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Oligacanthorhynchus tortuosa (Leidy, 1850) Schmidt
1972) (Acanthocephala: Oligacanthorhynchidae)

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Redescription of *Oligacanthorhynchus microcephalus* (Rudolphi, 1819) Schmidt 1972 (syn. *Oligacanthorhynchus tortuosa* (Leidy, 1850) Schmidt 1972) (Acanthocephala: Oligacanthorhynchidae)

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ABSTRACT: *Oligacanthorhynchus microcephalus* (Rudolphi, 1819) Schmidt, 1972 was originally described from the philander opossum *Caluromys philander* from Brazil. *Oligacanthorhynchus tortuosa* (Leidy, 1850) Schmidt, 1972 was originally described from the Virginia opossum (*Didelphis virginiana*) in North America. Six years after describing *O. tortuosa*, Leidy indicated the synonymy of *O. tortuosa* with *O. microcephalus*. This taxonomic view persisted for decades until Van Cleave, in 1924, recognized the validity of *O. tortuosa*, apparently without examining the type material of *O. microcephalus*. Subsequent workers have recognized 2 species of *Oligacanthorhynchus* from New World opossums: *O. microcephalus* from South American opossums and *O. tortuosa* from North American opossums. In this study, comparison of individuals of *O. tortuosa* from *D. virginiana* from the United States with the type specimen of *O. microcephalus* revealed the worms to be conspecific. It was thus determined that *O. tortuosa* is a junior synonym of *O. microcephalus* and *O. microcephalus* is redescribed on the basis of both laboratory-reared material and the type specimen. Additionally, comparison of the type material of *Oligacanthorhynchus tumida* (Van Cleave, 1947) Schmidt, 1972 revealed these specimens to be conspecific with *O. microcephalus*; thus *O. tumida* (Van Cleave, 1947) Schmidt, 1972 is considered a junior synonym of *O. microcephalus*. Analysis of the literature and museum specimens reveals that *O. microcephalus* exhibits a broad distribution throughout much of the New World, utilizing an array of hosts with substantially overlapping ranges.

KEY WORDS: *Oligacanthorhynchus microcephalus*, *Oligacanthorhynchus tortuosa*, *Didelphis virginiana*, *Didelphis marsupialis*, *Didelphis albiventris*, *Caluromys cayopollin*, Oligacanthorhynchidae, Acanthocephala.

Oligacanthorhynchus microcephalus was originally described as *Echinorhynchus microcephalus* by Rudolphi (1819) from the opossum, *Didelphis cayopollin*, in Brazil. Gardner (2007) later determined *D. cayopollin* to be a synonym of the philander, or bare-tailed woolly opossum, *Caluromys philander philander*. Leidy (1850) originally described *Oligacanthorhynchus tortuosa* as *Echinorhynchus tortuosa* from the Virginia opossum (*Didelphis virginiana*); however, the locality from which the opossum was collected was not given, nor apparently was type material deposited (Van Cleave, 1924). Leidy (1856) considered *E. tortuosa* to be a synonym of *E. microcephalus* but offered no rationale underlying this decision. The synonymy of *E. tortuosa* and *E. microcephalus* was recognized by Porta (1909) and Travassos (1917). Travassos (1915) transferred *E. microcephalus* to the genus *Hamanniella*. Van Cleave (1924) recognized the validity of *E. tortuosa* solely on the basis of comparison with eggs taken from an acanthocephalan purported to be

H. microcephalus collected from a black-eared opossum *Didelphis aurita* by Travassos in Brazil. Unfortunately, Van Cleave (1924) appears not to have examined the type specimen of *O. microcephalus* upon which Rudolphi based his original description. Southwell and Macfie (1925) determined that the genus *Hamanniella* was a junior synonym of *Oligacanthorhynchus*, although this synonymy was not widely accepted until its endorsement by Schmidt (1972) in his revision of the class Archiacanthocephala. In short, since the resurrection of *O. tortuosa* by Van Cleave (1924) most workers have recognized two species of *Oligacanthorhynchus* from New World opossums: *O. microcephalus* from South American opossums and *O. tortuosa* from North American opossums. For a detailed account of the sordid taxonomic history of this group see Schmidt (1972).

