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

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Background. Arvicoline rodents are one of the most speciose and rapidly evolving mammalian lineages. Fossil 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 two mitochondrial genes and three nuclear genes representing 146 (82% coverage) species and 100% of currently recognized arvicoline genera. We elucidate well-supported major clades, 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 previous molecular phylogenies, but we increased the support in many regions of the arvicoline tree that were previously poorly-sampled. Our sampling resulted in a better understanding of relationships within Clethrionomyini, the early-diverging position and close relationship of true lemmings (Lemmus and Myopus) and bog lemmings (Synaptomys), and provided support for recent taxonomic changes within Microtini. Our results indicate an origin of ~6.4 Ma for crown arvicoline rodents. These results have major implications (e.g., diversification rates, paleobiogeography) 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

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Abstract

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40   sampled. Our sampling resulted in a better understanding of relationships within
41   Clethrionomyini, the early-diverging position and close relationship of true lemmings
42   (Lemmus and Myopus) and bog lemmings (Synaptomys), and provided support for
43   recent taxonomic changes within Microtini. Our results indicate an origin of ~6.4 Ma for
44   crown arvicoline rodents. These results have major implications (e.g., diversification
45   rates, paleobiogeography) for our confidence in the fossil record of arvicolines and their
46   utility as biochronological tools in Eurasia and North America during the Quaternary.

48 ## Introduction

49   Arvicoline rodents (voles, lemmings, muskrats, and their extinct relatives) are the
50   subject of a complex history of taxonomic and phylogenetic research (Conroy and Cook,
51   1999, 2000; Galewski et al., 2006; Buzan et al., 2008; Robovský et al., 2008; Fabre et
52   al., 2012; Martínková and Moravec, 2012; Steppan and Schenk, 2017; Upham et al.,
53   2019; Withnell, 2020; Abramson et al., 2021). Previous phylogenetic studies focused on
54   subsets of Arvicolinae (i.e., North American *Microtus*; Conroy and Cook, 1999;
55   Martínková and Moravec, 2012), used only one or two genes (Buzan et al., 2008),
56   included arvicolines in larger studies investigating the phylogeny of all rodents (Fabre et
57   al., 2012; Steppan and Schenk, 2017), or focused on mitochondrial genomes
58   (Abramson et al., 2021). A comprehensive combined-evidence molecular and
59   morphological dataset was generated by Robovský et al. (2008). Although a great deal
60   of molecular data is available for arvicoline rodents, no study has synthesized all
61   available molecular data to examine phylogenetic relationships across the group at both
62   the generic and species levels—a new phylogeny has been warranted. Our objectives
63   with this study are two-fold. (1) We wanted to consolidate a current and succinct
64   understanding of the taxonomy and systematics of all the major clades of arvicolines
65   through an analysis of the molecular data available on GenBank. (2) We wanted to use
66   the fossil record to generate a time-calibrated phylogeny for the clade that can serve as
67   the foundation that will allow for quantitative modeling of paleobiogeography and
68   dispersal patterns of arvicolines across Beringia. To accomplish these objectives, we
69   compiled the most taxonomically complete molecular dataset of global Arvicolinae to
70   date (July, 2023), using published nuclear genes and mitochondrial markers, to provide
71   a well-sampled molecular hypothesis of extant Arvicolinae.
72

73 **Arvicoline Taxonomy and Systematics Through Time**
74   For the sake of simplicity we have organized our summary of arvicoline taxonomy
75   and systematics according to the Mammal Diversity Database (2023) of the American
76   Society of Mammalogists. Different tribal affinities have been designated over the years
77   and where relevant we have indicated this change. Tribal affinities in the headings reflect

78 the current (August 2023) understanding recognized by the Mammal Diversity Database
79 (2023).
80
81 Tribe Arvicolini (*Arvicola*)
82   The number of recognized species in *Arvicola* has varied from one to nine (Miller,
83 1912; Ellerman and Morrison-Scott, 1951; Wilson et al., 2017; Kryštufek and Shenbrot,
84 2022). The tribe Arvicolini has historically consisted of the members of the current tribe
85 Microtini + *Arvicola*. In a phylogenetic analysis by Abramson et al., (2021) *Arvicola* was
86 placed separate (sister to the tribe Lagurini) from the taxa included in Microtini, and
87 therefore the Mammal Diversity Database (2023) lists *Arvicola* as the only member of
88 the tribe Arvicolini with the rest of the previous members (*Alexandromys*, *Chionomys*,
89 *Hyperacrius*, *Lasiopodomys*, *Lemmiscus*, *Microtus*, *Mictomicrotus*, *Neodon*,
90 *Proedromys*, *Stenocranius*, and *Volemys*) being moved to the tribe Microtini.
91   .
92 Tribe Clethrionomyini (*Alticola*, *Antellomys*, *Caromys*, *Clethrionomys*, *Craseomys*, and
93 *Eothenomys*)
94   Tribe Clethrionomyini is one of the largest groups of arvicoline rodents with six
95 genera. Taxa that belong to this tribe have a long and complicated history of taxonomic
96 revision (e.g., Hinton, 1926; Miller, 1896; Kretzoi, 1969; von Koenigswald, 1980; Kohli et
97 al., 2014; Kryštufek et al., 2020; Kryštufek and Shenbrot, 2022). However, the
98 membership of this tribe has remained fairly stable, but generic affinity of the constituent
99 species has shifted frequently (Kryštufek and Shenbrot, 2022). The priority of
100 *Clethrionomys* as the valid genus name for red-backed voles was recently recognized
101 (Kryštufek et al., 2020); therefore, we have abandoned the taxonomy used by Musser
102 and Carleton (2005) that used the genus name *Myodes*. Historically, species that are
103 now listed in *Craseomys* and *Caromys* have been placed in *Clethrionomys* (Kryštufek
104 and Shenbrot, 2022). Tang and colleagues (2018) found a paraphyletic *Clethrionomys*
105 + *Craseomys* with respect to *Alticola*, which supports the hypothesis from Kohli et al.
106 (2014) that frequent episodes of hybridization have complicated our understanding of
107 their evolutionary history. The "mountain voles" (*Alticola*) were in the past classified
108 within *Arvicola* and *Microtus*, but both of those hypotheses were demonstrated to be
109 incorrect (Kryštufek and Shenbrot, 2022). Recent phylogenetic work with *Alticola* has
110 demonstrated that *Ascizomys*, a taxonomically disputed group, is sister to *Alticola* and
111 often ranked as a subgenus of *Alticola* (Kohli et al., 2014; Bodrov et al., 2016; Kryštufek
112 and Shenbrot, 2022). The "Chinese voles", *Anteliomys*, consists of seven species that
113 have historically been placed in *Eothenomys* (Liu et al., 2012). Recently *Anteliomys* was
114 elevated to generic distinction (Kryštufek and Shenbrot, 2022). The "Brownish voles",
115 *Caromys*, have been thought of as a clade in between *Microtus* and *Clethrionomys*
116 (Kryštufek and Shenbrot, 2022). Today, *Caromys* is considered a valid genus that is
117 sister to *Eothenomys* + *Anteliomys* (Liu et al., 2012; Tang et al., 2018; Kryštufek and

118 Shenbrot, 2022). Red-backed voles belonging to *Clethrionomys* today represent five
119 species. In phylogenetic studies the position of *Clethrionomys* relative to *Craseomys*
120 and *Alticola* has been demonstrated as problematic, most likely due to the recent age of
121 the radiation and frequent hybridization between its members (Kohli et al., 2014; Tang
122 et al., 2018). Oriental voles, *Eothenomys*, are native to southeast Asia and phylogenetic
123 works have demonstrated their sister position to *Anteliomys* (Liu et al., 2017). The exact
124 number of species of *Eothenomys* has been debated and more work is needed to clarify
125 this (Kryštufek and Shenbrot, 2022).
126   From a morphological perspective, species with rooted molars were lumped into
127 Clethrionomyini (Gromov and Polyakov, 1992) or the subtribe Myodina (Pavlinov and
128 Rossolimo, 1998). Appendicular myological and osteological data support the
129 monophyly of *Alticola* and its close relationship to *Clethrionomys* and *Eothenomys*
130 (Stein, 1987). Dental morphology (i.e., small, rooted teeth) alone may indicate that
131 *Clethrionomys* and *Alticola* are early diverging members of Arvicolinae, if rooted teeth
132 are the ancestral condition. Suzuki et al. (1999) and Musser and Carleton (2005) argued
133 that members of *Clethrionomys* may have independently evolved rooted molar
134 conditions. More recent systematic work using multilocus datasets provided some
135 support for that hypothesis (Kohli et al., 2014).
136
137 Tribe Dicrostonychini (*Dicrostonyx*)
138   Collared lemmings (*Dicrostonyx*) were historically thought to be close to true
139 lemmings (Miller, 1896). Early molecular and morphological analyses indicated that
140 *Dicrostonyx* was part of one of the earliest radiations of arvicolines (e.g., Carleton,
141 1981; Chaline and Graf, 1988; Conroy and Cook, 1999; Gromov and Polyakov, 1992).
142 For decades, the dominant viewpoint was that there was a single circumpolar species of
143 collared lemming, *Dicrostonyx torquatus*, but evidence from morphology, genetics,
144 ecology, and karyology indicates multiple species (Borowik and Engstrom, 1993; Eger,
145 1995; Musser and Carleton, 2005; Wilson et al., 2017; Kryštufek and Shenbrot, 2022).
146 Fedorov et al. (1999) further documented the complex biogreographic history for
147 *Dicrostonyx* and the interesting phylogeography of the distinct populations in the
148 Palearctic and Nearctic.
149
150 Tribe Ellobiusini (*Bramus* and *Ellobius*)
151   *Ellobius*, the Northern mole voles, and *Bramus*, the Southern mole voles are
152 morphologically specialized arvicolines (Corbet, 1978; Pavlinov et al., 1995; Tesakov,
153 2008, 2016; Kryštufek and Shenbrot, 2022). These genera are remarkable in that their
154 Pleistocene range included parts of Israel and North Africa, areas that no other
155 arvicoline has ever inhabited (or they did not leave a known fossil record; Jaeger, 1988).
156 *Arvicola* is a European, fossil-rich genus that was previously hypothesized to be closely

157 related to *Microtus* and within the tribe Arvicolini (Chaline and Graf, 1988; Mezhzherin et
158 al., 1993; Kryštufek and Shenbrot, 2022).
159
160 Tribe Lagurini (*Eolagurus* and *Lagurus*)
161   Lagurines have been classified close to lemmings, within *Myodes* and *Microtus*, as
162 its own genus *Lagurus*, and as a tribe or subtribe of Arvicolini (see Kryštufek and
163 Shenbrot, 2022 for a description). Early researchers postulated that the sagebrush vole,
164 *Lemmiscus curtatus* and *Hyperacrius* were members of Lagurini, but both genera have
165 subsequently been removed based on molecular and morphological data (Abramson et
166 al., 2021; Kryštufek and Shenbrot, 2022). Today, two genera, *Lagurus* and *Eolagurus*
167 are included in the tribe Lagurini (Gromov and Polyakov, 1992; Wilson et al., 2017;
168 Kryštufek and Shenbrot, 2022).
169
170 Tribe Lemmini (*Lemmus*, *Myopus*, and *Synaptomys*)
171   Bog lemmings (*Synaptomys* and/or *Mictomys*) have many morphological and
172 molecular characters thought to associate the group with the 'true lemmings' (*Myopus*
173 and *Lemmus*) (Abramson, 1993; Carleton, 1981; Chaline and Graf, 1988). Bog
174 lemmings are a strictly North American clade in the modern biota, but based on the
175 fossil record were hypothesized to have originated c. 4 Ma in Europe, with subsequent
176 dispersal through Beringia into North America (Repenning and Grady, 1988). Some
177 paleontologists posited that the northern bog lemming (*Synaptomys borealis*) should be
178 placed in its own genus, *Mictomys*, based on dental morphology (Repenning and
179 Grady, 1988). Neontologists (Hall, 1981; Musser and Carleton, 2005) argued that, at
180 best, *Mictomys* is a subgenus of *Synaptomys* based on morphology and ecology.
181   The 'true lemmings' *Myopus* and *Lemmus* are thought to be early diverging
182 arvicolines (Carleton, 1981; Chaline and Graf, 1988; Abramson, 1993). The monophyly
183 of the 'true lemmings' + *Synaptomys* (excluding *Dicrostonyx*) was supported by cladistic
184 analysis of allozyme data (Mezhzherin et al., 1995), nuclear DNA (Modi, 1996), and
185 mitochondrial DNA (Conroy and Cook, 1999). The taxonomic treatment of *Myopus* has
186 been complicated. Originally, Chaline (1972) treated *Myopus schisticolor* as a species
187 of *Lemmus*. Subsequently, Chaline et al. (1989) and von Koenigswald and Martin
188 (1984) cited molar similarity between *Myopus* and *Lemmus* and placed *Myopus* as a
189 subgenus within *Lemmus*. Karyotype, body size, fur coloration, other morphologies
190 (skull, feet, and eyes), habitat, and behavior were later invoked to demonstrate that
191 *Myopus* is readily distinguishable from *Lemmus* (Jarrell and Fredga, 1993). Therefore,
192 Musser and Carleton (2005), Wilson et al. (2017), Kryštufek and Shenbrot (2022), and
193 the Mammal Diversity Database (2023) treated it as a separate genus.
194
195 Tribe Microtini (*Alexandromys*, *Chionomys*, *Hyperacrius*, *Lasiopodomys*, *Lemmiscus*,
196 *Microtus*, *Mictomicrotus*, *Neodon*, *Proedromys*, *Stenocranius*, and *Volemys*)

197   *Alexandromys* is an historical term used to describe the grass voles (e.g., *A.*
198 *oeconomus*). For most of their named history its members have been classified into
199 *Microtus* and/or *Neodon* with *Alexandromys* often being used as a subgenus (Gromov
200 and Polyakov, 1977; Musser and Carleton, 2005). Karyology indicated that it might be
201 more complicated (see Kryštufek and Shenbrot, 2022 for an overview) and recent
202 phylogenetic work has demonstrated *Alexandromys* to be distinct and a valid genus
203 (Bannikova et al., 2010; Haring et al., 2015; Steppan and Schenk, 2017). Lissovsky et
204 al. (2018) provided new insight into the monophyly of *Alexandromys* and their recent
205 and complex radiation. The systematic relationships of the snow voles, *Chionomys*, are
206 historically controversial (Gromov and Polyakov, 1992; Yannic et al., 2012). Some
207 researchers posited that *Chionomys* is a member of Myodini (Mezhzherin et al., 1995),
208 just outside of *Microtus* (Yannic et al., 2012), and others argued based on known fossils
209 that *Chionomys* is closely related to *Clethrionomys* (=*Myodes*) (Kretzoi, 1969; Chaline,
210 1987). Some researchers place *Chionomys* closer to *Microtus* in the tribe *Arvicolini*
211 (Kryštufek and Shenbrot, 2022) although others elevated the subtribe Microtini to a tribe
212 and classified *Chionomys* there (Mammal Diversity Database, 2023). High-altitude
213 inhabitants of the Himalayas, Kashmir voles of the genus *Hyperacrius*, were originally
214 thought to be a subgenus of *Microtus* (Miller, 1896). However, Hinton (1926) named
215 *Hyperacrius* a valid genus that is closely related to but outside of *Microtus*.
216   Members of *Lasiopodomys* were considered by paleontologists to be the remnants
217 of a group that was previously more speciose and widespread (Gromov and Polyakov,
218 1992; Repenning, 1992). We note that the fossil *Lasiopodomys* referred to by
219 Repenning (1992) in North America is not the same as the extant Eurasian taxa, further
220 adding to the taxonomic confusion of the genus (Repenning and Grady, 1988).
221 Neontologists and paleontologists have recognized the morphological uniqueness of
222 *Lasiopodomys*, but in one allozyme analysis, *Lasiopodomys brandtii* was grouped with
223 *Microtis fortis* and *Microtus* (=*Stenocranius*) *gregalis*, thus questioning the generic
224 affinity of these species (Mezhzherin et al., 1993). However, Musser and Carleton
225 (2005) retained *Lasiopodomys* at the generic level, and Robovský et al. (2008)
226 recognized *Lasiopodomys* as the sister to *Stenocranius*. *Lemmiscus* is a monotypic
227 genus that was long considered a subgenus of *Lagurus* in order to segregate New
228 World sagebrush voles from Old World steppe voles (Carroll and Genoways, 1980).
229 Morphological and molecular data, however, indicate that *Lemmiscus* may be closely
230 related to *Microtus* (Carleton, 1981; Modi, 1987; Abramson et al., 2021).
231   The taxonomy and systematics of *Microtus* are complicated and historically difficult
232 to disentangle. Little consensus exists in the literature on how to treat generic-level
233 identifications of fossil *Microtus*, partially because many hypotheses of *Microtus*
234 relationships were based on tooth characters that have limited systematic potential and
235 have undergone rapid evolutionary change (Guthrie and Matthews, 1971; von
236 Koenigswald, 1980). Combined with the broad Holarctic distribution of the group, poor

