

Does morphological variation buffer against extinction? A test using veneroid bivalves from the Plio-Pleistocene of Florida

Sarah E. Kolbe, Rowan Lockwood, and Gene Hunt

Abstract.—Although morphological variation is known to influence the evolutionary fates of species, the relationship between morphological variation and survivorship in the face of extinction-inducing perturbations is poorly understood. Here, we investigate this relationship for veneroid bivalves in association with the Plio-Pleistocene extinction in Florida. Fourteen pairs of related species were selected for analysis, with each pair including one species that survived the Plio-Pleistocene extinction and another that became extinct during the interval. Morphological landmark data were acquired for more than 1500 museum specimens, representing 19 localities that encompass four well-known Plio-Pleistocene units in the study region. Procrustes superimposition was applied to each sample, and overall multivariate variation was calculated as the mean squared partial Procrustes distance between specimens and their mean form. Morphological variation was calculated at three geographic scales for each species, and differences in variation between survivors and victims were examined within each species pair. Results indicate that species surviving the Plio-Pleistocene extinction were significantly more variable morphologically than victims. Greater morphological variation may promote survivorship by directly enhancing species adaptations to changing conditions or by permitting the occupation of a larger geographic range. Alternatively, high morphological variation and survivorship may both be mediated by a third variable, such as large geographic range.

Sarah E. Kolbe. *Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221-0013. E-mail: kolbesh@mail.uc.edu*

Rowan Lockwood. *Department of Geology, College of William and Mary, Post Office Box 8795, Williamsburg, Virginia 23187*

Gene Hunt. *Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, MRC 121, Post Office Box 37012, Washington, D.C. 20013-7012*

Accepted: 5 October 2010

Introduction

Analyses of biological selectivity during mass extinctions have helped to identify factors that influence the extinction risk of taxa, as well as the causative roles of extinction events in morphological and ecological transitions (e.g., Stanley 1988; Jackson et al. 1996a; Lockwood 2004). A variety of organismal and species-level attributes have been the foci of past investigations of extinction selectivity, including geographic range, body size, abundance, and membership in particular trophic groups (Stanley 1990; McGhee 1995; Todd et al. 2002; Jablonski and Hunt 2006). A promising, but largely unexplored, factor is the potential for the morphological variation of a species to affect its susceptibility to extinction. Greater variation, or a wider range of forms, might afford a species more ecological flexibility during environmental perturbations or permit it to inhabit a greater geographic range, an attri-

bute that is known to promote survivorship (Lloyd and Gould 1993; Payne and Finnegan 2007; Jablonski 2008). Moreover, because a population's rate of evolution by natural selection is proportional to additive genetic variance (Lande 1976), and morphological variation may reflect additive genetic variance (Strauss 1991; Yezerinac 1992), greater variation, if heritable, will result in faster adaptation to changing selective conditions, which may be particularly important during intervals of environmental change associated with extinction. Here, we assess whether morphological variation affected the survivorship of veneroid bivalve species in Florida during the regional Plio-Pleistocene extinction.

The Plio-Pleistocene extinction affected marine communities of the western Atlantic, Caribbean, and eastern Pacific (Allmon 1993a), and was characterized by a protracted interval of elevated extinction from the mid-

Pliocene to the mid-Pleistocene, occurring asynchronously across these regions (Stanley 1986). Recent revisions to the Neogene time-scale (Ogg et al. 2008, with update from the International Commission on Stratigraphy [2009]) now place the extinction interval in Florida largely in the early Pleistocene. Mollusks, sea grasses, and corals were severely affected by the extinction, with approximately 65% of bivalve species becoming extinct regionally (Stanley 1986, 1990; Budd et al. 1996; Jackson et al. 1996b). The extinction was more severe in the western Atlantic than in the eastern Pacific, possibly because the western Atlantic contained a larger proportion of endemic species (Vermeij and Petuch 1986). Several potential triggers of the Plio-Pleistocene extinction have been proposed (e.g., Olsson 1961; Woodring 1966; Stanley and Campbell 1981; Petuch 1982a; Vermeij 1990; Jackson et al. 1993; Budd et al. 1996; Roopnarine 1996; Allmon 2001), but regardless of its ultimate cause(s), the event encompassed a myriad of environmental changes including shifts in temperature, ocean circulation, sea level, and productivity (Stanley and Campbell 1981; Stanley 1986; Vermeij and Petuch 1986; Allmon 1993b; Cronin and Dowsett 1996).

For this study, we first identified 14 pairs of congeneric or otherwise closely related veneroid bivalve species, each consisting of one species that was a victim of the Plio-Pleistocene extinction, and another that survived. We then quantified and compared morphological variation at multiple scales for each victim-survivor pair, and tested whether survivors were systematically more variable than the extinct species with which they were paired. If survivors consistently had greater morphological variation than victims, this could suggest that greater morphological variation acted as a buffer to extinction during the Plio-Pleistocene event.

