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

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

35

36 Introduction

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

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3 44 structures within this species in comparison to dormice. Ognev (1947) identified the animal as
4
5 45 a highly derived dormouse and emphasised the resemblance of this species to *Myomimus*. He
6
7 46 therefore created the subfamily Seleviniinae within the family Gliridae. More recent analyses
8
9 47 of the enamel structure in this animal and other dormice also incorporated *Selevinia* within
10
11 48 Gliridae, and no longer acknowledged Seleviniidae as a sister group of Gliridae (von
12
13 49 Koenigswald, 1992). Storch (1994) assigned *Myomimus* and *Chaetocauda* to Seleviniinae
14
15 50 alongside *Selevinia*, regarding it as the most primitive of all extant dormice subfamilies. In
16
17 51 contrast, Yachontov and Potapova (1991) considered *Selevinia* to be more closely related to
18
19 52 *Muscardinus* and *Glis*, belonging to the subfamily Glirinae. Later, Potapova reasserted the close
20
21 53 relationship between *Myomimus* and *Selevinia* based on middle ear morphology (Potapova,
22
23 54 2001). Wahlert et al. (1993) placed *Selevinia* and *Myomimus* in the tribe Seleviniini, which,
24
25 55 joined with the tribe Leithiini, formed the subfamily Leithiinae. Due to the scarcity of accessible
26
27 56 specimens, *Selevinia* was not included in the phylogenetic analyses of the Gliridae based on
28
29 57 molecular data by Montgelard et al. (2003) or Nunome et al. (2007). The exact placement of
30
31 58 the species within the dormouse phylogeny therefore remains unclear. However, the current
32
33 59 consensus is to place the monospecific genus within the subfamily Leithiinae and refrain from
34
35 60 the use of Seleviniinae (Holden-Musser et al. 2016).
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46 61
47 62 Eighty years after its first description in the literature, a great deal is still unknown about the
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49 63 desert dormouse. The inhospitable desert environment in which it lives has resulted in only a
50
51 64 few specimens being captured in the wild. We know of five specimens of the species caught
52
53 65 by hand during an expedition in 1938, and another specimen in 1946. The species appears to
54
55 66 be widely distributed in the south and east parts of Kazakhstan, especially in the deserts
56
57 67 surrounding Lake Balkhash, and has been documented as far south in Kara-Ungur, near the
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68 border with Kyrgyzstan (Bashanov and Belosludov, 1941; Holden, 2005). The animal is likely
69 predated on by birds of prey, as *Selevinia* material has been reportedly found in bird pellets
70 (Argyropulo and Vinogradov, 1939). Bashanov and Belosludov (1941) noted that the coat of
71 the animal is quite long and dense. It is light grey in colour dorsally, including some dark specks,
72 but light grey and slightly yellowish ventrally. The ears are rather large, including reddish hairs
73 on the outside. No clear facial mask, as seen in *Eliomys* for example, is apparent. The tail is
74 short haired and dark grey dorsally, but significantly lighter ventrally. The forepaw includes
75 four digits, and the hind leg has five, with the soles lacking in hair. The five specimens analysed
76 by Bashanov and Belosludov (1941) showed a total body length varying between 78 and 95
77 mm, with the tail length varying between 58 and 77 mm. Cranial length was only assessed in
78 three specimens, indicating a range between 21.5 and 22.1 mm.

79
80 Wahlert et al. (1993) described the cranial morphology of most extant dormouse genera using
81 a total of 54 cranial and mandibular characteristics. At the time, the authors did not have access
82 to cranial material of *Selevinia*, but instead used former descriptions and dated photographic
83 material to assess the morphological characteristics within the genus (Bashanov and
84 Belosludov, 1941; Ognev, 1947). Due to the resolution and orientation of the figures consulted,
85 the states of many cranial characters could not be reliably determined in the genus. Here, we
86 use microCT data of two adult specimens of *Selevinia betpakdalaensis* in order to describe the
87 cranial anatomy of this species and to complement the dataset created by Wahlert et al.
88 (1993). We believe this to be the first time this species has been scanned using microCT,
89 allowing us to assess the cranial morphology of this species in very high detail. This description
90 will result in a much greater understanding of the distinct morphological features present in

1 91 the desert dormouse, and will enable us to compare this species with other dormouse taxa
2
3 92 more accurately.
4

5 93

6 7 94 **Materials and methods**

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9
10 95 The sample comprised the skulls and mandibles of two adult specimens of the species *Selevinia*
11
12 96 *betpakdalaensis*, both housed in Russian institutions. Specimen ZIN 32206 is an adult male
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15 97 collected on the 21st August, 1946, by M. A. Musarov near the Meteo Station in Betpak-Dala
16
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18 98 Desert (46°02'N; 70°12'E). It was placed in the Zoological Institute of Kazakh Academy of
19
20
21 99 Sciences with the incoming number 34-1947. The specimen was later transferred to the
22
23 100 Zoological Institute in Saint Petersburg on the 27th May, 1947. The material, consisting of an
24
25
26 101 intact skull and a slightly broken mandible, was scanned at the Research Centre for X-ray
27
28 102 Diffraction Studies of Saint Petersburg State University (Saint Petersburg, Russia), using a high-
29
30
31 103 resolution X-ray computed micro-tomography scanner (SkyScan 1172) with an isometric voxel
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33
34 104 dimensions of 4.9 µm. The specimen was later downsampled to 9.8 µm in order to decrease
35
36 105 the computation time whilst rendering the object for analysis. Dentition was analysed using
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38
39 106 the original 4.9 µm resolution.
40

