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Bucephalidae) from Inland Fishes in Mississippi,  
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## ***Rhipidocotyle tridecapapillata* n. sp. and *Prosorhynchoides potamoensis* n. sp. (Digenea: Bucephalidae) from Inland Fishes in Mississippi, U.S.A.**

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**ABSTRACT:** *Rhipidocotyle tridecapapillata* n. sp. is described from the intestine of the white bass, *Morone chrysops* (Rafinesque, 1820), from the Luxapalila River in Lowndes County, Mississippi, U.S.A. The new species has 13 papillae that protrude laterally from the anterior rim of the dorsal lobe of the rhynchus, enabling easy differentiation from the only known freshwater North American congeners, *Rhipidocotyle papillosa* (Woodhead, 1929), which has 15 papillae, and *Rhipidocotyle septapapillata* Krull, 1934, which has 7 papillae. *Prosorhynchoides potamoensis* n. sp. is described from the pyloric ceca and intestine of the white crappie, *Pomoxis annularis* Rafinesque, 1818, from the Pascagoula River in Jackson County, Mississippi, U.S.A. The new species differs from the only other North American freshwater congener, *Prosorhynchoides pusilla* (Stafford, 1904), by having the anterior half of the body wider than the posterior body half rather than having a cylindrical body; a rhynchus-width to body-width ratio of 1:2.5–4.0 compared with 1:0.8–1.3; a pre-equatorial rather than equatorial mouth; a larger pharynx, testes, and ovary; and the Mehlis' gland located between the testes rather than immediately posterior to the ovary as in *P. pusilla* and most of the North American marine species in *Prosorhynchoides*. New combinations are created for 9 species of North American bucephalids belonging in *Prosorhynchoides* Dollfus, 1929.

**KEY WORDS:** Digenea, Bucephalidae, *Rhipidocotyle tridecapapillata* n. sp., *Prosorhynchoides potamoensis* n. sp., *Morone chrysops*, *Pomoxis annularis*, Luxapalila River, Pascagoula River, Mississippi, U.S.A.

Two previously unknown species belonging in Bucephalidae Poche, 1907 were collected from inland fishes in Mississippi, U.S.A., and are herein described as new species. One of the species has a rhynchus consisting of a simple sucker surmounted by a dorsal lobe, a pretesticular ovary, and a slightly bent prostatic duct and therefore belongs in *Rhipidocotyle* Diesing, 1858 (see Nicoll [1914]; Overstreet and Curran [2002]). The other new species has a rhynchus in the form of a simple sucker, a pretesticular ovary, and an ellipsoid seminal vesicle and therefore belongs in *Prosorhynchoides* Dollfus, 1929 (see Srivastava and Chauhan [1973]).

### **MATERIALS AND METHODS**

Specimens of the white bass, *Morone chrysops* (Rafinesque, 1820), were collected from the Luxapalila River in Lowndes County, Mississippi, U.S.A., transported to Mississippi State University at State College, Mississippi, U.S.A., and dissected while freshly dead in April 2001. Specimens of the white crappie, *Pomoxis annularis* Rafinesque, 1818, the blacktail shiner, *Cyprinella venusta* Girard, 1856, and the weed shiner, *Notropis texanus* (Girard, 1856) were collected from a small oxbow periodically contiguous with the Pascagoula River in Jackson County, Mississippi, U.S.A. and transported live to the Gulf Coast Research Laboratory of The University of Southern Mississippi and dissected while freshly dead in June 2007.

Adult digeneans were removed from the intestine and pyloric ceca of piscivorous hosts, and metacercariae were removed from the body cavity of shiners. All specimens were placed in 0.75% saline solution and killed with hot tap water. The specimens were then placed in 5% phosphate-buffered formalin solution and later stained using Van Cleave's hematoxylin or alcoholic Carmine stain. After staining, the specimens were dehydrated, cleared in clove oil, and mounted in Canada balsam on glass slides under cover slips. Drawings were made with the aid of a Wild drawing tube. Measurements are given as ranges in micrometers. Holotype and paratype specimens are deposited at the United States National Parasite Collection (USNPC), Beltsville, Maryland, U.S.A. For comparative purposes we also collected a variety of species belonging in *Prosorhynchoides* from freshwater and marine habitats. Representative voucher specimens of these are deposited at the Harold W. Manter Laboratory of Parasitology (HWML), Lincoln, Nebraska, U.S.A. The species studied with their hosts, collection localities, and museum accession numbers are in Table 1. Specimens listed in Table 1 were prepared using the above mentioned techniques.

### ***Rhipidocotyle tridecapapillata* n. sp. (Figs. 1–4)**

Description based on 4 adults: Body 1,291–1,515 long, 281–295 wide. Tegument entirely covered by dense scales. Rhynchus a simple muscular sucker surmounted by a muscular disc; entire structure 202–224 long, 175–213 wide, widest at anterior disc; disc ventrally notched, with 13 equidistant lateral papillae each protruding 9–14 from disc; papillae 11–14 in diameter at base. Mouth immediately pre-equatorial.

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**Table 1.** *Proserhynchoides* spp. from the United States examined with host, locality, and museum accession numbers for deposited specimens.

