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A New Species of *Catenotaenia* (Cestoda: Catenotaeniidae) from *Pygeretmus pumilio* Kerr, 1792 from the Gobi of Mongolia

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ABSTRACT: From 1999 through 2012, a total of 541 individual rodents (jerboas of the family Dipodidae) were collected from several habitat types, primarily from the Gobi region of Mongolia, and were examined for helminth and protistan parasites. Of those rodents, 25 were identified as *Pygeretmus pumilio* Kerr, 1792 (Rodentia: Dipodidae), whereas 516 were other species of jerboa from the provinces of Dornogobi, Dundgobi, Omnogobi, Ovorhangai, Bayanhongor, Gobi Altai, and Hovd. During our field work, we collected several cestodes; some of which represented undescribed species, and these new species occurred in 40% of *P. pumilio* from four separate collecting localities. We designate this new species as *Catenotaenia tuyae* n. sp. (Cyclophyllidea: Catenotaeniidae), which is characterized by having relatively long and narrow gravid proglottids and an ovary in mature segments that is located antiporally in the anterior portion of the mature proglottids. In addition, the position and the ratio of the genital pore toward the anterior end of the proglottids are unique and the ovary is elongate, being confined to the antiporal part of the mature proglottid. These morphological features serve to differentiate *Catenotaenia tuyae* from all other species in the genus included in the phylogenetic analysis and are supported by molecular phylogenetic evidence using the 28S ribosomal RNA gene. The intensity of *C. tuyae* infection in *Pygeretmus* ranged from 1 to 3 individual cestodes per infected host.

KEY WORDS: *Catenotaenia*, Catenotaeniidae, jerboa, Dipodidae, Gobi, *Pygeretmus*, Mongolia, taxonomy, parsimony, phylogeny.

Rodents of the family Dipodidae Fischer de Waldheim, 1817 have a mostly Holarctic distribution with only 4 extant species known from the Nearctic region, including 1 species of *Napaeozapus* Preble 1899 and 3 species of *Zapus* Coues 1875 (see Holden and Musser, 2005). In the Palearctic region, dipodids have substantial diversity, with about 46 species known. Most species of dipodids known from the Old World are adapted to more-xeric habitats, with geographic distributions extending from eastern Mongolia, west and south through central Asia and eastern Europe, into northern Africa (Holden and Musser, 2005).

The parasites of dwarf fat-tailed jerboas of the genus *Pygeretmus* Gloger, 1841 (Rodentia: Dipodidae) have been poorly studied. From 1999 to 2012, our field teams conducted a biodiversity survey of vertebrates in southern and southwestern Mongolia (Fig. 1). This expeditionary research was conducted as the Mongolian Vertebrate Parasite Project (MVPP). During this work, 541 individuals of the family Dipodidae were collected and examined for parasites; from that collection, 25 individuals of *Pygeretmus pumilio* Kerr, 1792 (Fig. 2), were obtained and examined for parasites in the field. The overall goal of this project was to discover, describe, and document the distribution of vertebrates and their parasites, with a focus on the south-central and southwestern areas of the Gobi desert and eastern Altai Mountains (Tinnin et al., 2008). The current article presents the results of a review of the cestodes of the species of *Pygeretmus* collected during the MVPP.

In the genus *Catenotaenia* Janicki, 1904 (Cyclophyllidea: Catenotaeniidae), 19 species have been described from 22 species of rodents from both Palearctic and Nearctic regions (Haukisalmi et al., 2010) (Table 1). Tinnin et al. (2011) summarized the data on these cestodes from central Asia and Mongolia; 7 species of *Catenotaenia* have been recorded from 17 species of rodents from, in, and around the geopolitical boundaries of Mongolia (Table 2) including: *Catenotaenia afghana* Tenora, 1977, *Catenotaenia asiatica* Tenora and Murai, 1975, *Catenotaenia cricetorum* Kirschenblatt, 1949, *Catenotaenia dendritica* Goeze, 1782, *Catenotaenia henttoneni* Haukisalmi and Tenora, 1993, *Catenotaenia pusilla* Goeze, 1782,

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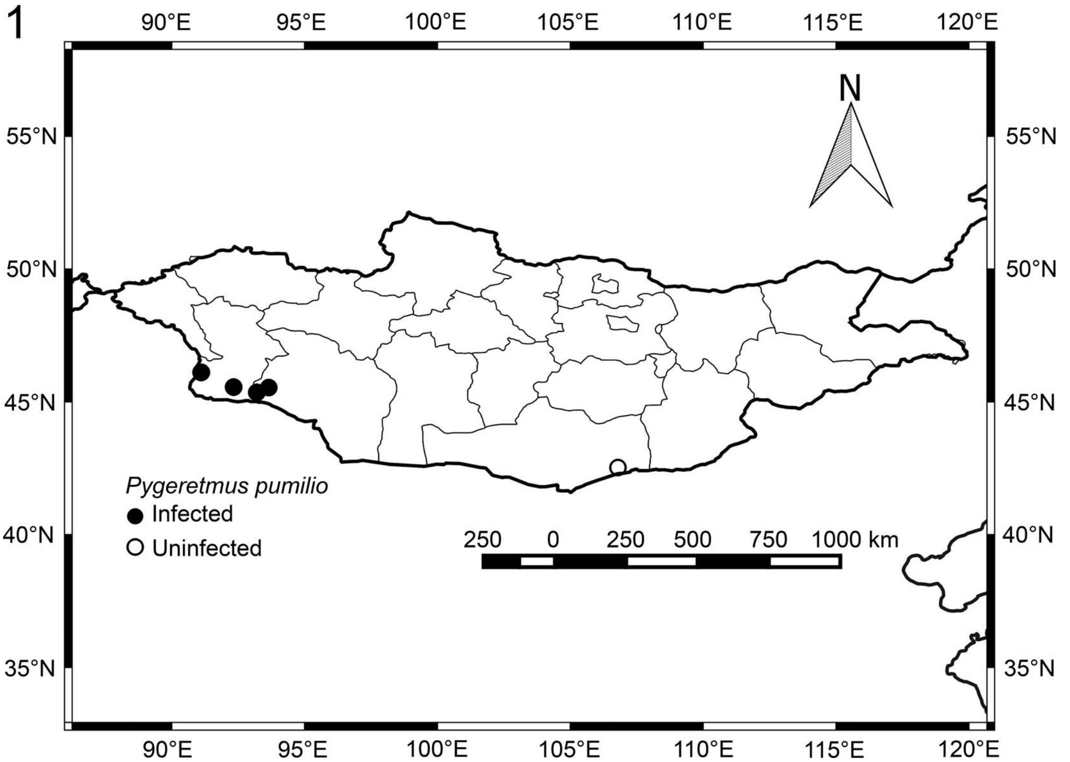
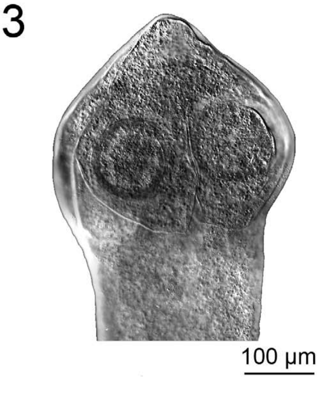