Geologic Setting

Plio-Pleistocene deposits are extensive in Florida, and contain abundant, well-preserved fossil assemblages representing a wide range of environments. The deposits were generally formed in shallow settings above

storm wave base, with wave energy and storm conditions similar to present-day conditions (Allmon 1993a,b; Missimer 2001a). Many of the Plio-Pleistocene deposits in Florida are highly fossiliferous because of high rates of biological productivity in combination with sediment winnowing, which produced condensed and time-averaged accumulations of fossil material (Allmon 1993a). Taphonomic evidence indicates that the fossil material experienced multiple episodes of reworking, but underwent little spatial transport (Allmon 1993a).

The Plio-Pleistocene deposits sampled in this study are largely unlithified and include the Pinecrest Beds, and the Caloosahatchee, Jackson Bluff, and Nashua Formations (Fig. 1). The Pinecrest Beds, exposed in southern and central Florida, are dominated by shells, shell fragments, and quartz sand (Petuch 1982b). These beds represent a wide variety of subtropical environments, including shoreface, offshore subtidal, estuarine, and lagoonal settings, as well as oyster reefs (Petuch 1982b; Willard et al. 1993). The Pinecrest Beds were deposited in two pulses during the late Pliocene and early Pleistocene (Jones et al. 1991; Missimer 2001b). (The 2009 International Commission on Stratigraphy Geologic Time Scale is used here and throughout the following sections.)

The Caloosahatchee Formation is exposed in southern and central Florida, and occurs stratigraphically above the Pinecrest Beds. The formation consists of gray, fossiliferous, calcareous marl and sandy limestones (DuBar et al. 1991). Like the Pinecrest Beds, the Caloosahatchee Formation was deposited in subtropical conditions, and tropical and subtropical mollusks are abundant (Willard et al. 1993; Allmon et al. 1996). Carbonate deposition predominated, with coastal influxes of quartz sand, and a diversity of depositional environments is represented, including carbonate-shelf, open-bay, and lagoon (Missimer 2001a). Helium-uranium dating suggests that the Caloosahatchee Formation is early Pleistocene in age, 1.8–2.5 Ma (Lyons 1991), but faunal and strontium isotope evidence suggests that the formation is slightly younger (Allmon et al. 1996; Missimer 2001b).