Parasite	Host	Locality	Specimens deposited
<i>P. ovatus</i> (Linton, 1900)	<i>Lobotes surinamensis</i> (Bloch, 1790)	The Mississippi Sound off Biloxi, Mississippi	HWML Nos. 48925 (3 specimens), 48926 (1 specimen)
<i>P. pusilla</i> (Stafford, 1904)	<i>Sander vitreus</i> (Mitchill, 1818)	Lake of the Woods, Minnesota	HWML No. 48927 (3 specimens)
<i>P. caecorum</i> (Hopkins, 1956)	<i>Bairdiella chrysoura</i> (Lecepede, 1802)	Ocean Springs, Mississippi	HWML No. 48928 (1 specimen)
	<i>Cynoscion nebulosus</i> (Cuvier, 1830)	Ocean Springs, Mississippi	HWML No. 48929 (1 specimen)
	<i>Sciaenops ocellatus</i> (Linnaeus, 1766)	Off Deer Island, Biloxi, Mississippi	HWML No. 48930 (1 specimen)
<i>P. paralichthydis</i> (Corkum, 1961)	<i>Paralichthys lethostigma</i> Jordan and Gilbert, 1884	Off Deer Island, Biloxi, Mississippi	HWML No. 48931 (2 specimens)
<i>P. megacirrus</i> (Riggins and Sparks, 1962)	<i>Sciaenops ocellatus</i> (Linnaeus, 1766)	Off Horn Island, Jackson County, Mississippi	HWML No. 48932 (1 specimen)

Pharynx nearly spherical, 63–70 long, 65–70 wide. Cecum a simple sac extending dorsally from pharynx then turning dextral and posteriorly, 136–156 long, 80–105 wide.

Testes 2, entire, tandem, dextral, subspherical, contiguous; anterior testis 111–119 long, 85–97 wide; posterior testis 108–119 long, 94–111 wide. Cirrus sac sinistral in posterior body end, extending to mid-level of anterior testis, 290–340 long, 95–106 wide, widest near middle, with wall approximately 4 thick. Seminal vesicle ovoid or ellipsoid, 71–128 long, 48–60 wide. Pars prostatica bent, 133–165 long, filling cirrus sac between seminal vesicle and distal end. Ejaculatory duct (portion of male duct extending beyond pars prostatica) 57–71 long. Genital atrium subspherical, 85–99 long, 80–119 wide, with wall approximately 4 thick, containing muscular protrusible genital lobe, surrounded by glandular cells.

Ovary pretesticular, subspherical, dextral, contiguous or nearly so with anterior testis, 99–128 long, 74–97 wide. Oviduct descending from ovary on dorsal side, containing sperm. Laurer's canal relatively short, extending from dorsal side of oviduct, bending anteriorly, and opening on dorsal surface at level of ovary. Mehlis' gland dorsal in the intertesticular region, receiving common vitelline duct. Vitelline follicles arranged in 2 lateral fields; fields in anterior body half (roughly in second fifth of body, not extending to level of rhynchus); sinistral field 244–290 long, consisting of 11–12 follicles; dextral field 234–296 long, consisting of 13–16 follicles. Uterus extending medially from ootype, extending anteriorly, occupying region between vitelline fields, then descending to and entering genital atrium. Common genital pore opening from genital atrium on ventral surface, submedian on left side, 60–80 from posterior end. Eggs numerous, 26–31 long, 17–18 wide (measured from eggs in distal uterus).

Excretory vesicle I-shaped, extending anteriorly to near anterior margin of vitelline fields; proximal end bending dorsally; pore terminal.

### Taxonomic summary

*Type host:* White bass, *Morone chrysops* (Rafinesque, 1820) (Perciformes: Moronidae).

*Sites:* Pyloric ceca and intestine.

*Type locality:* Luxapalila River, Lowndes County, Mississippi, U.S.A. (33°34'06''N, 88°20'35''W).