Representatives of the genus *Caluromys* occur as far north as southern Mexico, although *C. philander* is restricted to Venezuela, Trinidad, the Guianas, Brazil, and eastern Bolivia (Gardner, 2007). Didelphid marsupials were common in North America during the late Cretaceous, but had disappeared from

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North America by the Eocene (Dawson, 1967). Presently, 95 species of opossums representing 19 genera occur in South America, whereas only a single species of marsupial, *D. virginiana*, the largest marsupial occurring in the New World, occurs as far north as the United States. The genus *Didelphis* is represented by 3 groups of opossums comprised of 6 species: the black-eared opossums, *Didelphis marsupialis* and *D. aurita*, and the white-eared opossums *Didelphis albiventris*, *Didelphis pernigra*, and *Didelphis imperfecta*, all of which occur in South America. Of these, only *D. marsupialis* also occurs in North America, with a range extending northward well into Mexico. The sixth species, *D. virginiana*, occurs throughout much of North America. The range of *D. virginiana* extends as far south as Nicaragua and thus substantially overlaps the range of *D. marsupialis* in much of southern Mexico (Lowery, 1974). *Didelphis virginiana* is thought to have entered North America only after the Pliocene union of South and North America via land bridge (Gilmore, 1977) and was initially restricted to the eastern United States. However, the distribution of *D. virginiana* now includes the entire Pacific coast from southern Canada southward into Mexico. The western population of *D. virginiana* is presumably the result of opossums introduced by immigrants entering California from the eastern United States between 1870 and 1915, with the founding opossum populations being primarily from Missouri and Tennessee (Grinnell et al., 1937; Gilmore, 1977). *Didelphis virginiana* has also recently been introduced into Grand Junction, Colorado and parts of Arizona, New Mexico, and Idaho (Gardner, 1973; Gilmore, 1977; Sealander, 1979). In addition, within the past century, *D. virginiana* has extended its range north-eastward throughout much of New England as far north as extreme southern Maine (Whitaker and Hamilton, 1998).

The purpose of this paper is to clarify the taxonomic status of the putative North American *O. tortuosa* and South American *O. microcephalus* by critical comparison of North American material with both the type specimen of *O. microcephalus* and with material recently collected from South American opossums. Additionally, a brief review of previous reports of *O. microcephalus* is provided.

MATERIALS AND METHODS

Sixty-four 68-d-old adults of *O. tortuosa* were taken from laboratory-infected opossums (*D. virginiana*) infected with cystacanths taken from millipedes (*Narceus americanus*) collected from Honey Island Swamp on the Pearl River, east of Slidell, St. Tammany Parish, Louisiana (Richardson,

2006). These specimens were compared with the single type specimen, an immature male, originally described as *E. microcephalus* by Rudolphi (1819) and deposited in the helminth collection of the Zoologisches Museum, Berlin, now Museum für Naturkunde, Berlin, Germany, catalogue number 1154 (Hartwick et al., 1998). Additional specimens were obtained from the Colección Nacional de Helmintos, IBUNAM, México, Distrito Federal (collection numbers 610, 611, 618, 2965, 4497, 4779, and 5074); the Harold W. Manter Laboratory, University of Nebraska State Museum (HWML; collection numbers 35092, 49770, 60308, and 60600, 67230, 67231, 67232, and 67233); the Museu de Zoologia Universidade de São Paulo, São Paulo, Brazil (MZSP; collection numbers 131, 189, 190, 336, 390, 680, and 964); the United States National Parasite Collection (USNPC); collection numbers 8916, 28526, 30815, 37606, 38336, 44224, 61134, 61194, 61195, 61196, 61197, 61198, 61500, 61501, 61502, 61503, 61504, 61505, 61506, 61507, 69862, 74429, 74430, 83346, 90910, 97972, 97973, 97974, 97975, 97976, and 97977); and the personal collection of Dr. Brent B. Nickol, University of Nebraska-Lincoln, Lincoln, Nebraska.

Unmounted specimens were prepared, examined, and drawn as described by Richardson and Barger (2006). Measurements were made as described by Richardson (2005), are in micrometers unless otherwise stated, and are given as range followed by mean in parentheses. Terminology for plane shapes follows Clopton (2004).