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44 108 Specimen S-28487 was captured in the northern part of Betpak-Dala Desert by V. Selevin on
45
46 109 8th August 1938. The specimen is considered a paratype and was donated to the Zoological
47
48
49 110 Museum in Moscow. The external morphology of this specimen is shown in Fig. 1. A microCT
50
51
52 111 scan of the skull and two hemi-mandibles was created at the Geology department of Moscow
53
54 112 State University (Moscow, Russia) on a SkyScan 1172. The resolution of the scanned material
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57 113 is 15.42 µm.
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115 Three-dimensional virtual reconstructions of the skull and lower jaw of each specimen were
116 created from the microCT scans using the segmentation function of Avizo 9.2 (Thermo Fisher
117 Scientific, Waltham, MA, USA). Both surface files of the scanned dormice were uploaded to the
118 online database Morphosource (www.morphosource.org). Linear measurements of the
119 cranium and dentition were recorded from the reconstructions and are given in ESM 1. The
120 virtual reconstructions were used to produce detailed descriptions of the cranial, mandibular
121 and dental anatomy of *Selevinia betpakdalaensis*, and to determine the character states of the
122 54 anatomical characters used by Wahlert et al. (1993) in their analysis of dormouse cranial
123 anatomy (ESM 2). The morphology was also compared to all other dormouse genera, but in
124 particular *Myomimus* and *Muscardinus*, because the former has been hypothesised to have a
125 close phylogenetic relationship with *Selevinia* (Wahlert et al., 1993; Storch, 1994; Potapova,
126 2001) and the latter is a similarly small-sized dormouse. The character state data for *Selevinia*
127 were combined with data for all other dormouse genera (except *Chaetocauda*) and four
128 outgroup taxa (*Paramys*, *Sciurus*, *Sicista* and *Cricetulus*) taken from Wahlert et al. (1993) in a
129 parsimony analysis, conducted in PAUP* 4.0a167 (Swofford, 2003). The most parsimonious
130 tree was compared with the cladogram presented in Wahlert et al. (1993), as well as with
131 phylogenies of the Gliridae derived from molecular data (Montgelard et al. 2003; Nunome et
132 al. 2007).

133

134 Results

135 *Specimen descriptions*

136 The reconstruction of Specimen 32206 is shown in Fig. 2. The skull includes one incisor and
137 three molars on each side. The right pterygoid flange is broken, as is the ventralmost area of
138 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*

162 Numbers in square brackets correspond to the character list set out in the appendix of Wahlert
163 et al. (1993). A full scoring of these characters in *Selevinia betpakdalaensis* alongside the
164 character states for other dormice genera and four rodent outgroups from Wahlert et al.
165 (1993) is given in ESM 3.

166

167 *Cranium*

168 In order to facilitate comparison, the skull shape of various dormouse genera are presented in
169 Figs. 3-6. *Selevinia betpakdalaensis* is a small dormouse species, with the two specimens
170 analysed for this study having skull lengths of roughly 21 and 24 mm compared with a range of
171 18 to 40 mm in other species (Holden-Musser et al. 2016). When examined dorsally, the
172 posterior extent of the premaxilla is roughly at the same location as that of the nasal bones [1]
173 and extends farther than the maxilla [2]. As in all other dormice genera, the anterior end of the
174 premaxilla is tall and high above the most anterior part of the incisor alveolus [3]. The nasal
175 bone varies significantly between both skulls. Specimen S-28487 has a much broader anterior
176 part of the nasal bone in comparison with Specimen 32206. It is possible that this feature is
177 deformed in the former specimen, but it is difficult to determine if this happened post-mortem
178 or not. Nonetheless, both specimens indicate that the nasal bone is rather wide in comparison
179 with most dormice genera. The infraorbital foramen is similar in size and position to in
180 *Myomimus*, although *Myomimus* has more developed ridges on the lateral side of this foramen
181 and flares more strongly inferiorly, resulting in a very pronounced anterior extension of the
182 ventral margin. This extension is present, although less pronounced, in *Selevinia*. As *Selevinia*
183 has a clearly reduced molar row, the diastema is technically longer than is seen in other
184 dormice; however, there is a clear distinction between the area created by molar reduction
185 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.

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3 211 On the ventral aspect of the skull, the premaxillary-maxillary suture connects with the incisive
4
5 212 foramina near their midpoints [10], in a similar fashion to all other genera. The area between
6
7
8 213 the anterior part of the incisive foramen and the incisor is of similar length to that of *Myomimus*
9
10 214 and shorter than *Glis*. The ratio of incisive foramen length to diastema is roughly 85% [11] and
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12
13 215 therefore most similar to *Myomimus*. However, when using the full diastemal length (anterior
14
15 216 part molar row to posterior part of the incisor alveolus), the ratio is only 69% and falls within
16
17
18 217 the range of *Eliomys*. The anteromedial position of the palatine bone with respect to the molar
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20
21 218 row is located between the posterior part of M2 and the M2-M3 junction [12], relatively caudal
22
23 219 compared to all other genera. This is thought to be a by-product of the reduction of the molar
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25
26 220 row. Furthermore, the reduction in molar size results in a relatively large palatal width between
27
28 221 the M1 teeth in *Selevinia*, with a ratio of palatal width to condylobasilar length of 0.16 [13].
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31 222 This ratio is also similar in many *Dryomys* and *Glirulus* specimens, but smaller in other genera.
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34 223 The posterior palatine foramen is within the palatine bone and medial to the M3 [14], similar
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36 224 to *Glirulus*, *Myomimus* and some *Graphiurus*. The posteriorly orientated spine on the medial
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39 225 posterior end of the palate is absent in *Selevinia* [15], whereas it is very weakly present in
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41 226 *Myomimus* and *Glis*. The opening of the posterior maxillary notch or foramen is a difficult
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43
44 227 characteristic to determine. Wahlert et al. (1993) distinguish various options within species for
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46 228 *Glis* and *Dryomys*, in which the notch or foramen is either well enclosed or just enclosed. We
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49 229 examined multiple species ourselves in order to correctly assign this character to *Selevinia* and
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51
52 230 noticed that our *Glirulus* specimen has no maxillary notch or foramen. Instead a foramen is
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54 231 present within the alisphenoid, which is well enclosed and could easily be confused with a
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57 232 maxillary foramen. Wahlert et al. (1993) originally assigned the well enclosed option for the
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59 233 maxillary foramen for *Glirulus*, but it is unclear from their figures whether this is because of an
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3 235 species. *Selevinia* shows a maxillary notch rather than a foramen, which can be considered
4
5 236 either just enclosed, or well enclosed. It appears to be more enclosed than our *Graphiurus*
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8 237 specimen, in which the maxillary notch is assigned just enclosed according to Wahlert et al.
9
10 238 (1993). Following this reasoning, the characteristic of the enclosure of the maxillary notch in
11
12
13 239 *Selivinia* is determined to be well enclosed [16].

14
15 240

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18 241 Similar to all other dormice, the entrance of the lacrimal canal is situated anteromedially with
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20
21 242 respect to the infraorbital foramen [17]. The anterior part of the sphenopalatine foramen is
22
23 243 slightly posterior to the middle of M2 [18], similar to *Glirulus* and *Myomimus* as well as some
24
25
26 244 *Graphiurus* and *Dryomys* specimens. The non-ossification between the orbitosphenoid and the
27
28
29 245 frontal is present within one of our *Selevinia* specimens, but absent in the other [19]. Where
30
31 246 present it appears to have incorporated the ethmoid foramen. The anterior part of this area is
32
33
34 247 dorsal to M3 and extends posterodorsally beyond M3. In the specimen lacking the non-
35
36 248 ossification, the ethmoid foramen is more clearly identifiable and dorsal to M3 [20]. The optic
37
38
39 249 foramen is located even more posteriorly [21] and is quite small [22], similar to *Myomimus* and
40
41 250 *Glirulus*. The dorsal palatine foramen is positioned entirely posterodorsally to M3 [23] and
42
43
44 251 relatively close to the sphenopalatine foramen [24] in comparison to *Eliomys* and *Dryomys*. The
45
46 252 sphenofrontal foramen appears to be present in *Selevinia* [25], but the frontal bone does not
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49 253 extend all the way to this foramen [26]. There is no connection between the parietal bone and
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51
52 254 the alisphenoid [27].

