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The mammalian order Lagomorpha has been the subject of many morphometric studies aimed at understanding the relationship between form and function as it relates to locomotion, primarily in postcranial morphology. The leporid cranial skeleton, however, may also reveal information about their ecology, particularly locomotion and vision. Here we investigate the relationship between cranial shape and the degree of facial tilt with locomotion (cursoriality, saltation, and burrowing) within crown leporids. Our results suggest that facial tilt is more pronounced in cursors and saltators compared to generalists, and that increasing facial tilt may be driven by a need for expanded visual fields. Our phylogenetically informed analyses indicate that burrowing behavior, facial tilt, and locomotor behavior do not predict cranial shape. However, we find that variables such as bullae size, size of the splenius capitus fossa, and overall rostral dimensions are important components for understanding the cranial variation in leporids.

# ECOLOGICAL CORRELATES TO CRANIAL MORPHOLOGY IN LEPORIDS (MAMMALIA, LAGOMORPHA)

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24 **ABSTRACT**

25 The mammalian order Lagomorpha has been the subject of many morphometric studies aimed at

26 understanding the relationship between form and function as it relates to locomotion, primarily in

27 postcranial morphology. The leporid cranial skeleton, however, may also reveal information about their

28 ecology, particularly locomotion and vision. Here we investigate the relationship between cranial shape

29 and the degree of facial tilt with locomotion (cursoriality, saltation, and burrowing) within crown

30 leporids. Our results suggest that facial tilt is more pronounced in cursors and saltators compared to

31 generalists, and that increasing facial tilt may be driven by a need for expanded visual fields. Our

32 phylogenetically informed analyses indicate that burrowing behavior, facial tilt, and locomotor

33 behavior do not predict cranial shape. However, we find that variables such as bullae size, size of the

34 splenius capitus fossa, and overall rostral dimensions are important components for understanding the

35 cranial variation in leporids.

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47 **INTRODUCTION**

48    The relationship between form and function as it relates to locomotion has been extensively

49    studied in a wide range of vertebrate groups (Webb, 1984; Hildebrand, 1988; Rayner, 1988; Aerts et

50    al., 2000). The mammalian order Lagomorpha has been the subject of many morphometric studies

51    aimed at understanding this relationship in postcranial morphology (e.g., Reese et al., 2013; Fostowicz-

52    Frelik, 2007; Seckel and Janis, 2008, Young et al., 2014), and the impetus of these is largely to

53    understand the high-speed form of leaping observed in some leporids (rabbits and hares). Leporids are

54    peerless cursors for their size; some hares have been shown to achieve speeds greater than 70km/h

55    (Garland, 1983). Indeed, the leporid postcranial skeleton exhibits many derived features that are

56    strongly associated with saltation and cursoriality, including limb element elongation (Szalay, 1985;

57    Fostowicz-Frelik, 2007; Seckel and Janis, 2008).

58    The cranial skeleton is more often overlooked in studies of form and locomotion, though there

59    are biologically relevant associations between skull form and locomotor behavior, such as the role of

60    the skull in active headfirst burrowing (e.g., Gans 1974; Barros et al. 2011; Sherratt et al. 2014;

61    Hopkins and Davis, 2009; and see Wake 1993 for a review). In leporids, it has been suggested that

62    morphological transformations of the skull may also be related to their ecology, particularly

63    locomotion and vision (DuBrul, 1950; Bramble, 1989). The leporid skull is highly transformed,

64    exhibiting a combination of features that clearly distinguish it from a more typical mammalian skull. A

65    striking, yet often overlooked, characteristic is the broad dorsal arching of the cranium (Thompson,

66    1942), which is achieved via expansion and folding of the supraoccipital, and a distinct flexure near the

67    basisphenoid/presphenoid suture (Fig. 1). A prominent ridge on the dorsal portion of the posterior

68    cranial roof, which is superficially similar to an occipital crest, is actually a distinct flexure within the

69    supraoccipital bone. Based on the position of the rabbit skull in resting position (De Beer, 1947: Fig. 9;

70    Vidal et al. 1986: Fig. 4B, and see our Fig. 2), this flexure results in significant tilting of the facial

71    region ventrally relative to the basicranium, which we here refer to as Facial Tilt (FT). DuBrul (1950)

72 discusses this feature in detail within hares, and points out that the facial tilt of leporids is likely related

73 to their unique mode of locomotor behavior. DuBrul (1950) also discusses the similarities in leporid

74 skull transformations to those of our own lineage; in our hominin relatives, increased basicranial

75 flexion is associated with the onset of bipedal locomotion (Strait and Ross, 1999).

76      The goal of this study is to investigate the relationship between cranial shape and locomotion

77 (cursoriality, saltation, and burrowing) within crown leporids. Our study is driven by hypotheses

78 previously stated (DuBrul, 1950; Bramble, 1989) but never quantitatively tested. We use a large

79 morphometric dataset spanning 16 phylogenetically constrained extant taxa (table 1) to evaluate

80 hypotheses about the relationship between skull shape and facial tilt with locomotor ecology.

81

82 **STUDY SYSTEM AND HYPOTHESES**

83      The mammalian order Lagomorpha is composed of two families, Leporidae (rabbits and hares)

84 and Ochotonidae (pikas). Ochotonids are represented by one living genus, *Ochotona*, which includes

85 two North American and 28 Eurasian species (Alves and Hackländer, 2008). Leporids include 11

86 living genera with 62 species overall. The majority of species are found within two genera (Alves and

87 Hackländer, 2008); *Lepus* (hares, 32 species) and *Sylvilagus* (a portion of rabbits, 17 species). Of the

88 remaining nine genera, seven are monotypic, while two genera, *Nesolagus* and *Pronolagus*, only

89 include two and four species, respectively. Overall, sixteen leporids species are currently considered

90 endangered or critically endangered by the IUCN (Alves and Hackländer, 2008), and conservation

91 issues are compounded by the lack of natural history data for many of these species. Leporids are

92 found on every continent except Antarctica, from the high arctic to dry, hot deserts (Chapman and

93 Flux, 1990, 2008). Some leporids are nocturnal, some are social, and some live in dense cover as

94 opposed to the open plains often associated with these animals (Stoner et al., 2003). In terms of size,

95 our study includes (Appendix 1) the smallest leporid, *Brachylagus* (mean skull length ~ 50mm) to one

96   of the largest, *Lepus timidus* (mean skull length ~ 90mm). Genera such as *Pentalagus* and *Caprolagus*

97   have heavy, robust skulls, compared to the typically gracile skulls of most taxa. These cranial

98   differences manifest themselves morphometrically via a wide range of snout lengths and marked

99   differences in skull robustness and form (Fig. 1). While leaping abilities are common among most

100  leporid lineages, they are also known to be facultatively semiaquatic, scansorial, fossorial, or exhibit a

101  more generalized, non-hopping form of locomotion (Chapman and Flux, 2008). We distinguish here

102  between the saltatory locomotion (i.e., hopping) most typical among leporids (Table 1, Fig. 3), and its

103  cursorial form observed in some hare lineages (Gambaryan and Hardin, 1974; Bramble, 1989).

104  Generalists are recognized as those who don't exhibit clear hopping, but rather move in a more

105  scampering habit.

