

# RELATIONSHIP BETWEEN SPECIES CO-OCCURRENCE AND RATE OF MORPHOLOGICAL CHANGE IN *PERCINA* DARTERS (PERCIDAE: ETHEOSTOMATINAE)

Rose L. Carlson,<sup>1,2,3</sup> Peter C. Wainwright,<sup>1,4</sup> and Thomas J. Near<sup>5,6</sup>

<sup>1</sup>Center for Population Biology and Department of Evolution and Ecology, University of California, Davis, California 95616

<sup>2</sup>E-mail: rcarlson@oeb.harvard.edu

<sup>4</sup>E-mail: pcwainwright@ucdavis.edu

<sup>5</sup>Department of Ecology and Evolutionary Biology and Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520

<sup>6</sup>E-mail: thomas.near@yale.edu

Received December 18, 2007

Accepted October 28, 2008

When the morphological diversity of a clade of species is quantified as the among-species variance in morphology, that diversity is a joint consequence of the phylogenetic structure of the clade (i.e., temporal pattern of speciation events) and the rates of change in the morphological traits of interest. Extrinsic factors have previously been linked to variation in the rate of morphological change among clades. Here, we ask whether species co-occurrence is positively correlated with the rate of change in several ecologically relevant morphological characters using the North American freshwater fish clade *Percina* (Teleostei: Etheostomatinae). We constructed a time-calibrated phylogenetic tree of *Percina* from mtDNA sequence data, gathered data on eight morphological characters from 37 species, used a principal components analysis to identify the primary axes of morphological variation, and analyzed 16,094 collection records to estimate species co-occurrence. We then calculated standardized independent contrasts (SIC) of the morphological traits (rate of change) at each node, estimated ancestral species co-occurrence, and quantified the correlation between species co-occurrence and rate of morphological change. We find that morphology changes more quickly when co-occurrence is greater in *Percina*. Our results provide strong evidence that co-occurrence among close relatives is linked to the morphological diversification of this clade.

**KEY WORDS:** Character displacement, ecomorphology, morphological diversity, species co-occurrence.

Evolutionary biologists have long been intrigued by the observation that clades of closely related species often differ dramatically in morphological diversity (e.g., Simpson 1953; Rensch 1959; Foote 1997; Schluter 2000). When a clade's morphological diversity is measured as the total variance among species in one or more

morphological characters, the clade's diversity is the joint effect of the pattern of species diversification (phylogenetic structure of the clade) and the rate of change in the morphological characters of interest (Collar et al. 2005; O'Meara et al. 2006). Factors known to affect the rate at which lineages diversify in morphology fall into two categories: intrinsic features of a lineage, including the origin of characters that result in a change in morphological diversity, such as the evolution of flight and its resulting effects on the variety of locomotor morphology in birds (Gatesy and Middleton

<sup>3</sup>Current address: Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138

1997), and extrinsic factors such as the geographic context of speciation (e.g., isolated islands vs. continents; Schluter 1988), the variety of available prey types (Van Valkenburgh 1988), and, as has been the case in many adaptive radiations, the frequency of allopatric versus sympatric speciation (Schluter 2000). Here, we examine the effect of an additional extrinsic factor, co-occurrence with close relatives (other species in the same clade) on the rate of morphological diversification. Such an analysis is the first step in determining whether variation in species co-occurrence leads to differences in morphological diversity between clades of species.

Theoretical and empirical evidence suggests that ecologically identical individuals, populations, or species will be unable to co-occur in a community for extended periods of time because competition for limited resources will likely lead to the extinction of one or more of the community members (Hardin 1960; Bengtsson 1989). The coexistence of species in a community is therefore enabled by differences in resource and habitat use (MacArthur 1958; MacArthur and Levins 1964; Werner and Hall 1976) as well as by differential predation or susceptibility to parasites or disease (e.g., Paine 1966). The ecological differences that facilitate coexistence may evolve either before co-occurrence or as a result of interactions with other species in the community. The latter type of change most often takes the form of ecological niche shifts that are correlated with morphological divergence (i.e., character displacement) (Brown and Wilson 1956; Schoener 1965; Abrams 1986; Dayan and Simberloff 1994; Robinson and Wilson 1994). Furthermore, the amount of change that occurs during morphological divergence is expected to increase as the number of ecologically similar species in the community increases (Abrams 1986). Thus, all else being equal, species that occur in a community with two ecologically similar species should exhibit greater morphological change than species that occur with only one species. Closely related species (such as members of the same genus) are among the most likely to compete for limited resources when they occur in the same community because ecological similarity among these species is typically high as a result of their extensive shared history (Peterson et al. 1999; Losos et al. 2003; but see Knouft et al. 2006). Thus, we expect that there will be a positive relationship between co-occurrence with close relatives and the rate of change in ecologically relevant morphological characters. We test this prediction using *Percina*, a monophyletic lineage in the radiation of North American freshwater fish known as darters (Percidae: Etheostomatinae).

## Materials and Methods

### STUDY GROUP

*Percina* includes 45 described species (Page 2000; Near 2002, 2008; Near and Benard 2004; Page and Near 2007; Williams et al.

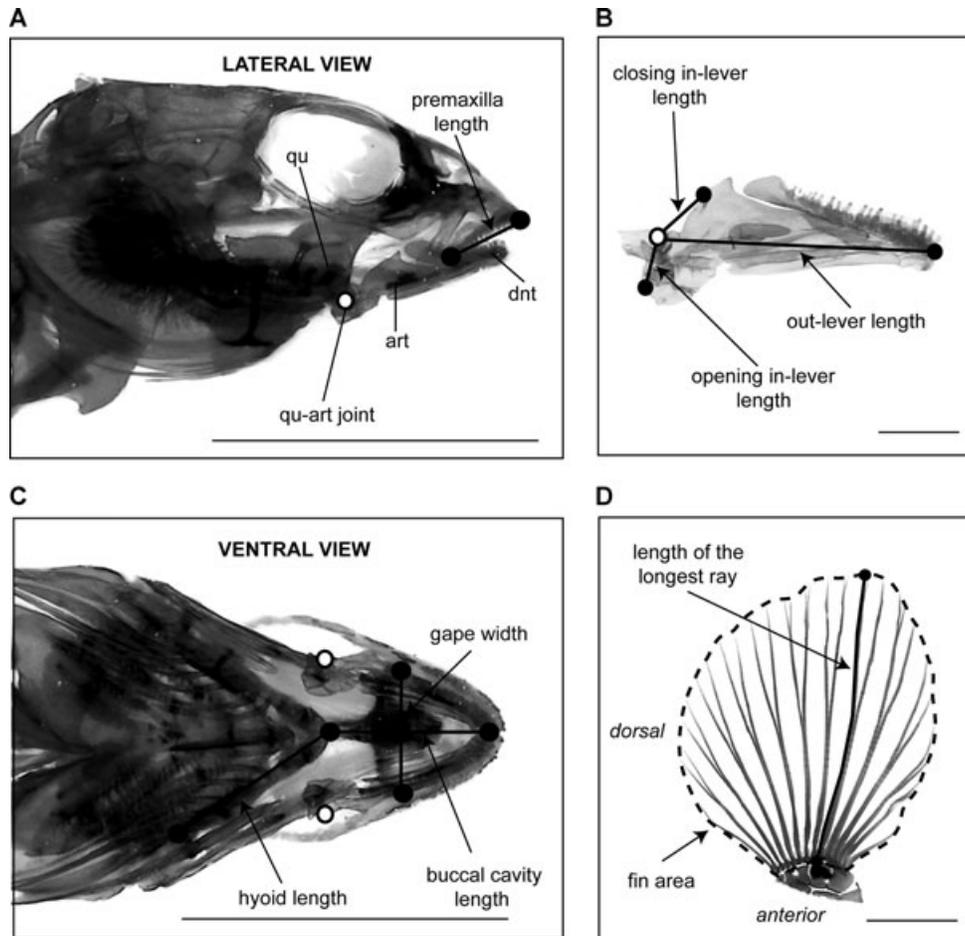
2007) and at least one undescribed species, *P. cf. nasuta* (Robison and Buchanan 1988). *Percina* includes both wide-ranging and geographically restricted species that inhabit a variety of freshwater habitats including creeks, streams, and rivers as well as lakes and reservoirs (Page 1983; Etnier and Starnes 1993; Boschung and Mayden 2004). Species occupy microhabitats ranging from shallow riffles to deep runs and slow pools (Page 1983) and are associated with a wide variety of substrates from large boulders to mixtures of sand and gravel (Carlson 2008). *Percina* is unique among darters in that many species occupy midwater (Greenberg 1991), a habit facilitated by the presence of an enlarged and putatively functional swim bladder in these species (Page 1983; Near 2002; Evans and Page 2003). All species of *Percina* are carnivorous; most species feed on aquatic insect larvae, especially midges, black flies, mayflies, and caddisflies (Page and Swofford 1984), although a few species, including the snail darter *P. tanasi* and its relatives, typically include a large quantity of gastropods in their diet (Page 1983; Haag and Warren 2006).

