The ecological morphology of darter fishes (Percidae: Etheostomatinae)

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Darters are a species-rich radiation of small benthic and benthic-associated stream fishes that comprise approximately 20% of the diversity of the North American freshwater fish fauna. Here, we gather data from 165, or 87%, of described species and use this information to characterize the morphological diversity of the darter radiation. We focus on characters of the oral jaws known to function in prey capture and consumption in other perciform taxa in order to explicitly link morphological diversity to ecological diversity. In addition to a quantitative description of the morphospace occupied by darters, we identify several instances of significant morphological convergence. We also describe three groups of darter species that exhibit unusual jaw morphologies that are used in previously undescribed prey capture behaviours. Despite these new ecomorphs, we find that darters exhibit relatively low variation in trophic morphology when compared with two other radiations of teleost fishes, and that the observed variation is related more to differences in microhabitat use than to differences in prey type. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **100**, 30–45.

ADDITIONAL KEYWORDS: convergence – *Etheostoma* – morphological diversity – oral jaw apparatus – *Percina* – premaxillary frenum.

INTRODUCTION

Darters (Percidae: Etheostomatinae) are a species-rich radiation of freshwater fishes. The 190 described and 30 undescribed species comprise approximately 20% of the recognized diversity of freshwater fishes in North America (Page, 1983; T. J. Near, unpubl. data). Darters are small, often very colourful inhabitants of aquatic environments ranging from small shallow creeks to wide deep rivers across the eastern, southern and south-eastern USA (Kuehne & Barbour, 1983; Page, 1983).

The ecomorphological diversity of the darter lineage is of particular interest for two reasons. First, darter species can exhibit high levels of sympatry (up to 14 species of darters co-occur at some sites on the Kentucky River in Kentucky, USA) (Carlson, Wainwright & Near, 2009). Second, dietary overlap among species is relatively high with selectivity occurring at the prey genus and species', but not family, levels (Alford & Beckett, 2007). Most species are consumers of small, benthic aquatic insect larvae and microcrustaceans, such as chironomids (midges), ephemeropterans (mayflies) and hydropsychids (caddisflies) (Wynes & Wissing, 1982; Page, 1983), although a few species are known to consume small gastropods, either by eating the entirety of the snail (Haag & Warren, 2006) or by removing (apparently by suction) the fleshy snail body from its shell (R. Carlson, pers. observ.). Understanding the variation in jaw morphology among species is therefore expected to provide insight into the differences in prey type and prey capture method that facilitate species' coexistence and, ultimately, the diversification of the lineage in ecology, morphology and number of species.

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Freshwater habitats vary along four primary axes: water depth, flow speed, substrate size and temperature. All darter species are benthic or benthic-associated fishes that either completely lack or possess a much reduced swimbladder (Evans & Page, 2003). Darter species therefore partition habitat along the first three of these axes (Matthews, Beck & Surat, 1982; Page & Swofford, 1984; Chipps, Perry & Perry, 1994; Stauffer *et al.*, 1996; Welsh & Perry, 1998). Species occupy microhabitats ranging from sandy pools to fast-flowing rocky riffles and from deep sand raceways to vegetation-filled springs (Carlson, 2008).

In this study, we describe the morphological diversity of darter fishes with a focus on characters of the skull that have been linked to feeding ecology in other perciform species, particularly prey type and capture method. In addition, we identify several instances of morphological and apparent ecological convergence among darter species. We also describe three novel associations between oral jaw morphology and feeding ecology in darters. The work presented here is a step towards understanding the forces driving the morphological and, by extension, ecological diversification of this species-rich radiation.

MATERIAL AND METHODS

We gathered data from 2–10 cleared and double-stained adult specimens of 164 darter species and one specimen of an additional species, the leopard darter *Percina pantherina* (Moore & Reeves, 1955). Both for simplicity and to facilitate future analyses of ecological diversification in darters, we divided our 165 study species into 11 clades that are thought to represent the major evolutionary lineages of darters (see Table 1 for a list of the study species in each clade). Our clades are based primarily on the major groups of species found in a molecular phylogeny reconstructed using data from 1.1 kb of the mitochondrial cytochrome *b* locus (T. J. Near, unpubl. data). We then found support for our phylogeny-based groups in several other types of data, including traditional generic and subgeneric classifications of species (Page, 1981), geographical range maps, microhabitat (Carlson, 2008), reproductive behaviour and male breeding coloration (Page, 1983). It is worth noting here that we also chose to follow Near & Keck (2005) and to elevate *Etheostoma* (*Nothonotus*) to generic status based on the monophyly of the subgenus and its well-supported position outside of *Etheostoma s.l.*, as indicated by strong Bayesian posterior probabilities on topologies estimated from both mitochondrial and nuclear loci (T. J. Near, unpubl. data).

In four instances, the mitochondrial locus-based phylogeny predicts sister species' relationships that are not supported by our other data: *E. uniporum*–*E. caeruleum*, *E. arteseae*–(*E. uniporum*–*E. caeruleum*), *E. fragi*–*E. variatum* clade and *E. podostomone*–*E. nigrum* (Bossu & Near, 2009; Heckman, Near & Alonzo, 2009). In only two cases, however, does the error place a species in a putatively incorrect clade. First, instead of being sister to *E. caeruleum* Storer, 1845 in the *E. boschungi* clade, as indicated by the mitochondrial data, ecological data and phylogenies reconstructed using multiple nuclear loci indicate that *E. uniporum* Distler, 1968 is more closely related to *E. spectabile* (Agassiz, 1854) and members of the *E. microperca* clade than it is to *E. caeruleum* (Bossu & Near, 2009). We therefore treat *E. uniporum* as a member of the *E. microperca* clade. Likewise, all sources of data other than the mitochondrial phylogeny indicate that *E. fragi* Distler, 1968 is more closely related to *E. spectabile* and members of the *E. microperca* clade than it is to members of the *E. variatum* clade. Thus, we also treat *E. fragi* as a member of the *E. microperca* clade (Table 1).

On each specimen, we measured seven aspects of head and oral jaw shape and size, as well as overall body size (BS). We measured this particular set of characters because each has previously been shown to have predictable consequences for performance in ecologically relevant tasks, including prey capture and consumption in other perciform species (mouth size, Keast, 1978; Richard & Wainwright, 1995; Wainwright, 1996; Carroll *et al.*, 2004; hyoid length, Svanbäck, Wainwright & Ferry-Graham, 2002; lower jaw lever ratios, Westneat, 1994; Wainwright & Richard, 1995); 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 in oral jaw structure (Wainwright & Bellwood, 2002). We measured the following: (1) the standard length (SL), or the distance from the anteriormost 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) (Fig. 1C); (3) the length of the dentigerous arm of the premaxilla (PL) (Fig. 1A); (4) the length of the buccal cavity (BCL) from the anteriormost tip of the dentary to the hyoid symphysis (Fig. 1C); (5) the gape width (GW), the distance between the left and right coronoid processes of the dentary of the closed mouth (Fig. 1A, C); (6) the length of the lower jaw out-lever, the distance from the anteriormost tip of the dentary to the centre of the quadrate–articular jaw joint (Fig. 1B); (7) the 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 centre of the quadrate–articular jaw joint (Fig. 1B); (8) the length of the lower jaw opening in-lever, the distance from the centre of the quadrate–articular joint to the

Table 1. Darter species in each of the 11 major clades. Clade membership was determined primarily by examination of a phylogenetic hypothesis based on 1.1 kb of the mitochondrial cytochrome *b* locus (T. J. Near, unpubl. data) and confirmed by ecological and other natural history data. Values in parentheses are the number of specimens examined in the morphological analysis

