A new perspective on the taxonomy and systematics of Arvicolinae (Gray, 1821) and a new time-calibrated phylogeny for the clade

Charles B Withnell [Corresp., 1, 2], **Simon G Scarpetta** [2, 3]

[1] Department of Medical Education/ Anne Burnett Marion School of Medicine, Texas Christian University, Fort Worth, Texas, United States

[2] Department of Geological Sciences/ Jackson School of Geosciences, The University of Texas at Austin, Austin, Texas, United States

[3] Museum of Vertebrate Zoology, University of California, Berkeley, Berkeley, California, United States

Corresponding Author: Charles B Withnell
Email address: c.withnell@tcu.edu

Background. Arvicoline rodents are one of the most speciose and rapidly evolving mammal lineages. Fossils arvicolines are also among the most common vertebrate fossils found in sites of Pliocene and Pleistocene age in Eurasia and North America. However, there is no taxonomically robust, well-supported, time-calibrated phylogeny for the group.

Methods. Here we present well-supported hypotheses of arvicoline rodent systematics using maximum likelihood and Bayesian inference of DNA sequences of three nuclear genes and two mitochondrial genes representing 132 (89% coverage) species of arvicolines. We elucidate well-supported major clades, and reviewed the relationships and taxonomy of many species and genera and critically compared our resulting molecular phylogenetic hypotheses to previously published hypotheses. We also used five fossil calibrations to generate a time-calibrated phylogeny of Arvicolinae that permitted some reconciliation between paleontological and neontological data.

Results. Our results are largely congruent with most previous molecular phylogenies, but we increased the confidence in many regions of the arvicoline tree that were previously poorly-sampled. Our approach allowed us to support the paraphyly of *Clethrionomys*, the basal position and close relationship of true lemmings (*Lemmus* and *Myopus*) and bog lemmings (*Synaptomys*, *Mictomys*), the monophyly of *Alticola*, and the need for a large-scale revision of *Microtus*. Our results indicate an evolutionary origin of ~8 Ma for crown arvicoline rodents with four primary radiations. These results have major implications for our confidence in the fossil record of arvicolines and their utility as biochronological tools in Eurasia and North America during the Quaternary.

A NEW PERSPECTIVE ON THE TAXONOMY AND SYSTEMATICS OF ARVICOLINAE (GRAY, 1821) AND A NEW TIME-CALIBRATED PHYLOGENY FOR THE CLADE

Charles B. Withnell[1,2], Simon G. Scarpetta[1,3]

[1] Department of Geological Sciences, Jackson School of Geosciences, The University of Texas at Austin, Texas 78712.
[2] Department of Medical Education, Anne Burnett Marion School of Medicine, Texas Christian University, Fort Worth, Texas, 76129
[3] Museum of Vertebrate Zoology, University of California Berkeley, California, 94720

Corresponding Author:
Charles Withnell[1]
Department of Medical Education, Anne Burnett Marion School of Medicine, Texas Christian University, Fort Worth, Texas, 76129
Email address: c.withnell@tcu.edu

Abstract

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Introduction

Arvicoline rodents (voles, lemmings, muskrats, and their extinct relatives) are the subject of a complex history of taxonomic and phylogenetic research (Conroy and Cook, 1999, 2000; Galewski et al., 2006; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Martínková and Moravec, 2012; Steppan and Schenk, 2017; Upham et al., 2019; Abramson et al., 2021). Previous phylogenetic studies focused on subsets of Arvicolinae (i.e., North American *Microtus*; Conroy and Cook, 1999; Martínková and Moravec, 2012), used only one or two genes (Buzan et al., 2008), included arvicolines in larger studies investigating the phylogeny of all rodents (Fabre et al., 2012; Steppan and Schenk, 2017), or focused on mitochondrial genomes (Abramson et al., 2021). A comprehensive combined-evidence molecular and morphological dataset was generated by Robovský et al. (2008). Although a great deal of molecular data is available for arvicoline rodents, no study has synthesized available molecular data to examine phylogenetic relationships across the group at both the generic and species levels—a new phylogeny has been warranted. We compiled the most taxonomically complete molecular dataset of global Arvicolinae to date (July, 2022), using both nuclear genes and mitochondrial markers, to provide a well-sampled molecular hypothesis of extant Arvicolinae. Additionally, we assess the rich fossil record of arvicolines to establish several node calibrations for divergence time analyses, and present the largest such analyses of Arvicolinae to date. Finally, we discuss the implications of our results on arvicoline taxonomy and systematics.

Arvicoline Taxonomy and Systematics Through Time

Bog lemmings of the genera *Synaptomys* (and/or *Mictomys*) have many morphological and molecular characters thought to associate the group with the ‘true lemmings’ (*Myopus* and *Lemmus*) (Abramson, 1993; Carleton, 1981; Chaline and Graf, 1988). Bog lemmings are a strictly North American clade in the modern biota, but based on the fossil record were hypothesized to have originated c. 4 Ma in Europe, with subsequent dispersal through Beringia into North America (Repenning and Grady, 1988). Some paleontologists posited that the northern bog lemming (*Synaptomys borealis*) should be placed in its own genus, *Mictomys*, based on dental morphology (Repenning and Grady, 1988). Neontologists (Hall, 1981; Musser and Carleton, 2005) argued that, at best, *Mictomys* is a subgenus of *Synaptomys* based on morphology and ecology.

The ‘true lemmings’ *Myopus* and *Lemmus* are early diverging arvicolines (Carleton, 1981; Chaline and Graf, 1988; Abramson, 1993). The monophyly of the ‘true lemmings’ + *Synaptomys* (excluding *Dicrostonyx*) was supported by cladistic analysis of allozyme data (Mezhzherin et al., 1995), nuclear DNA (Modi, 1996), and mitochondrial DNA (Conroy and Cook, 1999). The taxonomic treatment of *Myopus* has been complicated. Originally, Chaline (1972) treated *Myopus schisticolor* as a species of

Lemmus. Subsequently, Chaline et al. (1989) and von Koenigswald and Martin (1984) cited molar similarity between *Myopus* and *Lemmus* and placed *Myopus* as a subgenus within *Lemmus*. Karyotype, body size, fur coloration, other morphologies (skull, feet, and eyes), habitat, and behavior were later invoked to demonstrate that *Myopus* is readily distinguishable from *Lemmus* (Jarrell and Fredga, 1993). Therefore, Musser and Carleton (2005) treated it as a separate genus.

Collared lemmings (*Dicrostonyx*) were historically thought to be close to true lemmings (Miller, 1896). Early molecular and morphological analyses indicated that *Dicrostonyx* was part of one of the earliest radiations of arvicolines (e.g., Carleton, 1981; Chaline and Graf, 1988; Conroy and Cook, 1999; Gromov and Polyakov, 1992). For decades, the dominant viewpoint was that there was a single circumpolar species of collared lemming, *Dicrostonyx torquatus*, but evidence from morphology, genetics, ecology, and karyology indicates multiple species (Borowik and Engstrom, 1993; Eger, 1995; Musser and Carleton, 2005).

Phenacomys and *Arborimus* have a complicated taxonomic history. Similarities in dental morphology led some researchers to classify *Arborimus* as a subgenus of *Phenacomys* (Repenning and Grady, 1988), but others treated *Arborimus* as a separate genus (Musser and Carleton, 1993). Another study placed them together in the tribe Phenacomyini (Zagorodnyuk, 1990). Others placed *Phenacomys* with *Phaiomys* and other extinct genera (Repenning et al. 1990) or with the tribe Myodini (McKenna and Bell, 1997). Both *Phenacomys* and *Arborimus* have primitive molars that retain the plesiomorphic condition of retaining roots on molars, and they lack cementum in the reentrant angles on those molars; therefore some paleontologists argued that *Phenacomys* is an early relict lineage (Repenning, 1987).

Ellobius, the mole voles, is a morphologically specialized group (Corbet, 1978; Pavlinov et al., 1995; Tesakov, 2008; Tesakov, 2016). The genus is remarkable in that its Pleistocene range included parts of Israel and North Africa, areas that no other arvicoline has ever inhabited (or they did not leave a known fossil record; Jaeger, 1988). *Arvicola* is a European, fossil-rich genus that was previously hypothesized to be closely related to *Microtus* (Chaline and Graf, 1988; Mezhzherin et al., 1993). The number of recognized species in *Arvicola* has varied from one to seven (Miller, 1912; Ellerman and Morrison-Scott, 1951). *Lemmiscus* is a monotypic genus that was long considered a subgenus of *Lagurus* in order to segregate New World sagebrush voles from Old World steppe voles (Carroll and Genoways, 1980). Morphological and molecular data, however, indicate that *Lemmiscus* may be closely related to *Microtus* (Carleton, 1981; Modi, 1987; Abramson et al., 2021). *Lagurus* was hypothesized to be closely related to *Eolagurus* and was placed in the tribe Lagurini (Gromov and Polyakov, 1992).

The systematic relationships of the snow voles, *Chionomys*, are historically controversial (Gromov and Polyakov, 1992; Yannic et al., 2012). Some researchers posited that *Chionomys* is a member of Myodini (Mezhzherin et al., 1995), just outside

of *Microtus* (Yannic et al., 2012), and others argued based on known fossils that *Chionomys* is closely related to *Clethrionomys* (=*Myodes*) (Kretzoi, 1969; Chaline, 1987). Using morphological characters, *Proedromys* was hypothesized to be closely related to *Microtus*, but its diagnostic traits (massive cranium with wide, heavy, and grooved upper incisors and odd molars) were also used to support the hypothesis of a close relationship with extinct genera such as *Allophaiomys* (Gromov and Polyakov, 1992; Repenning, 1992). Molecular phylogenies also suggest that *Proedromys* is outside and thus separate from *Microtus*, although with low support (Chen et al., 2012). *Volemys* consists of two high-altitude alpine species native to western Sichuan, China. Species of *Volemys* were previously placed in *Microtus* or were found to be closely related to *Microtus*, and previously published phylogenetic analyses of molecular data hinted that the distribution of *Volemys* may be relictual due to geographic (and correspondingly, genetic) isolation during the Late Pleistocene (Lawrence, 1982; Zagorodnyuk, 1990). Voles of the genus *Neodon* are found throughout the mountainous regions of southern Asia. They have a long and complicated taxonomic history, but their close relationship to *Microtus* has been established, although systematic relationships of the genus relative to other arvicolines are still debated (Musser and Carleton, 2005; Pradhan et al., 2019). Recent taxonomic revision has seen the number of species belonging to *Neodon* grow (Pradhan et al., 2019).

The taxonomy and systematics of *Microtus* are complicated and historically difficult to disentangle. Little consensus exists in the literature on how to treat generic-level identification of fossil *Microtus*, partially because many hypotheses of *Microtus* relationships were based on teeth that have limited systematic potential and have undergone rapid evolutionary change (Guthrie and Matthews, 1971; von Koenigswald, 1980). Combined with the broad Holarctic distribution of the group, poor genetic sampling, and hypothesized recent origination and diversification, and the result has been taxonomic and systematic chaos.

