

# Skeletal Indicators of Ecological Specialization in Pika (Mammalia, Ochotonidae)

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**ABSTRACT** Pika species generally fall into two ecotypes, meadow-dwelling (burrowing) or talus-dwelling, a classification that distinguishes a suite of different ecological, behavioral, and life history traits. Despite these differences, little morphological variation has previously been documented to distinguish among ecotypes. The aim of this study was to test whether postcranial features related to burrowing are present in meadow-dwelling species and whether talus-dwelling species exhibit postcranial modifications related to frequent leaping between rocks. To test this, the scapula, humerus, ulna, radius, innominate, femur, tibia, and calcaneus of 15 species were studied and measured. Twenty-three measurements were taken on 199 skeletons, and 19 indices were constructed from these measurements. Indices were compared between the two ecotypes using Student's *t*-test. Comparisons among ecotypes, species, and subgenera were made using one-way ANOVA with the Tukey honest significant difference post hoc test. Multivariate results were generated using principal components analyses. Thirteen forelimb and hind limb indices proved significant in distinguishing the meadow-dwelling, talus-dwelling, and intermediate forms. A number of these indices are associated with burrowing or leaping in other mammals, providing some support for the hypothesis that postcranial modifications in pika are related to locomotor differences. This evidence of morphological responses to ecological specialization will be useful for reconstructing the paleobiology of extinct taxa, assessing the behavioral variability of extant species, and improving our understanding of the evolutionary history of pikas. *J. Morphol.* 274:585–602, 2013. © 2013 Wiley Periodicals, Inc.

**KEY WORDS:** digging; forelimb; functional morphology; hind limb; *Ochotona*

## INTRODUCTION

Postcranial morphology is expected to reflect differences in ecology and positional behaviors, such as digging or leaping. Despite the fact that digging and leaping behaviors have evolved several times within mammals, many of the same traits are found across a wide range of species (Salton and Sargis, 2008, 2009). Similar digging adaptations in the postcranium have been identified in several fossorial mammals (Hildebrand, 1985), small mammals such as

treeshrews and tenrecs (Sargis, 2002a,b; Salton and Sargis, 2008, 2009), and, in isolated cases, fossil lagomorphs (e.g., Averianov, 1995). Skeletal adaptations of the hind limbs for leaping have also been demonstrated in several mammals, particularly primates (Gabriel, 1984; Anemone, 1990; Connour et al., 2000; James et al., 2007). Such traits associated with digging and leaping may have evolved multiple times within pikas (see Fig. 1; Yu et al., 2000).

Pikas (Lagomorpha: Ochotonidae: *Ochotona*) are small, generalist herbivores currently distributed in the northern hemisphere (Smith et al., 1990). They are typically considered to belong to one of two ecotypes, each associated with a suite of distinct life history traits and behaviors (Smith, 1988, 2008). Meadow-dwellers, often referred to as burrowing pikas, excavate and occupy burrows in steppe, forest, or shrub habitats. They are short-lived, highly social, and highly fecund, and they exhibit large demographic fluctuations (Smith et al., 1990). Although they are known to burrow, little is known about the burrowing behavior of pika or the mechanics of their burrowing. Current evidence indicates that they primarily employ scratch-digging. They appear to use their fore- and hind feet to move dirt backwards out of the burrow (G. Schaller pers. comm.), and pika that are captured sometimes have a lot of soil on their forefeet (A. Lissovsky pers. comm.). Talus-dwelling species inhabit boulder, talus, or scree fields. They are generally nonburrowing, relatively long-lived, and

Additional Supporting Information may be found in the online version of this article.

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Received 22 August 2012; Revised 16 November 2012;  
Accepted 16 December 2012

Published online 5 February 2013 in  
Wiley Online Library (wileyonlinelibrary.com)  
DOI: 10.1002/jmor.20127

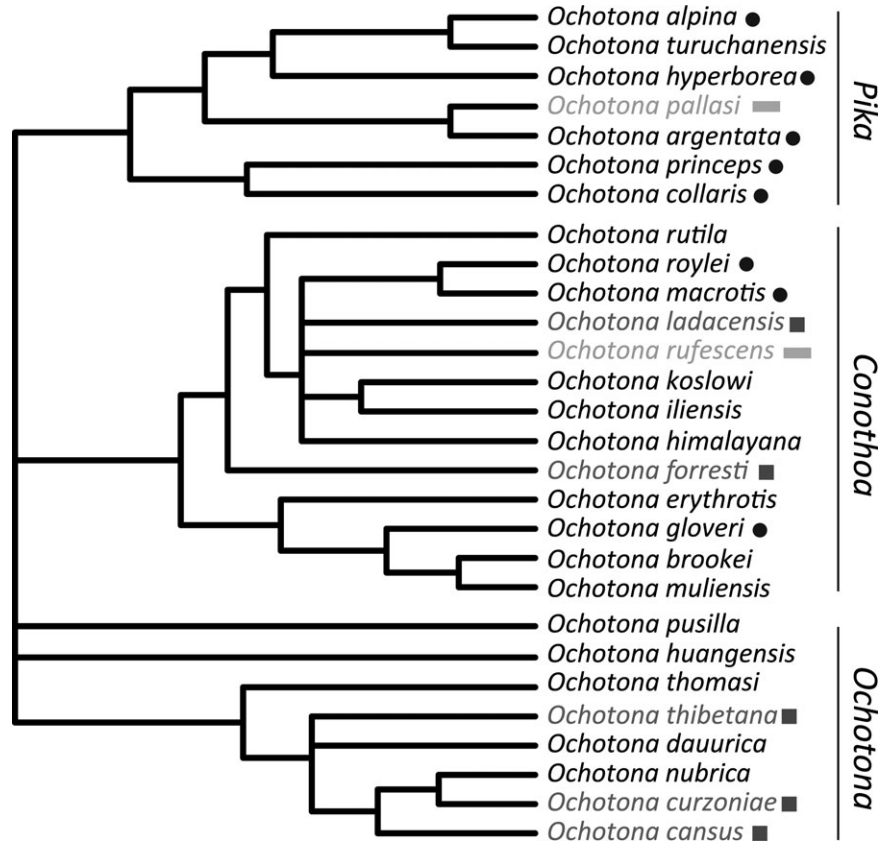


Fig. 1. Phylogeny of the genus *Ochotona* (after Lanier and Olson, 2009). Black circles denote talus-dwellers included in this study; dark gray squares denote meadow-dwellers included in this study; and light gray rectangles denote intermediate taxa included in this study.

asocial, and they exhibit much lower fecundity (Smith et al., 1990). Leaping (four-footed jumping between rocks that covers horizontal, and sometimes vertical, distances from a few centimeters to more than three times their body length) is a noteworthy component of their locomotor repertoire (pers. obs.). Previously, the only differences described to distinguish pika ecotypes were longer vibrissae and sharp, bent claws in the talus-dwelling forms, and shorter vibrissae and flat, broad claws in the meadow-dwelling forms (Fedosenko, 1974; Formozov, 1981).

Of the 30 named species, both American species (*O. princeps* and *O. collaris*) and approximately half of the Asian species are talus-dwelling, whereas the rest of the Asian species are steppe-, forest-, or shrub-dwelling (henceforth referred to as meadow-dwelling; Smith et al., 1990; Yu et al., 2000; Smith, 2008). A few species, such as Pallas's Pika (*O. pallasii*) and the Afghan Pika (*O. rufescens*), exhibit the life history characteristics of meadow-dwelling species (Smith, 1988) but are known to occur in both steppe and rocky environments, where they exhibit the behaviors associated with those habitats (Smith, 2008). They are thus termed "intermediate" species (Smith, 1988).

Pika species exhibit little morphological variation in body size or shape (Smith et al., 1990; Yu et al., 2000), but high intraspecific variation (particularly in pelage) has been noted (Corbet, 1978). Early attempts to explore the phylogenetic relationships of *Ochotona* focused on cranial attributes (Corbet, 1978; Weston, 1982; Yu et al., 1992) and offered little consistent taxonomic resolution (see Yu et al., 2000). Four recent molecular studies completed since 2000 (Yu et al., 2000; Niu et al., 2004; Lissovksy et al., 2007; Lanier and Olson, 2009), as well as a study that combined cranial and mandibular data (Fostowicz-Freluk et al., 2010), have provided more phylogenetic resolution within the genus.

Historically separated by palatal characteristics (Weston, 1982), three subgenera are currently recognized in *Ochotona* based on molecular results: *Pika*, *Ochotona*, and *Conothoa* (Lanier and Olson, 2009). However, there is continued debate regarding their constituent members (e.g., see Fostowicz-Freluk et al., 2010). *Pika* includes talus-dwelling species such as the two North American taxa, *O. collaris*, and *O. princeps*, as well as the intermediate species *O. pallasii*. The subgenus *Ochotona* comprises exclusively burrowing meadow-dwelling species. *Conothoa* is mixed, with approximately

TABLE 1. *Ochotona* species included in this study

Species	Subgenus	Ecotype	Range <sup>a</sup>	Body length (cm)	Abbrev.	<i>n</i>
<i>O. alpina</i> (Pallas, 1773)	<i>Pika</i>	Talus	China; Kazakhstan; Mongolia; Russia	15.2–23.5 <sup>a</sup>	AL	4
<i>O. argentata</i> Howell, 1928	<i>Pika</i>	Talus	China	20.8–23.5 <sup>a</sup>	AR	1
<i>O. collaris</i> (Nelson, 1893)	<i>Pika</i>	Talus	Canada; United States	18.9 <sup>b</sup>	CO	81
<i>O. gloveri</i> Thomas, 1922	<i>Conothoa</i>	Talus	China	16–22 <sup>a</sup>	G	1
<i>O. hyperborea</i> (Pallas, 1811)	<i>Pika</i>	Talus	China; Japan; North Korea; Mongolia; Russia	15–20.4 <sup>a</sup>	H	5
<i>O. macrotis</i> (Gunther, 1875)	<i>Conothoa</i>	Talus	Afghanistan; Bhutan; China; India; Kazakhstan; Kyrgyzstan; Nepal; Pakistan; Tajikistan	15–20.4 <sup>a</sup>	M	12
<i>O. princeps</i> (Richardson, 1828)	<i>Pika</i>	Talus	Canada; United States	16.2–21.6 <sup>c</sup>	PR	23
<i>O. roylei</i> (Ogilby, 1839)	<i>Conothoa</i>	Talus	China; India; Nepal; Pakistan	15.5–20.4 <sup>a</sup>	RO	10
<i>O. cansus</i> Lyon, 1907	<i>Ochotona</i>	Meadow	China	11.6–16.5 <sup>a</sup>	CA	6
<i>O. curzoniae</i> (Hodgson, 1858)	<i>Ochotona</i>	Meadow	China; India; Nepal	14–19.2 <sup>a</sup>	CU	8
<i>O. forresti</i> Thomas, 1923	<i>Conothoa</i>	Meadow	Bhutan; China; India; Myanmar	15.5–18.5 <sup>a</sup>	F	1
<i>O. ladacensis</i> (Gunther, 1875)	<i>Conothoa</i>	Meadow	China; India; Pakistan	18–22.9 <sup>a</sup>	L	1
<i>O. thibetana</i> (Milne-Edwards, 1871)	<i>Ochotona</i>	Meadow	Bhutan; China; India; Myanmar	14–18 <sup>a</sup>	T	17
<i>O. pallasi</i> (Gray, 1867)	<i>Pika</i>	Intermediate	China; Kazakhstan; Mongolia; Russia	16–22 <sup>a</sup>	PA	3
<i>O. rufescens</i> (Gray, 1842)	<i>Conothoa</i>	Intermediate	Afghanistan; Iran; Pakistan; Turkmenistan	11–25 <sup>d</sup>	RU	26

<sup>a</sup>IUCN, 2011.

<sup>b</sup>MacDonald and Jones, 1987.

<sup>c</sup>Smith and Weston, 1990.

<sup>d</sup>Fulk and Khokar, 1980.

