2015

Hymenolepis folkertsii n. sp. (Eucestoda:
Hymenolepididae) in the Oldfield Mouse
Peromyscus polionotus (Wagner) (Rodentia:
Cricetidae: Neotominae) from the Southeastern
Nearctic with Comments on Tapeworm Faunal
Diversity among Deer Mice

Arseny A. Makarikov

Russian Academy of Sciences, makarikov@mail.ru

Todd N. Nims

Georgia Perimeter College

Kurt E. Galbreath

Northern Michigan University

Eric P. Hoberg

United States Department of Agriculture, Agricultural Research Service, geocolonizer@gmail.com

Follow this and additional works at: <http://digitalcommons.unl.edu/parasitologyfacpubs>

Part of the [Biodiversity Commons](#), [Ecology and Evolutionary Biology Commons](#), [Parasitology Commons](#), and the [Zoology Commons](#)

Makarikov, Arseny A.; Nims, Todd N.; Galbreath, Kurt E.; and Hoberg, Eric P., "*Hymenolepis folkertsii* n. sp. (Eucestoda: Hymenolepididae) in the Oldfield Mouse *Peromyscus polionotus* (Wagner) (Rodentia: Cricetidae: Neotominae) from the Southeastern Nearctic with Comments on Tapeworm Faunal Diversity among Deer Mice" (2015). *Faculty Publications from the Harold W. Manter Laboratory of Parasitology*. 795.
<http://digitalcommons.unl.edu/parasitologyfacpubs/795>

This Article is brought to you for free and open access by the Parasitology, Harold W. Manter Laboratory of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications from the Harold W. Manter Laboratory of Parasitology by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Hymenolepis folkertsii n. sp. (Eucestoda: Hymenolepididae) in the oldfield mouse *Peromyscus polionotus* (Wagner) (Rodentia: Cricetidae: Neotominae) from the southeastern Nearctic with comments on tapeworm faunal diversity among deer mice

Arseny A. Makarikov · Todd N. Nims ·
Kurt E. Galbreath · Eric P. Hoberg

Received: 18 December 2014 / Accepted: 27 February 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract A previously unrecognized species of hymenolepidid cestode attributable to *Hymenolepis* is described based on specimens in *Peromyscus polionotus*, oldfield mouse, from Georgia near the southeastern coast of continental North America. Specimens of *Hymenolepis folkertsii* n. sp. differ from those attributed to most other species in the genus by having testes arranged in a triangle and a scolex with a prominent rostrum-like protrusion. The newly recognized species is further distinguished by the relative position and length of the cirrus sac, shape of seminal receptacle, and relative size of external seminal vesicle and seminal receptacle. Hymenolepidid cestodes have sporadically been reported among the highly diverse assemblage of *Peromyscus* which includes 56 distinct species in the Nearctic. Although the host genus has a great temporal duration and is endemic to the Nearctic, current evidence suggests that tapeworm faunal diversity reflects relatively recent assembly through bouts of

host switching among other cricetid, murid, and geomyid rodents in sympatry.

Keywords Eucestoda · Hymenolepididae · *Hymenolepis folkertsii* · New species · Morphology · Rodents · *Peromyscus polionotus* · Georgia

Introduction

Muroid rodents of the genus *Peromyscus* Gloger, 1841 (Cricetidae) are among the most diverse assemblage among the Neotominae and represent an endemic complex of 56 species occurring with restricted and overlapping distributions across a considerable geographic expanse of North America from near Arctic latitudes into central Mexico (Musser and Carleton 2005). The taxonomy and biogeography of these rodents are particularly intricate reflecting both the temporal duration of this group with origins in the late Miocene and early Pliocene in the Nearctic and the range of habitats that are occupied by various species (e.g., Kurtén and Anderson 1980; Avise et al. 1983; Dragoo et al. 2006). The extensive geographic range of this assemblage suggests the potential for substantial insights about the history and patterns of North American biogeography and ecology, which can be revealed by exploring diversity and faunal assembly of complex host-parasite systems (e.g., Whitaker Jr 1968; Whitaker and Hamilton 1998; Hoberg et al. 2012; Makarikov et al. 2013a).

Biodiversity inventory for helminths has involved few species within *Peromyscus* and has focused, for example, on the following: *Peromyscus maniculatus* (Wagner, 1845)

A. A. Makarikov (✉)
Institute of Systematics and Ecology of Animals, Siberian Branch of
the Russian Academy of Sciences, Frunze Str. 11,
Novosibirsk, Russia 630091
e-mail: makarikov@mail.ru

T. N. Nims
Science Department, Georgia Perimeter College, 239 Cedar Lane,
Covington, GA 30014, USA

K. E. Galbreath
Department of Biology, Northern Michigan University, 1401 Presque
Isle Ave., Marquette, MI 49855, USA

E. P. Hoberg
United States National Parasite Collection, Animal Parasitic Disease
Laboratory, USDA Agricultural Research Service, BARC East No.
1180, 10300 Baltimore Avenue, Beltsville, MD 20705, USA

(Michigan and Wisconsin—Rausch and Tiner 1949; Quebec—Schad 1954; central plains eastern Rocky Mountains—Smith 1954; Arizona—Kruidenier and Gallicchio 1956; Alberta—Lubinsky 1957; Utah—Grundmann and Frandsen 1960; Colorado and Idaho—Leiby 1961, 1962; Montana—Vaughn 2013), *Pe. maniculatus*, *Peromyscus eremicus* (Baird, 1857), *Peromyscus truei* (Shufeldt, 1885) and *Peromyscus crinitus* (Merriam, 1891) (Nevada—Babero and Matthias 1967), *Pe. maniculatus* and *Peromyscus leucopus* (Rafinesque, 1818) (Illinois—Barker et al. 1987), *Peromyscus californicus* (Gambell, 1848), *Pe. truei* and *Peromyscus boylii* (Baird, 1855) (coastal California—Voge 1952), *Pe. boylii* and *Pe. maniculatus* (central California—Tinkle 1972) and *Peromyscus gossypinus* (LeConte, 1853), *Peromyscus polionotus* (Wagner, 1843), and *Peromyscus floridanus* (Chapman, 1889) (Florida—Layne 1963; Kinsella 1991). Geographically extensive and often site intensive survey among species of *Peromyscus* were conducted by mammalogists associated with the Museum of Southwestern Biology (University of New Mexico) and in the Beringian Coevolution Project exploring diversity across high latitudes of the Nearctic. In excess of 800 potential hosts were examined including *Pe. maniculatus*, *Peromyscus keeni* (Rhoads, 1894), and *Peromyscus nasutus* (Allen, 1891) with cestodes documented in about 6 % of these rodents (Mariel Campbell,

Pers. Comm.; <http://arctos.database.museum/SpecimenSearch.cfm>). In contrast to the considerable diversity of these neotomine rodents, relatively few comprehensive studies of host-parasite diversity have been conducted and the helminth faunas for most species are completely unknown or are based on fragmentary survey data (e.g., species lists summarized in Erickson 1938; Doran 1954; Whitaker Jr 1968; Dyer 1969).

