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Revision of *Cryptogonimus* Osborn, 1903 and *Caecincola* Marshall et Gilbert, 1905 (Digenea: Cryptogonimidae), supplemental description of *Cryptogonimus chili* Osborn, 1903, and description of a new species of *Caecincola* infecting basses (Centrarchiformes: Centrarchidae) in Tennessee and Alabama rivers

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Abstract: We provide a supplemental description of the type species for *Cryptogonimus* Osborn, 1903 (Digenea: Cryptogonimidae), *Cryptogonimus chili* Osborn, 1903, based on newly-collected, heat-killed, formalin-fixed specimens infecting rock bass, *Ambloplites rupestris* (Rafinesque), and smallmouth bass, *Micropterus dolomieu* Lacepède (both Centrarchiformes: Centrarchidae), from the Duck River, Tennessee (USA). We emend *Cryptogonimus* to include features observed in the present specimens of its type species and in the descriptions of its congeners: a broad (wider than long) oral sucker, an intestine that bifurcates in the posterior half of the forebody, a bipartite seminal vesicle, a hermaphroditic duct that is dorsal to the ventral sucker, a preovarian seminal receptacle, and a Laurer's canal that opens dorsally at the level of the anterior testis. We describe *Caecincola duttonae* sp. n. (Cryptogonimidae) infecting largemouth bass, *Micropterus salmoides* (Lacepède), from Neely Henry Reservoir (Coosa River, Alabama, USA). The new species differs from its congeners by having a combination of a less elongate body, an intestine that bifurcates at the level of the ventral sucker, caeca that terminate at the level of the testes, diagonal testes in the middle of the hindbody, and a vitellarium predominantly distributed in the hindbody. We emend *Caecincola* Marshall et Gilbert, 1905 (type species *Caecincola parvulus* Marshall et Gilbert, 1905) to include features of the new species and recently-described congeners: an elongate body, an intestine that bifurcates in the posterior half of the forebody, caeca that extend posteriad beyond the testes, tandem testes, and a vitellarium that is wholly or primarily in the hindbody. Our 28S and ITS2 phylogenetic analyses recovered *Caecincola* and *Cryptogonimus* as sister taxa; *Caecincola* was recovered as paraphyletic with 28S but monophyletic with ITS2. This is the first phylogenetic study of Cryptogonimidae that includes a nucleotide sequence for a species of the type genus *Cryptogonimus*. We regard *Cryptogonimus diaphanus* (Stafford, 1904) Miller, 1941 as a *species inquirenda*.

Keywords: Gonotyl, protuberance, ventrogenital sac, phylogenetic analysis.

Species of *Cryptogonimus* Osborn, 1903 and *Caecincola* Marshall et Gilbert, 1905 (both Digenea: Cryptogonimidae) are morphologically similar and mature in the gastrointestinal tract of centrarchids in North America (Osborn 1903, Marshall and Gilbert 1905, Gibson 1996, Miller and Cribb 2008b, Curran and Overstreet 2009, Barger 2018). Osborn (1903) proposed *Cryptogonimus* for *Cryptogonimus chili* Osborn, 1903 (type species) infecting the stomach and intestine of smallmouth bass, *Micropterus dolomieu* Lacepède (Centrarchiformes: Centrarchidae) and "other fishes of Lake Chautauqua, New York and St. Mary's River, Michigan (USA)."

Osborn (1903) proposed, but did not explicitly diagnose, Cryptogoniminae Osborn, 1903 to accommodate *Cryptogonimus*. Ward (1917) ignored the proposal of Cryptogoniminae by Osborn (1903) and redundantly diagnosed a subfamily by the same name, Cryptogoniminae Ward, 1917. Miller and Cribb (2008b) dismissed the morphological evidence for cryptogonimid subfamilies, rejected the subfamilies, and accepted "Cryptogonimidae Ward, 1917."

The International Commission on Zoological Nomenclature (ICZN 1999; see also Notton et al. 2011). Article 29.1 (Formation of family-group names) states that, "A family-group name is formed by adding to the stem of the

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name [Art. 29.3] of the type genus, or to the entire name of the type genus [see Article 29.6], a suffix as specified in Article 29.2." Article 29.3 (Determination of stem in names of type genera) states that, "The stem of a family-group name is based on the name of its type genus."

Article 36 (Principal of coordination) states that, "A name established for a taxon at any rank in the family group (which includes the subfamily, family and superfamily) is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group; all of these taxa have the same type genus, and their names are formed from the stem of the name of the type genus [Art. 29.3] with appropriate change of suffix [Art. 34.1]. The name has the same authorship and date at every rank."

Hence, Cryptogonimidae Osborn, 1903 and Cryptogoniminae Osborn, 1903 are the correct authorities and dates for these taxa. Greer and Corkum (1979), without commenting on Cryptogoniminae *sensu* Ward (1917), accepted and emended Cryptogoniminae Osborn, 1903. Stafford (1904) and Greer and Corkum (1979) additionally described *Cryptogonimus diaphanus* (Stafford, 1904) Miller, 1941 and *Cryptogonimus spinovum* Greer et Corkum, 1979 that they collected from fish markets in Montreal (Canada) and from the False River (Pointe Coupee Parish, Louisiana, USA), respectively. Despite being the type genus for Cryptogonimidae, no DNA sequence is publicly available for any accepted species of *Cryptogonimus*.

Marshall and Gilbert (1905) erected *Caecincola* for *Caecincola parvulus* Marshall et Gilbert, 1905 (type species) infecting the pyloric caeca and stomach of largemouth bass, *Micropterus salmoides* (Lacepède), in Wisconsin (USA). Seven congeners have since been described, all of which infect black basses (*Micropterus* Lacepède) and white crappie, *Pomoxis annularis* Rafinesque (Centrarchidae) in North America (Premvati 1967, Greer and Corkum 1979, Curran and Overstreet 2009, Barger 2010, 2018, McAndrews and Barger 2017, Orcutt and Barger 2017). Marshall and Gilbert (1905) emphasised the morphological similarity between *Caecincola* and *Cryptogonimus* and diagnosed *Caecincola* by lacking a gonotyl and eyespot remnants (vs. *Cryptogonimus* that has a gonotyl and eyespot remnants).

Mueller (1934) differentiated *Caecincola* from *Cryptogonimus* by *Caecincola* lacking a gonotyl (vs. having a gonotyl), having minute tegumental spines (vs. large spines) and eggs having an abopercular protuberance (vs. lacking it). Gibson (1996) and Miller and Cribb (2008b) stated that *Caecincola* differed from *Cryptogonimus* only by lacking a gonotyl. Gibson (1996) and Curran and Overstreet (2009) suggested that *Caecincola* could be a junior subjective synonym of *Cryptogonimus* pending nucleotide-based phylogenetic analyses. Barger (2018), without a comment on the taxonomic identity of the two genera, regarded *Caecincola* as distinct from *Cryptogonimus*, accepted eight species of *Caecincola*, and provided a key to *Caecincola* spp. Prior to this study, the partial 18S and 28S ribosomal DNA sequences for *Ca. parvulus* comprise the only publicly available sequences representative of *Caecincola*.

In the present study, we provide a supplemental description of *Cr. chili*, describe a new species of *Caecincola*, emend the diagnoses for *Cryptogonimus* and *Caecincola*, provide keys to all accepted species of the two genera, and conduct the first phylogenetic analyses of Cryptogonimidae that includes species of its type genus (*Cryptogonimus*).

MATERIALS AND METHODS

Twelve largemouth bass were electrofished from Neely Henry Reservoir (33.7888N, 86.0526W, Coosa River, Alabama, USA) on 5 April 2022. Three rock bass, *Ambloplites rupestris* (Rafinesque) (Centrarchidae) and two smallmouth bass were also electrofished from Big Swan Creek (35.5608N, 87.3986W; Duck River, Tennessee, USA) on 29 August 2023. We also collected adult specimens of three other cryptogonimids to augment the phylogenetic analyses: *Caecincola longiscens* Curran et Overstreet, 2009 from three white crappie caught by hoop net in an oxbow of the Pascagoula River (30.6115N, 88.6387W; Jackson County, Mississippi, USA) on 6 June 2008; *Neochasmus sogandaresi* Overstreet, 1971 from a striped bass, *Morone saxatilis* (Walbaum) (Moronidae) caught by hook and line from Biloxi Bay (30.4309N, 89.0178W; northern Gulf of Mexico) on 16 March 2011; and *Pseudoacanthostomum floridense* Nahhas et Short, 1965 from a hardhead sea catfish, *Ariopsis felis* (Linnaeus) (Siluriformes: Ariidae) caught by hook and line from Davis Bayou (30.3918N, 88.7987W; northern Gulf of Mexico, Mississippi) on 19 June 2012.

Fishes were dissected in the field or transported to the laboratory alive or on ice and examined for parasites. Adult cryptogonimids were heat-killed using hot water (60°C), fixed in 10% neutral buffered formalin, stained overnight in Van Cleave's and Ehrlich's haematoxylins, dehydrated in an ethanol (EtOH) series, cleared in clove oil, and permanently mounted on glass slides using Canada balsam. Trematodes intended for DNA extraction were placed directly into 95% EtOH.

Line drawings were made with the aid of an Olympus BX51 microscope (Olympus Corporation of the Americas, Center Valley, Pennsylvania, USA). Jenoptik Gryphax® software version 2.1.0.724 (Jenoptik AG, Jena, Germany) was used for measurements and taking photomicrographs. Unless otherwise indicated, morphometric variations were reported in micrometres (µm) as the range, followed by the mean in parentheses. Measured eggs were from the distal uterus. Taxonomic authorities for fishes followed Fricke et al. (2024).

Anatomical terms for cryptogonimids followed Barger (2018), except that "prepharyngeal oesophagus", "postpharyngeal oesophagus", and "protuberance" (egg morphology) were used instead of "prepharynx", "esophagus", and "spinous process", respectively. Representatives of the adult cryptogonimids we collected herein were deposited as vouchers in the National Museum of Natural History's Invertebrate Zoology Collection (NMNH, Smithsonian Institution, Washington, D.C., USA) (see Table 1).

Twelve EtOH-preserved adult trematodes (two each from largemouth bass, rock bass, smallmouth bass, white crappie, striped bass, and hardhead sea catfish) were used to extract the genomic DNA using the DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany). DNA concentration was measured using a NanoDrop One spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA), diluted to 20 ng/µl, and stored at –20°C. The large

Table 1. New cryptogonimid specimens and sequences from the present study.

