doi:10.1111/evo.13168

Rare ecomorphological convergence on a complex adaptive landscape: Body size and diet mediate evolution of jaw shape in squirrels (Sciuridae)

Miriam Leah Zelditch,[1,2] Ji Ye,[3] Jonathan S. Mitchell,[4] and Donald L. Swiderski[5]

[1]*Museum of Paleontology, University of Michigan, Ann Arbor, Ann Arbor 48109*

[2]*E-mail: zelditch@umich.edu*

[3]*Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, MI 48109*

[4]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109*

[5]*Kresge Hearing Research Institute and Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109*

Received June 11, 2016
Accepted December 30, 2016

Convergence is widely regarded as compelling evidence for adaptation, often being portrayed as evidence that phenotypic outcomes are predictable from ecology, overriding contingencies of history. However, repeated outcomes may be very rare unless adaptive landscapes are simple, structured by strong ecological and functional constraints. One such constraint may be a limitation on body size because performance often scales with size, allowing species to adapt to challenging functions by modifying only size. When size is constrained, species might adapt by changing shape; convergent shapes may therefore be common when size is limiting and functions are challenging. We examine the roles of size and diet as determinants of jaw shape in Sciuridae. As expected, size and diet have significant interdependent effects on jaw shape and ecomorphological convergence is rare, typically involving demanding diets and limiting sizes. More surprising is morphological without ecological convergence, which is equally common between and within dietary classes. Those cases, like rare ecomorphological convergence, may be consequences of evolving on an adaptive landscape shaped by many-to-many relationships between ecology and function, many-to-one relationships between form and performance, and one-to-many relationships between functionally versatile morphologies and ecology. On complex adaptive landscapes, ecological selection can yield different outcomes.

KEY WORDS: Convergence, diet evolution, geometric morphometrics, jaw morphology, macroevolutionary adaptive landscape, shape evolution.

Convergence is widely regarded as compelling evidence for adaptation, often being portrayed as evidence that phenotypic outcomes are predictable from ecology, overriding contingencies of history (e.g., Losos et al. 1998; Melville et al. 2006; Mahler et al. 2013; Wollenberg et al. 2013; Collar et al. 2014; Friedman et al. 2016). But convergence itself may be contingent on a simple adaptive landscape, one characterized by a limited array of niches that is replicated across environments and by a single optimum per niche. Convergence is thus most likely when ecological constraints limit the array of niches and functional constraints specify a single optimum for each niche. On such a simple landscape, we would expect (1) lineages to converge on the array of niches and, (2) that species that converge ecologically will also converge morphologically, regardless of geographic context or ancestral morphologies. That combination of strong ecological and functional constraints is hypothesized to explain rampant convergence in damselfish (Cooper and Westneat 2009; Frederich et al. 2013) and desert iguanian lizards (Melville et al. 2006). The combination of strong ecological and functional constraints, however, may be very rare making convergence generally unlikely. One well-known explanation for the low frequency of convergence is the many-to-one mapping of form onto function; that mapping means that multiple morphologies are functionally equivalent (Hulsey and Wainwright 2002; Alfaro et al. 2005; Wainwright et al. 2005; Collar et al. 2014). Another explanation is the converse, the one-to-many mapping of form onto ecology: because a single functionally versatile morphology can exploit diverse resources; a species with a specialized morphology is not restricted to a specialized resource but can switch to it when other resources are limited and competition is most intense (Liem 1980; Robinson and Wilson 1998; Bellwood et al. 2006). Functional versatility reduces the probability of convergence because that versatile morphology persists despite ecological divergence or convergence.

The probability of convergence may be further reduced by the many-to-many mapping of ecological classes onto functions (Ross et al. 2012). This many-to-many relationship arises from the multidimensionality of both ecological classes and function. In some cases, it might be possible to treat niches as one dimensional, arrayed along a continuum with thresholds (Revell 2014). But diet classes, for example, cannot be arrayed along a single continuum. It may be possible to characterize two extremes, such as probing for colonial insects with a long tongue and gnawing hard nuts but others, including slicing leaves, crushing fruit or seeds, and gouging bark do not lie between them. Foods such as fruits can vary along multiple dimensions because they can be soft and pulpy, fibrous and tough, or hard shelled and resistant to fracture, and they can also be tiny such as blueberries or large like coconuts. Behaviors used to exploit foods with particular properties can also vary; for example, hard, fracture-resistant foods can be eaten by gouging, prying, shaving, puncturing, crushing, or even by using tools. Because of the many combinations of variation in material properties and feeding behaviors, species that belong to a single dietary class will experience different loading regimes resulting in different patterns of internal stresses and strains on their skeletons (Ross et al. 2012) and therefore have different optimal morphologies.

The many-to-many relationship between ecology and function is due to the multidimensionality of both ecology and function just as the many-to-one relationship between form and function is due to the multidimensionality of morphology. Multidimensionality, in general, reduces the probability of convergence (Stayton 2008) hence strong ecological and functional constraints increase the probability of convergence by limiting the array of accessible niches and optimal forms within them. Niche-dependent constraints on body size are a candidate for both ecological and functional constraints because many performance variables, such as bite force, scale with body size. If body size is not limited, animals can adapt to eating harder foods by simply increasing their size but when size is niche limited, adaptation to more challenging foods requires modifying proportions (e.g., increasing the ratio of input and output lever arm lengths) to increase output force exerted at the teeth relative to the input force applied to the bone. Animals that eat hard foods, such as nut-eating squirrels and tooth-digging gophers, have powerful incisor bites for their body size (Freeman and Lemen 2008), as do small-bodied carnivora (Christiansen and Wroe 2007). Niche-dependent limitations on body size may restrict the optimal shape for a functionally demanding niche. Limits on body size may not be enough to increase the probability of convergence because multiple configurations of a complex lever system perform equally well; different geometries produce the same bite force, exemplifying the many-to-one relationship between morphology and performance. Additional constraints, such as the inverse relationship between bite force and gape, can further narrow the set of equally optimal morphologies because adaptations that increase one necessarily reduce the other. That particular trade-off would be most consequential for animals eating foods that are both hard and large for their body size. The combination of constraints on body size and trade-offs limits the array of foods that can be eaten and can restrict the array of feeding behaviors that exploit those foods and may also produce niche-dependent scaling relationships.

Niche-dependent scaling relationships are likely when the optimal shape for a given size depends on niche and the optimal shape for a given niche depends on size. Despite the potential importance of size and niche-dependent scaling relationships, they are typically ignored in studies that aim to explain the relationship between shape and diet. In some cases, only shape is analyzed (Perez et al. 2009; Alvarez et al. 2011), or the relationship between size and shape is analyzed separately from that between niche and shape (Figueirido et al. 2010; Meloro et al. 2015), or size is viewed as a confounding variable (Hautier et al. 2011; Friedman et al. 2016) controlled either by including it as a covariate in the model (Baab et al. 2014) or by analyzing residuals from a regression (Metzger and Herrel 2005; Casanovas-Vilar and van Dam 2013; Collar et al. 2014). Omitting size from the model can lose potentially important information about adaptation because niche-dependent allometries, like niche-dependent morphologies, are evidence of ecological adaptation.

In this analysis, we examine size, dietary ecology, and mandibular morphology in squirrels (Sciuridae). Only one case of convergence is widely recognized in this group: bark-gouging miniatures that converge on a highly distinctive morphology as well as dietary niche (Ball and Roth 1995; Thorington and Darrow 1996; Casanovas-Vilar and van Dam 2013; Pecnerova et al. 2015; Zelditch et al. 2015). One explanation for the infrequency of convergence is that squirrels are highly conservative because of their functionally versatile trophic morphology (Roth 2005). That is consistent with the widespread view that squirrels are morphologically conservative, even constrained (e.g., Moore 1959; Roth 2005; Fabre et al. 2012; Casanovas-Vilar and van Dam 2013) and with the apparently contrary interpretations of squirrels as both specialized hard nut feeders (Cox et al. 2012) and as opportunistic generalists (Nowack 1999; Wilson and Reader 2005). That apparent contradiction between being specialists and generalists is characteristic of functional versatility (Liem 1980; Robinson and Wilson 1998; Bellwood et al. 2006). Many studies conclude that size accounts for little of the shape variation (Ball and Roth 1995; Thorington and Darrow 1996; Velhagen and Roth 1997; Caumul and Polly 2005; Hautier et al. 2009; Swiderski and Zelditch 2010; Casanovas-Vilar and van Dam 2013; Zelditch et al. 2015) despite the large range of body sizes (16–8000 g, Hayssen 2008), which could either mean that squirrels adapt to more challenging foods by increasing body size or that there are niche-dependent scaling relationships rather than a single allometric trend. Several studies have examined the relationship between squirrel trophic morphology and diet (Ball and Roth 1995; Thorington and Darrow 1996; Michaux et al. 2008; Casanovas-Vilar and van Dam 2013; Pecnerova et al. 2015) but have reached no consensus regarding that relationship and, to date, no study has used modern phylogenetic comparative methods to analyze it. In this study, we first reconstruct the evolutionary histories of diet and size, then test two hypotheses about the relationship between ecology and morphology: (1) size depends on dietary niche, and (2) jaw shape depends on both size and diet, with the effect of each being conditional on the value of the other. Finally, we examine the frequency and degree of convergence of jaw shape, testing the hypothesis that the degree of convergence is greatest in size-limited, functionally demanding dietary niches.

Materials and Methods

PHYLOGENY

The phylogeny used in this study was pruned from our previous analysis (Zelditch et al. 2015) and contains all 145 species for which we had morphological and molecular data and could obtain diet information.