Although ectoparasites of *Peromyscus* have been reasonably well characterized, there remains minimal information about helminth diversity in these hosts (Whitaker Jr 1968). Nematodes are prominent components of most communities where data are available, but cestodes appear to be relatively rare other than species of *Catenotaenia* Janicki, 1904 and *Choanotaenia* Railliet, 1896 and may be most often associated with other rodent hosts in sympatry (e.g., Erickson 1938; Smith 1954; Doran 1954; Grundmann and Frandsen 1960; Leiby 1961, 1962; Dyer 1969; Barker et al. 1987; Kinsella 1991) (Table 1). For example, hymenolepidids have sporadically been documented among *Peromyscus* spp. including unarmed cestodes referred to *Hymenolepis citelli* (McLeod, 1933) and *Hymenolepis diminuta* (Rudolphi, 1819) in *Pe. maniculatus* from Utah (Grundmann and Frandsen 1960) and armed *Rodentolepis nana* (Siebold, 1852) (as *Hymenolepis*) in *Pe. gossypinus*, *Pe. polionotus*, and *Pe. floridanus* from Florida (Kinsella 1991). Unidentified

Table 1 Checklist of cestodes reported from *Peromyscus* spp

Cestode species	Host species	Locality	Reference
<i>Catenotaenia peromysci</i> Smith, 1954	<i>Pe. maniculatus</i>	New Mexico, Colorado, Wyoming,	Smith (1954)
	<i>Pe. maniculatus</i>	Colorado	Leiby (1961)
	<i>Pe. maniculatus</i>	Illinois	Barker et al. (1987)
<i>Choanotaenia peromysci</i> (Erickson, 1938)	<i>Pe. maniculatus</i>	Minnesota	Erickson (1938)
(syn.: <i>Prochoanotaenia peromysci</i> Erickson, 1938)	<i>Pe. maniculatus</i>	Illinois	Barker et al. (1987)
<i>Hymenolepis</i> sp.	<i>Pe. maniculatus</i> , <i>Pe. eremicus</i>	Nevada	Babero and Matthias (1967)
	<i>Pe. maniculatus</i>	Minnesota	Erickson (1938)
	<i>Pe. maniculatus</i>	Arizona	Kruidenier and Gallicchio (1956)
	<i>Pe. maniculatus</i>	Nebraska	Hansen (1950)
	<i>Pe. maniculatus</i>	Montana	Vaughn (2013)
<i>Hymenolepis</i> sp. (cysticercoids)	<i>Pe. maniculatus</i>	Idaho	Leiby (1962)
<i>Hymenolepis bennetti</i> Freeman, 1960	<i>Pe. maniculatus</i>	Ontario	Freeman (1960)
	<i>Pe. maniculatus</i> , <i>Pe. leucopus</i>	Illinois	Barker et al. (1987)
<i>H. citelli</i> (McLeod, 1933)	<i>Pe. maniculatus</i>	Utah	Grundmann and Frandsen (1960)
<i>H. diminuta</i> (Rudolphi, 1819)	<i>Pe. maniculatus</i>	Utah	Grundmann and Frandsen (1960)
<i>H. horrida</i> (Linstow, 1901)	<i>Pe. truei</i> , <i>Pe. boylii</i> , <i>Pe. californicus</i>	California	Voge (1952)
<i>H. peromysci</i> Tinkle, 1972	<i>Pe. boylii</i> , <i>Pe. maniculatus</i>	California	Tinkle (1972)
<i>Rodentolepis nana</i> (Siebold, 1852)	<i>Pe. gossypinus</i> , <i>Pe. polionotus</i>	Florida	Kinsella (1991)
(syn.: <i>Hymenolepis nana</i> (Siebold, 1852))			
<i>Taenia rileyi</i> Loewen, 1929 (larva)	<i>Pe. gossypinus</i>	Florida	Kinsella (1991)

strobilate specimens of *Hymenolepis* sp. have been observed in *Pe. maniculatus* and *Pe. eremicus* from Nevada (Babero and Matthias 1967) and in *Pe. maniculatus* from Minnesota (Erickson 1938), Arizona (Kruidenier and Gallicchio 1956), Nebraska (Hansen 1950), and Montana (Vaughn 2013); cysticercoids attributed to *Hymenolepis* sp. were seen in *Pe. maniculatus* from Idaho (Leiby 1962). Strobilate specimens referred to the armed *Hymenolepis bennetti* Freeman, 1960, originally described based on specimens in *Napaeozapus insignis* (Miller, 1891) and *Pe. maniculatus* from Ontario, were also collected in *Pe. maniculatus* and *Pe. leucopus* from Illinois (Freeman 1960; Barker et al. 1987). Another species with an armed scolex, *Hymenolepis peromysci* Tinkle, 1972, was described based on specimens in *Pe. boylii* and also reported in *Pe. maniculatus* from central California (Tinkle 1972). Cestodes referred to *Hymenolepis horrida* (Linstow, 1901) were examined from *Pe. truei*, *Pe. boylii*, and *Pe. californicus* at localities along coastal California (Voge 1952). *H. horrida* (as *Arostrilepis* Mas-Coma and Tenora 1997) is now regarded as a complex of species across the Holarctic, and specimens originally examined by Voge (1952) were recently described as *Arostrilepis mariettavogae* Makarikov, Gardner et Hoberg, 2013 in these species of *Peromyscus* and the heteromyid, *Perognathus inornatus* Merriam, 1889 (Makarikov et al. 2012, 2013a).

Over the past century, it was generally accepted that among mammalian and rodent cestodes, many anoplocephalid, catenotaeniid, and hymenolepidid species were widespread, often with intercontinental distributions, and were characterized by considerable morphological variation without definable limits related either to geography or host association (Voge 1952; Schiller 1952; Ryzhikov et al. 1978). Studies across a spectrum of host taxa including rodents have increasingly identified the broad occurrence of poorly differentiated or cryptic parasite species, suggesting that considerable diversity remains to be discovered and characterized (e.g., Haukialmi et al. 2004, 2010b; Pérez-Ponce de León and Nadler 2010; Makarikov et al. 2013a; Makarikov and Tkach 2013). Increasing discrimination of species limits and molecular/morphological partitions among taxa contribute to nuanced observations about specificity. Some hymenolepidid cestodes in rodents appear to maintain specificity to host genera (Makarikov et al. 2013a, b; Makarikov and Tkach 2013). A similar specificity at the level of host genus was observed among hymenolepidids from various Soricidae (Binkienė et al. 2011). Faunal assembly and specificity are a reflection of historical and microevolutionary processes that have structured the biosphere and thus lead to predictions about the distribution of helminth diversity in space and time (e.g., Hoberg et al. 2012). Interacting abiotic and biotic mechanisms, and patterns of isolation over time, support the concept that endemic hosts may be predicted to have unique helminth faunas. Consequently, explorations among poorly

investigated hosts are critically important foundations in broader investigations of faunal diversity and contribute directly to empirical assessments of specificity among nominal taxa.

Our current study establishes a parasitological inventory of *Pe. polionotus*, or oldfield mouse, from Georgia, USA (Nims et al. 2008; additional data for publication in preparation), a species endemic to the southeastern region of North America occurring from central Tennessee to northern Florida. Prior records of cestodes in this region are limited to the cosmopolitan *R. nana* documented among species of *Peromyscus* including *Pe. polionotus* from Florida (Kinsella 1991). Building on this current picture of diversity, we now describe and name a previously unrecognized species of hymenolepidid belonging to *Hymenolepis* (s. str.) Weinland, 1858 which is differentiated from related cestodes based on comparative morphology. Further, we briefly discuss the biological and historical context for hymenolepidid tapeworm faunas in species of *Peromyscus* from North America.

