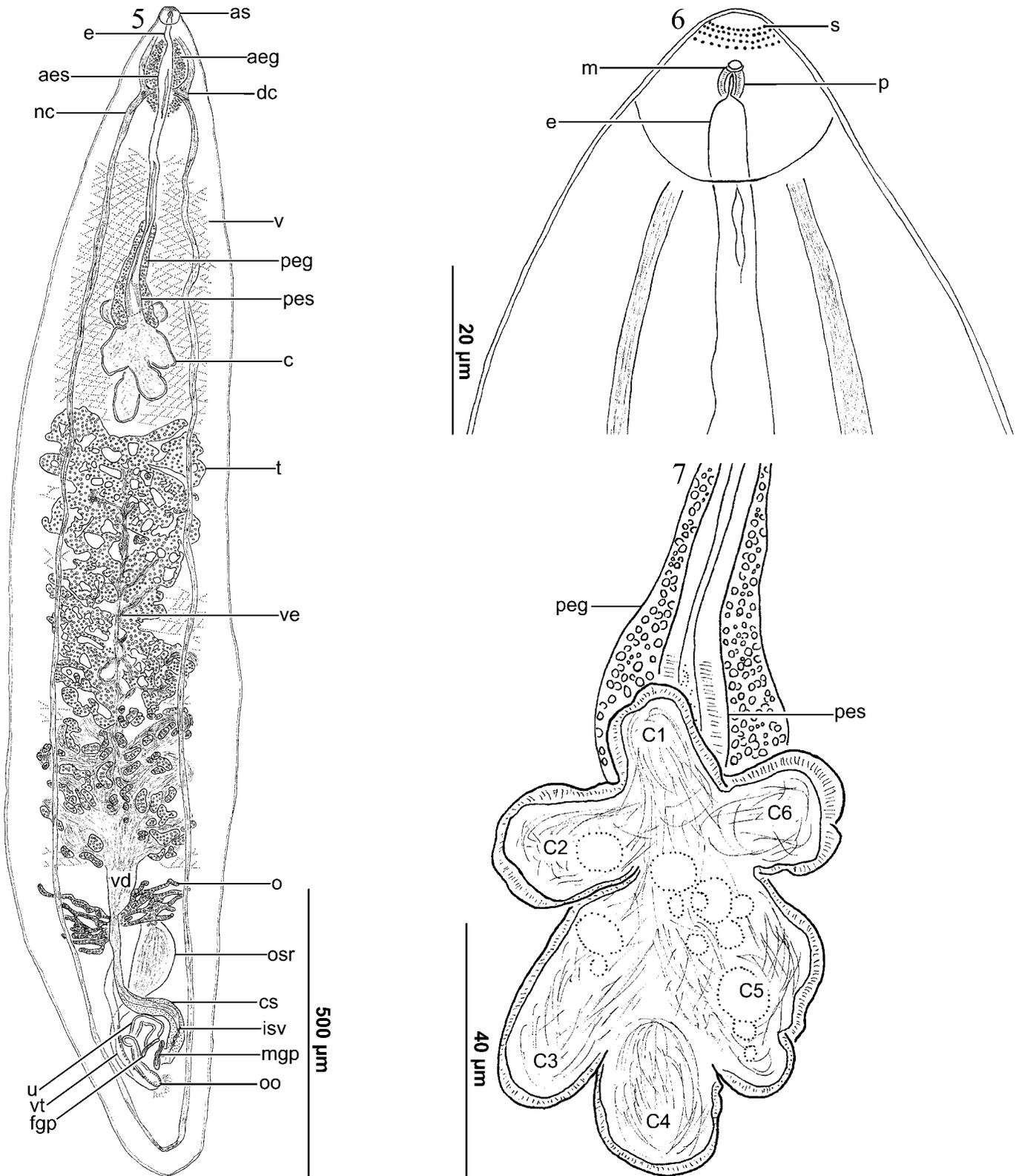
FIGURES 5–7.   *Kritsky platyrhynchi* n. gen., n. sp. (Digenea: Aporocotylidae) from the body cavity of porthole shovelnose catfish, *Hemisorubim platyrhynchos* Valenciennes, 1840 (Siluriformes: Pimelodidae), from the Itaya River, Peru. Scale values beside each bar. (**5**) Body of adult specimen (USNM Coll. No. 1254658) showing location of anterior sucker (as), esophagus (e), anterior esophageal gland (aeg), anterior esophageal swelling (aes), anterior commissure of dorsolateral nerve cord (dc), dorsolateral nerve cord (nc), posterior esophageal gland (peg), posterior esophageal swelling (pes), vittelarium (v), ceca (c), testis (t), vasa efferentia (ve), vas deferens (vd), ovary (o), oviducal seminal receptacle (osr), cirrus sac (cs), internal seminal
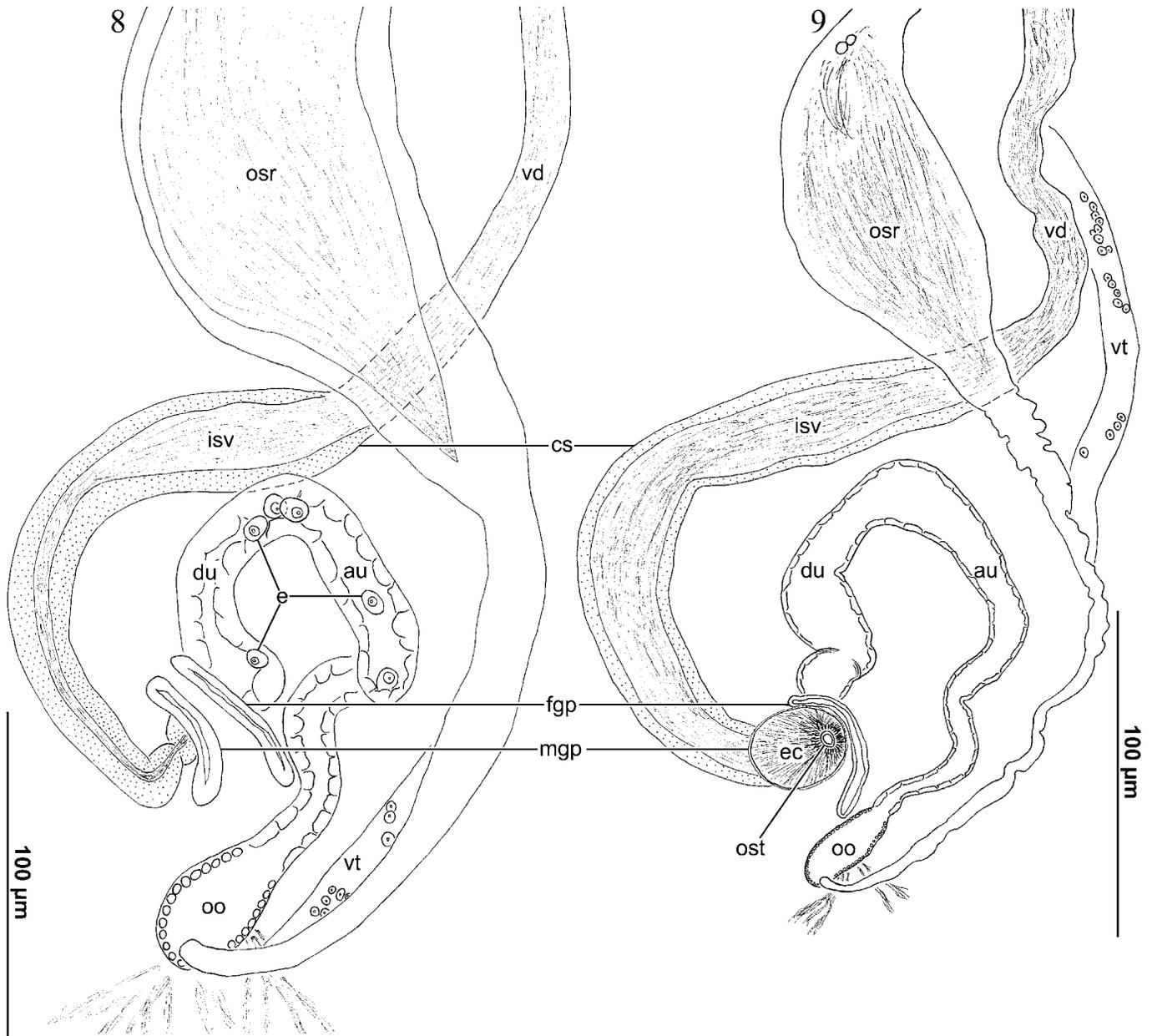
FIGURES 8, 9.  Genitalia of *Kritsky platyrhynchi* n. gen., n. sp. (Digenea: Aporocotylidae) from the body cavity of porthole shovelnose catfish, *Hemisorubim platyrhynchos* Valenciennes, 1840 (Siluriformes: Pimelodidae), dorsal views. Scale values beside each bar. Oviducal seminal receptacle (osr), vitelline duct (vt), oötype (oo), ascending uterus (au), descending uterus (du), female genital pore (fgp), vas deferens (vd), internal seminal vesicle (isv), cirrus sac (cs), male genital pore (mgp), everted cirrus (ec), opening of sperm tube (ost). (**8**) Voucher specimen (USNM Coll. No. 1254659) from Itaya River, Peru. (**9**) Paratype (CHIOC 34361a) from Baía River, Brazil.