The ecological communities in which *Percina* occur often include multiple other non-*Percina* darter species (R. Carlson, unpubl. data). However, the frequency of interactions between *Percina* and non-*Percina* darter species is expected to be low compared to the frequency of *Percina*–*Percina* interactions due to the large average body size (BS) of *Percina* relative to other darter clades as well as the species' tendency to inhabit midwater rather than strictly benthic microhabitats (Carlson 2008).

### DATA COLLECTION

We gathered morphological data from two to five cleared and doubled stained (bone and cartilage) specimens of 37 described species of *Percina*. These sample sizes were sufficient to differentiate among species in the measured morphological characters; interspecific variance of the individual traits was on average 4.73 times greater than intraspecific variance. Given that a high percentage of the total variance is between species (83% of the total), the probability of making either a type I or type II error as a result of small sample sizes is relatively small (Harmon and Losos 2005). We recognize, however, that by sampling individuals from only one population of each species we cannot quantify the extent of intraspecific geographic variation. Although this limits the generality of our conclusions, it is not expected to bias our results in a systematic way because sampled populations were chosen at random from available collections.

We measured 10 morphological characters on each specimen (see Fig. 1): (1) standard length (SL), the distance from the anterior-most tip of the upper jaw to the posterior edge of the hypurals at the base of the tail, (2) the combined length of the hypohyal and ceratohyal bones, or hyoid length (HL), (3) the length of the dentigerous arm of the premaxilla (PL), (4) The buccal cavity length (BCL) from the dentary to the hyoid symphysis, (5)



**Figure 1.** (A) Lateral view of the skull of a cleared and stained specimen of *P. palmaris*. Landmarks and bones used in the measurement of morphological characters are indicated. (B) Lower jaw of *P. palmaris*. (C) Ventral view of the skull of *P. palmaris* with relevant lengths shown. (D) Pectoral fin of *P. palmaris* with fin area and the longest fin ray indicated. Images in A, C, and D are of the same individual. Scale bar is equal to 1 cm in A and C and 20 mm in B and D.

gape width (GW), the distance between the left and right coronoid processes of the dentary of the closed mouth, (6) length of the lower jaw out-lever, the distance from the anterior-most tip of the dentary to the center of the quadrate–articular jaw joint, (7) length of the lower jaw closing in-lever, the distance from the insertion of the adductor mandibulae on the coronoid process of the articular to the center of the quadrate–articular jaw joint, (8) length of the lower jaw opening in-lever, the distance from the center of the quadrate–articular joint to the insertion of the interoperculo mandibular ligament on the retroarticular process of the articular, (9) area of the pectoral fin with fin rays expanded, and (10) the length of the longest pectoral fin ray. Characters (1–8) were measured using a dissecting scope and ocular micrometer. We attempted to control for variation in buccal expansion among preserved specimens (which could affect measurements of GW and BCL) by manually reducing lateral expansion of specimens during measurement. The pectoral fin characters were measured on digital images using National Institutes of Health Image (de-

veloped at the U.S. National Institutes of Health; available at <http://rsb.info.nih.gov/nih-image/>). The aspect ratio of the pectoral fin (PFR) was calculated by dividing the area of the fin by the squared length of the longest fin ray (Walker and Westneat 2002). Lower jaw in-lever and out-lever measurements were used to calculate opening- and closing-lever ratios (OLR and CLR, respectively) by dividing the length of the appropriate in-lever by the length of the out-lever (Westneat 1994).

We were not able to reliably measure body mass from all the specimens in this study because specimens of many species were obtained already cleared and stained from museum or institutional collections. We therefore measured the body size (BS) of each specimen as the geometric mean of five linear head and body measurements: SL, BCL, GW, HL, and PL. We chose this geometric-mean approach because no single linear measurement will allow one to remove size-dependent shape variation from a dataset (Rohlf and Marcus 1993). *Percina* species vary in shape (e.g., slender species like *P. caprodes* vs. robust species like

*P. roanoka*) and variation in shape is equivalent to differences in size along different morphological axes. The use of a geometric mean of the linear measures allowed us to capture some of the shape variation associated with size.

We measured the morphological characters listed above because each has predictable consequences for performance in ecologically relevant tasks. BS is strongly correlated with prey size and type and diet breadth in darters (Page 1983; Page and Swofford 1984). Likewise, PFR (and fin length) is correlated with habitat type in darters (Page and Swofford 1984). Variation in mouth size (BCL, GW, and PL each describe a dimension of the mouth), HL, CLR, and OLR has functional ramifications and performance consequences that have been correlated with patterns of habitat use and prey type among nondarter perciform species (mouth size: Richard and Wainwright 1995; Wainwright 1996; Carroll et al. 2004; HL: Svanbäck et al. 2002; CLR, OLR: Westneat 1994; Wainwright and Richard 1995). Although these associations between morphology and ecology have not been explicitly tested in darters, characters that perform a particular function in one perciform group are likely to have a similar function in a second perciform group as a result of broad similarities among taxa in oral jaw structure (Wainwright and Bellwood 2002).