33% meadow-dwellers and 66% talus-dwellers, as well as the intermediate species *O. rufescens* (see Fig. 1). These groupings accentuate the fact that the two ecotypes evolved multiple times, so variation may exist in the specializations of different lineages (subgenera and species) to their behavioral regimes (e.g., see Sargis et al., 2008). To date, no survey of pika systematics has included an analysis of the postcranial skeleton.

Although digging has been recorded in isolated cases for some American talus-dwelling species (Markham and Whicker, 1972), it represents an exceedingly small proportion of observed behaviors. It is expected that morphological modifications related to digging, such as a long olecranon process of the ulna and medial epicondyle of the humerus (Hildebrand, 1985), will be more pronounced in burrowing species, which perform this behavior habitually. In contrast, talus-dwelling species may exhibit more extensive hind limb modifications, including longer limb bones and feet, which may be advantageous in frequent leaping from rock to rock. Suites of characteristics associated with both of these behaviors are described in the literature on mammalian postcranial morphology (see Salton and Sargis, 2008, 2009), but the entire suite is not expected to be present in every burrowing or leaping group or taxon.

We analyzed the postcranial morphology of pikas representing both ecotypes, as well as intermediate species, from across the three recognized subgenera to test for morphological variation associated with the specific behavioral regimes. Identifying

whether such specializations exist could help to determine how behaviorally specialized these taxa are; allow for reconstructing the paleobiology of extinct species; improve our understanding of how different species within each ecotype vary in their postcranial specializations for similar locomotor behaviors (e.g., Sargis et al., 2008); and contribute to our understanding of the function of certain postcranial characters, which may be used in future phylogenetic analyses of this still poorly resolved taxon (Hoffman and Smith, 2005).

## MATERIALS AND METHODS

The scapula, humerus, ulna, radius, innominate, femur, tibia, and calcaneus (Fig. 2) of 199 specimens (Supporting Information), representing 15 species (Table 1), were studied and measured with fine-point digital calipers. Skeletal specimens were analyzed at the American Museum of Natural History, Canadian Museum of Nature, The Natural History Museum, University of Kansas Natural History Museum, United States National Museum of Natural History, University of Michigan Museum of Zoology, and Yale Peabody Museum of Natural History. Additional specimens were borrowed from the Harvard University Museum of Comparative Zoology, Museum of Southwestern Biology, University of California Berkeley Museum of Vertebrate Zoology, and University of Washington Burke Museum and measured at the Yale Peabody Museum. Only adult specimens, as identified by full epiphyseal fusion, dental eruption, and the presence of a mandibular crest for masseter attachment (Lissovsky, 2004), were measured.

Up to 23 linear measurements (Table 2, Fig. 2) were taken on each specimen. To control for size differences between species, measurements were transformed into 19 indices (Table 3). Most indices were created with measurements from a single bone, which allowed specimens with limited available elements to be included in the indices, and which will also allow comparisons

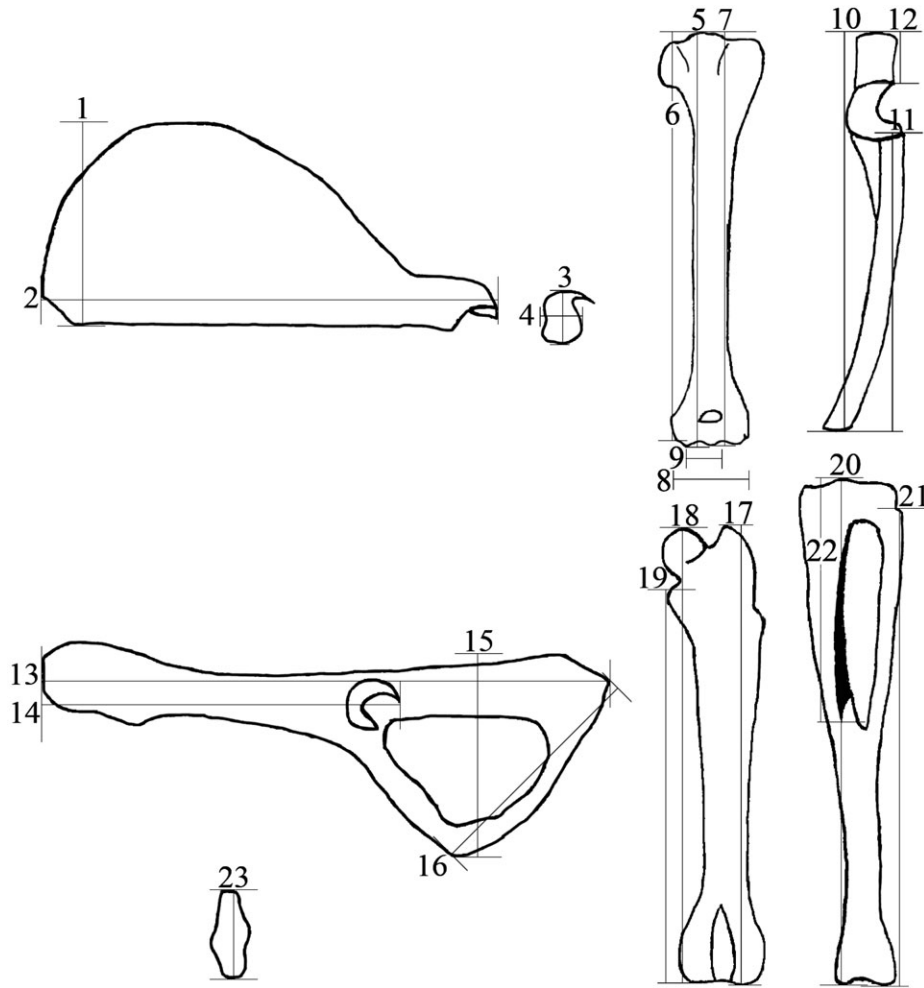


Fig. 2. Forelimb and hind limb measurements (see Table 2 for descriptions).

to isolated fossil specimens in the future. Four standard composite indices were also created with measurements from multiple bones. Statistical analyses were performed in STATISTICA (Version 6.0, StatSoft, Tulsa, OK) and in the R environment for statistical computing (Version 2.15, R Core Team, Vienna). Individual indices were compared between the two main ecotypes (i.e., meadow and talus, with intermediate species excluded) using Student's *t*-test. They were also compared among ecotypes (meadow, talus, and intermediate), species, and the three subgenera using one-way ANOVA, with the Tukey honest significant difference (HSD) post hoc test ( $P < 0.05$ ). Statistical results are available in Supporting Information.

To assess multivariate morphometrics, two principal components analyses (PCA) were conducted on correlation matrices computed from raw measurements, comparing individuals in one analysis and species means in another; the analysis of species means allowed the inclusion of variables that are missing in individual specimens. In both analyses, some taxa were not included (notably species for which only one specimen, with broken or missing elements, was measured) to maximize the number of variables analyzed. Some measurements were eliminated because the bones associated with them were missing or broken in many specimens. For the comparison of individuals, 14 measurements (Table 2; excluding measurements 8, 9, 13, 14, 15, 16, 20, 21, and 23) and 13 species (78 individuals) were included. For the comparison of species means, 21 measurements (Table 2; excluding measurements 16 and 23) and 13 taxa were included. In both analyses, the two species that could not be included were *Ochotona argentata* and *O.*

*forresti*, both of which were represented by single, largely incomplete specimens for which many measurements could not be taken.

## RESULTS

### Univariate

**Forelimb.** The scapula shape index separates the meadow and talus ecotypes when comparing only those two groups; however, it is significantly higher in the intermediate species than in either defined ecotype (Fig. 3A). The two intermediate species are significantly different from numerous taxa when analyzed at the species level (Fig. 3B). This index is also significantly lower in *O. collaris* than in the intermediate species, four other talus-dwelling taxa, or two of the meadow taxa. The scapula shape index is also higher in the subgenus *Conothoa* than in *Pika* (Fig. 3C). This difference appears to be driven by the extremely low value of *O. (Pika) collaris* (Fig. 3B).

The glenoid fossa shape index (Fig. 4A) is also significantly higher in the intermediate species than in either defined ecotype. Intermediate species differ

TABLE 2. Measurements (see Fig. 2 for illustrations)

1) Scapula width	Cranial angle to caudal angle with vertebral border oriented nearly vertically and the scapular spine oriented nearly horizontally
2) Scapula length	Supraglenoid tubercle to vertebral border with vertebral border oriented nearly vertically and the scapular spine oriented nearly horizontally
3) Glenoid fossa length	Cranial edge to caudal edge
4) Glenoid fossa width	Medial edge to lateral edge on caudal part of fossa
5) Humerus length to trochlea	Proximal edge of humeral head to distal edge of trochlea
6) Humerus length to medial epicondyle	Proximal edge of humeral head to distal edge of medial epicondyle
7) Humerus length to capitulum	Proximal edge of humeral head to distal edge of capitulum
8) Humeral distal end width	Medial edge of medial epicondyle to lateral edge of lateral epicondyle
9) Humeral distal articular surface width	Medial edge of trochlea to lateral edge of capitulum
10) Ulna length	Proximal edge of olecranon process to distal edge of styloid process
11) Radius length	Proximal edge of radial head to distal edge of styloid process
12) Olecranon process length	Proximal edge of olecranon process to proximal edge of trochlear notch (olecranon beak)
13) Innominate length	Cranial edge of ilium (iliac crest) to caudal edge of ischium
14) Distal extent of acetabulum	Cranial edge of ilium (iliac crest) to caudal edge of acetabulum
15) Ischium to pubis length	Ischial tuberosity to pubic symphysis
16) Pubis width	Ischial ramus to pubic symphysis with innominate oriented horizontally
17) Maximum femoral length	Proximal edge of greater trochanter to distal edge of lateral condyle
18) Femur length	Proximal edge of femoral head to distal edge of medial condyle
19) Proximal extent of lesser trochanter	Proximal edge of lesser trochanter to distal edge of medial condyle
20) Tibia length	Proximal edge of intercondylar tubercle to distal edge of medial malleolus
21) Fibula length	Proximal edge of fibular head to distal edge of lateral malleolus
22) Tibial crest length	Proximal edge of intercondylar tubercle to distal extent of tibial crest
23) Calcaneus length	Proximal edge of calcaneal tuber to distal edge of cuboid facet

significantly in the glenoid fossa shape index at the species level from two taxa, *O. collaris* and *O. curzoniae* (Fig. 4B). This index is also significantly higher in the meadow taxon *O. thibetana* than in either the talus-dweller *O. collaris* or the meadow-dweller *O. curzoniae*. In addition, the glenoid fossa shape index is significantly higher in the subgenus *Conothoa* than in *Pika* (Fig. 4C). This is most likely driven by the high values in *O. (Conothoa) rufescens* (Fig. 4B).

The humeral epicondylar width index is significantly lower in the talus group than in the intermediate forms (Fig. 5A). This reflects the species level difference between *O. rufescens* and *O. mac-*

*rotis* (Fig. 5B). The index is also higher in meadow forms than in talus forms, but the difference is not significant (Fig. 5A).