Laurer's canal (see Short, 1954; Van der Land, 1967; Maillard and Ktari, 1978; Bullard et al., 2006; Orélis-Ribeiro et al., 2013). *Kritsky* can be most easily differentiated from the blood fluke genera including species that infect basal fish lineages, e.g., *Acipensericola* Bullard, Snyder, Jensen, and Overstreet, 2008, *Elopicola* Bullard, 2014, and *Paracardicoloides* Martin, 1974, by lacking a bowl-shaped anterior sucker, lateral tegumental spines, U-shaped intestine, Laurer's canal, intergonadal oötype, and common genital atrium and pore (Martin, 1974; Bullard et al., 2008; Bullard, 2014). The new genus differs from aporocotylid genera accommodating species that infect higher bony fishes (Euteleostei) by the combination of lacking lateral tegumental body spines and an intestine comprising paired anterior and posterior

---

←

vesicle (isv), male genital pore (mgp), uterus (u), oötype (oo), vitelline duct (vt), female genital pore (fgp); ventral view. (**6**) Anterior end of voucher specimen (USNM Coll. No. 1254659) showing row of spines (s), mouth (m), pharynx (p), esophagus (e); dorsal view. (**7**) High-magnification view of ceca of voucher specimen (USNM Coll. No. 1254659) showing posterior esophageal gland (peg), posterior esophageal swelling (pes), ceca (C1–C6); dorsal view.

ceca (Bullard and Overstreet, 2003, 2004; Bullard, 2010, 2012, 2013; Bullard et al., 2012; McVay et al., 2011).