Members of *Lasiopodomys* were considered by paleontologists to be the remnants of a group that was previously more speciose and widespread (Gromov and Polyakov, 1992; Repenning, 1992). We note that the fossil *Lasiopodomys* referred to by Repenning (1992) in North America is not the same as the extant Eurasian taxa, further adding to the taxonomic confusion of the genus (Repenning and Grady, 1988). Neontologists and paleontologists have recognized the morphological uniqueness of *Lasiopodomys*, but in one allozyme analysis, *Lasiopodomys brandtii* was grouped with *Microtis fortis* and *Microtus gregalis*, thus questioning the generic affinity of these species (Mezhzherin et al., 1990). Musser and Carleton (2005) retained *Lasiopodomys* at the generic level, but recognized that there was a need for phylogenetic work to clarify the taxonomy of the genus. *Blanfordimys* is a geographically isolated group of voles found in south-central Asia (e.g., Afghanistan). They have retained dental characters that have been interpreted as ~~pleisiomorphic~~, but they have inflated auditory

bullae and a mastoid region that is so enlarged that it almost projects beyond the occipital condyle, both of which have been interpreted as highly apomorphic (Gromov and Polayakov, 1992). This led some researchers to place them as a subgenus of *Microtus* (Gromov and Polyakov, 1992) while others gave them full generic distinction (Musser and Carleton, 1993). Allozyme analysis by Mezhzherin et al. (1993) nested *B. afghanus* with ten species of *Microtus* and led Musser and Carleton (2005) to stress caution with the taxonomy of the group.

Ondatra and *Neofiber* are monotypic genera that have the largest body sizes of all arvicolines (both extant and extinct). Historically, they were placed together in the tribe Ondatrini (Chaline and Mein, 1979; Repenning et al., 1990) or subtribe Ondatrina (Pavlinov et al., 1995). Based on allozymic analysis, Mezhzherin et al. (1995) concluded that Ondatrina was one of the first groups of arvicolines to diverge from the ancestral arvicoline population during the late Miocene. Dental morphology however led some paleontologists to consider *Ondatra* and *Neofiber* as more distantly related. Although the most obvious similarity is that they are both large (Carleton, 1981; von Koenigswald, 1980; Martin, 1974; Martin 1996), *Ondatra* has rooted molars, and *Neofiber* has rootless molars. Molecular phylogenies support a sister taxon relationship between the genera (Modi, 1996; Fabre et al., 2012).

The Eurasian genera *Dinaromys* and *Prometheomys* are both monotypic in the extant biota. The plesiomorphic characteristics (e.g., rooted dentition) of *Dinaromys* caused it to be placed in many different groups: subfamily Dolomyinae (Chaline, 1975), Tribe Ondatrini (Corbet, 1978), Tribe Clethrionomyini (Gromov and Polyakov, 1992), or Tribe Prometheomyini (Pavlinov et al., 1995). To further complicate their systematic status, von Koenigswald (1980) found that the lone extant species of the genus, *Dinaromys bogdanovi*, has an enamel microstructure that is unlike any other known extant species. The ‘long clawed mole vole’, *Prometheomys schaposchnikowi*, is a monotypic species with plesiomorphic characters usually classified in its own tribe (Gromov and Polyakov, 1992). This led Repenning et al. (1990) to align *Prometheomys* with *Ellobius* in Prometheomyinae while other researchers place *Prometheomys* into Prometheomyini (Pavlinov et al., 1995; Pavlinov and Rossolimo, 1998). Whole mitochondrial genomes indicated that *Prometheomys* is a likely a basal arvicoline (Ibis et al., 2020).

The clade that includes the genera *Clethrionomys* (=*Myodes*), *Eothenomys*, and *Alticola* also has a long and complicated history of taxonomic revision (e.g., Hinton, 1926; Miller, 1896; Kretzoi, 1969; von Koenigswald, 1980; Kohli et al., 2014; Kryštufek et al., 2020). The priority of *Clethrionomys* as the valid genus name for red-backed voles was recently recognized (Kryštufek et al., 2020); therefore, we have abandoned the taxonomy used by Musser and Carleton (2005) that used the genus name *Myodes*. Traditionally, species with rooted molars were lumped into Clethrionomyini (Gromov and Polyakov, 1992) or the subtribe Myodina (Pavlinov and Rossolimo, 1998). Appendicular

myological and osteological data support the monophyly of *Alticola* and its close relationship to *Clethrionomys* and *Eothenomys* (Stein, 1987). Dental morphology (i.e., small, rooted teeth) alone may indicate that *Clethrionomys* and *Alticola* are early diverging members of Arvicolinae, if rooted teeth are the ancestral condition. Suzuki et al. (1999) and Musser and Carleton (2005) argued that members of *Clethrionomys* may have independently evolved rooted molar conditions. More recent work using multilocus datasets provided some support for that hypothesis (Kohli et al., 2014).

Materials & Methods

Taxon Sampling

Complete sampling of Arvicolinae has been challenging historically due to the high species diversity and global distribution of the clade, and the relative rarity of some species in museum collections. We attempted to sample all genera (n=28) and species (n=149) recognized by Musser and Carleton (2005) and Shenbrot and Krasnov (2005). We sampled all of the genera recognized by Musser and Carleton (2005). We included a species placed in *Phaiomys* by Musser and Carleton (2005) in *Neodon*. Species historically placed in *Caromys* (Musser and Carleton, 2005) were included here, but we follow Luo et al. (2004) in placing those species in the genera *Eothenomys*. The resulting dataset included 132 species of extant arvicolines, and is the most taxonomically complete dataset to date (July, 2022) for Arvicolinae (89% species coverage).

Concatenated dataset

Molecular data were obtained from GenBank (NCBI Resource Coordinators, 2016) (GenBank accession numbers are in Appendix A and deposited in Dryad). Three rodents outside of crown Arvicolinae were used as outgroups (Fabre et al., 2012), including *Cricetus cricetus*, *Mesocricetus auratus*, and *Neotoma fuscipes*. Five loci were chosen that previously were demonstrated to be useful for rodent phylogenetics (Galewski et al., 2006; Robovský et al., 2008; Fabre et al., 2012; Martinkova and Moravec, 2012; D'Elía et al., 2019; Upham et al., 2019; Abramson et al., 2021). We used two mitochondrial markers, Cytochrome b (Cytb) and Cytochrome c oxidase subunit 1 (COI), as well as the three nuclear genes, growth hormone receptor (Ghr) exon 10, iron responsive element binding protein/retinol binding protein 3 (IRBP/RBP3) exon 1, and the Breast Cancer gene 1 (BRCA1) exon 11. These genes were chosen because they had at least 40% coverage across all of the taxa included in this analysis. Other genes, such as ACP5, have been used in some phylogenetic analyses of arvicoline rodents (Bondareva et al., 2021a,b), but we chose not to include them because their coverage across all of the taxa included in these analyses was relatively low. Sequences selected for this project were compared to other sequences within GenBank by using BLAST. This allows us to increase our confidence in the taxonomic

identification of sequences before phylogenetic analysis was completed. In total there were 5220 base pairs, and each gene had the following coverage across the 135 taxa (132 arvicolines + outgroups): Cytb (100%), COI (43.0%), Ghr (64.4%), IRBP/RBP3 (74.4%), and BRCA1 (48.1%). Across the entire dataset there was 36.5% missing data. The degree of missing data for COI and BRCA1 led us to exclude these two markers from some of the analyses discussed below.

Sequences were aligned using the iterative refinement algorithm L-INS-I of MAFFT (Katoh and Standley, 2013). Aligned nexus files were imported into AliView (Larsson, 2014) and nuclear protein coding genes were checked for stop codons and trimmed where needed to ensure that they were in the proper reading frame for the first and third codon positions. PartitionFinder 2 (Lanfear et al., 2017) was used to partition the dataset (by codon position for the nuclear protein-coding genes) using the Akaike Information Criterion (AIC) (Burnham and Anderson, 2004).

Phylogenetic analyses

We conducted Maximum Likelihood (ML) and Bayesian Inference (BI) analyses of the concatenated datasets, including combined analyses of nuclear and mitochondrial loci of all five markers, nuclear markers with coverage >50% (Ghr and IRBP/RBP3), mitochondrial marker only with coverage >50% (Cytb), and a combined analysis of nuclear and mitochondrial markers >50% (Ghr, IRBP/RBP3, and Cytb), for a total of 12 phylogenetic analyses. Four analyses were conducted using ML: (1) all five markers (2) Cytb only (3) higher coverage nuclear markers (Ghr and IRBP) (4) all higher coverage markers (Ghr, IRBP, and Cytb). Four analyses using BI include analyses of (1) all five markers (2) Cytb only (3) Ghr and IRBP, and (4) Ghr, IRBP, and Cytb. Finally, four time-calibrated BI analyses were performed on (1) all five markers (2) Cytb only (3) Ghr and IRBP, and (4) Ghr, IRBP, and Cytb. The ML trees were estimated using RAxML v8.2.12 (Stamatakis, 2014) on the CIPRES cluster (Miller et al., 2010). We used GTR+ Γ or GTR + Γ + I molecular substitution models as suggested by PartitionFinder 2 (Lanfear et al., 2017). For ML analyses support values were estimated using 1000 nonparametric bootstrap pseudoreplicates. Bayesian inference of the partitioned and concatenated dataset was conducted using the Markov Chain Monte Carlo (MCMC) method in MrBayes 3.2.6 (Ronquist et al., 2012). The analysis ran for 3.0 x 10^7 generations sampled every 1000 generations and for two separate and independent runs. Beagle was used for high-performance phylogenetic statistical inference (Ayres et al., 2012). Results were examined in Tracer 1.7 (Rambaut et al., 2018) to ensure that the independent runs reached stationarity and that the effective sample size (ESS) values were >200 for all model parameters. Trees were summarized with majority-rule consensus trees and the first 30% of the samples were discarded as burn-in. All input files for the RAxML and MrBayes analyses are deposited on Dryad.

Node Calibration Selection

We used five internal node calibrations and a root calibration in divergence time analyses. These nodes were selected after non-calibrated phylogenies were produced. For all nodes, there were no suitable fossils available to help establish calibration maxima, so we used exponential calibration priors for each node. For each calibration, the fossil age was used as the offset. R scripts for calculating a suitable mean are in Appendix B.

Calibration 1: Cricetidae (Outgroup) Node

We chose as outgroups three muroid rodents previously found to be closely related to Arvicolinae (Fabre et al., 2012; D'Elía et al., 2019). These three species belong to the subfamilies Cricetinae *(Cricetus cricetus*, *Mesocricetus auratus*) and Neotominae (*Neotoma fuscipes*). The split between Arvicolinae and Cricetinae is reported to have occurred during the middle Miocene (Fabre et al., 2012). The split between (Arvicolinae, Cricetinae) and Neotominae was hypothesized to be during the early-Miocene (Fabre et al., 2012; Steppan and Schenk, 2017). We used a secondary calibration based on those divergence times (Fabre et al. 2012; Steppan and Schenk 2017) to constrain the root age. We used an offset exponential distribution with a minimum age of 7 Ma and a mean of 8.44 Ma. A minimum age of 7 Ma was chosen as the root of our tree based on the fossil record and divergence times estimated by Fabre et al. (2012) and Steppan and Schenk (2017).