106

107  **Hypothesis 1 — Facial Tilt**

108  *A high degree of facial tilting (e.g., ventral flexion of the facial region) should a) be positively*

109  *correlated with more active (e.g., saltatorial or cursorial) locomotor styles, and b) show no correlation*

110  *with burrowing habit.*

111  Variation in the degree of facial tilt among leporids has strong effects on orbital orientation (Fig. 3).

112  There is substantial literature discussing the relationship between orbit orientation and ecology within

113  vertebrates (Noble, et al., 2000; Cox, 2008; Heesy, 2008; Iwaniuk et al., 2008; Jeffery and Cox, 2010),

114  and Cartmill (1970) established the terms 'orbital convergence' and 'frontation' to understand these

115  relationships. While orbit orientation is influenced by brain size and jaw mastication (Lieberman et al.

116  2000; Cox, 2008), within primates, orbital convergence is also strongly associated with increased

117  binocular visual field overlap observed in nocturnal predatory species (Heesy, 2004, Heesy 2008).

118  Various groups exhibit a high degree of both orbital convergence and orbital frontation (Cox and

119  Jeffery, 2008), with hominids serving as an exemplar; orbital frontation is strongly positively

120 correlated with basicranial flexion (Ross, 1995). As DuBrul (1950) points out, facial tilt

121 transformations among leporids are nearly identical to basicranial flexion observed within anthropoids;

122 increased facial tilt and basicranial flexion both result in increased orbital frontation (see Fig. 2 for

123 changes in frontation related to increased FT). Several workers have shown that increased frontation is

124 positively correlated with arboreal taxa (Cartmill, 1970; Heesy, 2008); increased frontation changes the

125 visual field to allow for better visualization of substrate. Jeffery and Cox (2010) show that leporids

126 have relatively low degrees of convergence and frontation. As we discuss below, however, when facial

127 tilt is taken into consideration, leporids actually demonstrate a relatively higher degree of frontation (as

128 indicated by the orbital plane relative to the vertical plane). More importantly, regardless of the

129 absolute measure of frontation within leporids, we expect that frontation will vary among leporids

130 correlated with varying degrees of facial tilt. For this reason, we expect that facial tilt (as a proxy for

131 frontation) should be strongly correlated to locomotor styles that would require enhanced substrate

132 perception (saltatorial and cursorial), but we do not expect that facial tilt will be related to burrowing

133 habit.

134

135 **Hypothesis 2 — Skull shape**

136 *We expect that there will be significant skull shape differences among a) locomotor styles, and b)*

137 *burrowing habits.*

138 We have no a priori expectations about how overall skull shape might change with locomotor mode or

139 burrowing habit. Instead we will investigate the more fundamental question of whether skull shape is

140 related to locomotion and burrowing habit at all. Our interest in this question is therefore more a form

141 of exploratory data analysis than a test of a specific hypothesis.

142

143 **MATERIALS AND METHODS**

144   We collected morphometric data (Table 2; Appendix 1) from 140 leporid skulls spanning 16

145   taxa (Table 1) housed in the departments of Mammalogy at the American Museum of Natural History

146   (AMNH) and the Los Angeles County Museum of Natural History (LACM). Care was made to use

147   only adult specimens, characterized by fully fused occipital sutures (Hoffmeister and Zimmerman,

148   1967). Ten linear measurements (Table 3, Figure 3) were recorded per specimen using digital calipers

149   by three authors (BPK, MW, and NB), and a repeatability analysis (consisting of 10 specimens

150   measured 3 times, results not presented) was performed to ensure there was no intercollector bias

151   introduced. The ten cranial measurements were analyzed using the log-shape ratios approach

152   (Mosimann, 1970; Mosimann and James, 1979). For each specimen, size was computed as the

153   geometric mean of all measurements, and then each measurement was divided by size to obtain the

154   shape ratios. We then used the log of this quantity as raw data for the subsequent analyses.

155   Facial tilt was measured by photographing each skull in lateral view using a Nikon D80 digital

156   camera. The skulls were placed in a sandbox to ensure that the sagittal plane was orthogonal to the

157   focal direction. Facial tilt angle was acquired from the digital photos within Adobe Photoshop ©,

158   measured as the angular difference between the 'occipital plane' and a line parallel to the cranial

159   diastema (Fig. 3). Variation among individuals for the cranial variables weas explored using principal

160   components analysis on the covariance matrix of the log-shape ratios shape variables within the

161   statistical software R v3.1.1 (R Core Team 2014, http://cran.r-project.org/).

162

163   **Phylogenetically informed analyses**

164   To examine facial tilt angle and cranial shape in a phylogenetic context, we used the

165   phylogenetic relationships among species of Leporidae recently published by Matthee et al. (2004).

166   The original tree was constructed using seven genes (five nuclear and 2 mt) for 25 ingroup taxa. We

167   pruned the tree using Mesquite © (Maddison and Maddison, 2015) to include only the 16 taxa studied

168   here (Fig. 3), and retained the information on branch lengths (details of which are in Matthee et al.

169   2004).

170       We first examined the amount of phylogenetic signal in the morphometric variables, calculating

171   the $K$ statistic (Blomberg et al. 2003) for facial tilt angle, and the multivariate equivalent $K_{mult}$ (Adams

172   2014a) for all log-shape ratios. The $K$ statistics provide a measure of the strength of phylogenetic signal

173   for univariate and multivariate traits respectively, and in each case provides a single statistic. A value

174   of less than one implies that taxa resemble each other phenotypically less than expected under

175   Brownian motion, while values of more than 1 implies that close relatives are more similar to one

176   another phenotypically than expected under Brownian motion. Significance testing was performed

177   using a permutation procedure whereby the variables are randomized relative to the tree, and 1000

178   permutations were performed for each test (Blomberg *et al.* 2003).

179       Log-shape ratios and facial tilt angle were compared to several key ecological indicators,

180   including locomotor type and burrowing habit (Table 1). Ecological data were obtained from Chapman

181   and Flux (1990) and Stoner et al. (2003). We divided leporids into three locomotor categories:

182   generalized or 'scramble' locomotors, which tend to be the slowest-moving; saltatory or hopping

183   locomotors; and fast-moving taxa that practice cursorial (leaping and bounding) locomotion, which is

184   essentially a specialized form of saltation. Regarding burrowing habits, some leporids dig their own

185   burrows (e.g., *Oryctolagus* and *Romerolagus*), whereas others simply occupy preexisting burrows

186   excavated by other animals. For the purposes of this study, we refer to leporids as burrowers if they

187   occupy burrows consistently, regardless of whether they dig the burrows.

188       To test whether or not the degree of facial tilt differs among the three locomotor categories, we

189   performed a one-way Analysis of Variance (ANOVA) in an evolutionary context, under a Brownian

190   motion model of evolution. This was done by using species means of the FT angle in a distance-based

191   phylogenetic generalized least squares analysis (D-PGLS ; Adams 2014b). A distance-based approach

192    provides numerically identical estimates of evolutionary patterns to those obtained from standard

193    implementations of PGLS on univariate datasets, and was used here for consistency with analyses

194    below on the log-shape ratios. The statistical significance of each term in the D-PGLS was assessed

195    using 1000 permutations whereby the species means are shuffled among the tips of the phylogeny. We

196    performed a second ANOVA as above to test whether facial tilt differs between taxa that utilize

197    burrows ("burrowing") and those that do not ("non-burrowing"). Box and whisker plots were used to

198    visualize the individual variation in facial tilt angle among groups.

