

# FUNCTIONAL EQUIVALENCE OF MORPHOLOGIES ENABLES MORPHOLOGICAL AND ECOLOGICAL DIVERSITY

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Diversity in organismal forms among taxa is thought to reflect distinct selection pressures across environments. The central assumption underlying this expectation is that taxa experiencing similar selection have similar response to that selection. However, because selection acts on trait function, taxa similarity in selection response depends crucially on the relationship between function and morphology. Further, when a trait consists of multiple parts, changes in function in response to selection can result from modification of different parts, and adaptation to the same environment might result in functional but not morphological similarity. Here, we address the extent to which functional and morphological diversity in masticatory apparatus of soricid shrews reflects a shared ecological characteristic of their diet type. We examine the factors limiting morphological variation across shrew species by assessing the relative contribution of trait function (biomechanics of the jaw), ecology, and phylogeny to species similarity in mandibular traits. We found that species that shared diet type were functionally but not morphologically similar. The presence of multiple semi-independently varying traits enabled functional equivalence of composite foraging morphologies and resulted in variable response to selection exerted by similar diet. We show that functional equivalence of multiple morphologies enabled persistence of differences in habitat use (e.g., habitat moisture and coverage) among species that specialize on the same diet. We discuss the importance of developmental and functional integration among traits for evolutionary diversification of morphological structures that generate equivalent functions.

**KEY WORDS:** adaptation, biomechanics, mandible, morphological integration, redundancy, *Sorex*.

A central goal of evolutionary biology is to understand the origin of morphological diversity. Diversity in form is often associated with diversity of selection pressures experienced by taxa occupying different environments (Gatz 1979; Arnold 1983; Ricklefs and Miles 1994; Schluter 1996; Losos et al. 1998), such that morphological convergence among taxa is expected to result from similarity in selection pressures. However, convergence requires not only similarity in selection pressures, but also similarity in response to this selection (Gould 1985; Price et al. 2000; Van Buskirk 2002). Because selection acts at the level of trait function, trait similarity in response to selection depends on the concordance of functional and morphological variation (Koehl 1996; Schaefer and Lauder 1996; Alfaro et al. 2005).

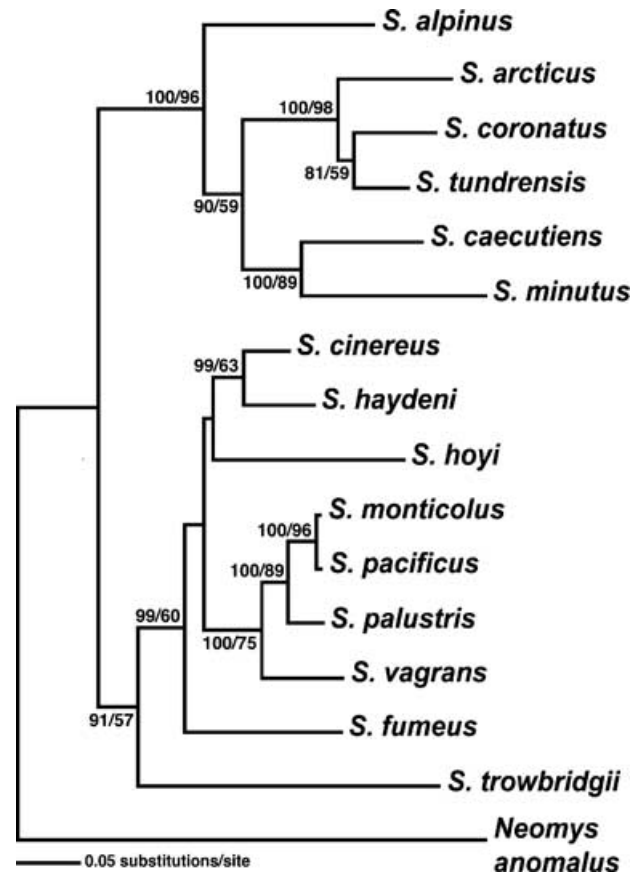
When a function favored by selection in one environment can be achieved by only one phenotype, adaptation to the same environment across taxa should result in morphological convergence (e.g., Schluter and McPhail 1993; Koehl 1996; Losos et al. 1998). However, when functional equivalence is produced by distinct morphologies (e.g., when different morphologies can generate the same physiological output), ecological and functional similarity of taxa might be achieved by different responses among taxa to similar selection pressures (Schaefer and Lauder 1996; Wainwright et al. 2005), facilitating the evolution of morphological diversity (Alfaro et al. 2004). In addition, variation in response to selection enabled by the functional equivalence of morphologies may resolve trade-offs produced by a trait's involvement in

multiple functions and thus allow species to adapt to multiple aspects of their environment (e.g., Toro et al. 2004; Alfaro et al. 2005; Westneat et al. 2005). Thus, species specializing to one ecological factor (e.g., particular diet) might be highly divergent in relation to other ecological factors (e.g., habitat type), and such differences may in turn generate diversity in responses to similar selection pressures (Schluter 2000).

Recent studies suggest that functional equivalence is an emergent property of complex morphologies (Alfaro et al. 2005; Wainwright et al. 2005). Because complex traits consist of multiple components that produce a particular function, change in that function can result from modification of any of the components of the complex trait resulting in a diversity of morphological solutions to the same functional requirement. Whereas, the importance of functional equivalence of morphologies for the evolution of diversity is well supported (Vermeij 1973; Koehl 1996; Wainwright et al. 2005), the factors that produce and limit this diversity are not well understood.

Here we test the hypotheses that functional equivalence facilitates morphological divergence among taxa that share an environmental characteristic, and allows otherwise ecologically divergent taxa to specialize on the same environmental resource. We predict that when functional similarity among taxa is achieved by multiple morphological solutions, species specializing on the same resource should be more similar in trait performance (e.g., biting force) than in trait morphology (e.g., skeletal structure). In addition, because functional equivalence of multiple morphologies enables variation in morphological response to shared selection pressures (e.g., Toro et al. 2004; Alfaro et al. 2005; Westneat et al. 2005), we predict that species experiencing similar functional requirements should likewise be more similar in trait performance than in characteristics of habitat use. Moreover, variation in morphological response to shared selection pressures should allow for the evolution of the same ecological specialization in distantly related taxa. Finally, we address the limitations on the diversity of morphological adaptations by examining the level of diversity across individual components of a complex morphological trait, and discuss factors that may constrain the development and evolution of some morphological variants.

