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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. However cranial shape does not differ significantly among these locomotor groups, nor does it differ significantly between species that burrow and those that do not.

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

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SHORT TITLE: Cranial morphology in leporids

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23 **ABSTRACT**

24 The mammalian order Lagomorpha has been the subject of many morphometric studies aimed at
25 understanding the relationship between form and function as it relates to locomotion, primarily in
26 postcranial morphology. The leporid cranial skeleton, however, may also reveal information
27 about their ecology, particularly locomotion and vision. Here we investigate the relationship
28 between cranial shape and the degree of facial tilt with locomotion (cursoriality, saltation, and
29 burrowing) within crown leporids. Our results suggest that facial tilt is more pronounced in
30 cursors and saltators compared to generalists. However cranial shape does not differ significantly
31 among these locomotor groups, nor does it differ significantly between species that burrow and
32 those that do not.

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INTRODUCTION

The relationship between form and function as it relates to locomotion has been well studied in a wide range of vertebrate groups. The mammalian order Lagomorpha has been the subject of many morphometric studies aimed at understanding this relationship in postcranial morphology (e.g., Reese et al., 2013; Fostowicz-Frelik, 2007; Seckel and Janis, 2008, Young et al., 2014). The impetus of these studies is largely to understand the high-speed form of cursoriality observed in some leporids (rabbits and hares). Leporids are peerless cursors for their size; some hares have been shown to achieve speeds greater than 70km/h (Garland, 1983). Indeed, the leporid postcranial skeleton exhibits many derived features that are strongly associated with saltation and cursoriality, including limb element elongation.

The cranial skeleton is more often overlooked in studies of form and locomotion, though there are biologically relevant associations between skull form and locomotory behavior, such as the role of the skull in active headfirst burrowing (e.g., Gans 1974; Barros et al. 2011; Sherratt et al. 2014; Hopkins and Davis, 2009; and see Wake 1993 for a review). In leporids, it has been suggested that morphological transformations of the skull may also be related to their ecology, particularly locomotion and vision (DuBrul, 1950; Bramble, 1989). The leporid skull is highly transformed, exhibiting a combination of features that clearly distinguish it from a more typical mammalian skull. A striking, yet often overlooked, characteristic is the broad dorsal arching of the cranium, which is achieved via expansion and folding of the supraoccipital, and a distinct flexure near the basisphenoid/presphenoid suture (Fig 1). A prominent ridge on the dorsal portion of the posterior cranial roof, which is superficially similar to an occipital crest, is actually a distinct flexure within the supraoccipital bone. Based on the position of the rabbit skull in resting position (De Beer, 1947: fig. 9; Vidal et al. 1986: fig. 4B), this flexure results in significant tilting of the facial region ventrally relative to the basicranium, which we here refer to as Facial Tilt

(FT). DuBrul (1950) discusses this feature in detail within hares, and points out that the facial tilt of leporids is likely related to their unique mode of locomotion. DuBrul (1950) also discussed the similarities in leporid skull transformations to those of our own lineage; in our hominin relatives, increased basicranial flexion was associated with the onset of bipedal locomotion.

The goal of this study is to investigate the relationship between cranial shape and locomotion (cursoriality, saltation, and burrowing) within crown leporids. Our study is driven by hypotheses previously stated (DuBrul, 1950; Bramble, 1989) but never quantitatively tested. We use a large morphometric dataset spanning 17 extant taxa (table 1) to evaluate hypotheses about the relationship between skull shape and facial tilt with locomotory ecology (details below).

STUDY SYSTEM AND HYPOTHESES

The mammalian order Lagomorpha is today composed of two families, Leporidae (rabbits and hares) and Ochotonidae (pikas). Ochotonids are represented by one living genus, *Ochotona*, which includes two North American and 28 Eurasian species (Alves and Hackländer, 2008). Leporids include 11 living genera with 62 species overall. The majority of species are found within two genera (Alves and Hackländer, 2008); *Lepus* (hares, 32 species) and *Sylvilagus* (a portion of rabbits, 17 species). Of the remaining nine genera, seven are monotypic, while two genera, *Nesolagus* and *Pronolagus*, only include two and four species, respectively. Overall, sixteen leporids species are currently considered endangered or critically endangered by the IUCN (Alves and Hackländer, 2008), and conservation issues are compounded by the lack of natural history data for many of these species.

Despite the perception that leporids are biologically conserved, the crown group exhibits a surprising level of ecological and morphological diversity. Leporids are found on every continent except Antarctica, from the high arctic to dry, hot deserts. Some leporids are nocturnal, some are social, and some live in dense cover as opposed to the open plains often associated with these

animals. In terms of size, our study includes the smallest leporid, *Brachylagus* (mean skull length ~ 50mm) to one of the largest, *Lepus timidus* (mean skull length ~ 90mm). Genera such as *Pentalagus* and *Caprolagus* have heavy, robust skulls, compared to the typically gracile skulls of most taxa. These cranial differences manifest themselves morphometrically via a wide range of snout lengths and marked differences in skull robustness and form. While leaping abilities are common among most leporid lineages, they are also known to be facultatively semiaquatic, scansorial, fossorial, or exhibit a more generalized, non-hopping form of locomotion (Chapman and Flux, 2008). We distinguish here between the saltatory locomotion (i.e., hopping) most typical among leporids (table 1), and its cursorial form observed in some hare lineages (Gambaryan and Hardin, 1974; Bramble, 1989). Generalists are recognized as those who don't exhibit clear hopping, but rather move in a more scampering habit.

