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SELECTION FOR MECHANICAL ADVANTAGE UNDERLIES MULTIPLE CRANIAL OPTIMA IN NEW WORLD LEAF-NOSED BATS

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Selection for divergent performance optima has been proposed as a central mechanism underlying adaptive radiation. Uncovering multiple optima requires identifying forms associated with different adaptive zones and linking those forms to performance. However, testing and modeling the performance of complex morphologies like the cranium is challenging. We introduce a three-dimensional finite-element (FE) model of the cranium that can be morphed into different shapes by varying simple parameters to investigate the relationship between two engineering-based measures of performance, mechanical advantage and von Mises stress, and four divergent adaptive zones occupied by New World Leaf-nosed bats. To investigate these relationships, we tested the fit of Brownian motion and Ornstein–Uhlenbeck models of evolution in mechanical advantage and von Mises stress using dated multilocus phylogenies. The analyses revealed three performance optima for mechanical advantage among species from three adaptive zones: bats that eat nectar; generalized insectivores, omnivores and some frugivores; and bats that specialize on hard canopy fruits. Only two optima, one corresponding to nectar feeding, were consistently uncovered for von Mises stress. These results suggest that mechanical advantage played a larger role than von Mises stress in the radiation of New World Leaf-nosed bats into divergent adaptive zones.

KEY WORDS: Feeding biomechanics, finite-element analysis, theoretical shape.

Studies of morphological adaptation aim to link form (morphology) to biomechanical function, and biomechanical function to performance, or the ability to carry out ecological tasks that influence fitness (Arnold 1983). Selection for performance is thought to drive the evolution of underlying form. Implicit in many studies is the assumption of the existence of performance optima, or values of peak performance toward which lineages evolve. Many morphological systems contain multiple performance optima, each of which offers the opportunity to evolve into a different adaptive zone (Simpson 1944, 1953). For example, limb length in lizards can serve to enhance sprint speed (long limbs) or confer greater stability on small and compliant substrates (short limbs) (e.g., Losos and Sinervo 1989; Losos and Irschick 1996; Macrini and Irschick 1998; Vanhooydonck et al. 2006). Similarly, alternative morphologies of the limbs in arthropods enhance either strength under compression (crabs), or resistance to bending (crickets; Taylor and Dirks 2012). Field-based studies of fishes, wildflowers, and insects illustrate the role of selection for divergent performance optima in driving speciation and adaptive

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radiation (e.g., Nosil et al. 2003; Langerhans 2009; Martin and Wainwright 2013; Streisfeld et al. 2013).

Linking form and performance can be as straightforward as measuring limb length and sprint speed, but evaluating the performance of a complex structure like the cranium is more challenging. The cranium performs many functions, but its role in feeding has drawn the most attention. In live animals, there are two ways to assess how the cranium performs during feeding. One is to attach strain gages to bone and measure how much it deforms (bone strain) when an animal bites and chews, the other is to measure bite force. Strain gages are difficult to use in very small animals, and even in large animals it is impossible to place strain gages on all parts of the cranium that are of interest. In addition, both bone strain and bite force are difficult to collect from the large number of species that are needed for comparative analyses of ecologically diverse clades.

As an alternative to assessing performance by measuring bone strain and bite force, comparative biologists have recently turned to finite-element (FE) modeling to evaluate the performance of the cranium during feeding (e.g., Tanner et al. 2008; Pierce et al. 2009; Strait et al. 2010; Attard et al. 2011; Dumont et al. 2011; Cox et al. 2012). FE modeling is a computational method of predicting how structures deform, and ultimately fail, when forces are applied to them. FE modeling is a mature engineering technology, reliable to the point that man-made structures and products designed using FE models perform as expected, reducing and sometimes even eliminating the need to build and test physical prototypes.

Biologists who use FE modeling to evaluate performance typically use two performance variables, von Mises stress and mechanical advantage. von Mises stress is a predictor of structural strength of systems that fail in a ductile manner, such as cortical bone (Keyak and Rossi 2000; Nalla et al. 2003; Nallaa et al. 2005). Comparative FE modeling studies assume that high structural strength (low von Mises stress) is optimal and argue, explicitly or implicitly, that it has been the object of natural selection (e.g., Tanner et al. 2008; Wroe 2008; Strait et al. 2010). For crania, mechanical advantage is a measure of the efficiency with which force is transferred from the masticatory muscles through the cranium and to whatever an animal is biting. Mechanical advantage is strongly correlated with bite force, and high bite force is often viewed as biologically optimal, as it allows animals to eat a wider range of foods (Anderson et al. 2008).

To date, only two comparative studies have used FE modeling to investigate the evolution of engineering-based performance optima. Stayton (2011) morphed a landmark-based model of a turtle shell into a wide range of real and hypothetical shapes, and used FE modeling to simulate dorsoventral crushing on each one. He used these data to construct a morphospace overlain with performance data—hereafter a morpho-performance space—that allowed him to visualize the location of existing species relative to regions of high and low von Mises stress. Stayton found that aquatic turtles were far from the stress optimum (low von Mises stress), but clustered near a separate optimum for hydrodynamic efficiency. A more recent study of carnivores used similar methods to generate a morpho-performance space and found that hypercarnivorous canids and hyaenids have converged on common local optima of high structural strength (low von Mises stress; Tseng 2013). These studies offered fresh approaches to exploring the interface between morphological diversity and engineering-based measures of performance, but each fell short of testing whether selection favored multiple performance optima.

In this study, we test the hypothesis that selection for multiple engineering-based performance optima is associated with the multiple adaptive zones occupied by New World Leaf-nosed bats (family Phyllostomidae). We accomplish this by using a morphable FE model to construct morpho-performance spaces for von Mises stress and mechanical advantage, and by using comparative methods to test for evidence of selection for performance optima among species representing four different adaptive zones (Fig. 1). We study phyllostomids for three reasons: (1) phyllostomids exhibit the greatest range of variation in the shape of the cranium within any single clade of mammals; (2) the form and function of their feeding apparatus is well-studied and corresponds to divergent adaptive zones (e.g., Santana et al. 2010; Dumont et al. 2012); and (3) we have collected data to generate well-sampled, dated phylogenies for the group with which to address evolutionary hypotheses.

