

This is a repository copy of *Cranial anatomy of the desert dormouse, Selevina betpakdalaensis (Rodentia, Gliridae), revealed with micro-computed tomography.*

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/158856/>

Version: Accepted Version

Article:

Hennekam, Jesse, Sadler, James, Golenischchev, Feodor et al. (4 more authors) (2021) Cranial anatomy of the desert dormouse, *Selevina betpakdalaensis* (Rodentia, Gliridae), revealed with micro-computed tomography. *Journal of mammalian evolution*. pp. 457-468. ISSN: 1064-7554

<https://doi.org/10.1007/s10914-020-09504-x>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

[Click here to view linked References](#)

1 Title: Cranial Anatomy of the Desert Dormouse, *Selevinia betpakdalaensis*
2
3
4 2 (Rodentia, Gliridae), revealed by Micro-Computed Tomography
5
6
7 3

8
9 4 Authors: Jesse J. Hennekam¹, James W.F. Sadler¹, Fedor N. Golenishchev², Lyudmila Yu.
10
11 5 Kryuchkova³, Dmitry Korost⁴, Olga Nanova⁵, Philip G. Cox^{1,6}
12
13
14 6

15
16
17 7 Affiliations:

18
19 8 ¹*Hull York Medical School, University of York, United Kingdom*
20
21

22 9 ²*Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia*
23
24

25 10 ³*Saint Petersburg State University, St. Petersburg, Russia*
26
27

28 11 ⁴*Department of Geology and Geochemistry of Fossil Fuels, Geological Faculty, M.V.*
29
30 12 *Lomonosov Moscow State University, Moscow, Russia*
31

32 13 ⁵*Zoological Museum, M.V. Lomonosov Moscow State University, Moscow, Russia*
33
34

35 14 ⁶*Department of Archaeology, University of York, United Kingdom*
36
37

38 15
39
40 16 Corresponding author: Jesse J. Hennekam
41

42
43 17 Address: PalaeoHub, University of York, Wentworth Way, York, YO10 5DD, UK
44

45 18 Email: jjh556@york.ac.uk
46
47
48 19
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Abstract

The dormice (Gliridae) represent a relatively small family of rodents, but exhibit considerable variation in their cranial anatomy. The skull morphology of almost all genera of dormice was described from osteological specimens by Wahlert et al. (1993). However, the rare desert dormouse, *Selevinia betpakdalaensis*, was only assessed using previous descriptions and photographic images, resulting in difficulties with assigning all cranial features within this particular genus. In this study, the crania and mandibles of two adult individuals of this genus were scanned using micro-computed tomography and virtually reconstructed. From these reconstructions, we describe in detail the highly unusual cranial and mandibular morphology of the desert dormouse and determine the states of the cranial and mandibular characters described by Wahlert et al. (1993). These morphological characters were used to compare this species with previously described dormouse genera, showing a clear resemblance between *Selevinia* and the small mouse-tailed dormouse genus *Myomimus*. Derived morphological features unique to *Selevinia* indicate clear adaptations to a desert-like environment, as well as hinting towards an insectivorous diet and burrowing lifestyle.

Introduction

The first description of the desert dormouse *Selevinia betpakdalaensis* dates back to 1939 by Belosludov and Bashanov, based on specimens collected in 1938 by B. A. Belosludov and V. A. Selevin (Bashanov and Belosludov, 1941). Initially placed in Muridae based on its dental formula, further analyses led to the first description of this species published in English (Bashanov and Belosludov, 1941), in which it was placed in a new monospecific family, Seleviniidae. These authors mentioned the close resemblance of the skull morphology of this species with that of members of Gliridae (Myoxidae), but highlighted the atypical dental

structures within this species in comparison to dormice. Ognev (1947) identified the animal as a highly derived dormouse and emphasised the resemblance of this species to *Myomimus*. He therefore created the subfamily Seleviniinae within the family Gliridae. More recent analyses of the enamel structure in this animal and other dormice also incorporated *Selevinia* within Gliridae, and no longer acknowledged Seleviniidae as a sister group of Gliridae (von Koenigswald, 1992). Storch (1994) assigned *Myomimus* and *Chaetocauda* to Seleviniinae alongside *Selevinia*, regarding it as the most primitive of all extant dormice subfamilies. In contrast, Yachontov and Potapova (1991) considered *Selevinia* to be more closely related to *Muscardinus* and *Glis*, belonging to the subfamily Glirinae. Later, Potapova reasserted the close relationship between *Myomimus* and *Selevinia* based on middle ear morphology (Potapova, 2001). Wahlert et al. (1993) placed *Selevinia* and *Myomimus* in the tribe Seleviniini, which, joined with the tribe Leithiini, formed the subfamily Leithiinae. Due to the scarcity of accessible specimens, *Selevinia* was not included in the phylogenetic analyses of the Gliridae based on molecular data by Montgelard et al. (2003) or Nunome et al. (2007). The exact placement of the species within the dormouse phylogeny therefore remains unclear. However, the current consensus is to place the monospecific genus within the subfamily Leithiinae and refrain from the use of Seleviniinae (Holden-Musser et al. 2016).

Eighty years after its first description in the literature, a great deal is still unknown about the desert dormouse. The inhospitable desert environment in which it lives has resulted in only a few specimens being captured in the wild. We know of five specimens of the species caught by hand during an expedition in 1938, and another specimen in 1946. The species appears to be widely distributed in the south and east parts of Kazakhstan, especially in the deserts surrounding Lake Balkhash, and has been documented as far south in Kara-Ungur, near the

border with Kyrgyzstan (Bashanov and Belosludov, 1941; Holden, 2005). The animal is likely predated on by birds of prey, as *Selevinia* material has been reportedly found in bird pellets (Argyropulo and Vinogradov, 1939). Bashanov and Belosludov (1941) noted that the coat of the animal is quite long and dense. It is light grey in colour dorsally, including some dark specks, but light grey and slightly yellowish ventrally. The ears are rather large, including reddish hairs on the outside. No clear facial mask, as seen in *Eliomys* for example, is apparent. The tail is short haired and dark grey dorsally, but significantly lighter ventrally. The forepaw includes four digits, and the hind leg has five, with the soles lacking in hair. The five specimens analysed by Bashanov and Belosludov (1941) showed a total body length varying between 78 and 95 mm, with the tail length varying between 58 and 77 mm. Cranial length was only assessed in three specimens, indicating a range between 21.5 and 22.1 mm.

Wahlert et al. (1993) described the cranial morphology of most extant dormouse genera using a total of 54 cranial and mandibular characteristics. At the time, the authors did not have access to cranial material of *Selevinia*, but instead used former descriptions and dated photographic material to assess the morphological characteristics within the genus (Bashanov and Belosludov, 1941; Ognev, 1947). Due to the resolution and orientation of the figures consulted, the states of many cranial characters could not be reliably determined in the genus. Here, we use microCT data of two adult specimens of *Selevinia betpakdalaensis* in order to describe the cranial anatomy of this species and to complement the dataset created by Wahlert et al. (1993). We believe this to be the first time this species has been scanned using microCT, allowing us to assess the cranial morphology of this species in very high detail. This description will result in a much greater understanding of the distinct morphological features present in

the desert dormouse, and will enable us to compare this species with other dormouse taxa more accurately.

