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Helminths of the American bullfrog, *Lithobates catesbeianus* (Shaw, 1802), from Pawnee Lake, Lancaster, Nebraska, USA with a checklist of its helminth parasites

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Abstract

The American bullfrog, *Lithobates catesbeianus*, is one of the most intensively studied host species. However, most of the records related to the parasites of this anuran are scattered through the literature. The purpose of our study is twofold: 1) to list the helmiths of this host from Pawnee Lake, Lancaster Co., Nebraska, USA, and 2) To compile all published records and those contained by several scientific collections to construct a checklist of helminth parasites associated with the American bullfrog through its range in both native and introduced geographical areas. Twenty-seven specimens of *L. catesbeianus* were collected and examined for helminth parasites; 20 frogs were infected. Nine species of helminths were collected: 4 digeneans: *Haematoloechus coloradensis*, *H. parviplexus*, *Gorgoderina attenuata*, and *Glypthelmins quieta*, and 5 nematodes: *Rhabdias ranae*, *Spinitectus gracilis*, *Cosmocercoides variabilis*, *Spiroxys* sp., and an unidentified ascarid nematode. Pawnee Lake represents a new locality record for *S. gracilis*. The digenean *H. parviplexus* had the highest prevalence and mean abundance (33.3% and 3, respectively). As a result of our study, the number of helminth taxa known for this host is 159 (75 digeneans, 4 monogeneans, 10 cestodes, 7 acanthocephalans, and 63 nematodes); these records come from 6 countries (Canada, Cuba, Japan, Korea, United Kingdom, and USA). Although well documented, the helminthological record of this host species could increase after further inventory work in poorly sampled regions.

Key words: *Lithobates catesbeianus*, American bullfrog, Pawnee Lake, helminths, Nematoda, Digenea, checklist

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Introduction

The American bullfrog, *Lithobates catesbeianus* (Shaw, 1802) (previously *Rana catesbeiana* Shaw, 1802, see Frost *et al*. 2006), is native to North America, occurring from sea level to 2,740 m elevation, from southern Atlantic Canada to eastern Colorado and eastern New Mexico and it has been introduced to many localities in the western United States as well as in 26 countries around the world (Santos-Barrera *et al*. 2006). To the best of our knowledge, only one study compiles the helminthological record of the American bullfrog in North America, listing 95 helminth species (Andrews *et al*. 1992). For hosts from Nebraska, 22 helminth species have been recorded (Brooks 1974, 1975a, 1976, 1977; Snyder & Tkach 2001; León-Règagnon & Brooks 2003; León-Règagnon *et al*. 2005; Brooks *et al*. 2006a; Bolek & Janovy 2007). The purpose of this study is to describe helminth parasites of *L. catesbeianus* in Pawnee Lake, Lancaster County, Nebraska, as well as to summarize and update the helminth records of this host species.

Materials and method

A total of 27 adult frogs were collected by hand on September, 2001 from a permanent, anthropogenic impoundment (Pawnee Lake), Lancaster Co., Nebraska (40°51' 31.6'' N, 96° 53' 20.2'' W). Amphibians were collected by hand and placed in plastic containers, transported alive to the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska, Lincoln, Nebraska and killed with an overdose of sodium pentobarbital within 48 hr of capture. The body cavity was opened and internal organs (lungs, stomach, intestine, gall bladder, liver, and urinary bladder) were removed, placed in individual Petri dishes with 0.65% saline solution and examined for helminths with a stereomicroscope. The integument and mouth cavity were also searched for helmiths. Helminths were counted *in situ*, collected and fixed with hot formalin 4% for morphological studies. Digeneans were stained with Mayer's paracarmin, dehydrated, cleared in a gradual series of methyl salicilate and mounted in Canada balsam. Nematodes were cleared with glycerol or Amman's lactophenol and mounted on temporary slides. Helminth infections were characterized following Bush *et al*. (1997). Hosts were initially fixed with 10% formalin, washed with tap water, stored in 70% ethanol and deposited in the collection of amphibians and reptiles of the Zoological Division of the University of Nebraska State Museum, with the following accession numbers: ZM 23694-23707, 23716-23728. Helminth voucher specimens were deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City. To create the checklist, we used the information from a retrospective bibliographical search, using different databases (CAB Abstracts, Biological Abstracts, Zoological Record, and ISI Web of Science) and searches in data bases of parasite collections. Larval stages are indicated by asterisk (*). Data are updated to October, 2009. The following acronyms are used reffering to parasitological collections: CMNPA: Canadian Museum of Nature, Parasitological Collection, Ottawa, Canada; CZACC: Colección del Instituto de Zoología, Academía de Ciencias de Cuba, Havana, Cuba; HWML: Harold W. Manter Laboratory of Parasitology, Lincoln, Nebraska, USA; IES: Instituto de Ecología y Sistematica, Havana, Cuba; NBM: New Brunswick Museum, New Brunswick, Canada; NSMT: National Science Museum, Tokyo, Japan; USNPC: US National Parasite Collection, Maryland, USA.

Results

Twenty seven American bullfrogs were examined (5.144-23.76±25.87 gr and 34-125 (61.78±17.68) mm snout-vent). Thirteen were males, 9 females and for 5, the sex could not be recognized. Of these 20 were parasitized (74%, 44.44% harbored 0-1 species of helminths). Two hundred and two specimens distributed across 9 helminth species were recovered, 4 digenean species: *Haematoloechus coloradensis* (Cort, 1915), *H. parviplexus* (Irwin, 1929), *Gorgoderina attenuata* (Stafford, 1902), and *Glypthelmins quieta* (Stafford, 1900), and 5 nematode species: *Rhabdias ranae* Walton, 1929, *Spinitectus gracilis* Ward & Magath, 1917, *Cosmocercoides variabilis* (Harwood, 1930), *Spiroxys* sp., and an unidentified ascarid nematode. The percentage of parasitism

by organ was: lungs 49.5%, stomach 23.27%, small intestine 12.87%, mesentery 9.4%, large intestine 3.96, and urinary bladder with 0.9%. The lungs were the most parasitized organs with 3 helminth species (*H. coloradensis*, *H. parviplexus* and *R. ranae*).

Three frogs showing site specific co-infection including *R. ranae* and *H. parviplexus*, *R. ranae* and *C. variabilis*, and *H. parviplexus* and *H. colorandensis*. Adult stages were predominant in both helminth classes, nematodes had the highest prevalence values in the overall sample; however, individually *H. parviplexus* showed the highest prevalence and mean abundance (33.3% and 3, respectively).

In the present checklist, 159 helminth taxa recorded as parasites of *L. catesbeianus* are listed, including digeneans (75 taxa), followed by nematodes (63 taxa), cestodes (10 taxa), acanthocephalans (7 taxa), and finally monogeneans with 4 taxa. Most of the helminth species enlisted was recorded in adult stage (111), while 48 taxa represent larval stages. Intestine and lungs constitute the most parasitized habitats in this host species, harbored 59 and 18 helminth taxa, respectively.

Checklist of helmith parasites of *L. catesbeianus* along its natural and introduced distribution range

Digenea van Beneden, 1858

Alaria sp.*

Site of infection: muscle, body cavity.

Recruitment: penetration.

Distribution: Canada: Ontario (Walters *et al*. 1975, experimental). USA: Arizona (Goldberg *et al*. 1998).

Specimens in collections: USNPC: 87070.

Remarks: Goldberg *et al*. (1998) did not consider this genus as typical of anurans, because it does not reach maturity in frogs. Frogs act as second intermediate host; definitive hosts are mammals.

Alaria arisaemoides Agustine & Uribe, 1927*

Site of infection: lungs, muscles, stomach.

Recruitment: penetration.

Distribtion: Canada: New Brunswick (McAlpine 1997; McAlpine & Burt, 1998a).

Specimens in collections: NBM.

Alaria marcianae (La Rue, 1917)*

Site of infection: muscle.

Recruitment: penetration.

Distribution: USA: Louisiana (Shoop 1985, experimental life cycle); Michigan (Bosma 1934).

No specimens in collections.

Remarks: Tadpoles have been reported as experimental second intermediate host of several species of *Alaria* (Johnson 1968).

Alaria mustelae Bosma, 1931*

Site of infection: muscle.

Recruitment: penetration.

Distribution: USA: Michigan (Bosma 1934, experimental life cycle).

Specimens in collections: USNPC: 8553.

Remarks: Bosma (1934) and Johnson (1979) described the life cycle of *Alaria* spp. from experimentally infected tadpoles and naturally infected frogs.

***Allassostomoides chelydrae* (MacCallum, 1919)**

Site of infection: rectum.

Recruitment: penetration.

Distribution: USA: Nebraska (Brooks 1975b; Brooks 1976; Brooks *et al*. 2006a).

No specimens in collections.

Remarks: Some authors have been considered this species synonym of *A. parvus* (Stunkard 1924; Travassos 1934; Skrjabin 1947); however, Yamaguti (1958, 1971) recognized it as a valid species. *Allassostomoides chelydrae* was re-described by Brooks (1975b) based on specimens from multiple host species.

***Allassostomoides parvus* (Stunkard, 1916)**

Site of infection: digestive system, colon, cloaca, rectum.

Recruitment: penetration.

Distribution: USA: Illinois (Beaver 1929); Louisiana (Bennett 1938); Nebraska (Brooks 1975a; Brooks 1976; Brooks *et al*. 2006a).

Specimens in collections: HWML: 20103; USNPC: 95702.

Apharyngostrigea pipientis* (Faust, 1918)

Site of infection: body cavity.

Recruitment: penetration.

Distribution: Canada: New Brunswick (McAlpine 1997).

Specimens in collections: NBM: 1410.

Remarks: This species has also been recorded in *Pseudacris triseriata* from Canada (Goldberg *et al*. 2002) and *Rana pipiens* from USA (Goldberg *et al*. 2001).

Auridistomum chelydrae* (Stafford 1900)

Site of infection: not specified.

Recruitment: penetration.

Distribution: USA: Oklahoma (Ralph 1938).

Specimens in collections: USNPC: 9260 (syntypes).

Remarks: This species was recorded as *Tetrapapillatrema concavocorpa* which is considered a synonym of *Auridistomum chelydrae* (Yamaguti 1971).

***Brachycoelium salamandrae* (Fröelich, 1789)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Georgia (Parker 1941).

No specimens in collections.

Remarks: Recorded as *Brachycoelium louisianae* Byrd, 1937, species synonymyzed with *B. salamandrae* by Rankin (1938) but Yamaguti (1971) included it among valid species of the genus. Reciently Yildirimhan *et al*. (2005) returned *B. louisianae* to synonymy with *B. salamandrae*.

Bunodera* sp.

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Kansas (USNPC).

Specimens in collections: USNPC: 91220.

Remarks: Species of this genus are typical parasites of freshwater fishes (Choudhury & León-Règagnon 2005).

***Cephalogonimus* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Kansas (USNPC).

Specimens in collections: USNPC: 91221.

Remarks: This is the only genus of the family Cephalogonimidae represented in amphibian hosts. Species of this genus are distributed from Canada to Brazil (Yamaguti 1971; Rodriguez-Ortíz *et al*. 2004; Brooks *et al*. 2006a).

***Cephalogonimus americanus* Stafford, 1902**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Massachusetts (Rankin 1945); Arizona (Goldberg *et al*. 1998); undetermined (USNPC).

Specimens in collections: USNPC: 51431.

