

Late Cenozoic history and the role of Beringia in assembling a Holarctic cestode species complex

Kurt E. Galbreath^{a,*}, Arseny A. Makarikov^b, Kayce C. Bell^c, Stephen E. Greiman^d, Julie M. Allen^e, Genevieve M. S. Haas^a, Chenhong Li^f, Joseph A. Cook^g, Eric P. Hoberg^g

^a Northern Michigan University, 1401, Presque Isle Ave, Marquette, MI 49855, United States

^b Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, Novosibirsk, Russia

^c Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007, United States

^d Department of Biology, Georgia Southern University, Statesboro, GA 30458, Georgia, United States

^e Biology Department, University of Nevada, Reno, NV 89557, United States

^f Key Laboratory of Exploration and Utilization of Aquatic Genetic Resources, Ministry of Education, Shanghai Ocean University, Shanghai 201306, People's Republic of China

^g Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM, United States

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ABSTRACT

The dynamic climate history that drove sea level fluctuation during past glacial periods mediated the movement of organisms between Asia and North America via the Bering Land Bridge. Investigations of the biogeographic histories of small mammals and their parasites demonstrate facets of a complex history of episodic geographic colonization and refugial isolation that structured diversity across the Holarctic. We use a large multi-locus nuclear DNA sequence dataset to robustly resolve relationships within the cestode genus *Arostrilepis* (Cyclophylidae: Hymenolepididae), a widespread parasite of predominantly arvicoline rodents (voles, lemmings). Using this phylogeny, we confirm that several Asian *Arostrilepis* lineages colonized North America during up to four distinct glacial periods in association with different rodent hosts, consistent with taxon-pulse dynamics. A previously inferred westward dispersal across the land bridge is rejected. We also refine interpretations of past host colonization, providing evidence for several distinct episodes of expanding host range, which probably contributed to diversification by *Arostrilepis*. Finally, *Arostrilepis* is shown to be paraphyletic with respect to *Hymenandrya thomomys*, a parasite of pocket gophers, confirming that ancient *Arostrilepis* species colonized new host lineages upon arriving in North America.

1. Introduction

The rich mosaic of mammal and parasite communities that occupy North America was largely assembled through waves of intercontinental colonization from Asian sources (Cook et al., 2017; Hoberg et al., 2012; Rausch, 1994). Prior to the Late Miocene, the northern continents were joined into a single landmass that allowed relatively unimpeded dispersal between the western and eastern hemispheres (Sher, 1999). Since the Miocene, dispersal between the continents has been mediated by pulses of climate cooling that periodically caused continental ice sheets to expand and sea levels to drop. During episodes of climate cooling, beginning in the late Pliocene and continuing through the Pleistocene, the Bering Land Bridge emerged from the Bering and Chukchi Seas, creating opportunities for terrestrial taxa to pass between

Asia and North America (Hoberg et al., 2017; Hopkins, 1959). During glacial stages of the Pleistocene, Beringia was delineated by a porous western boundary in central Siberia and a continuous barrier of glacial ice walling off its eastern flank (Arkhipov et al., 1986; Hoffmann, 1981). With global cooling beginning in the Late Pliocene and extending into the Pleistocene, the region increasingly functioned as a filter bridge that facilitated colonization by cold-resilient taxa and inhibited dispersal by temperate faunas. Temperature gradients structured ecological communities through cycles of geographic colonization and subsequent population fragmentation and isolation (Hoberg and Brooks, 2010; Kafle et al., 2020). The Beringian landscape resulted in more Asian taxa expanding eastward than North American taxa moving to the west (Waltari et al., 2007).

Mybp, million years before present

* Corresponding author.

E-mail address: kgalbrea@nmu.edu (K.E. Galbreath).

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Episodic, climate-driven pulses of transberingian colonization produced a complex patchwork or mosaic of ancient and recent faunas distributed across the Holarctic (Hoberg and Brooks, 2008). The processes that underlie this history of community assembly are described as elements of the Stockholm Paradigm, which provides a general framework for understanding how environmental change interacts with organismal capacity and opportunity for geographic colonization and expanding host range to explain the structure of biodiversity (Agosta and Brooks, 2020; Brooks et al., 2019). Across Beringia, pulses of geographic colonization and accompanying host colonization by parasites led to the formation of diverse parasite assemblages, the histories of which are refining our general understanding of regional and intercontinental biogeographic histories and ecological dynamics (e.g., Galbreath and Hoberg, 2012; Galbreath et al., 2020; Hoberg et al., 2012).

