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Source: Journal of Parasitology, 109(4) : 377-400

Published By: American Society of Parasitologists

URL: <https://doi.org/10.1645/23-6>

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ADULT TAPEWORM (PLATYHELMINTHES: CESTODA) PARASITES OF NORTH AMERICAN HERPETOFAUNA: CHECKLIST OF SPECIES AND IDENTIFICATION KEY TO FAMILIES AND GENERA

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KEY WORDS ABSTRACT

Canada	An updated checklist of adult tapeworms (Platyhelminthes: Cestoda) that parasitize wild North
Cestodes	American amphibians and reptiles is presented: A total of 58 species grouped in 15 genera, 5 fami-
Cestodiasis	lies, and 3 orders, are registered; these infect a total of 90 species of reptiles and 88 species of
Mexico	amphibians in the region. An illustrated identification key for the families and genera listed is
Neodermata	proposed.
United States	

The phylum Platyhelminthes is comprised of acoelomate and usually vermiform invertebrates commonly known as flatworms; they were traditionally grouped into 4 classes, of which Turbellaria included mostly free-living and aquatic forms, with a few terrestrial and parasitic exceptions; meanwhile, the remaining 3 classes, Cestoda, Monogenea, and Trematoda, included exclusively very derived parasitic forms (Lamothe-Argumedo, 1983; García-Prieto et al., 2014).

The members of the class Cestoda (sometimes spelled Cestoidea) are commonly known as tapeworms or cestodes and are distinguished from those parasitic flatworms in the classes Monogenea and Trematoda by their lack of a true gut, and by their mostly long and vermiform bodies which are divided into a scolex (the “head”), a neck region (the germinating zone), and a strobila (the “body”) formed by several proglottids in multiple stages of maturation (not to be confused with true segmentation, as seen in Annelida or Arthropoda; Schmidt, 1970; Lamothe-Argumedo, 1983). This class consists of 19 recognized orders (Caira et al., 2017). In their adult forms, tapeworms are endoparasites that typically inhabit the small intestines of vertebrates. Their life cycles are mostly indirect, requiring an intermediate and a definitive host in most of the cases, but sometimes more than 1 intermediate host is required to complete the cycle; very rarely (as in Nematotaeniidae), the life cycle is direct, and an intermediate host is not required (Schmidt, 1970; Lamothe-Argumedo, 1983; Caira et al., 2017). Two exceptional orders, Amphiliniidae and Gyrocotylidae,

inhabit the coelomic cavity of fishes and freshwater turtles, lack a divided body, and at least the first has members that possess a proboscis (Gibson, 1994a, 1994b); these were previously grouped into a subclass called Cestodaria, but no molecular support was found for their monophyly (Caira et al., 2017); in contrast, the remaining 17 orders were traditionally grouped in a subclass called Eucestoda; these conform to what is the norm for the class, the monophyly of which is supported by molecular evidence (Caira et al., 2017).

The reptile tapeworms of the world, along with their respective hosts, were listed in 1941 by Hughes et al. (1941a, 1941b, 1941c), who filled an important gap in the literature. In addition, the works of C. R. Bursey, S. R. Goldberg, C. T. McAllister, and associates have added a great deal to our knowledge of the tapeworms of select amphibians and reptiles. Although the aim of the current publication has a much narrower geographic scope, focusing on wild North American (continental United States, Canada, and Mexico) amphibians and reptiles, we believe it will serve as a basis for many future studies. Coupled with the checklist, an illustrated key is proposed for the families and genera included in said listing to aid in the process of identification.

MATERIALS AND METHODS

An extensive search of records of adult tapeworms parasitizing wild herpetofauna from continental North America was made;

these were compiled into 2 checklists: parasite–host and host–parasite. For the identification key, the works of Schmidt (1970), Jones (1987a, 1994), Beveridge (1994), Bray et al. (1994), Georgiev and Korniyushin (1994), Jones et al. (1994a, 1994b), Rego (1994), and Melo et al. (2011), were consulted, with some of their figures being redrawn to illustrate it.

RESULTS

Parasite–host checklist

Tapeworms are listed alphabetically by order, family, genus, and species; the hosts are listed alphabetically by family and species. The taxonomic arrangement and nomenclature follow Kuchta and Scholz (2017) for the order Bothriocephalidea; Mariaux et al. (2017) for the order Cyclophyllidea; and de Chambrier et al. (2017) for the order Onchoproteocephalidea. Next, the geographic location to state (Mexico and the United States) or province (Canada) level is provided. Finally, the source of the record is cited. Complete geographical distribution is not included, nor are any records of larval stages.

The only member of the Amphilinidea that is known to parasitize herpetofauna is *Australamphilina elongata* Johnston, 1931 (Amphilinidae), which inhabits the coelomic cavity of Australian chelid turtles (Rohde and Georgi, 1983); thus, the current North American checklist includes only species that are found in the small intestine, making the mention of the location of the parasite within the body of the host irrelevant.

Phylum PLATYHELMINTHES Gegenbaur, 1859

Class CESTODA Rudolphi, 1808

Order BOTHRIOCEPHALIDEA Kuchta, Scholz, Brabec, and Bray, 2008

I. Family BOTHRIOCEPHALIDAE Blanchard, 1849

i. Genus *Bothriocephalus* Rudolphi, 1808

Unidentified specimens of this genus have been found in *Eurycea wallacei* (Carr, 1939) from Georgia (McAllister et al., 2013a) and *Rana catesbeiana* from New Brunswick, Canada (McAlpine and Burt, 1998).

1. *Bothriocephalus euryciensis* Schaefer and Self, 1978

Plethodontidae: *Eurycea longicauda* from Oklahoma (Schaefer and Self, 1978 and has not been referenced since).

2. *Bothriocephalus rarus* Thomas, 1937

Plethodontidae: *Desmognathus fuscus* from New Hampshire (Muzzall et al., 1997); *Desmognathus quadramaculatus* from Tennessee (Dunbar and Moore, 1979); *Eurycea bislineata* from New Hampshire (Muzzall et al., 1997) and New York (Fischthal, 1955); *Eurycea longicauda* from Arkansas (McAllister and Bursey, 2004a; McAllister et al., 2015b); *Eurycea lucifuga* from Kentucky (O'Brien, 1979) and Oklahoma (McAllister et al., 2016); *Eurycea multiplicata* from Arkansas (McAllister et al., 2014b); *Eurycea quadridigitata* from Arkansas (McAllister and Bursey, 2003); *Eurycea spelaea* from Oklahoma (McAllister et al., 2016); *Eurycea tynnerensis* from Arkansas (McAllister et al., 2014b); *Gyrinophilus porphyriticus* from Ohio (Catalano et al., 1982); *Pseudotriton ruber* from Ohio (Catalano et al., 1982).

Salamandridae: *Notophthalmus viridescens* from Kentucky (del Fosse and Whitaker, 1971), Massachusetts (Rankin, 1945), Michigan (Thomas, 1937a; Muzzall, 1991), North Carolina (Rankin, 1937), New York (Fischthal, 1955), Pennsylvania (Jackson and Beaudoin, 1967; Thomas, 1937b), South Carolina (Thomas, 1937b) and West Virginia (Jarroll, 1979, 1980); *Taricha torosa* from Ohio (Lehmann, 1960).

3. *Bothriocephalus typhlotritonis* Reeves, 1949

Plethodontidae: *Eurycea longicauda* from Arkansas (Saltarelli, 1977); *Eurycea lucifuga* from Arkansas (Saltarelli, 1977); *Eurycea multiplicata* from Arkansas (Saltarelli, 1977); *Eurycea nerea* from Oklahoma (Reeves, 1949); *Eurycea spelaea* from Arkansas (McAllister et al., 2006) and Oklahoma (Reeves, 1949).

ii. Genus *Schyzocotyle* Akhmerov, 1960

4. *Schyzocotyle acheilognathi* (Yamaguti, 1934)

Ambystomatidae: *Ambystoma dumerili* from Michoacan, Mexico (García-Altamirano, 1992; García-Altamirano et al., 1993; in both, parasite as *Bothriocephalus acheilognathi*).

Natricidae: *Thamnophis melanogaster* from Michoacan, Mexico (Jiménez-Ruiz et al., 2002; parasite as *Bothriocephalus acheilognathi*).

Order CYCLOPHYLLIDEA Van Beneden, 1900

II. Family ANOPELOCEPHALIDAE Blanchard, 1891

iii. Genus *Mathevotaenia* Akhmerov, 1946

Although the species of this genus are known to parasitize mammals primarily (Beveridge, 1994), there are a few records in birds (Baugh and Saxena, 1976; Saxena and Baugh, 1978) and reptiles (Bursey et al., 2010b; Goldberg et al., 2010; Lunaschi et al., 2012).

5. *Mathevotaenia antrozoi* (Voge, 1954)

Corytophanidae: Undetermined species from Tabasco, Mexico (Flores-Barroeta et al., 1958, parasite as *Oochoristica antrozoi*; the host is named “Toloque”; this common name is employed in Mexico for *Basiliscus vittatus* Wiegmann, 1828, *Laemantus longipes* Wiegmann, 1834, and *Laemantus serratus* Cope, 1864, the 3 of which inhabit the state of Tabasco, making it impossible to determine the identity of the host with certainty).

Remarks

Both Paredes-León et al. (2008) and Merlo-Serna and García-Prieto (2018) mention the host of this record as “Lacértido,” an old generic name for a lizard (not to be associated with Old World lizards of the family Lacertidae); however, the host is referred to as a “Toloque” by Flores-Barroeta et al. (1958), a common name specifically applied to some lizards of the family Corytophanidae in Mexico.

iv. Genus *Oochoristica* Lühe, 1898

Unidentified adults of this genus have been recorded in several species of herpetofauna: *Rhinella horribilis* from Jalisco, Mexico (Velarde-Aguilar, 2011); *Anolis nebulosus* (Wiegmann, 1834) from Nayarit, Mexico (Mayen-Peña and Salgado-Maldonado, 1998); *Phyllodactylus lanei* Smith, 1935, from Nayarit, Mexico (Mayen-Peña and Salgado-Maldonado, 1998); and *Phyllodactylus unctus*

(Cope, 1863) from Baja California Sur, Mexico (Goldberg and Bursey, 2010); *Crotalus basiliscus* from Colima, Mexico (Paredes-León et al., 2008); *Ctenosaura acanthura* (Shaw, 1802) from Morelos, Mexico (Paredes-León et al., 2008); *Ctenosaura hemilopha* (Cope, 1863) from Baja California Sur, Mexico (Iturbe-González, 1998); *Ctenosaura pectinata* from Nayarit, Mexico (Mayen-Peña and Salgado-Maldonado, 1998); *Aspidoscelis dixonii* from Texas (McAllister et al., 1991); *Aspidoscelis gularis* from Oklahoma and Texas (McAllister, 1990d); *Aspidoscelis tigris* from Arizona (Benes, 1985); *Cophosaurus texanus* from Arizona (Walker and Matthias, 1973; Goldberg and Bursey, 1992); *Holbrookia maculata* from Arizona (Walker and Matthias, 1973); *Petrosaurus repens* (Van Denburgh, 1895) from Baja California Sur, Mexico (Bursey and Goldberg, 2007); *Phrynosoma solare* from Arizona (Benes, 1985); *Sceloporus magister* from Arizona (Benes, 1985); *Sceloporus merriami* from Texas (Goldberg et al., 1995b); *Sceloporus variabilis* from Texas (Goldberg et al., 1995b); *Uta stansburiana* from Arizona (Benes, 1985); *Urosaurus graciosus* from California (Goldberg et al., 1993c); *Urosaurus ornatus* from New Mexico (Goldberg et al., 1993e); *Uta stansburiana* from Arizona (Benes, 1985); *Coleonyx variegatus* (Baird, 1858) from Arizona (Benes, 1985); *Elgaria multicarinata* from California (Goldberg and Bursey, 1990b). See also Hughes (1940). This overly large genus is in dire need of revision.