The radius length index is one of two indices that separate the two ecotypes from each other, as well as from the intermediate species in the three-way comparison. It is significantly higher in the meadow group than in the talus group, which is significantly higher than in the intermediate species (Fig. 6A). Two meadow taxa, *O. cansus* and *O. thibetana*, are primarily driving the separation between the meadow taxa and the other forms (Fig. 6B). Both, when analyzed by species, show

TABLE 3. Indices

1) Scapula shape index	Scapula width/scapula length
2) Glenoid fossa shape index	Glenoid fossa length/glenoid fossa width
3) Humerus length 1 index	Humerus length to medial epicondyle/humerus length to capitulum
4) Humerus length 2 index	Humerus length to trochlea/humerus length to capitulum
5) Humeral epicondylar width index	(Humeral distal end width—humeral distal articular surface width)/humeral distal end width
6) Radius length index	Radius length/ulna length
7) Olecranon process length index	Olecranon process length/ulna length
8) Distal extent of the acetabulum index	Distal extent of acetabulum/innominate length
9) Innominate shape index	Ischium to pubis length/innominate length
10) Pubis width index	Pubis width/innominate length
11) Femur length index	Femur length/maximum femoral length
12) Proximal extent of the lesser trochanter index	Proximal extent of lesser trochanter/maximum femoral length
13) Fibula length index	Fibula length/tibia length
14) Tibial crest length index	Tibial crest length/tibia length
15) Calcaneus length index	Calcaneus length/tibia length
16) Brachial index	Radius length/humerus length to trochlea
17) Humero-femoral index	Humerus length to trochlea/maximum femoral length
18) Crural index	Tibia length/maximum femoral length
19) Intermembral index	(Humerus length to trochlea + radius length)/(maximum femoral length + tibia length)

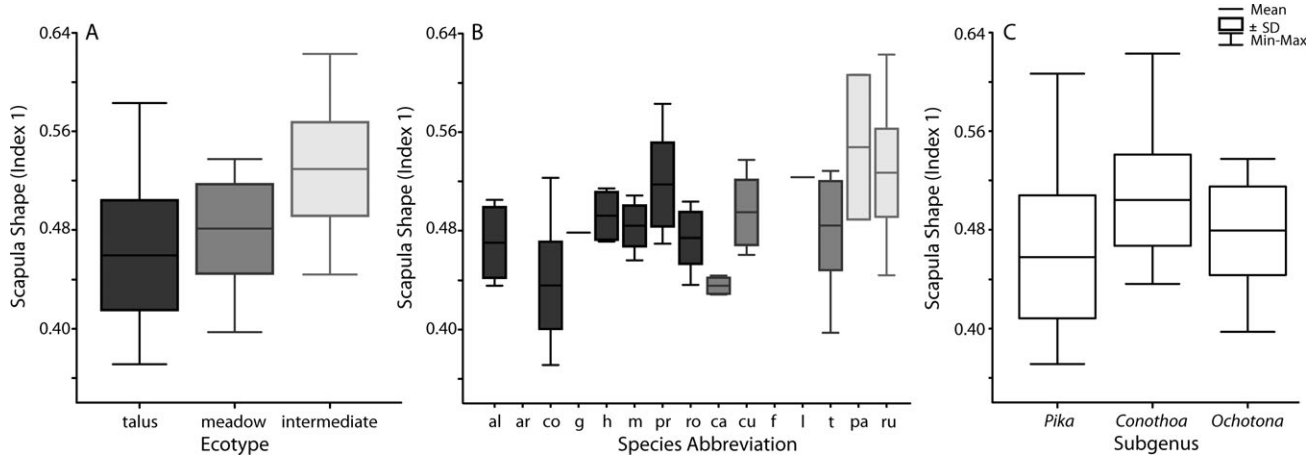


Fig. 3. Box plots of scapula shape index by **A:** ecotype, **B:** species, **C:** subgenus.

significant differences from two talus taxa (i.e., *O. hyperborea* and *O. princeps*) as well as the two intermediate species. The radius length index also separates one subgenus from the other two. It is lower in both *Pika* and *Conothoa* than in *Ochotona* (Fig. 6C). This is driven by *O. (P.) pallasii*, which has a significantly lower mean than *O. (C.) macrotis*, *O. (O.) cansus*, and *O. (O.) thibetana*. Also, *O. (P.) hyperborea* and *O. (P.) princeps* both have significantly lower means than *O. (O.) cansus* and *O. (O.) thibetana* (Fig. 6B).

The olecranon process length index also separates all three groups. It is highest in the intermediate species and lowest in the meadow taxa (Fig. 7A). As with the radius length index, much of the divergence between the groups is due to the extreme values in *O. cansus* and *O. thibetana* (Fig. 7B). When comparing among species, this index is significantly lower in these two taxa than in the talus-dwelling *O. collaris*, *O. macrotis*, and *O. princeps*, the meadow-dweller *O. curzoniae*, and

the intermediate species *O. rufescens*. It is also significantly lower in *O. thibetana* than in the talus form *O. alpina* and the intermediate species *O. pallasii*. The olecranon process length index also separates the subgenera *Pika* and *Conothoa* from the subgenus *Ochotona*, with lower values in *Ochotona* than in the other two subgenera (Fig. 7C). The differences in the olecranon process length index are likely driven by the low values of *O. (O.) cansus* and *O. (O.) thibetana* (Fig. 7B).

**Hind Limb.** The innominate shape index differs significantly between the two defined ecotypes in the two-way comparison, and it is higher in the talus taxa and intermediate species than in the meadow taxa when all three are compared (Fig. 8). The distal extent of the acetabulum index differs only between the subgenera *Ochotona* and *Conothoa* (Fig. 9).

The pubis width index is one of two hind limb indices that separate the two defined ecotypes and the intermediate species in the three-way compari-

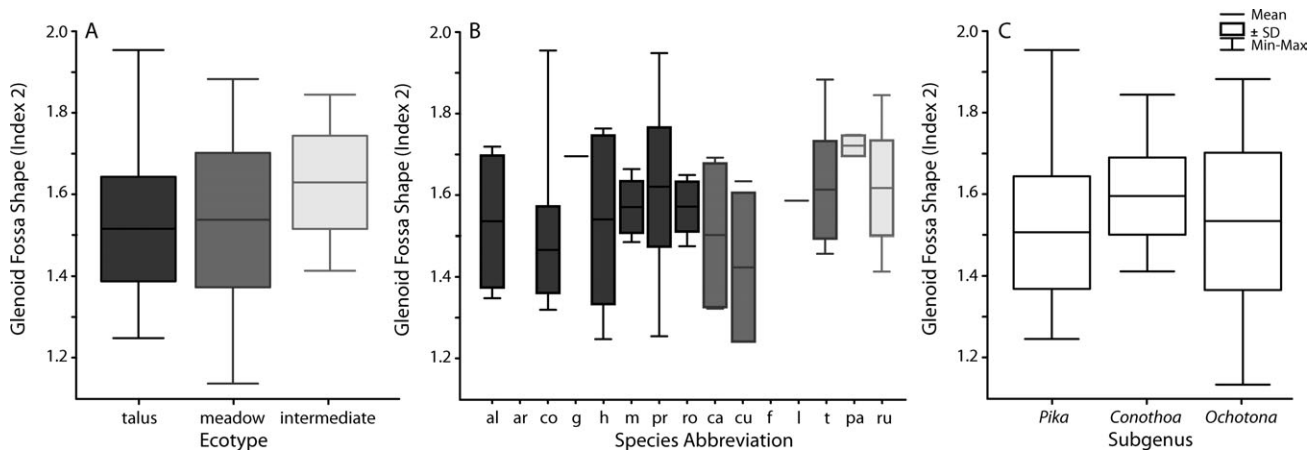


Fig. 4. Box plots of glenoid fossa shape index by **A:** ecotype, **B:** species, **C:** subgenus.

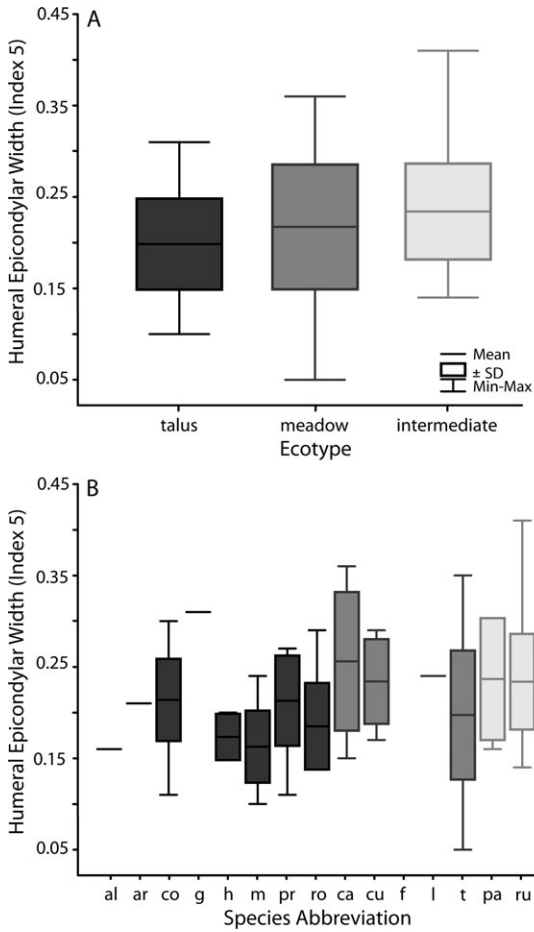


Fig. 5. Box plots of humeral epicondylar width index by A: ecotype, B: species.

son. It is higher in the talus-dwelling group than in the meadow-dwelling group, and it is highest in the intermediate species (Fig. 10A). At the species level, this is driven primarily by the intermediate species *O. rufescens*, which has a significantly higher value than 9 of the 11 species for which

comparison was possible, and the talus taxon *O. collaris*, which has a significantly higher mean than two of the meadow taxa, *O. cansus* and *O. thibetana* (Fig. 10B). Additionally, the pubis width index is higher in both *Pika* and *Conothoa* than in *Ochotona* (Fig. 10C). The difference is most likely driven solely by the high values in *O. (P.) collaris* and *O. (C.) rufescens* (Fig. 10B).

The femur length index also differs among subgenera, with lower values in *Conothoa* than in either of the other subgenera (Fig. 11A). The differentiation in the femur length index is most likely primarily driven by the low value of *O. (C.) macrotis* (Fig. 11B).

The proximal extent of the lesser trochanter index is the other hind limb index that divides both the ecotypes and the intermediate species. It is significantly higher in the meadow forms than in the talus-dwellers in the two-way comparison, and it is higher in both ecotypes than in the intermediate species in the three-way comparison (Fig. 12A). The separation of the meadow group is likely driven by *O. thibetana*, which has a higher mean than any other species (Fig. 12B). This difference was significant in comparisons with three talus species (*O. collaris*, *O. macrotis*, and *O. princeps*) and the intermediate species *O. rufescens*, but non-significant values may simply reflect smaller sample sizes for some species. The separation of the intermediates is driven by *O. rufescens*, which has a significantly lower mean than *O. thibetana* and *O. collaris* (Fig. 12B). The proximal extent of the lesser trochanter is one of two hind limb indices that separate all three subgenera. It is highest in *Ochotona*, intermediate in *Pika*, and lowest in *Conothoa* (Fig. 12C). This is driven by the high value of *O. (O.) thibetana* and the low value of *O. (C.) rufescens* (Fig. 12B).

The tibial crest index separates the two defined ecotypes in the two-way comparison, and it is significantly higher in both the talus-dwellers and the intermediate species than in the meadow-

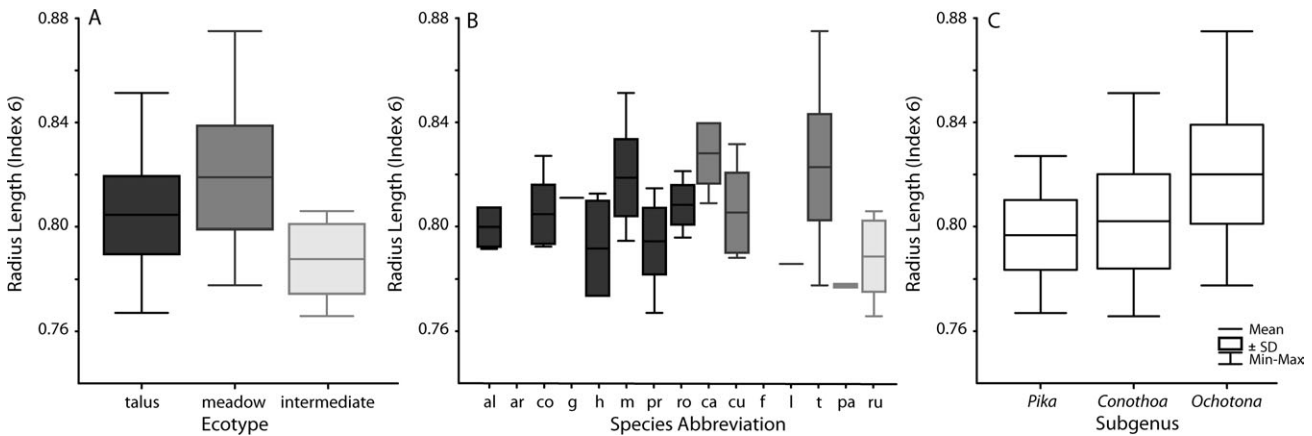


Fig. 6. Box plots of radius length index by A: ecotype, B: species, C: subgenus.