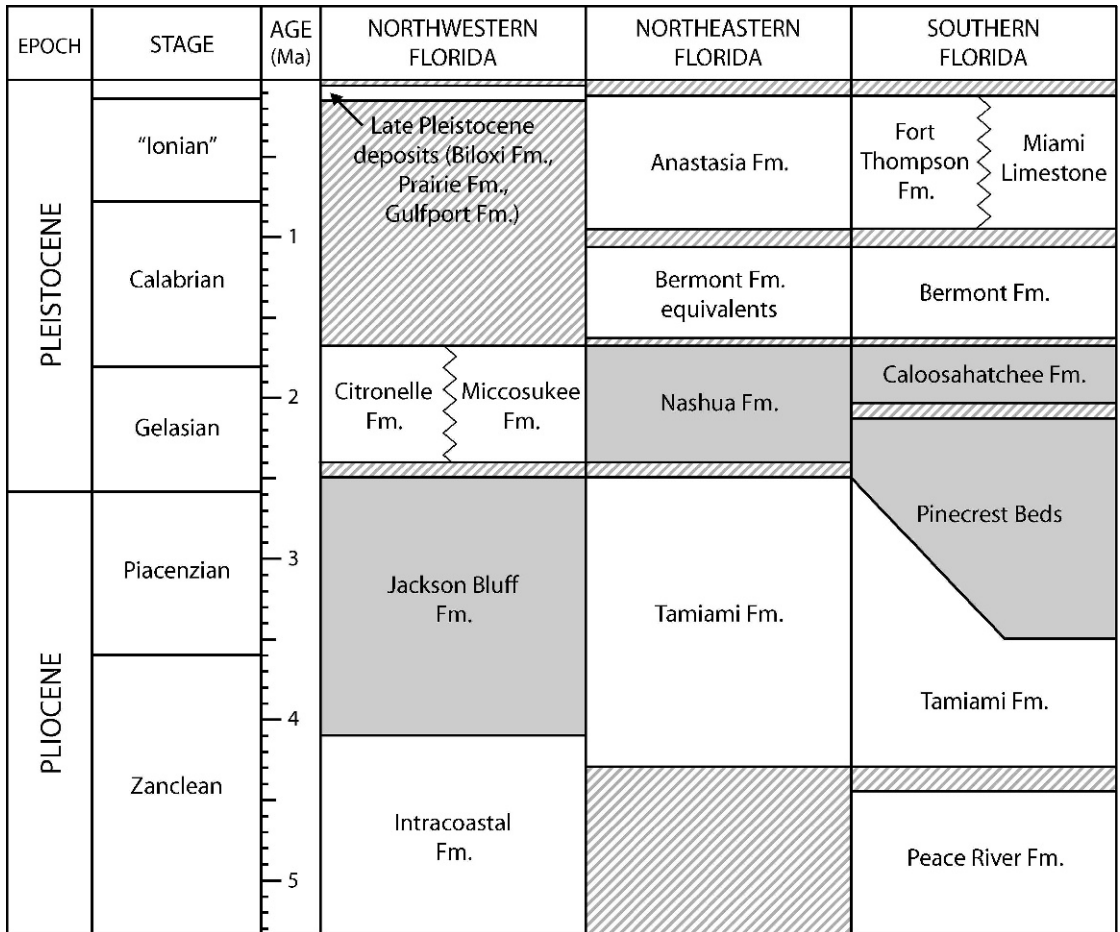


FIGURE 1. Generalized correlation chart of Pliocene and Pleistocene deposits in Florida (based on Akers 1972; Akers and Koeppl 1973; Huddleston 1988; Otvos 1988, 2005; Rupert 1990; DuBar et al. 1991; Jones et al. 1991; Lyons 1991; Allmon 1992; McCartan et al. 1995; and Missimer 2001a,b). The units sampled in this study are indicated by shading; known gaps are indicated by cross-hatching.

The Jackson Bluff Formation is exposed in northwestern Florida. It is composed of fossiliferous mixed clay and sand, and is siltier and less calcareous than the Pinecrest Beds and Caloosahatchee Formation to the south, representing deposition in an offshore environment (Akers 1972; Schmidt 1984; Ward 1992). Biostratigraphic correlation indicates a mid- to late Pliocene age (Akers and Koeppl 1973; Berggren et al. 1995).

The Nashua Formation, exposed in northeastern Florida, is a heterogeneous unit containing calcareous quartz sands and sandy shell coquina (Huddleston 1988). Considered a biostratigraphic equivalent of the Caloosahatchee Formation, the Nashua Formation contains less limestone and more quartz sand

and dark clays than its southern counterpart, and represents deposition in a shallow-water nearshore to open-marine neritic continental shelf (Huddleston 1988; DuBar et al. 1991). The Nashua Formation is considered to be early Pleistocene in age on the basis of evidence from planktonic foraminifera (Huddleston 1988).

Methods

Sampling.—We compared morphological variation between victims and survivors of the Plio-Pleistocene extinction for 14 pairs of species, each consisting of species from the same genus or related genera. To a large extent, this sampling scheme controls for phylogenetic non-independence of species,

TABLE 1. Species pairs included in the study. In each pair, the upper species was a victim of the Plio-Pleistocene extinction, while the lower species survived. The total number of localities and specimens examined for each species are indicated by columns 3 and 4, respectively.

Pair	Victim survivor	Number of localities	Number of specimens
A	<i>Linga amabilis</i> (Dall)	3	56
	<i>Linga pensylvanica</i> (Linnaeus)	4	94
B	<i>Radiolucina waccamawensis</i> (Dall)	3	86
	<i>Parvilucina multilineata</i> (Tuomey and Holmes)	3	95
C	<i>Miltha caloosaensis</i> (Dall)	3	78
	<i>Armillitha disciformis</i> (Heilprin)	3	58
D	<i>Carditamera arata</i> (Conrad)	3	68
	<i>Carditamera floridana</i> Conrad	3	52
E	<i>Eucrassatella meridionalis</i> (Dall)	2	35
	<i>Eucrassatella speciosa</i> (Adams)	2	40
F	<i>Crassinella acuta</i> (Dall)	2	28
	<i>Crassinella lunulata</i> (Conrad)	2	30
G	<i>Trachycardium emmonsii</i> (Conrad)	2	29
	<i>Trachycardium muricatum</i> (Linnaeus)	2	22
H	<i>Trigoniocardia willcoxi</i> (Dall)	2	31
	<i>Americardia media</i> (Linnaeus)	2	61
I	<i>Mulinia sapotilla</i> Dall	2	91
	<i>Mulinia lateralis</i> (Say)	3	72
J	<i>Panichone ulocyma</i> (Dall)	4	86
	<i>Lirophira latilirata</i> (Conrad)	3	66
K	<i>Anomalocardia caloosana</i> (Dall)	2	48
	<i>Anomalocardia auberiana</i> (d'Orbigny)	1	48
L	<i>Dosinia acetabula</i> (Conrad)	2	27
	<i>Dosinia elegans</i> (Conrad)	2	53
M	<i>Tellina strictolineata</i> Olsson and Harbison	1	15
	<i>Tellina alternata</i> Say	2	39
N	<i>Transennella caloosana</i> Dall	1	27
	<i>Transennella conradina</i> Dall	2	28

as each pair is phylogenetically independent of all the others (Felsenstein 1985). It is not necessary that each pair represents true sister species; they are phylogenetically independent as long as each species is more closely related to its paired species than it is to any other species in the analysis.