Cestodes of the genus *Arostrilepis* Mas-Coma et Tenora, 1997 (Cyclophyllidae: Hymenolepididae) make up a diverse parasite assemblage centered on Beringia that offers insight into the complex factors that shaped communities across the Holarctic (Haas et al., 2020; Makarikov et al., 2013). There are at least 20 major genetically distinct and divergent lineages of *Arostrilepis*, including both named species and unnamed lineages. These lineages evolved in close association with arvicoline rodents (voles and lemmings), which have provided perspectives on transberingian connectivity of northern ecosystems (Cook et al., 2004; Fedorov et al., 1999; Galbreath and Cook, 2004; Hope et al., 2013), instances of climate-driven range fluctuation (Fedorov, 1999; Kohli et al., 2015), changes in effective population size (Fedorov et al., 2020), and placement of glacial and interglacial refugial zones (Conroy and Cook, 2000b; Cook et al., 2001; Fedorov and Stenseth, 2002). Our prior work on *Arostrilepis* inferred 4 eastward and 2 westward geographic expansion events across Beringia, as well as up to 12 episodes of host colonization (Haas et al., 2020). Poor resolution of some nodes

and an inability to time-calibrate the phylogeny, however, limited clarification of parasites' histories in the context of their hosts. Further, monophyly of *Arostrilepis* was called into question, with another hymenolepidid, *Hymenandrya thomomyis* Smith, 1954, rendering *Arostrilepis* paraphyletic in a phylogeny based on the mitochondrial cytochrome *b* gene. A multi-locus phylogeny indicated monophyly for *Arostrilepis*, but with poor nodal support. Here we address these uncertainties by reconstructing a portion of the *Arostrilepis* phylogeny based on a large multi-locus nuclear sequence dataset that also includes *H. thomomyis*. We address the following questions, which are derived from our previous observations (Haas et al., 2020): 1) How many episodes of transberingian colonization by *Arostrilepis* took place, and in which directions? 2) How many host colonization events are required to reconcile the phylogeny to current host associations? 3) Is *Arostrilepis* monophyletic with respect to *H. thomomyis*?

2. Methods

2.1. Nuclear sequencing

We used target gene enrichment to acquire multi-locus nuclear sequence data from a single specimen of *H. thomomyis* and 24 *Arostrilepis* specimens (Supplemental Table S1) sampled from sites distributed across the Holarctic (Fig. 1). These represented nine nominal species and two undescribed lineages documented previously (Haas et al., 2020). This sequencing approach is described in detail elsewhere (Yuan et al., 2016), but in brief, RNA baits for targeted sequence capture of single-copy coding regions were designed using reference genomes from the cyclophyllidean cestodes *Echinococcus granulosus* (Batsch, 1786), *Taenia solium* Linnaeus, 1758, and *Rodentolepis microstoma* (Dujardin, 1845) (identified as *Hymenolepis microstoma* in GenBank). Baits were hybridized to sheared genomic DNA to create DNA libraries en-

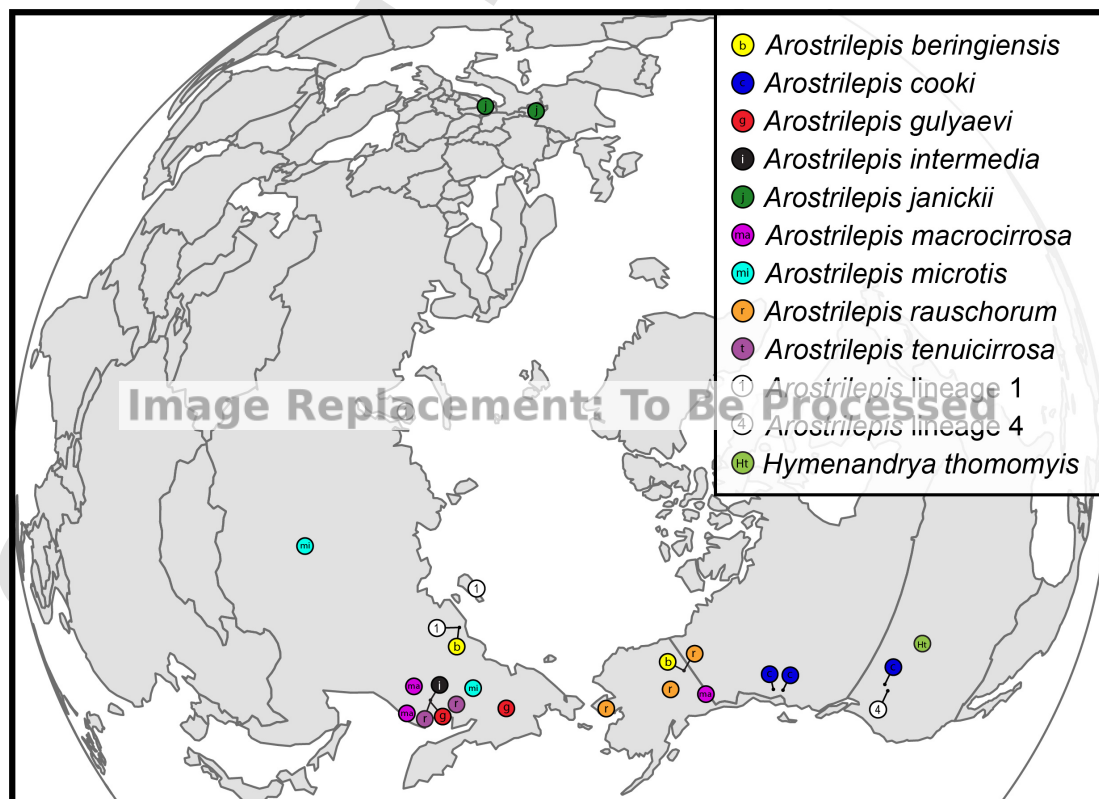


Fig. 1. Map showing sampling distribution across the Holarctic for *Arostrilepis* specimens from which DNA sequence data were collected for the current study. Color-coded circles with letter or number codes indicating species or lineage identity denote sampling localities. In instances where symbols would overlap, a line is used to denote the position of sampling localities.

riched for target loci. Enriched samples were PCR-amplified with indexed primers, pooled, and sequenced on an Illumina HiSeq 2500 sequencer (Illumina, Inc, San Diego, CA, USA). Raw sequence reads were organized by specimen and passed through a data processing pipeline that trimmed adapters and poor-quality sequence reads, mapped reads to target loci, and assembled contigs for each locus.