Materials and methods

Oldfield mice were captured using live traps baited with sunflower seeds at the Fifteenmile Creek Conservation Easement (32° 21' 21.8" N, 82° 01' 42.4" W) (The Nature Conservancy in Georgia), located in Candler County, Georgia, USA, from November 2002 to February 2003. This location represented a frequently burned (ca. every 3 years) longleaf pine/wiregrass habitat. Captured mice were euthanized in the field with chloroform. Mammal trapping and euthanasia were carried out using methods recommended by the American Society of Mammalogists (1998) and approved by Georgia Southern University's Animal Care and Use Committee. Trapping was further authorized by the Georgia Department of Natural Resources (permits 29-WMB-02-83 and 29-WMB-03-105).

Helminths were recovered from small mammals using a technique described by Pung et al. (2000). The gastrointestinal tracts from 30 oldfield mice were examined for helminths. The small intestine and large intestine were each placed in individual Petri dishes, covered with water, cut open, and then gently scraped with insect pins during examination using a dissecting microscope (×8 total magnification). Helminths were preserved overnight in 5 % formalin and then transferred to 70 % ethanol.

Cestodes were stained with Ehrlich's hematoxylin, dehydrated in an ethanol series, cleared in clove oil, and mounted in Canada balsam. In the description, measurements are given in micrometers except where otherwise stated; they are presented as the range followed by the mean and the number of the measurements (*n*) in parentheses. Host taxonomy is consistent with Wilson and Reeder (2005). The type specimens of the new species have been deposited in the collections

of the Harold W. Manter Laboratory of Parasitology, University of Nebraska State Museum, University of Nebraska-Lincoln, NE, under HWML-75144-75145.

The following type and voucher materials from previously described species deposited in the United States National Parasite Collection, Beltsville, MD (USNPC), were studied for comparative analysis: holotype of *Hymenolepis tualatinensis* Gardner, 1985 (USNPC 078418) in the geomyid *Thomomys bulbivorus* (Richardson, 1829) from Oregon, holotype of *Hymenolepis pitymi* Yarinsky, 1952 (USNPC 038261) in the arvicoline, *Pitymys* (= *Microtus*) *pinetorum* (LeConte, 1830) from Tennessee, and a voucher of *H. citelli* (USNPC 044825) in the sciurid, *Spermophilus* (= *Otospermophilus*) *beecheyi* (Richardson, 1829) from California. Other materials examined by us included tape-worms from the collections of Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, representing specimens of *H. diminuta* in *Rattus norvegicus* (Berkenhout, 1769) and *Hymenolepis megaloon* Linstow, 1901 in *Spermophilus undulatus* (Pallas, 1778).

Results

Description

Hymenolepis folkertsi n. sp. (Figs. 1 and 2)

Fig. 1 *Hymenolepis folkertsi* n. sp. **a** Paratype, dorsoventral view of scolex; **b** holotype, cirrus and vagina, ventral view; **c** holotype, hermaphroditic mature proglottids, dorsal view; and **d** holotype, genital ducts, dorsal view. Scale bars: **a**, **d**=100 μ m; **b**=50 μ m; and **c**=300 μ m

Description (based on two gravid specimens): Worms of medium size. Fully developed strobila 99–116 mm long, with maximum width at pregravid or gravid (but not terminal) proglottids, 1.71–1.85 mm. Strobila consisting of about 790–850 craspedote proglottids. Scolex slightly flattened dorsoventrally, 168 wide, clearly distinct from strobila (Fig. 1a). Suckers unarmed, round or oval, 93–102 $\times$ 70–86 (97 $\times$ 75, n =4), with thick muscular walls, extending beyond lateral margins of scolex. Rhynchus unarmed, 37 $\times$ 4, not fully invaginated in rostellar pouch and its evaginated part forms rostrum-like protrusion on apex of scolex; rostellum absent (Fig. 1a). Rostellar pouch 67 $\times$ 43, with muscular walls, not reaching beyond posterior margins of suckers, osmoregulatory canals penetrate through rostellar pouch wall. Neck narrower than scolex, 130–145.

Ventral osmoregulatory canals 25–52 (34, n =10) wide, connected by transverse anastomoses. Dorsal osmoregulatory canals 3–5 (3, n =10) wide, usually situated directly above ventral canals on both sides of proglottids. Genital pores unilateral, dextral. Genital ducts pass dorsally to both ventral and dorsal longitudinal osmoregulatory canals (Fig. 1c). Development of proglottids gradual, protandrous. External segmentation becomes evident at level of mature part of strobila.

Mature proglottids 90–150 $\times$ 810–1030 (116 $\times$ 919, n =10), transversely elongate, trapezoid (Fig. 1c). Testes relatively small, usually three, almost equal in size, 75–112 $\times$ 44–62 (91 $\times$ 52, n =19), oval, normally situated in triangle with flat

Fig. 2 *Hymenolepis folkertsi* n. sp. **a** Paratype, pregravid proglottid from ventral side, showing appearance of ventral uterine diverticula (immature eggs are illustrated only on the lateral sides of the uterus); **b** holotype, gravid proglottid from ventral side, showing saccate uterus with ventral uterine diverticula (mature eggs are illustrated only on the lateral sides of the uterus); **c** holotype, egg; and **d** holotype, embryonic hooks. Scale bars: **a**, **b**=300 μ m; **c**=20 μ m; and **d**=10 μ m

angle; poral testis separated from two antiporal testes by female gonads. Arrangement of testes may vary (triangle with right angle to linear). Cirrus sac pyriform, relatively short, $138\text{--}154 \times 30\text{--}39$ (145×34 , $n=14$), with thick muscular walls. Antiporal part of cirrus sac usually rarely overlapping ventral longitudinal canal but not crossing it (Fig. 1c, d). Genital atrium simple, infundibular, deep, situated approximately in middle or slightly anterior of lateral proglottid margin. Cirrus $45\text{--}58 \times 7\text{--}10$ (51×8 , $n=15$), conical in basal region, fully evaginated cirrus not available in material examined, armed with minuscule (less than one long) spines (Fig. 1b). Internal seminal vesicle oval, $78\text{--}110 \times 26\text{--}33$ (92×29 , $n=13$), more than half of cirrus sac length (Fig. 1d). External seminal vesicle elongate $65\text{--}98 \times 31\text{--}49$ (84×39 , $n=10$), clearly distinguishable from vas deferens, distinctly smaller than seminal receptacle.

Ovary $147\text{--}217$ (180 , $n=10$) wide, median, lobed, fan-shaped, ventral to male genital organs, occupying about third of median field width, usually not reaching testes or slightly overlapping one of them (Fig. 1c). Vitellarium $30\text{--}57 \times 55\text{--}98$ (43×72 , $n=11$), postovarian, median, scarcely lobed. Copulatory part of vagina $51\text{--}64 \times 4\text{--}12$ (59×7 , $n=11$), tubular, with thick walls, clearly distinct from seminal receptacle; ventral to cirrus sac. Vagina surrounded by circular musculature and covered externally by dense layer of intensely stained cells (Fig. 1b). Seminal receptacle relatively large, $275\text{--}365 \times 37\text{--}62$ (315×49 , $n=16$), elongated, usually curved, or twisted (Fig. 1d).