Materials and methods

The sample comprised the skulls and mandibles of two adult specimens of the species *Selevinia betpakdalaensis*, both housed in Russian institutions. Specimen ZIN 32206 is an adult male collected on the 21st August, 1946, by M. A. Musarov near the Meteo Station in Betpak-Dala Desert (46°02'N; 70°12'E). It was placed in the Zoological Institute of Kazakh Academy of Sciences with the incoming number 34-1947. The specimen was later transferred to the Zoological Institute in Saint Petersburg on the 27th May, 1947. The material, consisting of an intact skull and a slightly broken mandible, was scanned at the Research Centre for X-ray Diffraction Studies of Saint Petersburg State University (Saint Petersburg, Russia), using a high-resolution X-ray computed micro-tomography scanner (SkyScan 1172) with an isometric voxel dimensions of 4.9 µm. The specimen was later downsampled to 9.8 µm in order to decrease the computation time whilst rendering the object for analysis. Dentition was analysed using the original 4.9 µm resolution.

Specimen S-28487 was captured in the northern part of Betpak-Dala Desert by V. Selevin on 8th August 1938. The specimen is considered a paratype and was donated to the Zoological Museum in Moscow. The external morphology of this specimen is shown in Fig. 1. A microCT scan of the skull and two hemi-mandibles was created at the Geology department of Moscow State University (Moscow, Russia) on a SkyScan 1172. The resolution of the scanned material is 15.42 µm.

Three-dimensional virtual reconstructions of the skull and lower jaw of each specimen were created from the microCT scans using the segmentation function of Avizo 9.2 (Thermo Fisher Scientific, Waltham, MA, USA). Both surface files of the scanned dormice were uploaded to the online database Morphosource (www.morphosource.org). Linear measurements of the cranium and dentition were recorded from the reconstructions and are given in ESM 1. The virtual reconstructions were used to produce detailed descriptions of the cranial, mandibular and dental anatomy of *Selevinia betpakdalaensis*, and to determine the character states of the 54 anatomical characters used by Wahlert et al. (1993) in their analysis of dormouse cranial anatomy (ESM 2). The morphology was also compared to all other dormouse genera, but in particular *Myomimus* and *Muscardinus*, because the former has been hypothesised to have a close phylogenetic relationship with *Selevinia* (Wahlert et al., 1993; Storch, 1994; Potapova, 2001) and the latter is a similarly small-sized dormouse. The character state data for *Selevinia* were combined with data for all other dormouse genera (except *Chaetocauda*) and four outgroup taxa (*Paramys*, *Sciurus*, *Sicista* and *Cricetulus*) taken from Wahlert et al. (1993) in a parsimony analysis, conducted in PAUP* 4.0a167 (Swofford, 2003). The most parsimonious tree was compared with the cladogram presented in Wahlert et al. (1993), as well as with phylogenies of the Gliridae derived from molecular data (Montgelard et al. 2003; Nunome et al. 2007).

Results

Specimen descriptions

The reconstruction of Specimen 32206 is shown in Fig. 2. The skull includes one incisor and three molars on each side. The right pterygoid flange is broken, as is the ventralmost area of the right auditory bulla. The right orbitosphenoid appears to be displaced. The right occipital

139 area is slightly broken, showing small perforations of the skull. The ventralmost part of the left
140 auditory bulla is slightly dented. The dentaries are fused at the mandibular symphysis and both
141 have their full dentition intact: an incisor and three molars. The angular process of the right
142 dentary is slightly broken but otherwise intact. The left coronoid process is broken and the
143 most lateral tip of the left angular process is absent. No other features appear to be broken or
144 deformed in the remainder of the mandible.

145
146 The reconstruction of Specimen S-28487 is shown in Fig. 2. The skull is not deformed, although
147 it lacks multiple distinctive cranial features. Both upper incisors appear to have been cut and
148 M1 and M2 are missing in the right molar row. Both zygomatic arches are missing and the
149 auditory bullae are either broken or possibly sawn open. Some of the inner and middle ear
150 morphology is therefore absent. The basioccipital area is broken posteriorly, as is part of the
151 right occipital condyle. The part of the frontal bone located directly behind the zygomatic plate
152 is broken on the right side, as is a part of the hard palate on the same side. The superior part
153 of the infraorbital foramen on the left side is damaged when examined anteriorly. The
154 mandible of this specimen is not fused at the symphysis, resulting in two separated dentaries.
155 In the right dentary, the third molar is absent, the incisor alveolus is slightly broken laterally,
156 and the tip of the coronoid process is missing, as is the middle and upper part of the angular
157 process. All three molars are present in the left dentary. In addition, the incisor alveolus is very
158 slightly broken ventrally, and the coronoid and angular processes are broken in a similar
159 fashion to the right dentary of this individual.

160
161 *Anatomical description*

Numbers in square brackets correspond to the character list set out in the appendix of Wahlert et al. (1993). A full scoring of these characters in *Selevinia betpakdalaensis* alongside the character states for other dormice genera and four rodent outgroups from Wahlert et al. (1993) is given in ESM 3.

Cranium

In order to facilitate comparison, the skull shape of various dormouse genera are presented in Figs. 3-6. *Selevinia betpakdalaensis* is a small dormouse species, with the two specimens analysed for this study having skull lengths of roughly 21 and 24 mm compared with a range of 18 to 40 mm in other species (Holden-Musser et al. 2016). When examined dorsally, the posterior extent of the premaxilla is roughly at the same location as that of the nasal bones [1] and extends farther than the maxilla [2]. As in all other dormice genera, the anterior end of the premaxilla is tall and high above the most anterior part of the incisor alveolus [3]. The nasal bone varies significantly between both skulls. Specimen S-28487 has a much broader anterior part of the nasal bone in comparison with Specimen 32206. It is possible that this feature is deformed in the former specimen, but it is difficult to determine if this happened post-mortem or not. Nonetheless, both specimens indicate that the nasal bone is rather wide in comparison with most dormice genera. The infraorbital foramen is similar in size and position to in *Myomimus*, although *Myomimus* has more developed ridges on the lateral side of this foramen and flares more strongly inferiorly, resulting in a very pronounced anterior extension of the ventral margin. This extension is present, although less pronounced, in *Selevinia*. As *Selevinia* has a clearly reduced molar row, the diastema is technically longer than is seen in other dormice; however, there is a clear distinction between the area created by molar reduction and the area representing the diastemal palate in other genera. We will use the latter area for

186 assigning the diastema. This area appears to be very flat within *Selevinia* [4]. A tubercle defines
187 the position of the origin of the superficial masseter [5], in contrast to *Graphiurus*, *Muscardinus*
188 and *Glis*, in which the area is not always clearly separated by a tubercle. The zygomatic plate is
189 of similar thickness to *Muscardinus*, but positioned more inferiorly compared to this genus and
190 tilted more anteriorly. The presumed extension of the lateral masseter on to the zygomatic
191 plate on the rostrum is present in this genus, similar to most dormouse genera (except
192 *Graphiurus*) [6], and the medial masseter extends through the enlarged infraorbital foramen
193 [7], similar to all other dormice. The combined extension of both the lateral and medial
194 masseter on to the rostrum is characterised as the myomorphous condition.