Calibration 2: Lemmini (*Lemmus* + *Myopus* + *Synaptomys* + *Mictomys*) Node

There is a substantial fossil record of North American bog lemmings (*Synaptomys*), the earliest of which date to 3.95 Ma from the Hagerman Fossil Beds National Monument, Idaho (*Mictomys* = *Synaptomys vetus*; Ruez and Gensler, 2008). The offset for this node is anchored by a right m1 (lower first molar) housed at the Idaho Museum of Natural History (IMNH 67002/39517) that has radiometric age control (Ar-Ar) of a basaltic tephra located 30 m above the site and dated at 3.79 $\pm$ 0.03 Ma (Hart and Brueseke, 1999). Interpolation of depositional rates indicates that the age of the fossil from IMNH locality 67002 is ~3.95 Ma (Hart and Brueseke, 1999). IMNH 67002/39517 was identified as *Mictomys vetus* by having evergrowing molars with cementum in the reentrant angles. The m1 also has a posterior loop with three triangles, and an anterior loop (Ruez and Gensler, 2008). Triangles 1 and 2 are broadly confluent with the anterior loop and triangle three is joined by the anterior loop near the midline. Triangles 1 and 3 are nearly twice the width of triangle 2. Because *Synaptomys* was paraphyletic in some of our uncalibrated analyses, we used this fossil to calibrate the crown lemming node instead. We used an offset exponential distribution with a minimum age of 3.95 Ma and a mean of 4.74 Ma.

Calibration 3: Ondatrini (*Ondatra* + *Neofiber*) Node

Fossils of this clade of relatively large-bodied extant arvicoline rodent appeared during the Pliocene. The oldest known species, *Ondatra minor*, is found in the Hagerman Formation in Hagerman, Idaho at ~3.6 Ma (Hibbard, 1959). All of the fossils at Hagerman are constrained between two lava flows and ash units that have yielded ages of 4.0 Ma to 3.2 Ma using Ar-Ar dating methods (McDonald et al., 1996). We anchored the *Ondatra* + *Neofiber* node using a left m1 tooth of *Ondatra minor* (USNM 21830) from Hagerman. This m1 was identified as *Ondatra minor* by its relatively large size as well as being rooted and having a posterior loop, five alternating triangles, with a fifth triangle opening broadly into the anterior loop (Hibbard, 1959). We used an offset exponential distribution with a minimum age of 3.2 Ma and a mean of 4.9 Ma. The age of 3.2 Ma was chosen because it is the most conservative estimate of the age of the two ash layers described from Hagerman Idaho and deposition interpolation information were not available for the locality.

Calibration 4: Phenacomyini (*Phenacomys* + *Arborimus*) Node

Extant voles of the genera *Phenacomys* and *Arborimus* are today restricted to North America. Eurasian specimens of *Phenacomys* were identified from Krestovka, Kolyma Lowland Russia (Sher et al., 1979; Zazhigin, 1997) and Romanovo 1c, Western Siberia, Russia (Smirnov et al., 1986; Borodin, 2012). Recently, a new species (*Phenacomys europaeus*) was described from Europe in Zuurland, the Netherlands, and dated at 2.1 Ma via biochronology (van Kolfschoten et al., 2018). The oldest known record of *Phenacomys*, *P*. *gryci*, (type locality in the Gubik Formation) is from the Fish Creek fauna of Alaska. The Fish Creek Fauna is in the Gubik Formation, which is an alternating marine and coastal plain sedimentary unit. The Fish Creek Fauna is dated at ~2.4 Ma using amino acid racemization ratios, a reversed polarity zone, and the presence of the ancestral sea otter *Enhydrion* and the arvicoline rodent *Plioctomys mimomiformis* (Carter et al., 1986; Repenning et al., 1987; Repenning and Brouwers, 1992). We calibrated the (*Phenacomys* + *Arboriumus*) node based on the type specimen of *Phenacomys gryci* (a left m1 housed at the United States National Museum USNM 26495). This fossil was assigned to *Phenacomys gryci* by having a rooted m1 that lacked cementum in the reentrant angles. It also possesses a posterior loop, five asymmetrical alternating triangles with a "*Mimomys* Kante" on triangle four, and a complex anterior loop (Repenning et al., 1987). This node was calibrated using an offset exponential distribution with a minimum age 2.4 Ma and a mean of 3.27 Ma.

Calibration 5: Ellobiusini + Arvicolini + *Arvicola* + *Lemmiscus* + *Lagurini* Node: Includes the genera: *Ellobius* + *Neodon* + *Arvicola* + *Lemmiscus* + *Lagurus* + *Eolagurus* + *Chionomys* + *Proedromys* + *Volemys* + *Microtus* + *Lasiopodomys* + *Blanfordimys*

The timing of the origination and diversification of *Microtus* and its close relatives has been repeatedly contested among paleontologists (e.g., Repenning, 1992; Martin and Tesakov, 1998). It was argued that the genus *Allophaiomys* gave rise via anagenetic evolution to what is recognized today as *Microtus* (Martin and Tesakov, 1998), but that hypothesis is controversial (e.g., Bell et al., 2004; Bell and Bever, 2006). The oldest *Allophaiomys* with external age control is from Hansen Bluff (Colorado) and dated at 1.9 Ma (Rogers et al., 1992). The earliest occurrence of *Microtus,* as defined by Repenning (1992), was long thought to be from the Anza-Borrego Desert of California (Zakrzewski, 1972) from possibly 1.4 to 1.6 Ma (lacking firm age control). Unfortunately, the specimens from Anza-Borrego had questionable field data; one specimen was found in a fault block and from a different area in the park than originally reported, and a second specimen could not definitively be assigned to *Microtus* (Bell and Bever, 2006; Murray et al., 2011). The oldest known *Microtus* is, therefore, found in the type Irvington Fauna from California dated to 1.21 Ma based on paleomagnetic data (Bell and Bever, 2006).

Fossil evidence from *Ellobius*, the sister taxon to other members of this clade, was used here to calibrate the node. The oldest fossils of *Ellobius* are from the Late Pliocene of Kazakhstan and Tajikistan (Lytchev and Savinov, 1974; Zazhigin, 1988) and the Northern Caucasus (Tesakov, 2004). We chose to use a fossil mandible with m1-m3 (Paleontological Institute, Russian Academy of Sciences M-2049/58-KB) of *Ellobius primigenius* from Central Asia (Lytchev and Savinov, 1974). This fossil possesses rooted teeth with relatively high crowns, a posterior loop, five alternating triangles, and an anterior loop consistent with *Ellobius* (Lytchev and Savinov, 1974). This mandible is part of the Kiikbai fauna of Kazakhstan dated using biochronology (the occurrence of *Hypolagus brachygnathus*, *Ochotonoides complicidens*, and *Mimomys pliocaenicus*) to the Pliocene at ~2.4 Ma in the Matuyama Chron (Sotnikova et al., 1997). The Kiikbai fauna is described from the southern flank of the Ilian depression in the Alatau mountain and placed in the European middle Villafranchian land mammal age (Sotnikova et al, 1997). We used an offset exponential distribution with a minimum age of 2.4 Ma and a mean of 3.27 Ma.

Time-Calibrated Analyses

Microtus is one of the most diverse and rapidly evolving mammalian genera (Triant and DeWoody, 2006). Many phenotypic characters are convergent among distantly related species, and high genetic variation has been attributed to karyotypic differentiation, with diploid chromosomal numbers ranging from 17 to 64 (Triant and DeWoody, 2006). A previous study by Triant and DeWoody (2006) documented that *Microtus sensu stricto* has a time-corrected rate of nucleotide substitution of 0.08 substitutions per site. That is substantially higher than many if not most other mammals (i.e., *Pan*, *Bos*, *Ursus*) (Triant and DeWoody, 2006). We chose to use the substitution

rate of 0.08 substitutions per site as the mean clock rate prior for our time-calibrated analysis. We used the MrBayes command 'prset clockratepr' with a mean of -2.5 (natural log of 0.08) and a standard deviation of 0.005.

Calibrated nodes were constrained as monophyletic. We used MrBayes 3.2.6 for divergence time analyses. We used a birth-death model and an independent gamma rate relaxed-clock (igr), where each branch has an independent rate drawn from a gamma distribution that was empirically derived in MrBayes. The MCMC chain was run for 3.0×10^7 generations (sampled every 1000 generations) for two runs each with four chains. The time-calibrated analysis, completed using all five genes, required a longer run to reach stationarity, so 5.0×10^7 generations sampled every 1000 generations and for two separate and independent runs was used for that analysis only. A temperature of 0.05 was implemented for all analyses except for the analysis with all five genes that utilized a temperature of 0.1, and the first 30% of the data were discarded as burn-in. Results of the analyses were visualized in Tracer v1.7 (Rambaut et al., 2018) to ensure runs had reached stationarity and that the effective sample size (ESS) was >200 for all model parameters.

Results

Non-clock Analyses

Eight phylogenetic analyses were conducted on the concatenated dataset that included either all or a subset of the 135 sequences from *Cytb*; 58 from *COI*; 87 from *Ghr*; 100 from *IRBP/RBP3*; and 65 from *BRCA1*. 104 species (77%) included both mitochondrial and nuclear data. 31 species (23%) had only mitochondrial data. GenBank accession numbers are in Appendix A. Results from Maximum Likelihood, and Bayesian analyses were similar or identical, except where discussed below. For the ML and BI non-time calibrated analyses as well as the BI time-calibrated analyses we will describe the results of the combined analysis of all five genes and the nuclear loci >50% coverage (Ghr and IRBP/RBP3). The rest of the results are reported in Appendix C.

Maximum Likelihood (ML) Results

A summary of the ML tree including all five loci with rapid-bootstrapping values from RAxML v7.0.4 (lnL = -68877.47) is presented in Figure 1. Low support values (<70 nonparametric bootstrap (BS)) were inferred for 50 (37%) of the nodes. Moderate support (71-90 BS) was inferred for 12 (9%) of the nodes. High support (>90 BS) was found for 73 (54%) of the nodes. Most nodes with low support are near the base of major clades. A summary of the ML tree including the nuclear loci Ghr and IRBP with rapid-bootstrapping values from RAxML v7.0.4 (lnL = -14281.47) is presented in Figure 2. Low support values (<70 nonparametric bootstrap (BS)) were inferred for 41 (40%) of the nodes. Moderate support (71-90 BS) was inferred for 18 (17%) of the nodes. High

support (>90 BS) was found for 45 (43%) of the nodes. Most nodes with low support are near the base of major clades and the tree.