Uterus first appears as perforated transversely elongated sac, situated dorsally to other organs and extending laterally

beyond longitudinal osmoregulatory canals (Fig. 2a). With proglottid development, uterus forms numerous diverticula predominantly on ventral side of strobila (Fig. 2b). Testes remain in postmature proglottids; cirrus sac and vagina persist in pregravid proglottids. Gravid proglottids transversely elongate, $230\text{--}370 \times 1580\text{--}1845$ (286×1679 , $n=15$). Fully developed uterus occupying entire median field and extending laterally beyond longitudinal osmoregulatory canals, saccate, with ventral and dorsal diverticula, in terminal gravid proglottids uterine walls indistinguishable (Fig. 2b). Uterus contains numerous (up to 700–1000) large eggs. Eggs $46\text{--}56 \times 57\text{--}69$ (51×61 , $n=19$), subspherical, with relatively thin outer coat (up to 1.5), egg surface smooth; oncosphere $22\text{--}26 \times 26\text{--}35$ (23×31 , $n=17$) (Fig. 2c). Embryophore subspherical, thin, $23\text{--}29 \times 30\text{--}39$ (25×34 , $n=18$). Embryonic hooks of different shape and length (Fig. 2d), antero-lateral embryonic hooks ($16\text{--}16.5$, $n=11$) much more robust than slender postero-lateral ($15.7\text{--}16.5$, $n=7$) and median hooks ($17\text{--}18$, $n=6$).

Taxonomic summary

Site in the host: small intestine.

Type host: *Pe. polionotus* (Wagner, 1843) (Rodentia: Cricetidae: Neotominae).

Other hosts: currently unknown.

Type locality: Fifteenmile Creek Conservation Easement ($32^{\circ} 21' 21.8''$ N, $82^{\circ} 01' 42.4''$ W) (The Nature Conservancy in Georgia), Candler County, Georgia, USA.

Other localities: currently unknown.

Type specimens: holotype, HWML-75144, in type host (specimen labeled: ex. *Pe. polionotus* no. 01-23FEB03-076, Fifteenmile Creek Conservation Easement ($32^{\circ} 21' 21.8''$ N,

82° 01' 42.4" W) (The Nature Conservancy in Georgia), Candler County, Georgia, USA, 23 February 2003, coll. T. Nims). Paratype, HWML-75145, also in type host.

Symbiotype: skeleton and skin of type host retained and deposited in the Mammalogy collection of the Georgia Museum of Natural History, Georgia, USA.

Etymology: this species is named in memory of Dr. George W. Folkerts (1938–2007) in recognition of his significant contributions to the knowledge and conservation of native species and habitats of the Southeastern USA.

Remarks

H. folkertsii n. sp. has morphological characters typical of *Hymenolepis* (s. str.). Primary diagnostic attributes are a scolex with rudimentary rostellar apparatus, unarmed rhynchus invaginated in a rostellar pouch, ventral canals with transverse anastomoses, cirrus sac with muscular walls, vagina surrounded by circular musculature, and saccate uterus with ventral and dorsal diverticula and spherical eggs (Makarikov and Tkach 2013). *Hymenolepis* (s. str.) includes about 18 nominal taxa occurring among Rodentia in addition to four species in Chiroptera and one in Erinaceomorpha (Makarikov and Tkach 2013; Makarikov et al. 2013b; Gardner et al. 2014; Makarikov et al. 2015). It should be noted that two species in birds were attributed to *Hymenolepis* by Czaplinski and Vaucher (1994). These are *Hymenolepis megalops* (Nitzsch in Creplin, 1829) and *Hymenolepis biaculeata* Fuhrmann, 1909. Previously these species had been chosen as the type species of two independent genera: *H. megalops* for *Cloacotaenia* Wolffhügel, 1938 and *H. biaculeata* for *Amphipetrovia* Spassky and Spasskaja 1954 (Spassky and Spasskaja 1954; Spassky 1963). Subsequently, *Cloacotaenia* and *Amphipetrovia* were synonymized with *Hymenolepis* (s. l.) by Czaplinski and Vaucher (1994) without any explanation. However, the morphological characteristics of *H. megalops* and *H. biaculeata* significantly differ from species of *Hymenolepis* (s. str.). Among the most remarkable differences between *H. megalops* and *Hymenolepis* (s. str.) may be listed the following characters: cirrus sac reaching or crossing middle line of proglottids vs cirrus sac not reaching middle line of proglottids, velum well developed vs velum scarcely developed or absent, and fully developed uterus compact without pockets and septa not extending laterally beyond longitudinal osmoregulatory canals vs uterus with ventral and dorsal diverticula extending into both lateral fields. The following features distinguish *H. biaculeata* and *Hymenolepis* (s. str.): female gonads shifted to poral side of proglottids and testes not separated by ovary vs median female gonads and testes separated by ovary (see Spassky and Spasskaja 1954; Spassky 1963; Makarikov and Tkach 2013). In view of this, we are restoring independent status of the genera *Cloacotaenia* with type

species *C. megalops* and *Amphipetrovia* with type species *Amphipetrovia biaculeata*.

Among those species of *Hymenolepis* in rodents, specimens of *H. folkertsii* are readily distinguished by disposition of the testes arranged in triangle and a scolex with a rostrum-like protrusion. In contrast, most congeners in murid, geomyid, spalacid, or sciurid rodents are characterized by a linear arrangement of the testes and a fully invaginated rhynchus at the apex of the scolex (e.g., in North America: *H. diminuta*, *H. citelli*, and *Hymenolepis weldensis* Gardner and Schmidt 1988; in the Palearctic including Eurasia: *H. diminuta*, *H. megaloon*, *Hymenolepis hibernia* Montgomery, Montgomery et Dunn, 1986, and *Hymenolepis pseudodiminuta* Tenora, Asakawa et Kamiya, 1994, *Hymenolepis apodemi* Makarikov and Tkach 2013, *Hymenolepis rymzhanovi* Makarikov and Tkach 2013; in southern Asia/Philippines: *Hymenolepis bicauda* Makarikov and Tkach 2013, *Hymenolepis haukisalmi* Makarikov and Tkach 2013, *Hymenolepis bilateralis* Makarikov et al. 2015, and *Hymenolepis alterna* Makarikov et al. 2015; and in west Africa: *Hymenolepis uranomidis* Hunkeler, 1972).

In the Nearctic, cestodes of two species of *Hymenolepis* resemble *H. folkertsii* in having the testes arranged in a triangle and a scolex with a rostrum-like protrusion. These are *H. pitymi* in the cricetid (Arvicolinae) *M. pinetorum* (syn.: *Pi. pinetorum*) from Tennessee (Yarinsky 1952) and *H. tualatinensis* in the geomyid *T. bulbivorus* from western Oregon (Gardner 1985). *H. folkertsii* is distinguished from these species by a larger cirrus sac (138–154, mean 145, versus 79 in *H. pitymi*; 56–150, mean 99 in *H. tualatinensis*) and larger seminal receptacle (275–365×37–62, versus 155–241 in *H. pitymi*; 48–169×23–70 in *H. tualatinensis*). Furthermore, the cirrus sac of *H. folkertsii* rarely overlaps and does not cross the ventral longitudinal canal and the external seminal vesicle is distinctly smaller than the seminal receptacle. In contrast, the cirrus sac of *H. pitymi* and *H. tualatinensis* substantially crosses the poral osmoregulatory canals and the external seminal vesicle is almost equal in length relative to the seminal receptacle.