To select loci for phylogenetic analyses in this study, we first screened the full nuclear dataset to identify loci that were well-represented across species. Specifically, we selected loci for which a minimum of one individual per species was represented by > 75 % of the full locus sequence. This selection process identified 99 loci that matched these criteria, which were then screened for recombination using the default recombination detection methods implemented in RDP v4.97 (Martin et al., 2015). For a given locus, if putative recombination was detected, the locus was either trimmed to retain the largest non-recombining portion of the sequence, or excluded entirely if evidence for recombination occurred throughout. Seven loci were excluded due to strong evidence for recombination. Sequences for the remaining 92 loci are archived in GenBank (accession numbers OQ211676-OQ213903).

Finally, to incorporate an outgroup for phylogenetic analyses we used aTRAM v2.0 (Allen et al., 2015; Allen et al., 2018) to assemble homologous sequences from a shotgun sequence dataset (GenBank BioSample accession # SAMN30713040) previously generated for *Pseudobotrialepis globosoides* (Soltys, 1954) using the trinity *de novo* assembler (Grabherr et al., 2011). *Pseudobotrialepis* Schaldybin, 1957 is closely related to *Arostrilepis* (Haukisalmi et al., 2010; Neov et al., 2019). We were unable to identify orthologs from *P. globosoides* for 30 loci. Therefore, our final focal dataset included 62 loci, all of which included sequence data representing the outgroup and all ingroup species, though we also prepared the 62-locus and 92-locus datasets for phylogenetic analysis without the outgroup. Data matrices for each locus were aligned using MUSCLE (Edgar, 2004) as implemented in MEGA v11 (Tamura et al., 2021). Most loci aligned unambiguously, lacking indels and repetitive motifs that could introduce ambiguity into alignments. Alignments with indels were translated to amino acid sequences in MEGA to confirm that placement of indels did not alter the reading frame of the sequences. A repetitive motif present in a single locus that was part of the 92-locus dataset (GenBank numbers OQ213000 to OQ213024), but not the 62-locus dataset, resulted in a section of ambiguous alignment (12 to 27 nucleotides beginning at position 296) that was excluded from analyses.

2.2. Phylogenetic analysis

To evaluate relationships among *Arostrilepis* species, we performed both traditional and coalescent-based phylogenetic analyses. We first concatenated the loci of the outgroup-rooted 62-locus dataset to form a single data matrix approximately 28,430 nucleotides in length. Next, we used ModelFinder (Kalyaanamoorthy et al., 2017) in combination with a partition-scheme selection algorithm (Lanfear et al., 2012) implemented in IQ-TREE v2.0 (Nguyen et al., 2014) to determine an appropriate partitioning scheme and associated set of nucleotide substitution models for the data. A two-partition scheme was selected in which one partition grouped 42 loci (SYM + I + G model) and the other grouped 20 loci (K2P + G model). This partition scheme was applied in a maximum likelihood analysis using the edge-linked partition model in IQ-TREE (Chernomor et al., 2016). To assess nodal support, we generated 1000 bootstrap replicates using the ultra-fast bootstrap method implemented in IQ-TREE (Hoang et al., 2017).

Because concatenation of unlinked loci fails to account for independent genealogical histories among loci that can yield insight into the true species tree, we applied the multi-species coalescent approach implemented in StarBEAST2 (Ogilvie et al., 2017) using BEAST v2.67 (Bouckaert et al., 2019; Heled and Drummond, 2012). We applied a

strict molecular clock and linked the clock model among loci, but allowed the site models and trees to vary among loci. Individuals were assigned to species (or major lineages that may represent unnamed species) described previously (Haas et al., 2020), and we applied analytical population size integration to increase computational efficiency. We used the automodel function in PAUP* v4.0a169 (Swofford 2003) to select appropriate models of nucleotide substitution for each locus, and these were applied in BEAUti. In instances where a perfect match was not available in BEAUti, we applied the next more complex model that included all parameters from the originally selected model. Nucleotide frequencies were fixed to empirical values to reduce model complexity and the yule model was chosen for the tree prior. The StarBEAST2 analysis was completed via two independent runs of 1 billion generations each, with sampling every 500,000 generations. Stationarity of traces and convergence of parameter values between runs were confirmed using Tracer v1.7.1 (Rambaut et al., 2018). A burnin of 10 % was discarded prior to calculating the final tree topology and parameter estimates. All parameters achieved ESS values > 200.