RESULTS AND DISCUSSION

Specimens of putative *O. tortuosa* from Louisiana collected in this study were morphologically consistent with the type specimen of *O. microcephalus*, and thus in agreement with Leidy (1856), Porta (1909), and Travassos (1917), *O. tortuosa* was determined to be a junior synonym of *O. microcephalus*. In addition, contemporary specimens of *Oligacanthorhynchus* sp. collected from Bolivia were determined to be conspecific with *O. microcephalus*. Examination of the type series of *Hamanniella tumida* described by Van Cleave (1947) as *Travassosia tumida* from *D. virginiana* in Oklahoma, U.S.A. and transferred since first to the genus *Hamanniella* by Van Cleave (1953) and then to the genus *Oligacanthorhynchus* by Schmidt (1972), who revealed the 2 species to be conspecific. Thus, *O. tumida* is considered a junior synonym of *O. microcephalus*. Table 1 gives morphometric comparison of *O. tortuosa* from Louisiana, the type specimen of *O. microcephalus*, the type material of *O. tumida*, and contemporary specimens of *O. microcephalus* collected from Bolivia. Specimens collected from Bolivia were not included in the redescription of *O. microcephalus*, even though there were slight differences in ranges of proboscis length and width and lengths of hooks 1–4. In short, some of the Bolivian specimens were immature. Nevertheless, morphomet-

Table 1. Summary of morphometric data for the holotype of *Oligacanthorhynchus microcephalus* (Rudolphi, 1819) (specimen 1154 Museum für Naturkunde, Berlin, Germany), holotype and allotype of *Travassosia tumida* (Van Cleave, 1947) (USNPC37606), laboratory-reared specimens from Louisiana, United States of America (Yale Peabody Museum numbers YPM 68124-YPM68194 and YPM68466-YPM68468), and specimens collected from Bolivian opossums in the present study (Harold W. Manter Laboratory, University of Nebraska State Museum, Lincoln, Nebraska numbers HWML35092, 60308, and 60600). All measurements in micrometers unless otherwise stated.

Character	<i>O. microcephalus</i> type	<i>T. tumida</i>	Louisiana specimens	Bolivian specimens
Trunk (mm)				
Length, male	62.4	105.4	71–145 (114)	58.3–101.6 (76.9)
Maximum width male	3.3	3.5	3.2–5.5 (4.0)	3.1–4.9 (4.0)
Length, female	—	91.2	95–258 (179)	94–271 (143)
Maximum width female	—	3.7–6.9	4.0–9.0 (7.1)	3.9–10.0 (6.5)
Proboscis				
Length	261	264–270 (267)	246–350 (296)	236–309 (277)
Width	249	228–288 (258)	246–390 (313)	222–330 (280)
Length of hooks				
Hook 1	—	88–100 (95)	75–110 (92)	63–100 (83)
Hook 2	—	—	58–89 (73)	53–95 (69)
Hook 3	—	68	51–88 (66)	50–65 (57)
Hook 4	—	60–68 (64)	43–76 (60)	40–60 (51)
Hook 5	—	51–63 (58)	35–65 (49)	35–53 (49)
Hook 6	—	45	33–53 (43)	33–50 (40)
Testes length (mm)	3.7	5.5–5.8 (5.7)	4.0–7.9 (6.2)	3.4–7.6 (5.4)
Testes width (mm)	1.1	1.5–1.6 (1.6)	1.3–3.3 (2.1)	1.1–2.6 (1.9)
Seafftigen's pouch length (mm)	3.3	3.4	3.0–4.1 (3.6)	2.4–4.6 (3.5)
% trunk occupied by male system	36.3	34.6	25.7–41.9 (33.1)	27.2–39.0 (33.3)
% trunk occupied by female system	—	2.7	1.0–3.0	1.1–2.2
Egg length	—	—	83–110 (98)	90–101 (97)
Egg width	—	—	38–50 (44)	35–48 (42)

ric data for these specimens are provided in Table 1 to facilitate any future comparative analysis of North American and South American specimens of *O. microcephalus* as more material becomes available.