Our hypothesis requires that “co-occurring” species live in close enough proximity to possibly interact and specifically, when appropriate (i.e., the species’ niches overlap), compete with one another. Interaction between species is most likely when they occur in either the same or adjacent microhabitats. In addition, microhabitat displacement is a common outcome of competition and thus, the occupation of adjacent microhabitats may carry a signal of either historical post- or presympatry ecological change. We therefore considered that two or more species “co-occur” if they occupy the same or adjacent microhabitats. Given our rather stringent definition of species co-occurrence, we chose to gather co-occurrence data from collection records instead of geographic range maps because the former provides more definitive evidence that species co-occur. We note, however, that co-occurrence among species is closely tied to geographic range overlap; two species cannot co-occur unless their geographic ranges overlap.

Benthic stream fish such as darters are typically collected using a kick seine. When collections are made using this method, only a limited amount of habitat can be sampled. Thus, finding that two or more species were captured at the same collection site provides much stronger evidence that the species co-occur than finding that the geographic ranges of the species overlap.

We analyzed a total of 16,094 records from the Cornell University Museum of Vertebrates, the Illinois Natural History Survey, the Tulane University Museum of Natural History, and the University of Alabama Ichthyology Collection. To sample the largest possible geographic area and thereby more accurately estimate co-occurrence among species with both small and exten-

sive geographic ranges, we examined the collection records from institutions in three different geographic regions; a large proportion of a museum or university’s collections typically occur in the geographic region near the institution.

Each collection record in a database minimally includes the species’ name, the collection date, and the collection locality (typically: site description, drainage, county, and state). We sorted the database entries first by collection date and then by collection locality to identify unique collection events. Then, for each species in each collection event, we counted the number of other *Percina* with which it was collected. This number ranged from 0 (the species was collected alone) to a maximum of 7. We then counted the total number of collections in which each species occurred with 0, 1, . . . 7 other species. Finally, we combined the data from all of the databases and calculated the mean number of other species with which each *Percina* species co-occurs throughout its range.

#### PHYLOGENY RECONSTRUCTION AND DIVERGENCE TIME ESTIMATION

We used a 1.1 kb segment of the mitochondrial cytochrome b locus for which sequence data are available in GenBank to reconstruct the phylogenetic relationships among *Percina* species (Near 2002). We also included sequence data for five nondarter percid outgroup species, *Gymnocephalus cernuus*, *Perca flavescens*, *Sander vitreus*, *Romanichthys valsanicola*, and *Zingel zingel*, and seven centrarchid species, *Ambloplites cavifrons*, *A. ruprestris*, *Archoplites interruptus*, *Centrarchus macropterus*, *Lepomis macrochirus*, *L. miniatus*, *Micropterus salmoides*, and *M. dolomieu* for time calibration of the molecular phylogeny. Darters have a poor fossil record and as a result, there are no darter fossils with which to calibrate molecular phylogenies of darter taxa (Smith 1981; Cavender 1986). Centrarchid fish, on the other hand, have an extensive fossil record (Near et al. 2005) and fossil-calibrated centrarchid phylogenies offer a set of external calibrations that can be used to estimate divergence times in darters (Near and Benard 2004; Near and Keck 2005). We used Akaike Information Criteria (AIC) criteria in ModelTest (Posada and Crandall 1998, 2001) to identify the best-fit model of sequence evolution for each codon position and used the resulting models in a partitioned mixed model Bayesian analysis using MrBayes 3.1 (Ronquist and Hulsenbeck 2003). MrBayes 3.1 was run with  $5 \times 10^6$  generations to increase the probability of convergence of the algorithm in the estimation of model parameters, tree topology, and branch lengths. The “burn-in” period of the analysis was determined by plotting the marginal likelihood versus generation number at which likelihood values reach a plateau. Trees and parameter values sampled prior to the first million generations (i.e., the “burn-in”) were discarded. The posterior clade probabilities of node support were

determined by the frequency of their occurrence in the post “burn-in” distribution (Ronquist and Huelsenbeck 2003). MrBayes runs were repeated four times. There were no differences between runs and thus, the results from the first run were used for our analyses.

The *Percina* phylogeny was time-calibrated using an external fossil calibration from the North American freshwater perciform clade Centrarchidae. The age of the extinct fossil centrarchid species ( $\dagger$ *Archoplites clarki* (15.5 my) (Smith and Miller 1985; Golenberg et al. 1990) was used to calibrate the node in the phylogeny subtending the centrarchid *Archoplites* and *Ambloplites* lineages (Near et al. 2005). Previous studies have identified seven centrarchid fossil calibrations that provide consistent age molecular age estimates. Due to a limited taxon sampling of cytochrome *b* gene sequences for centrarchids, our analyses were limited to the use of one of these calibrations. We used the computer program r8s version 1.7 to perform penalized-likelihood analyses with the minimal age constraint treated as a fixed node (Sanderson 2002, 2003). The optimal smoothing parameter value for penalized likelihood was determined using a cross-validation procedure outlined in Sanderson (2002). Divergence times were estimated using a truncated Newton (TN) algorithm with five initial starts and with three perturbed restarts; the magnitude of perturbations was 0.05 in random directions. The resulting divergence time estimates were treated as the phylogenetic branch lengths in our comparative analyses. Following phylogeny reconstruction and divergence time estimation, we pruned eight species from the phylogeny for which morphological data could not be obtained: *P. williamsi*, *P. macrocephala*, *P. nasuta*, *P. cf. nasuta*, *P. bimaculata*, *P. pantherina*, *P. sipsi*, and *P. smithvanizi*.

#### DATA ANALYSIS

Measurements of BCL, GW, HL, and PL were log transformed to homogenize variance and linearize the relationship between each character and log-transformed BS. The log-transformed characters were positively correlated with log BS such that larger species had, on average, a wider GW, a longer BCL etc. Thus, an evolutionary change in BS implicitly includes change in SL, GW, BCL, HL, and PL such that the inclusion of the latter four linear measurements in subsequent statistical analyses is redundant. Thus, BS was removed from each variable prior to analysis. Change in BS-corrected GW, BCL, HL, and PL represents change in shape. Size-corrected values of log-transformed BCL, GW, HL, and PL are the residuals of a linear regression of each character against log BS; means from all species were used to estimate the best-fit regression line. We identified the primary axes of variation in jaw, mouth, and pectoral fin shape and BS using a principal components (PC) analysis on the correlations among size-corrected measurements of log-transformed BCL, GW, HL, and PL, OLR, CLR, PFR and log-transformed BS.

We used the Phenotypic Diversity Analysis Programs (PDAP) module (Midford et al. 2003) in Mesquite version 1.12 (build h66) (Maddison and Maddison 2004) to calculate standardized independent contrasts (SIC) for the scores on each of the eight principal component axes at each node in the *Percina* phylogeny. The standardized contrast at a node is the difference in morphology between the species subtending that node divided by its variance (equivalent to the square root sum of the branch lengths) (Garland 1992). When branch lengths are in absolute time, as they are in our phylogeny, the standardized contrast at a node is equivalent to the rate of change in morphology (Hutcheon and Garland 2004). We tested for adequate standardization of contrasts using a linear regression of the SIC at each node versus its variance. A nonsignificant correlation between the SICs and their variance indicates that the SICs are adequately standardized (Garland 1992).

