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DISCORDANCE BETWEEN MORPHOLOGICAL AND MECHANICAL DIVERSITY IN THE FEEDING MECHANISM OF CENTRARCHID FISHES

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Abstract.—Morphological diversity is routinely used to infer ecological variation among species because differences in form underlie variation in functional performance of ecological tasks like capturing prey, avoiding predators, or defending territories. However, many functions have complex morphological bases that can weaken associations between morphological and functional diversification. We investigate the link between these levels of diversity in a mechanically explicit model of fish suction-feeding performance, where the map of head morphology to feeding mechanics is many-to-one: multiple, alternative forms can produce the same mechanical property. We show that many-to-one mapping leads to discordance between morphological and mechanical diversity in the freshwater fish family, the Centrarchidae, despite close associations between morphological changes and their mechanical effects. We find that each of the model's five morphological variables underlies evolution of suction capacity. Yet, the major centrarchid clades exhibit an order of magnitude range in diversity of suction mechanics in the absence of any clear difference in diversity of the morphological variables. This cryptic pattern of mechanical diversity suggests an evolutionary history for suction performance that is unlike the one inferred from comparisons of morphological diversity. Because many-to-one mapping is likely to be common in functional systems, this property of design may lead to widespread discordance between functional and morphological diversity. Although we focus on the interaction between morphology and mechanics, many-to-one mapping can decouple diversity between levels of organization in any hierarchical system.

Key words.—*Lepomis*, many-to-one mapping, *Micropterus*, performance, *Pomoxis*, rate of character evolution, suction feeding.

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Morphology is widely used as a metric of biodiversity to infer the role of ecological mechanisms in the diversification of evolutionary lineages. Species' differences in form are thought to reflect variation in resource use patterns, and morphological diversity has been employed to identify adaptive radiations (Sundberg 1996; Warheit et al. 1999; Losos and Miles 2002; Lovette et al. 2002), infer modes of natural selection (Wagner 1995; Hansen and Martins 1996; Foote 1999; Ricklefs 2005), and investigate competitive interactions among species (Van Valkenburgh 1985, 1988). Given the utility of morphological diversity in evolutionary biology, an important question is what factors weaken the connection between morphological and ecological variety.

Because function is the intermediate link between morphology and its ecological consequences, the map of morphological variation to function in part determines associations between morphology and ecology. If functional variation does not mirror variation in form, then associations between morphology and resource use are unlikely (Losos 1990). Of course, the link between these levels of variation will be tighter for morphological traits that contribute to the function of interest. Nevertheless, several factors can weaken associations between a function and the morphological characters that influence it (Arnold 1983). These factors include aspects of organismal design or the environment that affect function independent of variation in the measured morphological characters, such as behavioral differences (Lauder 1995; Schrank and Webb 1998; Vanhooydonck and Van Damme 2001), uncontrolled variation in unmeasured morphological traits (Arnold 1983; Jayne and Bennett 1989), and effects of the fluid medium (water or air) in which the function is performed (Liem 1978, 1990). In addition, even when the measured morphological characters completely determine function (i.e., function is an emergent property of morphology), complexity in the form-function relationship has the potential to weaken associations between these levels of diversity (Koehl 1996; Hulsey and Wainwright 2002; Alfaro et al. 2004, 2005). In this paper, we investigate the link between diversity in feeding mechanics and the underlying head morphology in suction-feeding fishes. This biomechanical system exhibits many-to-one mapping (sensu Alfaro et al. 2004, 2005; Wainwright et al. 2005) of a suite of morphological characters to its emergent mechanical property, where multiple, alternative head shapes can produce the same suction mechanics. We ask how feeding morphology is modified during evolution to produce changes in suction-feeding capacity and whether diversity in mechanics reflects diversity in the underlying morphology.

Suction feeding is the primary mode of prey capture for the majority of bony fishes, including all 33 species of Centrarchidae (including sunfishes, black basses, and crappies). A coordinated series of movements of cranial elements rapidly expands the buccal (mouth) cavity, inducing a flow of water into the mouth and generating a drop in static pressure inside the buccal cavity. Differences in buccal pressure are associated with differences in the velocity and acceleration of water in front of the mouth (Muller et al. 1982; Van Leeuwen 1984; Higham et al. 2006b) and, thus, the forces exerted on prey. Because success rate of prey capture is in part a function of a fish's ability to use the induced flow to carry prey into its mouth, the maximum magnitude of the buccal pressure drop that a fish can generate (referred to hereafter as ''suction capacity'') is a mechanically meaningful measure of its suction-feeding performance (Van Leeuwen 1984; Nor-

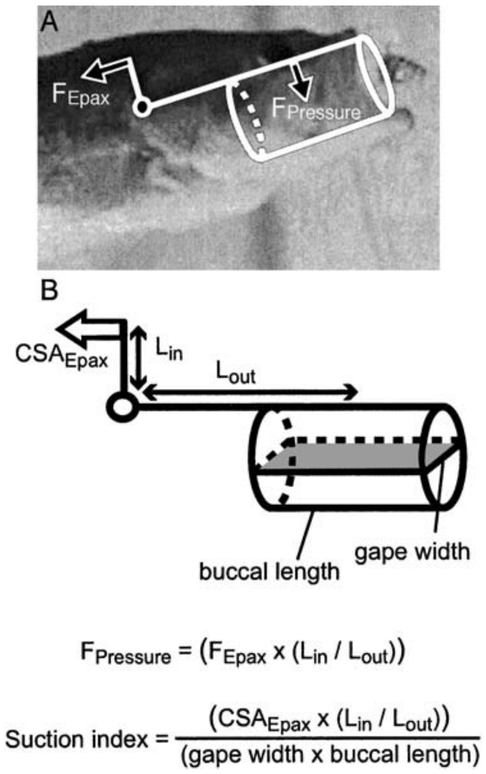

FIG. 1. Schematic diagram of the torque balance involved in neurocranial rotation and buccal expansion (based on Carroll et al. 2004) superimposed on a largemouth bass, *Micropterus salmoides*, striking goldfish prey (A), and the schematic diagram with morphological parameters labeled (B). Expansion of the buccal cavity, shown as a cylinder, results in a drop in buccal pressure, which resolves to a force (F_{Pressure}) that opposes neurocranial rotation and buccal expansion. The maximum F_{Pressure} that a fish can overcome is equal to the product of the force capacity of the epaxial muscles (F_{Epax}), which is proportional to their cross-sectional area (CSA_{Epax}), and their mechanical advantage, which is the ratio of L_{in} to L_{out}. Because the buccal pressure drop is distributed over the projected area of the bucccal cavity, which is equal to the product of gape width and buccal length, the maximum magnitude of buccal pressure drop that a fish can produce (i.e., its suction capacity) is proportional to the suction index.

ton and Brainerd 1993; Nemeth 1997; Van Wassenbergh et al. 2006).