Because the multi-species coalescent method does not require an outgroup to root species trees, rather establishing the root node in the phylogeny based on a clock model, we ran an additional StarBEAST2 analysis as described above (except with run length of 2 billion generations to achieve adequate ESS values) on the 62-locus dataset without *P. globosoides*. This allowed a test of the robustness of the root node estimate with and without the outgroup. Finally, to assess the effect of including additional sequence data on the tree topology, and in particular whether or not it would aid in resolving poorly supported relationships, we repeated the StarBEAST2 analysis as described above (except with run length of 2 billion generations) using the dataset of 92 non-recombining loci that were identified prior to eliminating 30 loci for which orthologs were not detected from *P. globosoides*. This analysis excluded the outgroup as well. Data alignments and BEAST XML files used in this study are accessible via the Mendeley archive (<https://doi.org/10.17632/dc4jhmzy8b.1>).

2.3. Biogeographic analysis

To estimate ancestral geographic ranges and instances of geographic dispersal, we used BioGeoBEARS v. 1.1.2 (Matzke, 2013; Matzke, 2018). We conducted this biogeographic analysis on the outgroup-rooted StarBEAST2 62-locus consensus tree with outgroup trimmed, and assigned each taxon in the tree to regions defined as the Palaearctic (*Arostrilepis gulyaevi*, *Arostrilepis janickii*, *Arostrilepis intermedia*, *Arostrilepis microtis*, *Arostrilepis tenuicirrosa*), the Nearctic (*Arostrilepis cooki*, *Arostrilepis* Lineage 1, *Arostrilepis* Lineage 4, *Arostrilepis rauschorum*, *H. thomomyis*), or the Holarctic (*Arostrilepis macrocirrosa*, *Arostrilepis beringiensis*). The basal node was constrained to the Palaearctic, which is currently considered to be the most likely origin for the group (Haas et al., 2020; Makarikov et al., 2013; Rausch, 1994). We calculated corrected AIC scores for dispersal extinction cladogenesis (DEC) (Ree and Smith, 2008), DIVALIKE (likelihood implementation of dispersal-vicariance) (Ronquist, 1997), BAYAREALIKE (likelihood implementation of BayArea) (Landis et al., 2013) and the + j formulation of each of these models, which incorporates jump dispersal into biogeographic estimations. We also used likelihood ratio tests to test the hypothesis that each pair of biogeographic models with and without the j parameter yields statistically equivalent likelihood scores.

2.4. Host association analysis

To reconstruct ancestral host associations for nodes within the *Arostrilepis* phylogeny, we used Bayesian Binary Markov chain Monte Carlo (BBM; Ronquist and Huelsenbeck, 2003) as implemented in RASP v4.2 (Yu et al., 2015). This analysis was performed on the outgroup-rooted StarBEAST2 62-locus consensus tree with outgroup trimmed. We

assigned each *Arostrilepis* lineage to the single host family, subfamily, or tribe with which it is most commonly associated. These were Myodini (*A. cooki*, *A. macrocirrosa*, *A. tenuicirrosa*, *A. intermedia*, *A. gulyaevi*), Arvicolini (*A. janickii*, *A. rauschorum*, *A. microtis*), Lemmini (*A. beringiensis*, Lineage 4), Neotominae (Lineage 1), and Geomyidae (*H. thomomys*). In the case of *A. cooki* and *A. macrocirrosa*, associations with host lineages other than the Myodini are documented but uncommon (Makarikov et al., 2013), and were therefore not considered in the host lineage assignment. Ancestral nodes were constrained to permit associations with a maximum of two host lineages.

3. Results

Phylogenies generated using maximum likelihood and Bayesian multi-species coalescent methods show the same relationships among species, with robust bootstrap and posterior probability support (Fig. 2). Most relationships within the phylogeny are consistent with patterns observed in the multi-locus phylogeny of our prior analysis (Haas et al. 2020), with three important exceptions. First, in the current analysis, *A. rauschorum* is shown to be sister to Lineage 4. Previously, *A. rauschorum* was found to be sister to Lineage 1. Second, *A. microtis* is here found to be closely related to *Arostrilepis rauschorum*, *A. janickii*, Lineage 1, and Lineage 4, whereas it was previously inferred to arise more deeply within the tree. Third, *Arostrilepis* is here shown to be paraphyletic with respect to *H. thomomys*, as the Palearctic *A. gulyaevi* and *A. tenuicirrosa*, and the Holarctic *Arostrilepis beringiensis*, all arise from deeper nodes in the tree. In all of these cases, the Haas et al. (2020) tree showed low nodal support for the relationships in question, while the current analysis yields a robust result. Only one node in the phylogeny remains poorly resolved, defining relationships between *A. microtis*, *A.*

janickii, and the clade comprised of *A. rauschorum*, Lineage 1 and Lineage 4. Resolution of this node did not improve with the inclusion of 30 additional nuclear loci to the primary 62-locus dataset (Supplemental Figure S1). Well-supported relationships inferred based on both the 62 and 92-locus datasets that excluded the outgroup matched the outgroup-rooted phylogeny with one exception. The position of *A. gulyaevi*/*A. tenuicirrosa* relative to *A. beringiensis* and the clade holding the rest of the *Arostrilepis* species was reversed in trees built with and without *P. globosoides* (Fig. 2; Supplemental Figures S1, S2).