199       To test whether or not cranial shape, as represented by ten morphometric variables, differs

200    among the three locomotor types, we performed a multivariate analysis of variance in an evolutionary

201    context under a Brownian motion model of evolution. This was done a D-PGLS with the species means

202    of the ten log-shape ratios. The D-PGLS performs better than a regular PGLS when the number of

203    variables begins to approach the number of species (Adams 2014b). The statistical significance of each

204    term in the D-PGLS was assessed using 1000 permutations of the species means. Similarly, we tested

205    whether or not cranial shape differs between burrowing and non-burrowing taxa using a D-PGLS as

206    above.

207       Finally, to test whether or not facial tilt is a significant predictor of cranial shape, we performed

208    a multivariate regression in an evolutionary context, under a Brownian motion model of evolution,

209    again using the D-PGLS approach. The statistical significance was assessed using 1000 permutations

210    of the species means of the log-shape ratios. All of the phylogenetically informed analyses were done

211    using the geomorph package (Adams et al. 2014) in the statistical software R v3.1.1 (R Core Team,

212    2014). The ANOVAs on FT, the MANOVAs on cranial log-shape rations, and the multivariate

213    regression were done using the *procD.pgls* function, and phylogenetic signal was calculated with the

214    *physignal* function.

215

216 **RESULTS**

217 **Facial Tilt**

218        Facial tilt (FT) summarizes the broad dorsal arching of the skull roof that is prominent among

219 living leporids (Fig. 3). Across the species in this study, the measure of facial tilt angle has a very low

220 value for $K$, implying that the taxa resemble each other morphologically less than expected under

221 Brownian motion, and the test is not significant ($K = 0.62$, $P = 0.53$). Overall, there is a nearly 30°

222 range of variation in FT among specimens of all species in this sample (Appendix 1). We found a

223 significant difference among locomotor types for facial tilt angle (D-PGLS, $F = 7.02$, $P = 0.016$; Fig.

224 5a). The mean FT angle for generalized locomotors (mean, $\mu = 44.0$, standard deviation, $\sigma = 5.48$) is

225 substantially higher than that of cursorial ($\mu = 36.3$, $\sigma = 5.46$) and saltatorial taxa ($\mu = 37.2$, $\sigma = 5.91$)

226 (Fig. 5a). This indicates that taxa that are either saltatorial or cursorial tend to have facial regions that

227 are more ventrally deflected. By contrast, we found no significant difference in FT angle between

228 burrowing and non-burrowing taxa (Fig. 5b; D-PGLS, $F = 0.0037$, $P = 0.973$; Fig. 5b).

229

230 **Cranial shape analyses**

231        In a principal components analysis of the ten log-shape ratios among individuals, the first four

232 PC axes account for 90.2% of total variance. PC1 accounts for 43.5% of cranial shape differences, PC2

233 accounts for 24.4%, PC3 accounts for 13.2%, and PC4 accounts for 9.0% of variance. (Table 3; Fig. 6).

234 The remaining PCs each contribute less than 10% of the total variation. A PCA of the species means

235 (not shown) produced equivalent results (PC1 = 42.6%, PC2 = 33.4%, PC3 = 11.3%, PC4 = 5.9%), and

236 with the same variables contributing highly on each axis, and thus we present only one analysis for

237 brevity.

238        The loadings of the PCA (Table 3) show that bullae diameter (BD; 0.85) has the strongest

239 influence on PC1, substantially more than other variables. PC1 strongly separates *Brachylagus,*

240   *Romerolagus*, and *Bunolagus* (all with larger bullae diameters) from all other leporid species (Fig. 6A).

241   In terms of locomotor styles, cursorial species are isolated towards the negative portion of the PC1

242   axis. Similarly, PC2 strongly shows the effects of size of the *splenius capitus* fossa (SCF; -0.91). While

243   this measure does not separate among saltators (Fig. 6B), there is some separation between generalists

244   and cursorial species. Loadings for PC3 indicate that three variables are strongly affecting the variance

245   along that axis: interorbital width (IOW; 0.68), nasal length (NL; -0.51), and diastema length (DILU; -

246   0.42). PC3 shows separation of species (Fig. 6C), but no clear broader groupings. It also does not

247   clearly distinguish locomotor modes, but saltators do occupy the negative portion of the axes where no

248   generalists or cursors are found (Fig. 6D). Parietal length (PAL; -0.87) loads strongly along PC4. This

249   axes does help to distinguish species (Fig. 6C), but shows little ability to distinguish among locomotor

250   modes (Fig. 6D).

251        There is significant phylogenetic signal is cranial shape described by the ten log-shape ratios

252   ($K_{mult} = 0.91$, $P = 0.035$). The value of kappa is substantially higher than that for facial tilt, but still

253   below 1, implying that close relatives are moderately less similar to one another phenotypically than

254   expected under Brownian motion. Phylogenetically informed analysis of variance (D-PGLS) indicates

255   that there is no significant effect of locomotor habit on cranial shape ($F = 1.3712$, $P = 0.28$). Likewise,

256   there is no significant effect on cranial shape by burrowing behavior ($F = 1.2831$, $P = 0.56$). Finally, a

257   phylogenetically informed multivariate regression suggests that facial tilt angle is not a significant

258   predictor of cranial shape ($R^2 = 0.097$, $P = 0.413$)

259

260   **DISCUSSION**

261        Given a clear correlation between the degree of facial tilt (FT) and locomotor style, and the lack

262   of significant phylogenetic signal in FT angle, it is evident that this aspect of cranial morphology is

263   strongly influenced by ecological factors within Leporidae. While the relationship between shape and

264     function is established, the specific aspects of cranial shape that inform ecological function are only

265     partially resolved from our multivariate analyses. Generalized locomotors exhibit less facial tilt, an

266     anatomical condition that could properly be thought to be primitive for the mammalian skull, and given

267     their fossil record, lagomorphs as well (Dice, 1933; Asher et al., 2005). Facial tilt within leporids is

268     allowed via the expansion of the supraoccipital bone on the dorsal skull (Fig. 2), and along the ventral

269     skull, there is a pronounced flexure near the basisphenoid/presphenoid juncture.

270     The complex architecture of the supraoccipital in leporids is the most marked change related to

271     the dorsal arching the skull roof, but there are additional effects on the orientation of the orbit (Fig. 2).

272     There is a vast literature on orbital orientation as it relates to locomotion, visual acuity, brain size, and

273     masticatory anatomy (Noble et al., 2000; Heesy, 2005; Heesy et al., 2007; Iwaniuk et al., 2008; Heesy,

274     2008; Cox, 2008; Jeffery and Cox, 2010), and perhaps most clearly, changes in orbit orientation have

275     direct affects on the range of visual fields. Both orbital convergence and frontation are commonly

276     measured orbital variables that seem to be functionally predictive (Cox, 2008); increased convergence

277     is thought to increase binocular field overlap within primates (Ross and Martin 2007; Heesy et al.,

278     2007), and orbital frontation allows for better substrate visualization (Cartmill, 1970; Heesy, 2008).

279     While Jeffery and Cox (2010) demonstrated that the rabbit shows low degrees convergence and

280     frontation, frontation in the rabbit is complicated by skull transformations associated with facial tilt.