We use a large series of new, dated phylogenies and Ornstein–Uhlenbeck (OU) models of trait evolution to evaluate the evolution of engineering-based optima within four different adaptive zones. Species within each zone have similar diets and their crania exhibit different combinations of palate length and width. The first adaptive zone contains nectar feeders, which have long rostra that support elongated tongues that can extract nectar from deep within the corollas of flowers (Freeman 1995; Muchhala and Thomson 2009; Gonzalez-Terrazas et al. 2012). In light of their long rostra and liquid diet, we predict that nectarivores occupy a local performance optimum of low mechanical advantage and high von Mises stress. The second adaptive zone contains the more generalized insectivores, omnivores, and carnivores (hereafter "generalists"). These species have shorter rostra than nectar feeders and are characterized by a limited range of biting behaviors during feeding and bite forces that, in general, scale with head size (see Santana and Dumont 2009; Dumont et al. 2012). We predict that these generalists occupy a local optimum of lower stress and higher mechanical advantage than nectar feeders. The third adaptive zone contains most of the species from the subfamily Stenodermatinae. All are frugivores (hereafter "frugivores") and have wider palates than the generalists. The origin of this

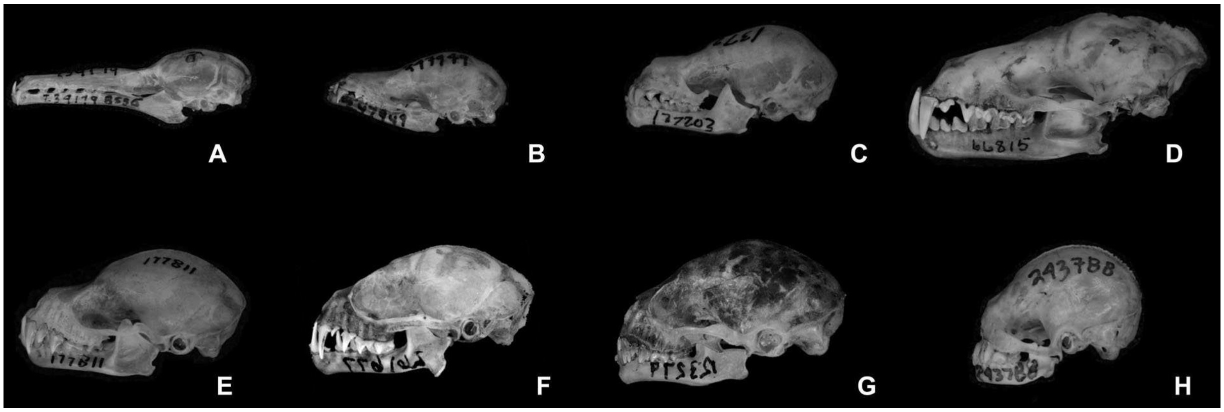

Figure 1. Morphological diversity among adaptive zones in phyllostomids. Nectarivores: (A) *Platalina genovensium*, (B) *Glossophaga soricina*; generalists: (C) *Carollia perspicillata*, (D) *Vampyrum spectrum*; fig-eating frugivores: (E) *Artibeus jamaicensis*, (F) *Chiroderma villosum*; and Short-faced bats: (G) *Phyllops falcatus*, (H) *Centurio senex*. Crania are not shown to scale.

subfamily was associated with a significant increase in species diversification rate and a novel cranial morphology that reflects increased biting performance (Dumont et al. 2012). We predict that frugivores occupy a local optimum of lower von Mises stress and a local optimum of mechanical advantage that is higher than that of generalist species. The fourth adaptive zone is occupied by a monophyletic subtribe of frugivores that have very short and wide palates (hereafter "Short-faced bats," Dávalos 2007). Short-faced bats eat hard fruits that are found high in the canopy and have high bite forces relative to their body size (Dumont et al. 2009b). We predict that their crania occupy local performance optima of very low von Mises stress and very high mechanical advantage.

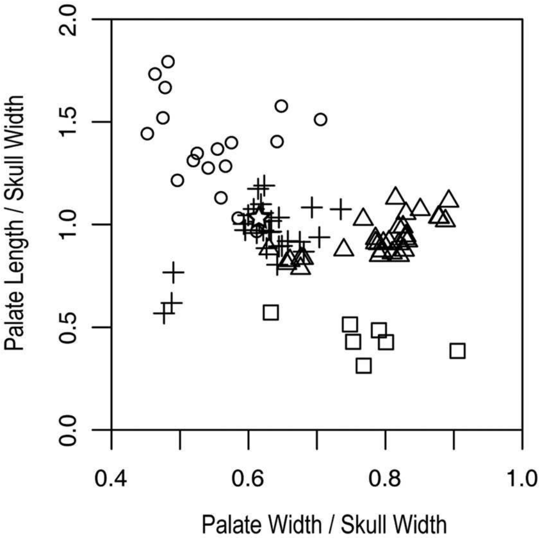

Figure 2. The distribution of phyllostomid species based on a morphospace defined by palate length and palate width normalized by cranium width. Squares, Short-faced bats; circles, nectarivores; triangles, frugivores; crosses, generalists. The location of *Carollia perspicillata* in the morphospace is indicated by a star.

Methods

DEFINING AND MODELING MORPHO-PERFORMANCE

To construct a morpho-performance space with which to study the evolution of cranial form in phyllostimid bats, we first needed to understand their primary axes of variation. Previous analyses of the evolution of cranial shape in this family identified two principal components that together describe 73% of variation among adult crania (Dumont et al. 2012). Variables associated with cranial length loaded strongly on PC1, whereas variables related to cranial width were strongly loaded on PC2. These results are echoed in a recent study of palate growth in phyllsotomids, in which allometric changes in palate length and width are suggested to have been a path of least resistance in the evolution of interspecific variation in cranial form (Sears 2013). Because our study focuses specifically on feeding, we chose to define a bivariate morphospace using palate length and width. There is substantial variation in body size among phyllostomids, (*Ectophylla alba* = 5–6 g [Timm 1982], *Vampyrum spectrum* = 134–172 g [Simmons et al. 1998]). Because von Mises stress is affected by size as well as shape (Dumont et al. 2009a), we normalized palate length and width for each of 85 species of phyllostomids by dividing them by the maximum width of the cranium posterior to the external auditory meatus (Fig. 2). The species we sampled include members of all subfamilies and encompassed the range of palate lengths and widths within the family.

To develop a morpho-performance space, we needed to document how von Mises stress and mechanical advantage vary across the morphospace of relative palate length and width. We began by creating a model of a phyllostomid cranium using computer-aided design (CAD) software (SolidWorks, Dassault Systems Solid Works Corporation, Waltham, MA; Supporting Information Methods; Tables S1, S2; Figs. S1, S2). The model was based on *Carollia perspicillata* because it is near the center of the morphospace (Fig. 2). The shape of the model was controlled by palate length and width, and so by changing the values of palate length and width we were able to create models from any point within the morphospace. We created 42 models from within the morphospace, performed FE analysis on each one, and we interpolated values of mechanical advantage and von Mises stress to create our morpho-performance spaces.