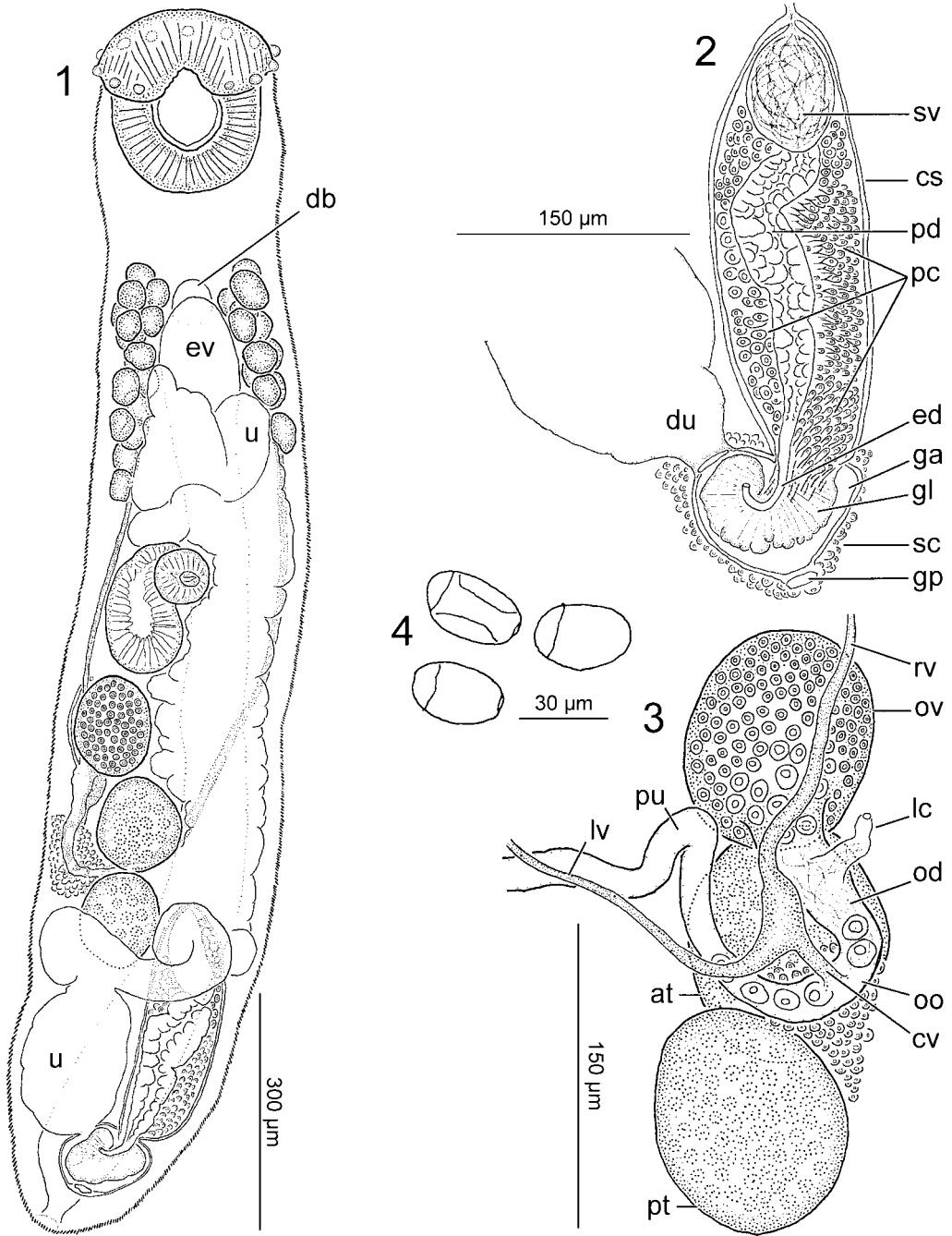
*Prevalence and intensity:* Two infected hosts/3 fish examined = 66%; 2 mature worms per infected host. Additionally, 13 immature worms were recovered from the 2 infected hosts but not included in the description.

*Specimens deposited:* Holotype USNPC No. 100981; 3 paratypes USNPC No. 100982.

*Etymology:* The specific name *tridecapapillata* is a feminine Greek adjective referring to the 13 papillae present on the rhynchal disc.

### Remarks

*Rhipidocotyle tridecapapillata* n. sp. is similar to its only 2 known congeners from North American freshwater, *Rhipidocotyle papillosa* (Woodhead, 1929) and *Rhipidocotyle septapapillata* Krull, 1934. *Rhipidocotyle tridecapapillata* differs from them most appreciably by having 13 papillae protruding laterally around the anterior rim of the dorsal lobe of the rhynchus. The new species is also larger than both others, ranging from 1,291–1,515  $\mu\text{m}$  long by 281–295  $\mu\text{m}$  wide and has a larger pharynx that measures 63–70  $\mu\text{m}$  long by 65–70  $\mu\text{m}$  wide. In contrast, *R. papillosa* has 15 rhynchal papillae, measures 728–



**Figures 1–4.** *Rhipidocotyle tridecapapillata* n. sp. **1.** Ventral view of holotype (USNPC No. 100981). **2.** Ventral view of cirrus sac, distal portion of uterus and genital atrium of paratype (USNPC No. 100982). **3.** Dorsal view of gonads from paratype (USNPC No. 100982). **4.** Eggs from distal portion of uterus of paratype (USNPC No. 100982). (at, anterior testis; cs, cirrus sac; cv, common vitelline duct; db, dorsal bend of the anterior end of the excretory vesicle; du, distal uterus; ed, ejaculatory duct; ev, excretory vesicle; ga, genital atrium; gl, genital lobe; gp, genital pore; lc, Laurer's canal; lv, left vitelline duct; od, oviduct; oo, ootype; ov, ovary; pc, prostatic cells; pd, prostatic duct; pt, posterior testis; pu, proximal uterus; rv, right vitelline duct; sc, secretory cells; sv, seminal vesicle; u, uterus drawn without eggs.).

1,024  $\mu\text{m}$  long by 168–256  $\mu\text{m}$  wide, and has a pharynx with an average diameter of 40–60  $\mu\text{m}$  (Woodhead, 1929). *Rhipidocotyle septapapillata* has 7 rhynchal papillae, a body averaging 938  $\mu\text{m}$  long by 195  $\mu\text{m}$  wide, and a pharynx averaging 52  $\mu\text{m}$  in diameter (Krull, 1934). In addition, *R. tridecapapillata* has smaller eggs than *R. septapapillata*, measuring 26–31  $\mu\text{m}$  long by 17–18  $\mu\text{m}$  wide compared with eggs averaging 38  $\mu\text{m}$  long by 17  $\mu\text{m}$  wide (Krull, 1934). *Rhipidocotyle tridecapapillata* differs from both congeners by having the vitellarium lying entirely anterior to the cecum rather than having the cecum located between the vitelline fields (Woodhead, 1929; Krull, 1934; VanCleave and Mueller, 1934).