Figure 1. Map of Mongolia with localities indicated from which individuals of *Pygeretmus pumilio* (Kerr, 1792) were collected during the years of expeditionary field work by the Mongolian Vertebrate Parasite Project (1999 –2012).

and *Catenotaenia rhombomidis* Schulz and Landa, 1934. The most recent taxonomic review of species in the genus *Catenotaenia* was published by Haukisalmi et al. (2010).

From the vicinity of the Karakum Canal in Turkmenistan (approximately 41°07′26″N; 60°36′24″E), 2 species of dipodids were shown to be infected with *C. cricetorum*, including *Allactaga elater* Lichtenstein, 1825 and *Alactagulus acontion* Pallas, 1811 (syn. *Pygeretmus pumilio* (Kerr, 1792)). This finding was the first reported record of a species of *Catenotaenia* from a dipodid (Babaev, 1976).



Figures 2, 3. Photographs of host and tapeworm. **2**. Image of *Pygeretmus pumilio* (Kerr, 1792) from southwestern Mongolia. **3**. Scolex of *Catenotaenia tuyae* n. sp. showing suckers and well developed apical organ.

Table 1. Known species of *Catenotaenia* Janicki, 1904, with type hosts and geographic distributions. All altitudes reported as meters above sea level.

Catenotaenia sp.	Host species	Collection localities	Coordinates
C. afghana Tenora, 1977	*Alticola roylei* (Gray,1842)	Unai, Salang, Afghanistan	34°45′N, 68°37′E, 3,283 m.
	Cricetulus migratorius (Pallas, 1773)	Unai, Salang, Afghanistan	34°45′N, 68°37′E, 3,283 m
C. apodemi Haukisalmi, Hardman and Henttonen, 2010	*Apodemus peninsulae* Thomas, 1907 *Apodemus uralensis* (Pallas, 1811)	Lower Tunguska River, North-Central Siberia, Republic of Buryata, Russia	51°57′N, 106°35′E, 920 m
C. asiatica Tenora and Murai, 1975	*Cricetulus barabensis* (Pallas, 1773)	Baruun Urt, Sukhbaatar Province, Mongolia	12°37′N, 47°18′E, 1,240 m
C. californica Dowell, 1953	*Dipodomys panamintinus* (Merriam, 1894)	Lovejoy Butte, California, U.S.A.	34°35′N, 117°51′W, 945 m
C. cricetorum Kirshenblat, 1949	*Mesocricetus brandti* (Nehring, 1898)	Armenia	locality not specified
	Alactagulus acontion (Pallas, 1811) (*syn Pygeretmus pumilio* (Kerr, 1792))	Turkmenistan	locality not specified
C. cricetuli Haukisalmi, Hardman and Henttonen, 2010	*Cricetulus barabensis* (Pallas, 1773)	Republic of Buryatia, Russia	51°30′N, 107°09′E, 909 m
C. dendritica Goeze, 1782	*Sciurus vulgaris* Linnaeus, 1758	Europe	locality not specified
C. gracilae Asakawa, Tenora, Kamiya, Harada and Borkovcova, 1992	*Myodes smithii* (Thomas, 1905)	Kami-kita-yama, Nara Prefecture, Japan	34°81′N, 135°59′E, 453 m
C. henttoneni Haukisalmi and Tenora, 1993	*Myodes glareolus* (Schreber, 1780)	Lapland, Pallasjarvi, Finland	68°03′N, 24°09′E, 382 m
C. kullmanni Tenora, 1977	*Blanfordimys afghanus* (Thomas, 1912)	Unai, Afghanistan	34°27′N, 68°22′E, 3,200 m
	Calomyscus bailwardi Thomas, 1905	Unai, Afghanistan	34°27′N, 68°22′E, 3,200 m
C. laguri Smith, 1954	*Lemmiscus curtatus* (Cope, 1868)	33 miles S, 22 miles E, Rock Springs, Wyoming, U.S.A.	41°13′N, 108°46′W, 2,071 m
C. microti Haukisalmi, Hardman and Henttonen, 2010	*Microtus socialis* (Pallas, 1773)	Bakanas, Kazakhstan	44°80′N, 76°26′E, 397 m
C. linsdalei McIntosh, 1941	*Thomomys bottae* (Eydoux and Gervais, 1836)	Monterey, California, U.S.A.	36°22′N, 121°33′W, 471 m.
C. neotomae Babero and Cattan, 1983	*Neotoma lepida* Thomas, 1893	Clark county, Nevada, U.S.A.	36°47′N, 115°56′W, 584 m
C. peromysci Smith, 1954	*Peromyscus maniculatus* (Wagner, 1845)	Rio Arriba County, New Mexico, U.S.A.	36°36′N, 106°43′W, 2,194 m
C. pusilla Goeze, 1782	*Mus musculus* Linnaeus, 1758	Europe	locality not specified
C. reggiae Rausch, 1951	*Marmota caligata broweri* Hall and Gilmore, 1934	Tolugak Lake, Alaska, U.S.A.	68°24′N, 161°41′W, 133 m
C. rhombomidis Shulz and Landa, 1935	*Rhombomys opimus* (Lichtenstein, 1823)	Kazakhstan, Uzbekistan	locality not specified
C. ris Yamaguti, 1942	*Sciurus lis* Temminck, 1844	Kiso, Nagano Prefecture, Japan	35°50′N, 137°41′E, 811 m
C. tuyae n. sp.	*Pygeretmus pumilio*	Takhi Station, Bij Gol, Bugat Soum, Gobi Altai province, Mongolia	45°53′N, 93°65′W, 1,689 m

