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# Acanthocephala of Arkansas, Including New Host and Geographic Distribution Records from Fishes

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Running Title: Acanthocephalans of Arkansas

#### **Abstract**

Little is known about the spiny- or thorny-headed worms (Phylum Acanthocephala) of Arkansas and there are no summaries on the acanthocephalans of the state. Here, we provide a checklist of the 22 acanthocephalans that occur in Arkansas' vertebrates based on previously published records and new data presented herein. In addition, we document a new state record as well as 13 new host records for some fish acanthocephalans.

#### Introduction

The phylum Acanthocephala includes at least 4 classes, 10 orders, 26 families, and about 1,300 species (Amin 2013). Adults are highly specialized, dioecious parasites of the intestinal tract of a variety of vertebrates. As adults acanthocephalans reside exclusively in the vertebrate small intestine. They have an indirect life cycle involving at least 2 hosts, either an aquatic intermediate host (Amphipoda, Copepoda, Isopoda, and Ostracoda) or terrestrial intermediate host, including insects, crustaceans and myriapods. Fishes, amphibians, reptiles, birds, and mammals serve as definitive hosts.

The purpose of this report is 2-fold: (1) provide a checklist of the acanthocephalans that occur in Arkansas based on previously published records, and (2) document new host and distributional records of some acanthocephalans from fishes.

#### Methods

Between April 2014 and July 2015, we collected fishes with backpack electrofishers, dipnets and seines. Fish were placed in habitat water and necropsied

within 24 hr. We followed accepted guidelines for the use of fish in research (AFS 2004). Specimens were overdosed with a concentrated Chloretone (chlorobutanol) solution and measured for total length (TL). A mid-ventral incision from anus up to the level of the stomach was made to expose the gastrointestinal tract and other internal viscera (including gallbladder) which was removed and placed in a Petri dish containing 0.6% w/v saline. Acanthocephalans were transferred to Petri dishes containing distilled water overnight to completely evert their proboscides. They were then placed in 70-95% v/v DNA-grade ethanol, stained with acetocarmine and mounted entire with Canada balsam or Damar gum. Voucher specimens were deposited in the Harold W. Manter Laboratory of Parasitology Parasite Collection (HWML), Division of Parasitology, University of Nebraska-Lincoln, State Museum. Host voucher specimens were deposited in the Henderson State University Museum (HSU), Arkadelphia, Arkansas. Prevalence, mean intensity, and range of infection are provided in accordance with terminology given in Bush et al. (1997).

We also examined the scientific literature for previous information on reports of acanthocephalans from Arkansas. Reports of unidentified acanthocephalan cystacanths from various Arkansas vertebrate hosts, were not included herein. We follow Amin's (2013) classification of the Acanthocephala.

The annotated list of data for fish hosts harboring acanthocephalans is as follows: host and TL (mean  $\pm$  1SD range, when available), prevalence, intensity (mean  $\pm$  1SD range, when available), collection site, collection date, HWML accession number.

#### **Results and Discussion**

The following species of acanthocephalans have

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been previously reported from vertebrate hosts in Arkansas:

#### ACANTHOCEPHALA OF ACTINOPTERYGII

### Eoacanthocephala: Neoechinorhynchida: Neoechinorhynchidae

Neoechinorhynchus sp. – Aphredoderus sayanus, Pirate Perch (McAllister et al. 2014a); Moxostoma duquesnei, Black Redhorse (McAllister et al. 2015a).

Neoechinorhynchus cylindratus (Van Cleave, 1911) Van Cleave, 1919 – Micropterus dolomieu, Smallmouth Bass, Micropterus punctulatus, Spotted Bass, Micropterus salmoides, Largemouth Bass (Becker et al. 1966); Ameiurus natalis, Yellow Bullhead, Lepomis macrochirus, Bluegill, M. punctulatus, M. salmoides (Becker and Houghton 1969); Pomoxis annularis, White Crappie, L. macrochirus, M. salmoides, M. punctulatus, Lepomis gularis, Warmouth (Becker and Cloutman 1975); M. salmoides, L. macrochirus (Cloutman 1975). At least 7 species of ostracods serve as the first intermediate host, with smaller non-game fishes as paratenic hosts.

*Neoechinorhynchus prolixus* Van Cleave and Timmons, 1952. *Carpiodes velifer*, Highfin Carpsucker (McAllister et al. 2015a).

*Paulisentis* sp. – *Campostoma anomalum*, Central Stoneroller (McAllister et al. 2015a).