### *Kritsky platyrhynchi* (Guidelli, Isaac, and Pavanelli, 2002) n. gen., n. comb.
(Figs. 5–9)

*Diagnosis of adult (measurements and illustrations based on 2 paratypes of* P. platyrhynchi *[CHIOC 34361a and 34361b] plus 4 stained, whole-mounted specimens):* Body 1,955–2,210 (2,075; 3) [1,868, 3,358] long, 272–518 (390; 4) [300, 600] wide or 5.4–7.2 (6.1; 3) [6.2, 5.6]✕ longer than wide (Fig. 5). Ventral and dorsal sensory papillae not evident with light microscopy. Dorsolateral nerve cords 6–12 (9; 4) [5, 8] wide near mid-body at widest level; 53–77 (67; 4) [65, 82] or 12–20% (18%; 4) [22%, 14%] of body width from body margin at mid-body, paired, contiguous anteriorly and posteriorly, becoming confluent with paired cord 35–55 (45; 3) [25, 67] or 2–3% (2%, 3) [1%, 2%] of BL from posterior body end; commissure of dorsolateral nerve cord 143–151 (148; 4) [148, 240] or 7% (7%; 3) [8%, 7%] of BL from anterior body end, 52–77 (65; 4) [70, 130] across width of the worm or 15–19% (17%; 4) [23%, 22%] of maximum body width, 4–7 (5; 4) [7, 10] in diameter, perpendicular to long axis of body, coursing dorsal to mid-portion of esophageal anterior swelling (Fig. 5). Anterior sucker base width 50–70 (58; 4) [52, 72] or 13–18% (15%; 4) [17%, 12%] of body width, 34–41 (38; 4) [34, 51] long or 1.3–1.7 (1.5; 4) [1.5, 1.4]✕ wider than long; 4 concentric rows of approximately 1 long 1 wide spines associated with anterior end; terminal papillae on anterior margin not present; denticles not present (Figs. 5, 6). Mouth 2–4 (3; 4) [3, 3] in diameter, 9–14 (12; 4) [10, 16] or 27–34% (30%; 4) [29%, 31%] of anterior sucker length from anterior end (Figs. 5, 6); pharynx immediately posterior to mouth, ovoid, 7–9 (8; 4) [9, 10] long or 1–2% (1%; 4) [2%, 1%] of esophagus length, 7–10 (9; 4) [8, 9] wide or 1 (1; 4) [1, 1]✕ longer than wide, with muscular wall 3–4 (4; 4) [4, 4] thick, not extending posteriad along esophagus beyond posterior margin of anterior sucker (Fig. 6). Esophagus 540–624 (570; 4) [588, 949] long or 26–28% (27%; 3) [32%, 28%] of BL, including (i) a distal portion, (ii) an anterior esophageal swelling portion, (iii) an elongated narrow portion, and (iv) a posterior swelling portion; distal portion typically (5 of 6 specimens) dilating to 9–15 (12; 4) [10, 7, not dilating] immediately after pharynx and extending straight posteriad for 18–25 (20; 4) [35, not dilating] or 3–4% (4%; 4) [6%, not dilating] of esophagus total length, narrowing to 5–8 (7; 4) [8, 10] and extending 30–44 (37; 4) [30, 84, not narrowing] or 5–9% (7%; 4) of esophagus total length before connecting with anterior esophageal swelling; anterior esophageal swelling 101–143 (124; 4) [110, 197] long or 19–23% (22%; 4) [19%, 21%] of esophagus total length, 19–26 (23; 4) wide or 5–7% (6%; 4) [7%, 4%] of maximum body width, with wall 7–8 (8; 4) [6, 6] thick, 66–83 (77; 4) [85, 106] or 3–4% (4%; 3) [5%, 3%] of BL from anterior body end; elongated narrow portion 11–15 (13; 4) [16, 22] wide, with wall 3–5 (4; 4) [3, 3] thick, extending directly posteriad 223–297 (265; 4) [273, 471] before connecting with posterior esophageal swelling; posterior esophageal swelling with elongate anterior portion and bulb-like posterior portion, anterior portion delineated anteriorly from narrow region of esophagus by slight bend of esophagus; posterior portion immediately anterior to cecal ramification 71–169 (111; 4) [70, 197] long or 13–27% (19%; 4) [12%, 21%] of esophagus length, 24–33 (30; 4) [21, 52] wide or 1.2–1.4 (1.3; 4) [1.1, 2]✕ maximum esophagus width, with wall 5–7 (6; 4) [6, 12] thick, ovoid, medial (Figs. 5, 7). Anterior esophageal gland 132–175 (149; 4) [indistinct, 235] long, 43–85 (62; 4) [indistinct, 135] wide or 2.3–3.3 (2.7; 4) [indistinct, 5.2]✕ width of anterior esophageal swelling (Fig. 5); posterior esophageal gland 154–207 (175) [140, 290] long or 27–38% (31%; 4) [24%, 31%] of esophagus length, 55–85 (70; 4) [58, 130] wide or 2.1–2.6 (2.4; 4) [2.8, 2.5]✕ width of posterior esophageal swelling, a loose aggregation of large gland-like cells bound by a thin and lightly-staining membrane (Figs. 5, 7). Intestine 532–623 (576; 4) [528, 963] or 27–28% (27%, 3) [28%, 29%] of BL from anterior body end; with six clearly differentiated ceca in all specimens examined, ceca (clockwise in ventral view from esophagus-intestine connection) 32–49 (43; 4) [63, 100], 46–79 (63; 4) [94, 145], 65–87 (74; 4) [75, 303], 61–111 (87; 4) [118, 224], 48–73 (61; 4) [90, 184], and 33–58 (46; 4) [75, 90] long or approximately 3–4% [5, 5] of BL and 10–14% [15, 18] of esophagus length, 21–47 (36; 4) [55, 106], 31–67 (55; 4) [47, 137], 37–75 (50; 4) [50, 94], 29–42 (36; 4) [63, 90], 40–56 (50; 4) [63, 90], and 34–47 (39; 4) [53, 72] wide or approximately 11–12% [18%, 16%] of maximum body width and 1.4–1.6 [2.6, 1.9]✕ maximum esophagus width, smooth (lacking diverticula), containing refractive content (not illustrated), cecal field 165–214 (191; 4) [215, 493] long or

9–10% (10%; 4) [12%, 15%] of BL and 26–39% (34%; 4) [37%, 52%] of esophagus length, 125–170 (140; 4) [221, 292] wide or 33–46% (37%, 4) [74%, 49%] of maximum body width; post-cecal distance 1,211–1,460 (1,330; 3) [1,135, 2,025] or 62–66% (64%; 3) [61%, 60%] of BL from posterior body end (Figs. 5, 7).