Additionally, in the Nearctic, *Hymenolepis robertrauschi* Gardner et al. 2014 also superficially resembles *H. folkertsii* in having testes disposed in a triangle but lacks a rostrum-like protrusion on the scolex. The former species was described in grasshopper mice (species of *Onychomys* Baird, 1858) from Nebraska and New Mexico, a cricetid (Neotominae) considered to be phylogenetically close to *Peromyscus* (e.g., Musser and Carleton 2005; Gardner et al. 2014). Consequently, we consider that it is necessary to distinguish these two congeners. *H. folkertsii* can be differentiated from *H. robertrauschi* by a smaller scolex (168 versus 199–257) and suckers (93–102×70–86 versus 119–164×82–95), shorter cirrus sac (138–154, mean 145 versus 147–233, mean 193), cirrus spination (length of spines less than 1 versus 1.3), and a larger seminal

receptacle (275–365×37–62 versus 190–246×45–121). Furthermore, the external seminal vesicle in *H. folkertsi* is distinctly smaller than the seminal receptacle, whereas these structures are almost equal in length in specimens of *H. robertrauschi* (see Gardner et al. 2014).

A representative series of voucher specimens of hymenolepidid cestodes from prior studies of *Peromyscus* spp. were not available for comparison, and strobilate cestodes were apparently not deposited following many surveys involving this assemblage of rodent species across North America (e.g., Erickson 1938; Hansen 1950; Grundmann and Frandsen 1960; Babero and Matthias 1967; Vaughn 2013). Access to new comparative materials for concurrent or integrated morphological/molecular analyses is essential to enhance our ability to more completely document parasite faunal diversity among *Peromyscus* spp. and other rodents (e.g., Haukisalmi et al. 2010a; Makarikov et al. 2013a, b). Deposition of specimens from inventories is a basic foundation for characterization of faunal structure (e.g., Hoberg et al. 2009) and is increasingly necessary given the expanding recognition of cryptic diversity across many groups of parasites and hosts (Pérez-Ponce de León and Nadler 2010).

Discussion

H. folkertsi n. sp. is described based on specimens in the oldfield mouse collected from central Georgia. As such, these tapeworms represent the first species of *Hymenolepis* (s. str.) to be formally described from the large assemblage of *Peromyscus* species from North America. Discovery and characterization of these cestodes afford the opportunity to discuss some anatomical characters typical among species of *Hymenolepis* (s. str.). Further, we explore our current understanding of hymenolepidid faunas documented among *Peromyscus* relative to patterns of host biogeography and diversity in North America.

Scolex anatomy and function

The rostellar hooks and rostellum are secondarily reduced among species of *Hymenolepis* (s. str.). However, the rudimentary rostellar apparatus is conserved. A uniform anatomy of the rostellar apparatus can be recognized among all known species of the genus, consisting of an unarmed rhynchus invaginated in the muscular-walled rostellar pouch (Makarikov and Tkach 2013). Thus, we consider that the apical organ of *Hymenolepis* species described in some publications as a rostellum is homologous with the rostellar pouch (Yarinsky 1952; Singh 1956; Arai 1980; Mas-Coma and Tenora 1997). This hypothesis is further supported by the observation that among mammalian hymenolepidids, the osmoregulatory

canals penetrate through the walls of the rostellar pouch rather than into the rostellum.

The microanatomic structure and functional significance of a rudimentary rostellar apparatus were well studied in the type species, *H. diminuta*. Wardle and McLeod (1952) postulated that the unarmed rostellum may serve as an apical sucker, helping in fixation to the host intestine. Such an assumption, however, was not supported due to the poor muscular development of the rudimentary rostellar apparatus in *H. diminuta* (Specian and Lumsden 1980). The presence of numerous sensilla in the tegument of the apical organ of *H. diminuta* suggested a sensory function (Specian and Lumsden 1980). In addition, glandular cells or tissue in the rostellar pouch indicates an excretory/secretory role for this organ. Secretions are released from the apex of the apical invagination (rhynchus) at the mucosal interface in the host intestine, although the function for materials secreted from the gland cells remains uncertain (Specian and Lumsden 1980, 1981). Secretory activity associated with the glands of the rostellar pouch may be involved in avoidance of host immune responses targeted toward tapeworms localized in the mucosa, though this requires further study (Pospekhova 2009).

The function of a modified and rudimentary rostellar apparatus of *H. folkertsi* (i.e., appearance of rostrum-like protrusion), and other species where this structure has been documented, remains to be determined. We suggest that the particular shape of the scolex may facilitate penetration into spaces among the intestinal villi leading to better adhesion and maintenance of position in the host intestinal tract. This would not exclude the possibility that the rostrum-like protrusion has a sensory function or that it could serve a role in release of cellular secretions.

Phylogeny

Spassky (1992) considered hymenolepidids with an unarmed scolex parasitizing mammalian hosts to be paraphyletic. Recent molecular phylogenetic studies (Haukisalmi et al. 2010a; Greiman and Tkach 2012) have corroborated this hypothesis and have demonstrated that the loss of the rostellum, or the rostellar armature, has occurred in several independent lineages of hymenolepidids among mammals. For example, this is exemplified by species of the *Arostrilepis horrida* complex (syn.: *Hymenolepis horrida*), which are not closely related to *Hymenolepis* (Haukisalmi et al. 2010a), yet they lack a rostellum.

Following numerous revisions, the genus *Hymenolepis* (s. str.) currently represents a morphologically homogenous and probably monophyletic group (see the generic diagnosis of *Hymenolepis* (s. str.) sensu Makarikov and Tkach 2013). However, the taxonomic significance of some morphological characters in this genus is not fully determined. Gulyaev and Mel'nikova (2005) considered differences in the cirrus sac

wall structure (absence or presence of distinct muscular walls of the cirrus sac) and relative position of dorsal and ventral osmoregulatory canals to be characters of generic level in this group. For example, there are four species of *Hymenolepis* in murid rodents from the Philippines, each of which have a unique relative positioning of the dorsal and ventral osmoregulatory canals and a cirrus sac wall with different thickness. If one accepts the generic-level characters proposed by Gulyaev and Mel'nikova (2005), all four species from the Philippines should be placed in four new genera because each of them has a unique combination of these features (Makarikov et al. 2013b, 2015). However, due to the lack of detailed phylogenetic studies within this lineage of mammalian hymenolepidids, we refrain from further generic splitting of the *Hymenolepis*. Future phylogenetic studies incorporating a greater number of *Hymenolepis* species from different hosts will allow us to better understand the evolution of this globally distributed lineage of hymenolepidid cestodes and to reevaluate the morphological characters currently used in their systematic arrangement (Tkach et al. unpublished observation).

Hymenolepidid diversity among rodents

Hymenolepidids among rodents constitute an assemblage of genera and species (e.g., Ryzhikov et al. 1978) that occur across all continents except Antarctica and are broadly but unevenly represented among cricetids, geomyids, heteromyids, murids, sciurids, spalacids, glirids, and dipodids. Diversity of *Hymenolepis* (*s. str.*) among rodent hosts including *H. folkertsii* now includes about 19 species. These cestodes are globally distributed as parasites in at least five families of Rodentia (i.e., Muridae, Geomyidae, Sciuridae, Cricetidae, and Spalacidae) (Gardner and Schmidt 1988; Makarikov and Tkach 2013; Makarikov et al. 2013b; Gardner et al. 2014; Makarikov et al. 2015). Geographic and host distribution suggests that diversification among species of *Hymenolepis* has been linked to colonization of unrelated taxa of Muroidea and other Rodentia during the process of host radiation. Furthermore, ecological similarity of some rodents, chiropterans, and soricomorphs is consistent with the possibility of mutual exchanges of these helminths between phylogenetically distinct groups of small mammals, supporting current ideas about the importance of host switching and ecological fitting in diversification of complex faunas (e.g., Hoberg and Brooks 2008; Agosta et al. 2010; Brooks et al. 2014).