281     Traditionally, frontation was considered as the degree to which the orbital plane is aligned vertically

282     (Cartmill, 1970; Ross, 1994); whereas, Jeffery and Cox (2010) used angular differences between the

283     lateral semicircular canal and the medial and lateral orbital rectus muscles as a proxy for frontation.

284     While these later measures are distinct for rabbits (Cox and Jeffery, 2008; Jeffery and Cox, 2010) as

285     compared to other mammals, due to the way rabbits hold there heads (De Beer, 1947; Vidal et al.

286     1986), angular differences between the lateral semi-circular canal and horizontal rectus muscles may

287     not be a perfect summary of the degree to which the orbital plane approaches vertical. Interestingly, as

288   Jeffery and Cox (2010) show, humans and rabbits are outliers with regard to this metric, as they both

289   demonstrate strong misalignment of semicircular canal and rectus muscle orientations. This may be

290   driven by the fact that both of these species exhibit skull shapes in which the basicranium is highly

291   transformed relative to the facial region (DuBrul, 1950). Most importantly, and regardless of the

292   absolute degree of frontation, facial tilting within leporids would have the effect of changing the

293   orientation of the orbit and increasing frontation. Our data show that variation in facial tilt among

294   leporids (~30°) is explained by mode of locomotion. Presumably, pronounced facial tilt and the

295   associated increase in frontation improve substrate visibility in fast-moving taxa.

296       In contrast to FT angle, overall cranial morphology as described by ten log-shape ratio

297   measurements is not significantly different among locomotor modes or between burrowers and non-

298   burrowers. Instead, the PCA of individual variation in our cranial variables clearly shows that among-

299   species variation is a strong driver of morphospace organization (Fig. 6). The phylogenetic structure

300   evident in the cranial variables shown in our PCA is supported by a high measure of phylogenetic

301   signal. However, there is some separation of the three locomotor modes in morphospace in (Fig. 6).

302   Saltatorial species have a wide-variety of cranial morphologies, while the generalized locomotors are

303   clustered in morphospace (in the negative quadrant of PC1 and PC2), likely due to their close ancestry.

304       Bulla length contributes the most to the first PCA axis, separating out a group of three species

305   (larger bullae; *Romerolagus, Bunolagus*, and *Brachylagus*) from all other leporids, and thus this

306   morphological trait is a candidate feature of adaptive differences between the different locomotors

307   styles. The external bulla is a complicated structure, which receives contributions from different bones

308   across Mammalia (Novaek, 1977). The external auditory bulla has been shown to be of significant

309   systematic importance within carnivorans (Hunt, 1974; Ivanoff, 2001), but the function of bulla size is

310   unclear for leporids. Pavlinov and Rogovin (2000) showed that bulla size is negatively correlated with

311   pinna size in specialized desert rodents. They specifically remark that faster, more agile rodents within

312     these groups tend toward smaller bulla and larger pinnae. While our data do not explicitly test this, our

313     cursorial species appear toward the negative PC1 axes, which are represented by smaller bullae. We

314     also note that while *Romerolagus* and *Brachylagus* exhibit large bullae and relatively small pinnae,

315     *Bunolagus* does not fit this pattern as it has both large bullae and large pinnae. Liao et al. (2007) shows

316     that bulla size is negatively correlated with altitude in the Daurian pika, *Ochotona dauurica*

317     (Lagomorpha, Ochotonidae). This patterns does not match our observations, as one of our large bullae

318     species, *Romerolagus*, is found at high elevations (Cervantes et al., 1990). We think that our PC1 axis

319     may also reflect the relative size of the basicranium to the facial region within leporids, in addition to

320     bullae size; we discuss this topic further below.

321        The second variable of interest, which loads strongly on PC2, is the *splenius capitus* fossae.

322     Lateral to the external occipital protuberance (EOP; i.e. Inion) are two large fossae that extend to the

323     parietal/occipital suture and allow for attachment of the *splenius capitus* mm. (Barone et al., 1973),

324     which are involved in head extension and lateral rotation. The fossae can be clearly identified via the

325     prominent superior nuchal line that extends rostrally from the EOP. The *longissimus capitus* m. inserts

326     with the *splenius capitus* m. in the lateral, mastoid area, of the occipital region. A final long extensor

327     muscle, the *semispinalus capitus* m., attaches to the lateral portions of the EOP. Together, these three

328     long erectors serve to extend, stabilize, and laterally rotate the head (Igarashi et al., 2000). Upon

329     comparison of leporid skulls (Fig. 1), it is apparent that those with significant facial tilt are expanding

330     the rostral portions of the supraoccipital bone relative to the caudal portion, and indeed, this seems to

331     be reflected in PC2 as the variance along that axis helps to separate out cursors (larger *splenius capitus*

332     fossa) and generalists (smaller *splenius capitus* fossa*). The expansion of the *splenius capitus* fossa

333     should serve to increase the attachment area for the long extensor muscles, allowing for improved

334     extension and lateral rotation of the head.

335    It is worth noting that all variables strongly affecting PC1, PC2, and PC4 are associated with

336    the neurocranium, and variables affecting PC3 are all associated with the splanchnocranium. It has

337    been thoroughly demonstrated within our own lineage, and mammals more broadly, that these

338    basicranial and facial regions demonstrate strong levels of phenotypic independence (see, for example,

339    Porto, et al., 2009; Drake and Klingenberg, 2010; Sanger, et al., 2012; Klingenberg, 2013) While this

340    pattern is debated within humans and other great apes  (Singh et al. 2011; Mitteroecker et al. 2012;

341    Martinez-Abadias et al. 2012 ), some similarities in skull transformation between humans and rabbits

342    have been noted in the literature (DuBrul, 1950; Moore and Spence, 1969). Moore and Spence (1969)

343    highlighted that both humans and rabbits transform the facial regions relative to the basicranium, but

344    also pointed out that the transformation seems to be driven in the facial regions within rabbits, whereas

345    it seems to be driven from the basicranium in humans. While our data do not directly address

346    modularity or developmental pathways within leporid skulls, it would be useful to understand how

347    relative transformation between the facial and basicranial regions within leporids, which seems to

348    influence facial tilt, could be explained mechanistically by these developmental trajectories.

349    Most importantly, it is striking that facial tilt *does* distinguish generalist locomotors clearly

350    from more active taxa within leporids. This suggests that FT represents a meaningful biological metric

351    among leporids, but may also summarize a specific aspect of cranial shape not recognized, but alluded

352    to, within our linear variables. While our linear measurements failed to strongly discern differences

353    among locomotor groups, this may be a function of the limited ability of these variables to capture

354    important shape differences among crania within leporids due to the highly transformed nature of their

355    skulls (e.g. pronounced dorsal arching). Nonetheless, our linear variables do separate taxonomic

356    groups, as has been done in other studies (see, for example, Palacios et al., 2008 and Pintur et al. 2014).

357    Our study demonstrates that the dorsal arching found within leporid skulls, mainly represented

358    here as facial tilt, has a strong relationship with how these animals moved. Facial tilt is related to a

359  complex transformation of nearly all aspects of the leporid skull, including basicranial rearrangement

360  and facial changes in the diastema region. Our linear variables, in addition to distinguishing taxonomic

361  groups, also capture some aspects of these changes related to locomotion. Based on the changes in

362  orbit orientation that are associated with increased facial tilt, it is likely that skull transformations in

363  crown leporids are driven by a need for increased visual perception of substrate.