237 genetic sampling, and hypothesized recent origination and diversification, and the result
238 has been taxonomic and systematic chaos. Currently, 60 species of *Microtus* are
239 recognized within six subgenera; *Blanfordimys*, *Euarvicola*, *Iberomys*, *Microtus*,
240 *Pitymys*, and *Terricola* (Kryštufek and Shenbrot, 2022; Mammal Diversity Database,
241 2023). *Microtus* (*Blanfordimys*) is a geographically isolated group of voles found in
242 south-central Asia (e.g., Afghanistan) (Shenbrot and Krasnov, 2005). They have
243 retained dental characters that have been interpreted as pleisiomorphic, but they have
244 inflated auditory bullae and a mastoid region that is so enlarged that it almost projects
245 beyond the occipital condyle, both of which have been interpreted as highly apomorphic
246 (Gromov and Polayakov, 1992). This led some researchers to place them as a
247 subgenus of *Microtus* (Gromov and Polyakov, 1992; Kryštufek and Shenbrot, 2022)
248 while others gave them full generic distinction (Musser and Carleton, 1993). Bannikova
249 and collegues (2009) and Steppan and Schenk (2017) recovered *Blanfordimys* as sister
250 to *Euarvicola* and this should be further examined.
251   *Euarvicola*, or the field voles, are a Palaearctic group that for most of their history
252 have been recognized as a single species (*M. agrestis*). However, there are now three
253 recognized species (Pardiñas et al. 2017; Kryštufek and Shenbrot, 2022). *Iberomys*
254 consists of a single species, *M. cabrerae*, native to the Iberian peninsula (Kryštufek and
255 Shenbrot, 2022). Historically, *M. cabrerae* has been considered a close relative to *M.*
256 *arvalis*, however recent studies have left its position unresolved (Fink et al., 2010), close
257 to *Stenocranius* (Cuenca Bescós et al., 2014) or close to the Nearctic *Microtus*
258 (Robovský et al. 2008, Martínková & Moravec 2012). *Microtus* (*Microtus*) consists of
259 three species "groups" (Steppan and Schenk, 2017; Kryštufek and Shenbrot, 2022).
260 These groups include: 1. *arvalis* "Grey voles" 2. *socialis* "Social voles" and 3.
261 *shelkovnikovi*. Grey voles are a group of morphologically cryptic species that, based on
262 studies of *cytb*, contains seven species and is sister to the social voles (Tougard et al.
263 2013; Mahmoudi et al. 2017; Golenishchev et al. 2019). The *socialis* "social vole" group
264 contains one to eight species (Jaarola et al., 2004; Steppan and Schenk, 2017; Thanou
265 et al., 2020; Kryštufek and Shenbrot, 2022). The *shelkovnikovi* group consists of a
266 single species (*M. shelkovnikovi*) that has been recovered as the sister taxon to the
267 *socialis* group (Martínková and Moravec, 2012; Steppan and Schenk, 2017). *Pitymys*
268 are a large subgenus of *Microtus* that consists exclusively of North American taxa
269 (Musser and Carleton, 2005). *Terricola*, or the pine voles, have commonly been
270 considered a subgenus under *Microtus* by neontologists or a genus all of its own by
271 paleontologists (Kryštufek and Shenbrot, 2022). All members of *Terricola* are united
272 morphologicaly by the confluence of triangles 4-5 on the upper first molar (Kryštufek
273 and Shenbrot, 2022). Molecular systematics have demonstrated the complexity in the
274 taxonomic richness for this subgenus with as many as five groups being recognized
275 (see Kryštufek and Shenbrot, 2022 for a summary).
276   *Mictomicrotus* is a recently named monotypic genus (Kryštufek and Shenbrot,
277 2022). Liu et al., (2007) originally placed *M. liangshanensis* in *Proedromys* (*P.*
278 *liangshanensis*). However, morphology and phylogenetic studies demonstrated that
279 *liangshanensis* is not the sister taxa to *Proedromys bedfordi* and therefore warrants a
280 genus of its own (Chen et al., 2012; Steppan and Schenk, 2017). Voles of the genus

281   *Neodon* are found throughout the mountainous regions of southern Asia. They have a
282   long and complicated taxonomic history, but their close relationship to *Microtus* has
283   been established, although systematic relationships of the genus relative to other
284   arvicolines are still debated (Musser and Carleton, 2005; Pradhan et al., 2019). Recent
285   taxonomic revision has seen the number of species belonging to *Neodon* grow (Liu et
286   al., 2017; Pradhan et al., 2019).
287   Using morphological characters, *Proedromys* was hypothesized to be closely
288   related to *Microtus*, but its diagnostic traits (massive cranium with wide, heavy, and
289   grooved upper incisors and odd molars) were also used to support the hypothesis of a
290   close relationship with extinct genera such as *Allophaiomys* (Gromov and Polyakov,
291   1992; Repenning, 1992). Molecular phylogenies also suggest that *Proedromys* is
292   outside of and thus separate from *Microtus*, although with low support (Chen et al.,
293   2012). Currently, *Proedromys* is considered a monotypic genus in the tribe Microtini and
294   thought to be closely related to but separate from *Microtus* (Mammal Diversity
295   Database, 2023). The narrow-headed voles, *Stenocranius*, have been considered as a
296   subgenus of *Microtus* as well as *Lasiopodomys* (Kryštufek and Shenbrot, 2022). For
297   many decades only one species (*S. gregalis*) was recognized, but recent molecular
298   work has detected a cryptic species, *S. raddei* (Petrova et al., 2015, 2016). *Volemys*
299   consists of two high-altitude alpine species native to western Sichuan, China (Liu et al.,
300   2017). Species of *Volemys* were previously placed in *Microtus* or were found to be
301   closely related to *Microtus*, and previously published phylogenetic analyses of molecular
302   data hinted that the distribution of *Volemys* may be relictual due to geographic (and
303   correspondingly, genetic) isolation during the Late Pleistocene (Lawrence, 1982;
304   Zagorodnyuk, 1990).
305
306   Tribe Ondatrini (*Ondatra* and *Neofiber*)
307   *Ondatra* and *Neofiber* are monotypic genera that have the largest body sizes of
308   all arvicolines (both extant and extinct). Historically, they were placed together in the
309   tribe Ondatrini (Chaline and Mein, 1979; Repenning et al., 1990) or subtribe Ondatrina
310   (Pavlinov et al., 1995). Based on allozyme analysis, Mezhzherin et al. (1995) concluded
311   that Ondatrina was one of the first groups of arvicolines to diverge from the ancestral
312   arvicoline population during the late Miocene. Dental morphology, however, led some
313   paleontologists to consider *Ondatra* and *Neofiber* as more distantly related. Although
314   the most obvious similarity is that they are both large (Carleton, 1981; von Koenigswald,
315   1980; Martin, 1974; Martin 1996), *Ondatra* has rooted molars, and *Neofiber* has rootless
316   molars. Molecular phylogenies support a sister taxon relationship between the genera
317   (Modi, 1996; Fabre et al., 2012).
318
319   Tribe Pliophenacomyini (*Arborimus* and *Phenacomys*)

320   Similarities in dental morphology led some researchers to classify *Arborimus* as a
321 subgenus of *Phenacomys* (Repenning and Grady, 1988), but others treated *Arborimus*
322 as a separate genus (Musser and Carleton, 1993). Another study placed them together
323 in the tribe Phenacomyini (Zagorodnyuk, 1990). Others placed *Phenacomys* with
324 *Phaiomys* and other extinct genera (Repenning et al. 1990) or with the tribe Myodini
325 (McKenna and Bell, 1997). Both *Phenacomys* and *Arborimus* have primitive molars that
326 retain the plesiomorphic condition of retaining roots on molars, and they lack cementum
327 in the reentrant angles on those molars; therefore some paleontologists argued that
328 *Phenacomys* is an early relict lineage (Repenning, 1987). Currently there are two
329 species of *Phenacomys* and three species of *Arborimus* recognized in two distinct but
330 closely related genera united within the tribe Pliophenacomyini (Wilson et al., 2017).
331
332 Tribe Pliomyini (*Dinaromys*)
333   The Eurasian genus *Dinaromys* is monotypic in the extant biota. The
334 plesiomorphic characteristics (e.g., rooted dentition) of *Dinaromys* caused it to be
335 placed in many different groups: subfamily Dolomyinae (Chaline, 1975), Tribe Ondatrini
336 (Corbet, 1978), Tribe Clethrionomyini (Gromov and Polyakov, 1992), or Tribe
337 Prometheomyini (Pavlinov et al., 1995). To further complicate their systematic status,
338 von Koenigswald (1980) found that the lone extant species of the genus, *Dinaromys*
339 *bogdanovi*, has an enamel microstructure that is unlike any other known extant species.
340
341 Tribe Prometheomyini (*Prometheomys*)
342   The 'long clawed mole vole', *Prometheomys schaposchnikowi*, is a monotypic
343 species with plesiomorphic characters usually classified in its own tribe (Gromov and
344 Polyakov, 1992). This led Repenning et al. (1990) to align *Prometheomys* with *Ellobius*
345 in Prometheomyinae, whereas other researchers place *Prometheomys* into
346 Prometheomyini (Pavlinov et al., 1995; Pavlinov and Rossolimo, 1998; Mammal
347 Diveristy Database, 2023). Whole mitochondrial genomes and subsequent research has
348 indicated that *Prometheomys* is likely a basal arvicoline (Ibis et al., 2020; Kryštufek and
349 Shenbrot, 2022).
350

Materials & Methods
Taxon Sampling
353   Complete sampling of Arvicolinae has been historically challenging due to the high
354 species diversity, global distribution of the clade, and the relative rarity of some species
355 in museum collections. We attempted to sample all genera (n=32) and species (n=178)
356 recognized by the Mammal Diversity Database (Mammal Diversity Database, 2023) in
357 July 2023. We used Musser and Carleton (2005), Wilson et al., (2017), and Kryštufek
358 and Shenbrot, (2022) to inform our taxonomic coverage, however we used the Mammal
359 Diversity Database (2023), the most current and widely accepted database of

360   mammalian taxonomy, when calculating our taxonomic coverage. That resulted in three
361   datasets; (1) a dataset of only taxa with mitochondrial data (n=146), (2) a dataset of only
362   taxa with nuclear data (n=107), (3) a concatenated dataset that includes both
363   mitochondrial and nuclear loci of n=146 species of extant arvicolines, and is the most
364   taxonomically complete dataset to date (August, 2023) for Arvicolinae (82% species and
365   100% generic coverage). Portions of this text were previously published as part of a
366   thesis (https://repositories.lib.utexas.edu/bitstream/handle/2152/82563/WITHNELL-
367   DISSERTATION-2020.pdf?isAllowed=y&sequence=1).
368
369   **Concatenated dataset**
370   Molecular data were obtained from GenBank (NCBI Resource Coordinators,
371   2016) (GenBank accession numbers are in Appendix A and deposited in Dryad). Three
372   rodents outside of crown Arvicolinae were used as outgroups (Fabre et al., 2012),
373   including *Cricetus cricetus*, *Mesocricetus auratus*, and *Neotoma fuscipes*. Five loci were
374   chosen that previously were demonstrated to be useful for rodent phylogenetics
375   (Galewski et al., 2006; Robovský et al., 2008; Fabre et al., 2012; Martinkova and
376   Moravec, 2012; D'Elía et al., 2019; Upham et al., 2019; Abramson et al., 2021). We
377   used two mitochondrial markers, Cytochrome b (Cytb) and Cytochrome c oxidase
378   subunit 1 (COI), as well as the three nuclear markers, growth hormone receptor (Ghr)
379   exon 10, iron responsive element binding protein/retinol binding protein 3 (IRBP/RBP3)
380   exon 1, and the Breast Cancer gene 1 (BRCA1) exon 11. Other genes, such as ACP5,
381   have been used in some phylogenetic analyses of arvicoline rodents (Bondareva et al.,
382   2021a,b), but we chose not to include them because their coverage across all of the
383   taxa included in these analyses was relatively low. Whenever possible, vouchered
384   specimens were used and the voucher numbers as well as author constributions are
385   noted in Appendix A. This allowed us to increase our confidence in the taxonomic
386   identification of sequences before phylogenetic analysis was completed. In total there
387   were 5857 base pairs, and each gene had the following coverage across the 149 taxa
388   (146 arvicolines + outgroups): Cytb (147 species for 99% coverage with n=122, 82%
389   vouchered), COI (64 species for 43.0% coverage with n=44, 30% vouchered), Ghr (90
390   species for 60% coverage with n=47, 32% vouchered), IRBP/RBP3 (105 species for
391   70% coverage with n=61, 41% vouchered), and BRCA1 (69 species for 46% coverage
392   with n=48, 32% vouchered). Across the entire dataset there was 36.5% missing data.
393   *Stenocranius gregalis* was the most complete across the five genes (5722/5857
394   nucleotides for 2.3% missing) while *Lemmus amurensis* had the most missing data
395   (356/5857 nucleotides for 93.9% missing).
396   Sequences were aligned using the iterative refinement algorithm L-INS-I of
397   MAFFT (Katoh and Standley, 2013). Aligned nexus files were imported into AliView
398   (Larsson, 2014) and nuclear protein coding loci were checked for stop codons and
399   trimmed where needed to ensure that they were in the proper reading frame for the first

400 and third codon positions. PartitionFinder 2 (Lanfear et al., 2017) was used to partition
401 the dataset (by codon position for the nuclear protein-coding genes) using the Akaike
402 Information Criterion (AIC) (Burnham and Anderson, 2004). With all analyses we used
403 GTR+ Γ or GTR + Γ + I molecular substitution models as suggested by PartitionFinder 2
404 (Lanfear et al., 2017). For the specific model used with each partition see the results of
405 the PartionFinder 2 analysis in Appendix B.
406

407 **Phylogenetic analyses**
408   We conducted Maximum Likelihood (ML) and Bayesian Inference (BI) analyses
409 of the concatenated datasets, including mitochondrial only (cytb and COI), nuclear only
410 (Ghr, IRBP/RBP3, BRCA1), and analyses of all five nuclear and mitochondrial markers,
411 for a total of 6 phylogenetic analyses. We did not estimate gene trees for the nuclear
412 exons or investigate a species tree approach because of uneven taxonomic sampling
413 within each locus relative to the total taxonomic sample. With more comprehensive
414 taxon sampling across loci, a species tree approach would be highly informative and
415 could possibly help resolve some of the more challenging areas of the tree (e.g., within
416 *Microtus*).
417   Three analyses were conducted using ML: (1) mitochondrial only (cytb and COI)
418 (2) nuclear only (Ghr, IRBP/RBP3, and BRCA1) (3) concatenated mitochondrial and
419 nuclear (cytb, COI, Ghr, IRBP/RBP3, and BRCA1). Three analyses were conducted
420 using BI: (1) mitochondrial only (cytb and COI) (2) nuclear only (Ghr, IRBP/RBP3, and
421 BRCA1) (3) concatenated mitochondrial and nuclear (cytb, COI, Ghr, IRBP/RBP3, and
422 BRCA1). The ML trees were estimated using RAxML v8.2.12 (Stamatakis, 2014) on the
423 CIPRES cluster (Miller et al., 2010). We used GTR+ Γ or GTR + Γ + I molecular
424 substitution models as suggested by PartitionFinder 2 (Lanfear et al., 2017). For ML
425 analyses support values were estimated using 1000 nonparametric bootstrap
426 pseudoreplicates. Bayesian inference of the partitioned and concatenated dataset was
427 conducted using the Markov Chain Monte Carlo (MCMC) method in MrBayes 3.2.7
428 (Ronquist et al., 2012). The analysis ran for 3.0×10^7 generations sampled every 1000
429 generations and for two separate and independent runs. Beagle was used for high-
430 performance phylogenetic statistical inference (Ayres et al., 2012). Results were
431 examined in Tracer 1.7 (Rambaut et al., 2018) to ensure that the independent runs
432 reached stationarity and that the effective sample size (ESS) values were >200 for all
433 model parameters. Trees were summarized with majority-rule consensus trees and the
434 first 30% of the samples were discarded as burn-in. All input files for the RAxML and
435 MrBayes analyses are deposited on Dryad.
436

437 **Time-Calibrated Analyses**
438   We conducted a time-calibrated BI analysis in MrBayes 3.2.7 using our
439 concatenated mitochondrial and nuclear datasets. We used a birth-death model and an

440 independent gamma rate relaxed-clock (igr), where each branch has an independent
441 rate drawn from a gamma distribution that was empirically derived in MrBayes. The
442 MCMC chain was run for 3.0 x 10^7 generations (sampled every 1000 generations) for
443 two runs each with four chains. A temperature of 0.1 was implemented and the first 30%
444 of the data were discarded as burn-in. Results of the analyses were visualized in Tracer
445 v1.7 (Rambaut et al., 2018) to ensure runs had reached stationarity and that the
446 effective sample size (ESS) was >200 for all model parameters.
447   *Microtus* is one of the most diverse and rapidly evolving mammalian genera
448 (Triant and DeWoody, 2006). Many phenotypic characters are convergent among
449 distantly related species, and high genetic variation has been attributed to karyotypic
450 differentiation, with diploid chromosomal numbers ranging from 17 to 64 (Triant and
451 DeWoody, 2006). Triant and DeWoody (2006) documented that *Microtus sensu stricto*
452 has a time-corrected mitochondrial rate of nucleotide substitution of 0.08 substitutions
453 per site per million years. This is higher than most other mammals (e.g., *Pan*, *Bos*,
454 *Ursus*) and obviously would affect divergence time analyses (Triant and DeWoody,
455 2006). We therefore calculated the rate of evolution for the mitochondrial only, nuclear
456 only, and concatenated mitochondrial and nuclear datasets using R code provided in
457 Gunnell et al., (2018). This code uses a user inputed tree-age along with branch lengths
458 to calculate the rate of evolution within the tree. The mitochondrial rate of evolution was
459 0.09 substitutions per site per million years, the nuclear rate of evolution was 0.01
460 substitutions per site per million years, and the concatenated dataset was 0.065
461 subtitutions per site per million years. This code is included in our Dryad submission
462 (Appendix C). Since we used the concatenated mitochondrial and nuclear dataset for
463 time-calibration we chose to use the substitution rate of 0.065 substitutions per site per
464 million years as the mean clock rate prior. We used the MrBayes command 'prset
465 clockratepr' with a mean of -2.72 (natural log of 0.065) and a standard deviation of 0.12
466 as calculated in the code from Gunnell et al. (2018).
467
468 **Node Calibration Selection**
469   We used four internal node calibrations and a root calibration in our divergence
470 time analyses. Calibrated nodes were constrained as monophyletic and these nodes
471 were selected after non-calibrated phylogenies were produced. For all nodes, there
472 were no suitable fossils available to help establish calibration maxima, so we used
473 exponential calibration priors for each node. For each calibration, the fossil age was
474 used as the offset. R scripts for calculating a suitable mean are in Appendix C.
475
476 **Calibration 1: Cricetidae (Outgroup) (Tree Root)**
477   We chose as outgroups three muroid rodents previously found to be closely
478 related to Arvicolinae (Fabre et al., 2012; D'Elía et al., 2019). These three species
479 belong to the subfamilies Cricetinae *(Cricetus cricetus*, *Mesocricetus auratus*) and