The diversity (56 species in the Nearctic; Musser and Carleton 2005), ecological distinctiveness (Nowak 1999), and deep phylogenetic distance (Steppan et al. 2004) between *Peromyscus* and other rodent genera suggest that these rodents could have a deep association with a unique cestode fauna. However, hymenolepidid cestodes have only sporadically been reported from *Peromyscus*, and those that are most often documented from these mice tend to be widespread species of

tapeworms, including some with obvious cosmopolitan distributions due to anthropogenic or natural introduction and invasion (i.e., *H. citelli*, *H. diminuta*, *A. horrida* (*s. l.*), and *R. nana*). In contrast, only five species of tapeworms have been described as specific parasites of deer mice, associated with *Pe. boylii*, *Pe. leucopus*, and *Pe. maniculatus* (i.e., *H. peromysci*, *H. bennetti*, *A. mariettavogae*, *Choanotaenia peromysci* (Erickson 1938) (syn.: *Prochoanotaenia peromysci* Erickson, 1938), and *C. peromysci* Smith, 1954). Such a small number of apparently host-specific and phylogenetically disparate cestodes in *Peromyscus* species may indicate relatively recent assembly of tapeworm faunas in these Nearctic rodents. These faunas contrast with the diverse hymenolepidids, anoplocephalids, and catenotaeniids among Arvicolinae, Neotominae, and other rodents across the Holarctic region (e.g., Haukisalmi et al. 2010b; Makarikov et al. 2013a; Haukisalmi et al. 2014). Conversely, our initial impression of a depauperate cestode fauna may reflect limited study of host species. We assume that a more comprehensive survey and inventory of the intestinal helminths among species of *Peromyscus* and a diverse assemblage of other temperate latitude rodents in the Nearctic will result in the discovery of additional previously unknown cestodes. Such a survey must be both geographically widespread and site intensive to ensure that parasite diversity is thoroughly documented. In the current study, only one of 30 *Pe. polionotus* was infected with specimens of *H. folkertsii*. Such low prevalence highlights the need for sampling efforts to be extensive.

Although the host genus has a relatively deep history and is endemic to the Nearctic, current evidence suggests that tapeworm faunal diversity reflects relatively recent bouts of host switching from sympatric geomyid, murine, neotomine, and arvicoline rodents, rather than deep ancestral host-parasite associations. Among Muroidea, rodents unequivocally recognized as *Peromyscus* appear in North America during the Miocene, with some extant species present by the Pleistocene (Kurtén and Anderson 1980; Musser and Carleton 2005). Extensive diversification among species of *Peromyscus* occurred over the past 2 million years under episodes of habitat fragmentation linked to glacial-interglacial cycles and shifting climate during the Quaternary (e.g., Avise et al. 1983; Dragoo et al. 2006). The late Pliocene and Quaternary also coincided with considerable development and diversification of rodent faunas with temporally circumscribed episodes of expansion out of Eurasia into North America (Repenning 2001; Hope et al. 2013). Episodic faunal mixing, cyclic isolation, and expansion may be reflected in the overall diversity of cestode faunas, assembled from multiple and disparate sources, and in the relatively depauperate and heterogeneous distributions that are now observed for hymenolepidids and other taxa among species of *Peromyscus*.

Faunal assembly involving temporal and geographic mosaics related to recurrent events of geographic expansion and

contact among potential host groups and host switching appear to be important drivers in establishing regional assemblages of cestodes among rodents (e.g., Haukisalmi et al. 2010b; Hoberg et al. 2012; Makarikov et al. 2012). For example, among hymenolepidids, the genus *Arostrilepis* appears to be the sister of tapeworms among Soricomorpha with origins then attributable to host colonization of Arvicolinae (e.g., Haukisalmi et al. 2010a); subsequent diversification reflects episodes of host colonization among geomyid and neotomine rodents (e.g., Makarikov et al. 2012; Hoberg et al. 2012). Considering *H. folkertsi*, morphological similarity among Nearctic species is observed for *H. tualatinensis* in a geomyid from central Oregon, *H. pitymi* in an arvicoline from Tennessee, and *H. robertrauschi* in species of *Onychomys* a related neotomine, and putative sister of *Peromyscus*, across west-central North America from southern Canada to northern Mexico. Extensive sampling and inventory of rodent faunas and a phylogenetic context for cestodes will contribute to evaluation of hypotheses for intricate histories of host and parasite association and regional faunal development over time.

Acknowledgments We thank Dr. Jean Mariaux (Natural History Museum, Geneva, Switzerland), Dr. Patricia Pilitt (US National Parasite Collection, Beltsville, MD, USA), and Dr. Scott L. Gardner (Harold W. Manter Laboratory of Parasitology, Lincoln, NE, USA), for specimen loans and/or providing conditions and laboratory space for examination of the type and voucher specimens. We thank Dr. Oscar Pung (Georgia Southern University (GSU), Statesboro, GA, USA) for his assistance with the mouse dissections. We thank The Nature Conservancy in Georgia for allowing access to their managed lands. We are grateful for access to the Arctos database through the Museum of Southwestern Biology, University of New Mexico, and a summary of inventory for parasites in species of *Peromyscus* prepared by Mariel Campbell. We sincerely thank Dr. Scott L. Gardner and an anonymous reviewer for their detailed comments that improved our manuscript. Research by AAM was supported in part by the Russian Fund for Fundamental Research (Project No. 14-04-00871-a). Further support for AAM was provided by the National Science Foundation (DEB 0819696 and 0818823) through grants addressing cestode diversity coordinated by Dr. Janine Caira, University of Connecticut. This is also a contribution to understanding history and diversity of mammalian helminth faunas supported by NSF through the Beringian Coevolution Project (DEB 0196095 and 0415668) and the Integrated Inventory of Biomes of the Arctic (DEB-Biodiversity Discovery and Analysis-1258010) to J.A. Cook (University of New Mexico), EPH, and KEG. Portions of this study were approved by the Institutional Animal Care and Use Committee (IACUC) at Georgia Southern University, permitted by the Georgia Department of Natural Resources, and done in partial completion of a Master of Science in Biology at GSU by TNN.