Hypothesis 1 — Facial Tilt

A high degree of facial tilting (e.g., ventral flexion of the facial region) should a) be positively correlated with more active (e.g., saltatorial or cursorial) locomotor styles, and b) show no correlation with burrowing habit.

Variation in the degree of facial tilt among leporids has strong effects on orbital orientation (fig. 1). There is substantial literature discussing the relationship between orbit orientation and ecomorphology, and Cartmill (1970) established the terms 'orbital convergence' and 'frontation' to understand these relationships. Within primates, various groups exhibit a high degree of both orbital convergence and orbital frontation. Orbital convergence is strongly associated with increased binocular visual field overlap (i.e., binocular vision; Heesy, 2004), and orbital frontation is strongly positively correlated with basicranial flexion (Ross, 1993). As DuBrul (1950) pointed out, facial tilt transformations among leporids are nearly identical to basicranial

flexion observed within anthropoids; increased facial tilt and basicranial flexion both result in increased orbital frontation (see figure 1 for changes in frontation related to increased FT). Several workers have shown that increased frontation is positively correlated with arboreal taxa (Cartmill, 1970; Heesy, 2008); increased frontation changes the visual field to allow for better visualization of substrate. Given these relationships, and the fact that leporids show relatively low degrees of convergence but high degree of frontation, we expect that facial tilt (as a proxy for frontation) should be strongly correlated to locomotor styles that would require enhanced substrate perception (saltatorial and cursorial), but we do not expect that facial tilt will be related to burrowing habit.

Hypothesis 2 — Skull shape

We expect that there will be significant skull shape differences among a) locomotor styles, and b) burrowing habits.

We have no a priori expectations about how overall skull shape might change with locomotor mode or burrowing habit. Instead we will investigate the more fundamental question of whether skull shape is related to locomotion and burrowing habit at all. Our interest in this question is therefore more a form of exploratory data analysis than a test of a specific hypothesis.

MATERIALS AND METHODS

We collected morphometric data (Appendix 1) from 140 leporid skulls spanning 16 taxa (Table 1) housed in the departments of Mammalogy at the American Museum of Natural History and the Los Angeles County Museum of Natural History. Care was made to use only adult specimens, characterized by fully fused occipital sutures (Hoffmeister and Zimmerman, 1967). Ten linear measurements (Table 2, Figure 2) were recorded per specimen using digital calipers by

three authors (BPK, MW, and NB), and a repeatability study (not shown) was performed to ensure there was no intercollector bias introduced. We also measured the first molar (M1) length and width, then calculated the M1 area to use as a proxy to body size, which been shown to be highly correlated with body mass in rabbits (Calzada et al. 2003).

Facial tilt was measured by photographing each skull in lateral view using a Nikon D80 digital camera. The skulls were placed in a sandbox to ensure that the sagittal plane was orthogonal to the focal direction. Facial tilt angle was acquired from the digital photos within Adobe Photoshop © (Fig. 1), measured as the angular difference between the 'occipital plane' and a line parallel to the cranial diastema. Variations among individuals for the cranial variables were explored using principal components analysis. To do this we took the natural log of body size (M1A) and the ten linear measurements, and using the covariance matrix of these variables performed a PCA, within the statistical software R v3.1.1 (R Development Core Team 2014).

Phylogenetically informed analyses

To examine facial tilt angle and cranial shape in a phylogenetic context, we used the phylogenetic relationships among species of Leporidae recently published by Matthee et al (2004). The original tree was constructed using seven genes (five nuclear and 2 mt) for 25 ingroup taxa. We pruned the tree to include only the 16 taxa studied here, and retained the information on branch lengths, which are scaled using a molecular clock (details of which are in Matthee et al 2004).

Morphometric data and facial tilt angle were compared to several key ecological indicators, including locomotor type and burrowing habit (Table 1). Ecological data were obtained from Chapman and Flux (1990). We divided leporids into three locomotor categories: generalized or 'scramble' locomotors, which tend to be the slowest-moving, saltatory or hopping locomotors, and fast-moving taxa that practice cursorial (leaping and bounding) locomotion,

which is essentially a specialized form of saltation. Regarding burrowing habits, some leporids dig their own burrows (e.g., *Oryctolagus* and *Romerolagus*), whereas others simply occupy preexisting burrows excavated by other animals. For the purposes of this study, we refer to leporids as burrowers if they occupy burrows consistently, regardless of whether they dig the burrows.

To test whether or not the degree of facial tilt differs among the three locomotor categories, we performed a one-way Analysis of Variance (ANOVA) under a Brownian motion model of evolution. This was done using species means of the FT angle and a distance-based phylogenetic generalized least squares analysis (D-PGLS ; Adams 2014). A distance-based approach provides numerically identical estimates of evolutionary patterns to those obtained from standard implementations of PGLS on univariate datasets, and was used here for consistency with analyses below on the cranial variables. The statistical significance of each term in the D-PGLS was assessed using 1000 permutations whereby the species means are shuffled among the tips of the phylogeny. We performed a second ANOVA as above to test whether facial tilt differs between taxa that utilize burrows (“burrowing”) and those that do not (“non-burrowing”). Box and whisker plots were used to visualize the individual variation in facial tilt angle among groups. Both ANOVAs were done using *procD.pgls* in the geomorph package (Adams et al. 2014) in the statistical software R v3.1.1 (R Development Core Team 2014).