***Prosorhynchoides potamoensis* n. sp.**  
(Figs. 5–6)

Description based on 4 adults: Body elongated, 618–888 long, 173–337 wide at widest portion, with anterior half wider than posterior half. Tegument entirely covered by small spines. Rhynchus a simple muscular sucker, 65–111 long, 68–108 wide. Mouth opening ventrally, pre-equatorial, directed posteriorly. Pharynx nearly spherical, 48–57 long, 48–63 wide. Cecum a simple sac extending dorsally from pharynx, 100–150 long, 72–135 wide.

Testes 2, entire, tandem, dextral, subspherical, slightly overlapping or separated by short distance (17–48); anterior testis 108–116 long, 122–144 wide; posterior testis 99–113 long, 85–105 wide. Cirrus sac sinistral in posterior body end, extending to level of anterior testis, 227–278 long, 45–71 wide, widest near middle, with wall approximately 3 thick. Seminal vesicle ellipsoid, 43–82 long, 31–48 wide. Pars prostatica slightly bending, 142–145 long, filling cirrus sac between seminal vesicle and posterior end. Ejaculatory duct 14–20 long. Genital atrium subspherical, 48–85 long, 40–94 wide, with wall approximately 3–5 thick, containing protrusible genital lobe.

Ovary pretesticular, subspherical, dextral, with posterior margin ventral to anterior testis, 90–99 long, 82–97 wide. Oviduct descending from dorsal side of ovary. Laurer's canal extending posteriorly from dorsal side of oviduct, opening on dorsal surface lateral to anterior testis. Mehli's gland intertesticular. Vitellarium arranged in 2 lateral fields anterior to ovary; fields extending anteriorly to about midway between rhynchus and cecum; sinistral field 142–201 long, consisting of approximately 12 follicles; dextral field 131–199 long, consisting of approximately 14 follicles. Uterus with anterior extent within 6–26 of rhynchus, lacking sphincter where entering genital

atrium. Common genital pore of genital atrium ventral, sinistral, 34–48 from posterior end. Eggs 31–34 long, 14–23 wide (measured eggs from distal portion of uterus only).

Excretory vesicle I-shaped, extending anteriorly to near mid-level of vitelline fields; pore terminal.

**Taxonomic summary**

*Type host:* White crappie, *Pomoxis annularis* Rafinesque, 1818 (Perciformes: Centrarchiidae).

*Sites:* Pyloric ceca and intestine.

*Type locality:* Pascagoula River, Jackson County, Mississippi, U.S.A. (30°36'42''N, 88°38'18''W).

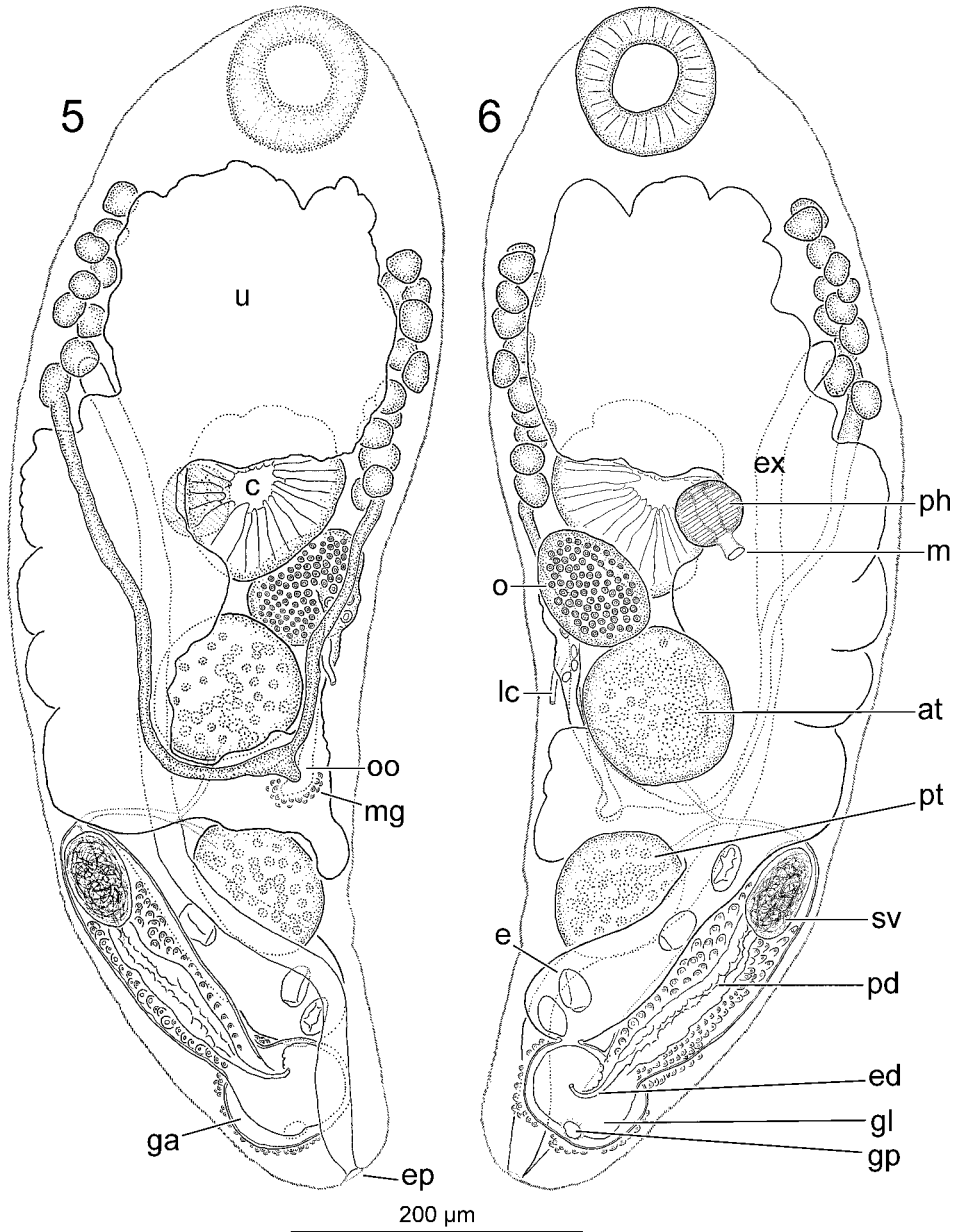
*Prevalence and intensity:* Four infected hosts/50 fish examined = 8.0%; 1.5 worms per infected host. One host had 2 worms that were fixed in ethanol for DNA extraction.