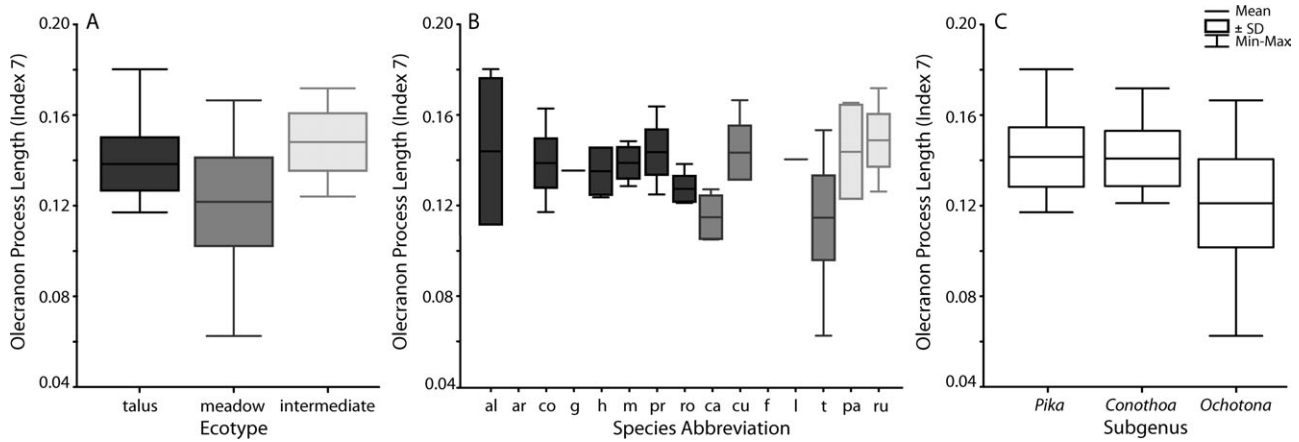


Fig. 7. Box plots of olecranon process length index by **A**: ecotype, **B**: species, **C**: subgenus.

dwellers when all three are compared (Fig. 13A). This separation is driven, primarily, by the high values in the talus taxa *O. collaris*, *O. hyperborea*, and *O. princeps*, the relatively high values in the intermediate species, and the low values in the meadow taxa *O. cansus* and *O. thibetana* (Fig. 13B). The tibial crest index is the other hind limb index that separates all three subgenera. It is highest in *Pika*, intermediate in *Conothoa*, and lowest in *Ochotona* (Fig. 13C). This division reflects the extremely high values of *O. (P.) collaris*, *O. (P.) hyperborea*, and *O. (P.) princeps*, and the low values of *O. (O.) cansus* and *O. (O.) thibetana* (Fig. 13B).

**Composite.** All four of the composite indices are significantly different between the meadow and talus ecotypes in the two-way comparison. In addition, each index also shows at least some significant differences among the intermediates and the other ecotypes.

The brachial index (radius length/humerus length) is significantly higher in the meadow eco-

type than in either the intermediate or talus ecotypes (Fig. 14A). This is primarily driven by the high values of *O. curzoniae* and *O. thibetana* (Fig. 14B). Additionally, this index is significantly lower in the subgenus *Pika* than in either *Conothoa* or *Ochotona* (Fig. 14C). This is likely driven by the low value of *O. (P.) princeps*, which is significantly lower than those of *O. (C.) macrotis*, *O. (C.) roylei*, *O. (O.) cansus*, *O. (O.) curzoniae*, and *O. (O.) thibetana* (Fig. 14B).

The humerofemoral index (humerus length/femur length) is significantly different among all the ecotypes and subgenera. The index is highest in the talus-dwellers, lowest in the meadow-dwellers, and intermediate in the intermediate ecotype (Fig. 15A). These separations are primarily driven by the high value of *O. princeps*, the extremely low values of *O. cansus* and *O. curzoniae*, and the intermediate values of both intermediate species (Fig. 15B). The index is highest in the subgenus *Pika*, intermediate in *Ochotona*, and lowest in

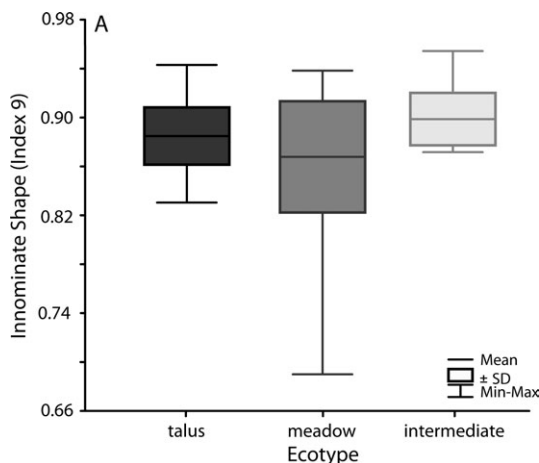


Fig. 8. Box plot of innominate shape index by ecotype.

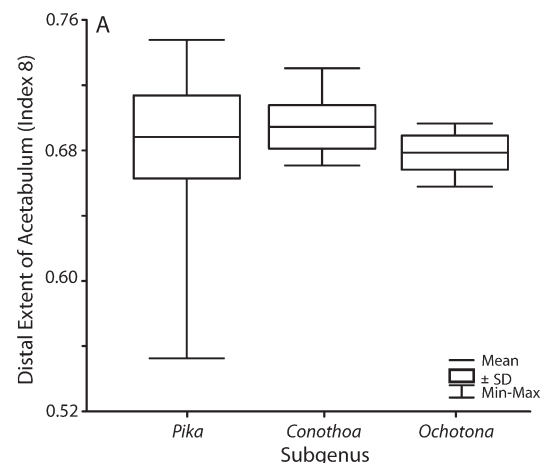


Fig. 9. Box plot of distal extent of the acetabulum index by subgenus.



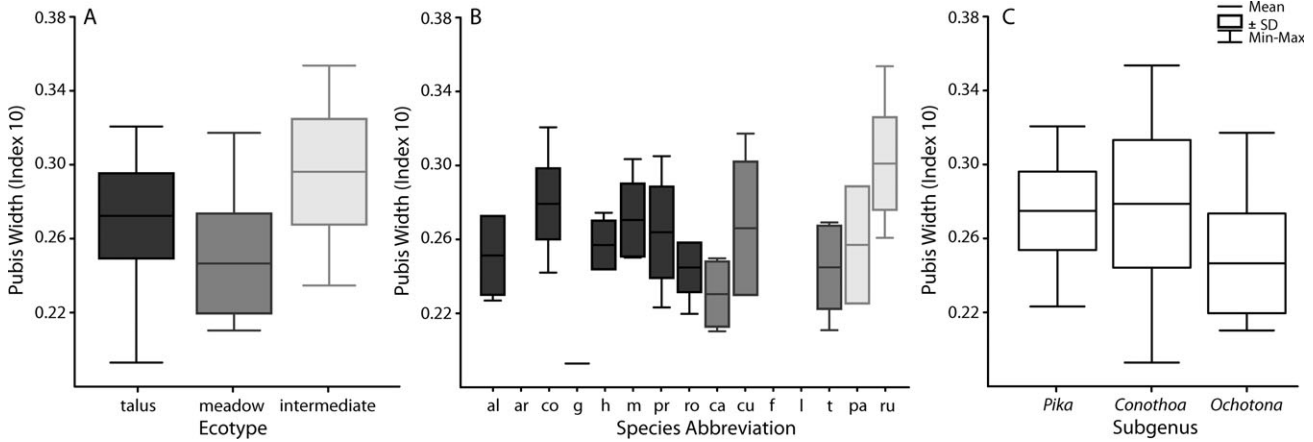


Fig. 10. Box plots of pubis width index by **A:** ecotype, **B:** species, **C:** subgenus.

*Conothoa* (Fig. 15C). This separation is primarily driven by the high values of *O. (P.) collaris* and *O. (P.) princeps* and the low values of *O. (C.) macrotis* and *O. (C.) roylei* (Fig. 15B).

The crural index (tibia length/femur length) is significantly higher in the meadow-dwellers than

in either the intermediates or the talus-dwellers (Fig. 16A). Most of this separation is likely due to the high values of *O. cansus* and *O. thibetana* (Fig. 16B). Additionally, the crural index in the subgenus *Pika* is significantly lower than in both *Conothoa* and *Ochotona* (Fig. 16C). This difference is most likely driven by the low values of *O. (P.) collaris*, *O. (P.) hyperborea*, and *O. (P.) princeps*, which are all lower than those of *O. (C.) roylei*, *O. (O.) cansus*, and *O. (O.) thibetana* (Fig. 16B).

Finally, the intermembral index [(humerus + radius length)/(femur + tibia length)] is significantly lower in the meadow-dwellers than in the other two ecotypes (Fig. 17A). This is most likely primarily driven by the extremely low value of *O. cansus* (Fig. 17B). This index is also significantly higher in the subgenus *Pika* than in either *Conothoa* or *Ochotona* (Fig. 17C). The separation of the subgenus *Pika* is most likely a reflection of the high values of *O. (P.) alpina*, *O. (P.) collaris*, *O. (P.) hyperborea*, and *O. (P.) princeps* (Fig. 17B).

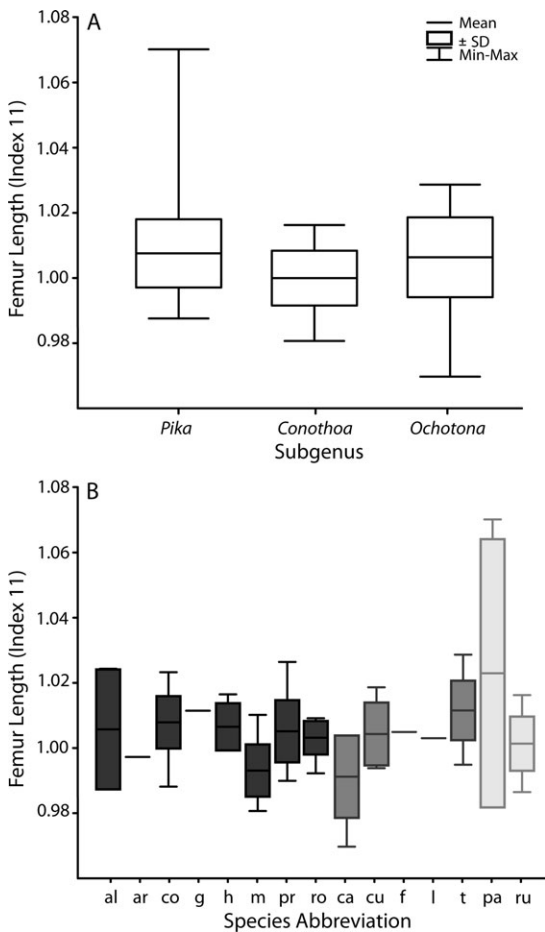


Fig. 11. Box plots of femur length index by **A:** subgenus, **B:** species.

**Multivariate**

**Individuals.** A PCA of raw measurement values was conducted on 14 measurements from 78 specimens, representing 13 taxa. The first three factors of the PCA account for approximately 92% of the variation (Fig. 18). For eigenvalues, see Table 4; factor loadings and factor coordinates are available in Supporting Information.