## Paleoacanthocephala: Echinorhynchida: Echinorhynchidae

Acanthocephalus tahlequahensis Oetinger and Buckner, 1976 – Cottus carolinae, Banded Sculpin (McAllister et al. 2014d); Ambloplites ariommus, Shadow Bass, Noturus exilis, Slender Madtom (McAllister et al. 2015a).

#### Heteroacanthocephalidae

Aspersentis sp. -A. sayanus (McAllister and Amin 2008).

#### Pomphorhynchidae

*Pomphorhynchus lucyi* Williams and Rodgers, 1984 – *A. sayanus* (McAllister and Amin 2008).

#### Illiosentidae

Leptorhynchoides sp. -A. sayanus (McAllister et al. 2014a).

Leptorhynchoides thecatus (Linton, 1891) Kostylev, 1924 – M. salmoides (Becker et al. 1966, Becker and Houghton 1969, Becker and Cloutman 1975). Note: Classification of this common parasite was recently revised by Steinauer and Nickol (2015); previous records from fishes need to be re-examined.

#### ACANTHOCEPHALANS OF AMPHIBIA

#### Fessisentidae

Fessisentis vancleavei – Eurycea tynerensis, Oklahoma salamander (Buckner and Nickol 1978, McAllister et al. 1995, 2014c).

#### ACANTHOCEPHALANS OF REPTILIA

#### Neoechinorhynchidae

Neoechinorhynchus chrysemydis Cable and Hopp, 1954 – Trachemys scripta elegans, red-eared slider (Cable and Fisher 1957, Fisher 1960, Rosen and Marquardt 1978).

*Neoechinorhynchus emydis* (Leidy, 1851) Van Cleave, 1916 – *Graptemys geographica*, common map turtle (McAllister et al. 2014b).

*Neoechinorhynchus emyditoides* Fisher, 1960 – *T. s. elegans* (Cable and Fisher 1957, Fisher 1960, Rosen and Marquardt 1978, Barger 2004).

*Neoechinorhynchus pseudemydis* Cable and Hopp, 1954 – *T. s. elegans* (Cable and Fisher 1957, Fisher 1960, Rosen and Marquardt 1978, Barger 2004).

*Neoechinorhynchus stunkardi* Cable and Fisher, 1961 – *T. s. elegans* (Rosen and Marquardt 1978).

#### Pomphorhynchidae

Pomphorhynchus bulbicolli Linkins in Van Cleave, 1919 – Nerodia sipedon pleuralis, Midland water snake (McAllister et al. 2015b). The presence of *P. bulbocolli* in this snake is considered to be an artifact of a piscivorous diet and the host should be considered accidental.

#### **ACANTHOCEPHALA OF AVES**

## Paleoacanthocephala: Polymorphida: Centrorhynchidae

Centrorhynchus conspectus Van Cleave and Pratt, 1940 — Bubo virginianus, great horned owl (Richardson and Nickol 1995).

#### ACANTHOCEPHALA OF MAMMALIA

## Archiacanthocephala: Moniliformida: Moniliformidae

*Moniliformis clarkii* (Ward, 1917) Chandler, 1921 – *Sciurus carolinensis*, eastern gray squirrel (Singleton et al. 1993).

#### **Acanthocephalans of Arkansas**

#### Oligachanthorhynchida: Oligacanthorhynchidae

*Macracanthorhynchus ingens* (von Linstow, 1879) Travassos, 1917 – *Procyon lotor*, raccoon (Richardson et al. 1992, Richardson 2014).

Oligacanthorhynchus microcephalus (Rudolphi, 1819) Schmidt, 1972 – (syn. O. tortuosa) Didelphis virginiana, Virginia opossum (Richardson 1993, Richardson and Barnawell 1995, Richardson et al. 2014).

### Palaeacanthocephala: Polymorphida: Centrorhynchidae

Centrorhynchus conspectus Van Cleave and Pratt, 1940. – D. virginiana (Richardson 1993); P. lotor (Richardson et al. 1992).

#### Plagiorhynchidae

*Plagiorhynchus cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966. – *D. virginiana* (Ellis et al. 1999).

#### NEW HOST AND GEOGRAPHIC RECORDS FOR ACANTHOCEPHALANS FROM ACTINOPTERYGII

Counties where acanthocephalans were collected from fishes are presented in Fig. 1. All hosts were taken from the Arkansas, Ouachita and White river drainages. Our findings are documented as new host records for each acanthocephalan listed below.

### *Pomphyrhynchus bulbocolli* Linkins in Van Cleave, 1919

Campostoma spadiceum, 1 male, 1 female, Garland Co., Walnut Creek (34.533874°N, 93.371049°W), 8 Jun. 2015. HWML 101937.