364

365  **AUTHOR CONTRIBUTIONS**

366  Conceived and designed the experiments: BPK, MJW. Performed the experiments: BPK, NB, ES.

367  Analyzed the data: BPK, NB, ES. Contributed reagents/materials/analysis tools: BPK, NB, ES, MJW.

368  Wrote the paper: BPK, NB, MJW, ES.

369

370

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379  Anatomy, Western University of Health Sciences.

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Disparity of leporid skulls

FIGURE 1 — Disparity in facial tilt and cranial shape in selected leporids, including a) *Brachylagus idahoensis* (LACM 447; SLD ~ 50mm), b) *Lepus capensis* (LACM 40152; SLD ~ 82mm), c) *Poelagus marjorita* (AMNH 51056; SLD ~ 80mm), d) *Pronolagus crassicaudatus* (AMNH 89033; SLD ~ 80mm), e) *Lepus americanus* (LACM 93737; SLD ~ 75mm), f) *Oryctolagus cuniculus* (AMNH 166951; SLD ~ 78mm), g) *Nesolagus timminsi* (AMNH 272419; SLD ~ 78mm), h) *Bunolagus monticularis* (AMNH 146662; SLD ~ 78mm), and i) *Romerolagus diazi* (AMNH 148181; SLD ~ 60mm). All skull images are scaled to approximately the same skull length, skull length measurements are an approximation based on our measured specimens.

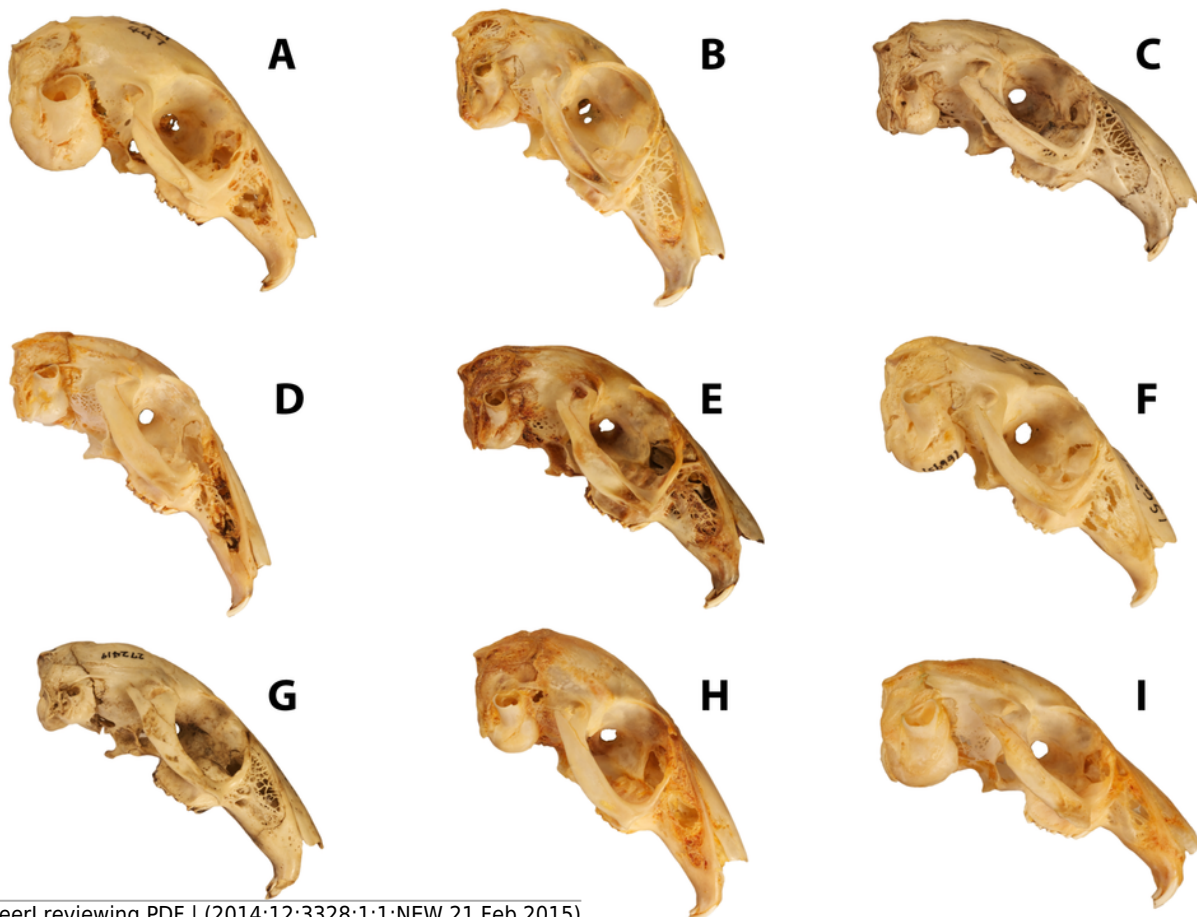
# 2

Facial tilt in leporids

FIGURE 2 — Facial tilt in leporids. The crania of a) *Caprolagus hispidus* (AMNH 54852, above) and b) *Pronolagus crassicaudatus* (AMNH 89033, below) are shown in left lateral view. Facial tilt (FT) is defined herein as the angle between the upper diastema and the occipital plane, where increased values indicated a skull orientation closer the horizontal plane. The triangle indicated the position of the external occipital protuberance (EOP), and from that, both the dorsal (red) and occipital (blue) extend of the supraoccipital bones is outlined.