We then used our database-derived estimates of co-occurrence for each extant species to reconstruct historical co-occurrence among *Percina* species. To do so, we assume a pure-birth (Yule) model of diversification because there is no fossil record from which to estimate the magnitude and frequency of *Percina* extinction. In addition, we use a method of ancestral state reconstruction that accounts for a decrease in the number of extant lineages with increasing depth in the phylogeny. Thus, a negative correlation between node height and species co-occurrence is an expected consequence of our reconstruction method.

To make our estimates, we first calculated the proportion of the total number of *Percina* species with which each extant species co-occurs by dividing our estimate of the number of species with which each species co-occurs (calculated from the collection records) by the total number of *Percina* species in the phylogeny minus one (because a species cannot co-occur with itself). For example, our analysis of the collection records indicated that *P. shumardi* occurs with an average of 1.82 other *Percina* species throughout its range. This is equivalent to 1.82/36 or 0.051 of the other species.

Beginning at the tips and moving toward the root, we then reconstructed the number of species with which each ancestor (node) would have co-occurred. Specifically, we calculated the mean proportion of species with which the pair of extant species subtending each node in the phylogeny co-occurs. This method assumes that the proportion of extant lineages with which a most recent common ancestor co-occurs is equivalent to the mean proportion of species with which the ancestor's descendent lineages co-occur. Because species co-occurrence is intrinsically linked to geographic range overlap, our method of ancestral state reconstruction is akin to estimating the range size of the most recent common ancestor of two species as the mean range size of the species (e.g., Coyne and Orr 1989; Berlocher and Feder 2002). For example, if *P. shumardi* co-occurs with 0.051 of the other

*Percina* species and its sister species *P. vigil* co-occurs with 0.033 of the other species, we would estimate that the ancestor of the two species co-occurred with  $(0.033 + 0.051)/2$  or 0.059 of the other species.

Next, we multiplied the proportion of total species with which an ancestor was expected to co-occur by the number of lineages extant at the same time as the ancestor (node) to convert the proportion back into a number of species, a value more relevant to our hypothesis. Returning to the example above, if the most recent common ancestor (MRCA) of *P. shumardi* and *P. vigil* was extant at the same time as 21 other *Percina* species, the *shumardi-i-vigil* ancestor would have been expected to co-occur with  $0.059 \times 21 = 1.23$  other species. This value, 1.23, represents the “reconstructed co-occurrence frequency” for the node subtending *P. shumardi* and *P. vigil* and was subsequently used to estimate ancestral co-occurrence at the node subtending *P. shumardi* and *P. vigil* and *P. lenticula* (*P. copelandi* [*P. aurora* + *P. brevicauda*]) in the same manner.

We paired our estimates of ancestral species co-occurrence with the standardized contrasts in morphology to ask whether species co-occurrence is positively correlated with the rate of morphological change in *Percina*. Due to the presence of outlying datapoints, we used nonparametric correlation analysis implemented in JMP version 8.1 (SAS Institute, Inc., Cary, NC) instead of standard linear regression. We estimated the correlation between reconstructed species co-occurrence and the SICs on each PC axis at each node in a total of eight correlation analyses, one for each PC axis. Instead of using the overly conservative sequential Bonferroni approach to account for multiple tests, we used a Bernoulli process to estimate the probability of obtaining  $k$  results of  $n$  total tests that are significant at a specified  $\alpha$  value due to chance alone (Moran 2003).

Reconstructions of ancestral states by all methods including ours become more and more uncertain with increasing depth in the tree. This uncertainty may affect the veracity of conclusions drawn from the data. To account for uncertainty in our reconstructions of co-occurrence at deeper nodes, we estimated the strength of correlation between co-occurrence and rate of morphological change using data only from the shallowest nodes: those subtending a pair of extant species. In cases in which data were not affected by outliers, we used parametric regression for our analyses.

## Results

The phylogenetic tree of *Percina* that resulted from our Bayesian analysis of the cytochrome *b* sequence data is very similar to trees that resulted from parsimony and maximum-likelihood analyses of the same data (Near 2002). Many of the internal nodes of our Bayesian tree are supported with high posterior probabilities

(Fig. 2). An optimal smoothing parameter of 3.16 was estimated from the penalized-likelihood cross-validation analysis and subsequent penalized-likelihood analysis estimated the age of the most recent common ancestor of *Percina* at 19.8 my (Fig. 2).

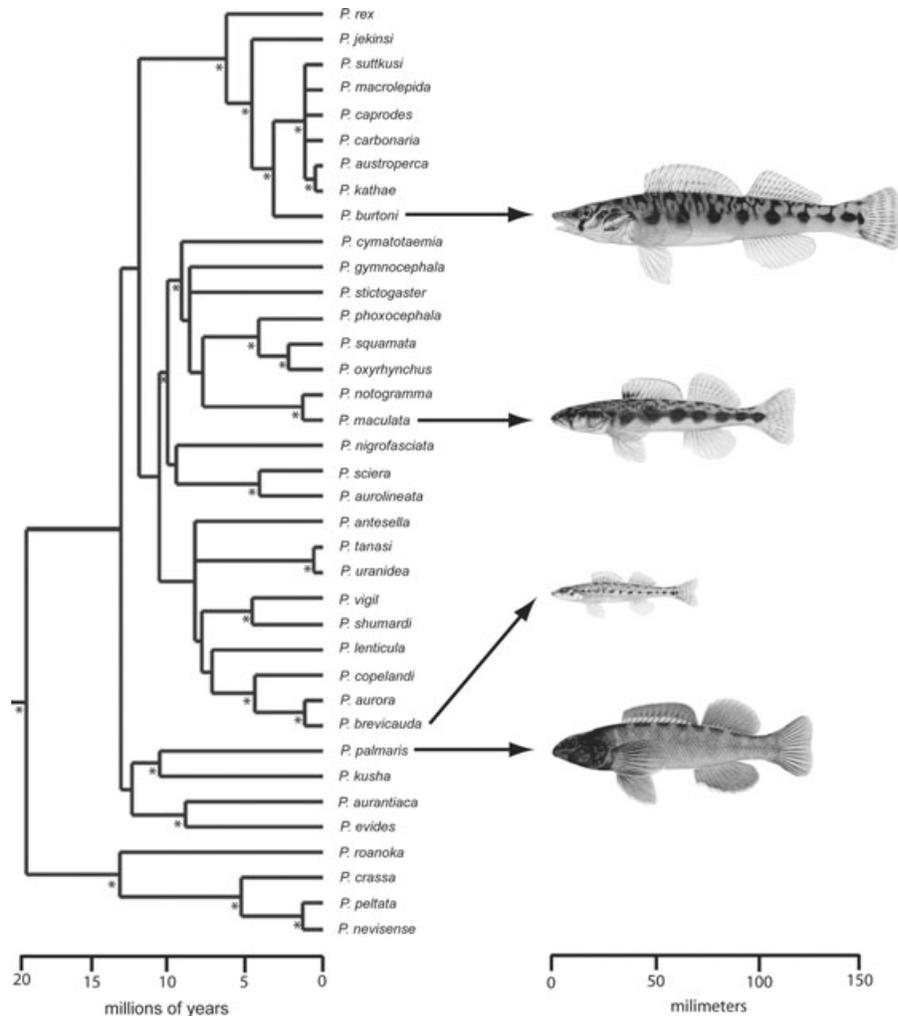
Independent contrasts (ICs) on PC axes 1, 2, 4, 5, 6, 7, and 8 are not adequately standardized by their variance (square root sum of the branch lengths subtending each node) (linear regression:  $P < 0.05$ ). Although log and power transformation did not significantly improve standardization, we chose to proceed with our analysis for three reasons. First, inadequate standardization of contrasts will not reduce the validity of our conclusions as long as our results are not dependent on inadequate contrast standardization (i.e., as long as co-occurrence is not significantly correlated with the rate of change along all seven of the PC axes for which contrasts could not be standardized). Second, interpretation of ICs as a rate of change is made considerably easier by the retention of untransformed branch lengths when those branch lengths are in absolute time. Third, the inadequate standardization of ICs by variance suggests either that stabilizing selection influenced the evolution of the character or that change in the character was punctuational (Diaz-Uriarte and Garland 1996). In contrast, when ICs in a character are adequately standardized by the variance, the character is most likely to have evolved in a manner consistent with a random walk representing a pattern of undirected change. Competition for limited resources has been shown to place selection pressure on the competing organisms (Slatkin 1980; Taper and Case 1992) and is therefore expected to produce a pattern of morphological change that is directed rather than random.