195
196 The posterior edge of the anterior root of the zygoma is located anterior to the first cheek
197 tooth [8]. This characteristic is also present in *Graphiurus*, whereas in all other genera it is
198 lateral to the first premolar. The lack of premolars in *Selevinia* is unique within extant dormice
199 and could well be impacting this characteristic. The lacrimal bone does not appear to be
200 present in either of the two *Selevinia* specimens, although the scarcity of crania available to us
201 makes it impossible to rule out the absence of this bone in all members of this genus. The
202 lacrimal bone appears to be often broken or missing in dormice skulls, as it is often not
203 completely fused with the cranium. In *Selevinia*, the jugo-maxillary suture is positioned
204 posteriorly along the zygomatic arch to such an extent, that it seems very unlikely that any
205 potential lacrimal bone would contact the jugal [9]. The zygomatic arches flare dorsally midway
206 along the arch (forming a small postorbital process) and are similar in shape to *Muscardinus*,
207 although the flaring occurs more posteriorly in *Selevinia*. The zygomatic arches are only slightly
208 wider than the posterior part of the cranium, a trait not seen in other dormouse species. This
209 results in a narrowing of the overall skull width.

210

211 On the ventral aspect of the skull, the premaxillary-maxillary suture connects with the incisive
212 foramina near their midpoints [10], in a similar fashion to all other genera. The area between
213 the anterior part of the incisive foramen and the incisor is of similar length to that of *Myomimus*
214 and shorter than *Glis*. The ratio of incisive foramen length to diastema is roughly 85% [11] and
215 therefore most similar to *Myomimus*. However, when using the full diastemal length (anterior
216 part molar row to posterior part of the incisor alveolus), the ratio is only 69% and falls within
217 the range of *Eliomys*. The anteromedial position of the palatine bone with respect to the molar
218 row is located between the posterior part of M2 and the M2-M3 junction [12], relatively caudal
219 compared to all other genera. This is thought to be a by-product of the reduction of the molar
220 row. Furthermore, the reduction in molar size results in a relatively large palatal width between
221 the M1 teeth in *Selevinia*, with a ratio of palatal width to condylobasilar length of 0.16 [13].
222 This ratio is also similar in many *Dryomys* and *Glirulus* specimens, but smaller in other genera.
223 The posterior palatine foramen is within the palatine bone and medial to the M3 [14], similar
224 to *Glirulus*, *Myomimus* and some *Graphiurus*. The posteriorly orientated spine on the medial
225 posterior end of the palate is absent in *Selevinia* [15], whereas it is very weakly present in
226 *Myomimus* and *Glis*. The opening of the posterior maxillary notch or foramen is a difficult
227 characteristic to determine. Wahlert et al. (1993) distinguish various options within species for
228 *Glis* and *Dryomys*, in which the notch or foramen is either well enclosed or just enclosed. We
229 examined multiple species ourselves in order to correctly assign this character to *Selevinia* and
230 noticed that our *Glirulus* specimen has no maxillary notch or foramen. Instead a foramen is
231 present within the alisphenoid, which is well enclosed and could easily be confused with a
232 maxillary foramen. Wahlert et al. (1993) originally assigned the well enclosed option for the
233 maxillary foramen for *Glirulus*, but it is unclear from their figures whether this is because of an

incorrect identification of the alisphenoid canal or because of intraspecific variation within this species. *Selevinia* shows a maxillary notch rather than a foramen, which can be considered either just enclosed, or well enclosed. It appears to be more enclosed than our *Graphiurus* specimen, in which the maxillary notch is assigned just enclosed according to Wahlert et al. (1993). Following this reasoning, the characteristic of the enclosure of the maxillary notch in *Selivinia* is determined to be well enclosed [16].

Similar to all other dormice, the entrance of the lacrimal canal is situated anteromedially with respect to the infraorbital foramen [17]. The anterior part of the sphenopalatine foramen is slightly posterior to the middle of M2 [18], similar to *Glirulus* and *Myomimus* as well as some *Graphiurus* and *Dryomys* specimens. The non-ossification between the orbitosphenoid and the frontal is present within one of our *Selevinia* specimens, but absent in the other [19]. Where present it appears to have incorporated the ethmoid foramen. The anterior part of this area is dorsal to M3 and extends posterodorsally beyond M3. In the specimen lacking the non-ossification, the ethmoid foramen is more clearly identifiable and dorsal to M3 [20]. The optic foramen is located even more posteriorly [21] and is quite small [22], similar to *Myomimus* and *Glirulus*. The dorsal palatine foramen is positioned entirely posterodorsally to M3 [23] and relatively close to the sphenopalatine foramen [24] in comparison to *Eliomys* and *Dryomys*. The sphenofrontal foramen appears to be present in *Selevinia* [25], but the frontal bone does not extend all the way to this foramen [26]. There is no connection between the parietal bone and the alisphenoid [27].

The foramen ovale is distant from the posterior entrance of the alisphenoid canal [28], in a similar fashion to *Eliomys*. An accessory foramen ovale appears to be absent [29], which

corresponds with all other dormice. There is a fenestra anterodorsal to the masticatory foramen [30], which is absent in some *Muscardinus* and *Eliomys* specimens, and in all *Glis* and *Glirulus* specimens. The lateral pterygoid flange very is weakly developed in *Selevinia* [31] as opposed to *Glis glis*. Wahlert et al. (1993) indicate this pterygoid flange to be present also within *Muscardinus*, whereas it is clearly absent in our specimen of this species. Similar to all other dormice genera, the sphenopalatine vacuity in *Selevinia* extends to the edge of the anterior alar fissure, but is not visible in the orbit [32] as in *Eliomys* and some *Dryomys* specimens. The ratio of the distance between the posterior edge of M3 and the anterior part of the foramen ovale to the condylobasilar length for *Selevinia* is between 0.12 and 0.14 [33]. This is similar to most dormice genera – only the genus *Muscardinus* appears to have a ratio smaller than 0.1. The stapedial artery and the foramen in which the stapedius muscle takes its origin are present within *Selevinia*. These features are similar in size compared to those in our *Myomimus* specimens and therefore considered small [34].

The posterior part of the zygomatic arch is orientated relatively inferiorly with the most lateral part not extended posteriorly, as is seen in *Myomimus*, for example. The area bounded by the zygomatic arch is oblong in dorsal view, which is representative for smaller dormice species. Furthermore, the interparietal and parietal bones are curved, another feature often observed in smaller genera and juvenile dormice. A dorsal orbital ridge is quite strongly developed (compared to other dormouse genera) in both specimens. A groove potentially related to muscle attachment of the temporalis muscle is clearly visible on the squamosal when observed laterally. This groove is less apparent in *Muscardinus*, but much more pronounced in *Myomimus*. *Selevinia* and all other dormice genera have the postglenoid foramen positioned between the auditory bulla and the squamosal bone [35]. The posterior part of the squamosal

bone is solid [36], similar to *Glirulus*, *Glis*, *Graphiurus* and *Muscardinus*. No clear temporal foramen is present at the squamosal-parietal suture [37], and neither is this foramen present in any other genus.