Carroll et al. (2004) derived and empirically validated a biomechanical model that predicts the suction capacity of individual fish based on the transmission of muscular force to buccal cavity expansion, and we briefly review this model here. Dorsal rotation of the neurocranium contributes to buccal expansion and is actuated by contraction of the epaxial muscles that attach to the supraoccipital crest and posterior portion of the neurocranium (Lauder 1980). Force from the epaxial muscles is transmitted through their moment arm (L_{in}) to rotate the neurocranium at the joint between the surpracleithrum and posttemporal bone (S-PT joint; Fig. 1). This torque is opposed by the force due to subambient pressure inside the buccal cavity acting through its moment arm (L_{out}; Fig. 1). Even though additional cranial kinematics, such as hyoid depression and suspensorial abduction, contribute to buccal expansion, the force generated by neurocranial elevation must be able to resist the force due to subambient buccal pressure in order for the buccal cavity to expand. The maximum force that a fish can resist is equal to the product of the epaxial muscles' force capacity (F_{Epax}) and its mechanical advantage, which is the ratio of L_{in} to L_{out}. The force due to the pressure drop is distributed across the projected area of the buccal cavity, which is equal to the product of gape width and buccal length (Fig. 1), and an individual fish's suction capacity can be predicted from the following equation:

$$\text{suction capacity} = \frac{[F_{\mathrm{Epax}}(L_{\mathrm{in}}/L_{\mathrm{out}})]}{(\text{gape width} \times \text{buccal length})}. \qquad (1)$$

Because F_{Epax} is proportional to the cross-sectional area of the epaxial muscles (CSA_{Epax}), we modified this equation to calculate a suction index (which approximates the variable, ''morphological potential'' in Carroll et al. 2004) that is proportional to maximum suction capacity:

$$\text{suction index} = \frac{[CSA_{\mathrm{Epax}}(L_{\mathrm{in}}/L_{\mathrm{out}})]}{(\text{gape width} \times \text{buccal length})}. \qquad (2)$$

Suction index times specific tension of the epaxial muscle is an accurate estimate of a fish's maximum suction pressure capacity (Carroll et al. 2004).

The suction model exhibits many-to-one mapping of morphology to mechanics; multiple combinations of morphological parameter values can produce the same suction index. For example, centrarchid species with relatively low suction indexes span the range of variation in buccal length for the entire radiation; low suction indexes are achieved in species that have relatively long buccal lengths and average values for the remaining morphological parameters as well as in species with relatively short buccal lengths and short L_{in} lengths (Fig. 2). Furthermore, the potential exists for different parameters to drive change in suction index in different lineages. For example, decreases in suction index can result from increases in buccal length or decreases in length of L_{in}. Because many head morphologies can produce the same suction index, this biomechanical system has the potential to exhibit a weak relationship between morphological and mechanical diversification (Alfaro et al. 2004).

We investigated diversity in suction index and its morphological parameters in the lineages of the North American freshwater fish family, the Centrarchidae. A recent, well-resolved phylogenetic hypothesis for the extant centrarchid species identified three major clades (Near et al. 2005) and provided three monophyletic groups for our diversity comparisons: *Lepomis*, the sunfishes (12 of 13 species are represented here), are sister to *Micropterus*, the black basses (seven of eight species), and these two clades are sister to a third clade containing the genera *Pomoxis*, *Enneacanthus*, *Centrarchus*, *Archoplites*, and *Ambloplites* (eight of 11 species; referred to hereafter as ''*Pomoxis* et al.'') (Fig. 3). We used rates of evolution (estimates of the Brownian motion rate parameter, σ^2) as phylogenetically correct estimates of mechanical and morphological diversity (Hutcheon and Garland 2004; Collar et al. 2005; O'Meara et al. 2006) and tested whether the differences between clades in rates of suction index evolution correspond with differences in rates of evo-