A

Frontation angle of the orbit

Cranial diastema line

B

Facial tilt angle

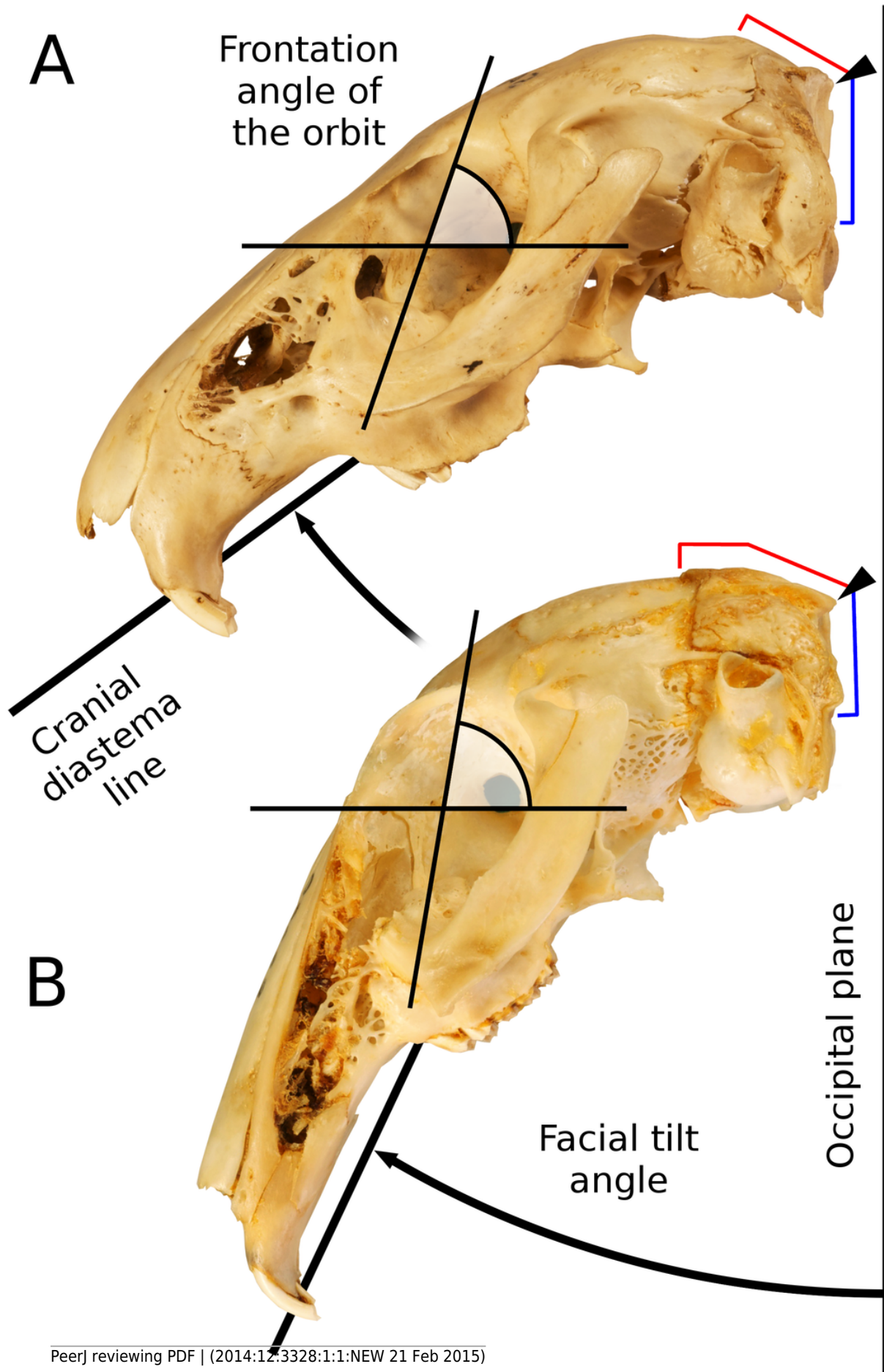
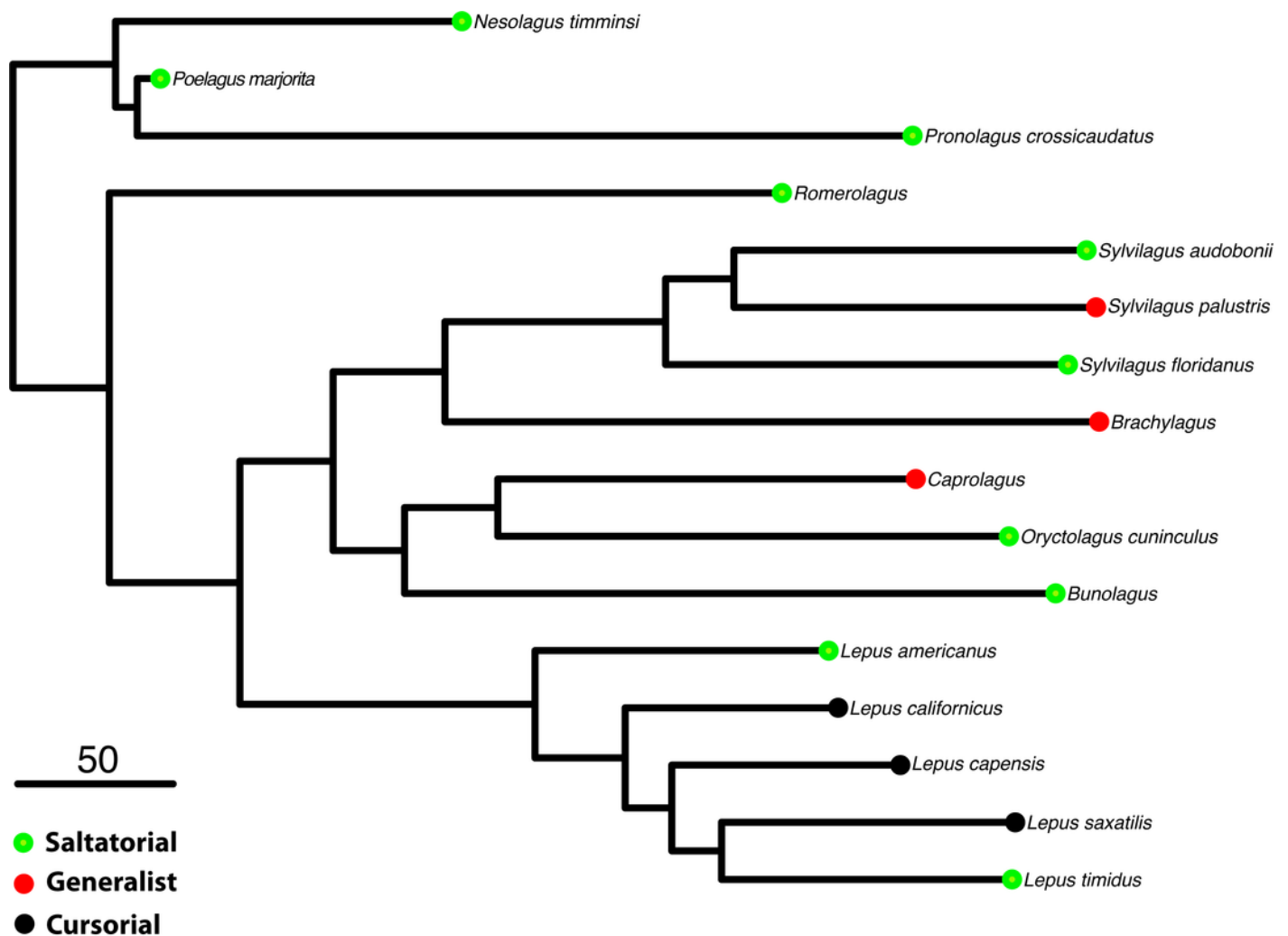
Occipital plane

Phylogeny of Leporidae

FIGURE 3 — The phylogenetic hypothesis of the 16 taxa used in this study, pruned from the supermatrix maximum likelihood phylogeny in Matthee et al (2004). Locomotor styles from Table 1.