Species	GenBank accession number	Museum number
Cryptogonimus chili Osborn, 1903	PQ628042 (28S)[a], PQ628050 (ITS2)[a], PQ628041 (28S)[b], PQ628049 (ITS2)[b]	Vouchers USNM 1741945–947, 1741949
Caecincola duttonae Truong et Bullard sp. n.	PQ628043 (28S), PQ628052 (ITS2)	Holotype USNM 1741937, paratypes USNM 1741938–941
Caecincola longiscens Curran et Overstreet, 2009 n. comb.	PQ628051 (28S and ITS2)	Vouchers USNM 1741942–944
Neochasmus sogandaresi Overstreet, 1971	PQ628048 (28S and ITS2)	Vouchers USNM 1741950–953
Pseudoacanthostomum floridense Nahhas et Short, 1965	PQ628047 (28S and ITS2)	Vouchers USNM 1741954–957

[a]ex rock bass; [b]ex smallmouth bass.

subunit ribosomal DNA (partial 28S) was amplified using forward primer (digl2: 5′–AAGCATATCACTAAGCGG–3′) and reverse primer (1500R: 5′–GCTATCCTGAGGGAAACTTCG–3′) (Tkach et al. 2003). The complete internal transcribed spacer 2 region (ITS2) was amplified using GA1 (5'–AGAACATCGACATCTTGAAC–3') and ITS2.2 (5'–CCTGGTTAGTTTCTTTTCCTCCGC–3') (Anderson and Barker 1998, Cribb et al. 1998).

PCR reactions were performed with the following thermocycling parametres: initial denaturation step of 94°C for 4 min, followed by 40 cycles of 94°C for 40 s, 52°C for 30 s, 72°C for 2 min, with a final extension step of 72°C for 5 min. PCR product was purified using the QIAquick PCR Purification kit (Qiagen). Both PCR primers (digl2, 1500R, GA1, and ITS2.2) were used in DNA sequencing reactions. Two internal primers 300F (5'–CAAGTACCGTGAGGGAAAGTTG–3') and 1200R (5'–GCATAGTTCACCATCTTCGG–3') were also used to improve 28S sequencing coverage (Lockyer et al. 2003). Additional DNA sequences of other cryptogonimids were presented in Table 1. DNA sequencing was performed by Genewiz (South Plainfield, New Jersey, USA). Representative nucleotide sequences of species lacking intraspecific variation and all generated sequences of species exhibiting intraspecific variation were deposited in the NCBI GenBank (see Table 1).

Taxon and outgroup selection was based on previous phylogenetic studies of Cryptogonimidae of Kmentová et al. (2020) and Yong et al. (2023). Selected sequences were from Olson et al. (2003), Miller and Cribb (2007a–c, 2008a, 2009, 2013), Katokhin et al. (2008), Bray et al. (2009), Miller et al. (2009, 2010a,b, 2018), Thaenkham et al. (2011), Jayawardena et al. (2013), Wongsawad et al. (2017), Kvach et al. (2018), Pantoja et al. (2018), Hernández-Orts et al. (2019), Kmentová et al. (2020), Miller and Adlard (2020), Solodovnik et al. (2021), Martin and Cutmore (2022), Santacruz et al. (2022), and Yong et al. (2023).

Sequences were aligned using MAFFT (Katoh and Standley 2013). The alignments were exported as .phy files to run the phylogenetic analyses using Maximum Likelihood. Trees were inferred with IQ-TREE v.1.16.12 (Nguyen et al. 2015). Substitution model testing was done with ModelFinder (Kalyaanamoorthy et al. 2017) as implemented in IQ-TREE. After model testing, tree inference was done using the best-fitting substitution model GTR + F + I + G4 (Chernomor et al. 2016).

Default tree search parametres 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 (Hoang et al. 2018). The inferred phylogenetic trees were visualised using FigTree v1.4.4 (Rambaut et al. 2014) and further edited with Adobe Illustrator 28.5 version (2024) (Adobe Systems, San Jose, California, USA).

RESULTS

Cryptogonimus Osborn, 1903, emended

Synonym: *Protenteron* Stafford, 1904

Type species: *Cryptogofzoobannimus chili* Osborn, 1903.

Other species: *Cryptogonimus diaphanus* (Stafford, 1904) Miller, 1941 (*species inquirenda*); *Cryptogonimus spinovus* Greer et Corkum, 1979.

Diagnosis: Body elongate. Tegument spinous; spines minute, scale-like, distributing over entire body surface except on suckers. Eyespot remnants compacted or dispersed in pharyngeal region. Oral sucker funnel-shaped, terminal, wider than long. Enlarged circumoral spines absent. Ventrogenital sac in anterior half of body. Ventral sucker subspherical, smaller than oral sucker, in anterior half of body, deeply embedded in ventrogenital sac. Gonotyl sucker-like, single, median, immediately anterior to or slightly overlapping anterior margin of ventral sucker, smaller or larger than ventral sucker, embedded in ventrogenital sac.

Prepharynx shorter or longer than pharynx. Oesophagus distinct, shorter or longer than pharynx. Pharynx subspherical or ovoid. Intestine bifurcating in posterior half of forebody; caeca blindly ending at level of or beyond testes.

Testes two, ovoid or ellipsoid, tandem, diagonal, or nearly opposite, separate, abutting or slightly overlapping, at middle of hindbody. Seminal vesicle bipartite, wholly in hindbody, pretesticular. *Pars prostatica*, cirrus and genital atrium indistinct or absent. Hermaphroditic duct dorsal to ventral sucker, wholly internal to ventrogenital sac. Genital pore immediately anterior to ventral sucker, opening into ventrogenital sac cavity.

Ovary lobed, median or submedian, pretesticular or ventrally overlapping testes. Mehlis' gland and Laurer's canal present. Seminal receptacle canalicular, anterodorsal to ovary. Uterus comprising descending and ascending portions, occupying body space from ventral sucker to near posterior body end. Eggs numerous, ovoid, operculate; abopercular end broadly rounded or having protuberance.

Vitellarium follicular, in two separate lateral fields; vitelline fields distributing into forebody and hindbody. Excretory bladder Y-shaped; main stem bifurcating at level of testes; arms extending anteriad to level of pharynx; pore terminal.

Adults infecting pyloric caeca, stomach, and intestine of freshwater fishes (Centrarchiformes) in North America.

Differential diagnosis: Body elongate. Oral sucker funnel-shaped. Enlarged circumoral spines absent. Gonotyl sucker-like, single, immediately anterior to or slightly

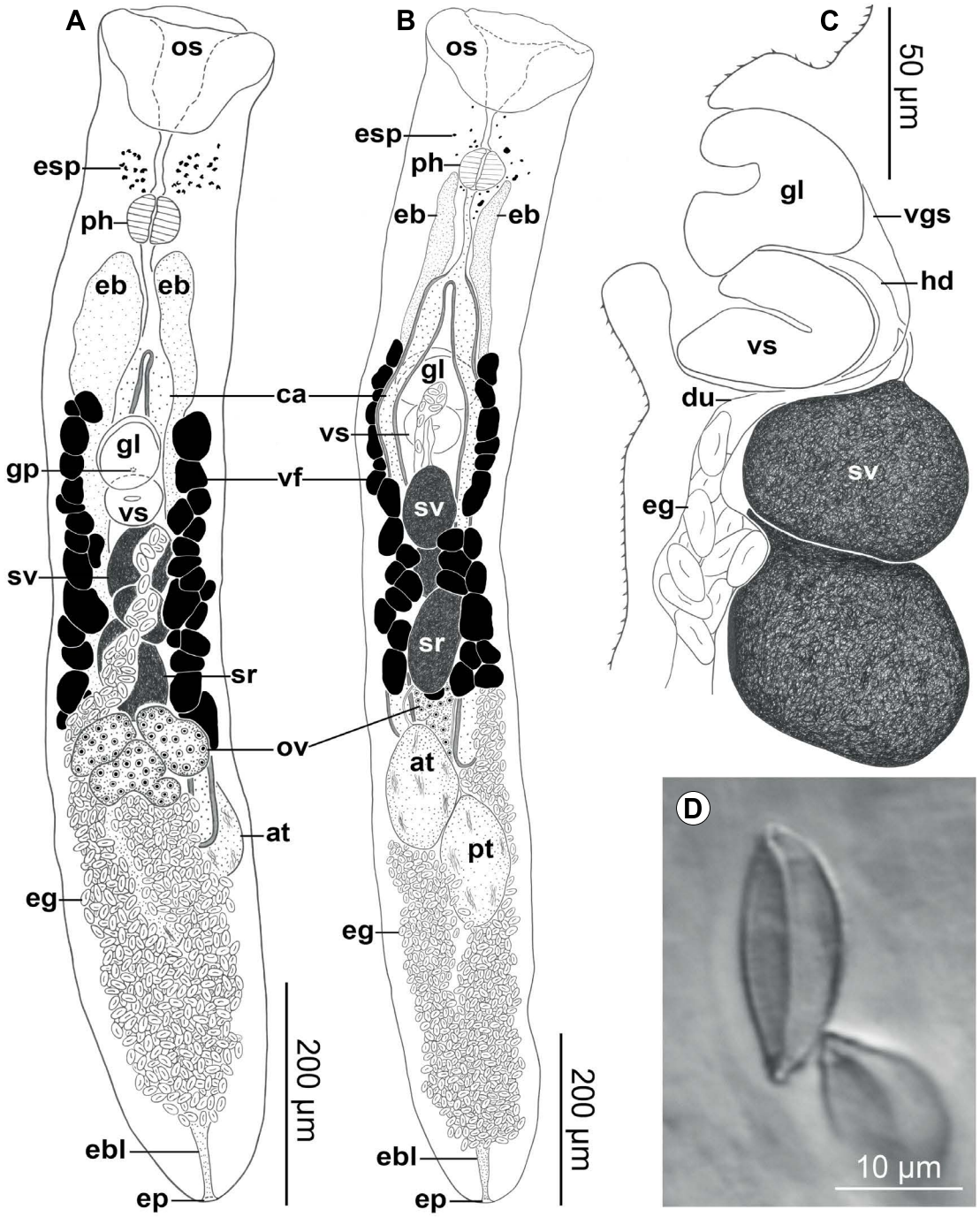

Fig. 1. *Cryptogonimus chili* Osborn, 1903 (Digenea: Cryptogonimidae) infecting rock bass, *Ambloplites rupestris* (Rafinesque) (Centrarchiformes: Centrarchidae) from the Duck River, Tennessee, USA. **A** – ventral view of voucher USNM 1741945 showing anatomical organs; **B** – dorsal view of voucher USNM 1741946; **C** – lateral view of voucher USNM 1741949 showing the terminal male and female genitalia; **D** – photomicrograph of mature eggs. *Abbreviations*: at – anterior testis; ca – caecum; du – distal uterus; eb – excretory branch; ebl – excretory bladder; eg – egg; ep – excretory pore; esp – eyespot remnant; gl – gonotyl; gp – genital pore; hd – hermaphroditic duct; os – oral sucker; ph – pharynx; pt – posterior testis; sr – seminal receptacle; sv – seminal vesicle; vf – vitelline follicles; vgs – ventrogenital sac; vs – ventral sucker.

overlapping ventral sucker. Caeca ending blindly. Testes two. Seminal vesicle bipartite. Eggs with abopercular end broadly rounded or having protuberance.

