Abstract.—We conducted a geometric morphometric analysis of interspecific body shape variation among representatives of 31 species of darters (Pisces: Percidae) to determine whether there is evidence of a phylogenetic effect in body shape variation. Cartesian transformation grids representing relative shape differences of individual species and subspecies revealed qualitative similarities within most traditionally recognized taxonomic groups (genera and subgenera). Canonical variates analysis and a UPGMA cluster analysis were conducted to explore further the relationships among body shapes of species; both analyses revealed patterns of variation consistent with the interpretation that shape is associated with taxonomic affinities. Normalized Mantel statistics revealed a significant positive association between body shape differences and phylogenetic interrelatedness for each of four recent phylogenetic hypotheses, providing evidence of a phylogenetic effect. This result is somewhat surprising, however, given the largely incompatible nature of these four phylogenies. We provide evidence that this result may be due to (1) the inclusion of multiple sets of closely related species to represent the traditionally recognized genera and subgenera within each phylogeny and/or (2) the inclusion of several species with relatively divergent shapes and their particular positions within the phylogenies relative to one another or to the other species of darters. [Body shape variation; geometric morphometrics; phylogenetic effect; thin-plate spline.]

Variations in body form have important fitness consequences for organisms because these variations can affect the ability to occupy particular habitats successfully (Gatz, 1979a, 1979b; Douglas, 1987; Losos and Sinervo, 1989; Irschick et al., 2000), to prevail in predator–prey interactions (Tolimier and Baker, 1993; Carpenter, 1996; Walker, 1997; Nagel and Schluter, 1998), and to reproduce successfully (Fleming and Gross, 1989; Foster et al., 1992; Abell et al., 1999). As with all patterns of phenotypic variation, however, the effects of phylogenetic nonindependence must be evaluated as part of a complete understanding of body shape variation (Harvey and Pagel, 1991; Martins, 1996; Garland et al., 1999). To our knowledge, there has been no prior quantification of the phylogenetic effect in the context of a geometric morphometric analysis, although an effect is beginning to be assumed and preemptively controlled for (e.g., Ruber and Adams, 2001; Rosenberg, 2002).

The darters (subfamily Etheostomatinae, family Percidae) are a diverse clade of small, mostly benthic stream fishes that are endemic to North America. A great deal of research effort has been focused on their ecologies, behavioral patterns, life histories, and evolutionary relationships. One recurring theme has been the association of their generally small body size with other aspects of their biology (e.g., Page and Swoford, 1984; Paine, 1990; Bart and Page, 1992). Body shape variation—indepedent of size—is, however, an essentially unexplored component of darter morphology. Many taxonomic descriptions and other studies of darters have included general qualitative assessments of body form (e.g., fusiform, deep-bodied, laterally compressed, or cylindrical), although few such studies have analyzed interspecific variation in these traits quantitatively. Two notable exceptions are the investigations by Page (1983) and Page and Swoford (1984), who examined large numbers of darter species for correlations among a suite of traditional morphological measures and various ecological and behavioral traits. These analyses underscored the primary importance of body size in the observed patterns of variation in all of the other meristic, mensural, habitat, and behavioral characters that were examined. Although these authors attempted to explore some aspects of shape variation beyond the effects of size, the techniques employed (i.e., ratios and ordination of linear measurements) have since been shown to be problematic (Bookstein, 1991; Reyment, 1991).

Darter systematics is currently an active topic of research (Nar, 2000; Kinzinger et al., 2001; Near, 2002), and the publication of several new broad phylogenies (Wood and Mayden, 1997; Song et al., 1998) presented the opportunity to assess darter shape variation in the context of possible phylogenetic effects (Felsenstein, 1985; Martins, 1996; Garland et al., 1999). The substantial differences between the phylogenies proposed by Wood and Mayden (1997) and Song et al. (1998; see Fig. 1) have somewhat complicated this analysis but have also afforded the opportunity to examine our results in terms of a real-world case of nontrivial phylogenetic uncertainty. In the present study therefore, we examined the correlations between these four hypotheses of darter evolutionary relationships and a set of rigorous estimates of overall body shape obtained using modern geometric morphometric techniques.