Oligacanthorhynchus microcephalus
(Rudolphi, 1819) Schmidt, 1972

Syn. *Echinorhynchus microcephalus* Rudolphi, 1819; *Echinorhynchus tortuosa* Leidy, 1850; *Hamanniella microcephalus* (Rudolphi, 1819) Travassos, 1915; *Hamanniella tortuosa* (Leidy 1850) Van Cleave, 1924; *Hamanniella tumida* (Van Cleave, 1947) Van Cleave, 1953; *Oligacanthorhynchus tortuosa* (Leidy, 1850) Schmidt, 1972; *Oligacanthorhynchus tumida* (Van Cleave, 1947) Schmidt, 1972; *Travassosia tumida* Van Cleave, 1947 (Figs. 1–5)

General: (on the basis of 64 68-d-old worms (25 females, 37 males, and 2 worms of undetermined sex) acquired from laboratory infections of Virginia

opossums (*Didelphis virginiana*) infected with *cystacanths* taken from millipedes (*Narceus americanus*) collected from Honey Island Swamp on the Pearl River, east of Slidell, St. Tammany Parish, Louisiana (Richardson, 2006): Elongate, narrowly constricted at anterior end. Proboscis very broadly to broadly elliptoid to ovoid, 246–350 (296) long, 246–390 (313) wide, armed with 6 longitudinally arranged spiral rows of 6 shallowly rooted hooks each. Anterior-most hooks semifalciform to narrowly semifalciform or semilunifiform to narrowly semilunifiform, 75–110 (92), exceptionally as short as 65 (see Richardson, 2005); second hooks in each row deeply to very deeply semifalciform or semilunifiform, 58–89 (73); third and fourth hooks in each row deeply to narrowly semifalciform or semilunifiform. Third hook in each row 51–81 (66). Fourth hook in each row 43–76 (60). Fifth and sixth hooks in each row shallowly to very deeply semifalciform or semilunifiform. Fifth hook in each row 35–65 (49). Sixth hook in each row 33–53 (43). Neck 180–264 (229) long by 213–380 (270) wide. Proboscis receptacle approximately 810–1,440 (1,078) long by 230–500 (333) wide with thick muscular wall. Distinct collar

formed at about or just anterior to point of origin of dorsal, ventral, and lateral protruder muscles near the base of the neck (see Schmidt, 1972). Collar variable in length and width depending on degree of extension of neck and proboscis; 30–198 (106) long by 248–540 (370) wide. Collar less distinct when neck and proboscis fully extended. Lemnisci about equal in length, often highly coiled, extending 10–24 (18) mm beyond posterior end of proboscis receptacle, each containing several conspicuous nuclei. Cerebral ganglion in posterior half of proboscis receptacle and narrowly elliptoid or fusiform to elliptoid or fusiform, 150–228 (182) long by 55–113 (81) wide.

Female: (on the basis of 25 gravid females): Trunk 95–258 (179) mm long, exceptionally females may achieve a length of up to 350 mm (see Richardson and Barnawell, 1995). Trunk 0.3–0.7 (0.4) mm wide at anterior end just posterior to collar formed at origin of protruder muscles. Width at widest point in middle portion of trunk to posterior half of trunk, 4.0–9.0 (7.1) mm. Tapering to 1.4–3.0 (2.1) mm at posterior end. Length-to-width ratio (at widest point) 17.9–33.9 (25.3:1). Reproductive tract (from anterior edge of uterine bell to genital pore) occupying 1–3% of length of trunk. Genital pore slightly subterminal. Fully embryonated eggs narrowly elliptoid to elliptoid, 83–110 (98) long by 38–50 (44) wide; outer membrane sculpted; fertilization membrane often exhibits polar thickening or prolongation.