The foramen magnum, although incomplete in S-28487, appears to be relatively enlarged. The foramen magnum is orientated caudally in a similar fashion to *Myomimus*. The auditory bullae in are greatly inflated in all dormice genera but *Glis*, in which this feature is only slightly inflated. *Selevinia* however shows exceptionally well-inflated auditory bullae [38], resulting in the length of this feature representing 36% and 37% of the total skull length respectively, significantly larger than in any other dormouse genus. Three primary septa appear to be present within the auditory bullae [39], similar to all other genera, with the exception of *Glirulus*.

Mandible

The mandibles of various dormouse genera are illustrated in Fig. 7. The mandibular material of *Selevinia* available for this study is slightly broken. However, most features are present and intact in Specimen 32206. The diastema is rather flat when considering other genera. The mandible of *Selevinia* is quite distinctive compared to other dormice, characterised by robust incisors, a lack of premolars, extremely small molars and a condyle that is posteriorly extended with respect to the angular process. The angular processes in the two specimens observed here are perforated with a single, large fenestra [40] in a similar fashion to that often seen in *Myomimus*, *Muscardinus*, *Dryomys* and *Eliomys*. The flaring of the angular process is not very significant and the muscle attachment area relatively small. The condyle stretches out posteriorly and has a relatively small condylar head. The coronoid process is only intact in one dentary, and it flares posteriorly and slightly laterally, as is common in other dormice species.

The inclination of the leading edge of the coronoid relative to the occlusal plane is a relatively difficult character to evaluate, as this can be affected by the orientation in which the specimen is examined. However, the coronoid margin appears to be more horizontal than that of *Myomimus*, a genus Wahlert et al. (1993) described as being orientated at less than 60° to the occlusal plane. Measuring this angle with the dentary in as flat an orientation as possible indicates an angle of 45° [41]. The concealing of the molars by the coronoid process is also a difficult character to assess, as it is not clearly specified how the dentary should be positioned in order to establish a lateral view. This is of importance due to the three-dimensionality of this bone, however flat it might appear. We evaluated mandibles of various genera and positioned them laterally in such manner that our findings were similar to that of Wahlert et al. (1993). When positioning the *Selevinia* mandibles in a similar way, the coronoid either concealed the posterior part of the m3, or no molar at all [42]. The masseteric ridge protrudes clearly and the most anterior part of the masseteric fossa is ventral to the anterior margin of the first molar [43]. This is relatively similar to all other dormice, with the exception of *Glis*, in which the fossa is positioned slightly more posteriorly. The bone in the region caudal to the posterior part of the incisor alveolus is noticeably thin. Furthermore, a large number of openings are present on the ventral side of the mandible, exposing parts of the embedded enlarged incisor.

Dentition

The dental formula for the upper and lower jaws is 1/0/0/3 in *Selevinia*. The upper incisors are very unlike the incisors of other dormice except for *Chaetocauda*, owing to the deep groove running down the lateral side of the enamel surface. *Chaetocauda* is the only dormouse genus lacking in our comparative dataset; however, Wang (1985) describes a deep groove in the medial anterior surface of the upper incisors. This description of the upper incisors of

Chaetocauda corresponds with what is seen in *Selevinia*, although it should be noted that the pictures in Wang (1985) are not clear enough to compare this feature accurately with our *Selevinia* specimens. The segmented incisor shows that this groove is already apparent at the origin of the incisor, located medially to the zygomatic plate. The enamel is relatively thin and evenly spread throughout the anterior part of the incisor. In our evaluation of the enamel characteristic we presume the enamel cap to grade into the lateral surface [44]. The incisors are orientated downwards and ever so slightly posteriorly.

The curvature of the lower incisors is similar to other dormice species, with the incisor root located inferoposteriorly to the last molar. The lower incisors are very robust in comparison to any of the other dormice species, but lack the anterior groove characterising the upper incisors. However, the lower incisors show a ridge on their occlusal surface which is likely a result of wear from the grooved upper incisors.

The ratio of upper cheek teeth crown length to condylobasilar length is very small (less than 0.2) in *Selevinia* [45], as a result of the very small, brachydont molars characterising this genus. The genus is also the only one in which all upper and lower premolars appear to be absent [46,47], although both *Muscardinus* and *Myomimus* show reduced premolars, in contrast to other genera. In the adult *Selevinia* specimens studied here, small cavities can be seen located anterior to the first upper molar. As Bashanov (1951) observed two deciduous premolars in juvenile *Selevinia* specimens, the cavities in our specimens are therefore identified as (remnants of) the alveoli of the deciduous fourth premolars.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

353 The upper molars are concave and very simplistic, lacking any clear dental patterns on the
354 occlusal surface, which is considered to be weakly helical in shape [48] compared to other
355 genera. The occlusal surface of the molar row consists solely of enamel, with no dentine visible
356 externally. The M2 is the largest molar in both specimens, being slightly larger than M1. Both
357 M1 and M2 include two lingual lobes, but this is less clearly expressed in M1. M3 lacks these
358 lobes completely and is roughly half the size of M2. The simplified molars in *Selevinia* do not
359 include any cusps, and the buccal ridge of the molars is not more pronounced than the lingual
360 ridge [49]. No distinct accessory crests or cusps are present within any of the molars of
361 *Selevinia*. The root morphology varies per molar (Fig. 8), with the M1 having three roots, with
362 the palatal root being the longest and the only one including a canal. The M2 also includes
363 three roots, with the palatal root being the most developed. The anterior accessory root here
364 fuses with the palatal root in both our specimens. The posterior accessory root appears to be
365 shorter in M2 in comparison to M1 and flares more posteriorly. One canal is present within the
366 M2, located in the palatal root. M3 is much more simplistic in comparison with the other
367 molars in the molar row, including only a single canalized root. None of the other molar
368 characteristics [50-54] is identifiable in *Selevinia* due to the reduced state of these teeth.

369
370 The lower molars are similar to those in the upper jaw, being concave, reduced in size and
371 relatively simplistic in morphology. The relative molar sizes are similar as well, with m2 being
372 the largest of the three molars and m3 clearly the smallest. No room for a premolar appears
373 to be present within this species. Interestingly, the occlusal surface of the lower molar row
374 appears to be larger than that of the upper molar row. Root morphology is more simplistic in
375 the lower molar row, with all molars having one well developed root. m1 and m2 show

indications of a large posterior root fused with an anterior accessory root. Only one canal is present in every molar, similar to the upper molars.