DIET INFORMATION AND CODING

Information about diets of squirrels is obtained primarily from the recent summary of the literature (Thorington et al. 2012) and by consulting the cited primary literature. Nearly all species observed in multiple seasons or multiple localities have variable diets; those that eat nuts with thick, tough shells (e.g., walnuts, *Juglans*) may also eat soft fruits, flowers, and buds when available, or insects, tougher buds, and bark of twigs when preferred foods are not available. Our coding scheme (Table S1) is based on the most challenging foods eaten by that species, taking into account its body size, because the same food item might be a large and hard object for a small-bodied species but neither large nor hard for a large-bodied species. Our coding scheme is based on both the foods that are routinely eaten or are critical fall-back foods eaten during shortages of preferred foods. Foods were divided into those requiring large bite forces at the incisors (hard nuts and seeds, cones, and the bark of large branches and boles), those that could be effectively processed by simple crushing during mastication (seeds, soft fruits, leaves, buds, terminal branches), and those that require grinding (i.e., leaves of herbaceous plants). We further divided incisor biting to distinguish gouging or plucking bark from eating nuts and cones, reasoning that bark gouging requires not only large forces but also low mechanical advantage because the animal is biting a surface outside of its mouth. We also distinguish browsers that include soft or thin-shelled nuts such as chestnuts (*Castanea*) or acorns (*Quercus*) in their diet from those that do not. Animals that eat harder nuts are classified as nut eaters even if much of their diet is less challenging because they are capable of processing hard nuts even if they rarely do so. This food type is further divided to distinguish between extremely hard nuts, such as panda nuts (*Panda oleosa*), and nuts of intermediate hardness (e.g., *Juglans*, *Carya*, and *Corylus*). Hard nuts of tropical forests, such as *P. oleosa*, may have husks more than 10 mm thick (Emmons 1980), and a peak force to failure more than 13 times that of the hardest nuts of Nearctic forests (Peters 1987; Visalberghi et al. 2008). Thus, we distinguish eight diet classes as follows: (1) nuts, (2) hard nuts, (3) bark, (4) seeds, (5) browse that does not include nuts, (6) browse that does include nuts, (7) grass, and (8) soft foods (including specialized insectivory).

RECONSTRUCTING THE EVOLUTION OF DIET

Before we can test for ecomorphological convergence, we need to identify ecological convergence. To that end, we reconstructed ancestral diets, evaluating three models for transition rates between diets: (1) equal rates, predicting that all transitions between classes occur at equal rates; (2) symmetric rates, predicting that rates of forward and backward shifts between a pair of classes are equal but transitions between different pairs of classes may differ in rates; and (3) all rates differ, predicting that rates of all transitions differ, including forward and backward shifts between a pair of classes. This approach presumes that rates are constant, which is unlikely in Sciuridae given that some diet classes are unique to arboreal or terrestrial squirrels. We thus fit the models separately to the lineage of primarily arboreal squirrels and the lineage of primarily terrestrial squirrels.

Models were fit using a joint estimation procedure, meaning that all information from each node is used (in a two-pass optimization). The relative fit of these models was assessed by a likelihood ratio test. We then assessed the conservatism of diets by the probability of being in one state given the initial state and 10 million years (Ma), which is a long time relative to a stem age of 36 Ma. Ambiguities in the ancestral reconstructions are conveyed

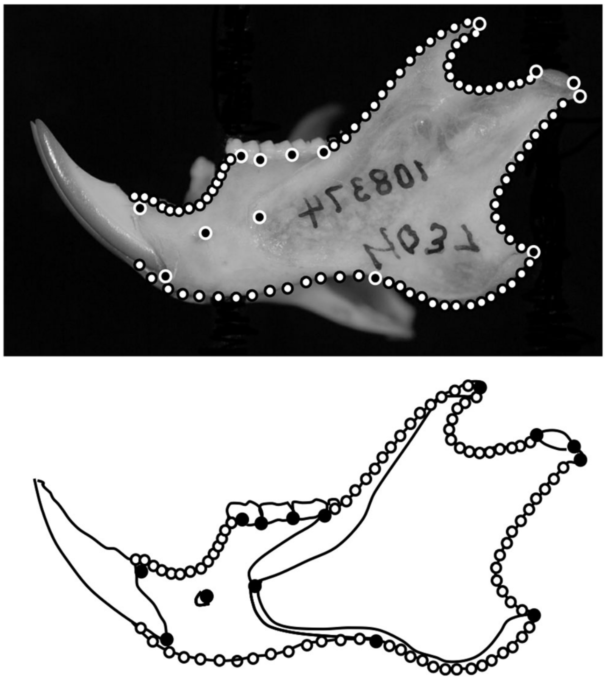

Figure 1. Landmarks (in black) and semilandmarks (in white) shown on a representative mandible of *Tamiasciurus douglassi*.

by a pie chart at each node that shows the relative probability of the states. These analyses were done using ace, a function in ape 3.4 (Paradis et al. 2004) in R 3.3.1 (R Core Team 2016).

SIZE AND SHAPE DATA

Fourteen landmarks and 84 semilandmarks were digitized to capture information about shape, including the curvature of the incisor alveolus, ventral horizontal ramus, and the three mandibular processes (Fig. 1). Landmarks were superimposed by a General Procrustes Analysis (Rohlf and Slice 1990); semilandmarks were slid using the bending energy criterion, which does not slide semilandmarks beyond the endpoint of a curve or onto another structure (Gunz and Mitteroecker 2013). Size was measured by mandibular centroid size, which is highly correlated ($r = 0.97$) with body size (Zelditch et al. 2015). Sample sizes ranged from 1 to 31, with a mean of nine. Procrustes superimposition, including semilandmark sliding, was done in geomorph 3.0.2 (Adams and Otarola-Castillo 2013), an R package for geometric morphometrics.

RECONSTRUCTING THE EVOLUTION OF SIZE

The evolution of size was inferred by a generalization of the Brownian motion model that relaxes the assumptions of neutrality and gradualism, allowing for the possibility that traits evolve at different rates over the tree due to a mixture of neutral drift, large changes due to directional selection, and low rates due to stabilizing selection (Elliot and Mooers 2014). Allowing rates to vary can result in having too many parameters to estimate but the model can be fit by sampling from a heavy-tailed distribution. In the case of Brownian motion, a trait evolves by incremental changes drawn from a random distribution and the variance is finite and constant; in contrast, the variation in rates due to a mix of directional selection, stabilizing selection and random genetic drift generates a heavy-tailed distribution. Stochastic processes with variable variances and heavy tails can be modeled using stable distributions parameterized by an index of stability and the scale; the sum of several stable distributions is stable, with the same value for the stability parameter. In the case of Brownian motion, that parameter $= 2$; if it is <2, the distribution is shallower with heavier tails. We used StableTraits (Elliot and Mooers 2014) (available at http://www.michaelelliot.net/stabletraits.html) to reconstruct the evolution of size; two MCMC chains were run for 1,000,000 iterations and the first 10% of each was discarded as burn-in resulting in a scale reduction factor of 1.02.

Reconstruction of ancestral values of shape was done by maximum likelihood using the Brownian motion model; although that may be an unrealistic model for shape, the outcome, a summary of the pattern of shapes in relation to the phylogeny, that is, a phylomorphospace (Sidlauskas 2008), depends very little on that model. A phylomorphospace is a principal components analysis of the observed and inferred ancestral shapes with the phylogeny projected onto the plane of the principal components. The phylomorphospace was obtained using the plotGMPhyloMorphoSpace function in the geomorph package.

STATISTICAL ANALYSIS OF THE RELATIONSHIP BETWEEN DIET AND SHAPE

To examine the relationship between diet and both size and shape, we first assessed the dependence of size on diet and then of shape on size, diet, and the interaction between size and diet. In these analyses, we used phylogenetic generalized least squares, adapted to high-dimensional shape data (Adams 2014). As in nonphylogenetic Procrustes Anova (Goodall 1991), sums of squares are the sums of squared Procrustes distances; from those sums of squares, F-ratios and R^2 values are calculated for all the terms in the model and the statistical significance of the terms is assessed by resampling the residuals from the reduced model. Using the reduced model makes it possible to control for the effects of covariates or other factors previously entered in the model (Anderson 2001; Collyer et al. 2015). PGLS (for size and shape) was done using the procD.pgls function in geomorph.

Because PGLS, by default, assumes Brownian motion and may give misleading results when that model does not fit the residuals of the statistical model, we estimated the residuals and assessed the fit of a Brownian motion model relative to two other models, a single stationary peak Ornstein-Uhlenbeck (OU) model and an “Early Burst” (EB) model, selecting the one yielding the lowest value for the Akaike information criterion, corrected for small sample size (AICc). Models for size were fit using the fitContinuous function in geiger 2.06 (Harmon et al. 2008). Models for shape were fit using the transformPhylo.ML function in the R package motmot (Thomas and Freckleton 2012) and the fitContinuousMV function kindly provided by Graham Slater. Previous analysis showed that these yield accurate estimates of shape disparity when the model fits the data (Zelditch et al. 2015). Fitting these models requires reducing the dimensionality of the data, which can lead to inaccurate parameter estimates if too few dimensions are included in the analysis, hence, in analyses of Sciuridae, we fit the models to the first 21 PCs as a single multidimensional set. Those axes explain 99% of the variance. Similarly, in separate analyses of tree and ground squirrels we used the first 19 PCs, which explain 99% of the variance in those data. When BM did not fit the residuals, we rescaled the tree according to the parameters of the better-fitting model (invariably, OU) and refit the model to determine if, after that rescaling, the residuals meet the assumption of BM. In all cases, phylogenetic signal of the residuals from the refit model, $K_{\text{multi}} \approx 1.00$ (ranging from 1.004 to 1.02) and the best-fitting model for those residuals is BM, meeting the assumptions of the test. We used this approach rather than estimating Pagel's λ (Pagel 1999) because that transform treats tips and nodes of the phylogeny differently when rescaling the tree, a procedure difficult to justify by either evolutionary or statistical theory.