Materials and Methods

Phylogenetic Hypotheses

The hypotheses of phylogenetic relationships employed in the present study were derived from analyses of allozymes (Wood and Mayden, 1997) and mitochondrial cytochrome b DNA sequences (Song et al., 1998). Both studies proposed several possible phylogenies resulting from different analytical models. In the present study, we used two trees proposed by Wood and Mayden (1997: Figs. 1, 3, hereinafter WM1 and WM3, respectively) and two proposed by Song et al. (1998: Figs. 3, 4, hereinafter SNP3 and SNP4, respectively). These four
FIGURE 1. Dissimilarity of four hypotheses of darter phylogenetic relationships. These trees are abstractions to the subgeneric level of the phylogenies presented by Song et al. (1998) and Wood and Mayden (1997), limited to the subgenera common to both of those studies. The strict consensus of these trees contains only a single resolved node: Boleosoma + Ioa. (A) Song et al. (1998), Figure 3. (B) Song et al. (1998), Figure 4. (C) Wood and Mayden (1997), Figure 1. (D) Wood and Mayden (1997), Figure 3.

FIGURE 2. Two of the four hypotheses of the darter phylogenetic relationships. (A) Redrawn from figure 3 of Wood and Mayden (1997:269): the most-parsimonious tree resulting from frequency analysis based on 32 allozyme loci. Estimates of node support were not presented. (B) Redrawn from figure 3 of Song et al. (1998:349): the most-parsimonious tree resulting from maximum parsimony analysis of cytochrome b (1,140 bp) DNA sequence data. Bootstrap values (1,000 replications) are indicated. Species in parentheses are closely related substitutes for those species we were unable to represent; dotted terminal branches indicate species for which no suitable substitute could be made and therefore were not considered in the present analyses. Morphometric data were gathered for the following additional species but were not included in the phylogenetic analyses: Percina sciera, Etheostoma exile, E. inscriptum, E. lynceum, E. radiosum, and E. simoterum (including both E. s. simoterum and E. s. atripinne).

Data Collection
The present analyses include shape data collected from a total of 1,089 adult female specimens representing 31 species and two subspecies of darters. Adult females were used to avoid the possible confounding
effects of ontogenetic allometry and sexual dimorphism. Our choice of species generally followed those of Wood and Mayden (1997) and Song et al. (1998). For some species included by those authors, however, sufficient numbers of specimens could not be obtained (Fig. 2). For most of these cases, it was possible to substitute an adequate number of specimens of relatively uncontroversially closely related species (cf. Butler et al., 2000).

Shape data were collected and analyzed following the protocol outlined by Hood and Heins (2000) and Guill et al. (2003) using tpsRegr (Rohlf, 1997) and NTSYSpc (Rohlf, 2001b). Eight two-dimensional landmarks were digitized, including the most anterior point on the head, the anterior junctions of the first and second dorsal fins with the dorsal midline, the junctions of the caudal fin with the dorsal and ventral midline, the anterior junction of the anal fin with the ventral midline, the point on the ventral midline between the anterior junctions of the pelvic fins with the body, and the dorsal junction of the left pectoral fin with the body (Fig. 3A).

**Figure 3.** Cartesian transformation grids illustrating the average landmark configuration for 31 species and two subspecies of darters (A) and the relative shape differences of species representing the genera *Ammocrypta* (B, C), *Crystallaria* (D), and *Percina* (E–I). Deformations are exaggerated three times to aid interpretation.
The digitized landmark data were used to generate consensus configurations (average shapes) for each of the 32 taxa using the orthogonal generalized least squares method (Rohlf and Slice, 1990), and these consensuses were used to generate a grand consensus of all 32 species. The grand consensus was generated using the 32 consensuses rather than configurations for all of the individual specimens because species were represented by unequal numbers of specimens. Cartesian transformation grids (CTGs) were then generated to illustrate relative shape differences between each species’ consensus and the grand consensus.

Statistical Analysis

The program tpsSmall (Rohlf, 1998) was used to verify the assumption that the amount of shape variation represented by the landmark data set was sufficiently small that analyses could be performed on their projections into linear tangent space. Canonical variates analysis (CVA) was used as an inferential and ordination technique to examine variation in overall body shape among species and to illustrate the associations among species of various taxonomic affiliation in the space defined by the canonical variate axes. The shape data used in the CVA consisted of the affine and partial warps scores of each individual specimen relative to the consensus of all 1,089 specimens. A UPGMA cluster analysis was conducted using the generalized (Mahalanobis) distances between all pairs of species calculated from the matrix of species’ affine and partial warps scores, following Rohlf et al. (1996) and Marcus et al. (2000). Affine and partial warps scores are measures of shape differences in one configuration of landmarks relative to another (Bookstein, 1991). In the present analyses, these scores collectively describe the shape of individual specimens or species relative to the average (consensus) of all specimens or species.