We examine the association between morphology, ecology, and function in mandibles of 15 species of soricid shrews (Fig. 1), insectivorous predators in which the combination of rapid metabolism and variation across taxa in diet specialization results in strong selection on the masticatory apparatus (Genoud 1988; Churchfield 1990; Zakharov et al. 1991; Carraway and Verts 1994). Moreover, because diet specialization is distributed across the phylogeny (Fig. 1), this system provides an opportunity to examine ecological and evolutionary factors that influence interspecific diversity in both morphology and function. Here, we first assess morphological similarity among species with simi-



**Figure 1.** The maximum-likelihood phylogeny of the *Sorex* species used in this study. The numbers at each node in the phylogeny represent Bayesian posterior probabilities/maximum-likelihood bootstrap values (if > 50%).

lar diet type. Second, we model mechanical potential of the jaw and associated bite force to characterize the relationship between mandible morphology and function (Carraway and Verts 1994). We examine concordance of morphological and functional variation and establish functional equivalence of multiple morphologies. Lastly, to assess constraints on across-species morphological variation associated with diet type, we compare observed diversity in each mandible component across species that share diet type with potential diversity generated using mandible morphologies simulated for each species assuming no developmental or evolutionary constraints on proportionality among components of the mandible.

## Materials & Methods

### DATA COLLECTION

#### Morphological Measurements

In 15 species of *Sorex* shrews (species and sample sizes shown in Fig. 1 and Table 1), we measured mandibles of fully grown individuals. Left mandibles were placed on a slide and photographed

**Table 1.** Species sample size and means (coefficient of variation) for morphological and functional traits measured in this study.

Species	<i>N</i>	Coronoid–condyle length [mm]	Distance to molar [mm]	Force angle [°]	Mandible size [centroid]	Mechanical potential
<i>S. alpinus</i>	13	3.53(4.6)	6.52(7.7)	33.1(7.0)	13.78(5.9)	0.453(8.7)
<i>S. arcticus</i>	17	3.75(8.7)	6.20(4.5)	28.5(7.2)	12.57(6.5)	0.530(6.6)
<i>S. caecutiens</i>	13	3.46(3.8)	5.81(5.5)	32.3(7.3)	11.82(3.6)	0.503(4.7)
<i>S. cinereus</i>	15	2.77(2.4)	5.06(2.8)	33.9(9.3)	9.9(4.2)	0.454(5.3)
<i>S. coronatus</i>	20	3.91(3.5)	6.34(2.9)	32.6(7.1)	13.15(3.1)	0.519(3.6)
<i>S. fumeus</i>	19	3.39(3.6)	6.06(4.5)	33.4(10.8)	12.21(4.1)	0.468(4.7)
<i>S. haydeni</i>	20	2.95(5.3)	5.20(7.9)	30.9(9.0)	10.29(5.2)	0.488(8.9)
<i>S. hoyi</i>	20	2.77(4.4)	4.56(4.7)	31.7(5.9)	9.03(5.2)	0.517(6.4)
<i>S. minutus</i>	20	2.83(4.8)	5.06(6.5)	31.4(10.2)	10.42(4.3)	0.477(6.9)
<i>S. monticolus</i>	15	3.08(13.9)	5.36(8.6)	38.8(3.6)	11.11(10.9)	0.446(7.0)
<i>S. pacificus</i>	20	5.02(3.9)	7.35(3.6)	26.7(11.5)	15.13(3.6)	0.610(4.1)
<i>S. palustris</i>	20	4.14(5.7)	6.85(2.9)	29.9(12.4)	14.38(4.8)	0.522(5.4)
<i>S. trowbridgii</i>	18	3.45(5.0)	6.00(4.2)	31.2(5.4)	12.16(4.0)	0.491(5.2)
<i>S. tundrensis</i>	20	3.46(3.1)	6.04(3.2)	34.7(7.4)	12.4(3.2)	0.470(3.5)
<i>S. vagrans</i>	14	3.28(4.6)	5.47(4.1)	31.8(8.5)	10.9(6.5)	0.509(5.6)

at high resolution using an Olympus (Tokyo, Japan), Camedia E-20, 5-megapixel digital camera mounted in a standard position, or photographed under 10× magnifications using a Leica DC 300 (Bannockburn, IL) microscope (right mandibles were used in 24 individuals due to damage on the left mandible). We scaled all images to standard size using a ruler photographed with each mandible. Analyses of all images were conducted using Sigma-Scan 5.0 Pro software (SPSS, Inc., Chicago, IL). From mandible images, we obtained three measurements associated with bite force in shrews: coronoid–condyle length, distance from condyle to molar bite point, and gape angle (Fig. 2; Carraway and Verts 1994; Carraway et al. 1996). In addition to their importance for overall mandible function, these morphological measurements correspond with hypothesized developmental and functional units and, are thus, semi-independent traits of the mammalian mandible (Atchley and Hall 1991; Atchley 1993). We calculated mandible size as centroid size using 15 landmarks commonly used in studies of shrew mandible morphology (Fig. 2; also see Badyaev and Foresman 2000 for more details). Centroid size was calculated as the square root of the summed squared distance between each landmark and the mandible center. We calculated repeatability of all measurements from the intraclass correlation coefficient (Lessels and Boag 1987) of ANOVA from a subset of 30 individuals (two from each species) measured three times. Repeatability of all measurements was > 97%.