Before the FE models were analyzed, we assigned material properties and applied forces to them, and constrained them from rigid body motion (i.e., fixed them in space so that the applied forces deformed them, and we could calculate von Mises stress from those deformations). We assigned isotropic material properties to the FE models (Young's modulus = 25.12 GPa and Poisson's ratio = 0.3) that have been applied successfully to cortical bone in bats (Dumont et al. 2005). The FE models were loaded by applying forces over the origin of the temporalis muscle, which, on average, accounts for more than 70% of muscle force provided by the jaw adductors in phyllostomid bats ($N = 28$ species, data from Herrel et al. 2008; Santana et al. 2010). The applied force per surface area was conserved in all models according to the scaling axiom of Dumont et al. (2009a), which preserves states of stress and strain in the absence of shape differences. The temporomandibular joints and molar tooth (or teeth) were constrained (as in Dumont et al. 2011) to model two loading regimes: biting with the first molar on one side of the mouth (unilateral biting) and biting with the first molars on both sides (bilateral biting). Both theoretical and modeling studies predict that bilateral biting bends the rostrum, whereas unilateral biting twists and bends it.

We extracted von Mises stress values from the rostrum because the models varied primarily in palate length and width; the brain case did not vary in size or shape. In FE modeling, stress is artificially high near idealized constraints and loads, such as single point constraints or single points where loads are applied. Therefore, we recorded the highest von Mises stress at 98% of each model's volume, and disregarded the 2% of volume that was most highly stressed and occurred at the idealized constraints. Mechanical advantage was simply defined as the reaction force at the bite point divided by the applied muscle load. All models were solved in ANSYS WorkBench 13.0 (ANSYS Inc., Canonsburg, PA).

DOCUMENTING THE RELATIONSHIP BETWEEN ECOLOGICAL AND ENGINEERING-BASED PERFORMANCE

To evaluate the evolution of engineering performance and its relationship to ecological performance, we tested the relationship between mechanical advantage calculated from the FE models to bite force measured in live bats of the same species. We used bite force data for 35 species that included representatives from each of the four adaptive zones (nectar feeders [$n = 1$], generalists [$n = 16$], frugivores [$n = 15$], and Short-faced bats [$n = 1$]; Dumont et al. 2012). Previous analyses have shown that bite force in phyllostomids is a function of body size (Dumont et al. 2012). Head height is commonly used as a proxy for body size in studies of bite force (reviewed in Anderson et al. 2008), and so we included head height as a predictor in models of bite force as a function of mechanical advantage (Freckleton 2002). To evaluate the relationship between bite force and mechanical advantage, we used phylogenetic generalized least-square regressions (Grafen 1989), and two alternative models of the correlation structure of the residuals, Brownian motion (BM) and the lambda transformation on internal branch lengths (Pagel 1999). Two models were fitted for each type of correlation structure, a null mode including only head height as a predictor, and a model including both head height and mechanical advantage. All models were fitted across a random sample of 500 dated Bayesian phylogenies using the *pgls* function within the R package caper version 0.5 (Orme et al. 2011; see Phylogeny reconstruction, below).

PHYLOGENY RECONSTRUCTION

Dated phylogenies were inferred using new and recently published sequence data from seven nuclear loci (official gene symbols: *thy*, *stat5a*, *plcb4*, *bdnf*, *ttn6*, *rag2*, and *atp7a* (Dávalos et al. in press), and published *rag2* and mitochondrial sequences (Baker et al. 2003; Clare et al. 2007; Clare et al. 2011) (Supporting Information Methods, Table S3). Taxonomic sampling covered all the subfamilies of the family Phyllostomidae, and one species from the outgroup family Mormoopidae (*Mormoops blainvelli*). Protein-coding regions were aligned using transAlign (Bininda-Emonds 2005) and the *einsi* routines in MAFFT for noncoding regions (Katoh et al. 2005). Published alignments for the mitochondrial ribosomal RNAs were also used (Dávalos et al. 2012). The concatenated multilocus alignment consisted of 8209 bp after trimming ends to reduce missing data. Partitioning for downstream analyses was carried out using PartitionFinder (Lanfear et al. 2012) (Table S4). Maximum likelihood (ML) was used to infer an initial tree, with 100 rapid bootstrap replicates on optimized partitioned schemes using RAxML (Stamatakis 2006; Stamatakis et al. 2008). This ML phylogeny was then time calibrated using the "r8s" algorithm (Sanderson 2003). Three non-nested nodes were calibrated by constraining them to ages within the range of the minimum and maximum ages for the stratigraphic layers in which Miocene and Pleistocene fossils of phyllostomids were found (Dávalos et al. in press). This time-calibrated and node-constrained phylogeny was then used as a starting point for three independent Metropolis-coupled Markov chain Monte Carlo Bayesian searches in Beast (Drummond et al. 2012). The monophyly of phyllostomids was enforced to add an additional Oligocene calibration point for outgroup divergence, and to facilitate convergence. The alignment and summaries of resulting phylogenies were deposited in TreeBASE under ID 14654. A random sample of 500 dated posterior trees resulting from analyses in Beast was used in subsequent comparative analyses. A summary phylogram of all posterior trees is presented in Figure 3.

EVALUATING SELECTION FOR PERFORMANCE OPTIMA

We compared five OU models of trait evolution to test for potential adaptive optima in each of the three performance variables: mechanical advantage; von Mises stress in the snout during unilateral molar biting; and von Mises stress in the snout during bilateral molar loading. OU models break down evolutionary change in continuous traits into a deterministic component that describes the strength of selection, and a stochastic component that represents other nonmodeled forces (Blomberg et al. 2003; Butler and King 2004). An OU model with one phenotypic optimum has three parameters: the strength of selection or α, an optimum given by θ, and a measure of the intensity of random walk fluctuations, or σ (Hansen 1997; Butler and King 2004). This last parameter is shared with a BM model, which serves as the null model for hypothesis testing.

We evaluated the fit of OU models that reflect our predictions about performance optima among species representing the four adaptive zones. These include optima for nectarivores θ_N, generalists θ_G, frugivores θ_F, and Short-faced bats θ_{SF}. The simplest OU model evaluated a single optimum for all phyllostomids independent of diet (OU1: $\theta_{SF} = \theta_F = \theta_N = \theta_G$), and the most complex included four peaks corresponding to each dietary specialization (OU4: $\theta_{SF} \neq \theta_F \neq \theta_N \neq \theta_G$). Three additional models collapsed two or more diet categories into potential optima. The most complex of these proposed three optima corresponding to nectarivores, the frugivorous lineages, and other species (OU3: $\theta_{SF} = \theta_F \neq \theta_N \neq \theta_G$). The last two models each included two optima; one that separated nectarivores from all other phyllostomids (OU2a: $\theta_{SF} = \theta_F = \theta_G \neq \theta_N$), and another that separated frugivores from all other phyllostomids (OU2b: $\theta_{SF} = \theta_F \neq \theta_N = \theta_G$).