A broad-scale comparison of all cestode specimens collected during the course of the MVPP field expeditions revealed an undescribed species of *Catenotaenia* from *Pygeretmus pumilio*. This species is described herein.

MATERIALS AND METHODS

The material used for the following description was collected between August 2011 and July 2012. We include in the general numbers of specimens collected during the MVPP those specimens of mammals and parasites col-

Table 2. ***Catenotaenia* Janicki, 1904 infection host records in Central Asia (after Tinnin et al., 2011).**

Host species	Host family	*Catenotaenia* species
Apodemus agrarius (Pallas 1771) striped field mouse	Muridae	*Catenotaenia pusilla* (Goeze 1782)
Apodemus peninsulae (Thomas 1907) Korean field mouse	Muridae	*Catenotaenia pusilla* (Goeze 1782)
Clethrionomys (= *Myodes*) *rufocanus* (Sundevall 1846) gray red-backed vole	Cricetidae	*Catenotaenia sp.*
Clethrionomys (= *Myodes*) *rutilus* (Pallas 1779) northern red-backed vole	Cricetidae	*Catenotaenia cricetorum* (Kirschenblatt 1949) *Catenotaenia henttoneni* (Haukisalmi and Tenora 1993) *Catenotaenia pusilla* (Goeze 1782) *Catenotaenia sp.*
Cricetulus barabensis (Pallas 1773) striped dwarf hamster	Cricetidae	*Catenotaenia asiatica* (Tenora and Murai 1975) *Catenotaenia cricetorum* (Kirschenblatt 1949)
Cricetulus migratorius (Pallas 1773) gray hamster	Cricetidae	*Catenotaenia afghana* (Tenora 1977) *Catenotaenia cricetorum* (Kirschenblatt 1949) *Catenotaenia dendritica* (Goeze 1782)
Lasiopodomys brandtii (Radde 1861) Brandt's vole	Cricetidae	*Catenotaenia afghana* (Tenora 1977)
Meriones meridianus (Pallas 1773) mid-day gerbil	Muridae	*Catenotaenia pusilla* (Goeze 1782) *Catenotaenia rhombomidis* (Schulz and Landa 1934)
Microtus arvalis (Pallas 1778) common vole	Cricetidae	*Catenotaenia cricetorum* (Kirschenblatt 1949) *Catenotaenia pusilla* (Goeze 1782)
Microtus gregalis (Pallas 1779) narrow-headed vole	Cricetidae	*Catenotaenia pusilla* (Goeze 1782)
Mus musculus (Linnaeus 1758) house mouse	Muridae	*Catenotaenia cricetorum* (Kirschenblatt 1949) *Catenotaenia pusilla* (Goeze 1782)
Ochotona alpina (Pallas 1773) alpine pika	Ochotonidae	*Catenotaenia sp.*
Phodopus campbelli (Thomas 1905) Campbell's hamster	Cricetidae	*Catenotaenia sp.*
Rattus norvegicus (Berkenhout 1769) Norway rat	Muridae	*Catenotaenia pusilla* (Goeze 1782)
Rhombomys opimus (Lichtenstein 1832) great gerbil	Muridae	*Catenotaenia pusilla* (Goeze 1782) *Catenotaenia rhombomidis* (Schulz and Landa 1934)
Sciurus vulgaris (Linnaeus 1758) Eurasian red squirrel	Sciuridae	*Catenotaenia dendritica* (Goeze 1782)
Spermophilus undulatus (Pallas 1778) long-tailed ground squirrel	Sciuridae	*Catenotaenia cricetorum* (Kirschenblatt 1949)

lected during a brief trip by our team to central Mongolia in 1999; no specimens attributable to the new species were collected then. From western Mongolia, dwarf fat-tailed jerboas were captured from 4 different localities, including: Zuun Haats, Bulgan River Valley, Bulgan soum, Hovd province (46°6′39.88″N, 91°6′45.86″E); Takhi Station, Bij River, Dzungarian Gobi, Bugat soum, Gobi Altai province (45°32′19.21″N, 93°39′3.85″E); south of Yolhon Oasis, Altai soum, Gobi Altai province (45°33′19.59″N, 92°19′45.19″E); and north of Honin Us Spring, Dzungarian Gobi, Tonhil soum, Gobi Altai province (45°21′19.65″N, 93°12′14.22″E) (Fig. 1). A total of 25 *P. pumilio* were collected from these localities; all specimens of mammals referred to herein have been deposited in the Mammal Division, Museum of Southwestern Biology, Department of Biology, University of New Mexico (Albuquerque, New Mexico, U.S.A.).

Specimens of *P. pumilio* (Fig. 2) were either trapped using Sherman™ live-traps baited with peanut butter and oatmeal or caught at night by hand with insect nets using illumination provided by vehicle spotlights and personal headlamps. Mammals collected in the field were immediately killed with chloroform and examined for both ectoparasites and endoparasites (Gardner and Jiménez-Ruiz, 2009). With a dissecting microscope, the mucosal surface and the contents of each organ of the gastrointestinal tract were examined separately for the presence of helminths.