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57 256 The foramen ovale is distant from the posterior entrance of the alisphenoid canal [28], in a
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59 257 similar fashion to *Eliomys*. An accessory foramen ovale appears to be absent [29], which
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3 259 corresponds with all other dormice. There is a fenestra anterodorsal to the masticatory
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5 260 foramen [30], which is absent in some *Muscardinus* and *Eliomys* specimens, and in all *Glis* and
6
7 261 *Glirulus* specimens. The lateral pterygoid flange very is weakly developed in *Selevinia* [31] as
8
9 262 opposed to *Glis glis*. Wahlert et al. (1993) indicate this pterygoid flange to be present also
10
11 263 within *Muscardinus*, whereas it is clearly absent in our specimen of this species. Similar to all
12
13 264 other dormice genera, the sphenopalatine vacuity in *Selevinia* extends to the edge of the
14
15 265 anterior alar fissure, but is not visible in the orbit [32] as in *Eliomys* and some *Dryomys*
16
17 266 specimens. The ratio of the distance between the posterior edge of M3 and the anterior part
18
19 267 of the foramen ovale to the condylobasilar length for *Selevinia* is between 0.12 and 0.14 [33].
20
21 268 This is similar to most dormice genera – only the genus *Muscardinus* appears to have a ratio
22
23 269 smaller than 0.1. The stapedial artery and the foramen in which the stapedius muscle takes its
24
25 270 origin are present within *Selevinia*. These features are similar in size compared to those in our
26
27 271 *Myomimus* specimens and therefore considered small [34].
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34 272 The posterior part of the zygomatic arch is orientated relatively inferiorly with the most lateral
35
36 273 part not extended posteriorly, as is seen in *Myomimus*, for example. The area bounded by the
37
38 274 zygomatic arch is oblong in dorsal view, which is representative for smaller dormice species.
39
40 275 Furthermore, the interparietal and parietal bones are curved, another feature often observed
41
42 276 in smaller genera and juvenile dormice. A dorsal orbital ridge is quite strongly developed
43
44 277 (compared to other dormouse genera) in both specimens. A groove potentially related to
45
46 278 muscle attachment of the temporalis muscle is clearly visible on the squamosal when observed
47
48 279 laterally. This groove is less apparent in *Muscardinus*, but much more pronounced in
49
50 280 *Myomimus*. *Selevinia* and all other dormice genera have the postglenoid foramen positioned
51
52 281 between the auditory bulla and the squamosal bone [35]. The posterior part of the squamosal
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3 283 bone is solid [36], similar to *Glirulus*, *Glis*, *Graphiurus* and *Muscardinus*. No clear temporal
4
5 284 foramen is present at the squamosal-parietal suture [37], and neither is this foramen present
6
7
8 285 in any other genus.

9
10 286 The foramen magnum, although incomplete in S-28487, appears to be relatively enlarged. The
11
12 287 foramen magnum is orientated caudally in a similar fashion to *Myomimus*. The auditory bullae
13
14 288 in are greatly inflated in all dormice genera but *Glis*, in which this feature is only slightly inflated.
15
16 289 *Selevinia* however shows exceptionally well-inflated auditory bullae [38], resulting in the length
17
18 290 of this feature representing 36% and 37% of the total skull length respectively, significantly
19
20 291 larger than in any other dormouse genus. Three primary septa appear to be present within the
21
22 292 auditory bullae [39], similar to all other genera, with the exception of *Glirulus*.

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29 30 31 294 *Mandible*

32
33 295 The mandibles of various dormouse genera are illustrated in Fig. 7. The mandibular material of
34
35 296 *Selevinia* available for this study is slightly broken. However, most features are present and
36
37 297 intact in Specimen 32206. The diastema is rather flat when considering other genera. The
38
39 298 mandible of *Selevinia* is quite distinctive compared to other dormice, characterised by robust
40
41 299 incisors, a lack of premolars, extremely small molars and a condyle that is posteriorly extended
42
43 300 with respect to the angular process. The angular processes in the two specimens observed
44
45 301 here are perforated with a single, large fenestra [40] in a similar fashion to that often seen in
46
47 302 *Myomimus*, *Muscardinus*, *Dryomys* and *Eliomys*. The flaring of the angular process is not very
48
49 303 significant and the muscle attachment area relatively small. The condyle stretches out
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51 304 posteriorly and has a relatively small condylar head. The coronoid process is only intact in one
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53 305 dentary, and it flares posteriorly and slightly laterally, as is common in other dormice species.
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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.

46 324 *Dentition*

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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

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3 330 *Chaetocauda* corresponds with what is seen in *Selevinia*, although it should be noted that the
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5 331 pictures in Wang (1985) are not clear enough to compare this feature accurately with our
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7 332 *Selevinia* specimens. The segmented incisor shows that this groove is already apparent at the
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9 333 origin of the incisor, located medially to the zygomatic plate. The enamel is relatively thin and
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11 334 evenly spread throughout the anterior part of the incisor. In our evaluation of the enamel
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13 335 characteristic we presume the enamel cap to grade into the lateral surface [44]. The incisors
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15 336 are orientated downwards and ever so slightly posteriorly.

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20 338 The curvature of the lower incisors is similar to other dormice species, with the incisor root
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22 339 located inferoposteriorly to the last molar. The lower incisors are very robust in comparison to
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24 340 any of the other dormice species, but lack the anterior groove characterising the upper
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26 341 incisors. However, the lower incisors show a ridge on their occlusal surface which is likely a
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28 342 result of wear from the grooved upper incisors.

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34 344 The ratio of upper cheek teeth crown length to condylobasilar length is very small (less than
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36 345 0.2) in *Selevinia* [45], as a result of the very small, brachydont molars characterising this genus.