Factor 1 accounts for almost 84% of the total variance and is most likely driven by size. It does not clearly separate the individuals by ecotype, phylogeny, or geography. Factor 2 accounts for almost 5% of the variance. It is driven primarily by the negatively weighted tibial crest length measurement and the positively weighted radius length. When considering phylogeny, factor 2 strongly separates the two subgenera that include leapers, *Pika* and *Conothoa*, but both groups are intersected by the

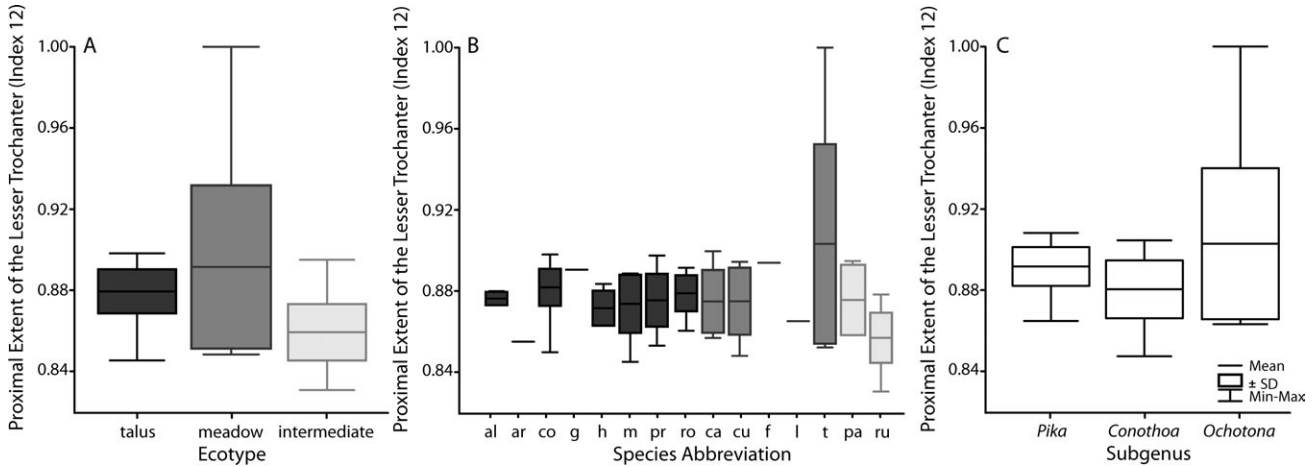


Fig. 12. Box plots of proximal extent of the lesser trochanter index by **A:** ecotype, **B:** species, **C:** subgenus.

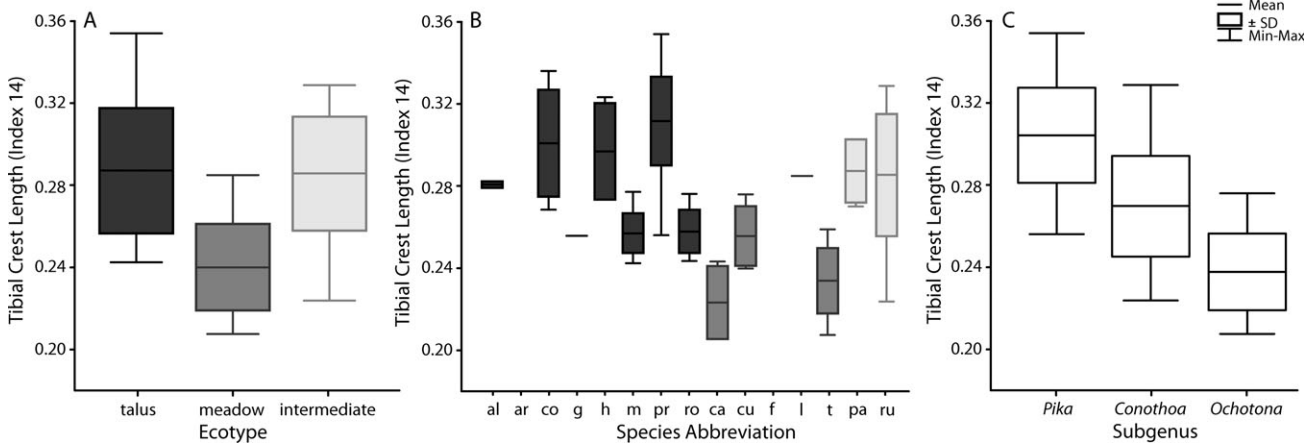


Fig. 13. Box plots of tibial crest length index by **A:** ecotype, **B:** species, **C:** subgenus.

widely spread subgenus *Ochotona*. However, when considering ecotype, factor 2 groups the meadow forms, whereas the talus-dwellers and intermediate species are spread broadly (Fig. 18).

Factor 3, which accounts for more than 3% of the variance, is also driven by the negatively weighted tibial crest length in addition to the positively weighted olecranon process length and gle-

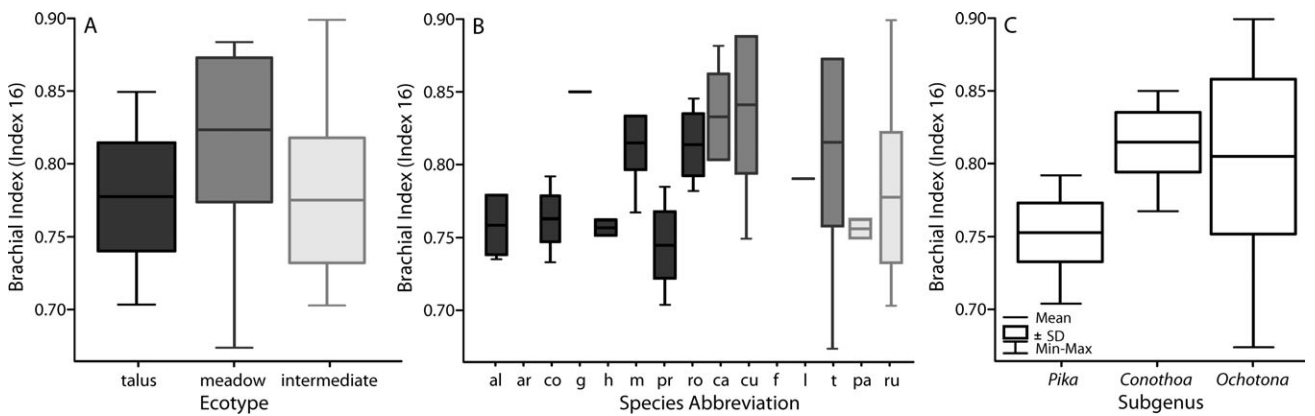


Fig. 14. Box plots of brachial index by **A:** ecotype, **B:** species, **C:** subgenus.

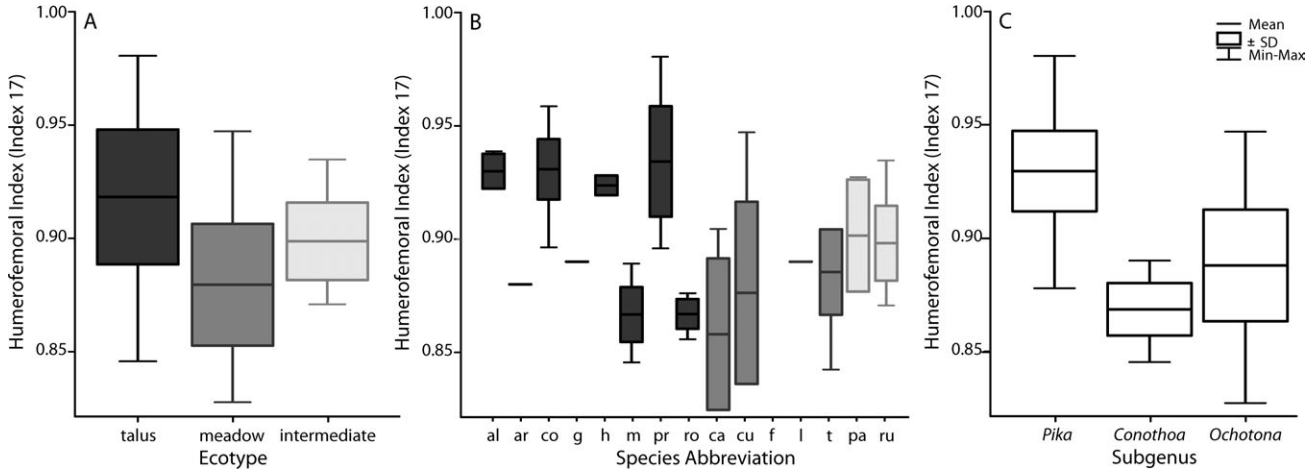


Fig. 15. Box plots of humerofemoral index by **A:** ecotype, **B:** species, **C:** subgenus.

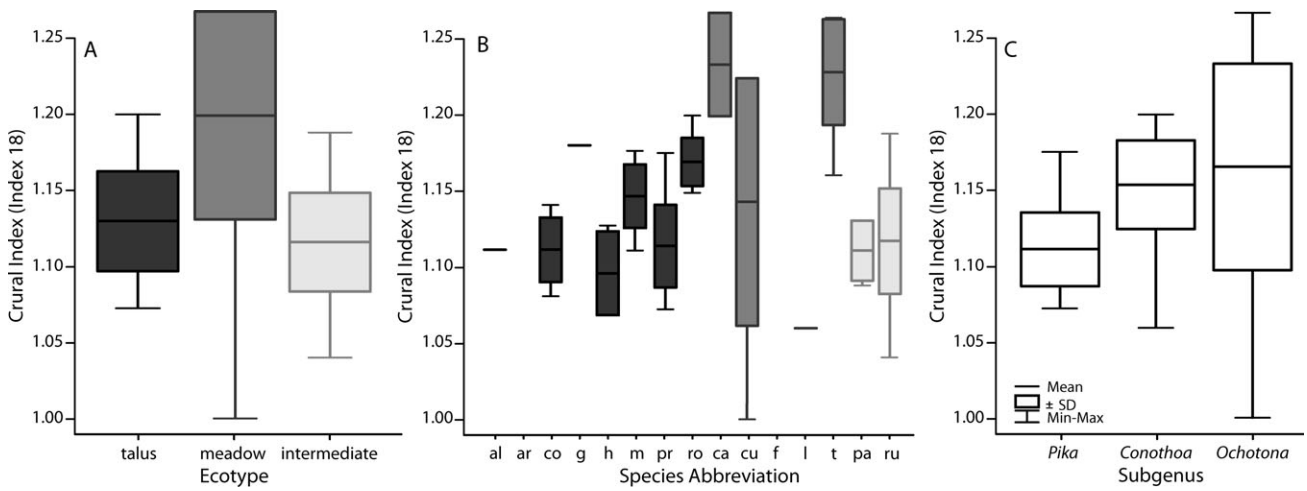


Fig. 16. Box plots of crural index by **A:** ecotype, **B:** species, **C:** subgenus.

noid fossa width. There is divergence along factor 3 between the talus species and the meadow species, but it is less striking than for factor 2.

**Means.** A PCA of species means, which included 21 measurement means from 13 species, was conducted. The first three factors of the PCA

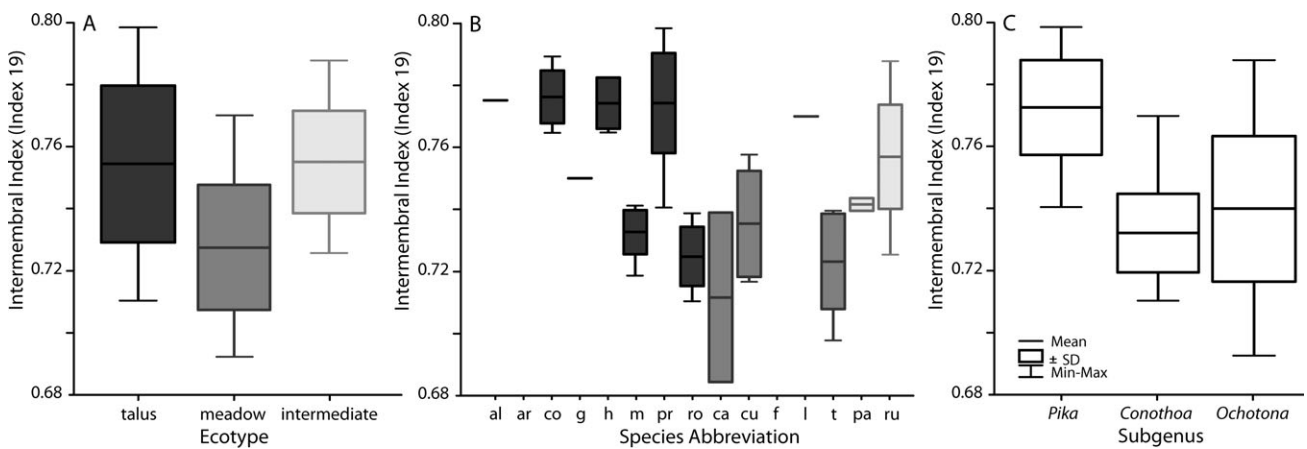


Fig. 17. Box plots of intermembral index by **A:** ecotype, **B:** species, **C:** subgenus.