Principal components 1–3 have eigenvalues greater than or equal to one and in combination, these axes describe more than half (64.5%) of the morphological variation among species. PC axis 1 captures variation in head shape among species, PC axis 2 captures variation in the length of the lower jaw and the size of the mouth opening, and PC axis 3 describes variation in BS and pectoral fin shape (Table 1).

The rates of change along PC axes 1, 3, 4, 6, 7, and 8 are positively correlated with species co-occurrence across the *Percina* phylogeny (Table 2; Fig. 3). The probability of obtaining six of eight correlations significant at  $\alpha = 0.05$  is very small ( $P = 3.95 \times 10^{-7}$ ), suggesting a strong overall trend of a correlation between co-occurrence and the rate of morphological evolution in *Percina*. When an analysis is limited to the 10 nodes subtending extant species, correlation strength decreases due to a reduction in power but remains greater than zero.

## Discussion

We found a positive correlation between the rate of change in ecologically relevant morphological features and species co-occurrence in *Percina*. Specifically, we determined that the rate



**Figure 2.** Phylogenetic tree of 37 *Percina* species based on a Bayesian analysis of 1.1 kb of the mitochondrial cytochrome *b* locus. Branch lengths are given in absolute time. Nodes with an asterisk have  $\geq 95\%$  Bayesian posterior probability. The four *Percina* species are shown approximately to scale (*P. burtoni* [150 mm SL], *P. maculata* [95 mm SL], *P. brevicauda* [50 mm SL], and *P. palmaris* [100 mm SL]) and illustrate the degree of variation among species in body size and head and fin shape.

of change in head, jaw, and pectoral fin shape and BS is higher at nodes that are reconstructed to co-occur with a greater number of other *Percina* species. Based on these results, we conclude that the morphological diversification of *Percina* is linked to co-occurrence with congeners such that co-occurrence with more congeners is either a cause or a result of elevated rates of morphological change. This result is in general accordance with previous studies that have used alternative methodologies to study patterns of community-wide morphological change in a variety of fish and nonfish taxa (e.g., Seehausen and Schluter 2004; Dayan and Simberloff 2005; Rabosky et al. 2007).

The rates of change along six of the eight morphological axes are positively correlated with species co-occurrence when data from all nodes are included. Of the six significant axes, axes 1 and 3 (eigenvalues = 2.04 and 1.49 respectively) explain the greatest amount of morphological variation among species. The

characters that are most strongly correlated with these two axes, include, on axis 1, size-corrected GW, hyoid length, and BCL and, on axis 3, BS and PFR. Each of these characters is likely to have functional and ecological consequences based on research in darters or other perciform taxa. BS and head shape (described by a combination of size-corrected GW, HL, and BCL) are correlated with feeding ecology (i.e., prey size and type) whereas the PFR is linked to habitat use and more specifically to depth in the water column. These results suggest that feeding ecology and habitat use are the two axes along which *Percina* exhibit the greatest ecological divergence.

BS is positively correlated with prey size and diet breadth in darters (Miller 1983; Page 1983; Page and Swofford 1984). Specifically, greater diet breadth has been shown to be one of the consequences of larger BS in darters (Page and Swofford 1984). SL (effectively, body length) varies over 100 mm in *Percina*; it

**Table 1.** Results of a principal components analysis based on the correlations among eight morphological characters.

PC axis	1	2	3	4	5	6	7	8
Eigenvalue	2.04	1.63	1.49	0.95	0.82	0.53	0.44	0.11
Percent total variance	25.5	20.4	18.6	11.8	10.3	6.65	5.45	1.31
Cumulative percent variance	25.5	45.9	64.5	76.3	86.6	93.2	98.7	100
Variable loadings								
BS	0.087	-0.029	0.65	-0.047	0.51	0.40	0.35	-0.16
CLR	-0.028	-0.47	0.27	0.61	-0.30	-0.27	0.37	0.18
OLR	-0.00012	0.56	0.15	0.38	0.44	-0.53	-0.14	0.15
PFR	-0.17	0.093	-0.64	0.30	0.30	0.18	0.55	-0.19
Size-corrected GW	0.55	0.11	-0.12	0.40	-0.024	0.53	-0.22	0.43
Size-corrected PL	0.098	-0.58	-0.22	-0.23	0.57	-0.211	-0.095	0.42
Size-corrected HL	0.50	0.26	-0.028	-0.41	-0.19	-0.26	0.58	0.27
Size-corrected BCL	-0.63	0.21	0.092	-0.12	-0.079	0.24	0.13	0.67

ranges from 50 mm (Coal Darter *P. brevicauda*) (Suttkus et al. 1994) to 180 mm (Southern Logperch *P. austroperca*) (Boschung and Mayden 2004). Small amphipods, isopods, and crayfishes are too large to be consumed by small species. In contrast, both large and small species are capable of consuming aquatic insect larvae such as midge and black flies, mayflies, and caddisflies (Matthews et al. 1982; Page and Swofford 1984; van Snik Gray et al. 1997).