Clade	Species (sample size)	Clade	Species (sample size)
Ammocrypta clade	*Allohistium cinereum* (3)	*E. variatum* clade	*E. euzonum* (3)
	Ammocrypta beani (3)		*E. kanawhae* (5)
	A. bifascia (2)		*E. osburni* (5)
	A. clara (3)		*E. sagitta* (3)
	A. meridiana (3)		*E. tetrazonum* (2)
	A. pellucida (3)		*E. variatum* (5)
	A. vivax (3)	*E. blennioides* clade	*E. atripinne* (3)
	Crystallaria asprella (3)		*E. baileyi* (2)
Nothonotus	*N. acuticeps* (10)		*E. barrenense* (3)
	N. aquali (3)		*E. bellator* (2)
	N. bellus (10)		*E. blennioides* (2)
	N. camurus (3)		*E. blennius* (3)
	N. chlorobranchius (5)		*E. brevirostrum* (3)
	N. chuckwachatte (3)		*E. cervus* (3)
	N. douglasi (5)		*E. chermocki* (2)
	N. jordani (4)		*E. colorosum* (3)
	N. juliae (3)		*E. coosae* (3)
	N. maculatus (3)		*E. duryi* (3)
	N. microlepidus (8)		*E. etnieri* (2)
	N. moorei (4)		*E. flavum* (3)
	N. rufilineatus (3)		*E. histrio* (3)
	N. sanguifluus (10)		*E. inscriptum* (3)
	N. tippecanoe (9)		*E. lachneri* (3)
	N. vulneratus (10)		*E. lynceum* (3)
Etheostoma fusiforme clade	*E. chlorosomum* (2)		*E. pyrrhogaster* (4)
	E. collis (3)		*E. rafinesquei* (3)
	E. davisoni (5)		*E. ramseyi* (2)
	E. edwini (4)		*E. raneyi* (2)
	E. fricksium (5)		*E. rupestre* (3)
	E. fusiforme (4)		*E. scotti* (3)
	E. gracile (3)		*E. simoterum* (3)
	E. hopkinsi (2)		*E. swannanoa* (3)
	E. jessiae (4)		*E. tallapoosae* (3)
	E. mariae (4)		*E. thallassinum* (2)
	E. okaloosae (4)		*E. zonale* (3)
	E. parvipinne (3)		*E. zonisitum* (3)
	E. saludae (2)	*E. nigrum* clade	*E. longimanum* (8)
	E. serrifer (3)		*E. nigrum* (2)
	E. stigmaeum (3)		*E. olmstedi* (3)
	E. zonifer (6)		*E. perlongum* (3)
E. microperca clade	*E. bison* (4)		*E. podostomone* (10)
	E. burri (5)		*E. vitreum* (10)
	E. fonticola (5)	*E. forbesi* clade	*E. chienense* (3)
	E. fragi (5)		*E. corona* (3)
	E. kantuckeenese (4)		*E. crossopterum* (3)
	E. microperca (2)		*E. forbesi* (3)
	E. proeliare (3)		*E. neopterum* (3)
	E. punctulatum (5)		*E. nigripinne* (3)
	E. spectabile (5)		*E. olivaceum* (3)
	E. techumsei (4)		*E. squamiceps* (3)
	E. uniporum (5)		

Table 1. *Continued*

| Clade	Species (sample size)	Clade	Species (sample size)
E. barbouri clade	*E. barbouri* (3)		*P. copelandi* (3)
	E. flabellare (3)		*P. crassa* (3)
	E. kennicotti (3)		*P. cymatotaenia* (3)
	E. obeyense (3)		*P. evides* (2)
	E. smithi (3)		*P. gymnocephala* (2)
	E. striatulum (2)		*P. jenkinisi* (3)
E. boschungi clade	*E. artesiae* (5)		*P. kathae* (3)
	E. asprigene (3)		*P. kusha* (3)
	E. boschungi (4)		*P. lenticula* (3)
	E. caeruleum (3)		*P. maculata* (3)
	E. collettei (2)		*P. macrocephala* (3)
	E. craigini (5)		*P. microlepida* (3)
	E. ditrema (5)		*P. nasuta* (3)
	E. exile (5)		*P. nevisense* (2)
	E. grahami (4)		*P. nigrofasciata* (3)
	E. lepidum (3)		*P. notogramma* (3)
	E. luteovinctum (5)		*P. oxyrhynchus* (3)
	E. radiosum (3)		*P. palmaris* (3)
	E. swaini (3)		*P. pantherina* (1)
	E. trisella (3)		*P. peltata* (3)
	E. tuscumbia (3)		*P. phoxocephala* (3)
	E. whipplei (2)		*P. rex* (3)
Percina	*P. antesella* (3)		*P. roanoka* (3)
	P. aurantiaca (4)		*P. sciera* (3)
	P. aurolineata (3)		*P. shumardi* (3)
	P. aurora (2)		*P. squamata* (3)
	P. austroperca (3)		*P. stictogaster* (3)
	P. brevicauda (3)		*P. suttkusi* (3)
	P. burtoni (3)		*P. tanasi* (3)
	P. caprodes (3)		*P. uranidea* (3)
	P. carbonaria (3)		*P. vigil* (3)

insertion of the interoperculomandibular ligament on the retroarticular process of the articular (Fig. 1B). The lower jaw in-lever and out-lever measurements were then used to calculate the 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). Finally, we estimated the BS of each specimen as the geometric mean of five linear head and body measurements: SL, BCL, GW, HL and PL. We used this composite metric of BS instead of a more traditional measure such as SL because, by virtue of its multidimensionality, the geometric mean provides a more synthetic estimate of overall BS and is therefore particularly well suited to groups of organisms, such as darters, that vary not only in BS but also in body shape (Rohlf & Marcus, 1993; Zani, 2000).

Prior to statistical 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. 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 each species were used to estimate the best-fit regression line. We identified the major axes of variation in head, jaw and mouth shape and BS using a principal component (PC) analysis on the correlations among size-corrected measurements of log-transformed BCL, GW, HL, and PL, OLR and CLR, and log-transformed BS. We then used a series of discriminant function analyses to determine whether each species could be assigned to the correct clade using the PC axes.