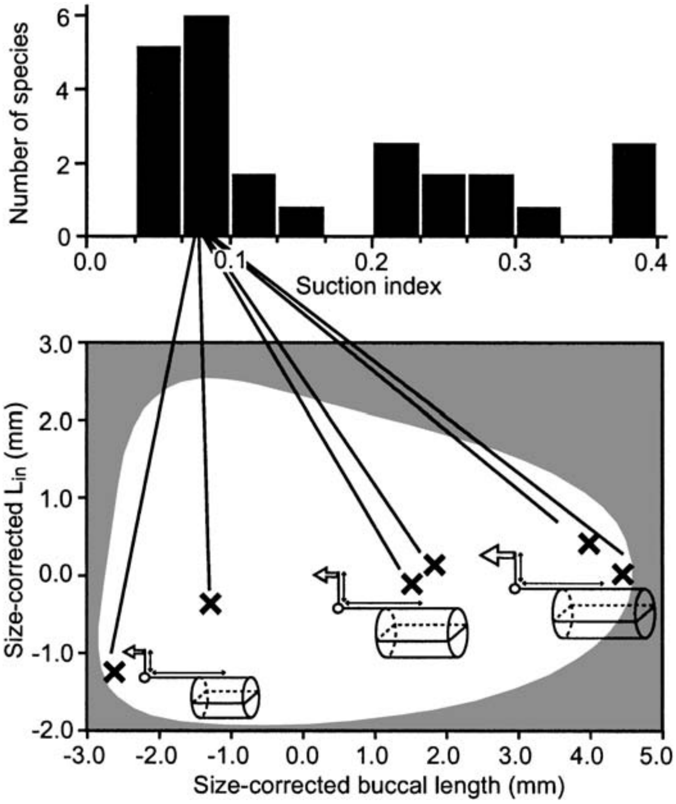

FIG. 2. Redundancy in the relationship between suction index and morphological parameters. The histogram (top) shows the distribution of suction index in 27 centrarchid species measured in this study. Six species that have suction indexes between 0.067 and 0.100, spanning less than 10% of the centrarchid suction index range, are mapped onto a morphospace defined by size-corrected buccal length and L_{in} (bottom). The white area in this plot indicates the range of morphospace occupied by all 27 species. Despite a narrow range of suction indexes, these six species span the range of buccal lengths for all measured centrarchid species. Schematic diagrams of the suction model are superimposed on the morphospace to illustrate the noticeably disparate morphologies of these fishes.

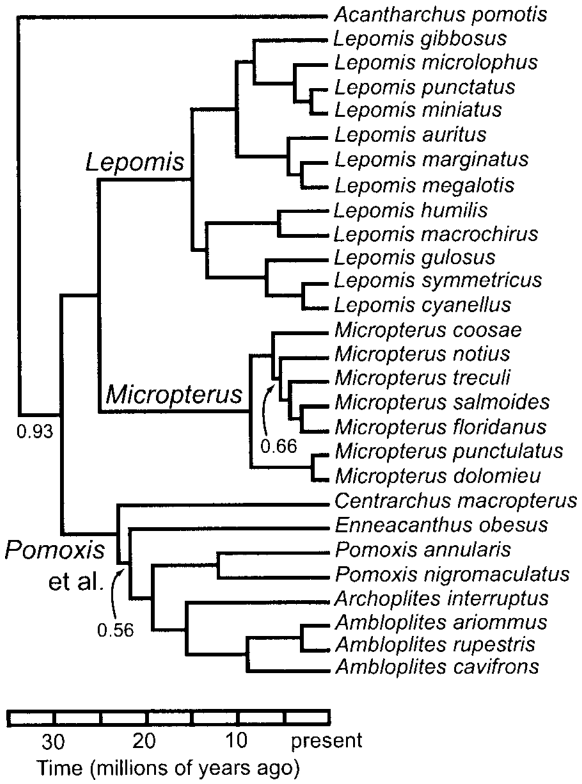

FIG. 3. Chronogram from Near et al. (2005) modified to show relationships between the 27 centrarchid species involved in this analysis. The major centrarchid clades, *Lepomis*, *Micropterus*, and *Pomoxis* et al., are labeled along their stems and serve as the groups between which we compare morphological and mechanical diversity. Branch lengths are given in millions of years. Nodes are supported by greater than 0.95 Bayesian posterior probabilities, unless otherwise noted.

lution of the underlying morphology. In addition, we asked what morphological parameters are responsible for evolution of the suction index and to what extent have different combinations of morphological changes been exploited in different lineages.

MATERIALS AND METHODS

Specimens and Sampling

We estimated species' parameter values as means from three individuals and calculated species' suction indexes from their parameter values using equation (2) (see Appendix 1). Specimens of the following species were collected from Florida, fixed in 10% formalin, and stored in 70% ethanol: *Lepomis auritus*, *L. gulosus*, *L. macrochirus*, *L. marginatus*, *L. microlophus*, *L. punctatus*, *Micropterus notius*, *M. salmoides*, and *Pomoxis nigromaculatus*. Preserved specimens of the remaining species were borrowed from museum collections. This study did not include the recognized centrarchid species *Acantharchus pomotis*, *Ambloplites constellatus*, *Enneacanthus chaetodon*, *E. gloriosus*, *Lepomis peltastes*, and *Micropterus cataractae*. The complete list of species involved in this study is provided in Appendix 1. All specimens were cleared using trypsin and double stained in alcian blue cartilage stain and alizarin red bone stain (Taylor 1967). This method restored pliability to connective tissue, permitting manipulation of the specimens, and allowed accurate identification of relevant landmarks (see next section).

Morphological Measurements

All measurements were made on cleared and stained specimens using dial calipers. We modeled the buccal cavity as an expanding cylinder and used the product of gape width and buccal length as the projected area of the cavity (Fig. 1). We measured gape width in a maximally opened mouth as the distance between the left and right coronoid processes of the mandible. Gape width was multiplied by 0.67 to correspond with its value at the time of minimum buccal pressure, as measured for the largemouth bass, *M. salmoides* (Sanford and Wainwright 2002). Buccal length was taken as the distance between the anterior tip of the mandible and the posteriormost point of the basihyal in a maximally expanded buccal cavity. These landmarks correspond to the ones measured on silicone buccal casts as in Carroll et al. (2004). The length of L_{out} was taken as the distance between the S-PT joint and the midpoint of the dorsal surface of the buccal cavity. We estimated CSA_{Epax} as the area of a semi-ellipse, where half the major axis is the distance between the S-PT joint and the dorsalmost aspect of the epaxial muscle mass and the minor axis is the distance between lateral extremes of the epaxial muscle mass along the axis containing the S-PT joint. As long as fascicle orientation and specific muscle tension do not vary systematically among centrarchid species, CSA_{Epax} should accurately reflect differences in force capacity of the epaxial muscles. Length of L_{in} was taken as the vertical distance between the centroid of the epaxial muscles' cross-section and the S-PT joint.