This sampling scheme, with its reliance on survivor-victim species pairs, differs from the traditional approach that would instead assemble aggregate sets of victim species and survivor species and then determine whether, on average, survivor species are more variable than victims. However, as argued by Purvis (2008), comparisons that do not take into account the phylogenetic relatedness of species can mislead inferences about extinction selectivity because they can be confounded by differences among clades. An example of this effect was reported by Smith and Roy (2006), who found that large body size conferred a survivorship advantage for scallop species. But, this body-size selectivity was only detectable when species were compared within

phylogenetic units (genera): a lumped survivor-victim comparison showed no significant difference with respect to body size. Purvis (2008) provides a detailed list of similar studies. Assessing variation difference in survivor-victim pairs is consistent with previous approaches that rely on phylogenetically informed contrasts (Felsenstein 1985; Maddison 2000). No phylogenetic hypothesis exists for the Veneroidea as a whole that would allow us to more fully integrate topology and divergence times into this analysis, but our paired approach uses phylogenetic information to the extent it is available.

Victims and survivors were designated from the literature; for the purposes of this study, victims were defined as species that had a last occurrence in the latest Pliocene or early Pleistocene. Because the reliability of stratigraphic ranges is limited by the quality of mid- to late Pleistocene deposits in Florida, survivors were defined as species that are extant today (Table 1). The species were sampled from an aggregate set of 19 localities

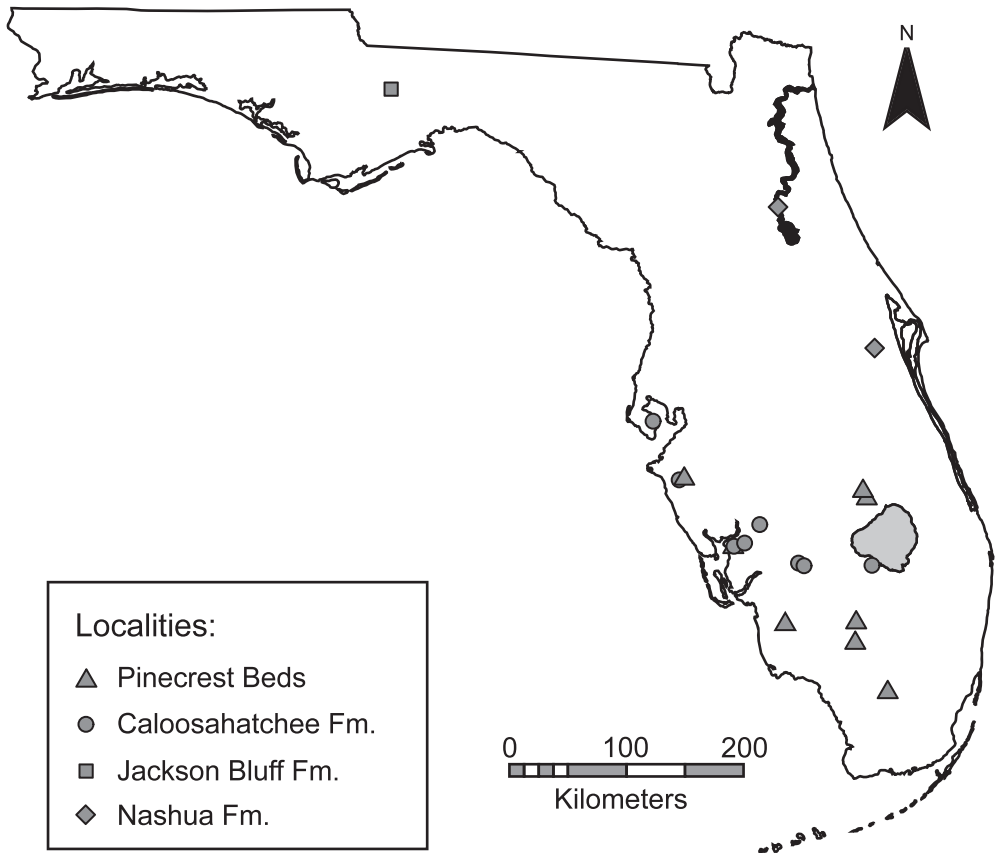


FIGURE 2. Sample localities in Florida. Specimens from these localities were examined from museum collections at the Florida Museum of Natural History.

across Florida encompassing the aforementioned Plio-Pleistocene units from collections at the Florida Museum of Natural History in Gainesville, Florida. (Fig. 2, supplemental Appendices 1 and 2 online at Dryad: <http://dx.doi.org/10.5061/dryad.8679>).