480   Neotominae (*Neotoma fuscipes*). The split between Arvicolinae and Cricetinae is
481   reported to have occurred during the middle Miocene (Fabre et al., 2012). The split
482   between (Arvicolinae, Cricetinae) and Neotominae was hypothesized to be during the
483   early-Miocene (Fabre et al., 2012; Steppan and Schenk, 2017). We chose to calibrate
484   the root of our tree using the oldest purported fossil neotomid, *Lindsaymys* sp. cf. *L.*
485   *takeuchii* (Kelly and Whistler, 2014; Martin and Zakrzewski, 2019). This calibration is
486   anchored by a lower first molar (m1) housed at the Los Angeles County Museum
487   (LACM 157168). LACM 157168 is diagnosed as belonging to *Lindsaymys* based on. (1)
488   a moderately hyposodont molar that is smaller than the more temporally recent
489   specimens (2) an m1 with an anteroconid that is not bifurcated and positioned close to
490   the metaconid (3) a metalophulid that connects to the protolophulid I at the junction with
491   the anterolophid (4) presence of an entoconid spur and (5) a moderately deep valley
492   between the metaconid and the lingual edge of the anteroconid and anterlophid (Kelly
493   and Whistler, 2014). This last feature is key to distinguishing it from other contemporary
494   taxa such as *Abelmoschomys*, *Antecalomys*, *Prosigmodon*, *Bensonomys*, *Baiomys*,
495   *Symmetrodontomys*, and *Jacobsomys* (Kelly and Whistler, 2014). LACM 157168 was
496   found in locality LACM 5720 which is thought to be Latest Clarendonian to early
497   Hemphillian (C13-Hh1, ~9.2-8.7 Ma) (Kelly and Whistler, 2014). LACM Locality 5720 is
498   found in the El Paso Mountains within the Dove Spring Formation of the western Mojave
499   Desert, California (Kelly and Whistler, 2014). The site lies underneath Dove Spring Ash
500   number 16 dated via Ar/Ar at 8.5 ± 0.13 Ma and above Dove Spring Ash number 15
501   dated via fission tract at 8.4 ± 1.8 Ma (Whistler et al., 2009). Biochronology and
502   paleomagnetics place this site in Chron C4A, with a maximum age of ~9.2 Ma (Kelly
503   and Whistler, 2014). We chose to use 8.8 Ma as a conservative estimate of the
504   minimum age of the site, since it is a middle point between 8.5 Ma and 9.2 Ma (Whistler
505   et al., 2009; Kelly and Whistler, 2014). The soft maximum for the node was based on
506   the divergence time analysis of Steppan and Schenk (2017). We used an offset
507   exponential distribution with a minimum age of 8.8 Ma and a mean of 10.8 Ma. 10.8 Ma
508   was chosen as the mean because it produced an 95% upper bound of the distribution at
509   15 Ma.
510
511   **Calibration 2: Lemmini Node**
512   The earliest North American bog lemmings (*Synaptomys*) are from the
513   Hagerman Fossil Beds National Monument, Idaho (*Mictomys = Synaptomys vetus*;
514   Ruez and Gensler, 2008). The offset for this node is anchored by a right m1 (lower first
515   molar) housed at the Idaho Museum of Natural History (IMNH 67002/39517) that has
516   radiometric age control (Ar-Ar) of a basaltic tephra located 30 m above the site and
517   dated at 3.79 ± 0.03 Ma (Hart and Brueseke, 1999). Interpolation of depositional rates
518   indicates that the age of the fossil from IMNH locality 67002 is ~3.95 Ma (Hart and
519   Brueseke, 1999). IMNH 67002/39517 was identified as *Mictomys vetus* by having

520 evergrowing molars with cementum in the reentrant angles. The m1 also has a posterior
521 loop with three triangles, and an anterior loop (Ruez and Gensler, 2008). Triangles 1
522 and 2 are broadly confluent with the anterior loop and triangle three is joined by the
523 anterior loop near the midline. Triangles 1 and 3 are nearly twice the width of triangle 2.
524 Because *Synaptomys* was paraphyletic in some of our uncalibrated analyses, we used
525 this fossil to calibrate the crown lemming node instead. We used an offset exponential
526 distribution with a minimum age of 3.95 Ma and a mean of 4.74 Ma (see Appendix C for
527 this calculation).
528
529 **Calibration 3: Ondatrini Node**
530   The oldest known species of this clade, *Ondatra minor*, is found in the Hagerman
531 Formation in Hagerman, Idaho at ~3.6 Ma (Hibbard, 1959). All of the fossils at
532 Hagerman are constrained between two lava flows and ash units that have yielded ages
533 of 4.0 Ma to 3.2 Ma using Ar-Ar dating methods (McDonald et al., 1996). We anchored
534 the *Ondatra + Neofiber* node using a left m1 tooth of *Ondatra minor* (USNM 21830) from
535 Hagerman. This m1 was identified as *Ondatra minor* by its relatively large size as well
536 as being rooted and having a posterior loop, five alternating triangles, with a fifth triangle
537 opening broadly into the anterior loop (Hibbard, 1959). We used an offset exponential
538 distribution with a minimum age of 3.2 Ma and a mean of 4.9 Ma. The age of 3.2 Ma
539 was chosen because it is the most conservative estimate of the age of the two ash
540 layers described from Hagerman Idaho and deposition interpolation information were
541 not available for the locality.
542
543 **Calibration 4: Pliophenacomyini Node**
544   Extant voles of the genera *Phenacomys* and *Arborimus* are today restricted to
545 North America. Eurasian specimens of *Phenacomys* were identified from Krestovka,
546 Kolyma Lowland Russia (Sher et al., 1979; Zazhigin, 1997) and Romanovo 1c, Western
547 Siberia, Russia (Smirnov et al., 1986; Borodin, 2012). Recently, a new species
548 (*Phenacomys europaeus*) was described from Europe in Zuurland, the Netherlands,
549 and dated at ~2.1 Ma based on biochronology (van Kolfschoten et al., 2018). The oldest
550 known record of *Phenacomys*, *P. gryci*, (type locality in the Gubik Formation) is from the
551 Fish Creek fauna of Alaska. The Fish Creek Fauna is in the Gubik Formation, which is
552 an alternating marine and coastal plain sedimentary unit. The Fish creek Fauna is dated
553 at ~2.4 Ma using amino acid racemization ratios, a reversed polarity zone, and the
554 presence of the ancestral sea otter *Enhydrion* and the arvicoline rodent *Plioctomys*
555 *mimomiformis* (Carter et al., 1986; Repenning et al., 1987; Repenning and Brouwers,
556 1992). We calibrated the (*Phenacomys + Arboriumus*) node based on the type
557 specimen of *Phenacomys gryci* (a left m1 housed at the United States National Museum
558 USNM 26495). This fossil was assigned to *Phenacomys gryci* by having a rooted m1
559 that lacked cementum in the reentrant angles. It also possesses a posterior loop, five

560 asymmetrical alternating triangles with a "*Mimomys* Kante" on triangle four, and a
561 complex anterior loop (Repenning et al., 1987). This node was calibrated using an offset
562 exponential distribution with a minimum age 2.4 Ma and a mean of 3.27 Ma (see
563 Appendix C for this calculation).
564
565 **Calibration 5: Ellobiusini**
566   The timing of the origination and diversification of *Microtus* and its close relatives
567 has been repeatedly contested among paleontologists (e.g., Repenning, 1992; Martin
568 and Tesakov, 1998). It was argued that the genus *Allophaiomys* gave rise via
569 anagenetic evolution to what is recognized today as *Microtus* (Martin and Tesakov,
570 1998), but that hypothesis is controversial (e.g., Bell et al., 2004; Bell and Bever, 2006).
571 The oldest *Allophaiomys* with external age control is from Hansen Bluff (Colorado) and
572 dated at 1.9 Ma (Rogers et al., 1992). The earliest occurrence of *Microtus,* as defined
573 by Repenning (1992), was long thought to be from the Anza-Borrego Desert of
574 California (Zakrzewski, 1972), possibly from 1.4 to 1.6 Ma (lacking firm age control).
575 Unfortunately, the specimens from Anza-Borrego had questionable field data; one
576 specimen was found in a fault block and from a different area in the park than originally
577 reported, and a second specimen could not definitively be assigned to *Microtus* (Bell
578 and Bever, 2006; Murray et al., 2011). The oldest known *Microtus* is, therefore, found in
579 the type Irvington Fauna from California dated to 1.21 Ma based on paleomagnetic data
580 (Bell and Bever, 2006).
581   Fossil evidence from *Ellobius*, an early diverging member of the clade that
582 includes *Microtus*, was used here to calibrate the node. The oldest fossils of *Ellobius*
583 are from the Late Pliocene of Kazakhstan and Tajikistan (Lytchev and Savinov, 1974;
584 Zazhigin, 1988) and the Northern Caucasus (Tesakov, 2004). We chose to use a fossil
585 mandible with m1-m3 (Paleontological Institute, Russian Academy of Sciences M-
586 2049/58-KB) of *Ellobius primigenius* from Central Asia (Lytchev and Savinov, 1974).
587 This fossil possesses rooted teeth with relatively high crowns, a posterior loop, five
588 alternating triangles, and an anterior loop consistent with *Ellobius* (Lytchev and Savinov,
589 1974). This mandible is part of the Kiikbai fauna of Kazakhstan dated using
590 biochronology (the occurrence of *Hypolagus brachygnathus*, *Ochotonoides*
591 *complicidens*, and *Mimomys pliocaenicus*) to the Pliocene at ~2.4 Ma in the Matuyama
592 Chron (Sotnikova et al., 1997). The Kiikbai fauna is described from the southern flank of
593 the Ilian depression in the Alatau mountain and placed in the European middle
594 Villafranchian land mammal age (Sotnikova et al, 1997). We used an offset exponential
595 distribution with a minimum age of 2.4 Ma and a mean of 3.27 Ma (see Appendix C for
596 this calculation).
597
598 **Results**
599 **Non-clock Analyses**

600   Six phylogenetic analyses were conducted on the concatenated dataset that
601 included either all or a subset of the 147 sequences from *Cytb*; 64 from *COI*; 90 from
602 *Ghr*; 105 from *IRBP/RBP3*; and 69 from *BRCA1*. 110 species (74%) included both
603 mitochondrial and nuclear data. 39 species (26%) had only mitochondrial data.
604 GenBank accession numbers are in Appendix A. Results from Maximum Likelihood and
605 Bayesian analyses were similar or identical except where discussed below.
606
607 **Maximum Likelihood (ML) Results**
608   A tribe-level summary of the ML tree including only the mitochondrial loci (Cytb
609 and COI) with rapid-bootstrapping values from RAxML v7.0.4 (lnL = -55015.19) is
610 presented in Figure 1a. Moderate support (71-89 BS) was inferred for 3 (8%) of the
611 nodes (Figure 1a). High support (>90 BS) was found for 2 (6%) of the nodes (Figure
612 1a). A species-level tree is presented in Appendix D. Moderate support was inferred for
613 18 (12%) of the nodes (Appendix D). High support was found for 51 (35%) of the nodes
614 (Appendix D). A tribe-level summary of the ML tree including only the nuclear loci (Ghr,
615 IRBP/RBP3, and BRCA1) with rapid-bootstrapping values from RAxML v7.0.4 (lnL = -
616 21229.90) is presented in Figure 2a. Moderate support was inferred for 1 (4%) of the
617 nodes (Figure 2a). High support was found for 14 (52%) of the nodes (Figure 2a). A
618 species-level tree is presented in Appendix E. Moderate support was inferred for 10
619 (9%) of the nodes (Appendix E). High support was found for 56 (53%) of the nodes
620 (Appendix E). Finally, another tribe-level summary of the ML tree including all five loci
621 (Cytb, COI, Ghr, IRBP/RBP3, and BRCA1) with rapid-bootstrapping values from RAxML
622 v7.0.4 (lnL = -77750.23) is presented in Figure 3a. Moderate support was inferred for 2
623 (7%) of the nodes (Figure 3a). High support was found for 9 (32%) of the nodes (Figure
624 3a). A species-level tree is presented in Appendix F. Moderate support was inferred for
625 13 (9%) of the nodes (Appendix F). High support was found for 72 (49%) of the nodes
626 (Appendix F).
627
628 **Bayesian Inference (BI) Results**
629   A tribe-level summary of the BI tree including only the mitochondrial loci (Cytb
630 and COI) with posterior probability values is presented in Figure 1b. High support (>95
631 PP) was found for 11 (32%) of the nodes (Figure 1b). A species-level tree is presented
632 in Appendix G. High support was found for 80 (54%) of the nodes (Appendix G). A tribe-
633 level summary of the BI tree including only the nuclear loci (Ghr, IRBP/RBP3, and
634 BRCA1) with posterior probability values is presented in Figure 2b. High support was
635 found for 20 (74%) of the nodes (Figure 2b). A species-level tree is presented in
636 Appendix H. High support was found for 68 (63%) of the nodes (Appendix H). Finally a
637 tribe-level summary of the BI tree including all five loci (Cytb, COI, Ghr, IRBP/RBP3,
638 and BRCA1) with posterior probability values is presented in Figure 3b. High support

639 was found for 17 (57%) of the nodes (Figure 3b). A species-level tree is presented in
640 Appendix I. High support was found for 88 (60%) of the nodes (Appendix I).
641
642 **Major Clade Systematic Results**
643   The tribe Arvicolini was variably placed in the different analyses (Figure 1-3). In
644 the mitochondrial analyses (Figure 1) Arvicolini is weakly placed near the root of the
645 arvicoline tree. In the nuclear and combined analyses (Figure 2-3) it is placed with
646 stronger support in the derived clade that includes Ellobiusini, Pliomyini, Lagurini, and
647 Microtini. Clethrionomyini is consistently found in all analyses to be a large clade in the
648 middle of the arvicoline tree (Figures 1-3). Within this tribe there are two clades that are
649 found in all analyses. (1) A clade that consists of *Caryomys*, *Eothenomys*, and
650 *Anteliomys* (Figures 1-3), and (2) A clade that consists of *Craseomys*, *Clethrionomys*,
651 and *Alticola* (Figures 1-3). *Anteliomys* is paraphyletic with strong support with respect to
652 *Eothenomys* in the nuclear analysis (Figure 2) but monophyletic and the sister to
653 *Eothenomys* in the other analyses (Figures 1 and 3). The paraphyly/monophyly of
654 *Clethrionomys* and *Alticola* vary among analyses (Figures 1-3). *Clethrionomys* is
655 paraphyletic in the ML and BI mitochondrial and nuclear analyses as well as the
656 combined BI analysis (Figures 1-3). In the combined ML analysis, *Clethrionomys* was
657 monophyletic (Figure 3a). *Alticola* was found to be paraphyletic in the mitochondrial
658 analyses (Figure 1) and the combined ML analysis (Figure 3a) and monophyletic in the
659 nuclear analysis (Figure 2) and combined BI (Figure 3b).
660   Dicrostonychini is weakly inferred as the sister to Ondatrini in the mitochondrial
661 analyses (Figure 1), and strongly supported as the sister to Pliophenacomyini in the
662 nuclear and combined analyses (Figure 2-3). Ellobiusini is consistently found at the
663 base of the large clade that includes Lagurini, Arvicolini (in the nuclear and combined
664 analyses), Pliomyini (in the nuclear and combined analyses), and Microtini (Figures 1-
665 3). Lagurini is found to be the sister to Microtini in the mitochondrial analyses (Figure 1)
666 but sister to the clade containing Arvicolini + Microtini in the nuclear and combined
667 analyses (Figures 2-3). Lemmini is consistently found near the base of the arvicoline
668 tree (Figures 1-3), but relationships within the tribe vary across analyses. *Myopus* is the
669 first diverging member of Lemmini in the mitochondrial analysis (Figure 1 and Appendix
670 D and G), but earliest diverging 'true-lemming' in the nuclear and combined analyses
671 (Figures 2-3 and Appendix E,H and F,I). *Synaptomys* is paraphyletic or polyphyletic in
672 the mitochondrial analyses (Figure 1) and combined ML analysis (Figure 3a) but
673 monophyletic in the nuclear analyses (Figure 2) and combined BI analysis (Figure 3b).
674   Microtini was consistently the most crownward tribe of arvicolines (Figures 1-3).
675 *Chionomys* is sister to the rest of Microtini in the nuclear and combined analyses
676 (Figures 2-3), but in the mitochondrial analyses (Figure 1), a split between *Microtus*
677 *ochrogaster* and the rest of Microtini was the first divergence. *Volemys* are early
678 diverging within Microtini, and are polyphyletic in the ML mitochondrial analysis (Figure