Phylogenetic analysis The most parsimonious tree of dormouse genera based on cranio-mandibular and dental characters had a length of 150 and is given in Fig. 9. *Selevinia* is found to be most similar to *Myomimus*, and then to a grouping of *Eliomys* and *Dryomys*. These four genera are then most closely related to *Graphiurus*, with *Glis*, *Muscardinus* and *Glirulus* forming a separate group. Tree support values were CI = 0.613, RI = 0.536 and RC = 0.329.

Discussion

A number of unusual and highly derived morphological features within the skull and lower jaw of *Selevinia betpakdalaensis* were described using the virtual reconstruction of two specimens. The most obvious of these are the extremely reduced and simplified cheek teeth. Loss of the premolars is not unusual within rodents, occurring widely throughout the order, notably in the Muridae (although not in any other dormouse species). However, a reduction in the size and complexity of the molars is much less common, with the only other known examples of this phenomenon in rodents being specialist worm-eating taxa from Southeast Asia, such as *Paucidentomys*, *Pseudohydromys* and *Rhynchomys* (Esselstyn et al. 2012; Charles et al. 2013). Such a vermivorous diet is unlikely in *Selevinia* given the lack of an elongated rostrum and the presence of robust incisors, although it should be noted that the precise diet of this species is at the moment unclear. Captive specimens of this species were observed to consume mostly insects (Ognev, 1947), but an analysis of stomach contents of a wild specimen revealed undigested leaves of a desert plant, *Salsola laricifolia* (Bashanov and Belosludov, 1941). An insectivorous diet is most likely given the small, simple molars, but the robust incisors have

also been suggested as an adaptation to cropping tough vegetation (Holden-Musser et al. 2016).

The upper incisors of *Selevinia* are also highly unusual, displaying a prominent groove antero-laterally, which gives them an irregular cross-section. Analogues for this morphology seem to be present in some other rodents (Ohazama et al. 2010), such as the meadow jumping mouse (*Zapus hudsonius*) and the capybara (*Hydrochoerus hydrochaeris*), as well as being found in lagomorphs including pikas (Ochotonidae). It is unclear at the moment what advantage such a groove may convey.

The auditory bullae of most dormouse species are enlarged (Wahlert et al. 1993), but this trait is taken to the extreme in *Selevinia*, which has the largest bullae relative to cranial length of all Gliridae. This is perhaps not surprising as hypertrophied auditory bullae are known to be common in small desert mammals (Alhajeri et al. 2015; Mason, 2016). Such morphology increases the acuity of low frequency hearing and has the potential advantages to desert dwelling species of improving communication over long distances or better seismic detection. Enlarged auditory bullae are also common in fossorial rodents owing to the slower attenuation of low frequency sounds in subterranean tunnels (Schleich and Vassallo, 2003). Thus, it is possible that *Selevinia* is spending at least part of its life underground. This interpretation is also supported by other characters such as the relatively narrow width of the cranium, with the zygomatic arches being only slightly more laterally extended than the posterior part of the skull, and the caudal orientation of the foramen magnum. The latter character indicates a rectilineal posture, similar to *Myomimus*, which would be advantageous for moving through

underground tunnels. Considering the barren landscape of the Betpak-Dala Desert and the hibernating characteristics within most dormice, adaptations to burrowing would not be surprising in the desert dormouse.

The parsimony analysis of dormouse genera and four rodent outgroups produced a shortest tree very similar to that presented in Wahlert et al. (1993). The only difference was in the placement of *Graphiurus*, which was found to be the sister-group to all other dormouse genera in Wahlert et al. (1993), but was recovered as the sister-group to the Leithiinae (minus *Muscardinus*) in our analysis (Fig. 9). Although Wahlert et al. (1993) did not formally include *Selevinia* in their cladistic analysis, they hypothesised that it would be the sister-genus to *Myomimus*, and this is what we found here. More recent molecular phylogenies of the Gliridae (Montgelard et al. 2003; Nunome et al. 2007) show roughly similar topologies to that recovered here, but differ in the placement of *Muscardinus* which is found to be the sister-genus to the Leithiinae, and not closely related to *Glis* and *Glirulus*. This has led to the inclusion of *Muscardinus* within Leithiinae in recent classifications (Wilson & Reeder, 2005; Holden-Musser et al. 2016). There is also continued uncertainty in the position of *Graphiurus*, with Montgelard et al. (2003) placing it as the first branching genus (as also seen in Wahlert et al. 1993), but Nunome et al. (2007) finding it to be sister-group to the Leithiinae, thus agreeing more closely with the analysis presented here. At the time of writing, *Selevinia* has yet to be included in a molecular-based phylogenetic analysis of dormice.

As noted above, the reduced state of the molars in *Selevinia* prevents accurate coding of characters 50-54 (they were scored as missing in the parsimony analysis conducted here). Thus, these are excluded in all further discussion, leaving a total of 49 characters. When

compared with the taxa analysed by Wahlert et al. (1993), *Selevinia* appears to resemble the small dormouse genus *Myomimus* most closely, sharing 39 of the 49 characters (Table 1). *Dryomys* follows *Myomimus* with 36 corresponding characters, closely followed by *Graphiurus* (35). Interestingly, the genus *Muscardinus* does not seem to resemble *Selevinia* greatly (23 shared characters) despite being similar in cranial size, i.e. very small for dormice. Notwithstanding some controversy over the phylogenetic position of *Muscardinus* (Wahlert et al. 1993; Montgelard et al. 2003; Nunome et al. 2007) it is clear that this genus is not particularly closely related to *Selevinia*. This evolutionary distance may have led to the morphological differences between the genera. Alternatively, strong functional adaptation of the teeth (relatively large and densely ridged molars in *Muscardinus*, and simplified and reduced molars in *Selevinia*) may have driven a divergence in overall cranial morphology. Both *Myomimus* and *Muscardinus* are characterised by a size reduction of the premolars. We hypothesise that *Selevinia* went through a similar premolar size reduction phase before losing its premolars completely.

The similarity of *Selevinia* to *Myomimus* was expected and predicted by Wahlert et al. (1993). Furthermore, the similarity to *Dryomys* is understandable, as *Myomimus* has previously been proposed as a subgenus of *Dryomys*. However, the number of shared characteristics with *Graphiurus* was surprising, as *Muscardinus* is phylogenetically closer to *Myomimus* and *Dryomys* than to *Graphiurus* (Montgelard et al. 2003). Initially we hypothesised that the broad range of *Graphiurus* species may have resulted in many variable characters to be present within the genus, explaining the large potential correlation with *Selevinia*. However, when analysing the number of characters that are polymorphic within *Graphiurus*, we did not find an exceptionally large number (4 out of 49), especially when compared with *Dryomys* (8 out of

49). Potentially, some primitive cranial characteristics are present in both the sub-Saharan dormice and the desert dormouse. It would be extremely interesting to include *Selevinia* in a phylogenetic study, in order to know the placement of this peculiar species within Gliridae.