Landmark Collection.—Digital images of specimens were collected using an Epson Perfection 1640 SU scanner (600–1200 dpi) and an Olympus DP12 digital microscope camera (1×–3×). Images were adjusted and rotated to a uniform orientation using Adobe Photoshop v.7.0.1 to facilitate the consistent collection of data on maximum height and width. Landmark coordinate points for morphometric analysis were collected using tpsDig v.2.05 (Rohlf 2006). Nine landmarks common to all study species were digitized, and scale data were collected for each specimen (Fig. 3). The beak, the posterior and anterior ends of the hinge plate, and the

intersections of the posterior and anterior adductor muscles with the pallial line were selected as Type I landmark points, and four additional Type III landmark points were digitized along the shell outline at points representing maximum length and height to capture additional aspects of shell shape. These landmarks were chosen as homologous, repeatable, and functionally important aspects of form, but of course other approaches can be used to capture other aspects of bivalve morphology, such as valve outline.

Quantifying Morphological Variation.—Generalized Procrustes analysis (GPA) was applied to each species separately to quantify morphological variation using the *shapes* package (Dryden 2006) in R (R Core Development Team 2006). GPA translates, scales, and rotates all landmark sets within a group to minimize the sum of the squared distances between them (Rohlf 1990; Dryden and Mardia

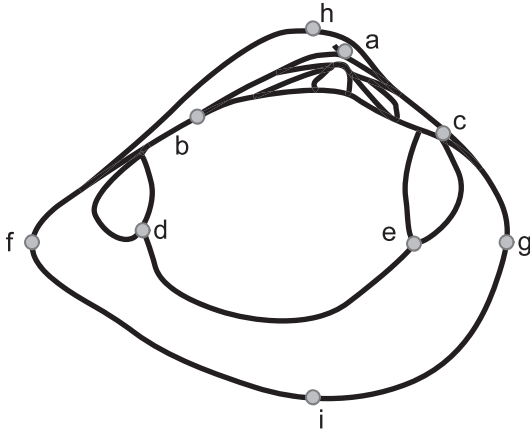


FIGURE 3. Location of landmark points on an idealized veneroid shell: beak (a); posterior end of hinge plate (b); anterior end of hinge plate (c); posterior intersection of adductor muscle scar with pallial line (d); anterior intersection of adductor muscle scar with pallial line (e); points representing maximum width (f, g); points representing maximum height (i, j).

1998). A mean form is calculated during GPA by averaging the x and y coordinates of each of the fitted landmark points (Rohlf 1990). Procrustes residuals then provide a vector record of the distance from the landmark of each specimen to the corresponding landmark of the mean form (Chapman 1990); these residuals retain all information about shape difference from the mean after the removal of specimen size, location, and orientation. Importantly, although size is removed, size-related shape variation is not. Potential effects of this allometric shape variation will be discussed below.

To quantify morphological variation, we calculated what Zelditch et al. (2004) refer to as morphological disparity (*MD*), which is equal to the mean-squared Procrustes distance $(D_p)_i$ between specimens and their mean form; $(D_p)_i$, in turn, is the square root of the summed squared distances between a specimen and the mean form for each of k landmarks ($k = 9$ in this study):

$$MD = \frac{\sum_{i=1}^N (D_p)_i^2}{(N-1)},$$

$$\text{where } (D_p)_i = \sqrt{\sum_{j=1}^k [(x_{ij} - \bar{x}_j)^2 + (y_{ij} - \bar{y}_j)^2]},$$

where \bar{x}_j and \bar{y}_j represent the j^{th} landmark coordinates of the mean form, and x_{ij} and y_{ij} represent the coordinates for the j^{th} landmark of the i^{th} specimen (Zelditch et al. 2004; Hopkins and Webster 2009).

Using this procedure, *MD* values were calculated separately by locality for each species. An overall estimate of variation for each species was computed as the average of its within-locality variances in partial Procrustes distance. Because *MD* values, like all measures of variation, are more precisely measured with increasing sample size, the average *MD* values were weighted by each locality's sample size. Unweighted average *MD* values were also calculated and yielded similar results to the weighted average *MD* values; only the weighted average *MD* values are reported here. Confidence intervals for *MD* values were estimated via 1000 bootstrap samples of each population. A measure of total *MD* was also calculated for each species by combining all samples of a given species into one group, applying GPA, and calculating the resulting *MD* value. This total *MD* value, unlike the average within-locality *MD* value, incorporates both variation within sites and differences in morphology *between* sites.