References

- Agosta SJ, Janz N, Brooks DR (2010) How generalists can be specialists: resolving the “parasite paradox” and implications for emerging infectious disease. *Zoologia* 27:151–162
- American Society of Mammalogists (1998) Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *J Mammal* 79:1416–1431
- Arai H (1980) Biology of the Tapeworm *Hymenolepis diminuta*. New York Academic Press, New York
- Avise JC, Shapira JF, Daniel SW, Aquadro CF, Lansman RA (1983) Mitochondrial DNA differentiation during the speciation process in *Peromyscus*. *Mol Biol Evol* 1:38–56
- Babero BB, Matthias D (1967) *Protospirura peromysci* n. sp. (Nematoda: Spiruridea) and other helminths from *Peromyscus* spp. in Nevada. *Proc Helminthol Soc Wash* 34:255–261
- Barker CM, Dyer WG, Feldhamer GA (1987) Helminths of *Peromyscus leucopus*, *P. maniculatus* and *Blarina carolinensis* from southern Illinois. *Trans Ill Acad Sci* 80:119–127
- Binkienė R, Kontrimavichus V, Hoberg EP (2011) Overview of the cestode fauna of European shrews of the genus *Sorex* with comments on the fauna in *Neomys* and *Crociodura* and an exploration of historical processes in post-glacial Europe. *Helminthologia* 48:207–228. doi:10.2478/s11687-011-0031-5
- Brooks DR, Hoberg EP, Boeger WA, Gardner SL, Galbreath KE, Herczeg D, Mejía-Madrid HH, Rácz SE, Dursahinhan AT (2014) Finding them before they find us: informatics, parasites, and environments in accelerating climate change. *Comp Parasitol* 81:155–164. doi:10.1654/4724b.1
- Doran DJ (1954) A catalogue of the Protozoa and helminths of North American rodents. II. Cestoda. *Am Midl Nat* 52:469–480
- Dragoo JW, Lackey JA, Moore KE, Lessa EP, Cook JA, Yates TL (2006) Phylogeography of the deer mouse (*Peromyscus maniculatus*) provides a predictive framework for research on hantaviruses. *J Gen Virol* 87:1997–2003. doi:10.1099/vir.0.81576-0
- Dyer WG (1969) A checklist of the Protozoa and helminths of the deer mouse *Peromyscus maniculatus* in North America. *Am Midl Nat* 81:258–262
- Erickson AB (1938) Parasites of some Minnesota Cricetidae and Zapodidae, and a host catalogue of helminth parasites of native American mice. *Am Midl Nat* 20:575–589
- Freeman RS (1960) Another hymenolepidid with great morphological variation, *Hymenolepis bennetti* n. sp. (Cestoda) from *Napaeozapus insignis algonquinensis* Prince. *Can J Zool* 38:737–743
- Gardner SL (1985) Helminth parasites of *Thomomys bulbivorus* (Richardson) (Rodentia: Geomyidae), with the description of a new species of *Hymenolepis* (Cestoda). *Can J Zool* 63:1463–1469
- Gardner SL, Schmidt GD (1988) Cestodes of the genus *Hymenolepis* Weinland, 1858 sensu stricto from pocket gophers *Geomys* and *Thomomys* spp. (Rodentia: Geomyidae) in Colorado and Oregon, with a discriminant analysis of four species of *Hymenolepis*. *Can J Zool* 66:896–903
- Gardner SL, Luedders BA, Duszynski DW (2014) *Hymenolepis robertrauschi* n. sp. from grasshopper mice *Onychomys* spp. in New Mexico and Nebraska, U.S.A. *Occas Pap Mus Texas Tech Univ* 322:1–10
- Greiman SE, Tkach VV (2012) Description and phylogenetic relationships of *Rodentolepis gnoskei* n. sp. (Cyclophyllidae: Hymenolepididae) from a shrew *Suncus varilla minor* in Malawi. *Parasitol Int* 61:343–350
- Grundmann AW, Frandsen JC (1960) Definitive host relationships of the helminth parasites of the deer mouse, *Peromyscus maniculatus*, in the Bonneville Basin of Utah. *J Parasitol* 46:673–677
- Gulyaev VD, Mel’nikova YA (2005) New genus of Cestoda from moles *Talpolepis* gen. n. and the redescription of *T. peipingensis* (Hsü, 1935) comb. n. (Cyclophyllidae: Hymenolepididae). *Probl Cestodol* 3:130–139 (In Russian)
- Hansen MF (1950) A new dilepidid tapeworm and notes on other tapeworms of rodents. *Am Midl Nat* 43:471–479
- Haukisalmi V, Wickström LM, Henttonen H, Hantula J, Gubányi A (2004) Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Cestoda, Anoplocephalidae)