To study the morphological convergence among darter species, we first used the scatterplots of species' means in morphospace to qualitatively identify species that were nearer to a cluster of nonclade mates (members of a different clade) than to members of the same clade. Next, we estimated the morphological distance between each species and the clade to which it had converged as the Euclidean distance between the species and the clade mean on the seven
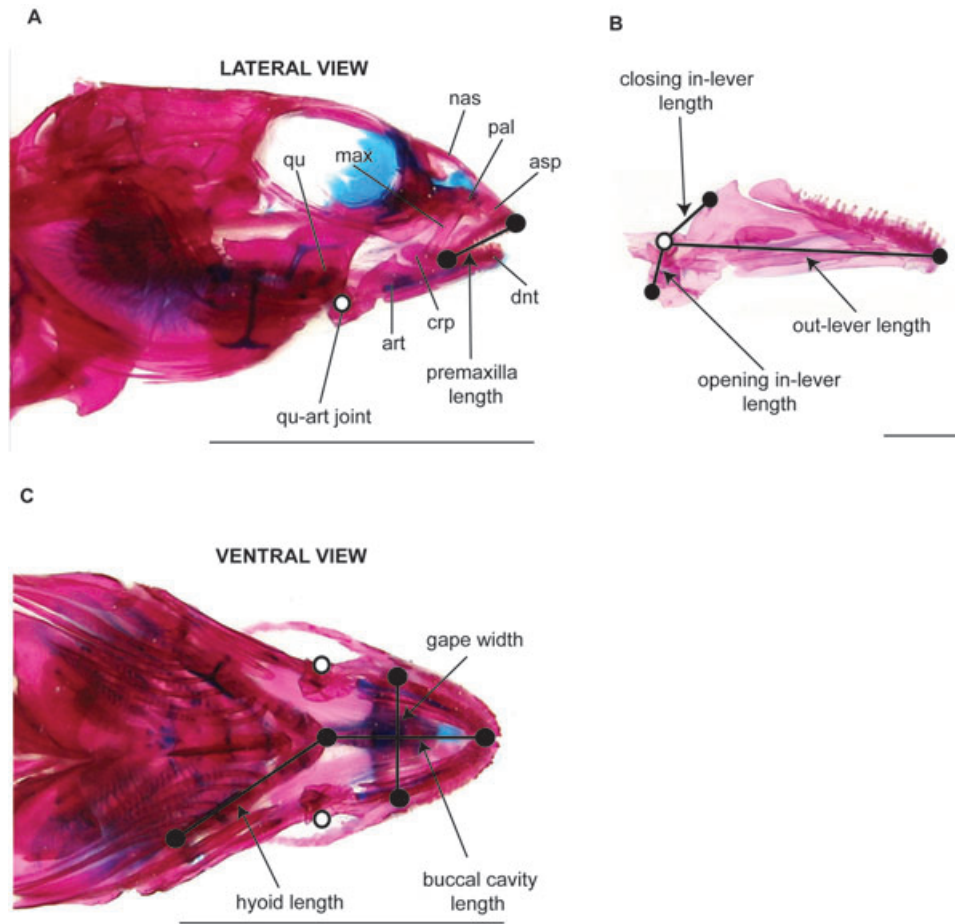
Figure 1. A, Lateral view of the skull of a cleared and stained specimen of *Percina palmaris* (Bailey, 1940). Landmarks and bones used in the measurement of morphological characters are indicated. B, Lower jaw of *P. palmaris*. C, Ventral view of the skull of *P. palmaris* with relevant lengths shown. Images in (A) and (C) are from the same individual. Scale bars: A, C, 1 cm; B, 20 mm. art, articular; asp, ascending process of the premaxilla; crp, coronoid process of the dentary; dnt, dentary; max, maxilla; nas, nasal; pal, palatine; qu, quadrate.

PC axes. To incorporate branch length data, we also reconstructed the ancestral state on each PC axis for each clade using the *ace* function in the *ape* package (Paradis, Claude & Strimmer, 2004) for the R Statistical Language, and calculated the Euclidean distance between these estimates and the focal species. We then estimated the probability with which the observed morphological similarity between each species and the appropriate clade would be expected to occur simply as a result of undirected (Brownian) movement through morphospace over the evolutionary history of the lineage. To do this, we used the *sim.char* function in the *Geiger* package (Harmon *et al.*, 2008) for R to simulate continuous character evolution under Brownian motion across the phylogeny 1000 times, whilst maintaining a fixed, empirically derived variance–covariance relationship among the PC axes. We estimated the Euclidean distance between each species and the clade mean or between

each species and the reconstructed ancestral state for each of the simulated matrices. We compared the observed distance calculated under both methods with the distribution of simulated distances to estimate the probability that the observed similarity was the result of chance rather than directed movement through morphospace.

We gathered previously published morphological data for two additional teleost lineages, North American freshwater sunfishes and black basses (Centarchidae) (Collar, Near & Wainwright, 2005) and marine wrasses and parrotfishes [Labridae: note that the family Scaridae (parrotfishes) is phylogenetically nested within Labridae] (Wainwright *et al.*, 2004), in order to determine the relative diversity of darters in several shared morphological features. We calculated the variance among species in lower jaw OLR and CLR, log-transformed body size (SL) and SL-corrected and log-transformed gape distance (GW) for

Table 2. Principal components analysis of seven characters of the head, oral jaws and body using data from 165 species of darter. Entries in the main table are the correlations between each principal component and each character

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Percentage of variance explained	37.2	24.1	15.0	11.8	6.9	3.7	1.3
Eigenvalue	2.61	1.69	1.05	0.83	0.49	0.26	0.089
Body size*	0.048	−0.27	0.72	0.62	−0.0035	0.12	0.021
Closing ratio	−0.20	0.62	−0.19	0.38	−0.058	0.63	0.045
Opening ratio	−0.38	0.50	0.12	0.24	0.15	−0.71	0.10
BCL†	−0.55	−0.28	0.033	−0.17	0.035	0.16	0.75
GW†	0.36	0.38	0.38	−0.32	−0.60	−0.036	0.35
PL†	0.38	−0.18	−0.52	0.52	−0.24	−0.24	0.42
HL†	0.49	0.21	0.11	−0.094	0.75	0.75	0.36

*Logarithmic transformation of the geometric mean of SL, BCL, GW, PL and HL.
†Residuals from log–log regression of the character vs. body size.
BCL, buccal cavity length; GW, gape width; HL, hyoid length; PL, premaxilla length; SL, standard length.

eachlineage using data from 122 labrid, 27 centrarchid and 165 darter species.

Morphological diversity, measured as variance among species, is a joint effect of lineage age and the pattern of species' diversification (Peterson, Soberón & Sánchez-Cordero, 1999; O'Meara et al., 2006). We therefore note that labrids are thought to be about twice as old as darters (65 vs. 35 million years) (Kazancioglu et al., 2009) and have about three times as many species (600 labrids vs. 200 darters). In contrast, there are only 32 species of centrarchids and the lineage is approximately equal in age to darters (Near, Bolnick & Wainwright, 2005). Based only on the differences in age among the groups, and assuming a constant rate of Brownian character evolution, we expect labrids to exhibit twice the variance in morphology of either darters or centrarchids. By extension, we expect centrarchids and darters to exhibit similar levels of diversity. Deviations from these expectations are likely to be the result of different rates of diversification along the morphological axes related to prey capture, consumption and other ecologically relevant tasks (Collar et al., 2009).

RESULTS

Major axes of morphological diversity

The first three PCs explain more than three-quarters of the morphological variation among darter species (Table 2). PC1 accounts for 37.2% of the total variation and is dominated by four characters: BCL, PL, HL and GW. Species with high scores on PC1 have a relatively long hyoid, wide gape and long premaxilla, but a short buccal cavity (Fig. 2A, B). The second PC axis explains 24.1% of the variation among species. Species with high scores on PC2 have high lower jaw

OLR and CLR (Fig. 2C, D). The third PC primarily describes variation in BS and explains 15.0% of the total morphological variation among species. Axes 4–7 describe additional aspects of head and jaw shape and BS but, as indicated by the magnitude of their respective eigenvalues, are relatively less important axes of variation among species.

The scatterplots of species' means indicate that species in the E. blennioides clade are morphologically distinguishable from other darters along PC1 and PC2 (Fig. 3A). Only 20% of the species in the E. blennioides clade were incorrectly classified in a discriminant function analysis. All other species, however, are relatively similar in PC1 and PC2 scores. Again, this observation is confirmed quantitatively by discriminant function analysis: more than 60% of species were incorrectly classified using only the first two PC axes. In addition to overall similarity in head and jaw morphology, most species of darter are similar in BS (Fig. 3B).