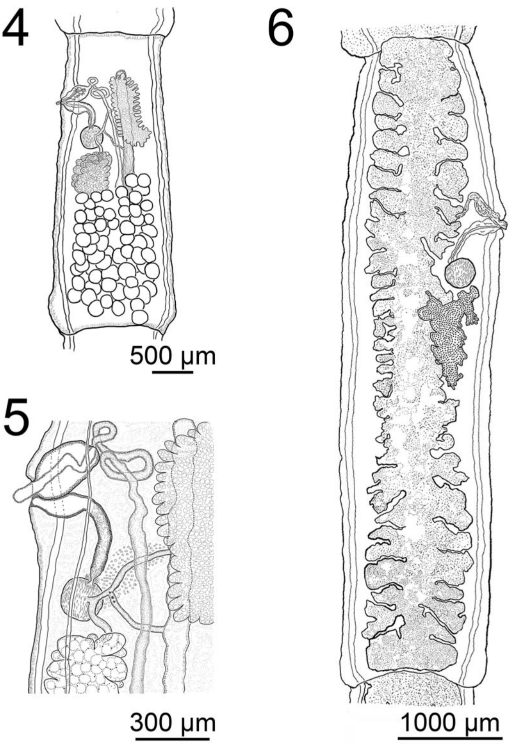
All cestodes recovered were transferred to distilled water for a minimum of 20 min to allow the strobilae to relax. They were subsequently killed and fixed in hot 10% (v/v) aqueous formalin solution in which it was stored until later study. A part of each individual specimen was removed before fixation and stored for molecular analysis as noted below. In the laboratory, specimens were stained with Semichon's acetic carmine, dehydrated in an ethanol series, cleared in terpineol and xylene, and mounted permanently on a microscope slide in Damar gum. For most of these specimens, the last gravid proglottid was either frozen in liquid nitrogen or preserved in 98% ethanol (in the field) and was subsequently frozen at −80°C in the Parasite Genomic Research Facility in the H.W. Manter Laboratory of Parasitology (University of Nebraska-Lincoln, Lincoln, Nebraska, U.S.A.) for future investigations using molecular approaches.

Measurements are given in micrometers unless otherwise indicated and are presented as range followed by mean ± SD and the number of structures examined (*N*). Measurements of organs in mature proglottids were taken from the last mature proglottid, which was the one immediately anterior to the first observed proglottid in which eggs begin to appear in the developing uterus. For measurements of the characteristics of eggs and testes only, $N =$ the average of 10 individual structures measured.

Molecular analysis: DNA was extracted from cestodes that were frozen (-80°C) using a standard phenol–chloroform protocol. Samples were subjected to polymerase chain reaction (PCR) using the primers LSU-forward (5′-TAG GTC GAC CCG CTG AAY TTY AGC A-3′) and 1200-reverse (5′-GCA TAG TTC ACC ATC TTT CGG-3′), which amplified approximately 1.5 kilobase (kb) of the 28S ribosomal (r)RNA gene (all citations and protocols follow that given in Haukisalmi et al., 2010). Samples were subjected to PCR under the following conditions: an initial denaturing step of 95°C for 3 min, followed by 30 cycles of 94°C for 30 sec, 53–55°C for 1 min, 72°C for 1 min, and a final elongation step of 72°C for 7 min. Crude PCR products were sent to Functional Biosciences, Inc. (Madison, Wisconsin, U.S.A.) for sequencing. The specimen with collection number NK224420 produced multiple bands that could not be eliminated by manipulation of the annealing temperature or salt concentrations; therefore, that sample was further processed using the QIAquick Gel Extraction Kit (Qiagen, Valencia, California, U.S.A.), following the manufacturer's protocol to isolate the band of the correct size for sequencing.

Phylogenetic analysis: An additional specimen of *Catenotaenia* (collected at the Bij River valley in the Dzungarian Gobi) was included in our analysis and is represented by specimen NK224347 (from *Dipus saggita* (Pallas, 1773)). Although that specimen could potentially represent an undescribed species, it is nevertheless closely associated on our tree with *Catenotaenia microti* Haukisalmi et al., 2010, with a genetic distance of 0.8%, with samples of *C. microti* reported from *Microtus socialis* (Pallas, 1773) from GenBank (National Center for Biotechnology Information, Bethesda, Maryland, U.S.A.; see Haukisalmi et al., 2010), indicating a relatively close genetic relationship (see genetic distance Table 3).

Comparative sequences from cestodes in the Catenotaeniidae were downloaded from GenBank (GU254039–GU254058), manually edited with the BioEdit Sequence Alignment Editor (Hall, 1999), and then, aligned with our sequences from Mongolia using multiple sequence comparison by log-expectation (MUSCLE) (Edgar, 2004). Aligned sequences representing samples of individual cestodes were analyzed under the criterion of maximum parsimony with the program TNT 1.1 (Willi Hennig Society Edition, New York, New York, U.S.A.; Goloboff et al., 2008). Bootstrap and symmetric resampling replicates indicated on the tree were based on 1,000 cycles of removals and additions. The consistency index (CI) and retention index (RI) were calculated using scripts in the TNT software (Goloboff et al., 2008). The species *Meggittina baeri* Lynsdale, 1953 and *Skrjabinotaenia lobata* Baer, 1925 were used as outgroups, and the sequences were also downloaded from GenBank (see Haukisalmi et al., 2010).



Figures 4–6. Line drawings of *Catenotaenia tuyae* n. sp. **4**. Mature proglottid, dorsal view. **5**. Details of the genital pore, dorsal view. **6**. Gravid proglottid, dorsal view.