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38 346 The genus is also the only one in which all upper and lower premolars appear to be absent
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40 347 [46,47], although both *Muscardinus* and *Myomimus* show reduced premolars, in contrast to
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42 348 other genera. In the adult *Selevinia* specimens studied here, small cavities can be seen located
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44 349 anterior to the first upper molar. As Bashanov (1951) observed two deciduous premolars in
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46 350 juvenile *Selevinia* specimens, the cavities in our specimens are therefore identified as
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48 351 (remnants of) the alveoli of the deciduous fourth premolars.

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

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

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3 376 indications of a large posterior root fused with an anterior accessory root. Only one canal is
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5 377 present in every molar, similar to the upper molars.

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8 379 *Phylogenetic analysis* The most parsimonious tree of dormouse genera based on
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10 380 cranio-mandibular and dental characters had a length of 150 and is given in Fig. 9. *Selevinia* is
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12 381 found to be most similar to *Myomimus*, and then to a grouping of *Eliomys* and *Dryomys*. These
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14 382 four genera are then most closely related to *Graphiurus*, with *Glis*, *Muscardinus* and *Glirulus*
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16 383 forming a separate group. Tree support values were CI = 0.613, RI = 0.536 and RC = 0.329.
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22 23 385 Discussion

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25 386 A number of unusual and highly derived morphological features within the skull and lower jaw
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27 387 of *Selevinia betpakdalaensis* were described using the virtual reconstruction of two specimens.

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29 388 The most obvious of these are the extremely reduced and simplified cheek teeth. Loss of the
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31 389 premolars is not unusual within rodents, occurring widely throughout the order, notably in the
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33 390 Muridae (although not in any other dormouse species). However, a reduction in the size and
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35 391 complexity of the molars is much less common, with the only other known examples of this
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37 392 phenomenon in rodents being specialist worm-eating taxa from Southeast Asia, such as
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39 393 *Paucidentomys*, *Pseudohydromys* and *Rhynchomys* (Esselstyn et al. 2012; Charles et al. 2013).

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41 394 Such a vermivorous diet is unlikely in *Selevinia* given the lack of an elongated rostrum and the
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43 395 presence of robust incisors, although it should be noted that the precise diet of this species is
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47 396 at the moment unclear. Captive specimens of this species were observed to consume mostly
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49 397 insects (Ognev, 1947), but an analysis of stomach contents of a wild specimen revealed
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53 398 undigested leaves of a desert plant, *Salsola laricifolia* (Bashanov and Belosludov, 1941). An
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55 399 insectivorous diet is most likely given the small, simple molars, but the robust incisors have
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3 400 also been suggested as an adaptation to cropping tough vegetation (Holden-Musser et al.
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5 401 2016).

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11 403 The upper incisors of *Selevinia* are also highly unusual, displaying a prominent groove antero-
12 404 laterally, which gives them an irregular cross-section. Analogues for this morphology seem to
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14 405 be present in some other rodents (Ohazama et al. 2010), such as the meadow jumping mouse
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16 406 (*Zapus hudsonius*) and the capybara (*Hydrochoerus hydrochaeris*), as well as being found in
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19 407 lagomorphs including pikas (Ochotonidae). It is unclear at the moment what advantage such a
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22 408 groove may convey.

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27 410 The auditory bullae of most dormouse species are enlarged (Wahlert et al. 1993), but this trait
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29 411 is taken to the extreme in *Selevinia*, which has the largest bullae relative to cranial length of all
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32 412 Gliridae. This is perhaps not surprising as hypertrophied auditory bullae are known to be
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34 413 common in small desert mammals (Alhajeri et al. 2015; Mason, 2016). Such morphology
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37 414 increases the acuity of low frequency hearing and has the potential advantages to desert
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40 415 dwelling species of improving communication over long distances or better seismic detection.
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42 416 Enlarged auditory bullae are also common in fossorial rodents owing to the slower attenuation
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45 417 of low frequency sounds in subterranean tunnels (Schleich and Vassallo, 2003). Thus, it is
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48 418 possible that *Selevinia* is spending at least part of its life underground. This interpretation is
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50 419 also supported by other characters such as the relatively narrow width of the cranium, with
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53 420 the zygomatic arches being only slightly more laterally extended than the posterior part of the
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55 421 skull, and the caudal orientation of the foramen magnum. The latter character indicates a
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58 422 rectilinear posture, similar to *Myomimus*, which would be advantageous for moving through

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1 423 underground tunnels. Considering the barren landscape of the Betpak-Dala Desert and the
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3 424 hibernating characteristics within most dormice, adaptations to burrowing would not be
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5 425 surprising in the desert dormouse.

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10 427 The parsimony analysis of dormouse genera and four rodent outgroups produced a shortest
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13 428 tree very similar to that presented in Wahlert et al. (1993). The only difference was in the
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15 429 placement of *Graphiurus*, which was found to be the sister-group to all other dormouse genera
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18 430 in Wahlert et al. (1993), but was recovered as the sister-group to the Leithiinae (minus
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20 431 *Muscardinus*) in our analysis (Fig. 9). Although Wahlert et al. (1993) did not formally include
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23 432 *Selevinia* in their cladistic analysis, they hypothesised that it would be the sister-genus to
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26 433 *Myomimus*, and this is what we found here. More recent molecular phylogenies of the Gliridae
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28 434 (Montgelard et al. 2003; Nunome et al. 2007) show roughly similar topologies to that
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31 435 recovered here, but differ in the placement of *Muscardinus* which is found to be the sister-
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34 436 genus to the Leithiinae, and not closely related to *Glis* and *Glirulus*. This has led to the inclusion
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36 437 of *Muscardinus* within Leithiinae in recent classifications (Wilson & Reeder, 2005; Holden-
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39 438 Musser et al. 2016). There is also continued uncertainty in the position of *Graphiurus*, with
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41 439 Montgelard et al. (2003) placing it as the first branching genus (as also seen in Wahlert et al.
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44 440 1993), but Nunome et al. (2007) finding it to be sister-group to the Leithiinae, thus agreeing
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46 441 more closely with the analysis presented here. At the time of writing, *Selevinia* has yet to be
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49 442 included in a molecular-based phylogenetic analysis of dormice.