The shape of the pectoral fin (measured as the PFR) has been correlated with swimming performance and patterns of habitat use in a wide variety of fish taxa (Webb 1984). Among wrasses and parrotfishes, in particular, round, low-PFRs are characteristic of midwater species that inhabit quiet water (Bellwood and Wainwright 2001). In contrast, wing-like, high-PFRs facilitate precise maneuvering and are characteristic of species that live in high-complexity habitats (Webb 1984) or in areas of high-velocity water flow (Bellwood and Wainwright 2001). *Percina* differs from other darter lineages in its possession of a functional swim bladder (Evans and Page 2003). Thus, species are capable of occupying either midwater or benthic microhabitats (Greenberg 1991; Welsh

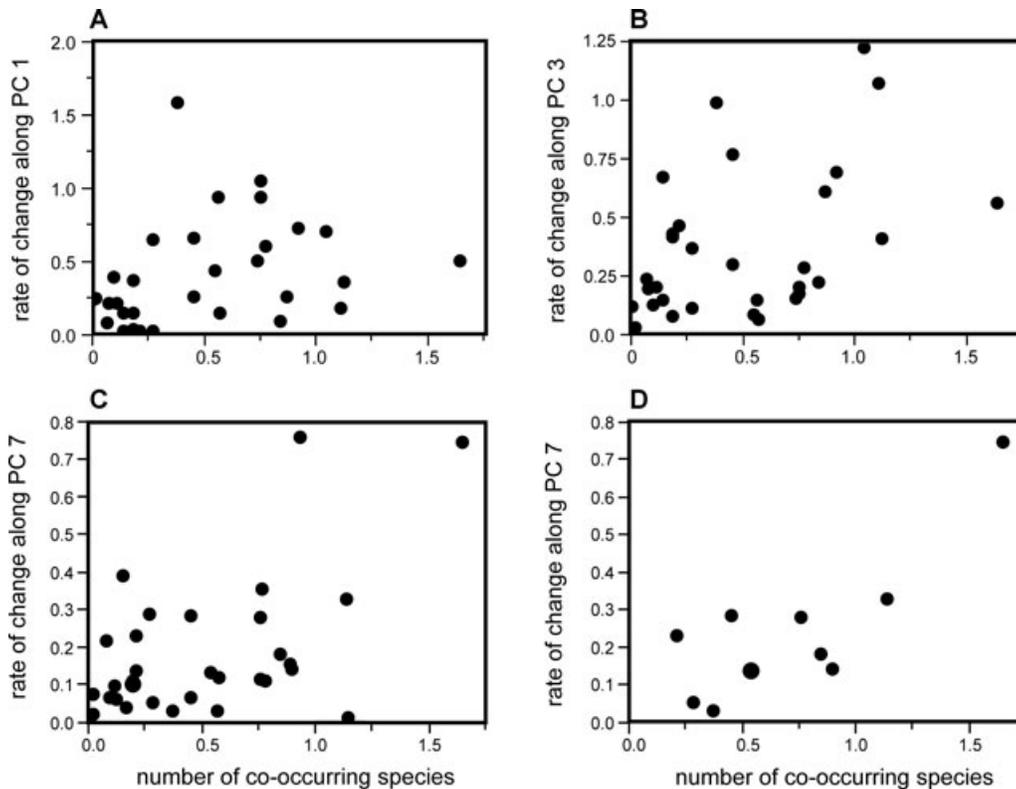
and Perry 1998; Near 2002). Based on functional data from other taxa, paddle-shaped, low-aspect ratio fins are likely to be better suited for life in midwater due to their high efficiency whereas wing-like, high-aspect ratio fins are useful for holding position on the substrate and should therefore be characteristic of only the most benthic species of *Percina*.

Head shape (described by a combination of size-corrected GW, HL, and BCL) is correlated with prey type as well as with prey-capture technique among darters. *Percina* species exhibit considerable variation in this character. Most species of *Percina* have blunt snouts (GW only slightly shorter than BCL) and feed on the surface of rocks (Carlson 2008). However, two subgroups of *Percina* have relatively long, thin snouts (low GW relative to BCL), the *P. caprodes* group (*P. caprodes*, *P. burtoni*, *P. jenkinsi*, *P. carbonaria*, *P. nebulosa*, *P. kathae*, and *P. austroperca*) and species in the *P. phoxocephala* group (*P. phoxocephala*, *P. oxyrhynchus*, and *P. squamata*). Species in the *P. caprodes* group use their snout to flip over rocks and other debris (Etnier and Starnes 1993) whereas species in the *P. phoxocephala* group use their snout to probe between rocks (Page 1983; Carlson 2008).

Although we did not use geographic range overlap per se to quantify species co-occurrence, our estimates of co-occurrence are implicitly linked to geographic range size; species cannot co-occur by our metric unless their geographic ranges overlap. It follows that as the size and shape of a species' range changes over time, so, too, might the number of species with which it co-occurs change. Geographic ranges typically have a high rate of expansion or contraction (Losos and Glor 2003) and it is difficult to reconstruct with certainty either the geographic range of an extinct taxon or, by extension, the number of species with which an extinct taxon co-occurs. Reconstruction of ancestral ranges becomes increasingly difficult with increasing depth in the tree (Fitzpatrick and Turelli 2006). We therefore recognize that our estimates of species co-occurrence at deeper nodes in the phylogeny are likely to be associated with error and performed an

**Table 2.** Strength of the correlation between rate of morphological change (SIC) along each of the eight PC axes and reconstructed number of co-occurring species across all nodes in the phylogeny. *P*-values in bold are significant at  $\alpha=0.05$ .

PC Axis	Spearman's $\rho$	<i>P</i> -value
1	0.43	<b>0.015</b>
2	0.30	0.10
3	0.43	<b>0.016</b>
4	0.39	<b>0.029</b>
5	0.25	0.18
6	0.45	<b>0.010</b>
7	0.39	<b>0.031</b>
8	0.45	<b>0.010</b>



**Figure 3.** Scatterplot of the mean number of co-occurring species and rate of change along three PC axes at each node in the phylogeny (A) PC 1, (B) PC 3, (C) PC 7, and only at those nodes subtending extant species, (D) PC 7. Each of the PC axes describes one of the most important axes of morphological variation among species of *Percina*.

additional set of correlation analyses restricted to nodes subtending pairs of extant species to account for this error. The correlations resulting from these analyses were positive but markedly weaker than those including all nodes. These results indicate that the rate of morphological change is less strongly associated with species co-occurrence at younger nodes. This is not expected, however, given that of the 10 species pairs included in the analysis, only two include species that actually co-occur.

Ecological communities that include one or more species of *Percina* also typically include one or more *Etheostoma* and/or *Nothonotus* or *Ammocrypta* species. Species in the latter two groups rarely co-occur as a result of occupying drastically different microhabitats and geographic areas (Carlson 2008). Due to the ecological differences between *Percina* and non-*Percina*, we expect that *Percina*–*Percina* interactions are both more likely to occur and more likely to be correlated with morphological change than *Percina*–non-*Percina* interactions. To test the hypothesis that co-occurrence among *Percina* and non-*Percina* species is less closely linked to morphological change than *Percina*–*Percina* interactions, we performed an analysis that was identical to our previous analysis except that we estimated and then reconstructed co-occurrence among each *Percina* and all non-*Percina* at each node. The resulting correlations were weaker than those includ-

ing only *Percina* (mean  $\rho$ : *Percina* = 0.39, non-*Percina* = 0.33) indicating that *Percina*–*Percina* co-occurrence is more closely linked to morphological change than *Percina*–non-*Percina* co-occurrence.

Our finding that the rates of change of several ecologically important morphological characters are positively correlated with species co-occurrence supports our hypothesis that co-occurrence among close relatives is linked to morphological change. There are, however, other means by which ecologically similar species can come to co-occur. For example, differential predation or susceptibility to parasites has also been shown to facilitate the coexistence of ecologically similar species (e.g., Paine 1966). We cannot rule out the possibility that co-occurrence among *Percina* species is made possible either fully or in part by one or more of these forces.

