DOI: 10.2478/s11686-013-0170-6

Acta Parasitologica, 2013, 58(4), 441–452; ISSN 1230-2821

VERSITA

A widespread distribution for *Arostrilepis tenuicirrosa* (Eucestoda: Hymenolepididae) in *Myodes* voles (Cricetidae: Arvicolinae) from the Palearctic based on molecular and morphological evidence: historical and biogeographic implications

Kurt E. Galbreath[1]*, Kristina Ragaliauskaitė[2], Leonas Kontrimavichus[2], Arseny A. Makarikov[3] and Eric P. Hoberg[4]

[1]Department of Biology, Northern Michigan University, 1401 Presque Isle Ave., Marquette, Michigan 49855, USA.
[2]Institute of Ecology of Nature Research Centre, Akademijos 2, Vilnius 08412, Lithuania.
[3]Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, Frunze Str. 11, 630091 Novosibirsk, Russia.
[4]United States National Parasite Collection, Animal Parasitic Disease Laboratory, USDA, Agricultural Research Service, BARC East No. 1180, 10300 Baltimore Avenue, Beltsville, Maryland 20705, USA

Abstract

Hymenolepidid cestodes in *Myodes glareolus* from Lithuania and additional specimens originally attributed to *Arostrilepis horrida* from the Republic of Belarus are now referred to *A. tenuicirrosa*. Our study includes the first records of *A. tenuicirrosa* from the European (western) region of the Palearctic, and contributes to the recognition of *A. horrida* (*sensu lato*) as a complex of cryptic species distributed broadly across the Holarctic. Specimens of *A. tenuicirrosa* from Lithuania were compared to cestodes representing apparently disjunct populations in the eastern Palearctic based on structural characters of adult parasites and molecular sequence data from nuclear (ITS2) and mitochondrial (cytochrome *b*) genes. Morphological and molecular data revealed low levels of divergence between eastern and western populations. Phylogeographic relationships among populations and host biogeographic history suggests that limited intraspecific diversity within *A. tenuicirrosa* may reflect a Late Pleistocene transcontinental range expansion from an East Asian point of origin.

Keywords

Hymenolepididae, *Arostrilepis tenuicirrosa*, Beringia, Eurasia, Arvicolinae, *Myodes glareolus*, phylogeography

Introduction

Over the past century the hymenolepidid cestode *Arostrilepis horrida* (Linstow, 1901) was regarded as a single hyper-variable species occurring in a diverse assemblage of rodent definitive hosts encompassing the Holarctic region (e.g., Schiller 1952; Voge 1952; Rausch 1952; Ryzhikov *et al*. 1978; Fedorov 1986). Although the possibility of a widespread complex of poorly differentiated species was periodically considered, little consensus emerged regarding specific morphological criteria to define particular taxa (Johri 1956; Mas-Coma *et al*. 1980; Mas-Coma and Tenora 1997; Asakawa *et al*. 2002; Hwang *et al*. 2007; Haukisalmi *et al*. 2009, 2010). Recognition of *A. beringiensis* (Kontrimavichus et Smirnova, 1991) in lemmings and *A. microtis* Gulyaev et Chechulin, 1997 among voles (*Microtus* Schrank and *Arvicola* Lacépède) from east-central Siberia led to initial resolution and definition of limits on species diversity within the genus based on comparative morphology (Kontrimavichus and Smirnova 1991; Gulyaev and Chechulin 1997).

Currently a minimum of 12 species may be recognized within *Arostrilepis* Mas-Coma et Tenora, 1997 across temperate to high latitudes of the Holarctic (Hoberg *et al*. 2012). Among these, *A. horrida* in the Palearctic, and *A. mariettavogeae* Makarikov, Gardner et Hoberg, 2012 and *A. schilleri* Makarikov, Gardner et Hoberg, 2012 in the Nearctic are based solely on morphological criteria (Makarikov *et al*. 2011, 2012). An additional 10 molecular-based lineages of *Aros-*

*Corresponding author: kgalbrea@nmu.edu

trilepis have been correlated with unequivocal morphological attributes. Among these, nominal *Arostrilepis* now include 5 endemic species in the Palearctic (and a minimum of 1 undescribed), 4 endemic species in the Nearctic, 2 species with amphiberingian distributions spanning northwestern North America and northeastern Eurasia, and one species with a disjunct distribution that includes localities in Europe and northwestern North America (Cook *et al*. 2005; Makarikov and Kontrimavichus 2011; Makarikov *et al*. 2011, 2012; Makarikov *et al*. 2013). Our studies have clearly demonstrated the value of integrated morphological/molecular approaches in exploring the distribution and limits of species diversity relative to host associations and geography.

Advances in our understanding of diversity in *Arostrilepis* resulted from (1) a clear definition and re-description of the type species, *A. horrida* (e.g., Makarikov *et al*. 2011); (2) recognition and validation of the suites of diagnostic characters associated with the cirrus (e.g., Makarikov *et al*. 2011; Makarikov and Kontrimavichus 2011; Makarikov *et al*. 2012; Makarikov *et al*. 2013); and (3) integration of molecular and sequence-based criteria in defining species limits (Hoberg *et al*. 2003; Cook *et al*. 2005; Makarikov *et al*. 2013). Where new field collections have been conducted they have confirmed the existence of considerable species diversity within *Arostrilepis*, highlighting the need for a broad-based re-examination of those specimens of cestodes in arvicolines and other rodents that had originally been identified as *A. horrida*. This is necessary to clearly define species diversity, along with the host and geographic distributions within this assemblage (e.g., Makarikov *et al*. 2012).

Investigations over the past decade have examined the structure of arvicoline parasite faunas from the Beringian region linking North America and eastern Siberia, and further west extending into central Eurasia (Cook *et al*. 2005; Makarikov 2008; Hoberg *et al*. 2012). Records of tapeworm diversity in arvicolines from the western Palearctic and central Europe have also been assembled, including numerous reports of *A. horrida* (syn: *Hymenolepis horrida*) (e.g., Baer 1932; Żarnowski 1955; Erhardová 1958; Rybicka 1959; Mozgovoi *et al*. 1966; Prokopic and Mahnert 1970; Murai and Tenora 1973; Merkusheva and Bobkova 1981; Genov 1984; Mas-Coma and Tenora 1997). Our current understanding of the genus and the status of *A. horrida* as a complex of species, however, indicates that these records now can only be confirmed or validated based on the availability of voucher specimens held in various museum archives. Additionally, new and continued biodiversity inventory remains necessary to explore patterns of cestode diversity and historical, evolutionary and ecological determinants of host and geographic distributions. We examine these challenges in the current study based on data accumulated for *A. tenuicirrosa* Makarikov, Gulyaev et Kontrimavichus, 2011 across the Palearctic region.

Within the assemblage of *Arostrilepis* species, *A. tenuicirrosa* was described in red-backed voles: *Myodes rutilus* (Pallas); *M. rufocanus* (Sundevall); *M. glareolus* (Schreber) and *M. rex* (Imaizumi) (originally *M. sikotanensis* (Tokuda); see Abramson e*t al*. 2009) from the Asian region of Russia extending across Western Siberia to the Russian Far East (Makarikov *et al*. 2011). Additional field collections and specimens in red-backed voles (*Myodes* Pallas) from western Beringia (Magadanskaya Oblast') have confirmed this general geographic distribution; there is no evidence that *A. tenuicirrosa* occurs in the Nearctic (Makarikov *et al*. 2013). Thus, *A. tenuicirrosa* has been considered a species typical of red-backed voles, often occurring in sympatry and mixed infections with other species of *Arostrilepis*, with an overall distribution potentially limited to eastern Eurasia.

During our field surveys of the helminth fauna of red-backed voles (specifically *M. glareolus*) from Lithuania we found hymenolepidid cestodes considered to be conspecific with *A. tenuicirrosa*. Although hymenolepidids of arvicolines have been reported from across the Palearctic (e.g., Ryzhikov *et al*. 1978), there are few voucher specimens or substantiated records that define the distribution of *Arostrilepis* in the Baltic region. Several studies on the helminth fauna of rodents reported cestodes identified as *A. horrida* (*sensu lato*) in voles [*M. glareolus*, *Microtus arvalis* (Pallas) and *M. oeconomus* (Pallas)] from Republic of Belarus (see Merkusheva and Bobkova 1981).