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54 444 As noted above, the reduced state of the molars in *Selevinia* prevents accurate coding of
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57 445 characters 50-54 (they were scored as missing in the parsimony analysis conducted here).
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59 446 Thus, these are excluded in all further discussion, leaving a total of 49 characters. When
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3 447 compared with the taxa analysed by Wahlert et al. (1993), *Selevinia* appears to resemble the
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5 448 small dormouse genus *Myomimus* most closely, sharing 39 of the 49 characters (Table 1).
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7 449 *Dryomys* follows *Myomimus* with 36 corresponding characters, closely followed by *Graphiurus*
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9 450 (35). Interestingly, the genus *Muscardinus* does not seem to resemble *Selevinia* greatly (23
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11 451 shared characters) despite being similar in cranial size, i.e. very small for dormice.
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13 452 Notwithstanding some controversy over the phylogenetic position of *Muscardinus* (Wahlert et
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15 453 al. 1993; Montgelard et al. 2003; Nunome et al. 2007) it is clear that this genus is not
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17 454 particularly closely related to *Selevinia*. This evolutionary distance may have led to the
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19 455 morphological differences between the genera. Alternatively, strong functional adaptation of
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21 456 the teeth (relatively large and densely ridged molars in *Muscardinus*, and simplified and
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23 457 reduced molars in *Selevinia*) may have driven a divergence in overall cranial morphology. Both
24
25 458 *Myomimus* and *Muscardinus* are characterised by a size reduction of the premolars. We
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27 459 hypothesise that *Selevinia* went through a similar premolar size reduction phase before losing
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29 460 its premolars completely.
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39 462 The similarity of *Selevinia* to *Myomimus* was expected and predicted by Wahlert et al. (1993).
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41 463 Furthermore, the similarity to *Dryomys* is understandable, as *Myomimus* has previously been
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43 464 proposed as a subgenus of *Dryomys*. However, the number of shared characteristics with
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45 465 *Graphiurus* was surprising, as *Muscardinus* is phylogenetically closer to *Myomimus* and
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47 466 *Dryomys* than to *Graphiurus* (Montgelard et al. 2003). Initially we hypothesised that the broad
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49 467 range of *Graphiurus* species may have resulted in many variable characters to be present
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51 468 within the genus, explaining the large potential correlation with *Selevinia*. However, when
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53 469 analysing the number of characters that are polymorphic within *Graphiurus*, we did not find an
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55 470 exceptionally large number (4 out of 49), especially when compared with *Dryomys* (8 out of
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1 471 49). Potentially, some primitive cranial characteristics are present in both the sub-Saharan
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3 472 dormice and the desert dormouse. It would be extremely interesting to include *Selevinia* in a
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5 473 phylogenetic study, in order to know the placement of this peculiar species within Gliridae.
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10 475 Our analysis of the cranial and mandibular morphology of the desert dormouse, *Selevinia*
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12 476 *betpakdalaensis*, shows that this species is morphologically very similar to the mouse-tailed
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14 477 dormice in the genus *Myomimus*. Derived cranial features are suggested to be adaptations to
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16 478 a burrowing lifestyle in a desert environment; these include extremely enlarged auditory
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18 479 bullae, and a reduced molar row both in number and size of teeth, as well as a less lateral
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20 480 extension of the zygomatic arch, relative to the posterior part of the skull. The detailed
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22 481 description of the cranial morphology will facilitate more reliable comparisons of *Selevinia* with
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24 482 other dormice, leading to a more complete overview of cranial and mandibular shape variation
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26 483 within the rodent family Gliridae.
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37
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39
40 487 within *Selevinia* and allowing them to modify the schematic figures by including *Selevinia*;
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54 494 Medical School.
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3 **496 Author contributions**

4
5 497 JJH and PGC conceived the study. JJH segmented the data and undertook the character
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7 498 analysis. JWFS produced the illustrations. FNG, LYK, DK, ON provided access to specimens. JJH
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10 499 and PGC drafted the manuscript. All authors contributed to the editing of the final manuscript
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13 500 and gave final approval before submission.

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57 563 **Tables**
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564 Table 1: Number of shared characters between dormouse genera included by Wahlert
 565 et al. (1993) and the desert dormouse *Selevinia betpakdalaensis*.

Number of characters shared with <i>Selevinia</i>	Dormouse genus
39	<i>Myomimus</i> 567
36	<i>Dryomys</i>
35	<i>Graphiurus</i> 568
34	<i>Eliomys</i>
29	<i>Glirulus</i> 569
23	<i>Muscardinus</i>
21	<i>Glis</i> 570

571

572 Figure captions

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

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

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

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

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3 588 Abbreviations for bones and their processes: as, alisphenoid; ab, auditory bulla; bo,
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5 589 basioccipital; bs, basisphenoid; f, frontal; ip, interparietal; j, jugal; 1, lacrimal; m, maxilla; mst,
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7 590 mastoid region; n, nasal; oc, occipital; os, orbitosphenoid; p, parietal; pl, palatine; pm,
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9 591 premaxilla; ps, presphenoid (continuous with orbitosphenoid); sq, squamosal.

10 592 This image is modified with permission from Wahlert et al. (1993) by the inclusion of the
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13 593 *Selevinia* skull.

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19 595 Figure 4: Glirid skulls, ventral view. See Figure 3 for abbreviations. Image is modified
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22 596 with permission from Wahlert et al. (1993) by the inclusion of *Selevinia*.

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28 598 Figure 5: Glirid skulls, dorsal view. See Figure 3 for abbreviations. Image is modified with
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31 599 permission from Wahlert et al. (1993) by the inclusion of *Selevinia*.

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38 601 Figure 6: Glirid skulls, frontal view. See Figure 3 for abbreviations. Image is modified
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41 602 with permission from Wahlert et al. (1993) by the inclusion of *Selevinia*.

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47 604 Figure 7: Glirid mandibles, right buccal views. Abbreviations: an, angle; con, condyloid
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50 605 process; cor, coronoid process; d, dentary bone; fen fenestra; mfos, masseteric fossa; mt,
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52 606 mental foramen; san, superior angular process. Image is modified with permission from
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55 607 Wahlert et al. (1993) by the inclusion of *Selevinia* and the coronoid process of *Glirulus*.

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609 Figure 8: (a) Rendering of specimen 32206 with the dentition segmented separately
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3 610 showing the extent of the molar roots and the origin of the incisors. (b) Enlarged lateral (lingual)
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5 611 view of the upper and lower molar rows (left, mesial; right distal) in the original resolution (4.9
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7 612 μm).