We used the sample of 500 trees drawn from the Bayesian posterior analyses for comparing the fit of alternative comparative models while accounting for variation in topology and branch lengths. To prepare for the OU analyses, we estimated the ancestral states for diet for each of the groupings used for the OU models using the *ace* function in the Ape version 3.0–7 R package (Paradis et al. 2004). We used equal-rate models as they consistently performed better in reconstructing ancestral diets than did either symmetrical or unequal rate models (Table S5). We then fitted each of the trait evolution models using the *hansen* (OU) and *brown* (BM) functions in the Ouch version 2.8–2 R package (Butler and King 2004), and calculated the modified Akaike information criterion (AICc) to evaluate the ML fit of each model to each tree (Burnham and Anderson 2002). We then calculated the harmonic mean of model parameters and measures of fit across the entire sample of 5 posterior trees. This provided a summary of trait evolution results that accounted for variation in topology and branch lengths. Finally, we used the AICc values to calculate Akaike weights, which indicate the relative support of each model relative to the others. Akaike weights range from 0 (no support) to 1 (highest support).

Results

THE MORPHO-PERFORMANCE SPACE

Values of the performance variables, von Mises stress and mechanical advantage, vary across the morphospace (Fig. 4). The distribution of mechanical advantage was mediated solely by palate length and did not vary between the unilateral biting and bilateral biting loading regimes (Fig. 4B). Variation in values of von Mises stress had a more complex pattern (Fig. 4C, D). For both unilateral and bilateral molar biting, von Mises stress was lowest near the center of the morphospace and increased rapidly as relative palate length and width increased. In both cases, the highest values of von Mises stress were predicted for the longest and narrowest palates. Unlike the results for mechanical advantage, slight differences in von Mises stress were predicted for unilateral and bilateral biting. Relative to bilateral biting, von Mises stress was lower for models with long, narrow palates but slightly higher for models with the shortest, widest palates.

Phyllostomid species are widely distributed across the morpho-performance space, and so values of mechanical advantage and von Mises stress vary among them (Fig. 4). Nectar feeders have the lowest mechanical advantage, while mechanical advantage is highest among the Short-faced bats. All other species have intermediate values of mechanical advantage. The lowest values of von Mises stress are found among the generalists under both bilateral and unilateral biting. Under bilateral biting, most nectarivores and some frugivores lie in regions of high stress. Von Mises stress is relatively lower in some nectarivores and higher in some Short-faced bats under unilateral biting.

THE LINK BETWEEN ECOLOGICAL AND ENGINEERING-BASED PERFORMANCE

Mechanical advantage was a significant predictor of observed bite force (Table 1). Including the lambda transformation in the regressions significantly improved the fit to the correlation structure of the residuals ($N = 35$, $\chi^2_1 = 4.60$, $P = 0.019$). The lambda-transformed model that included mechanical advantage was significantly better than the lambda model that included only head height as a predictor ($N = 35$, $\chi^2_1 = 3.78$, $P = 0.031$).

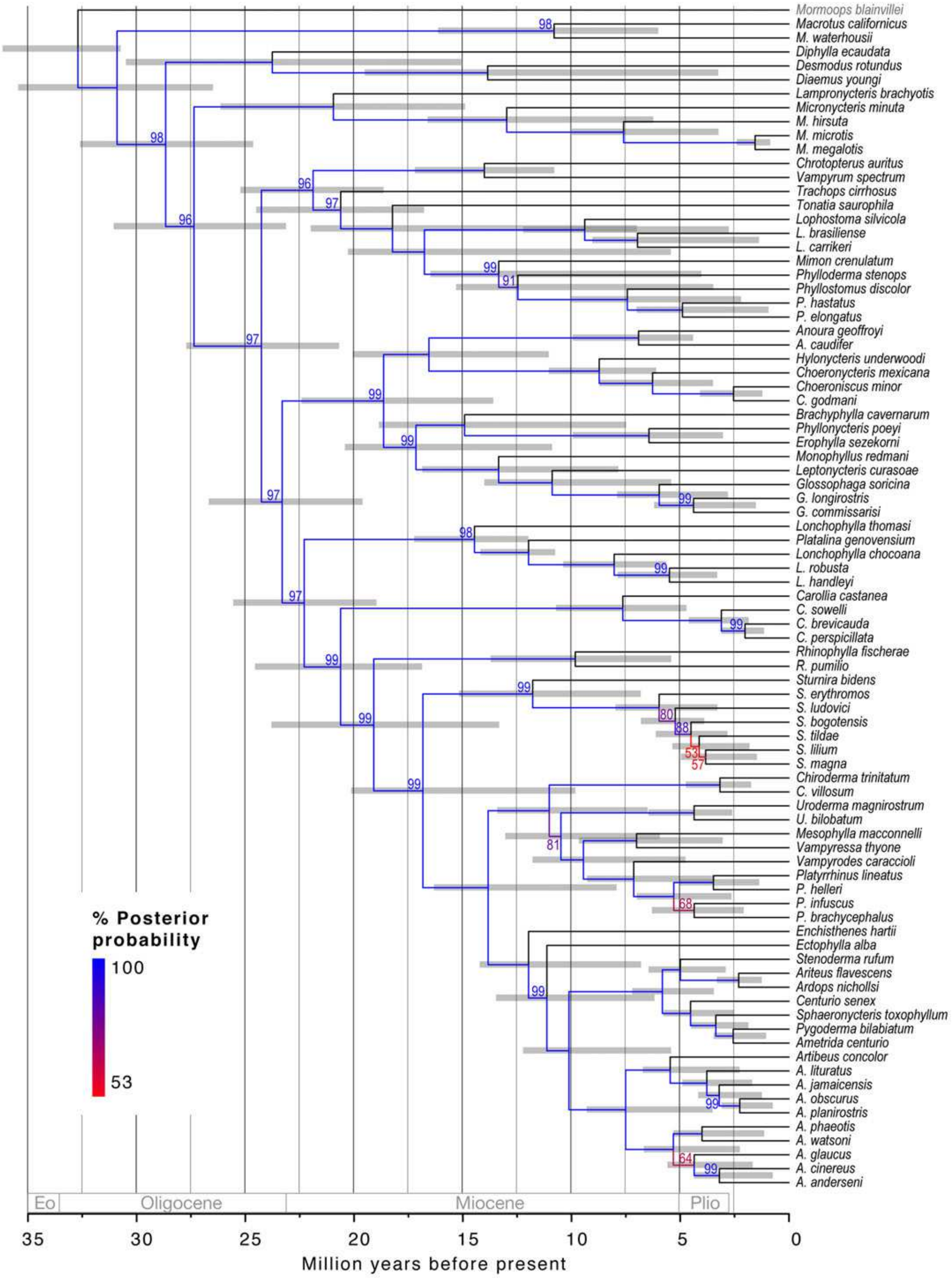

Figure 3. Summary phylogram of posterior trees from three independent runs of Bayesian relaxed molecular clock analyses of DNA sequence data calibrated with fossil-based node constraints. The mean of the posterior log-likelihood of the model given the data was −97,556 (lower 95% high probability density [HPD] = −97,583, higher HPD = −97,531). Branch colors are scaled to percent posterior probability. Posterior probabilities ≤0.99 are indicated below branches. The sole outgroup is shown in gray font. Geological epochs: Eo., Eocene; Plio., Pliocene.