Following our initial discovery, we examined museum specimens from the northwestern Palearctic that were originally identified as *A. horrida* or *Hymenolepis horrida*. Specimens of *H. horrida* in *M. glareolus* from Belarus are held in the archives of the Scientific and Practical Center for Bioresources, Minsk, Republic of Belarus (SPCB) (see Merkusheva and Bobkova 1981). Other cestodes in *M. glareolus* from Lithuania had been deposited at the Institute of Ecology of Nature Research Center, Vilnius, Lithuania (IENRC) (V. Stunzenas, V. Kontrimavichus, and S. Bondarenko, pers. obs. and data not shown). All of these specimens, originally considered to be *A. horrida*, were redetermined as *A. tenuicirrosa* and no other species of *Arostrilepis* were discovered. Here we report the first records of *A. tenuicirrosa* from Lithuania and Belarus based on specimens collected from *M. glareolus*. These series of specimens now indicate an apparently extensive trans-Palearctic distribution for *A. tenuicirrosa* based on its occurrence in the East European Plain.

Among cyclophyllideans there have been few studies documenting patterns of genetic diversity and the historical processes related to host association, dispersal, faunal expansion and geographic isolation (Santalla *et al*. 2002; Wickström *et al*. 2003; Padgett *et al*. 2005; Haukisalmi *et al*. 2007; Hoberg *et al*. 2012). In this investigation we take advantage of geographically extensive field collections to evaluate transcontinental genetic structure and phylogenetic relationships among discrete populations of *A. tenuicirrosa* from the East European Lowlands (Lithuania), Western Siberia (Tyumenskaya Oblast'), and the Russian Far East (Kunashir Island and Magadanskaya Oblast'). Comparisons are based on morphological and multi-locus DNA sequence data. Our results es-

tablish testable hypotheses regarding the broader biogeographic history of the Palearctic region and the structure and assembly of parasite faunas in small mammals.

Materials and Methods

Specimens collected and examined

Specimens of *Arostrilepis* in multiple species of *Myodes* from localities spanning the Palearctic region were examined. (1) In the Russian Far East cestodes consistent with *A. tenuicirrosa* in arvicoline rodents (6 *M. rufocanus* and 9 *M. rex*) were collected during July 2006 from the Kurilskiy Reserve located on Kunashir Island (44°11′N, 146°01′E). (2) Also from the Russian Far East, based on collections of the Beringian Coevolution Project (BCP; Cook *et al*. 2005), *A. tenuicirrosa* was found in 5 *M. rutilus* and 2 *M. rufocanus* during July 2002 on the Buynda River, Magadanskaya Oblast' (62°20′N, 153°21′E); in 2 *M. rutilus* and 2 *M. rufocanus* during August 2000 along the Omolon River, Magadanskaya Oblast' (63°20′N, 158°35′E, and 64°26′ 52″N, 161°07′ 47″E); and in 2 *M. rutilus* during August 2000 on the upper Kolyma River, Magadanskaya Oblast' (62°31′30″N, 151°16′34″E) (see Makarikov *et al*. 2013). (3) In south-central Russia, another series of cestodes in *M. glareolus* was collected from Yarkovskiy Raion (57°26′N, 66°59′E), Tyumenskaya Oblast' during July to August 2007. (4) European specimens of *A. tenuicirrosa* in 16 *M. glareolus* were collected during July 2011 near the Lake Stirniai Hydrographic Reserve, Labanoras Regional Park (55°14′N, 25°36′E) located in the Molėtai district, Lithuania. All examined specimens are described in Table I.

Specimens originally attributed to *A. horrida* in the collections of the SPCB and IENRC were also examined morphologically. Cestodes from SPCB were collected from *M. glareolus* by Iya Vasilyevna Merkusheva between 1958 and 1972 from different regions of Belarus: Luninets Raion (52°17′N, 26°40′E), Pyetrykawski Raion (52°08′N, 28°29′E), suburbs of the city of Vitebsk (55°09′N, 29°46′E). Cestodes deposited in IENRC were collected from *M. glareolus* during October 2005 from the Molėtai district (55°14′N, 25°36′E) of Lithuania by Vytautas Kontrimavichus and Svetlana Bondarenko. Additional specimens in *Myodes* spp. from Siberia and the Russian Far East represent the original type series for *A. tenuicirrosa* (e.g., Makarikov *et al*. 2011). Identification of *A. tenuicirrosa* was based on criteria established by Makarikov *et al*. (2011). Morphological characters from cestodes representing apparently disjunct populations of *A. tenuicirrosa* were compared. Measurements are given in micrometers unless otherwise specified; the range for each measurement is followed by the mean in parentheses.

Specimens of *A. tenuicirrosa* with numbers 18.28.4.29–18.28.4.41 were deposited into the collections of the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia (ISEA). Other specimens of *A. tenuicirrosa* with numbers 301,

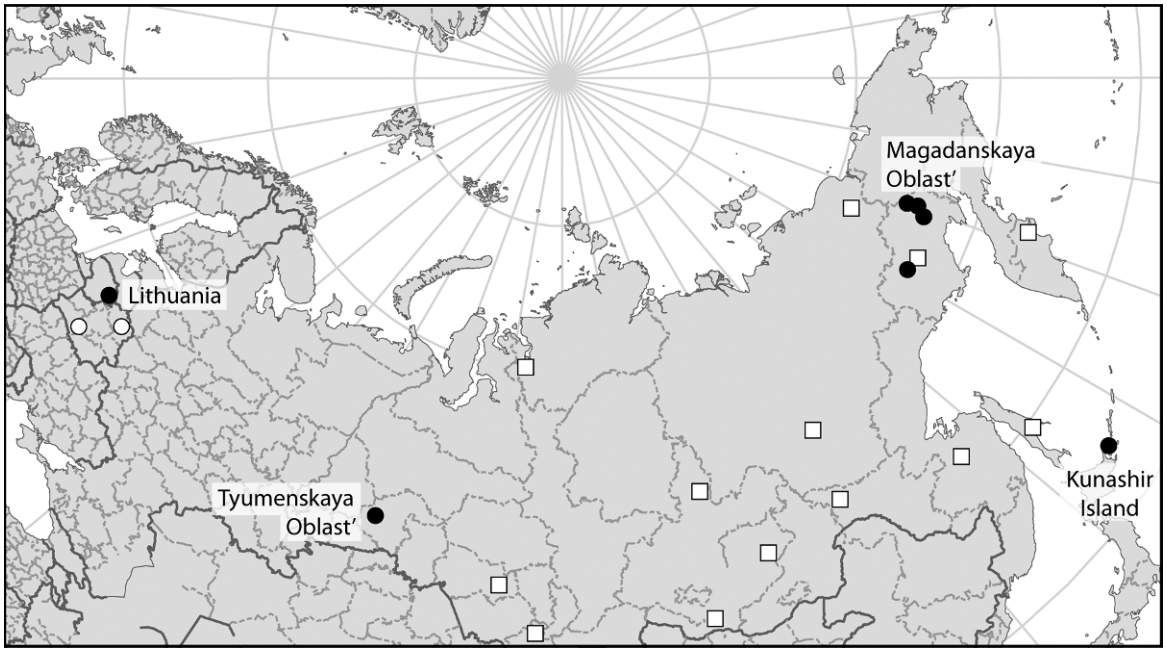

Fig. 1. Map of sampling localities for *Arostrilepis tenuicirrosa*. Black-filled circles associated with locality names indicate approximate localities for specimens that are represented in the molecular dataset used in this study. The Magadanskaya Oblast' sample was pooled from the four marked localities that lie in relatively close proximity in eastern Siberia. Approximate localities from which *A. tenuicirrosa* has been identified based solely on morphological criteria are denoted by either white-filled squares (eastern Palearctic; Makarikov *et al*. 2013; Makarikov *et al*. 2011) or white-filled circles (Belarus; this study)

Table I. *Arostrilepis* specimens included in the present analysis of ITS2 and cyt-*b* sequences and their GenBank accession numbers