***Cryptogonimus chili* Osborn, 1903** Fig. 1A–D

Supplemental description (based on light microscopy of 20 heat-killed, formalin-fixed, stained, whole-mounted adult specimens): Body elongate, 727–1,674 (998) long, 128–255 (177) wide (4.5–6.8× [5.7×] longer than wide); forebody 273–560 (360) long, (32–41% [36] of body length); hindbody 406–1,031 (592) long (55–72% [59] of body length), 1.4–2.0× (1.6×) longer than forebody (Fig. 1A,B). Eyespot pigment compact or dispersed near dorsal body surface between oral sucker and pharynx. Oral sucker

wider than long, 89–151 (124) long, 104–239 (159) wide (66–99% [90%] of body width). Ventral sucker 32–67 (49) long, 38–76 (56) wide (25–39% [32%] of body width). Oral sucker 1.7–3.9× (2.8×) wider than ventral sucker (Fig. 1A,B). Gonotyl slightly overlapping anterior margin of ventral sucker, 43–85 (60) long, 48–97 (61) wide (28–42% [35%] of body width), 0.9–1.5× (1.2×) longer than ventral sucker, 0.8–1.3× (1.1×) wider than ventral sucker. Prepharynx oesophagus 14–82 (33) long (2–5% [3%] of body length). Pharynx subspherical, 36–59 (45) long (3–6% [5%] of body length), 38–58 (46) wide (20–34% [26%] of body width). Oesophagus longer than prepharynx and pharynx, 42–143 (77) long (5–11% [8%] of body length). Intestine bifurcating in posterior half of forebody, 189–392 (263) from anterior body end (22–33% [27%] of body length); caeca thick-walled along its length, unequal in length, extending posteriad to level of testes; postcaecal space 271–579 (403) long (25–42% [34%] of body length) (Fig. 1A,B).

Testes longer than wide, median, diagonal, typically abutting, occasionally slightly overlapping or separate by some distance, in middle of hindbody; anterior testis 98–180 (131) long (9–16% [13%] of body length), 45–102 (70) wide (28–52% [39%] of body width); posterior testis 98–186 (139) long (9–18% [14%] of body length), 45–118 (75) wide (28–59% [42%] of body width); pretesticular space 420–1,017 (593) long (54–69% [58%] of body length); post-testicular space 137–394 (227) long (17–29% [23%] of body length) (Fig. 1A,B). Vasa efferentia extending anteriad from anterior margin of each testis, their courses incompletely observed; vas deferens not observed. Seminal vesicle filled with sperm, occupying most of anterior half of inter-caecal space between ventral sucker and ovary, anteriorly merging with distal uterus to form hermaphroditic duct dorsal to ventral sucker; anterior part ovoid, 51–140 (77) long, 38–108 (60) wide; posterior part ovoid, shorter than anterior part, 30–109 (55) long, 27–89 (46) wide (Fig. 1A–C). Genital pore median, immediately anterior to ventral sucker and posterior to gonotyl (Fig. 1A).

Ovary comprising 4–5 unequal lobes, median, wider than long, anterior to and ventrally overlapping testes, 65–159 (100) long (8–13% [10%] of body length), 78–162 (113) wide (51–76% [63%] of body width); preovarian space 391–925 (544) long (50–66% [54%] of body length) (Fig. 1A,B). Mehlis' gland cells numerous, primarily preovarian. Seminal receptacle ovoid or ellipsoid, median, pretesticular, dorsally overlapping posterior part of seminal vesicle and anterior half of ovary, filled with sperm, 71–128 (98) long, 45–75 (59) wide (Fig. 1A,B). Oviduct and Laurer's canal difficult to discern in whole-mounted specimens.

Vitelline fields wholly pretesticular, extending from slightly anterior to gonotyl or at level of ventral sucker posteriad to level of ovary, surrounding caeca, 183–505 (300) long (22–41% [30%] of body length); previtelline space 207–605 (301) long (21–41% [30%] of body length); postvitelline space 275–661 (407) long (35–47% [41%] of body length) (Fig. 1A,B); transverse vitelline ducts symmetrical, primarily dorsal to and at level of ovary, approximately branching at 131–420 (243) from anterior extent of each vitelline field (61–95% [79%] of body length), extending posteromedian 31–142 (64) to form vitelline reservoir. Vitelline reservoir oblong or subtriangular in outline, median, pretesticular, immediately posterior to or ventrally overlapping posterior margin of seminal receptacle, 10–21 (15) long, 9–36 (23) wide.

Uterus primarily ventral to testes, comprising several post-testicular coils, filling most post-testicular space in fully mature specimens, dorsally originating from ovary, descending posteriad sinistrally to near posterior body end, ascending dextrally to level of ovary, entering ventrogenital sac ventral to seminal vesicle and seminal receptacle; distal end of uterus lacking muscular layer (metraterm absent) (Fig. 1A–C). Eggs having smooth surface, transparent in proximal uterus, becoming tanned in distal uterus, 19–24 (21) long, 10–13 (11) wide; abopercular end broadly rounded, lacking protuberance (Fig. 1A–D).

Excretory bladder slender proximally; excretory branches enlarged distally, ventral to caeca, extending anteriad to level of or slightly posterior to pharynx (Fig. 1A,B).

Type host: Smallmouth bass, *Micropterus dolomieu* Lacepède (Centrarchiformes: Centrarchidae).

Hosts of present study: Rock bass, *Ambloplites rupestris* (Rafinesque) (Centrarchiformes: Centrarchidae) and smallmouth bass.

Type locality: Osborn (1903) did not designate the type locality. He collected adults of *Cr. chili* from Chautauqua Lake, Chadakoin River, New York and Saint Mary's River, Michigan (both USA).

Locality of present study: Big Swan Creek (35.5608N, 87.3986W), Duck River, Tennessee (USA).

Site of infection: Stomach and intestine.

Prevalence and intensity of infection: Three of 3 rock bass (100%) were infected by 2, 7 and 7 adult worms; 1 of 2 smallmouth bass (50%) were infected by 34 adult worms.

Specimens and sequences deposited: See Table 1.

Museum specimens examined: vouchers of *Cr. chili* (also labelled as *Cryptogonimus chyli*), including USNM 1350346 (1 slide), USNM 1356183 (28 slides), USNM 1372215 (1 slide), USNM 1374145 (1 slide), USNM 1385104 (6 slides), USNM 1390661 (8 slides), USNM 1395254 (1 slide), 1395257 (1 slide), and USNM 1396895 (2 slides); holotype of *Cr. spinovus* USNM 1370367 (labelled as *Cr. spinovum*).

Taxonomic remarks

Miller and Cribb (2008b) diagnosed *Cryptogonimus* as having an oral sucker that was longer than wide, an intestine that bifurcated immediately anterior to the ventral sucker, and a tubular (unipartite) seminal vesicle. They did not treat the fine features of the male and female reproductive systems, i.e., the hermaphroditic duct, seminal receptacle and Laurer's canal.

We herein emend *Cryptogonimus* to include features observed in the newly-collected, properly heat-killed specimens of *Cr. chili* and in the holotype of *Cr. spinovus*. These features comprise an oral sucker that is wider than long (present in *Cr. chili* and *Cr. spinovus*), an intestine that

bifurcates in the posterior half of the forebody (*Cr. chili*), a bipartite seminal vesicle (*Cr. chili* and *Cr. spinovus*), a hermaphroditic duct that is dorsal to the ventral sucker (*Cr. chili* and *Cr. spinovus*), a seminal receptacle that is anterodorsal to the ovary (*Cr. chili* and *Cr. spinovus*), and a Laurer's canal that dorsally opens at the level of the anterior testis (*Cr. spinovus*).

The original description of *Cr. diaphanus* by Stafford (1904) (as *Protenteron diaphanum* Stafford, 1904; based on unspecified number of adult specimens infecting the intestine of rock bass from Montreal, Canada, collected by Stafford from 1901 to 1903) was incomplete and included outlier features, i.e., a ventral sucker (0.62 mm wide) twice as wide as the body (0.385 mm), short caeca terminating at the posterior margin of or slightly beyond the ventral sucker, and eggs that were 0.22 mm long and 0.011 mm wide (Stafford's measurements for *Cr. diaphanus* were probably misprints). No illustration of *Cr. diaphanus* was provided by Stafford (1904).

A redescription (with a single figure of laterally-mounted whole body) of *Cr. diaphanus* by Miller (1941) (based on a single unnamed, poorly-mounted, poorly-stained trematode specimen infecting rock bass from an unspecified locality, collected by Stafford in 1904) was also incomplete and comprised some doubtful features: an oral sucker that was longer than wide, an entire ovary and eggs that were 0.2 mm long and 0.1 mm wide (probably also misprinted measurements). These unusual features reported for *Cr. diaphanus* clearly do not fit the present emended diagnosis of *Cryptogonimus*. *Cryptogonimus diaphanus* needs a redescription based on fresh, properly heat-killed, formalin-fixed, stained specimens from the type host and type locality or nearby areas. Hence, until a sufficient redescription of *Cr. diaphanus* is available, we herein consider *Cr. diaphanus* as a *species inquirenda*.

Cryptogonimus chili required a morphological reappraisal because the narrative descriptions of this species by Osborn (1903, 1910) were incomplete and dubious. Osborn (1903, 1910) described *Cr. chili* (also spelled as *Cr. chyli* by Osborn 1910, Mueller 1934, Van Cleave and Mueller 1934, Miller 1941) as "The worms appear to the naked eye as extremely minute black spots…" and "The minute worms are detected as black spots of elongate form". Osborn (1903) reported that *Cr. chili* was 0.525–9.3 mm long. Osborn (1910), perhaps re-examining the same specimens, reported the length of *Cr. chili* with a much narrower range (0.525–1.3 mm).