*Specimens deposited:* Holotype USNPC No. 100983; 3 paratypes USNPC No. 100984; 1 metacercaria from body cavity of the blacktail shiner, *Cyprinella venusta* Girard, 1856, (Cypriniformes: Cyprinidae) USNPC No. 100985.

*Etymology:* The neuter, adjectival specific name *potamoensis* refers to the Greek word "potamo," which means "river" and "ensis," which means "dwelling in."

**Remarks**

*Prosorhynchoides potamoensis* n. sp. resembles *Prosorhynchoides pusilla* (Stafford, 1904), the only other North American freshwater congener, which occurs in perciform fishes in northern United States and Canada (Stafford, 1904; Woodhead, 1930; Gibson, 1996). The new species differs from *P. pusilla* by being slightly larger and having a non-cylindrical body, measuring 618–888  $\mu\text{m}$  long by 173–337  $\mu\text{m}$  wide compared with 549–770  $\mu\text{m}$  long by 122–350  $\mu\text{m}$  wide as reported by Stafford (1904) and Woodhead (1930). Specimens of *P. pusilla* that we collected from the walleye, *Sander vitreus* (Mitchill, 1818), from Lake of the Woods, Minnesota, U.S.A., and examined ( $n = 12$ ) ranged from 607–776  $\mu\text{m}$  long by 123–167  $\mu\text{m}$  wide. The anterior body half of *P. potamoensis* was always wider than the posterior half, but the entire body of *P. pusilla* was approximately cylindrical. Additionally, the rhynchus was narrower in *P. potamoensis*, measuring 68–108  $\mu\text{m}$  wide compared with 116–148  $\mu\text{m}$  wide and approximately 100  $\mu\text{m}$  wide in the illustration of



**Figures 5, 6.** *Prosorhynchoides potamoensis* n. sp. Eggs are omitted from the illustrations except from the extreme distal portion of uterus. **5.** Dorsal view of holotype (USNPC No.100983). **6.** Ventral view of holotype. (at, anterior testis; c, cecum; e, egg; ed, ejaculatory duct; ep, excretory pore; ex, excretory vesicle; ga, genital atrium; gl, genital lobe; gp, genital pore; lc, Lauer's canal; m, mouth; mg, Mehlis' gland; o, ovary; oo, ootype; pd, prostatic duct; ph, pharynx; pt, posterior testis; sv, seminal vesicle; u, uterus.).

*P. pusilla* by Woodhead (1930). Consequently, the ratio of the rhynchus width to maximum body width was 1:2.5–4.0 in *P. potamoensis* and 1:0.8–1.3 in *P. pusilla*. *Prosorhynchoides potamoensis* differed further from *P. pusilla* by having the mouth opening pre-

equatorial rather than equatorial; a larger pharynx, measuring 48–57  $\mu\text{m}$  long by 48–63  $\mu\text{m}$  wide compared with one reported as 32  $\mu\text{m}$  in diameter by Woodhead (1930) and measuring 37–40  $\mu\text{m}$  long by 40–43  $\mu\text{m}$  wide in our 12 specimens of *P. pusilla*;

larger testes, measuring approximately 100  $\mu\text{m}$  or more in diameter compared with 60  $\mu\text{m}$  in diameter reported by Woodhead (1930) and measuring 54–71  $\mu\text{m}$  long by 59–80  $\mu\text{m}$  wide in our specimens; and a larger ovary, measuring 90–99  $\mu\text{m}$  long by 82–97  $\mu\text{m}$  wide compared with 42  $\mu\text{m}$  average width reported by Woodhead (1930) and 40–68  $\mu\text{m}$  long by 43–65  $\mu\text{m}$  wide in our specimens.