PC4–7 explain slightly less than one-quarter of the morphological variance among species (Table 2). As a result, species do not fall into morphologically distinct clusters on any of the axes. Instead, most species group near the centre of each axis with a few morphologically extreme outliers. When a discriminant function analysis was performed using all seven PCs, 44% of species were misclassified, only a 6% decrease compared with the analysis that included only PC1–3.

Evidence for morphological convergence

We identified five cases of apparent morphological convergence among darter species from the scatterplots of species' means in PC space (Fig. 3). In three cases, a distantly related species occurred within the
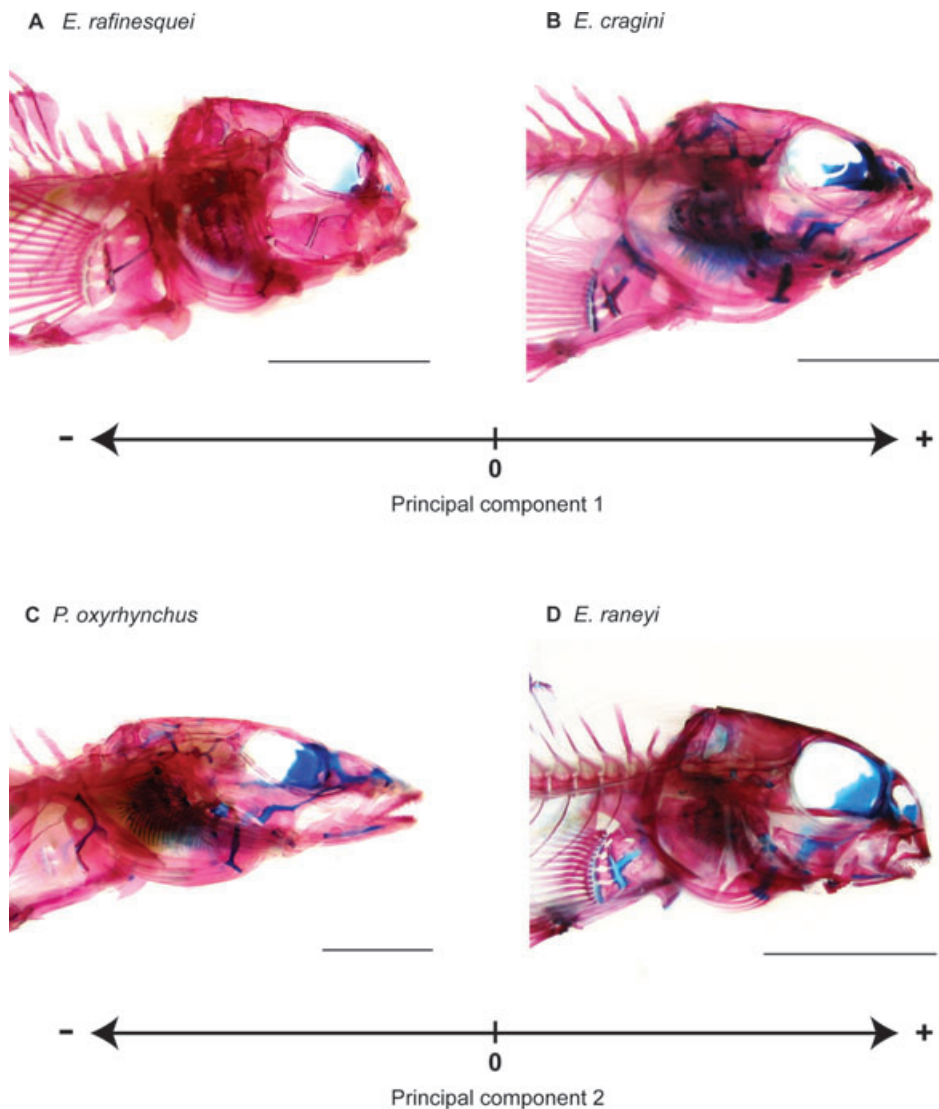
Figure 2. Extent of variation among darter species along the first two principal components (PCs). The species included in this figure fall at the extremes of morphospace. A, *Etheostoma rafinesquei* has the lowest score on PC1; B, *E. cragini* Gilbert, 1885 has the highest score on PC1; C, *Percina oxyrhynchus* has the lowest score on PC2; D, *E. raneyi* Suttkus & Bart, 1994 has the highest score on PC2. Scale bar, 5 mm.

morphospace otherwise occupied only by species in the *E. blennioides* clade: *E. chlorosomum*, *E. podostemone* Jordan & Jenkins, 1889 and *E. longimanum* Jordan, 1888. In a fourth case, *E. sagitta* (Jordan & Swain, 1883) occurred near the cluster of *P. nasuta* (Bailey, 1941), *P. oxyrhynchus* (Hubbs & Raney, 1939), *P. squamata* (Gilbert & Swain, 1887) and *P. phoxocephala* (Nelson, 1876) in morphospace. Finally, *E. vitreum* (Cope, 1870) and species of *Ammocrypta* occupied the same morphospace.

Convergence between *E. longimanum* and species in the *E. blennioides* clade (Fig. 4A), between *E. sagitta* and *P. nasuta*, *P. phoxocephala*, *P. oxyrhynchus*