Morphological variation of victim and survivor species was compared with the paired Wilcoxon signed rank test, which evaluates the null hypothesis that the median survivor-victim difference is equal to zero. A binomial test was also applied to determine whether the number of pairs in which the surviving species had greater morphological variation than the victim was significantly different than what would be expected by chance. Victim and survivors were compared in three ways: (1) at the species level, by averaging the *MD* values across all localities of a given species to calculate variation as described above ("average within-locality morphological variation"), (2) at the locality level, comparing only specimens from particular sites in which a victim and survivor co-occurred ("locality-controlled morphological variation"), and (3) at the species level, using the measure of total variation described above ("total regional morphological variation").

Alternative Measure of Morphological Variation and Allometry.—An alternative measure of morphological variation was also examined that takes into account variation in shape potentially related to allometric growth. If allometry is significant, samples with a great range of sizes may exhibit inflated shape variation relative to samples with a narrow range of sizes. Because the range of body sizes represented in a sample is not easy to standardize, the following procedure was used to measure variation excluding allometric shape differences. Principal components analysis (PCA) was applied to the landmark variables for each sample following Procrustes superimposition, producing 14 meaningful PC axes representing shape. Each resulting PC axis was regressed against the log centroid size values of the sample to remove the effects of allometry (“size standardization” [Hopkins and Webster 2009]), and the residuals of the regression were calculated. The morphological variation of the sample was calculated as the sum of the variances of each of the PC residuals.

To evaluate how well linear regression of shape onto log centroid size accounted for allometry, we visually examined each cross-plot of each PC axis against log centroid size, and analyzed the R^2 and significance for the regression of each PC axis against log centroid size. If allometric growth is a significant factor, a strong relationship would be expected between log centroid size and one or more PC axes.

As an alternative to *MD*, we also compared variation within species pairs by calculating the similar Procrustes root mean square metric (Dryden and Mardia 1998) of each species using full Procrustes distance, which produced results identical to the results produced by the *MD* metric.

Quantification of Digitizing Error.—Repeatability analyses were conducted to determine the magnitude of landmark digitizing error. A group of 20 replicate landmark sets were collected from a single specimen of *Panichone ulocyma*, a species with relatively low morphological variation, and landmark sets were collected from 20 additional specimens in a second group. Procrustes superimposition

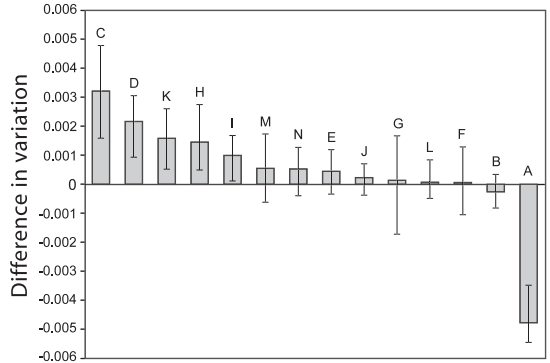


FIGURE 4. Difference in average within-locality variation between survivors and victims, with 95% confidence intervals based on bootstrapping (1000 replicates). For pairs that plot above the $y = 0$ line, the survivor species had greater average within-locality variation than the victim, whereas for pairs that plot below the $y = 0$ line, the victim species was more variable. Pair differences are individually statistically significant when the error bars do not cross the $y = 0$ line. In this and subsequent figures, letters A through N represent the 14 species pairs designated in Table 1.

was applied to each group separately, and an *MD* value was calculated for each group. Variation in the replicate sets, representing measurement error, was compared with variation among the landmark sets of the multiple-specimen group. Variation in the replicate sets was much lower than variation among specimens, with variation due to digitizing error representing less than 3% of the magnitude of among specimen variation.

Results

Average Within-Sample Morphological Variation.—Overall, surviving veneroid species had significantly greater average morphological variation than their non-surviving counterparts during the Plio-Pleistocene extinction when the weighted average *MD* values of all localities of each species were calculated (Fig. 4, Wilcoxon signed rank test, $n = 14$, $V = 86$, $p = 0.035$; binomial test, $n = 14$, $p = 0.013$). Considered individually, surviving species were more variable than their victim counterparts for 12 of the 14 pairs. Of the 12 cases, the difference was statistically significant ($p < 0.05$) in five instances; this was true in one of the two cases in which the victim was more variable.