Testis 718–1054 (871; 4) [595, 1,238] long or 37–42% (39%; 3) [32%, 37%] of BL, 183–302 (239; 4) [220, 480] wide or 58–67% (62%; 4) [73%, 80%] of body width or 3.5–3.9 (3.7; 4) [2.7, 2.6]✕ longer than wide, containing dense field of vasa efferentia intertwining among densely packed testicular cells; testicular cells circular, each measuring 2 (2; 20) [2, 2] in diameter; post-testicular space 498–588 (539; 3) [430, 857] long or 26–27% (26%; 3) [23%, 26%] of BL. Vasa efferentia secondary ducts 2–13 (8; 15) [6{3}, 21{5}] wide, extending from lateral margins of testicular lobes (Fig. 5). Vas deferens a thin-walled duct, including a proximal portion ventral to testis and a post-testicular portion; proximal portion robust, comprising approximately 3–6 (5; 4) [3, 7] swollen trunks 9–40 (26; 17) [12{3}, 30{7}] wide, extending from lateral margins of testicular lobes before uniting in post-testicular portion; post-testicular portion 236–297 (259; 3) [172, 353] long or 11–13% (13%; 3) [9%, 11%] of BL, 44–65 (53; 4) [14, 95] wide at the level of posterior margin of testis, narrowing to 11–12 (11; 3) [12, 45] at level of ovary before curving sinistrad to connect with cirrus sac and internal seminal vesicle, ventral to ovary, containing sperm in all specimens (Figs. 5, 8, 9). Cirrus sac appendix-like, 159–178 (167; 3) [224, 343] long or 8% (8%; 4) [12%, 10%] of BL, 21–31 (26; 3) [27, 32] in maximum width or 7–8% (8%; 3) [9%, 5%] of body width, with glandular wall 1 (1, 3) [1, 1] thick (Figs. 5, 8, 9); internal seminal vesicle robust, occupying breadth and length of cirrus sac to varying degrees depending on amount of sperm present in duct, 15–21 (18; 3) [27, 14] in maximum width or 9.6–10.6 (8.5; 3) [8.3, 24.5]✕ longer that wide, extending toward sinistral margin before continuing posteriad approximately in parallel with sinistral body margin (Figs. 5, 8, 9); inverted cirrus opening in ventral view obliquely angled at ~70° from midline, 31–41 (35; 3) [not inverted, 52] wide, 4–10 (7; 3) [not inverted, 5] height, opening 57–88 (76; 3) [not inverted, 102] or 21–23% (22%; 3) [not inverted, 17%] of maximum body width from sinistral body margin, 85–143 (117; 3) [not inverted, 145] or 31–37% (33%; 3) [not inverted, 24%] of maximum body width from dextral body margin, posterolateral to female genital pore; 162–192 (173; 3) [not inverted, 260] or 8–9% (8%; 3) [not inverted, 8%] of BL from posterior body end; everted cirrus proximal base [25, not everted] wide, distal portion [8, not everted] wide, opening [54, not everted] or [18%, not everted] of maximum body width from sinistral body margin, [87, not everted] or [29%, not everted] of maximum body width from dextral body margin, posterolateral to female genital pore; [124, not everted] or [7%, not everted] of BL from posterior body end.

Ovary divided into dextral and sinistral fields of dendritic branches, having approximately 7 (7; 2) [indistinct, 7] dextral and 4 (4; 2) [indistinct, 5] sinistral narrow branches each 2–3 (3; 33) [indistinct, 7 {10}] wide, branches may coalesce, dextral and sinistral fields measuring 133–155 (142; 2) [indistinct, 212] and 70–113 (92; 2) [indistinct, 141] in maximum length or approximately 7% (7; 2) [indistinct, 6%] and 4–6% (5%; 2) [indistinct, 4%] of BL, 165–253 (209; 2) [indistinct, 354] in maximum width or 60–67% (64%; 2) [indistinct, 59%] of body width, 1.6–1.9 (1.8; 2)✕ wider than long; post-ovarian space 379–387 (383; 3) [indistinct, 640] long or 19% (19%; 2) [indistinct, 19%] of BL. Oviduct curving sinistrally immediately posterior to ovary and lateral to vas deferens, 325–368 (367; 3) [326, 675] long or 17–18% (18%; 3) [17%, 20%] of BL, including (i) an abbreviated proximal duct, (ii) a dilated portion (=oviducal seminal receptacle), and (iii) a narrow distal portion; proximal duct emanating from posteroventral surface of ovary extending sinistrally 27–38 (31; 3) [33, 75] with 8–12 (10; 3) [5, 8] maximum width, curving posteromediad to connect with oviducal seminal receptacle; oviducal seminal receptacle filled with sperm and ova in all specimens, 154–203 (182; 3) [153, 367] long or 47–51% (49%; 3) [47%, 54%] of total oviduct length, 23–79 (57; 3) [49, 134] wide or 5.2–14.1 (8.2; 3) [6.7, 5]✕ longer than wide, occupying space between vas deferens and sinistral body margin, crossing vas deferens dorsally, post-ovarian, distal portion of oviduct 7–8 (8; 3) [6, 11] or 9–35% (19%, 3) [12%, 8%] of oviducal seminal vesicle width, continuing posteriad approximately in parallel with dextral body margin before uniting with vitelline duct. Oötype 25–40 (31; 3) [23, 58] long, 12–26 (17; 3) [10, 23] wide, 1.5–2.1 (1.9; 3) [2.3, 2.5]✕ longer than wide, connecting with vitelline duct and oviduct dorso-posteriorly, slightly dextral, orienting diagonally (not parallel with longitudinal body axis); post-oötype distance 135–147 (140; 3) [95, 204] or 7% (7%; 3) [5%, 6%] of BL from posterior

body end (Figs. 5, 8, 9). Uterus occupying space between oötype and cirrus sac; 179–230 (209; 3) [214, 280] long or 9–11% (10; 3) [11%, 8%], 17–21 (19; 3) [21, 36] in maximum width, beginning with an ascending uterus 89–127 (112; 3) [136, 172] long or 5–7% (6; 3) [7%, 6%] of BL, typically (3 of 5 specimens) convoluted dorsally along ascending segment length, descending uterus 71–81 (77; 3) [77, 107] long or 62–80% (70%; 3) [57%, 62%] ascending uterus length; uterine eggs thin-shelled, ovoid, 4–10 (6; 22) [no eggs, 15 {5}] long, 3–8 (5; 22) [no eggs, 11 {5}] wide. Female genital pore in ventral view obliquely angled at ∼45° from midline, 37–55 (48; 3) [45, 71] wide, 2–5 (3; 3) [3, 5] height, 67–88 (81; 3) [70, 115] or 23–25% (23%; 3) [23%, 19%] of BL from sinistral body margin, 79–114 (98; 3) [79, 160] or 27–29% (28%; 3) [26%, 27%] of BL from dextral body margin, 182–192 (188; 3) [120, 311] or 9–10% (9%; 3) [6%, 9%] of BL from posterior body end.

Excretory system indistinct.

*Type and only host:* Porthole shovelnose catfish, *Hemisorubim platyrhynchos* Valenciennes, 1840 (Siluriformes: Pimelodidae).

*Type locality:* Baía River, floodplain of upper Paraná River Basin, Brazil.

*Other localities:* Itaya River, Amazon River Basin, Iquitos, Peru.

*Site in host:* Body cavity.

*Intensity of infection:* 10 specimens infected 1 porthole shovelnose catfish.

*Specimens examined:* CHIOC paratypes 34361a and 34361b plus 4 stained, whole-mounted adult specimens from body cavity of porthole shovelnose catfish (field number PI 432a; 15 cm total length; collection date: 13 September 2006) in the Itaya River (03°45′60″S, 73°14′44″W), Amazon River Basin, near Iquitos, Peru.