and *P. squamata* (Fig. 4B) and between *E. vitreum* and *Ammocrypta* (Fig. 4C) is unlikely to be explained by chance (Table 3; $P < 0.05$). In contrast, the similarity between *E. chlorosomum* and species in the *E. blennioides* clade can be attributed to either random or nonrandom movement through morphospace, depending on the test employed (ancestral state reconstruction, $P < 0.037$; extant species only, $P > 0.053$). We did not test for convergence between *E. podostemone* and species in the *E. blennioides* clade because, in the mitochondrial phylogeny, *E. podostemone* falls out as sister to *E. nigrum* Rafinesque, 1820 rather than to *E. logimanum* as predicted by nuclear
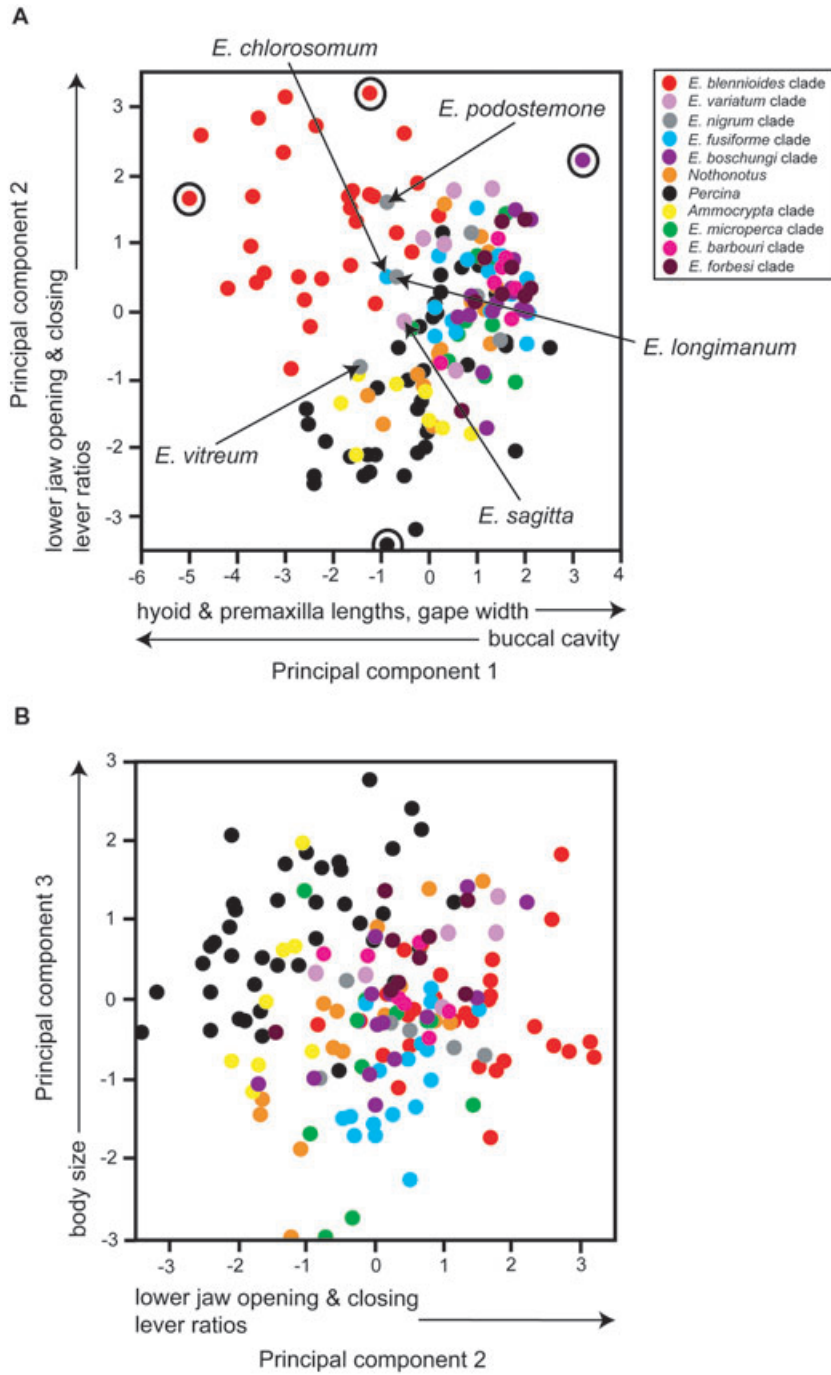
Figure 3. Scatterplots of species' mean scores on principal component 1 (PC1) and PC2 (A) and PC2 and PC3 (B). Character loadings on each axis are shown in Table 1. Circled points correspond to the species in Figure 2. Arrows indicate species that are putatively convergent with another clade (Figure 4).

loci and our other data (Heckman *et al.*, 2009). Thus, any simulation data based on this relationship are likely to lead to inaccurate conclusions about the nature of convergence between *E. podostemone* and other darter species.

THREE NOVEL ECOMORPHS

The prober

Four species of *Percina* and one species of *Etheostoma* exhibit the *prober* ecomorph, including the monophyletic group consisting of *P. nasuta*, *P. squamata*, *P.*
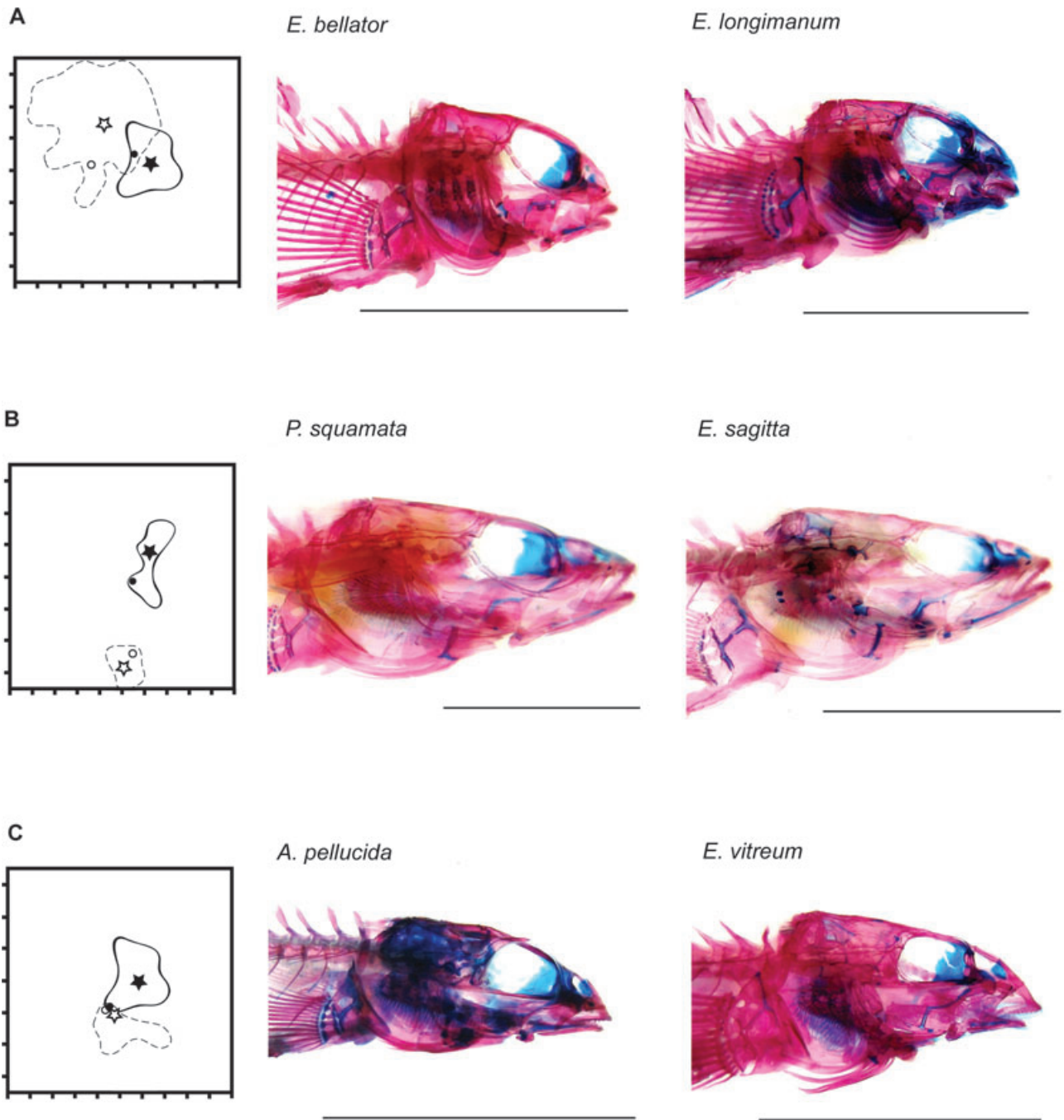
Figure 4. Morphological convergence among darter species. Middle and right-hand images: independent evolution of a blunt snout and short lower jaw in *Etheostoma bellator* Suttkus & Bailey, 1993 and *E. longimanum* (A), a pointed snout and elongate lower jaw in *Percina squamata* and *E. sagitta* (B), and an elongate head, lower jaw and protrusible premaxilla in *Ammocrypta pellucida* (Putnam, 1863) and *E. vitreum* (C). Scale bar, 1 cm. Left-hand images: scatterplots illustrate the area of the morphospace defined by principal component (PC) axes 1 and 2 that is occupied by species in the *E. blennioides* clade (broken line) and *E. nigrum* clade (full line), the four *prober* species of *Percina* (broken line) and the *E. variatum* clade (full line), and species of *Ammocrypta* (broken line) and species in the *E. nigrum* clade (full line). Open stars indicate the morphology reconstructed for the ancestor of each clade or group of species outlined by a broken line, and filled stars indicate the ancestor of clades outlined by a full line. Locations in morphospace of *E. bellator*, *P. squamata* and *A. pellucida* are indicated by an open circle, and locations of *E. longimanum*, *E. sagitta* and *E. vitreum* are indicated by filled circles.