ANALYSIS OF CONVERGENCE

The only method for assessing convergence that is suitable for the high-dimensional data of shape requires first identifying the species that converge. Our a priori hypothesis is that species within the same dietary class converge, but convergence might not be ecomorphological, hence we also examined cases of convergence between species within different dietary classes. Methods that can identify convergence in the absence of a priori hypotheses exist for multivariate data (Ingram and Mahler 2013; Khabbazian et al. 2016) but they are not suitable for high-dimensional data because they assume that each trait has an independent rate of adaptation (α) and diffusion (σ^2); also, including traits that lack a biological interpretation limits the ability of those methods to recover convergence (Ingram and Mahler 2013). Such analyses could be done using principal components of shape, but those are unlikely to have independent rates of adaptation and diffusion, or a biological interpretation; they are merely the axes of a convenient coordinate system. Estimating rates of adaptation and diffusion along those axes presumes that evolution occurs along them, not within the full shape space; in contrast, distances between shapes are always measured within the full space (by the Procrustes distance), not separately along each axis. Thus, to examine convergence, we first visualized patterns of morphological similarity relative to phylogenetic relationships using a tanglegram, which pairs two branching diagrams. Here, the phylogeny is one branching diagram and a phenogram produced by clustering shapes using UPGMA is the other. After a rotation to optimize the vertical matching of tips, a line is drawn for each species, connecting its positions in the two diagrams; discrepancies in those positions reveal convergence. The tanglegram was done using the cophylo function in the phytools package (Revell 2012).

We examined the degree of convergence using methods that can distinguish between similarity due to convergence and long-term stasis (Stayton 2015). To that end, the distance between the putatively convergent taxa (D_{tip}) is compared to the maximum distance between any pair of living or ancestral species within the lineages of the putatively convergent taxa ($D_{\max}$). The index of convergence, C1, is

$$\mathrm{C1} = 1 - D_{\text{tip}}/D_{\max} \tag{1}$$

This measures how similar two extant taxa are relative to how distinct their lineages have been in the past (i.e., the proportion of the maximum distance between two lineages that is closed by the evolution of the putatively convergent taxa). A value of zero indicates that species have not converged at all; they are as different as members of their lineage have ever been. A value of 1 would mean that they evolved to be identical, thus values closer to 1 indicate greater evolved similarity. We did not estimate the frequencies of convergence because that requires having more putatively convergent species than variables and some diet classes have just four to six species. Because convergence is expected even in randomly evolving clades (Stayton 2008), the degree of convergence is tested to determine whether it is any greater than expected for randomly evolving clades. The degree of convergence is compared to values obtained by simulating evolution under a model of Brownian motion. For cases in which species are inferred to converge to a significant degree, we examined the degree of similarity between them; it is possible that the putatively convergent species close up a large proportion of the distance between their lineages without closely resembling each other. Analyses of convergence were done using R code provided in Supporting Information.

Results

EVOLUTION OF DIET

In the analyses of tree squirrels, the equal rates model is favored over the more complex ones; for ground squirrels, the symmetric rate model fits best (Table S2). Based on these models, within tree squirrels, the most probable diet at the root is nuts ($P = 0.56$) and the next most probable is bark ($P = 0.12$). For ground squirrels, the diet at the root of the tree is more ambiguous; two

Table 1. Probability of switching from a given diet class (along rows) to another over 10 Ma for largely arboreal (Tree) and largely terrestrial (Ground) squirrels.

Tree	Nuts	Hard	Bark	Seeds	Browse1	Grass	Browse2	soft
Nuts	0.541							
Hard	0.077	0.541						
Bark	0.077	0.077	0.541					
Seeds	0.077	0.077	0.077	0.541				
Browse1	0.077	0.077	0.077	0.077	0.541			
Browse2	0.077	0.077	0.077	0.077	0.077	NA		
Soft	0.077	0.077	0.077	0.077	0.077	NA	0.077	0.541
Ground								
Nuts	0.337							
Hard	0.007	0.361						
Bark	0.011	0.340	0.327					
Seeds	0.349	0.005	0.008	0.362				
Browse1	0.204	0.035	0.044	0.194	0.290			
Grass	0.059	0.004	0.006	0.054	0.142	0.714		
Browse2	0.033	0.248	0.263	0.027	0.091	0.020	0.318	NA

"NA" refers to diets that do not evolve within the lineage.

diets, nuts ($P = 0.34$) and seeds ($P = 0.35$), are equally probable and browse is only slightly less so ($P = 0.24$). For tree squirrels, all diet transitions are equally improbable; far more probable is retaining the same diet over 10 Ma (Table 1). For ground squirrels, the probability of retaining the same diet depends on the diet; transitions between nut eating and seed eating are only slightly less probable than retaining either of those two diets but neither nut eaters nor seed eaters are likely to switch to grazing (Table 1). Grazing appears to be the most conservative diet in this clade and browsers are most likely to switch diets, but not preferentially to any other one.

Despite the low probabilities of most diet transitions, convergent evolution of diets is common. All diets have appeared, or in the case of nuts, reappeared multiple times (Fig. 2). Transitions away from nuts occurred early in Callosciurinae and Pteromyini and convergent returns to this diet occurred in both clades, possibly multiple times in each. Convergent returns to the nut diet also are probable for *Tamias* (Marmotini), more so if divergence from that diet occurred early rather than late. The diet that appears to have arisen most frequently is seed eating (excluding nuts), which arose independently in three clades of tree squirrels (Callosciurinae, Pteromyini, and Sciurini) and two clades of ground squirrels (Protoxerini and Marmotini), and multiple times in most of those clades.

Such a high frequency of convergence on seed eating may not be surprising for a diet found in 19% of the species in this study, but other diets have even higher rates of convergence relative to the number of living species within that dietary niche. Considering only the species analyzed herein, bark gouging arose at least seven times but is present in just 10 species, and hard nut eating arose three times but is present in just four species. In contrast, grazing arose just two or three times even though it is present in 23% of the species. The number of times that this diet arose is ambiguous largely because of its conservatism; were it less so, two independent origins in Marmotini would be probable, one in *Marmota* and the other in the S*permophilus*–*Cynomys* lineage.

MORPHOLOGY

Evolutionary history of size

Most major clades exhibit numerous increases and decreases in size, but changes typically are small and sister taxa usually are not dramatically different (Fig. 3). Although rare, some changes do result in sizes outside the typical range (60–135 mm centroid size, corresponding to body masses of 60–1000 g). Most of the large changes are reductions leading to the bark-gouging miniatures *Sciurillus pusillus*, *Exilisciurus exilis*, *Nannosciurus melanotis*, and *Myosciurus pumilio* (<30 g). By far, the largest change in size is the increase to the giant grazing squirrels in *Marmota* (>2500 g). Another size increase occurred during the evolution of the giant flying squirrels (*Petaurista*), and although they are half the size of the smallest *Marmota*, they are larger than most arboreal squirrels. Another increase occurred in the lineage leading to the Bornean hard nut specialist, *Rheithrosciurus macrotis*. Interestingly, mandibular size of this species is comparable to that of a small marmot but its body mass (1200 g) is comparable to that of large prairie dogs (*Cynomys*) and the giant flying squirrels.

Species that have extreme sizes usually do differ in diet from their sister clades but those diets are not restricted to species at

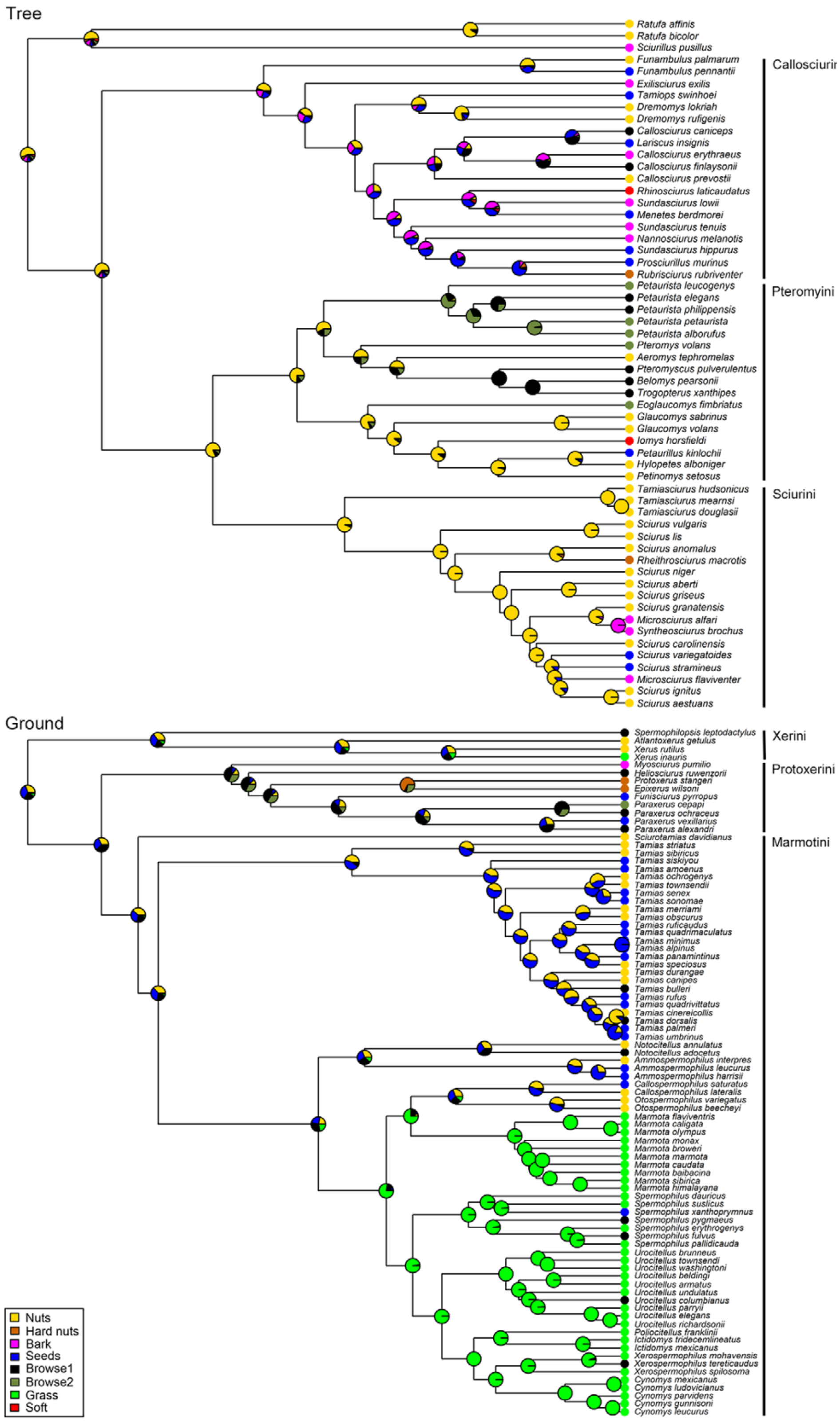

Figure 2. Reconstruction of the evolutionary history of diet for the largely arboreal (Tree) squirrels and largely terrestrial (Ground) squirrels. Piecharts at nodes depict the relative probability of the ancestral diets.