Body Size Corrections

We corrected for differences in species' morphological parameter values that are due to differences in body size of specimens using a method described by Blomberg et al. (2003). We regressed $\log_{10}$-transformed parameter values on $\log_{10}$-transformed standard length (SL; $n = 27$), but in order to account for the confounding effects of phylogeny (Felsenstein 1985), we constrained the slope coefficients to be equal to those estimated from least-squares regressions involving standardized contrasts ($n = 26$). We note that the slope coefficients estimated from species' values and from standardized contrasts do not differ significantly for any morphological parameter. We fit the intercepts of the species' values regressions by least-squares and obtained residual parameter values for each species from these regression lines. We obtained standardized contrasts using the computer program CAIC (Purvis and Rambaut 1995) and the phylogenetic topology and branch lengths calibrated in millions of years presented in Near et al. (2005; see Fig. 3). This procedure provided size-corrected morphological parameter values for each of the 27 species in $\log_{10}$ scale. Suction index required no size correction because it showed no relationship with SL ($r^2 = 0.004$, $P = 0.75$).

Comparing Mechanical and Morphological Diversity among Clades

We tested whether differences among the centrarchid clades in suction index diversity correspond with differences in morphological diversity. We used the rate of evolution as a metric of phenotypic (morphological and mechanical) diversity. The rate of evolution is the time-independent variance parameter, σ^2, of the Brownian motion model of continuous character evolution (Felsenstein 1985). We chose this metric over estimates of within-clade variance because it accounts for the confounding effects of phylogeny on the accumulation of variance (Collar et al. 2005; O'Meara et al. 2006). In this context, comparisons of rates of evolution are phylogenetically correct tests of heterogeneity of variance among groups (Hutcheon and Garland 2004).

To account for correlations between morphological parameters and to reduce dimensionality of the morphological dataset, we applied principal-components analysis (PCA) to the correlation matrix of species' size-corrected morphological parameter values. We note that size-corrected species' values are the residuals from the regressions of morphological parameters against SL, and these were antilog$_{10}$-transformed prior to PCA to facilitate comparisons between variation in suction index and morphological parameters. We retained only PCs that cumulatively accounted for up to 95% of the total morphological variation, and we estimated rates of morphological evolution within clades using these PCs.

We compared rates of evolution of the suction index and morphological PCs among the three centrarchid clades. We applied the computer program Brownie (O'Meara et al. 2006) to find maximum likelihood estimates for the rates of evolution of the suction index and morphological PCs in *Lepomis*, *Micropterus*, and *Pomoxis* et al. and to compare rates between each pair of clades using a modified likelihood ratio test. The branch length covariance matrices for this program were obtained from the centrarchid phylogeny presented in Near et al. (2005; see Fig. 3), where branch lengths were estimated in millions of years. The likelihood ratio (LR) for each test was the ratio of the maximum likelihood of the model given equal rates in the two clades to the maximum likelihood of the model allowing rates to differ. *P*-values were obtained by comparison to a distribution of LR statistics based on 1000 pseudoreplicates of simulated Brownian motion evolution on the branch length covariance matrix given equal rates of evolution (O'Meara et al. 2006). We used this parametric bootstrapping procedure instead of employing the χ^2 distribution because the latter test could inflate Type I error rates when sample sizes are not large. For each rate comparison, we applied Bonferroni corrections to account for the three comparisons between pairs of clades ($\alpha = 0.017$).

We tested the hypothesis that the rate differences between clades are concordant for the suction index and morphological PCs using a parametric bootstrapping procedure that we implemented in Brownie (O'Meara et al. 2006). For each clade, we obtained 1000 pseudoreplicates of species' values given a Brownian motion model of evolution and rate parameter equal to its maximum likelihood estimate for the suction index. We then estimated the rate for each pseudoreplicate within each clade. For each pairwise comparison, we obtained a distribution of rate differences, where the rate difference of a pseudoreplicate was the ratio of the rate in the clade whose suction index evolved more rapidly to the rate of the clade whose suction index evolved more slowly. *P*-values were obtained by comparing rate differences for morphological PCs to this distribution. We also used this bootstrapping procedure to test concordance between differences in rates of suction index evolution and differences in the sum of rates of morphological PC evolution. We interpreted the sum of rates of PC evolution as an estimate of overall morphological diversity within each clade.

Because application of rate comparisons is valid only for characters that have evolved in a manner consistent with Brownian motion, we also tested the assumption that the suction index and morphological PCs fit the Brownian motion model in each of the three clades. We applied the computer program Continuous (Pagel 1997, 1999) to test three predictions of the Brownian motion model: (1) covariance between species is proportional to total shared branch length; (2) character change along each branch of the phylogeny is proportional to the length of the branch; and (3) the rate of evolution

TABLE 1. Principal component loadings on original variables and summary statistics. We considered a morphological parameter to be strongly correlated with a principal component if its loading is greater than 0.40 in magnitude (shown in bold).

Variable	PC1	PC2	PC3
Gape width	**−0.43**	**0.46**	0.39
Buccal length	−0.15	**0.80**	**−0.42**
L_{out}	**0.44**	0.31	**0.76**
L_{in}	**0.55**	0.13	−0.17
CSA_{Epax}	**0.54**	0.20	−0.25
Eigenvalue	3.01	1.28	0.46
% total variance	60.1	25.6	9.2