6. *Oochoristica acapulcoensis* Brooks, Pérez-Ponce de León, and García 1999

Iguanidae: *Ctenosaura pectinata* from Guerrero, Mexico (Brooks et al., 1999; Merlo-Serna and García-Prieto, 2018).

7. *Oochoristica ameivae* (Beddard, 1914)

Gekkonidae: *Hemidactylus turcicus* from Texas (McAllister and Bursey, 2016).

8. *Oochoristica americana* Harwood, 1932

Dipsadidae: *Farancia abacura* from Texas (Harwood, 1932).

9. *Oochoristica anniellae* Stunkard and Lynch, 1944

Anniellidae: *Anniella pulchra* from California (Stunkard and Lynch, 1944).

10. *Oochoristica anolis* Harwood, 1932

Dactyloidae: *Anolis carolinensis* from Louisiana (Conn, 1985) and Texas (Harwood, 1932).

11. *Oochoristica bezyi* Bursey and Goldberg, 1992

Gekkonidae: *Hemidactylus turcicus* from California (McAllister et al., 2021a).

Xantusiidae: *Xantusia arizonae* from Arizona (Goldberg et al., 2015); *Xantusia bezyi* from Arizona (Goldberg et al., 2015); *Xantusia henshawi* from California (Amrein, 1951; Telford, 1970; in the latter 2, parasite as *Oochoristica scelopori*; Goldberg et al., 1993a; Bezy et al., 2022); *Xantusia sierrae* from California (Goldberg et al., 2015); *Xantusia vigilis* from California (Telford, 1970, parasite as *Oochoristica scelopori*; Bursey and Goldberg, 1992a; Goldberg et al., 1993a; Bezy et al., 2022).

12. *Oochoristica bivittellolata* Loewen, 1940

Teiidae: *Aspidoscelis dixonii* from Texas (McAllister et al., 1991); *Aspidoscelis exsanguis* from New Mexico and Texas (McAllister, 1990c); *Aspidoscelis gularis* from Oklahoma and

Texas (McAllister, 1990d; McAllister et al., 1995b); *Aspidoscelis inornata* from Arizona (Goldberg and Bursey, 1990a); *Aspidoscelis marmorata* from Texas (McAllister et al., 2003); *Aspidoscelis neomexicana* from New Mexico and Texas (McAllister, 1990b); *Aspidoscelis sexlineata* from Kansas (Loewen, 1940), Nebraska (Brooks and Mayes, 1976; Shoop and Janovy, 1978), and South Dakota (Dyer, 1971); *Aspidoscelis sonora* from Arizona (McAllister, 1992; Goldberg et al., 1997a) and New Mexico (McAllister, 1992); *Aspidoscelis stictogrammus* from Arizona (Goldberg and Bursey, 1989); *Aspidoscelis tessellatus* from Texas (McAllister, 1990a, parasite as *Oochoristica* sp.); *Aspidoscelis tigris* from Arizona (Goldberg et al., 1997a), California (Telford, 1970), Idaho (Lyon, 1986), and Utah (Grundmann, 1959); *Aspidoscelis uniparens* from Arizona (Goldberg and Bursey, 1990a); *Aspidoscelis velox* (McAllister, 1992).

13. *Oochoristica crotaphyti* McAllister, Trauth, and Ubelaker, 1985

Crotaphytidae: *Crotaphytus collaris* from Arkansas (McAllister et al., 1985).

14. *Oochoristica elaphis* Harwood, 1932

Colubridae: *Pantherophis obsoletus* from Texas (Harwood, 1932).

15. *Oochoristica eumecis* Harwood, 1932

Anguidae: *Elgaria kingii* from Arizona (Goldberg et al., 1999a).

Iguanidae: *Ctenosaura pectinata* from Morelos, Mexico (Flores-Barroeta et al., 1958).

Scincidae: *Plestiodon fasciatus* from Texas (Harwood, 1932); *Scincella lateralis* from Arkansas (McAllister et al., 2014a).

16. *Oochoristica gracewileyae* Loewen, 1940

Viperidae: *Crotalus* sp. from Texas (Loewen, 1940).

17. *Oochoristica harschi* McAllister and Bursey, 2017

Gekkonidae: *Hemidactylus turcicus* from Texas (McAllister and Bursey, 2017).

18. *Oochoristica islandensis* Bursey and Goldberg, 1992

Xantusiidae: *Xantusia riversiana* from California (Telford, 1970; Bursey and Goldberg, 1992b, parasite as *Oochoristica scelopori*; Bezy et al., 2022).

19. *Oochoristica javaensis* Kennedy, Killick, and Beverley-Burton, 1982

Gekkonidae: *Hemidactylus turcicus* from Louisiana (Criscione and Font, 2001) and Texas (Caballero et al., 2015).

20. *Oochoristica leonregagnonae* Arizmendi-Espinoza, García-Prieto, and Guillen-Hernández, 2005

Iguanidae: *Ctenosaura pectinata* from Oaxaca, Mexico (Arizmendi-Espinoza et al., 2005; Merlo-Serna and García-Prieto, 2018).

21. *Oochoristica macallisteri* Bursey and Goldberg, 1996

Gekkonidae: *Hemidactylus turcicus* from Arizona (Goldberg et al., 2000b).

Phrynosomatidae: *Uma rufopunctata* from Sonora, Mexico (Goldberg et al., 2014b); *Uta stansburiana* from California (Bursey and Goldberg, 1996; Goldberg et al., 1999b).

Teiidae: *Aspidoscelis sonora* from Arizona (Goldberg et al., 1997a).

22. *Oochoristica natricis* Harwood, 1932

Natricidae: *Nerodia rhombifer* from Texas (Harwood, 1932).

23. *Oochoristica osheroffi* Meggitt, 1934

Colubridae: *Pituophis catenifer* from Nebraska (Meggitt, 1934).

Iguanidae: *Ctenosaura pectinata* from Morelos, Mexico (Flores-Barroeta, and Hidalgo-Escalante, 1960).

Viperidae: *Crotalus atrox* from New Mexico (Goldberg et al., 2002b); *Crotalus cerastes* from California (Alexander and Alexander, 1957, parasite as *Oochoristica crotalicola*; Widmer, 1966); *Crotalus helleri* from California (Alexander and Alexander, 1957, parasite as *Oochoristica crotalicola*; Widmer, 1966); *Crotalus viridis* from Colorado (Widmer and Olsen, 1967).

24. *Oochoristica parvula* (Stunkard, 1938)

Bipedidae: *Bipes biporus* from Baja California Sur, Mexico (Goldberg and Bursey, 2012a).

Eublepharidae: *Coleonyx elegans* from Yucatan, Mexico (Stunkard, 1938).

Teiidae: *Aspidoscelis maxima* from Baja California Sur, Mexico (Goldberg and Bursey, 2012a).

25. *Oochoristica phrynosomatis* (Harwood, 1932)

Phrynosomatidae: *Phrynosoma braconieri* from Puebla, Mexico (Goldberg and Bursey, 1991a); *Phrynosoma cornutum* from Arizona (Goldberg et al., 1993b, parasite as *Diachetos phrynosomatis*), Oklahoma (Steelman, 1939a, parasite as *Oochoristica parvovaria*), Texas (Harwood, 1932, parasite as *Diachetos phrynosomatis*; Vincent, 1948), and from an unspecified US locality (Loewen, 1940); *Phrynosoma douglassii* from Arizona (Walker and Matthias, 1973); *Phrynosoma platyrhinos* from Idaho (Lyon, 1986), Nevada (Babero and Kay, 1967), and Utah (Grundmann, 1959); *Phrynosoma solare* from Arizona (Benes, 1985; Goldberg et al., 1993b).

Remarks

Although *Oochoristica parvovaria* was listed as a valid species by McAllister and Bursey (2017), it had been synonymized with *Oochoristica phrynosomatis* by Goldberg et al. (1993b). Given that the only difference between the species is that *Oochoristica parvovaria* is smaller, which can be explained by dwarfism, we decided to follow the assessment of Goldberg et al. (1993b) and consider *Oochoristica parvovaria* as a junior synonym of *Oochoristica phrynosomatis*.

26. *Oochoristica scelopori* Voge and Fox, 1950

Crotaphytidae: *Gambelia wislizenii* from California (Telford, 1970).

Gekkonidae: *Hemidactylus turcicus* from Texas (McAllister and Bursey, 2016).

Phrynosomatidae: *Phrynosoma ditmarsii* from Sonora, Mexico (Goldberg and Bursey, 2000b); *Sceloporus clarkii* from Arizona (Goldberg et al., 1994); *Sceloporus graciosus* from California (Telford, 1970; Goldberg et al., 1997b) and Idaho (Lyon, 1986); *Sceloporus consobrinus* (Goldberg et al., 1994); *Sceloporus grammicus* from unspecified localities in Mexico (Goldberg et al., 2003, source lists Ciudad de Mexico, Estado de Mexico, Hidalgo, Nuevo Leon, and Oaxaca); *Sceloporus jarrovi* from Chihuahua,

Durango, Guanajuato, Hidalgo, Queretaro, and Zacatecas, Mexico (Goldberg et al., 1996a) and Arizona (Goldberg and Bursey, 1990c; Bursey and Goldberg, 1994; Goldberg et al., 1995a); *Sceloporus magister* from Arizona (Walker and Matthias, 1973) and Texas (Goldberg et al., 1995b); *Sceloporus megalepidurus* from Puebla, Mexico (Goldberg et al., 2003); *Sceloporus mucronatus* from unspecified localities in Mexico (Goldberg et al., 2003, source lists from Ciudad de Mexico, Estado de Mexico, Hidalgo, Oaxaca, Puebla, and Veracruz); *Sceloporus occidentalis* from California (Telford, 1970; Goldberg et al., 1998b) and Idaho (Lyon, 1986); *Sceloporus olivaceus* from Texas (Goldberg et al., 1995b); *Sceloporus orcutti* from California (Goldberg and Bursey, 1991e); *Sceloporus parvus* from Hidalgo, Mexico (Goldberg et al., 2003); *Sceloporus poinsettii* from Texas (Goldberg et al., 1993d); *Sceloporus scalaris* from Arizona, (Goldberg et al., 1996d); *Sceloporus variabilis* from unspecified localities in Mexico (Goldberg et al., 2003, source lists Coahuila and Puebla); *Uma notata* from California, (Telford, 1970); *Urosaurus graciosus* from California (Telford, 1970).

Teiidae: *Aspidoscelis calidipes* from Michoacan, Mexico (Goldberg et al., 2014a); *Aspidoscelis cozumelae* from Quintana Roo, Mexico (Goldberg et al., 2014a); *Aspidoscelis lineatissimus* from Michoacan, Mexico (Goldberg et al., 2014a); *Aspidoscelis sackii* from Oaxaca, Mexico (Goldberg et al., 2014a); *Aspidoscelis tigris* from California (Goldberg et al., 1998c).

27. *Oochoristica whitentoni* Steelman, 1939

Emydidae: *Terrapene carolina* from Oklahoma (Steelman, 1939b; Ernst and Ernst, 1977; McAllister and Bursey, 2015).