Remarks: Adult and juvenile specimens of this species have been recorded as parasites of Ranidae and Ambystomatidae (Paredes-León *et al*. 2008). Tadpoles of *Anaxyrus fowleri* (Hinckley) were experimentally infected by Lang (1968).

***Cephalogonimus brevicirrus* Ingles, 1932**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Nevada (Brooks, 1976).

No specimens in collections.

Clinostomum* sp.

Site of infection: muscle, mesentery.

Recruitment: penetration.

Distribution: Canada: Ontario (USNPC). USA: Arizona (Goldberg *et al*. 1998); Louisiana (USNPC); Michigan (Muzzall 1991; USNPC); Texas (Yoder & Gomez 2007; HWML); undetermined locality (Lemke *et al*. 2008).

Specimens in collections: HWML: 48351. USNPC: 50105, 51495, 81461, 87071.

Remarks: Freshwater fish species represent the most common intermediate hosts for species of this genus.

Clinostomum attenuatum* Cort, 1913

Site of infection: peritoneum, body cavity.

Recruitment: penetration.

Distribution: USA: Oklahoma (Trowbridge & Hefley 1934); undetermined (HWML).

Specimens in collections: HWML: 30326, 40122.

Remarks: The definitive hosts of this species are several fish-eating birds.

Clinostomum marginatum* Rudolphi, 1819

Site of infection: peritoneum.

Recruitment: penetration.

Distribution: Kansas (Jinks & Johnston 1971).

No specimens in collections.

Remarks: Baer (1933) and Ukoli (1966) synonymyzed *C. marginatum* with *C. complanatum* (Rudolphi, 1819), but recently both species were separated based on differences in ribosomal DNA (Dzikowski *et al*. 2004).

Cystagora tetracystis* (Gastaldi, 1854)

Site of infection: muscles of throat.

Recruitment: unknown.

Distribution: Canada (Stafford 1900, 1905; CMNPA).

Specimens in collections: CMNPA: 1900-1680, 1900-1681.

Remarks: Yamaguti (1971) listed this species among the larval digeneans of amphibians.

***Diplodiscus* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Indiana (USNPC).

Specimens in collections: USNPC: 51953.01.

Remarks: In accordance with Jones *et al*. (2005), species of *Diplodiscus* are distributed in Europe, Asia and Africa. Identification of these specimens needs to be confirmed.

Echinostoma trivolvis* (Cort, 1914)

Site of infection: kidney.

Recruitment: penetration.

Distribution: Canada: New Brunswick (McAlpine 1997). USA: Pennsylvania (Fried & Bradford, 1997).

Specimens in collections: NBM: 1493.

Remarks: Identification of Canada material was based on adult specimens obtained from experimental infection in *Gallus gallus*.

Euryhelmis squamula* (Rudolphi, 1819)

Site of infection: skin.

Recruitment: penetration.

Distribution: USA: Washington (USNPC).

Specimens in collections: USNPC: 44419.

Remarks: Specific identification of these metacercariae was based on experimental infection in mice (USNPC).

***Glypthelmins* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Nebraska (HWML); Oregon (USNPC); Wisconsin (HWML).

Specimens in collections: HWML: 19720, 19722, 19723, 23832. USNPC: 66142.

Remarks: Based on morphological and molecular evidence, Razo-Mendivil and Pérez-Ponce de León (2008) redefined the genus *Glypthelmins*, including only 10 species; from these, *G. quieta, G. californiensis, G. intestinalis, G. hyloreus, G. pennsylvaniensis, G. parva, and G. shastai* are distributed in USA.

***Glypthelmins californiensis* (Cort, 1919)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: not specified (HWML).

Specimens in collections: HWML: 31390.

Remarks: Valid species following Razo-Mendivil and Pérez-Ponce de León (2008).

***Glypthelmins quieta* (Stafford, 1900)**

Site of infection: intestine.

Recruitment: ingestion.

Prevalence, mean intensity, and intensity range: 25.9%, 3.71, 1-13.

Specimens deposited: CNHE: 5374.

Distribution: Canada: New Brunswick (McAlpine 1997a, 1997b; 1998; McAlpine & Burt 1998a; NBM); Ontario (Stafford 1900; Stafford 1905; Walton 1938; Walton 1947); Quebec (CMNPA). Cuba: Havana (Odening 1968; Martínez *et al*. 1982). USA: Arkansas (Rosen & Manis 1976; USNPC); California (Goldberg & Bursey 2002a); Florida (Manter 1938); Georgia (USNPC; HWML; Parker 1941; Sullivan 1972; Sullivan 1976); Illinois (Miller 1930; Leigh 1937a, 1937b, 1946; Andrews *et al*. 1992; USNPC); Indiana (Lank 1971); Iowa (Ulmer 1970); Kansas (Jinks & Johnston 1971); Louisiana (Bennett 1938; Sullivan 1972; Sullivan 1976; HWML); Massachusetts (Rankin 1944a); Michigan (Najarian 1955; Muzzall 1991); Mississippi (Sullivan 1972; Sullivan 1976; Brooks 1979; HWML); Nebraska (Brooks 1975a; Brooks 1976; Brooks 1979; Brooks *et*

al. 2006a; Razo-Mendivil *et al*. 2006; HWML); Nevada (Babero & Golling 1974); New England (Rankin 1944a; Leigh & Van Cleave 1945); North Carolina (Brandt 1936; Rankin 1944a; Leigh & Van Cleave 1945); Ohio (Odlaug 1954; Ashton & Rabalais 1978); Oklahoma (Trowbridge & Hefley 1934; Brooks 1979); Oregon (O'Grady 1987; USNPC); Seattle (Rankin 1944a; Leigh & Van Cleave 1945); South Carolina (USNPC); Texas (Harwood 1932; Slagle 1966; Hollis 1972; Mayberry *et al*. 2000; Smythe & Font 2001); Virginia (Britt 1947; Campbell 1968); Washington (Rankin 1944a; Leigh & Van Cleave 1945); Winsconsin (Schell 1962); undetermined locality (Walton 1938, 1947; USNPC).

Specimens in collections: CMNPA: 1900-1696, 1900-1697, 1900-1698. HWML: 19721, 20174-20178, 20183, 20187, 20229, 20643, 20925, 20938, 20956, 22675, 31273. NBM: 746. USNPC: 66142.02, 72269, 72270, 82012, 84282, 84283, 84802, 84814, 91248, 95554.

Remarks: Type species of the genus *Glypthelmins* sensu stricto (Razo-Mendivil *et al*. 2006). Harwood (1932) described *Glypthelmins subtropica* Harwood, 1932 based on specimens from *L. catesbeianus* (USNPC: 30878); this name was used also by Parker (1941); however, in a recent phylogenetic analysis and revision of the genus, this species was considered synonym of *G. quieta* (Razo-Mendivil *et al*. 2006; Razo-Mendivil & Pérez-Ponce de León 2008).

***Gorgodera* sp.**

Site of infection: intestine, urinary bladder.

Recruitment: ingestion.

Distribution: Canada: Ontario (CMNPA); Quebec (Fantham & Portes 1948). USA: Kansas (HWML); Louisiana (HWML); Michigan (Hunt 1952); New York (USNPC); West Virginia (NBM).

Specimens in collections: CMNPA: 1900-1617c. HWML 22682, 24896. NBM: 1376. USNPC: 36360.

Remarks: This genus is apparently distributed in the Nearctic, Palearctic and Oriental Realms (Yamaguti 1971). Some species have been found in sympatry with species of *Gorgoderina* in *L. catesbeianus* (Odlaug 1937; Andrews *et al*. 1992). Material from Michigan was obtained experimentally, and recorded as *Gorgodera vivata* Hunt, 1952, which is *nomen nudum* (Yamaguti 1971).

***Gorgodera amplicava* Looss, 1899a**

Site of infection: kidneys and urinary bladder (in adult specimens); bladder, excretory ducts, stomach, intestine, colon, cloaca, Wolffian duct, oviduct, mesonephroi (in young specimens).

Recruitment: ingestion.

Distribution: Canada: Ontario (Bensley, 1897; Looss 1899a, 1899b; Stafford 1903; Cort 1912; CMNPA; USNPC). USA: Arkansas (Parker 1941; Rosen & Manis 1976); Illinois (Andrews *et al*. 1992; USNPC); Indiana (Lank 1971); Iowa (Ulmer 1970); Kentucky (Parker 1941); Louisiana (Bennett 1938; Goodchild 1954, 1955; HWML); Massachusetts (Odlaug 1937; Goodchild 1945, 1948, 1950, 1955); Michigan (Krull 1935); Mississippi (Brooks 1979); Missouri (Goodchild 1948,1950, 1954; HWML); Nebraska (Brooks 1976; Brooks *et al*. 2006a); North Carolina (Brandt 1936; HWML); Ohio (Odlaug 1936; Guberlet 1920); Oklahoma (Guberlet 1919; Trowbridge & Hefley 1934); Tennessee (Parker 1941); Texas (Harwood 1932; Hollis 1972; Mayberry *et al*. 2000; Yoder & Gomez 2007; HWML); Virginia (Campbell 1968); Wisconsin (HWML); undetermined locality (Odlaug 1936; Lemke *et al*. 2008; USNPC).

Specimens in collections: CMNPA: 1900-1617a. HWML: 20127-20131, 20957, 22683, 23424, 23425, 33140, 33141, 48349, 49007. USNPC: 50312, 50313, 51638, 51642, 51643, 82013, 84815.

Remarks: This species has been registered exclusively in North America; the only record out of this region (Kirghizia, Asia by Skarvilovich, 1950 in Yamaguti 1971) needs to be confirmed. Records of this

species from Oklahoma (representing a new species, *Gorgodera circava*) were transferred to *G. amplicava* by Harwood (1932); unfortunately, no type specimens were deposited for specific status confirmation. In the same way, specimens from Ontario, Canada (Cort 1912), Illinois (USNPC 51642, 51643 and HWML 20957), Mississippi (Brooks 1979) and Texas (Hollis 1972) were identified as *Gorgodera minima*, but Yamaguti (1971) considered this species synonym of *G. amplicava*.

***Gorgodera cygnoides* (Zeder, 1800)**

Site of infection: urinary bladder.

Recruitment: ingestion.

Distribution: USA: New York Aquarium (USNPC).

Specimens in collections: USNPC: 36351.

Remarks: Material recorded as *Distomum cygnoides*, which is currently included in the genus *Gorgodera*. Distribution of this species is exclusively Palearctic and Oriental (Walton 1949; Prudhoe & Bray 1982); for this reason, identity of these specimens needs to be confirmed.

Gorgoderidae gen. sp.

Site of infection: urinary bladder.

Recruitment: ingestion.

Distribution: USA: California and Nebraska (HWML).

Specimens in collections: HWML: 31427, 45868, 45873.

Remarks: These specimens were found in adult stage; nevertheless, its identity remains unknown.

***Gorgoderina* sp.**

Site of infection: kidney.

Recruitment: ingestion.

Distribution: USA: Nebraska (HWML).

Specimens in collections: HWML: 48997.

***Gorgoderina attenuata* (Stafford, 1902)**

Site of infection: kidney, urinary bladder.

Recruitment: ingestion.

Prevalence, mean intensity: 7.4%, 1.

Specimens deposited: CNHE: 6943.