Our analysis of the cranial and mandibular morphology of the desert dormouse, *Selevinia betpakdalaensis*, shows that this species is morphologically very similar to the mouse-tailed dormice in the genus *Myomimus*. Derived cranial features are suggested to be adaptations to a burrowing lifestyle in a desert environment; these include extremely enlarged auditory bullae, and a reduced molar row both in number and size of teeth, as well as a less lateral extension of the zygomatic arch, relative to the posterior part of the skull. The detailed description of the cranial morphology will facilitate more reliable comparisons of *Selevinia* with other dormice, leading to a more complete overview of cranial and mandibular shape variation within the rodent family Gliridae.

Acknowledgements

The authors would like to thank John Wahlert for discussions on certain anatomical features within *Selevinia* and allowing them to modify the schematic figures by including *Selevinia*; Nathan Jeffery, for providing operable scan data and his comments on the manuscript; Nedko Nedyalkov, for alerting us to the presence of skeletal material of this genus in Russian institutes; and Vladimir Lebedev and Leonid Voyta aiding in the communication between the different institutes. This work was also supported by Moscow State University Grant for Leading Scientific Schools "Depository of the Living Systems" in frame of the MSU Development Program. Jesse Hennekam was funded by a graduate teaching assistantship at the Hull York Medical School.

495

496 **Author contributions**

497 JJH and PGC conceived the study. JJH segmented the data and undertook the character
498 analysis. JWFS produced the illustrations. FNG, LYK, DK, ON provided access to specimens. JJH
499 and PGC drafted the manuscript. All authors contributed to the editing of the final manuscript
500 and gave final approval before submission.

501

502 **References**

- 503 Alhajeri BH, Hunt OJ, Steppan SJ (2015) Molecular systematics of gerbils and deomyines
504 (Rodentia: Gerbillinae, Deomyinae) and a test of desert adaptation in the tympanic
505 bulla. J Zool Syst Evol Res 53:312-330
- 506 Argyropulo AJ, Vinogradov B (1939) O novom zamechatelnom ghizune nashej fauni (*Selevinia*
507 *paradoxa* gen. et spec. nov.). Priroda 1:81-83
- 508 Bashanov BS (1951) Some peculiarities of rodents belonging to the family Seleviniidae, and
509 endemic in Kazakhstan. Izvest Akad Nauk SSSR 80:469-472 [In Russian]
- 510 Bashanov BS, Belosludov BA (1941) A remarkable family of rodents from Kasakhstan, U.S.S.R.
511 J Mammal 22:311-315
- 512 Belosludov BA, Bashanov BS (1938) A new genus and species of rodent from the Central
513 Kasakhstan (USSR). Uchen Zap Kazak Univ Alma-Ata, Biol 1:81-86 [In Russian]
- 514 Charles C, Solé F, Gomes Rodrigues H, Viriot L (2013) Under pressure? Dental adaptations to
515 termitophagy and vermivory among mammals. Evol 67:1792-1804
- 516 Esselstyn JA, Achmadi AS, Rowe KC (2012) Evolutionary novelty in a rat with no molars. Biol
517 Lett 8:990-993

518 Holden ME (2005) Family Gliridae. In: Wilson DE, Reeder DM (eds) Mammal species of the
 1 world, a taxonomic and geographic reference, 3rd edition. Johns Hopkins University
 2
 3 519 Press, Baltimore, MD, pp. 819-841
 4
 5 520
 6
 7 521 Holden-Musser ME, Juškaitis R, Musser GM (2016) Gliridae. In: Wilson DE, Lacher TE,
 8
 9 Mittermeier RA (eds) Handbook of the Mammals of the World, Vol. 6. Lagomorphs
 10 522
 11 and Rodents I. Lynx Edicions, Barcelona, pp. 838-889
 12
 13 523
 14
 15 524 von Koenigswald W (1993) Die Schmelzmuster in den Schneidezähnen der Gliroidea (Gliridae
 16
 17 und Seleviniidae, Rodentia, Mammalia) und ihre systematische Bedeutung. Zeit
 18 525
 19 Säugetierkd 58:92-115
 20
 21 526
 22
 23 527 Mason MJ (2016) Structure and function of the mammalian middle ear. I: Large middle ears
 24
 25 in small desert mammals. J Anat 228:284-299
 26 528
 27
 28 529 Montgelard C, Matthee CA, Robinson TJ (2003) Molecular systematics of dormice (Rodentia:
 29
 30 Gliridae) and the radiation of *Graphiurus* in Africa. Proc R Soc Lond B 270: 1947-1955
 31 530
 32
 33 531 Nunome M, Yasuda SP, Sato JJ, Vogel P, Suzuki H (2007) Phylogenetic relationships and
 34
 35 divergence times among dormice (Rodentia, Gliridae) based on three nuclear genes.
 36 532
 37 Zool Scripta 36:537-546
 38
 39 533
 40
 41 534 Ognev SI (1947) Mammals of the USSR and adjacent countries. Mammals of Eastern Europe
 42
 43 and Northern Asia, Vol 5. Rodents. Israel Program Scientific Translations, Jerusalem
 44 535
 45 (Translated 1963)
 46 536
 47
 48 537 Ohazama A, Blackburn J, Porntaveetus T, Ota MS, Choi HY, Johnson EB, Myers P, Oommen S,
 49
 50 Eto K, Kessler JA, Kondo T (2010) A role for suppressed incisor cuspal morphogenesis
 51 538
 52 in the evolution of mammalian heterodont dentition. Proc Natl Acad Sci U S A,
 53
 54 107:92-97
 55
 56
 57 540
 58
 59
 60
 61
 62
 63
 64
 65

- 541 Potapova EG (2001) Morphological patterns and evolutionary pathways of the middle ear in
542 dormice (Gliridae, Rodentia). Trakya Uni J Sci Res B 2:159-170
- 543 Schleich CE, Vassallo AI (2003) Bullar volume in subterranean and surface-dwelling
544 caviomorph rodents. J Mammal 84:184-189
- 545 Storch G (1994) Affinities among living dormouse genera. Hystrix 6: 51-62
- 546 Swofford DL (2003) PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods)
547 v4.0a. Sinauer Associates, Sunderland, Massachusetts
- 548 Wahlert JH, Sawitzke SL, Holden ME (1993) Cranial anatomy and relationships of dormice
549 (Rodentia, Myoxidae). Am Mus Novit 3061:1-32
- 550 Wang Y (1985) A new genus and species of Gliridae, *Chaetocauda sichuanensis* gen. et sp.
551 nov. Acta Theriol Sinica 5:67-75
- 552 Wilson DE, Reeder DM (2005) Mammal Species of the World. Johns Hopkins Press, Baltimore
- 553 Yachontov EL, Potapova EG (1991) On the position of dormice (Gliroidea) in the system of
554 rodents. Proc Zool Inst Acad USSR 243:127-147
- 555
- 556
- 557
- 558
- 559
- 560
- 561
- 562
- 563 Tables

Table 1: Number of shared characters between dormouse genera included by Wahlert et al. (1993) and the desert dormouse *Selevinia betpakdalaensis*.