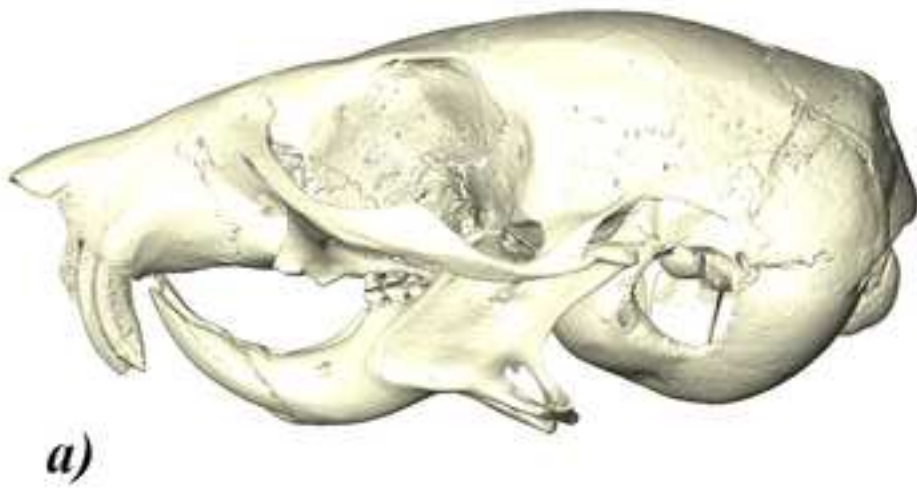
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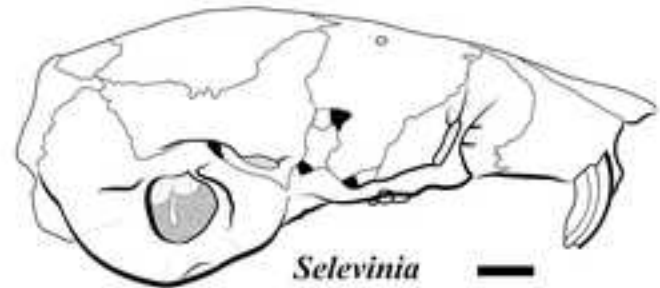
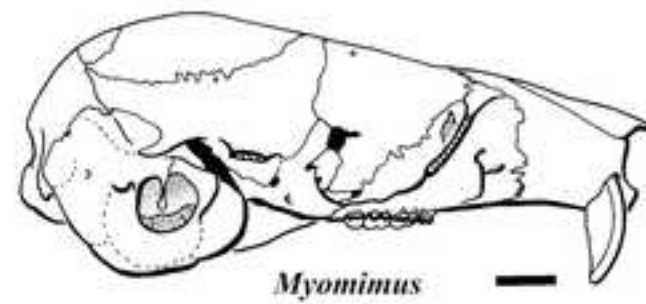
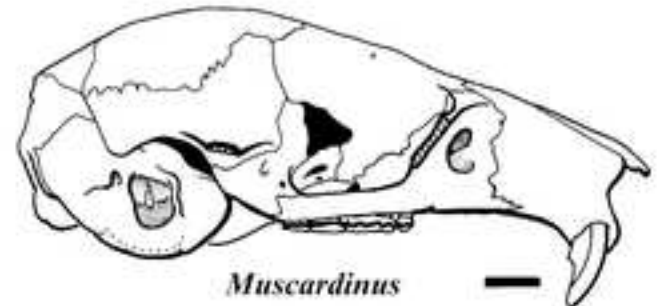
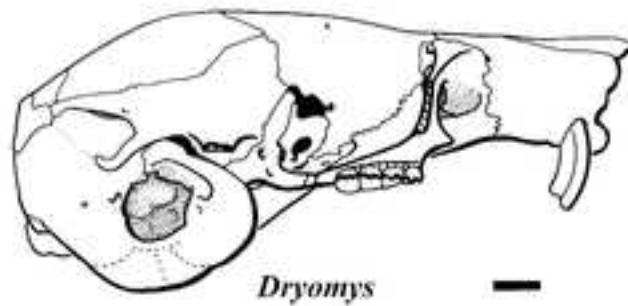
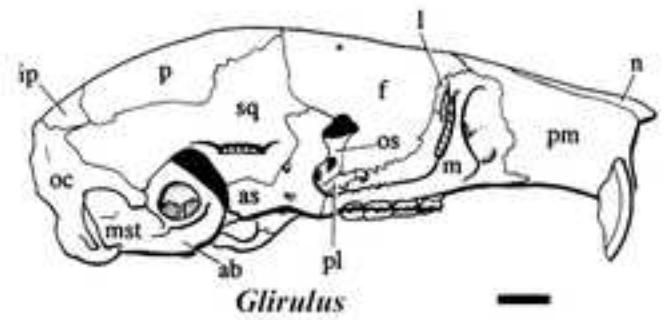
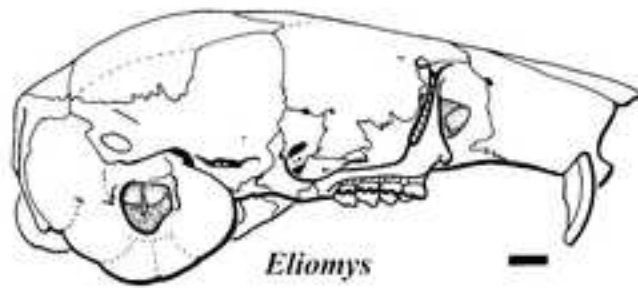
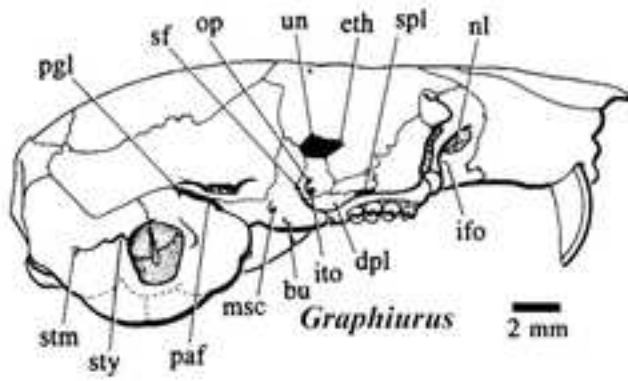
12 614 Figure 9: Most parsimonious tree recovered from analysis of 54 cranial, mandibular and
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15 615 dental characters. Character states for all taxa except *Selevinia* taken from Wahlert et al.
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17 616 (1993).