*Luxilus pilsbyri*, 110 mm TL, 3 specimens, Izard Co., Calico Creek (36.122557°N, 92.143797°W), 7 Jul. 2015. HWML 101941.

Although this acanthocephalan is widely-distributed in North American freshwater fishes (Amin 1987, Hoffman 1999), this is the first report of *P. bulbocolli* from Arkansas fishes.

### Neoechinorhynchus prolixus Van Cleave and Timmons, 1952

Carpiodes cyprinus, Marion Co., Crooked Creek (36.244433°N, 92.716531°W), 23 Jul. 2014, HWML 75374. McAllister et al. (2015a) previously reported *N. prolixus* from *C. velifer* from Arkansas.

Acanthocephalus dirus (Van Cleave, 1931) Van Cleave and Townsend, 1936

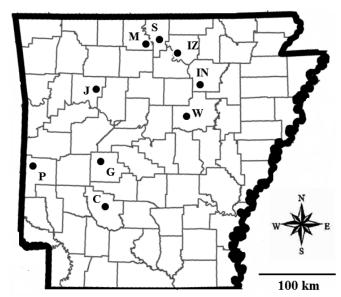


Figure 1. Nine Arkansas counties containing streams where fishes harbored acanthocephalans. Abbreviations: C (Clark), G (Garland), IN (Independence), IZ (Izard), J (Johnson), Marion (M), P (Polk), S (Sharp), W (White).

Etheostoma artesiae, 5 gravid females. Clark Co., Mill Creek off St. Hwy 7 (34.033599°N, 92.935703°W), 9 Apr. 2015. HWML 101943.

Etheostoma whipplei, 74 mm TL, 2 females, 1 juvenile, Johnson Co., Washita Creek (35.654197°N, 93.593527°W), 7 Jun. 2015. HWML 101938.

Lepomis cyanellus, 1 male, 2 gravid females, White Co., Gin Creek in Searcy (35.2511°N, 91.716288°W), 4 Apr. 2014. HWML 101947.

Luxilus zonatus, 1 female, Sharp Co., N Big Creek at St. Hwy 354 (36.157657°N, 91.5141°W), 8 Jul. 2015. HWML 101981. This is the first report of any helminth from this host.

Acanthocephalus dirus has the widest geographical and host distribution and is found in at least 16 families of fish mostly in the Mississippi River drainage in 13 states in the USA (Amin 1985). We document 4 new host records and document A. dirus for the first time from Arkansas.

### Acanthocephalus tahlequahensis Oetinger and Buckner, 1976

Etheostoma radiosum, 2 males, Garland Co., Walnut Creek (34.533874°N, 93.371049°W), 26 Nov. 2014, HWML 101949; 1 male, 2 males, Garland Co., Bear Creek at Bear (34.534784°N, 93.285969°W), 2 specimens, 63 mm TL, 26 Nov. 2014, 22 May 2015, HWML 101934, 101950; Polk Co., Carter Creek (34.543342°N, 94.165758°W), 22 May 2015, HWML 101935; 1 female, Garland Co., Middle Branch Gulpha Creek (34.510095°N, 93.008682°W), 8 Jun. 2015. Not

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deposited.

Lepomis cyanellus, 1 male, Polk Co., Carter Creek (34.543342°N, 94.165758°W), 22 May 2015. HWML 101936.

McAllister et al. (2014d) previously reported A. tahlequahensis in Arkansas from C. carolinae. This species was described from adjacent Oklahoma in the Illinois River drainage and reported from Sunburst Darter (Etheostoma mihileze), Orangethroat Darter (Etheostoma spectabile), Redspot Chub (Nocomis asper), and Cardinal Shiner (Notropis cardinalis) (Oetinger and Buckner 1976). McAllister et al. (2015a) extended the host range in fishes of the Centrarchidae and Ictaluridae and here we add 2 new hosts and a new river drainage (Ouachita).

#### Neoechinorhynchus sp.

*Etheostoma spectabile*, 1 male, White Co., Dennard Creek (35.257397°N, 91.744696°W), 4 Apr. 2015. HWML 101948.

*Esox americanus*, 1 juvenile, Polk Co., Abernathy Spring (34.468162°N, 93.947976°W), 23 May 2015. HWML 101939.

Hypentelium nigricans, 159 mm TL, 1 juvenile, Marion Co., Crooked Creek (36.244433°N, 92.716531°W), 23 Jul. 2014. Not deposited.