Helodermatidae: *Heloderma suspectum* from Arizona (Goldberg and Bursey, 1991d).

Iguanidae: *Ctenosaura pectinata* from Guerrero, Mexico (Flores-Barroeta, 1955a).

28. *Oochoristica whitfieldi* Guillén-Hernández, García-Prieto, and Armendariz-Espinosa, 2007

Iguanidae: *Ctenosaura oaxacana* from Oaxaca, Mexico (Guillén-Hernández et al., 2007; Merlo-Serna and García-Prieto, 2018).

Phrynosomatidae: *Urosaurus auriculatus* from Colima, Mexico (Goldberg and Bursey, 2012b).

III. Family NEMATOTAENIIDAE Lühe, 1910 v. Genus *Bitegmen* Jones, 1987

Unidentified adults of this genus have been recorded in *Scincella lateralis* from Florida (Telford and Bursey, 2003).

29. *Bitegmen gerrhonoti* (Telford, 1965)

Anguidae: *Elgaria multicarinata* from California (Telford, 1965, 1970; Jones, 1987a; in the first 2, parasite as *Baerietta gerrhonoti*).

Plethodontidae: *Ensatina eschscholtzii* from California (Goldberg et al., 1998a).

Xantusiidae: *Lepidophyma gaigeae* from Hidalgo, Mexico (Goldberg et al., 2002a).

vi. Genus *Cylindrotaenia* Jewell, 1916

30. *Cylindrotaenia americana* Jewell, 1916

Ambystomatidae: *Ambystoma texanum* from Texas (McAllister and Upton, 1987a).

Bufonidae: *Anaxyrus americanus* from Iowa (Ulmer and James, 1976b), and from an unspecified US locality (Jewell, 1916);

Anaxyrs canorus from California (Walton, 1941); *Anaxyrs fowleri* from Virginia (Campbell, 1967, 1968, in both); *Anaxyrs kelloggi* from Sonora, Mexico (Goldberg and Bursey, 2002a); *Anaxyrs microscaphus* from Utah (Parry and Grundmann, 1965); *Anaxyrs terrestris* from Florida (McAllister et al., 2015c), Washington (Jones, 1987a) and from an unspecified US locality (Jewell, 1916); *Incilius nebulifer* from an unspecified US locality (Jones, 1987a).

Hylidae: *Acris blanchardi* from Illinois (Jewell, 1916; Jones, 1987a), Iowa (Ulmer and James, 1976b), Nebraska (Brooks, 1976; Jones, 1987a), Oklahoma (Trowbridge and Hefley, 1933), and Texas (Harwood, 1932); *Dryophytes arenicolor* from Tennessee (Dunbar and Moore, 1979; Goldberg et al., 1996b); *Dryophytes avivoca* from Arkansas (McAllister et al., 1993a); *Dryophytes squirellus* from Texas (Harwood, 1932); *Dryophytes wrightorum* from Arizona (Goldberg et al., 1996b); *Osteopilus septentrionalis* from Florida (Oliver et al., 2007; Ortega et al., 2015); *Pseudacris clarkii* from Texas (McAllister, 1991); *Pseudacris fouquettei* from Oklahoma (Bouchard, 1953; McAllister et al., 2015a) and Texas (Harwood, 1932); *Pseudacris triseriata* from Alberta, Canada (Goldberg et al., 2002d).

Leptodactylidae: *Leptodactylus melanonotus* from Sonora, Mexico (Goldberg and Bursey, 2002a).

Microhylidae: *Gastrophryne olivacea* from Texas (McAllister and Upton, 1987b).

Natricidae: *Thamnophis sirtalis* from Quebec, Canada (Rau and Gordon, 1978).

Plethodontidae: *Desmognathus brimleyorum* from Arkansas (McAllister et al., 1995a) and Oklahoma (Bouchard, 1953); *Desmognathus carolinensis* from Tennessee (Dunbar and Moore, 1979); *Desmognathus fuscus* from New York (Fischthal, 1955); *Desmognathus marmoratus* from North Carolina (Goater et al., 1987); *Desmognathus monticola* from North Carolina (Goater et al., 1987) and Tennessee (Dunbar and Moore, 1979); *Desmognathus ochrophaeus* from North Carolina (Goater et al., 1987) and Tennessee (Dunbar and Moore, 1979); *Desmognathus quadramaculatus* from North Carolina (Goater et al., 1987); *Eurycea tynesensis* from Arkansas (McAllister et al., 2014b); *Plethodon albagula* from Arkansas (McAllister et al., 1993b) and Texas (McAllister, 2006); *Plethodon angusticlavius* from Arkansas (McAllister et al., 2013b); *Plethodon cinereus* from Tennessee (Dunbar and Moore, 1979, parasite as *Cylindrotaenia idahoensis*) and Pennsylvania (Bursey and Schibli, 1995); *Plethodon glutinosus* from Tennessee (Dunbar and Moore, 1979); *Plethodon jordani* from North Carolina (Dyer, 1983); *Plethodon richmondi* from Tennessee (Dunbar and Moore, 1979).

Ranidae: *Rana berlandieri* from Oklahoma (Jones, 1987a); *Rana catesbeiana* from Massachusetts (Rankin, 1945), Virginia (Campbell, 1967, 1968), and from New Brunswick, Canada (McAlpine and Burt, 1998); *Rana clamitans* from New Brunswick, Canada (McAlpine and Burt, 1998); *Rana pipiens* from Iowa (Ulmer and James, 1976b), Illinois, Nebraska (Jones, 1987a), and Michigan (Lawler, 1939, parasite as *Cylindrotaenia quadrijugosa*; Jewell, 1916; Jones, 1987a; in the 3); *Rana septentrionalis* from Maine (Bouchard, 1951); *Rana sylvatica* from Quebec, Canada (Jones, 1987a); *Rana* sp. "Colima form" from Guerrero, Mexico (Cabrera-Aguilar et al., 2007).

Scincidae: *Scincella lateralis* from Florida (Harwood, 1932, 1936; Brooks, 1972).

Trionychidae: *Apalone spinifera* (Ernst and Ernst, 1977; McKnight, 1959).

Remarks

McAllister et al. (2013b) mention several North American species as hosts for this species of tapeworm, but some of the sources do contain records for the following hosts *Dendropsophus microcephalus* (Cope, 1886), *Pseudacris triseriata* (Wied-Neuwied, 1838) (Goldberg et al., 2002c), *Rana aurora* and *Rana pretiosa* Baird and Girard, 1853 (Lehmann, 1954).

31. *Cylindrotaenia idahoensis* (Waitz and Mehra, 1961)

Plethodontidae: *Plethodon caddoensis* from Arkansas (McAllister et al., 2002); *Plethodon idahoensis* from Idaho (Waitz and Mehra, 1961, parasite as *Baerietta idahoensis*); *Plethodon jordani* from North Carolina (Jones, 1987a); *Plethodon ouachitae* from Arkansas and Oklahoma (McAllister et al., 2002); *Plethodon sequoyah* from Oklahoma (McAllister and Bursey, 2004b); *Plethodon serratus* from Arkansas and Oklahoma (McAllister et al., 2002).

vii. Genus *Distoichometra* Dickey, 1921

32. *Distoichometra bufonis* Dickey, 1921

Bufoidea: *Anaxyrs americanus* from Georgia (Dickey, 1921) and from an unspecified locality (Jones, 1987a); *Anaxyrs boreas* from the United States (Jones, 1987a); *Anaxyrs cognatus* from Arizona (Goldberg and Bursey, 1991c) and New Mexico (Goldberg et al., 1995c); *Anaxyrs canorus* from California (Jones, 1987a); *Anaxyrs compactilis* from Ciudad de Mexico, Mexico (Jones, 1987a; Walton, 1940, 1964; in the last 2, parasite as *Cylindrotaenia americana*); *Anaxyrs debilis* from New Mexico (Goldberg et al., 1995c); *Anaxyrs fowleri* from Virginia (Campbell, 1967, 1968); *Anaxyrs microscaphus* from Arizona (Goldberg et al., 1996c); *Anaxyrs punctatus* from Arizona (Goldberg and Bursey, 1991b); *Anaxyrs retiformis* from Arizona (Goldberg et al., 1996c); *Anaxyrs terrestris* from Georgia and Washington (Jones, 1987a); *Anaxyrs woodhousii* from Arizona (Goldberg et al., 1996c), Nebraska (Jones, 1987a), and Texas (McAllister et al., 1989); *Anaxyrs* hybrid (*microscaphus* × *woodhousii*) from Arizona (Goldberg et al., 1996c); *Incilius nebulifer* from Nuevo Leon, Mexico (Martínez-Villarreal, 1969); *Rhinella horribilis* from Nuevo Leon, Mexico (Martínez-Villarreal, 1969; León-Régagnon et al., 2005).

Hylidae: *Pseudacris crucifer* from Maryland (Jones, 1987a); *Pseudacris regilla* from Baja California, Mexico (Goldberg et al., 2001); *Smilisca fodiens* from Arizona (Goldberg et al., 1999c).

Ranidae: *Rana berlandieri* from Nuevo Leon, Mexico (Martínez-Villarreal, 1969); *Rana boylei* from California (Bursey et al., 2010a).

Scaphiropodidae: *Scaphiopus couchii* from Arizona (Goldberg and Bursey, 1991c); *Spea intermontana* from Nevada (Goldberg and Bursey, 2002b); *Spea multiplicata* from New Mexico (Goldberg et al., 1995c), and Ciudad de Mexico, Mexico (Walton, 1940, 1964; Jones, 1987a; in the last 2, parasite as *Cylindrotaenia americana*).

Plethodontidae: *Aneides lugubris* from California (Jones, 1987a).

viii. Genus *Nematotaenia* Lühe, 1899

33. *Nematotaenia dispar* (Goeze, 1782)

Bufoidea: *Incilius alvarius* from Arizona (Goldberg and Bursey 1991c); *Incilius mazatlanensis* from Sonora, Mexico (Goldberg and Bursey, 2002a); *Rhinella horribilis* from Colima and Guerrero (Paredes-León et al., 2008), and Veracruz (Goldberg et al., 2002c), Mexico.

IV. Family PARUTERINIDAE Fuhrmann, 1907**ix. Genus *Anonchotaenia* Cohn, 1900****34. *Anonchotaenia ranae* (Ulmer and James, 1976)**

Ranidae: *Rana pipiens* from Iowa (Ulmer and James, 1976a, parasite as *Nematotaenoides ranae*; Jones, 1987b).

x. Genus *Metroliasthes* Ranson, 1900**35. *Metroliasthes mexicana* (Macías-Palacios and Flores-Barroeta, 1967)**

Ranidae: *Rana montezumae* from Estado de Mexico, Mexico (Macías-Palacios and Flores-Barroeta, 1967, parasite as *Hexaparuterina mexicana*; Merlo-Serna and García-Prieto, 2018).

Order ONCHOPROTEOCEPHALIDEA Caira, Jensen, Waeschenbach, Olson, and Littlewood, 2014

Unidentified adults of this order have been found in the tree frog *Tripion spatulatus* Günther, 1882 in Jalisco, Mexico (Velarde-Aguilar, 2011).