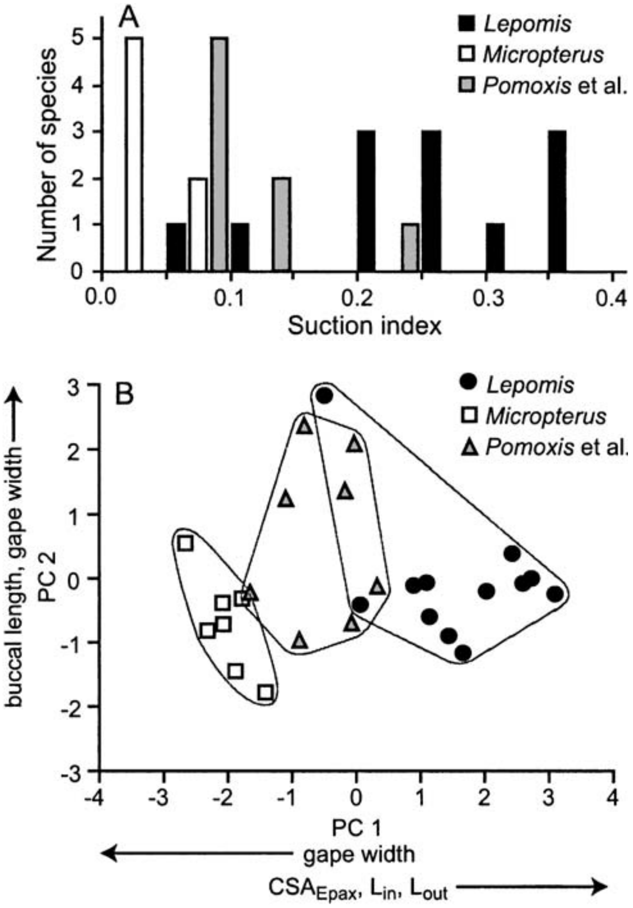

FIG. 4. (A) Histogram showing the distribution of suction index in *Lepomis* (black), *Micropterus* (white), and *Pomoxis* et al. (gray); and (B) scatterplot of species' scores on principal components 1 and 2 for 12 *Lepomis* species (black circles), seven *Micropterus* species (open squares), and eight *Pomoxis* et al. species (gray triangles). Principal component 1 accounts for 60% of the variation among species and correlates positively with L_{in}, CSA_{Epax}, and L_{out} and negatively with gape width. Principal component 2 explains 26% of the variation and correlates positively with buccal length and gape width. These distributions of extant species' values suggest that the differences between clades in suction index variation do not correspond with the differences in morphological variation; however, rather than compare variance between clades, we used the rate of evolution as a metric of diversity, which accounts for phylogenetic relationships between species. Rates of evolution for the suction index and morphological parameters were estimated using the chronogram shown in Figure 3 and the species' values represented here.

is constant throughout the history of the clade. These three predictions correspond to three parameters, λ, κ, and δ, whose values are all equal to one for a trait evolving under Brownian motion (Pagel 1997, 1999). Therefore, we tested the hypothesis that each parameter equals one for the suction index and morphological PCs, using LR tests. We adjusted significance levels by sequential Bonferroni corrections (Rice 1989) to account for multiple (i.e., three) tests, which were applied separately to the suction index and each morphological PC.

Regression and Correlation Analysis

We used multiple linear regression to determine what morphological parameters are responsible for evolutionary change in suction index. Evolutionary changes at nodes in the centrarchid phylogeny were estimated as standardized independent contrasts (Felsenstein 1985). We obtained standardized contrasts of $\log_{10}$-transformed suction index and $\log_{10}$-transformed, size-corrected morphological parameter values ($n = 26$ for each variable) using CAIC (Purvis and Rambaut 1995). To ensure that the confounding effects of phylogeny had been adequately controlled for each variable, we regressed standardized contrasts for each node against the square root of the descendant branch lengths and found no relationship (Garland et al. 1992). We applied least-squares optimization to a multiple linear regression model involving these standardized contrasts; the response variable of the model was suction index, and the predictors were the five morphological parameters. We tested for normality of residuals of the model and linearity of the relationship between each predictor and the response and found no evidence that these model assumptions have been violated. We also examined pairwise Pearson correlation coefficients between predictor variables and adjusted significance levels for multiple (i.e., 10) comparisons by Bonferroni correction ($\alpha = 0.005$).

RESULTS

PCA provides three axes that together account for 95% of the total variation in morphological parameters among centrarchid species (Table 1). PC1 accounts for 60% of the variation and correlates ($|\mathrm{loading}| > 0.40$) positively with L_{in}, CSA_{Epax}, and L_{out} and negatively with gape width. PC2 explains 26% of the variation and correlates positively with buccal length and gape width. PC3 accounts for 9% of the variation and correlates positively with L_{out} and negatively with buccal length. We note that inclusion of the remaining two PCs does not qualitatively alter results.

Although we used rates of evolution to test for differences in diversity between clades, discordance between morphological and mechanical diversity is evident in the variation among the extant species of each clade. Figure 4 illustrates the distributions of species' values of the suction index and morphological PCs for *Lepomis*, *Micropterus*, and *Pomoxis* et al. We note that comparisons of variance using Levene's test provide qualitatively similar results to those revealed in rates comparisons.

Differences among clades in rate of suction index evolution

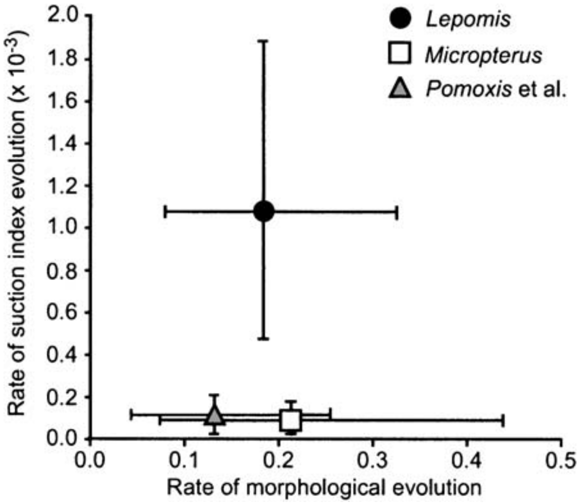

FIG. 5. Plot showing maximum likelihood estimates for rates of morphological evolution and rates of suction index evolution for *Lepomis* (black circle), *Micropterus* (open square), and *Pomoxis* et al. (gray triangle). For each clade, the rate of morphological evolution is the sum of maximum likelihood estimates for principal components 1, 2, and 3. Bars represent 95% confidence intervals for each rate estimate based on parametric bootstrapping. Although these clades exhibit similar rates of evolution of morphological parameters, *Lepomis* has experienced an order of magnitude higher rate of suction index evolution.

TABLE 2. Results from the multiple linear regression of standardized contrasts of $\log_{10}$-transformed suction index (response variable) on contrasts of $\log_{10}$-transformed, size-corrected model parameters (predictor variables). Partial regression coefficient estimates with standard errors are based on least-squares regression. Significance tests for each predictor variable are based on Type III sums of squares. The model explains 99% of the variation in the response variable, has 20 degrees of freedom, and has a mean squared error equal to 2.6×10^{-5}.