*Specimens deposited:* USNM Coll. Nos. 1254658 and 1254659 (2 vouchers); CHIOC No. 38217 (1 voucher).

### Remarks

Our observations of the paratypes and newly collected specimens of *Kritsky platyrhynchi* n. gen., n. comb. differed from the original description in several regards. Guidelli et al. (2002) did not report observations of an anterior sucker but one is clearly present, albeit comprising the typically diminutive anterior sucker of fish blood flukes. They described the mouth as "apical and very small, surrounded by 4 rows of denticles" (see Guidelli et al. [2002], Fig. 2d). They related these sclerites with those of *Plehniella dentata* Paperna, 1964 (very likely a species of *Nomasanguinicola*; see Truong and Bullard [2013]). Truong and Bullard (2013) argued that all clariid aporocotylids (Siluriformes: Clariidae) (i.e., *Nomasanguinicola canthoensis* Truong and Bullard, 2013, *P. dentata*, and *Sanguinicola clarias* Imam, El-Askalany, Hassan, and Itman, 1984) are congeners and likely have 2 columns of 4 denticles each that flank the mouth. These denticles should not be confused with the minute, straight spines arranged in 4 concentric rows described herein (see Truong and Bullard [2013] for a discussion on homology of spines). We regard the presence of this spinous anterior sucker as an important generic feature differentiating *K. platyrhynchi* from members of *Nomasanguinicola*, *Plehniella*, and *Sanguinicola*. Guidelli et al. (2002) described the diminutive pharynx as a "muscular organ" posterior to the mouth and summarized published descriptions of the pharynx in *S. inermis* Plehn, 1905, *S. argentinensis* Szidat, 1951, and *P. coelomicola* Szidat, 1951. The pharynx of the *K. platyrhynchi* resembles that of *N. canthoensis* and other species of *Plehniella* (Truong and Bullard, 2013; Orélis-Ribeiro and Bullard, 2015). Guidelli et al. (2002) indicated the presence of the posterior esophageal swelling as "enlarged and surrounded by numerous cells." We confirmed that the anterior esophageal swelling and its associated gland is present in all of the specimens we studied. Guidelli et al. (2002) described the vas deferens as "directed toward the posterior extremity of the body parallel and to the left of the uterus." The paratypes and newly collected specimens clearly show that the vas deferens is dextral to the oviducal seminal receptacle (Figs. 5, 8, 9). In addition, Guidelli et al. (2002) described the vas deferens as, "bending to the right and again to the medial region of the body." The vas deferens curves sinistrad once before connecting with a cirrus sac and an internal seminal vesicle (Figs. 5, 8, 9). Guidelli et al. (2002) described the female genital pore as dorsal to the ovary (see Guidelli et al.'s [2002] Fig. 2a, c), but in all specimens we studied the pore is clearly lateral to the male genital pore (Figs. 5, 8, 9). Perhaps related to this error, Guidelli et al. (2002) described the oviducal seminal receptacle as a distal portion of the uterus, the vitelline duct as the oviduct, and the uterus as a "prolonged and ascending seminal receptacle."

## DISCUSSION

The species and genus-level taxonomic diversity of catfish blood flukes (Table I) and the large proportion of catfishes that have yet to be thoroughly examined for infections together underscore the potential for aporocotylid species discovery. Including the present study, 9 species of blood flukes in 4 genera infect 11 catfishes of 7 genera among Auchenipteridae, Clariidae, Claroteidae, Mochoidae, and Pimelodidae (Table I). Yet no data are available for blood fluke infections in some species-rich catfish families. For example, the Neotropical family Loricariidae (907 species; Eschmeyer and Fong, 2015) is the fifth most diverse vertebrate family (Lujan et al., 2015) but lacks a single blood fluke record. This comprises a markedly under-sampled fish lineage for blood fluke infections.

Like in other fish blood fluke lineages (Bullard et al., 2008; Bullard and Overstreet, 2004, 2006; Orélis-Ribeiro et al., 2013; Bullard, 2014), morphologically similar blood flukes seemingly infect phylogenetically related catfishes (Orélis-Ribeiro and Bullard, 2015). The present study revealed some uncanny similarities between *K. platyrhynchi* and *Plehniella* spp., all of which infect body cavity of South American pimelodid catfishes (Remarks; Table I); for example, Truong and Bullard (2013) reported that congeneric aporocotylids infect walking catfishes (Clariidae) (see Table I).

Although redescriptions of *P. dentata* and *S. clarias* are needed, the presence of 2 columns of 4 denticles flanking either side of the mouth of those blood flukes and *N. canthoensis* likely indicates that they are congeners. Moreover, recollection and redescription of new specimens of *Sanguinicola chalmersi* Odhner, 1924, sourced from the type host and type locality in Africa may result in its assignment to a new genus. If so, the blood flukes of African catfishes (a multifamily clade informally named by Sullivan et al. [2006] as "Big Africa") may also comprise a taxonomically diverse and closely related group. Likewise, the relationship between catfish ancestry and the evolution of their blood flukes will be greatly advanced by examining additional South American catfishes for infections.

Because catfishes range or have ranged on all continents, including Antarctica (Grande and Eastman, 1986; Armbruster, 2011), focused collections targeting body cavity and vascular system of extant species for the presence of blood fluke infections could provide data to test biogeographic hypothesis regarding intra- and inter-continental relationships among the catfish blood flukes. The South American catfish blood flukes *C. tomasscholzi* and *K. platyrhynchi* and the African-Asian catfish blood flukes *N. canthoensis*, *P. dentata*, and *S. clarias* have a combination of a minute pharynx, an esophagus with anterior and posterior esophageal swellings enveloped by esophageal glands, a single testis that is pre-ovarian, a cirrus sac, a butterfly wing-shaped ovary, a post-ovarian uterus having ascending and descending segments, and separate genital pores as well as lacking a Laurer's canal. Thus, available morphological evidence suggests that the ancestor of those catfish blood flukes infected a Gondwanaland catfish.