V. Family PROTEOCEPHALIDAE La Rue, 1911**xi. Genus *Crepidobothrium* Monticelli, 1900****36. *Crepidobothrium gerrardii* (Baird, 1860)**

Boidae: *Boa* sp. from an unspecified locality, Mexico (MacCallum, 1921, parasite as *Tetrabothrius brevis*).

xii. Genus *Nomimoscolex* Woodland, 1934

Unidentified adults of this genus have been found in the dipsadid snake *Leptodeira annulata* (Hallowell, 1861) from Guerrero, Mexico (Rosas-Valdéz, 2002, parasite as *Proteocephalus* sp.).

xiii. Genus *Ophiotaenia* La Rue, 1911

Unidentified adults of this genus have been recorded in *Rana megapoda* (Taylor, 1942) from Jalisco, Mexico (Velarde-Aguilar, 2011), in *Agkistrodon contortrix* (Linnaeus, 1766) and *Agkistrodon piscivorus* from North Carolina (Davis et al., 2016) as well as *Farancia abacura* from Oklahoma (McAllister and Bursey, 2012).

37. *Ophiotaenia agkistrodontis* Harwood, 1933

Viperidae: *Agkistrodon piscivorus* from Louisiana (Brooks, 1978, parasite as *Proteocephalus agkistrodontis*; Fontenot and Font, 1996, parasite as *Proteocephalus agkistrodontis*), Oklahoma (Roberts, 1956, parasite as *Ophiotaenia grandis*), and Texas (Brooks, 1978, parasite as *Proteocephalus agkistrodontis*; Harwood, 1933, parasite as *Proteocephalus (Ophiotaenia) agkistrodontis*).

38. *Ophiotaenia alternans* Riser, 1942

Amphiumidae: *Amphiuma tridactylum* from Tennessee (Riser, 1942).

39. *Ophiotaenia amphiumae* (Zeliff, 1932)

Amphiumidae: *Amphiuma tridactylum* from Louisiana (Brooks, 1978, parasite as *Proteocephalus amphiumae*; Zeliff, 1932, parasite as *Crepidobothrium amphiumae*).

Plethodontidae: *Desmognathus fuscus* from Ohio (Odlaug, 1954, parasite as *Crepidobothrium amphiumae*); *Eurycea spelaea* from Missouri (Smith, 1948).

40. *Ophiotaenia cryptobranchi* La Rue, 1914

Cryptobranchidae: *Cryptobranchus alleganiensis* from Missouri (Dyer and Brandon, 1973) and Pennsylvania (La Rue, 1914; Brooks, 1978, parasite as *Proteocephalus cryptobranchi*).

Plethodontidae: *Desmognathus fuscus* from North Carolina (Rankin, 1937, parasite as *Crepidobothrium cryptobranchi*); *Desmognathus ochrophaeus* from North Carolina (Rankin, 1937, parasite as *Crepidobothrium cryptobranchi*); *Desmognathus quadramaculatus* from North Carolina (Rankin, 1937, parasite as *Crepidobothrium cryptobranchi*); *Eurycea lucifuga* from Alabama (Dyer and Peck, 1975, parasite as *Batrachotaenia cryptobranchi*); *Plethodon metcalfi* from North Carolina (Rankin, 1937, parasite as *Crepidobothrium cryptobranchi*); *Pseudotriton ruber* from North Carolina (Rankin, 1937, parasite as *Crepidobothrium cryptobranchi*).

41. *Ophiotaenia faranciae* MacCallum, 1921

Dipsadidae: *Farancia abacura* from Arkansas (McAllister et al., 2008, parasite as *Proteocephalus faranciae*) and Texas (Harwood, 1932, parasite as *Proteocephalus faranciae*).

Natricidae: *Nerodia cyclopion* from Florida (Brooks, 1978, parasite as *Proteocephalus faranciae*); *Nerodia floridana* from Florida (Brooks, 1978, parasite as *Proteocephalus faranciae*).

42. *Ophiotaenia filaroides* (La Rue, 1909)

Ambystomatidae: *Ambystoma tigrinum* from Kansas and Nebraska (La Rue, 1909, parasite as *Proteocephalus filaroides*); *Ambystoma* sp. from Estado from Mexico, Mexico (García-Prieto, 1986, parasite as *Batrachotaenia filaroides*).

Ranidae: *Rana berlandieri* from Nuevo Leon, Mexico (León-Régagnon et al., 2005); *Rana dunni* from Michoacan, Mexico (Pulido-Flores, 1994); *Rana montezumae* from Ciudad de Mexico (Macías-Palacios, 1963) and Estado de Mexico (Paredes-León et al., 2008), Mexico.

43. *Ophiotaenia grandis* La Rue, 1911

Natricidae: *Nerodia cyclopion* from Louisiana (Brooks, 1978, parasite as *Proteocephalus grandis*); *Nerodia floridana* from Florida (Brooks, 1978, parasite as *Proteocephalus grandis*); *Thamnophis ordinoides* from Montreal, Canada (Fantham and Porter, 1954); *Thamnophis sirtalis* from Montreal, Canada (Fantham and Porter, 1954).

Viperidae: *Agkistrodon piscivorus* from Oklahoma (Roberts, 1956; McAllister et al., 2021b).

Remarks

Fantham and Porter (1954) mention this species from *Agkistrodon piscivorus* from Canada; however, this species is not found as far north; thus this record is treated in the present work as dubious.

44. *Ophiotaenia gracilis* Jones, Cheng and Gillespie 1958

Ranidae: *Rana catesbeiana* from Virginia (Jones et al., 1958); *Rana clamitans* from Ohio (Bursey and DeWolf, 1998).

45. *Ophiotaenia lonnbergii* (Fuhrmann, 1895) nom. emend.

Proteidae: *Necturus maculosus* from Illinois (Brooks, 1978, parasite as *Proteocephalus lonnbergii*), Indiana (La Rue, 1909, parasite as *Proteocephalus lonnbergii*), Ohio (La Rue, 1909, parasite as *Proteocephalus lonnbergii*; Odlaug, 1954, parasite as *Crepidobothrium lonnbergii*), and Wisconsin (Coggins and Sajdak, 1982, parasite as *Proteocephalus lonnbergii*).

Remarks

The original spelling of the name of this species, by Fuhrmann (1895), was *Ichthyotaenia lonnbergii*; while the omission of the

dieresis was needed, the addition of an additional “e” to the name was not (Brooks, 1978); therefore, we hereby recommend the use of the specific epithet *lonnbergii* instead of *loennbergii*.

46. *Ophiotaenia magna* Hannum, 1925

Ranidae: *Rana berlandieri* from Texas (Goldberg and Bursey, 2020); *Rana blairi* from Texas (Goldberg et al., 2000b); *Rana catesbeiana* from Colorado (Buhler, 1970; Brooks, 1976), Nebraska (Brooks, 1976, 1978, parasite as *Proteocephalus magnus*), Oklahoma (Hannum, 1925), and Texas (Harwood, 1932, parasite as *Proteocephalus magnus*); *Rana clamitans* from Texas (Brooks, 1978, parasite as *Proteocephalus magnus*); *Rana montezumae* from Ciudad de Mexico, Mexico (Macías-Palacios, 1963); *Rana tarahumarae* from Sonora, Mexico (Bursey and Goldberg, 2001).

47. *Ophiotaenia marenzelleri* (Barrois, 1898)

Viperidae: *Agkistrodon piscivorus* from North Carolina (Collins, 1969), Louisiana (Brooks, 1978, parasite as *Proteocephalus marenzelleri*; Fontenot and Font, 1996, parasite as *Proteocephalus marenzelleri*), Texas (Harwood, 1933, parasite as *Proteocephalus (Ophiotaenia) marenzelleri*), and from an unspecified U.S. locality (Barrois, 1898, parasite as *Ichthyotaenia marenzelleri*).

Remarks

Fantham and Porter (1954) mention this species from *Agkistrodon piscivorus* from Canada; however, this species is not found as far north; thus this record is treated in the present work as dubious.

48. *Ophiotaenia micruricola* (Shoop and Corkum 1982)

Elapidae: *Micrurus diastema* from Oaxaca, Mexico (Shoop and Corkum, 1982, parasite as *Proteocephalus micruricola*).

49. *Ophiotaenia nattereri* (Parona, 1901)

Unknown (Serpentes): Undetermined species of snake from Chiapas, Mexico (Flores-Barroeta, 1955b, host mentioned as *Culebra roja*, meaning red snake).

Remarks

In Mexico, the name “culebra” could refer to any snake, but in the scientific context, it is typically applied to colubroid snakes of the families Colubridae, Dipsadidae, Sibynophiidae, and Natricidae. It is deemed impossible to determine the identity of the host with certainty, as there are multiple species of red colubroid snakes in the state of Chiapas, from where Flores-Barroeta (1955b) made the report.

50. *Ophiotaenia olor* (Ingles, 1936)

Ranidae: *Rana aurora* from California (Ingles, 1936, parasite as *Crepidobothrium olor*).

51. *Ophiotaenia perspicua* La Rue, 1911

Dipsadidae: *Diadophis punctatus* from Oklahoma (McAllister and Bursey, 2012).

Natricidae: *Nerodia cyclopion* from Florida (Brooks, 1978, parasite as *Proteocephalus perspicua*) and Louisiana (Fontenot and Font, 1996, parasite as *Proteocephalus perspicua*); *Nerodia erythrogaster* from Nuevo Leon, Mexico (García-Prieto, 1986); *Nerodia fasciata* from Louisiana (Brooks, 1978, parasite as *Proteocephalus perspicua*; Fontenot and Font, 1996, parasite as *Proteocephalus perspicua*);

Nerodia floridana from Florida (Brooks, 1978, parasite as *Proteocephalus perspicua*); *Nerodia rhombifer* from Illinois (La Rue, 1911), Louisiana (Brooks, 1978, parasite as *Proteocephalus perspicua*; Fontenot and Font, 1996, parasite as *Proteocephalus perspicua*), and Oklahoma (Herde, 1938; McAllister et al., 2021b), and Veracruz, Mexico (Goldberg et al., 2012); *Nerodia sipedon* from North Carolina (Collins, 1969), Ohio (Anderson, 1935; Gibson and Rabalais, 1973), Mississippi (Brooks, 1978, parasite as *Proteocephalus perspicua*), and Texas (Thomas, 1941); *Nerodia taxispilota* from North Carolina (Collins, 1969); *Thamnophis sirtalis* from Ohio (Gibson and Rabalais, 1973) and Oklahoma (McAllister et al., 2021b).

Viperidae: *Agkistrodon piscivorus* from North Carolina (Collins, 1969); *Crotalus atrox* from Hidalgo, Mexico (Flores-Barroeta et al., 1961).

Remarks

Fantham and Porter (1954) mention this species from *Nerodia rhombifer* from Canada; however, this species is not found as far north; thus this record is treated in the present work as dubious. The record made by Flores-Barroeta et al. (1961) is quite unusual, as this parasite is associated with aquatic snakes and *Crotalus atrox* is completely terrestrial. Specimens akin to this species were found by McAllister et al. (2021b) in Oklahoma, from the water-snakes *Nerodia erythrogaster* and *Nerodia fasciata*.

52. *Ophiotaenia racemosa* (Rudolphi, 1819)

Natricidae: *Thamnophis eques* from Ciudad de Mexico and Estado de Mexico, Mexico (Cruz-Reyes, 1974); *Thamnophis melanogaster* from Michoacan, Mexico (Cruz-Reyes, 1974).

53. *Ophiotaenia saphena* Osler, 1931

Bufonidae: *Anaxyrus americanus* from Iowa (Ulmer and James, 1976b).

Ranidae: *Rana clamitans* from North Carolina (Brandt, 1936) and Michigan (Osler, 1931; Thomas, 1934); *Rana pipiens* from Iowa (Ulmer and James, 1976b).