We consider the maximum body length of *Cr. chili* presented in Osborn (1903) as a misprint (body length probably ranges from 0.525 to 0.93 or to 1.3 mm) as compared to his two narrative descriptions of this species. Further, Osborn (1903, 1910) inconsistently (erroneously) described the anatomy of this species. The seminal vesicle was depicted as elongated and unipartite by Osborn (1903; fig. 1) but later illustrated as tripartite in Osborn (1910; figs. 2, 3). We suspect that Osborn (1910) misinterpreted the seminal receptacle as a part of the seminal vesicle because Osborn (1903, 1910) erroneously stated that *Cr. chili* lacked a seminal receptacle.

Regarding the female complex, Osborn (1903; figs. 1, 2) drew the ovary of *Cr. chili* with smooth margins and as pretesticular or intertesticular, whereas Osborn (1910; fig. 1) illustrated the ovary of *Cr. chili* as trilobed and ventral to both testes. Van Cleave and Mueller (1934; fig. 4) collected specimens of *Cr. chili* from rock bass and smallmouth bass in Oneida Lake (New York, USA) that were 0.88 mm long and had a preovarian seminal receptacle and an ovary with 7–8 lobes.

The present specimens of *Cr. chili* from the Duck River are important and potentially good vouchers for future studies of this species and related cryptogonimids because they were well-fixed, well-stained, properly-mounted, and matched the voucher specimens of *Cr. chili*. At the time of writing this paper, we could not locate a type specimen of *Cr. chili* from Osborn's (1903, 1910) studies nor a voucher of *Cr. chili* deposited by Van Cleave and Mueller (1934) to confirm the body measurements and the dubious features of *Cr. chili* reported by Osborn (1903, 1910).

We studied a voucher specimen of *Cr. chili* (USNM 1350346) collected and identified by Osborn (1903) from smallmouth bass from Minnesota (USA). This specimen was 0.57 mm long, contracted and poorly-fixed such that the gonads, hermaphroditic duct and distal portions of the male and female genitalia were indiscernible. Other vouchers of *Cr. chili* (see Taxonomic summary; all in poor condition) we examined were 0.82–1.45 mm long and had a bipartite seminal vesicle, an ovoid seminal receptacle immediately posterior to or slightly overlapping the posterior part of the seminal vesicle, and an ovary having 4–5 lobes and ventral to the testes.

Our supplemental description of *Cr. chili* herein includes several new observations, including a body that is 727–1,674 long (4.5–6.8× longer than wide), an oral sucker that is wider than long, an intestine that bifurcates in the posterior half of the forebody, a bipartite seminal vesicle, a hermaphroditic duct that is dorsal to the ventral sucker, a pretesticular seminal receptacle, and an ovary having 4–5 unequal lobes. Some of our specimens of *Cr. chili*, however, were slightly longer than those reported in Osborn (1903, 1910) and Van Cleave and Mueller (1934), perhaps related to specimen age.

We provide a key to accepted species of *Cryptogonimus*:

1a. Caeca extending into post-testicular space; vitellarium extending anteriad to level of pharynx; eggs having pointed abopercular protuberance .... *Cryptogonimus spinovus*

1b. Caeca terminating at level of testes; vitellarium extending anteriad to slightly anterior to gonotyl; eggs lacking abopercular protuberance ..... *Cryptogonimus chili*

Caecincola Marshall et Gilbert, 1905, emended

Type species: *Caecincola parvulus* Marshall et Gilbert, 1905.

Other accepted species: *Caecincola aubergine* Barger, 2018; *Caecincola autumnae* Barger, 2010; *Caecincola cookorum* McAndrews et Barger, 2017; *Caecincola latostomus* Greer et Corkum, 1979; *Caecincola longiscens* Curran et Overstreet, 2009; *Caecincola septimus* Orcutt et Barger, 2017; *Caecincola wakullata* Premvati, 1967.

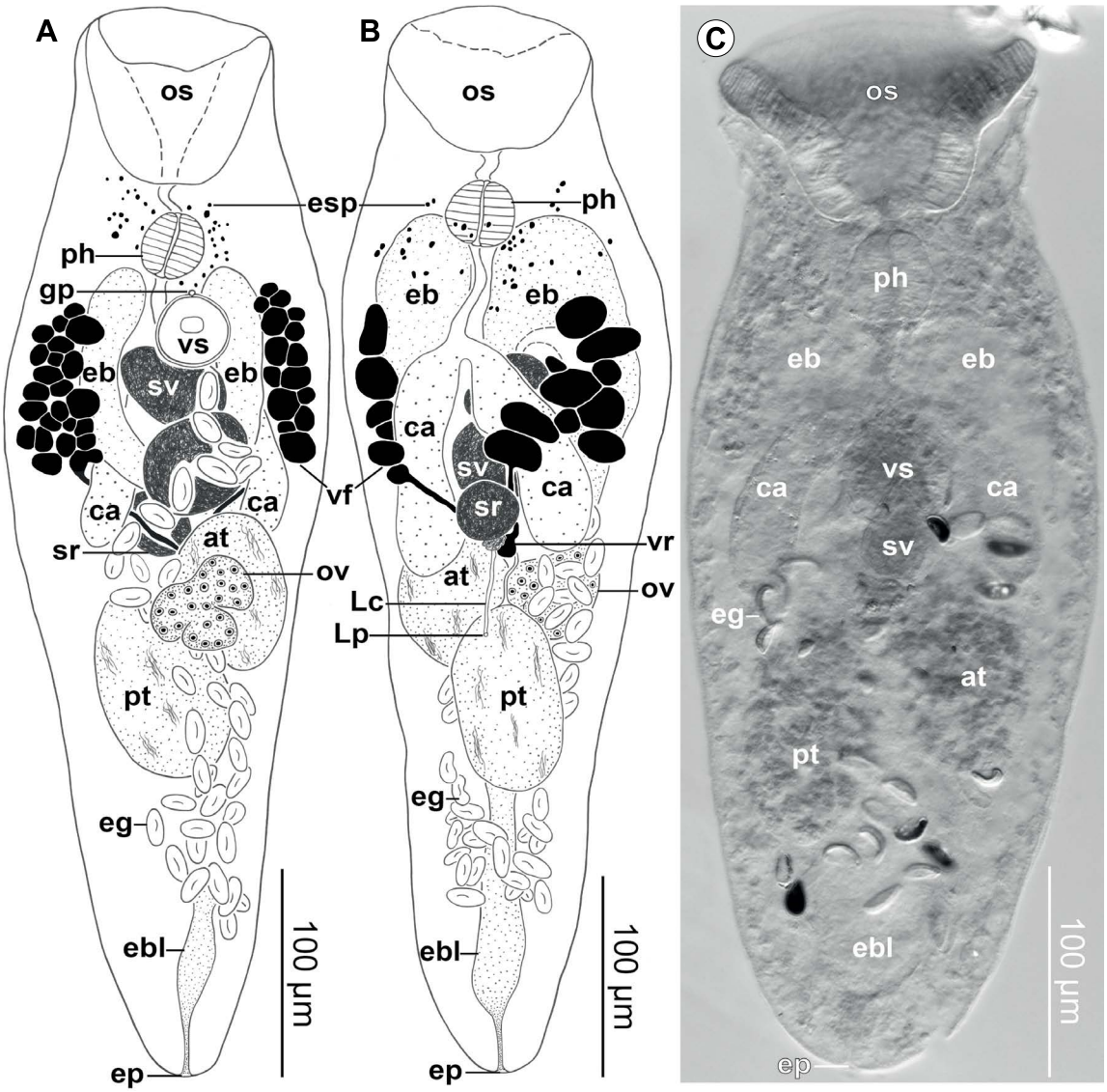

Fig. 2. *Caecincola duttonae* Truong et Bullard sp. n. (Digenea: Cryptogonimidae) infecting largemouth bass, *Micropterus salmoides* (Lacepède) (Centrarchiformes: Centrarchidae) from Neely Henry Reservoir, Coosa River, Alabama, USA (A, B) and *Caecincola parvulus* Marshall et Gilbert, 1905 infecting largemouth bass from Wisconsin, USA (C). **A** – ventral view of the holotype USNM 1741937 showing anatomical organs; **B** – dorsal view of a paratype USNM 1741938; **C** – photomicrograph of a syntype (USNM 1350225, dorsal view). *Abbreviations*: at – anterior testis; ca – caecum; eb – excretory branch; ebl – excretory bladder; eg – egg; ep – excretory pore; esp – eyespot remnant; gp – genital pore; Lc – Laurer's canal; Lp – Laurer's canal pore; os – oral sucker; ov – ovary; ph – pharynx; pt – posterior testis; sr – seminal receptacle; sv – seminal vesicle; vf – vitelline follicles; vr – vitelline reservoir vs – ventral sucker.

Diagnosis: Body subovoid, elongate-ovoid, or elongate. Tegument spinous; spines minute, scale-like, distributing over entire body surface except on suckers. Eyespot remnants compacted or dispersed in pharyngeal region. Oral sucker funnel-shaped, terminal, ranging from wider than long to longer than wide. Enlarged circumoral spines absent. Ventrogenital sac in anterior half or middle of body. Ventral sucker subspherical, smaller than oral sucker, embedded in ventrogenital sac. Gonotyl absent.

Subspherical or ovoid. Prepharynx indistinct, shorter or longer than pharynx. Pharynx oesophagus distinct, shorter or longer than pharynx. Intestine bifurcating in posterior half of forebody or at level of ventral sucker; caeca blindly ending, wholly pretesticular or terminating at level of or slightly beyond testes.

Testes two, ovoid or ellipsoid, tandem, diagonal, or nearly opposite, separate, abutting or slightly overlapping, at middle or posterior half of hindbody. Seminal vesicle bipartite, typically in hindbody (exceptionally extending into forebody in *Ca. wakullata*), pretesticular, rarely extending into forebody. *Pars prostatica*, cirrus and genital atrium indistinct or absent. Hermaphroditic duct dorsal to ventral sucker, wholly internal to ventrogenital sac. Genital pore immediately anterior to ventral sucker, opening into ventrogenital sac cavity.