679 1a), nuclear analyses (Figure 2), and combined analyses (Figure 3). However, *Volemys*
680 was found to be monophyletic in BI mitochondrial analysis (Figure 1b). In all analyses,
681 *Proedromys* was placed as sister to *Volemys musseri* (Figures 1-3). *Lasiopodomys* is
682 the sister to *Stenocranius* in the BI mitochondrial only (Figure 1b) and the nuclear and
683 combined analyses (Figure 2-3). In the ML mitochondrial only analysis, *Lasiopodomys*
684 is sister to *Alexandromys*, albeit weakly (Figure 1a). In the ML mitochondrial only
685 analysis, *Stenocranius* was sister to a paraphyletic *Neodon* (containg a nested *Volemys*
686 *millicens*) (Figure 1a), but in the others it is sister to *Lasiopodomys* (Figures 1b-3).
687 *Neodon* is found to be monophyletic in the mitochondrial BI analysis (Figure 1b),
688 nuclear ML (Figure 2a) and paraphyletic in the other analyses (Figure 1a, 2b, and 3).
689 *Mictomicrotus* is deeply nested within Microtini (Figures 1a, 2 and 3) or is nested within
690 *Microtus* (Figures 1b). *Alexandromys* is one of the most nested members of Microtini
691 (Figures 1-3). *Microtus* is the most nested arvicoline and was monophyletic in the
692 nuclear and combined analyses (Figures 2-3) but paraphyletic or polyphyletic in the
693 mitochondrial analyses (Figure 1). Endemic species of North American *Microtus* are
694 monophyletic in the nuclear and combined analyses (Figures 2-3).
695   Ondatrini is a rootward tribe of arvicolines in all analyses, but its sister
696 relationships vary (Figures 1-3). In the mitochondrial analyses Ondatrini is sister to
697 Dicrostonychini (Figure 1), and in the nuclear and combined analyses it is sister to
698 Pliophenacomyini + Dicrostonychini + Lemmini (Figure 2-3), Pliophenacomyini is
699 recovered as an early diverging arvicoline sister to Dicrostonychini in the nuclear and
700 combined analyses (Figure 2-3). Pliomyini is found towards the base of the arvicoline
701 tree in the mitochondrial analyses (Figure 1), but within the clade that includes
702 Ellobiusini, Lagurini, Arvicolini, and Microtini in the nuclear and combined analyses
703 (Figure 2-3). Prometheomyini is found at the base of the arvicoline tree in the nuclear
704 and combined analysis (Figure 2-3), but at the base of the clade that includes
705 Ellobiusini, Lagurini, and Microtini in the mitochondrial analyses (Figure 1).
706
707 **Time-Calibrated Analysis**
708   A tribel-level time-calibrated majority rule consensus tree of the combined
709 dataset is presented in Figure 4. A species-level tree is presented in Appendix J. 105
710 nodes (72%) had posterior probability values >0.95.
711
712 **Divergence-Time Results**
713   Crown arvicoline rodents were inferred to have diverged ~6.4 Ma. For a list of all
714 the major clades and their divergence estimates see Table 1.
715

716 # Discussion
717 **Systematic Position of Genera and Discussion of Intrageneric Relationships**

718   The overall topology of our ML and BI analyses are largely congruent with
719 previously published molecular phylogenies (e.g., Conroy and Cook, 1999, 2000;
720 Galewski et al., 2006; Buzan et al., 2008; Fabre et al., 2012; Martínková and Moravec,
721 2012; Steppan and Schenk, 2017; Upham et al., 2019; Abramson et al., 2021) except
722 for Robovský et al. (2008), which included morphological characters in their analyses.
723 We did find some different topological arrangements than previous works, especially in
724 relatively earlier divergences, but few of those nodes were well-supported. There are
725 some topological differences based on marker set inclusion (e.g., nuclear,
726 mitochondrial, or combined). Below we outline the implications of our results for the
727 taxonomy and evolutionary understanding of Arvicolinae.
728
729 **Basal position of Prometheomyini?**
730   Prometheomyini is sister to all other arvicolines in several studies though with
731 weak support (Galewski et al., 2006; Fabre et al., 2012; Steppan and Schenk, 2017;
732 Upham et al., 2019; Ibis et al., 2020). In other studies, it was placed close to the base of
733 Arvicolinae but not as the first diverging arvicoline (Buzan et al., 2008; Robovský et al.,
734 2008; Abramson et al., 2021). Our nuclear analyses and combined BI analysis placed
735 Prometheomyini as sister to other arvicolines with strong support (Figures 2 and 3b).
736 Prometheomyini was deeply nested (though with weak support) in the mitochondrial-
737 only analyses (Figure 1), and sister to arvicolines besides *Lemmiscus* in the combined
738 ML analysis. Therefore, we stress caution in considering *Prometheomys* as the most
739 basal arvicoline. Discrepancy between the mitochondrial and nuclear loci warrants
740 further investigation (Pardiñas et al., 2017; Kryštufek and Shenbrot, 2022).
741
742 **Systematic relationships within Lemmini**
743   Bog lemmings (*Synaptomys*) and 'true lemmings' (*Myopus*, *Lemmus*) are
744 consistently placed in a clade at or near the base of the arvicoline tree. One previous
745 study placed lemmings as sister to all other arvicolines (Abramson et al., 2021),
746 whereas most have found lemmings to be near but not at the base of the tree (Galewski
747 et al., 2006; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Steppan and
748 Schenk, 2017; Upham et al., 2019). Studies that sampled both species of extant bog
749 lemming found that *Synaptomys* (as defined by Musser and Carleton, 2005) is
750 paraphyletic with respect to 'true lemmings' (Buzan et al., 2008; Fabre et al., 2012;
751 Steppan and Schenk, 2017; Upham et al., 2019). Our results unfortunately do not add
752 any clarity on whether bog lemmings should be one or two genera, because 50% of our
753 trees recover a weakly supported clade. However, it should be noted that analyses
754 based either entirely or predominantly on nuclear markers recovered a weakly
755 supported clade, while those that included mitochondrial-only data tended not to. Based
756 on dental morphology, many paleontologists have considered the northern bog
757 lemming, *Synaptomys borealis* (following Musser and Carleton, 2005), to be a member

758 of a distinct genus known as *Mictomys* (Fejfar and Repenning, 1998; Repenning and
759 Grady, 1988). Musser and Carleton (2005) and Pardiñas et al. (2017) argued that there
760 may be enough evidence to place *Mictomys* and *Synaptomys* as distinct genera, but
761 they tentatively kept them in the same genus. Along with other studies (e.g., Buzan et
762 al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017), our analyses do not support
763 or reject the monophyly of bog lemmings.
764
765 **Systematic Status of Dicrostonychini and Pliophenacomyini**
766   Voles belonging to *Phenacomys* and *Arborimus* are consistently found to be
767 sister genera (Robovský et al., 2008; Fabre et al., 2012; Steppan and Schenk, 2017;
768 Upham et al., 2019). Recently, the clade (*Phenacomys, Arborimus*) was found to be
769 sister to *Dicrostonyx* (Galewski et al., 2006; Buzan et al., 2008; Robovský et al., 2008;
770 Fabre et al., 2012; Steppan and Schenk, 2017; Abramson et al., 2021). Historically
771 *Dicrostonyx* was thought to be closely related to the other lemmings, but that was not
772 found in recent studies (Galewski et al., 2006; Buzan et al., 2008; Robovský et al.,
773 2008; Fabre et al., 2012; Steppan and Schenk, 2017; Abramson et al., 2021). Our
774 nuclear and combined mitochondrial and nuclear analyses are in agreement with
775 Abramson et al. (2021) that *Dicrostonyx*, *Phenacomys*, and *Arborimus*, are united in a
776 clade that Abramson et al. (2021) called Dicrostonychini. However, we have followed
777 the tribal terminology of Kryštufek and Shenbrot (2022) in which Dicrostonychini
778 (*Dicrostonyx* only) and Pliophenacomyini (*Phenacomys + Arborimus*) are closely related
779 but separate tribes. Lemmings and ((*Phenacomys, Arborimus*), *Dicrostonyx*) were
780 consistently placed in a clade at or near the base of Arvicolinae in our analyses.
781 Although it is true that *Dicrostonyx* are not sister to Lemmini, they are part of a more
782 inclusive clade that is often plaed as sister to Lemmini.
783
784 **Systematic Status of Clethrionomyini**
785   Using molecular data (and to a lesser extent morphology), *Alticola*, *Anteliomys*,
786 *Caryomys*, *Clethrionomys*, *Craseomys*, and *Eothenomys* were consistently found to be
787 closely related and united in the tribe Myodini (Luo et al., 2004; Galewski et al., 2006;
788 Lebedev et al., 2007; Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Liu
789 et al., 2012; Zeng et al., 2013; Steppan and Schenk, 2017; Upham et al., 2019;
790 Abramson et al., 2021). We use the tribal name Clethrionomyini rather than Myodini,
791 because Myodini is no longer a valid term (Kryštufek and Shenbrot, 2022). Interestingly,
792 dental morphology alone suggests that *Clethrionomys*, *Craseomys rex* and *Craseomys*
793 *rufocanus* (rooted molars) should be more distantly related to *Anteliomys*, *Caryomys*,
794 *Eothenomys*, *Alticola*, and the rest of *Craseomys* (rootless molars) (Luo et al., 2004;
795 Lebedev et al., 2007; Liu et al., 2012; Zeng et al., 2013; Kryštufek and Shenbrot, 2022).
796 However, they are consistently united together into Clethrionomyini (Luo et al., 2004;
797 Buzan et al., 2008; Robovský et al., 2008; Fabre et al., 2012; Liu et al., 2012; Zeng et

798 al., 2013; Steppan and Schenk, 2017; Abramson et al., 2021). We also found that clade
799 here, and, furthermore, found two major clades within Clethrionomyini, (1) *Caryomys* +
800 *Eothenomys* + *Anteliomys*, and (2) *Craseomys* + *Clethrionomys* + *Alticola*.
801   *Alticola* was poorly sampled in many previous studies. Depending on which
802 species of *Alticola* were included, studies variably inferred monophyly (Fabre et al.,
803 2012) or paraphyly (Lebedev et al., 2007; Steppan and Schenk, 2017; Upham et al.,
804 2019; Abramson et al., 2021) of the genus. Our study includes a robust sampling of
805 currently recognized species of *Alticola* and our mitochondrial only and combined ML
806 analyses are similar to Upham et al. (2019) in finding a paraphyletic *Alticola* with respect
807 to *Clethrionomys*. More sampling within *Alticola* is warranted to get a more complete
808 understanding of this clade.
809
810 **Systematic Status of *Hyperacrius***
811   The systematic position of the Subalpine Kashmir Vole (*Hyperacrius fertilis*) has
812 been relatively understudied. Using morphology alone, *Hyperacrius* was hypothesized
813 to be closely related to *Alticola* (Hinton, 1926), or as a member of the tribe
814 Clethrionomyini (Gromov and Polyakov, 1977). Kohli et al. (2014) included *Hyperacrius*
815 for the first time in a molecular analysis, and its relationship to Clethrionomyini was
816 doubted. We found weakly-supported close relationships between *Hyperacrius* and
817 Clethrionomyini (mitochondrial only and combined ML) and near Pliomyini (combined
818 BI). Recently, *Hyperacrius* was hypothesized to be the earliest diverging member of
819 what was previously considered Arvicolini (i.e., Microtini minus *Arvicola*) (Abramson et
820 al., 2020; 2021). Given that only *cytb* data were available for *Hyperacrius* our results
821 should be considered equivocal and more sampling is needed.
822
823 **Systematic Status of *Lemmiscus curtatus***
824   Until recently, the sagebrush vole, *Lemmiscus curtatus*, had not been included in
825 molecular phylogenies (Steppan and Schenk, 2017; Abramson et al., 2021). Those two
826 analyses produced conflicting results for the systematic position of *Lemmiscus*. Both
827 studies found that *Lemmiscus* and *Microtus* are not sister taxa. Steppan and Schenk
828 (2017) placed *Lemmiscus* as sister to *Arvicola*, whereas Abramson et al. (2021) placed
829 it as sister to *Chionomys*. Some of our results, though weakly supported, are similar to
830 Steppan and Schenk (2017), probably because we used the same genetic data for
831 *Lemmiscus* for our phylogeny, whereas Abramson et al. (2021) used an entire
832 mitochondrial genome of *Lemmiscus*. Our combined ML analysis placed *Lemmiscus* as
833 sister to other arvicolines whereas our other analyses place it close to Arvicolini. More
834 data from transcriptomes or nuclear genes will help to refine the systematic position of
835 this species, so we do not make any taxonomic recommendations based on the
836 systematic position of *Lemmiscus* in our analyses.
837

Systematic Status of Ellobiusini, Arvicolini, Lagurini, and Pliomyini

838
839   Over the past decade, Ellobiusini, Arvicolini and Lagurini have been the subject
840 of several phylogenetic studies (Bondareva et al., 2020; Mahmoudi et al., 2020).
841 Ellobiusini (including *Ellobius* and *Bramus*) was placed as an early diverging arvicoline
842 (Bondareva et al., 2020; Robovský et al., 2008), or as an early diverging member of the
843 radiation that includes *Lagurus*, *Eolagurus*, *Lemmiscus*, *Neodon*, *Arvicola*, *Chionomys*,
844 *Proedromys*, *Volemys*, *Lasiopodomys*, and *Microtus* (Fabre et al., 2012; Steppan and
845 Schenk, 2017; Upham et al., 2019; Abramson et al., 2021). Our results support that
846 Ellobiusini is an early diverging member of the large radiation that includes Arvicolini +
847 Lagurini + Microtini, and not an early diverging arvicoline (see Figures 1-3). However,
848 that relationship was not strongly supported in any analysis that included mitochondrial
849 data.
850   Arvicolini has been used to describe a large number of genera including *Arvicola*,
851 *Chionomys*, *Neodon*, *Lasiopodomys*, and *Microtus*. We recognize the tribe Arvicolini as
852 having a single genus, *Arvicola*, based on the Mammal Diversity Database (2023). We
853 inferred a monophyletic Arvicolini with a weak sister taxon relationship to *Lemmiscus*
854 *curtatus* (in mitochondrial only BI), similar to the results of Steppan and Schenk (2017).
855 That is an interesting biogeographic result given the large distance between the extant
856 members of these genera. We also recovered Arvicolini as the sister clade to Microtini
857 (in both nuclear and combined analyses) and as in Abramson et al. (2021).
858   Lagurini was placed as the sister to Pliomyini (Steppan and Schenk, 2017), as
859 the sister to *Arvicola* (Abramson et al., 2021), and as sister to Microtini (Fabre et al.,
860 2012). Our nuclear only and combined results are most similar to Fabre et al. (2012)
861 and Abramson et al. (2021) in that we found Lagurini to be closely related to Arvicolini
862 and Microtini. Pliomyini was found to be sister to Lagurini (Steppan and Schenk, 2017),
863 and as the sister to *Arvicola* (Fabre et al., 2012; Abramson et al., 2021). Regardless of
864 its sister taxon relationship all three of these studies recovered Pliomyini close to
865 Ellobiusini, Arvicolini, and Lagurini. Our analyses placed Pliomyini as (1) sister to
866 Arvicolini and Clethrionomyini wth mitochondrial data only, or (2) as closely related to
867 Arvicolini, Lagurini, Ellobiusini, and Microtini in the nuclear only and combined analyses.
868 Based on those results, Pliomyini is part of the major radiation that includes Ellobiusini,
869 Lagurini, Arvicolini, and Microtini.
870

Systematic Status of Microtini

871
872   Microtini is the largest tribe of arvicoline rodents. Recently, the Mammal Diversity
873 Database (2023) recognized Microtini as distinct from Arvicolini based on Abramson et
874 al. (2021), who found that *Arvicola* was not in a clade with the other members of
875 Microtini. We found the same result (see Figures 1-3). Therfore we retain the genera
876 *Chionomys*, *Proedromys*, *Volemys*, *Mictomicrotus*, *Neodon*, *Lasiopodomys*,
877 *Stenocranius*, *Alexandromys*, and *Microtus* within a monophyletic Microtini.

878   Historically, *Chionomys* was placed in *Arvicola*, in *Microtus*, its own genus, or as
879   a subgenus of *Microtus* (Yannic et al., 2012). This complicated history can be attributed
880   in part to the fragmented geographic distribution and isolation in high alpine
881   environments of *Chionomys*. Jaarola et al. (2004) used analyses of *cytb* to solidify
882   *Chionomys* as a valid genus separate from *Microtus*, and several other studies placed
883   *Chionomys* as a nested member of what is now considered Microtini, but outside of
884   *Microtus* (Galewski et al., 2006; Robovský et al., 2008; Fabre et al., 2012; Abramson et
885   al., 2021). Our results further support that hypothesis and provide evidence to suggest
886   that *Chionomys* is a basal member of Microtini. *Proedromys* has historically been
887   thought to be closely related, or even included in, *Microtus* (Ellerman and Morrison-
888   Scott, 1951; Gromov and Polyakov, 1977; Musser and Carleton, 2005). We concur with
889   other phylogenetic studies (Fabre et al., 2012; Steppan and Schenk, 2017; Abramson et
890   al., 2021) that place *Proedromys* in Microtini and close to but outside of *Microtus*. We
891   consistently found *Volemys musseri* as sister to *Proedromys* with strong support (see
892   Figures 1-3). Given the geographical overlap of the two genera that result is not
893   suprising and recapitulates previous studies (Steppan and Schenk, 2017; Upham et al.,
894   2019). *Mictomicrotus* is a recently named genus that is monotypic (*M. liangshanensis*)
895   and was previously included in *Proedromys* (Liu et al., 2007; Kryštufek and Shenbrot,
896   2022; Steppan and Schenk, 2017). Our results further support the hypothesis that
897   *Mictomicrotus* is a distinct genus.
898   Recent systematic and taxonomic work altered our understanding of *Microtus*
899   (Bannikova et al., 2010; Liu et al., 2012; Liu et al., 2017; Pradhan et al., 2019). For
900   example, *Neodon* was previously recognized as its own genus or as a subgenus of
901   *Microtus* (see Musser and Carleton, 2005; Pardiñas et al. (2017)), or was placed in
902   *Pitymys* (Ellerman and Scott, 1951). It has become increasingly apparent that *Microtus*
903   was historically used as a taxonomic garbage bin. Several species previously allocated
904   to *Microtus* are now placed in *Neodon* (*N. leucurus*, *N. clarkei*, and *N. fuscus*) (Pradhan
905   et al., 2019; Abramson et al., 2021). We found a paraphyletic *Neodon* with respect to
906   *Volemys millicens* in most analyses (mitochondrial only ML, Nuclear only BI, and
907   combined ML and BI), and a monophyletic *Neodon* that is sister to *Alexandromys* in the
908   others (Mitochondrial only BI and Nuclear only ML). The relationship between *Volemys*
909   *millicens* and *Neodon* warrants further exploration.
910   *Volemys* was considered a distinct genus or a subgenus of *Microtus*, with Musser
911   and Carleton (2005) recognizing two species, *V. musseri* and *V. millicens*. That
912   classification is based on morphology alone, and the monophyly of *Volemys* has not
913   been supported by molecular datasets (Jaarola et al., 2004; Steppan and Schenk, 2017;
914   Upham et al., 2019). We inferred a weakly monophyletic *Volemys* in one analysis
915   (mitochondrial only BI). We suggest further systematic study of *Volemys* and further
916   examination to understand potential morphological homoplasy between *V. millicens* and
917   *V. musseri*.