Number of characters shared with <i>Selevinia</i>	Dormouse genus
39	<i>Myomimus</i>
36	<i>Dryomys</i>
35	<i>Graphiurus</i>
34	<i>Eliomys</i>
29	<i>Glirulus</i>
23	<i>Muscardinus</i>
21	<i>Glis</i>

Figure captions

Figure 1: Skin of *Selevinia betpakdalaensis*, specimen S-28487 (paratype), in (a) dorsal and (b) ventral view.

Figure 2: Virtual reconstructions of the cranium and mandible of *Selevinia betpakdalaensis* in left lateral view, (a) specimen 32206, (b) specimen S-28487. Note the characteristic grooved upper incisors, the robust lower incisors, reduced size of the molars and the greatly inflated auditory bullae.

Figure 3: Glirid skulls, right lateral view, zygomatic arch removed.

Abbreviations for foramina and other apertures: ac, alisphenoid canal, posterior end; bu, buccinator; dpl, dorsal palatine; eth, ethmoid; fo, foramen ovale; hy, hypoglossal; ifo, infraorbital; in, incisive; ito, interorbital; ju, jugular; mlf, middle lacerate; msc, masticatory; nl, nasolacrimal; op, optic; paf, posterior alar fissure; pgl, postglenoid; pom, posterior maxillary; ppl, posterior palatine; sf, sphenofrontal; spl, sphenopalatine; spv, sphenopalatine vacuity; stm, stapedius muscle canal; sty, stylomastoid; trc, transverse canal; un, unossified area.

588 Abbreviations for bones and their processes: as, alisphenoid; ab, auditory bulla; bo,
589 basioccipital; bs, basisphenoid; f, frontal; ip, interparietal; j, jugal; 1, lacrimal; m, maxilla; mst,
590 mastoid region; n, nasal; oc, occipital; os, orbitosphenoid; p, parietal; pl, palatine; pm,
591 premaxilla; ps, presphenoid (continuous with orbitosphenoid); sq, squamosal.

592 This image is modified with permission from Wahlert et al. (1993) by the inclusion of the
593 *Selevinia* skull.

594

595 Figure 4: Glirid skulls, ventral view. See Figure 3 for abbreviations. Image is modified
596 with permission from Wahlert et al. (1993) by the inclusion of *Selevinia*.

597

598 Figure 5: Glirid skulls, dorsal view. See Figure 3 for abbreviations. Image is modified with
599 permission from Wahlert et al. (1993) by the inclusion of *Selevinia*.

600

601 Figure 6: Glirid skulls, frontal view. See Figure 3 for abbreviations. Image is modified
602 with permission from Wahlert et al. (1993) by the inclusion of *Selevinia*.

603

604 Figure 7: Glirid mandibles, right buccal views. Abbreviations: an, angle; con, condyloid
605 process; cor, coronoid process; d, dentary bone; fen fenestra; mfos, masseteric fossa; mt,
606 mental foramen; san, superior angular process. Image is modified with permission from
607 Wahlert et al. (1993) by the inclusion of *Selevinia* and the coronoid process of *Glirulus*.

608

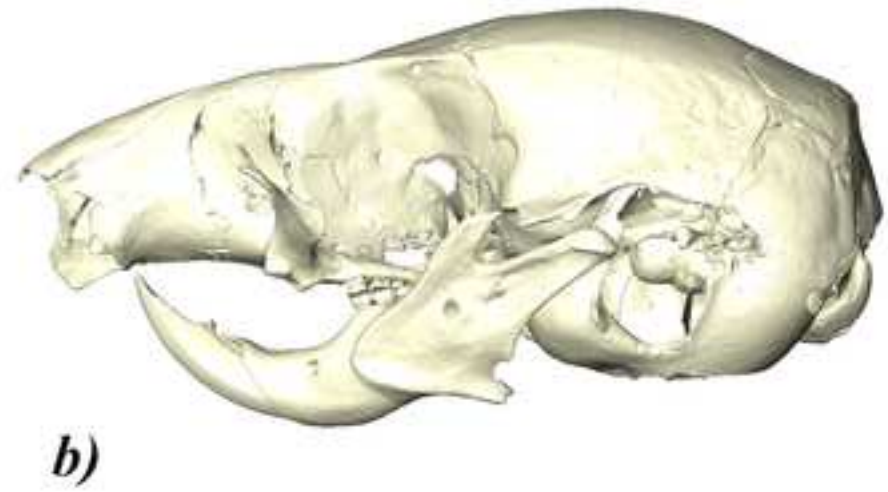
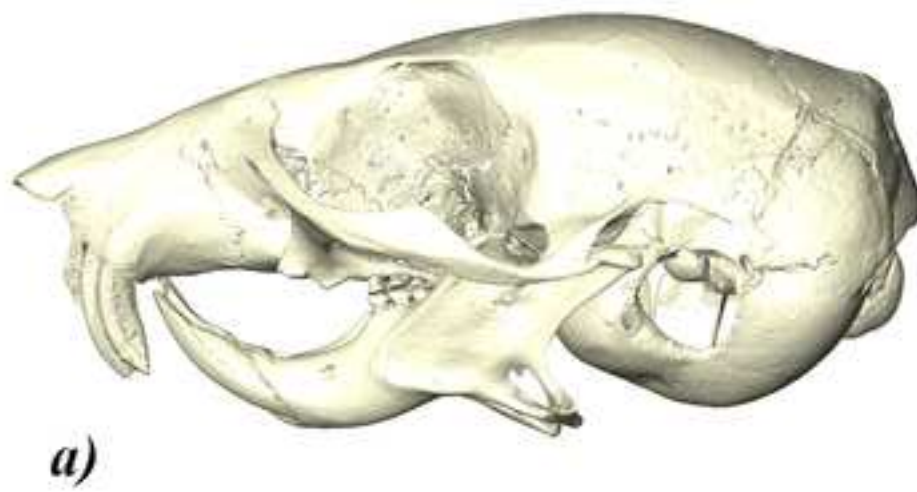
Figure 8: (a) Rendering of specimen 32206 with the dentition segmented separately showing the extent of the molar roots and the origin of the incisors. (b) Enlarged lateral (lingual) view of the upper and lower molar rows (left, mesial; right distal) in the original resolution (4.9 μm).