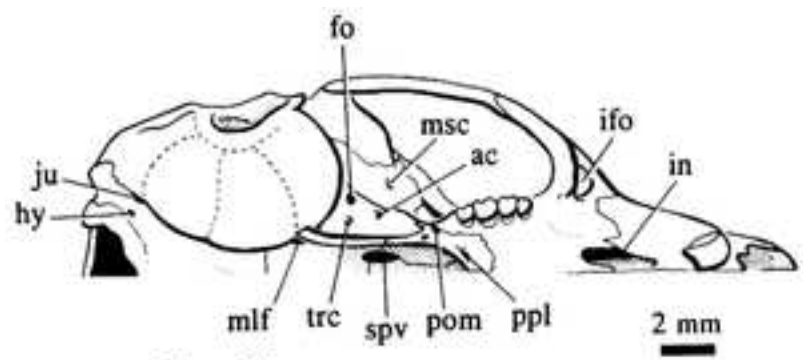
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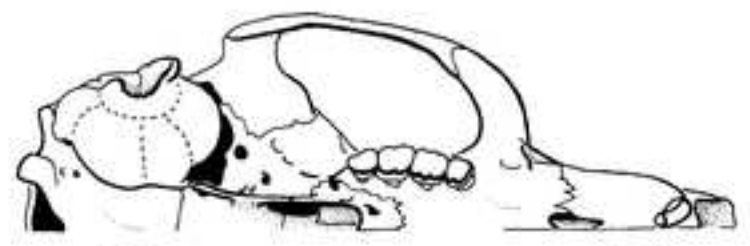




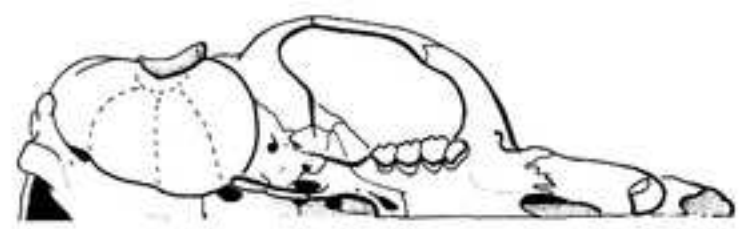




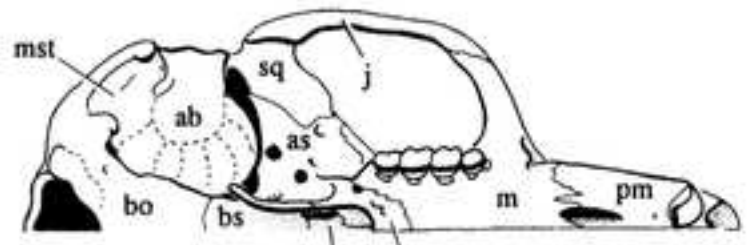
Graphiurus



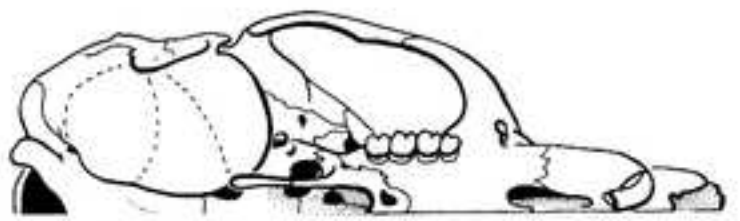
Glis



Eliomys



Glirulus



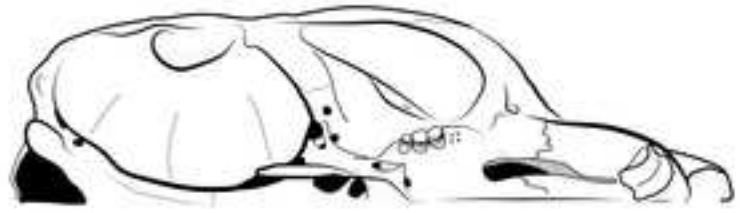
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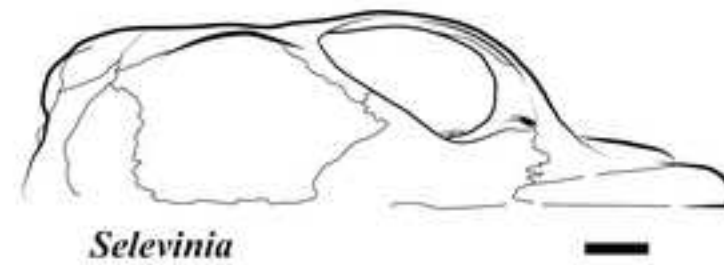
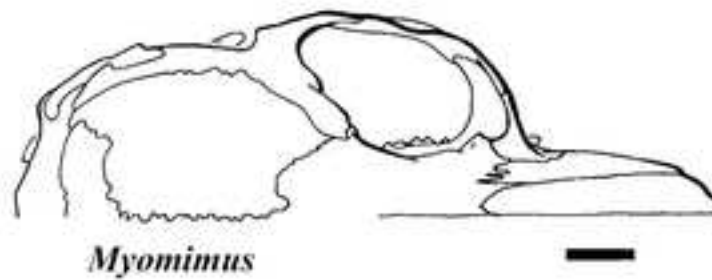
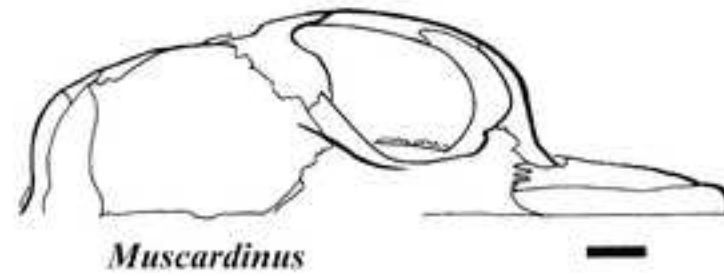
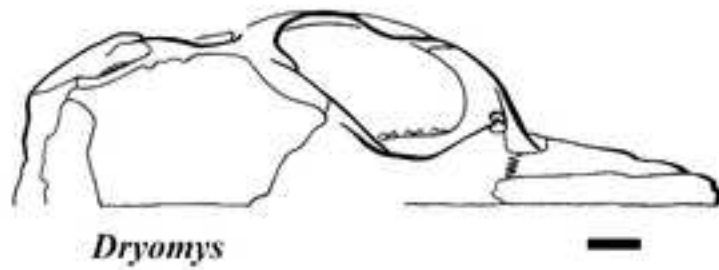
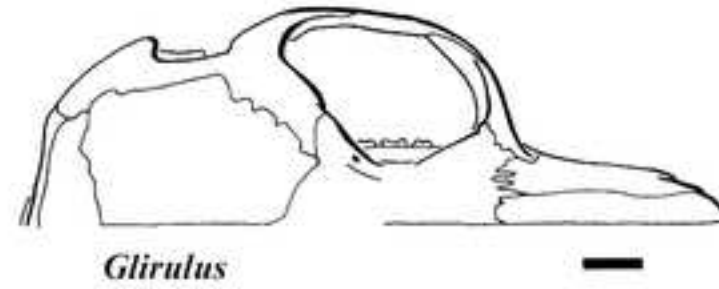
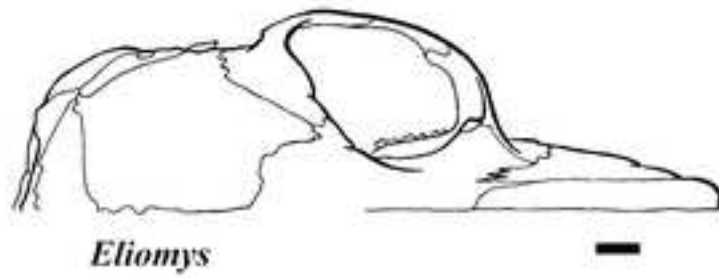
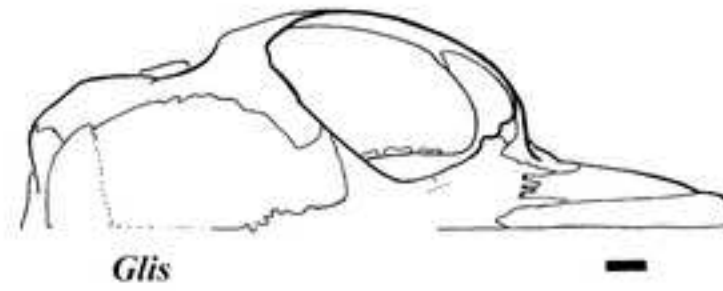
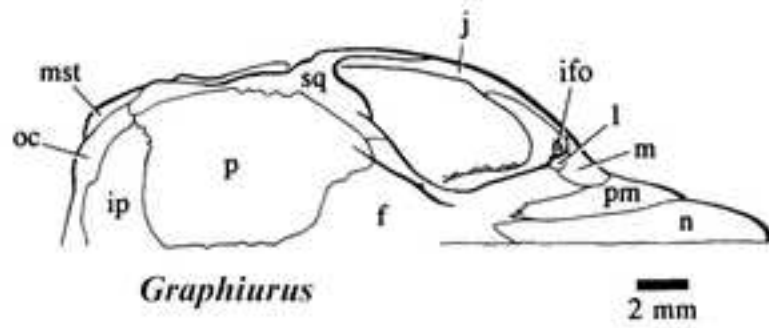
Muscardinus