54. *Ophiotaenia variabilis* (Brooks, 1978)

Natricidae: *Nerodia cyclopion* from Louisiana (Brooks, 1978, parasite as *Proteocephalus variabilis*; Fontenot and Font, 1996, parasite as *Proteocephalus variabilis*); *Nerodia rhombifer* from Louisiana (Brooks, 1978, parasite as *Proteocephalus variabilis*); *Thamnophis eques* from Estado de Mexico, Jalisco and Michoacan, Mexico (Pérez-Ponce de León et al., 2001, parasite as *Proteocephalus variabilis*); *Thamnophis melanogaster* from Estado de Mexico, Jalisco and Michoacan, Mexico (Pérez-Ponce de León et al., 2001, parasite as *Proteocephalus variabilis*).

xiv. Genus *Proteocephalus* Weinland, 1858

55. *Proteocephalus aberrans* Brooks, 1978

Sirenidae: *Siren lacertina* from Florida (Brooks, 1978)

56. *Proteocephalus amphiumicola* Brooks, 1978

Amphiumidae: *Amphiuma means* from Alabama and Mississippi (Brooks, 1978).

57. *Proteocephalus sireni* (Brooks and Buckner, 1976)

Sirenidae: *Siren intermedia* from Arkansas (McAllister et al., 1994), Illinois (Brooks and Buckner 1976, parasite as *Ophiotaenia sireni*), and Louisiana (Brooks, 1978).

xv. Genus *Testudotaenia* Freze, 1965**58. *Testudotaenia testudo* (Magath, 1924)**

Trionychidae: *Apalone spinifera* from Minnesota (Acholonu, 1970, parasite as *Proteocephalus testudo*; Magath, 1924, parasite as *Ophiotaenia testudo*), Louisiana (Acholonu, 1970, parasite as *Proteocephalus testudo*), and Tennessee (de Chambrier et al., 2009).

Emydidae: *Graptemys pseudogeographica* from Oklahoma (McKnight, 1959); *Trachemys scripta* from Oklahoma. (McKnight, 1959).

Host–parasite checklist

Here the hosts are listed alphabetically by class, order, family, and species; and the tapeworms are listed alphabetically by family and species. Tapeworms not identified to species level are not included (see under each family and genus).

AMPHIBIA**ANURA****BUFONIDAE*****Anaxyrus americanus* (Holbrook, 1836)**

Nematotaeniidae: *Cylindrotaenia americana*, *Distoichometra bufonis*

Proteocephalidae: *Ophiotaenia saphena*

***Anaxyrus boreas* (Baird and Girard, 1852)**

Nematotaeniidae: *Distoichometra bufonis*

***Anaxyrus canorus* (Camp, 1916)**

Nematotaeniidae: *Cylindrotaenia americana*, *Distoichometra bufonis*

***Anaxyrus cognatus* (Say, 1822)**

Nematotaeniidae: *Distoichometra bufonis*

***Anaxyrus compactilis* (Wiegmann, 1833)**

Nematotaeniidae: *Distoichometra bufonis*

***Anaxyrus debilis* (Girard, 1854)**

Nematotaeniidae: *Distoichometra bufonis*

***Anaxyrus fowleri* (Hinckley, 1882)**

Nematotaeniidae: *Cylindrotaenia americana*, *Distoichometra bufonis*

***Anaxyrus kelloggi* (Taylor, 1938)**

Nematotaeniidae: *Cylindrotaenia americana*

***Anaxyrus microscaphus* (Cope, 1867)**

Nematotaeniidae: *Cylindrotaenia americana*, *Distoichometra bufonis*

***Anaxyrus punctatus* (Baird and Girard, 1852)**

Nematotaeniidae: *Distoichometra bufonis*

***Anaxyrus retiformis* (Sanders and Smith, 1951)**

Nematotaeniidae: *Distoichometra bufonis*

***Anaxyrus terrestris* (Bonaterre, 1789)**

Nematotaeniidae: *Cylindrotaenia americana*, *Distoichometra bufonis*

***Anaxyrus woodhousii* (Girard, 1854)**

Nematotaeniidae: *Distoichometra bufonis*

***Anaxyrus hybrid* (*microscaphus* × *woodhousii*)**

Nematotaeniidae: *Distoichometra bufonis*

***Incilius alvarius* (Girard, 1859)**

Nematotaeniidae: *Nematotaenia dispar*

***Incilius mazatlanensis* (Taylor, 1940)**

Nematotaeniidae: *Nematotaenia dispar*

***Incilius nebulifer* (Girard, 1854)**

Nematotaeniidae: *Cylindrotaenia americana*, *Distoichometra bufonis*

***Rhinella horribilis* (Wiegmann, 1833)**

Nematotaeniidae: *Distoichometra bufonis*, *Nematotaenia dispar*

HYLIDAE***Acris blanchardi* Harper, 1947**

Nematotaeniidae: *Cylindrotaenia americana*

***Dryophytes arenicolor* (Cope, 1866)**

Nematotaeniidae: *Cylindrotaenia americana*

***Dryophytes avivoca* (Viosca, 1928)**

Nematotaeniidae: *Cylindrotaenia americana*

***Dryophytes squirellus* (LeConte, 1825)**

Nematotaeniidae: *Cylindrotaenia americana*

***Dryophytes wrightorum* (Taylor, 1939)**

Nematotaeniidae: *Cylindrotaenia americana*

***Osteopilus septentrionalis* (Duméril and Bibron, 1841)**

Nematotaeniidae: *Cylindrotaenia americana*

***Pseudacris clarkii* (Baird, 1854)**

Nematotaeniidae: *Cylindrotaenia americana*

***Pseudacris crucifer* (Wied-Neuwied, 1838)**

Nematotaeniidae: *Distoichometra bufonis*

***Pseudacris fouquettei* Lemmon, Lemmon, Collins and Cannatella, 2008**

Nematotaeniidae: *Cylindrotaenia americana*

***Pseudacris regilla* (Baird and Girard, 1852)**

Nematotaeniidae: *Distoichometra bufonis*

***Pseudacris triseriata* (Wied-Neuwied, 1838)**

Nematotaeniidae: *Cylindrotaenia americana*

***Smilisca fodiens* (Boulenger, 1882)**

Nematotaeniidae: *Distoichometra bufonis*

LEPTODACTYLIDAE***Leptodactylus melanonotus* (Hallowell, 1861)**

Nematotaeniidae: *Cylindrotaenia americana*

MICROHYLIDAE***Gastrophryne olivacea* (Hallowell, 1856)**

Nematotaeniidae: *Cylindrotaenia americana*

RANIDAE

Rana aurora* Baird and Girard, 1852**Proteocephalidae: *Ophiotaenia olor*Rana berlandieri* (Baird, 1859)**Nematotaeniidae: *Cylindrotaenia americana*, *Distoichometra bufonis*Proteocephalidae: *Ophiotaenia filaroides*, *Ophiotaenia magna****Rana blairi* (Mecham, Littlejohn, Oldham, Brown and Brown, 1973)**Proteocephalidae: *Ophiotaenia magna****Rana boylei* Baird, 1854**Nematotaeniidae: *Distoichometra bufonis****Rana catesbeiana* (Shaw, 1802)**Nematotaeniidae: *Cylindrotaenia americana*Proteocephalidae: *Ophiotaenia gracilis*, *Ophiotaenia magna****Rana clamitans* (Latreille, 1801)**Nematotaeniidae: *Cylindrotaenia americana*Proteocephalidae: *Ophiotaenia gracilis*, *Ophiotaenia magna*, *Ophiotaenia saphena****Rana dunni* (Zweifel, 1957)**Proteocephalidae: *Ophiotaenia filaroides****Rana montezumae* (Baird, 1854)**Paruterinidae: *Metroliaesthes mexicana*Proteocephalidae: *Ophiotaenia filaroides*, *Ophiotaenia magna*.***Rana pipiens* (Schreber, 1782)**Nematotaeniidae: *Cylindrotaenia americana*Paruterinidae: *Anonchotaenia ranae*Proteocephalidae: *Ophiotaenia saphena****Rana septentrionalis* (Baird, 1854)**Nematotaeniidae: *Cylindrotaenia americana****Rana sylvatica* LeConte, 1825**Nematotaeniidae: *Cylindrotaenia americana****Rana tarahumarae* (Boulenger, 1917)**Proteocephalidae: *Ophiotaenia magna****Rana* sp. "Colima form"**Nematotaeniidae: *Cylindrotaenia americana*

SCAPHIOPODIDAE

Scaphiopus couchii* Baird, 1854**Nematotaeniidae: *Distoichometra bufonis*Spea intermontana* (Cope, 1883)**Nematotaeniidae: *Distoichometra bufonis****Spea multiplicata* (Cope, 1863)**Nematotaeniidae: *Distoichometra bufonis*

CAUDATA

AMBYSTOMATIDAE

Ambystoma dumerili* (Dugès, 1870)**Bothriocephalidae: *Schyzocotyle acheilognathi*Ambystoma texanum* (Matthes, 1855)**Nematotaeniidae: *Cylindrotaenia americana****Ambystoma tigrinum* (Green, 1825)**Proteocephalidae: *Ophiotaenia filaroides****Ambystoma* sp.**Proteocephalidae: *Ophiotaenia filaroides*

AMPHIUMIDAE

Amphiuma means* Garden, 1821**Proteocephalidae: *Proteocephalus amphiumicola*Amphiuma tridactylum* Cuvier, 1827**Proteocephalidae: *Ophiotaenia alternans*, *Ophiotaenia amphiumae*

CRYPTOBRANCHIDAE

***Cryptobranchus alleganiensis* (Sonni de Manoncourt and Latreille, 1801)**Proteocephalidae: *Ophiotaenia cryptobranchi*

PLETHODONTIDAE

Aneides lugubris* (Hallowell, 1849)**Nematotaeniidae: *Distoichometra bufonis*Desmognathus brimleyorum* Stejneger, 1895**Nematotaeniidae: *Cylindrotaenia americana****Desmognathus carolinensis* Dunn, 1916**Nematotaeniidae: *Cylindrotaenia americana****Desmognathus fuscus* (Green, 1818)**Bothriocephalidae: *Bothriocephalus rarus*Nematotaeniidae: *Cylindrotaenia americana*Proteocephalidae: *Ophiotaenia amphiumae*, *Ophiotaenia cryptobranchi****Desmognathus marmoratus* (Moore, 1899)**Nematotaeniidae: *Cylindrotaenia americana****Desmognathus monticola* Dunn, 1916**Nematotaeniidae: *Cylindrotaenia americana****Desmognathus ochrophaeus* Cope, 1859**Nematotaeniidae: *Cylindrotaenia americana*Proteocephalidae: *Ophiotaenia cryptobranchi****Desmognathus quadramaculatus* (Holbrook, 1840)**Bothriocephalidae: *Bothriocephalus rarus*Nematotaeniidae: *Cylindrotaenia americana*Proteocephalidae: *Ophiotaenia cryptobranchi****Ensatina eschscholtzii* Gray, 1850**Nematotaeniidae: *Bitegmen gerrhonoti*