The method used to test for evidence of an overall phylogenetic effect in body shape variation among species was adapted from a technique used by Rohlf (2001a:2152; see also Böhning-Gaese and Oberrath, 1999). A matrix of ultrametric distances between all possible pairs of species was generated for each of the four phylogenies under consideration, which were pruned to exclude species that were detected. To explore these possible effects, the CVA, UPGMA cluster analysis, and Mantel tests for phylogenetic effect on full and reduced data sets were replicated using data sets regenereated from phylogenies and landmark data from which A. beanii, A. vivax, and C. asprella were excluded.

Results

The CTGs (Figs. 3–6) illustrate the grand consensus body shape of all species presently considered (Fig. 3A) and the ways in which the consensuses of individual species differ from the grand consensus (Figs. 3B–6I). Qualitative similarities among species within traditionally recognized higher taxa (e.g., subgenera) are readily discernable. For example, the CTGs representing two species of the genus Ammocrypta clearly exhibit the markedly shallow profiles characteristic of the sand darters. The profile of C. asprella is similarly shallow, although its tail region is much elongated and the caudal peduncle is much narrower. In contrast, a wider range of body forms is exhibited by five species representing the genus Percina, although they all exhibit relatively short head and tail regions (or, conversely, elongated midsections). Among these fishes, the two species (P. nigrofasciata and P. sciera) representing the subgenus Hadropterus are the most similarly shaped, exhibiting somewhat shallower body profiles, a posterior displacement of landmark 3, and narrow caudal peduncles (distance between landmarks 4 and 5).

The remaining 24 taxa we examined are members of the genus Etheostoma s.l. and represent nine traditionally recognized subgenera. Within subgenera represented by two or more species, common shape features are evident
FIGURE 4. Cartesian transformation grids illustrating shape differences of species of the genus *Etheostoma*, subgenera *Boleichthys* (A–C), *Boleosoma* (D, E), *Catonotus* (F, G), and *Doration* (H). Deformations are exaggerated three times.

in most cases. The three species representing subgenus *Boleichthys* exhibit a somewhat shallow profile overall and a markedly shorter midsection than the consensus configuration. The two species representing subgenus *Boleosoma* also exhibit a shortening of the midsection in addition to a dorsal displacement of landmarks 2, 3, and 6 (particularly evident in the CTG for *E. olmstedi*) and the posterior displacement of landmark 4. Both of the species representing subgenus *Catonotus* exhibit deep body profiles, short first dorsal fins (indicated by the distance between landmarks 2 and 3), and a dorsal displacement of the anteriormost point on the head (landmark 1). In contrast, all five species representing subgenus *Etheostoma* (s.s.) have landmark 1 displaced ventrally to some extent. Additional features common to *Etheostoma* s.s. include a short head region, and relatively deep body profile. The two species representing subgenus *Nothonotus* are relatively deep-bodied, with shortened tail regions. *Etheostoma juliae* exhibits a markedly dorsal displacement of landmark 1, a minor feature in *E. jordani*. The only readily apparent feature common to the two species representing subgenus *Ulocentra* is a slightly shortened head region. These species differ in displacement of landmark 1 (ventrally in *E. coosae* and somewhat dorsally in *E. simoterum*). The two subspecies of *E. simoterum* are highly similar, although minor differences are discernible regarding the dorsal displacement of landmarks 1 (*E. simoterum atripinne*) and 2 (*E. s. simoterum*) relative to the consensus and the relative depth of the caudal peduncle (landmarks 4 and 5). *Oligocephalus* is the only subgenus for which the representative species show no readily discernable common deviations from the consensus.
configuration. Among the five species considered, *E. radiosum* and *E. whipplei* appear to be most similar in body form.

The regression of all pairwise distances between shapes in tangent space onto their Procrustes distances in Kendall’s shape space yields a line with slope 0.999, and the two measures are perfectly correlated ($r = 1.0$); therefore, statistical analyses based on measures in tangent space should be valid. The CVA of shape variability among species clearly shows that the differences among species are highly significant (Wilks’ $\Lambda = 6.14 \times 10^{-6}$; $F_{164,8971} = 190.865$; $P < 10^{-8}$), and ordination plots based on the first three canonical variates axes (Fig. 7) further support the conclusion that relatively closely related species (as defined by their traditional taxonomic affiliations, i.e., genus and subgenus) are generally similarly shaped; species centroids tend to cluster by taxon. The UPGMA cluster analysis of generalized distances between species lends additional support to this conclusion (Fig. 8). Of the 11 traditionally recognized taxonomic groups (genera and subgenera) that were represented by two or more species, 5 clustered unequivocally: *Ammocrypta, Hadropterus, Boleosoma, Catonotus*, and *Ulocentra*. Additionally, two of the three representatives of subgenus *Boleichthys* clustered, as did three of the five representatives of *Etheostoma* s.s. and four of the five