Cestode species	Host species	Region, locality	Geographical coordinates	Slide number	GenBank accession numbers for ITS2 sequences	GenBank accession numbers for cyt-*b* sequences
Arostrilepis tenuicirrosa	*Myodes glareolus*	Tyumenskaya Oblast'	57°26′N, 66°59′E	18.28.4.29	HQ174772	JX126909
A. tenuicirrosa	*M. glareolus*	Tyumenskaya Oblast'	57°26′N, 66°59′E	18.28.4.30	HQ174773	JX126910
A. tenuicirrosa	*Myodes rex*	Kunashir Island	44°11′N, 146°01′E	18.28.4.35	HQ174774	no sequence
A. tenuicirrosa	*M. rex*	Kunashir Island	44°11′N, 146°01′E	18.28.4.36	HQ174775	JX126911
A. tenuicirrosa	*M. glareolus*	Tyumenskaya Oblast'	57°26′N, 66°59′E	18.28.4.37	HQ174776	no sequence
A. tenuicirrosa	*Myodes rufocanus*	Kunashir Island	44°11′N, 146°01′E	18.28.4.41	HQ174777	no sequence
A. tenuicirrosa	*M. glareolus*	Lithuania	55°14′N, 25°36′E	301	JX121629	JX121634
A. tenuicirrosa	*M. glareolus*	Lithuania	55°14′N, 25°36′E	302	JX121630	JX121635
A. tenuicirrosa	*M. glareolus*	Lithuania	55°14′N, 25°36′E	341	JX121631	JX121636
A. tenuicirrosa	*M. glareolus*	Lithuania	55°14′N, 25°36′E	342	JX121632	JX121637
A. tenuicirrosa	*M. glareolus*	Lithuania	55°14′N, 25°36′E	351	JX121633	no sequence
A. tenuicirrosa	*M. rutilus*	Magadanskaya Oblast'	63°20′N, 158°35′E	38038c1	JX104768	JX104762
A. tenuicirrosa	*M. rutilus*	Magadanskaya Oblast'	63°20′N, 158°35′E	38038c2	JX104769	JX104763
A. tenuicirrosa	*M. rufocanus*	Magadanskaya Oblast'	64°26′N, 161°07′E	38237c1	JX104770	JX104764
A. tenuicirrosa	*M. rufocanus*	Magadanskaya Oblast'	64°26′N, 161°07′E	38238c4	JX104771	JX104765
A. tenuicirrosa	*M. rufocanus*	Magadanskaya Oblast'	65°18′N, 160°20′E	38289c3	JX104772	JX104766
A. tenuicirrosa	*M. rutilus*	Magadanskaya Oblast'	62°31′N, 151°16′E	38814c2	JX104773	JX104767
A. macrocirrosa	*M. rutilus*	Magadanskaya Oblast'	63°20′N, 158°35′E	38004c1	no sequence	JX841310

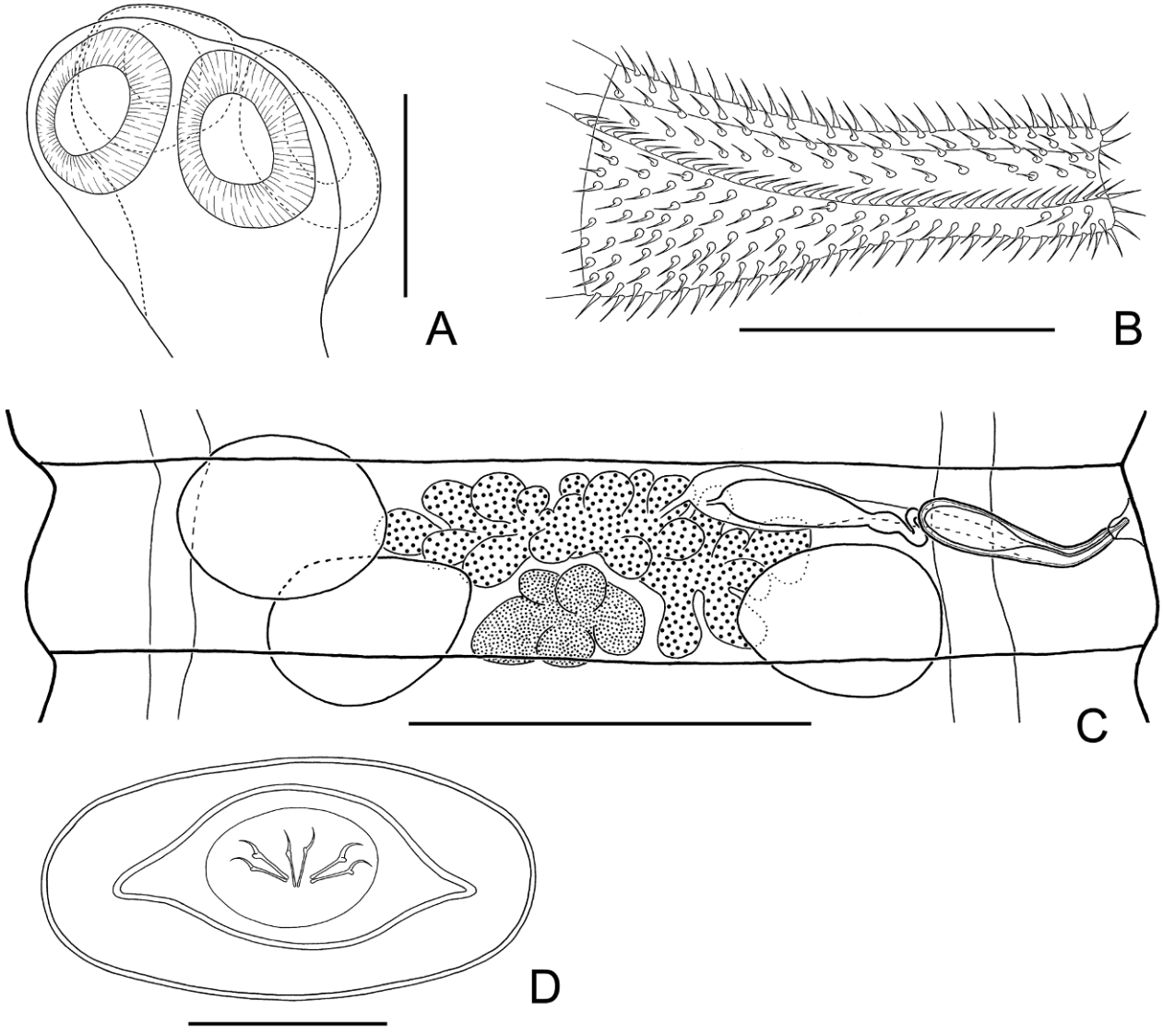

Fig. 2. Morphology of specimens attributed to *Arostrilepis tenuicirrosa* Makarikov, Gulyaev et Kontrimavichus, 2011 from the European zone of the Palearctic. **A** – dorsoventral view of scolex; **B** – cirrus; **C** – hermaphroditic mature proglottis; **D** – egg. Scale bars: A = 200 μm; B = 20 μm; C = 300 μm, D = 25 μm

302, 341, 342, 351 were deposited into the IENRC. Specimens attributed to the BCP have been deposited in the Parasitology Division of the Museum of Southwestern Biology, University New Mexico (see Makarikov *et al*. 2013).

Molecular data collection and analysis

To evaluate patterns of genetic structure and relatedness across the range of *A. tenuicirrosa*, we collected DNA sequence data from specimens representing the full geographic range of the species (Fig. 1, Table I). We sequenced a portion of the mitochondrial cytochrome *b* gene (cyt-*b*; ~570 base pairs; 10 individuals) and the second internal transcribed spacer of nuclear ribosomal DNA (ITS2; ~630 base pairs; 11 individuals) to obtain independent perspectives on the history of the species. We also sequenced the homologous portion of cyt-*b* from one individual of *A. macrocirrosa* Makarikov, Gulyaev et Kontrimavichus, 2011 to serve as an outgroup. Whole genomic DNA was extracted from tissue subsamples (3–10 posterior proglottids) using Qiagen™ DNeasy Tissue Kits®. We PCR amplified cyt-*b* using published primers HYM01 and HYM08 (Makarikov *et al*. 2013), and ITS2 using published primers 3S and A28 (Okamoto *et al*. 1997). PCR products were sequenced in both directions on an ABI 3100 genetic analyzer (Applied Biosystems Inc., Foster City, CA, USA) using ABI PRISM® BigDye™ sequencing chemistry. Newly obtained data were supplemented with published cyt-*b* (GenBank numbers JX104763-JX104765; Makarikov *et al*. 2013) and ITS2 (GenBank numbers HQ174772-HQ174777) sequences for *A. tenuicirrosa*. In addition, ITS2 sequences for

A. macrocirrosa were acquired from GenBank to serve as outgroups in analyses for that marker (HM561418 and HM561423; Makarikov *et al*. 2011).