Distribution: Canada: New Brunswick (McAlpine 1997; McAlpine & Burt 1998a; NBM); Ontario (Stafford 1903; Cort 1912; Pande 1937; USNPC); Quebec (Fantham & Porter 1948). USA: Arizona (Goldberg *et al*. 1998); Arkansas (Rosen & Manis 1976); Illinois (Andrews *et al*. 1992; USNPC); Indiana (Lank 1971); Kansas (Jinks & Johnston 1971); Massachusetts (Odlaug 1937; Rankin 1945; Goodchild 1950); Michigan (Muzzall 1991); Mississippi (Brooks 1979; HWML); Nebraska (Brooks 1976; Brooks *et al*. 2006a; HWML); North Carolina (Brandt 1936); South Carolina (USNPC); Texas (Hollis 1972; Mayberry *et al*. 2000); Virginia (Britt 1947); Washington (USNPC).

Specimens in collections: HWML: 20121, 20122, 20124, 20126, 20955, 48985, 48989, 48992-94, 48996. NBM: 791, 1448, 1484. USNPC: 44421, 50314, 82014, 84803.

Remarks: Distribution of this species extends from Canada to Guatemala, parasitizing a large variety of amphibian species, but it has not been recorded in *L. catesbeianus* from Mexico and Guatemala (Muzzall *et al*. 2001; Bolek & Coggins 2003; Mata-López *et al*. 2005; Pérez-Ponce de León *et al*. 2007).

***Gorgoderina bilobata* Rankin, 1937**

Site of infection: urinary bladder.

Recruitment: ingestion.

Distribution: USA: Georgia (Parker 1941); Virginia (Campbell 1968).

No specimens in collections.

Remarks: This species has also been found in Caudata (*Pseudotriton* spp. and *Notophthalmus*) and other species of anurans (Yamaguti 1971; Mata-López *et al*. 2005).

***Gorgoderina simplex* (Looss, 1899)**

Site of infection: urinary bladder.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997; McAlpine & Burt 1998a; NBM); Ontario (Stafford 1903; Cort 1912; CMNPA; USNPC). USA: Michigan (Najarian 1955); Nebraska (Brooks 1976; Brooks *et al*. 2006a); undetermined locality (Bensley 1897).

Specimens in collections: CMNPA: 1900-1607, 1900-1617b. HWML: 20117, 20120. NBM: 784, 785, 788, 789, 790, 1395, 1396, 1486. USNPC 50315, 51645.

Remarks: This species was originally named *Gorgodera simplex* (Looss 1899a, 1899b) based on Canadian specimens and transferred to *Gorgoderina* by Looss (1905) who established it as the type species of the genus. Material identified by Bensley (1897) as *Distoma cygnoides* var. B was proposed as synonym of *G. simplex* by Looss (1905). Pande (1937) and Kaw (1950) considered this species as member of the genus *Phyllodistomum*.

***Haematoloechus* sp.**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: USA: California (HWML); Louisiana (USNPC); Nebraska (HWML); North Carolina (Brandt 1936); Texas (Knight *et al*. 1965; Morrison 1966); West Virginia (NBM).

Specimens in collections: HWML: 19716, 19840, 31435, 45945. NBM: 1372. USNPC: 59141, 59175, 59180.

Remarks: To date, 8 species of *Haematoloechus* have been recorded as parasites of *L. catesbeianus*, all of them recorded within its native distribution range.

***Haematoloechus breviplexus* Stafford, 1902**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: Canada: Ontario (Stafford 1905; Cort 1915; CMNPA); Quebec (Fantham & Porter 1948). USA: Arizona (Snyder & Tkach 2001); Arkansas (Rosen & Manis 1976; USNPC); Illinois (USNPC); Indiana (Lank 1971; Whitehouse 2002); Kentucky (Whitehouse 2002); Louisiana (Bennett 1938; USNPC; HWML); Mississippi (Clark & Longest 1969; Brooks 1979; HWML); Nebraska (Brooks *et al*. 2006a; HWML); Nevada (Babero & Golling 1974); North Carolina (Brandt 1936); New Mexico (Dronen 1977); Oklahoma (Cort 1915;

Trowbridge & Hefley 1934); South Carolina (USNPC); Texas (Knight *et al*. 1965; Slagle 1966; Hollis 1972; Underwood & Dronen 1977; Mayberry *et al*. 2000; Yoder & Gomez 2007; HWML); Virginia (Campbell 1968).

Specimens in collections: CMNPA: 1900-1621. HWML: 20293, 21957, 22681, 48350. USNPC: 50473, 82015, 84816, 95563.

Remarks: Some specimens identified by Cort (1915) as *H. breviplexus* were re-determined by León-Règagnon *et al*. (2005) as *H. floedae*. Material from Quebec was included into the genus *Pneumobites*, a synonym of *Haematoloechus* (Yamaguti 1971).

***Haematoloechus buttensis* Ingles, 1936**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: USA: Nevada (Babero & Golling 1974).

No specimens in collections.

***Haematoloechus coloradensis* (Cort, 1915)**

Site of infection: lungs.

Recruitment: ingestion.

Prevalence, mean intensity, and range: 3.7%, 0.11, 3.

Specimens deposited: CNHE: 6944.

Distribution: USA: Nebraska (Bolek & Janovy 2007).

Specimens in collections: HWML: 48480.

Remarks: *Haematoloechus coloradensis* is found from the western United States to Central Mexico and the Pacific coast as the result of expansion and contraction of distribution ranges of Nearctic fauna following geologic events from the early Eocene to the Pleistocene (León-Règagnon & Brooks 2003).

***Haematoloechus complexus* (Seely, 1906)**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: USA: Nebraska (Bolek & Janovy 2007; HWML); South Carolina (USNPC).

Specimens in collections: HWML: 15298, 15299, 48481. USNPC: 84805.

Remarks: *Haematoloechus complexus* has shown some specificity to leopard frogs (León-Règagnon & Brooks 2003); records in American bullfrogs may be considered as accidental infections.

***Haematoloechus floedae* Harwood, 1932**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: USA: Arizona (Mayberry *et al*. 2000; Snyder & Tkach 2001); California (León-Règagnon *et al*. 2005); Florida (Manter 1938); Georgia (León-Règagnon & Brooks 2003); Nebraska (HWML); Texas (Harwood 1932; Jacobs & Morrison 1966);

Specimens in collections: CNHE: 4663, 4664; HWML: 1251, 21945. USNPC: 30879 (holotype), 84804, 91507.

Remarks: Some authors consider *H. floedae* as junior synonym of *H. breviplexus* (Odening 1960; Kennedy 1981); however, according to morphological and molecular data, *H. floedae* is a valid species (León-Règagnon & Brooks 2003). Voucher specimens from *L. catesbeianus* identified as *H. breviplexus* by Snyder and Tkach (2001), as well as specimens deposited at the USNPC (84804), were re-assigned to *H. floedae* (León-Règagnon & Brooks 2003).

***Haematoloechus lobatus* (Seno, 1907)**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: Japan: Chiba and Kagagua Prefectures (Uchida & Itagaki 1976). Korea: Chonnam-Kohung Podu (Kim *et al*. 1992).

No specimens in collections.

Remarks: This species was described originally as *Pneumonoeces lobatus*, but the original description lacks morphological characters (Seno 1907). Uchida and Itagaki (1976) redescribed in detail this species as parasite of *Lithobates catesbeianus.*

***Haematoloechus longiplexus* Stafford, 1902**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997a, 1997b; 1998; McAlpine & Burt 1998a; NBM); Nova Scotia (Stafford 1903); Ontario (Stafford 1903; Cort 1915; CMNPA); Quebec (Stafford 1903). Cuba (Odening 1968). USA: Arizona (Goldberg *et al*. 1998; Snyder & Tkach 2001; USNPC); Arkansas (Rosen & Manis 1976); California (Shields 1987; Goldberg & Bursey 2002a); Connecticut (Brooks, 1976); Georgia (HWML); Idaho (Waitz 1961; Waitz 1962); Illinois (Cort 1915); Indiana (Cort 1915; Lank 1971); Iowa (Ulmer 1970; Cain & French 1975); Kentucky (Whitehouse 2002); Louisiana (Bennett 1938); Michigan (Krull 1932; Muzzall 1991; Najarian 1955); Mississippi (Clark & Longest 1969); Nebraska (Brooks 1974; Brooks 1976; Snyder & Tkach 2001; León-Règagnon & Brooks 2003; Brooks *et al*. 2006a; Bolek & Janovy 2007; HWML; USNPC); Nevada (Babero & Golling 1974); North Carolina (Brandt 1936); Ohio (Ashton & Rabalais 1978; Bursey & DeWolf 1998); Oklahoma (Trowbridge & Hefley 1934; Brooks 1979); Oregon (HWML); Texas (Harwood 1932); Washington (Schell 1965); West Virginia (USNPC).

Specimens in collections: CMNPA: 1900-1624, 1900-1625, 1900-1626, 1900-1631, 1900-1634. HWML: 15282, 15301, 15304, 19843, 20144-20150, 20939, 21947, 23255, 48432, 48482. NBM: 793, 1244, 1245, 1248, 1249, 1251, 1460, 1479, 3523-3526. USNPC: 79466, 87069, 91244, 91509, 91510, 102161, 102175.

Remarks: León-Règagnon *et al*. (1999) synonymyzed *H. macrorchis* with *H. longiplexus*, but molecular evidence provided by Snyder & Tkach (2001) and León-Règagnon and Brooks (2003) support that they are independent species with very similar morphology.

***Haematoloechus medioplexus* Stafford, 1902**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: Canada: Quebec (Fantham & Porter 1948). USA: Iowa (Cain & French 1975).

No specimens in collections.

Remarks: Some species parasitizing *Lithobates* spp. in Mexico were recorded as *H. medioplexus*; further, they were re-determined as *H. danbrooksi* (León-Règagnon & Paredes-Calderón 2002). This species is a second intermediate host specialist, parasitizing only anisopteran odonates (Krull 1930; Snyder & Janovy 1994).

***Haematoloechus parviplexus* (Irwin 1929)**

Site of infection: lungs.

Prevalence, mean intensity, and intensity range: 33.3%, 9, 1-28.

Specimens deposited: CNHE: 6945.

Recruitment: ingestion.

Distribution: USA: Connecticut (Brooks 1976); Louisiana (Bennett 1938; USNPC); Michigan (Muzzall 1991); Nebraska (Brooks 1974; Brooks 1976; León-Règagnon & Brooks 2003; León-Règagnon *et al*. 2005; Brooks *et al*. 2006a; Bolek & Janovy 2007); Nevada (Babero & Golling 1974); Washington (USNPC).

Specimens in collections: CNHE: 4405. HWML: 20142, 20143, 20753, 21660, 48433, 48483. USNPC: 75445, 81467, 95564, 102174.

Remarks: Kennedy (1981) proposed the synonymy of *H. parviplexus* with *H. varioplexus*; however, León-Règagnon and Brooks (2003) and León-Règagnon *et al*. (2005) supported the validity of this species based on molecular and morphological evidence.

***Haematoloechus variegatus* (Rudolphi, 1819)**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: Canada: Ontario (Stafford 1900). USA: New York Aquarium (USNPC).

Specimens in collections: USNPC: 35195.

Remarks: Material deposited in USNPC as *Distomum variegatum* Rudolphi; later this species was transferred to the genus *Haematoloechus* (Looss). This is a typical European species (Yamaguti 1971). Identification of this material needs to be revised.