Although *P. potamoensis* occurs in freshwater, it resembles several species of *Prosorhynchoides* that are present in the estuary and marine environment near the mouth of the Pascagoula River more closely than it resembles *P. pusilla*. The most similar of the local coastal species are *Prosorhynchoides ovatus* (Linton, 1900) from the Atlantic tripletail, *Lobotes surinamensis* (Bloch, 1790); *Prosorhynchoides strongyluræ* (Hopkins, 1954) from the Atlantic needlefish, *Strongylura marina* (Walbaum, 1792); *Prosorhynchoides caecorum* (Hopkins, 1956) from the silver perch, *Bairdiella chrysoura* (Lecepede, 1802), the spotted seatrout, *Cynoscion nebulosus* (Cuvier, 1830), the sand seatrout, *Cynoscion arenarius* Ginsberg, 1929, the red drum, *Sciaenops ocellatus* (Linnaeus, 1766), and the Atlantic croaker, *Microgogonias undulatus* (Linnaeus, 1766); *Prosorhynchoides bennetti* (Hopkins and Sparks, 1958) from the southern flounder, *Paralichthys lethostigma* Jordan and Gilbert, 1884; *P. paralichthydis* (Corkum, 1961) also from the southern flounder; and *Prosorhynchoides megacirrus* (Riggins and Sparks, 1962) from the red drum.

*Prosorhynchoides potamoensis* differs from *P. ovatus* by having an intestine in the form of a simple sac extending dorsally from the pharynx that measures 100–150  $\mu\text{m}$  long by 72–135  $\mu\text{m}$  wide compared with a long, tubular intestine that extends dorsally and anteriorly from the pharynx before turning and extending posteriorly to the testicular level (Dollfus, 1929). *Prosorhynchoides potamoensis* differs from *P. strongyluræ* by having the anterior body half wider than the posterior half rather than having the widest portion of the body in the middle, by having the anterior extent of the uterus separated from the rhynchus by a much shorter distance, by having larger eggs (31–34  $\mu\text{m}$  long by 14–23  $\mu\text{m}$  wide compared with 20–22  $\mu\text{m}$  long by 12–14  $\mu\text{m}$  wide), and by having the excretory vesicle extending anteriorly to the level of the vitellarium rather than the ovary (Hopkins, 1954). *Prosorhynchoides potamoensis* differs from *P. caecorum* by having a relatively narrow body that is always less than half as wide as long compared with a body about half as wide as long, being wider anteriorly than posteriorly

rather than being roughly oval in outline and, and having the larger eggs (compared with 20–24  $\mu\text{m}$  long by 12–14  $\mu\text{m}$  wide) (Hopkins, 1956). *Prosorhynchoides potamoensis* differs from *P. bennetti* by being smaller, measuring 618–888  $\mu\text{m}$  long by 173–337  $\mu\text{m}$  wide compared with 1,090–1,720  $\mu\text{m}$  long by 500–720  $\mu\text{m}$  wide, having a much shorter distance between the anterior extent of the uterus and the rhynchus, having testes further posterior in the body, and having eggs much larger than 19  $\mu\text{m}$  long by 11  $\mu\text{m}$  wide (Hopkins and Sparks, 1958). *Prosorhynchoides potamoensis* is approximately the same size and shape as *P. paralichthydis* and has similarly sized eggs and anterior extent of the uterus, but it differs from specimens we collected in Ocean Springs, Mississippi, U.S.A., and the description by Corkum (1961) by having a relatively smaller rhynchus (65–111  $\mu\text{m}$  long by 68–108  $\mu\text{m}$  wide compared with 110–170  $\mu\text{m}$  long by 120–200  $\mu\text{m}$  wide), a pre-equatorial mouth rather than a postequatorial one, an ovary that is more or less contiguous with rather than well separated from the anterior testis, and the Mehlis' gland lies between the testes rather than between the ovary and anterior testis. *Prosorhynchoides potamoensis* differs from *P. megacirrus* by having a pre-equatorial rather than postequatorial mouth and a cirrus sac extending anteriorly to the middle of the testicular level only rather than to the ovarian level.

Further investigation into the identity of digeneans in fishes from the Pascagoula River, Mississippi, U.S.A., revealed that specimens of the largemouth bass, *Micropterus salmoides* (Lacepede, 1802), collected from the same location as the infected white crappie were infected with *P. potamoensis*; furthermore, the intensity of infection was markedly higher in largemouth bass, with some harboring as many as 20 worms in the pyloric ceca. However, none of the specimens found in largemouth bass possessed eggs and none had mature gonads, suggesting that the largemouth bass is not a suitable host for *P. potamoensis*. Comparison of gene sequences from specimens from both hosts will be featured in a future investigation pertaining to interrelationships of bucephalids.

## DISCUSSION

### Freshwater fish digenean diversity in the Southeastern United States

The inland waters of the Southeastern United States, defined here as the area including eastern Texas, Louisiana, Mississippi, Alabama, Georgia, Kentucky, Tennessee, North Carolina, and northern