*Moxostoma carinatum*, 325mm TL, 1 juvenile female, Independence Co., White River at Batesville (35.756648°N, 91.638512°W), 5 Apr. 2014. HWML 101946.

Since a male and 3 juveniles were found in these 4 hosts, no specific identification was possible; however, we document 4 new host records for the genus.

In summary, we provide a checklist of the 22 acanthocephalans now known from Arkansas as well providing 13 new host records and a new state record (A. dirus) for fish acanthocephalans. Additional surveys, particularly of birds along the eastern corridor and southern tier of counties, and of fishes from other Arkansas river drainages, will undoubtedly increase our knowledge of these parasites.

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#### **Literature Cited**

- American Fisheries Society (AFS). 2004. Guidelines for the use of fishes in research [web application]. JG Nickum (Chair). American Fisheries Society, Bethesda, Maryland.http://fisheries.org/docs/policy\_useoffishes.pdf. Accessed 2015 Dec. 27.
- Amin OM. 1985. Hosts and geographic distribution of *Acanthocephalus* (Acanthocephala: Echinorhynchidae) from North American freshwater fishes, with a discussion of species relationships. Proceedings of the Helminthological Society of Washington 52:210–220.
- **Amin OM.** 1987. Acanthocephala from lake fishes in Wisconsin: Ecology and host relationships of *Pomphorhynchus bulbocolli* (Pomphorhyncidae). Journal of Parasitology 73:278–289.
- **Amin OM**. 2013. Classification of the Acanthocephala. Folia Parasitologica 60:273–305.
- **Barger MA**. 2004. The *Neoechinorhynchus* of turtles: Specimen base, distribution, and host use. Comparative Parasitology 71:118–129.
- **Becker DA** and **DG Cloutman**. 1975. Parasites of selected game fishes of Lake Fort Smith, Arkansas. Proceedings of the Arkansas Academy of Science 29:12–18.
- **Becker DA, RG Heard** and **PD Holmes**. 1966. A preimpoundment survey of helminth and copepod parasites of *Micropterus* spp. of Beaver Reservoir in northwest Arkansas. Transactions of the American Fisheries Society 95:23–34.
- **Becker DA** and **WC Houghton**. 1969. A survey of the helminth parasites of selected game fishes of Lake Fort Smith, Arkansas. Proceedings of the Arkansas Academy of Science 23:110–117.
- **Buckner RL** and **BB Nickol**. 1978. Redescription of *Fessisentis vancleavei* (Hughes and Moore, 1943) Nickol, 1972 (Acanthocephala: Fessisentidae). Journal of Parasitology 64:635–637.
- **Bush AO, KD Lafferty, JM Lotz** and **AW Shostak**. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83:575–583.
- **Cable RM** and **FM Fisher Jr**. 1957. A fourth species of *Neoechinorhynchus* (Acanthocephala) in turtles in the United States. Abstract 62. Journal of Parasitology 43: (Supplement):29.

#### **Acanthocephalans of Arkansas**

- Cloutman DG. 1975. Parasite community structure of Largemouth Bass, Warmouth and Bluegill in Lake Fort Smith, Arkansas. Transactions of the American Fisheries Society 104:277–283.
- **Ellis RD, OJ Pung** and **DJ Richardson**. 1999. Site selection by intestinal helminths of the Virginia opossum (*Didelphis virginiana*). Journal of Parasitology 85:1–5.
- **Fisher FM Jr.** 1960. On Acanthocephala of turtles, with the description of *Neoechinorhynchus emyditoides* n. sp. Journal of Parasitology 46:257–266.
- **Hoffman GL**. 1999. Parasites of North American freshwater fishes. Second Ed. Ithaca (NY): Comstock Publishing Associates. 539 p.
- McAllister C and O Amin. 2008. Acanthocephalan parasites (Echinorhynchida: Heteracanthocephalidae; Pomphorhynchidae) from the Pirate Perch (Percopsiformes: Aphredoderidae), from the Caddo River, Arkansas. Journal of the Arkansas Academy of Science 62:151–152.
- McAllister CT, MA Barger, TJ Fayton, MB Connior, DA Neely and HW Robison. 2015a. Acanthocephalan parasites of select fishes (Catostomidae, Centrarchidae, Cyprinidae, Ictaluridae), from the White River Drainage, Arkansas. Journal of the Arkansas Academy of Science 69:132–134.
- McAllister CT, MA Barger and HW Robison. 2015b. Natural history notes: *Nerodia sipedon pleuralis*. Herpetological Review 46:648.
- McAllister CT, CR Bursey, HW Robison, DA Neely, MB Connior and MA Barger. 2014a. Miscellaneous fish helminth parasite (Trematoda, Cestoidea, Nematoda, Acanthocephala) records from Arkansas. Journal of the Arkansas Academy of Science 68:78–86.
- McAllister CT, CR Bursey, HW Robison and MA Barger. 2014b. *Haemogregarina* sp. (Apicomplexa: Haemogregarinidae), *Telorchis attenuata* (Digenea: Telorchiidae) and *Neoechinorhynchus emydis* (Acanthocephala: Neoechinorhyncidae) from map turtles (*Graptemys* spp.), in Northcentral Arkansas. Journal of the Arkansas Academy of Science 68:154–157.
- McAllister CT, MB Connior, CR Bursey and HW Robison. 2014c. A comparative study of helminth parasites of the many-ribbed salamander, Eurycea multiplicata and Oklahoma salamander, Eurycea tynerensis (Caudata: Plethodontidae), from Arkansas and Oklahoma. Journal of the Arkansas Academy of Science 68:87–96.