RESULTS

Catenotaenia tuyae n. sp. (Figs. 3–6)

Description

Sixteen specimens were examined. Scolex (Fig. 3) 262–402 (318 ± 39; $N = 12$) in maximum width. Suckers 119–250 (154 ± 21; $N = 12$) long by 99–195 (133 ± 18) wide. Scolex unarmed. Neck, 244–1076 (464 ± 216; $N = 11$) long by 213–523 (294 ± 84) in maximum width. Strobila 11–110 mm (41 ± 34 mm; $N = 13$) long with 12–32 (20.46 ± 7; $N = 12$) proglottids; maximum width 0.5–1 (1 ± 0.3) attained late in gravid proglottids. Anlagen of genital organs appearing as early as proglottid 5 and as late as proglottid 7 (5 ± 1; $N = 12$). Strobilar margins serrate, intersegmental boundaries well defined in mature and gravid proglottids (Fig. 4). Proglottids longer than they are wide; strobila attenuated anteriorly, with increase in relative length beginning in mature proglottids; length/width ratio of mature and gravid proglottids 2–5 (3 ± 1; $N = 15$) and 4–7

Table 3. Estimates of genetic distance between sequences. The number of base substitutions per site from between sequences are shown. Analyses were conducted using the Maximum Composite Likelihood model (Tamura et al., 2004). The analysis involved 24 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 1,196 positions in the final dataset. Evolutionary analyses were conducted in MEGA6 (Tamura et al., 2013).

		Genetic distance between samples.																							
	Cestode Species Name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	*Meggittina baeri* (GU254056)	0.000																							
2	*Skrjabinotaenia lobata* (GU254058)	0.082	0.000																						
3	*S. lobata* (GU254045)	0.082	0.000	0.000																					
4	*Catenotaenia sp. (*GU443958)	0.168	0.154	0.154	0.000																				
5	*Catenotaenia sp. (*GU254050)	0.155	0.125	0.125	0.100	0.000																			
6	*C. cricetuli (*GU254057)	0.145	0.118	0.118	0.099	0.027	0.000																		
7	*C. cricetuli (*GU254055)	0.145	0.118	0.118	0.099	0.027	0.000	0.000																	
8	*C. henttoneni* (GU254054)	0.153	0.124	0.124	0.101	0.008	0.025	0.025	0.000																
9	*C. henttoneni* (GU254053)	0.153	0.124	0.124	0.101	0.008	0.025	0.025	0.000	0.000															
10	*C. henttoneni* (GU254051)	0.153	0.124	0.124	0.101	0.008	0.025	0.025	0.000	0.000	0.000														
11	*C. henttoneni* (GU254049)	0.152	0.122	0.122	0.100	0.008	0.024	0.024	0.001	0.001	0.001	0.000													
12	*C. henttoneni* (GU254048)	0.153	0.124	0.124	0.101	0.008	0.025	0.025	0.000	0.000	0.000	0.001	0.000												
13	*C. henttoneni* (GU254044)	0.153	0.124	0.124	0.101	0.008	0.025	0.025	0.000	0.000	0.000	0.001	0.000	0.000											
14	*C. apodemi* (GU254052)	0.136	0.106	0.106	0.102	0.055	0.038	0.038	0.051	0.051	0.051	0.050	0.051	0.051	0.000										
15	*C. apodemi* (GU254047)	0.136	0.106	0.106	0.102	0.055	0.038	0.038	0.051	0.051	0.051	0.050	0.051	0.051	0.000	0.000									
16	*C. apodemi* (GU254046)	0.138	0.108	0.108	0.103	0.056	0.039	0.039	0.052	0.052	0.052	0.051	0.052	0.052	0.003	0.003	0.000								
17	*C. microti* (GU254041)	0.150	0.122	0.122	0.097	0.013	0.023	0.023	0.010	0.010	0.010	0.009	0.010	0.010	0.049	0.049	0.050	0.000							
18	*C. microti* (GU254040)	0.150	0.122	0.122	0.097	0.013	0.023	0.023	0.010	0.010	0.010	0.009	0.010	0.010	0.049	0.049	0.050	0.000	0.000						
19	*C. dendritica* (GU254039)	0.139	0.126	0.126	0.118	0.066	0.065	0.065	0.061	0.061	0.061	0.061	0.061	0.061	0.064	0.064	0.066	0.066	0.066	0.000					
20	*C. kirgizica* (GU254043)	0.129	0.104	0.104	0.111	0.069	0.054	0.054	0.065	0.065	0.065	0.064	0.065	0.065	0.047	0.047	0.048	0.065	0.065	0.068	0.000				
21	*C. kirgizica* (GU254042)	0.130	0.106	0.106	0.113	0.071	0.056	0.056	0.067	0.067	0.067	0.066	0.067	0.067	0.049	0.049	0.050	0.067	0.067	0.068	0.003	0.000			
22	*C. tuyae* n. sp. NK223985	0.135	0.111	0.111	0.104	0.064	0.059	0.059	0.060	0.060	0.060	0.059	0.060	0.060	0.068	0.068	0.069	0.057	0.057	0.076	0.067	0.067	0.000		
23	*C. tuyae* n. sp. NK224420	0.135	0.111	0.111	0.104	0.064	0.059	0.059	0.060	0.060	0.060	0.059	0.060	0.060	0.068	0.068	0.069	0.057	0.057	0.076	0.067	0.067	0.000	0.000	
24	*C. sp.* NK224347	0.153	0.124	0.124	0.097	0.016	0.030	0.030	0.015	0.015	0.015	0.014	0.015	0.015	0.056	0.056	0.057	0.008	0.008	0.067	0.069	0.069	0.055	0.055	0.000