***Haematoloechus varioplexus* Stafford, 1902**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997a, 1997b; 1998; McAlpine & Burt 1998a; NBM); Ontario (Stafford 1900); Quebec (Stafford 1903). USA: Louisiana (USNPC); Nebraska (Snyder & Tkach 2001; Bolek & Janovy 2007); Virginia (Campbell 1968).

Specimens in collections: NBM: 792, 797, 798, 1257-1259, 1496-1500, 1503-1505, 3536-3538. USNPC: 84817, 91515.

Remarks: Many species of *Haematoloechus* were synonymyzed with *H. varioplexus* by Kennedy (1981). Based on morphological and molecular evidence, León-Règagnon *et al*. (2005) re-established the validity of these species and the close phylogenetic relationships of *H. varioplexus* with *H. parviplexus* and *H. colorandensis*.

***Haematoloechus viguerasi* Martinez, Coy-Otero & Ventosa, 1982**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: Cuba: Havana (Martínez *et al*. 1982; IES).

Specimens in collections: IES: 12.4075 (holotype), 12.4076 (paratypes).

Remarks: This species closely resembles to *H. breviplexus* and *H. floedae*; however, it can be distinguished from *H. breviplexus* by the position of the acetabulum and uterus, as well as form and size of testes; from *H. floedae* is differentiated by body lenght/width and oral sucker/acetabulum ratios, absence of esophagus, ovary shape, and distribution of vitelline glands (Martínez *et al*. 1982).

***Halipegus* sp.**

Site of infection: Eustachian tube, stomach.

Recruitment: ingestion.

Distribution: USA: Arkansas (Rosen & Manis 1976); Louisiana (USNPC); Michigan (Muzzall 1991); Nebraska (HWML).

Specimens in collections: HWML: 19715. USNPC: 84818.

Remarks: Zelmer and Brooks (2000) restricted the genus *Halipegus* to those species lacking genital sacs, permanent sinus organs, and well-developed hermaphroditic ducts.

***Halipegus amherstensis* Rankin, 1944**

Site of infection: Eustachian tube, mouth.

Recruitment: ingestion.

Distribution: USA: Massachusetts (Rankin 1944b; Rankin 1945).

Specimens in collections: USNPC: 36882 (holotype), 36883 (paratype).

Remarks: McAlpine and Burt (1998b) reassigned two specimens from the type material of *H. amhertensis* to *H. occidualis*.

***Halipegus eccentricus* Thomas, 1944**

Site of infection: Eustachian tubes.

Recruitment: ingestion.

Distribution: USA: Michigan (Thomas 1939; Muzzall 2005, in tadpoles); Nebraska (Brooks *et al*. 2006a).

Specimens in collections: USNPC: 9203 (holotype and paratypes).

Remarks: This species was described by Thomas (1939) based on immature specimens parasitizing *L. catesbeianus*, but the material was deposited in USNPC as parasite of *L. clamitans*. McAlpine and Burt (1998b) considered this species a junior synonym of *H occidualis*, but Zelmer and Esch (1999) and McAlpine (2006) rejected this suggestion.

***Halipegus occidualis* Stafford, 1905**

Site of infection: Eustachian tubes, mouth, stomach.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997a, 1997b; 1998; McAlpine & Burt 1998b; NBM); Ontario (Stafford 1905; CMNPA). USA: Massachusetts (McAlpine & Burt 1998b); Nebraska (Brooks 1976); Pennsylvania (USNPC).

Specimens in collections: CMNPA: 1900-1629 (type). HWML: 20098-20101. NBM: 759-761, 1242, 1243, 1254, 1255. USNPC: 31124, 36883.02.

Remarks: This digenean species has been recorded from southern Canada, across USA to Mexico, in different species of amphibians (Zelmer & Brooks 2000).

***Halipegus ovocaudatus* (Vulpian, 1860)**

Site of infection: Eustachian tube, tongue.

Recruitment: ingestion.

Distribution: Canada: Ontario (Stafford 1900).

No specimens in collections.

Remarks: According with Stunkard (1973), *H. ovocaudatus* is distributed exclusively in Europe.

***Langeronia macrocirra* Caballero & Bravo, 1949**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Nevada (Babero & Golling 1974).

No specimens in collections.

Remarks: These specimens were originally recorded as *Loxogenes provitellaria*, which is considered synonym of *L. macrocirra* by Ubelaker (1965). Recently, Martínez- Salazar (2004) re-examined type material of *L. provitellaria*, confirming Ubelaker's proposal.

***Levinseniella ophidea* Nicol, Demaree & Wootton, 1985**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: California (Nicol *et al.* 1985; Goldberg & Bursey 2002a).

No specimens in collections.

Remarks: Nicol *et al*. (1985) distinguished *L. ophidea* from other members of the genus because it uses *L. catesbeianus* as the definitive host. This same authors recorded leeches as a second intermediate host for this species.

***Loxogenes* sp.**

Site of infection: pylorus.

Recruitment: ingestion.

Distribution: Canada: Ontario (CMNPA).

Specimens in collections: CMNPA: 1900-1619.

***Loxogenes arcanum* (Nickerson, 1900)**

Site of infection: liver (immature cyst), duodenum, pyloric caeca, intestine,

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997); Ontario (Stafford 1900; Stafford 1905; CMNPA). USA: Louisiana (USNPC; HWML); Michigan (Muzzall 1991); South Carolina (USNPC).

Specimens in collections: CMNPA: 1900-1711. HWML: 22234-22242, 22354, 22684, 22697. USNPC: 84807, 84819.

Remarks: *Loxogenes arcanum* was originally described as *Distomum arcanum* by Nickerson (1900) from an undetermined North American frog species (distinct of *L. catesbeianus*) and later transferred into the genus *Loxogenes* (Stafford 1905). It has been recorded from other North American (McAlpine & Burt 1998a) and tropical frog species (Goldberg & Bursey 2007).

***Loxogenoides bicolor* (Krull, 1933)**

Site of infection: hepatic-duodenal junction.

Recruitment: ingestion.

Distribution: USA: Carolina (USNPC); Georgia (HWML); Nebraska (Brooks *et al*. 2006a); North Carolina (Brandt 1936).

Specimens in collections: HWML: 22350, 22351. USNPC: 84808.

Remarks: This species was described as *Loxogenes bicolor* by Krull (1933), type species of the new genus *Loxogenoides* proposed by Kaw (1945).

***Loxogenoides loborchis* Christensen, 1981**

Site of infection: liver, bile ducts.

Recruitment: ingestion.

Distribution: USA: Georgia, Kentucky, North Carolina (Christensen 1981).

Specimens in collections: HWML: 21193 (paratype). USNPC: 76097 (holotype), 76320 (paratype).

Remarks: This species and *L. bicolor* reach apparently low prevalence and intensity of infection in *L. catesbeianus*. Christensen (1981) mentioned that studies on life histories and host specifity are needed to further clarify relationships between these species.

***Megalodiscus* sp.**

Site of infection: colon, excretory system, rectum.

Recruitment: ingestion.

Distribution: USA: Florida (Loftin 1960); Georgia (HWML); Michigan (Smith 1953).

Specimens in collections: HWML: 22244.

Remarks: This genus, erected by Chandler (1923), was considered synonym of *Diplodiscus* by Cort (1926) and Führmann (1928); however, Yamaguti (1971) enlisted *Megalodiscus* as valid genus. Specimens from Michigan were obtained experimentally and named *Megalodiscus ferrisianus* Smith, 1953, currently *nomen nudum* (Yamaguti 1971).

***Megalodiscus americanus* Chandler, 1923**

Site of infection: rectum.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997).

Specimens in collections: NBM.

***Megalodiscus intermedius* (Hunter, 1930)**

Site of infection: rectum.

Recruitment: ingestion.

Distribution: USA: Louisiana (Hunter 1930; Brooks *et al*. 2006a); North Carolina (Brandt 1936).

Specimens in collections: USNPC: 8116 (type), 45881 (paratypes), and 8117.

Remarks: Originally described as *Diplodiscus intermedius* and transferred to *Megalodiscus* by Harwood (1932). Zamparo and Brooks (2005) considered that this species could be synonym of *M. temperatus*.

***Megalodiscus microphagus* Ingles, 1936**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Arkansas (Rosen & Manis 1976).

No specimens in collections.

Remarks: This species was described as parasite of *Anaxyrus boreas* (Baird & Girard); besides of *L. catesbeianus*, it has been recorded from *Dicamptodon ensatus* (Eschscholtz), *Pseudacris regilla* (Baird & Girard), *Rana aurora* Baird and Girard, *Taricha granulosa* (Skilton), and *Rana cascadae* Slater (Zamparo & Brooks 2005).

***Megalodiscus temperatus* (Stafford, 1905)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997a, 1997b; McAlpine & Burt 1998a); Ontario (Stafford 1905). USA: Arkansas (Rosen & Manis 1976; USNPC); California (Ingles 1936; Goldberg & Bursey 2002a); Georgia (Parker 1941); Illinois (Andrews *et al*. 1992); Iowa (Ulmer 1970); Louisiana (USNPC); Michigan (Krull & Price 1932; Muzzall 1991; Najarian 1955); North Carolina (Brandt 1936; Brooks *et al*. 2006a; HWML); Nebraska (Brooks 1977; Brooks *et al*. 2006a); South Carolina (USNPC); Tennessee (Parker 1941); Texas (Harwood 1932; Slagle 1966; Hollis 1972; Mayberry *et al*. 2000; Yoder & Gomez 2007; HWML; USNPC); Virginia (Campbell 1968).

Specimens in collections: HWML: 4809, 4903, 20081, 20082, 20084, 33178, 48348. NBM: 1374, 1413. USNPC: 31683, 31684, 31697, 31698, 51953.02, 84284, 84285, 84809, 84820, 91245.

Remarks: Specimens of HWML (33178) were deposited as *Diplodiscus temperatus*, species currently included in *Megalodiscus*. Material from USNPC (4903) pertaining to Leidy Collection and identified as *Diplodiscus subclavatus* (Pallas) Diesing, was considered by Yamaguti (1971) synonym of *M. temperatus*.

***Mesocoelium brevicaecum* Ochi, 1930**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Japan (Ochi 1930).

No specimens in collections.

Remarks: *Lithobates catesbeianus* has been introduced to Japan in several occasions from 1918 (Goldberg & Bursey 2002b).

Neogogatea kentuckiensis* (Cable, 1935)

Site of infection: muscles.

Recruitment: penetration

Distribution: USA: Ohio (Myer 1960).

No specimens in collections.

Remarks: This species was described as *Cercaria kentuckiensis* based on metacercariae obtained experimentally from tadpoles of *L. clamitans*, *L. catesbeianus* and *L. pipiens* (Cable 1935). Later, it was transferred to *Mesostephanus* by Myer (1960), and finally included into the genus *Neogogatea* (Hoffman & Dunbar 1963).

Paramphistomidae gen. sp.

Site of infection: rectum.
Recruitment: ingestion.
Distribution: Canada: New Brunswick (NBM).
Specimens in collections: NBM: 1419, 1420.

Pharyngostomum cordatum* (Diesing, 1850)

Site of infection: mesentery and connective tissues.
Recruitment: penetration.
Distribution: Japan: Aichi Prefecture (Uchida & Itagaki 1980); Kagawa Prefecture (Uchida *et al*. 1977).
No specimens in collections.