On a continental scale, we report the first locality record of *K. platyrhynchi* from the upper Amazon Basin (Itaya River, Peru), approximately 3,000 km away from its type locality in the upper Paraná Basin (Baía River, Brazil). This distribution is consistent with the existence of a dispersal route between the Amazon and

Paraná basins (Hubert and Renno, 2006; Hubert et al., 2007). Given that no catfish blood fluke life cycle has been demonstrated, the identity of the molluscan (or polychaete) intermediate host represents an obvious gap in our knowledge that should be closed in order to test hypotheses concerning their biogeography: a given blood fluke's distribution may just as well be explained by the geographic distribution of its intermediate host(s).

Most blood flukes infect a variety of sites within the blood vascular system; many fewer infect the body cavity. In fact, these are the only blood flukes (Schistosomatoidea) that mature outside of the circulatory system. *Kritsky platyrhynchi* and *Plehniella* spp. represent 2 lineages of freshwater fish blood flukes that reportedly infect the body cavity of South American pimelodids (see Table I). *Deontacylix* spp., which are morphologically unlike the aforementioned genera in many ways, are the only lineage of marine fish blood flukes that infect the body cavity of sea chubs: *Deontacylix ovalis* Linton, 1910 (type species), from yellow sea chub, *Kyphosus incisor* Cuvier, 1831; Bermuda sea chub, *K. sectatrix* Linnaeus, 1758, and Cortez sea chub, *K. elegans* Peters, 1869 (Linton, 1910; Manter, 1947; Léon-Régagnon et al., 1997); and *D. kyphosi* Yamaguti, 1970, from blue sea chub, *K. cinerascens* Forsskål, 1775 (Yamaguti, 1970). Such a departure from infecting circulatory system likely has a physiological basis and associated advantages and disadvantages that would be exciting to explore. For example, perhaps body cavity flukes avoid the host immune response but have access to fewer host resources, given that they are no longer associated with blood. Such studies would require that we learn what fish blood flukes in both sites eat. Noteworthy also is that no information exists regarding the sites of egg deposition from any of these lineages. Szidat (1951) pointed out that, although he had thoroughly searched for eggs of *P. coelomicola* in the kidney and gill of fishes infected by adult flukes, he observed undeveloped eggs in the body cavity only; however, he did not detail the disposition or location of undeveloped eggs in the body cavity. Perhaps there are significant advantages to infecting the body cavity with respect to egress of eggs through the host's intestine, which would apparently represent a significant evolutionary departure from that of other fish blood flukes wherein miracidia are assumed to hatch from eggs embedded in gill epithelium and bore out of the fish (references in Bullard and Overstreet, 2008; Orélis-Ribeiro et al., 2014).

## ACKNOWLEDGMENTS

## LITERATURE CITED

ARMBRUSTER, J. W. 2011. Global catfish biodiversity. American Fisheries Society Symposium **77:** 15–37.

AVENDAÑO DE MAC INTOSH, F., AND M. OSTROWSKI DE NÚÑEZ. 1998. Seasonal dynamics of *Plehniella coelomica* (Trematoda: Aporocotylidae) in two catfish, *Pimelodus albicans* and *P. maculatus* (Pisces: Siluriformes), from La Plata River, Argentina. Folia Parasitologica **45:** 253–255.

BRASIL-SATO, M. C. 2003. Parasitos de peixes da bacia do São Francisco. *In* Águas, peixes e pescadores do São Francisco das Minas Gerais, H. P. Godinho and A. L. Godinho (eds.). PUC Minas, Belo Horizonte, Brazil, p. 149–165.

BRASIL-SATO, M. C., AND G. C. PAVANELLI. 2004. Digenea de *Pimelodus maculatus* (Osteichthyes: Pimelodidae) das bacias dos rios São Francisco e Paraná, Brasil. Parasitologia Latinoamericana **59:** 123–131.

BROWN, C. E. 1956. Composition of scientific words—A manual of methods and a lexicon of materials for the practice of logotechnics. Smithsonian Institution Press, Washington, D.C., 881 p.

BULLARD, S. A. 2010. A new species of *Cardicola* Short, 1953 (Digenea: Aporocotylidae) from the heart and branchial vessels of two surfperches (Perciformes: Embiotocidae) in the Eastern Pacific Ocean off California. Journal of Parasitology **96:** 382–388.

BULLARD, S. A. 2012. *Pearsonellum lemusi* n. sp. (Digenea: Aporocotylidae) from blood vascular system of gag grouper, *Mycteroperca microlepis*, (Perciformes: Serranidae) off Alabama, with an emendation of *Pearsonellum* Overstreet and Koie, 1989. Journal of Parasitology **98:** 323–327.

BULLARD, S. A. 2013. *Cardicola langeli* sp. n. (Digenea: Aporocotylidae) from heart of sheepshead, *Archosargus probatocephalus* (Actinopterygii: Sparidae) in the Gulf of Mexico, with an updated list of hosts, infection sites and localities for *Cardicola* spp. Folia Parasitologica **60:** 17–27.

BULLARD, S. A. 2014. Blood flukes (Digenea: Aporocotylidae) of Elopomorpha: emended diagnosis of *Paracardicoloides*, supplemental observations of *Paracardicoloides yamagutii*, and a new genus and species from ladyfish, *Elops saurus* in the northern Gulf of Mexico. Journal of Parasitology **100:** 305–316.

BULLARD, S. A., K. JENSEN, AND R. M. OVERSTREET. 2009. Historical account of the two family-group names in use for the single accepted family comprising the "fish blood flukes." Acta Parasitologica **54:** 78–84.

BULLARD, S. A., AND R. M. OVERSTREET. 2003. *Elaphrobates euzeti* gen. and sp. n. (Digenea: Sanguinicolidae) from snappers (Lutjanidae) in the Gulf of Mexico. *In* Taxonomie, écologie et évolution des métazoaires parasites. Taxonomy, ecology and evolution of metazoan parasites. Tome 1. C. Combes and J. Jourdane (eds.). PUP, Perpignan, France, p. 97–113.

BULLARD, S. A., AND R. M. OVERSTREET. 2004. Two new species of *Cardicola* (Digenea: Sanguinicolidae) in drums (Sciaenidae) from Mississippi and Louisiana. Journal of Parasitology **90:** 128–136.

BULLARD, S. A., AND R. M. OVERSTREET. 2006. *Psettarium anthicum* sp. n. (Digenea: Sanguinicolidae) from the heart of cobia *Rachycentron canadum* (Rachycentridae) in the northern Gulf of Mexico. Folia Parasitologica **53:** 117–124.