Predictor	Partial regression coefficient	Sum of squares	F	P
Gape width	-1.00 ± 0.05	0.0117	450.6	<0.001
Buccal length	-1.07 ± 0.07	0.0056	215.4	<0.001
L_{out}	-1.18 ± 0.16	0.0015	56.5	<0.001
CSA_{Epax}	0.99 ± 0.07	0.0047	179.7	<0.001
L_{in}	1.08 ± 0.10	0.0031	117.6	<0.001

are discordant with differences in rate of evolution of morphological parameters. The rate of suction index evolution is greater in *Lepomis* by a factor of 10 relative to *Pomoxis* et al. ($-2\ \ln(\text{LR}) = 9.8$, $P = 0.008$) and by a factor of 14 relative to *Micropterus* ($-2\ \ln(\text{LR}) = 10.4$, $P = 0.002$). Comparisons involving rates of morphological evolution do not mirror this pattern (Fig. 5). The sum of rates of evolution for the first three morphological PCs suggests that morphological evolution is most rapid in *Micropterus* (faster than *Lepomis* and *Pomoxis* et al. by factors of 1.1 and 2, respectively) and slowest in *Pomoxis* et al. (the rate in *Lepomis* is greater by a factor of 1.5). These rate differences are significantly discordant with those based on rates of suction index evolution ($P < 0.001$ for *Lepomis*-*Micropterus* and *Lepomis*-*Pomoxis* et al. comparisons and $P = 0.009$ for *Micropterus*-*Pomoxis* et al.).

Comparisons involving individual morphological PCs revealed that only rates of PC1 evolution show a rank ordering of clades similar to that of the suction index. *Lepomis* exhibits a higher rate than *Micropterus* and *Pomoxis* et al. by factors of three and five, respectively. However, the rate differences involving PC1 are much lower in magnitude and significantly discordant with those based on the suction index ($P < 0.001$ for comparisons involving *Lepomis* and $P = 0.009$ for *Micropterus*-*Pomoxis* et al.). PC2 has evolved fastest in *Micropterus* (greater than *Lepomis* and *Pomoxis* et al. by a factor of two), and PC3 has evolved fastest in *Pomoxis* et al. (greater than *Lepomis* and *Micropterus* by factors of 1.5 and 2, respectively).

We found insufficient evidence to reject the Brownian motion model, with one exception. Within *Micropterus*, covariance among species in the suction index does not reflect shared evolutionary history ($\hat{\lambda} = 0.0$, $P = 0.008$). This result seems to be due to a large difference in suction index between *M. dolomieu* and *M. punctulatus*, which are sister species that diverged only about 1.7 million years ago (Near et al. 2005); removing either species from the test produces a nonsignificant result. While this outcome suggests non-Brownian motion evolution of the suction index in *Micropterus*, the relatively large, recent divergence in suction index acts to elevate the estimate of the rate of suction index evolution relative to the Brownian expectation. Because the suction index has evolved slowest in *Micropterus*, this violation does not confound the rank ordering among clades in rate of suction index evolution.

All five morphological parameters are responsible for evolutionary change in the suction index in Centrarchidae. In a multiple linear regression model, standardized contrasts of $\log_{10}$-transformed, size-corrected morphological parameters explain 99% of the variation in standardized contrasts of the $\log_{10}$-transformed suction index. Estimates of partial regression coefficients for the five predictor variables do not differ significantly from positive or negative one (Table 2), indicating that the contrasts for log-transformed morphological parameters have similar magnitudes of effect on contrasts of log-transformed suction index. Moreover, contrasts for all morphological parameters account for highly significant proportions of variation in suction index contrasts. However, they explain different amounts of this variation (Table 2). Comparisons among predictors' Type III sums of squares (SS) indicate that gape width accounts for the largest proportion of variation in suction index that is not explained by the other morphological parameters. Gape width alone explains 43% of the total variation in suction index, buccal length explains 21%, CSA_{Epax} explains 17%, L_{in} explains 11%, and L_{out} explains 5% (Table 2). We also found that correlations for nine of the 10 combinations of morphological parameters are low and nonsignificant in Centrarchidae (Table 3). Only L_{in} and CSA_{Epax} have evolved in association ($r = 0.82$, $P < 0.001$).

DISCUSSION

The pattern of diversity in suction capacity among centrarchid clades is discordant with the pattern of diversity in

TABLE 3. Pearson correlation coefficients between standardized contrasts of $\log_{10}$-transformed, size-corrected morphological parameters. *P*-values for nonsignificant correlations are greater than 0.05.

Variable	Gape width	Buccal length	L_{out}	CSA_{Epax}
Buccal length	0.28			
L_{out}	−0.04	−0.19		
CSA_{Epax}	0.26	0.13	0.33	
L_{in}	0.12	0.22	0.36	0.82*

* Significant correlation after Bonferroni correction.

the underlying morphology. Despite similar rates of evolution among the clades in the morphological features that determine the suction index, *Lepomis* has experienced an order of magnitude higher rate of suction index evolution (Fig. 5). Differences between clades in the rate of mechanical evolution suggest an evolutionary history for the suction mechanism that is unlike the one inferred from comparisons of rates of morphological evolution. The elevated rate of suction index evolution in *Lepomis* suggests a history of divergent selection on suction performance in the lineages of *Lepomis* that may not have been experienced in *Micropterus* and *Pomoxis* et al. Yet, there is no evidence of these disparate evolutionary histories in the pattern of morphological diversity. Furthermore, because species' differences in suction capacity likely reflect differences in prey capture abilities, the pattern of suction index diversity may also indicate a history of selection for divergent prey resources in the lineages of *Lepomis* that was absent in *Micropterus* and *Pomoxis* et al. Of course, suction capacity is only one aspect of feeding performance, and species' differences in prey capture ability and diet will be affected by other functional variables in addition to suction capacity. For example, prey capture is likely influenced by other aspects of feeding morphology such as buccal cavity volume and upper jaw protrusion as well as features of the locomotor and sensory systems. Therefore, further investigation is necessary to determine whether species' differences in suction capacity reflect diet differences. Nevertheless, the patterns of diversity in suction mechanics and its underlying morphology lead to different inferences regarding the role of natural selection in the evolutionary histories of suction capacity in these clades.