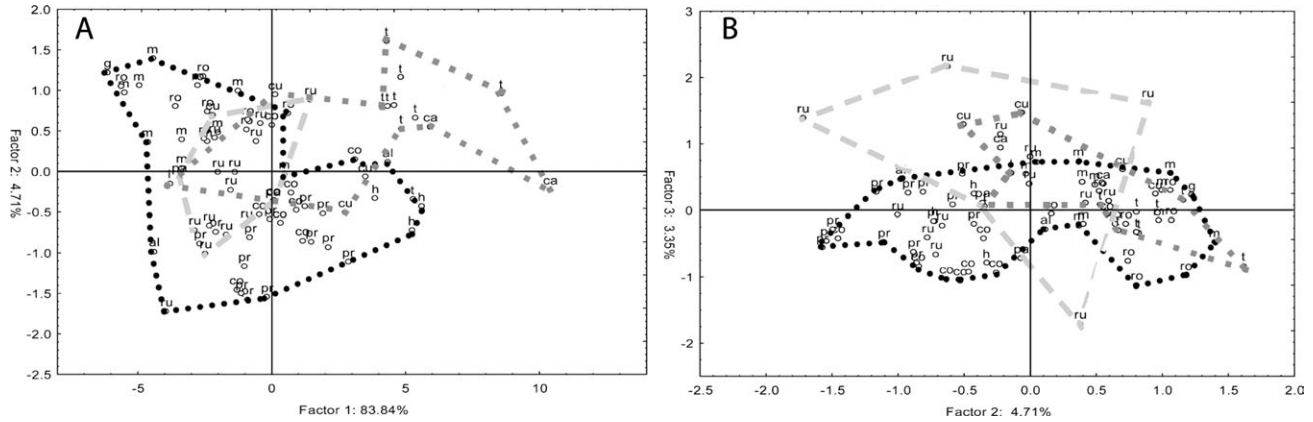


Fig. 18. (A) Bivariate plot of factors 1 and 2 from PCA of individuals. (B) Bivariate plot of factors 2 and 3 from PCA of individuals. Area denoted by black circles contains talus-dwellers; dark gray squares denote meadow-dwellers; and light gray rectangles denote intermediates.

account for over 96% of the total variation (Fig. 19). For eigenvalues, see Table 5; factor loadings and factor coordinates are available in Supporting Information.

Factor 1, which accounts for 89% of the variance, again appears to be driven by size. Factor 2, which accounts for approximately 6% of the variation, is most highly influenced by the positively weighted humeral distal end and humeral distal articular surface width measurements and the negatively weighted tibia and fibula lengths. Neither factor definitively separates the species by ecotype, phylogeny, or geography, although the subgenus *Pika* is separated from the other two subgenera.

Factor 3, which accounts for almost 1.4% of the variation, is affected most by the positively weighted tibial crest length and the negatively weighted glenoid fossa width. It is also influenced by four negatively weighted forelimb variables, i.e., radius length, humeral distal end width, olecranon process length, and ulna length, as well as the positively weighted distal extent of the acetabulum variable. This factor separates the species between the two defined ecotypes, with the intermediate species spanning the two groups (Fig. 19). There is less divergence when the species are grouped by subgenus, with *Ochotona* and *Conothoa* overlapping, but *Pika* remains separate from these subgenera.

## DISCUSSION

We documented a number of the predicted postcranial modifications for digging in meadow-dwelling

TABLE 4. Eigenvalues from PCA of individuals

Factor	Eigenvalues	% of total variance	Cumulative eigenvalues	Cumulative % of total variance
1	11.74	83.84	11.74	83.84
2	0.66	4.71	12.40	88.55
3	0.47	3.35	12.87	91.90

pikas and for leaping in some of the talus-dwelling forms. However, and perhaps unsurprisingly, because meadow-dwelling pikas are not specialized for a strictly fossorial lifestyle and many digging mammals show morphological adaptations for other specialized locomotor modes, we did not find support for all the typical skeletal features associated with digging behavior in these species.

## Forelimb

The difference in the scapula shape index (Fig. 3; see Tables 6 and 7 for index and measurement means) indicates a broader vertebral border, caudal angle, and infrapinous fossa in the burrowers. These structures represent the areas of origin for the teres major and infrapinatus muscles, both of which retract the humerus, which is likely important during digging, as is stabilization of the shoulder by the infrapinatus (Morgan, 2009). A broad scapula is also found in other burrowers, including armadillos, some rodents, and some tenrecs (Smith and Savage, 1956; Stein, 2000; Salton and Sargis, 2008; Morgan, 2009).

The high value of the glenoid fossa shape index in the burrowers (Fig. 4) is driven by their narrow glenoid fossa. The ovoid shape of their fossa may restrict shoulder mobility in relation to parasagittal movements during digging (see Sargis, 2002a). Furthermore, the glenoid fossa is typically more rounded in nondiggers than in fossorial forms (Stein, 2000; Salton and Sargis, 2008).

The higher humeral epicondylar width index in burrowers (Fig. 5) is indicative of a large medial epicondyle. This serves as a larger area of origin for the wrist and digital flexor muscles, which powerfully flex the manus during digging. Similar enlargement of the medial epicondyle has been documented in several other diggers (Hildebrand, 1985; Stein, 2000; Sargis, 2002a; Lessa et al.,

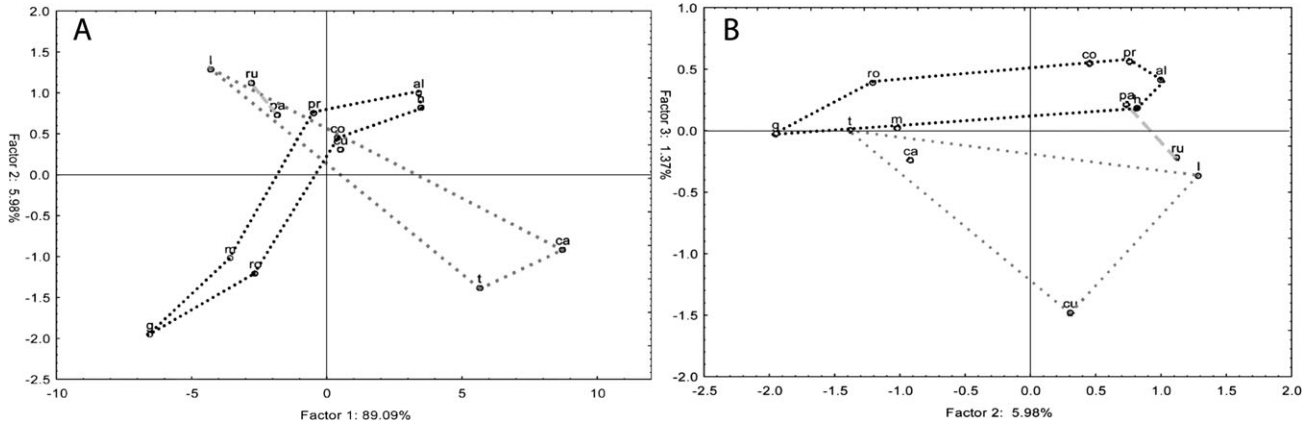


Fig. 19. (A) Bivariate plot of factors 1 and 2 from PCA of means. (B) Bivariate plot of factors 2 and 3 from PCA of means. Area denoted by black circles contains talus-dwellers; dark gray squares denote meadow-dwellers; and light gray rectangles denote intermediates.

2008; Salton and Sargis, 2008; Samuels and Van Valkenburgh, 2008).

A longer olecranon process serves as a longer in-lever for the insertion of the triceps brachii muscle, thereby increasing the force that can be exerted by the forearms during burrowing via powerful extension of the elbow (Hildebrand, 1985; Stein, 2000). This is captured by the most consistent skeletal metric for fossorial behavior, i.e., the ratio of the length of the olecranon process to the length of the ulna (Hildebrand, 1985; Stein, 2000; Vizcaíno and Milne, 2002; Lessa et al., 2008; Salton and Sargis, 2008; Samuels and Van Valkenburgh, 2008; Hopkins and Davis, 2009). Contrary to typical morphological specializations for fossoriality, the olecranon process is significantly shorter in the burrowing species than in the nonburrowing leapers, and both are significantly shorter when compared to the intermediate species (Fig. 7). All three groups have a ratio of olecranon process to ulna length (Fig. 7) that is comparable to nonfossorial mammals, such as raccoons ( $< 0.15$ ; Hildebrand, 1985). Similarly, a low radius to ulna length ratio should coincide with a long olecranon process, but the highest index values were found in the meadow-dwelling species (Fig. 6). Both of these metrics indicate that the meadow-dwelling species have not acquired this common skeletal specialization for fossorial behavior. This is not entirely surprising because the meadow forms are not fossorial specialists, and the specific mechanics of pika digging remain unstudied.

TABLE 5. Eigenvalues from PCA of means

Factor	Eigenvalues	% of total variance	Cumulative eigenvalues	Cumulative % of total variance
1	18.71	89.09	18.71	89.09
2	1.26	5.98	19.97	95.07
3	0.29	1.37	20.26	96.44

**Hind Limb**

A reduction of pubis width and ischium to pubis length in the meadow-dwelling pikas is captured in their lower pubis width (Fig. 10) and innominate shape index (Fig. 8) values. Reduced pelvis size is typically found in fossorial forms because it allows for greater maneuverability in tunnels (Stein, 2000; Salton and Sargis, 2009).

A high proximal extent of the lesser trochanter index value (Fig. 12) indicates that the lesser trochanter is close to the proximal end of the femur. The iliopsoas muscle inserts on the lesser trochanter, and a more proximal lesser trochanter allows this muscle to rapidly flex the thigh (Smith and Savage, 1956; Hildebrand, 1985). Rapid flexion of the thigh would be advantageous during leaping in the talus-dwellers (see Jungers, 1977; Dagosto, 1983). In the burrowers, which also have a more proximal lesser trochanter, rapid thigh flexion may be advantageous for moving dirt. Because the same condition is present in both meadow- and talus-dwelling forms, though not in the intermediate species, further study will be necessary to understand the ancestral condition and determine if any morphological specialization has occurred.