In the biogeographic analysis, corrected AIC scores identified DEC + J as the best fitting model, with addition of the jump parameter providing a statistically significant improvement in the likelihood score of the biogeographic model. Four instances of either dispersal or range expansion from Asia into North America were inferred (Fig. 2), in addition to the complex history of bidirectional transberingian dispersal that was previously described for *A. macrocirrosa* (Haas et al., 2020), and regarding which our current data do not provide additional insight.

Inference of ancestral host associations suggested that the common ancestor of extant *Arostrilepis* parasitized lemmings (tribe Lemmini), though support for this seems tenuous, particularly given ambiguity regarding the position of the lemming-associated *A. beringiensis* in the phylogeny. More convincing is the conclusion that most early diversification of *Arostrilepis* took place in association with tribe Myodini, which includes the red-backed voles. Subsequently, members of the Geomyidae, Arvicolini, Neotominae, and Lemmini were colonized.

4. Discussion

This study improves on the results of our more taxonomically complete, but data-limited, investigation of relationships among *Arostrilepis*

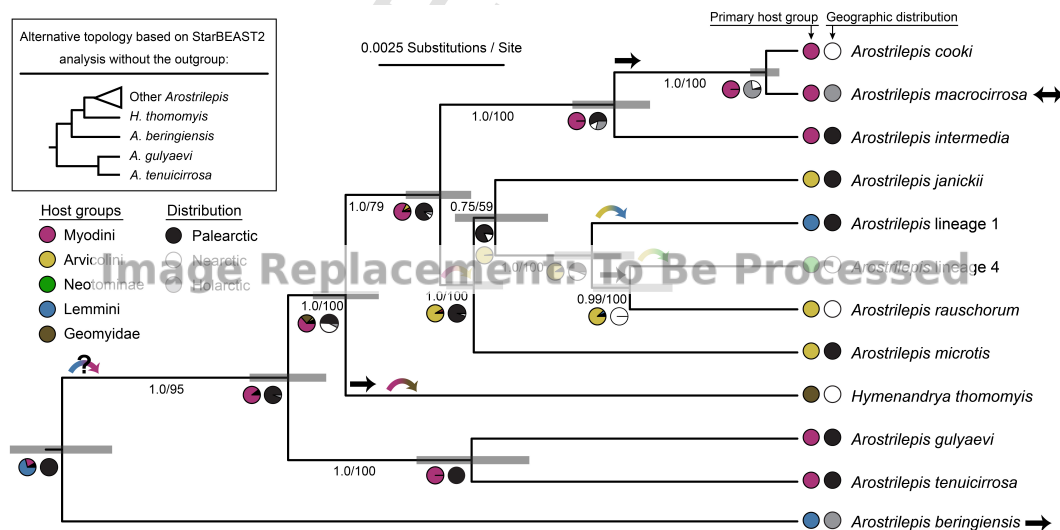


Fig. 2. Multi-species coalescent-based phylogeny of *Arostrilepis* based on 62 nuclear loci. The outgroup used to root the analysis, *Pseudobotrilepis globosoides*, was removed to improve clarity of ingroup relationships and branch lengths. Nodal support values adjacent to branches are Bayesian posterior probabilities followed by maximum likelihood ultrafast bootstrap values. Shaded bars on nodes depict 95 % highest probability density intervals for node age. Shaded circles in gray scale (right-hand circle in each pair) adjacent to tips indicate geographic areas of species distributions (see key for color code), and pie charts in gray scale indicate probabilities of alternative geographic areas inferred for the adjacent node under the DEC + J model using BioGeoBears. Shaded circles in color adjacent to tips (left-hand circle in each pair; digital version of figure is in color) indicate major host groups of species (see key for color code), and pie charts in color indicate probabilities of alternative host associations inferred for the adjacent node using the Bayesian Binary Markov Chain Monte Carlo method in RASP. Probabilities of internal nodes being associated with two host lineages were minimal in all cases and therefore are not reflected in the key. Dispersal events are indicated by black arrows above branches, all involving expansion from Asia into North America. Host colonization events are indicated by curved, colored arrows, with colors denoting the ancestral and colonized host groups, respectively. A question mark (?) on the Lemmini to Myodini host colonization event at the base of the tree indicates ambiguity regarding that inference in light of uncertain basal relationships. Timing of geographic and host colonization events is uncertain and could fall anywhere along the length of the associated branch. A small double-headed arrow at *Arostrilepis macrocirrosa* indicates the complex history of bidirectional intercontinental dispersal inferred previously for that species (2 dispersal events; Haas et al. 2020). A small single-headed arrow at *Arostrilepis beringiensis* indicates presumed intraspecific expansion from Asia into North America, which resulted in a Holarctic distribution for the species. The inset phylogeny depicts relationships at the root of the phylogeny inferred using alternative multi-species coalescent phylogenetic analyses that did not include the outgroup (Supplemental Figures S1, S2). All nodes depicted in the inset tree were supported with posterior probability values of 1.0.

species (Haas et al., 2020). In that earlier analysis, which was based on just two nuclear and two mitochondrial markers, several nodes deep within the phylogeny were not resolved with strong support. Here we found that a large sample of independent nuclear loci provided sufficient signal to clarify most relationships among the species for which these multi-locus data were available, with implications for our understanding of historical biogeography, development of host associations, and evolution of key diagnostic features used in hymenolepidid taxonomy.