(5 ± 1; *N* = 11), respectively. Ratio of measurements of distance from anterior end of proglottid to genital pore relative to total length of proglottid, defined as poral distance ratio (PDR). The PDR for mature proglottids: 3–5 (4 ± 0.6; *N* = 15); PDR for gravid proglottids, 3–5 (4 ± 0.6; *N* = 11). Genital atrium, 22–61.4 (44 ± 15; *N* = 16) deep. Genital pores irregularly alternating, situated in anterior fourth of the proglottid. Ventral longitudinal osmoregulatory canals, 9.5–57 (26 ± 12; *N* = 16) wide, transverse canals not seen. Dorsal longitudinal osmoregulatory canals, 3.3–14 (8.5 ± 3.7; *N* = 16) wide, situated more toward the center of the proglottid and overlapping the seminal receptacle and distal one eighth of the cirrus sac (Fig. 5). Cirrus unarmed (Fig. 5). Cirrus sac elongate, fusiform 173.5–298 (236 ± 47; *N* = 14) in maximum length by 36–160 (103 ± 37; *N* = 14) in maximum width; cirrus sac overlapping ventral longitudinal osmoregulatory canals. Testes subspherical and spherical, 48–112 (67 ± 17; *N* = 15) long and 42–100 (60 ± 15.2) wide. Number of testes 67–92 (77 ± 8; *N* = 13). Gravid proglottids with 29–53 (41 ± 8.3; *N* = 9) pairs of primary branches of uterus (Fig. 6). Vagina, 28–632 (360 ± 163; *N* = 13) long by 52–141 (85 ± 23.5) in maximum width entering genital atrium posterior to the exit of cirrus (Figs. 4 and 5). Vagina narrow at first then expanding slightly, then narrowing to form a tube of consistent diameter running posteriad to seminal vesicle. Seminal receptacle 52.4–245.4 (130 ± 62; *N* = 13) long by 45–222 (111 ± 60) in maximum width, extending porad, mostly anterior to ovary. Ovary lobate, distinctly elongate and narrow and confined almost entirely to the antiporal side in anterior portion of proglottid, 241–1503 (889 ± 374; *N* = 13) in maximum length by 168.5–387.3 (274.5 ± 62) in maximum width. Vitellarium initially globular, becoming elongate and posteriorly tapered in postmature proglottids, 171–874 (463 ± 185.5; *N* = 13) long by 140–395 (223 ± 66.5) in maximum length. Both female and male genital ducts always visible. Eggs, subspherical with thin outer shell, 18–34 (24 ± 4.8; *N* = 7) long by 17–23 (19 ± 1.6) wide.

Taxonomic summary

Symbiotype host: Dwarf fat-tailed jerboa, *Pygeretmus pumilio* (Kerr, 1792) (Rodentia: Dipodidae). Museum of Southwestern Biology, Division of Mammals, MSB267856 (adult, female).

Type locality: Takhi Station, Bij Gol, Dzungarian Gobi, Bugat soum, Gobi Altai province, Mongolia, 45°32′19.212″N; 93°39′3.852″W, July 20, 2012 (Fig. 1).

Site of infection: Small intestine.

Prevalence: 10 of 25 *P. pumilio* examined (40%).

Intensity of infection (number of individual cestodes per infected rodent): 1–3 (mean = 1.6)

Specimen deposited: Holotype, HWML68323 (deposited as a permanent slide mounted in gum Damar). Paratypes HWML67537, HWML68400, HWML67775, HWML67757, HWML68167, HWML67755, HWML68391, HWML68382, and HWML67666.

Fecal samples deposited in HWML and stored permanently in 2% $K_2Cr_2O_7$ solution at 2°C in the parasite collection of the Harold W. Manter Laboratory of Parasitology.

Etymology: This species was named after Enkhtuya Jamiyansuren Taravjav—who was the dedicated mother of the first author, in addition to being a cutting-edge aerial cartographer in Mongolia in the 1980s.

Differential diagnosis

Of the 19 species of *Catenotaenia* known from rodents in the Holarctic (Table 4), all use rodents as the definitive host with no records of species of this genus yet reported from Africa (Haukisalmi et al., 2010).

From the species of *Catenotaenia* described from rodents in the Nearctic region, *C. tuyae* can be recognized as distinct by the following characters: from *Catenotaenia californica*, by the width of the mature proglottid (smaller in *C. tuyae*); from *Catenotaenia laguri*, by a larger strobila (larger in *C. tuyae*); from *Catenotaenia linsdalei*, by having segments that are wider in the posterior end versus uniform width in *C. linsdalei* and by having fewer testes (in *C. tuyae*); from *Catenotaenia neotomae*, by *C. tuyae* having a smaller strobila, many fewer testes, and fewer branches of the uterus; from *Catenotaenia peromysci*, by the width of the gravid proglottid, which is wider in the anterior part of *C. tuyae*; and finally from *Catenotaenia reggiae*, as described by Rausch (1951) from *Marmota caligata* from near Anaktuvuk Pass in the Brooks Range of Alaska, by being much smaller.

Catenotaenia tuyae n. sp. can be recognized as distinct from *C. asiatica* Tenora and Murai, 1975, *C. cricetorum* Kirshenblat, 1949, *Catenotaenia gracilae* Asakawa, Tenora, Kamiya, Harada and Borkovcova, 1992, *C. henttoneni* Haukisalmi and Tenora, 1993, *C. microti* Haukisalmi, Hardman and Henttonen, 2010, *C. pusilla* Goeze, 1782, and *C. rhombomidis* Shulz and Landa, 1934 by the greater number of branches of the uterus.

Catenotaenia tuyae n. sp. can be recognized as distinct from *C. afghana* based on the following characters: larger scolex width, more uterine branches, larger egg length, and ovoid egg shape (outer membrane) in the new species.

Catenotaenia tuyae n. sp. can be recognized as distinct from *Catenotaenia apodemi* Haukisalmi, Hardman and Henttonen, 2010, with *C. tuyae* having a longer body length, a mature proglottid that is wider at the posterior-most part of the segment (relative to the widest point at the position of the genital pore in *C. apodemi*), and a greater number of uterine branches (Table 4).

Catenotaenia tuyae n. sp. can be recognized as distinct from *Catenotaenia cricetuli* Haukisalmi, 2010 by having a smaller strobila, a different position of the widest point of the gravid proglottid, fewer testes, a shorter anterior free space, and the shape of the outer membrane of the egg in the new species (Table 4).

Catenotaenia tuyae n. sp. can be separated from *Catenotaenia dendritica* Goeze, 1782 in having a smaller overall strobila, a different widest point of the mature proglottids, and many fewer testes.