TABLE 1. Results of Mantel matrix correlation analyses of the relationship between body shape with phylogeny based upon two phylogenies (SNP3 and SNP4) presented by Song et al. (1998) and two phylogenies (WM1 and WM3) presented by Wood and Mayden (1997); $r$ is the normalized Mantel statistic and $P$ is its estimated probability value. Analyses were conducted with the full data set of species (full set) and with a reduced data set with a single representative species per subgenus.

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representatives of *Percina* s.l. Three of the four traditionally recognized pairs of sister species (or subspecies) in our data set also clustered: *E. radiosum*/*E. whipplei*, *E. nigrum*/*E. ohmstedi*, and *E. simoterum* *s. atripinne*; the exception was *E. lynceum*/*E. zonale*.

The Mantel matrix correlations (Table 1) tested the hypothesis that closely related species tend to be similarly shaped across the entire clade of darters, while taking into account the proposed relationships among and within the traditionally recognized genera and subgenera. Although there were the substantial differences among the phylogenies, all four tests showed a significant positive correlation between phylogenetic distances among species and their relative similarities in
FIGURE 7. Relative body shape variation in darters as revealed by CVA. (A) First canonical variate plotted against the second. (B) First canonical variate plotted against the third. Overall similarities of body shapes are proportional to physical proximity of species’ centroids in these three dimensions. Species are indicated by abbreviations consisting of the first four letters of their specific epithet (e.g., E. proeliare = proe), except in the cases of E. blennius (blus), E. simoterum atripinne (atri), and P. nigrofasciata (nfas). Genera are represented by triangles (Ammocrypta), a square (Crystallaria), circles (Etheostoma), and diamonds (Percina).
body shape. The results of the reanalyses of the reduced data sets (which in these tests include *Ammocrypta* and *Crystallaria*) are presented in the right half of Table 1. For three of the four phylogenies (SNP3, SNP4, and WM1), these reductions rendered the correlations nonsignificant (*P* > 0.05), suggesting that in these cases much of the phylogenetic effect demonstrated in the initial analyses was indeed attributable to the inclusion of multiple closely related species.

The preceding analyses were repeated with *A. beanii*, *A. vivax*, and *C. asprella* (or individuals of these species in the case of the CVA) excluded because their extreme body shapes (see Figs. 3B–D, 7) were suspected of exerting a disproportionate influence. For the CVA and UPGMA cluster analysis, this exclusion resulted in very little changed. The differences among species revealed by CVA remained highly significant (Wilks’ *λ* = 2.64 × 10⁻⁵; *F*₁₄₄,₈₀₅₅₉ = 135,739; *P* < 10⁻⁸), and the relative locations of the remaining species’ centroids in the ordination plot (not shown) of the recalculated CV2 (hereinafter CV2*) against recalculated CV1 (CV1*) were very similar to the configuration shown.
in Figure 7A, except rotated 90° counterclockwise. The plot of CV3* against CV1* (not shown) displayed an arrangement of species’ centroids not seen previously but consistent with the interpretation that in most cases the centroids of taxonomically closely related species tend to cluster. The recalculated UPGMA cluster analysis yielded a phenogram (not shown) that differed from the arrangement of species in the original phenogram (exclusive of *A. beanti, A. vivax,* and *C. asprella*) in only two minor ways (cf. Fig. 8): the clades (*E. blemnioides, E. lyncneum*), *E. inscriptum* and (*P. nigrofasciata, P. sciara*), *P. ouachitae* and *P. caprodes*). Neither of these changes alters any of the conclusions drawn from examination of the cluster analysis on the complete data set.

In contrast, substantial differences were found for the the Mantel correlations of phylogenetic and morphometric distance matrices that were recalculated from data sets from which *Ammocrypta* and *Crystallaria* had been excluded (Table 2). Only one of the correlations based on the full data sets (which included all species except *A. beanti, A. vivax,* and *C. asprella*) was significant, and none were significant for the reduced data set from which these species also were excluded.