To test whether or not cranial shape, as represented by ten morphometric variables, differs among the three locomotor types, we performed a multivariate analysis of covariance (MANCOVA) in an evolutionary context under a Brownian motion model of evolution. This was done using species means of the natural log of the ten variables and D-PGLS, which performs better than a regular PGLS when the number of variables begins to approach the number of species (Adams 2014). The MANCOVA model used body size as a covariate. We used the area of the first upper molar as a proxy for body size, which is commonly used among mammals (see

Alroy, 1998), but has also been shown to be useful within leporids (Calzada, et al., 2013). The statistical significance of each term in the D-PGLS was assessed using 1000 permutations of the species means. Similarly, we tested whether or not cranial shape differs between burrowing and non-burrowing taxa using a MANCOVA as described above. These analyses were done in *procD.pgls* within the geomorph package (Adams et al. 2014) in the statistical software R v3.1.1 (R Development Core Team 2014).

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189 RESULTS

190 Facial Tilt

191 Facial tilt (FT) summarizes the broad dorsal arching of the skull roof that is prominent
192 among living leporids (Fig. 1). Overall, there is a nearly 30° range of variation in this trait among
193 specimens of all species in this sample (Appendix 1). We found a significant difference among
194 locomotor types for facial tilt angle ($F = 7.02$, $P = 0.016$; Fig. 3a). The mean FT angle for
195 generalized locomotors (mean, $\mu = 44.0$, standard deviation, $\sigma = 5.48$) is substantially higher than
196 that of cursorial ($\mu = 36.3$, $\sigma = 5.46$) and saltatorial taxa ($\mu = 37.2$, $\sigma = 5.91$) (Fig. 3a). This
197 indicates that taxa that are either saltatorial or cursorial tend to have facial regions that are more
198 ventrally deflected. By contrast, we found no significant difference in FT angle between
199 burrowing and non-burrowing taxa ($F = 0.0037$, $P = 0.973$; Fig. 3b).

200

201 Cranial shape analyses

202 Principal components analysis shows that PC1 accounts for 75.6% of cranial shape
203 differences, PC2 accounts for 10.3%, and PC3 accounts for 4.1%. (Table 3; Fig. 4). Body size has
204 a significant effect on cranial shape, as described by the ten linear variables ($F = 11.43$, $P = 0.001$
205 in the model with locomotor mode, and $F = 11.76$, $P = 0.002$). However, there is no significant

effect of locomotor habit on cranial shape ($F = 1.603$, $P = 0.28$), nor was there significant interaction between body size and locomotor habit ($F = 0.896$, $P = 0.570$). Likewise, there is no significant effect on cranial shape by burrowing behavior ($F = 2.416$, $P = 0.263$), nor a significant interaction of body size and burrowing behavior ($F = 1.005$, $P = 0.452$). These results indicate that the variation in cranial shape observed among modern species is partly due to evolutionary allometry, but not to the ecological diversification of leporids into different locomotor modes or burrowing behavior.

DISCUSSION

Given a clear correlation between the degree of facial tilt (FT) and locomotor style, understanding the anatomical basis of facial tilt is important to discerning its function. Generalized locomotors exhibit less facial tilt, an anatomical condition that could properly be thought to be primitive for the mammalian skull, and given their fossil record, lagomorphs as well (Dice, 1933; Asher et al., 2005). However, the extent of dorsal arching of the skull roof and associated facial tilt seen within extant saltatorial and cursorial leporids is exceptional among mammalian skulls. Our own species is one of the few others that exhibit such a dramatic transformation between the basicranial and facial regions of the skull. Facial tilt within leporids is allowed via the expansion of the supraoccipital bone on the dorsal skull. Along the ventral skull, there is a pronounced flexure near the basisphenoid/presphenoid juncture. The ‘crest’ in the occipital region, which looks like an occipital crest in lateral view, is actually the external occipital protuberance (EOP) of the supraoccipital bone. The complex architecture of the supraoccipital in leporids is the most marked change related to the dorsal arching the skull roof. Lateral to the EOP are two large fossa that extend to the parietal/occipital suture that allow for

attachment of the *splenius capitus* mm., which are involved in head extension and lateral rotation. The fossae can be clearly identified via the prominent superior nuchal line that extends rostrally from the EOP. The *longissimus capitus* m. inserts with the *splenius capitus* m. in the lateral, mastoid area, of the occipital region. A final long extensor muscle, the *semispinalus capitus* m., attaches to the lateral portions of the EOP. Together, these three long erectors serve to extend, stabilize, and laterally rotate the head. Deep to these long erectors are an occipital group of muscles that attach to the first two cervical vertebrae and occipital bones to serve as fine motor control of the head. Upon comparison of leporid skulls, it is apparent that those with significant facial tilt are expanding the rostral portions of the supraoccipital bone relative to the caudal portion. This serves to increase the attachment area for the long extensor muscles, allowing for improved extension and lateral rotation of the head. Most importantly, it is clear that the transformations of facial tilt observed with in leporids are driven by a highly dynamic musculature and osteological system. As outlined above, increasing facial tilt would have the consequence of increasing frontation, and in turn, increasing the visual field to allow for better visualization of substrate. Our results indicate that more active leporids (cursorial and saltatorial species) exhibit greater facial tilt and that this may be driven by a need to better substrate visualization, although we have not tested that explicitly.