- McAllister CT, MB Connior, WF Font and HW Robison. 2014d. Helminth parasites of the Banded Sculpin, *Cottus carolinae* (Scorpaeniformes: Cottidae), from Northern Arkansas, U.S.A. Comparative Parasitology 81:203–209.
- McAllister CT, SE Trauth and CR Bursey. 1995.

  Metazoan parasites of the graybelly salamander,

  Eurycea multiplicata griseogaster (Caudata:

  Plethodontidae), from Arkansas. Journal of the

  Helminthological Society of Washington 62:66–69.
- Oetinger DF and RL Buckner. 1976. Acanthocephalus tahlequahensis sp. n. (Acanthocephala, Echinorhynchidae) from the Stippled Darter, Etheostoma punctulatum (Agassiz) in northeastern Oklahoma. Journal of Parasitology 62:237-241.
- **Richardson DJ**. 1993. Acanthocephala of the Virginia opossum (*Didelphis virginiana*) in Arkansas, with a note on the life history of *Centrorhynchus wardae* (Centrorhynchidae). Journal of the Helminthological Society of Washington 60:128–130.
- **Richardson DJ.** 2005. Identification of cystacanths and adults of *Oligacanthorhynchus tortuosa*, *Macracanthorhynchus ingens*, and *Macracanthorhynchus hirudinaceus* based on proboscis and hook morphometrics. Journal of the Arkansas Academy of Science 59:205–209.
- **Richardson DJ**. 2014. Acanthocephala of the raccoon (*Procyon lotor*) with a faunal review of *Macracanthorhynchus ingens* (Acanthocephala: Oligacanthorhynchidae). Comparative Parasitology 81:44–52.
- **Richardson DJ** and **EB Barnawell.** 1995. Histopathology of *Oligacanthorhynchus tortuosa* (Oligacanthorhynchidae) infection in the Virginia opossum (*Didelphis virginiana*). Journal of the Helminthological Society of Washington 62:253–256.
- Richardson DJ and BB Nickol. 1995. The genus Centrorhynchus (Acanthocephala) in North America with description of Centrorhynchus robustus n. sp., redescription of Centrorhynchus conspectus, and a key to species. Journal of Parasitology 81:767–772.
- Richardson DJ, SL Gardner and JW Allen Jr. 2014.

  Redescription of Oligacanthorhynchus microcephalus (Rudolphi, 1819) Schmidt, 1972 (syn. Oligacanthorhynchus tortuosa (Leidy, 1850) Schmidt, 1972) (Acanthocephala: Oligacanthorhynchidae). Comparative Parasitology 81:53–60.

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- **Richardson DJ, WB Owen** and **DE Snyder.** 1992. Helminth parasites of the raccoon (*Procyon lotor*) from North-central Arkansas. Journal of Parasitology 78:163-166.
- **Rosen R** and **WC Marquardt**. 1978. Helminth parasites of the red-eared turtle (*Pseudemys scripta elegans*) in central Arkansas. Journal of Parasitology 64:1148–1149.
- Singleton J, DJ Richardson and JM Lockhart. 1993. Severe moniliformiasis (Acanthocephala: Moniliformidae) in a gray squirrel, *Sciurus carolinensis*, from Arkansas, USA. Journal of Wildlife Diseases 29:165–168.
- **Steinauer ML** and **BB Nickol**. 2015. Revision of *Leptorhynchoides thecatus* (Acanthocephala: Illiosentidae), with morphometric analysis and description of six new species. Journal of Parasitology 101:193–211.