### Mechanical Potential Modeling

To model mechanical potential, we assumed the shrew mandible to be a simple lever in which the point of articulation between the mandible and skull (the condyloid process) serves as the fulcrum (after Fearnhead et al. 1955), and the distance from the tip

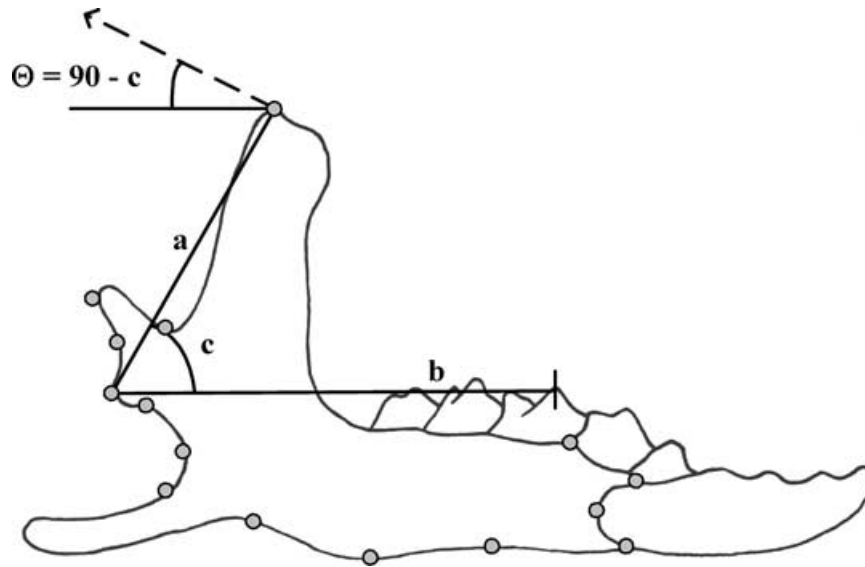
of the coronoid process (the primary cite of insertion of *M. temporalis*; Badyaev et al. 2005; R. L. Young, unpubl. data) to the lower condyloid process represents the length of the muscle moment arm **a**. The muscle moment arm was set at an acute angle **c** to the resistance arm. The resistance moment arm was measured as the distance from the condyloid process to the tip of the bite point or the highest cusp on the first molar **b** (Fig. 2; after Carraway and Verts 1994; Carraway et al. 1996). This bite point is the major location of prey crushing and has been found to yield the highest values in empirical measurements of bite force in *Sorex* (R. L. Young, unpubl. data). From these measurements, mechanical potential, **MP**, was calculated as:

$$MP = a/b \cos(\Theta),$$

where,  $\Theta = 90 - c$ , referred to as the force angle, and  $\cos \Theta$  is the proportion of force directed at a right angle to the muscle moment arm (after Carraway and Verts 1994 and consistent with the general orientation of the *M. temporalis* originating at the suture point of the left and right parietal bones). This measure of function indicates that bite force is independent of (1) overall mandible size such that larger mechanical potentials signify greater bite forces and (2) any compensatory effects of musculature. Therefore, MP provides a measurement of potential function of the mandible and assumes (1) a single source of force responsible for jaw closure (i.e., the temporalis muscle on the coronoid process); (2) a constant input force across all samples; and (3) the application of force at a right angle to the muscle moment arm.

### Diet, Foraging, and Habitat Categorizations

To categorize species diet type, habitat coverage and moisture association, and foraging type, we collected published data on diet



**Figure 2.** Morphological measurements used to calculate bite force and characterize morphology: a: coronoid-condyle length, b: distance to the highest cusp on the first molar, c: gape angle, and  $\Theta$ : force angle. Mechanical potential  $MP = a/b \cos \Theta$ .

type, stomach contents, species ranges, foraging behavior, and habitat associations (Table 2). Foraging type was defined as the location of foraging activity (Table 2). Habitat moisture levels were defined as either moist or dry and moist. Species strictly associated with swampy, boggy, or riverine habitats were labeled as moist. Because all species found in dry habitats (e.g., grass or scrublands) were also found in forest and riverine habitats associated with higher moisture levels, these species were categorized as dry and moist. Diet type was determined by prey hardness. Hard prey items (e.g., beetles and snails) were given a value of 1, soft prey items (e.g., earthworms, slugs, and larvae)—a value of 0, and intermediate prey items (e.g., spiders and moths)—a value of 0.5. Species with a mean diet score over 0.7 were categorized as “hard-bodied specialists,” species with diet scores between 0.3 and 0.7 were categorized as “generalists,” and species with diet scores less than 0.3 as “soft-bodied specialists” (Table 2).

## DATA ANALYSIS

### Phylogenetic Analysis

We constructed phylogenetic trees for the *Sorex* species used in the study using partial cytochrome *b* nucleotide sequences. We obtained 30 samples of 1011 bp sequence from Genbank (two individuals from each the 15 *Sorex* species) and aligned them with the program Se-Al (Rambaut 1996). The water shrew, *Neomys anomalus*, was used as an outgroup. Phylogenetic reconstructions were performed using distance (neighbor-joining), maximum likelihood, and Bayesian analyses. These methods add to previous phylogenetic analyses of *Sorex* shrews by allowing calculation of branch lengths (Fumagalli et al. 1999; Ohdachi et al. 2006). Distance and maximum-likelihood analyses were determined using Paup version 4.0b10 (Swofford 2000). We first built

neighbor-joining trees using two individuals from each species and the Tamura-Nei model of substitution. Once monophyly for each species was confirmed, one individual per species was used for maximum-likelihood analyses. Maximum-likelihood trees were reconstructed using the GTR +  $\Gamma$  + I model of nucleotide substitution, as determined by Modeltest (Posada and Crandall 1998) to be the best-fit model, and 1000 bootstrap replicates were run to assess phylogenetic support. We ran Bayesian analyses with Markov chain Monte Carlo sampling (MCMC) in MrBayes version 3.0b4 (Huelsenbeck and Ronquist 2001) using the GTR +  $\Gamma$  + I model. The search was run with four chains for 1,000,000 generations sampling trees every 1000 generations, with the first 10,000 generations discarded. We ran the analysis three times, and the trees from all three runs were combined to determine posterior probabilities.

### Morphological and Functional Variation

To examine the concordance of mandible morphology and diet type, we first used canonical discriminant analysis to summarize morphological variation between diet types, with each species weighted equally (SAS Institute Inc. 2004). Second, we calculated means for each of the four morphological measurements for each species (Table 1) and for each diet categorization. Means for each diet categorization were calculated as the mean of all species included in a diet category and group means of each measurement were compared using *t*-tests. All size and linear measurements were log transformed and angular measurements were arcsine transformed prior to analyses to achieve normal distribution (Sokal and Rohlf 1995). To examine concordance of function and diet type, we compared group mean mechanical potentials with *t*-tests.