Florida contain a diverse assemblage of digenean species that parasitize fishes. Recent digenean collections from rivers draining into the Gulf of Mexico east of the Mississippi River revealed a substantial undiscovered fauna in the region. The North American freshwater digeneans have several possible origins. Some modern North American species have close relatives that only occur in Central and South America (i.e., some Allocreadiidae, Callodistomidae, and Derogenidae). Others have close relatives in Europe, suggesting a possible holarctic origin (i.e., some Allocreadiidae, Deropristidae, Lissorchiidae, and Macroderoididae). Still others have a marine ancestry (i.e., Apocreadiidae, Azigiidae, Bucephalidae, Cladorchiidae, Cryptogonimidae, Cyathocotylidae, Gorgoderidae, Microphallidae, Monorchidae, Opecoelidae, Ptychogonimidae, and Sanguinicolidae or Aporocotylidae depending on one's view). Regardless of historic origin, many species present in the Southeastern Region have apparent close relatives residing in the Mississippi River Basin or on the Atlantic Slope, suggesting that radiation of the freshwater digenean fauna has occurred in North America. We attribute the apparent pocket of digenean diversity in the Southeastern United States to a combination of factors summarized as follows: 1) The region contains the world's most diverse native assemblage of freshwater molluscs that serve as intermediate hosts for digeneans. The Southeastern mollusc fauna includes 269 species of mussels (Unionoida: Unionidae), 20 species of finger-nail clams (Veneroida: Sphaeriidae), and about 313 species of snails (Gastropoda: Megogasteropoda, Basommatophora) (Neves et al., 1997). 2) The region contains a rich aquatic arthropod fauna comprising aquatic insects and crustaceans that serve as intermediate hosts for some digeneans. Approximately 4,212 species of aquatic insects occur in the Southeastern United States, representing about 40% of the 11,053 species of aquatic insects present in North America north of Mexico (Morse et al., 1997); and freshwater crustaceans exhibit a high degree of endemism in the Southeastern United States (Schuster, 1997). 3) The region contains relatively high fish diversity, with 106 species present in the Pearl River Drainage, 86 species in the Pascagoula River Drainage, 157 species in the Mobile Bay Drainage, and 86 species in the Apalachicola River Drainage (Swift et al., 1986). For comparison, North America contains approximately 1,061 species of inland and diadromous fishes, about 790 of which occur within the United States (Warren and Burr, 1994). Further, the fish fauna has persisted without

any major extinctions in the last 5 million years (Robison, 1986; Ross, 2001). 4) Multiple Pleistocene glacier events led to fluctuations in climate in North America, causing the Southeastern Region to periodically serve as a temperate refuge from ice sheets (Brown and Lomolino, 1998). Associated sea level changes caused adjacent river drainages to be captured and subsequently isolated over approximately the past 2 million years (Robison, 1986). The connection and separation of river basins may have provided a mechanism for creating allopatric populations of digeneans.

### North American freshwater species in Bucephalinae Poche, 1907

Bucephalinae Poche, 1907 consists mostly of marine species but has freshwater species in North America, South America, Europe, East Asia, and India. In North America, the subfamily is well represented in marine waters, which contain 1 species of *Alcicornis* MacCallum, 1917; about 8 species in *Bucephalus* Baer, 1827; 10 species in *Prosorhynchoides*; and about 11 species in *Rhipidocotyle* (Yamaguti, 1971). *Bucephalus elegans* Woodhead, 1930, *P. pusilla*, *R. papillosa*, *R. septapillata*, and the 2 new species, *R. tridecapapillata* and *P. potamoensis*, represent all the known freshwater North American bucephalines.

*Rhipidocotyle tridecapapillata* from the Luxapalila River, a tributary of the Mobile Bay Drainage, is morphologically very similar to its 2 North American inland congeners, *R. papillosa* from the upper Mississippi River Drainage and Great Lakes and *R. septapillata* from the Potomac River in the Chesapeake Bay Drainage. The 3 species have a rhynchus that consists of a simple sucker surmounted by a muscular disc that has papillae protruding in a ring outward from the disc. This arrangement is unique among species in *Rhipidocotyle*. Among North America marine species, *Rhipidocotyle longleyi* Manter, 1934, *Rhipidocotyle angusticolle* Chandler, 1941, *Rhipidocotyle adbaculum* Manter, 1940, *Rhipidocotyle capitata* (Linton, 1940), *Rhipidocotyle nagatyi* Manter, 1940, and *Rhipidocotyle barracudae* Manter, 1940 have a rhynchus consisting of a simple sucker surmounted by some sort of muscular hood or disc that has large muscular lobes (Manter, 1934; Manter, 1940; Linton, 1940; Chandler, 1941). Some other marine species, *Rhipidocotyle baculum* (Linton, 1905), *Rhipidocotyle elongatum* McFarlane, 1936, and *Rhipidocotyle lepisostei* Hopkins, 1954, all have a simple sucker surmounted by a disc with 2 barely