Differences in facial tilt are important to discuss in terms of the allometric scaling of cranial shape found within remaining linear morphometric dataset. Given that size is a major predictor of cranial shape within our ten linear variables and that locomotor style has little relationship to cranial shape, it is striking that facial tilt *does* distinguish generalist locomotors clearly from more active taxa. This suggests that FT represents a meaningful biological metric among leporids, but may also summarize a specific aspect of cranial shape not recognized within

our linear variables. While our linear measurements failed to discern differences among locomotor groups, this may be function of the limited ability of these variables to capture important shape differences among crania within leporids due to the highly transformed nature of their skulls (e.g. pronounced dorsal arching). Nonetheless, our linear variables do discriminate taxonomic groups (Fig. 4a) based on both size (PC1) and our first shape component (PC2); which has been shown in other cranial morphometric studies (see, for example, Palacios et al., 2008 and Pintur et al. 2014).

Our study demonstrates that the dorsal arching found within leporid skulls (summarized here as facial tilt) has a strong relationship with how these animals moved. Facial tilt summarized a complex transformation of nearly all aspects of the leporid skull, including basicranial rearrangement of the occipital bones and facial changes in the diastema region. Our linear variables, while distinguishing taxonomic groups, do not capture shapes changes as they relate to locomotion; which is likely do to the simplified, two dimensional nature of these metrics. Based on the changes in orbit orientation that are associated with increased facial tilt, it is likely that skull transformations in crown leporids are driven by a need for increased visual perception of substrate.

AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: BPK, MJW. Performed the experiments: BPK, NB, ES. Analyzed the data: BPK, NB, ES. Contributed reagents/materials/analysis tools: BPK, NB, MJW. Wrote the paper: BPK, NB, MJW, ES.

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282 continue that work. Travel to the AMNH by MJW was made possibly by funds from the
283 Department of Anatomy, Western University of Health Sciences.

284 APPENDIX 1 All measurements

285 FIGURE 1 — Facial tilt in leporids. The crania of *Caprolagus hispidus* (AMNH 54852, above)
286 and *Pronolagus crassicaudatus* (AMNH 89033, below) are shown in left lateral view. Facial tilt
287 (FT) is defined herein as the angle between the upper diastema and the occipital plane, where
288 increased values indicated a skull orientation closer the horizontal plane.

289

290 FIGURE 2 — A representative leporid skull showing measurements used in this analysis. The
291 cranium of *Bunolagus monticularis* (AMNH 146662) is shown in right lateral (top), dorsal (lower
292 left), and ventral (lower right) views. Abbreviations follow Table 1. Three measurements
293 included in the analysis are not shown here: lower diastema length (DILL; measured similar to
294 DILU), M1 area (M1A; M1 length x M1 width), and facial tilt (FT; illustrated in fig. 2).

295

296 FIGURE 3 — Box and whisker plot summarizing facial tilt angle for all specimens, showing how
297 the angle differs between locomotor types (a) and burrowing behavior (b).

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299 FIGURE 4 — Principal components analysis of 11 linear measurements describing cranial shape
300 for all specimens. a) Colored symbols by species. b) colored by LOC.

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FIGURE 1

Facial tilt in leporids. The crania of *Caprolagus hispidus* (AMNH 54852, above) and *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.