Bayesian Inference (BI) Results

Most nodes (85, or 64%) in the non-clock BI analysis that included all five genes were highly supported (>0.95 posterior probability values (PP)). The majority rule consensus tree for this analysis is presented in Figure 3. In the analysis of the two high coverage nuclear markers Ghr and IRBP/RBP3, 59 nodes (57%) were highly supported (>0.95 posterior probability values (PP)). The majority rule consensus tree for this analysis is presented in Figure 4.

Major Clade Systematic Results

Prometheomys was consistently placed as the most basal, or nearly most basal arvicoline (see Figures 1-4). The two species of bog lemming (*Synaptomys*, *Mictomys*) were paraphyletic in the ML and BI analyses of all five genes (100 BS, 1.00 PP), and monophyletic (92 BS) in the ML and BI (0.83 PP) Ghr and IRBP only analyses. All analyses inferred a relatively basal position for the 'true lemmings' (see Figures 1-4). *Myopus* was inferred as the sister taxon to *Lemmus* in both ML analyses (100-98 BS) and BI (1.00 PP) analyses. *Lemmus* was monophyletic, with relationships among the species of *Lemmus* identical for both ML and BI analyses and with high support (ML: 97-100 BS; BI: 1.00 PP. *Ondatra* and *Neofiber* were inferred as sister genera in all analyses with high support (ML: 100 BS: BI: 1.00 PP) and placed near the base of the arvicoline tree.

Interspecies relationships among *Dicrostonyx* were highly supported but different between analyses (see Figures 1-4). *Dicrostonyx* was consistently placed as sister to the clade (*Phenacomys*, *Arborimus*) with moderate to strong support. We found generic resolution between *Phenacomys* and *Arborimus* similar to Robovský et al. (2008) and Fabre et al. (2012). In the ML analysis (see Figures 1-2) we found a (*Phenacomys*, *Arborimus*) clade (100 BS) that had high bootstrap values throughout (100 BS). The BI analysis also had high posterior probabilities (1.00) for all relationships within (*Phenacomys*, *Arborimus*) (see Figure 3-4).

All of our ML and BI analyses inferred a large clade that includes the genera *Ellobius*, *Lagurus*, *Eolagurus*, *Neodon*, *Dinaromys*, *Lemmiscus*, *Arvicola*, *Chionomys*, *Proedromys*, *Volemys*, *Microtus* (including both North American and Eurasian species), *Lasiopodomys*, and *Blanfordimys* (see Figures 1-4). The overall topology among the genera varies little between the analyses, but some species level relationships did vary with poor interspecies resolution throughout. *Arvicola* was placed towards the base of this large clade and as monophyletic (with identical species level topology) and with high support (ML: 100 BS; BI: 1.00 PP). However, the interspecies relationships within *Arvicola* were not well supported in all analyses. *Neodon* was found to be monophyletic

with high support (ML: 99 BS; BI: 1.00 PP) and near the base of the large clade. *Chionomys* is well supported (98-100 BS; 1.00 PP) as a clade that, in the ML analysis of all five genes, is sister to the clade including *Volemys*, *Proedromys*, *Microtus*, *Blanfordimys*, and *Lasiopodomys*. In all analyses, *Proedromys bedfordi* is the sister to *Volemys musseri* with high support in the ML (99-100 BS) and the BI (1.00 PP) analyses. *Volemys millicens* is inferred to be the sister to *Neodon* (ML: 98-100 BS; BI: 1.00 PP). All analyses indicate that *Volemys* is polyphyletic. *Lasiopodomys* is inferred as monophyletic in all analyses with moderate to high support (71-100 BS and 1.00 PP). In the BI analysis of Ghr and IRBP, *Lasiopodomys* is inferred to be nested within North American *Microtus* (1.00 PP) (see Figure 4). *Blanfordimys* is found to be monophyletic in all analyses with high support (100 BS and 1.00 PP). North American *Microtus* is inferred as monophyletic in half the analyses (BI Ghr, IRBP, cytb; ML and BI of all five genes), however, this clade is weakly supported (ML: 40 BS; BI: 0.31-0.73 PP). *Alticola* was weakly to moderately supported as monophyletic (ML: 68-90 BS; BI: 0.82 PP), with similar but not identical species level topology, and nested within *Clethrionomys* in all analyses. *Clethrionomys* is thus rendered paraphyletic by *Alticola*.

Time-Calibrated Analysis

In the analysis that included Ghr and IRBP, 57 nodes (55%) had posterior probability values >0.95. The time-calibrated majority rule consensus tree is presented in Figure 5. In the analysis that included all five genes, 94 nodes (71%) had posterior probability values >0.95. The time-calibrated majority rule consensus tree is presented in Figure 6.

Divergence-Time Results

Crown arvicoline rodents were inferred to have diverged ~8 Ma. For a list of all the major clades and their divergence estimates see Table 1.

Discussion

Systematic Position of Genera and Discussion of Intrageneric Relationships

The overall topology of our ML and BI analyses are largely congruent with previously published molecular phylogenies (e.g., Conroy and Cook, 1999, 2000; Galewski et al., 2006; Buzan et al., 2008; Fabre et al., 2012; Martínková and Moravec, 2012; Steppan and Schenk, 2017; Upham et al., 2019; Abramson et al., 2021) with the main exception being Robovský et al. (2008). This exception is likely tied to the fact that this is the only study that included morphological characters in the analysis. With our increased sample size we did find some differences, especially in relatively earlier divergences, but few of those nodes were well-supported. There are some topological differences based on which genes are included in the analysis (e.g., nuclear,

mitochondrial, or combined). Below we outline the implications of our results for the taxonomy and evolutionary understanding of Arvicolinae.

Basal position of *Prometheomys*

Prometheomys was placed as the most basal arvicoline with weak support in several studies (Galewski et al., 2006; Fabre et al., 2012; Steppan and Schenk, 2017; Upham et al., 2019; Ibis et al., 2020). In other studies, it was placed close to the base of Arvicolinae but not as the first diverging arvicoline (Buzan et al., 2008; Robovský et al., 2008; Abramson et al., 2021). Our results provide conflicting results depending on which markers and method was used to reconstruct the phylogeny. Our ML and BI analyses that included only nuclear markers placed *Prometheomys*, as the most basal arvicoline with strong support (100 BS and 1.00 PP). However, when mitochondrial markers were included, *Prometheomys* is placed near the base, but not as the most basal arvicoline (weak support). Therefore, we stress caution in assigning *Prometheomys* the title of the 'most basal arvicoline'.

Monophyly of Bog Lemmings?

Bog lemmings (*Synaptomys* and *Mictomys*) and 'true lemmings' (*Myopus*, *Lemmus*) are consistently placed in a clade at or near the base of the arvicoline tree. One study placed lemmings as sister to all other arvicolines (Abramson et al., 2021), while most have found lemmings to be near but not at the base of the tree (Galewski et al., 2006; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017; Upham et al., 2019). Studies that sampled both species of extant bog lemmings found that *Synaptomys* (as defined by Musser and Carleton, 2005) is paraphyletic with respect to 'true lemmings' (Buzan et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017; Upham et al., 2019). Our results unfortunately do not add any clarity on whether bog lemmings should be one or two genera, with 50% of our trees recovering a weakly supported clade. However, it should be noted that analyses based either entirely or predominantly on nuclear markers recovered a weakly supported clade, while those that included mitochondrial data tended not to. Based on dental morphology, many paleontologists have considered the northern bog lemming, *Synaptomys borealis* (following Musser and Carleton, 2005), to be a member of a distinct genus known as *Mictomys* (Fejfar and Repenning, 1998; Repenning and Grady, 1988). Musser and Carleton (2005) argued that there may be enough evidence to place *Mictomys* and *Synaptomys* as distinct genera, but they tentatively kept them in the same genus. Along with other studies (e.g., Buzan et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017), our analyses do not support the monophyly of bog lemmings and so *Mictomys* and *Synaptomys* are likely distinct genera that are united with *Myopus* and *Lemmus* in Lemmini.

Systematic Status of Dicrostonychini (*Phenacomys*, *Arborimus*, and *Dicrostonyx*)

Voles belonging to *Phenacomys* and *Arborimus* are consistently found to be sister genera (Robovský et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017; Upham et al., 2019). Recently, the clade (*Phenacomys, Arborimus*) was found to be sister to *Dicrostonyx* (Galewski et al., 2006; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017; Abramson et al., 2021). Historically *Dicrostonyx* was thought to be closely related to the other lemmings, but that was not viewed as valid in recent studies (Galewski et al., 2006; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017; Abramson et al., 2021). Our study uses robust sampling of *Dicrostonyx* and *Phenacomys* (and to a lesser extent *Arborimus*) to further substantiate the hypothesis that they are not closely related to other lemmings as hypothesized based on morphology alone. All of our data are also in agreement with Abramson et al. (2021) that *Dicrostonyx*, *Phenacomys*, and *Arborimus*, are united into a clade that Abramson et al. (2021) called Dicrostonychini. Lemmings and ((*Phenacomys*, *Arborimus*), *Dicrostonyx*) were consistently placed in a clade at or near the base of Arvicolinae in our analyses. More complete taxonomic sampling is needed, especially within *Phenacomys* and *Arborimus* (e.g., *Arborimus albipes*, which was not included here) to further parse these relationships and provide further support for the close affinity of Dicrostonychini and Lemmini.

Systematic Status of Myodini (*Clethrionomys*, *Alticola*, and *Eothenomys*)

Using molecular data (and to a lesser extent morphology), *Clethrionomys*, *Alticola*, and *Eothenomys* were consistently found to be closely related and united in the tribe Myodini (Luo et al., 2004; Galewski et al., 2006; Lebedev et al., 2007; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Liu et al., 2012; Jin et al., 2013; Steppan and Schenk, 2017; Upham et al., 2019; Abramson et al., 2021). Dental morphology alone suggests that *Clethrionomys* (rooted molars) would likely be more distantly related to voles of the genera *Eothenomys* and *Alticola* (rootless molars) (Luo et al., 2004; Lebedev et al., 2007; Liu et al., 2012; Zeng et al., 2013). We consistently recovered *Eothenomys* in a clade closely related to *Clethrionomys*, which is similar to previous studies (Luo et al., 2004; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Liu et al., 2012; Zeng et al., 2013; Steppan and Schenk, 2017; Abramson et al., 2021). We found that *Clethrionomys* is paraphyletic with respect to *Alticola*. Species currently placed in *Clethrionomys* and *Alticola* form the sister clade of *Eothenomys*. Clearly the taxonomy of species assigned to *Clethrionomys* is problematic, but we suggest that phylogenomic analyses should be performed to establish a stable taxonomy.

Alticola has been under-sampled in many previous studies. Depending on what taxa of *Alticola* are included, studies have found it to be monophyletic (Fabre et al., 2012; this study) or paraphyletic (Lebedev et al., 2007; Steppan and Schenk, 2017;

Upham et al., 2019; Abramson et al., 2021). Our study includes a nearly complete sampling of currently recognized species of *Alticola* (n=11). Our well-supported results indicate that species currently placed in *Alticola* compose a clade. This result is different than what was recovered by Upham and colleagues (2019), the only other study to include 11 species of *Alticola*. They recovered a paraphyletic *Alticola* with respect to *Clethrionomys*. This suggests that more work needs to be done on these two genera to further clarify there systematic status.