**Table 2.** Diet type and ecological characteristics of species used in this study.

Species	Diet type	Foraging type	Habitat moisture	Habitat coverage	References
<i>S. alpinus</i>	soft-bodied specialist	surface and litter	moist habitats	open and closed habitats	(Hutterer 1982; Wilson and Reeder 1993)
<i>S. arcticus</i>	hard-bodied specialist	surface and litter	moist habitats	closed habitats	(Jackson 1961; Peterson 1966)
<i>S. caecutiens</i>	generalist	surface	dry and moist habitats	open and closed habitats	(Churchfield 1990; Churchfield et al. 1999)
<i>S. cinereus</i>	generalist	surface and litter	moist habitats	open and closed habitats	(French 1984; Pagels et al. 1994; Brannon 2000; Bellocq and Smith 2003)
<i>S. coronatus</i>	generalist	surface and litter	moist habitats	closed habitats	(Yalden et al. 1973; Churchfield 1990)
<i>S. fumeus</i>	soft-bodied specialist	litter and soil	moist habitats	closed habitats	(Whitaker and Cudmore 1987; Churchfield 1990; Brannon 2000)
<i>S. haydeni</i>	generalist	surface and litter	dry and moist habitats	open habitats	(van Zyll de Jong 1980; Clark and Stromberg 1987)
<i>S. hoyi</i>	hard-bodied specialist	surface, litter, and soil	dry and moist habitats	closed habitats	(Clark and Stromberg 1987; Whitaker and Cudmore 1987; Churchfield 1990; Kurta 1995)
<i>S. minutus</i>	generalist	litter and soil	dry and moist habitats	closed habitats	(Crowcroft 1955; Yalden 1981; Churchfield 1990, 1994)
<i>S. monticolus</i>	soft-bodied specialist	litter	moist habitats	closed habitats	(Whitaker and Maser 1976; Terry 1981; Carraway and Verts 1994)
<i>S. pacificus</i>	hard-bodied specialist	surface	dry and moist habitats	closed habitats	(Whitaker and Maser 1976; Carraway and Verts 1994)
<i>S. palustris</i>	generalist	water	moist habitats	closed habitats	(van Zyll de Jong 1983; Beneski and Stinson 1987; Clark and Stromberg 1987)
<i>S. trowbridgii</i>	generalist	litter and soil	dry habitats	closed habitats	(Whitaker and Maser 1976; Terry 1981)
<i>S. tundrensis</i>	soft-bodied specialist	surface, litter, and soil	dry and moist habitats	closed habitats	(Youngman 1975; van Zyll de Jong 1983)
<i>S. vagrans</i>	generalist	surface and litter	moist habitats	open and closed habitats	(Terry 1981; Whitaker et al. 1983; Gillihan and Foresman 2004)

### Consequences of Morphological Variability

To examine the contribution of coronoid–condyle length, distance to molar, and force angle to overall morphological diversity, we compared mechanical potential and morphological variation for each trait among species using regression analysis. We examined the relationship between species' diet categorization and their foraging and habitat type while controlling for phylogenetic distance between species (Table 2) by creating between-species dissimilarity matrices for foraging type, habitat coverage, and habitat moisture. Differences in diet type were ranked as 0, 0.5, or 1, with 0 representing a species pair that share diet type, 0.5 representing a comparison between a generalist and a specialist, and 1 representing a comparison between hard and soft specialists. Phylogenetic distance was estimated using branch lengths from the phylogenetic tree (see Methods above). We calculated the distances between pairs of species by adding the lengths of the branches between them. This was done for distance, maximum likelihood, and Bayesian analyses. Between-species divergence in each of

the remaining ecological characters, coverage, moisture and foraging type, were similarly calculated as a value between 0 and 1, 0 sharing the foraging or habitat type and 1 differing in foraging or habitat type.

Between-species dissimilarity matrices of morphological distance, mechanical potential, diet type, phylogenetic relatedness, and ecological divergence were compared using Mantel's and partial Mantel's tests. Partial Mantel's test allows for the comparison of two matrices while controlling for the effect of the third (Smouse et al. 1986; Legendre and Legendre 1998); thus, it was used to control for species relatedness in comparisons between morphological, ecological, and functional distances. Morphological distances between all species pairs were estimated with Mahalanobis distances using canonical discriminant analysis. Functional difference between species pairs was the absolute value of the difference in mechanical potential. Ecological divergence between species was measured as dissimilarity in foraging, coverage, and moisture type combined. Each species pair

was scored with a value between 0 and 1, species pairs that share all habitat (i.e., coverage and moisture) and foraging characteristics were scored as 0, and species pairs with divergent habitat and foraging characteristics were scored as 1. Ecological dissimilarity scores for species pairs sharing some habitat or foraging characteristics were calculated as the average of the species-pair dissimilarity scores for coverage, moisture, and foraging characteristics. All matrix correlations (Mantel's statistic) were estimated with R (R Development Core Team 2004; Oksanen et al. 2005).

### Constraints on Diversity Mandible Components

To characterize constraints on morphological variation in relation to diet, we compared observed diversity in morphological adaptation to null models of predicted potential morphological diversity for each diet type. To estimate potential diversity for each diet type, 20 morphologies were randomly generated for each species such that their coronoid–condyle length (*a*), distance to bite point (*b*), and force angle ( $\Theta$ ) were limited within the range of values observed for the species and their mechanical potential fell within the interquartile range for the species. This was repeated 1000 times for each species. First, for each iteration, we calculated means for all three morphological variables. Second, one iteration was sampled without replacement for each species within a diet category, and the interspecific means, coefficients of variation (CVs), and variances were calculated for each mandible character until all iterations had been selected. Finally, observed means, CVs, and variances for each trait and diet type were compared to simulated distribution of means, CVs, and variances using *z*-tests. Among species sharing diet type, variation in each of the three morphological character was considered constrained when observed CV and variance for a component of the mandible were lower than those generated by the model.