4.1. Origins of *Arostrilepis*

It is generally assumed that *Arostrilepis* arose in Asia (Rausch, 1994), and we base our biogeographic inferences on that assumption, though comprehensive sampling of *Arostrilepis* diversity across both Asia and North America remains incomplete and will be necessary to rigorously test that hypothesis. Certainly, the arvicoline rodents that currently represent the primary hosts for *Arostrilepis* originated in Asia, colonizing North America in successive waves (Fink et al., 2010; Repenning, 1990). Ambiguity regarding relationships at the base of the tree requires clarification (i.e., considering differences between phylogenies produced with and without an outgroup), but to date most phylogenies for *Arostrilepis* are consistent with a Palearctic origin (Haas et al., 2020; Makarikov et al., 2020; Makarikov et al., 2013; this study). Recently, the North American *Arostrilepis mariettavogae* Makarikov, Gardner et Hoberg, 2012 was identified based on morphological traits as sister to the remaining species in the genus (Altangerel et al., 2022). Molecular data are currently unavailable for this species due to a lack of recent specimen collections. This phylogenetic placement implies that the history of *Arostrilepis* in North America could be deeper than we show here, though this hypothesis remains to be tested using DNA sequence data.

Arostrilepis probably arose from an ancestor that parasitized shrews of the genus *Sorex* (Haukioja et al., 2010), a group of insectivores that began diversification across the Holarctic as early as 17 million years before present (Mybp; Bannikova et al., 2018). In contrast, Arvicolines first appear in the fossil record of Asia and North America roughly 5 to 6 Mybp (Chaline et al., 1999; Fejfar et al., 2011; Shotwell, 1956). Though we lack a taxon-specific molecular clock rate to date the origin of *Arostrilepis* with confidence, application of an average mutation rate calculated for protein-coding nuclear genes from another group of cestodes (genus *Schizorchis*; 0.00137 substitutions/site/million years; Galbreath et al., 2020) suggests an origin > 10 Mybp. This suggests that *Arostrilepis* could have originated in association with the microtoid cricetids, an assemblage of early cricetid rodents with arvicoline-like dental morphology that are generally considered to represent the ancestral group from which the true arvicolines arose (Fejfar et al., 2011). The earliest microtoid cricetids were present in Asia by 17 Mybp (Maridet et al., 2012) and may have arrived in North America as early as 9 Mybp (Maul et al., 2017). Modern arvicolines would have subsequently acquired *Arostrilepis* species via host colonization (e.g., Hoberg and Brooks, 2008). We acknowledge, however, that the average rate of molecular evolution across the current dataset is undoubtedly not identical to that calculated for *Schizorchis*, given that the nuclear genes in question are not the same and the two genera are deeply divergent. A more accurate timing estimate will require internal calibration points that permit a robust molecular clock to be inferred for *Arostrilepis*.

Incomplete sampling of species diversity prevents us from clarifying the pattern of diversification across the *Arostrilepis* phylogeny. Four described species have never been incorporated into DNA sequence datasets, including *A. mariettavogae*, *Arostrilepis horrida* (*sensu stricto*) (Linstow, 1901), *Arostrilepis kontrimavichusi* Makarikov et Hoberg, 2016, and *Arostrilepis schilleri* Makarikov, Gardner et Hoberg, 2012. Nine additional lineages beyond those included here have been de-

tected using molecular data (Altangerel et al., 2022; Haas et al., 2020; Makarikov et al., 2020), but were not available for sequencing for the current study. Several of these lineages may be close relatives of either the *A. macrocirrosa*/*A. cooki* clade or the Lineage 4/*A. rauschorum* clade.

4.2. Historical biogeography

Arostrilepis species became distributed across the Holarctic via multiple episodes of geographic expansion between Asia and North America, consistent with taxon-pulse dynamics (Erwin, 1985). This history of colonization was probably mediated primarily by the arvicoline definitive hosts. Collembola, which serve as intermediate hosts of *Arostrilepis* (Ishigenova et al., 2013; Smirnova and Kontrimavichus, 1977), are hyperabundant soil-dwelling arthropods that occur globally and are therefore unlikely to constrain the geographic distribution of these tapeworms, though their limited vagility also makes them unlikely to facilitate cestode dispersal. Several dispersal events by arvicolines during the Pliocene and Pleistocene have been identified based on paleontological and molecular systematic evidence (e.g., Conroy and Cook, 2000a; Cook et al., 2004; Fink et al., 2010; Repenning, 1990; Waltari et al., 2007). We previously estimated that six intercontinental dispersals across Beringia by *Arostrilepis* took place during a minimum of three sequential glacial stages in association with the movements of different host lineages (Haas et al., 2020).

Of the six previously inferred transberingian dispersals, three are associated with the two *Arostrilepis* species that maintain Holarctic distributions. *Arostrilepis macrocirrosa* may have its origins in a westward dispersal out of North America before an intraspecific lineage traveled back across the land bridge to return to North America (Haas et al., 2020). This complex history was undoubtedly tied to that of its primary hosts, the red-backed voles (genus *Myodes*) (Kohli et al., 2015; Kohli et al., 2014), but a more thorough phylogeographic analysis of *A. macrocirrosa* is required to clarify the relative timing of host and parasite dispersals. Another intercontinental colonization took place in the history of *A. beringiensis*, presumably facilitated by its lemming hosts (genus *Lemmus*), which also have a complex history of isolation in and dispersal across Beringia (Fedorov et al., 2003; Fedorov et al., 1999).