The correlation between rates of morphological change and species co-occurrence in *Percina* is intriguing. However, it is not possible at this time to determine whether rapid morphological change in *Percina* enables greater co-occurrence (i.e., change occurs prior to co-occurrence and species that are more different in morphology are more likely to co-occur) or whether greater co-occurrence and hence, a greater potential for interactions with other *Percina* species, causes more rapid morphological change

(i.e., change occurs subsequent to co-occurrence). We do know, however, that morphological change following co-occurrence, (i.e., character displacement) (Brown and Wilson 1956), has been recorded in darters. In a recent study of several species of *Etheostoma*, Knouft (2003) found that populations of the same species differ in morphology between areas in which they occur in sympatry with an ecologically similar species and in which they occur in allopatry. In addition, morphological divergence among populations of the same species was greater when those populations occurred with more close relatives (Knouft 2003). In a different study, Carlson (2008) found evidence of ecologically relevant morphological change in the native Tessellated Darter *Etheostoma olmstedi* following the introduction of its competitively superior congener, *E. zonale*. Thus, character displacement represents a viable mechanism of morphological change in darters. Other mechanisms, however, may also underlie the observed pattern of correlated co-occurrence and rates of morphological change.

The relationship between the rate of morphological change and co-occurrence with close relatives has not yet been examined for other taxa. The results of our analysis in the darter clade *Percina*, however, suggest that co-occurrence with close relatives may be an extrinsic factor that affects the rate of morphological diversification of a lineage and is therefore a factor that is worthy of study in additional lineages of plants and animals.

#### ACKNOWLEDGMENTS

We thank C. Dardia and J. Friel at the Cornell University Museum of Vertebrates, M. Retzer at the Illinois Natural History Survey, H. Bart at the Tulane Museum of Natural History, and B. Kuhajda at the University of Alabama Ichthyology Collection for generously loaning specimens and/or supplying collection databases for this study. J. Kendrick and D. Etnier provided collection assistance at the University of Tennessee Research Collection of Fishes. Illustrations in Figure 2 were provided J. Tomelleri. Discussions with B. O'Meara and J. Whittall were crucial to development of the analytical methods used in this study. D. Collar, B. O'Meara, S. Heard, and several anonymous reviewers provided insightful comments and useful suggestions on earlier drafts of this manuscript. Funding for RLC provided by a National Science Foundation Graduate Research Fellowship, the Center for Population Biology at UC Davis, and a Graduate Research Mentorship Fellowship at UC Davis. Research support for PCW was provided by National Science Foundation grant DEB-0717009.

#### LITERATURE CITED

- Abrams, P. A. 1986. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theor. Popul. Biol.* 29:107–160.
- Bellwood, D. R., and P. C. Wainwright. 2001. Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* 20:139–150.
- Bengtsson, J. 1989. Interspecific competition increases local extinction rate in a metapopulation system. *Nature* 340:713–715.
- Berlocher, S. H., and J. L. Feder. 2002. Sympatric speciation in phytophagous insects: moving beyond controversy? *Annu. Rev. Entomol.* 47:773–815.
- Boschung, H. T. Jr., and R. L. Mayden. 2004. The fishes of Alabama. Smithsonian Books, Washington, D.C.
- Brown, W. L. Jr., and E. O. Wilson. 1956. Character displacement. *Syst. Zool.* 5:49–64.
- Carlson, R. L. 2008. Morphological change in the Tessellated Darter (*Etheostoma olmstedi*) following the introduction of the Banded Darter (*E. zonale*) to the Susquehanna River Drainage. *Copeia* 3:661–668.
- . 2008. Evolution of ecological and morphological diversity in darter fishes (Percidae: Etheostomatinae). Unpubl. Ph.D. Dissertation, Univ. of California, Davis. 134 pp.
- Carroll, A. M., P. C. Wainwright, S. H. Huskey, D. C. Collar, and R. G. Turnigan. 2004. Morphology predicts suction feeding performance in centrarchid fishes. *J. Exp. Biol.* 207:3873–3881.
- Cavender, T. M. 1986. Review of the fossil history of North American freshwater fishes. Pp. 699–724 in C. H. Hocutt, and E. O. Wiley, eds. The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.
- Collar, D. C., T. J. Near, and P. C. Wainwright. 2005. Comparative analysis of morphological diversity: does disparity accumulate at the same rate in two lineages of centrarchid fishes? *Evolution* 59:1783–1794.
- Coyne, J. A., and H. A. Orr. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43:362–381.
- Dayan, T., and D. Simberloff. 1994. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. *Ecology* 75:1063–1073.
- . 2005. Ecological and community-wide character displacement: the next generation. *Ecol. Lett.* 8:875–894.
- Diaz-Uriarte, R. and T. Garland Jr. 1996. Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. *Syst. Biol.* 45:27–47.
- Etnier, D. A., and W. C. Starnes. 1993. Fishes of Tennessee. Univ. of Tennessee Press, Knoxville, TN.
- Evans, J. D., and L. M. Page. 2003. Distribution and relative size of the swim bladder in *Percina*, with comparisons to *Etheostoma*, *Crystallaria*, and *Ammocrypta* (Teleostei: Percidae). *Environ. Biol. Fish.* 66:61–65.
- Fitzpatrick, B. M., and M. Turelli. 2006. The geography of mammalian speciation: mixed signals from phylogenies and range maps. *Evolution* 60:601–615.
- Foote, M. 1997. The evolution of morphological diversity. *Annu. Rev. Ecol. Syst.* 28:129–152.
- Garland, T. Jr. 1992. Rate tests for phenotypic evolution using phylogenetically independent contrasts. *Am. Nat.* 140:509–519.
- Gatesy, S. M., and K. M. Middleton. 1997. Bipedalism, flight, and the evolution of theropod locomotor diversity. *J. Vertebr. Paleontol.* 17:308–329.
- Golenberg, E. M., D. E. Giannasi, M. T. Clegg, C. J. Smiley, M. Durbin, D. Henderson, and G. Zurawski. 1990. Chloroplast DNA sequence from a Miocene Magnolia species. *Nature* 344:656–658.
- Greenberg, L. A. 1991. Habitat use and feeding behavior of thirteen species of benthic stream fishes. *Environ. Biol. Fish.* 31:389–401.
- Haag, W. R., and J. M. L. Warren. 2006. Seasonal feeding specialization on snails by river darters (*Percina shumardi*) with a review of snail feeding by other darter species. *Copeia* 2006:604–612.
- Hardin, G. 1960. The competitive exclusion principal. *Science* 131:1292–1297.
- Harmon, L. J., and J. B. Losos. 2005. The effect of intraspecific sample size on the type I and type II error rates in comparative studies. *Evolution* 59:2705–2710.
- Hutcheon, J. M., and T. Garland Jr. 2004. Are megabats big? *J. Mammal. Evol.* 3–4:257–277.