918   Voles placed within *Lasiopodomys* and *Stenocranius* have a long history of
919 taxonomic change, with some studies placing them within *Microtus*, while others have
920 placed them all within *Lasiopodomys* (see Musser and Carleton, 2005; Pardiñas et al.
921 2017; Kryštufek and Shenbrot, 2022). We follow the taxonomy recognized by Kryštufek
922 and Shenbrot (2022) and the Mammal Diversity Databse (2023) in which there are two
923 species of *Lasiopodomys* and two species of *Stenocranius*. All but one of our analyses
924 (mitochondrial only ML) found *Lasiopodomys* and *Stenocranius* to be sister taxa with
925 medium to strong support, in agreement with past studies (Fabre et al., 2012; Steppan
926 and Schenk, 2017; Abramson et al., 2021).

927   *Alexandromys* was used for holarctic grass voles for more than a century, but its
928 usage has waxed and waned (Kryštufek and Shenbrot, 2022). Voles that the Mammal
929 Diversity Database (2023) assign to *Alexandromys* have historically been placed in
930 *Microtus*, *Iberomys* (Gromov and Polyakov, 1977), *Neodon* (Musser and Carleton,
931 2005), and in various subgeneric groups within *Microtus* (Kryštufek and Shenbrot,
932 2022). Phylogenetic analyses, however indicate the validity of *Alexandromys* as a
933 genus separate from *Microtus*. Steppan and Schenk (2017) and Abramson et al., (2021)
934 found a monophyletic *Alexandromys* but Fabre et al. (2012) found the genus to be
935 paraphyletic with respect to *Volemys musseri*. All of our analyses used a robust
936 sampling within *Alexandromys* and all found a monophyletic genus that is closely
937 related to but outside of crown *Microtus* (see Figures 1-3). Given the aforementioned
938 issues with *Volemys* it is likely that *Alexandromys* is a monophyletic genus whose
939 recognition helps to make *Microtus* monophyletic.

940   Voles of the genus *Microtus* are frequently studied but have presented a long-
941 term systematic enigma (e.g., Conroy and Cook, 2000; Fabre et al. 2012; Abramson et
942 al., 2021). *Microtus* is one of the most rapidly evolving lineages of rodents and contains
943 over sixty extant species (Mammal Diversity Database, 2023). To attempt to clarify the
944 taxonomy of *Microtus*, researchers have used subgenera such as *Pedomys*,
945 *Alexandromys*, *Terricola*, *Iberomys*, *Agricola*, and *Neodon*, but these subgenera are
946 variably considered genera by different authors. Thus, the genus *Microtus* was in need
947 of being redefined (Barbosa et al., 2018; Abramson et al., 2021). Recent taxonomic
948 work concerning *Alexandromys*, *Neodon*, *Lasiopodomys*, *Stenocranius*, *Chionomys*,
949 *Proedromys*, and *Mictomicrotus* has helped to address this issue and our results (a
950 monophyletic *Microtus* in our nuclear only and combined analyses; see Figure 2-3)
951 further help to support those changes (Kryštufek and Shenbrot, 2022). This is a key
952 step to clarifying this complicated genus and getting closer to being able to have an
953 answer for 'What is *Microtus*?'

954

955 **Systematic Status of North American *Microtus***

956   The species of *Microtus* that are endemic to North America have in the past been
957 inferred as a clade (Conroy and Cook, 1999, 2000; Upham et al., 2019; Abramson et

958   al., 2021). Our mitochondrial only results conflict with that hypothesis (see species level
959   trees in Appendix D and G) in that North American *Microtus* is paraphyletic with respect
960   to *M. cabrerae* (a species endemic to the Iberian Penninsula), while our nuclear only
961   and combined analyses (see species level trees in Appendix E,H and F,I) found a
962   weakly-supported clade. The relationship between *M. cabrerae* and the North American
963   *Microtus* should be further examined using transcriptome and genomic data. Whether or
964   not North American *Microtus* is monophyletic has important implications for
965   paleobiogeography and our understanding of the fossil record in relation to North
966   American Land Mammal Ages (NALMAs), which is largely based on the immigration of
967   voles and other mammals into North America at various times during the Pliocene and
968   Pleistocene (Bell et al., 2004).
969
970   **Diversification of arvicolines**
971   Time-calibrated phylogenies rely on several important factors to assure their
972   accuracy and reproducibility. Node calibrations must leverage appropriate fossils to
973   avoid erroneous divergence times. As recommended by Parham et al. (2012), care
974   must be taken to insure that a fossil that is used for a calibration has (1) a museum
975   number, (2) a systematic position established with an apomorphy based diagnosis or
976   phylogenetic analysis, (3) reconciliation of morphological and molecular data with
977   respect to the fossil's position, (4) detailed locality and geological data, and (5)
978   reference to a published radiographic age. Following this protocol insures that a
979   calibration is as accurate as possible, given the understanding of the fossil record at the
980   time of the analysis. Studies have also demonstrated that secondary calibrations can
981   dramatically affect the age of a node (Schenk, 2016). Secondary calibrations can
982   certainly be used to help inform node calibrations, but we advise the use of primary
983   fossil calibrations, when possible. In our divergence-time analysis we chose to
984   implement a node-dating approach rather than tip-dating or the fossilized birth-death
985   model (FBD) (Heath et al., 2014), because there are currently so few phylogenetically
986   constrained arvicoline fossils. We acknowledge that the use of single fossils for node
987   age minima and maxima (node-dating) is potentially problematic (Heath et al. 2014). In
988   the future when there are more phylogenetically constrained fossils, we recommend a
989   reexamination of this issue using FBD methods.
990   We argue that one of the strengths of our paper is our justification of our fossil
991   calibrations following Parham et al. (2012). Our results are largely congruent with the
992   published fossil record and our divergence time estimates are younger (closer to the
993   known fossil record) than those produced by Steppan and Schenk (2017), Upham et al.
994   (2019), and Abramson et al. (2021). This is not surprising given the density of fossil
995   calibrations that we used across the arvicoline tree. We estimated a median age of
996   crown Arvicolinae at ~6.4 Ma, which is slightly younger than the age (7.4 Ma) inferred
997   by Abramson et al. (2021). These ages are very close to the age of the earliest known

998   possible arvicoline rodent fossils (~9-8 Ma, which are probably Pliocene in age (e.g.,
999   *Pannonicola, Microtoscoptes*, or *Goniodontomys*; Maul et al., 2017). Abramson et al.
1000 (2021) included a calibration at the crown Arvicolinae node (7 Ma FAD, 10 Ma max age)
1001 whereas we did not, potentially accounting for some discrepancy in our results. We did
1002 not use a calibration at the root of Arvicolinae because of the uncertain phylogenetic
1003 placement of putative early arvicoline fossils (Repenning, 1987; Fejfar et al., 2011).
1004 Thus we hypothesize an origin of arvicolines at 6.4 Ma, with dentally distinct arvicoline
1005 rodents evolving slightly later. For ages of major tribes and clades of arvicolines found
1006 in our study, see Table 1.
1007

Conclusions

1009   A consolidated understanding of the phylogeny of arvicoline rodents has been
1010 warranted given their remarkable evolutionary history and abundance across high
1011 latitudes. We provide phylogenetic support for systematic hypotheses across
1012 Arvicolinae and some direction for future systematic and taxonomic work. We show that
1013 the earliest diverging arvicolines likely includes the Tribes Prometheomyini, Ondatrini,
1014 Lemmini, Dicrostonychini, and Pliophenacomyini. *Prometheomys* is probably the sister
1015 taxon of all other arvicolines, but work still needs to be done to solidify that hypothesis.
1016 The monophyly of bog lemmings (*Synaptomys*) is doubted, however their close
1017 relationship to the "true lemmings" (*Myopus* and *Lemmus*) is clear. *Hyperacrius* and
1018 *Lemmiscus* need to be sampled using phylogenomic data to better clarify their
1019 systematic positon. Clethrionomyini is a valid Tribe consisting of *Caryomys*,
1020 *Eothenomys*, *Anteliomys*, *Craseomys*, *Alticola*, and *Clethrionomys*. The paraphyly of
1021 *Clethrionomys* relative to *Alticola* needs to be explored. Pliomyini, Ellobiusini, Lagurini,
1022 Arvicolini, and Microtini represent a clade that forms a large portion of the arvicoline
1023 tree. We found some evidence for a monophyletic endemic North American *Microtus*,
1024 however this was not found in all analyses, and could benefit from larger scale sampling
1025 across the genome. Finally, we estimated divergence times among the major clades,
1026 which were concordant with the published fossil record. This will provide valuable
1027 insight into the evolutionary and paleobiogeographical history of this clade. Overall our
1028 understanding of the evolutionary history of arvicolines is improving and this study is a
1029 step in the right direction for both taxonomic and systematic clarity for Arvicolinae.
1030

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1041

References

1043   Abramson, N.I., 1993. Evolutionary trends in the dentition of true lemmings (Lemmini,
1044   Cricetidae, Rodentia): functional-adaptive analysis. *Journal of Zoology*, *230*(4),
1045   687-699. https://doi.org/10.1111/j.1469-7998.1993.tb02717.x.
1046   Abramson, N.I., Golenishchev, F.N., Bodrov, S.Y., Bondareva, O.V., Genelt-Yanovskiy,
1047   E.A., Petrova, T. V., 2020. Phylogenetic relationships and taxonomic position of
1048   genus *Hyperacrius* (Rodentia: Arvicolinae) from Kashmir based on evidences
1049   from analysis of mitochondrial genome and study of skull morphology. PeerJ, 8,
1050   e10364. https://doi.org/10.7717/peerj.10364.
1051   Abramson, N.I., Bodrov, S.Y., Bondareva, O.V., Genelt-Yanovskiy, E.A., Petrova, T.V.,
1052   2021. A mitochondrial genome phylogeny of voles and lemmings (Rodentia:
1053   Arvicolinae): Evolutionary and taxonomic implications. PloS one, *16*(11),
1054   e0248198. https://doi.org/10.1371/journal.pone.0248198.
1055   Abramson, N., Petrova, T., Dokuchaev, N. 2022. Analysis of "historical" DNA of
1056   museum samples resolve taxonomic, nomenclature and biogeography issues:
1057   case study of true lemmings. Bio. Comm. 67(4): 340–348. https://doi.
1058   org/10.21638/spbu03.2022.408
1059   Ayres, D.L., Darling, A., Zwickl, D.J., Beerli, P., Holder, M.T., Lewis, P.O., Huelsenbeck,
1060   J.P., Ronquist, F., Swofford, D.L., Cummings, M.P., Rambaut, A., Suchard, M.A.,
1061   2012. BEAGLE: an application programming interface and high-performance
1062   computing library for statistical phylogenetics. Systematic biology, 61(1), 170-
1063   173. https://doi.org/10.1093/sysbio/syr100.
1064   Bannikova, A.A., Lebedev, V.S., Golenishchev, F.N., 2009. Taxonomic position of
1065   Afghan vole (Subgenus *Blanfordimys*) by the sequence of the mitochondrial cytb
1066   gene. Russian Journal of Genetics, 45(1), 91-97.
1067   https://doi.org/10.1134/S102279540901013X.
1068   Bannikova, A.A., Lebedev, V.S., Lissovsky, A.A., Matrosova, V., Abramson, N.I.,
1069   Obolenskaya, E.V., & Tesakov, A.S., 2010. Molecular phylogeny and evolution of
1070   the Asian lineage of vole genus *Microtus* (Rodentia: Arvicolinae) inferred from
1071   mitochondrial cytochrome b sequence. Biological Journal of the Linnean Society,
1072   99(3), 595-613. https://doi.org/10.1111/j.1095-8312.2009.01378.x.
1073   Barbosa, S., Paupério, J., Pavlova, S.V., Alves, P.C., Searle, J.B., 2018. The *Microtus*
1074   voles: Resolving the phylogeny of one of the most speciose mammalian genera
1075   using genomics. Molecular phylogenetics and evolution, 125, 85-92.
1076   https://doi.org/10.1016/j.ympev.2018.03.017.

1077   Bell, C.J., Bever, G.S., 2006. Description and significance of the *Microtus* (Rodentia:
1078   Arvicolinae) from the type Irvington fauna, Alameda County, California. Journal of
1079   Vertebrate Paleontology, 26(2), 371-380. https://doi.org/10.1671/0272-
1080   4634(2006)26[371:DASOTM]2.0.CO;2.
1081   Bell, C.J., Lundelius, E.L., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez, D.R.,
1082   Semken, H.A., Webb, S.D., Zakrzewski, R.J., 2004. 7. The Blancan, Irvingtonian,
1083   and Rancholabrean Mammal Ages. In Late Cretaceous and Cenozoic Mammals
1084   of North America (pp. 232-314). Columbia University Press.
1085   Bodrov S.Yu., Kostygov A.Yu., Rudneva L.V., Abramson N.I. 2016. Revision of the
1086   taxonomic position of the Olkhon mountain vole (Rodentia, Cricetidae). Biol. Bull.
1087   43:136–145.
1088   Bondareva, O.V., Mahmoudi, A., Bodrov, S.Y., Genelt-Yanovskiy, E.A., Petrova, T.V.,
1089   Abramson, N.I., 2020. The complete mitochondrial genomes of three *Ellobius*
1090   mole vole species (Rodentia: Arvicolinae). Mitochondrial DNA Part B, 5(3), 2485-
1091   2487. https://doi.org/10.1080/23802359.2020.1778567.
1092   Bondareva, O.V., Genelt-Yanovskiy, E., Petrova, T., Bodrov, S., Smorkatcheva, A.,
1093   Abramson, N., 2021a. Signatures of Adaptation in Mitochondrial Genomes of
1094   Palearctic Subterranean Voles (Arvicolinae, Rodentia). Genes, 12(12), 1945.
1095   https://doi.org/10.1371/journal.pone.0248198.
1096   Bondareva,O.V., Potapova, N.A., Konovalov, K.A., Petrova, T.V., Abramson, N.I.
1097   2021b. Searching for signatures of positive selection in cytochrome b gene
1098   associated with subterranean lifestyle in fast-evolving arvicolines (Arvicolinae,
1099   Cricetidae, Rodentia). BMC Ecology and Evolution. 21(92). doi: 10.1186/s12862-
1100   021-01819-4.
1101   Borodin, A.V., 2012. Voles (Arvicolinae, Rodentia) of Urals and Western Siberia
1102   (Eopleistocene-Recent). Abridged thesis. Canadian Science Institute of Ecology
1103   of Plants and Animals. Uralian Branch of the Russian Academy of Science.
1104   Ekaterinburg. [In Russian].
1105   Borowik, O.A., Engstrom, M.D., 1993. Chromosomal evolution and biogeography of
1106   collared lemmings (*Dicrostonyx*) in the eastern and High Arctic of
1107   Canada. Canadian journal of zoology, 71(8), 1481-1493.
1108   https://doi.org/10.1139/z93-209.
1109   Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and
1110   BIC in model selection. Sociological methods & research, 33(2), 261-304.
1111   https://doi.org/10.1177%2F0049124104268644.
1112   Buzan, E. V., Krystufek, B., Hänfling, B., Hutchinson, W.F., 2008. Mitochondrial
1113   phylogeny of Arvicolinae using comprehensive taxonomic sampling yields new
1114   insights. Biological Journal of the Linnean Society, 94(4), 825-835.
1115   https://doi.org/10.1111/j.1095-8312.2008.01024.

1116   Carleton, M.D., 1981. A survey of gross stomach morphology in Microtinae (Rodentia:
1117   Muroidea).
1118   Carroll, L.E., Genoways, H.H., 1980. *Lagurus curtatus*. Mammalian Species, 124, 1–6.
1119   https://doi.org/10.2307/3503931.
1120   Carter, L. D., Brigham-Grette, J., Marincovich Jr, L., Pease, V.L., Hillhouse, J.W., 1986.
1121   Late Cenozoic Arctic Ocean sea ice and terrestrial paleoclimate. Geology, 14(8),
1122   675-678. https://doi.org/10.1130/0091-
1123   7613(1986)14%3C675:LCAOSI%3E2.0.CO;2.
1124   Chaline, J., 1972. Les rongeurs du Pléistocène moyen et supérieur de France. –
1125   Cahiers de Paléontologie du CNRS, Paris. 410 pp.
1126   Chaline, J., 1975. Taxonomie des Campagnols (Arvicolidae, Rodentia) de la sous-
1127   famille des Dolomyinae nov. dans l'hemisphere nord: Acad. Sci., Paris. Compt.
1128   Rend., Ser. D, 281, 33.
1129   Chaline, J., 1987. Arvicolid data (Arvicolidae, Rodentia) and evolutionary concepts. In
1130   Evolutionary biology (pp. 237-310). Springer, Boston, MA.
1131   Chaline, J., Graf, J.D., 1988. Phylogeny of the Arvicolidae (Rodentia): biochemical and
1132   paleontological evidence. *Journal of Mammalogy*, *69*(1), 22-33.
1133   https://doi.org/10.2307/1381744.
1134   Chaline, J., Mein, P., 1979. Les rongeurs et l'évolution.
1135   Chaline, J., Brunet-Lecomte, P., Brochet, G., Martin, F., 1989. Les lemmings fossiles du
1136   genre Lemmus (Arvicolidae, Rodentia) dans le Pléistocène de France. Geobios,
1137   22(5), 613-623. https://doi.org/10.1016/S0016-6995(89)80115-9.
1138   Chen, W.C., Hao, H.B., Sun, Z.Y., Liu, Y., Liu, S.Y., Yue, B.S., 2012. Phylogenetic
1139   position of the genus *Proedromys* (Arvicolinae, Rodentia): Evidence from nuclear
1140   and mitochondrial DNA. Biochemical Systematics and Ecology, 42, 59-68.
1141   https://doi.org/10.1016/j.bse.2012.01.002.
1142   Conroy, C.J., Cook, J.A., 1999. MtDNA evidence for repeated pulses of speciation
1143   within arvicoline and murid rodents. Journal of Mammalian Evolution, *6*(3), 221-
1144   245. https://link.springer.com/article/10.1023/A:1020561623890.
1145   Conroy, C.J., Cook, J.A., 2000. Molecular systematics of a Holarctic rodent (*Microtus*:
1146   Muridae). Journal of Mammalogy, 81(2), 344-359. https://doi.org/10.1644/1545-
1147   1542(2000)081<0344:MSOAHR>2.0.CO;2.
1148   Corbet, G.B., 1978. The mammals of the Palaearctic region: A taxonomic review.
1149   Cornell University press.
1150   Cuenca Bescós, G., López-García, J.M., Galindo-Pellicena, M.A., García-Perea, R.,
1151   Gisbert, J., Rofes, J., Ventura, J., 2014. The Pleistocene history of *Iberomys*, an
1152   endangered endemic rodent from South Western Europe. Int. Zool. 9:481–497.
1153   D'Elía, G., Fabre, P.H., Lessa, E.P., 2019. Rodent systematics in an age of discovery:
1154   recent advances and prospects. Journal of Mammalogy, 100(3), 852-871.
1155   https://doi.org/10.1093/jmammal/gyy179.