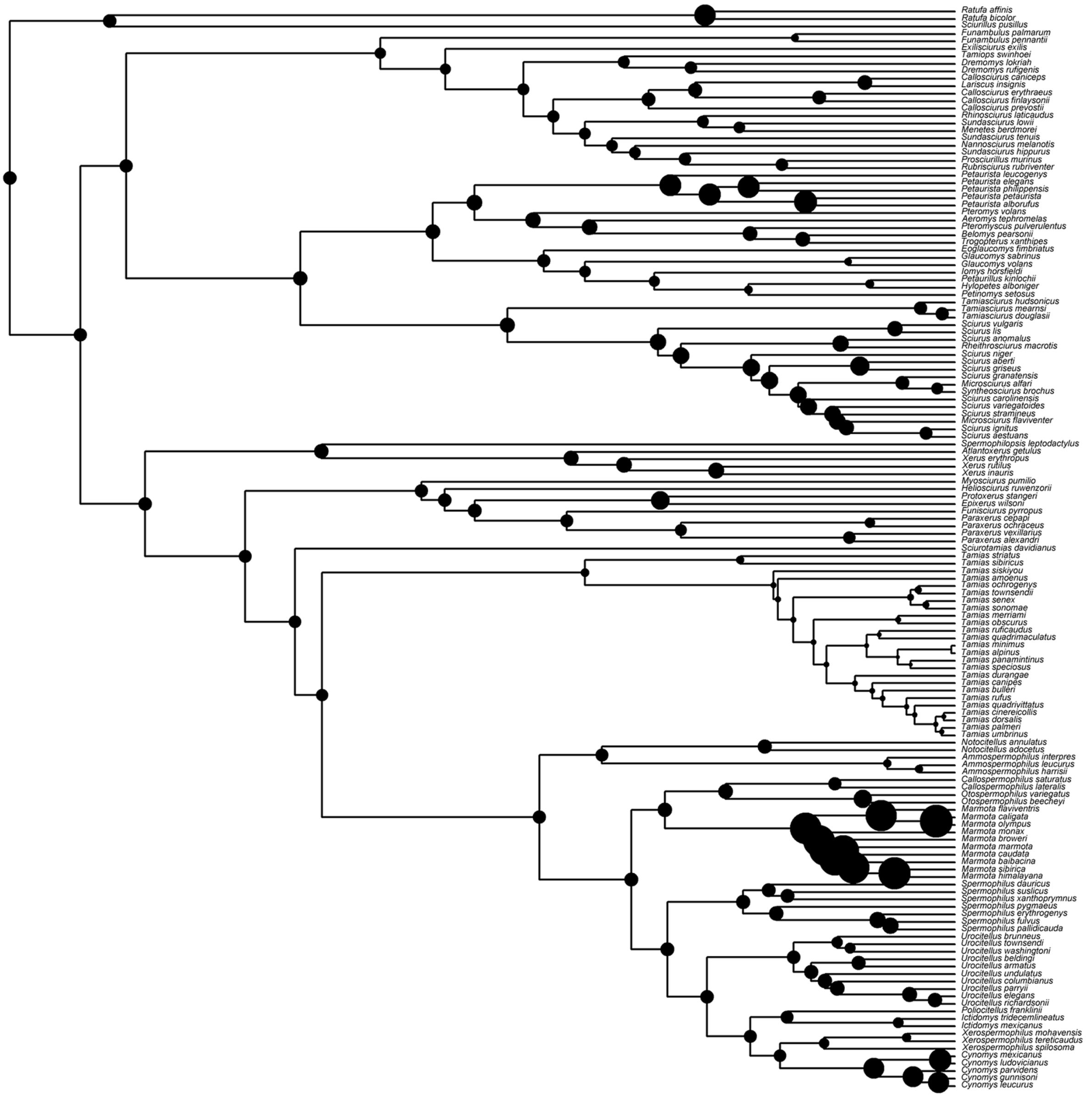

Figure 3. **Reconstruction of the evolutionary history of jaw size; the size of the circles at the nodes show the deviation of the inferred ancestral size from the minimum ancestral log-centroid size (multiplied by 1.5).**

the extremes of the size range. Bark gouging is not restricted to the smallest miniatures; bark-gouging species of *Sundasciurus* and *Callosciurus* are not miniatures, nor were their ancestors. Similarly, grazers are not all giants and grazing either predates the evolution of giants or is independent of it. Although the hard nut feeders are typically large bodied and vary little in size, the most extreme size classes are not the least varied in either size or diet (Fig. 4).

Phylomorphospace

Three principal components explain 83% of the variation in the data comprising morphologies of living species and inferred ancestral shapes. PC1 (Fig. 5) explains 52.6% of the shape variation and describes the divergence of ground squirrels (Xerini and Marmotini) from tree squirrels. A prominent feature along this axis is the posterior extension of the angular process, on which many of the major masticatory muscles insert. Two ground foraging callosciurine taxa, (*Rhinosciurus laticaudatus* and *Menetes berdmorei*) and two flying squirrels (*Belomys pearsonii* and *Trogopterus xanthipes*) also diverge along this axis, reflecting general elongation of the mandible. All Xerini and Marmotini are distinguished from tree squirrels along this axis, even those that retain the nut and seed diets. The greatest divergence is in the grazing ground squirrels (e.g., *Marmota*, and the lineage including *Cynomys* and *Spermophilus*). In contrast, Protoxerini, the arboreal clade in Xerinae, cannot be distinguished from the

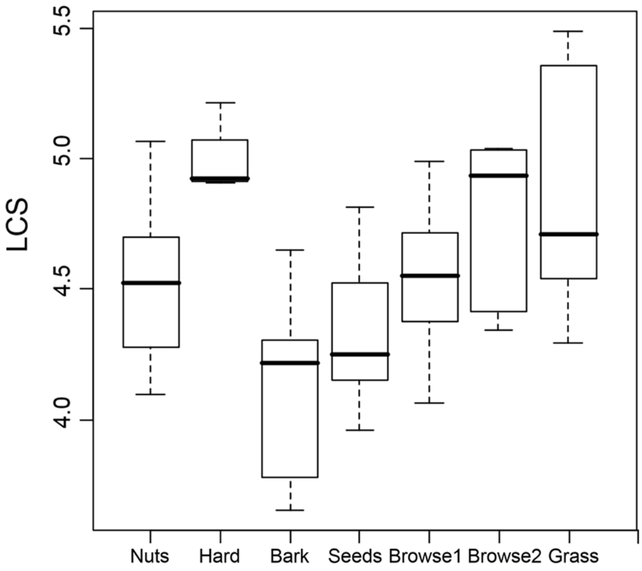

Figure 4. Distribution of jaw size within diets, in units of ln-transformed centroid size (LCS). The horizontal line is at the median; the box shows the interquartile range, and the whiskers extend 1.5 of the interquartile range.

other arboreal clades in these plots. PC2 and PC3 are relatively short and nearly equal in length, explaining 16.2 and 14.4% of the shape variation, respectively. The three smallest bark gougers have some of the lowest scores on PC2; their shorter coronoid is associated with a more robust condyloid process and ramus and a broader angular process. On PC3, the most prominent features are contrasting changes in the length of the condyloid process and breadth of the angular process; along this axis, the specialized insectivore *Rhinosciurus* has the most extreme scores owing to its slender mandibular processes and elongate horizontal ramus.

Within this three-dimensional space, only two diets, specialized insectivory and bark gouging by miniatures, occupy exclusive regions. Browsers, nut eaters and seed eaters each occupy large and broadly overlapping regions. Those occupied by grazers, hard nut specialists and larger-bodied bark gougers are smaller but also encompass species with other diets; however, overlap within such a low-dimensional plot does not mean that the shapes actually do overlap (they may be separated in another dimension). The hard nut specialists and grazers are the least disparate in shape, considering only the diet classes containing more than two species (Fig. 6).

PGLS: THE RELATIONSHIPS AMONG DIET, SIZE, AND SHAPE

Diet has a statistically significant but only moderate impact on size (Table 2); at most (in tree squirrels) it explains 42% of the variance. In the analysis of shape (Table 3), the effects of size, diet and the interaction term are all statistically significant but taken together, the model explains less than half of the variation in Sciuridae. That proportion increases when tree and ground squirrels are analyzed separately, but we cannot ascribe the variation to any of the terms in the model because the effect of each one depends on the other; the variation explained by each depends on whether it is entered first or second in the model.

CONVERGENCE

The tanglegram (Fig. 7) shows several cases of ecomorphological convergence; the most obvious being the bark-gouging species and another is the hard nut eating squirrels (*Rheithrosciurus*, *Rubriscurus*, *Protoxerus*, and *Epixerus*); although two protoxerines cluster more closely with smaller New World nut-eating squirrels (*Tamiasciurus* and *Sciurus*). These are the only cases in which ecomorphological convergence is significantly greater than expected for a randomly evolving clade (Table 4). Depending on the reconstruction of the ancestral diet, there are two cases of morphological convergence that might be ecomorphological: (1) two nut eaters (*Sciurotamias davidianus* and smaller-bodied *Tamias striatus*) and (2) two grazers (*Ictidomys mexicanus* and *Xerospermophilus spilosoma*). An interesting case that might be considered ecomorphological convergence even though the species are classified within two diet classes is between the large-bodied protoxerine hard nut specialists, *Protoxerus stangeri* and *Epixerus wilsoni*, and smaller-bodied nut-eating sciurines. Size also clearly plays an important role in the degree of convergence of bark gougers; these species do not all form a single tight cluster, rather, they form three: (1) mouse-sized miniatures (*Exilisciurus*, *Nannosciurus*, and *Myosciurus*); (2) miniatures comparable in size to small chipmunks (*Microsciurus* and *Sciurillus*); and (3) a loose cluster of species that are not small for tree squirrels (*Sundasciurus lowii*, *Sundasciurus tenuis*, and *Callosciurus erythraeus*). The degree of convergence is greatest for the three smallest miniatures ($C1 = 0.443$; $P < 0.005$), although not all are highly similar morphologically—the distances between them range from 0.055 to 0.0793.