Ovary lobed, median or submedian, pretesticular or ventrally overlapping testes. Mehlis' gland and Laurer's canal present. Seminal receptacle canalicular, dorsal to ovary. Uterus comprising descending and ascending portions, occupying body space from ventral sucker to near posterior

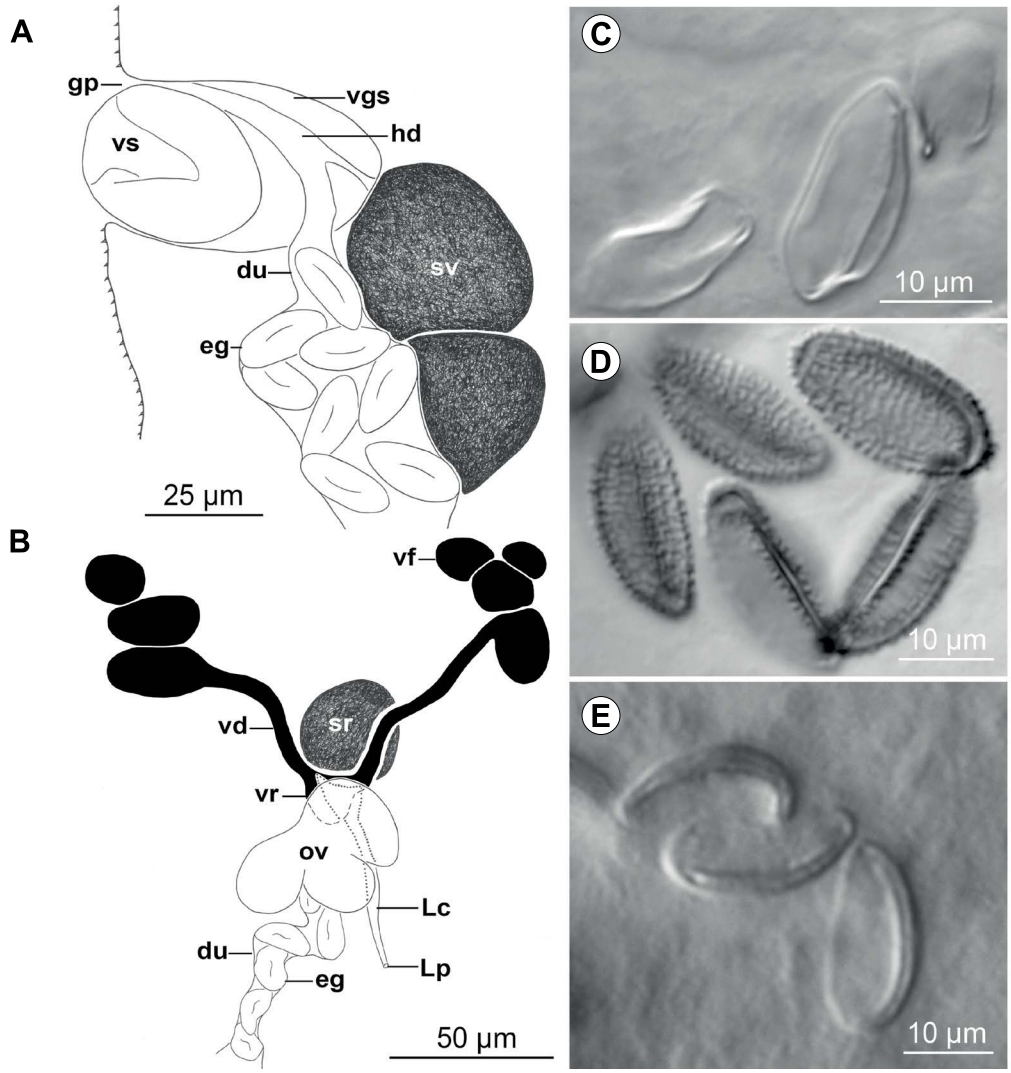

Fig. 3. *Caecincola duttonae* Truong et Bullard sp. n. (Digenea: Cryptogonimidae) infecting largemouth bass, *Micropterus salmoides* (Lacepède) (Centrarchiformes: Centrarchidae) from Neely Henry Reservoir, Coosa River, Alabama, USA (A–D) and *Caecincola parvulus* Marshall et Gilbert, 1905 infecting largemouth bass from Wisconsin, USA (E). **A** – lateral view of a paratype USNM 1741939 showing the terminal male and female genitalia; **B** – ventral view of a paratype USNM 1741940 showing the ovarian complex; **C** – photomicrograph of immature eggs; **D** – photomicrograph of mature eggs; **E** – photomicrograph of eggs of a syntype (USNM 1350225). *Abbreviations*: du – distal uterus; eg – egg; gp – genital pore; hd – hermaphroditic duct; Lc – Laurer's canal; Lp – Laurer's canal pore; ov – ovary; sr – seminal receptacle; sv – seminal vesicle; vd – vitelline duct; vf – vitelline follicles; vgs – ventrogenital sac; vr – vitelline reservoir; vs – ventral sucker.

body end. Eggs numerous, ovoid, operculated; abopercular end broadly rounded or having protuberance.

Vitellarium follicular, in two separate lateral fields; vitelline fields confined to forebody or to hindbody or distributed into forebody and hindbody. Excretory bladder Y-shaped; main stem bifurcating at level of testes; arms extending anteriorly to level of pharynx; pore terminal. Adults infecting pyloric caeca, stomach, and intestine of freshwater fishes (Centrarchiformes) in North America.

Differential diagnosis: Body subovoid, elongate-ovoid, or elongate. Oral sucker funnel-shaped. Enlarged circumoral spines absent. Gonotyl absent. Caeca ending blindly. Testes two. Seminal vesicle bipartite. Eggs with abopercular end broadly rounded or having protuberance.

Caecincola duttonae Truong et Bullard sp. n.

Figs. 2A,B, 3A–C

ZooBank number for species:
urn:lsid:zoobank.org:act:A3A607FA-B812-433D-A3C6-E36AD8B6B2F4

Description (measurements based on light microscopy of 18 heat-killed, formalin-fixed, stained, whole-mounted adult specimens): Body elongate-ovoid or slightly elongate with broadly rounded body ends, 420–605 (508) long, 140–224 (181) wide (body 2.6–3.3× [2.9×] longer than wide); forebody 125–161 (142) long (24–32% [28%] of body length); hindbody 214–418 (324) long (47–69% [63%] of body length), 1.6–2.9× (2.3×) longer than forebody (Fig. 2A,B). Eyespot pigment dispersed near dorsal body surface in pharyngeal region. Oral sucker wider than long,

80–134 (90) long, 90–179 (120) wide (55–96% [69%] of body width). Ventral sucker 30–40 (36) long, 34–42 (37) wide (17–25% [21%] of body width). Oral sucker 2.3–5.3× (3.4×) wider than ventral sucker (Fig. 2A,B). Prepharynx shorter than pharynx, 12–30 (18) long (2–5% [3%] of body length). Pharynx subspherical, 32–51 (37) long (6–10% [7%] of body length), 29–49 (35) wide (16–26% [20%] of body width). Oesophagus longer than prepharynx, 14–151 (31) long (3–9% [6%] of body length. Intestine bifurcating at level of ventral sucker, 133–188 (162) from anterior body end (28–35% [32%] of body length); caeca extending posteriad to level of anterior testis; postcaecal space 177–312 (245) long (39–52% [47%] of body length) (Fig. 2A,B).

Testes ovoid or ellipsoid, longer than wide, primarily postcaecal, diagonal, abutting or nearly abutting, occasionally slightly overlapping, in middle of hindbody; anterior testis 74–126 (98) long (15–22% [19%] of body length), 43–94 (66) wide (27–45% [37%] of body width); posterior testis slightly larger than anterior testis, 87–166 (115) long (17–27% [22%] of body length), 53–95 (73) wide (32–48% [41%] of body width); pretesticular space 224–291 (250) long (45–53% [50%] of body length); post-testicular space 82–133 (107) long (18–25% [21%] of body length) (Fig. 2A,B). Vasa efferentia extending anteriad from anterior margin of each testis, their courses difficult to trace in whole-mounted specimens; vas deferens not observed. Seminal vesicle ventral to caeca, filled with sperm, occupying space between ventral sucker and testes, merging anteriorly with distal uterus to form hermaphroditic duct within ventrogenital sac; anterior part ovoid, 33–54 (44) long, 26–48 (37) wide; posterior part ovoid, approximately equal in size to anterior part, 32–54 (40) long, 32–54 (42) wide (Figs. 2A,B, 3A). Genital pore immediately anterior to ventral sucker (Figs. 2A,B, 3A).

Ovary deeply trilobed, median or submedian, wider than long, ventral to and entirely overlapping testes, 36–70 (53) long (8–12% [10%] of body length), 45–92 (64) wide (28–44% [37%] of body width); preovarian space 235–304 (262) long (47–58% [51%] of body length) (Figs. 2A,B, 3B). Mehlis' gland cells numerous, primarily preovarian. Seminal receptacle ovoid or ellipsoid, median, immediately preovarian or slightly overlapping anterior margin of ovary, dorsally overlapping posterior part of seminal vesicle and anterior testis, filled with sperm, 23–71 (38) long, 24–56 (35) wide (Figs. 2A,B, 3B). Oviduct difficult to discern in whole-mounted specimens. Laurer's canal straight and slender along its length, originating from posterior margin of seminal vesicle, extending posteriad 49–87 (67) (10–17% [14%] of body length); pore submedian, opening dorsally at level of middle of posterior testis (Figs. 2B, 3B).

Vitelline fields compact, primarily extra-caecal, wholly pretesticular, extending anteriad to level of or slightly posterior to pharynx and posteriad to level of posterior part of seminal vesicle, 80–144 (100) long (16–25% [19%] of body length); previtelline space 118–167 (136) long (20–30% [26%] of body length); postvitelline space 236–362 (287) long (50–62% [55%] of body length); transverse vitelline ducts nearly symmetrical, dorsal to caeca, branching at or nearly at posterior end of each vitelline field), extending posteromedian 46–87 (63) to form vitelline reservoir; vitelline reservoir oblong or subtriangular in outline, median or submedian, immediately preovarian, dorsal to anterior half of anterior testis, 228–304 (259) from anterior body end (44–56% [52%] of body length), 8–16 (12) long, 10–21 (17) wide (Figs. 2A,B, 3B).

Uterus ventral to testes along its course, originating from ovary, descending posteriad sinistrally to middle of post-testicular space or to near posterior body end, ascending dextrally to level of testes before winding slightly to midline, entering ventrogenital sac ventral to seminal vesicle and seminal receptacle; metraterm absent (Figs. 2A,B, 3A). Uterine eggs transparent and smooth in proximal uterus, becoming darkly tanned and having a wholly textured surface with irregularly ridges in distal uterus, 21–24 (22) long, 10–12 (11) wide; abopercular end broadly rounded, lacking abopercular protuberance (Figs. 2A,B, 3A–D).