1156 Eger, J.L., 1995. Morphometric variation in the Nearctic collared lemming
1157   (*Dicrostonyx*). Journal of Zoology, 235(1), 143-161.
1158   https://doi.org/10.1111/j.1469-7998.1995.tb05134.x.
1159 Ellerman, J.R., Morrison-Scott, R.C.S., 1951. Checklist of Palearctic and Indian
1160   Mammals. British Museum of Natural History), London.
1161 Fabre, P.H., Hautier, L., Dimitrov, D., Douzery, E.J.P., 2012. A glimpse on the pattern of
1162   rodent diversification: a phylogenetic approach. BMC Evolutionary Biology, 12(1),
1163   1-19. https://bmcecolevol.biomedcentral.com/articles/10.1186/1471-2148-12-88.
1164 Fedorov, V.B., Fredga, K., Jarrell, G.H. 1999. Mitochondrial DNA variation and the
1165   evolutionary history of chromosome races of collared lemmings (Dicrostonyx) in
1166   the Eurasian Arctic. Journal of Evolutionary Biology, 12(1), pp.134-145.
1167 Fejfar, O., Repenning, C.A., 1998. The ancestors of the lemmings (Lemmini,
1168   Arvicolinae, Cricetidae, Rodentia) in the early Pliocene of Wölfersheim near
1169   Frankfurt am Main; Germany. Senckenbergiana lethaea, 77(1), 161-193.
1170   https://doi.org/10.1007/BF03043739.
1171 Fejfar, O., Heinrich, W.D., Kordos, L., Maul, L.C., 2011. Microtoid cricetids and the early
1172   history of arvicolids (Mammalia, Rodentia). Palaeontologia Electronica, 14(3), 1-
1173   38.
1174 Fink S., Fischer M.C., Excoffier L., Heckel G., 2010. Genomic scans support repetitive
1175   continental colonization events during the rapid radiation of voles (Rodentia:
1176   Microtus). Syst. Biol. 59:548–572.
1177 Galewski, T, Tilak, M.K., Sanchez, S., Chevret, P., Paradis, E., Douzery, E.J., 2006.
1178   The evolutionary radiation of Arvicolinae rodents (voles and lemmings): relative
1179   contribution of nuclear and mitochondrial DNA phylogenies. BMC Evolutionary
1180   Biology, 6(1), 1-17. https://link.springer.com/article/10.1186/1471-2148-6-80.
1181 Golenishchev, F., Malikov, V., Petrova, T., Bodrov, S., Abramson, N. 2019. Toward
1182   assembling a taxonomic puzzle: Case study of Iranian gray voles of the
1183   subgenus *Microtus* (Rodentia, Cricetidae). Mamm. Bio. 94:98–105.
1184 Gromov, I.M., Polyakov, I.Y., 1977. Fauna SSSR: Mammals. Voles (Microtinae)
1185   Leningrad: Nauka. [In Russian]; 1977.
1186 Gromov, I.M., Polyakov, I.Y., 1992. *Voles (microtinae)*. Fauna of the USSR. Mammals.
1187   Vol. 3, No. 8.
1188 Gunnell, G.F., Boyer, D.M., Friscia, A.R., Heritage, S., Manthi, F.K., Miller, E.R., Sallam,
1189   H.M., Simmons, N.B., Stevens, N.J., Seiffert, E.R., 2018. Fossil lemurs from
1190   Egypt and Kenya suggest an African origin for Madagascar's aye-aye. Nature
1191   communications, 9(1), p.3193.
1192 Guthrie, R.D., Matthews, J.V., 1971. The Cape Deceit fauna—early Pleistocene
1193   mammalian assemblage from the Alaskan Arctic. Quaternary Research, 1(4),
1194   474-510. https://doi.org/10.1016/0033-5894(71)90060-3.

1195 Hall, E.R., 1981. The mammals of North America. Second ed. John Wiley and Sons,
1196   New York, 1:1-600 + 90, 2: 601-1181 + 90.

1197 Haring, E., Voyta, L.L., Däubl, B., Tiunov, M.P., 2015. Comparison of genetic and
1198   morphological characters in fossil teeth of grey voles from the Russian Far East
1199   (Rodentia: Cricetidae: Alexandromys). Mammalian Biology, 80, 496-504.

1200 Hart, W.K., Brueseke, M.E., 1999. Analysis and dating of volcanic horizons from
1201   Hagerman Fossil Beds National Monument and a revised interpretation of
1202   eastern Glenns Ferry Formation chronostratigraphy. National Park Service
1203   Report, 1443, 1-37.

1204 Heath, T.A., Huelsenbeck, J.P., Stadler, T., 2014. The fossilized birth–death process for
1205   coherent calibration of divergence-time estimates. Proceedings of the National
1206   Academy of Sciences, 111(29), E2957-E2966.
1207   https://doi.org/10.1073/pnas.1319091111.

1208 Hibbard, C.W., 1959. Late Cenozoic microtine rodents from Wyoming and Idaho.
1209   University of Michigan Press.

1210 Hinton, M.A.C., 1926. Monograph of the voles and lemmings (Microtinae) living and
1211   extinct. Brit. Mus. Nat. Hist., (London).

1212 İbiş, O., Selçuk, A.Y., Sacks, B.N., Yıldız, B., Özcan, S., Kefelioğlu, H., Tez, C., 2020.
1213   Whole mitochondrial genome of long-clawed mole vole (*Prometheomys*
1214   *schaposchnikowi*) from Turkey, with its phylogenetic relationships. Genomics,
1215   112(5), 3247-3255. https://doi.org/10.1016/j.ygeno.2020.06.008.

1216 Jaarola, M., Martínková, N., Gündüz, İ., Brunhoff, C., Zima, J., Nadachowski, A., Amori,
1217   G., Bulatova, N.S., Chondropoulos, B., Fraguedakis-Tsolis, S., González-
1218   Esteban, J., López-Fuster, M.J., Kandaurov, A.S., Kefelioglu, H., da Luz Mathias,
1219   M, Villate, I., Searle, J.B., 2004. Molecular phylogeny of the speciose vole genus
1220   *Microtus* (Arvicolinae, Rodentia) inferred from mitochondrial DNA sequences.
1221   Molecular Phylogenetics and evolution, 33(3), 647-663.
1222   https://doi.org/10.1016/j.ympev.2004.07.015.

1223 Jaeger, J.J. 1988. Origine et evolution du genre *Ellobius* (Mammalia, Rodentia) en
1224   Afrique Nord- Occidentale. Folia Quaternaria 57:3-50.

1225 Jarrell, G.H., Fredga, K.A.R.L. 1993. How many kinds of lemmings? A taxonomic
1226   overview. The biology of lemmings, 45-57.

1227 Katoh, K., Standley, D.M. 2013. MAFFT multiple sequence alignment software version
1228   7: improvements in performance and usability. Molecular biology and evolution,
1229   30(4), 772-780. https://doi.org/10.1093/molbev/mst010.

1230 Kelly, T.S., Whistler, D.P. 2014. New late Miocene (latest Clarendonian) to early
1231   Hemphillian cricetid rodents from the upper part of the Dove Spring Formation,
1232   Mojave Desert, California. Paludicola, 10, 1-48.

1233 Kretzoi, M., 1969. Sketch of the Late Cenozoic (Pliocene and Quaternary) terrestrial
1234   stratigraphy of Hungary. Földrajzi Közlemények, 93, 179-204.

1235 Kryštufek, B., Tesakov, A.S., Lebedev, V.S., Bannikova, A.A., Abramson, N.I.,
1236   Shenbrot, G., 2020. Back to the future: the proper name for red-backed voles is
1237   *Clethrionomys* Tilesius and not *Myodes* Pallas. Mammalia, 84(2), 214-217.
1238   https://doi.org/10.1515/mammalia-2019-0067.
1239 Kryštufek, B., Shenbrot, G., 2022. *Voles and lemmings (Arvicolinae) of the palaearctic*
1240   *region* (p. 449). University of Maribor, University Press.
1241 Kohli, B.A., Speer, K.A., Kilpatrick, C.W., Batsaikhan, N., Damdinbaza, D., Cook, J.A.,
1242   2014. Multilocus systematics and non-punctuated evolution of Holarctic Myodini
1243   (Rodentia: Arvicolinae). Molecular Phylogenetics and Evolution, 76, 18-29.
1244   https://doi.org/10.1016/j.ympev.2014.02.019.
1245 Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2017. PartitionFinder
1246   2: new methods for selecting partitioned models of evolution for molecular and
1247   morphological phylogenetic analyses. Molecular biology and evolution, 34(3),
1248   772-773. https://doi.org/10.1093/molbev/msw260.
1249 Larsson, A., 2014. AliView: a fast and lightweight alignment viewer and editor for large
1250   datasets. Bioinformatics, 30(22), 3276-3278.
1251   https://doi.org/10.1093/bioinformatics/btu531.
1252 Lawrence, M.A. 1982. Western Chinese arvicolines (Rodentia) collected by the Sage
1253   Expedition. American Museum Novitates; no. 2745.
1254   http://hdl.handle.net/2246/5289.
1255 Lebedev, V.S., Bannikova, A.A., Tesakov, A.S., Abramson, N.I., 2007. Molecular
1256   phylogeny of the genus *Alticola* (Cricetidae, Rodentia) as inferred from the
1257   sequence of the cytochrome b gene. Zoologica Scripta, 36(6), 547-563.
1258   https://doi.org/10.1111/j.1463-6409.2007.00300.x.
1259 Lissovsky, A.A., Petrova, T.V., Yatsentyuk, S.P., Golenishchev, F.N., Putincev, N.I.,
1260   Kartavtseva, I.V., Sheremetyeva, I.N. and Abramson, N.I., 2018. Multilocus
1261   phylogeny and taxonomy of East Asian voles Alexandromys (Rodentia,
1262   Arvicolinae). Zoologica Scripta, 47(1), pp.9-20.
1263 Liu, S., Sun, Z., Zeng, Z. and Zhao, E., 2007. A new vole (Cricetidae: Arvicolinae:
1264   proedromys) from the Liangshan Mountains of Sichuan province, China. Journal
1265   of Mammalogy, 88(5), pp.1170-1178.
1266 Liu, S., Liu, Y., Guo, P., Sun, Z., Murphy, R.W., Fan, Z., Fu, J., Zhang, Y., 2012.
1267   Phylogeny of oriental voles (Rodentia: Muridae: Arvicolinae): molecular and
1268   morphological evidence. Zoological Science, 29(9), 610-622.
1269   https://doi.org/10.2108/zsj.29.610.
1270 Liu, S., Jin, W., Liu, Y., Murphy, R.W., Lv, B., Hao, H., Liao, R., Sun, Z., Tang, M.,
1271   Chen, W., Fu, J., 2017. Taxonomic position of Chinese voles of the tribe
1272   Arvicolini and the description of 2 new species from Xizang, China. Journal of
1273   Mammalogy, 98(1), 166-182. https://doi.org/10.1093/jmammal/gyw170.

1274   Luo, J., Yang, D., Suzuki, H., Wang, Y., Chen, W.J., Campbell, K.L., Zhang, Y.P., 2004.
1275   Molecular phylogeny and biogeography of Oriental voles: genus *Eothenomys*
1276   (Muridae, Mammalia). Molecular Phylogenetics and Evolution, 33(2), 349-362.
1277   https://doi.org/10.1016/j.ympev.2004.06.005.
1278   Lytchev, G.F., Savinov, P.F., 1974. Late Pliocene lagomorphs and rodents from Kiikbai.
1279   Materialy po Istorii i Faune Kazakhstana, 6, 39-57.
1280   Mahmoudi A., Darvish J., Aliabadian M., Moghaddam F.Y., Kryštufek B. 2017. New
1281   insight into the cradle of the grey voles (subgenus *Microtus*) inferred from
1282   mitochondrial cytochrome b sequences. Mammalia, 81:583–593.
1283   Mahmoudi, A., Maul, L.C., Khoshyar, M., Darvish, J., Aliabadian, M., Kryštufek, B.,
1284   2020. Evolutionary history of water voles revisited: confronting a new
1285   phylogenetic model from molecular data with the fossil record. Mammalia, 84(2),
1286   171-184. https://doi.org/10.1515/mammalia-2018-0178.
1287   Mammal Diversity Database., 2023. Mammal Diversity Database (Version 1.11) [Data
1288   set]. Zenodo. https://doi.org/10.5281/zenodo.7830771
1289   Martin, R.A., 1974. Fossil mammals from the Coleman IIA Fauna, Sumter County. Pp.
1290   35-99, in Pleistocene mammals of Florida (S.D. Webb, ed.). The University
1291   Presses of Florida, Gainesville, 270 pp.
1292   Martin, R.A., 1996. Dental evolution and size change in the North American muskrat:
1293   Classification and tempo of a presumed phyletic sequence. In Palaeoecology
1294   and Palaeoenvironments of Late Cenozoic Mammals: Tributes to the Career of
1295   C.S. (Rufus) Churcher (pp. 431-457). Toronto: University of Toronto Press.
1296   https://doi.org/10.3138/9781487574154-022.
1297   Martin, R.A., Tesakov, A., 1998. Introductory remarks: does *Allophaiomys* exist.
1298   Paludicola, 2(1), 1-7.
1299   Martin, R.A., Zakrzewski, R.J. 2019. On the ancestry of woodrats. Journal of
1300   Mammalogy, 100(5), pp.1564-1582.
1301   Martínková, N., Moravec, J., 2012. Multilocus phylogeny of arvicoline voles (Arvicolini,
1302   Rodentia) shows small tree terrace size. Folia Zoologica, 61(3–4), 254-267.
1303   https://doi.org/10.25225/fozo.v61.i3.a10.2012.
1304   Maul, L.C., Rekovets, L.I., Heinrich, W.D., Bruch, A.A., 2017. Comments on the age and
1305   dispersal of Microtoscoptini (Rodentia: Cricetidae). Fossil Imprint, 73(3-4), 495-
1306   514.
1307   McDonald, H.G., Link, P.K., Lee, D.E., 1996. An overview of the geology and
1308   paleontology of the Pliocene Glenns Ferry Formation, Hagerman Fossil Beds
1309   National Monument. Northwest Geology, 26, 16-45.
1310   McKenna, M.C., Bell, S.K., 1997. *Classification of mammals: above the species level*.
1311   Columbia University Press.
1312   Mezhzherin, S.V., Zykov, A.E., Morozov-Leonov, S.Y.u., 1993. Biochemical variation
1313   and genetic divergence in Palearctic voles (Arvicolidae): meadow voles *Microtus*

1314   Schrank 1798, snow voles *Chionomys* Miller 1908, water voles *Arvicola*
1315   Lacepede 1799. Genetika 29, 28–41 (in Russian with English summary).
1316 Mezhzherin, S.V., Morozov-Leonov, S.Yu., Kuznetsova, I.A., 1995. Biochemical
1317   variation and genetic divergence in Palearctic voles (Arvicolidae): subgenus
1318   *Terricola*, true lemmings *Lemmus* Link 1795, pied lemmings *Dicrostonyx* Gloger
1319   1841, steppe lemmings *Lagurus* Gloger 1842, mole voles *Ellobius* Fischer von
1320   Waldheim 1814. Genetika 31, 788–797 (in Russian with English summary).
1321 Miller, G.S., 1896. *Genera and subgenera of voles and lemmings* (No. 12). US
1322   Government Printing Office.
1323 Miller, G.S., 1912. Catalogue of the mammals of Western Europe (Europe exclusive of
1324   Russia) in the collection of the British Museum. British Museum (Natural History),
1325   London, 1019. Pp.
1326 Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for
1327   inference of large phylogenetic trees. In 2010 gateway computing environments
1328   workshop (GCE) (pp. 1-8). Ieee. https://doi.org/10.1109/GCE.2010.5676129.
1329 Modi, W.S., 1987. Phylogenetic analyses of chromosomal banding patterns among the
1330   nearctic Arvicolidae (Mammalia: Rodentia). Systematic Zoology, 36(2), 109–136.
1331   https://doi.org/10.2307/2413264.
1332 Modi W.S., 1996. Phylogenetic history of LINE-1 among arvicolid rodents. Molecular
1333   Biology and Evolution, 13(5), 633–641.
1334   https://doi.org/10.1093/oxfordjournals.molbev.a025623.
1335 Murray, L.K., Ruez Jr, D.R., Bell, C.J., 2011. New perspectives on lagomorph and
1336   rodent biochronology in the Anza-Borrego Desert of southern California, USA.
1337   Palaeontologia Electronica, 14(3), 36A.
1338 Musser, G.G., Carleton, M.D., 1993. Family Muridae. In: Wilson, D.E. and Reeder,
1339   D.M., Eds., Mammals Species of the World: A Taxonomic and Geographic
1340   Reference, Smithsonian University Press, Washington DC, 1206.
1341 Musser, G.G., Carleton, M.D., 2005. Superfamily Muroidea. In: Wilson, D.E. and
1342   Reeder, D.M., Eds., Mammal Species of the World: A Taxonomic and
1343   Geographic Reference, The Johns Hopkins University Press, Baltimore, 2142.
1344 NCBI Resource Coordinators (2016). Database resources of the National Center for
1345   Biotechnology Information. Nucleic acids research, 44(D1), D7–D19.
1346   https://doi.org/10.1093/nar/gkv1290.
1347 Pardiñas U.F.J., Myers P., Léon-Paniagua L., Ordóñez Garza N., Cook J.A., Kryštufek
1348   B., Haslauer R., Bradley R.D., Shenbrot G.I., Patton J.L., 2017. Family Cricetidae
1349   (True hamsters, voles, lemmings and New World rats and mice). In: Wilson D.E.,
1350   Lacher T.E. & Mittermeier R.A. (Eds.), Handbook of the Mammals of the World.
1351   Vol. 7. Rodents II. Lynx Edicionas, Barcelona, pp. 204–535.
1352 Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A.,
1353   Inoue, J.G., Irmis, R.B., Joyce, J.E., Ksepka, D.T., Patané, J.S.L., Smith, N.D.,