Finally, the tibial crest is longer in the talus-dwellers (Fig. 13). The quadriceps femoris muscle inserts on the most proximal part of the tibial crest, the tibial tuberosity, via the quadriceps tendon and patellar ligament. The longer crest also provides a larger area of attachment for the tibialis anterior muscle, which originates from this crest. A longer tibial crest may allow for more powerful extension of the knee by the quadriceps femoris muscle, which would be advantageous for leaping. Furthermore, tibialis anterior inverts the foot, which may be important for landing and moving on uneven talus substrates. A large tibial tuberosity has been documented previously in other leapers, as well as in terrestrial runners (Taylor,

TABLE 6. Ecotype and species index values\*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Talus</i>	Mean 0.46	1.51	1.00	1.00	0.20	0.80	0.14	0.69	0.89	0.28	1.01	0.88	0.95	0.29	0.22	0.78	0.92	1.13	0.75
	StDev 0.04	0.13	0.01	0.01	0.05	0.01	0.01	0.02	0.89	0.11	0.01	0.01	0.03	0.03	0.02	0.04	0.03	0.03	0.03
	<i>n</i>	119	124	111	54	57	52	65	118	96	125	124	56	56	23	56	110	58	48
<i>Intermediate</i>	Mean 0.53	1.63	1.01	1.01	0.23	0.79	0.15	0.69	0.90	0.30	1.00	0.86	0.95	0.29	0.26	0.78	0.90	1.12	0.76
	StDev 0.04	0.11	0.01	0.01	0.05	0.01	0.01	0.02	0.02	0.03	0.02	0.01	0.04	0.03	0.15	0.04	0.02	0.03	0.02
	<i>n</i>	26	26	27	27	21	22	27	16	18	26	27	20	20	17	20	25	19	16
<i>Meadow</i>	Mean 0.48	1.54	1.01	1.01	0.22	0.82	0.12	0.68	0.87	0.25	1.01	0.89	0.96	0.24	0.21	0.82	0.88	1.20	0.73
	StDev 0.04	0.16	0.01	0.01	0.07	0.02	0.02	0.01	0.05	0.03	0.01	0.04	0.05	0.02	0.02	0.05	0.03	0.07	0.02
	<i>n</i>	25	26	29	26	28	28	21	24	16	30	30	21	21	16	26	25	20	17
<i>O. alpina</i>	Mean 0.47	1.54	1.00	1.01	0.16	0.80	0.14	0.69	0.88	0.25	1.01	0.88	1.00	0.28	0.76	0.93	1.11	0.78	
	StDev 0.03	0.16	0.01	0.00	0.16	0.01	0.03	0.00	0.02	0.02	0.02	0.00	0.03	0.00	0.02	0.02	0.01	0.11	0.78
	<i>n</i>	4	4	4	1	3	3	3	3	3	3	3	2	2	3	3	3	1	1
<i>O. argentata</i>	Mean 0.99	1.00	0.21	1.00	0.21	1.00	0.86	0.88	0.89	0.86	1.00	0.86	0.96	0.30	0.23	0.76	0.93	1.11	0.78
	StDev <i>n</i>	0.44	1.47	1.00	0.21	0.80	0.14	0.69	0.88	0.30	1.01	0.88	0.96	0.30	0.23	0.76	0.93	1.11	0.78
<i>O. collaris</i>	Mean 0.04	0.11	0.01	0.01	0.04	0.01	0.01	0.04	0.02	0.13	0.01	0.01	0.03	0.03	0.03	0.02	0.01	0.02	0.01
	StDev <i>n</i>	73	76	64	13	11	11	17	71	68	77	76	11	11	5	11	62	11	7
<i>O. glomeri</i>	Mean 0.48	1.70	0.99	1.00	0.31	0.81	0.14	0.69	0.90	0.19	1.01	0.89	0.97	0.26	0.85	0.89	1.18	0.75	
	StDev <i>n</i>	0.01	0.06	0.01	0.05	0.01	0.01	0.01	0.02	0.02	0.01	0.02	0.03	0.01	0.02	0.01	0.02	0.01	0.01
<i>O. hyperborea</i>	Mean 0.49	1.54	1.00	1.00	0.16	0.82	0.14	0.69	0.90	0.27	1.00	0.87	0.96	0.26	0.81	0.87	1.15	0.73	
	StDev <i>n</i>	0.01	0.06	0.01	0.05	0.01	0.01	0.01	0.02	0.02	0.01	0.02	0.03	0.01	0.02	0.01	0.02	0.01	0.01
<i>O. princeps</i>	Mean 0.52	1.62	1.00	1.00	0.21	0.79	0.14	0.69	0.89	0.26	1.01	0.88	0.94	0.31	0.22	0.74	0.93	1.11	0.77
	StDev <i>n</i>	0.03	0.15	0.01	0.05	0.01	0.01	0.02	0.03	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.03	0.02
<i>O. roylei</i>	Mean 0.47	1.57	1.01	1.00	0.19	0.81	0.13	0.69	0.89	0.24	1.00	0.88	0.96	0.26	0.20	0.81	0.87	1.17	0.72
	StDev <i>n</i>	0.02	0.06	0.01	0.05	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.02	0.01
<i>O. cansus</i>	Mean 0.44	1.50	1.01	1.01	0.26	0.83	0.11	0.69	0.85	0.23	0.99	0.88	0.94	0.22	0.20	0.83	0.86	1.23	0.71
	StDev <i>n</i>	0.01	0.18	0.02	0.08	0.01	0.01	0.01	0.11	0.02	0.01	0.02	0.02	0.02	0.01	0.03	0.03	0.03	0.03
<i>O. curzoniae</i>	Mean 0.49	1.42	1.01	1.01	0.23	0.81	0.14	0.67	0.87	0.27	1.00	0.88	0.98	0.26	0.23	0.84	0.88	1.14	0.74
	StDev <i>n</i>	0.03	0.18	0.01	0.05	0.02	0.01	0.01	0.01	0.04	0.01	0.02	0.05	0.01	0.04	0.04	0.04	0.07	0.01
<i>O. forresti</i>	Mean 0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70
	StDev <i>n</i>	0.52	1.59	1.00	0.24	0.79	0.14	0.71	0.93	0.28	1.00	0.87	0.90	0.28	0.28	0.79	0.89	1.06	0.77
<i>O. ladacensis</i>	Mean 0.48	1.61	1.00	1.00	0.20	0.82	0.11	0.68	0.87	0.24	1.01	0.90	0.96	0.23	0.20	0.82	0.89	1.23	0.72
	StDev <i>n</i>	0.04	0.12	0.01	0.07	0.02	0.02	0.01	0.02	0.02	0.01	0.05	0.06	0.02	0.01	0.06	0.02	0.03	0.02
<i>O. thibetana</i>	Mean 0.55	1.72	1.01	1.00	0.24	0.78	0.14	0.67	0.88	0.26	1.02	0.88	0.89	0.29	0.22	0.76	0.9	1.11	0.74
	StDev <i>n</i>	0.06	0.03	0.01	0.07	0.00	0.02	0.00	0.01	0.03	0.04	0.02	0.05	0.02	0.01	0.01	0.02	0.02	0.02
<i>O. pallasi</i>	Mean 0.53	1.62	1.01	1.01	0.23	0.79	0.15	0.70	0.90	0.30	1.00	0.86	0.96	0.29	0.27	0.78	0.9	1.12	0.76
	StDev <i>n</i>	0.04	0.12	0.01	0.05	0.01	0.01	0.01	0.02	0.02	0.01	0.02	0.03	0.03	0.03	0.04	0.04	0.07	0.01
<i>O. rufescens</i>	Mean 0.49	1.42	1.01	1.01	0.23	0.81	0.14	0.67	0.87	0.27	1.00	0.88	0.98	0.26	0.23	0.84	0.88	1.14	0.74
	StDev <i>n</i>	0.03	0.18	0.01	0.05	0.02	0.01	0.01	0.01	0.04	0.01	0.02	0.05	0.01	0.04	0.04	0.04	0.07	0.01
<i>O. forresti</i>	Mean 0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70	0.89	0.70
	StDev <i>n</i>	0.52	1.59	1.00	0.24	0.79	0.14	0.71	0.93	0.28	1.00	0.87	0.90	0.28	0.28	0.79	0.89	1.06	0.77

\*See Table 3 for index descriptions.

TABLE 7. Ecotype and species raw measurement values\*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Talus	Mean	11.33	24.62	4.34	2.87	27.02	27.03	26.96	4.93	3.95	26.35	21.22	3.63	28.87	20.41	25.54	7.76	29.50	29.66	25.95	34.00	32.35	9.65	6.95
	StDev	1.66	2.04	0.48	0.25	1.78	1.82	1.79	0.35	0.28	2.48	2.21	0.41	2.05	1.65	1.93	0.81	2.33	2.25	2.03	3.83	3.79	0.88	0.87
	n	124	127	128	128	115	115	115	111	58	58	57	65	126	69	123	102	129	129	128	60	74	28	28
Intermediate	Mean	13.31	25.17	4.93	3.04	28.03	28.05	27.89	5.93	4.53	27.64	21.89	4.11	31.10	21.58	28.42	9.22	31.43	31.59	27.00	32.44	33.16	9.87	7.69
	StDev	1.17	1.81	0.32	0.24	1.53	1.49	1.49	0.45	0.33	1.55	1.01	0.36	1.71	1.12	1.68	1.05	1.50	1.52	1.25	7.98	2.41	1.21	0.42
	n	26	26	26	26	27	27	27	27	27	24	21	24	24	27	18	18	27	26	27	22	21	22	18
Meadow	Mean	10.51	21.74	3.82	2.51	22.59	22.60	22.48	3.96	3.07	22.75	18.59	2.82	25.38	17.46	22.03	5.97	25.67	25.82	22.85	31.28	30.05	7.53	6.26
	StDev	1.76	2.89	0.66	0.51	2.87	2.90	2.89	0.87	0.66	3.61	2.82	0.72	3.77	2.58	3.56	1.33	3.13	3.14	2.71	3.37	3.73	1.14	0.94
	n	25	26	26	26	28	28	28	28	27	27	28	23	23	23	15	29	29	29	20	21	22	22	22
O. alpina	Mean	10.79	22.84	3.90	2.53	24.20	23.98	23.97	4.12	4.15	23.52	18.79	3.32	23.93	16.50	21.05	6.02	26.70	26.88	23.40	27.47	27.41	8.72	7.46
	StDev	2.43	4.13	0.96	0.45	4.46	4.65	4.52	0.58	0.44	4.53	3.44	1.19	2.36	1.57	1.66	0.82	5.39	5.57	4.65	1.82	2.69	1.80	1.80
	n	4	4	4	4	4	4	4	4	1	3	3	4	3	3	3	3	3	3	3	2	2	2	3
O. argentata	Mean					32.06	31.92	32.15	5.36	4.22								36.64	36.54	31.34				
	StDev																							
O. collaris	Mean	10.36	23.77	4.16	2.84	26.83	26.77	26.76	4.99	3.98	25.43	20.46	3.56	28.22	19.96	24.82	7.85	28.83	29.06	25.43	31.93	30.67	9.49	6.78
	StDev	1.03	0.98	0.38	0.16	1.04	1.02	1.03	0.21	0.20	0.84	0.63	0.22	1.25	1.17	1.10	0.68	1.17	1.19	1.03	1.22	1.36	0.89	1.00
	n	74	75	76	76	64	64	64	63	13	11	11	19	74	17	72	69	77	77	76	11	11	23	8
O. glomeri	Mean	14.47	30.25	5.34	3.15	30.92	30.7	30.89	5.53	3.83	32.48	26.34	4.4	34.21	23.55	30.85	6.6	34.88	35.28	31.07	41.3	40	10.57	
	StDev																							
O. hyperborea	Mean	11.22	22.78	4.06	2.69	23.42	23.59	23.42	4.09	3.38	22.36	17.69	3.02	27.07	18.63	24.17	6.68	26.47	26.64	23.09	27.73	25.93	8.24	5.81
	StDev	1.07	1.77	0.25	0.54	0.75	0.87	0.90	0.12	0.20	0.96	0.48	0.25	3.05	2.14	2.62	0.63	2.40	2.40	2.33	0.73	1.15	0.83	0.35
	n	5	5	5	5	3	3	3	3	3	3	3	3	5	5	5	4	4	4	4	3	3	3	3
O. macrotis	Mean	13.47	27.90	4.94	3.15	28.70	28.78	28.59	4.85	4.05	28.56	23.39	3.96	31.45	21.63	28.07	8.55	33.13	32.89	28.95	37.98	36.20	9.76	5.22
	StDev	0.60	1.11	0.30	0.22	1.44	1.55	1.48	0.37	0.27	1.44	1.34	0.23	1.65	1.12	1.68	0.56	1.72	1.54	1.49	2.09	2.16	0.52	
	n	11	12	12	12	12	12	12	11	11	12	12	12	12	12	12	8	12	12	12	12	12	12	12
O. princeps	Mean	12.98	25.05	4.64	2.88	26.83	26.91	26.81	4.98	3.92	25.18	19.98	3.62	29.88	20.64	26.65	7.76	28.87	29.02	25.29	32.12	30.18	9.99	7.18
	StDev	0.96	1.34	0.39	0.27	1.28	1.37	1.29	0.31	0.29	1.04	1.01	0.24	1.33	1.02	1.14	0.84	1.30	1.28	1.31	1.52	1.54	0.73	0.72
	n	19	20	20	20	21	21	21	20	18	17	17	17	17	21	21	11	21	21	21	21	21	22	15
O. roylei	Mean	12.95	27.29	4.59	2.92	28.11	28.36	28.12	4.97	4.04	28.27	22.85	3.60	30.32	20.96	26.96	7.54	32.42	32.52	28.50	37.90	36.24	9.78	7.82
	StDev	1.03	1.56	0.28	0.19	1.39	1.39	1.37	0.40	0.17	1.47	1.19	0.19	1.67	0.90	1.55	0.53	1.54	1.54	1.20	1.88	1.88	0.66	
	n	10	10	10	10	9	9	9	8	8	10	10	9	10	10	10	6	10	10	10	10	10	10	1
O. cansus	Mean	8.39	19.26	3.21	2.15	19.37	19.35	19.19	3.25	2.39	19.57	16.20	2.25	20.79	14.28	17.43	4.79	22.68	22.49	19.84	28.15	26.45	6.29	5.28
	StDev	0.87	2.07	0.34	0.23	1.80	1.61	1.94	0.43	0.20	1.72	1.35	0.33	1.77	1.27	0.98	0.55	1.26	1.40	0.90	2.83	2.18	0.76	0.61
	n	4	4	4	4	5	5	5	5	5	6	6	6	4	4	4	4	5	5	5	3	3	3	6
O. curzoniae	Mean	12.15	24.01	4.39	3.10	24.91	24.96	24.76	4.99	3.90	26.76	21.55	3.81	29.14	19.94	25.32	7.41	28.25	28.34	24.69	31.88	31.27	8.12	7.53
	StDev	0.59	2.10	0.45	0.24	2.42	2.45	2.43	0.64	0.42	2.64	2.20	0.19	2.53	1.49	2.05	1.49	3.72	3.49	2.98	5.26	4.95	1.19	0.57
	n	7	8	8	8	7	7	7	6	5	6	6	6	7	6	7	4	6	6	6	5	5	5	3
O. forresti	Mean																	28.34	28.48	25.34				
	StDev																							
O. ladacensis	Mean	14.23	27.19	5.25	3.31	29.42	29.54	29.58	6.35	4.8	29.41	23.11	4.13	30.82	21.98	28.57		32.92	33.02	28.49	35.03	31.38	9.98	
	StDev																							
O. thibetana	Mean	10.00	20.69	3.55	2.21	22.13	22.13	22.04	3.64	2.91	21.91	18.03	2.53	23.87	16.45	20.71	5.82	25.02	25.30	22.60	31.51	30.32	7.40	6.41
	StDev	1.14	2.14	0.41	0.27	1.59	1.62	1.55	0.27	0.25	2.45	2.18	0.41	1.70	0.64	1.72	0.71	1.78	1.84	1.89	2.07	3.32	0.82	0.66
	n	13	13	13	13	15	15	15	15	15	14	14	15	10	8	10	7	16	16	16	11	12	13	13
O. pallasi	Mean	13.43	24.68	5.02	2.92	27.69	27.68	27.63	5.47	4.19	26.31	21.31	3.77	30.75	20.47	27.47	8.01	30.73	31.40	26.90	34.14	30.57	9.82	7.54
	StDev	0.79	2.61	0.20	0.14	1.72	1.56	1.73	0.23	0.51	2.29	1.41	0.46	1.79	1.27	2.06	0.44	2.14	1.52	1.62	2.46	3.78	1.10	0.22
	n	3	3	3	3	3	3	3	3	3	3	2	3	3	3	2	2	3	3	3	3	3	3	2
O. rufescens	Mean	13.29	25.24	4.92	3.05	28.08	28.07	27.93	5.99	4.58	27.85	21.96	4.16	31.14	21.72	28.56	9.37	31.52	31.61	27.01	34.96	33.59	9.88	7.71
	StDev	1.22	1.75	0.33	0.25	1.54	1.52	1.50	0.44	0.30	1.37	0.99	0.33	1.74	1.05	1.67	1.01	1.44	1.55	1.24	1.84	1.94	1.26	0.44
	n	23	23	23	23	24	24	24	24	24	19	19	21	24	24	14	16	24	23	24	17	18	19	16