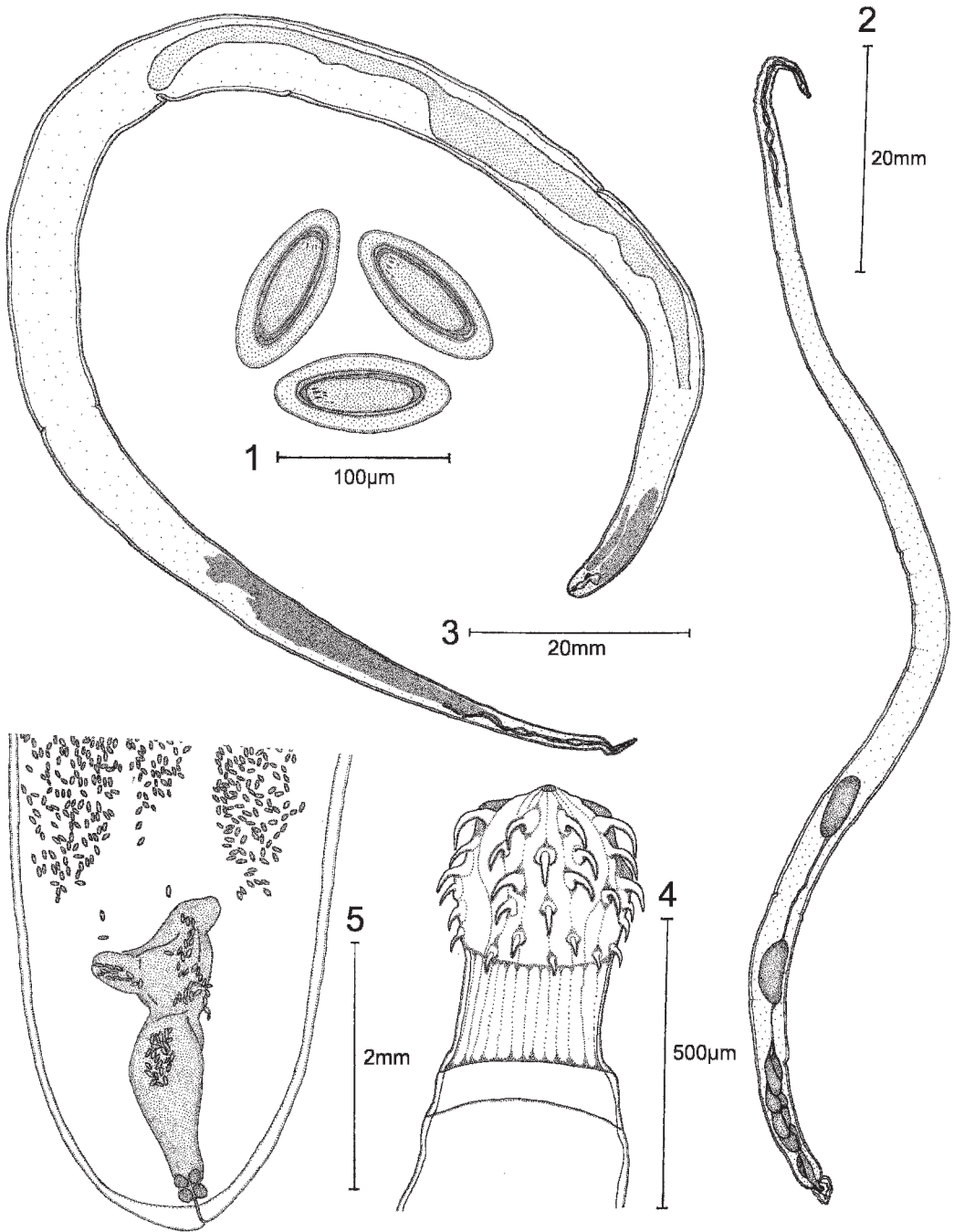
Male: (on the basis of 37 males): Trunk 71–145 (114) mm long by 294–600 (386) wide at anterior end just posterior to collar formed at origin of protruder muscles; widest point at level of anterior testis, or exceptionally just anterior to anterior testis, 3.2–5.4 (4.0) mm. Tapering to 1.2–2.2 (1.7) mm at posterior end. Length-to-width (at widest point) ratio 21.1–36.0 (28.4):1. Testes in tandem, narrowly elliptoid to elliptoid. Anterior testis 3,950–7,900 (6,209) long by 1,300–3,300 (2,151) wide. Posterior testis 4,225–7,825 (6,282) long by 1,275–2,925 (2,072) wide. Distance between posterior end of anterior testis to anterior end of posterior testis 2.3–17.3 (9.0) mm. Eight reniform cement glands, obovoid or teardrop to reniform shaped, originating 0.5–8.8 (3.4) mm posterior to posterior end of posterior testis and extending 7.0–13.5 (10.1) mm. Saeftigen's pouch 3.0–4.1 (3.6) mm long. Copulatory bursa roughly orbicular, varying in shape from very broadly to broadly elliptoid, 0.7–2.6 (1.9) mm long by 0.8–2.5 (1.8) mm long. Entire male reproductive system occupying posterior 25.7–41.9% (33.1%) of trunk.