The most surprising cases of convergence are morphological but not ecological (Table 5). Some small-bodied, nut-eating flying squirrels (*Glaucomys* and *Petinomys*) converge on an ecologically diverse group of protoxerines (*Heliosciurus ruwenzorii*, *Funisciurus pyrropus*, and *Paraxerus* species; some browsers, some seed eaters). Similarly, a browser (*Spermophilopsis leptodactylus*) converges on a group that includes two grazers (*I. mexicanus* and *X. spilosoma*), some nut eaters (*Callospermophilus lateralis*, *Otospermophilus beecheyi*, *Otospermophilus variegatus*, and *Notocitellus annulatus*), and a browser that does not include nuts in its diet (*Notocitellus adocetus*). Convergence between a bark-gouging sciurine (*Syntheosciurus brochus)* and a seed-eating callosciurine (*Prosciurillus murinus)* is among the most impressive in degree because their ancestors are very different, not because

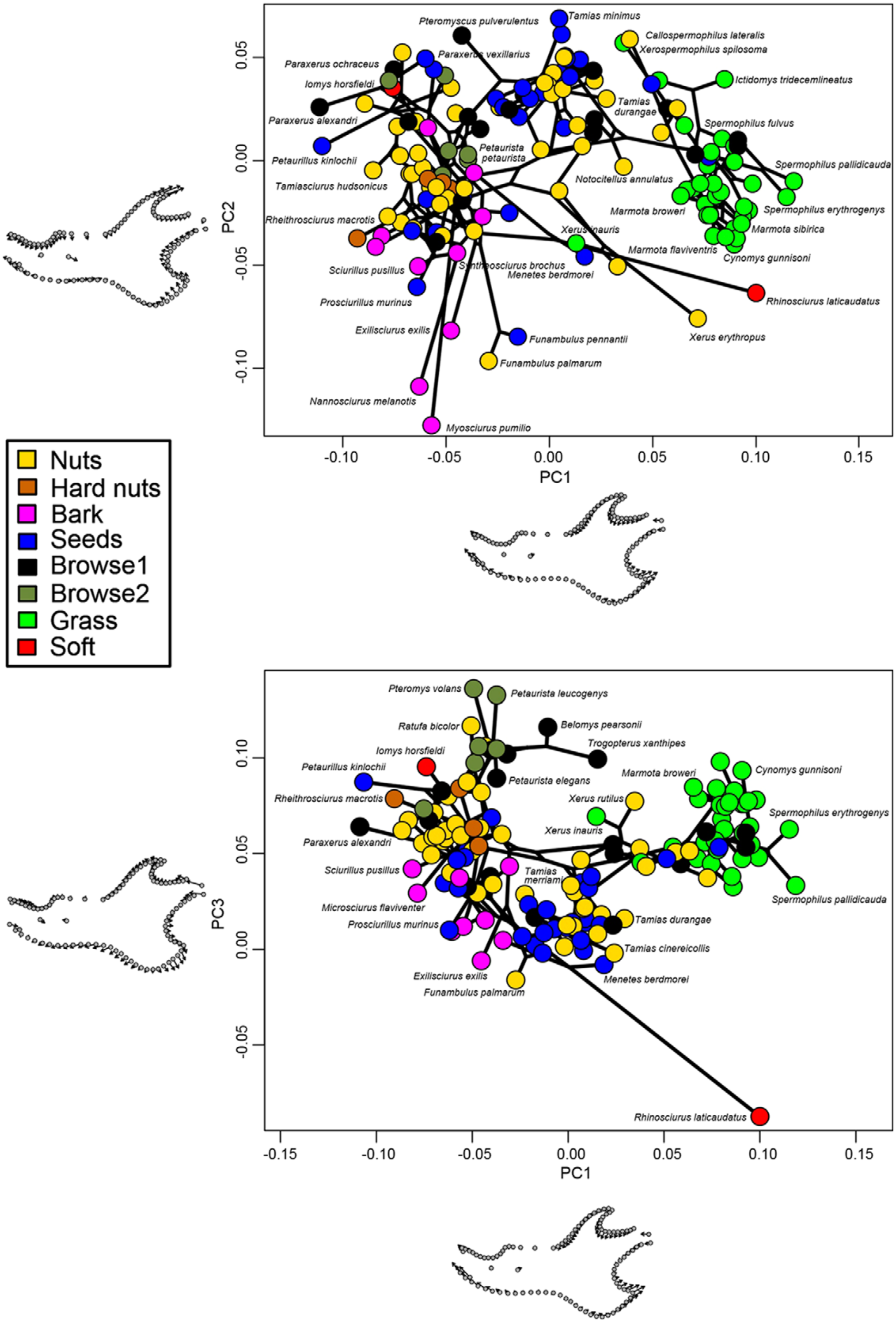

Figure 5. Principal components analysis of the shapes of living species and their estimated ancestors; the phylogeny is projected onto the space of PC1 × PC2 (above) and PC1 × PC3 (below).

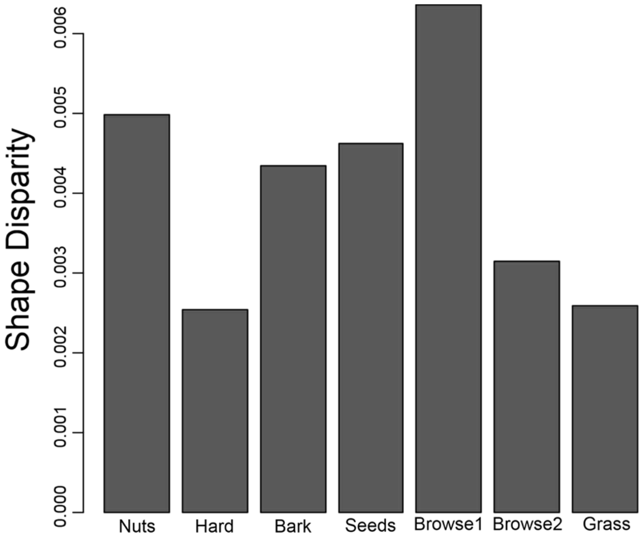

Figure 6. Disparity of shape within diet classes.

the descendants are highly similar. One case that might seem compelling from the tanglegram and the numerically high degree of convergence ($C1 = 0.273$) is between a bark-gouging sciurine (*Microsciurus alfari*) and a seed-eating callosciurine (*Sundasciurus hippurus)* but that one does not exceed what would be expected from a randomly evolving lineage ($P = 0.108$).

In addition to convergence, the tanglegram also reveals the broad overlap between nut eaters and seed eaters within clades and, more strikingly, the distinctness of nut eaters and seed eaters from different clades. Despite convergence on their similar complex diets, the squirrels and chipmunks do not converge in morphology

Discussion

We predicted that ecomorphological convergence would be rare except in size-constrained niches owing to the many-to-many relationship between ecology and function and the many-to-one and/or one-to-many mapping of form onto function. We further predicted that size would play an important role in both dietary ecology and convergence because, in the absence of constraints on size, species might adapt to more challenging foods by increasing body size, but when size is limiting, species would adapt by modifying their shape. Convergence on shape would thus be most likely when dietary niches limit size and feeding function limits the optimal form for that diet niche at that given size. That reasoning presumes that the optimal size depends on diet, and the optimal shape for a given diet depends on size. Our results clearly show that in the absence of constraints on size, ecomorphological convergence is rare: we found only four cases in which dietary niches and shapes converge, and in three, size is either constrained or limiting and foods are challenging. The results of the phylogenetic Procrustes Anova offers some support for the general premise of the hypothesis, but diet explains only 40% or less of the variance in size and the model predicting shape from size, diet, and diet-dependent scaling explains, at most, only 60% of the variance in jaw shape. We also find substantial support for the hypothesis of a many-to-many mapping of shape onto dietary ecology, which may explain the most surprising result: morphological convergence without ecological convergence is as common between dietary classes as within them.

The three cases of ecomorphological convergence all involve the evolution of functionally demanding diets at a limiting or constrained size. One is the well-known convergence of mandibular morphology in bark-gouging miniatures and convergence of mandibular morphology is greatest for the small-bodied species. The similarity among these species is responsible for debates about their phylogenetic relationships and the role of miniaturization in convergence (e.g., Forsyth Major 1893; Pocock 1923; Moore 1959; Heaney 1985). Miniaturization, in general, is not a cause of convergence in squirrels—the chipmunk-sized tree squirrels do not resemble chipmunks, and among miniatures, it is only bark gougers that converge in mandibular morphology. The second and third cases involve the large bodied to giant hard nut specialists. They occupy the most size-constrained niche, one that is also functionally demanding because powerful bites are required to open these nuts (Peters 1987) and the large size of the nuts requires powerful bites at large gapes. Hard nut eaters from three tribes (Sciurini, Protoxerini, Nannosciurini) close up nearly half the distance between their ancestral mandibular shapes, although one other (*Reithrosciurus macrotis*) has a notably different shape. The third case is the convergence of the protoxerine hard nut specialists on the sciurine nut eaters. In this case, body size is also important because the hard nut specialists are far larger than all but the largest sciurine nut eaters. Finally, mandibular shape of nut-eating *S. davidianus* converges on that of nut-eating *T. striatus*, a species that is only 50% of its body weight, which is the sole case in which ecomorphological convergence is not predicted by a shared size-limited or constrained niche.