***Phyllodistomum* sp.**

Site of infection: "cloacal bladder".
Recruitment: ingestion.
Distribution: Canada: Quebec (Fantham & Porter 1948).
No specimens in collections.

***Plagiorchis* sp.**

Site of infection: intestine.
Recruitment: ingestion.
Distribution: unknown.
Specimens in collections: HWML: 42995.

***Pleurogenoides* sp.**

Site of infection: not specified.
Recruitment: ingestion.
Distribution: USA: California, Oregon and Washington (Lehmann 1965).
No specimens in collections.
Remarks: Species of *Pleurogenoides* are parasites of reptiles (Travassos 1921); however, they can mature in *Rana* sp. (Macy 1964).

***Pleurogenoides stromi* Travassos, 1930**

Site of infection: intestine.
Recruitment: ingestion.
Distribution: USA: Louisiana (HWML).

Specimens in collections: HWML: 23752.

Remarks: This material needs revision; the species is typical from Europe and Asia (Rao 1977).

***Proterometra albacauda* Anderson & Anderson, 1967**

Site of infection: esophagus, stomach.

Recruitment: ingestion.

Distribution: not specified (experimental infection by Krissinger and Mehra 1968).

No specimens in collections.

Remarks: The life cycle of this species was studied by Anderson and Anderson (1967) and Krissinger and Mehra (1968); later authors used *L. catesbeianus* as second intermediate host. This genus is a characteristic parasite of birds.

***Pseudosonsinotrema catesbeianae* Christian, 1971**

Site of infection: duodenum.

Recruitment: ingestion.

Distribution: USA: Louisiana (USNPC); Tennessee (Christian 1971).

Specimens in collections: USNPC: 70789 (holotype), 70790 (paratype), 84821.

Remarks: This genus is parasite of reptiles and occasionally of amphibians (Yamaguti 1971).

***Rauschiella linguatula* (Rudolphi, 1819)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Nevada (Babero & Golling 1974).

No specimens in collections.

Remarks: originally recorded as *Glypthelmins linguatula* (Rudolphi 1819), but based on morphological evidence, this species was transferred to *Rauschiella* (Razo-Mendivil *et al*. 2006).

***Rauschiella proxima* (Freitas, 1941)**

Site of infection: no specified.

Recruitment: ingestion.

Distribution: USA: Nevada (Babero & Golling 1974).

No specimens in collections.

Remarks: originally recorded as *Glypthelmins proxima* Freitas, 1941, but this species was transferred to *Rauschiella* (Razo-Mendivil *et al*. 2006).

Ribeiroia* sp.

Site of infection: not specified.

Recruitment: ingestion.

Distribution: USA: California (Johnson *et al*. 1999; Goldberg & Bursey 2002a); western United States (Johnson *et al*. 2002).

No specimens in collections.

Remarks: Johnson *et al*. (1999; 2002) associated the presence of larvae of this parasite with malformations in host amphibians.

Strigea elegans* Chandler & Rausch, 1947

Site of infection: muscles of tadpoles.

Recruitment: penetration.

Distribution: USA (Miller *et al*., 1965a, 1965b, 1965c).

No specimens in collections.

Remarks: This species is parasite of strigiformes. *Lithobates catesbeianus* and other anurans were infected with the mesocercariae of this species under experimental conditions (Miller *et al*. 1965a, 1965b, 1965c), but it has never been recorded in amphibians in the wild.

***Teloporia aspidonectes* (MacCallum, 1917)**

Site of infection: lungs.

Recruitment: ingestion.

Distribution: USA: Michigan (Esch & Kocan 1966).

Specimens in collections: USNPC: 61205.

Remarks: This species was described as *Paramphistomum aspidonectes* by MacCallum (1921), transferred to *Opisthoporus* by Fukui (1929) and finally included in *Teloporia* by Fukui (1933). Species of the genus *Telporia* are common parasites of turtles.

Monogenea Bychowsky, 1937

***Gyrodactylus* sp.**

Site of infection: skin.

Recruitment: contact.

Distribution: Canada: Ontario (Crawshaw 1997). USA: New Jersey (Stunkard & Dunihue 1933a, 1933b).

No specimens in collections.

Remarks: Stunkard and Dunihue (1933a, 1933b) considered that these specimens represent a new species of *Gyrodactylus*. This has also been suggested by Wootton *et al*. (1993), who pointed out that this material could pertain to *Gyrodactylus catesbeianae*.

***Gyrodactylus arcuatus* Bychowsky, 1933**

Site of infection: skin of tadpoles.

Recruitment: contact.

Distribution: Unknown (Paetow *et al*. 2009).

No specimens in collections.

Remarks: In accordance with Paetow *et al*. (2009), tadpoles of this anuran species acts as accidental hosts.

***Gyrodactylus catesbeianae* Wootton, Ryan, Demaree, & Critchfield, 1993**

Site of infection: skin of tadpoles.

Recruitment: contact.

Distribution: USA: California (Wootton *et al*. 1993).

Specimens in collections: HWML: 39479. USNPC: 75997 (holotype), 75998 (paratype).

Remarks: In accordance with Wooten *et al*. (1993), large infestations with this gyrodactylid species resulted in abnormal growth, deformation of the tail and eventual death of the tadpoles.

***Gyrodactylus jennyae* Paetow, Cone, Huyse Mcaughlin & Marcogliese, 2009**

Site of infection: skin of tadpoles.

Recruitment: contact.

Distribution: Unknown, but believed to be an American bullfrog farm in Missouri, USA (Paetow *et al*. 2009).

Specimens in collections: HWML: 49087.

Remarks: This species represents the fifth described from frogs and salamanders in North America, and the second for *L. catesbeianus* (Paetow *et al*. 2009).

Cestoidea Rudolphi, 1808

***Cylindrotaenia americana* Jewell, 1916**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997). USA: Massachussets (Rankin 1945; Cabrera-Guzmán *et al*. 2007); Virginia (Campbell 1968; Cabrera-Guzmán *et al*., 2007).

Specimens in collections: NBM: 1388.

Remarks: *Cylindrotaenia americana* is a western hemisphere species that infect species of several families of Anura (Goldberg & Bursey 2008).

***Bothriocephalus* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997).

Specimens in collections: NBM: 1399.

Remarks: Species of this genus are typical parasites of marine and freshwater teleosts (Bray *et al*. 1994); however, some species, e.g., *Bothriocephalus acheilognathi* Yamaguti, have been recorded parasitizing amphibians and reptiles (Paredes-León *et al*. 2008).

***Ophiotaenia* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Cuba: Provincia Habana, Provincia Pinar del Río (Martínez *et al*. 1982).

No specimens in collections.

Remarks: Specimens collected in Cuba were immature; this condition precluded its specific determination. To date, the only species of *Ophiotaenia* recorded in Cuba as parasite of amphibians is *Ophiotaenia bufonis* Pérez-Vigueras, 1942, in the "bufo" *Peltophryne peltocephala* (Pérez-Vigueras 1942; Freze & Rysavy 1976; de Chambrier *et al*. 2006).

***Ophiotaenia gracilis* Jones, Cheng & Gillespie, 1958**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Colorado (Buhler 1968, 1970; HWML); Virginia (Jones *et al*. 1958).

Specimens in collections: HWML: 33913, 37201.

Remarks: *Ophiotaenia gracilis* and *Ophiotaenia magna* share *Lithobates catesbeianus* as type host. Position of genital pore in mature proglottids (pre-equatorial in *O*. *magna* and equatorial in *O*. *gracilis*) differentiate them (Hannum 1925; Jones *et al*. 1958).

***Ophiotaenia magna* Hannum, 1925**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: California (Goldberg & Bursey 2002a); Nebraka (Brooks 1976; Brooks *et al*. 2006a; HWML); Nevada (Babero & Golling 1974); Oklahoma (Hannum 1925; Trowbridge & Hefley 1934; Kuntz & Self 1944); Texas (Harwood 1932; Hollis 1972; Mayberry *et al*. 2000).

Specimens in collections: HWML: 20205. USNPC: 91249.

Remarks: see comments on *O*. *gracilis*.

***Ophiotaenia saphena* Osler, 1931**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997a 1997b, 1998; McAlpine & Burt 1998a; NBM). USA: Nebraska (Brooks *et al*. 2006a); North Carolina (Brandt 1936).

Specimens in collections: NBM: 1402, 1404, 1406.

Remarks: This species is a common parasite of *Lithobates clamitans* (Muzzall 2005).

Proteocephalidae gen. sp.*

Site of infection: stomach.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997a, 1997b; McAlpine & Burt 1998a; NBM).

Specimens in collections: NBM: 1409.

***Proteocephalus* sp.**

Site of infection: no specified.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997). USA: California (Lehmann 1965); Nebraska (Brooks, 1976); North Carolina (Brandt 1936; cysts); Oregon (Lehmann 1965); Washington (Lehmann 1965).

No specimens in collections.

Remarks: *Proteocephalus* species are fundamentally parasites of Palaearctic fishes (de Chambrier *et al*. 2004).

Spirometra mansonoides* (Mueller, 1935)

Site of infection: femoral muscle.

Recruitment: ingestion.

Distribution: USA: Louisiana (Corkum 1966).

No specimens in collections.

Remarks: This cestode is parasite of mammals, mainly canids and felids, but it has also been registered as parasite of man (Tantaleán & Michaud 2005). Amphibians and reptiles act as intermediate hosts of this parasite (Mueller 1974).

Spirometra ranarum* (Meggitt 1925)

Site of infection: muscle.

Recruitment: ingestion.

Distribution: Canada: Quebec (Fantham & Porter 1948)

No specimens in collections.

Remarks: recorded as *Diphyllobothrium ranarum* Meggitt, 1925 (Fantham & Porter 1948).

Acanthocephala (Rudolphi, 1808)

***Acanthocephalus* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Massachusetts (USNPC).

Specimens in collections: USNPC: 38679.

Remarks: species of *Acanthocephalus* are common intestinal parasites of fishes, amphibians, and snakes (Bursey & Goldberg 2003). Members of this genus show low levels of specificity for the definitive host, e.g. *Acanthocephalus ranae* has been found in 8 genera of amphibians (Nagasawa & Egusa 1981).

Centrorhynchus* sp.

Site of infection: body cavity.

Recruitment: ingestion.

Distribution: USA: North Carolina (Brandt 1936); Texas (Hollis 1972; Mayberry *et al*. 2000); Virginia (Campbell 1968).

No specimens in collections.

Remarks: Species of genus *Centrorhynchus* include diurnal or nocturnal rapacious birds (Falconiforms or Strigiforms) as definitive hosts, and terrestrial isopods or insects, as intermediate hosts. Their various paratenic hosts (amphibians, reptiles, and mammals), play a fundamental role in their transmission to birds (Torres & Puga 1996).

Echinorhynchus* sp.

Site of infection: peritoneum.

Recruitment: ingestion.

Distribution: USA: New York Aquarium (USNPC).

Specimens in collections: USNPC: 36613.

Remarks: These acanthocephalans are common parasites of freshwater and marine fishes (Yamaguti 1963).

***Fessisentis friedi* Nickol, 1972**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1996, 1998; McAlpine & Burt 1998a; NBM).

Specimens in collections: NBM: 1412.

Remarks: this species is a common parasite of freshwater fishes (Choudhury & Dick 1998).

Neoechinorhynchus* sp.

Site of infection: between skin and muscles, lungs and peritoneum.