- in *Microtus* voles (Arvicolinae). Zool Scr 33:277–290. doi:[10.1111/j.0300-3256.2004.00148.x](https://doi.org/10.1111/j.0300-3256.2004.00148.x)
- Haukisalml V, Hardman LM, Foronda P, Feliu C, Laakonen J, Niemimaa J, Lehtonen JT, Henttonen H (2010a) Systematic relationships of hymenolepidid cestodes of rodents and shrews inferred from sequences of 28S ribosomal RNA. Zool Scr 39:631–641. doi:[10.1111/j.1463-6409.2010.00444.x](https://doi.org/10.1111/j.1463-6409.2010.00444.x)
- Haukisalml V, Hardman LM, Henttonen H (2010b) Taxonomic review of the genus *Catenotaenia* Janicki, 1904 in Eurasia and molecular phylogeny of the Catenotaeniidae (Cyclophyllidae). Zootaxa 2489:1–33
- Haukisalml V, Hardman LM, Hoberg EP, Henttonen H (2014) Phylogenetic relationships and taxonomic revision of *Paranoplocephala* Lühe, 1910 sensu lato (Cestoda, Cyclophyllidae, Anoplocephalidae). Zootaxa 3873:371–415. doi:[10.11646/zootaxa.3873.4.3](https://doi.org/10.11646/zootaxa.3873.4.3)
- Hoberg EP, Brooks DR (2008) A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host-parasite systems. J Biogeogr 35:1533–1550. doi:[10.1111/j.1365-2699.2008.01951.x](https://doi.org/10.1111/j.1365-2699.2008.01951.x)
- Hoberg EP, Pilitt PA, Galbreath KE (2009) Why museums matter: a tale of pinworms (Oxyuroidea: Heteroxynematidae) among pikas (*Ochotona princeps* and *O. collaris*) in the American west. J Parasitol 95:490–501. doi:[10.1645/GE-1823.1](https://doi.org/10.1645/GE-1823.1)
- Hoberg EP, Galbreath KE, Cook JA, Kutz SJ, Polley L (2012) Northern host-parasite assemblages: history and biogeography on the borders of episodic climate and environmental transition. Adv Parasitol 79:1–97. doi:[10.1016/B978-0-12-398457-9.00001-9](https://doi.org/10.1016/B978-0-12-398457-9.00001-9)
- Hope AG, Takebayashi N, Galbreath KE, Talbot SL, Cook JA (2013) Temporal, spatial and ecological dynamics of speciation among amphi-Beringian small mammals. J Biogeogr 40:415–429. doi:[10.1111/jbi.12056](https://doi.org/10.1111/jbi.12056)
- Kinsella JM (1991) Comparison of helminths of three species of mice, *Peromyscus floridanus*, *Peromyscus gossypinus*, and *Peromyscus polionotus*, from southern Florida. Can J Zool 69:3078–3083
- Kruidenier FJ, Gallicchio V (1956) A survey of cestodes in mammals from Grand Canyon National Park. J Parasitol 42:42
- Kurtén B, Anderson E (1980) Pleistocene mammals of North America. Columbia University Press, New York
- Layne JN (1963) A study of the parasites of the Florida mouse, *Peromyscus floridanus*, in relation to host and environmental factors. Tulane Stud Zool 11:1–27
- Leiby PD (1961) Intestinal helminths of some Colorado mammals. J Parasitol 47:311
- Leiby PD (1962) Helminth parasites recovered from some rodents in southeastern Idaho. Am Midl Nat 67:250
- Lubinsky G (1957) List of helminths from Alberta rodents. Can J Zool 35:623–627
- Makarikov AA, Tkach VV (2013) Two new species of *Hymenolepis* (Cestoda: Hymenolepididae) from Spalacidae and Muridae (Rodentia) from eastern Palearctic. Acta Parasitol 58:37–49. doi:[10.2478/s11686-013-0115-0](https://doi.org/10.2478/s11686-013-0115-0)
- Makarikov AA, Gardner SL, Hoberg EP (2012) New species of *Arotrilepis* (Eucestoda: Hymenolepididae) in members of Cricetidae and Geomyidae (Rodentia) from the Western Nearctic. J Parasitol 98:617–626. doi:[10.1645/GE-2943.1](https://doi.org/10.1645/GE-2943.1)
- Makarikov AA, Galbreath KE, Hoberg EP (2013a) Parasite diversity at the Holarctic nexus: species of *Arotrilepis* (Eucestoda: Hymenolepididae) in voles and lemmings (Cricetidae: Arvicolinae) from greater Beringia. Zootaxa 3608:401–439. doi:[10.11646/zootaxa.3608.6.1](https://doi.org/10.11646/zootaxa.3608.6.1)
- Makarikov AA, Tkach VV, Bush SE (2013b) Two new species of *Hymenolepis* (Cestoda: Hymenolepididae) from murid rodents (Rodentia: Muridae) in the Philippines. J Parasitol 99:847–855. doi:[10.1645/12-173.1](https://doi.org/10.1645/12-173.1)
- Makarikov AA, Tkach VV, Villa SM, Bush SE (2015) Description of two new species of *Hymenolepis* Weinland, 1858 (Cestoda: Hymenolepididae) from rodents on Luzon Island, Philippines. Syst Parasitol 90:27–37. doi:[10.1007/s11230-014-9528-x](https://doi.org/10.1007/s11230-014-9528-x)
- Mas-Coma S, Tenora F (1997) Proposal of *Arotrilepis* n. gen. (Cestoda: Hymenolepididae). Res Rev Parasitol 57:93–101
- Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE (ed) Reeder DM (eds) mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, pp 894–1531
- Nims TN, Durden LA, Chandler CR, Pung OJ (2008) Parasitic and phoretic arthropods of the oldfield mouse (*Peromyscus polionotus*) from burned habitats with additional ectoparasite records from the eastern harvest mouse (*Reithrodontomys humulis*) and southern short-tailed shrew (*Blarina carolinensis*). Comp Parasitol 75:102–106. doi:[10.1654/4273.1](https://doi.org/10.1654/4273.1)
- Nowak RM (1999) Walker's mammals of the world, vol 2. The Johns Hopkins University Press, Baltimore
- Pérez-Ponce de León G, Nadler SL (2010) What we don't recognize can hurt us: a plea for awareness about cryptic species. J Parasitol 96:453–464. doi:[10.1645/GE-2260.1](https://doi.org/10.1645/GE-2260.1)
- Pospekhova NA (2009) Rostellar sac gland in *Cloacotaenia megalops* (Cestoda: Hymenolepididae). Invertebr Zool 6:33–46 (In Russian)
- Pung OJ, Durden LA, Patrick MJ, Conyers T, Mitchell LR (2000) Ectoparasites and gastrointestinal helminths of southern flying squirrels in southeast Georgia. J Parasitol 86:1051–1055. doi:[10.1645/0022-3395\(2000\)086\[1051:EAGHOS\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2000)086[1051:EAGHOS]2.0.CO;2)
- Rausch RL, Tiner JD (1949) Studies on the parasitic helminths of the north-central states. II. Helminths of voles (*Microtus* spp.) preliminary report. Am Midl Nat 41:665–694
- Repenning CA (2001) Beringian climate during intercontinental dispersal: a mouse eye view. Quat Sci Rev 20:25–40
- Ryzhikov KM, Gvozdev EV, Tokobaev MM, Shaldybin LS, Matzaberidze GV, Merkusheva IV, Nadtochii EV, Khohlova IG, Sharpilo LD (1978) Keys to the helminths of the rodent fauna of the USSR. Cestodes and trematodes. Izdatel'stvo Nauka, Moskva, 232 pp. (In Russian)
- Schad GA (1954) Helminth parasites of mice in northeastern Quebec and the coast of Labrador. Can J Zool 32:215–224
- Schiller EL (1952) Studies on the helminth fauna of Alaska. X. Morphological variation in *Hymenolepis horrida* (von Linstow, 1901) (Cestoda: Hymenolepididae). J Parasitol 38:554–568. doi:[10.2307/3273983](https://doi.org/10.2307/3273983)
- Singh KS (1956) *Hymenolepis vogeae* n. sp., from an Indian Field Mouse, *Mus buduga* Thomas, 1881. Trans Am Microsc Soc 75:252–255. <http://www.jstor.org/stable/3224018>
- Smith CF (1954) Four new species of cestodes of rodents from the high plains, central and southern Rockies and notes on *Catenotaenia dendritica*. J Parasitol 40:245–254
- Spassky AA (1963) Hymenolepidid cestodes—tapeworms of wild and domestic birds, vol 2. Izdatel'stvo Akademii Nauk SSSR, Moscow, 418 pp. (In Russian)
- Spassky AA (1992) To the phylogeny and systematics of hymenolepidoid tapeworms (Cestoda: Cyclophyllidae). Buletinul Academiei de Stiinta Republicii Moldova, Stiinte Biologice si Chimice 6:41–47 (In Russian)
- Spassky AA, Spasskaja LP (1954) Systematics of Hymenolepididae parasitizing birds. Trudy Gel'mintologicheskoy Laboratorii Akademii Nauk SSSR 7:55–119, In Russian
- Specian RD, Lumsden RD (1980) The microanatomy and fine structure of the rostellum of *Hymenolepis diminuta*. Z Parasitenkd 63:71–88. doi:[10.1007/bf00927728](https://doi.org/10.1007/bf00927728)
- Specian RD, Lumsden RD (1981) Histochemical, cytochemical and autoradiographic studies on the rostellum of *Hymenolepis diminuta*. Z Parasitenkd 64:335–345. doi:[10.1007/BF00927380](https://doi.org/10.1007/BF00927380)
- Steppan SJ, Adkins RM, Anderson J (2004) Phylogeny and divergence-date estimates of rapid radiations in muroid rodents

- based on multiple nuclear genes. Syst Biol 53:533–553. doi:[10.2307/4135423](https://doi.org/10.2307/4135423)
- Tinkle DP (1972) Description and natural intermediate hosts of *Hymenolepis peromysci* n. sp., a new cestode from deer mice (*Peromyscus*). Trans Am Microsc Soc 91:66–69, <http://www.jstor.org/stable/3224860>
- Vaughn JW (2013) Parasite fauna of 3 sympatric Montana rodents. Unpublished Masters of Science Thesis, Western Illinois University, pp 1–23
- Voge M (1952) Variation in some unarmed Hymenolepididae (Cestoda) from rodents. Univ Calif Publ Zool 57:1–52
- Whitaker JO, Jr (1968) Parasites. In: King JA (ed) Biology of *Peromyscus* (Rodentia). Special Publication American Society of Mammalogy, No. 2, pp 254–311
- Whitaker JO Jr, Hamilton WJ Jr (1998) Mammals of the Eastern United States. Cornell University Press, Ithaca, 583 pp
- Wilson DE, Reeder DM (2005) Mammal species of the world a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore
- Yarinsky A (1952) *Hymenolepis pitymi* n. sp., a hymenolepidid cestode from the pine mouse. J Tenn Acad Sci 27:150–152