SELECTION FOR ENGINEERING-BASED PERFORMANCE

We found evidence supporting adaptive optima in each of the three performance variables: mechanical advantage; von Mises stress in the snout during unilateral molar biting; and von Mises stress in the snout during bilateral molar loading. Table 2 summarizes the rate of evolution, strength of selection, optima, and log-likelihood of the OU models fitted to the data. The BM model of evolution was rejected for both mechanical advantage and von Mises stress. As predicted, mechanical advantage had multiple optima

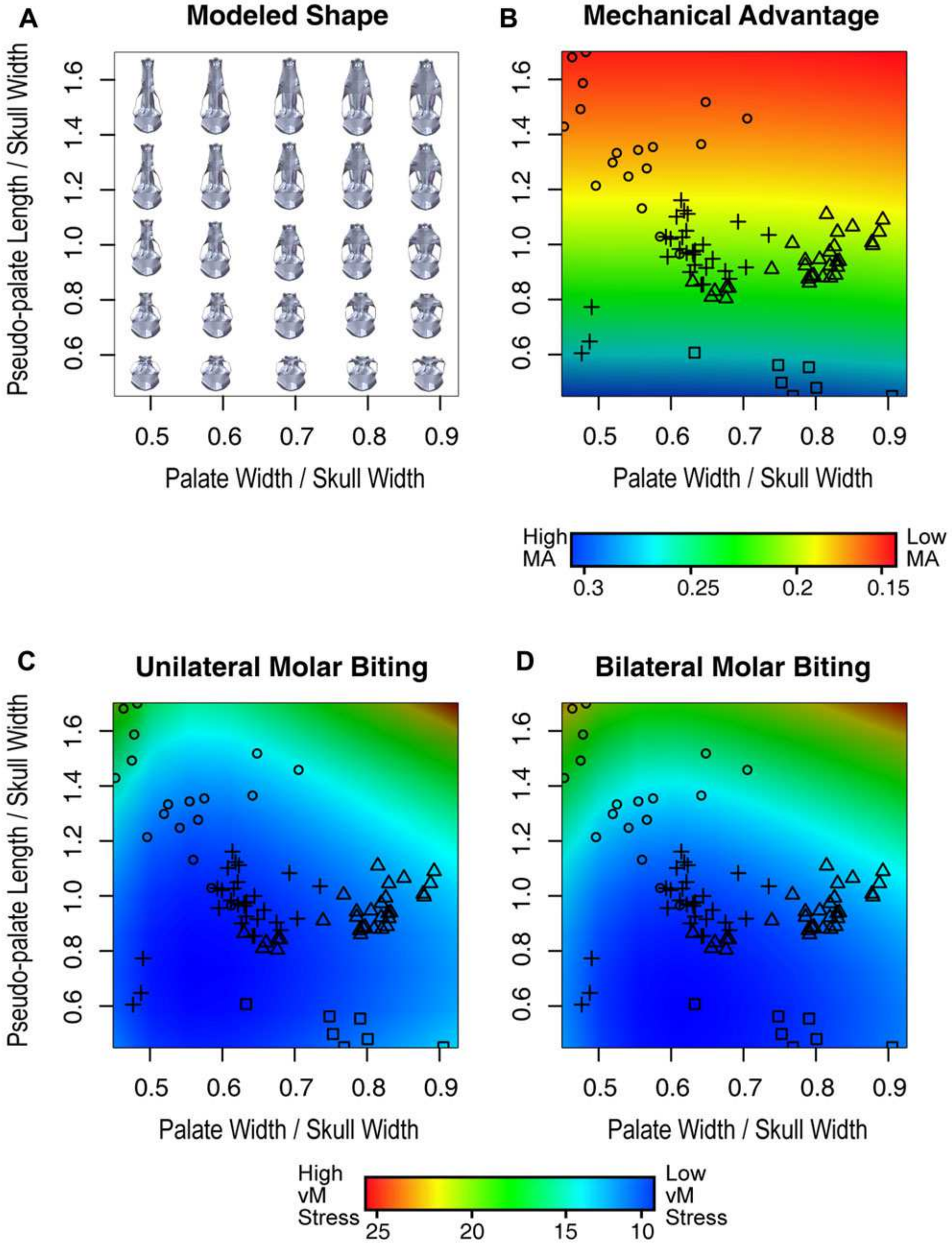

Figure 4. Distribution of species in morpho-performance space. The model was morphed to represent the entire morphospace to calculate performance (A). The locations of species are mapped onto morpho-performance spaces for mechanical advantage (B) and von Mises stress (in MPa) during unilateral and bilateral molar biting (C, D). Squares, Short-faced bats; circles, nectarivores; triangles, frugivores; crosses, generalists.

corresponding to groups occupying different adaptive zones. Short-faced bats had the highest optimum of mechanical advantage, and the lowest was found among nectar-feeding species (Fig. 4B). The optimum for mechanical advantage of the frugivores was not significantly different from that of more generalized species. von Mises stress under unilateral biting had three optima: high stress in nectarivores, intermediate levels of stress in frugivores and Short-faced bats, and low stress in generalists (Fig. 4C). von Mises stress under bilateral molar biting had two distinct optima, with high stress among nectarivorous lineages and low stress among all other phyllostomids (Fig. 4D).

Discussion

This study advances our understanding of adaptation by natural selection by relating multiple adaptive zones to engineering-based performance optima. FE modeling is increasingly popular among comparative biomechanists, and many draw conclusions about

Table 1. Regression models of log-transformed bite force as a function of mechanical advantage (MA) while controlling for head size (i.e., head height).