Type host: *Caluromys philander philander* (philander or bare-tailed woolly opossum).

Type locality: Brazil.

Site of infection: Small intestine.

Other reported hosts and localities: Previous reports of *O. microcephalus* from *D. virginiana* confirmed by examination of voucher material include: Alabama (USNPC44224); Arkansas (USNPC 8916, Yale Peabody Museum, New Haven, Connecticut, U.S.A. number YPM68124 [Richardson, 1993]); California (YPM68125-YPM68127); Florida (Van Cleave, 1953); Georgia (Ellis et al., 1999); Illinois (Babero, 1957; Alden, 1995); Louisiana (YPM68130) (Van Cleave, 1953); Mississippi (USNPC30815 and 69862); Oklahoma (Van Cleave, 1924, 1947, 1953); South Carolina (USNPC90910); and Texas (Van Cleave 1924, 1953) in the United States and Michoacán and Oaxaca in Mexico (García-Prieto et al., 2010). Additionally, unconfirmed reports of *O. microcephalus* from *D. virginiana* in the literature include Georgia (Babero, 1960); Stewart and Dean, 1971); Illinois (Miller and Dunagan, 1978; Wong et al., 1979; Dunagan and Miller, 1981); Louisiana (Babero, 1957); North Carolina (Feldman et al., 1972); and Pennsylvania (Blumenthal and Kirkland, 1976) in the United States and Colima and Vera Cruz in Mexico (García-Prieto et al., 2010). In a summary of helminths recorded from *D. virginiana* by Alden (1995), *O. tortuosa* was erroneously listed as having been reported from Colorado (Krupp and Quillin, 1964) and Washington (Richardson, 1993). Although Krupp and Quillin (1964) briefly discussed *O. tortuosa* in their review, they did not report it as occurring in Colorado. The report by Richardson (1993) of *O. tortuosa* referred to specimens from Van Buren, Yell, and Washington counties in Arkansas, not Washington State. *Oligacanthorhynchus microcephalus* was confirmed from *D. albiventris* from: Oaxaca, Mexico (García-Prieto et al., 2010); *D. cayopollin* from Chaco Boreal, Paraguay (USNPC74430); French Guiana (HWML67230-67233); Beni and Santa Cruz in Bolivia (HWML60308, 60388, and 60600); and Brazil (Rudolphi, 1819); and from *D. marsupialis* from São Paulo, Brazil (MZSP680) and Tabasco and Vera Cruz in Mexico (García-Prieto et al., 2010). Díaz-Ungría (1958) provided an unconfirmed report of *O. microcephalus* from *D. marsupialis* in Venezuela. *Oligacanthorhynchus microcephalus* was also confirmed from the woolly mouse opossum, *Marmosa demerarae* (HWML 49770), the murine opossum, *Marmosa murina* (HWML 67230-67233) from French Guiana (Byles



Figures 1–5. Drawings of 68-d-old specimens of *Oligacanthorhynchus microcephalus* from laboratory-infected Virginia opossums, *Didelphis virginiana* fed cystacanths taken from the hemocoels of millipedes (*Narceus americanus*) collected from Honey Island Swamp on the Pearl River, east of Slidell, St. Tammany Parish, Louisiana. **1.** Eggs from YPM68467. **2.** Adult male (YPM68468). **3.** Adult female (YPM68466). **4.** Proboscis of YMP68174. **5.** Female reproductive system (YPM68466).