Recruitment: ingestion.

Distribution: Cuba: Provincia Pinar del Río (Martínez *et al*. 1982).

Specimens in collections: CZACC: 114077.

Remarks: In accordance with Amin (2002), only 1 species of the genus *Neoechinorhynchus* has been recorded parasitizing amphibians: *Neoechinorhynchus cyanophlytic* Kaw from India.

***Neoechinorhynchus* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Texas (Yoder & Gomez 2007; HWML).

Specimens in collections: HWML: 48355.

Remarks: This material can not be identified to specific level because only one specimen was collected; this suggests the accidental nature of this association (Yoder & Gomez 2007).

***Neoechinorhynchus rutili* (Müller, 1780)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1996, 1997a, 1997b, 1998; McAlpine & Burt 1998a; NBM).

Specimens in collections: NBM: 1401.

Remarks: This acanthocephalan species is a common parasite of freshwater fishes (Merritt & Pratt 1964), but it can be accidental parasite of frogs and turtles (Van Cleave & Lynch 1950).

Nematoda Rudolphi, 1808

Abbreviata* sp.

Site of infection: intestine, stomach.

Recruitment: ingestion.

Distribution: Cuba: Provincia Pinar del Río (Martínez *et al*. 1982). USA: Virginia (Campbell 1968).

No specimens in collections.

Remarks: Anderson (2000) pointed out that species of *Abbreviata* require insects as intermediate host. Larval specimens of this genus have been recorded from lizards, mainly in Australia and Borneo (Myers & Kuntz 1969; Goldberg *et al*. 2000) and from Cuba in 10 species of reptiles and one amphibian species (Barus 1972; Coy-Otero & Barus 1979).

Abbreviata ranae* (Walton, 1931)

Site of infection: intestine, stomach.

Recruitment: ingestion.

Distribution: USA: Columbia, Illinois, Indiana, Louisiana, South Carolina (Walton 1931).

Specimens in collections: Walton (1931) pointed out that type material was deposited in Ward Collection, University of Illinois, catalogue number 12211.

Remarks: Larval forms of this species [originally described as *Physaloptera ranae* by Walton (1931)] have been reported in frogs (Reiber *et al*. 1940; Campbell 1968; Ashton & Rabalais 1978); adults have not been described. *Physaloptera ranae* was transferred by Morgan (1941) to the genus *Abbreviata*, but Baker (1987) considered it a *species inquirendae*, because it is possible that more than one physalopterid species is envolved in these reports. On the other hand, Bursey *et al*. (2006a) pointed out that amphibians are probably intermediate hosts for species of *Abbreviata*.

Agamascaris odontocephala* Steiner, 1924

Site of infection: body cavity, liver, and stomach cysts.

Recruitment: unknown.

Distribution: USA: North Carolina (Brandt 1936); South Carolina (Walton 1933).

Specimens in collections: USNPC: 1569, 50576, 50577.

Remarks: *A. odontocephala* was described based on larval specimens collected from the stomach wall and liver of *Hyla carolinensis* (Steiner 1924).

Agamonema* sp.

Site of infection: entire body.

Recruitment: unknown.

Distribution: USA: North Carolina (Brandt 1936).

No specimens in collections.

Remarks: Definitive hosts for species of this genus are fishes; amphibians probably act as intermediate hosts.

***Angiostrongylus cantonensis* (Chen, 1933)**

Site of infection: no specified.

Recruitment: ingestion.

Distribution: Japan (Uchida 1976; Otsuru 1977; Hasegawa & Asakawa 2004).

No specimens in collections.

Remarks: This species is parasite of rodents around the world, and can also be parasite of man (Slom *et al*. 2002).

Anisakinae gen. sp.*

Site of infection: bladder mesentery.

Recruitment: ingestion.

Distribution: USA: Oklahoma (USNPC).

Specimens in collections: USNPC: 44302.

Remarks: immature specimens. Members of Anisakinae are parasites mainly of marine mammals, turtles, fish-eating birds, and elasmobranches (Anderson 2000). Probably, *L. catesbeianus* represents an accidental host.

***Aplectana* sp.**

Site of infection: cloaca, intestine.

Recruitment: ingestion.

Distribution: USA: Michigan (Muzzall 1991).

No specimens in collections.

Remarks: Species of the genus *Aplectana* are common intestinal parasites of reptiles and amphibians (Anderson 2000).

***Aplectana cubana* Barus, 1972**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Cuba: Provincia Pinar del Río and Provincia Habana (Barus 1972; Martínez *et al*. 1982).

No specimens in collections.

Remarks: Species considered *incerta sedis* by Baker (1987).

***Aplectana haematospicula* Walton, 1940**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Cuba: Provincia Santiago de Cuba (Martínez *et al*. 1982).

No specimens in collections.

Remarks: this species has been recorded in Cuba from 12 other amphibian host species (Walton 1940; Barus 1973; Coy-Otero & Ventosa 1984).

Ascarididae gen. sp.*

Site of infection: bladder.

Recruitment: ingestion.

Prevalence, mean intensity, and intensity range: 18.5%, 0.70, 1-12.

Specimens deposited: CNHE: 6950.

Distribution: USA: Arizona (Goldberg *et al*. 1998).

No specimens in collections.

Ascaris* sp.

Site of infection: peritoneum.

Recruitment: ingestion.

Distribution: USA: Massachussetts (USNPC); New York Aquarium (USNPC).

Specimens in collections: USNPC: 34634, 34635.

Remarks: this record is doubtful. Species of *Ascaris* are exclusively parasites of mammals. Sometimes this generic name is used in place of the family or superfamily name and is sometimes used as a common term for an elongate parasitic worm.

Brevimulticaecum* sp.

Site of infection: muscle.

Recruitment: ingestion.

Distribution: USA: Florida (Walton 1937).

No specimens in collections.

Remarks: *Lithobates catesbeianus* is considered by Bursey & Goldberg (2005) as paratenic host for this nematode.

***Camallanus* sp.**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Illinois (USNPC).

Specimens deposited: USNPC: 82017.

Remarks: Species of *Camallanus* are parasites of fishes; they are recruited by ingestion of infected copepods (Cheng 1973). This record could be accidental.

***Camallanus multilineatus* Kung, 1948**

Site of infection: stomach.

Recruitment: ingestion.

Distribution: UK: London Zoo (Baker 1987).

No specimens in collections.

Remarks: Baker (1987) pointed out that despite numerous parasitological surveys on *L. catesbeianus* in its native range, this nematode species has never been found there.

Contracaecum* sp.

Site of infection: coelom, muscles, stomach.

Recruitment: ingestion.

Distribution: Cuba: Provincia Pinar del Río (Martínez *et al*. 1982). USA: California (Goldberg & Bursey 2002a; USNPC); Pennsylvania (USNPC).

Specimens in collections: USNPC: 31123, 91247.

Remarks: Life cycle of *Contracaecum* spp. includes invertebrates and fishes as intermediate hosts; records in *L. catesbeianus* are probably accidental.

***Cosmocercoides* sp.**

Site of infection: intestine.

Recruitment: penetration.

Distribution: USA: Kansas (USNPC); Michigan (Muzzall 1991).

Specimens in collections: USNPC: 91217.

Remarks: The genus *Cosmocercoides* Wilkie comprises 17 species parasites of amphibians and reptiles from different bio-geographic Realms (Vanderburgh & Anderson 1987a, 1987b); only 2 of them have been recorded in *L. catesbeianus* (see below).

***Cosmocercoides dukae* (Holl, 1928)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997). USA: California (Lehmann 1965); Illinois (USNPC); Massachusetts (Rankin 1945); Mississipi basin (Walton 1929); North Carolina (Brandt 1936); Oregon (Lehmann 1965); Texas (Harwood 1932; Slagle 1966; Hollis 1972; Mayberry *et al*. 2000); Virginia (Campbell 1968); Washington (Lehmann 1965).

Specimens in collections: USNPC: 82018.

Remarks: This species is a common parasite of mollusks; accidentally infects frogs and salamanders (Vanderburgh & Anderson 1987a, 1987c). In accordance with these authors, many records of this species in amphibian hosts may have been confused with its closely related species *C. variabilis*.

***Cosmocercoides variabilis* (Harwood, 1930)**

Site of infection: intestine.

Recruitment: penetration.

Prevalence, mean intensity, and range: 14.8%, 2, 1-3.

Specimens deposited: CNHE: 6946.

Distribution: Canada: New Brunswick (McAlpine & Burt 1998a); Quebec (Rau *et al*. 1978). USA: California (Ingles 1936; Lehmann 1965; Goldberg & Bursey 2002a); Illinois (Andrews *et al*. 1992); Michigan (Muzzall 1991); Mississippi (Walton 1929); North Carolina (Brandt 1936); Ohio (Bursey & DeWolf 1998); Oklahoma (Trowbridge & Hefley 1934); Oregon (Lehmann 1965). Texas (Harwood 1932; Hollis 1972; Mayberry *et al*. 2000); Virginia (Campbell 1968); Washington (Lehmann 1965).

Specimens in collections: USNPC: 91250.

Remarks: This nematode species is considered as a true parasite of amphibians (Bolek 1997).

Dioctophyma renale* (Goeze, 1782)

Site of infection: body cavity.

Recruitment: ingestion.

Distribution: Canada: Ontario (Mace & Anderson 1975).

No specimens in collections.

Remarks: This parasite has been found encapsulated in fishes; larvae can be transmitted along food chain of paratenic hosts (Karmanova 1961). Possibly American bullfrogs became infected with *D. renale* by eating parasitized frogs of different species (Mace & Anderson 1975).

Dioctophymidae gen. sp.*

Site of infection: muscles.

Recruitment: ingestion.

Distribution: USA: Nevada (USNPC).

Specimens in collections: USNPC: 66950.

Remarks: Species of this family are associated with the kidneys and alimentary tract of carnivore mammals and birds, respectively (Anderson & Bain 1982).

Dujardinascaris* sp.

Site of infection: body cavity.

Recruitment: ingestion.

Distribution: USA: North Carolina (Brandt 1936).

No specimens in collections.

Remarks: Originally recorded as *Dujardinia* by Brandt (1936). Adults of *Dujardinascaris* spp. are parasites of fishes and aquatic reptiles (Sprent 1977).

***Enterobius vermicularis* Linnaeus, 1758**

Site of nfection: intestine.

Recruitment: ingestion.

Distribution: USA: New York Aquarium (USNPC).

Specimens in collections: USNPC: 34738.

Remarks: This identification is doubtful; *E. vermicularis* is a human parasite (Lamothe-Argumedo & García-Prieto 1988). Specimens deposited at USNPC as *Oxyuris vermicularis*.

Eustrongylides* sp.

Site of infection: body cavity attached to mesenteries, under skin.

Recruitment: ingestion.

Distribution: Cuba (Coy-Otero & Martínez 1987). USA: California (Goldberg & Bursey 2002a).

Specimens in collections: USNPC: 44423, 72571, 91252.

Remarks: Adult forms of *Eustrongylides* inhabit the pro-ventriculus of aquatic birds, whereas the infective larval stage is found in the tissues of fishes, amphibians and reptiles (Panesar & Beaver 1979).

Eustrongylides wenrichi* Canavan, 1929

Site of infection: eye, kidneys, liver, mesentery, mouth, muscle, peritoneum, skin, spleen, stomach.

Recruitment: ingestion.