# 4

Skull measurements

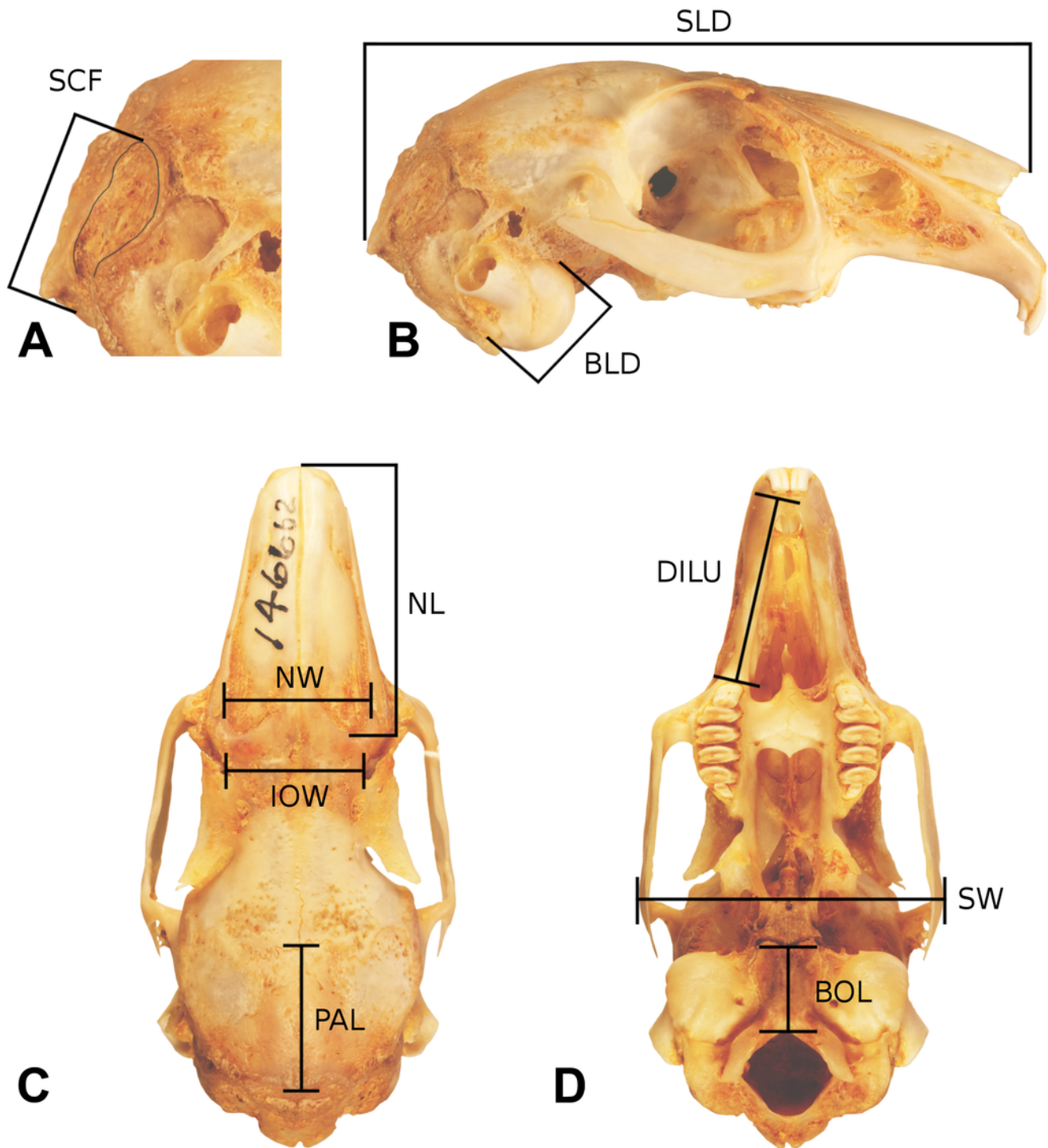
FIGURE 4 — A representative leporid skull showing measurements used in this analysis. The cranium of *Bunolagus monticularis* (AMNH 146662) is shown in (a and b) right lateral (top), (c) dorsal (lower left), and (d) ventral (lower right) views. Abbreviations follow Table 1. See figure 3 for a description of Facial Tilt (FT).

Facial tilt ANOVA

FIGURE 5 — Box and whisker plot summarizing facial tilt angle for all specimens, showing how the angle differs between locomotor types (a) and burrowing behavior (b).

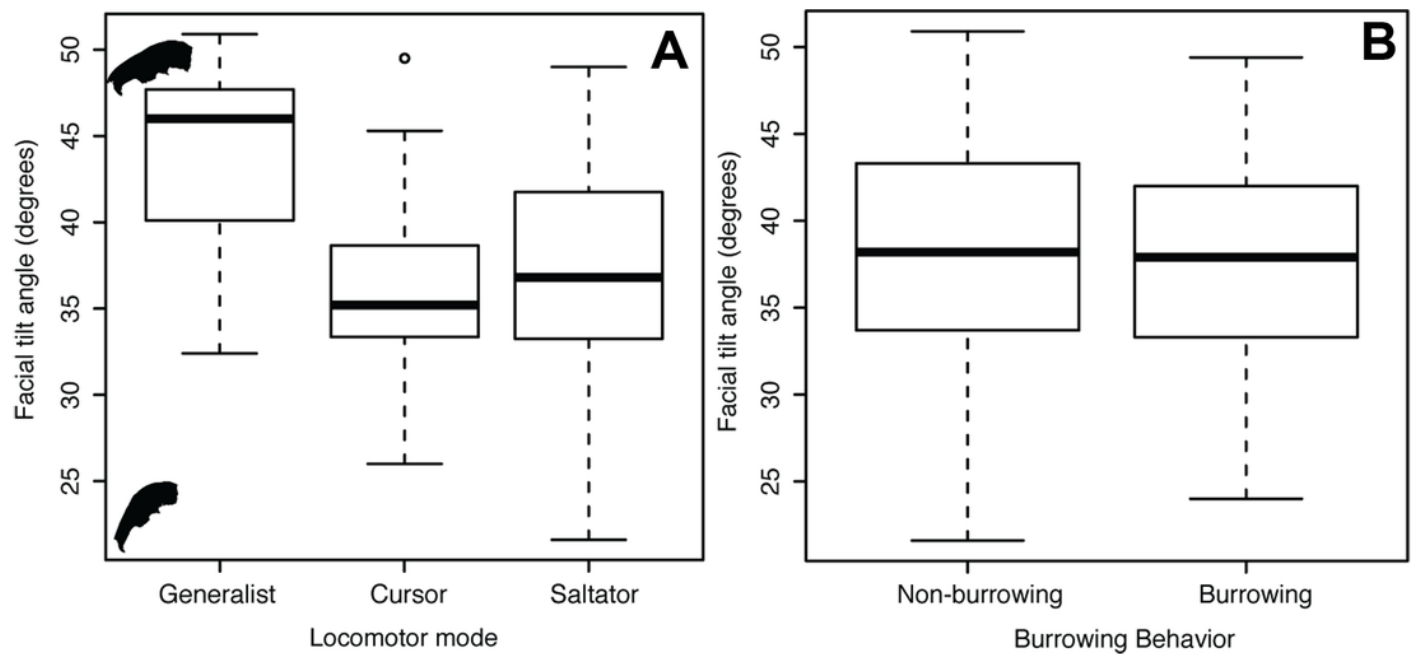
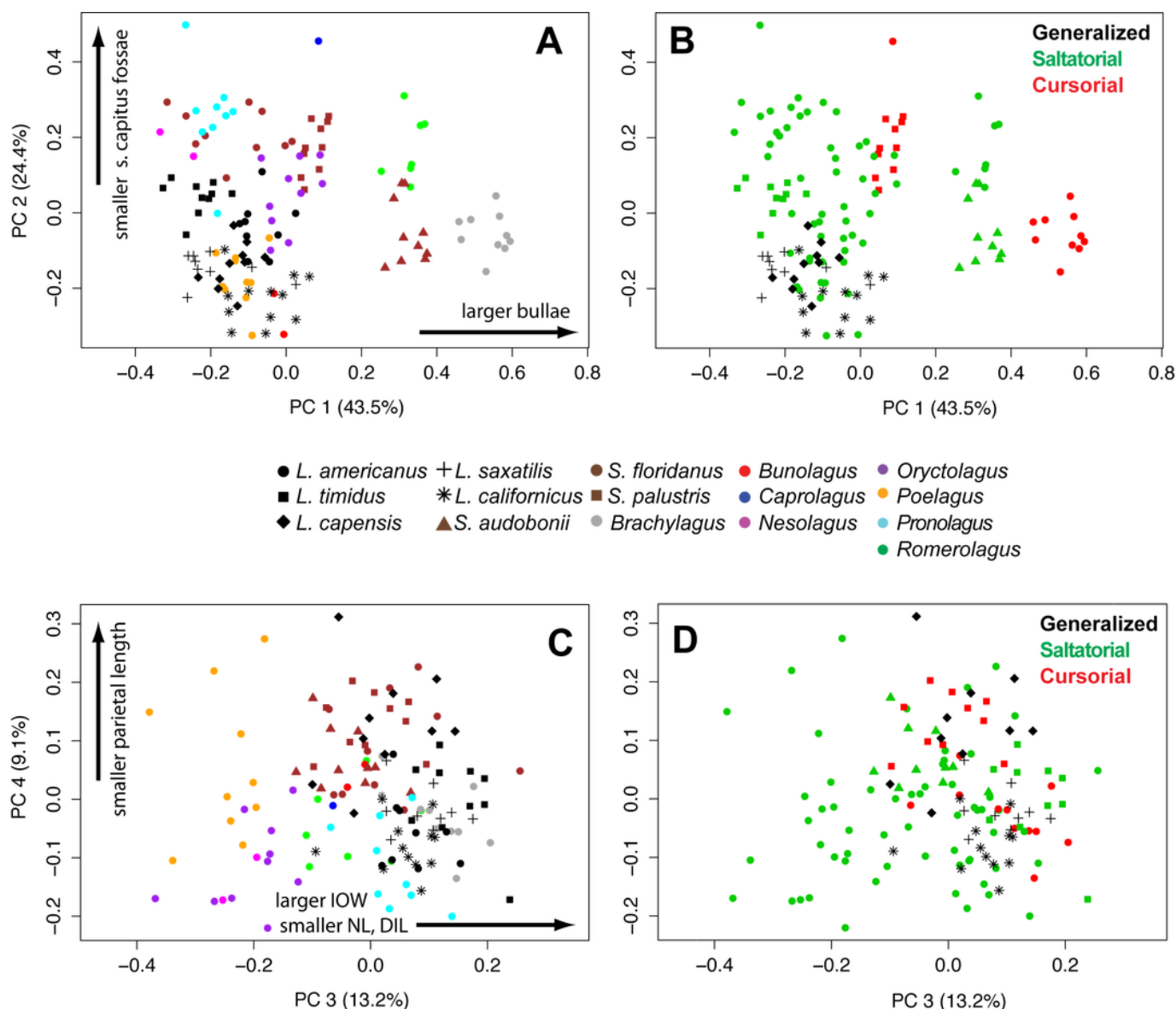
# 6