Evolution of the Suction Mechanism in Centrarchidae

Differences between centrarchid clades in mechanical diversity do not reflect differences in morphological diversity despite close linkage between evolutionary changes in suction index and its underlying morphology. The multiple linear regression revealed that contrasts for the five morphological parameters explain nearly all the variation in suction index contrasts, and each of the five morphological parameters accounts for a highly significant proportion of variation in suction index evolution (Table 2). Moreover, partial regression coefficient estimates for the five morphological variables are approximately equal in magnitude (Table 2), indicating that each morphological variable has had the same proportional effect on the suction index throughout centrarchid evolution. We note that these conclusions could have been reached by direct inspection of equation (2), which was used to calculate species' suction indexes from their measured morphological parameter values. Either way, morphological and mechanical changes are closely linked in the evolution of suction capacity in centrarchids, and discordance between morphological and mechanical diversity in this system refines expectations regarding the weakening effects of many-to-one mapping on associations between these levels of diversity. Previous authors demonstrated weak relationships between morphological and mechanical diversity in many-to-one biomechanical systems that are highly nonlinear, where the mechanical effect of change in one morphological variable depends on its initial value and the values of other morphological characters (Koehl 1996; Hulsey and Wainwright 2002). In these systems, morphological change can have disproportionately large or small effects on the mechanical property, and associations between evolutionary changes in morphology and mechanics are expected to be weak (Alfaro et al. 2004). In the suction mechanism, however, change in any morphological parameter has the same proportional effect on suction index regardless of the values of the other parameters, and the link between morphological and mechanical evolution is tighter in the suction mechanism than in these highly nonlinear systems.

Many combinations of morphological changes have been exploited during the evolution of the cetrarchid suction index. Each morphological parameter independently explains a highly significant amount of variation in suction index evolution (Table 2), indicating that all five morphological parameters have been modified during diversification of the suction index. Moreover, correlations among most pairs of contrasts of morphological parameters are weak (Table 3) and reveal a surprising degree of independence in the evolution of the morphological parameters underlying suction mechanics. These results suggest a limited role for constraints that would restrict combinations of morphological changes, such as low genetic variation or genetic correlations underlying these morphological variables. Instead, different morphological changes are responsible for suction index evolution in different centrarchid lineages. However, the morphological parameters account for different amounts of variation in suction index evolution (Table 2). In the multiple linear regression model, gape width and buccal length independently explained the highest proportions of variation in suction index evolution, suggesting that evolutionary changes in size of the buccal cavity generate much of the variation in suction mechanics. Additionally, the force capacity of the epaxial muscles, as represented by CSA_{Epax}, and their moment arm, L_{in}, seem constrained to evolve in close association (Table 3) because they are both proportional to the height of the epaxial muscle mass at the S-PT joint (Fig. 1). This correlation reduces the amount of variation in suction index that each of these variables explains independently but implies that evolutionary change in L_{in} affects suction index both directly and through its effect on CSA_{Epax} and vice versa. Changes in L_{out} seem to be the least important of the morphological parameters in generating variation in suction mechanics among centrarchid species.

Although *Micropterus* and *Pomoxis* et al. exhibit levels of morphological diversity similar to *Lepomis*, these two clades show relatively low suction index diversity. This result is partly a consequence of evolutionary changes in morphological parameters that have opposite effects on the suction index. Within *Micropterus* ($n = 6$), there is a high negative correlation between contrasts of buccal length and L_{out} ($r = -0.70$, $P = 0.12$). While increases in buccal length result in decreases in suction index, the corresponding decreases in L_{out} have the opposite effect. In *Pomoxis* et al. ($n = 7$) a high negative association between buccal length and L_{out} also exists ($r = -0.71$, $P = 0.07$) as well as a positive correlation between changes in gape width and L_{in} ($r = 0.80$, $P = 0.03$). The decreases in suction index resulting from increases in gape width offset the effects of increases in L_{in}. Although these correlations are at best only marginally statistically significant because of small sample sizes within clades and limited power, these comparisons offer insights into the discordance between morphological and mechanical diversity. Associations between evolutionary changes that have opposite effects on the suction index result in increased morphological variation without concomitant increases in mechanical variation.

Selection for multiple functions may in part explain the incongruity in morphological and mechanical diversity in *Micropterus* and *Pomoxis* et al. The morphological parameters that make up the suction-feeding mechanism contribute to other ecologically important functions, including other aspects of feeding mechanics and locomotor performance. Buccal length and gape width contribute to the volume of the buccal cavity (Fig. 1), which affects the volume of water ingested during a strike (Higham et al. 2006a) as well as maximum prey size (Werner 1977). Both L_{in} and CSA_{Epax} contribute to body depth (Fig. 1), which influences aspects of locomotor performance such as body acceleration (Webb 1978) and maneuverability (Walker 2004). A many-to-one biomechanical system is capable of mitigating trade-offs between multiple functions because it permits one or more morphological components to evolve for some other function without changing its mechanical property (Alfaro et al. 2005). The low suction index diversity in *Micropterus* and *Pomoxis* et al. is consistent with a history of stabilizing selection for suction capacity, and the substantial level of morphological variation could be due to divergent selection on some morphological parameters for locomotor performance or prey size. Associated changes in morphological parameters that have opposite effects on suction index illustrate how many-to-one biomechanical systems conserve mechanics while permitting evolution of morphological components for other functions. For example, in *Micropterus* and *Pomoxis* et al. the negative association between buccal length and L_{out} permit changes in buccal length, and thus ingested volume, without divergence in suction capacity. It should be noted, however, that the levels of morphological diversity in *Micropterus* and *Pomoxis* et al. might reflect neutral phenotypic drift rather than selection for other functions.