BULLARD, S. A., AND R. M. OVERSTREET. 2008. Digeneans as enemies of fishes. *In* Fish diseases. J. Eiras, H. Segner, T. Wahil, and B. G. Kapoor (eds.). Science Publishers, Enfield, New Hampshire, p. 817–976.

BULLARD, S. A., R. M. OVERSTREET, AND J. K. CARLSON. 2006. *Selachohemecus benzi* n. sp. (Digenea: Sanguinicolidae) from the blacktip shark *Carcharhinus limbatus* (Carcharhinidae) in the northern Gulf of Mexico. Systematic Parasitology **63:** 143–154.

BULLARD, S. A., S. D. SNYDER, K. JENSEN, AND R. M. OVERSTREET. 2008. New genus and species of Aporocotylidae (Digenea) from a basal actinopterygian, the American paddlefish, *Polyodon spathula* (Acipenseriformes: Polyodontidae) from the Mississippi Delta. Journal of Parasitology **94:** 487–495.

BULLARD, S. A., E. H. WILLIAMS JR., AND L. BUNKLEY-WILLIAMS. 2012. New genus and species of fish blood fluke (Aporocotylidae Odhner, 1912) from stoplight parrotfish, *Sparisoma viride* (Bonnaterre, 1788), (Perciformes: Scaridae: Sparisomatinae) in the Caribbean Sea. Journal of Parasitology **98:** 1139–1143.

CHAPMAN, A. D. 2009. Numbers of living species in Australia and the world. Australian Biological Resources Study. 2nd ed. Canberra, Australia. Available at: https://www.environment.gov.au/system/files/pages/2ee3f4a1-f130-465b-9c7a-79373680a067/files/nlsaw-2nd-complete.pdf. Accessed 1 May 2015.

EJSMONT, L. 1926. Morphologische, systematische und entwick- lungsgeschichtliche Untersuchungen an Arten des genus *Sanguinicola* Plehn. Bulletin International de l'Académie Polonaise des Sciences et des Lettres. Classe des Sciences Mathématiques et Naturelles. Serie B, Sciences Naturelles, **9–10B:** 877–966.

ESCHMEYER, W. N. 2015. Catalog of fishes. Available at: http://www.calacademy.org/scientists/projects/catalog-of-fishes, version of 2 September 2015. Accessed 18 September 2015.

ESCHMEYER, W. N., AND J. D. FONG. 2015. Species of fishes by family/subfamily. Available at: http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp, version of 2 September 2015. Accessed 18 September 2015.

FROESE, R., AND D. PAULY. 2015. FishBase, version 02/2015. World Wide Web electronic publication. Available at: www.fishbase.org. Accessed 15 May 2015.

GRANDE, L., AND J. T. EASTMAN. 1986. A review of Antarctic ichthyofaunas in the light of new fossil discoveries. Paleontology **29:** 113–137.

GUIDELLI, G. M., A. ISAAC, AND G. C. PAVANELLI. 2002. *Sanguinicola platyrhynchi* sp. n. (Digenea: Sanguinicolidae) parasite of visceral cavity of *Hemisorubim platyrhynchos* (Valenciennes, 1840) (Pisces: Pimelodidae) from the floodplain of the upper Paraná River. Brazilian Journal of Biology **64:** 801–806.

GUIDELLI, G. M., A. ISAAC, R. M. TAKEMOTO, AND G. C. PAVANELLI. 2003. Endoparasite infracommunities of *Hemisorubim platyrhynchos* (Valenciennes, 1840) (Pisces: Pimelodidae) of the Baía River, upper Paraná River floodplain, Brazil: Specific composition and ecological aspects. Brazilian Journal of Biology **63:** 261–268.

HUBERT, N., F. DUPONCHELLE, J. NUÑEZ, C. GARCIA-DAVILA, D. PAUGY, AND J.-F. RENNO. 2007. Phylogeography of the piranha genera *Serrasalmus* and *Pygocentrus*: Implication for the diversification of the Neotropical ichthyofauna. Molecular Ecology **16:** 2115–2136.

HUBERT, N., AND J.-F. RENNO. 2006. Historical biogeography of South American freshwater fishes. Journal of Biogeography **33:** 1411–1436.

IMAM, E. A., AND M. A. EL-ASKALANY. 1990. An approach to helminth parasites of catfish (*Clarias lazera*) in Beni-Suef Governorate. Assiut Veterinary Medical Journal **24:** 96–107.

IMAM, E. A., M. S. M. MARZOUK, A. A. HASSAN, AND R. H. ITMAN. 1984. Studies on *Sanguinicola* sp. (Trematoda) of Nile fishes. Veterinary Medical Journal **32:** 1–13.

KHALIL, L. F. 1969. Studies on the helminth parasites of freshwater fishes of the Sudan. Journal of Zoology **158:** 143–170.

KHALIL, L. F. 1971. Checklist of the helminth parasites of African freshwater fishes. Technical Communications 42, Commonwealth Institute of Helminthology, St. Albans, U.K., 80 p.

KIRK, R. S., AND J. W. LEWIS. 1993. The life-cycle and morphology of *Sanguinicola inermis* Plehn, 1905 (Digenea: Sanguinicolidae). Systematic Parasitology **25:** 125–133.

LÉON-RÉGAGNON, V., G. PÉREZ-PONCE DE LEÓN, AND L. GARCÍA-PRIETO. 1997. Description of *Heteroplectanum oliveri* n. sp. (Monogenea: Diplectanidae) and comments on the helminth fauna of *Kyphosus elegans* (Perciforms: Kyphosidae) from Chamela Bay, México. Journal of Helminthological Society of Washington **64:** 9–16.

LINTON, E. 1910. Helminth fauna of the Dry Tortugas. II. Trematodes. Carnegie Institution of Washington **133:** 11–98.

LUJAN, N. K., J. W. ARMBRUSTER, N. LOVEJOY, AND H. LÓPEZ-FERNÁNDEZ. 2015. Multilocus molecular phylogeny of the suckermouth armored catfishes (Siluriformes: Loricariidae) with a focus on subfamily Hypostominae. Molecular Phylogenetics and Evolution **82:** 269–288.

LUNASCHI, L. I. 1985. Helmintos parasitos de peces de agua dulce de la Argentina IV. Acerca de la validez del género *Plehniella* Szidat, 1951 (Trematoda-Sanguinicolidae). Neotropica **31:** 149–154.