Systematic Status of *Hyperacrius* and *Proedromys*

The systematic positions of the Subalpine Kashmir Vole (*Hyperacrius fertilis*) and the Duke of Bedford's Vole (*Proedromys bedfordi*) have been relatively understudied. Using morphology alone, *Hyperacrius* was historically hypothesized to be closely related to *Alticola* (Hinton, 1926), or as a member of the tribe Clethrionomyini (=Myodini) (Gromov and Polyakov, 1977). Kohli et al. (2014) included *Hyperacrius* for the first time in a molecular analysis, and its relationship to Clethrionomyini was doubted. None of our analyses recovered *Hyperacrius* with strong support. Some placing it with Myodini and others placing it near Arvicolini. Recently, *Hyperacrius* was hypothesized to be the earliest diverging member of Arvicolini (Abramson et al., 2020; 2021). More robust sampling is needed to firmly establish *Hyperacrius* systematic position.

Proedromys has historically been thought to be closely related, or even included in, *Microtus* (Ellerman and Morrison-Scott, 1951; Gromov and Polyakov, 1977; Musser and Carleton, 2005). We concur with other phylogenetic studies that have included *Proedromys* (Fabre et al., 2012; Steppan and Schenk, 2017; Abramson et al., 2021) that it is likely a member of the tribe Arvicolini and closely related to but outside of *Microtus*. We consistently recovered *Volemys musseri* as the sister to *Proedromys*. Given the geographical overlap of the two this is not suprising and others have recovered this as well (Steppan and Schenk, 2017; Upham et al., 2019).

Systematic Status of *Ellobius*, *Arvicola*, *Neodon* and *Chionomys*

Over the past decade, *Ellobius*, *Arvicola*, *Neodon*, and *Chionomys* have been the subject of several phylogenetic studies (Yannic et al., 2012; Pradhan et al., 2019; Bondareva et al., 2020; Mahmoudi et al., 2020). *Ellobius* has been placed as an early diverging arvicoline (Bondareva et al., 2020; Robovský et al., 2008), or as an early diverging member of the radiation that includes *Lagurus*, *Eolagurus*, *Lemmiscus*, *Neodon*, *Arvicola*, *Chionomys*, *Proedromys*, *Volemys*, *Lasiopodomys*, *Blanfordimys*, and *Microtus* (Fabre et al., 2012; Steppan and Schenk, 2017; Upham et al., 2019; Abramson et al., 2021). We found here that *Ellobius* is an early diverging member of the large, nested radiation that includes *Microtus*, and not an early diverging arvicoline (see Figures 1-4), but this relationship was not strongly supported in any analysis that included mitochondrial data. In the calibrated and uncalibrated nuclear trees, *Ellobius* is

the earliest diverging member of the large clade with strong support (Figures 2, 4, and 6).

Arvicola is frequently inferred to be a basal member of Arvicolini, and our results further support this hypothesis (Galewski et al., 2006; Robovský et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017; Upham et al., 2019; Mahmoudi et al., 2020). We inferred a monophyletic *Arvicola* with most commonly a weak sister taxon relationship to *Lemmiscus curtatus* (in analyses that included mitochondrial data with the exception being the ML 5 gene analysis), similar to the results of Steppan and Schenk (2017). That is an interesting biogeographic result given the large distance between the extant members of these genera.

Neodon has been recognized as a genus or as a subgenus of *Microtus* (see Musser and Carleton, 2005) or placed in *Pitymys* (Ellerman and Scott, 1951). Recent systematic and taxonomic work has altered our understanding of the clade (Bannikova et al., 2010; Liu et al., 2012; Liu et al., 2017; Pradhan et al., 2019). As more molecular data have been added across Arvicolinae, it is now apparent that, historically, *Microtus* has been used as a taxonomic garbage bin. With the recent recognition of *M. leucurus* as *Neodon leucurus*, *M. clarkei* as *N. clarkei*, *M. fuscus* as *N. fuscus*, and *N. juldaschi* as *Blanfordimys juldaschi*, we have achieved some taxonomic clarity for *Neodon* (Pradhan et al., 2019; Abramson et al., 2021). With these taxonomic revisions in mind, our analyses inferred, with high support, a monophyletic *Neodon*, that is an early diverging member of Arvicolini. We also found a strongly supported sister relationship between *Volemys millicens* and *Neodon*, which suggest a need for further exploration of the relationships between these two and possibly a need for taxonomic revision for *V. millicens*.

Historically, *Chionomys* was placed in *Arvicola*, in *Microtus*, its own genus, or as a subgenus of *Microtus* (Yannic et al., 2012). This complicated history can be attributed in part to a highly fragmented geographic distribution and isolation in high alpine environments. Jaarola et al. (2004) used *cytb* to solidify *Chionomys* as a valid genus separate from *Microtus*, and several other studies placed *Chionomys* as a nested member of Arvicolini outside of *Microtus* (Galewski et al., 2006; Robovský et al., 2008; Fabre et al., 2012; Abramson et al., 2021). Our results further support that hypothesis and further substantiate the claim that *Chionomys* is a valid genus.

Systematic Status of *Lemmiscus curtatus*

Lemmiscus curtatus has been poorly sampled in phylogenetic analyses. Until recently, the sagebrush vole, *Lemmiscus curtatus*, was not included in phylogenetic analyses based on molecular data (Steppan and Schenk, 2017; Abramson et al., 2021). Those two analyses produced conflicting results for the systematic position of *Lemmiscus*. Both studies found that *Lemmiscus* and *Microtus* are not sister taxa. Steppan and Schenk (2017) placed *Lemmiscus* as sister to *Arvicola*, whereas

Abramson et al. (2021) placed it as sister to *Chionomys*. Some of our results, though weakly supported, are similar to Steppan and Schenk (2017), probably because we used the same genetic data for *Lemmiscus* for our phylogeny, whereas Abramson et al. (2021) used an entire mitochondrial genome of *Lemmiscus*. Our ML analyses placed *Lemmiscus* as the most basal arvicoline whereas our BI analyses placed it weakly as the sister to *Arvicola*. We reject the most basal arvicoline hypothesis, because it is likely the product of only using a single mitochondrial marker. More data from transcriptomes or nuclear genes will likely help to refine the systematic position of this species so we do not make any recommendations on the systematic position of *Lemmiscus*.

Systematic Status of *Blanfordimys*, *Volemys*, and *Lasiopodomys*

Blanfordimys has been variably considered a distinct genus, a subgenus of *Microtus*, or as a member of *Neodon* (see Musser and Carleton, 2005). Bannikova et al. (2009) showed with high support that *B*. *bucharensis* was sister to what was then called *Microtus* (*Neodon*) *juldaschi*, and the two of them were considered sister to *B*. *afghanus*. That work laid the framework for Liu et al. (2012) to propose abandoning *M*. (*Neodon*) *juldaschi* for *B*. *juldaschi* to resolve the paraphyly of *Blanfordimys* (Fabre et al. 2012). Our results support this taxonomic decision, which would make *Blanfordimys* monophyletic (although the genus and several others still make *Microtus* paraphyletic; see below). *Blanfordimys* is sister to *Microtus agrestis* in our analyses. The taxonomy of that species is unclear, and *M*. *agrestis* could defensibly be assigned to *Blanfordimys* or *Microtus* depending on the taxonomic future of the latter genus.

Historically, *Volemys* has been considered a distinct genus or a subgenus of *Microtus*, with Musser and Carleton (2005) recognizing two species, *V*. *musseri* and *V*. *millicens*. That classification is based on morphology alone, and the monophyly of *Volemys* has not been supported using molecular data (Jaarola et al., 2004; Steppan and Schenk, 2017; Upham et al., 2019). We also did not infer a monophyletic *Volemys*, so we suggest further systematic study of voles currently placed within *Volemys*, because the molecular evidence points to the two species belonging to separate genera. Further examination should be undertaken to understand potential morphological homoplasy between *V*. *millicens* and *V*. *musseri*, which would explain their historical placement in the genus *Volemys*.

In the past, four species of voles have been included in *Lasiopodomys*; *Microtus gregalis*, L. *brandtii*, *L*. *mandarinus*, and *L*. *fuscus*. However, a combined evidence phylogeny suggested that *L*. *fuscus* should be removed from *Lasiopodomys* and placed in *Neodon* (Liu et al., 2012). This conclusion is supported in both our ML and BI analysis, and we support this taxonomic realignment. There is also disagreement on the generic allocation of *Lasiopodomys gregalis* to that genus or *Microtus* (see Abramson and Lissovsky, 2012; Petrova et al., 2015; Musser and Carleton, 2005). Our phylogenetic analysis supports the placement of the species in *Lasiopodomys*.

722
723 **Systematic Status of *Microtus***
724 Voles of the genus *Microtus* are frequently studied but have presented a long-
725 term systematic enigma (e.g., Conroy and Cook, 2000; Fabre et al. 2004; Abramson et
726 al., 2021). *Microtus* is one of the most rapidly evolving lineages of rodents and contains
727 over sixty extant species (Musser and Carleton, 2005). The species of *Microtus* that are
728 endemic to North America have in the past been recovered as a clade (Conroy and
729 Cook, 1999, 2000; Upham et al., 2019; Abramson et al., 2021). Our results fail to
730 definitively support this hypothesis, with half of our analyses recovering a paraphyletic
731 endemic North American *Microtus*. To attempt to clarify the taxonomy of *Microtus*,
732 researchers have used subgenera such as *Pedomys*, *Alexandromys*, *Terricola*,
733 *Iberomys*, *Agricola*, and *Neodon*, but these subgenera are variably considered genera
734 by different authors. Thus, the genus *Microtus* needs to be redefined (Barbosa et al.,
735 2018; Abramson et al., 2021), because without a redefinition, *Microtus* is a large
736 paraphyletic genus, with genera such as *Lasiopodomys*, *Blanfordimys*, *Arvicola*, and
737 *Neodon* nested within it (Conroy and Cook, 1999, 2000; Jaarola et al., 2004; Galewski
738 et al., 2006; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Martínková
739 and Moravec, 2012; Steppan and Schenk, 2017; Barbosa et al., 2018; Abramson et al.,
740 2021). We therefore recommend phylogenomic data be collected to stabilize this
741 taxonomy. Until then we do not suggest sweeping taxonomic changes within *Microtus*
742 but again emphasize the probable and widespread paraphyly of the genus.
743
744 **Diversification of arvicolines**
745 Our results are largely congruent with the published fossil record and the
746 divergence time estimates of Steppan and Schenk (2017), Upham et al. (2019), and
747 Abramson et al. (2021). We estimated a mean age of crown Arvicolinae at ~8 Ma, which
748 is only slightly older than the age (7.4 Ma) inferred by Abramson et al. (2021). These
749 ages are older than the earliest possible arvicoline rodent fossils, which are probably
750 Pliocene in age (e.g., *Pannonicola, Microtoscoptes*, or *Goniodontomys*). Abramson et
751 al. (2021) included a calibration at the crown Arvicolinae node whereas we did not,
752 potentially accounting for the slight discrepancy in our results. We did not use a
753 calibration because of the uncertain phylogenetic placement of putative early arvicoline
754 fossils (Repenning, 1987; Fejfar et al., 2011). Abramson et al (2021) also ran an
755 analysis without that calibration, and they found an age close to their fully calibrated tree
756 and the result of our study. This gives us confidence in an origin of arvicolines ~7-8 Ma,
757 with dentally distinct arvicoline rodents evolving later (~6-5 Ma). For ages of major tribes
758 and clades of arvicolines found in our study, see Table 1. Of note is the discrepancy in
759 the age of clades between analyses that included only nuclear markers, mitochondrial
760 markers only, or a combined analysis. Node ages did not vary by more than ~2 Ma
761 across our analyses.