**DISCUSSION**

We employed several complementary approaches to test how evolutionary relatedness is correlated with patterns of body shape variation among 32 taxa of darters. Readily discernible similarities were observed among species representing most of the traditionally recognized higher taxa (i.e., subgenera and genera) and were illustrated by ordination and cluster analysis. These observations generally support the descriptive accounts of previous authors (Kuehne and Barbour, 1983; Page, 1983; Page and Swofford, 1984; Bailey and Etnier, 1988). For example, Page and Swofford (1984:152) noted that *Percina roanoka* more closely resembles species of *Ethoestoma* s.l. that occur in similar stream-riffle habitats than it does other members of *Percina* s.l. Their observation was confirmed by the present CTGs (Figs. 3, 5) and by the relative position of *P. roanoka* in the ordination plots (Fig. 7) and UPGMA phenogram (Fig. 8).

In addition to permitting the statistically robust quantification of size-free shape (Bookstein, 1991), our use of landmark-based geometric morphometrics has considerably expanded upon previous observations regarding darter shape variation based on traditional morphometric methods. In the present study, we emphasized the unifying characteristics of shape found in most of the traditionally recognized taxa. However, the examination of CTGs readily exposes differences between otherwise relatively similarly shaped fishes such as *E. nigrum* and *E. stigmaceum* (Figs. 4D, 4H) that had not been investigated (Guill et al., 2003).

**Phylogenetic Effects**

Given that taxonomic categories fail to represent a large number of relationships within and among taxa, an explicitly phylogenetic approach was needed to verify these observations and to determine whether despite apparent cases of convergent evolution such as that of *P. roanoka* with other ecologically similar darters there was evidence of a phylogenetic effect across the entire set of species studied. The analysis was complicated by the existence of multiple competing phylogenies of the darters (Wood and Mayden, 1997; Song et al., 1998). Some authors have overcome similar predicaments by using composite or consensus phylogenies (e.g., Vanhooydonck and Van Damme, 1999; Jones and MacLarnon, 2001); however, such an approach for the present analyses would collapse almost all of the phylogenetically interesting nodes (see Fig. 1). We therefore opted to run analyses based upon all four phylogenies, as recommended by Harvey and Pagel (1991).

Because shape data of the sort generated by geometric morphometric analyses are inherently multivariate, measures of autocorrelation such as Moran’s *I* (Gittleman and Kot, 1990) are inappropriate. The present analyses employ normalized Mantel statistics (Smouse et al., 1986) to evaluate the overall correlation of pairs of matrices representing the phylogenetic and phenotypic distances between species (Böhning-Gaese and Öberrath, 1999; Rohlf, 2001a). These correlations were significant and positive for matrices calculated from all four competing phylogenies, indicating that (1) body shape does exhibit phylogenetic effects in these species as a group as hypothesized and (2) despite their considerable differences, all four phylogenies convey sufficient phylogenetic signal to detect this effect.

These conclusions immediately raise the question of how four such different hypotheses of evolutionary relationship could all convey nontrivial phylogenetic signal. Several potential explanations were investigated through reanalysis of subsets of the data. One explanation involves the fact that each of the four phylogenies under consideration contains pairs and triplets of species that belong to traditionally recognized subgenera, and these groups invariably cluster at the tips of the phylogenies. Thus, much of the phylogenetic effect that was detected could have arisen from the fact that these species were grouped and not necessarily from the branching patterns within or among these groups. To test this proposal, we randomly excluded one or two species from each of these clusters and reran the analyses. For three

**Table 2. Results of Mantel matrix correlation reanalyses of the relationship between body shape and phylogeny based on a full data set of species (full data) and a reduced data set with a single species per genus. The morphometrically distinct species *Ammocrypta beanti, A. vivax,* and *Crystallaria asprella* were excluded from both data sets.**

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of the four phylogenies (SNP3, SNP4, and WM1), the resulting reductions in correlation and significance are consistent with the possibility that much of the phylogenetic signal was carried in these subgeneric nodes near the tips of the trees. The obvious objection that this could simply be a function of reduced sample sizes is countered by the fact that for the fourth case (WM3), the reduced data set yielded a slightly higher correlation, which remained significant at the 0.05 level.