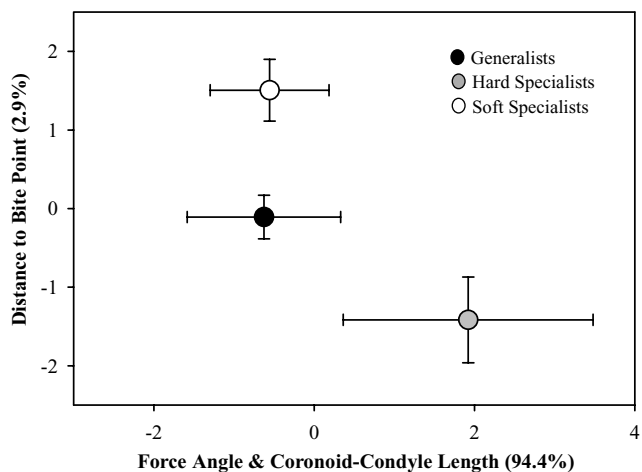
## Results

### PHYLOGENETIC ANALYSIS

Distance (neighbor-joining), maximum likelihood, and Bayesian methods all yielded the same topology with good phylogenetic support for most clades (Fig. 1), corroborating phylogenetic relationships among soricid shrews found in a previous analysis (Fumagalli et al. 1999; Ohdachi et al. 2006).

### MORPHOLOGICAL AND FUNCTIONAL VARIATION

Morphological divergence between diet types differed among the four measured traits, coronoid–condyle length, distance to the first molar, force angle, and mandible size (Tables 1 and 2; Figs. 3, 4). The first canonical axis accounted for 94.4% of the differences between diet types and consisted of variation in force angle,  $\Theta$ , and

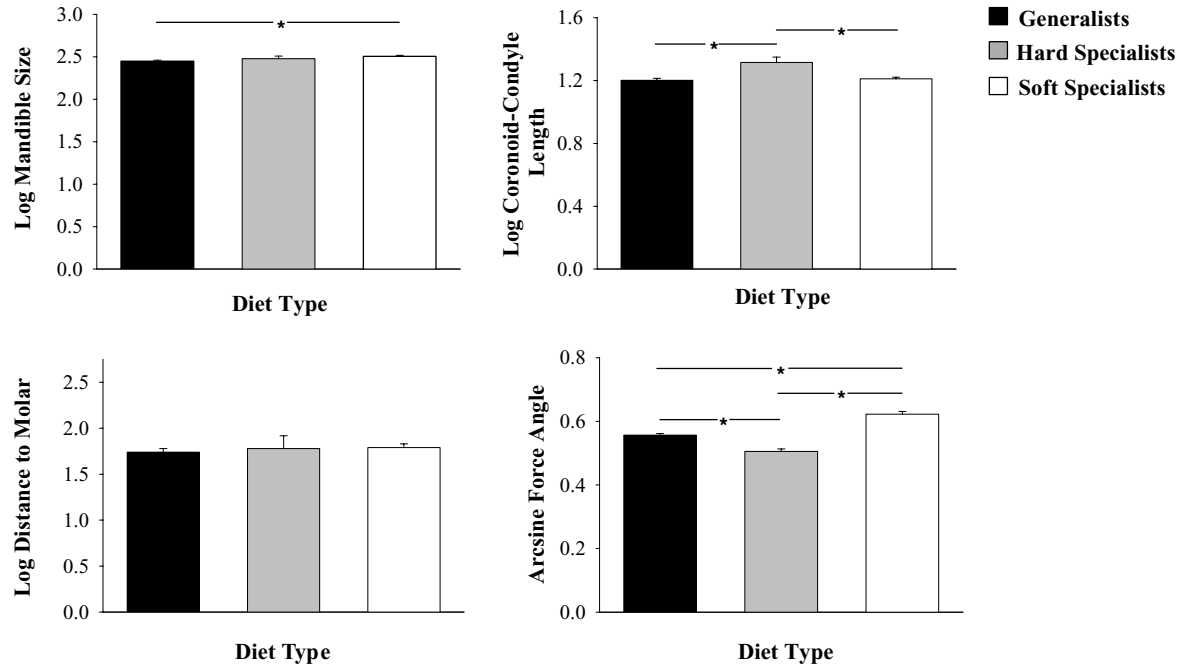


**Figure 3.** Canonical discriminant analysis of morphological variation among diet types. Abscissa is the first canonical axis; ordinate is the second canonical axis. Shown are mean  $\pm$  1SD for each diet category for the first two canonical axes. Closed circles show diet generalists, gray circles—hard specialists, and open circles—soft specialists.

coronoid–condyle length, *a*, whereas the second canonical axis contributed only 2.9% of the morphological divergence between diet types and consisted of distance to the first molar, *b* (Figs. 2, 3). Force angle differed among all three diet categories (general vs. hard:  $t = 5.5$ ,  $P < 0.001$ ; generalist vs. soft:  $t = -7.1$ ,  $P < 0.001$ ; hard vs. soft:  $t = -9.8$ ,  $P < 0.001$ ) and distance to the bite point did not differ between groups (general vs. hard:  $t = -0.27$ ,  $P = 0.8$ ; generalist vs. soft:  $t = -0.89$ ,  $P = 0.4$ ; hard vs. soft:  $t = -0.08$ ,  $P = 0.9$ ; Fig. 4). Hard specialists differed in coronoid–condyle length (Fig. 4; general vs. hard:  $t = -3.1$ ,  $P = 0.003$ ; generalist vs. soft:  $t = -0.58$ ,  $P = 0.6$ ; hard vs. soft:  $t = 2.91$ ,  $P = 0.005$ ), and mandible size differed between generalists and soft specialists (Fig. 4; general vs. hard:  $t = -0.9$ ,  $P = 0.4$ ; generalist vs. soft:  $t = -3.5$ ,  $P < 0.001$ ; hard vs. soft:  $t = -0.9$ ,  $P = 0.4$ ). Although coronoid–condyle length, distance to incisor, and mandible size did not differ among all diet categorizations (Fig. 4), mechanical potential differed among all three diet categories (general vs. hard:  $t = -2.13$ ,  $P = 0.06$ ; generalist vs. soft:  $t = 3.63$ ,  $P < 0.05$ ; hard vs. soft:  $t = 4.49$ ,  $P = 0.05$ ; Fig. 5).