Full sequence datasets were aligned using ClustalW as implemented in MEGA v5 (Tamura *et al*. 2011) and alignments were checked by eye. We excluded indels and sites of ambiguous alignment from further analyses. Because subsequent analyses were based on models of nucleotide evolution that assume neutrality, we tested for evidence of selection in the cyt-*b* and ITS2 datasets using HKA tests (Hudson *et al*. 1987) as implemented in DnaSP v5 (Librado and Rozas 2009). For each of these tests, a single *A. macrocirrosa* sequence was compared to the full *A. tenuicirrosa* datasets to evaluate levels of interspecific polymorphism. Neither genetic locus exhibited significant deviations from expectations based on a model of neutral evolution (cyt-*b*: $p = 0.12$; ITS2: $p = 0.75$).

To understand how levels of intraspecific genetic divergence within *A. tenuicirrosa* compare to interspecific variation we used MEGA v5 to calculate uncorrected *p* genetic distances between sets of samples representing distinct geographic localities and the outgroup, *A. macrocirrosa*. We also used DnaSP to calculate overall nucleotide diversity (π) for *A. tenuicirrosa* based on both genetic markers.

To evaluate relationships among populations we constructed separate phylogenetic trees for both loci using maximum likelihood (ML) and Bayesian methods. We first selected appropriate models of nucleotide substitution for the datasets using Akaike's information criterion (counting branch lengths as parameters) as implemented in Modeltest v3.8 (Posada and Crandall 1998). Modeltest selected the K81 (Kimura 1981) model with unequal base frequencies and invariant sites for cyt-*b*. For ITS2 the HKY (Hasegawa *et al*. 1985) model was chosen. We used Garli v2.0 (Zwickl 2006) to determine the best ML phylogeny based on 5 independent searches. Support for relationships within the trees was evaluated using 200 bootstrap replicates (2 searches per replicate). Bayesian analyses were conducted using MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001). Analyses included 5 chains and 10 million generations and were repeated 3 times from different random seeds. Trees were sampled every 1000 generations, and we discarded the first one million generations as burn-in after confirming stationarity of all parameter trends using Tracer v1.5 (Rambaut and Drummond 2007). Convergence of independent runs on consistent tree topologies was confirmed by ensuring that the standard deviation of split frequencies approached zero (both <0.01). Final topologies were produced by combining the results of all three runs.

The traditional phylogenetic methods described above do not take into account stochastic genealogical variation that can result from coalescent processes, nor do they offer an effective way to synthesize information from multiple loci into a single phylogenetic perspective. To address these shortcomings we also applied the multi-locus coalescent-based *BEAST method (Heled and Drummond 2010) implemented

Table II. Comparison of measurements of *Arostrilepis tenuicirrosa* from its original description and present study (measurements in micrometres except where otherwise stated)

Characters	Makarikov *et al.* 2011	Present study
Strobila: width	1.7–2.3 mm	1.3–2.3 mm
Scolex	280–360	260–397
Suckers: size	150–180 × 110–140	154–179 × 131–165
Neck	160–210	110–190
Ventral osmoregulatory canals	50–130	17–58
Hermaphroditic mature proglottis: size	210–270 × 1200–1700	190–330 × 825–1460
Testes: size	200–300 × 140–170	194–270 × 120–193
Cirrus-sac: size	175–225 × 35–45	174–213 × 35–49
Cirrus: size	64–71 × 6–12	67–75
Spines: size	2–2.5	2.2–2.8
Internal seminal vesicle	75–95 × 28–35	80–130 × 35–46
External seminal vesicle	170–240 × 40–68	110–135 × 28–92
Ovary: width	400–570	350–600
Vitellarium: size	80–110 × 140–200	90–130 × 170–290
Copulative part of vagina: size	72–83 × 6–10	83–95
Seminal receptacle: size	175–290 × 35–50	180–290 × 40–90
Gravid proglottis: size	250–380 × 1500–2000	270–380 × 1300–2320
Egg: size	30–34 × 50–57	31×62
Oncosphere: size	14–17 × 18–22	10 × 16
Embryophore: size	18–22 × 35–44	22 × 46
Embryonic hooks	7–8	7.5–8

in BEAST v1.6.1 (Drummond and Rambaut 2007) to infer relationships among the geographic regions represented in our molecular dataset (Magadanskaya Oblast', Tyumenskaya Oblast', Kunashir Island, and Lithuania). The outgroup, *A. macrocirrosa*, was also included in the analysis. We applied the Yule tree prior and allowed rates to vary between loci, but fixed the molecular clock for each locus. Analyses were run for 300 million generations, with 10% of each run discarded as burn-in. We assessed stationarity by examining parameter trend plots and effective sample size (ESS) values (all >200) using TRACER 1.5 (Rambaut and Drummond 2007), and repeated the analysis twice from different random starting seeds to confirm that all parameters converged on similar values.

Results

Hymenolepidid cestodes in *Myodes glareolus* from localities in Lithuania and additional specimens originally attributed to *A. horrida* from the western Palearctic are referred to *A. tenuicirrosa* based on comparative morphology and molecular sequence data outlined below. These are the first records of this species of *Arostrilepis* from the European region of the Palearctic. Redetermination of the species identity of specimens from the Molėtai district of Lithuania indicates that cytochrome c oxidase subunit I sequences previously obtained from these samples and archived in GenBank (DQ340976, DQ340977, and DQ340978, representing voucher specimens K117, K209, and K234, respectively) should now be referred to *A. tenuicirrosa* rather than *A. horrida*.

Morphological comparisons

Partial description of *A. tenuicirrosa* from Lithuania (based on 5 specimens; IENRC Nos. 301, 302, 341, 342, 351) (Figs 2A-D): Strobila 1.3-2.3 mm in maximum width when fully developed in pregravid or gravid proglottides. Scolex slightly compressed dorso–ventrally, 260–397 (317, n = 5) wide, clearly wider than neck, 110–190. Suckers unarmed, ovoid, 154–179 × 131–165 (165 × 141, n = 8), prominent, with thick walls (Fig. 2A).

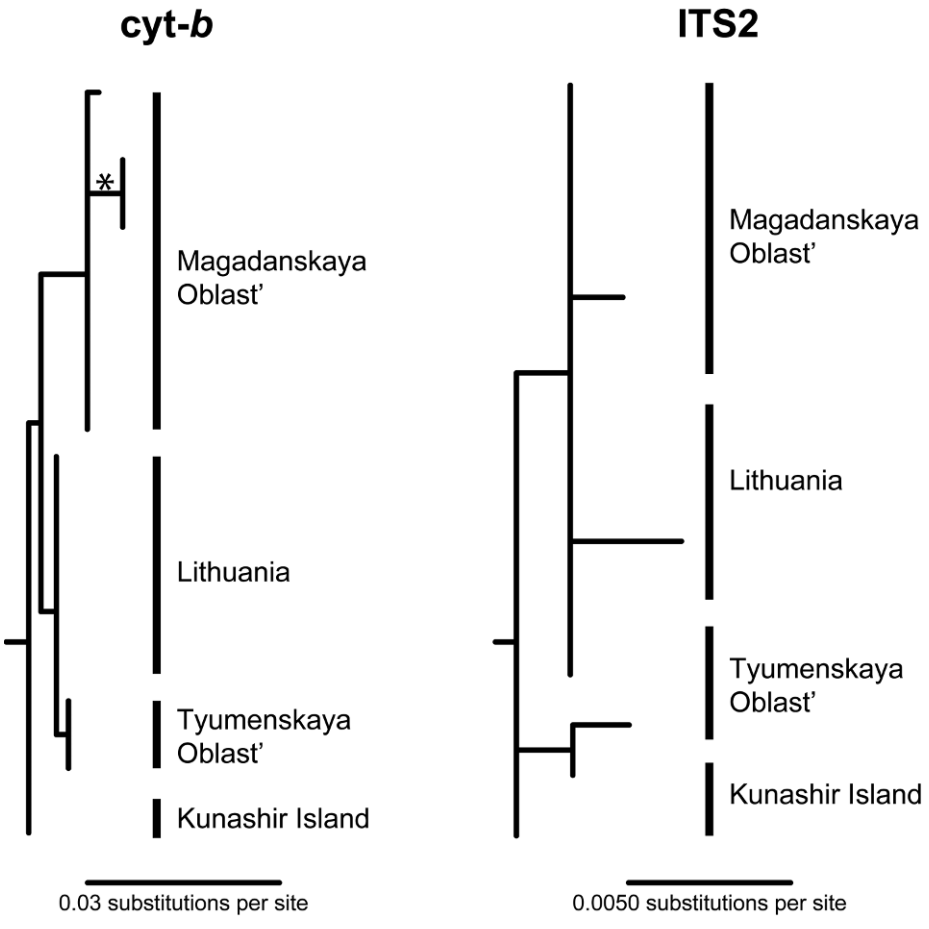

Fig. 3. Best maximum likelihood phylogenies for *Arostrilepis tenuicirrosa* based on cyt-b and ITS2. The node denoted by an asterisk (*) indicates the only relationship that was strongly supported by maximum likelihood bootstrap values (>80) and Bayesian posterior probabilities (>0.95). Outgroups have been removed for clarity