The low frequency of ecomorphological convergence is due to the complex relationship between diet and shape, which clearly is not one-to-one. Instead, it is both one-to-many and many-to-one. That it is one-to-many is suggested by the extensive morphological overlap between nut eaters and seed eaters within lineages, suggesting that the nut- and seed-eating morphology is functionally versatile, as proposed for squirrels' trophic morphology (Roth 2005). The reason for anticipating that nut eaters and seed eaters would differ morphologically is that nut eaters should maximize incisor-bite forces whereas seed eaters should maximize molar-crushing forces. However, there need not be any trade-off between incisor- and molar-bite forces because they can be jointly maximized by shortening the diastema (and face), bringing the in-

Table 2. Effect of diet on size analyzed by phylogenetic generalized least squares for Sciuridae and for tree squirrels and ground squirrels, analyzed separately.

Group	Effect	df	SS	MS	R^2	F	P
Sciurdae	Diet	7	0.424	0.061	0.305	8.59	0.001
	Residuals	137	0.966	0.007			
	Total	144	1.390				
Tree	Diet	6	0.379	0.063	0.421	6.18	0.001
	Residuals	51	0.521	0.010			
	Total	57	0.900				
Ground	Diet1.Ground	6	0.147	0.024	0.233	3.99	0.025
	Residuals	79	0.485	0.006			
	Total	85	0.632				

df, degree of freedom.

Table 3. Effects of size and diet on jaw shape analyzed by phylogenetic generalized least squares for Sciuridae and for tree squirrels and ground squirrels, analyzed separately.

Group	Effect	df	SS	MS	R^2	F	P
Sciuridae	Size	1	0.029	0.029	0.080	18.72	0.001
	Diet	7	0.090	0.016	0.256	8.58	0.001
	Size x diet	7	0.045	0.007	0.115	3.85	0.001
	Residuals	129	0.243	0.002			
	Total	144	0.441				
Tree	Size	1	0.038	0.038	0.117	11.45	0.001
	Diet	6	0.071	0.012	0.218	3.54	0.002
	Size x diet	6	0.069	0.011	0.213	3.46	0.001
	Residuals	44	0.146	0.003			
	Total	57	0.324				
Ground	Size	1	0.329	0.329	0.264	51.89	0.001
	Diet	6	0.374	0.062	0.300	9.83	0.001
	Size x diet	4	0.074	0.019	0.060	2.92	0.002
	Residuals	74	0.470	0.006			
	Total	85	1.248				

df, degree of freedom.

cisors closer to the molars. The many-to-one relationship between shape and diet may be due to the resultant trade-off between bite force and gape, a trade-off most consequential for species that eat foods large for their body size, such as chipmunks. To a chipmunk, an acorn is a large, hard object but chipmunks nonetheless eat them and transport them whole in their cheek pouches. Chipmunks must therefore fit whole acorns in their mouths even when their cheek pouches are filled with seeds and must later be able to bite through the shells of those same acorns. Compared to tree squirrels, chipmunks' jaw adductor muscles have low mechanical advantages, although reliable estimates for chipmunks are limited to a single species, *T. striatus* (Velhagen and Roth 1997; Casanovas-Vilar and van Dam 2013). Chipmunks and other small-bodied species may not maximize feeding efficiency; instead caching large or well-protected items more often than larger-bodied species do (Ivan and Swihart 2000). Adaptations that increase bite force at the expense of gape could compromise foraging efficiency.

Feeding efficiency clearly does matter when foods are extremely well protected or cannot be transported or stored, which may explain convergence among hard nut eaters and among bark gougers. Hard nuts eaten by squirrels are so well protected that most animals that eat them are much larger than squirrels, such as elephants, ruminants, and African brush-tailed porcupines, *Atherurus africanus* (Gautier-Hion et al. 1985) and some larger animals also use tools, such as the hammers and anvils fashioned by chimpanzees and capuchin monkeys (Boesch and Boesch 1983; Visalberghi et al. 2007). Trees gouged by bark gougers obviously cannot be transported. Feeding efficiency may explain the most specialized and divergent trophic morphology in squirrels, that of the insectivore (*Rhinosciurus laticaudatus*). This species,

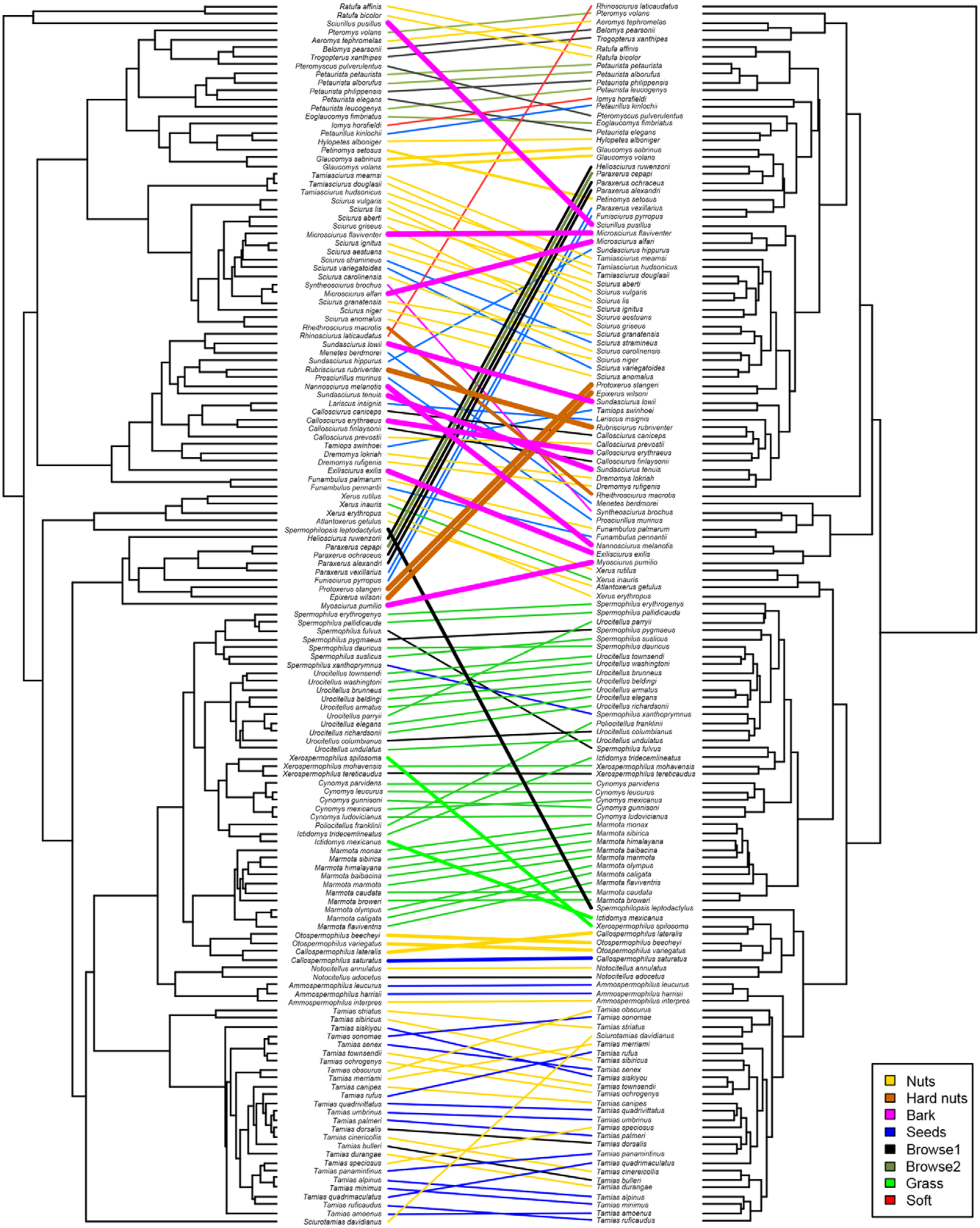

Figure 7. Tanglegram depicting convergence in jaw shape. The phylogeny is shown on the left and a phenogram from a cluster analysis (UPGMA) on the right. After rotation to maximize the similarity in ordering of tip labels, lines are drawn connecting the position of each species in the phylogeny to its position in the phenogram. Cases of convergence discussed in the text are shown by the thicker lines in the figure.

Table 4. Degree of convergence (C1), the probability that the degree of convergence exceeds what would be expected from a randomly evolving lineage (*P*), and the range of Procrustes distances between convergent species (ProcD) for cases of statistically significant convergence.

Diet	C1	*P*	ProcD
Nuts	0.091	0.735	
Hard nuts	0.210	0.001	0.042–0.090
Seeds	0.058	0.802	
Bark	0.165	0.001	0.038–0.175
Browse1	0.068	0.713	
Browse2	0.044	0.430	
Grass	0.067	0.861	
S. davidianus + *T. striatus*	0.440	0.010	0.031
Protoxerine hard nut + sciurines	0.210	0.009	0.044
I. mexicanus + *X. spilosoma* +	0.422	0.010	0.037
Two grazing lineages	0.034	0.840	

Table 5. Degree of convergence (C1), the probability that the degree of convergence exceeds what would be expected from a randomly evolving lineage (P), and the range of Procrustes distances between convergent species (ProcD) for cases of significant morphological convergence.

Convergent groups	CI	P	ProcD
Protoxerines + pteromyines	0.23	0.001	0.048–0.072
S. leptodactylus + some Marmotina	0.109	0.020	0.062–0.076
S. leptodactylus + grazers	0.35	0	0.062–0.077
S. brochus+ *P. murinus*	0.353	0.03	0.062

commonly known as the shrew-faced squirrel, may actually be the most remarkable case of convergence in the lineage though it converges not on another sciurid but rather on insectivorous treeshrews (Scandentia: Tupaiidae). What convergence on morphologies that maximize feeding or foraging efficiency cannot explain is the convergence of arboreal browsing protoxerines and small-bodied, nut-eating flying squirrels. This case is surprising because browsers typically eat softer foods than nuts and they are larger bodied than the nut eaters. They are thus presumably capable of generating more powerful bites than the species that eat harder foods. The even odder case is convergence among grazing and nut-eating marmotines. The convergence of two grazers is not surprising but the convergence of a grazer and a nut eater is surprising in light of evidence of a trade-off between nut-eating and grazing performance (Cox and Jeffery 2011). However, that evidence comes from a comparison between animals with divergent trophic anatomy (a nut-eating sciuromorphic squirrel and a grazing hystricomorphic guinea pig), leaving open the question of whether there are trade-offs between nut eating and grazing performance given a common trophic anatomy.