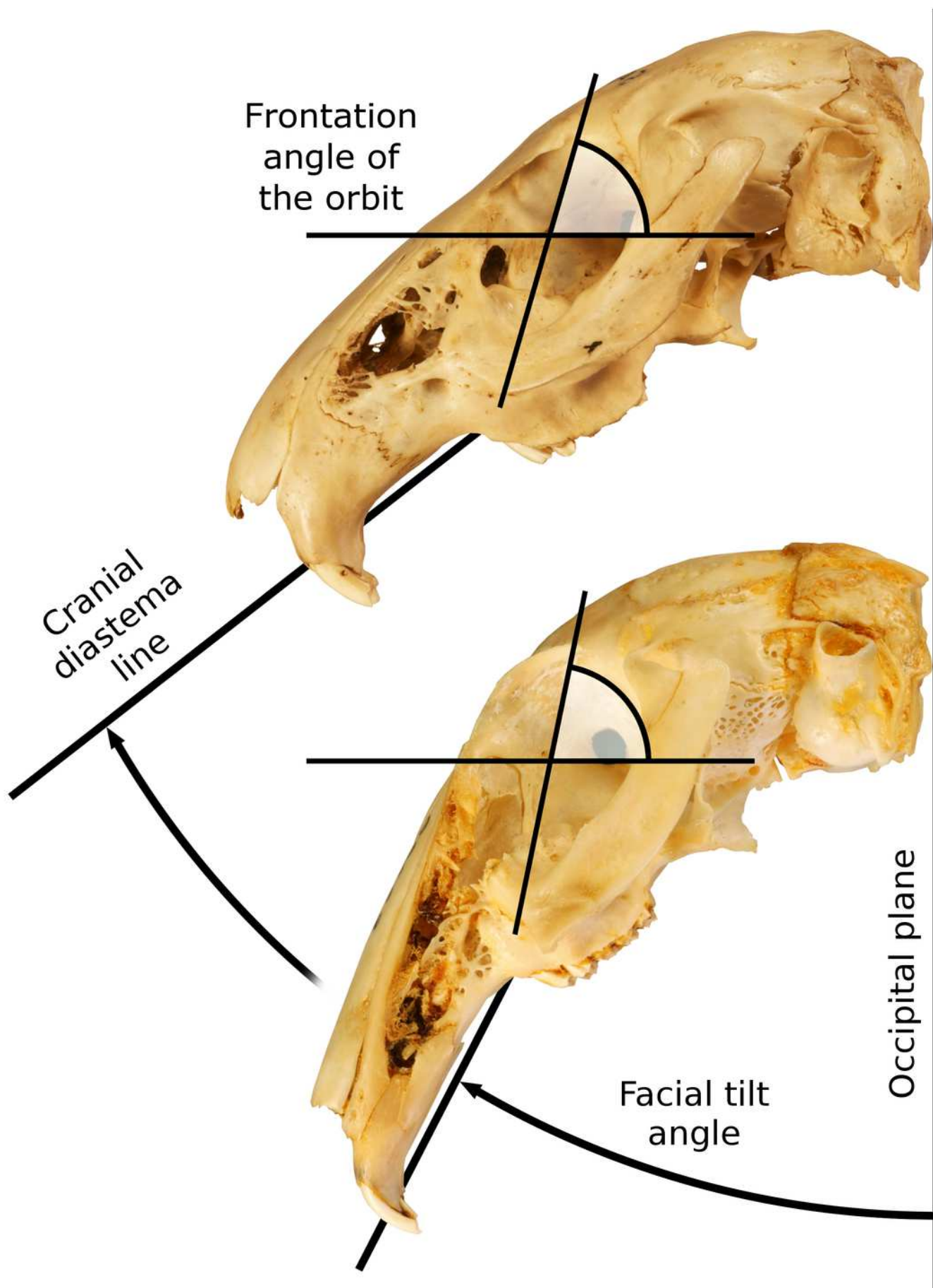


FIGURE 2

A representative leporid skull showing measurements used in this analysis. The cranium of *Bunolagus monticularis* (AMNH 146662) is shown in right lateral (top), dorsal (lower left), and ventral (lower right) views. Abbreviations follow Table 1. Three measurements included in the analysis are not shown here: lower diastema length (DILL; measured similar to DILU), M1 area (M1A; M1 length x M1 width), and facial tilt (FT; illustrated in fig. 2).