- Knouft, J. H. 2003. Convergence, divergence, and the effect of congeners on body size differences in stream fishes. *Evolution* 57:2374–2382.
- Knouft, J. H., J. B. Losos, R. E. Glor, and J. J. Kolbe. 2006. Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology* 87:S29–S39.
- Losos, J. B., and R. E. Glor. 2003. Comparative methods and the geography of speciation. *Trends Ecol. Evol.* 18:220–227.
- Losos, J. B., M. Leal, R. E. Glor, K. de Queiroz, R. E. Hertz, L. Rodriguez Schettino, A. Chamizo Lara, T. R. Jackman, and A. Larson. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* 424:542–545.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599–619.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. *Proc. Natl. Acad. Sci. USA* 51:1207–1210.
- Maddison, W. P., and D. R. Maddison. 2004. Mesquite: a modular system for evolutionary analysis. Version 1.05.
- Matthews, W. J., J. R. Bek, and E. Stuart. 1982. Comparative ecology of the darters *Etheostoma podostemone*, *E. flabellare* and *Percina roanoka* in the Upper Roanoke River Drainage, Virginia. *Copeia* 4:805–814.
- Midford, P. E., T. Garland Jr., and W. P. Maddison. 2003. PDAP Package.
- Miller, G. L. 1983. Trophic resource allocation between *Percina sciera* and *P. ouachitae* in the Tombigbee River, Mississippi. *Am. Midl. Nat.* 110:299–313.
- Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405.
- Near, T. J. 2002. Phylogenetic relationships of *Percina* (Percidae: Etheostomatinae). *Copeia* 1:1–14.
- . 2008. Rescued from synonymy: a redescription of *Percina bimaculata* Haldeman. *B. Yale Mus. Nat. Hist.* 49:3–18.
- Near, T. J., and M. F. Benard. 2004. Rapid allopatric speciation in logperch darters (Percidae: Percina). *Evolution* 58:2798–2808.
- Near, T. J., and B. P. Keck. 2005. Dispersal, vicariance, and timing of diversification in *Nothonotus* darters. *Mol. Ecol.* 14:3485–3496.
- Near, T. J., D. I. Bolnick, and P. C. Wainwright. 2005. Fossil calibrations and molecular divergence time estimates in centrarchid fishes (Teleostei: Centrarchidae). *Evolution* 59:1768–1782.
- O'Meara, B. C., C. M. Ané, M. J. Sanderson, and P. C. Wainwright. 2006. Testing for different rates of continuous trait evolution in different groups using likelihood. *Evolution* 60:922–933.
- Page, L. M. 1983. *Handbook of Darters*. TFH Publications, Inc., Neptune City, NJ.
- . 2000. Etheostomatinae. Pp. 225–253 in J. F. Craig, ed. *Percid fishes: systematics, ecology and exploitation*. Blackwell Science, Oxford, U.K.
- Page, L. M., and T. J. Near. 2007. *Percina williamsi*, a new darter from the Upper Tennessee River Drainage related to *Percina macrocephala* (Percidae: Etheostomatinae). *Copeia* 3:605–613.
- Page, L. M., and D. L. Swofford. 1984. Morphological correlates of ecological specialization in darters. *Environ. Biol. Fish.* 11:139–159.
- Paine, R. 1966. Food web complexity and species diversity. *Am. Nat.* 100:65–75.
- Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches over evolutionary time. *Science* 285:1265–1267.
- Posada, D., and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- . 2001. Selecting the best-fit model of nucleotide substitution. *Syst. Biol.* 50:580–601.
- Rabosky, D. L., J. Reid, M. A. Cowan, and J. Foulkes. 2007. Overdispersion of body size in Australian desert lizard communities at local scales only: no evidence for the Narcissus effect. *Oecologia* 154:561–570.
- Rensch, B. 1959. *Evolution above the species level*. Columbia Univ. Press, New York, NY.
- Richard, B. A., and P. C. Wainwright. 1995. Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *J. Exp. Biol.* 198:419–443.
- Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: a neglected literature. *Am. Nat.* 144:596–627.
- Robison, H. W., and T. M. Buchanan. 1988. *Fishes of Arkansas*. Univ. of Arkansas Press, Fayetteville, AR.
- Rohlf, F. J. and L. F. Marcus. 1993. A revolution in morphometrics. *Trends Ecol. Evol.* 8:129–132.
- Ronquist, F., and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Mol. Biol. Evol.* 19:101–109.
- . 2003. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* 19:301–302.
- Schluter, D. 1988. Character displacement and the adaptive radiation of finches on islands and continents. *Am. Nat.* 131:799–824.
- . 2000. *The Ecology of Adaptive Radiation*. Oxford Univ. Press, Oxford, U.K.
- Schoener, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19:189–213.
- Seehausen, O. and D. Schluter. 2004. Male-male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proc. R. Soc. Lond. B* 271:1345–1353.
- Simpson, G. G. 1953. *The major features of evolution*. Simon and Schuster, New York, NY.
- Slatkin, M. 1980. Ecological character displacement. *Ecology* 61:163–177.
- Smith, G. R. 1981. Late Cenozoic freshwater fishes of North America. *Annu. Rev. Ecol. Syst.* 12:163–193.
- Smith, G. R., and R. R. Miller. 1985. Taxonomy of fishes from Miocene Clarkia Lake beds, Idaho. Pp. 75–83 in C. J. Smiley, ed. *Late Cenozoic history of the Pacific Northwest*. American Association for the Advancement of Science, San Francisco.
- Suttkus, R. D., B. A. Thompson, and H. L. Bart. 1994. Two new darters, *Percina (Cottogaster)*, from the southeastern United States, with a review of the subgenus. *Occ. Pap. Tulane U. Mus. Nat. Hist.* 4:1–46.
- Svanbäck, R., P. C. Wainwright, and L. A. Ferry-Graham. 2002. Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. *Physiol. Biochem. Zool.* 75:532–543.
- Taper, M. L. and T. J. Case. 1992. Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* 46:317–333.
- van Snik Gray, E. S., J. M. Boltz, K. A. Kellogg, and J. Stauffer, Jr. 1997. Food resource partitioning by nine sympatric darter species. *T. Am. Fish. Soc.* 126:822–840.
- Van Valkenburgh, B. 1988. Trophic diversity in past and present guilds of large predatory animals. *Paleobiology* 14:155–173.
- Wainwright, P. C. 1996. Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* 77:1336–1343.
- Wainwright, P. C., and D. R. Bellwood. 2002. Ecomorphology of feeding in coral reef fishes. Pp. 33–55 in P. F. Sale, ed. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, CA.
- Wainwright, P. C., and B. A. Richard. 1995. Predicting patterns of prey use from morphology with fishes. *Environ. Biol. Fish.* 44:97–113.

- Walker, J. A., and M. W. Westneat. 2002. Performance limits of labriform propulsion and correlates with fin shape and motion. *J. Exp. Biol.* 205:177–187.
- Webb, P. W. 1984. Body form, locomotion, and foraging in aquatic vertebrates. *Am. Zool.* 24:107–120.
- Welsh, S. A., and S. A. Perry. 1998. Habitat partitioning in a community of darters in the Elk River, West Virginia. *Environ. Biol. Fish.* 51:411–419.
- Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. *Science* 191:404–406.
- Westneat, M. W. 1994. Transmission of force and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorphology* 114:103–18.
- Williams, J. D., D. A. Neely, S. J. Walsh, and N. M. Burkhead. 2007. Three new percid fishes (Percidae: *Percina*) from the Mobile Basin drainage of Alabama, Georgia, and Tennessee. *Zootaxa* 1549:1–28.

Associate Editor: F. Galis