When the relationship between ecology and function is many-to-many, and when trophic morphology may be optimized for different functions, diet is not likely to be a good predictor of jaw shape. In that context, it is surprising that our model predicts shape as well as it does. However, that is only because we included size as part of the ecological model for shape. This may be unconventional in studies that examine the relationship between trophic morphology and diet by phylogenetically informed comparative methods, but size and scaling relationships have long been a major focus of functional morphology. One study directly quantified morphological correlates of bite force, finding that, in phyllostomid bats, size explains approximately 74% of the variation in bite force, and species with stronger bites than expected for their size have a shorter rostrum and mandible and more developed muscle attachment areas (Nogueira et al. 2009). Not surprisingly, we also find that tree squirrels, which have stronger bites than expected for their size (Freeman and Lemen, 2008), have a relatively short, robust ramus or diastema and well-developed angular process. Bark gougers too have a robust ramus, broad angular process and robust condyloid process but the smallest miniatures have nearly no coronoid process. We expected that scaling relationships would vary across diets, and given the statistical support for that hypothesis, it would be useful to characterize the diet-dependent scaling relationships; when functional equivalence of jaws is maintained by geometric scaling, allometry indicates that species in that diet class are not maintaining functional equivalence across their range of body sizes.

Ecomorphological convergence in squirrel mandibular shape is far rarer and much lower in degree than that found in many other studies of convergence. For example, several analyses of adaptations of squamate locomotory and foraging mode to habitat structure document community wide, intercontinental convergence, including Australian and North American snakes (Grundler and Rabosky 2014), desert lizards (Melville et al. 2006), and island (Mahler et al. 2013) and mainland *Anolis* (Moreno-Arias and Calderón-Espinosa 2016). Studies of cranial and mandibular morphology also find frequent convergence, to a remarkably high degree, especially between boas and pythons (Esquerre and Scott Keogh 2016) and across iterated radiations of damselfishes (Frederich et al. 2013) as well as consistent ecomorphological convergence to specialized planktivory in surgeonfishes (Friedman et al. 2016). The pattern we find in squirrels more closely resembles the pattern found in reef fishes (Bellwood et al., 2006): broad morphological overlap among some dietary classes, and a distinctive shape for other classes, albeit with extreme shapes in a few specialized classes. In both these groups the broad overlap may be due to functional versatility. However, these studies use different methodologies and rely on diverse types of data (e.g., shape vs non-shape; high vs low dimensionality data) that makes comparisons between studies difficult, and what constitutes convergence may even vary between studies. In particular, it is difficult to say whether the low degree of convergence we find in squirrel mandibular morphology is simply typical of high-dimensional shape data (where convergence is inherently less likely) or due to functional versatility and the many-to-many relationships between shape, function, and ecology.

Although ecomorphological convergence is rare in squirrels, we do find cases of morphological without ecological convergence and those are difficult to reconcile with the hypothesis that convergence is rare in the absence of strong functional and ecological constraints. We found few such cases but there may be more than we detected because our method requires identifying convergent species prior to conducting the tests. At present, there is no method for automatically detecting convergence in high-dimensional data hence we may have overlooked other cases of morphological without ecological convergence. Another limitation of the present study is that data on the diets of many squirrels are sparse aside from a wealth of detail on several west African protoxerines (Emmons 1980), diurnal Malaysian squirrels (Harrison 1962; MacKinnon 1978; Payne 1980), and the North American species used to test theories of optimal foraging (Lewis 1980; Belovsky 1986; Ritchie 1991; Thomas and Weigl 1998) and mechanisms of coexistence (Ackerman and Weigl 1970; Brown and Batzli 1984; Dyni and Yensen 1996; Kotler and Brown 1999). More complete ecological information might reveal more cases of morphological without ecological convergence or add to the evidence for functional versatility.

Cases of morphological without ecological convergence are particularly interesting because they are difficult to reconcile with the idea that convergence provides compelling evidence that ecological selection yields repeatable outcomes. But it is no less difficult to reconcile rare ecomorphological convergence with the idea that historical contingency overrides ecological selection. The difference between commonly replicated morphologies, on one hand, and rarely but unexpectedly replicated outcomes on the other is due to the structure of their adaptive landscapes. Convergence will be most common when the relationship between ecology and form is one-to-one, yielding one optimum per niche. When adaptive landscapes are instead characterized by a many-to-one relationship between form and function, there may be multiple equally optimal morphologies (Hulsey and Wainwright 2002; Alfaro et al. 2004; Alfaro et al. 2005; Swiderski and Zelditch 2010), and when it is characterized by a one-to-many relationship between form and ecology there may be one ecologically and functionally versatile optimum (Roth 2005; Bellwood et al. 2006). The structure of the adaptive landscape can be further complicated by a many-to-many relationship between ecology and function because that could result in more than one adaptive peak for some ecological classes and less than one for others. The combination of one-to-many, many-to-one, and many-to-many relationships gives a complex structure to adaptive landscapes. On complex adaptive landscapes, ecological selection can yield different outcomes; replicated outcomes are, therefore, predictably rare.

ACKNOWLEDGMENTS

We thank the curators and staff for access to the specimens in their care. P. Tucker (UMMZ), E. Lacey (MVZ), K. Helgen (NMNH), J. Searle (CUMV), and L. Heaney and B. Patterson (FMNH). We thank Graham Slater for generously sharing the R code for the multivariate function (fitContinuousMV).

DATA ARCHIVING

The doi for our data is: doi: 10.5061/dryad.kq1g6.

Literature Cited

Ackerman, R., and P. D. Weigl. 1970. Dominance relations of red and gray squirrels. Ecology 51:332–334.

Adams, D. C. 2014. A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. Evolution 9:2675–2688.

Adams, D. C., and E. Otarola-Castillo. 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods Ecol. Evol. 4:393–399.

Alfaro, M. E., D. I. Bolnick, and P. C. Wainwrigh. 2004. Evolutionary dynamics of complex biomechanical systems: an example using the four-bar mechanism. Evolution 58:495–503.

———. 2005. Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. Am. Nat. 165:E140–E154.

Alvarez, A., S. I. Perez, and D. H. Verzi. 2011. Ecological and phylogenetic influence on mandible shape variation of South American caviomorph rodents (Rodentia: Hystricomorpha). Biol. J. Linn. Soc. 102:828–837.

Anderson, M. J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fisheries and Aquat. Sci. 58:626–639.

Baab, K. L., J. M. G. Perry, F. J. Rohlf, and W. L. Jungers. 2014. Phylogenetic, ecological, and allometric correlates of cranial shape in Malgasy lemuriforms. Evolution 68:1450–1468.

Ball, S. S., and V. L. Roth. 1995. Jaw muscles of New World squirrels. J. Morphol. 224:265–291.

Bellwood, D. R., P. C. Wainwright, C. J. Fulton, and A. S. Hoey. 2006. Functional versatility supports coral reef biodiversity. Proc. Biol. Sci. 273:101–107.

Belovsky, G. E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70:35–52.

Boesch, C., and H. Boesch. 1983. Optimization of nut-cracking with natural hammers by wild chimpanzees. Behaviour 83:265–286.

Brown, B. W., and G. O. Batzli. 1984. Habitat selection by fox and gray squirrels: a multivariate analysis. J. Wildl. Manag. 48:616–621.

Casanovas-Vilar, I., and J. van Dam. 2013. Conservatism and adaptability during squirrel radiation: what is mandible shape telling us? Plos One 8:e61298.

Caumul, R., and P. D. Polly. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). Evolution 59:2460–2472.

Christiansen, P., and S. Wroe. 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivores. Ecology 88:347–358.

Collar, D. C., J. S. Reece, M. E. Alfaro, P. C. Wainwright, and R. S. Mehta. 2014. Imperfect morphological convergence: variable changes in cranial structures underlie transitions to durophagy in moray eels. Am. Nat. 183:E168–E184.

Collyer, M. L., D. J. Sekora, and D. C. Adams. 2015. A method for analysis of phenotypic change for phenotypes described by high-dimensional data. Heredity (Edinb) 115:357–365.

Cooper, W. J., and M. W. Westneat. 2009. Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. BMC Evol. Biol. 9:24.

Cox, P. G., and N. Jeffery. 2011. Reviewing the morphology of the jaw-closing musculature in squirrels, rats, and guinea pigs with contrast-enhanced MicroCT. Anat. Rec. 294:915–928.

Cox, P. G., E. J. Rayfield, M. J. Fagan, A. Herrel, T. C. Pataky, and N. Jeffery. 2012. Functional evolution of the feeding system in rodents. Plos One 7:e36299.

Dyni, E. J., and E. Yensen. 1996. Dietary similarity in sympatric Idaho and Columbian ground squirrels *(Spermophilus brunneus* and *S. columbianus*). Northwest Sci. 70:99–108.

Elliot, M. G., and A. Ø. Mooers. 2014. Inferring ancestral states without assuming neutrality or gradualism using a stable model of continuous character evolution. BMC Evol. Biol. 14:1–15.

Emmons, L. H. 1980. Ecology and resource partitioning among nine species of African rain-forest squirrels. Ecol. Monograph. 50:31–54.

Esquerre, D., and J. Scott Keogh. 2016. Parallel selective pressures drive convergent diversification of phenotypes in pythons and boas. Ecol. Lett. 19:800–809.

Fabre, P. H., L. Hautier, D. Dimitrov, and E. J. P. Douzery. 2012. A glimpse on the pattern of rodent diversification: a phylogenetic approach. BMC Evol. Biol. 12:88.