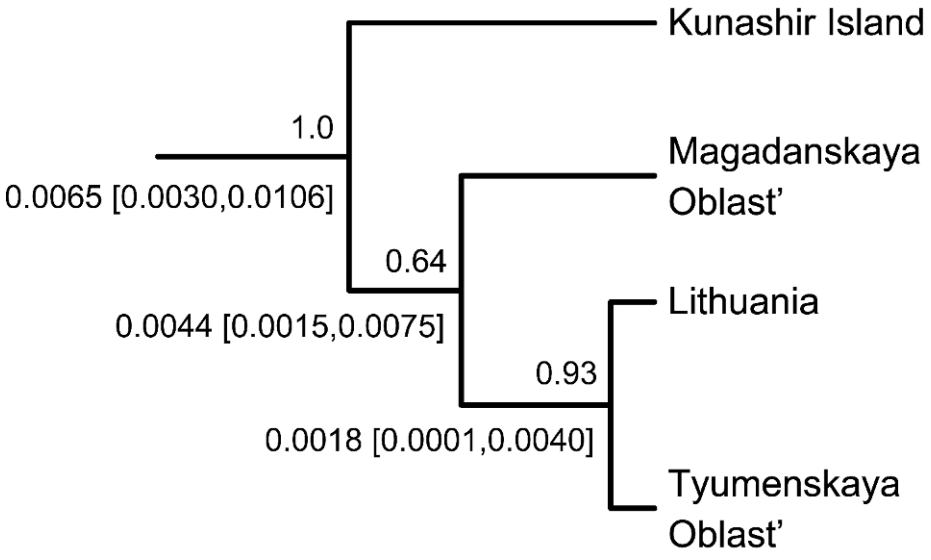

Fig. 4. Results of the multi-locus coalescent-based analysis of relationships among regional populations. Numbers above branches represent Bayesian posterior probabilities for associated nodes. Numbers below branches represent the age of nodes in units of substitutions per site, with 95% highest probability distributions for age estimates enclosed in brackets. The outgroup has been removed for clarity

Ventral osmoregulatory canals 17–58 wide, without transverse anastomoses. Dorsal osmoregulatory canals very thin, hardly seen, located predominantly in same sagittal plane as ventral canals. Genital pores unilateral, dextral.

Mature proglottides 190–330 × 825–1460 (251 × 1148, n = 6) wide, transversely elongate, trapeziform (Fig. 2C). Testes relatively large, usually three, almost of equal size, 194–270 × 120–193 (220 × 154, n = 10), pear-shaped, commonly situated in triangle; poral testis separated from two antiporal testes by female gonads. Cirrus–sac relatively short, 174–213 × 35–49 (199 × 42, n = 7), antiporal part slightly overlaps or crosses ventral longitudinal canal. Genital atrium simple, deep, opens laterally about middle of lateral proglottis margin. Cirrus 67–75 (71, n = 5) length, with relatively wide conical basal region and narrow cylindrical distal region, armed with small needle-shaped spines (2.2–2.8) along its entire length (Fig. 2B). Internal seminal vesicle ovoid, 80–130 × 35–46. External seminal vesicle, 110–135 × 28–92, slightly smaller than seminal receptacle.

Ovary median, 350–600 (431, n = 10) wide, fan–shaped, irregularly lobed, overlapping testes. Vitellarium 90–130 × 170–290 (104 × 203, n = 10), median, weakly lobed. Vagina tubular, ventral to cirrus–sac. Copulatory part of vagina 83–95 length. Seminal receptacle relatively small, transversely elongate, 180–290 × 40–90.

Gravid proglottides transversely elongate, 270–380 × 1300–2320 (329 × 1675, n = 4). Fully developed uterus labyrinthine. Eggs 31×62, oblong, with thin outer coats; oncosphere 10 × 16 (Fig. 2D). Embryophore fusiform, with straight polar processes, 22 × 46. Embryonic hooks small, 7.5–8 long.

Specimens from the western Palearctic agreed in most details with those originally described in *Myodes* voles from Siberia and the Russian Far East (Table II). No significant differences in the form and size of the cirrus, and its armature were detected among specimens of *A. tenuicirrosa* from the original type series (Sakhalin and Kunashir Islands), cestodes distributed at higher latitudes in the Russian Far East (e.g., Magadanskaya Oblast'), those from south-central Russia (Tyumenskaya Oblast'), and those examined from the western Palearctic (Lithuania and Belarus). In specimens from Lithuania, however, the cirrus was slightly longer than in cestodes from the Asian part of Russia. Additionally, in cestodes from the western Palearctic, the dimensions of the hermaphroditic mature proglottids and external seminal vesicle were smaller, and the vitellarium was larger than those observed in specimens from the Russian Far East. However, specimens from Lithuania were macerated and the relatively poor condition may have contributed to observed variation in morphometric characters.

Genetic variation and structure

Independent analyses of mitochondrial and nuclear loci yielded shallow patterns of genetic variation within *A. tenuicirrosa*. Mean uncorrected genetic distances between localities ranged from 0.002 to 0.011 substitutions per site for cyt-*b* and 0.001 to 0.003 substitutions per site for ITS2. This lack of structure is underscored by the occurrence of the same ITS2 allele in populations from Lithuania, Tyumenskaya Oblast', and Magadanskaya Oblast' (Russian Far East). Nucleotide diversity values were similarly low (cyt-*b*: 0.25%; ITS2: 0.14%). In contrast, *A. tenuicirrosa* differed from *A. macrocirrosa* by roughly 0.10 (cyt-*b*) and 0.04 (ITS2) substitutions per site. Low intraspecific levels of divergence are also apparent in independent phylogenies for the two loci. Support is weak for almost all relationships within the phylogenies (Fig. 3). The only consistent pattern that we detected at both loci is a relatively

deep divergence for samples from Kunashir Island. Two shallow clades within the cyt-*b* tree subdivide populations from eastern and western Eurasia, but this structure is not supported by ITS2, from which identical sequences were retrieved from geographically widespread localities. The combined coalescent-based analysis provided slightly better resolution of relationships among the four major geographic regions represented in our sample (Fig. 4). Specifically, specimens from Tyumenskaya Oblast' and Lithuania were found to be sister with reasonably strong support. The relatively early origin of the Kunashir Island lineage is also evident in this result, though support for this relationship remains weak. All sequence data are archived in the GenBank database (Table I).

Discussion

Records for *A. tenuicirrosa* and other *Arostrilepis* spp.

Arostrilepis tenuicirrosa is a specific parasite of red-backed voles (*Myodes*) and its distribution in the Palearctic generally conforms to that of its definitive hosts, which inhabit northern forests, tundra and bogs. Prior records supported recognition of a restricted regional distribution for *A. tenuicirrosa* in the Asian part of Russia extending from the Kurile Islands in the south to near the Arctic Circle in the north (e.g., Makarikov *et al*. 2011; Makarikov *et al*. 2013). Discovery of specimens consistent with *A. tenuicirrosa* from the western Palearctic (Lithuania and Belarus), however, unequivocally demonstrates a broad trans-Palearctic range for this assemblage of hosts and parasites.