Model	Intercept	Log HH	Log MA	Lambda	−log-Lik	AICc
BM	0.72 (−0.54, 0.37)	0.74 (0.57, 0.93)	–	–	28.12 (26.97, 29.97)	60.25 (57.94, 62.78)
BM	−1.77 (−2.33, −1.29)	0.76 (0.59, 0.95)	8.05 (7.38, 8.74)	–	27.28 (26.01, 28.63)	61.34 (58.79, 64.03)
Lambda	−0.91 (−1.10, −0.78)	1.09 (1.04, 1.13)	–	0.61 (0.62, 072)	26.44 (25.94, 26.90)	57.26 (56.25, 58.17)
Lambda	−3.78 (−4.02, −3.54)	1.21 (1.18, 1.24)	12.35 (11.59, 13.17)	0.47 (0.40, 0.56)	24.39 (24.06, 24.66)	55.55 (54.89, 56.10)

Two types of models were fitted to the residuals of the regression, Brownian motion (BM) and lambda (Freckleton 2002). Coefficients for the relevant variables and fits are summarized using the harmonic mean followed by 2.5% and 97.5% percentiles (in parentheses) of the distribution of parameters from fitted to 500 posterior trees. Model fit parameters: −log-Lik = negative log-likelihood of the model fit; and AICc = modified Akaike information criterion.

functional adaptations based on values of von Mises stress and mechanical advantage. To our knowledge, this is the first study to test for and to demonstrate selection for these measures of performance. This study also provides new insights into the evolution of the most morphologically diverse family of mammals. A previous study demonstrated that the evolution of the fruit-feeding adaptive zone was associated with a rapid increase in the rate of species diversification and significant slowing of the rate of evolution of cranial morphology (Dumont et al. 2012). This study distinguishes among biomechanical performance variables that are and are not associated with these changes. It also demonstrates selection for mechanical performance optima among nectar feeders, which evolved twice from insectivorous ancestors (Rojas et al. 2011). Finally, the morphable FE model introduced here is a novel and very flexible approach to modeling morphological variation. Here we use it to demonstrate that simply varying relative palate dimensions can successfully approximate the range of variation in the hypervariable crania of phyllostomid bats. The model morphing technique can be extended to other organisms and also used for studies of intraspecific variation.

We found evidence for selection toward multiple evolutionary optima in mechanical advantage within the Phyllostomidae that correspond to three different adaptive zones (Table 2, Fig. 4). As predicted, the Short-faced bats exhibit very high mechanical advantage. In these bats, mechanical advantage is associated with high bite force, which corresponds to their ecological specialization in hard canopy fruits. Also as predicted, the nectarivores occupy an optimum of extremely low mechanical advantage, which is associated with their relatively low bite forces (Dumont et al. 2012). In this case, low bite force is the trade-off for having long, narrow snouts that support long mop-like tongues that sop up the nectar from deep within flowers (Harper et al. 2013). The third optimum of mechanical advantage is shared by a heterogeneous mixture of frugivores and generalists.

We proposed that the evolution of a low, broad cranium at the base of the subfamily Stenodermatinae (including Short-faced bats) conferred higher bite forces and lead to the invasion of a new adaptive zone that includes feeding on hard fruit (Dumont et al. 2012). In bats, mechanical advantage is correlated with relative bite force—a proximate performance variable that determines an animal's ability to process foods of different hardness (Anderson et al. 2008; Santana et al. 2010). In this study, an evolutionary optimum for increased mechanical efficiency was restricted to the highly derived Short-faced bats. Mechanical advantage in most stenodermatines (frugivores) is no different from that of more generalized species (Table 2, Fig. 4B). Nevertheless, all stenodermatines produce the absolutely high bite force needed to feed on hard fruits. This suggests that high bite force may have been achieved, at least initially, by factors other than increased mechanical advantage, including changes in muscle morphology, biting style, and fruit handling behavior (Freeman 1988; Dumont 1999; Santana et al. 2010, 2012). By allowing us to quantify selection for mechanical advantage, the engineering models help illuminate the role of other traits in enabling stenodermatines to enter the adaptive zone associated with eating hard fruits.

There are three optima for von Mises stress in unilateral molar biting and two in bilateral molar biting (Table 2, Fig. 4C, D). In each case, one optimum corresponds to nectar feeders, which cluster around a high-stress optimum that indicates the low structural strength of their long, narrow palates under loads that simulate biting. This does not, however, imply that the palates of nectar feeders routinely experience high stress. A liquid diet does not require a strong bite, and so nectar feeders may be "released" from the need for structural strength during biting. The high stress predicted in the crania of nectar feeders during biting is more likely an epiphenomenon of selection for increased palate length to facilitate access to nectar. Moreover, nectar feeders do not bite and chew as frequently or with as much

Table 2. Null (Brownian motion —BM) and Ornstein–Uhlenbeck (OU) models of functional trait evolution, parameter estimates, and fit.