**Table 2.** North American species of bucephalids transferred to *Prosorhynchoides* Dollfus, 1929.

Nominal species	Accepted combination
<i>Gasterostomum arcuatum</i> Linton, 1900	<i>P. arcuatus</i> (Linton, 1900) Love and Moser, 1983
<i>Gasterostomum ovatum</i> Linton, 1900	<i>P. ovatus</i> (Linton, 1900) Dollfus, 1929
<i>Gasterostomum pusillum</i> Stafford, 1904	<i>P. pusilla</i> (Stafford, 1904) Margolis and Arthur, 1979
<i>Bucephaloides basargini</i> Layman, 1930	<i>P. basargini</i> (Layman, 1930) Margolis and Arthur, 1979
<i>Bucephalopsis longicirrus</i> (Nagaty, 1937)	<i>P. longicirrus</i> (Nagaty, 1937) n. comb.
<i>Bucephalopsis longoviferus</i> Manter, 1940	<i>P. longoviferus</i> (Manter, 1940) n. comb.
<i>Bucephalopsis labiatus</i> Manter and Van Cleave, 1951	<i>P. labiata</i> (Manter and Van Cleave, 1951) n. comb.
<i>Bucephaloides strongyluræ</i> Hopkins, 1954	<i>P. strongyluræ</i> (Hopkins, 1954) n. comb.
<i>Bucephaloides trichiuri</i> Sogandares-Bernal, 1955	<i>P. trichiuri</i> (Sogandares-Bernal, 1955) n. comb.
<i>Bucephaloides caecorum</i> Hopkins, 1956	<i>P. caecorum</i> (Hopkins, 1956) Bott and Cribb, 2005
<i>Bucephaloides bennetti</i> Hopkins and Sparks, 1958	<i>P. bennetti</i> (Hopkins and Sparks, 1958) n. comb.
<i>Bucephaloides paralichthydis</i> Corkum, 1961	<i>P. paralichthydis</i> (Corkum, 1961) n. comb.
<i>Bucephaloides megacirrus</i> Riggins and Sparks, 1962	<i>P. megacirrus</i> (Riggins and Sparks, 1962) n. comb.
<i>Bucephaloides scomberomorus</i> Corkum, 1968	<i>P. scomberomorus</i> (Corkum, 1968) n. comb.

discernable dorso-lateral lobes (Eckmann, 1932; McFarlane, 1936; Hopkins, 1954). *Rhipidocotyle transversale* Chandler, 1935, another North American marine species, has a simple sucker surmounted by a muscular disc with no lobe or papilla and *Rhipidocotyle lintoni* Hopkins, 1954, the only other North American marine species, differs from it by having a smaller muscular disc that also lacks lobes or papillae (Chandler, 1935; Hopkins, 1954). The configuration of the rhynchus, arrangement of the gonads, and position of the vitellarium in the 3 freshwater North American species of *Rhipidocotyle* suggest a closer relationship with *B. elegans* than to any forementioned marine *Rhipidocotyle* spp. We suspect that molecular comparison among *R. tridecapapillata*, *R. papillosa*, *R. septapapillata*, and *B. elegans* plus marine representatives from *Bucephalus* and *Rhipidocotyle* may reveal that the 3 freshwater species presently in *Rhipidocotyle* belong in *Bucephalus* or their own genus closely related to *Bucephalus*.

*Prosorhynchoides potamoensis* is similar to the only other freshwater congener in North America, *P. pusilla*, which occurs in the upper Mississippi River Drainage and Great Lakes but resembles several coastal marine species from the Gulf of Mexico more closely than *P. pusilla*. Life histories for most North American bucephalids are at least partially known, and these suggest that members of the family are well adapted for colonizing freshwater from the marine environment. Euryhaline tolerant intermediate hosts may have allowed bucephalids to bridge these disparate aquatic habitats, resulting in colonization of freshwater over evolutionary time. Known bivalve first intermediate hosts for bucephalids like oysters and certain species of unionids are common in or

near euryhaline habitats between Nova Scotia, Canada, and Texas, U.S.A., and small diadromous fishes are common second intermediate hosts for marine bucephalines throughout this range. For example, the metacercaria of *P. strongyluræ* utilizes the diadromous inland silverside, *Menidia beryllina* (Cope, 1867), as an intermediate host in Port Aransas, Texas, U.S.A. (Hopkins, 1954). And, while examining fishes from the Pascagoula River at the type locality for *P. potamoensis* during this study, we found what appears to be the metacercaria for that species free in the body cavity of *N. texanus* and *C. venusta*. Both of these shiners occur in freshwater but are subjected to some degree of salinity during dry annual periods and multiyear drought events. Regardless, the metacercaria occurs in more than 1 host, suggesting it may occur in diadromous fishes or more saline-tolerant sympatric species like the coastal shiner, *Notropis petersoni* Fowler, 1942, making it easy to imagine how a coastal digenean species might adapt to a freshwater habitat by utilizing certain hosts. Thus, life history and morphological features mentioned previously in the Remarks section suggest that *P. potamoensis* may be more closely related to some of its marine congeners than to its freshwater relative *P. pusilla* from northern North America. Clearly, molecular studies would provide interesting insights into the relationships of bucephaline genera and about their origins and acquisition of freshwater.

#### North American species in *Prosorhynchoides*

Historically, the generic name for bucephalid species having a simple sucker for a rhynchus was not uniformly agreed upon by taxonomists. North American species of *Prosorhynchoides* were formerly

contained in either *Gasterostomum* von Siebold, 1848, *Bucephalopsis* Deising, 1855, or *Bucephaloides* Hopkins, 1954. The type species, *P. ovatus*, was even once misplaced in a separate genus and subfamily in *Prosorhynchus* Odhner, 1905 (Linton, 1940). Presently, certain species formerly included in *Gasterostomum* and all species formerly considered in *Bucephalopsis* or *Bucephaloides* are considered to belong in *Prosorhynchoides* (Srivastava and Chauhan, 1973; Overstreet and Curran, 2002). New combinations for some of the North American species belonging in *Prosorhynchoides* have already been formally established (Dollfus, 1929; Margolis and Arthur, 1979; Love and Moser, 1983; Bott and Cribb, 2005). Table 2 summarizes the old nominal species names for all North American bucephalids with a simple sucker for a rhynchus that belong in *Prosorhynchoides* and provides new combinations for the remaining species formally in need of such treatment.

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