Context

Although behavior or unmeasured performance variables may further weaken the link between diversity in morphology and function, we focus on many-to-one mapping of morphology to mechanics as an intrinsic property of biomechanical systems that promotes incongruous diversity at these levels of organization. Our results contribute to previous work that has advocated cautious application of morphology as an indicator of ecological variety because of complexity in the form-function relationship. Koehl (1996) reviewed examples of nonlinearity and context dependence, in which morphological changes have disproportionately large or small effects on function. In these cases, no statistical association between morphological and functional change is expected. Hulsey and Wainwright (2002) found that morphological and mechanical diversity show no relationship in the jaw linkage system of labrid fishes, and they attributed this result to many-to-one mapping of the shape of a four-bar mechanical transmission mechanism to its mechanical advantage. Through computer simulation, Alfaro et al. (2004) demonstrated that this result is a likely outcome, as the four-bar shows only a weak relationship between morphological and mechanical diversity over many replicates of evolution. Here, we show that many-to-one mapping leads to discordance between morphological and mechanical diversity even though evolution of morphology and mechanics are tightly coupled.

The extent to which many-to-one mapping of form to function has widespread effects on associations between morphological and functional diversity depends in part on the prevalence of many-to-one mapping in functional systems. Although a comprehensive review of many-to-one systems in physiology or biomechanics is beyond the scope of this work, we speculate that this property of design is common. Several examples support this claim. First, vertebrate skeletal muscles with different fiber lengths, fiber orientations, and specific tensions are capable of equivalent tension production (Powell et al. 1984). Second, as mentioned above, many-to-one mapping is a well-established feature of the four-bar linkage transmission system (Hulsey and Wainwright 2002; Alfaro et al. 2004), which has been applied to model kinematics and force transmission in a variety of vertebrate functional systems (reviewed by Muller 1996). Third, equivalent jumping performance in lizards can be achieved through multiple combinations of muscle and limb dimensions (Toro et al. 2004). Organismal functions that involve the musculoskeletal system have at least the potential to be many-to-one because movement is a function of both muscle properties and the skeletal transmission system. Indeed, any functional property that is determined by three or more underlying features can show many-to-one mapping. Because almost all biological functions have complex underpinnings, we suggest that many-to-one mapping is likely to be a pervasive feature of biological design.

Moreover, we expect that many-to-one mapping can weaken associations between levels in any hierarchically organized system. The role of many-to-one mapping in molecular evolution is well established; many genotypes can result in the same phenotype, and genotypic diversity is not expected to be a good predictor of phenotypic diversity (Bromham et al. 2002). For example, genotypic variation has been shown to increase despite uniform selection for alcohol resistance in parallel fruit-fly lines (Hoffmann and Cohan 1987; Cohan and Hoffmann 1989). At higher levels of organization, different combinations of functional performance can produce the same level of whole-organism performance. Juvenile gobiid fishes achieve similar waterfall climbing speeds despite employing disparate locomotor styles (Blob et al. 2006). Also, tree seedlings may attain similar growth rates given various combinations of functional traits, including features of the wood, leaves, and roots as well as properties of nutrient allocation (Marks and Lechowicz 2006). We illustrate one consequence of many-to-one mapping for the evolution of phenotypic diversity, but future researchers may discover additional roles for this phenomenon in other aspects of organismal design.

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APPENDIX 1.

Species' mean standard lengths (SL), morphological parameter values, and suction indexes.

Species	SL (mm)	Gape width (mm)	Buccal length (mm)	L_{out} (mm)	CSA_{Epax} (mm^2)	L_{in} (mm)	Suction index
Ambloplites ariommus	80	8.8	16.8	19.8	47.7	4.3	0.07
Ambloplites cavifrons	119	13.5	21.6	29.5	130.9	6.1	0.09
Ambloplites rupestris	103	10.3	18.2	26.3	80.4	4.9	0.08
Archoplites interruptus	102	8.1	18.5	20.6	69.8	4.5	0.10
Centrarchus macropterus	61	4.9	8.7	16.9	17.5	2.7	0.07
Enneacanthus obesus	57	4.7	9.1	14.5	42.3	3.3	0.22
Lepomis auritus	95	4.7	14.2	24.0	88.1	5.1	0.28
Lepomis cyanellus	96	7.9	15.0	22.7	84.7	4.4	0.14
Lepomis gibbosus	98	5.9	15.4	25.0	117.6	6.3	0.33
Lepomis gulosus	88	9.7	18.5	22.3	72.1	4.2	0.08
Lepomis humilis	81	6.9	12.2	20.7	79.1	4.8	0.22
Lepomis macrochirus	93	5.0	15.1	23.7	110.6	6.4	0.40
Lepomis marginatus	61	3.2	8.4	16.9	45.8	3.8	0.38
Lepomis megalotis	97	6.9	14.2	24.9	133.4	7.1	0.39
Lepomis microlophus	93	5.5	15.3	26.0	98.1	5.3	0.24
Lepomis miniatus	101	6.3	16.5	24.9	122.2	6.1	0.29
Lepomis punctatus	97	6.4	15.3	23.5	99.2	5.2	0.22
Lepomis symmetricus	62	5.1	9.2	16.3	54.0	3.7	0.26
Micropterus coosae	106	9.8	16.7	23.5	55.8	3.4	0.05
Micropterus dolomieu	105	9.5	14.4	23.4	66.0	3.8	0.08
Micropterus floridanus	103	10.7	18.7	22.4	51.6	3.4	0.04
Micropterus notius	98	10.2	15.5	22.4	59.9	3.4	0.06
Micropterus punctulatus	85	8.6	13.9	19.5	33.2	2.5	0.04
Micropterus salmoides	99	9.4	14.2	23.0	45.9	3.2	0.05
Micropterus treculi	101	9.5	16.0	21.8	51.2	3.1	0.05
Pomoxis annularis	100	8.2	15.7	21.8	71.2	4.5	0.12
Pomoxis nigromaculatus	105	11.2	18.8	24.5	74.5	5.2	0.07