\*See Table 2 for measurement descriptions.

1976; Szalay and Sargis, 2001; Argot, 2002; Sargis, 2002b; Salton and Sargis, 2009), though the tibial spine index is not related to limb function in caviomorph rodents (Elissamburu and Vizcaíno, 2004).

### Composite and Multivariate

The results of the composite index analyses are less obviously associated with digging or leaping and are somewhat difficult to explain without more detailed information about pika locomotor behavior. The meadow-dwellers' higher ratio of distal to proximal elements (Figs. 14 and 16) is a feature typically seen in cursorial mammals (Smith and Savage, 1956). Although pikas are not cursorial, this difference may be related to faster terrestrial locomotion in meadow forms because they are running on a more continuous substrate. It could also be related to a lower center of gravity in talus forms, which may be advantageous on angled and discontinuous rocky surfaces. The humeri and forelimbs of pika are short relative to the femora and hind limbs (Figs. 15 and 17), respectively, just as they are in some other small mammals, such as treeshrews (Sargis, 2002a, fig. 2). Talus-dwellers would have been predicted to have the lowest intermembral indices because longer hind limbs are expected in leapers, so it is surprising that the meadow-dwellers have the lowest values for this ratio.

Overall, our morphometric analyses of the postcranium were useful for separating the two pika ecotypes (Figs. 18 and 19). The main features that contributed to distinguishing ecotypes in multivariate space were: glenoid fossa width, humeral distal end width, humeral distal articular surface width, radius length, olecranon process length, tibia length, fibula length, and tibial crest length. It is notable that although the forearm (antebrachium) measurements were important metrics for separating the ecotypes in the multivariate analyses, they did not always differ in the predicted manner in the univariate analyses.

Somewhat surprisingly, ecologically intermediate species were often significantly different from both ecotypes rather than spanning intermediate morphospace between the two ecotypes. In some cases, they were at an extreme with the meadow forms (scapula shape, glenoid fossa shape, and humeral epicondylar width indices), but in others they were more similar to the talus forms (tibial crest length, brachial, crural, and intermembral indices) or isolated. Because the intermediate species are known to burrow (Smith, 1988; Smith, 2008), the indices in which the intermediate and meadow-dwelling taxa are most similar are very likely some of the pika specializations for burrowing, whereas the reduction of pubis width and ischium to pubis length seen only in the meadow-dwelling pikas may contribute less to burrowing or indicate differ-

ences in how these forms perform this behavior or use burrows.

Variation between the ecotypes cannot be solely explained as an artifact of phylogeny. No indices differed solely between the subgenera *Ochotona* and *Pika*, each of which is primarily composed of one ecotype. It is notable, though, that some indices captured differences between the subgenera *Conothoa* and *Pika* (scapula shape and glenoid fossa shape indices) or *Conothoa* and *Ochotona* (distal extent of acetabulum index; Fig. 9), so these may be useful morphological features for assigning fossil taxa to subgenera. However, most features documented differences between one subgenus and the other two (radius length, olecranon process length, innominate shape, pubis width, femur length, brachial, crural, and intermembral indices) or among all of the subgenera (proximal extent of the lesser trochanter, tibial crest length, and humero-femoral indices). This lack of consistent differences among the subgenera contrasted with the differences related to ecotype indicates that variation in postcranial morphology is being driven by function and not just phylogeny.

The two species most frequently associated with burrowing specializations are *O. (O.) cansus* and *O. (O.) thibetana*, which are both members of the subgenus *Ochotona* (Lanier and Olson, 2009). For five indices, one (glenoid fossa shape and proximal extent of the lesser trochanter indices) or both (radius length, olecranon process length, and pubis width indices) of these taxa drove the separation between ecotypes. Unfortunately, few representatives of meadow-dwelling species in the subgenus *Conothoa* were available for study, thereby limiting our ability to determine with certainty if morphological features related to burrowing are restricted primarily to the subgenus *Ochotona* or have evolved convergently in both lineages.

### Implications

In summary, many of the metrics associated with fossoriality proved useful for differentiating between meadow-dwelling and talus-dwelling forms, though some were either not observed or were contrary to expectations. Knowledge of the respective postcranial specializations associated with pika ecotypes will be helpful in reconstructing the behavior of understudied or extinct species, as well as for assessing the behavioral variability of extant species. However, it is important to note that several of the well-cited mammalian postcranial features associated with scratch-digging did not always correspond to burrowing specializations in pika (e.g., an elongated olecranon process), so special attention to extant close relatives among *Ochotona* species will be essential for making accurate paleobiological inferences in this group.



Furthermore, in conjunction with future studies that incorporate more measurements and more taxa, including fossil species, these results could be used to help determine when and under what conditions these specializations evolved. It is clear that the postcranium of pika differs in ways that reflect the well-documented behavioral variation seen between the ecotypes. Based on the historical range of pika (Dawson, 1967; Ge et al., 2012), the ancestral ecotype for this group may have been a burrowing, meadow-dwelling form. In addition to the biogeographic evidence, there is also phylogenetic support for this inference, as some phylogenetic reconstructions (Niu et al., 2004; Fostowicz-Frelik et al., 2010) suggest that the burrowing pika *Ochotona pusilla* is the only extant member of a lineage that is the sister taxon to all other pika species (though see Formozov et al., 2006 and Ge et al., 2012 for alternative placements). If meadow-dwelling was the ancestral ecotype, then leaping specializations and the loss of burrowing features in talus-dwelling forms likely evolved in relation to their change in habitat.

Understanding the relationship between pika behavior and morphology may be important for future conservation efforts, as their survival may depend on their potential for behavioral variability. Pikas are considered particularly vulnerable to climate change because most are found at high elevations, are adapted to boreal/alpine environments, and exhibit low vagility (Smith et al., 1990). Previous warming events have resulted in the decline and disappearance of pika populations (Brown, 1971, 1978; Kniazev and Savinetski, 1988; Beaver et al., 2003). Whether the postcranial specializations documented here will limit their ability to respond to climate change remains to be seen.

Finally, this study serves to augment a growing body of research on the functional morphology of small mammal limbs. In conjunction with the work done on small viverrid carnivorans (Taylor, 1974, 1976), marsupials (Szalay and Sargis, 2001; Argot, 2001, 2002), treeshrews (Sargis, 2002a,b), rodents (Samuels and Van Valkenburgh, 2008), and tenrecs (Salton and Sargis, 2008, 2009), we are beginning to understand how small mammal postcranial morphology varies with substrate preference and locomotor differences. Such studies are crucial for reconstructing the paleobiology of fossil small mammals because it is critical to distinguish those specializations that are found across therian mammals from those that are taxon-specific.

## ACKNOWLEDGMENTS

For access to specimens, we thank the following people and institutions: Eileen Westwig and Teresa Pacheco, Department of Mammalogy, American Museum of Natural History, New York; Kamal Khidas, Department of Vertebrates, Canadian Mu-

seum of Nature, Ottawa; Judith Chupasko and Hopi Hoekstra, Department of Mammalogy, Harvard University Museum of Comparative Zoology, Cambridge; Jon Dunnum, Mammal Division, Museum of Southwestern Biology, Albuquerque; Louise Tomsett and Roberto Portela-Miguez, Department of Zoology, The Natural History Museum, London; Suzy Peurach, Division of Mammals, United States National Museum of Natural History, Washington, DC; Chris Conroy, Department of Mammalogy, University of California Berkeley Museum of Vertebrate Zoology, Berkeley; Bob Timm, Department of Mammalogy, University of Kansas Museum of Natural History, Lawrence; Philip Myers, Department of Mammals, University of Michigan Museum of Zoology, Ann Arbor; Jeff Bradley, Department of Mammalogy, University of Washington Burke Museum, Seattle; and Kristof Zyskowski and Greg Watkins-Colwell, Division of Vertebrate Zoology, Yale Peabody Museum of Natural History, New Haven.

We thank Aldo Vassallo and one anonymous reviewer for their comments, which greatly improved the manuscript. For funding support, we thank the following sources: Yale College Dean's Research Fellowship in the Sciences; Yale Environmental Fellowship; and the Yale Peabody Museum of Natural History Summer Internship Program. Finally, we also want to thank Andrew Smith, David Hik, and Link Olson for their help and advice, as well as Andrey Lissovsky and George Schaller for information on pika burrowing.

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