Eurycea bislineata* (Green, 1818)**Bothriocephalidae: *Bothriocephalus rarus*Eurycea longicauda* (Green, 1818)**Bothriocephalidae: *Bothriocephalus euryciensis*, *Bothriocephalus rarus*, *Bothriocephalus typhlotritonis****Eurycea lucifuga* Rafinesque, 1822**Bothriocephalidae: *Bothriocephalus rarus*, *Bothriocephalus typhlotritonis*Proteocephalidae: *Ophiotaenia cryptobranchi****Eurycea multiplicata* (Cope, 1869)**Bothriocephalidae: *Bothriocephalus rarus*, *Bothriocephalus typhlotritonis****Eurycea nerea* (Bishop, 1944)**Bothriocephalidae: *Bothriocephalus typhlotritonis****Eurycea quadridigitata* (Holbrook, 1842)**Bothriocephalidae: *Bothriocephalus rarus****Eurycea spelaea* (Stejneger, 1892)**Bothriocephalidae: *Bothriocephalus rarus*, *Bothriocephalus typhlotritonis*Proteocephalidae: *Ophiotaenia amphiumae****Eurycea tynnerensis* Moore and Hughes, 1939**Bothriocephalidae: *Bothriocephalus rarus*Nematotaeniidae: *Cylindrotaenia americana****Gyrinophilus porphyriticus* (Green, 1827)**Bothriocephalidae: *Bothriocephalus rarus****Plethodon albagula* Grobman, 1944**Nematotaeniidae: *Cylindrotaenia americana****Plethodon angusticlavius* Grobman, 1944**Nematotaeniidae: *Cylindrotaenia americana****Plethodon caddoensis* Pope and Pope, 1951**Nematotaeniidae: *Cylindrotaenia idahoensis****Plethodon cinereus* (Green, 1818)**Nematotaeniidae: *Cylindrotaenia americana****Plethodon glutinosus* (Green, 1818)**Nematotaeniidae: *Cylindrotaenia americana****Plethodon idahoensis* Slater and Slipp, 1940**Nematotaeniidae: *Cylindrotaenia idahoensis****Plethodon jordani* Blatchley, 1901**Nematotaeniidae: *Cylindrotaenia americana*, *Cylindrotaenia idahoensis****Plethodon metcalfi* Brimley, 1912**Proteocephalidae: *Ophiotaenia cryptobranchi****Plethodon ouachitae* Dunn and Heinze, 1933**Nematotaeniidae: *Cylindrotaenia idahoensis****Plethodon richmondi* Netting and Mittleman, 1938**Nematotaeniidae: *Cylindrotaenia americana****Plethodon sequoyah* Highton, 1989**Nematotaeniidae: *Cylindrotaenia idahoensis****Plethodon serratus* Grobman, 1944**Nematotaeniidae: *Cylindrotaenia idahoensis****Pseudotriton ruber* (Sonnini de Manoncourt and Latreille, 1801)**Bothriocephalidae: *Bothriocephalus rarus*Proteocephalidae: *Ophiotaenia cryptobranchi***PROTEIDAE*****Necturus maculosus* (Rafinesque, 1818)**Proteocephalidae: *Ophiotaenia lonnbergii***SALAMANDRIDAE*****Notophthalmus viridescens* (Rafinesque, 1820)**Bothriocephalidae: *Bothriocephalus rarus****Taricha torosa* (Rathke, 1833)**Bothriocephalidae: *Bothriocephalus rarus***SIRENIDAE*****Siren intermedia* Barnes, 1826**Proteocephalidae: *Proteocephalus sireni****Siren lacertina* Österdam, 1766**Proteocephalidae: *Proteocephalus aberrans***REPTILIA****SQUAMATA****ANGUIDAE*****Elgaria kingii* Gray, 1838**Anoplocephalidae: *Oochoristica eumecis****Elgaria multicarinata* (Blainville, 1835)**Nematotaeniidae: *Bitegmen gerrhonoti***ANNIELLIDAE*****Anniella pulchra* Gray, 1852**Anoplocephalidae: *Oochoristica annuellae***BIPEDIDAE*****Bipes biporus* (Cope, 1894)**Anoplocephalidae: *Oochoristica parvula***BOIDAE*****Boa* sp.**Proteocephalidae: *Crepidobothrium gerrardii***COLUBRIDAE*****Pantherophis obsoletus* (Say, 1823)**Anoplocephalidae: *Oochoristica elaphis****Pituophis catenifer* (Blainville, 1835)**Anoplocephalidae: *Oochoristica osheroffi*

CORYTOPHANIDAE

“Tolouque”

Anoplocephalidae: *Mathevotaenia antrozoi*

CROTAPHYTIDAE

***Crotaphytus collaris* (Say, 1823)**

Anoplocephalidae: *Oochoristica crotaphyti*

***Gambelia wislizenii* Baird and Girard, 1852**

Anoplocephalidae: *Oochoristica scelopori*

DACTYLOIDAE

***Anolis carolinensis* Voigt, 1832**

Anoplocephalidae: *Oochoristica anolis*

DIPSADIDAE

***Diadophis punctatus* (Linnaeus, 1766)**

Proteocephalidae: *Ophiotaenia perspicua*

***Farancia abacura* Holbrook, 1836**

Anoplocephalidae: *Oochoristica americana*

Proteocephalidae: *Ophiotaenia faranciae*

ELAPIDAE

***Micrurus diastema* (Duméril, Bibron and Duméril, 1854)**

Proteocephalidae: *Ophiotaenia micruricola*

EUBLEPHARIDAE

***Coleonyx elegans* Gray, 1845**

Anoplocephalidae: *Oochoristica parvula*

GEKKONIDAE

***Hemidactylus turcicus* (Linnaeus, 1758)**

Anoplocephalidae: *Oochoristica ameivae*, *Oochoristica bezyi*, *Oochoristica harschi*, *Oochoristica javaensis*, *Oochoristica macalisteri*, *Oochoristica scelopori*

HELODERMATIDAE

***Heloderma suspectum* Cope, 1869**

Anoplocephalidae: *Oochoristica whitentoni*

IGUANIDAE

***Ctenosaura pectinata* Wiegmann, 1834**

Anoplocephalidae: *Oochoristica acapulcoensis*, *Oochoristica eumecis*, *Oochoristica leonregagnonae*, *Oochoristica osheroffi*, *Oochoristica whitentoni*

***Ctenosaura oaxacana* Köhler and Hasbún, 2001**

Anoplocephalidae: *Oochoristica whitfieldi*

NATRICIDAE

***Nerodia cyclopion* (Duméril, Bibron and Duméril, 1854)**

Proteocephalidae: *Ophiotaenia faranciae*, *Ophiotaenia grandis*, *Ophiotaenia perspicua*, *Proteocephalus variabilis*

***Nerodia erythrogaster* (Forster, 1771)**

Proteocephalidae: *Ophiotaenia perspicua*

***Nerodia fasciata* (Linnaeus, 1766)**

Proteocephalidae: *Ophiotaenia perspicua*

***Nerodia floridana* (Goff, 1936)**

Proteocephalidae: *Ophiotaenia faranciae*, *Ophiotaenia grandis*, *Ophiotaenia perspicua*

***Nerodia rhombifer* (Hallowell, 1852)**

Anoplocephalidae: *Oochoristica natricis*

Proteocephalidae: *Ophiotaenia perspicua*, *Ophiotaenia variabilis*

***Nerodia sipedon* Linnaeus, 1758**

Proteocephalidae: *Ophiotaenia perspicua*

***Nerodia taxispilota* (Holbrook, 1838)**

Proteocephalidae: *Ophiotaenia perspicua*

***Thamnophis eques* (Reuss, 1834)**

Proteocephalidae: *Ophiotaenia racemosa*, *Ophiotaenia variabilis*

***Thamnophis melanogaster* Wiegmann, 1830**

Bothriocephalidae: *Schyzocotyle acheilognathi*

Proteocephalidae: *Ophiotaenia racemosa*, *Ophiotaenia variabilis*

***Thamnophis ordinoides* (Baird and Girard, 1852)**

Proteocephalidae: *Ophiotaenia grandis*

***Thamnophis sirtalis* (Linnaeus, 1758)**

Nematotaeniidae: *Cylindrotaenia americana*

Proteocephalidae: *Ophiotaenia grandis*, *Ophiotaenia perspicua*

PHRYNOSOMATIDAE

***Phrynosoma braconneri* Duméril, 1870**

Anoplocephalidae: *Oochoristica phrynosomatis*

***Phrynosoma cornutum* (Harlan, 1825)**

Anoplocephalidae: *Oochoristica phrynosomatis*

***Phrynosoma ditmarsii* Stejneger, 1906**

Anoplocephalidae: *Oochoristica scelopori*

***Phrynosoma douglassii* (Bell, 1828)**

Anoplocephalidae: *Oochoristica phrynosomatis*

***Phrynosoma platyrhinos* Girard, 1852**

Anoplocephalidae: *Oochoristica phrynosomatis*

***Phrynosoma solare* Gray, 1845**

Anoplocephalidae: *Oochoristica phrynosomatis*

***Sceloporus clarkii* Baird and Girard, 1852**

Anoplocephalidae: *Oochoristica scelopori*

***Sceloporus consobrinus* Baird and Girard, 1854**

Anoplocephalidae: *Oochoristica scelopori*

***Sceloporus graciosus* Baird and Girard, 1852**

Anoplocephalidae: *Oochoristica scelopori*

***Sceloporus grammicus* Wiegmann, 1828**

Anoplocephalidae: *Oochoristica scelopori*

Sceloporus jarrovi* Cope, 1875**Anoplocephalidae: *Oochoristica scelopori*Sceloporus magister* Hallowell, 1854**Anoplocephalidae: *Oochoristica scelopori****Sceloporus megalepidurus* Smith, 1934**Anoplocephalidae: *Oochoristica scelopori****Sceloporus mucronatus* Cope, 1885**Anoplocephalidae: *Oochoristica scelopori****Sceloporus occidentalis* Baird and Girard, 1852**Anoplocephalidae: *Oochoristica scelopori****Sceloporus olivaceus* Smith, 1934**Anoplocephalidae: *Oochoristica scelopori****Sceloporus orcutti* Stejneger, 1893**Anoplocephalidae: *Oochoristica scelopori****Sceloporus parvus* Smith, 1934**Anoplocephalidae: *Oochoristica scelopori****Sceloporus poinsettii* Baird and Girard, 1852**Anoplocephalidae: *Oochoristica scelopori****Sceloporus scalaris* Wiegmann, 1828**Anoplocephalidae: *Oochoristica scelopori****Sceloporus variabilis* Wiegmann, 1834**Anoplocephalidae: *Oochoristica scelopori****Uma notata* Baird, 1858**Anoplocephalidae: *Oochoristica scelopori****Uma rufopunctata* Cope, 1895**Anoplocephalidae: *Oochoristica macallisteri****Urosaurus auriculatus* (Cope, 1871)**Anoplocephalidae: *Oochoristica whitfieldi****Urosaurus graciosus* Hallowell, 1854**Anoplocephalidae: *Oochoristica scelopori****Uta stansburiana* Baird and Girard, 1852**Anoplocephalidae: *Oochoristica macallisteri***SCINCIDAE*****Plestiodon fasciatus* (Linnaeus, 1758)**Anoplocephalidae: *Oochoristica eumecis****Scincella lateralis* (Say, 1823)**Anoplocephalidae: *Oochoristica eumecis*Nematotaeniidae: *Cylindrotaenia americana***TEIIDAE*****Aspidoscelis calidipes* (Duellman, 1955)**Anoplocephalidae: *Oochoristica scelopori****Aspidoscelis cozumelae* (Gadow, 1906)**Anoplocephalidae: *Oochoristica scelopori****Aspidoscelis dixonii* (Scudday, 1973)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis exsanguis* (Lowe, 1956)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis gularis* (Baird and Girard, 1852)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis inornata* (Baird, 1859)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis lineatissima* (Cope, 1878)**Anoplocephalidae: *Oochoristica scelopori****Aspidoscelis marmorata* (Baird and Girard, 1852)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis maxima* (Cope, 1864)**Anoplocephalidae: *Oochoristica parvula****Aspidoscelis neomexicana* (Lowe and Zweifel, 1952)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis sackii* (Wiegmann, 1834)**Anoplocephalidae: *Oochoristica scelopori****Aspidoscelis sexlineata* (Linnaeus, 1766)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis sonorae* (Lowe and Wright, 1964)**Anoplocephalidae: *Oochoristica bivitellobata*, *Oochoristica macallisteri****Aspidoscelis stictogramma* (Burger, 1950)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis tessellata* (Say, 1823)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis tigris* (Baird and Girard, 1852)**Anoplocephalidae: *Oochoristica bivitellobata*, *Oochoristica scelopori****Aspidoscelis uniparens* (Wright and Lowe, 1965)**Anoplocephalidae: *Oochoristica bivitellobata****Aspidoscelis velox* (Springer, 1928)**Anoplocephalidae: *Oochoristica bivitellobata***VIPERIDAE*****Agkistrodon piscivorus* (Lacépède, 1789)**Proteocephalidae: *Ophiotaenia agkistrodantis*, *Ophiotaenia grandis*, *Ophiotaenia marenzelleri*, *Ophiotaenia perspicua****Crotalus atrox* Baird and Girard, 1853**Anoplocephalidae: *Oochoristica osheroffi*Proteocephalidae: *Ophiotaenia perspicua****Crotalus cerastes* Hallowell, 1854**Anoplocephalidae: *Oochoristica osheroffi****Crotalus helleri* Meek, 1905**Anoplocephalidae: *Oochoristica osheroffi*