Abramson et al. (2021) documented three radiations of arvicoline rodents, whereas we establish four radiations. The “first radiation” of Abramson et al. (2021) consists of the tribes Lemmini, Prometheomyini, Ondatraini, and Dicrostonychini (see Table 1 and Figure 5-6 for ages). This “first radiation” of Abramson et al. (2021) is taxonomically equivalent to our first three radiations. Our “first radiation” consists only of the tribe Prometheomyini with ancestors of the modern long-clawed mole vole (*P. schaposchnikowi*), diverging from all other arvicolines between 8-7 Ma. Our “second radiation” consists of the tribes Ondatraini, Lemmini, and Dicrostonychini. Between 7-6 Ma we see a divergence between these three tribes, and the rest of the arvicoline rodents (e.g., Myodini, Arvicolini). Our “third radiation” consists of Myodini and *Hyperacrius*. This radiation diverged from the MRCA with Arvicolini, Lagurini, and Ellobiusini between 6-5 Ma. Finally our “fourth radiation” consists of all of the other arvicolines, including Arvicolini, *Lemmiscus*, *Chionoys*, *Proedromys*, Ellobiusini and Lagurini. These arvicolines diverged from the MRCA with the rest of the arvicolines mentioned previously between 5-4 Ma.

Conclusions

A better understanding of the phylogeny of arvicoline rodents has been warranted given their remarkable evolutionary history and abundance across high latitudes. We provide new systematic hypotheses across Arvicolinae and some direction for future systematic and taxonomic work. We show that the first “wave” of arvicolines (our first “two radiations”) likely includes the genera *Ondatra*, *Neofiber*, *Lemmus*, *Myopus*, *Synaptomys*, *Mictomys*, *Dicrostonyx*, *Prometheomys*, *Phenacomys*, and *Arborimus*. The earliest diverging arvicoline clade is likely *Prometheomys*, but work still needs to be done to solidify this hypothesis. The monophyly of bog lemmings (*Synaptomys* and *Mictomys*) is doubted, however their close relationship to the “true lemmings” (*Myopus* and *Lemmus*) is clear. Similar to Abramson et al. (2021) we also recovered evidence to support the inclusion of *Phenacomys* and *Arborimus* with *Dicrostonyx* in Dicrostonychini. The second “wave” (our “third” and “fourth” radiations) include *Alticola*, *Clethrionomys*, *Eotheonomys*, *Ellobius*, *Lagurus*, *Arvicola*, *Lemmiscus*, *Chionomys*, *Neodon*, *Proedromys*, *Volemys*, *Lasiopodomys*, *Blanfordimys*, and *Microtus*. *Clethrionomys*, *Eothenomys*, and *Alticola* clearly form a large monophyletic clade, however the paraphyly of *Clethrionomys* relative to *Alticola* needs to be explored. Our study made progress in clarifying the taxonomy and systematics for this large clade, however we recommend more robust sampling (particularly within *Microtus*), before any large scale taxonomic revisions are made. We founds some evidence for a monophyletic endemic North American *Microtus*, however this was not recovered in all analyses, and could benefit from larger scale sampling across the genome. Finally, we estimated divergence times among the major clades, which were concordant with the

published fossil record. This will provide valuable insight into the evolutionary and paleobiogeographical history of this clade.

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Figure 1

Figure 1: Maximum Likelihood (ML) tree of concatenated molecular dataset of all five genes representing 132 arvicolines and 3 members of Cricetidae.

Tree was rooted with *Neotoma fuscipes*. Abbreviations: On = Ondatrini; Di = Dicrostonychini; El = Ellobiusini. La = Lagurini. Symbols at nodes represent bootstrap values.

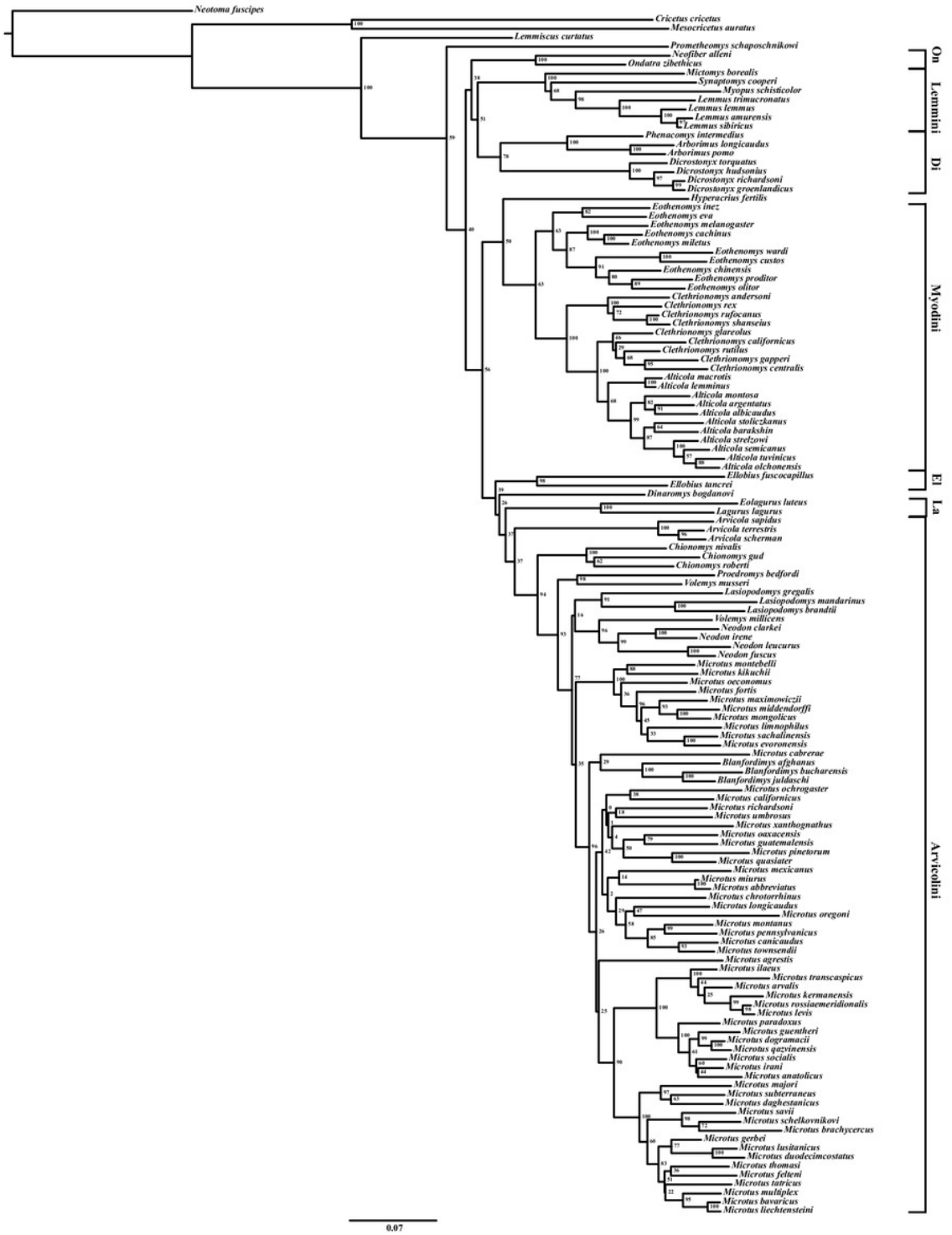
ML Ghr, IRBP/RBP3, BRCA1, Cytb, and COI Combined
Neotoma fuscipes
Cricetus cricetus
Mesocricetus auratus
Lemmiscus curtatus
Prometheomys schaposchnikowi
Neofiber alleni
Ondatra zibethicus
Mictomys borealis
Synaptomys cooperi
Myopus schisticolor
Lemmus trimucronatus
Lemmus lemmus
Lemmus amurensis
Lemmus sibiricus
Phenacomys intermedius
Arborimus longicaudus
Arborimus pomo
Dicrostonyx torquatus
Dicrostonyx hudsonius
Dicrostonyx richardsoni
Dicrostonyx groenlandicus
Hyperacrius fertilis
Eothenomys inez
Eothenomys eva
Eothenomys melanogaster
Eothenomys cachinus
Eothenomys miletus
Eothenomys wardi
Eothenomys custos
Eothenomys chinensis
Eothenomys proditor
Eothenomys olitor
Clethrionomys andersoni
Clethrionomys rex
Clethrionomys rufocanus
Clethrionomys shanseius
Clethrionomys glareolus
Clethrionomys californicus
Clethrionomys rutilus
Clethrionomys gapperi
Clethrionomys centralis
Alticola macrotis
Alticola lemminus
Alticola montosa
Alticola argentatus
Alticola albicaudus
Alticola stoliczkanus
Alticola barakshin
Alticola strelzowi
Alticola semicanus
Alticola tuvinicus
Alticola olchonensis
Ellobius fuscocapillus
Ellobius tancrei
Dinaromys bogdanovi
Eolagurus luteus
Lagurus lagurus
Arvicola sapidus
Arvicola terrestris
Arvicola scherman
Chionomys nivalis
Chionomys gud
Chionomys roberti
Proedromys bedfordi
Volemys musseri
Lasiopodomys gregalis
Lasiopodomys mandarinus
Lasiopodomys brandtii
Volemys millicens
Neodon clarkei
Neodon irene
Neodon leucurus
Neodon fuscus
Microtus montebelli
Microtus kikuchii
Microtus oeconomus
Microtus fortis
Microtus maximowiczii
Microtus middendorffi
Microtus mongolicus
Microtus limnophilus
Microtus sachalinensis
Microtus evoronensis
Microtus cabrerae
Blanfordimys afghanus
Blanfordimys bucharensis
Blanfordimys juldaschi
Microtus ochrogaster
Microtus californicus
Microtus richardsoni
Microtus umbrosus
Microtus xanthognathus
Microtus oaxacensis
Microtus guatemalensis
Microtus pinetorum
Microtus quasiater
Microtus mexicanus
Microtus miurus
Microtus abbreviatus
Microtus chrotorrhinus
Microtus longicaudus
Microtus oregoni
Microtus montanus
Microtus pennsylvanicus
Microtus canicaudus
Microtus townsendii
Microtus agrestis
Microtus ilaeus
Microtus transcaspicus
Microtus arvalis
Microtus kermanensis
Microtus rossiaemeridionalis
Microtus levis
Microtus paradoxus
Microtus guentheri
Microtus dogramacii
Microtus qazvinensis
Microtus socialis
Microtus irani
Microtus anatolicus
Microtus majori
Microtus subterraneus
Microtus daghestanicus
Microtus savii
Microtus schelkovnikovi
Microtus brachycercus
Microtus gerbei
Microtus lusitanicus
Microtus duodecimcostatus
Microtus thomasi
Microtus felteni
Microtus tatricus
Microtus multiplex
Microtus bavaricus
Microtus liechtensteini
0.07
On
Lemmini
Di
Myodini
El
La
Arvicolini

Figure 2

Figure 2: Maximum Likelihood (ML) tree of concatenated molecular dataset of the nuclear genes Ghr and IRBP/RPB3, representing 101 arvicolines and 3 members of Cricetidae.