Excretory system comprising main stem that bifurcating at level of posterior testis; excretory bladder becoming diminutive and narrow proximally; excretory branches enlarged distally, ventral to caeca, extending anteriad to level of pharynx (Fig. 2A,B).

Type host: Largemouth bass, *Micropterus salmoides* (Lacepède) (Centrarchiformes: Centrarchidae).

Type locality: Neely Henry Reservoir (33.7888N, 86.0526W, Coosa River, Alabama, USA).

Sites of infection: Pyloric caeca, stomach and intestine.

Prevalence of infection: Ten of 12 largemouth bass (83%) were infected.

Specimens and sequences deposited: Table 1.

Museum specimens examined: All labelled as *Ca. parvulus*, including the syntypes USNM 1350225 (1 slide) and vouchers USNM 1320377 (1 slide), USNM 1350224 (1 slide), USNM 1372172 (1 slide), USNM 1390610 (3 slides), USNM 1390611 (3 slides), USNM 1396895 (2 slides), and BMNH 2002.4.9.40 (1 slide; Natural History Museum, London, UK).

Etymology: The species name honours Haley Rebecca Dutton (Auburn University, Southeastern Cooperative Fish Parasite and Disease Laboratory) for her contributions to the parasitology and disease diagnostics of freshwater fishes in the southeastern United States.

Taxonomic remarks

Miller and Cribb (2008b) diagnosed *Caecincola* as having an oblong body, an intestine that bifurcates immediately anterior or dorsal to the ventral sucker, caeca that extend posteriad in the anterior half of the hindbody (caeca wholly pretesticular or extend posteriad to the level of the testes), testes that are symmetrical or slightly diagonal, and a vitellarium predominantly distributed in the forebody or extends posteriad to the posterior margin of the ventral sucker. When Miller and Cribb (2008b) diagnosed *Caecincola*, only three species (*Ca. parvulus*, *Ca. latostomus*, and *Ca. wakullata*) had been described.

We emend *Caecincola* to include features of the new species as well as of the other five recently-described congeners after Miller and Cribb (2008b): an elongate body (present in *Ca. aubergine*, *Ca. autumnae*, *Ca. cookorum*,

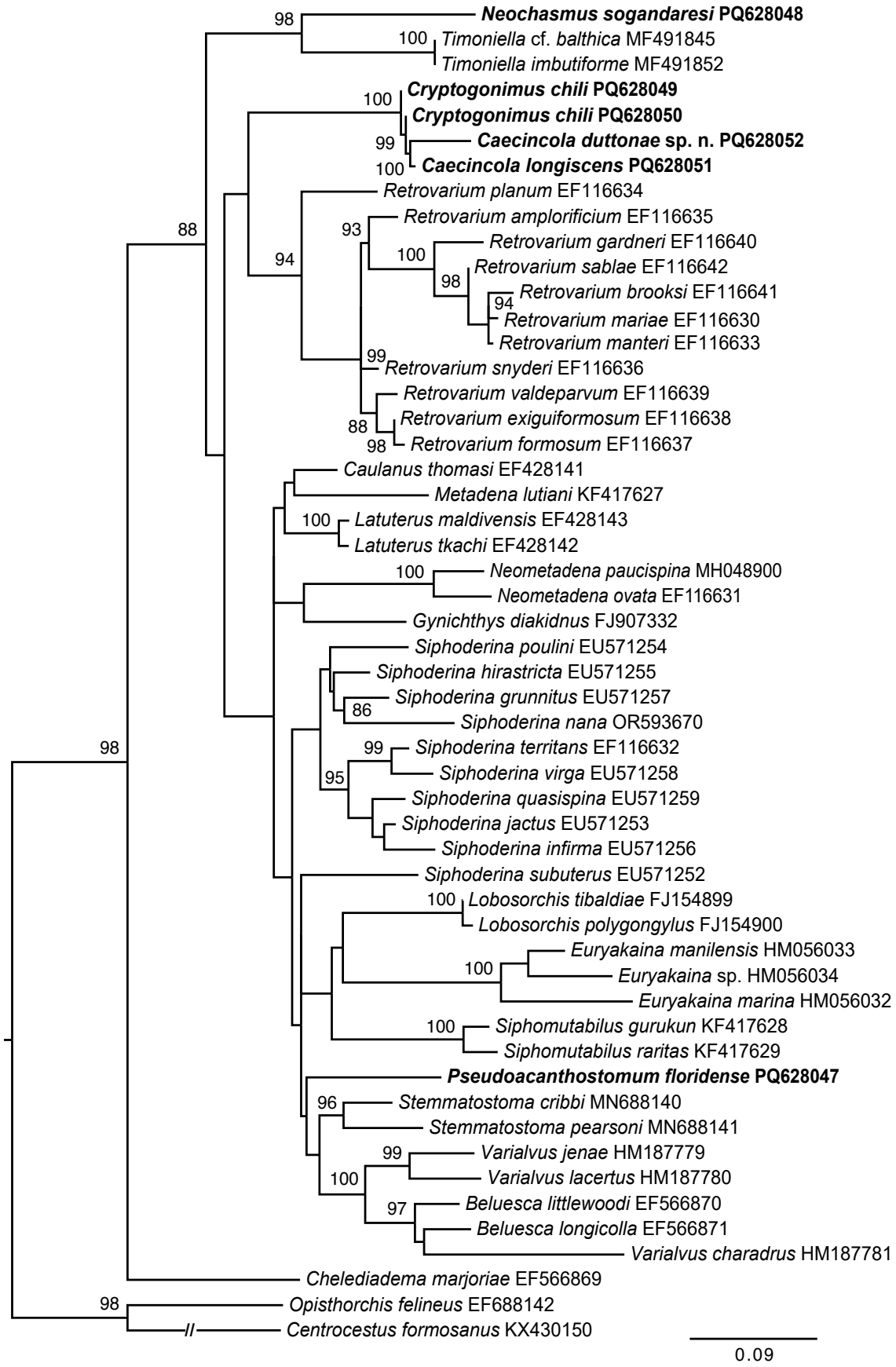

Fig. 4. 28S phylogeny of Cryptogonimidae. Sequences in bold are from the present study. Nodal supports lower than 85 are not shown. Scale bar is in substitutions per site.

Ca. longiscens, *Ca. septimus*), an intestine that bifurcates at the level of the ventral sucker (the new species) or farther anteriad in the posterior half of the forebody (*Ca. aubergine*, *Ca. autumnae*, *Ca. cookorum*, *Ca. longiscens*, *Ca. septimus*), caeca that extend posteriad beyond the testes (*Ca. cookorum*), tandem or nearly tandem testes (*Ca. aubergine*, *Ca. autumnae*, *Ca. cookorum*, *Ca. longiscens*, *Ca. septimus*), and a vitellarium that is wholly in the hindbody (*Ca. longiscens*) or primarily in the hindbody (*Ca. aubergine* and the new species).

Curran and Overstreet (2009) described *Ca. longiscens* (infecting the pyloric caeca and intestine of white crappie from Lake Chotard (Issaquena County, Mississippi River, Mississippi) and from an oxbow of the Pascagoula River (Jackson County, Mississippi) as uniquely having an elongate body (5.5–7.5× longer than wide), tandem testes, an elongate, tubular (unipartite) seminal vesicle, and a vitellarium that was wholly confined to the hindbody.

We collected adult cryptogonimid specimens from the intestine of the same host (white crappie) and same locality (a small oxbow near the Pascagoula River). The present specimens from the Pascagoula River matched those *Ca. longiscens* as per Curran and Overstreet (2009) except that they all had a bipartite seminal vesicle (more prominently visible in laterally-mounted specimens). No species of *Caecincola* reportedly has a unipartite seminal vesicle. Hence, the restricted distribution of the vitellarium in the hindbody is the most reliable feature that readily distinguishes *Ca. longiscens* from its congeners.

The new species most closely resembles *Ca. parvulus sensu* Marshall and Gilbert (1905) by having an elongate-ovoid to a slightly elongate body, short caeca that terminate at the level of the testes, diagonal testes in the middle of the hindbody, and a trilobed ovary. The new species differs from *Ca. parvulus* by having an intestine that bifurcates at the level of the ventral sucker (vs. immediately anterior to the ventral sucker) and a vitellarium predominantly distributed in the hindbody from the level of or slightly posterior to the pharynx posteriad to the level of the posterior part of the seminal vesicle (vs. a vitellarium that is wholly confined to the forebody in the pharyngeal region) (Fig. 2A,B).

We examined the syntypes of *Ca. parvulus* (USNM 1350225, comprising three incomplete adult specimens, one young complete adult having ~20 eggs, and one juvenile) and found that they were in poor condition (destained and poorly-mounted). Marshall and Gilbert (1905) used the only complete adult specimen to illustrate fig. 1, plate 15 in Marshall and Gilbert (1905). The four mature specimens had eyespot remnants dispersed in the pharyngeal region, an intestine that bifurcated immediately anterior to the ventral sucker, and eggs that had a transparent and smooth surface (likely representing immature eggs; cf. eggs of *Ca. duttonae*) and a broadly rounded abopercular end (lacking an abopercular protuberance; see Figs. 2C, 3E).

The vitellarium was indiscernible in all syntypes of *Ca. parvulus* (Fig. 2C). It was described as "yolk-glands lateral, far forward in the body lying at each side of the prepharynx and pharynx, never extending as far back as the intestinal caeca." Marshall and Gilbert (1905) illustrated the vitellarium (fig. 1) as symmetrical, bilateral fields of small follicles confined to the pharyngeal region from the posterior margin of the oral sucker posteriad to slightly beyond the pharynx (the vitellarium is wholly confined to the forebody).

The new species differs from *Ca. autumnae*, *Ca. cookorum*, *Ca. latostomus*, *Ca. septimus*, and *Ca. wakullata* by having a vitellarium predominantly distributed in the hindbody (vs. a vitellarium that is wholly or predominantly distributed in the forebody). The new species differs from *Ca. aubergine* and *Ca. longiscens* by having a less elongate body (2.6–3.3× vs. 5.0–8.8× and 5.5–7.5× longer than wide in *Ca. aubergine* and *Ca. longiscens*, respectively), caeca that terminate at the level of the anterior testis (vs. at the level of the posterior testis), and diagonal testes (vs. tandem testes).