Our dataset for the current study does not yield additional insight into the histories of *A. macrocirrosa* and *A. beringiensis*, but it does inform our understanding of the three remaining colonization events (Haas et al., 2020). Two of these, one preceding the origin of the clade that includes *A. cooki* and *A. macrocirrosa* (historically associated with Myodini) and the other leading to the clade that includes Nearctic *A. rauschorum* and Lineage 4 (historically associated with Arvicolini, though Lineage 4 colonized mice of the genus *Peromyscus*), are confirmed by this study. However, in contrast to the results of our earlier analysis, here we see evidence that these colonization events may have occurred simultaneously. Early Pleistocene episodes of dispersal from Asia into North America by *Myodes* (Kohli et al., 2015; Kohli et al., 2014) and *Microtus* (Conroy and Cook, 2000a; Repenning, 1990) voles could have mediated dispersal by the cestodes.

The remaining colonization that we previously inferred is rejected by the current analysis. Previously we found the Palearctic Lineage 1 to be sister to Nearctic *A. rauschorum*, which necessitated an inference of a westward dispersal to reconcile the biogeographic pattern (Haas et al., 2020). However, low support for relationships among those lineages cast doubt on that conclusion. In the current better-supported phylogeny, we show that *A. rauschorum* is sister to Nearctic Lineage 4, eliminating the need to invoke dispersal from North America into Asia in this clade, and simplifying our understanding of the biogeographic history of the assemblage.

Finally, the placement of *H. thomomyis* within the *Arostrilepis* clade reflects an intercontinental dispersal that we did not previously infer and which may represent a fourth temporally discrete episode of transberingian colonization. This cestode, which is associated with pocket

gophers (Geomyidae), evidently is descended from what may have been the first *Arostrilepis* colonists of North America. In this case the host association offers little insight into the history of colonization, as geomyid rodents occur only in North America. Presumably dispersal from Asia was facilitated by another host species, and a host colonization event led to the association with geomyids, which were already well-established in North America by the time the parasite lineage arrived (Tedford et al., 2004). It is plausible that geographic expansion from Asia by the ancestor of *H. thomomys* might have accompanied the initial arrival of arvicolines in North America (Chaline et al., 1999; Fejfar et al., 2011; Shotwell, 1956).

4.3. Evolution of host associations

Arostrilepis is associated with a diverse assemblage of rodent lineages, and determining the ancestral host lineage has been elusive (Haas et al., 2020). Here we see an indication that the Myodini may have been one of the original hosts for these cestodes, from which the Arvicolini were colonized. Construction of a taxonomically comprehensive multi-locus phylogeny is necessary to confirm this result. Despite this limitation, our results confirm separate instances of colonization of diverse rodent lineages by *Arostrilepis* (Haas et al., 2020). Within the predominantly Arvicolini-associated clade, *Arostrilepis* lineages were acquired by species of *Peromyscus* (*Arostrilepis* lineage 4) and *Lemmus* (*Arostrilepis* lineage 1). Another *Peromyscus*-associated species, *A. mariettavogae*, is not included in the molecular phylogeny, but available evidence suggests that it is deeply divergent from the Arvicolini-associated group (Altangerel et al., 2022), implying that it arose from an additional host colonization event separate from that of lineage 4. Similarly, evidence that *A. schilleri* may be phylogenetically nested within the Myodini-associated clade that includes *A. macrocirrosa*, *A. intermedia*, *A. cooki*, *Arostrilepis gardneri* Makarikov, Galbreath, Eckerlin, and Hoberg 2020, and *Arostrilepis insperata* Makarikov, Galbreath, Eckerlin, and Hoberg 2020 (Altangerel et al., 2022), indicates the occurrence of a colonization of *Thomomys* pocket gophers that is distinct from that which led to *H. thomomys*. These events demonstrate extensive capacity for host range expansion through ecological fitting within *Arostrilepis* given environmental and ecological opportunity concurrent with a history of geographic colonization (Agosta et al., 2010; Brooks et al., 2019).

An instance of phylogenetic incongruence between the results of this study and those of our previous work refines understanding of past host colonization in the Arvicolini. Here we show with strong support that *A. microtis*, together with *A. janickii*, *A. rauschorum* and their kin, form a clade that is predominantly associated with the Arvicolini. Previously, *A. microtis* arose more deeply in the phylogeny (though with weak nodal support), necessitating multiple instances of host colonization to reconcile the distribution of host associations across the tree. The current result yields a more parsimonious explanation of host history, with all Arvicolini-associated lineages occurring in a single clade. Such a cophylogenetic framework, however, remains consistent with a complex history of colonization and limited cospeciation (Brooks et al., 2019).