Table 3. Morphological convergence among darter species. We calculated the probability of achieving such extensive morphological similarity in two ways. First, we calculated the Euclidean distance along the seven principal component (PC) axes between each species and the mean of the clade to which it had putatively converged ('extant' method). We then compared this distance with the distribution of distances calculated from 1000 datasets simulated on the phylogeny under Brownian motion. Second, in order to incorporate branch length information, we calculated the Euclidean distance between each species and the estimated ancestor of the clade ('reconstruction' method). We then used a similar simulation approach to estimate the probability of the observed convergence between the focal species and ancestor of the clade

Species – clade or group	Observed distance (extant)	Simulated distance (range)	P value	Observed distance (reconstruction)	Simulated distance (range)	P value
E. longimanum–E. blennioides clade	2.00	1.39–12.5	< 0.008	1.80	1.43–12.3	< 0.006
E. chlorosomum–E. blennioides clade	2.96	1.50–12.2	< 0.054	2.75	1.61–12.0	< 0.037
E. sagitta–P. nasuta, P. squamata, P. oxyrhynchus & P. phoxocephala	2.76	2.35–15.4	< 0.006	2.76	2.33–15.4	< 0.006
E. vitreum–Ammocrypta spp.	1.69	1.41–15.4	< 0.002	1.71	1.76–15.4	< 0.001

oxyrhynchus and *P. phoxocephala* and *E. sagitta* (Figs 4B, 5A). Although we did not examine specimens of *E. nianguae* Gilbert & Meek, 1887, the putative sister species of *E. sagitta*, because of its listing as 'Federally Threatened', the external morphological similarity between *E. sagitta* and *E. nianguae* suggests that the latter species is most likely also a *prober*.

The snouts of the *prober* species are highly elongate and pointed as a result of both a lengthening of the upper and lower jaw bones and fixing of the premaxilla in a maximally protruded position. In the upper jaw, both the nasal and palatine bones extend well beyond the anteriormost part of the orbit and provide support for the long ascending process of the premaxilla. The distalmost tip of the ascending process rests in a bifurcate setting at the intersection of the head of the maxilla and palatine bones. In the lower jaw, the articular bone is approximately equal in length to the dentary and includes a relatively low coronoid process. GW is relatively narrow at the anteriormost tip of the jaw, but widens posteriorly, producing a triangle-like shape when the individual is viewed ventrally. In addition, the anteriorly oriented hyoid bones are long and gracile. Both the dentigerous arm of the premaxilla and the dentary bones are completely lined with several rows of tiny, needle-like teeth.

The length of the hyoid bones relative to the body, the long ascending process of the premaxilla and the elongate lower jaw suggest a morphology that is well suited to the generation and use of suction forces to capture and consume highly mobile prey (Motta, 1984). However, the particular combination of morphological features exhibited by the *prober* species departs from the classical design of a suction-feeder in several ways (Alexander, 1967; Gosline, 1987). First, the slenderness of the hyoid bone suggests that the structure is not well built to withstand the bending forces that would be generated during the forceful hyoid depression characteristic of suction-feeding kinematics (Sanford & Wainwright, 2002). Second, because the premaxilla is fixed, lower jaw depression neither results in jaw protrusion nor do the upper jaw bones rotate to fill the notch created by mouth opening. As a result, the open mouth of these species has a conspicuous lateral notch and would be expected to produce poorly directed and inefficient suction flows (Day *et al.*, 2005).

Anecdotal evidence suggests that *Percina* species feed by inserting their long snout between rocks and boulders in search of prey items (T. Near pers. comm.). In fact, the elongate jaws and narrow head appear to be well suited for reaching into narrow crevices between boulders and large rocks. In addition, the tooth-lined premaxilla and dentary would be expected to facilitate prey seizure and extraction by providing extensive grasping surfaces.

A *P. oxyrhynchus*
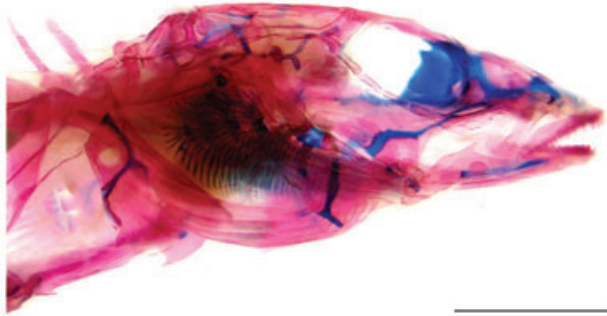
B *P. caprodes*

C *E. atripinne*
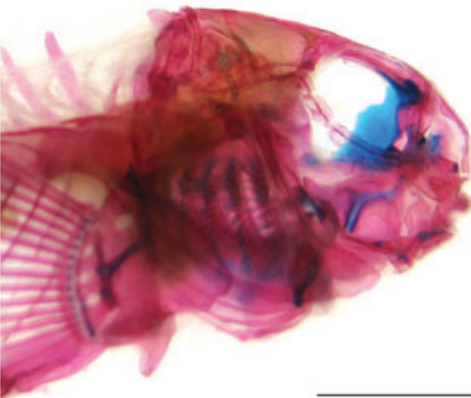
Figure 5. Three previously undescribed ecomorphs: A, the *prober* ecomorph as found in *Percina oxyrhynchus* (see also Figure 4B for images of two other *prober* species); B, the *rock flipper* ecomorph found in *Percina caprodes* (Rafinesque, 1818); C, the *manipulator* ecomorph as characteristic of *E. atripinne* (see also Figure 2A for a second *manipulator* species). Scale bar, 5 mm.

The rock flipper

All of the *Percina* commonly called 'logperches' exhibit the *rock flipper* ecomorph (Fig. 5B). In these species, the nasal and palatine bones extend anteriorly beyond the orbit to produce the distinct snout. However, neither bone is as long as that in the *prober* species. The short ascending process of the premaxilla is highly modified to provide a bony support for the soft snout of connective tissue. Like the *prober* species, the distal end of the ascending process of the premaxilla is seated in a bifurcate setting at the union of the head of the maxilla and palatine bones. From there, the process extends anteriorly for a short distance and bends ventrally at an angle of nearly 60°. The post-bend section of the process is broader and flatter than the pre-bend section and appears to provide a bony support for the bulbous snout that lies directly over it.

Compared with the thin, gracile lower jaws of the *probers*, the dentary and articular bones of the *rock flippers* are shorter and the coronoid processes on both bones are expanded dorsally. The premaxilla and dentary are both lined with multiple rows of short and robust, moderately recurved teeth. Depression of the lower jaw in cleared and stained *rock flippers* causes forward rotation of the premaxilla, but no anterior protrusion of the bone along the ascending process. Forward maxillary rotation, however, produces a nearly circular, ventrally oriented mouth opening.

Rock flippers swim just above the substrate, apparently in search of suitable small flat rocks and other pieces of debris. The fish then inserts the tip of its bulbous snout under one edge of the object and lifts up and moves or flips over (i.e. causes a 180° rotation) the rock or piece of debris. Once the item has been overturned or moved, the fish will investigate the uncovered substrate and consume any newly exposed prey items (Page, 1983; R. Carlson, pers. observ.). It is likely that the shape and orientation of the ascending process of the premaxilla provide the support for the bulbous snout that is required to flip over relatively large rocks.