Trait	Model	σ^2 (My^{-1})	α (My^{-1})	θ_{SF}	θ_F	θ_N	θ_G	−log-Lik	AICc	W
Mechanical										
advantage	BM	6.01 (5.56, 6.54)	–	–	–	–	–	−237 (−239, −235)	−470 (−475, −466)	0.00
	OU1	6.35 (5.83, 6.97)	1.12 (0.90, 1.42)				0.21 (0.21, 0.21)	−235 (−237, −233)	−464 (−468, −460)	0.00
	OU2a	6.28 (5.77, 6.89)	1.23 (0.98, 1.56)		0.41 (0.36, 0.47)		0.21 (0.21, 0.21)	−236 (−238, −234)	−463 (−468, −459)	0.00
	OU2b	6.03 (5.45, 6.74)	2.56 (1.83, 3.79)			0.00 (−0.06, 0.07)	0.22 (0.21, 0.22)	−240 (−242, −238)	−472 (−476, −468)	0.00
	OU3	6.02 (5.44, 6.74)	2.61 (1.88, 3.86)		0.25 (0.24, 0.27)	0.03 (−0.04, 0.08)	0.22 (0.21, 0.22)	−240 (−243, −238)	−470 (−474, −466)	0.00
	OU4	**3.40 (3.09, 3.77)**	**3.43 (2.59, 4.55)**	**0.89 (0.74, 1.08)**	**0.21 (0.20, 0.22)**	**0.05 (0.03, 0.10)**	**0.22 (0.21, 0.22)**	**−266 (−268, −265)**	**−519 (−523, −516)**	**1.00**
Unilateral										
molar biting	BM	9.7 (8.3, 11.6)	–	–	–	–	–	175 (169, 181)	353 (343, 366)	0.02
(vM stress)	OU1	12.4 (9.8, 16.6)	0.66 (0.38, 1.13)				15.4 (15.3, 15.5)	175 (171, 179)	355 (347, 365)	0.01
	OU2a	12.4 (9.8, 16.6)	0.67 (0.38, 1.14)		17.1 (16.4, 18.4)		15.3 (15.2, 15.4)	174 (170, 179)	357 (349, 367)	0.00
	OU2b	14.0 (10.9, 18.6)	1.37 (0.94, 1.94)			20.2 (19.2, 21.6)	14.8 (14.7, 14.9)	169 (166, 174)	347 (340, 356)	0.33
	OU3	**14.9 (11.5, 20.1)**	**1.68 (1.16, 2.39)**		**17.3 (16.8, 17.9)**	**19.9 (19.1, 21.1)**	**14.5 (14.4, 14.5)**	**168 (164, 172)**	**346 (340, 354)**	**0.49**
	OU4	14.9 (11.4, 20.1)	1.68 (1.17, 2.39)	16.6 (16.3, 17.1)	17.3 (16.9, 18.0)	19.9 (19.1, 21.1)	14.5 (14.4, 14.5)	168 (164, 172)	349 (342, 356)	0.16
Bilateral										
molar biting	BM	5.05 (4.37, 6.14)	–	–	–	–	–	−147 (142, 155)	298 (288, 314)	0.01
(vM stress)	OU1	5.81 (4.73, 8.01)	0.32 (0.17, 0.78)				10.9 (10.8, 10.9)	−148 (144, 155)	302 (294, 316)	0.00
	OU2a	5.81 (4.73, 8.02)	0.32 (0.17, 0.79)		8.9 (7.1, 10.2)		10.9 (10.8, 11.0)	−148 (144, 155)	304 (296, 318)	0.00
	OU2b	**6.68 (4.98, 9.78)**	**1.19 (0.70, 1.99)**			**15.8 (14.5, 18.4)**	**10.3 (10.3, 10.3)**	**−140 (136, 146)**	**289 (281, 300)**	**0.57**
	OU3	6.77 (5.02, 10.02)	1.25 (0.74, 2.10)		11.4 (11.0, 11.9)	15.8 (14.5, 18.3)	10.2 (10.2, 10.2)	−140 (136, 145)	290 (283, 301)	0.26
	OU4	6.69 (4.95, 9.98)	1.27 (0.75, 2.14)	8.1 (6.8, 9.0)	11.6 (11.2, 12.2)	15.8 (14.4, 18.2)	10.2 (10.2, 10.2)	−139 (135, 145)	291 (284, 302)	0.16

Transitions among categorical diet states were calculated for each of 500 phylogenies for all but the BM and OU1 models (which have no transitions between categories). Parameters and fits are summarized using the harmonic mean followed by 2.5% and 97.5% percentiles (in parentheses) from the distribution of models fitted to a series of trees. Functional traits: mechanical advantage, von Mises (vM) stress (in MPa) in the snout during unilateral molar biting, and vM stress in the snout during bilateral molar biting. Model parameters: σ^2 = random walk rate of evolution; α = strength of selection; θ_{SF} = optimum Short-faced bats; θ_F = optimum for frugivores; θ_N = optimum for nectarivorous lineages; and θ_G = optimum for dietary generalists. Model fit parameters: −log-Lik = negative log-likelihood of the model fit; AICc = modified Akaike information criterion; and W = Akaike weight. Models of trait evolution: BM = Brownian motion; OU1 = single-optimum OU; OU2a = two-optimum OU, where $\theta_{SF} = \theta_F = \theta_G \neq \theta_N$; OU2b = two-optimum OU, where $\theta_{SF} = \theta_F \neq \theta_G = \theta_N$; OU3 = three-optimum OU, where $\theta_{SF} = \theta_F \neq \theta_G \neq \theta_N$; and OU4 = four-optimum OU, where $\theta_{SF} \neq \theta_F \neq \theta_G \neq \theta_N$. For mechanical advantage (MA), the σ^2 parameter is shown as a factor of 10^{-4} and the α parameter as a factor of 10^{-1}. Best-fit models are in bold.

force as other bats. This adds weight to the suggestion that nectarivores have given up structural strength in exchange for an exceptionally long rostrum.

Nectarivores aside, the best-supported optima of von Mises stress for frugivores are either higher than or intermediate relative to other phyllostomids (Table 2, Fig. 4C, D). If, as we predicted and many other studies assume, low stress is optimal, there should be a signature of selection for low stress (and structurally strong crania) in lineages that exhibit the highest bite forces (frugivores and Short-faced bats). This is not the case and there are at least two alternative interpretations of this result. First, it may be that the relatively high stress exhibited by frugivores and Short-faced bats fall within acceptable biological limits and that selection simply does not "see" stress. This is supported by studies pointing out that the cranium never approaches the critical stress (i.e., the material strength of bone) during normal activities, and therefore routine stress is unlikely to play a role in shaping the evolution of cranial form (Hylander and Johnson 1997; Metzger et al. 2005). Our models predict stress based on static analyses that included forces attributed to the temporalis muscle. We did not evaluate the dynamic impact of head butting that is common in artiodactlys, and may occur in some dinosaurs and whales (Carrier et al. 2002; Farke 2008; Lambert et al. 2011; Snively and Theodor 2011; Peterson et al. 2013). However, there is no evidence to suggest that the heads of bats are subject to impacts from anything other than made-made obstacles (e.g., wind turbines and windows). Second, it may be that statistical power to identify additional optima is lacking. This is improbable because we were able to detect differences between more than two optima for mechanical advantage with the same sample of species.

The presence of multiple optima in von Mises stress depends, in part, on the validity of the assumptions built into our modeling process. Although our model does a good job of replicating the variety of shapes among phyllostomid crania, it also assumes that the force generated by the temporalis muscle scales isometrically with the surface area of the skull and the force generated by other jaw adductors. If these assumptions are not reasonable, then the distribution of von Mises stress across the morphospace may be more or less exaggerated than our results suggest. We investigated the two assumptions using phylogenetic least-squares (pgls) regression and phylogenetic anova on the residuals for 24 species of phyllostomids (nectarivores, $n = 2$; generalists, $n = 15$, frugivores, $n = 5$; Short-faced bats, $n = 2$; data from Santana et al. (2010). To assess the assumption that the ratio of the force produced by the temporalis muscle and the surface area of the cranium does not vary across the four adaptive zones, we regressed the physiological cross-sectional area (pcsa, a proxy for muscle force) of the temporalis muscle against the surface area of the cranium (Fig. S3). Three species fell outside of the 95% confidence intervals of the regression, but each represented a different group. A phylogenetic ANOVA of residuals failed to demonstrated differences among the four groups ($F = 1.445$, $P = 0.51$). To investigate the assumption that the force produced by the temporalis muscle is proportionate to the forces produced by the other jaw adductors, we regressed the pcsa of the masseter muscle, and the combined pcsa of the masseter and medial pterygoid muscles against the pcsa of the temporalis muscle (Figs. S4, S5). In both cases, the Short-faced bats were either below or nearly below the lower bound of the 95% confidence interval. However, the phylogenetic ANOVA on the residuals failed to uncover differences among the four groups (masseter: $F = 4.460$, $P = 0.15$; masseter + medial pterygoid: $F = 3.68$, $P = 0.19$). If anything, these results suggest that the forces applied by the jaw adductors to the Short-faced bats are lower than they should be. Increasing those forces would increase von Mises stress, perhaps adding further support to a distinct optimum of high stress, high mechanical advantage for the group.