Alternative Measure of Variation and Allometry.—For each within-pair comparison of

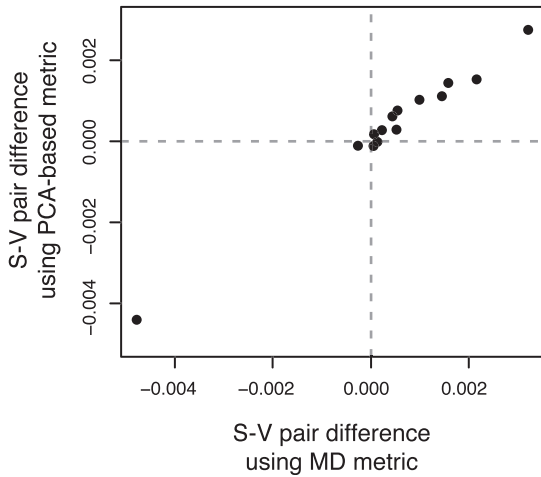


FIGURE 5. Comparison of difference in average within-locality morphological variation using *MD* versus the PCA-based metric. The metrics are significantly correlated (Spearman rank test, $n = 14$, $S = 6$, $p < 0.000$), suggesting that results are robust to differences in the morphological variation metric used.

variation, including average within-locality variation, the PCA-based measure of morphological variation produced results that were similar to those obtained using *MD* values (Fig. 5). Because the PCA-based approach uses the residuals of PCA shape variables regressed against centroid size to remove shape differences due to allometry, the similarity between the PCA-based results and the results based on the *MD* metric likely reflects a lack of strong allometry in the bivalves studied, at least over the range of sizes observed. The regressions of log centroid size against each of the 14 meaningful PC axes for each species also indicate a lack of strong allometry; the mean coefficient of determination between log centroid size and the 14 PC axes for each species ranged from 0.022 to 0.071. Of the 392 total regressions performed, 66 were statistically significant at the $\alpha = 0.05$ level, and the median R^2 of these significant regressions was 0.124, further indicating a lack of strong correlation between shape and log centroid size. Additionally, some curvilinearity was evident in the relationship between PC axes and log centroid size for at least 82 of the 392 regressions, potentially rendering simple linear regression of one variable on the other inappropriate. Because of this curvilinearity and because

allometry appeared to be minimal in most cases, the *MD* metric was favored over the PCA-based metric.

Locality-Controlled Comparisons of Morphological Variation.—Because many species respond morphologically to local environmental conditions, one species of a given pair may display greater morphological variation than its counterpart simply because it was present in environments that fostered greater ecophenotypic variation, or because it was sampled from a wider range of environments. To assess this possibility, we repeated our analysis, but limited it to localities in which the victim and survivor of a given pair both occurred. After removing victim-survivor pairs that never co-occurred at a locality, 11 pairs remained, with one to three shared localities per pair; each pair's difference in survivor and victim *MD* was calculated only on the basis of its shared localities. In addition, to avoid weighting the comparison toward cases in which species pairs had multiple localities in common, the difference in *MD* for survivor-victim pairs that co-occurred at more than one locality was calculated as the average of all shared localities. A pattern similar to the initial analyses results, with survivor variation exceeding that of victims for most species pairs (Fig. 6). However, the variation differences are not significant for this comparison, although this may reflect the reduced power due to the reduction in the number of pairs and in the number of specimens per pair (Wilcoxon signed rank test, $n = 11$, $V = 47$, $p = 0.240$; binomial test, $n = 11$, $p = 0.065$). Differences in average within-locality variation were significantly correlated with these locality-controlled differences in morphological variation, indicating that results of the average within-locality comparison were not systematically altered by differences in sampling between victims and survivors in each pair (Fig. 7).

Total Regional Morphological Variation.—The analysis of total regional morphological variation, based on lumping all localities of a given species into one group and calculating the resulting *MD* value, produced results roughly similar to the results of the average

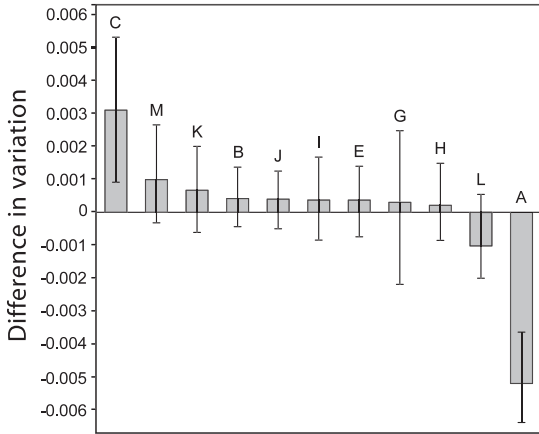


FIGURE 6. Locality-controlled comparison of morphological variation in survivors and victims. In this analysis, survivors and victims were compared only within localities where both species of a given pair both occurred. For survivor-victim pairs that had more than one locality in common, the average difference in morphological variation among those shared localities is depicted in this plot; 95% confidence intervals are based on bootstrapping (1000 replicates). Abbreviations as in Figure 4.