Several cryptogonimid records from centrarchids in the eastern United States are dubious. Regarding *Ca. parvulus*, after Marshall and Gilbert's (1905) description, Mueller (1934) and Van Cleave and Mueller (1934) (perhaps studied the same specimens) reported and deposited voucher specimens identified as *Ca. parvulus* (USNM 1390611) infecting the pyloric caeca, stomach and intestine of largemouth bass from Oneida Lake. These specimens had some bizarre features clearly distinct from the original description and type specimens of *Ca. parvulus*: an oral sucker that was longer than wide (vs. wider than long) and that was <1/2 maximum body width (vs. >1/2 maximum body width), an ovary that had 3–4 lobes (vs. having 3 lobes), and eggs (both immature and mature) that had a pointed abopercular protuberance (vs. lacking an abopercular protuberance).

Lundahl (1941) reported adult specimens identified as *Ca. parvulus* infecting largemouth bass from the Huron River (Michigan). These specimens of Lundahl (1941) matched the morphological descriptions and voucher specimens of *Ca. parvulus* as per Mueller (1934) and Van Cleave and Mueller (1934). Mueller (1934), Van Cleave and Mueller (1934), and Lundahl (1941) apparently did not examine the syntypes of *Ca. parvulus* nor morphologically compare these type specimens to their cryptogonimid specimens.

Amin (1982) reported a single adult specimen also identified as *Ca. parvulus* (USNM 1372172, poorly fixed) infecting largemouth bass from Silver Lake, Fox River (Wisconsin) that had eggs with a pointed, recurved abopercular protuberance. Another poorly fixed adult voucher of *Ca. parvulus* (USNM 1320377; collected and identified by Pearse in 1921), infecting rock bass from Sturgeon Bay, Lake Michigan (Wisconsin), had a sucker-like gonotyl immediately anterior to the ventral sucker; thereby this specimen was obviously a species of *Crytogonimus*, not *Ca. parvulus*.

We herein confirm that cryptogonimid records identified as *Ca. parvulus* in Mueller (1934), Van Cleave and Mueller (1934), Lundahl (1941), and Amin (1982) were taxonomically misidentified and likely represent undescribed species of *Caecincola* (cf. *Cr. spinovus*, which is the only accepted

species of *Cryptogonimus* having eggs [both immature and mature] with a pointed abopercular protuberance – Greer and Corkum 1979). A recollection of these specimens and their nucleotide sequences are needed to determine their proper taxonomic identity or new species description.

Barger (2018) presented a dichotomous key to *Caecincola* spp. that partly adopted the egg morphology (having a pointed protuberance at the abopercular end) in Mueller (1934), Van Cleave and Mueller (1934), and Lundahl (1941) to diagnose *Ca. parvulus*. We herein provide a key to nine accepted species of *Caecincola*:

1b. Body subovoid or elongate-ovoid (<880 μm long), caeca terminating at level of anterior testis or farther anteriad.. 5
2a. Vitellarium primarily in forebody 3
2b. Vitellarium wholly confined to or primarily in hindbody 4
3a. Caeca terminating at level of anterior testis; eggs 15–19 μm long..... *Caecincola septimus*
3b. Caeca extending posteriad into post-testicular space; eggs 20–31 μm long ..... *Caecincola cookorum*
4a. Vitellarium wholly in hindbody; ovary having three lobes ..... *Caecincola longiscens*
4b. Vitellarium extending anteriad into forebody; ovary having three to five lobes ..... *Caecincola aubergine*
5a. Vitelline follicles transversely elongate; eggs having abopercular protuberance 6
5b. Vitelline follicles not transversely elongate; eggs lacking abopercular protuberance 7
6a. Ovary four lobed; eggs 18–20 μm long .... *Caecincola autumnae*
6b. Ovary trilobed; eggs 22–26 μm long ....*Caecincola latostomus*
7a. Vitellarium primarily in hindbody ....*Caecincola duttonae* Truong et Bullard sp. n.
7b. Vitellarium confined to forebody 8
8a. Oral sucker longer than wide; seminal vesicle extending anteriad into forebody; ovary bilobed .... *Caecincola wakullata*
8b. Oral sucker wider than long; seminal vesicle not extending anteriad into forebody; ovary trilobed .... *Caecincola parvulus*

Phylogenetic results

The two 28S sequences (1,269 base pairs) of *Cr. chili* infecting rock bass were identical and differed from those (1,264 bp) of *Cr. chili* infecting smallmouth bass (all Duck River) by 1 nucleotide. The two ITS2 sequences (407–433 bp) of *Cr. chili* infecting rock bass were also identical and differed from those (406–411 bp) of *Cr. chili* infecting smallmouth bass by 1 nucleotide. We regard these as intraspecific differences because these specimens of *Cr. chili* are morphologically indistinguishable. Our two 28S (1,549–1,556 bp) and two ITS2 (414 bp) sequences of *Ca. duttonae* (Coosa River) were respectively identical.

The 28S sequences of *Cr. chili* were most similar to that of *Ca. longiscens* and differed by 7–8 bp (0.6–0.7%); they differed from that of *Ca. duttonae* by 22–23 bp (1.8–1.9%) (Table 2). The ITS2 of *Cr. chili* were most similar to that of *Ca. longiscens* and differed by only 2–3 bp (0.5–0.8%); they differed from that of *Ca. duttonae* by 16–17 bp (4.2–4.4%) (Table 3). The 28S of *Ca. duttonae* was most similar to a sequence identified as *Ca. parvulus* (AY222231, infecting largemouth bass from the Pascagoula River (Wilkerson's Ferry, Mississippi); see Olson et al. 2003) and differed by only 3 bp (0.2%) (Table 2).

We examined voucher specimens (BMNH 2002.4.9.40; 9 adults) associated with the only available 28S sequence of *Ca. parvulus* (AY222231) and found that these specimens had some features that did not match the syntypes and/or the original description of *Ca. parvulus* as per Marshall and Gilbert (1905): an intestine that bifurcated at the level of the ventral sucker, a transversely elongate ovary (vs. not transversely elongate), and a vitellarium that comprised transversely elongate follicles and that were predominantly in the forebody (from the level of the pharynx posteriad to the posterior margin of or slightly beyond the ventral sucker).

The ITS2 of *Ca. duttonae* was most similar to those of *Ca. longiscens* and *Cr. chili* and differed from them by 16–17 bp (4.2–4.4%) (Table 3). No ITS2 sequence of *Ca. parvulus* from the Pascagoula River (Mississippi) is publicly available.

Our 28S (1,236 bp; including only three species of *Caecincola* and *Cr. chili*) and ITS2 (384 bp; including only two species of *Caecincola* and *Cr. chili*) phylogenetic analyses each recovered the species of *Caecincola* and *Cryptogonimus* as sharing a recent common ancestor (Figs. 4, 5). The 28S tree suggested paraphyly of *Caecincola*: *Ca. duttonae* was recovered as sister to *Ca. parvulus* in a clade sharing a recent common ancestor with a clade comprising *Cr. chili* (which has a gonotyl) sister to *Ca. longiscens* (which lacks a gonotyl) (Fig. 4). The clade comprising all species of *Caecincola* and *Cryptogonimus* was recovered sister to a cryptogonimid metacercaria (MK359083) infecting Patagonian flounder, *Paralichthys patagonicus* Jordan (Pleuronectiformes: Paralichthyidae) from the San Matias Gulf, Río Negro, Argentina. The ITS2 tree recovered the two species of *Caecincola* as sister taxa in a clade that shared

Table 2. 28S comparisons among *Caecincola* spp. and *Cryptogonimus chili* (1236 bp; above diagonal: percent nucleotide similarity; below diagonal: nucleotide differences).

Species	*Cr. chili* (PQ628042)[a]	*Cr. chili* (PQ628041)[b]	*Ca. duttonae* sp. n. (PQ628043)	*Ca. parvulus* (AY222231)	*Ca. longiscens* (PQ628051)
Cryptogonimus chili (PQ628042)[a]	–	99.9	98.2	98.1	99.4
Cryptogonimus chili (PQ628041)[b]	1	–	98.1	98.0	99.3
Caecincola duttonae Truong et Bullard sp. n. (PQ628043)	22	23	–	99.8	98.0
Caecincola parvulus (AY222231)	23	24	3	–	97.9
Caecincola longiscens (PQ628051)	7	8	25	26	–