Prior to our study, two valid species of *Arostrilepis* were known in the western Palaearctic. The first of these is *A. horrida* (*sensu stricto*) with the type reported to have come from *Rattus norvegicus* (Berkenhout) among the Muridae. This host association has remained enigmatic and is likely incorrect (Linstow 1901; Makarikov *et al*. 2011; Makarikov and Kontrimavichus 2011). The second species is *A. janickii* Makarikov & Kontrimavichus, 2011, which occurs among voles of the genera *Arvicola*, *Microtus* and *Chionomys*. The geographic range for *A. janickii* bears some similarities to that of *A. tenuicirrosa* in that it appears to span the northern Palearctic, having been identified from both Europe and Alaska's Seward Peninsula (Makarikov *et al*. 2013). Species-level diversity of *Arostrilepis* is considerably greater in the eastern Palearctic than it is in the western Palearctic. Five *Arostrilepis* species in addition to *A. tenuicirrosa* are known from Siberia and the Russian Far East (Makarikov *et al*. 2013). Three of these (*A. gulyaevi* Makarikov, Galbreath & Hoberg, 2013, *A. intermedia* Makarikov & Kontrimavichus, 2011, *A. microtis*) may be endemic to the eastern Palearctic while the remaining two (*A. beringiensis*, *A. macrocirrosa*) have distributions that extend across Beringia into the Nearctic. Diversity in North America is also relatively high, with at least four endemic species (*A. cooki* Makarikov, Galbreath & Hoberg, 2013, *A. mariettavogeae*, *A. rauschorum* Makarikov, Galbreath & Hoberg, 2013, *A. schilleri*). Thus, it appears that the major centre of diversity for *Arostrilepis* lies across the Beringian region, with a gradient of declining species richness extending toward the western Palearctic. Overall these distributions may reflect a history of expansion, probably emerging from a center of diversification in eastern Eurasia with periodic episodes of geographic colonization occurring in the Nearctic and the European zone of the Palearctic (e.g., Hoberg *et al*. 2012). We note, however, that the distributional limits of most of these species remain poorly delineated in the absence of geographically extensive taxonomic surveys, particularly in Central Asia (Fig. 1).

In general, cestodes of the genus *Arostrilepis* exhibit specificity at the level of host genus (Makarikov and Kontrimavichus 2011; Makarikov *et al*. 2011, 2012; Makarikov *et al*. 2013). Of the arvicoline rodents that represent primary hosts for *Arostrilepis*, the red-backed voles (genus *Myodes*) harbor the most diverse suite of *Arostrilepis* species, hosting at least four species in addition to *A. tenuicirrosa*. These include apparent eastern Palearctic endemics (*A. gulyaevi, A. intermedia*), a Nearctic endemic (*A. cooki*), and one species with a Holarctic distribution (*A. macrocirrosa*).

Though *A. tenuicirrosa* represents the only species of the genus that is definitively known to parasitize *Myodes* in the western Palearctic, our growing understanding of diversity in this cestode complex emphasizes the need to critically re-evaluate previous reports of *A. horrida* in red-backed voles from Europe and western Asia (e.g. Rybicka 1959; Mozgovoi *et al*. 1966; Murai and Tenora 1973). It is likely that some of these previous records could be attributed to *A. tenuicirrosa* or other species. Further sampling of parasites of small mammals will also be necessary to fully characterize the *Arostrilepis* community in the region. For example, the north-western sector of the Palearctic (Fennoscandia) is of particular interest given that *Arostrilepis* has not been detected in this region despite the abundant presence of various potential host species and extensive helminthological surveys, particularly in Finland. There is only a single record of specimens identified as *H. horrida* in *M. glareolus* from the borders of south-eastern Fennoscandia (Karelia) with very low prevalence (1.7%) (Mozgovoi *et al*.1966). In subsequent helminthological studies of arvicoline rodents from Fennoscandia, *Arostrilepis* was not detected (Tenora *et al*. 1979; Tenora *et al*. 1983; Tenora *et al*. 1985; Haukisalmi 1986; Haukisalmi and Henttonen 1993; Haukisalmi and Henttonen 2001; Laakkonen *et al*. 2001).

Population structure and historical biogeography of *A. tenuicirrosa*

Results of both our morphological and molecular analyses of geographic structure within *A. tenuicirrosa* demonstrate no evidence of deep phylogeographic structure across the range of the species. This is striking given that the species has an extensive distribution across the heterogeneous and paleoecologically dynamic Asian landscape. If the parasite occupied this broad range over deep time (e.g., spanning multiple gla-

cial-interglacial cycles), we would predict that repeated opportunities for climate-driven population fragmentation would have produced separate regional lineages evolving along independent trajectories. Such a history might explain why the three most important hosts of *A. tenuicirrosa* (*M. rutilus*, *M. rufocanus*, *M. glareolus*) all exhibit deep phylogeographic structure (up to 4% cyt-*b* sequence divergence in the voles versus ≤1.1% in the cestode) across smaller spatial scales (Iwasa *et al*. 2000; Iwasa *et al*. 2002; Deffontaine *et al*. 2005).

Shallow inter-population genetic structure with low levels of nucleotide diversity may reflect 1) long or short-term persistence across the current broad distribution with a reduction in diversity caused by a recent selective sweep, 2) long or short-term persistence across the current distribution coupled with a low rate of molecular evolution, or 3) recent geographic expansion from a relatively small founder population. A selective sweep seems to be an unlikely explanation for low levels of diversity given that we failed to detect evidence of selection at either locus. Further, both cyt-*b* and ITS2 exhibited similar patterns of genetic variation, yet these unlinked loci are unlikely to be influenced by the same selective pressures. Thus, a selective sweep that decreases diversity at one locus would be expected to leave ancestral polymorphism undiminished at an independent locus.

Rates of molecular evolution in hymenolepidid and other cyclophyllidean tapeworms have not been well-studied, leaving open the possibility that an exceptionally slow rate of nucleotide substitution could explain the observed lack of deep structure among populations. However, our previous phylogenetic investigations of the *Arostrilepis* complex suggest that evolutionary rates within the group should be rapid enough to produce ample genetic variation over moderate time scales. For example, two *Arostrilepis* sister species associated with *Myodes* voles (*A. cooki* and *A. macrocirrosa*) differ by 4.5% sequence divergence at the cyt-*b* locus (Makarikov *et al*. 2013). Biogeographic histories for the hosts suggest that isolation between these two cestode species may have occurred in the Late Pliocene or Early Pleistocene (ca. 2 to 3 Ma; Cook *et al*. 2004). Thus, the considerably lower levels of divergence evident within *A. tenuicirrosa* probably reflect variation that has accumulated over a much shallower (e.g., Late Pleistocene) time scale.

A more likely explanation for the widespread distribution of *A. tenuicirrosa* and limited genetic diversity may be that the cestode underwent a Late Pleistocene range expansion from a geographically restricted founder population and has yet to accumulate deep phylogeographic structure across its current range. Our data are insufficient to provide a definitive perspective on relationships among *A. tenuicirrosa* populations, but the indication that eastern populations are derived from the deepest splits in the multi-locus phylogeny (Fig. 4) suggests an East Asian source for extant populations. Population range dynamics are presumably closely linked to host biogeographic histories, suggesting that geographic expansion by the parasite from an eastern source might be mirrored by a similar zoogeographic history in its hosts. Of the four known hosts of *A. tenuicirrosa*, *M. rutilus* and *M. rufocanus* have the widest distributions, linking Northern Europe and East Asia. Thus, if we assume that host associations have been relatively constant over time, a scenario of expansion from the east would most likely involve dispersal mediated by one or both of these hosts. Colonization of *M. glareolus*, which is currently restricted to western Eurasia, might therefore represent an instance of host-switching following a range expansion event that created novel host-parasite interactions (taxon pulse with ecological fitting; Hoberg and Brooks 2008; Hoberg *et al*. 2012). This presumed host-switch apparently allowed *A. tenuicirrosa* to expand into Lithuania and surrounding regions, which lie beyond the current distribution of *M. rutilus* and *M. rufocanus*. Though the demographic histories of Eurasian *Myodes* have not been thoroughly examined, evidence from the fossil record suggests that *M. rufocanus* probably originated in East Asia during or before the Middle Pleistocene and subsequently expanded its range westward to Europe (Chaline and Graf 1988). Such a history is consistent with patterns of genetic diversity observed in *A. tenuicirrosa*.

This biogeographic scenario represents a testable hypothesis that makes several predictions regarding the distribution of diversity across Eurasia. First, *A. tenuicirrosa*, *M. rufocanus*, and possibly *M. rutilus* are expected to exhibit signatures of demographic expansion, particularly in the western Palearctic. If range expansion occurred rapidly, western populations would be predicted to be phylogenetically nested within eastern populations and may exhibit lower levels of genetic diversity due to founder events along the leading edge of expansion ("pioneer" dispersal; Hewitt 1996). Under these conditions, the distribution of parasites can also lag behind the host range due to parasites "missing-the-boat" (Paterson and Banks 2001), which would result in a declining species diversity gradient from east to west across Eurasia. The occurrence of four *Arostrilepis* parasites of *Myodes* in East Asia and only one in the western Palearctic is consistent with this scenario, which could also explain the apparent absence of *A. tenuicirrosa* from most of Fennoscandia. That region was colonized during the Holocene by *Myodes* voles following the retreat of glacial ice roughly 10 ka. Robust tests of these hypotheses will require extensive geographic sampling of mammal and parasite populations across Eurasia to fully characterize range-wide patterns of diversity. Further, to resolve species histories (e.g., population structure, change in effective population size over time, range fluctuation) it will be necessary to estimate demographic parameters using coalescent approaches applied to multi-locus DNA sequence datasets.