Catenotaenia tuyae can be recognized as distinct from all other species of *Catenotaenia* in the Palearctic region by the PDR (defined above); in *C. tuyae*, the PDR is always greater than 1:4, which is greater than the PDR of all other species of *Catenotaenia* currently described (for a summary see Haukisalmi, 2010).

Catenotaenia tuyae n. sp. can be distinguished from all other species of *Catenotaenia*, from which data on DNA are available by its placement in the molecular phylogeny based on analysis of approximately 1.5 kb of the 28S rRNA gene (Fig. 7). The maximum-parsimony tree (Fig. 7) shows that both samples of *C. tuyae* n. sp. (NK223985 and NK224420), from different host–individuals, have identical sequence positions for the area of DNA that was amplified and analyzed. In the results of our analysis, it is clear that *C. dendritica* (a parasite of sciurids in Eurasia) is the sister taxon of *C. tuyae*; for the tree in Fig. 7, the calculated CI was 73% and the RI was 82%, indicating a relatively high degree of concordance of the characters with the structure of the tree (Goloboff et al., 2008; Goloboff and Catalano 2016). Although the resampling values shown on the tree are relatively low, the clade with the two samples of *C. tuyae* and one of *C. dendritica* were consistently recovered (100% of the time) using both the new technology search (NT) and implicit enumeration searches in TNT.

DISCUSSION

That the species of *Catenotaenia* found in *P. pumilio* in south-central and southwestern Mongolia represents an undescribed species is supported by both the morphological and molecular evidence presented herein. The relatively high prevalence of this parasite in individuals of *P. pumilio* collected in SW Mongolia indicates that this may be a common parasite in *P. pumilio* in the areas near the base of the Altai Mountains. Additional collections of this species of rodent from further to the east in Mongolia will enable testing of the idea of parasites potentially acting as probes for biodiversity (Gardner and Campbell, 1992). Individuals of *P. pumilio* were collected from five geographically separate localities in the area of the Gobi, but the parasite was found only from the southwestern regions of the Gobi desert. The presence of the cestode in *P. pumilio* in these areas suggests that the Dzungarian Gobi and Bulgan River valley areas have cryptic ecological similarities that enable *P. pumilio*, *C. tuyae*, and an as-yet-unknown arthropod intermediate host to exist in this area. Somewhat surprisingly, individuals of *C. tuyae* were not found in any other species of Dipodidae collected in the area. This result indicates that *P. pumilio* has different ecological and food prefer-

Table 4. Some morphometric features of the nominal species of *Catenotaenia* (table from Haukisalmi et al., 2010, with *C. tuyae* [boldface] added). All measurements are in millimeters.

Catenotaenia sp.	Body length*	Body width	Scolex width	Mature proglottids widest point	Gravid proglottids widest point	Number of testes	Anterior "free space"	Number of uterine branches	Total egg length	Egg shape (outer membrane)	Source†
C. afghana	120	2.0	0.141–0.24	Posterior	Posterior	80–113	Short	28–34	12–22	Caudate	8
C. apodemi	48–62	0.8–0.9	0.28–0.38	Middle	Middle	70–90	Short	29–34	35–42	Ovoid	1
C. asiatica	60–75	1.0–1.5	0.25	Uniform	Middle	60–80	Short	18–22	20–21	Caudate	2
C. californica	Max 82	3.3	0.15–0.2	Middle	Middle	72–90	Short	25–30	24–33	Ovoid	3
C. cricetorum	335	—	0.45	Posterior	Pore	110–130	Short	20–24	13–15	—	4
C. cricetuli	81–208	1.0–1.6	0.32–0.39	Posterior	Uniform	130–166	Long	27–43	37–55	Caudate	1
C. dentritica	85–170	1.3–1.8	2.29–0.35	Middle/pore	Uniform	140–233	Long	35–60	18–33	Ovoid	1,5,6,7,8
C. gracilae	25	0.7	0.17–0.22	Posterior	Uniform/posterior	ca. 150	Short	13–25	33–39	Ovoid/elongate	9
C. henttoneni	62–136	1.0–1.7	0.24–0.3	Posterior	Posterior	103–137	Short	16–28	20–31	Ovoid	1
C. laguri	30–50	0.7	0.22–0.26	Posterior	Uniform	70–80	Long	35–40	20–24	Ovoid	10
C. microti	56–106	1.1–1.6	0.25–0.27	Posterior	Uniform/middle	88–110	Short	21–27	35–40	Caudate	1
C. linsdalei	135	1.0	—	Uniform	Uniform	ca. 130	Intermediate	45–50	6–7	—	11
C. neotomae	160–205	1.3	0.41–0.47	Posterior/pore	Middle/pore	130–190	Intermediate	25–30	21–31	Ovoid/elongate	12
C. peromysci	65	1.2–1.7	0.33–0.36	Uniform/ posterior	Posterior	70–80	Intermediate	25–30	39	Ovoid	10
C. pusilla	30–160	0.8–1.7	0.19–0.4	Middle	Middle	70–150	Short	9–17	22–45	Ovoid/elongate	1,5,6,7
C. reggiae	Max 360	3.0	0.36–0.49	Posterior	Middle	ca. 300	Intermediate	25–40	17–28	Spherical	13
C. rhombomidis	100	—	0.43	Posterior	Middle	>400	Short	18–22	—	—	14
C. ris	>120	Up to 2.5	0.27–0.33	Middle/pore	Uniform	140–190	Long	30–40	18–33	Ovoid	15
***C. tuyae* N. sp.**	**12.5–110.6**	**0.51–1.3**	**0.26–0.40**	**Posterior**	**Middle/anterior**	**68–92**	**Short**	**29–53**	**18–34**	**Ovoid**	**16**

* Max, maximum.

† Sources: (1) Haukisalmi et al., 2010; (2) Tenora et al., 1975; (3) Dowell, 1953; (4) Kirshenblat, 1949; (5) Joyeux and Baer, 1945; (6) Spasskii, 1951; (7) Genov, 1984; (8) Ganzorig et al., 1999; (9) Asakawa et al., 1992; (10) Smith, 1954; (11) McIntosh, 1941; (12) Babero and Cattan, 1983; (13) Rausch, 1951; (14) Ryzhikov et al., 1978; (15) Yamaguti, 1942; (16) Present study, 2017.