Distribution: USA: Louisiana (Modzelewski & Culley 1974); Nevada (Babero & Golling 1974); Pennsylvania (USNPC); undetermined (Walton 1935).

Specimens in collections: USNPC: 80887 (paratype).

Remarks: Panesar & Beaver (1979) described the third larval stage of this parasite.

Falcaustra* sp.

Site of infection: musculature.

Recruitment: ingestion.

Distribution: USA: Texas (Yoder & Gomez 2007).

Specimens in collections: HWML: 48354.

***Falcaustra* sp.**

Site of infection: intestine, stomach.

Recruitment: ingestion.

Distribution: USA: Oklahoma (Kuntz & Self 1944).

Specimens in collections: USNPC: 44288.

Remarks: There are currently 69 nominal species of *Falcaustra* that occur in the digestive tract of fishes, amphibians, and reptiles (Bursey & Goldberg 2001). Specimens were deposited as *Spironoura*, junior synonym of *Falcaustra* (Freitas & Lent 1941).

***Falcaustra catesbeianae* Walton, 1929**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: Ontario (Baker 1986a; CMNPA). Japan: Hasama Oita (Hasegawa 2006). USA: Arkansas (McAllister *et al*. 2008; USNPC); California (Goldberg & Bursey 2002a); Georgia (Reiber *et al*. 1940); Illinois (Walton 1929; Walton 1933; USNPC); Louisiana (Walton 1929; USNPC); Maryland (USNPC); Michigan (Muzzall 1991); Nevada (Babero & Golling 1974); North Carolina (Brandt 1936); Ohio (Ashton & Rabalais 1978); Oklahoma (Walton 1929; Trowbridge & Hefley 1933; Kuntz & Self 1944; USNPC); South Carolina (USNPC); Tennessee (Reiber 1941); Texas (Harwood 1932; Slagle 1966; USNPC).

Specimens in collections: CMNPA: 1985-0161. NSMT-As: 3031. USNPC: 33061, 44272, 44299, 50683, 50685, 50808, 50809, 52137, 91246, 52131, 66528, 84247, 84248, 84796, 84810, 91246.

Remarks: Specimens from USNPC 44299, 50808, 50809, 52131, 66528 were recorded as *Spironoura catesbianae*. Record from Japan is considered an introduction by American bullfrogs imported from North America (Hasegawa 2006).

***Falcaustra inglisi* (Anderson, 1964)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997); Ontario (Anderson 1964; Baker 1986a; CMNPA; USNPC).

Specimens in collections: CMNPA: 1978-1196, 1985-0162. USNPC: 60164.

Remarks: Species originally described as *Oxysomatium inglisi* (Anderson 1964) and transferred to *Falcaustra* by Baker (1980).

***Filaria nitida* Leidy, 1856**

Site of infection: intestine.

Recruitment: vector.

Distribution: USA: New York Aquarium (USNPC).

Specimens in collections: USNPC: 34734.

Remarks: *Species inquerendae* (Baker 1987).

Filaria quadrituberculata* Leydi, 1856

Site of infection: peritoneum and mesentery.

Recruitment: vector.

Distribution: USA: Louisiana (Walton 1927); New Jersey (Benach 1972); Oklahoma (Trowbridge & Hefley 1934; Kuntz & Self 1944).

No specimens in collections.

Remarks: *Species inquirendae* (Baker 1987).

***Foleyella* sp.**

Site of infection: body cavity around the liver and spleen, intestinal mesentery, mesentery about the kidneys.

Recruitment: vector.

Distribution: USA: New Jersey (Crans 1969; USNPC); Oklahoma (USNPC).

Specimens in collections: USNPC: 44293, 71484, 71485, 71486, 71487.

Remarks: Bartlett (1986) emended the diagnosis of *Foleyella* including only 3 species and 1 subspecies: *F. candezei* (Fraipont) Seurat; *F. furcata* (Linstow) Witenberg & Gerichter; *F. brevicauda brevicauda* Chabaud & Brygoo; *F. b. magnilarvata* Bain, and *F. philistinae* Schacher & Khalil. USNPC 71484–71487 were recorded as *Foleyella seasonalis*, which is considered *nomen nudum*.

***Foleyellides* sp.**

Site of infection: body cavity, encysted on peritoneum and mesentery.

Recruitment: vector.

Distribution: USA: New Jersey (Crans 1969; Benach 1972, experimental); Oklahoma (Trowbridge & Hefley 1934; Kuntz & Self 1944); Texas (Yoder & Gomez 2007).

Specimens in collections: HWML: 48352.

***Foleyellides americana* (Walton, 1929)**

Site of infection: body cavity, mesentery, bladder.

Recruitment: vector.

Distribution: USA: Texas (Hollis 1972; Mayberry *et al*. 2000); North Carolina (Brandt 1936); Virginia (Campbell 1968); Ohio (Ashton & Rabalais 1978).

No specimens in collections.

Remarks: This species was described as *Foleyella americana* (Walton 1929), and transferred to *Foleyellides* by Esslinger (1986).

***Foleyellides flexicauda* (Schacher & Crans, 1973)**

Site of infection: blood, body cavity, mesentery.

Recruitment: vector.

Distribution: USA: New Jersey (Schacher & Crans 1973; Terwedow & Craig 1977a, 1977b; Baker 1987); experimental (Benach & Crans 1973).

Specimens in collections: USNPC: 72555 (holotype), 72556 (allotype), 72557 (male paratypes), 72558 (female paratypes), 72559 (microfilariae), 72600-72603 (vouchers).

Remarks: This species was registered as *Foleyella flexicauda* (Schacher & Crans 1973), which is considered synonym of *Foleyellides flexicauda* in accordance with Bartlett (1986) and Esslinger (1986).

***Foleyellides ranae* (Walton, 1929)**

Site of infection: encysted in body cavity and mesentery.

Recruitment: vector.

Distribution: USA: Louisiana (Walton 1929; Walton 1935; Causey 1939a, 1939b; Kotcher 1941; Baker 1987); North Carolina (Brandt 1936).

No specimens in collections.

Remarks: This species was described as member of the genus *Foleyella* (Walton, 1929); however, Esslinger (1986) re-established the genus *Foleyellides* to include those species of *Foleyella* parasites of amphibians.

Gnathostoma spinigerum* Owen, 1836

Site of infection: muscles.

Recruitment: ingestion.

Distribution: Japan (Uchida 1975; Hasegawa & Asakawa 2004).

No specimens in collections.

Remarks: Specimens of these records were collected as larvae; frogs act as paratenic hosts of this nematode.

***Gyrinicola batrachiensis* (Walton, 1929)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (Adamson 1981a); Ontario (Adamson 1981a; Pryor & Greiner 2004; CMNPA); Quebec (Adamson 1981a; Pryor & Greiner 2004). USA: Florida (Pryor & Greiner 2004); Ohio (Pryor & Greiner 2004); undetermined (Pryor & Bjorndal 2005).

Specimens in collections: CMNPA: 1980-1671a, 1980-1671b. USNPC: 92589.

Remarks: *Gyrinicola batrachiensis* can infect the gastrointestinal tracts of anuran larvae, but it is not observed in metamorphosing tadpoles or adult frogs (Adamson 1981b; Adamson 1981c; Bursey & DeWolf 1998).

***Hedruris* sp.**

Site of infection: not specified.

Recruitment: ingestion.

Distribution: USA: California (Lehmann 1965); New Hampshire (Muzzall 1991); Oregon (Lehmann 1965); Washington (Lehmann 1965).

No specimens in collections.

Remarks: To date, 21 nominal species of *Hedruris* have been described; they occur in the digestive tract of fishes, frogs, salamanders, lizards, and turtles (Bursey & Goldberg 2007).

***Hedruris pendula* (Leidy, 1851)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: Ontario (Baker 1986b).

Specimens in collections: CMNPA: 1986-0003.

Remarks: *H. pendula* and *H. siredonis* are the only two valid *Hedruris* species distributed in North America (Baker 1986b) parasitizing aquatic vertebrates.

***Hedruris siredonis* (Baird, 1858)**

Site of infection: stomach.

Recruitment: ingestion.

Distribution: USA: New Hampshire (Muzzall & Baker 1987).

No specimens in collections.

Remarks: Although this species is more frequently recorded as parasite of salamanders, infections in American bullfrogs do not appear to be accidental, and they can acquire the infection by predation on aquatic infected isopods (Muzzall & Baker 1987).

Kathlaniidae gen. sp.

Site of infection: intestine, stomach.

Recruitment: ingestion.

Distribution: USA: Texas (USNPC).

Specimens in collections: USNPC: 31180.

Onchocercidae gen. sp.*

Site of infection: blood vessels.

Recruitment: vector.

Distribution: USA: North Carolina (Brandt 1936); Virginia (Campbell 1968).

No specimens in collections.

Remarks: these larvae were referred to the informal collective group Microfilariae.

***Oswaldocruzia* sp.**

Site of infection: intestine.

Recruitment: penetration.

Distribution: USA: Michigan (Ridgeway 1964; Muzzall 2005); Tennessee (USNPC).

Specimens in collections: USNPC: 42061.

Remarks: the 81 species assigned to *Oswaldocruzia* are typically found in the intestine of amphibians and reptiles (Bursey *et al*. 2006b; Durette-Desset *et al*. 2006).

***Oswaldocruzia leidyi* Steiner, 1924**

Site of infection: intestine.

Recruitment: penetration.

Distribution: USA: Tennessee (USNPC).

Specimens in collections: USNPC: 42061.

Remarks: Baker (1977) considered *Oswaldocruzia leydi* Travassos, 1917 as a *nomen nudum*; Ben Slimane & Durette-Desset (1997) re-established its validity, noted that the first description of this species was provided by Steiner (1924), becoming Stainer the author of the name.

***Oswaldocruzia lenteixeirai* Pérez Vigueras, 1938**

Site of infection: intestine.

Recruitment: penetration.

Distribution: Cuba: Provincia Santiago de Cuba and Provincia Habana (Moravec & Kaiser 1995).

Specimens in collections: USNPC: 42061.

Remarks: Besides *L. catesbeianus*, this species has been recorded from Cuba parasitizing 22 species of reptiles and 9 species of amphibians (Barus & Moravec 1967; Barus 1972; Barus 1973; Coy-Otero & Barus 1979).

***Oswaldocruzia pipiens* Walton, 1929**

Site of infection: intestine.

Recruitment: penetration.

Distribution: Canada: New Brunswick (McAlpine 1997); Ontario (Baker 1978a). USA: California (Goldberg & Bursey 2002a; USNPC); Louisiana (USNPC); North Carolina (Brandt 1936); Oklahoma (Trowbridge & Hefley 1934); Virginia (Campbell 1968).

Specimens in collections: USNPC: 91241, 84811, 91251.

Remarks: Ben Slimane and Durette-Desset (1997) considered that *O. pipiens* constitutes a species complex inhabiting North American amphibians.

Oxysomatium* sp.

Site of infection: not specified.

Recruitment: unknown.

Distribution: USA: Oklahoma (Trowbridge & Hefley 1934).

No specimens in collections.

Oxyurida gen. sp.*

Site of infection: not specified.

Recruitment: ingestion.

Distribution: Canada: Ontario (CMNPA).

Specimens in collections: CMNPA: 1979-0492.

***Parapharyngodon bassi* (Walton, 1940)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Cuba: Provincia Habana and Provincia Santiago de Cuba (Martínez *et al*. 1982).