There are no phyllostomid species in regions of the morpho-performance space with the highest stresses (Fig. 4C, D). It is tempting to suggest that the absence of species in the high stress region indicates that stress limits the evolution of morphological diversity within the group, but there are at least two alternative explanations for this phenomenon. First, it may be that this region is inaccessible given existing developmental regimes. A recent study of palate growth and development in phyllostomids suggests that allometric growth of palate length and width may represent a path of least resistance in the evolution of facial form (Sears 2013). This is supported by previous studies of adult crania (Dumont et al. 2012) and our engineering models, which demonstrate that changes in palate length and width underlie variation among phyllostomid species. A second factor that could exclude species from the regions of the morphospace with the highest stress is the improbable combination of those forms and ecological function. For example, vampires, with their short and narrow palates, are near the region of lowest stress. It is difficult to envision what other dietary niches are available to species with vampire-like morphology. Narrow palates are good for feeding on nectar but those palates also need to be long to feed on flowers efficiently. Similarly, short palates and concomitant high bite forces are good for eating hard foods, but the large teeth needed to masticate hard fruits cannot fit on an absolutely narrow palate, and Short-faced bats are near that limit. The mechanical, developmental, and ecological processes that define the limits of cranial form in phyllostomids remain to be explored.

We found that species with generalized diets, the ancestral condition (Rojas et al. 2011; Dumont et al. 2012), have intermediate values of mechanical advantage and von Mises stress, whereas species that evolved to specialize on fruit and nectar have more extreme values. There are more optima for mechanical advantage than for von Mises stress, suggesting that it played a stronger role in the movement of phyllstomids into the entire range of adaptive zones. Species with high mechanical advantage have short palates and feed on hard canopy fruits, whereas species with low mechanical advantage feed have elongated palates and feed on nectar. It is noteworthy that variation in relative palate length is closely associated with dietary niche in many vertebrate lineages, including mammals, birds, crocodylians, and fishes (Paradis et al. 2004; Hulsey and De Leon 2005; Foster et al. 2008; Pierce et al. 2008; Samuels 2009; Goswami et al. 2011). The link between mechanical advantage and multiple optima that we found among phyllostomids offers the possibility that mechanical advantage is the object of selection in those clades as well.

The method of building a morphable 3D FE model offers a new and flexible approach to studying the evolution of morphological diversity in any group of organisms. The most common method of mesh morphing requires 2D or 3D landmarks and use geometric morphometrics to morph a model of one shape into models of known target shapes (Pierce et al. 2008; Stayton 2009; O'Higgins et al. 2011, 2012; Parr et al. 2012). This makes it easy to generate intermediate forms. However, geometric morphometric methods require large numbers of landmarks. Our morphable model was able to replicate values of mechanical advantage and von Mises stress for species with very different cranial morphologies by changing only two parameters, palate length and width (Supporting Information Methods; Tables S1, S2; Figs. S1, S2). The surprising fidelity of our engineering-based models to analyses of crania built from CT scans points to the fundamental importance of these two variables in the evolution of diversity among phyllostomids. Because our models are parameterized by only two continuous variables, it is also easy to visualize ancestral forms based on evolutionary analyses that can incorporate distributions of posterior trees and alternative models of evolution.

Conclusions

This study suggests a role for selection on engineering-based values of performance in the evolution of the cranium in a hyperdiverse family of mammals. We found multiple optima for mechanical advantage that accord well with adaptive zones characterized by differences in diet, the hardness of foods that are eaten, and feeding behaviors. In contrast, there are only two or three optima for von Mises stress. Both of these analyses reflect the structural weakness that stems from the elongated rostrum of nectarivorous species. The three-optimum model separates frugivores from other bats but, contrary to our predictions, predict an intermediate stress optimum. Mechanical advantage appears to have had a stronger influence on the movement of phyllostomid bats into a broad array of dietary niches.

Within the broader context of comparative studies based on FE analyses, the association between relatively high stress and relatively high bite force calls into question the common assumption that structures that exhibit low stress are adapted for high loading. Whether this is true of vertebrates other than bats will require large samples of models from other well-documented radiations and careful comparative analyses. The method we propose for building morphable, 3D FE models can make a significant contribution to this challenge by generating large number of morphologically diverse models with relative ease. Beyond uncovering robust signal for multiple evolutionary optima, the integration of morphable models with large samples of phylogenies, in turn, opens the door for future studies predicting ancestral morphologies and comparing their performance to that of extant or fossil forms.

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DATA ARCHIVING

Data will be archived in GenBank, Treebase, and Dryad (doi:10.5061/dryad.f77k3).

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Supporting Information

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

Supplementary Methods

Figure S1. The distribution of phyllostomid species based on a morphospace defined by (A) palate length and palate width normalized by cranium width, and (B) pseudo-palate length and palate width normalized by cranium width.

Figure S2. Visual comparison of the shapes of the STL (light blue) and engineering (dark blue) models for the base model *Carollia perspcillata* (A) and the morphed models for *Glossophaga soricina* (B), and *Centurio senex* (C).

Figure S3. Relationship between the physiological cross-sectional area (pcsa) of the temporalis muscle against the surface area of the skull (mm^2).

Figure S4. Relationship between the pcsa of the masseter muscle against the pcsa of temporalis.

Figure S5. Relationship between the combined pcsa of the masseter and medial pterygoid muscles against the pcsa of temporalis.

Table S1. Bone thicknesses of the surface models and the volumes and surface areas of the surface and solid models of *Centurio senex*, *Carollia perspicillata*, and *Glossophaga soricina*.

Table S2. Mechanical advantage and von Mises stress under bilateral and unilateral molar biting conditions in the surface and solid models of *Centurio senex*, *Carollia perspicillata,* and *Glossophaga soricina*.

Table S3. Species and GenBank accession numbers for each locus analyzed.

Table S4. Best partitioning scheme and optimal models of sequence evolution as determined using the Bayesian information criterion (BIC).

Table S5. Akaike information criterion (AIC) for models of evolution of diet with different categorizations corresponding to two, three, or four diet categories (as applied in subsequent Orsntein–Uhlenbeck models), and estimated rates of change for the best-fit model of equal rates.