Multivariate PCAs

FIGURE 6 — Principal components analysis of 10 log-shape ratios measurements describing cranial shape for all specimens. Biplots show PC1 vs PC2 (top) and PC3 vs PC4 (bottom). a) Colored symbols by species. b) colored by LOC (with species symbols). Details of the loadings of each variable in the PCA are presented in Table 3.

Leporid species studied

2    Table 1. Leporid species included in this study

| Species | Locomotion Type | Burrowing | Abbreviation | n |
|---------|-----------------|-----------|--------------|---|
| *Romerolagus* | Saltatorial | Yes | Ro | 7 |
| *Bunolagus* | Saltatorial | Yes | Bu | 2 |
| *Caprolagus* | Generalized | Yes | Ca | 2 |
| *Brachylagus* | Generalized | Yes | Br | 10 |
| *Sylvilagus floridanus* | Saltatorial | No | Sfl | 10 |
| *Sylvilagus palustris* | Generalized | No | Spal | 10 |
| *Sylvilagus audobonii* | Saltatorial | Yes | Sau | 10 |
| *Poelagus marjorita* | Saltatorial | No | Po | 10 |
| *Pronolagus crossicaudatus* | Saltatorial | No | Pc | 10 |
| *Oryctolagus cuninculus* | Saltatorial | Yes | Oc | 10 |
| *Nesolagus timminsi* | Saltatorial | Yes | Nt | 2 |
| *Lepus americanus* | Saltatorial | No | Lam | 10 |
| *Lepus timidus* | Saltatorial | Yes | Lti | 10 |
| *Lepus capensis* | Cursorial | Yes | Lcap | 10 |
| *Lepus californicus* | Cursorial | No | Lcal | 12 |
| *Lepus saxatilis* | Cursorial | No | Lsax | 9 |

Skull measurements used.

Table 2. Variables used in this study and description; see figures 2 and 4 for illustrations of the measurement conventions.

| Abbr. | Variable | Measurement Convention |
|-------|----------|------------------------|
| BLD | bulla diameter | maximum diameter (in any direction) of right bulla |
| BOL | basioccipital length | maximum midsagittal length from anterior basioccipital to foramen magnum |
| DIL | diastema length | maximum distance between right I2 and M1 |
| IOW | interorbital width | minimum transverse width between dorsal rims of orbits |
| NL | nasal length | maximum parasagittal length of nasal bones (i.e., orthogonal antero-posterior but not along midline) |
| NW | nasal width | maximum transverse width across posterior nasal bones |
| PAL | parietal length | maximum midsagittal length of parietal bones |
| SCF | splenius capitis fossa | maximum parasagittal length from anterior margin of *M. splenius capitis* insertion fossa to opisthocranion |
| SLD | skull length dorsal | maximum midsagittal length from anterior nasal bones to Opisthocranion (just dorsal to incisors) to opisthocranion |
| SW | skull width | maximum transverse width across zygomatic processes |

PCA loadings

2    Table 3. The first four principal component (PC) axes contribute to 90.2% of the total variation of
3    the ten log normal variables. For each PC, the proportion of total variance (%) and the loadings
4    on these are given. The variables with the highest loading are shown in bold and are discussed
5    within the text.

|  | PC1 | PC2 | PC3 | PC4 |
|---|---|---|---|---|
| **Proportion of variance** | 43.5 | 24.4 | 13.2 | 9.1 |
| **BLD** | **0.85046873** | 0.02545804 | 0.016857617 | 0.272291215 |
| **BOL** | 0.159862063 | 0.161106564 | 0.012761305 | -0.070830236 |
| **DIL** | -0.246528468 | -0.026035317 | **-0.415136231** | 0.156169866 |
| **IOW** | -0.249260494 | 0.331660879 | **0.681589555** | 0.259415969 |
| **NL** | -0.175108112 | 0.062932441 | **-0.505939657** | 0.130829626 |
| **NW** | -0.296951523 | 0.01926985 | 0.131337875 | 0.224903873 |
| **PAL** | 0.027064391 | 0.140782388 | 0.078947604 | **-0.866213361** |
| **SCF** | -0.050436754 | **-0.905402173** | 0.218089373 | -0.039704014 |
| **SLD** | -0.064043373 | 0.114113325 | -0.185926838 | 0.027064132 |
| **SW** | 0.044933539 | 0.076114004 | -0.032580602 | -0.093927069 |