No specimens in collections.

Remarks: This species has been recorded in Cuba from other amphibian hosts by Walton (1940), Barus and Moravec (1967) and Barus (1973).

Physalopteridae gen. sp.*

Site of nfection: stomach.

Recruitment: ingestion.

Distribution: USA: Oklahoma (USNPC).

Specimens in collections: USNPC: 44286.

Physaloptera* sp.

Site of infection: body cavity, intestinal wall, mesentery, stomach.

Recruitment: ingestion.

Distribution: USA: Arizona (Goldberg *et al*. 1998); California (Goldberg & Bursey 2002a); Indiana (Walton 1935; USNPC); North Carolina (Brandt 1936); Ohio (Ashton & Rabalais 1978); Virginia (Campbell 1968).

Specimens in collections: USNPC: 50789, 87072, 91253.

Porrocaecum* sp.

Site of infection: body cavity, intestine.

Recruitment: ingestion.

Distribution: Cuba: Provincia Pinar del Río and Provincia Santigo de Cuba (Martínez *et al*. 1982; Moravec & Kaiser 1995).

No specimens in collections.

Remarks: Larvae of this genus have been reported in 24 species of reptiles and three species of amphibians from Cuba (Barus 1972; Barus 1973; Coy-Otero & Barus 1979).

***Raillietnema longicaudata* (Walton, 1929)**

Site of infection: intestine.

Recruitment: unknown.

Distribution: USA: Indiana (Brandt 1936; Lank 1971); North Carolina (Brandt 1936).

No specimens in collections.

Remarks: specimens recorded as *Oxysomatium longicaudata*, species included in *Raillietnema* by Baker (1985).

***Rhabdias americanus* Baker, 1978b**

Site of infection: lungs.

Recruitment: vector.

Distribution: Canada: Quebec (Fantham & Porter 1948).

No specimens in collections.

Remarks: specimens recorded by Fantham and Porter (1948) as *Rhabdias bufonis* (Schrank, 1788); Baker (1987) included this record in *R. americanus*.

***Rhabdias* sp.**

Site of infection: body cavity, lungs.

Recruitment: vector.

Distribution: USA: California (Lehmann 1965); North Carolina (Brandt 1936); Oklahoma (USNPC); Oregon (Lehmann, 1965); Washington (Lehmann 1965).

Specimens in collections: USNPC: 44295.

Remarks: Species of *Rhabdias* Stiles and Hassall could be identified based on their relatively strict host specificity (Martínez-Salazar 2006).

***Rhabdias ranae* Walton, 1929**

Site of infection: lungs.

Recruitment: vector.

Prevalence, mean intensity and range: 25.9%, 2.28, 1-4.

Specimens deposited: CNHE: 6947.

Distribution: USA: Arizona (Goldberg *et al*., 1998); Louisina (USNPC); North Carolina (Brandt 1936); Ohio (Ashton & Rabalais 1978; Bursey & DeWolf 1998); Oklahoma (Morrison 1967); Texas (Harwood 1932; Hollis 1972; Mayberry *et al*. 2000); Virginia (Campbell 1968).

Specimens in collections: USNPC: 84812.

Remarks: In accordance with Kuzmin *et al*. (2003), this species is restricted to North American frogs; however, it is more common in hosts from northern United States and Canada.

***Spinitectus* sp.**

Site of infection: stomach.

Recruitment: ingestion.

Distribution: USA: Oklahoma (Trowbridge & Hefley 1934); Tennessee (Christian 1970); South Carolina (USNPC).

Specimens in collections: USNPC: 84800.

Remarks: According to Moravec (1998), species of this genus mainly parasitize marine and freshwater fishes; only four species have been recorded in amphibian hosts (Baker 1987).

***Spinitectus gracilis* Ward & Magath, 1917**

Site of infection: intestine, stomach.

Recruitment: ingestion.

Prevalence, mean intensity, and intensity range: 25.9%, 6.43, 2-12.

Specimens deposited: CNHE: 6948.

Distribution: USA: Michigan (Muzzall 1991); Oklahoma (Kuntz & Self 1944; USNPC).

Specimens in collections: USNPC: 44274.

Remarks: This species rarely parasitizes amphibian hosts, and is unlikely that its life cycle ends successfully in this group of vertebrates (Baker 1987).

"Spiroptera mugientis"* von Linstow, 1898

Site of infection: intestine, stomach.

Recruitment: ingestion.

Distribution: USA: undetermined (Walton, 1935).

No specimens in collections.

Remarks: Walton (1935) refers the uncertain position of this species; Yamaguti (1961) considered *Spiroptera* synomym of *Acuaria* (in part) and *Spirura* (in part).

Spiroxys* sp.

Site of infection: intestine, mesentery.

Recruitment: ingestion.

Prevalence, mean intensity, and intensity range: 3.7%, 0.07.

Specimens deposited: CNHE: 6949.

Distribution: USA: Arizona, Michigan (Muzzall 1991); North Carolina (Brandt 1936); Texas (Yoder & Gomez 2007; HWML)

Specimens deposited: HWML: 48353.

***Spiroxys contorta* (Rudolphi, 1819)**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: Canada: New Brunswick (McAlpine 1997; NBM).

Specimens in collections: NBM: 1833.

Remarks: This species is a common parasite of turtles (Yamaguti 1961). Record in *L. catesbeiana* is accidental.

***Spiroxys constricta* (Leidy, 1856)**

Site of infection: stomach.

Recruitment: ingestion.

Distribution: USA: Louisiana (USNPC).

Specimens in collections: USNPC: 84813.

Remarks: fishes, tadpoles and frogs serve as second intermediate hosts for *S. constricta*, as well as *S. contorta* (Hedrick 1935).

***Strongyluris ranae* Reiber, Byrd & Parker, 1940**

Site of infection: intestine.

Recruitment: ingestion.

Distribution: USA: Georgia (Reiber *et al*. 1940; Baker 1987).

Specimens in collections: USNPC: 9383 (holotype).

Remarks: This species has been exclusively found in *L. catesbeiana*.

Discussion

All helminth species found in Pawnee Lake, Nebraska, have previously been reported for this host species. However, this is the first report of the nematode *S. gracilis* for this locality; its presence in this host species is considered an accidental infection (Baker 1987), due to the overlapping ecological niche of fishes and bull frogs. Helminth richness in this host species was 9, with 5 species of nematodes and 4 of digeneans. Only 2 of the 9 species were collected as larval forms, which indicate the important role of this frog as definitive host in Pawnee Lake. Helminth taxa were collected from 5 sites within the hosts, with lungs being the most parasitized (3 taxa). The most frequent mode of parasite recruitment was ingestion of intermediate hosts; thus, 56% of the species were recruited through the food web. In contrast, 22% of helminth species were acquired by skin penetration, while 22% (*G. attenuata* and *G. quieta*) enter to the host using both vias (ingestion or penetration) (Yamaguti 1975; Anderson 2000).

Ecological parameters of infection recorded in *L. catesbeianus* from Pawnee Lake were low, similarly to those recorded for other species of amphibians in general (Muzzall 1991; McAlpine 1997; Goldberg *et al*., 2000; Muzzall *et al*., 2001; Goldberg *et al*., 2001; Bolek & Coggins 2003; Goldberg *et al*., 2002; Paredes-Calderón *et al*., 2004; Cabrera-Guzmán 2007). Vagility and feeding habits of hosts, as well as particular ecological conditions of each locality, have been used to explain these low levels of infection.

Because it is an opportunistic and voracious predator and has high adaptability, *L. catesbeianus* is considered to be one of the most successful species in the world by the Global Invasive Species Database (2009). As so, populations of this anuran species are currently established in various parts of the world, but its helminth fauna has not been exhaustively studied. Moreover, most of the species that have been found parasitizing this amphibian represent point localityl records; only two studies about its parasites cover states or regions (Lank 1971; Babero & Golling 1974). Prior to this study, the most comprehensive compilation about its parasite fauna was made in the United States (Andrews *et al*. 1992); this compilation included 95 helminth species (one monogenean, 51 digeneans, seven cestodes, one acanthocephalan, and 35 nematode species). As a result of our survey, and by the addition of records published or included in scientific collections, the number of helminth taxa known for this host in its native and introduced range of distribution increased to 159 (67% more); these records come from 6 countries (Canada, Cuba, Japan, Korea, United Kingdom, and USA), most of them from USA (121), followed by Canada (44). Three of the 159 species registered in this amphibian host have been considered *species inquirendae*; seven more were recorded experimentally. In addition, we found 7 unidentified records in the USNPC; their inclusion in the list of helminth taxa parasitizing *L. catesbeianus* is pending of a more precise determination.

As in other amphibian hosts, species richness is influenced by local availability of helminth species and their possibility of colonization; however, the presence of most of the helminth species is due to host diet (117 species are recruited through this via while 22 enter by penetration, and 11 more via vector transmission). Infections by accidental parasites in American bullfrogs (at least 9 species), are result of the generalist predator condition of this host species. For example, accidental infection by *G. spinigerum* in Japanese bullfrogs can be explained by ingestion of natural intermediate (copepods) or paratenic hosts (fishes) (Miyazaki 1991).

The helminth fauna of this host throughout its range is composed of 2 groups of species: generalists (comprised of helminth species that commonly occur in other groups of animals but can also infect amphibians, or that use *L. catesbeianus* as a paratenic host), and specialists (comprised of species with an "historic relationship" with the amphibian hosts, sensu Brooks & McLennan 2003). In the first group are genera such as *Alaria* and *Clinostomum*, represented by 3 species each; among specialists to anurans, two other digenean genera, *Haematoloechus* and *Halipegus*, are widely represented in the helminthological record of this frog, with 13 and 5 species, respectively, although some of the species of these genera more commonly parasitize other frog groups and are rarely found in *L. catesebeianus*, for example, *H. complexus* or *H. medioplexus*, that are more frequently found in leopard frogs (León-Règagnon 2003).

Of the 159 taxa recorded infecting American bullfrogs worldwide, only 16 species have been added to their helminth fauna from localities outside of its native distribution range. Although numerous, the helminthological record of this host species will increase after further inventory work, since this species has been introduced at least to 15 countries and helmith records come from only 4 of them (Cuba, Japan, Korea, and

United Kingdom). On the other hand, only one record of colonization of helminths from *Lithobates catesbeianus* to local amphibian fauna has been documened (León-Règagnon *et al*. 2005), but considering that host switching is a relatively frequent event in parasite evolution (Brooks & Ferrao 2005; Brooks *et al*. 2006b), it is imperative to evaluate the potential impact of introducing American bullfrogs (or any species) and their parasites, not only helminths, but also other emerging pathogens (Garner *et al*. 2006) into new environments, before doing so.

To the best of our knowledge, the only other species of anuran host that has been intensively studied from a helminthological point of view is the cane toad *Rhinella marina* (L.). Even though the natural and introduced distribution of cane toad is greater than those of the American bullfrog (*R. marina* is naturally distributed in 19 American countries and has been introduced to other 38 around the world), this bufonid species is parasitized by only 113 helminth species along its natural and introduced distribution range (Espinoza-Jiménez *et al*. 2007). Differences between helminth fauna harbored by both host species could be attributed to the particular biological characteristics of each one (e.g., *L. catesbeianus* spends time both on land and in water while *R. marina* usually stay on dry land and reproduce in any shallow water), or a merely effect of a distinct sampling effort.

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