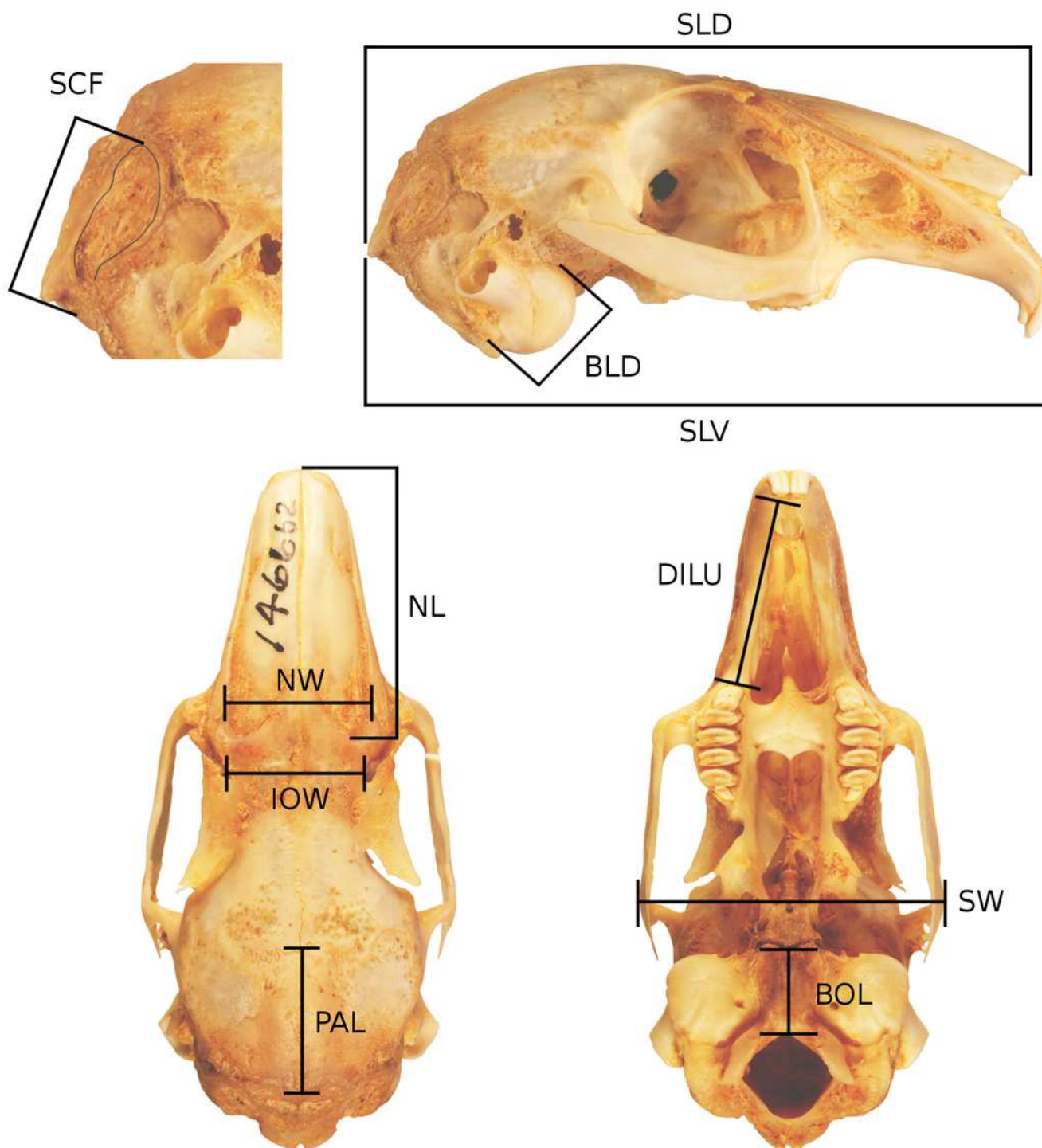


FIGURE 3

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

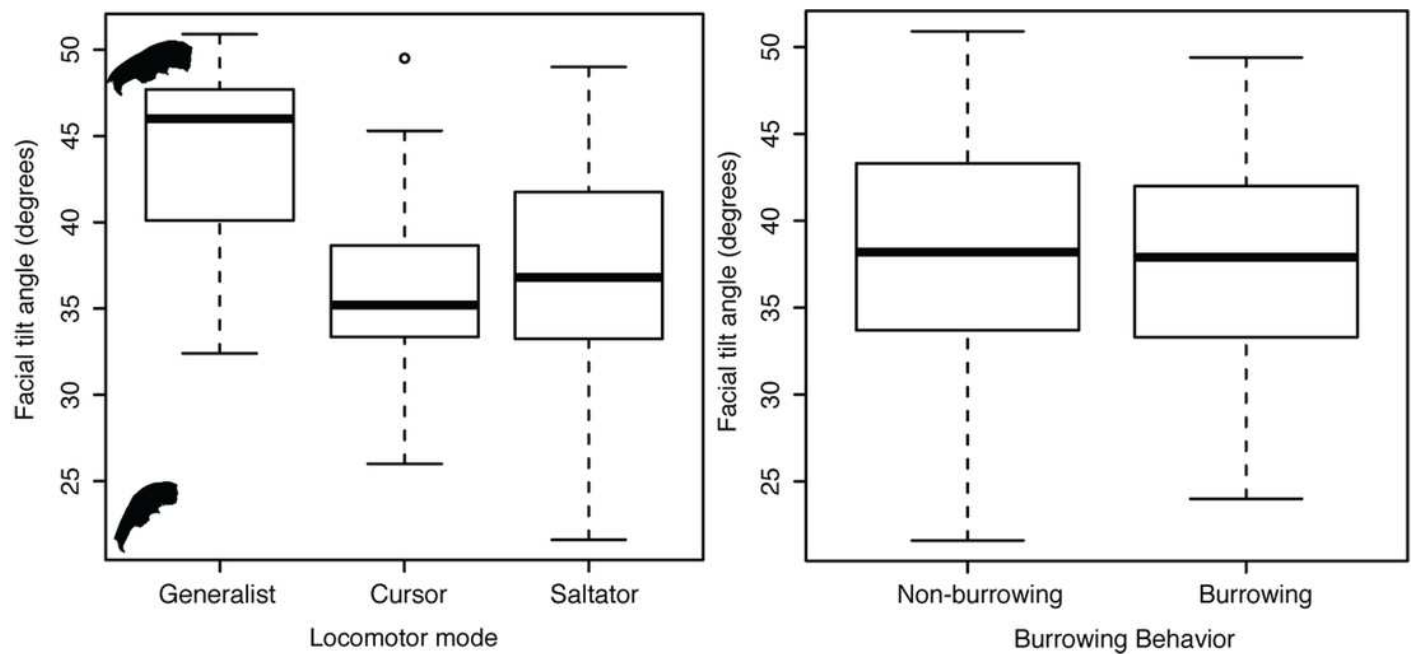


FIGURE 4

Principal components analysis of 11 linear measurements describing cranial shape for all specimens. a) Colored symbols by species. b) colored by LOC.