### FUNCTIONAL EQUIVALENCE OF MULTIPLE MORPHOLOGIES

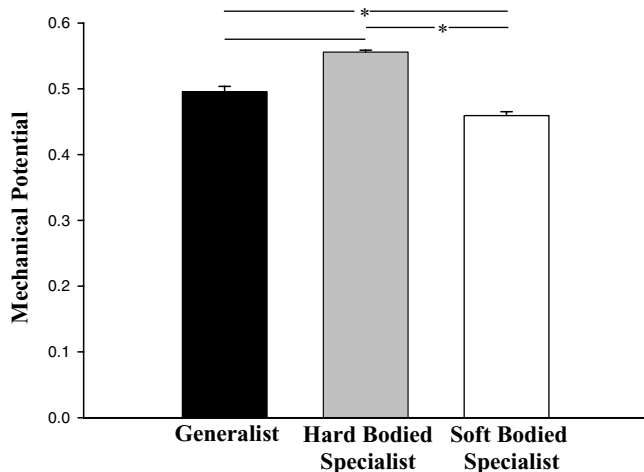
Across study species, different mandible morphologies produced the same mechanical potential. As a result, functional, but not morphological divergence was correlated with species differences in diet type (Table 4, comparisons of mechanical potential and morphology indicated that the relationship differed among traits). Across taxa, variation in morphological response to diet type was produced by modification of some traits, but persistence of others (Fig. 6). Both coronoid–condyle length ( $r^2 = 0.39$ ,  $P = 0.02$ )



**Figure 4.** Morphological divergence among diet types. Shown are mean  $\pm 1SE$ . Closed bars indicate diet generalists, gray bars—hard specialists, and open bars—soft specialists. Lines with asterisks connect means that are significantly different ( $\alpha < 0.05$ ).

and force angle ( $r^2 = 0.67$ ,  $P < 0.001$ ) positively correlated with mechanical potential, whereas distance to the bite point ( $r^2 = 0.13$ ,  $P = 0.18$ ) and mandible size ( $r^2 = 0.11$ ,  $P = 0.24$ ) did not vary with mechanical potential (Fig. 6). There was no correlation among matrices of diet type, foraging, and habitat characteristics indicating no association among ecological characteristics across species (Table 3). Phylogenetic divergence among species was not

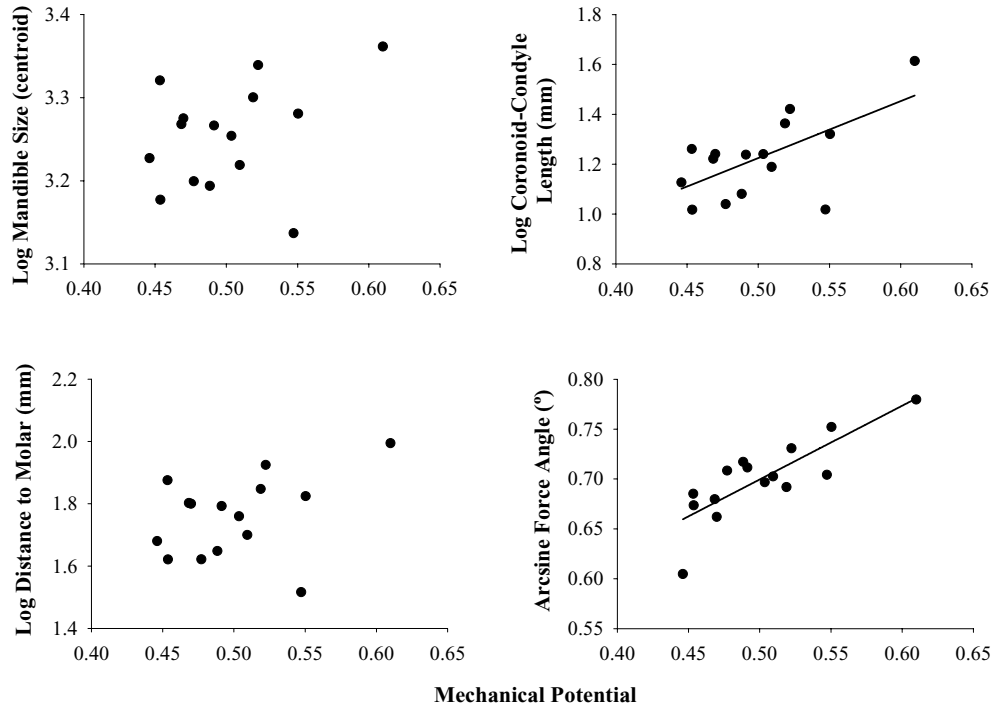
concordant with species divergence in morphology, function, diet type, and ecology ( $r = -0.18$ ,  $P = 0.85$ ;  $r = -0.23$ ,  $P = 0.98$ ;  $r = -0.14$ ,  $P = 0.14$ ;  $r = -0.12$ ,  $P = 0.89$ ). Morphological divergence was not consistent with ecological divergence among species; matrix correlations between Mahalanobis distances of species pairs did not vary with ecological divergence among species (i.e., morphological distance was not consistent with divergence in diet type or habitat coverage, moisture, and foraging characteristics among taxa; Table 4).



**Figure 5.** Comparison of mean mechanical potential among diet categories. Shown are mean  $\pm 1SE$ . Closed bars indicate diet generalists, gray bars—hard specialists, and open bars—soft specialists. Lines with asterisks connect means that are significantly different ( $\alpha < 0.05$ ); blank lines indicate differences in means ( $\alpha < 0.07$ ).

#### Constraints on Diversity in Mandible Components

Comparisons of observed and potential variation in each trait show that response to shared diet varied across traits for some diet types (Fig. 7). For coronoid–condyle length, observed variation was similar to the potential variation in generalists (CV:  $z = -0.45$ ,  $P = 0.33$ ; variance:  $z = -0.56$ ,  $P = 0.29$ ) and hard specialists (CV:  $z = -1.45$ ,  $P = 0.07$ ; variance:  $z = -1.13$ ,  $P = 0.13$ ). However, in soft specialists, variation of coronoid–condyloid values among species was greater than expected (CV:  $z = 8.31$ ,  $P > 0.99$ ; variance:  $z = 14.83$ ,  $P > 0.99$ ). Observed variation in distance to the molar bite point was greater than the potential variation in both generalists and soft specialists (generalists CV:  $z = 1.87$ ,  $P = 0.97$ , variance:  $z = 1.89$ ,  $P = 0.97$ ; soft specialists CV:  $z = 7.8$ ,  $P = 0.99$ , variance:  $z = 8.3$ ,  $P = 0.99$ ), and indistinguishable from potential variation in hard specialist (CV:  $z = 0.23$ ,  $P = 0.59$ ; variance:  $z = 0.34$ ,  $P = 0.63$ ). For force angle, the observed variation was consistent with potential variation in generalists and hard specialists (generalists CV:  $z = 0.15$ ,  $P = 0.56$ ;



**Figure 6.** Relationship between mandible morphology and mechanical potential. Coronoid–condyle length and force angle are significantly correlated with mechanical potential, and mandible size and distance to the molar are not correlated with mechanical potential. Lines indicate significance ( $P < 0.05$ ) in the regression of the morphological characters on mechanical potential.

variance:  $z = 0.1$ ,  $P = 0.54$ ; hard specialists CV:  $z = -0.95$ ,  $P = 0.17$ ; variance:  $z = -0.89$ ,  $P = 0.19$ ), and was greater than expected for soft specialists (CV:  $z = 7.59$ ,  $P = 0.99$ ; variance:  $z = 17.55$ ,  $P > 0.99$ ). CVs and variances yielded similar results, thus only variances are shown (Fig. 7).