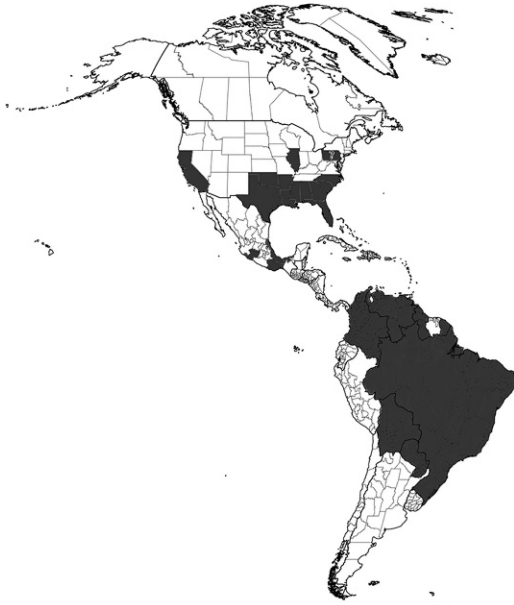


Figure 6. Distribution of *Oligacanthorhynchus microcephalus*. States in the United States and Mexico, and countries in South America from which *O. microcephalus* is being, or has been, reported are shown in gray. Question mark indicates unconfirmed distribution record for Pennsylvania.

et al., 2013), and the brown four-eyed opossum (*Metachirus nudicaudatus*) from Curiche, Choco Department, Columbia (YPM68128 and YPM68129). *Oligacanthorhynchus microcephalus* has been reported from 2 species of armadillos, *Dasyus novemcinctus* from Texas, U.S.A. (Chandler, 1946) and *Euphractus sexcinctus* from Chaco Boreal, Paraguay (USNPC74429). The extent to which armadillos serve as host of *O. microcephalus* is unclear because the intestinal helminth fauna of armadillos is relatively understudied. Richardson et al. (1992) erroneously identified two individuals from the small intestine of a single raccoon (*Procyon lotor*) from Arkansas as *O. tortuosa*. Re-examination of these specimens (USNPC81431) revealed them to be *Macracanthorhynchus ingens*. Figure 6 shows the known distribution of *O. microcephalus*.

Specimens deposited: YPM68124–YPM68194 and YPM68466–YPM68468.

Remarks

The results of this study revealed *O. tortuosa* and *O. tumida* to be conspecific with *O. microcephalus*. *Oligacanthorhynchus microcephalus* exhibits a broad distribution throughout much of the New World

(Fig. 6). In the United States, *O. microcephalus* has only been observed from the Southeast, Deep South, Southwest, Midwest, and California. A survey of 30 opossums from Connecticut by Richardson and Campo (2005) failed to reveal the presence of *O. microcephalus*, suggesting that the range of this helminth does not extend into the New England states, although *D. virginiana* occurs in New England as far north as southern Maine (Whitaker and Hamilton, 1998). Although the acanthocephalan reported by Feldman et al. (1972) from North Carolina opossums is listed herein as an unconfirmed report of *O. tortuosa*, the microphotograph provided by Feldman et al. (1972) is clearly of an individual of *O. tortuosa*. Because the unconfirmed report of *O. microcephalus* from Pennsylvania opossums by Blumenthal and Kirkland (1976) extends its known range so greatly, further surveys are warranted to confirm this report. Surveys of populations of *D. virginiana* throughout and particularly along the periphery of its range are warranted to delineate the range of *O. microcephalus* and other parasites of *D. virginiana* in North America. It is likely that *O. microcephalus* arrived in North America with *D. virginiana* after the Pliocene union of South America and North America. *Oligacanthorhynchus microcephalus* utilizes opossums as its primary definitive hosts, although there are two reports from armadillos.

The life cycle of *O. microcephalus* was described by Richardson (2006), who found the millipede *N. americanus* to serve as intermediate host. Although the range of *N. americanus* covers the range of *O. microcephalus* throughout the eastern United States (Shelley et al., 2006), surveys of millipedes throughout the range of *O. microcephalus*, especially in California, Mexico, and Central and South America, are warranted to identify other intermediate hosts because the range of *O. tortuosa* greatly transcends that of *N. americanus*.

The histopathology of *O. microcephalus* was described by Richardson and Barnawell (1995). Dunagan and Miller (1981) provided detailed anatomical description of the cerebral ganglion in *O. microcephalus*. Kilian (1932) described the general morphology of the body wall of *O. microcephalus* and Miller and Dunagan (1978) provided detailed description of the organization of the lacunar system.

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