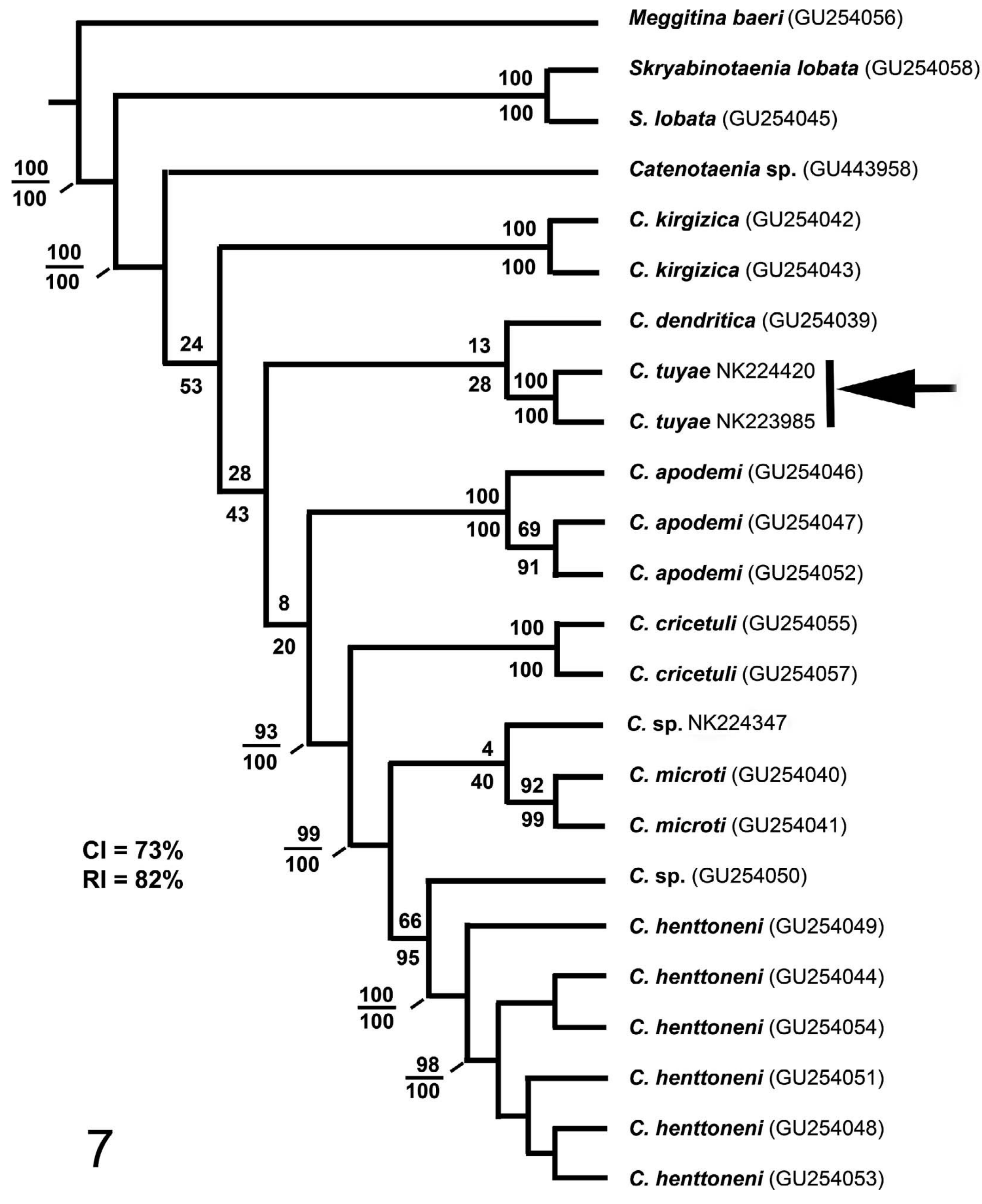


Figure 7. Phylogenetic relationships of *Catenotaenia* spp. in the Palearctic region estimated by TNT software (Goloboff et al., 2008) for ca. 1.5 kb of 28S rRNA using maximum parsimony. *Catenotaenia dendritica* (a parasite of sciurids in Eurasia) is the sister taxon of *Catenotaenia tuyae* n. sp. Node values reported include standard bootstrap values (top number) and symmetric resampling value (bottom number). Arrow indicates *C. tuyae* n. sp. described from *Pygeretmus pumilio* (Kerr, 1792).

ences from other species in the family Dipodidae that live in the same areas. Additional collecting should be conducted in these areas and further to the east to confirm the specificity of this host–parasite system.

Our parsimony analysis, which included individuals of *Catenotaenia* collected in Mongolia, shows that *C. tuyae* is located on the tree well-embedded within the in-group, with *C. dendritica* as its sister species; thus, both *C. dendritica* and *C. tuyae* shared a most recent common ancestor.

We chose the method of parsimony as the optimality criterion to examine the ancestor descendant relationships among species based on characters of the DNA because it has been shown numerous times that analyses using other methods (maximum-likelihood, Bayesian, or other phylogenetic systematics–based approaches) will converge upon a very similar, or the same, answer, given enough data (Brooks et al., 2007).

The molecular phylogenetic analysis, genetic distance analysis (Table 3), and morphological comparisons indicate that *C. tuyae* shares a high degree of genetic similarity with *C. dentritica* (about 92.4%). Our report of *C. tuyae* n. sp. from *P. pumilio* is only the third helminth species recorded from a species of the genus *Pygeretmus*. Our research suggests that the parasite diversity of Dipodidae is still relatively unknown throughout the geographic range of these rodents, indicating that further work should be conducted on this interesting group of rodents and its parasites (Brooks and McLennan, 2002).

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