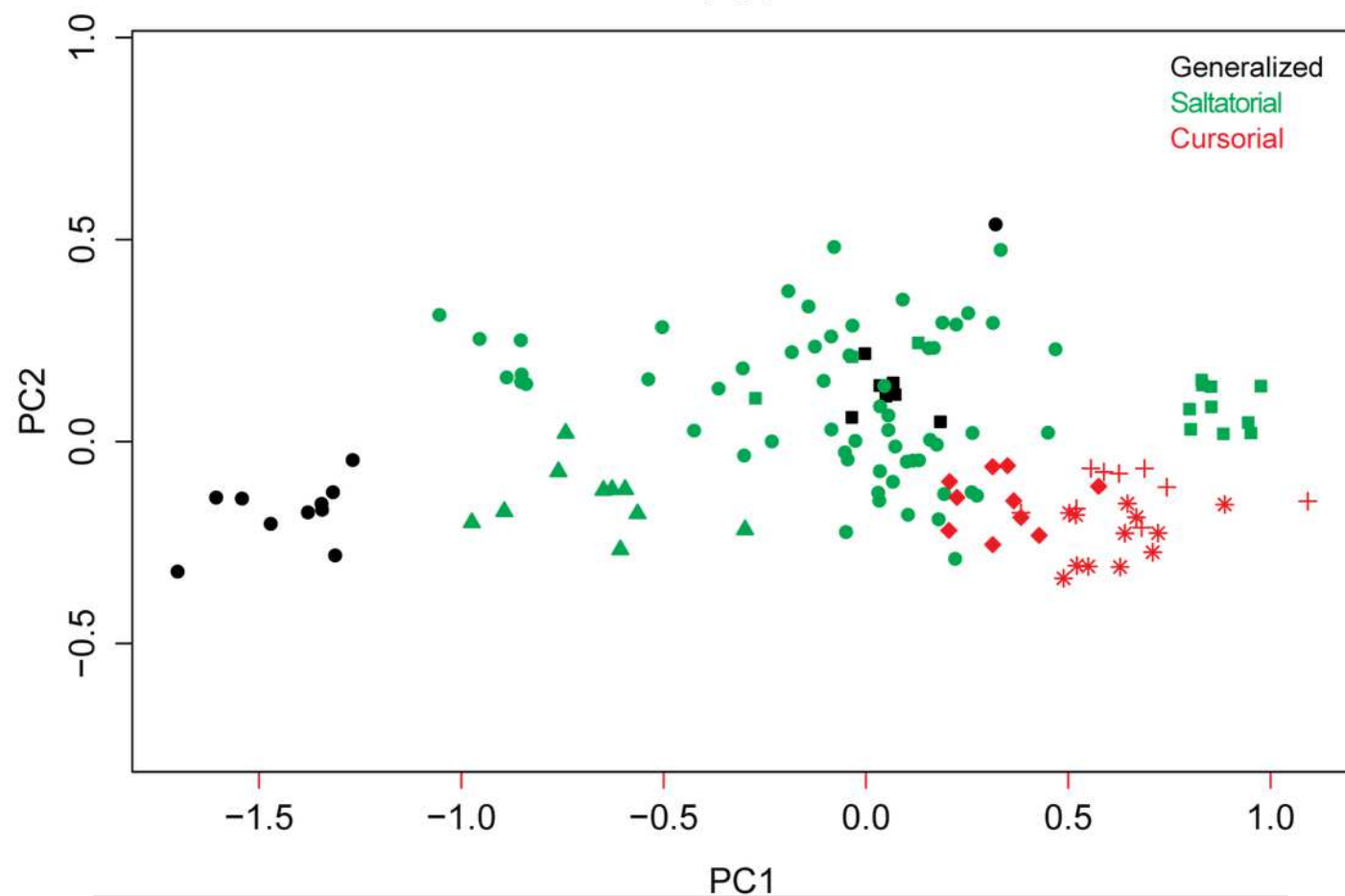
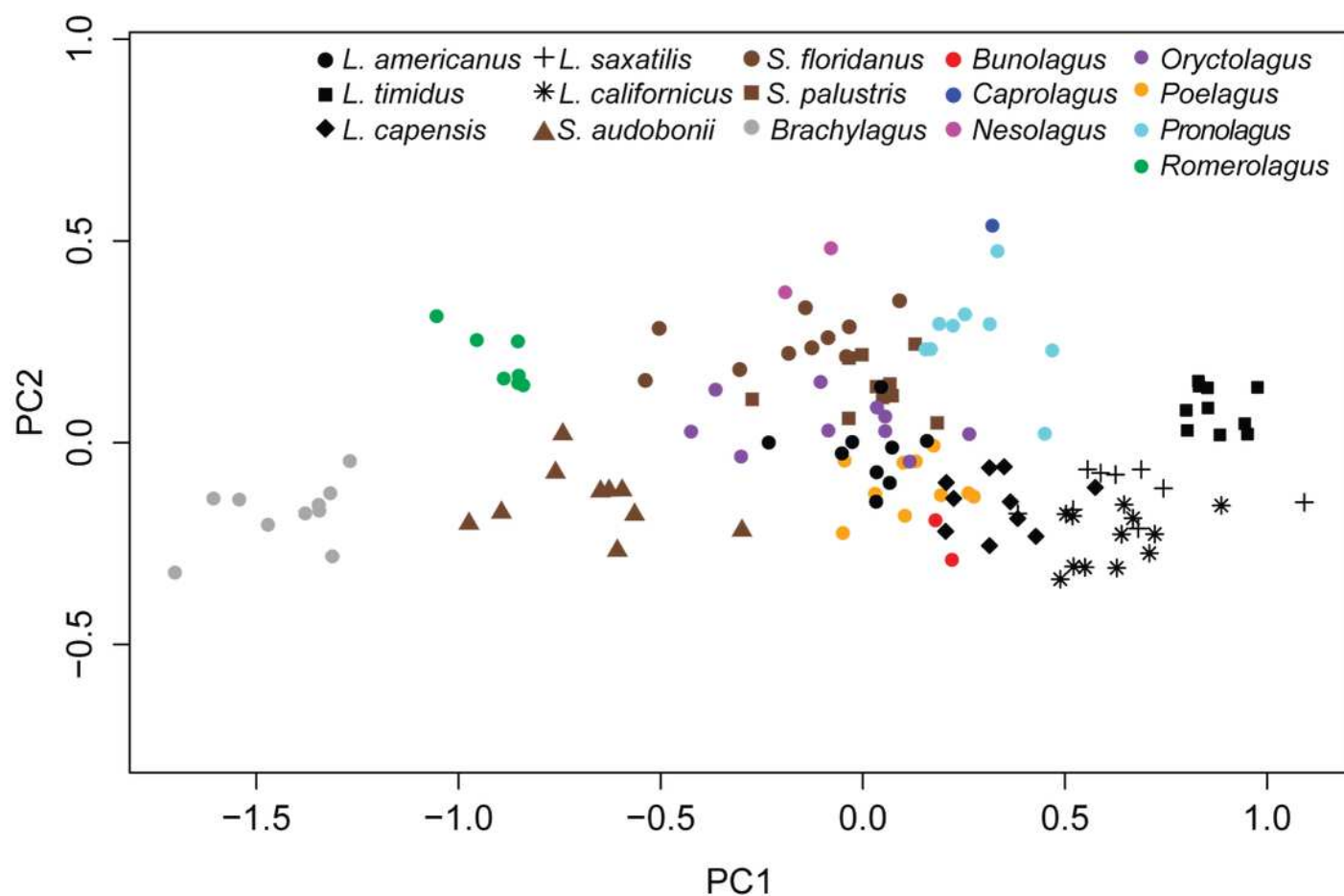