### Discussion

Discordance in patterns of ecological and morphological diversity across taxa can result from variation in response to similar selection pressures. Such variation is often attributed to historical contingency—the constraining effects of taxa-specific evolutionary histories (Schluter and Nagel 1995; Losos et al. 1998;

Langerhans and DeWitt 2004). However, if equivalent adaptive solutions are accomplished by multiple morphologies, then morphological variation among taxa specializing on the same environment can result from the ability of a trait to adapt to different combinations of environmental characteristics across taxa, such that, diversity in form would result from trait versatility in adaptation rather than constraints imposed by evolutionary history. In this case, morphological diversity depends on trait lability and the degree of independence among the components of a trait

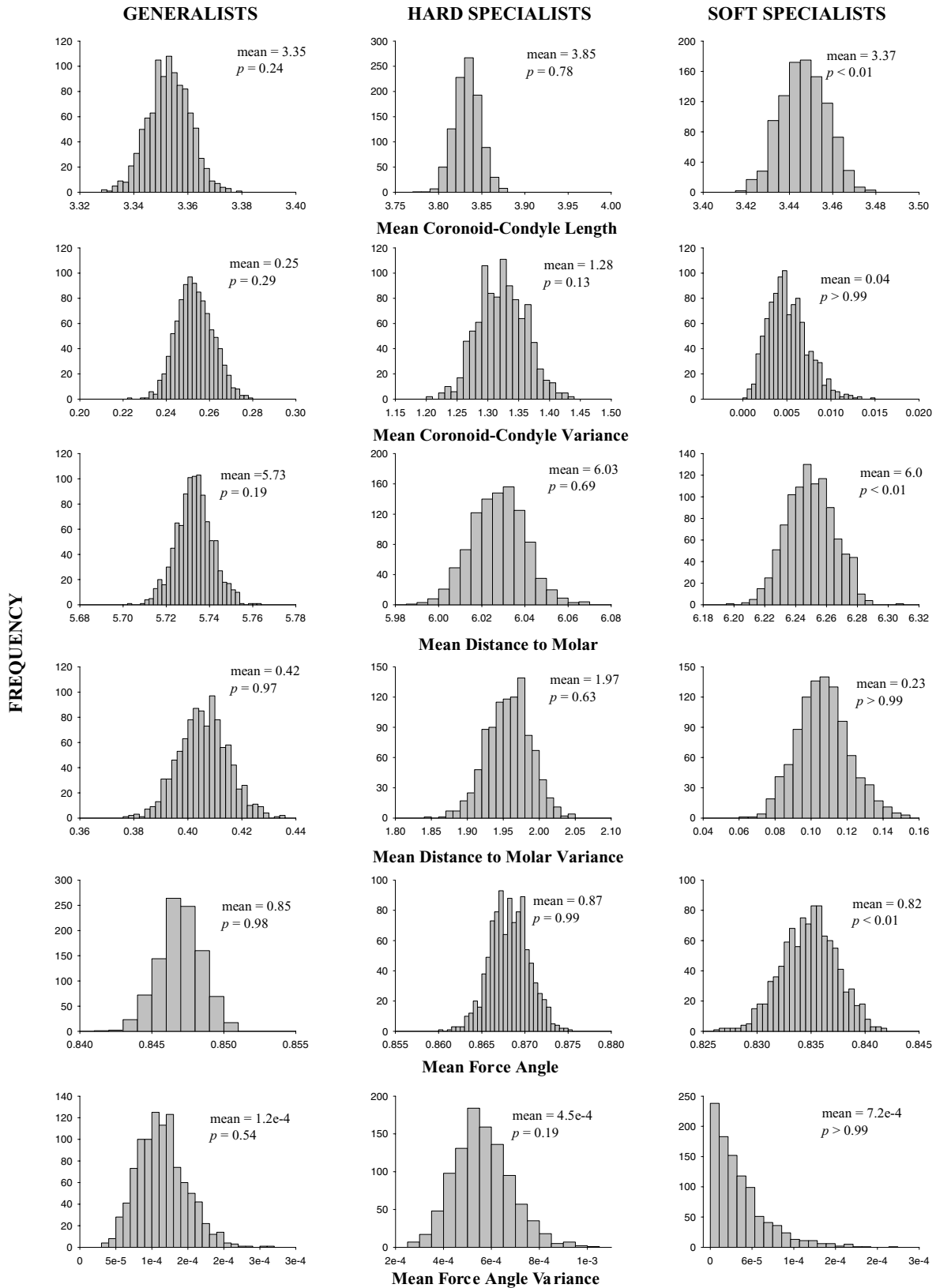
**Table 3.** Comparison of between-species divergence in diet type, foraging type, habitat moisture and coverage characteristics to test for concordance in use of resources and habitat type among taxa. Mantel’s statistic ( $r$ ) below the diagonal,  $P$ -values are shown above diagonal.

	Diet type	Foraging type	Habitat moisture	Habitat coverage
Diet type	.	0.4	0.9	0.8
Foraging type	0.01	.	0.2	0.8
Habitat moisture	-0.09	0.07	.	0.8
Habitat coverage	-0.09	-0.15	-0.07	.

**Table 4.** Comparison of morphological and functional (MP, mechanical potential) divergence among species controlling for species relatedness. We examine the relationship among trait morphology and function and organismal diet and environmental characteristics to identify factors that are important for species divergence in morphology and function. Partial Mantel’s statistic ( $r$ ) below the diagonal,  $P$ -values above diagonal. Significant correlations are highlighted in bold.