The only node that is not resolved with high confidence in the current analysis, other than that which defines the basal relationships in the tree, may offer insight into the process of diversification among *Arostrilepis* lineages predominantly associated with voles of tribe Arvicolini. The fact that resolution remained poor regardless of the number of loci included in the analysis might indicate that this is a “hard” polytomy, such as might result from diversification that occurs too rapidly for lineage sorting to be completed in the time between speciation events. A period of rapid Arvicolini diversification in Asia 3 to 5 Mybp could have been responsible for such a pattern in the parasites (Abramson et al., 2021). Rapid population fragmentation across broad spatial scales driven by a transition to cooler and drier climate condi-

tions in the Late Pliocene could have initiated near-simultaneous divergence of multiple cestode lineages from a single ancestor. Such a scenario has been described to explain the more recent origin of multiple lineages of *Myodes* voles across the Holarctic (Kohli et al., 2014).

4.4. Paraphyly of *Arostrilepis*

An unexpected result of this study was confirmation that *H. thomomys* renders *Arostrilepis* paraphyletic. In our prior work, *H. thomomys* was inferred to be either sister to *Arostrilepis* or phylogenetically nested within *Arostrilepis* (Haas et al., 2020). The current analysis robustly confirms the latter scenario. This raises questions regarding the utility of morphological features that have long been considered to be important to diagnosing *Arostrilepis* and its closest relatives. Differences in the number of testes provide a particularly striking example. The genus *Hymenandrya* Smith, 1954 is in part distinguished from *Arostrilepis* by the presence of 7 to 15 testes (Smith, 1954), whereas in *Arostrilepis*, proglottids typically hold 3 testes, with occasional instances of 2 to 4 testes (Mas-Coma and Tenora, 1997; Voge, 1952). Testis number has historically been used as a key distinguishing feature of hymenolepidid genera, though its utility for supraspecific taxonomy has been questioned given variation among individuals within a species, and even among proglottids within an individual (Mas-Coma and Galan-Puchades, 1991).

A discussion of evolution of testis number in the hymenolepidids is beyond the scope of the current study, but it may be central to understanding the implications of *Arostrilepis* paraphyly. Our phylogenetic result indicates a need for an emended generic diagnosis for *Hymenandrya* and taxonomic re-arrangement of *Arostrilepis* species, given that *Hymenandrya* has established priority. This decision and a broader discussion of testis number will require a thorough evaluation of phylogenetic and anatomical patterns across an extensive assemblage of related hymenolepidid genera.

4.5. Conclusions

Given the diversity of host associations and as many as four episodes of intercontinental dispersal during separate glacial stages, the *Arostrilepis* species assemblage is probably relatively ancient, with a history that spanned the geological changes and climatological oscillations of the Late Cenozoic. This antiquity indicates that the structure of diversity within the genus in part may reflect events that took place before its current hosts evolved, in host groups that are now extinct (e.g., colonization of *Thomomys* by the ancestor of *H. thomomys*). Subsequent colonization of new host lineages involved capacity to exploit widespread host-based resources among arvicolines and other rodents, and opportunity for colonization mediated by ecological fitting, as has been postulated for diverse parasite groups (Araujo et al., 2015; Brooks et al., 2019; Hoberg and Brooks, 2008). Contemporary diversity within *Arostrilepis* therefore retains the echoes of an early “ghost assemblage” of hosts and parasites from which it arose (e.g., Galbreath et al., 2020). Subsequent episodes of geographic range fluctuation (taxon pulses; Erwin, 1985) driven by climatic shifts and shaped by the interplay of glacial ice, sea level change, and tectonic activity across the northern hemisphere, created opportunities for new host associations to be established via ecological fitting (Janzen, 1985), and for new diversity to arise. These dynamics resulted in a rich mosaic of parasite-host diversity and interactions (Thompson, 2005) distributed across the Holarctic, as expected under the model of biogeographic, ecological, and evolutionary history known as the Stockholm Paradigm (Agosta and Brooks, 2020; Brooks et al., 2019; Hoberg and Brooks, 2008; Hoberg et al., 2017).

Work remains in our effort to understand the history of *Arostrilepis* and its arvicoline hosts. Most important is the need to thoroughly sample extant *Arostrilepis* diversity and sequence homologous gene regions,

which will allow these species to be included in a comprehensive phylogenetic and biogeographic analysis. Areas of particular interest, where unsampled helminth diversity abounds, are the American West and Asia, which are a focus for ongoing biodiversity inventories (Cook et al., 2017; Cook et al., 2005) using integrated protocols for mammal-parasite collection (Brooks et al., 2014; Colella et al., 2020; Galbreath et al., 2019). Comprehensive sampling will be critical for constraining the timing of North American colonization events, especially along the branch leading to *H. thomomys*, and identification of internal molecular clock calibration points for *Arotrilepis* will further refine our understanding of the timeline for speciation. As the pattern of intercontinental dispersal is clarified, it will help to delineate the timing of past openings of the Bering Land Bridge, which will enrich our general understanding of the historical events that shaped diversity and complex patterns of faunal assembly across the northern continents.

CRediT authorship contribution statement

Kurt E. Galbreath : Conceptualization, Writing – original draft, Formal analysis. **Arseny A. Makarikov** : Writing – review & editing. **Kayce C. Bell** : Data curation. **Stephen E. Greiman** : Investigation. **Julie M. Allen** : Data curation. **Genevieve M. S. Haas** : Data curation. **Chenhong Li** : Investigation. **Joseph A. Cook** : Resources. **Eric P. Hoberg** : Conceptualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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