[a]ex. rock bass; [b]ex. smallmouth bass

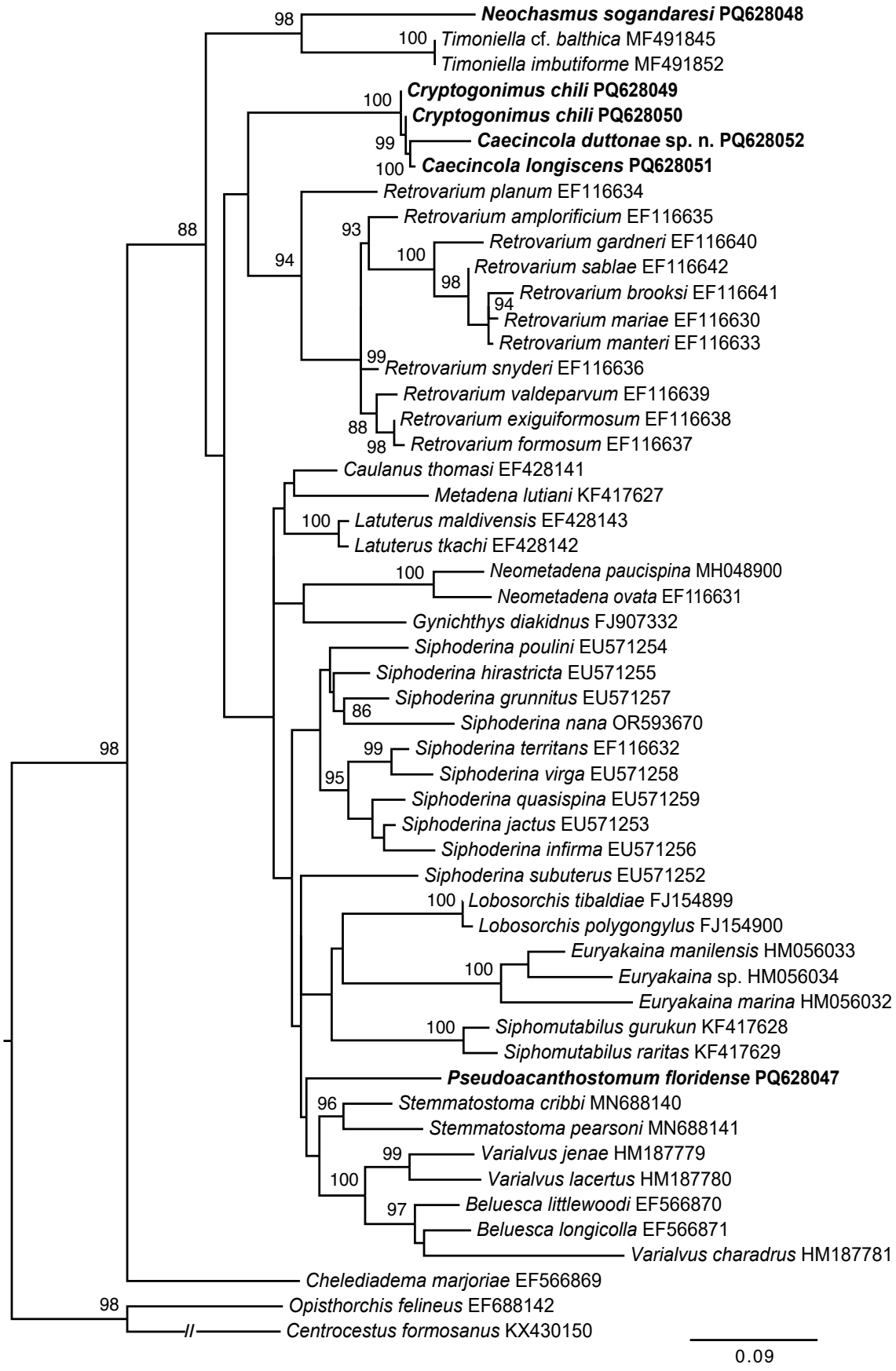

Fig 5. ITS2 phylogeny of Cryptogonimidae. Sequences in bold are from the present study. Nodal supports lower than 85 are not shown. Scale bar is in substitutions per site.

Table 3. ITS2 comparisons among *Caecincola* spp. and *Cryptogonimus chili* (384 bp; above diagonal: percent nucleotide similarity; below diagonal: nucleotide differences).

Species	*Cr. chili* (PQ628050)[a]	*Cr. chili* (PQ628049)[b]	*Ca. duttonae* sp. n. (PQ628052)	*Ca. longiscens* (PQ628051)
Cryptogonimus chili (PQ628050)[a]	–	99.7	95.6	99.5
Cryptogonimus chili (PQ628049)[b]	1	–	95.4	99.2
Caecincola duttonae Truong et Bullard sp. n. (PQ628052)	16	17	–	95.6
Caecincola longiscens (PQ628051)	2	3	16	–

[a]ex. rock bass; [b]ex. smallmouth bass.

a common ancestor to a clade comprising *Retrovarium* spp. (Fig. 5). The present study comprises the first cryptogonimid phylogeny that includes a nucleotide sequence of its type genus, *Cryptogonimus*. Additional sequences of *Caecincola* and *Cryptogonimus* are needed to adequately test monophyly of each genus because of low taxon sampling currently.

Pseudoacanthostomum panamense Caballero, Bravo-Hollis et Grocott, 1953 (Cryptogonimidae) was originally described from tete sea catfish, *Ariopsis seemanni* (Günther) from the Pacific Ocean off Panama. Scholz et al. (1999) redescribed *P. panamense* and expanded the known geographic range to include Atlantic Colombia and the host range to include Mayan sea catfish, *Ariopsis assimilis* (Günther) (Atlantic Mexico) and blue sea catfish, *Ariopsis guatamalensis* (Günther) (Pacific Mexico). Furthermore, they reported metacercariae of *P. panamense* infecting Pacific fat sleeper, *Dormitator latifrons* (Richardson) and Pacific sleeper, *Gobiomorus maculatus* (Günther) (both Gobiiformes: Eleotridae) (Pacific Mexico). Scholz et al. (1999) regarded *P. floridense*, which was described from hardhead sea catfish from the northern Gulf of Mexico, as a junior subjective synonym of *P. panamense*.

We accept *P. floridense* as the second species in the genus with a geographic range limited to the Atlantic Ocean. Adults of *P. floridense* have thus-far been reported from hardhead sea catfish in coastal waters of Alabama (present study), Louisiana (Corkum 1959), Mississippi (present study), and northwestern Florida (USA) (Nahhas and Short 1965). We also collected metacercariae of *P. floridense* encysted in the muscle (head and pelvic girdle) of a clown goby, *Microgobius gulosus* (Girard) (Gobiiformes: Gobiidae) from coastal Alabama.

Overstreet et al. (2009) considered specimens reported by Aguirre-Macedo et al. (2007) (identified as *P. panamense*) infecting blue sea catfish in the Caribbean Sea (Chetumal Bay, Quintana Roo, Mexico) to be *P. floridense*. Our acceptance of *P. floridense* is based on observations from ten heat-killed adult specimens that were fixed without pressure and collected from hardhead sea catfish from Mobile Bay, Alabama and coastal Mississippi, and from seven metacercariae infecting clown gobby from Alabama. Ten adult specimens from the northern Gulf of Mexico each had 28 oral spines, a greatly elongate body (2580–4950 µm long and 310–569 µm wide, widest in the forebody), testes that are tandem and well-separated from each other by approximately one testis length or more (102–324 µm), an ovary that is distinctly trilobed, 185–198 µm long and 159–227 µm wide, and a vitellarium that extends well into the forebody (to the level of the intestinal bifurcation or to the posterior margin of the pharynx).

Additionally, seven metacercariae from Alabama had 28 oral spines. In contrast, specimens of *P. panamense* studied by Scholz et al. (1999) (excluding those from hardhead sea catfish [USA] and from Mayan sea catfish [Mexico] because these may represent *P. floridense*) have 27 oral spines (all 26 individuals, including the four metacercariae from Pacific fat sleeper), a body that is smaller (1850–2580 µm long and 332–512 µm wide, with the widest part in the hindbody rather than forebody), testes that are contiguous or nearly contiguous, an ovary that is entire or slightly lobed, 99–129 µm long and 133–272 µm wide, and a vitellarium that is typically confined between the ventral sucker and the anterior testis. When Scholz et al. (1999) synonymised the two species, only three vouchers of *P. floridense* existed. We herein clearly differentiate these species and therefore reject the aforementioned synonymy of Scholz et al. (1999). The complete ITS2 and partial 28S from two adult specimens of *P. floridense* and one metacercaria were respectively identical. Comparable ribosomal DNA sequences of *P. panamense* from the Pacific Ocean and Caribbean Sea are needed.

DISCUSSION

Based on morphology and life history, we consider *Caecincola* and *Cryptogonimus* as closely related cryptogonimid genera. The emended diagnoses herein of *Caecincola* and *Cryptogonimus* fundamentally differ from each other by species of *Caecincola* lacking a gonotyl and *Cryptogonimus* spp. having a sucker-like gonotyl anterior to the ventral sucker. Previous experimental life cycle studies (Lundahl 1941, Greer and Corkum 1979) indicated that two species of *Caecincola* (*Caecincola latostomus* and a species identified as *Caecincola parvulus*; see Remarks on *Caecincola*) and *Cryptogonimus spinovus* had a similar three-host life cycle: a pleurolophocercous cercaria is shed by a hydrobiid snail, encysts in the muscle and fins of sunfishes (Centrarchidae), and matures in the gastrointestinal tract of primarily black basses (Centrarchiformes).

The Duck River is perhaps the most biodiverse river in North America (Ahlstedt et al. 2017, TWRA 2024). It is approximately 442 km long, begins in the eastern portion of south-central Tennessee, and flows westerly across Middle Tennessee until its mainstem connects to the Tennessee River (Schilling and Williams 2002, Ahlstedt et al. 2017). The Nature Conservancy states that the Duck River has more fish species (151 spp.) than all of Europe and more fish diversity per km than any other North American river (Ahlstedt et al. 2017, TWRA 2024). It belongs to the

Tennessee-Cumberland Rivers Ecoregion (TCRE) (*sensu* Abell et al. 2000), which has the highest species diversity of fishes, freshwater mussels and crayfishes as well as the highest number of endemic aquatic species (Schilling and Williams 2002, Ahlstedt et al. 2017). Considering all taxa, the TCRE is considered to be among the most diverse temperate freshwater ecoregions worldwide.

The Coosa River is also among North America's most diverse rivers regarding its aquatic biodiversity of fishes (147 spp.), freshwater mussels (53 spp.) and snails (91 spp.) (Boschung 1961, Mettee et al. 1996, Boschung and Mayden 2004, Young and Hall 2009, Duncan 2013, Chitwood 2016). Running for approximately 450 km, it originates in the Blue Ridge Mountains and Cumberland Plateau and flows southward to the Coastal Plain before becoming confluent with the Tallapoosa River, which ultimately joins the Alabama River (Mobile-Tensaw River Basin; the largest Gulf of Mexico drainage east of the Mississippi River). Both the Duck and Coosa Rivers course through urban areas, and the fishes and invertebrates ranging there face severe threats from dams, eutrophication and loss of critical habitat.

Despite the renowned biodiversity of these river systems, scant information is available on the parasites infecting the endemic and biodiverse fishes, snails and freshwater mussels that range in the Duck River and Coosa River. As parasitologists, we find it noteworthy that a group of parasites, i.e., freshwater mussels (Bivalvia: Unionida), are among the most imperilled and diverse taxa in the southeastern United States. These and other hosts likely harbour a correspondingly diverse parasite (or hyperparasite) fauna.

Taxonomic knowledge and life history information on the parasites infecting fishes and invertebrates of these rivers are of critical importance. This information can be used for habitat assessments and aquatic ecosystem connectivity estimates because many of the parasites infecting these organisms have indirect life cycles that require both invertebrate and vertebrate hosts. Correspondingly, parasites with direct life cycles could be indicative of water quality and host health. Hence, a high diversity of parasites (including those with direct and indirect life cycles) in the Coosa River and Duck River, for example, should indicate a high level of free-living biodiversity.

We lament the loss of so many snail and freshwater mussel species in the region (Benz and Collins 1997). The construction of dams during the first half of the 20th century destroyed critical habitat for many snails and freshwater mussels, many of which subsequently became extinct. Consequently, we will never know the true, full picture of lost biodiversity in these systems because the parasites were made extinct when their required hosts became extinct. The conservation trend for both of these rivers seems optimistic; however, the fact remains that both of these rivers begin and flow through urban areas that are not going to stop growing or developing. All of these facts underscore the critical importance of describing parasites from fishes of the Duck River and Coosa River; some of these extant parasites could be someday extinct.

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