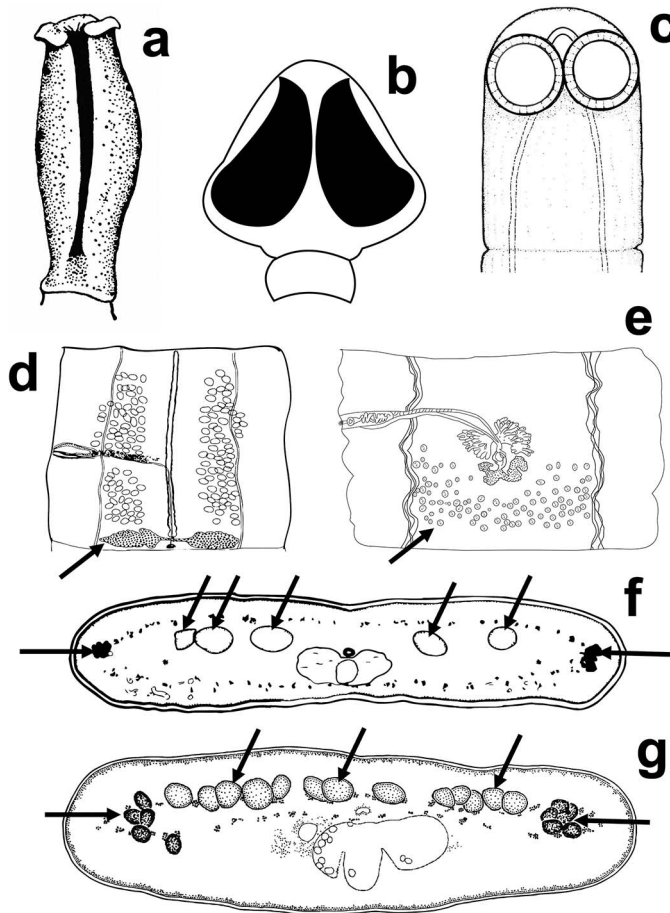
Crotalus viridis* (Rafinesque, 1818)**Anoplocephalidae: *Oochoristica osheroffi*Crotalus* sp.**Anoplocephalidae: *Oochoristica gracewileyae***XANTUSIIDAE*****Lepidophyma gaigeae* Mosauer, 1936**Nematotaeniidae: *Bitegmen gerrhonoti****Xantusia arizonae* Klauber, 1931**Anoplocephalidae: *Oochoristica bezyi*

Figure 1. Diagnostic characters of North American tapeworms used in the key, part 1. (a) Scolex of *Bothriocephalus rarus* (only 1 bothria is visible) (redrawn from Thomas, 1937b). (b) Scolex of *Schyzocotyle acheilognathi* (drawn from Choudhury et al., 2006). (c) Scolex of *Oochoristica macallisteri* (only 2 suckers are visible) (redrawn from Bursey and Goldberg, 1996). (d) Mature proglottid of *Ophiotaenia micuricola*, arrow points to the vitellarium (redrawn from Shoop and Corkum, 1982). (e) Mature proglottid from *Oochoristica leonregagnonae*, arrow points to the vitellarium (redrawn from Arizmendi-Espinoza et al., 2005). (f) Transverse section of posterior region of a gravid proglottid of *Nomimoscolex touzeti*, angled arrows point to the testes, straight arrows point to the vitellaria (redrawn from de Chambrier and Vaucher, 1992). (g) Transverse section of pregravid proglottids of *Testudotaenia testudo* at the level of the uterus, angled arrows point to the testes, straight arrows point to the vitellaria (redrawn from de Chambrier et al., 2009).

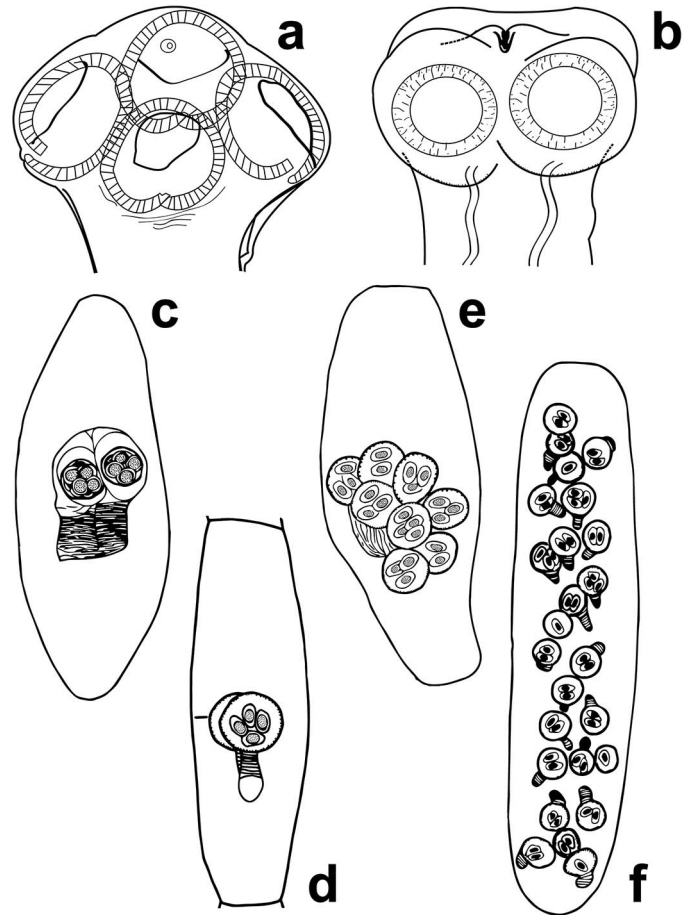


Figure 2. Diagnostic characters of North American tapeworms used in the key, part 2. (a) Scolex of *Crepidobothrium gerrardi* (redrawn from de Chambrier, 1989). (b) Scolex of *Ophiotaenia micuricola* (redrawn from Shoop and Corkum, 1982). (c) Gravid proglottid of *Bitegmen gerrhonoti* (redrawn from Jones, 1994). (d) Gravid proglottid of *Cylindrotaenia americana* (redrawn from Jones, 1994). (e) Gravid proglottid of *Distoichometra bufonis* (redrawn from Jones, 1994). (f) Gravid proglottid of *Nematotaenia dispar* (redrawn from Jones, 1994).

Xantusia bezyi* Papenfuss, Macey and Schulte, 2001**Anoplocephalidae: *Oochoristica bezyi*Xantusia henshawi* Stejneger, 1893**Anoplocephalidae: *Oochoristica bezyi****Xantusia riversiana* Cope, 1883**Anoplocephalidae: *Oochoristica islandensis****Xantusia sierrae* Bezy, 1967**Anoplocephalidae: *Oochoristica bezyi****Xantusia vigilis* Baird, 1859**Anoplocephalidae: *Oochoristica bezyi***UNKNOWN****"Red snake"**Proteocephalidae: *Ophiotaenia nattereri*

TESTUDINES EMYDIDAE

Graptemys pseudogeographica (Gray, 1831)

Proteocephalidae: *Testudotaenia testudo*

Terrapene carolina Linnaeus, 1758

Anoplocephalidae: *Oochoristica whitentoni*

Trachemys scripta (Thunberg, 1792)

Proteocephalidae: *Testudotaenia testudo*

TRIONYCHIDAE

Apalone spinifera (Lesueur, 1827)

Nematotaeniidae: *Cylindrotaenia americana*

Proteocephalidae: *Testudotaenia testudo*

KEY TO THE TAPEWORM (PLATYHELMINTHES: CESTODA) FAMILIES AND GENERA WHICH PARASITIZE NORTH AMERICAN HERPETOFAUNA.

- 1a. Scolex with 2 bothria (Fig. 1a, b)..... **BOTHRIOCEPHALIDAE: 2**
- 1b. Scolex with 4 suckers (Fig. 1c, 2a, b) **3**
- 2a. Scolex subcylindrical, longer than wide, the anterior and posterior portions being about the same width (Fig. 1a); bothria linear (Fig. 1a); commonly found in Nearctic caudates **Bothriocephalus**
- 2b. Scolex heart-shaped, with posterior portion wider than anterior 1 (Fig. 1b); bothria tear-shaped, slightly curved (Fig. 1b); rarely found in aquatic caudates and snakes (accidental hosts) **Schyzocotyle**
3. Mature proglottids with follicular vitellarium **PROTEOCEPHALIDAE: 4**
4. Mature proglottids with compact vitellarium (Fig. 1e) **8**
4. Mature proglottids with either testes or vitellarium placed in the cortex (Fig. 1f–g) **5**
4. Mature proglottids with both testes and vitellarium placed in the medulla **6**
5. Proglottids with testes in the medulla and vitellarium in the cortex (Fig. 1f); rarely found in **Nomimoscolex**
5. Proglottids with testes in the cortex and vitellarium in the medulla (Fig. 1g); found in freshwater turtles..... **Testudotaenia**
6. Suckers notched, heartlike (Fig. 2a); found in snakes (in the region it has only been found in boas)..... **Crepidobothrium**
6. Suckers circular (Fig. 2b); found in amphibians and snakes **7**
7. Testes in a single continuous field **Proteocephalus**
7. Testes in 2 fields, separated medially (Fig. 1d)..... **Ophiotaenia**
8. Strobila cylindrical, with strobilation that is only clear in the posterior region; gravid proglottids with 2 or more paruterine capsules (Fig. 2c–f); mature proglottids with 2 or more paruterine organs **NEMATOTAENIIDAE: 9**