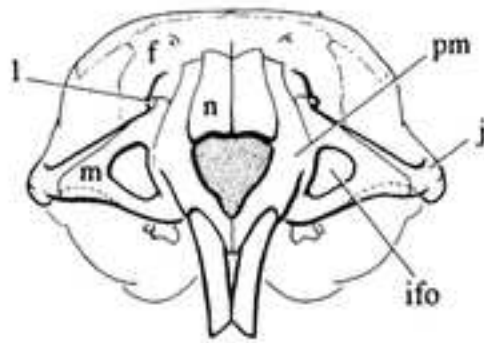


Myomimus

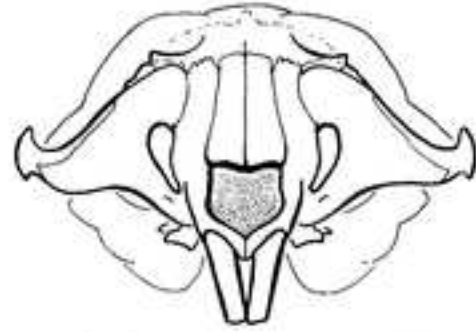
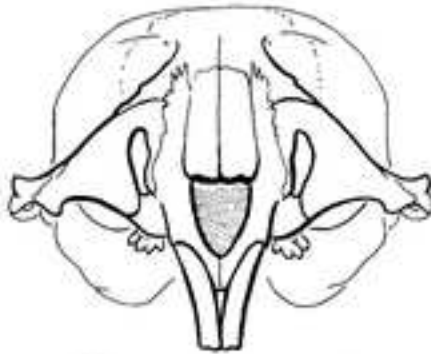
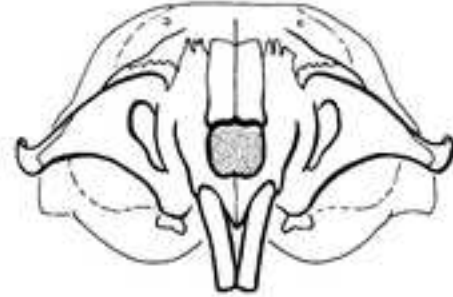
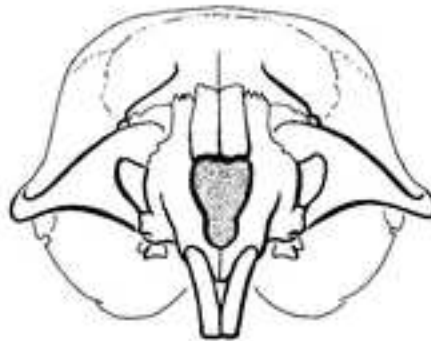
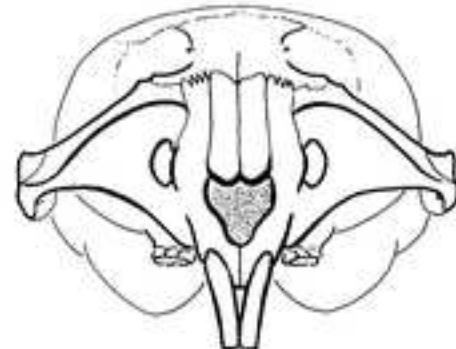
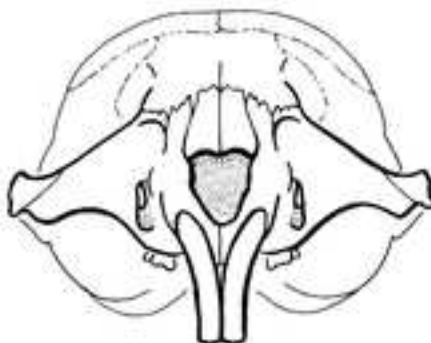
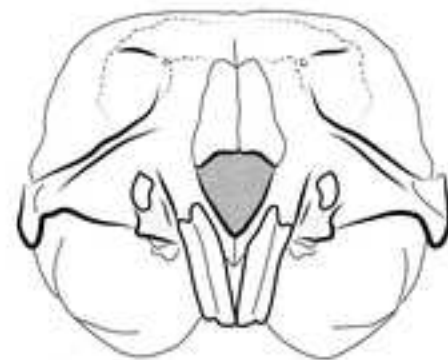


Selevinia



*Graphiurus*

2 mm

*Glis**Eliomys**Glirulus**Dryomys**Muscardinus**Myomimus**Selevinia*