A second possible explanation involves the potentially disproportionate effects that the inclusion of species of Ammocrypta and Crystallaria may have had on the analyses. Relative to other darters, species of these genera are highly distinct morphologically (although they are somewhat similar to each other; see Fig. 8), and in all four phylogenies, these genera are either sister to one another, partially or fully basal to the remainder of the phylogenies, or both (see Fig. 1). Reanalysis of the otherwise full data sets (from which the three species representing these genera had been excluded) yielded nonsignificant correlations for three of the four phylogenies (SNP3, SNP4, and WM3), suggesting that in these cases, one or both of these factors were responsible for much of the phylogenetic effect seen in the previous analyses that had included Ammocrypta and Crystallaria. In the fourth case (WM1), however, exclusion of these species nevertheless yielded a significant correlation that was somewhat higher than that found with them included. This correlation was rendered nonsignificant by eliminating redundant species, as was done in the previous analyses. Therefore, the phylogenetic effect originally found for each of the four phylogenies appears largely attributable to some combination of these factors, i.e., inclusion of multiple representatives for many of the subgenera and/or inclusion of species with highly distinct body shape.

**Ecomorphology**

The relationships between freshwater fish body shape variation and various ecological and functional variables have been described by many authors (Gatz, 1979a, 1979b; Douglas, 1987; Winemiller, 1992; Toline and Baker, 1993; Wood and Bain, 1995). Webb (1984) presented a classification of fish body forms based on modes of locomotion and suggested that body form associates strongly with trophic niche and predator–prey relationships. Based on their general body shapes, most darters would likely be classified as body/caudal fin transient propulsion species under Webb’s (1984) model and would therefore be expected to avoid sustained swimming, specialize on nonelusive prey, and use bursts of speed and rapid turns to avoid predators. As indicated by the common name “darter,” this description is a fair characterization of these species. Most darters feed almost exclusively on benthic invertebrates, gleaning small, nonelusive prey from the substrate where most species also seek refuge from predators (Kuehne and Barbour, 1983; Page, 1983). Given these overall similarities in locomotion and feeding ecology, some other factor or factors likely produced the variety of body shapes exhibited among the subgroups of darters.

Various authors (Page, 1983; Page and Swofford, 1984; Wood and Bain, 1995) have found associations between darter body shapes and environmental parameters such as current speed, water depth, substrate composition, and availability of cover (see also Fisher and Pearson, 1987; Welsh and Perry, 1998). Several of the observations made by these authors are corroborated by the CTGs generated for the present study: (1) species primarily found in high-current environments (e.g., E. caeruleum, E. juliae, E. jordani, and P. roonoka) have deep caudal peduncles and generally robust forms (Page, 1983; Page and Swofford, 1984); (2) species found in moderate to slow currents (e.g., E. exile, E. fusiforme, E. nigrum, and E. stigmamum) tend to be more fusiform and have narrow caudal peduncles (Wood and Bain, 1995); and (3) species inhabiting sandy environments (e.g., A. beinii, A. vivax, C. asprella, and E. whipplei) tend to be especially elongate, with narrow peduncles (Page and Swofford, 1984). The results of the present study show that correlation for phylogenetic effects will indeed be necessary in future investigations of darter body shape variation, because there is significant correlation between evolutionary relationships and body shape no matter which of the presently considered phylogenies is employed.

Although almost two decades of active research into the effects of phylogeny on phenotypic variation have preceded the present study, much of this research has been focused on developing and refining the appropriate methodologies. Here, we provide a robust application of these new methods. Much basic research that includes the recognition and appropriate control for phylogenetic effects remains to be conducted. The combination of comparative methods appropriate to multivariate data sets with the powerful new tools of geometric morphometrics represents a potentially fruitful avenue of investigation into the effects of body shape on the biology of organisms.

**ACKNOWLEDGMENTS**

We are indebted to the curators and collection managers of the museums listed in the Appendix for the loan of specimens in their care and to F. James Rohlf for advice and assistance with the statistical analyses. Henry L. Bart, Jr., Duncan J. Irschick, Thomas W. Sherry, Paul M. Magwene, and one anonymous reviewer provided valuable comments on the manuscript. This paper represents a portion of a Ph.D. dissertation by J.M.G. C.S.H. was supported by a Faculty Research Grant and the Mullahy Fund, Loyola University. Morphometric software is available at http://life.bio.sunysb.edu/morph.

**REFERENCES**


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Associate Editor: Junhong Kim

APPENDIX

MATERIAL EXAMINED

Material was provided by the following institutions: Tulane University Museum of Natural History (TU), University of Louisiana at Monroe Museum of Zoology (ULM), University of Michigan Museum of Zoology (UMMZ), and Cornell University Museum of Vertebrates (CU). The following species were examined: Ammocrypta