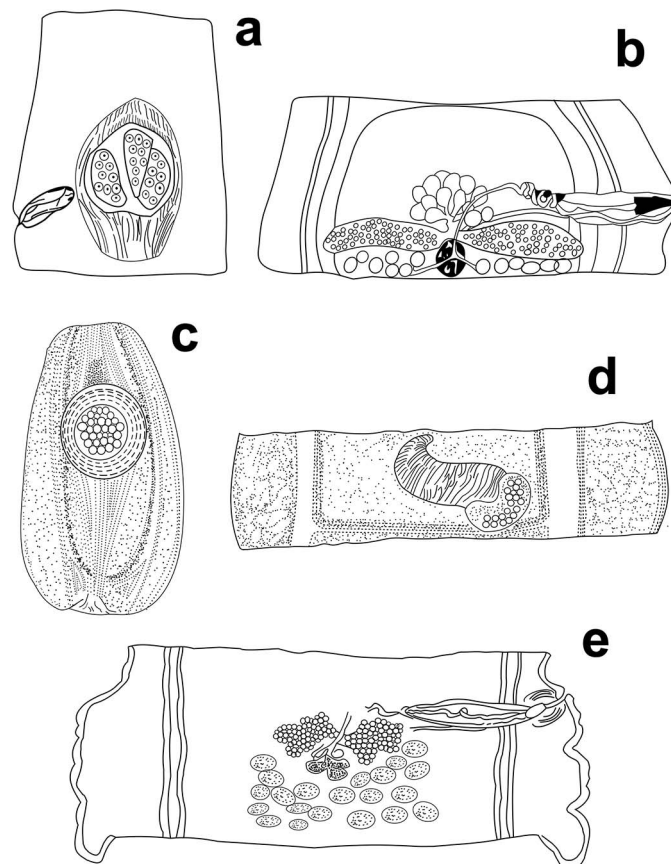


Figure 3. Diagnostic characters of North American tapeworms used in the key, part 3. (a) Formation of the paruterine organ in a proglottid of *Metroliaesthes mexicana* (redrawn from Macias-Palacios and Flores-Barroeta, 1967). (b) Fully formed paruterine organ in a proglottid of *Metroliaesthes mexicana*, only 3 compartments visible (redrawn from Macias-Palacios and Flores-Barroeta, 1967). (c) Paruterine organ in an early stage of formation in a proglottid of *Anonchotaenia ranae* (redrawn from Ulmer and James, 1976a). (d) Gravid proglottid of *Anonchotaenia ranae* showing a fully formed paruterine organ (redrawn from Ulmer and James, 1976a). (e) Mature proglottid of *Mathevotaenia chaquensis* (redrawn from Lunaschi et al., 2012).

- Strobila flattened, with clear strobilation throughout; proglottids usually without paruterine organs or capsules, if present, there is 1 per proglottid..... **12**
9. Gravid proglottids with 2 paruterine capsules (Fig. 2c, d); mature proglottids with 2 paruterine organs **10**
9. Gravid proglottids with more than 2 paruterine capsules (Fig. 2e, f); mature proglottids with more than 2 paruterine organs..... **11**
- 10a. Paruterine capsules of gravid proglottids enveloped in an additional membrane (Fig. 2c); paruterine organs of mature proglottids anteriorly bordered by massive cellular growth; found in lizards and caudates..... **Bitegmen**
- 10a. Paruterine capsules of gravid proglottids without additional membrane (Fig. 2d); paruterine organs of mature proglottids anteriorly bordered by small cellular growth; found in amphibians, rarely in reptiles **Cylindrotaenia**

11. Gravid proglottids with 4–12 paruterine capsules grouped in the posterior half (Fig. 2e); mature proglottids with paruterine organs in rows of 2–6 pairs; found in anurans, occasionally in caudates...
..... *Distoichometra*
Gravid proglottids with 5–150 paruterine capsules spread throughout (Fig. 2f); mature proglottids with paruterine organs unpaired; found in anurans (in the region it has been only found in true toads).
..... *Nematotaenia*
12. Gravid proglottids with a single paruterine organ (Fig. 2a–d), which can be divided in up to 6 compartments; rarely found in true frogs
..... **PARUTERINIDAE: 13**
Gravid proglottids without paruterine organ; commonly found in reptiles
..... **ANOPLOCEPHALIDAE: 14**
13. Paruterine organ of gravid proglottids divided in 4–6 compartments, located at distal end of proglottid (Fig. 3a); uterus bilobed in early stages (pregnate) of formation of the paruterine organ (Fig. 3b)
..... *Metroliaesthes*
Paruterine organ of gravid proglottids located at the center of the proglottid (Fig. 3c); uterus not bilobed in early stages (pre-gravid) of the paruterine organ, which can be horn-like (Fig. 3d) *Anonchotaenia*
14. Proglottids acraspedote (Fig. 1e); commonly found in lizards and snakes, rarely in turtles *Oochoristica*
Proglottids craspedote (Fig. 3e); rarely found in lizards *Mathevotaenia*

DISCUSSION

De Chambrier et al. (2006, 2017) cited *Ophiotaenia hernandezii* (Flores-Barroeta, 1955) for Mexico; however, Flores-Barroeta (1955b) states that this species was found in an unidentified *Rana* from the Sololá department in Guatemala. Paredes-León et al. (2008) mentioned *Anaxyrs compactilis* and *Spea multiplicata* as hosts of *Cylindrotaenia americana* citing the works of Walton (1940, 1964); however, these records correspond to *Distoichometra bufonis* (Jones, 1987a). Meggitt (1934) mentioned *Oochoristica fibrata* Meggitt, 1927 from *Pituophis catenifer* from Nebraska, and this record was later cited in a listing of species of reptile tapeworms (Hughes et al., 1941a, 1941b, 1941c); however, this species is a parasite of Asian snakes (Meggitt, 1934; Hughes et al., 1941a, 1941b, 1941c) and monitor lizards (Jadhav et al., 2010). As this species has not been recorded since from any American snake, and the report from Meggitt (1934) was made with less than desirable material (a few loose proglottids and a single strobila without a scolex), this record is treated in the present work as dubious.

Tetraphidium trionychium Lönnberg, 1894 was described from the small intestine of the softshell turtle *Apalone ferox* from Florida (Lönnberg, 1894), and was later recorded in another softshell turtle, *Apalone spinifer*, from Oklahoma (McKnight, 1959, parasite as *Proteocephalus trionychium*). The description of this species is considered too general to differentiate it from other members of the family Proteocephalidae adequately (Magath, 1924; Yamaguti,

1959); Brooks (1978) mentioned its status as unsolved. In the present publication, this species is considered a nomen dubium.

Larval stages of cestodes are found in many amphibians and reptiles (Merlo-Serna and García-Prieto, 2018). The most remarkable of these are the tetrathyridia of *Mesocostoides* Vailant, 1863 (Cyclophyllidae: Mesocostoididae) (Goldberg, 1984, 1987; Conn and McAllister, 1990; Goldberg and Bursey, 2000a) which sometimes can undergo asexual reproduction in this stage (Specht and Voge, 1965; Etges, 1991); these actively migrate to many organs including the liver, ovaries, coelomic cavity, and intestines of their intermediate host.

The methods of fixation, staining, and mounting of tapeworms vary greatly (Schmidt, 1970; Cable, 1977; Georgiev and Genov, 1986; Chubb et al., 1987; Jensen, 2005; Tyler, 2006; Ruhnke, 2011). The method we currently employ is the following: Once out of the intestine of the amphibian or reptilian host, it is untangled (easier done while completely submerged in 0.65% saline solution); the strobilae are arranged straight (if small enough) or in the shape of an M or an S in a petri dish with very little saline, then we place a microscope slide on top of the worm and, after that, we observe if the worm is making knots of itself; if not, we place a few other slides on top of the initial 1 (not necessary for very small worms) and drop enough alcohol, formalin, acetic acid (AFA) solution to cover the first 1 or 2 slides, killing and fixing the worm this way. We let the specimen stay in the AFA overnight, and, the next morning, we carefully remove the microscope slides on top of it; once free, it is washed in tap water and placed in 70% ethanol for long-term storage. For staining we place the specimens in Semichon's acetocarmine for around 20 min, destained as needed with acidic ethanol, and finally stabilized in carbonated ethanol for around 5 min. Once stained, the specimen is dehydrated in a series of ethanols (70, 80, 90, and 96%) for 10 min each; it is then passed through a series of xylene-ethanol solutions (1:3, 2:2, and 3:1) for 15 min each; finally, it goes into pure xylene for another 15 min. A xylene-based synthetic resin is used as a mounting medium, a drop is poured and dispersed in a slide, the specimen is placed above, and then an additional drop or 2 are poured onto the specimen, and finally, a coverslip is placed on top, which distributes the mounting medium evenly. The mounted specimen is left to dry for about a month at ambient temperature in a dry, well-ventilated room, out of direct sunlight. Excess of the mounting medium can be cleaned with paper towels moistened in pure xylene or left to dry and cleaned afterward with a flat metallic tool; the drying process can be accelerated by using an oven. Another technique recommended is rinsing the live tapeworms in 0.9% saline and fix them in almost boiling 4% formaldehyde, staining them in Meyer's carmine, dehydrating them in a series of ethanol, clear them in eugenol (clove oil) and mounting them in Canada balsam; it is recommended to store a few strobila in 96% ethanol for molecular work.

CONCLUSIONS

Fifty-eight (58) species of tapeworms (phylum Platyhelminthes, class Cestoda) were registered as intestinal parasites of wild North American herpetofauna (classes Amphibia and Reptilia). These are divided into 3 orders: Bothriocephalidae with 1 family (Bothriocephalidae), 2 genera (*Bothriocephalus* [3 sp.] and *Schyzocotyle* [1 sp.]), and 4 species; Cyclophyllidae with 3 families (Anoplocephalidae, Nematotaeniidae, and Paruterinidae), 8 genera (*Anonchotaenia* [1 sp.], *Bitegmen* [1 sp.], *Cylindrotaenia* [2 sp.], *Distoichometra* [1 sp.], *Mathevotaenia* [1 sp.], *Metroliaesthes* [1 sp.],

Nematotaenia [1 sp.], and *Oochoristica* [23 sp.]), and 31 species; and Onchoproteocephalidea with 1 family (Proteocephalidae), 5 genera (*Crepidobothrium* [1 sp.], *Nomimoscolex* [not identified to species level], *Ophiotaenia* [18 sp.], *Proteocephalus* [3 sp.], and *Testudotaenia* [1 sp.]) and 23 species.

Ninety (90) species of reptiles (21 snakes, 65 lizards, and 4 turtles; not including those not identified to species level) are recorded to be parasitized by adult tapeworms, the families represented are Anguillidae (2), Anniellidae (1), Bipedidae (1), Colubridae (2), Crotophytidae (2), Dactyloidae (1), Dipsadidae (2), Elapidae (1), Eublepharidae (1), Gekkonidae (1), Helodermatidae (1), Iguanidae (2), Natricidae (11), Phrynosomatidae (26), Scincidae (2), Teiidae (18), Viperidae (5), Xantusiidae (7), Emydidae (3), and Trionychidae (1). Additionally, 88 species of amphibians (46 anurans and 42 caudates; not including those not identified to species level or hybrids) are recorded to be parasitized by adult tapeworms, the families represented are Bufonidae (17), Hylidae (12), Leptodactylidae (1), Microhylidae (1), Ranidae (13), Scaphiopodidae (3), Ambystomatidae (4), Cryptobranchidae (1), Plethodontidae (31), Proteidae (1), Salamandridae (2), and Sirenidae (2).

ACKNOWLEDGMENTS

The authors thank Dr. Vasyl Tkach and Víctor Manuel Sosa Jiménez for their help in getting us literature we could not find elsewhere. M.D.L. and R.G.B. want to thank M.Sc. Gerardo Guajardo Martínez for inspiring and preparing us to pursue parasitological research, and the anonymous reviewers for their helpful comments and dedication.

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