Figueirido, B., F. J. Serrano-Alarcon, G. J. Slater, and P. Palmqvist. 2010. Shape at the cross-roads: homoplasy and history in the evolution of the carnivoran skull towards herbivory. J. Evol. Biol. 23:2579–2594.

Forsyth Major, C. J. 1893. On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. Proc. Zool. Soc. London 1893:179–215.

Frederich, B., L. Sorensen, F. Santini, G. J. Slater, and M. E. Alfaro. 2013. Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). Am. Nat. 181:94–113.

Freeman, P. W., and C. A. Lemen. 2008. A simple morphological predictor of bite force in rodents. J. Zool. 275:418–422.

Friedman, S. T., S. A. Price, A. S. Hoey, and P. C. Wainwright. 2016. Ecomorphological convergence in planktivorous surgeonfishes. J. Evol. Biol. 29:965–978.

Gautier-Hion, A., J. M. Duplantier, R. Quris, F. Feer, C. Sourd, J. P. Decoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, et al. 1985. Fruit characters as a basis of food choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65:324–337.

Goodall, C. 1991. Procrustes methods in the statistical analysis of shape. J. R. Stat. Soc. Series B Methodol. 53:285–339.

Grundler, M. C., and D. L. Rabosky. 2014. Trophic divergence despite morphological convergence in a continental radiation of snakes. Proc. R. Soc. B Biol. Sci. 281:20140413. DOI: 10.1098/rspb.2014.0413.

Gunz, P., and P. Mitteroecker. 2013. Semilandmarks: a method for quantifying curves and surfaces. Hystrix Ital. J. Mammal. 24:103–109.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Harrison, J. L. 1962. The distribution of feeding-habits among animals in a tropical rain-forest. J. Anim. Ecol. 31:53–63.

Hautier, L., P. H. Fabre, and J. Michaux. 2009. Mandible shape and dwarfism in squirrels (Mammalia, Rodentia): interaction of allometry and adaptation. Naturwissenschaften 96:725–730.

Hautier, L., R. Lebrun, S. Saksiri, J. Michaux, M. Vianey-Liaud, and L. Marivaux. 2011. Hystricognathy vs. sciurognathy in the rodent jaw: a new morphometric assessment of hystricognathy applied to the living fossil *Laonastes* (Diatomyidae). PLoS One 6:e18698.

Hayssen, V. 2008. Patterns of body size and tail length and body mass in Sciuridae. J. Mammal. 89:852–873.

Heaney, L. R. 1985. Systematics of oriental pygmy squirrels of the genera Exilosciurus and Nannosciurus (Mammalia: Sciuridae). Misc. Publ. Mus. Zool. Univ. Mich. 170:1–58.

Hulsey, C. D., and P. C. Wainwright. 2002. Projecting mechanics into morphospace: disparity in the feeding system of labrid fishes. Proc. R. Soc. B Biol. Sci. 269:317–326.

Ingram, T., and D. L. Mahler. 2013. SURFACE: detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise Akaike Information Criterion. Methods Ecol. Evol. 4:416–425.

Ivan, J. S., and R. K. Swihart. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. J. Mammal. 81:549–562.

Khabbazian, M., R. Kriebel, K. Rohe, and C. E. An′e. 2016. Fast and accurate detection of evolutionary shifts in Ornstein-Uhlenbeck models. Methods Ecol. Evol. 7:811–824.

Kotler, B. P., and J. S. Brown. 1999. Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. J. Mammal. 80:361–374.

Lewis, A. R. 1980. Patch use by gray squirrels and optimal foraging. Ecology 61:1371–1379.

Liem, K. F. 1980. Adaptive significance of intraspecific and interspecific differences in the feeding repetoires of cichlid fishes. Am. Zool. 20:295–314.

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.

MacKinnon, K. S. 1978. Stratification and feeding differences among Malayan squirrels. Malay. Nat. J. 30:593–608.

Mahler, D. L., T. Ingram, L. J. Revell, and J. B. Losos. 2013. Exceptional convergence on the macroevolutionary landscape in island lizard radiations. Science 341:292–295.

Meloro, C., N. C. Caceres, F. Carotenuto, J. Sponchiado, G. L. Melo, F. Passaro, and P. Raia. 2015. Chewing on the trees: constraints and adaptation in the evolution of the primate mandible. Evolution 69:1690–1700.

Melville, J., L. J. Harmon, and J. B. Losos. 2006. Intercontinental community convergence of ecology and morphology in desert lizards. Proc. R. Soc. B Biol. Sci. 273:557–563.

Metzger, K. A., and A. Herrel. 2005. Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. Biol. J. Linn. Soc. 86:433–466.

Michaux, J., L. Hautier, T. Simonin, and M. Vianey-Liaud. 2008. Phylogeny, adaptation and mandible shape in Sciuridae (Rodentia, Mammalia). Mammalia 72:286–296.

Moore, J. C. 1959. Relationships among the living squirrels of the Sciurinae. Bull. Am. Mus. Nat. History 118:153–206.

Moreno-Arias, R. A., and M. L. Calderón-Espinosa. 2016. Patterns of morphological diversification of mainland *Anolis* lizards from northwestern South America. Zool. J. Linn. Soc. 176:632–647.

Nogueira, M. R., A. L. Peracchi, and L. R. Monteiro. 2009. Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. Funct. Ecol. 23:715–723.

Nowack, R. M. 1999. Walker's mammals of the world. Johns Hopkins Univ. Press, Baltimore.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Payne, J. B. 1980. Synecology of Malayan tree squirrels with special reference to the genus *Ratufa*. Univ. of Cambridge, Cambridge.

Pecnerova, P., J. C. Moravec, and N. Martinkova. 2015. A skull might lie: modeling ancestral ranges and diet from genes and shape of tree squirrels. Syst. Biol. 64:1074–1088.

Perez, S. I., J. A. F. Diniz, F. J. Rohlf, and S. F. Dos Reis. 2009. Ecological and evolutionary factors in the morphological diversification of South American spiny rats. Biol. J. Linn. Soc. 98:646–660.

Peters, C. R. 1987. Nut-like oil seeds: Food for monkeys, chipmanzees, humans and probably ape-men. Am. J. Phys. Anthropol. 73:333–363.

Pocock, R. I. 1923. The classification of the Sciuridae. Proc. Zool. Soc. London (1944) 1923:209–246.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3:217–223.

Revell, L. J. 2014. Ancestral character estimation under the threshold model from quantitative genetics. Evolution 68:743–759.

Ritchie, M. E. 1991. Inheritance of optimal foraging behavior in Columbian ground squirrels. Evol. Ecol. 5:146–159.

Robinson, B. W., and D. S. Wilson. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. Am. Nat. 151:223–235.

Rohlf, F. J., and D. E. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst. Zool. 39:40–59.

Ross, C. F., J. Iriarte-Diaz, and C. L. Nunn. 2012. Innovative approaches to the relationship between diet and mandibular morphology in primates. Int. J. Primatol. 33:632–660.

Roth, V. L. 2005. Variation and versatility in macroevolution *in* B. Hallgrimsson, and B. K. Hall, eds. Variation: a central concept in biolgoy. Academic Press, Burlington, MA.

Sidlauskas, B. 2008. Continuous and arrested morphological diversification in sister clades of characiform fishes: a phylomorphospace approach. Evolution 62:3135–3156.

Stayton, C. T. 2008. Is convergence surprising? An examination of the frequency of convergence in simulated datasets. J. Theor. Biol. 252:1–14.

———. 2015. The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. Evolution 69:2140–2153.

Swiderski, D. L., and M. L. Zelditch. 2010. Morphological diversity despite isometric scaling of lever arms. Evol. Biol. 37:1–18.

Thomas, G. H., and R. P. Freckleton. 2012. MOTMOT: models of trait macroevolution on trees. Methods Ecol. Evol. 3:145–151.

Thomas, R. B., and P. D. Weigl. 1998. Dynamic foraging behavior in the southern flying squirrel (*Glaucomys volans*): test of a model. Am. Midl. Nat. 140:264–270.

Thorington, R. W., and K. Darrow. 1996. Jaw muscles of old world squirrels. J. Morphol. 230:145–165.

Thorington, R. W., J. L. Koprowski, M. A. Steele, and J. F. Whatton. 2012. Squirrels of the world. Johns Hopkins Univ. Press, Baltimore.

Velhagen, W. A., and V. L. Roth. 1997. Scaling of the mandible in squirrels. J. Morphol. 232:107–132.

Visalberghi, E., D. Fragaszy, E. Ottoni, P. Izar, M. G. de Oliveira, and F. R. D. Andrade. 2007. Characteristics of hammer stones and anvils used by wild bearded Capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. Am. J. Phys. Anthropol. 132:426–444.

Visalberghi, E., G. Sabbatini, N. Spagnoletti, F. R. D. Andrade, E. Ottoni, P. Izar, and D. Fragaszy. 2008. Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). Am. J. Primatol. 70:884–891.

Wainwright, P. C., M. E. Alfaro, D. I. Bolnick, and C. D. Hulsey. 2005. Many-to-one mapping of form to function: a general principle in organismal design? Integr. Comp. Biol. 45:256–262.

Wilson, D. E., and D. M. Reader. 2005. Mammals species of the world. Johns Hopkins Univ. Press, Baltimore.

Wollenberg, K. C., I. J. Wang, R. E. Glor, and J. B. Losos. 2013. Determinism in the diversification of Hispaniolan trunk-ground anoles (*Anolis cybotes* species complex). Evolution 67:3175–3190.

Zelditch, M. L., J. Li, L. A. P. Tran, and D. L. Swiderski. 2015. Relationships of diversity, disparity and their evolutionary rates in squirrels (Sciuridae). Evolution 69:1284–1300.

Associate Editor: G. Thomas
Handling Editor: P. Tiffin

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1: Phylogenies rescaled according to the value for alpha obtained from the residuals of PGLS.
Table S1: Species included in this analysis (in alphabetical order) and their diet classes.
Table S2: Evaluating models for rates of diet evolution.
Table S3: Evaluation of evolutionary models for the residuals from PGLS analysis of shape.