The manipulator

Several species in the *E. blennioides* clade exhibit the shortest jaws and tiniest mouths of all darter species. The small size of the mouth, combined with the high protrusibility of the premaxilla, suggests that these species are expert manipulators of small benthic prey items. Hence, we deem *E. atripinne* (Jordan, 1877), *E. simoterum* (Cope, 1868) and other species in the *E. simoterum* complex (Powers & Mayden, 2007), as well as *E. baileyi* Page & Burr, 1982, *E. barrenense* Page & Burr, 1982 and *E. rafinesquei* Burr & Page, 1982, *manipulators* (Fig. 5C).

The characteristic blunt snout of *manipulator* species is the result of a shortening of the lower jaw bones (dentary + articular) combined with a re-orientation of the nasal bone. Instead of extending anteriorly, as it does in the *prober* and *rock flipper* species, the nasal bone bends sharply downwards. The result is a small, hollow cavity just anterior to the orbit. The 90° bend of the nasal bone causes a re-orientation of the premaxilla, such that its ascending process is angled ventrally. In addition, the ascending process is shortened and laterally expanded at its distal end. This distal end is then hugged by the head of the maxilla and the anteriormost tip of the palatine bone. In addition to shortening the lower jaw, the coronoid processes of both the dentary and the articular are dorsally expanded.

The width and shortness of the ascending process of the premaxilla, combined with its ventral orientation, mean that only minimal protrusion is possible. The same features, however, in addition to the absence of a premaxillary frenum, allow for considerable back-and-forth rocking. Depression of the lower jaw results in downward (ventral) movement of the premaxilla that is sufficient to form the top half of a nearly circular, ventrally oriented mouth opening. The small size of the dentigerous arm of the premaxilla is mirrored by a short, often curved tooth-bearing process of the dentary. Both bones are densely lined with thick, recurved teeth.

Manipulator species have been observed taking prey from the top of large rocks, as well as foraging in the smaller diameter substrate that often accumulates between large rocks (Page & Mayden, 1981). The subterminal mouth and ventral opening appear to facilitate efficient removal of small prey from rock surfaces (Wehnes, 1973), and the small, highly mobile jaws are expected to be effective for taking very small prey items from crevices and fissures within and between rocks.

Relative morphological diversity

As expected on the basis of the known differences in age among the three lineages and the assumption of Brownian character evolution, darters and centrarchids exhibit lower variance among species than do labrids in all four characters (Fig. 6). Comparing only centrarchids and darters, lineages of similar age, we find that the two clades are similar in the diversity of the lower jaw OLR (Fig. 6) (darters, 0.0021; centrarchids, 0.0028). However, darters exhibit approximately twice as much variance in SL (darters, 0.014; centrarchids, 0.0070) than do centrarchids, whereas the reverse is true of GW (darters, 0.0058; centrarchids, 0.011) and lower jaw CLR (darters, 0.0012; centrarchids, 0.0023).
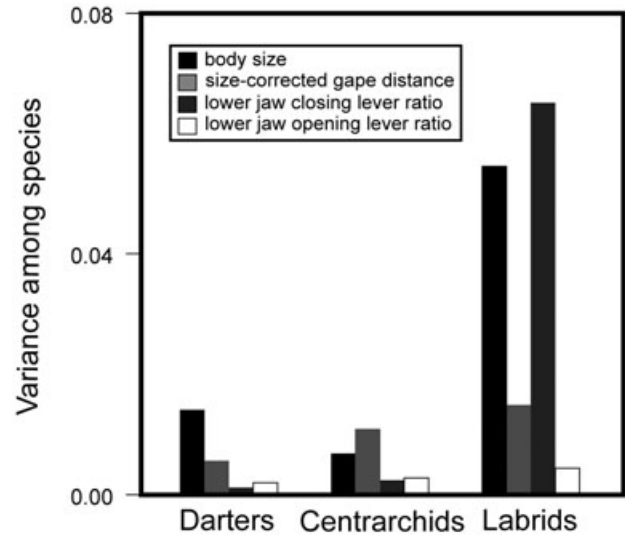
Figure 6. Variance in four ecologically relevant morphological characters among species in three radiations of teleost fishes. Estimates based on published data for 27 centrarchid species and 122 labrid species. Gape distances were body size corrected using the residuals derived from a linear regression of gape distance against body size. Size correction was performed separately for each group to account for any differences in the allometric relationship between gape and body size.

DISCUSSION

Rafinesque's (1819) decision to assign darters the generic epithet *Etheostoma*, or 'many mouths', has proven to be excellent. Darter species exhibit measurable variations in features of the head and jaws that are, on the basis of studies of homologous structures in other perciform species, likely to have performance consequences for prey capture and consumption. Multiple instances of convergent morphological evolution provide further support for the hypothesized functional significance and ecological relevance of the characters, whilst also contributing to the lineage's relatively low morphological diversity. Variance among darter species in several of these characters is comparable with that among species of Centrarchidae (sunfishes and black basses), a North American fish lineage of similar age. In addition to the subtle variation in jaw morphology among species, a few species, most notably within *Percina*, have evolved more extreme morphologies that are associated with methods of prey capture previously undescribed in stream fishes.

With the exception of species in the *E. blennioides* clade, most other darter species are remarkably similar in the shape and size of the head and oral jaws. This similarity is highlighted by comparing the variance among darter species with that exhibited by

the radiations of centrarchid and labrid fishes in four aspects of trophic morphology. Darters are less diverse than labrids in all four characters and less diverse than centrarchids in three characters. Only in body size (SL) do darters exhibit greater diversity than centrarchids.

Most of the variation in head and jaw shape among darter species is subtle and is the result of differences in the size (width, height) of the mouth, the length of the lower jaw (out-lever, articular + dentary) and the length of the dentigerous arm of the premaxilla. In fact, we find that evolution in these characters appears to be highly correlated in darters: species that have a short lower jaw typically have a short, often slightly recurved, premaxilla and a small mouth, whereas the reverse is true of species with a long lower jaw. Extreme lengthening or shortening of the lower jaw characterizes species such as the *manipulator*, *prober* and *rock flipper* ecomorphs that fall at the edges of darter morphospace.

The magnitudes of the lower jaw CLR and OLR provide an indication of the relative importance of force during jaw closing and velocity during jaw opening (Westneat, 1994). Darter species with high CLRs, such as those in the *E. blennioides* clade, are therefore capable of transferring a large fraction of the adductor mandibulae muscle contraction force, but relatively little motion and speed of movement, to the tip of the jaw. High CLRs are typically seen in species that feed primarily by biting either relatively slow-moving prey or prey items that are attached to the substrate (e.g. Wainwright & Richard, 1995; Wainwright *et al.*, 2004). Across darters, the magnitude of the OLR is also highest in members of the *E. blennioides* clade. This result suggests that prey capture by these species requires forceful rather than rapid mouth opening, and supports the observation that the species capture prey by biting and picking. In contrast, low OLR and CLR have the opposite mechanical properties and are characteristic of species that rely on suction and fast strikes to capture their elusive prey feed (Westneat, 1994). In darters, species with low OLR and CLR include the eight species in the *Ammocrypta* clade, the logperches (*Percina*) and the gastropod-eating species *P. antesella* Williams & Etnier, 1977 and *P. tanasi* Etnier, 1976 (Haag & Warren, 2006; R. Carlson, unpubl. data). Sand darters (*Ammocrypta* spp.) and their relatives live and feed on loose substrates, including sand and fine gravel. The ability to generate strong suction forces is expected to facilitate the capture of benthic prey items on such easily disturbed substrates (Page, 1983). The exact manner in which snail-eating *Percina* acquire prey is not known. However, individuals probably use a combination of suction and biting to remove snails from the substrate. Field

observations of logperch feeding suggest that individuals take quick bites at prey items uncovered by lifting rocks with the bulbous snout (R. Carlson, pers. observ.).