1354   Tarver, J.E., van Tuinen, M., Yang, Z., Angielczyk, K.D., Greenwood, J.M.,
1355   Hipsley, C.A., Jacobs, L., Makovicky, P.J., Müller, J., Smith, K.T., Theodor, J.M.,
1356   Warnock, R.C.M., Benton, M.J., 2012. Best practices for justifying fossil
1357   calibrations. Systematic Biology, 61(2), 346-359.
1358   https://doi.org/10.1093/sysbio/syr107.
1359 Pavlinov, I.Y., Rossolimo, O.L., 1998. Systematics of mammals of USSR: supplements.
1360   The study of fauna). MGU, Moscow.
1361 Pavlinov, I.Ya., Yakhontov, E.L., Agadzhanyan, A.K., 1995. [Mammals of Eurasia. I.
1362   Rodentia. Taxonomic and geographic guide.] Archives of the Zoological
1363   Museum, Moscow State University, 32:289 pp. (In Russian).
1364 Pradhan, N., Sharma, A.N., Sherchan, A.M., Chhetri, S., Shrestha, P., Kilpatrick, C.W.,
1365   2019. Further assessment of the Genus *Neodon* and the description of a new
1366   species from Nepal. PloS one, 14(7), e0219157.
1367   https://doi.org/10.1371/journal.pone.0219157.
1368 Petrova, T.V., Zakharov, E.S., Samiya, R., Abramson, N.I., 2015. Phylogeography of
1369   the narrow-headed vole *Lasiopodomys* (*Stenocranius*) *gregalis* (Cricetidae,
1370   Rodentia) inferred from mitochondrial cytochrome b sequences: an echo of
1371   Pleistocene prosperity. Journal of Zoological Systematics and Evolutionary
1372   Research, 53(2), 97-108. https://doi.org/10.1111/jzs.12082.
1373 Petrova T.V., Tesakov A.S., Kowalskaya Y.M. & Abramson N.I., 2016. Cryptic
1374   speciation in the narrow-headed vole, *Lasiopodomys* (*Stenocranius*) *gregalis*,
1375   (Rodentia: Cricetidae). Zool. Scr. 45:618–629.
1376 Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior
1377   summarization in Bayesian phylogenetics using Tracer 1.7. Systematic biology,
1378   67(5), 901-904. https://doi.org/10.1093/sysbio/syy032.
1379 Repenning, C.A., 1987. Biochronology of the microtine rodents of the United States, in,
1380   Woodburne, MO, ed., Cenozoic mammals of north America: Geochronology and
1381   biostratigraphy: Berkeley and Los Angeles.
1382 Repenning, C.A., 1992. *Allophaiomys* and the age of the Olyor Suite, Krestovka
1383   sections, Yakutia (No. 2035-2037). US Government Printing Office.
1384 Repenning, C.A., Grady, F., 1988. The microtine rodents of the Cheetah Room fauna,
1385   Hamilton Cave, West Virginia, and the spontaneous origin of *Synaptomys* (No.
1386   1853). USGPO, https://pubs.er.usgs.gov/publication/b1853.
1387 Repenning, C.A., Brouwers, E.M., 1992. Late Pliocene-early Pleistocene ecologic
1388   changes in the Arctic Ocean borderland. Washington, DC: US Government
1389   Printing Office.
1390 Repenning, C.A., Brouwers, E.M., Carter, L.D., Marincovich Jr, L., Ager, T.A., 1987. The
1391   Beringian ancestry of *Phenacomys* (Rodentia: Cricetidae) and the beginning of
1392   the modern Arctic Ocean borderland biota (p. 31). Department of the Interior, US
1393   Geological Survey.

1394 Repenning, C.A., Fejfar, O., Heinrich, W-D., 1990. Arvicolid rodent biochronology of the
1395   Northern Hemisphere. In: Fejfar, O., and Heinrich, W-D. (eds.): International
1396   Symposium: Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia,
1397   Mammalia). 385-418.
1398 Robovský, J., Řlčánková, V., Zrzavý, J., 2008. Phylogeny of Arvicolinae (Mammalia,
1399   Cricetidae): utility of morphological and molecular data sets in a recently radiating
1400   clade. Zoologica Scripta, 37(6), 571-590. https://doi.org/10.1111/j.1463-
1401   6409.2008.00342.x.
1402 Rogers, K.L., Larson, E.E., Smith, G., Katzman, D., Smith, G.R., Cerling, T., Wang, Y.,
1403   Baker, R.G., Lohmann, K.C., Repenning, C.A., Patterson, P., Mackie, G., 1992.
1404   Pliocene and Pleistocene geologic and climatic evolution in the San Luis Valley
1405   of south-central Colorado. Palaeogeography, Palaeoclimatology, Palaeoecology,
1406   94(1-4), 55-86. https://doi.org/10.1016/0031-0182(92)90113-J.
1407 Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S.,
1408   Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2:
1409   efficient Bayesian phylogenetic inference and model choice across a large model
1410   space. Systematic Biology, 61(3), 539-542.
1411   https://doi.org/10.1093/sysbio/sys029.
1412 Ruez Jr, D.R., Gensler, P.A., 2008. An unexpected early record of *Mictomys vetus*
1413   (Arvicolinae, Rodentia) from the Blancan (Pliocene) Glenns Ferry Formation,
1414   Hagerman Fossil Beds National Monument, Idaho. Journal of Paleontology,
1415   82(3), 638-642. https://doi.org/10.1666/06-098.1.
1416 Schenk, J.J., 2016. Consequences of secondary calibrations on divergence time
1417   estimates. PLoS ONE, 11(1), 1-17. https://doi.org/10.1371/journal.pone.0148228.
1418 Shenbrot, G.I., Krasnov, B.R., 2005. Atlas of the geographic distribution of the arvicoline
1419   rodents of the world (Rodentia, Muridae: Arvicolinae). Pensoft Publishing.
1420 Sher, A.V., Kaplina, T.N., Giterman, R.E., Lozhkin, A.V., Arkhangelov, A.A., Kiselyov,
1421   S.V., Kouznetsov, YuV., Virina, E.I., Zazhigin, V.S., 1979. Late Cenozoic of the
1422   Kolyma Lowland, Excursion Tour XI Guide-Book. In XIV Pacific Science
1423   Congress, USSR, Khabarovsk August 1979. USSR Academy of Sciences,
1424   Moscow.
1425 Smirnov, N.G., Bolshakov, V.N., Borodin, A.V., 1986. Pleistocene rodents of the North
1426   of Western Siberia. In Acad. Sci. USSR, Ural Sci. Centr (pp. 1-118). Moskva:
1427   Nauka.
1428 Sotnikova, M.V., Dodonov, A.E., Pen'Kov, A.V., 1997. Upper Cenozoic biomagnetic
1429   stratigraphy of Central Asian mammalian localities. Palaeogeography,
1430   Palaeoclimatology, Palaeoecology, 133(3-4), 243-258.
1431   https://doi.org/10.1016/S0031-0182(97)00078-3.

1432 Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-
1433   analysis of large phylogenies. Bioinformatics, 30(9), 1312-1313.
1434   https://doi.org/10.1093/bioinformatics/btu033.
1435 Stein, B.R., 1987. Phylogenetic relationships among four arvicolid genera. Zeitschrift für
1436   Säugetierkunde, 52(3), 140-156.
1437 Steppan, S.J., Schenk, J.J., 2017. Muroid rodent phylogenetics: 900-species tree
1438   reveals increasing diversification rates. PloS one, 12(8), e0183070.
1439   https://doi.org/10.1371/journal.pone.0183070.
1440 Suzuki, H., Iwasa, M., Harada, M., Wakana, S., Sakaizumi, M., Han, S.-H., Kitahara, E.,
1441   Kimura, Y., Kartavtseva, I., Tsuchiya, K., 1999. Molecular phylogeny of red-
1442   backed voles in far east Asia based on variation in ribosomal and mitochondrial
1443   DNA. Journal of Mammalogy, 80(2), 512–521. https://doi.org/10.2307/1383297.
1444 Tang, M.K., Jin, W., Tang, Y., Yan, C.C., Murphy, R.W., Sun, Z.Y., Zhang, X.Y., Zeng,
1445   T., Liao, R., Hou, Q.F. and Yue, B.S., 2018. Reassessment of the taxonomic
1446   status of Craseomys and three controversial species of Myodes and Alticola
1447   (Rodentia: Arvicolinae). Zootaxa, 4429(1), pp.1-52.
1448 Tesakov, A.S., 2004. Biostratigraphy of middle Pliocene-Pleistocene of Eastern Europe
1449   (based on small mammals). Transactions of the Geological Institute, Vol. 554,
1450   Nauka Moskow, 247 pp.
1451 Tesakov A.S., 2008. Early Pleistocene mammalian fauna of Sarkel (Lower Don River
1452   area, Russia): mole voles (Ellobiusini, Rodentia). Russian Journal of Theriology.
1453   Vol.7. No.2. P.81–88.
1454 Tesakov, A.S., 2016. Early Middle Pleistocene *Ellobius* (Rodentia, Cricetidae,
1455   Arvicolinae) from Armenia. Russian Journal of Theriology, 15(2), 151-158.
1456 Thanou, E., Paragamian, K., Lymberakis, P. 2020. Social but lonely: Species
1457   delimitation of social voles and the evolutionary history of the only *Microtus*
1458   species living in Africa. J. Zool. Syst. Evol. Res. 58:475–498.
1459 Tougard, C., Montuire, S., Volobouev, V.Y., Markova, E., Contet, J., Aniskin, V., Quere,
1460   J-P. 2013. Exploring phylogeography and species limits in the Altai vole
1461   (Rodentia: Cricetidae). Biol. J. Linn. Soc. 108:434–452.
1462 Triant, D.A., DeWoody, J.A., 2006. Accelerated molecular evolution in *Microtus*
1463   (Rodentia) as assessed via complete mitochondrial genome sequences.
1464   Genetica, 128(1), 95-108. https://doi.org/10.1007/s10709-005-5538-6.
1465 Upham, N.S., Esselstyn, J.A., Jetz, W. 2019. Infering the mammal tree: Species-level
1466   sets of phylogenies for questions in ecology, evolution, and conservation. PLOS
1467   Biology, 17(2): e3000494.
1468 van Kolfschoten, T., Tesakov, A.S., Bell, C.J., 2018. The first record of *Phenacomys*
1469   (Mammalia, Rodentia, Cricetidae) in Europe (Early Pleistocene, Zuurland, The
1470   Netherlands). Quaternary Science Reviews, 192, 274-281.
1471   https://doi.org/10.1016/j.quascirev.2018.06.005.

von Koenigswald, W., 1980. Schmelzmuster und Morphologie in den Molaren der Arvicolidae (Rodentia). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 539:1-129.

von Koenigswald, W.V., Martin, L.D. 1984. Revision of the fossil and recent Lemminae (Rodentia, Mammalia). Papers in Vertebrate Paleontology Honoring Robert Warren Wilson. Carnegie Museum of Natural History Special Publication, 9, 122-137.

Whistler, D.P., Tedford, R.H., Takeuchi, G.T., Wang, X., Tseng, Z.J., Perkins, M.E. 2009. Revised Miocene biostratigraphy and biochronology of the Dove Spring Formation, Mojave Desert, California: Museum of Northern Arizona Bulletin. *Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne*, *65*, 331-362.

Wilson, D.E., Lacher, T.E., Jr., Millermeier, R.A. eds. 2017. Handbook of the Mammals of the World. Vol 7. Rodents II. Lynx Edicions, Barcelona.

Withnell, C.B., 2020. A new perspective on the systematics and paleobiogeography of arvicoline rodents and the first radiometric age of the fauna from Cumberland Bone Cave, Maryland (Doctoral dissertation). https://repositories.lib.utexas.edu/bitstream/handle/2152/82563/WITHNELL-DISSERTATION-2020.pdf?isAllowed=y&sequence=1.

Yannic, G., Burri, R., Malikov, V. G., & Vogel, P., 2012. Systematics of snow voles (*Chionomys*, Arvicolinae) revisited. Molecular Phylogenetics and Evolution, 62(3), 806-815. https://doi.org/10.1016/j.ympev.2011.12.004.

Zagorodnyuk, I.V., 1990. Karyotypic variablity and systematics of the Arvicolini (Rodentia). Bestn. Zoologii., 2, 26-37.

Zakrzewski, R.J., 1972. Fossil microtines from Late Cenozoic Deposits in the Anza-Borrego Desert, Californiᴀ: with the description of a new subgenus of *Synaptomys*. Natural History Museum.

Zazhigin V.S. 1988. Paleontological descriptions: Insectivora, Lagomorpha, Rodentia. Vangengeim E.A., Nikiforova K.V. (eds.). In Biostratigraphy of Late Pliocene-Early Pleistocene of Tadzhikistan (Mammalian Fauna). Moskva: Nauka. P.18-24 [in Russian].

Zazhigin, V.S. 1997. Late-Pliocene and Pleistocene rodent faunas in the Kolyma lowland: possible correlations with North America. In Terrestrial Paleoenvironmental Studies in Beringia, pp. 25–29. Edited by M. E. Edwards, A. V. Sher & R. D. Guthrie. Fairbanks, AK: University of Alaska Museum.

Zeng, T., Jin, W., Sun, Z.Y., Liu, Y., Murphy, R.W., Fu, J.R., Wang, X., Hou, Q.F., Tu, F.Y., Liao, R., Liu, S.Y., Yue, B.S., 2013. Taxonomic position of *Eothenomys wardi* (Arvicolinae: Cricetidae) based on morphological and molecular analyses with a detailed description of the species. Zootaxa, 3682(1), 085-104. https://doi.org/10.11646/zootaxa.3682.1.3.

Figure 1

Figure 1: Higher-order mitochondrial (cytb and COI) only analyses

(**A**) Maximum Likelihood (ML) tree of mitochondrial dataset comprising 146 arvicolines and 3 members of Cricetidae. Tree was rooted with *Neotoma fuscipes*. For a species level tree see Appendix D. (**B**) Majority-rule consensus tree produced using Bayesian Inference (BI) methods of the mitochondrial only dataset comprising 146 arvicolines and 3 members of Cricetidae. For a species level tree see Appendix G.