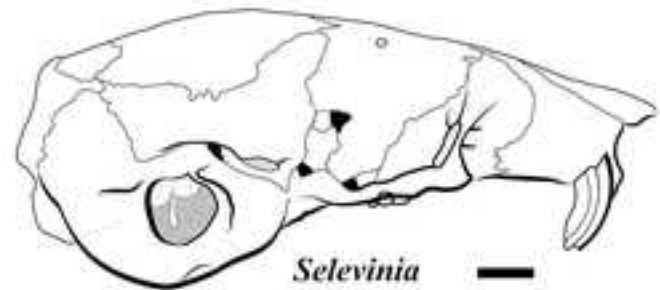
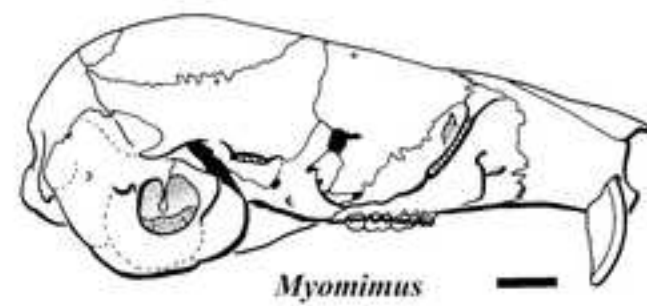
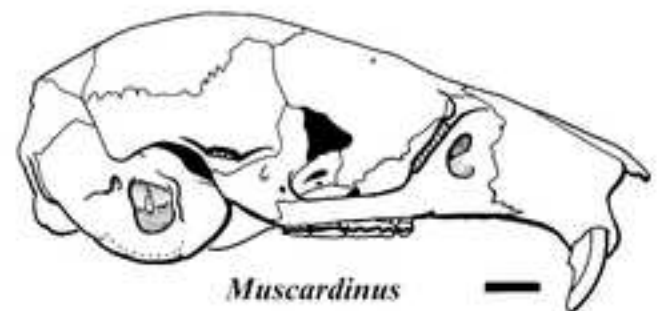
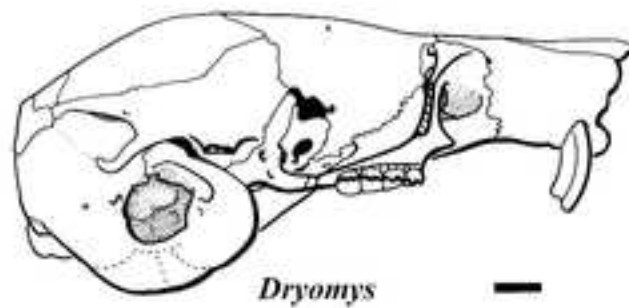
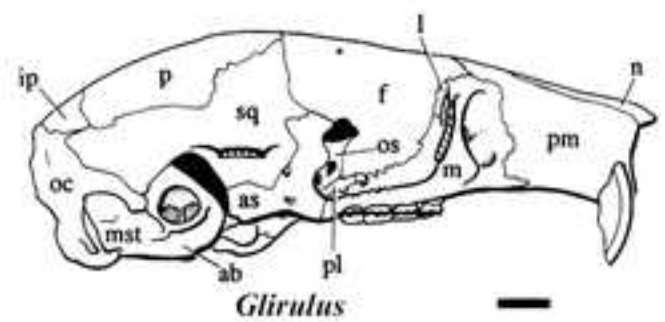
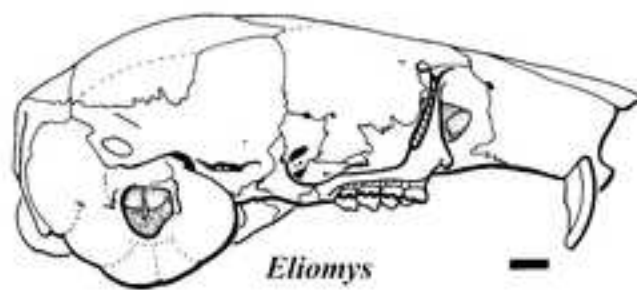
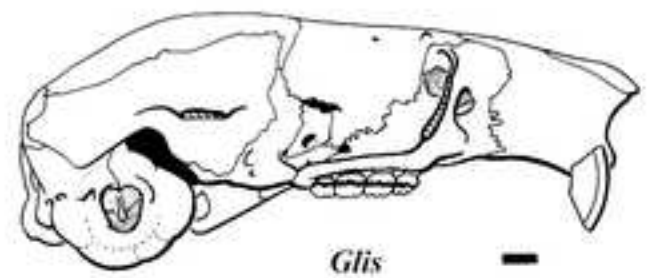
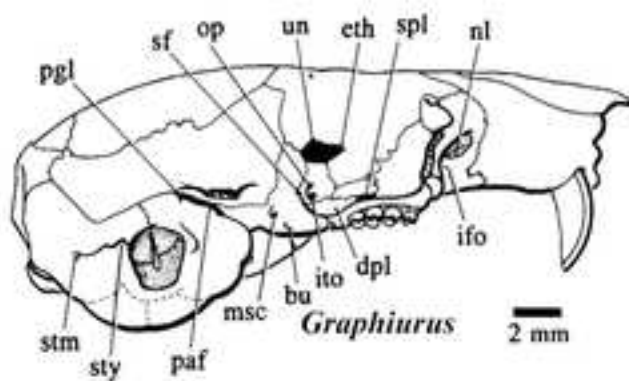
Figure 9: Most parsimonious tree recovered from analysis of 54 cranial, mandibular and dental characters. Character states for all taxa except *Selevinia* taken from Wahlert et al. (1993).

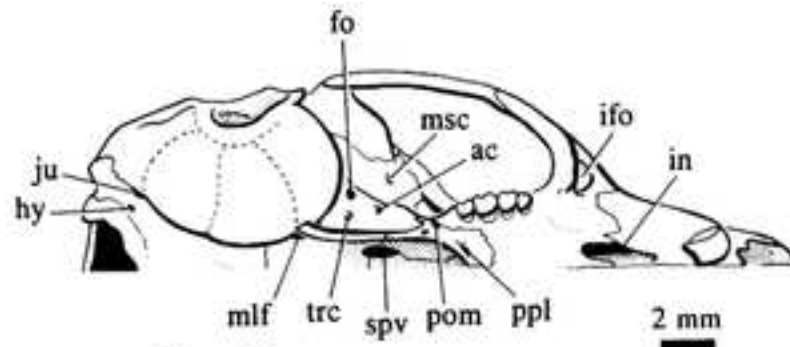
Figure 1

[Click here to access/download;Figure;Figure 1 skins.tif](#)









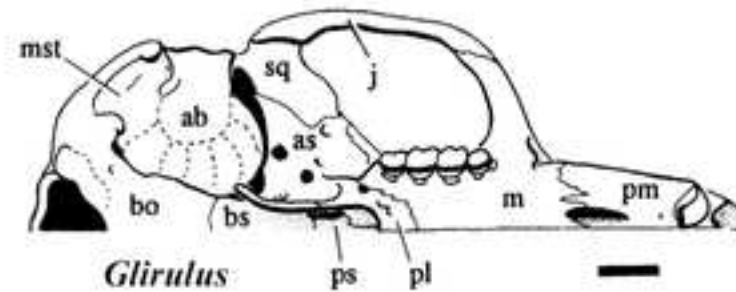
Graphiurus



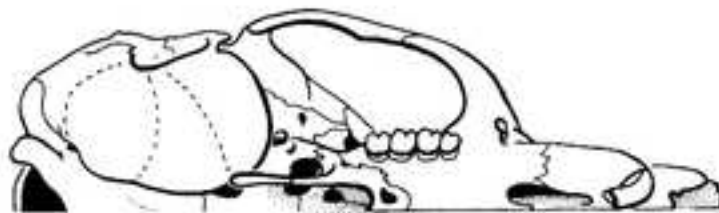
Glis



Eliomys



Glirulus



Dryomys



Muscardinus



Myomimus



Selevinia