Tree was rooted with *Neotoma fuscipes*. Abbreviations: On = Ondatrini; Di = Dicrostonychini; El = Ellobiusini. La = Lagurini. Symbols at nodes represent bootstrap values.


ML Ghr and IRBP/RBP3 (Nuclear)
Neotoma fuscipes
Mesocricetus auratus
Cricetus cricetus
Prometheomys schaposchnikowi
Ondatra zibethicus
Neofiber alleni
Arborimus longicaudus
Phenacomys intermedius
Dicrostonyx hudsonius
Dicrostonyx groenlandicus
Dicrostonyx torquatus
Myopus schisticolor
Lemmus trimucronatus
Lemmus lemmus
Lemmus sibiricus
Synaptomys cooperi
Mictomys borealis
Eothenomys inez
Eothenomys eva
Eothenomys proditor
Eothenomys cachinus
Eothenomys melanogaster
Eothenomys miletus
Eothenomys custos
Eothenomys olitor
Eothenomys wardi
Eothenomys chinensis
Clethrionomys andersoni
Clethrionomys shanseius
Clethrionomys rufocanus
Clethrionomys rex
Clethrionomys rutilus
Clethrionomys centralis
Clethrionomys gapperi
Clethrionomys californicus
Clethrionomys glareolus
Alticola argentatus
Alticola albicaudus
Alticola tuvinicus
Alticola barakshin
Alticola semicanus
Alticola strelzowi
Alticola olchonensis
Alticola macrotis
Alticola lemminus
Ellobius fuscocapillus
Ellobius tancrei
Dinaromys bogdanovi
Lagurus lagurus
Eolagurus luteus
Arvicola sapidus
Arvicola scherman
Arvicola terrestris
Chionomys nivalis
Chionomys gud
Chionomys roberti
Volemys musseri
Proedromys bedfordi
Lasiopodomys gregalis
Lasiopodomys brandtii
Lasiopodomys mandarinus
Blanfordimys juldaschi
Blanfordimys bucharensis
Blanfordimys afghanus
Microtus agrestis
Microtus schelkovnikovi
Microtus irani
Microtus guentheri
Microtus socialis
Microtus qazvinensis
Microtus transcaspicus
Microtus levis
Microtus rossiaemeridionalis
Microtus arvalis
Microtus lusitanicus
Microtus duodecimcostatus
Microtus gerbei
Microtus thomasi
Microtus subterraneus
Microtus majori
Microtus daghestanicus
Microtus miurus
Microtus ochrogaster
Microtus richardsoni
Microtus chrotorrhinus
Microtus pennsylvanicus
Microtus montanus
Microtus longicaudus
Microtus californicus
Microtus pinetorum
Microtus limnophilus
Microtus middendorffi
Microtus mongolicus
Microtus fortis
Microtus montebelli
Microtus oeconomus
Microtus kikuchii
Microtus maximowiczii
Microtus evoronensis
Microtus cabrerae
Volemys millicens
Neodon irene
Neodon leucurus
Neodon fuscus
0.02
On
Di
Lemmini
Myodini
El
La
Arvicolini

Figure 3

Figure 3: Majority-rule consensus tree produced using Bayesian Inference (BI) methods of the concatenated molecular dataset of all five genes representing 132 arvicolines and 3 members of Cricetidae.

Tree was rooted with *Neotoma fuscipes*. Abbreviations: On = Ondatrini; Di = Dicrostonychini; El = Ellobiusini. La = Lagurini. Symbols at nodes represent posterior probability values.

BI Ghr, IRBP/RBP3, BRCA1, Cytb, and COI Combined

Figure 4

Figure 4: Majority-rule consensus tree produced using Bayesian Inference (BI) methods of the concatenated molecular dataset of the nuclear genes Ghr and IRBP/RBP3 representing 101 arvicolines and 3 members of Cricetidae.

Tree was rooted with *Neotoma fuscipes*. Abbreviations: On = Ondatrini; Di = Dicrostonychini; El = Ellobiusini. La = Lagurini. Symbols at nodes represent posterior probability values.


BI GHR and IRBP/RBP3 (Nuclear) 30 Million Generations
Neotoma fuscipes
Cricetus cricetus
Mesocricetus auratus
Prometheomys schaposchnikowi
Ondatra zibethicus
Neofiber alleni
Arborimus longicaudus
Phenacomys intermedius
Dicrostonyx hudsonius
Dicrostonyx groenlandicus
Dicrostonyx torquatus
Mictomys borealis
Synaptomys cooperi
Myopus schisticolor
Lemmus trimucronatus
Lemmus lemmus
Lemmus sibiricus
Eothenomys inez
Eothenomys eva
Eothenomys proditor
Eothenomys miletus
Eothenomys melanogaster
Eothenomys cachinus
Eothenomys wardi
Eothenomys olitor
Eothenomys chinensis
Eothenomys custos
Clethrionomys andersoni
Clethrionomys rex
Clethrionomys rufocanus
Clethrionomys shanseius
Clethrionomys rutilus
Clethrionomys gapperi
Clethrionomys centralis
Clethrionomys californicus
Clethrionomys glareolus
Alticola lemminus
Alticola macrotis
Alticola argentatus
Alticola albicaudus
Alticola tuvinicus
Alticola olchonensis
Alticola barakshin
Alticola semicanus
Alticola strelzowi
Ellobius fuscocapillus
Ellobius tancrei
Dinaromys bogdanovi
Lagurus lagurus
Eolagurus luteus
Arvicola sapidus
Arvicola terrestris
Arvicola scherman
Chionomys roberti
Chionomys gud
Chionomys nivalis
Volemys musseri
Proedromys bedfordi
Volemys millicens
Neodon irene
Neodon fuscus
Neodon leucurus
Microtus fortis
Microtus maximowiczii
Microtus evoronensis
Microtus montebelli
Microtus oeconomus
Microtus kikuchii
Microtus limnophilus
Microtus mongolicus
Microtus middendorffi
Microtus cabrerae
Blanfordimys afghanus
Blanfordimys bucharensis
Blanfordimys juldaschi
Microtus miurus
Microtus pinetorum
Microtus californicus
Lasiopodomys gregalis
Lasiopodomys brandtii
Lasiopodomys mandarinus
Microtus richardsoni
Microtus ochrogaster
Microtus chrotorrhinus
Microtus longicaudus
Microtus montanus
Microtus pennsylvanicus
Microtus agrestis
Microtus subterraneus
Microtus daghestanicus
Microtus majori
Microtus thomasi
Microtus gerbei
Microtus duodecimcostatus
Microtus lusitanicus
Microtus schelkovnikovi
Microtus arvalis
Microtus transcaspicus
Microtus rossiaemeridionalis
Microtus levis
Microtus qazvinensis
Microtus irani
Microtus socialis
Microtus guentheri
0.009
On
Di
Lemmini
Myodini
El
La
Arvicolini

Figure 5

Figure 5: Time-Calibrated Bayesian (BI) tree of concatenated molecular dataset of all five genes representing 132 arvicolines and 3 members of Cricetidae.

Tree was rooted with *Neotoma fuscipes*. Abbreviations: On = Ondatrini; Di = Dicrostonychini; El = Ellobiusini. La = Lagurini. Symbols at nodes represent places where fossil calibrations were enforced. Red bars are the 95% confidence interval for the age of a node. Numbers 1-4 represent the four different radiation events.

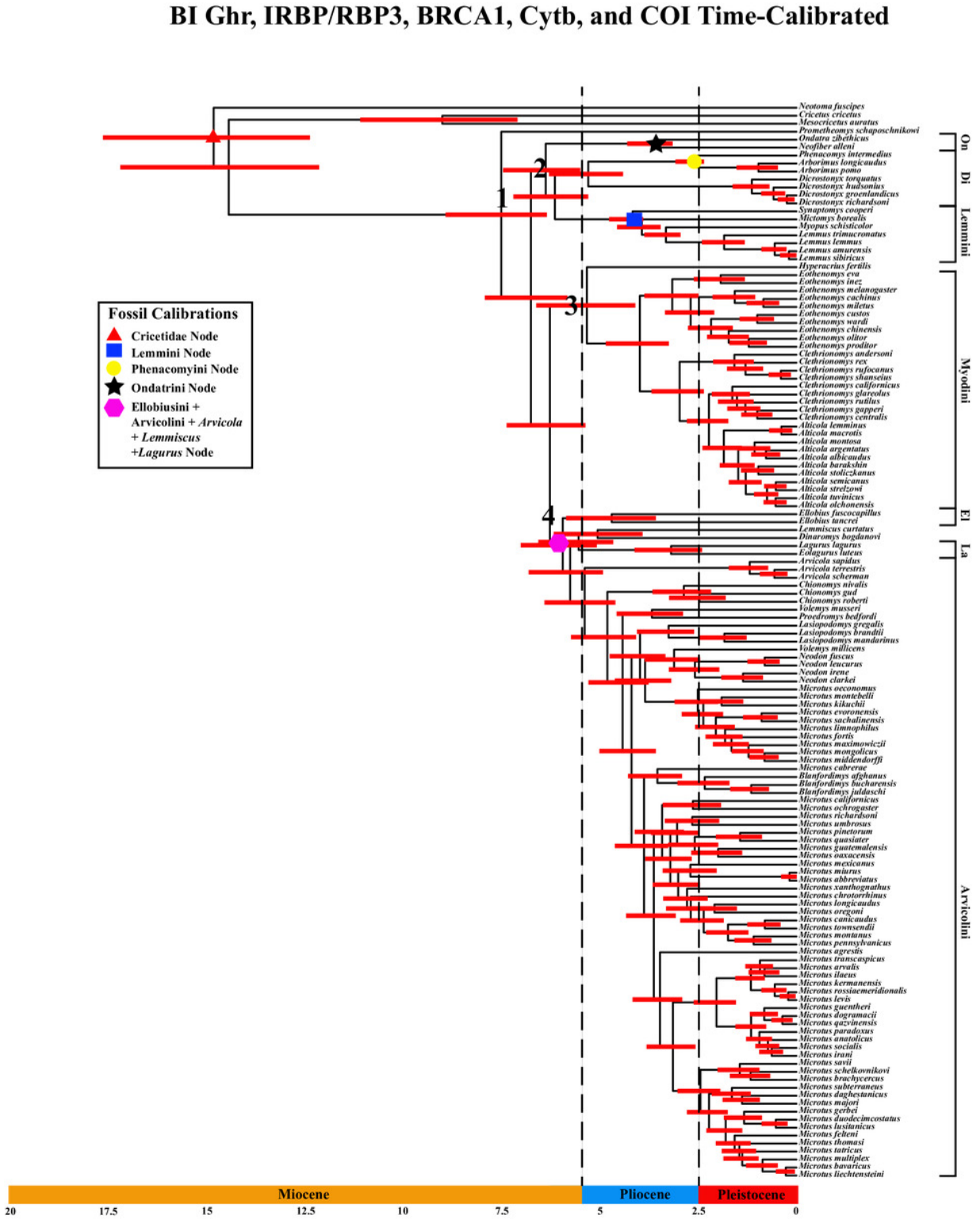
BI Ghr, IRBP/RBP3, BRCA1, Cytb, and COI Time-Calibrated
Fossil Calibrations
Cricetidae Node
Lemmini Node
Phenacomyini Node
Ondatrini Node
Ellobiusini + Arvicolini + Arvicola + Lemmiscus +Lagurus Node
1
2
3
4
On
Di
Lemmini
Myodini
El
La
Arvicolini
Miocene
Pliocene
Pleistocene
20
17.5
15
12.5
10
7.5
5
2.5
0