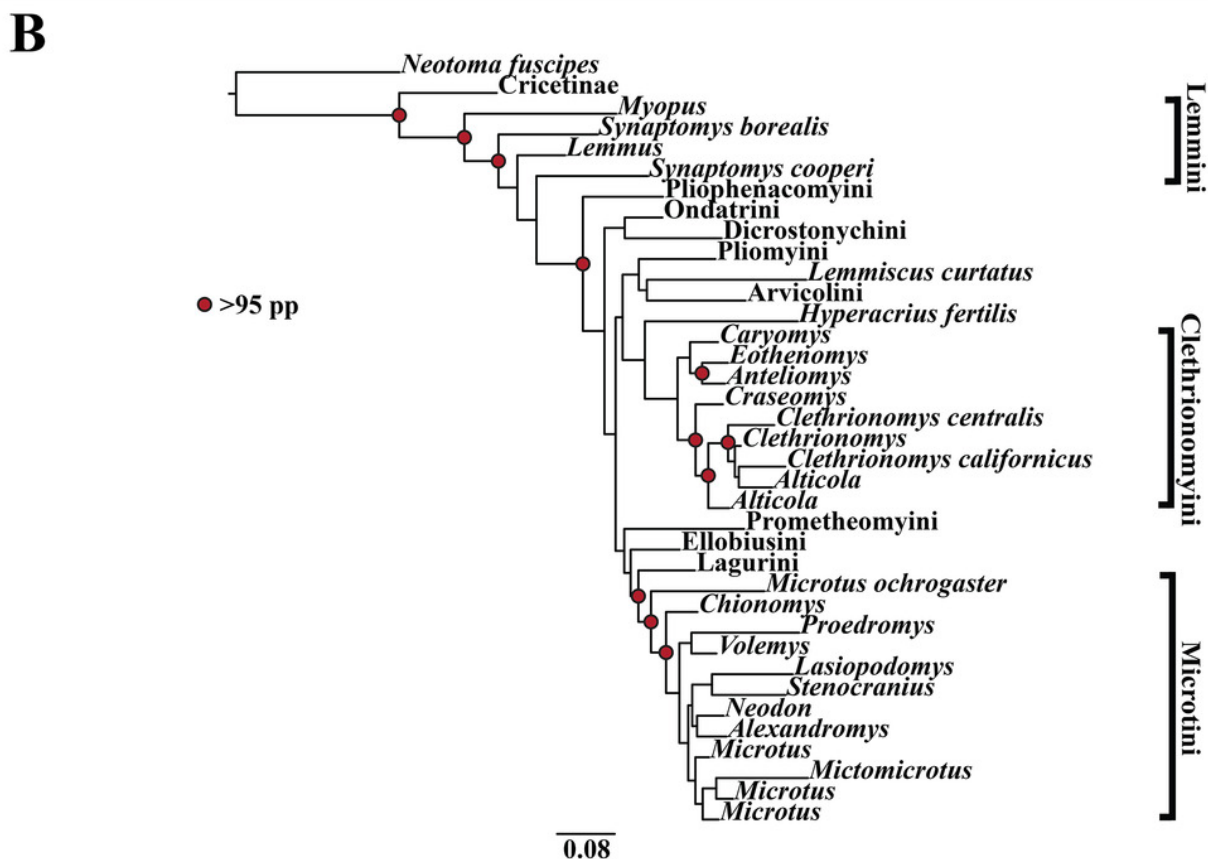
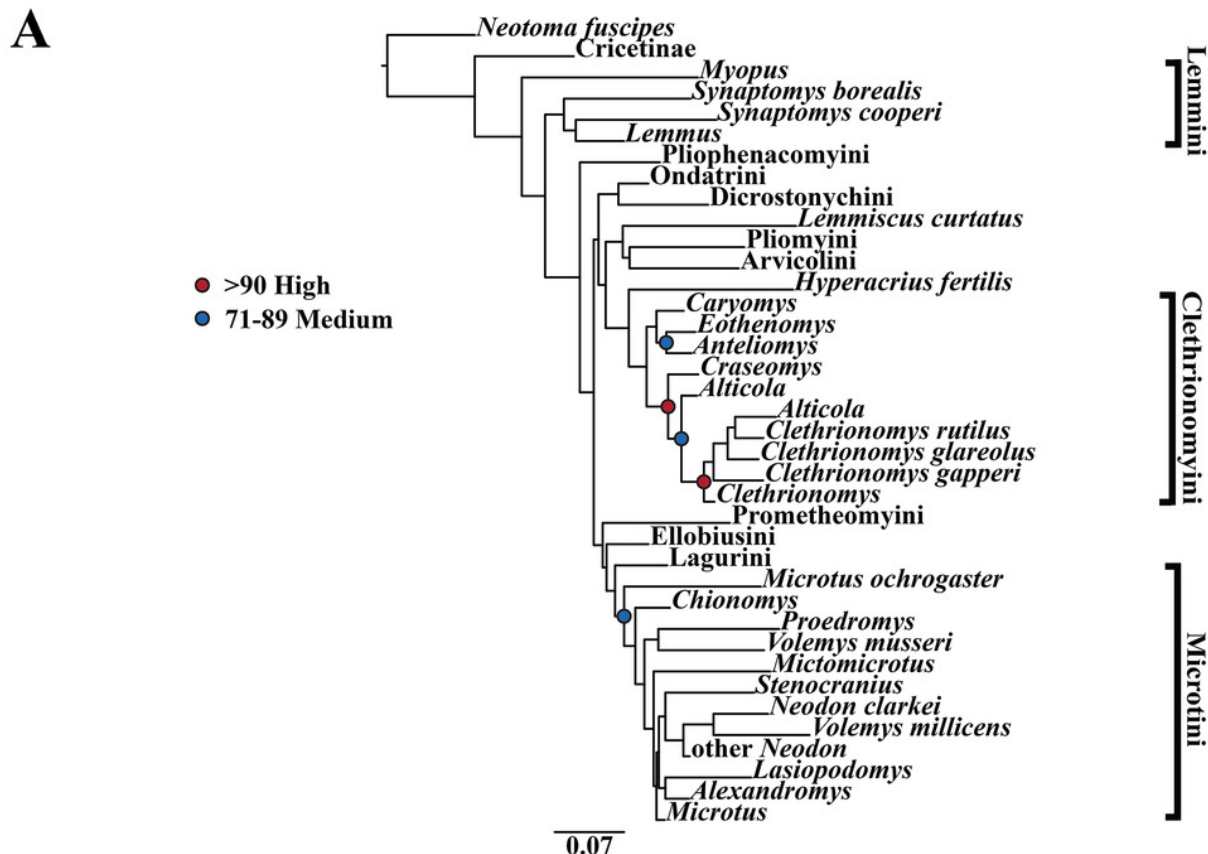



Figure 2

Figure 2: Higher-order nuclear (Ghr, IRBP/RBP3, and BRCA1) only analyses

(**A**) Maximum Likelihood (ML) tree of nuclear dataset comprising 107 arvicolines and 3 members of Cricetidae. Tree was rooted with *Neotoma fuscipes*. For a species level tree see Appendix E. (**B**) Majority-rule consensus tree produced using Bayesian Inference (BI) methods of the nuclear dataset comprising 107 arvicolines and 3 members of Cricetidae. For a species level tree see Appendix H.

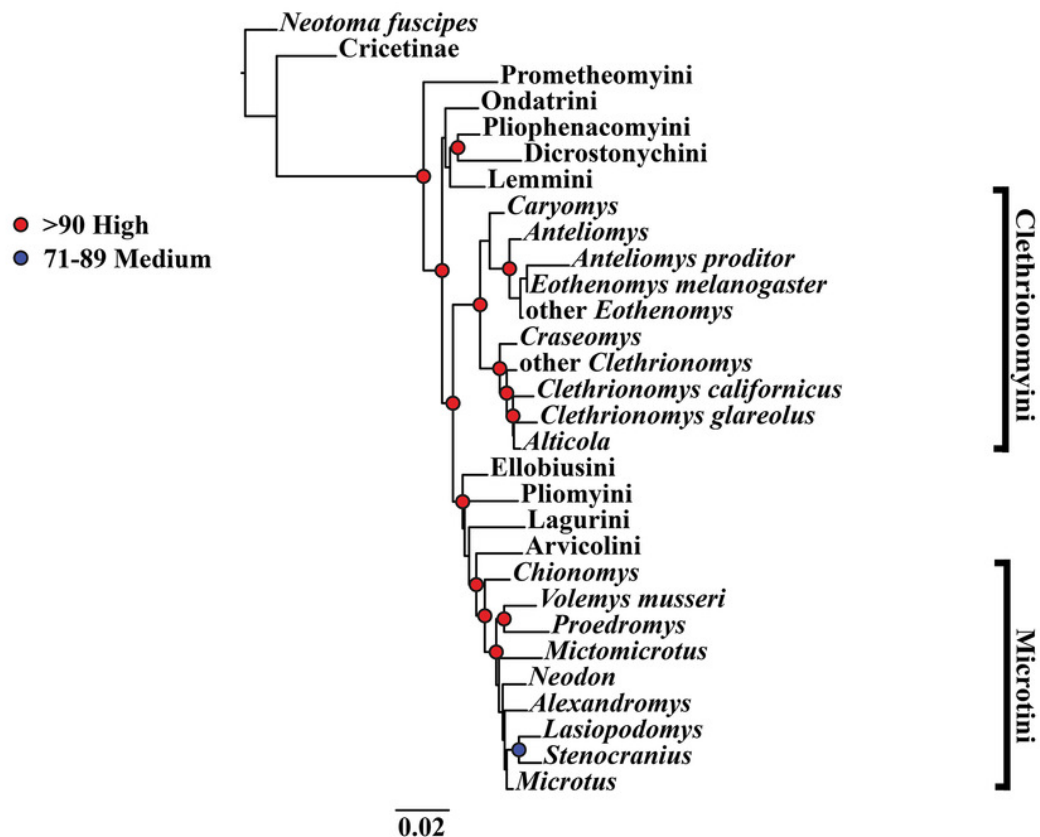
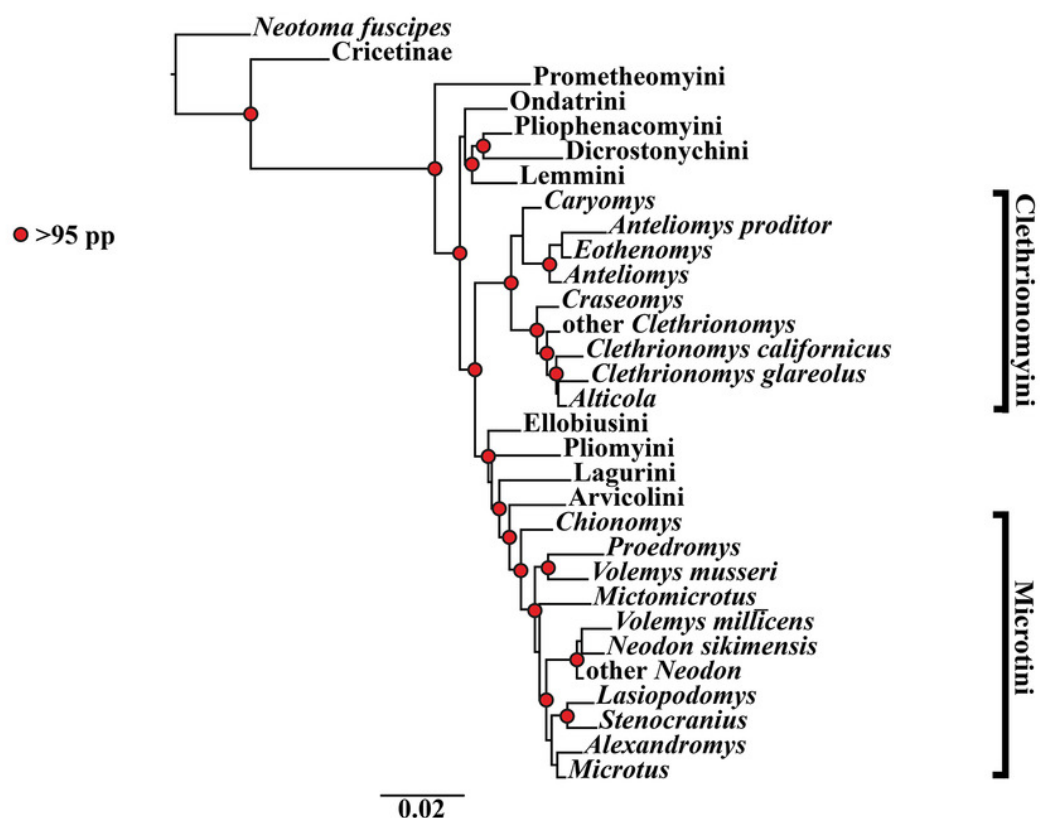
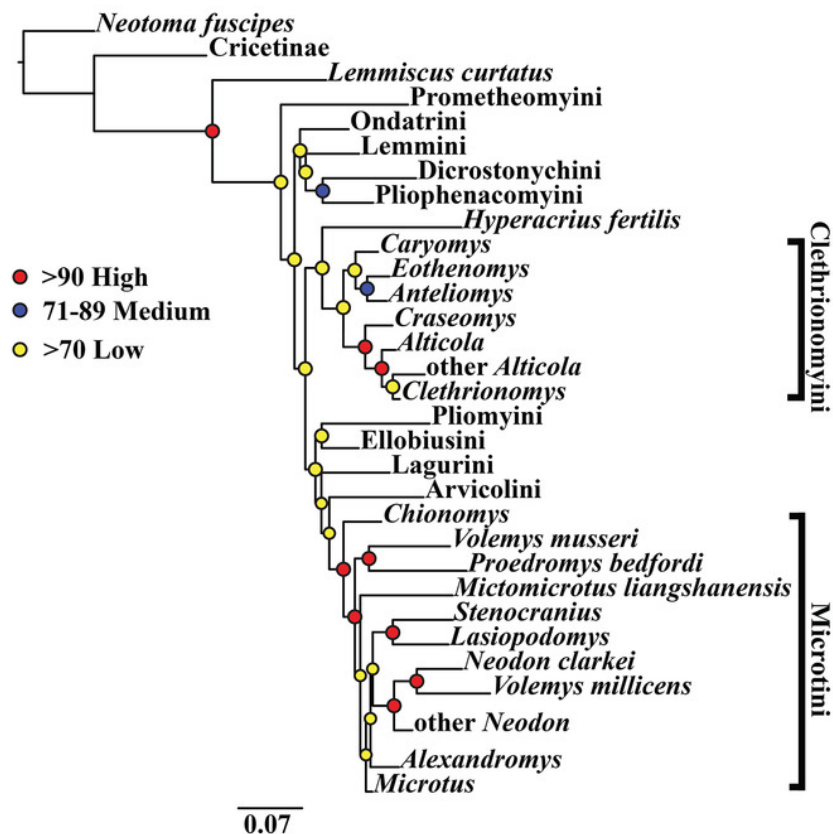



Figure 3

Figure 3: Higher-order concatenated mitochondrial and nuclear (cytb, COI, Ghr, IRBP/RBP3, and BRCA1) analyses

(**A**) Maximum Likelihood (ML) tree of concatenated dataset comprising 146 arvicolines and 3 members of Cricetidae. Tree was rooted with *Neotoma fuscipes*. For a species level tree see Appendix F. (**B**) Majority-rule consensus tree produced using Bayesian Inference (BI) methods of the concatenated dataset comprising 146 arvicolines and 3 members of Cricetidae. For a species level tree see Appendix I.

A

B

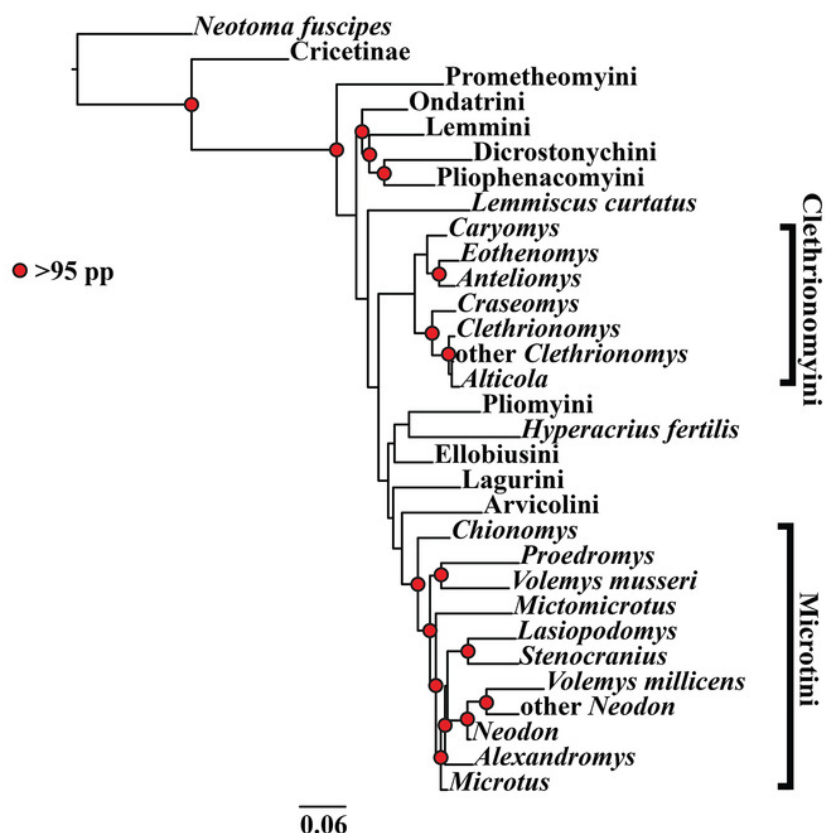



Figure 4

Figure 4: Time-Calibrated phylogeny of Arvicolinae.

Blue vertical dashed lines represent boundaries between geologic epoch. Red horizontal bar at each node represent the 95% HPD for the age of the node. Age in scale bar is in millions of years. PLE=Pleistocene. Orange Box=Holocene. For a species level time-calibrated phylogeny see Appendix J.

Concatenated Time-Calibrated BI

Neotominae
Cricetinae
Prometheomyini
Ondatrini
Lemmini
Dicrostonychini
Pliophenacomyini
Lemmiscus

Caryomys
Eothenomys
Anteliomys
Craseomys
Alticola
Clethrionomys
Alticola

Clethrionomyini

Pliomyini
Hyperacrius
Ellobiusini
Lagurini
Arvicolini

Chionomys
Proedromys
Volemys musseri
Mictomicrotus
Volemys millicens
Neodon clarkei
other *Neodon*
Lasiopodomys
Stenocranius
Alexandromys
Microtus

Microtini

Fossil Calibrations

- ● **Cricetidae**
- ● **Lemmini**
- ● **Ondatrini**
- ● **Pliophenacomyini**
- ● **Ellobiusini**

Miocene	Pliocene	PLE	

15   12.5   10   7.5   5   2.5   0

Table 1: Divergence ages of various clades within this study.

Age is in millions of years before present.

Subfamily	Tribe	Genera	Mean	Median	Minimum Age	Maximum Age
Neotominae			12.23	12.2	10.53	13.89
Cricetinae			7.86	7.85	6.5	9.27
Arvicolinae			6.41	6.4	5.7	7.17
	Prometheomyini		6.41	6.4	5.7	7.17
	Ondatrini		3.47	3.42	3.2	3.91
	Lemmini		4.05	4.02	3.95	4.23
		Synaptomys	3.67	3.69	3.18	4.11
		Myopus	3.11	3.11	2.62	3.61
		Lemmus	1.65	1.64	1.22	3.09
	Dicrostonychini		0.96	0.95	0.62	1.33
	Phenacomyini		2.57	2.53	2.4	2.85
		Lemmiscus	5.65	5.64	5.06	6.3
	Clethrionomyini		3.39	3.38	2.89	3.92
		Caryomys	1.68	1.67	1.24	2.16
		Eothenomys	1.06	1.05	0.74	1.41
		Anteliomys	1.83	1.82	1.47	2.18
		Craseomys	1.45	1.45	1.08	1.83
		Alticola	2.03	2.03	1.69	2.4
		Clethrionomys	1.43	1.42	1.13	1.74
	Pliomyini		4.2	4.23	3.15	5.17
		Hyperacrius	4.2	4.23	3.15	5.17
	Ellobiusini		3.75	3.74	3.11	4.42
	Lagurini		2.92	2.91	2.33	3.51
	Arvicolini		1.5	1.49	1.08	1.94
	Microtini		4.25	4.24	3.75	4.75
		Chionomys	2.56	2.55	2.02	3.09
		Proedromys	3.25	3.25	2.69	3.82
		Mictomicrotus	3.77	3.77	3.34	4.21
		Neodon	2.56	2.55	2.18	2.96
		Lasiopodomys	1.54	1.53	1.12	1.98
		Stenocranius	1.25	1.24	0.86	1.66
		Alexandromys	2.15	2.14	1.77	2.51
		Microtus	3.43	3.43	3.03	3.85
		NA Microtus	2.92	2.91	2.54	3.3

2 NA=North American