Table 1 (on next page)

Table 1

Leporid species included in this study

Species	Locomotion Type	Burrowing	Geographic Range	Abbreviation	n
<i>Romerolagus</i>	Saltatorial	Yes	Central Mexico	Ro	7
<i>Bunolagus</i>	Saltatorial	Yes	South Africa	Bu	2
<i>Caprolagus</i>	Generalized	Yes	Himalayas	Ca	2
<i>Brachylagus</i>	Generalized	Yes	NW United States	Br	10
<i>Sylvilagus floridanus</i>	Saltatorial	No	Americas	Sfl	10
<i>Sylvilagus palustris</i>	Generalized	No	SE United States	Spal	10
<i>Sylvilagus audubonii</i>	Saltatorial	Yes	Americas	Sau	10
<i>Poelagus marjorita</i>	Saltatorial	No	NE Africa	Po	10
<i>Pronolagus crossicaudatus</i>	Saltatorial	No	South Africa	Pc	10
<i>Oryctolagus cuniculus</i>	Saltatorial	Yes	Global	Oc	10
<i>Nesolagus timminsi</i>	Saltatorial	Yes	Vietnam/Laos	Nt	2
<i>Lepus americanus</i>	Saltatorial	No	North America	Lam	10
<i>Lepus timidus</i>	Saltatorial	Yes	Old World, Palearctic	Lti	10
<i>Lepus capensis</i>	Cursorial	Yes	Africa, Arabia, Europe, Asia	Lcap	10
<i>Lepus californicus</i>	Cursorial	No	SW North America	Lcal	12
<i>Lepus saxatilis</i>	Cursorial	No	South Africa; Namibia	Lsax	9

Table 1. Leporid species included in this study

Table 2(on next page)

Table 2

Variables used in this study and description; see figures 1 and 2 for illustrations of the measurement conventions.

Table 2. Variables used in this study and description; see figures 1 and 2 for illustrations of the measurement conventions.

Abbr.	Variable	Measurement Convention
BLD	bullae 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
M1A	M1 area (size proxy)	area of right M1, approximated as length x width
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 <i>M. splenius capitis</i> insertion fossa to opisthocranium
SLD	skull length dorsal	maximum midsagittal length from anterior nasal bones to opisthocranium (just dorsal to incisors) to opisthocranium
SW	skull width	maximum transverse width across zygomatic processes

Table 3(on next page)

Table 3

PCA loadings

Table 3. PCA loadings

	PC1	PC2	PC3
BLD	-0.04539695	-0.910565077	-0.16457026
BOL	0.31643982	-0.163364441	-0.32589829
DILU	0.3289936	0.053918587	0.25801961
DSLL	0.26485601	-0.348738236	0.641238
IOW	0.30539101	0.005297391	-0.44448898
M1A (Body size)	0.31974629	0.084227328	-0.19956786
NL	0.31995934	0.082793999	0.26130228
NW	0.32710183	0.052330681	0.09654871
PAL	0.29599664	0.011295643	-0.26889153
SLD	0.34095647	0.048591476	0.03475742
SW	0.33269084	-0.021292115	-0.02091868