Mouth height and width are positively correlated with prey size (Werner, 1977; Wainwright *et al.*, 2004), but negatively correlated with overall jaw dexterity in biting species (Konow *et al.*, 2008) and suction force in suction-feeding species (Carroll *et al.*, 2004). In biting species, small mouths and jaws are capable of more precise movements than are large mouths and jaws. Small mouths are therefore likely to be the most effective for removing small prey items from shallow crevices and fissures in rocks. In fact, this behaviour has been observed in many species of *Etheostoma* and, particularly, members of the *E. blennioides* clade (R. Carlson, pers. observ.).

All else being equal (i.e. BCL and HL), species with a smaller diameter mouth opening are also capable of generating greater suction forces than species with a larger diameter mouth opening (Carroll *et al.*, 2004). Thus, one might hypothesize that many darter species, and especially species of *Percina*, use suction to capture prey. Additional morphological evidence, however, suggests that this is unlikely to be the case. First, upper jaw protrusion that occurs in conjunction with lower jaw depression is an important aspect of suction force production (Alexander, 1967; Gosline, 1987; Holzman *et al.*, 2008). The correlated depression and rotation/protrusion of the upper and lower jaws produce the round, un-notched mouth opening that is essential for efficient and forceful suction flow generation (Day *et al.*, 2005). As a result, the efficient suction-feeding species [i.e. *Lepomis macrochirus* (Centrarchidae); Higham, Day & Wainwright, 2006] are capable of rapid premaxillary protrusion and rotation (Holzman *et al.*, 2008). However, 78% of darter species are incapable of significant jaw protrusion and, by extension, the formation of an un-notched circular mouth opening, because of the presence of a well-developed premaxillary frenum (R. Carlson, unpubl. data).

The location (terminal, subterminal, ventroterminal) and orientation (upturned, downturned) of the mouth are revealing about the feeding ecology of many species of perciform fishes (Keast & Webb, 1966; Gatz, 1981; Bhat, 2005). In darters, mouth location and orientation are informative about the primary location (i.e. surface or sides of rocks) from which prey are taken. A subterminal mouth, such as that which is characteristic of *E. blennioides* and *E. zonale* (Cope, 1868), is expected to be ideally suited for removing prey from the top of bare or algae-covered rocks, because prey can be removed with high efficiency, i.e. little or no lateral head movement. Similarly, a terminal mouth is characteristic of many

darter species, including *E. flabellare* Rafinesque, 1819, *Nothonotus* and most *Percina*, and these species typically take prey from the sides of rocks (Paine, Julian & Power, 1982). The ventroterminal mouth (so-called because it is mid-way between the terminal and subterminal) is characteristic of *E. variatum* Kirtland, 1840, and its relatives. Species with a ventroterminal mouth are able to remove prey from both the tops and sides of rocks with relative ease (Wehnes, 1973; Chipps *et al.*, 1994).

Morphological convergence provides strong evidence for the adaptive significance of traits (Stayton, 2006; Revell *et al.*, 2007), and has been known to occur in a variety of characters across a diversity of freshwater fish taxa (e.g. Winemiller, 1991; Bhat, 2005) including body size in darters (Knouft & Page, 2003). The observation of the convergence in head and jaw shape among darters that occupy the same type of microhabitat implies that the characters are adaptive for some aspects of life, including prey capture, in that habitat. We identified three strong examples of ecomorphological convergence in darters: *E. longimanum* and species in the *E. blennioides* clade, *E. sagitta* and the four *prober* species of *Percina*, and *E. vitreum* and species of *Ammocrypta*. Although qualitative analysis suggested that *E. chlorosomum* is convergent with species in the *E. blennioides* clade, our two quantitative tests of convergence yielded conflicting results.

In each of the cases of significant morphological convergence, the species involved occupy similar microhabitats. This suggests that comparable selection pressures may have led to morphological resemblance among species. *Etheostoma longimanum* occupies microhabitats with moderate to high water flow over rocks. The same types of microhabitat are occupied by several species in the *E. blennioides* and *E. variatum* clades. Species in the former clade have a short snout and tiny, subterminal mouth. *Etheostoma longimanum* exhibits a very similar head and jaw morphology that is unlikely to have evolved by chance alone. Similarly, *E. sagitta* inhabits the same microhabitat (low to moderate water flow over rocky substrate) as does *P. nasuta* and probably captures prey in a similar manner. *Etheostoma vitreum* occupies the sand raceway microhabitats otherwise occupied only by species of *Ammocrypta* (Carlson, 2008). In addition to a similarity in head and jaw morphology, *E. vitreum* exhibits the elongate body shape and transparent coloration that is otherwise unique to the sand darters.

Additional support for the hypothesized ecomorphological similarity among species comes from the observation that the convergent species never occur in the same ecological community. *Etheostoma longimanum* never co-occurs with any species in the *E. blennioides* clade, *E. sagitta* does not co-occur with *P. nasuta*, *P. oxyrhynchus* or *P. squamata*, and *E. vitreum* never co-occurs with species of *Ammocrypta* (R. Carlson, unpubl. data).

The relatively low diversity exhibited by darters in lower jaw CLR and OLR, and GW, is consistent with the hypothesis that darters have diversified more in the type of microhabitat from which prey are taken than in the type of prey consumed (Page & Swofford, 1984; Alford & Beckett, 2007). As a point of contrast, labrids have diversified along an axis of prey hardness; species consume prey ranging from coral skeletons (some parrotfishes) to mucus and small ectoparasites (*Labroides* spp.) to fish (*Epibulus* spp.). This diversity is reflected by the group's relatively high variance in lower jaw CLR, a feature that varies predictably in magnitude with prey hardness (Westneat, 1994). Centrarchids are similar to darters in that species have diversified in prey capture method, but differ in that species have also diversified in prey type. The centrarchid lineage includes species that take invertebrate prey from a variety of substrates, including rocks and vegetation (*Enneacanthus* spp.), as well as species, such as the largemouth bass *Micropterus salmoides* (Lacepède, 1802), that capture large, elusive prey (Collar *et al.*, 2005, 2009). Correlated variation among centrarchid species in prey capture method and prey type is reflected in the group's high diversity in GW and, to a lesser extent, the magnitude of the lower jaw CLR.

CONCLUSIONS

Darter species exhibit subtle variations in head and jaw shape that appear to be related to feeding ecology, specifically the manner in which prey are captured and the microhabitat in which they are taken. The extent of variation among darter species in several ecologically relevant features is comparable with that exhibited by the North American freshwater fish radiation of sunfishes and black basses, except in BS and gape distance. Several instances of remarkable convergence in head and jaw shape lend support to the hypothesis that our head and jaw characters have adaptive significance in darters as well as other perciform fishes. Ongoing research will use the data presented here to identify the abiotic and biotic mechanisms underlying the evolution of ecomorphological diversity in darters.

ACKNOWLEDGEMENTS

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