	Mahalanobis distance	Difference in MP	Diet type	Habitat type
Mahalanobis distance	.	<b>0.001</b>	0.3	0.59
Difference in MP	<b>0.72</b>	.	<b>0.006</b>	0.86
Diet type	0.12	<b>0.36</b>	.	0.9
Habitat type	-0.04	-0.12	-0.14	.





**Figure 7.** Comparison of observed and potential trait means and variances for each trait (in rows) and diet type (in columns). Distributions show the frequency of means and variances generated by simulation. Observed means or variances and significance are given on each distribution.

(Vermeij 1973). Thus, characterizing the relationship between morphological and functional variation can not only distinguish among alternative explanations for the evolution of morphological diversity (e.g., historical contingency vs. versatility), but also provide insight into the limitations on diversity of a morphological structure (Vermeij 1973; Wagner 2001; Wainwright et al 2004; Alfaro et al. 2005; Westneat et al. 2005; Young and Badyaev 2006).

We tested the a priori prediction that the combination of functional equivalence of form, shared functional requirements, and ecological diversity among shrew species should result in different evolutionary responses among taxa to similar selective pressures, ultimately producing functional but not morphological similarity among species that share a diet type. Our results supported this prediction—species with distinct diets differed in mandible function (Fig. 5), but were similar in mandible morphology (Fig. 3). Similarly, we found that within diet type, multiple individual morphologies generated identical mechanical potentials supporting the hypothesis that functional equivalence of multiple morphologies might be common in complex structures (Alfaro et al. 2005; Wainwright et al. 2005). As predicted, variation in response to selection facilitated different morphological solutions to selection exerted by a diet type (Table 4) and allowed for the evolution of diet specialization across distantly related species (Tables 2; Fig. 1). Moreover, functional equivalence of morphologies may have facilitated diet specialization among taxa with otherwise dissimilar ecological characteristics, because between-species similarity in diet type differed from between-species similarities in moisture, coverage, or foraging (Table 3). We found that functional equivalence of morphologies resulted from high variability in mandible characters among species that share diet type, because for each diet type variance in at least one morphological character was greater than expected. Interestingly, across diet type this high variability was found in different mandible components. Together, these results indicate that variation in morphological adaptation requires lability in only a subset of trait components (Fig. 7).

When a complex morphological structure consists of multiple components, such complexity can facilitate the evolution of differing morphological responses to shared selection pressures, and the variability in selection response should depend on the number of semi-independently varying parts (Vermeij 1973) and the strength of their integration (Vermeij 1973; Lande and Arnold 1983; Bonner 1988; Raff and Raff 2000). Theory predicts that the correlational structure among components of a complex trait should be consistent with functional relationships among components (Cheverud 1982, 1988, 1996; Wagner 1996), and thus the generation of variation during development and over evolutionary time in complex morphologies should reflect functional relationships among components. Here, we found that mandible traits of shrews differed in their response to changing functional requirements such that some characters were more variable across diet

types (e.g., force angle, Fig. 4) than others. Variation in lability among mandible characters across diet types may reflect difference among components in their contribution to overall mandible function (Atchley and Hall 1991). These distinct roles may favor the evolution of weak developmental and genetic integration among these structures through exploitation of variation across mandible components generated as a result of variation in functional roles during trait development. For example, during development of skeletal traits, epigenetic interactions between muscle and bone strongly influence morphological structure (e.g., see Herring 1993; Huiskes 2000), and regions of the same skeletal structure often experience distinct extrinsic pressures from differences in growth of surrounding tissues (e.g., vascular development or brain growth), or attachment and loading of connective tissues (i.e., tendons and ligaments; Henderson and Carter 2002). Furthermore, temporal and spatial distribution of mechanical stresses (e.g., muscle loading) may enable independence in development among components of the mandible through differential growth (Henderson and Carter 2002; Badyaev et al. 2005; Zelditch 2005) and decoupling of ossification timing among units (Smith 2002). This variation in stresses can result in differences in gene expression regulating rates of cell division and differentiation among components of a skeletal trait, and strongly influence correlation structure among regions of the mandible (reviewed in Henderson and Carter 2002; Zelditch 2005; Young and Badyaev 2007). Here, we found that later ossifying tissues (e.g., the coronoid and condyloid processes) were the most variable across diet types (Fig. 4, force angle and coronoid–condyle length; Atchley 1993; Ramaesh and Bard 2003), suggesting that timing of ossification may be important in determining correlation structure among mandible components. Furthermore, variation in trait response to changes in functional requirements may reflect differences in sensitivity of trait development to epigenetic signals. We found that force angle and coronoid–condyle length, traits associated with the muscle attachment region of the mandible, were the most variable both within and among diet categories (Fig. 7). These results corroborate previous findings of the importance of epigenetic signals and suggest that interactions between muscle and bone are crucial in determining developmental relationships among components of the shrew mandible (Badyaev et al. 2005; Young and Badyaev 2006, 2007).

Given our finding of variation in morphological response to selection for diet type, we expected to find high variability in mandible components across species that share diet type. In fact, we found few constraints on diversity of morphological solutions to diet specialization across taxa—observed variation was indistinguishable from or higher than potential variation simulated with the null model of diversity (e.g., force angle, Fig. 7). Interestingly, however, means of some traits differed from those predicted under the simulation model (e.g., mean force angle, Fig. 7) suggesting

bias in the production of variation in this system. Consistent with the idea that diversity in form among taxa specializing on the same diet can result from versatility of a trait to adapt to different combinations of environmental characteristics across taxa, such biased production of some morphologies is expected when some traits are used in multiple functions and are favored by selection for other jaw functions (e.g., grooming or social interactions). Overall, our findings of high realized levels of morphological diversity among taxa experiencing similar selection suggest high lability in morphological response to selection in this system.

Variation in adaptive response to changing functional requirements can generate morphological diversity among taxa by allowing functional similarity of multiple morphologies and, correspondingly, unique evolutionary solutions to similar selective pressures. The findings that mandible characters exhibiting the greatest variability are also the most sensitive to external effects (e.g., epigenetic interaction between muscle and bone, Atchley 1993; Ramaesh and Bard 2003), suggest that differences among traits in response to changing functional requirements may result from variation in timing and environmental sensitivity of trait development.

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