Acknowledgements. This study is a contribution of the Beringian Coevolution Project supported in part by the National Science Foundation (DEB 0196095 and 0415668) organized by Joseph Cook at the Museum of Southwestern Biology, University of New Mexico and EPH at the USNPC to explore the structure and distribution of

complex host-parasite systems across Beringia and the Holarctic. AAM was supported by the National Science Foundation (PBI grants DEB 0818696 and 0818823) coordinated by J. Caira, University of Connecticut. KEG received a reassigned time award from Northern Michigan University to support this project. We are grateful to Dr. Vytautas Kontrimavichus and Dr. Svetlana Bondarenko, who made useful contributions in preparation of the manuscript. We wish to thank Dr. Elizaveta Bychkova and Dr. Tatiana Shendrik, the curators of the cestode collections of the Scientific and Practical Center for Bioresources, Minsk, Republic of Belarus.

References

Abramson N.I., Abramov A.V., Baranova G.I. 2009. New species of red-backed vole (Mammalia: Rodentia: Cricetidae) in fauna of Russia: molecular and morphological evidences. *Proceedings of the Zoological Institute RAS*, 313, 3–9.

Asakawa M., Tenora F., Koubkova B. 2002. *Arostrilepis horrida* (Linstow, 1901) (Cestoda: Hymenolepididae) from *Eothenomys* spp. (Rodentia) in Japan. *Biogeography*, 4, 51–55.

Baer J.G. 1932. Contribution á la faune helminthologique de Suisse. *Revue Suisse de Zoologie*, 39, 1–57.

Chaline J., Graf J.-D. 1988. Phylogeny of the Arvicolidae (Rodentia): biochemical and paleontological evidence. *Journal of Mammalogy*, 69, 22–33.

Cook J.A., Hoberg E.P., Koehler A., Henttonen H., Wickström L., Haukisalmi V., Galbreath K., Chernyavski F., Dokuchaev N., Lahzuhtkin A., MacDonald S.O., Hope A., Waltari E., Runck A., Veitch A., Popko R., Jenkins E., Kutz S., Eckerlin R. 2005. Beringia: Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study*, 30, S33–S44. DOI: 10.3106/1348-6160(2005)30[33:BIEADO]2.0.CO;2.

Cook J.A., Runck A.M., Conroy C.J. 2004. Historical biogeography at the crossroads of the northern continents: molecular phylogenetics of red-backed voles (Rodentia : Arvicolinae). *Molecular Phylogenetics and Evolution*, 30, 767–777. DOI: 10.1016/S1055-7903(03)00248-3.

Deffontaine V., Libois R., Kotlík P., Sommer R., Nieberding C., Paradis E., Searle J. B., Michaux J. R. 2005. Beyond the Mediterranean peninsulas: evidence of central European glacial refugia for a temperate forest mammal species, the bank vole (*Clethrionomys glareolus*). *Molecular Ecology*, 14, 1727–1739. DOI: 10.1111/j.1365-294X.2005.02506.x.

Drummond A., Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7, 214. DOI:10.1186/1471-2148-7-214.

Erhardová B. 1958. (Parasitic worms of rodents in Czecho-Slovakia). *Čs. Parasitologie*, 5, 52–53 (In Czech).

Fedorov K.P. 1986. Patterns of spatial distribution of parasitic worms. Izdatel'stvo Nauka, Novosibirsk, 256 pp. (In Russian).

Genov T. 1984. [Helminths of insectivores and rodents in Bulgaria.] Izdatelstvo na Bulgarskata Akademiya na Naukite, Sofia, 348 pp. (In Bulgarian).

Gulyaev V.D., Chechulin A.I. 1997. *Arostrilepis microtis* n. sp. (Cyclophyllidea: Hymenolepididae), a new cestode species from Siberian rodents. *Research and Reviews in Parasitology*, 57, 103–107.

Hasegawa M., Kishino K., Yano T. 1985. Dating the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, 22, 160–174.

Haukisalmi V. 1986. Frequency distributions of helminths in microtine rodents in Finnish Lapland. *Annales Zoologici Fennici*, 23, 141–150.

Haukisalmi V., Hardman L.M., Niemimaa J., Henttonen H. 2007. Taxonomy and genetic divergence of *Paranoplocephala kalelai* (Tenora, Haukisalmi & Henttonen, 1985) (Cestoda: Anoplocephalidae) in the grey-sided vole *Myodes rufocanus* in northern Fennoscandia. *Acta Parasitologica*, 52, 335–341. DOI: 10.2478/s11686-007-0043-y.

Haukisalmi V., Henttonen H. 1993. Coexistence in helminths of the bank vole *Clethrionomys glareolus*. I. Patterns of co-occurrence. *Journal of Animal Ecology*, 62, 221–229.

Haukisalmi V., Henttonen H. 2001. Biogeography of helminth parasitism in *Lemmus* Link (Arvicolinae), with the description of *Paranoplocephala fellmani* n. sp. (Cestoda: Anoplocephalidae) from the Norwegian lemming *L. lemmus* (Linnaeus). *Systematic Parasitology*, 49, 7–22.

Haukisalmi V., Hardman L.M., Henttonen H., Laakonen J., Niemimaa J., Hardman M., Gubányi A. 2009. Molecular systematics and morphometrics of *Anoplocephaloides dentata* (Cestoda: Anoplocephalidae) and related species in voles and lemmings. *Zoologica Scripta*, 38, 199–220.

Haukisalmi V., Hardman L.M., Foronda P., Feliu C., Laakkonen J., Niemimaa J., Lehtonen J.T., Henttonen H. 2010. Systematic relationships of hymenolepidid cestodes of rodents and shrews inferred from sequences of 28S ribosomal RNA. *Zoologica Scripta*, 39, 631–641. DOI: 10.1111/j.1463-6409.2010.00444.x.

Heled J., Drummond A.J. 2010. Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution*, 27, 570–580. DOI: 10.1093/molbev/msp274.

Hewitt G.M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, 58, 247–276.

Hoberg E.P., Brooks D.R. 2008. A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host-parasite systems. *Journal of Biogeography*, 35, 1533–1550. DOI: 10.1111/j.1365-2699.2008.01951.x.

Hoberg E.P., Galbreath K.E., Cook J.A., Kutz S.J., Polley L. 2012. Northern host-parasite assemblages: history and biogeography on the borderlands of episodic climate and environmental transition. *Advances in Parasitology*, 79, 1–97. DOI: 10.1016/B978-0-12-398457-9.00001-9.

Hoberg E.P., Kutz S.J., Galbreath K.E., Cook J. 2003. Arctic biodiversity: From discovery to faunal baselines- revealing the history of a dynamic ecosystem. *Journal of Parasitology*, 89, S84–S95.

Hudson R.R., Kreitman M., Aguadé M. 1987. A test of neutral molecular evolution based on nucleotide data. *Genetics*, 116, 153–159.

Huelsenbeck J.P., Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755.

Hwang Y.T., Gardner S.L., Millar J.S. 2007. *Hymenolepis horrida* (Cestoda: Hymenolepididae) and *Catenotaenia peromysci* (Cestoda: Anoplocephalidae) in voles from the Canadian Rockies. *Comparative Parasitology*, 74, 160–163. DOI: 10.1654/4256.1.

Iwasa M.A., Kartavtseva I.V., Dobrotvorsky A.K., Panov V.V., Suzuki H. 2002. Local differentiation of *Clethrionomys rutilus* in northeastern Asia inferred from mitochondrial gene sequences. *Mammalian Biology*, 67, 157–166. DOI: 10.1078/1616-5047-00023.

Iwasa M.A., Utsumi Y., Nakata K., Kartavtseva I.V., Nevedomskaya I.A., Kondoh N., Suzuki H. 2000. Geographic patterns of cytochrome b and Sry gene lineages in the gray red-backed vole *Clethrionomys rufocanus* from Far East Asia Including Sakhalin and Hokkaido. *Zoological Science*, 17,477-484. DOI: 10.2108/0289-0003(2000)17[477:GPOCBA]2.0.CO;2.