Figure 6

Figure 6: Time-Calibrated Bayesian (BI) tree of concatenated molecular dataset of the nuclear genes Ghr and IRBP/RBP3 representing 101 arvicolines and 3 members of Cricetidae.

Tree was rooted with *Neotoma fuscipes*. Abbreviations: On = Ondatrini; Di = Dicrostonychini; El = Ellobiusini. La = Lagurini. Symbols at nodes represent places where fossil calibrations were enforced. Red bars are the 95% confidence interval for the age of a node. Numbers 1-4 represent the four different radiation events.

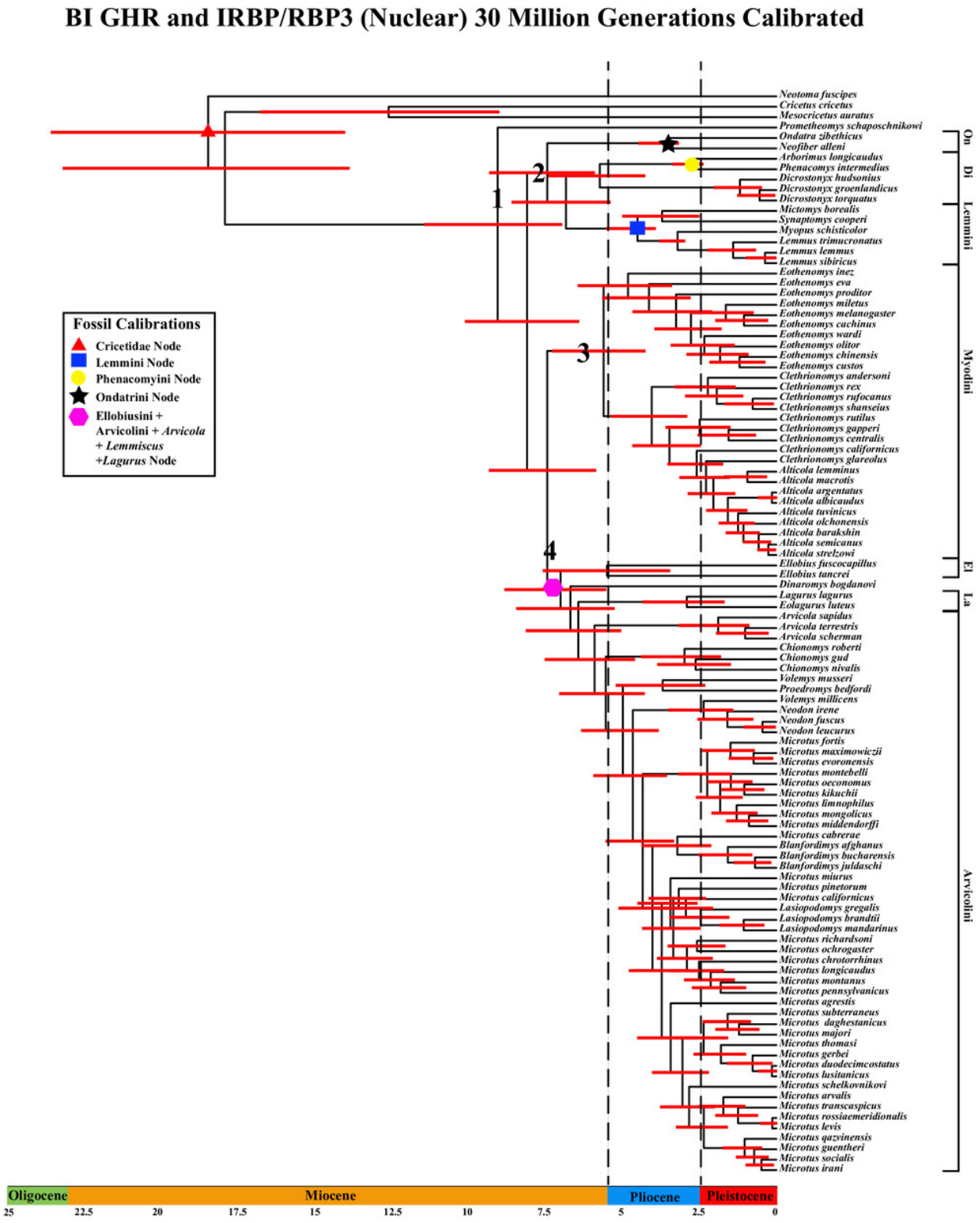
BI GHR and IRBP/RBP3 (Nuclear) 30 Million Generations Calibrated
Fossil Calibrations
Cricetidae Node
Lemmini Node
Phenacomyini Node
Ondatrini Node
Ellobiusini + Arvicolini + Arvicola + Lemmiscus +Lagurus Node
1
2
3
4
Neotoma fuscipes
Cricetus cricetus
Mesocricetus auratus
Prometheomys schaposchnikowi
Ondatra zibethicus
Neofiber alleni
Arborimus longicaudus
Phenacomys intermedius
Dicrostonyx hudsonius
Dicrostonyx groenlandicus
Dicrostonyx torquatus
Mictomys borealis
Synaptomys cooperi
Myopus schisticolor
Lemmus trimucronatus
Lemmus lemmus
Lemmus sibiricus
Eothenomys inez
Eothenomys eva
Eothenomys proditor
Eothenomys miletus
Eothenomys melanogaster
Eothenomys cachinus
Eothenomys wardi
Eothenomys olitor
Eothenomys chinensis
Eothenomys custos
Clethrionomys andersoni
Clethrionomys rex
Clethrionomys rufocanus
Clethrionomys shanseius
Clethrionomys rutilus
Clethrionomys gapperi
Clethrionomys centralis
Clethrionomys californicus
Clethrionomys glareolus
Alticola lemminus
Alticola macrotis
Alticola argentatus
Alticola albicaudus
Alticola tuvinicus
Alticola olchonensis
Alticola barakshin
Alticola semicanus
Alticola strelzowi
Ellobius fuscocapillus
Ellobius tancrei
Dinaromys bogdanovi
Lagurus lagurus
Eolagurus luteus
Arvicola sapidus
Arvicola terrestris
Arvicola scherman
Chionomys roberti
Chionomys gud
Chionomys nivalis
Volemys musseri
Proedromys bedfordi
Volemys millicens
Neodon irene
Neodon fuscus
Neodon leucurus
Microtus fortis
Microtus maximowiczii
Microtus evoronensis
Microtus montebelli
Microtus oeconomus
Microtus kikuchii
Microtus limnophilus
Microtus mongolicus
Microtus middendorffi
Microtus cabrerae
Blanfordimys afghanus
Blanfordimys bucharensis
Blanfordimys juldaschi
Microtus miurus
Microtus pinetorum
Microtus californicus
Lasiopodomys gregalis
Lasiopodomys brandtii
Lasiopodomys mandarinus
Microtus richardsoni
Microtus ochrogaster
Microtus chrotorrhinus
Microtus longicaudus
Microtus montanus
Microtus pennsylvanicus
Microtus agrestis
Microtus subterraneus
Microtus daghestanicus
Microtus majori
Microtus thomasi
Microtus gerbei
Microtus duodecimcostatus
Microtus lusitanicus
Microtus schelkovnikovi
Microtus arvalis
Microtus transcaspicus
Microtus rossiaemeridionalis
Microtus levis
Microtus qazvinensis
Microtus guentheri
Microtus socialis
Microtus irani
On
Di
Lemmini
Myodini
El
La
Arvicolini
Oligocene
Miocene
Pliocene
Pleistocene
25
22.5
20
17.5
15
12.5
10
7.5
5
2.5
0

Table 1(on next page)

Table1: Chart comparing the ages reported in Abramson et al. (2021) and this study.

All ages represent mean ages in millions of years.

Node	Abramson et al. (2021) (mean)	Mean Age	Median Age	95% confidence interval
Arvicolinae + Cricetinae	11.31	13.39	13.33	(15.72-11.04)
Arvicolinae	7.36	6.66	6.62	(7.73-5.69)
Lemmini	4.81	4.36	4.29	(5-3.95)
Ondatraini	6	3.55	3.48	(4.14-3.2)
Dicrostonychini (*Phenacomys*, *Arborimus*, *Dicrostnyx*)	4.89	4.92	4.88	(5.85-4.04)
Prometheomyini	6.3	5.6	5.57	(6.58-4.73)
Clethrionomyini (*Clethrionomys*, *Eothenomys*, *Alticola*) = Myodini	4.02	3.66	3.64	(4.31-3.04)
Alticola	0.9	1.63	1.62	(2-1.28)
Eothenomys	3.6	3.15	3.13	(3.75-2.57)
Ellobiusini	4.97	4.17	4.15	(5.21-3.13)
Lagurini	3.1	5.22	5.19	(6.04-4.39)
Arvicolini s.str (excluding *Hyperacrius*)	4.9	4.47	4.44	(5.19-3.77)
Lemmiscus	4.04	4.51	4.49	(5.47-3.61)
Chionomys	3.29	2.82	2.81	(3.51-2.18)
Proedromys	4.32	3.42	3.4	(4.13-2.71)
North American *Microtus*	3.41	3.6	3.58	(4.17-3.04)
Paraphyletic Crown *Microtus*	3.8	3.76	3.74	(4.37-3.19)
Neodon	3.16	2.46	2.45	(3.1-1.87)
Lasiopodomys	3.09	3.11	3.1	(3.74-2.52)

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