MAILLARD, C., AND M. H. KTARI. 1978. *Hyperandrotrema cetorhini* n. g. n. sp. (Trematoda, Sanguinicolidae) parasite du système circulatoire de *Cetorhinus maximus* (Selacii). Annales de Parasitologie **53:** 359–365.

MANTER, H. W. 1947. The digenetic trematodes of marine fishes of Tortugas, Florida. American Midland Naturalist **38:** 257–416.

MARTIN, W. E. 1974. *Paracardicoloides yamagutii* gen. et sp. n. from an Australian eel (Trematoda: Sanguinicolidae). Proceedings of the Helminthological Society of Washington **41:** 22–25.

MCVAY, M. J., M. D. BAKENHASTER, AND S. A. BULLARD. 2011. *Cardicola laruei* Short, 1953 (Digenea: Aporocotylidae) from heart of seatrouts, *Cynoscion* spp., (Perciformes: Sciaenidae) in the Gulf of Mexico and Atlantic Ocean: Taxonomic redescription, first observations of egg and miracidium, and comments on geographic distribution and host specificity. Comparative Parasitology **78:** 291–305.

MITCHELL, M. A., AND T. N. TULLY JR. 2008. Manual of exotic pet practice. Saunders Elsevier, St. Louis, Missouri, 560 p.

NELSON, J. S. 2006. Fishes of the world. 4th ed. John Wiley and Sons, Hoboken, New Jersey, 601 p.

ODHNER, T. 1924. Remarks on *Sanguinicola*. Quarterly Journal of Microscope Science **68:** 403–411.

ORÉLIS-RIBEIRO R., C. R. ARIAS, K. M. HALANYCH, T. H. CRIBB, AND S. A. BULLARD. 2014. Diversity and ancestry of flatworms infecting the blood of non-tetrapod craniates "fishes." Advances in Parasitology **85:** 1–64.

ORÉLIS-RIBEIRO, R., AND S. A. BULLARD. 2015. Blood flukes (Digenea: Aporocotylidae) infecting body cavity of South American catfishes (Siluriformes: Pimelodidae): Two new species from rivers in Bolivia, Guyana, and Peru with a re-assessment of *Plehniella* Szidat, 1951. Folia Parasitologica **62**(050): 1–17.

ORÉLIS-RIBEIRO, R., C. F. RUIZ, S. S. CURRAN, AND S. A. BULLARD. 2013. Blood flukes (Digenea: Aporocotylidae) of lamniforms: Redescription of *Hyperandrotrema cetorhini* from basking shark (*Cetorhinus maximus*) and description of a new congener from shortfin mako shark (*Isurus oxyrinchus*) off Alabama. Journal of Parasitology **99:** 835–846.

PAPERNA, I. 1964. Parasitic helminths of inland-water fishes in Israel. Israel Journal of Zoology **13:** 1–20.

PAPERNA, I. 1996. Parasites, Infections and diseases of fishes in Africa. An update. Committee for Inland Fisheries of Africa (CIFA) Technical Paper No. 31, FAO, Rome, Italy, 220 p.

PLEHN, M. 1905. *Sanguinicola armata* und *inermis* (n. gen., sp. n.) n. fam. rhynchostomida. Ein entoparasitisches Turbellar im Blut von Cypriniden. Zoologischer Anzeiger **29:** 224–252.

QUEIROZ, J. F., J. N. P. LOURENÇO, AND P. C. KITAMURA. 2002. A Embrapa e a aqüicultura: demandas e prioridades de pesquisa. Embrapa Informação Tecnológica, Brasília, Brazil, 38 p.

REIS, R. E., S. O. KULLANDER, AND C. J. FERRARIS. 2003. Checklist of the freshwater fishes of South and Central America. Edipucrs, Porto Alegre, Brazil, 735 p.

SCHELL, S. C. 1974. The life history of *Sanguinicola idahoensis* sp. n. (Trematoda: Sanguinicolidae), a blood parasite of steelhead trout, *Salmo gairdneri* Richardson. Journal of Parasitology **60:** 561–566.

SHORT, R. B. 1954. A new blood fluke, *Selachohemecus olsoni*, n.g., n. sp. (Aporocotylidae) from the sharp-nosed shark, *Scoliodon terra-novae*. Proceedings of the Helminthological Society of Washington **21:** 78–82.

SULLIVAN, J. P., J. G. LUNDBERG, AND M. HARDMAN. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei, Siluriformes) using rag1 and rag2 nuclear gene sequences. Molecular Phylogenetics and Evolution **41:** 636–662.

SZIDAT, L. 1951. Neue Arten der Trematodenfamilie Aporocotylidae aus dem Blut und der Leibeshöhle von Süsswasserfischen des Rio de la Plata. Zeitschrift für Parasitenkunde **15:** 70–86.

TAKEMOTO, R. M., G. C. PAVANELLI, M. A. P. LIZAMA, A. C. F. LACERDA, F. H. YAMADA, L. H. A. MOREIRA, T. L. CESCHINI, AND S. BELLAY. 2009. Diversity of parasites of fish from the upper Paraná River floodplain, Brazil. Brazilian Journal of Biology **69:** 691–705.

TRUONG, T. N., AND S. A. BULLARD. 2013. Blood flukes (Digenea: Aporocotylidae) of walking catfishes (Siluriformes: Clariidae): New genus and species from the Mekong River (Vietnam) with comments on related catfish aporocotylids. Folia Parasitologica **60:** 237–247.

VAN DER LAND, J. 1967. A new blood fluke (Trematoda) from *Chimaera monstrosa* L. Proceedings. Koninklijke Nederlandse Akademie van

Wetenschappen, Section C, Biological and Medical Sciences **70:** 110–120.

WELCOMME, R. L., J. VALBO-JORGENSEN, AND A. S. HALLS. 2014. Inland fisheries evolution and management—Case studies from four continents. FAO Fisheries and Aquaculture Technical Paper No. 579. Rome, Italy, 77 p.

WOODLAND, W. N. F. 1923. *Sanguinicola* from the Sudan. Quarterly Journal of Microscopical Science 67: 233–242.

WOODLAND, W. N. F. 1924. Note on *Sanguinicola* from the Sudan: A correction. Quarterly Journal of Microscopical Science **68:** 411–412.

YAMAGUTI, S. 1970. Digenetic trematodes of Hawaiian fishes. Keigaku Publishing Company, Tokyo, Japan, 436 p.