Johri G.N. 1956. On a new cestode from the palm squirrel, *Funambulus palmarum* Linn. *Proceedings of the National Academy of Sciences of Allahabad*, 26 (Series B), 274–277.

Kimura M. 1981. Estimation of evolutionary distances between homologous nucleotide sequences. *Proceedings of the National Academy of Sciences of the U.S.A.*, 78, 454–458.

Kontrimavichus V.L., Smirnova L.V. 1991. *Hymenolepis beringiensis* sp. n. from the Siberian lemming (*Lemmus sibiricus* Kerr) and the problem of the sibling species in helminthology. In: (Eds. Krasnosohekov G.P., Roitman V.A., Sonin M.D., Chesnova L.V.). Evoljucia parazitov. *Materialy I Vsesojuznogo Simpoziuma*. Tol'yatti, Akademiya Nauk SSSR, pp. 90–104 (In Russian).

Laakkonen J., Haukisalmi V., Niemimma J., Henttonen H. 2001. Parasite diversity of Norweigian lemmings (*Lemmus lemmus*). *Zoological Journal*, 253, 549–553. DOI: 10.1017/S0952836901000504.

Librado P., Rozas J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25, 1451–1452.

Linstow O. 1901. *Taenia horrida*, *Tetrabothrium macrocephalum*, und *Heterakis distans*. *Archiv für Naturgeschichte*, 67, 1–10.

Makarikov A.A. 2008. Cestodes of the family Hymenolepididae Perrier, 1897 in rodents from the Asian part of Russia. PhD Thesis, Rossiiskaja Akademija Nauk Sibirskoe Otdelenie Institut Sistematiki I Ekologii Zhivotnikh, Novosibirsk, Russia.

Makarikov A.A., Galbreath K.E., Hoberg E.P. 2013. Diversity at the Holarctic nexus: species of *Arostrilepis* (Eucestoda: Hymenolepididae) in arvicoline rodents (Cricetidae: Arvicolinae) from greater Beringia. *Zootaxa*, 3608, 401–439.

Makarikov A.A., Gardner S.L., Hoberg E.P. 2012. New species of *Arostrilepis* (Eucestoda: Hymenolepididae) in members of Cricetidae and Geomyidae (Rodentia) from the Western Nearctic. *Journal of Parasitology*, 98, 617–626. DOI: 10.1645/GE-2943.1.

Makarikov A.A., Gulyaev V.D., Kontrimavichus V.L. 2011. A redescription of *Arostrilepis horrida* (Linstow, 1901) and descriptions of two new species from Palaearctic microtine rodents, *Arostrilepis macrocirrosa* sp. n. and *A. tenuicirrosa* sp. n. (Cyclophyllidea: Hymenolepididae). *Folia Parasitologica*, 58, 108–120.

Makarikov A.A., Kontrimavichus V.L. 2011. A redescription of *Arostrilepis beringiensis* (Kontrimavichus et Smirnova, 1991) and descriptions of two new species from Palearctic microtine rodents, *Arostrilepis intermedia* sp. n. and *A. janickii* sp. n. (Cestoda: Hymenolepididae). *Folia Parasitologica*, 58, 289–301.

Mas-Coma S., Tenora F. 1997. Proposal of *Arostrilepis* n. gen. (Cestoda: Hymenolepidae). *Research and Reviews in Parasitology*, 57, 93–101.

Mas-Coma S., Tenora F., Gallego J. 1980. Consideraciones sobre los Hymenolepídidos inermes de Roedores, con especial referencia a la problemática entorno a *Hymenolepis diminuta*. *Circular Farmacéutica*, 38, 137–152.

Merkusheva I.V., Bobkova A.F. 1981. [Helminths of domesticated and wild animals in Belarus.] Nauka i Tehnika, Minsk, 120 pp. (In Russian).

Mozgovoi A.A., Semenova M.K., Mishchenko R.I., Tsibatova S.W. 1966. [Helminthofauna of rodents and leporids of Karelia]. *Trudy Gel'mintologicheskoi Laboratorii*, 17, 95–103 (In Russian).

Murai E., Tenora F. 1973. *Hymenolepis horrida* (Linstow, 1901) from Microtinae in Hungary. *Parasitologia Hungarica*, 6, 111–116.

Okamoto M., Agatsuma T., Kurosawa T., Ito A. 1997. Phylogenetic relationships of three hymenolepidid species inferred from nuclear ribosomal and mitochondrial DNA sequences. *Parasitology*, 115, 661–666.

Padgett K.A., Nadler S.A., Munson L., Sacks B., Boyce W.M. 2005. Systematics of *Mesocestoides* (Cestoda: Mesocestoididae): evaluation of molecular and morphological variation among isolates. *Journal of Parasitology*, 91, 1435–1443. DOI: 10.1645/GE-3461.1.

Paterson A.M., Banks J. 2001. Analytical approaches to measuring cospeciation of host and parasites: through a glass, darkly. *International Journal for Parasitology*, 31, 1012–1022. DOI: 10.1016/S0020-7519(01)00199-0.

Posada D., Crandall K.A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.

Prokopic J., Mahnert V. 1970. Uber Helminthen der Kleinsauger (Insectivora, Rodentia) Tirols (Österreichs). *Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck*, 58, 143–154.

Rambaut A., Drummond A.J. 2007. Tracer v1.5. Available from http://beast.bio.ed.ac.uk/Tracer.

Rausch R.L. 1952. Studies on the helminth fauna of Alaska. XI. Helminth parasites of microtine rodents – taxonomic considerations. *Journal of Parasitology*, 38, 415–444.

Rybicka K. 1959. Tapeworms of forest micromammals (Rodentia and Insectivora) from Kampinos Wilderness. *Acta Parasitologica Polonica*, 7, 393–421.

Ryzhikov K.M., Gvozdev E.V., Tokobaev M.M., Shaldybin L.S., Matzaberidze G.V., Merkusheva I.V., Nadtochii E.V., Khohlova I.G., Sharpilo L.D. 1978. [Keys to the helminths of the rodent fauna of the USSR. Cestodes and trematodes.] Izdatel'stvo Nauka, Moskva, 232 pp. (In Russian).

Santalla F., Casanova J.C., Durand P., Vaucher C., Renaud F., Feliu C. 2002. Morphometric and genetic variability of *Rodentolepis asymmetrica* (Hymenolepididae) from the Pyrenean mountains. *Journal of Parasitology*, 88, 983–988. DOI: 10.1645/0022-3395(2002)088[0983:MAGVOR]2.0.CO;2.

Schiller E.L. 1952. Studies on the helminth fauna of Alaska. X. Morphological variation in *Hymenolepis horrida* (von Linstow, 1901) (Cestoda: Hymenolepididae). *Journal of Parasitology*, 38, 554–568.

Tamura K., Peterson D., Peterson N., Stecher G., Nei M., Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739. DOI: 10.1093/molbev/msr121.

Tenora F., Henttonen H., Haukisalmi V. 1983. On helminths of rodents in Finland. *Annales Zoologici Fennici*, 20, 37–45.

Tenora F., Henttonen H., Haukisalmi V. 1985. New findings of helminths in rodents in Finland. *Folia Parasitologica*, 32, 33.

Tenora F., Wiger R., Baruš V. 1979. Seasonal and annual variations in the prevalence of helminths in a cyclic population of *Clethrionomys glareolus*. *Holarctic Ecology*, 2, 176–181.

Voge M. 1952. Variation in some unarmed Hymenolepididae (Cestoda) from rodents. *University of California Publications in Zoology*, 57, 1–52.

Wickström L.M., Haukisalmi V., Varis S., Hantula J., Fedorov V.B., Henttonen H. 2003. Phylogeography of the circumpolar *Paranoplocephala arctica* species complex (Cestoda: Anoplocephalidae) parasitizing collared lemmings (*Dicrostonyx* spp.). *Molecular Ecology*, 12, 3359–3371. DOI: 10.1046/j.1365-294X.2003.01985.x.

Żarnowski E. 1955. [Parasitic worms of forest small mammals (Rodentia and Insectivora) near Pulawy (Lublin). I. Cestoda]. *Acta Parasitologica Polonica*, 3, 279–368 (In Polish).

Zwickl D.J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. Thesis, University of Texas at Austin, USA.

(Accepted: June 14, 2013)