within-locality variation and locality-controlled variation analyses. Ten survivor species were observed to be more variable than their victim counterparts. Of these ten cases,

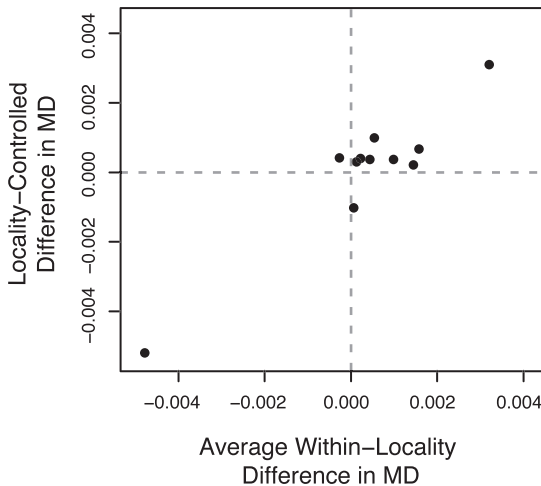


FIGURE 7. Comparison of average within-locality morphological variation versus locality-controlled morphological variation for survivors and victims. The significant correlation demonstrated here (Spearman rank test, $n = 11$, $S = 84$, $p = 0.04587$, $r^2 = 0.4113$) suggests that average within-locality differences in MD are robust to sampling biases potentially introduced by including different samples for the victim and survivor species within each pair.

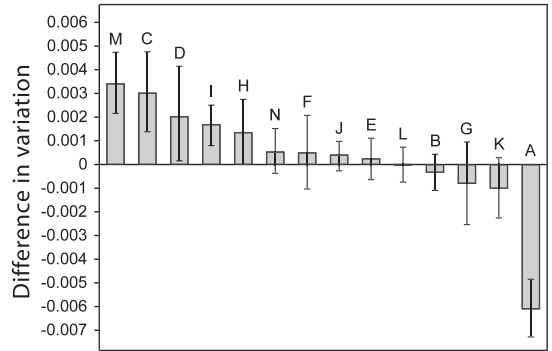


FIGURE 8. Difference in total regional variation between survivors and victims. For each species, variation was calculated for a lumped sample that included all specimens of the species, and variation of survivors and victims were compared within species pairs; 95% confidence intervals are based on bootstrapping (1000 replicates). Abbreviations as in Figure 4.

the difference was statistically significant ($p < 0.05$) in five instances; as before, this was true in only one of the four cases where the victim was more variable (Fig. 8).

When these aggregate differences in survivor and victim variation were tested using a Wilcoxon signed rank test, the results were not statistically significant ($n = 14$, $p = 0.217$). This difference from the previous analysis is related to the behavior of two victim-survivor pairs, K (*Anomalocardia caloosana* and *A. auberiana*) and G (*Trachycardium emmonsii* and *T. muricatum*). For both pairs, the victim increased in variation when samples were combined much more than the survivor did, either because the survivor was present at only one locality (Pair K) or because the mean forms at different localities differed more for the victim than for the survivor (Pair G). Because mean morphologies generally varied somewhat from locality to locality, total regional variation must be higher for each species than average within-sample variation, and the contributions of each sample to the regional variation of a species could be evaluated using an analysis of partial disparity (Foote 1993). However, given the limited and variable number of locations examined per species, an extensive comparison among species of the contributions of within and between-sample variation to total regional variation is not currently feasible.

Taxon Age and Survivorship.—Because extinction susceptibility may be related to taxon age (e.g., Doran et al. 2006; Finnegan et al. 2008), we also examined differences in taxon age, or time since a taxon's origination, at the time of the Plio-Pleistocene extinction (taxon age at event). First occurrences of each species were compiled from the literature (e.g., Anderson 1929; Mansfield 1932; Richards and Harbison 1942) and the Paleobiology Database. Although first occurrences are unlikely to represent the true origination of each species, given the high quality of preservation and sampling within the Florida Plio-Pleistocene, they are likely to record accurately the order of first occurrence within each species pair. Taxon age at the Plio-Pleistocene extinction event was calculated for each species as the number of stages elapsed since the species' first occurrence, and taxon ages at event were compared between victims and survivors. Victim species were older than their corresponding survivor species at the time of the Plio-Pleistocene extinction in four cases; survivors were older than victims in seven cases, and for three pairs, the survivor and victim species had the same stage of first occurrence. There was no significant difference in taxon age at the extinction event between victims and survivors when compared within pairs (Wilcoxon Signed Rank test, $n = 14$, $V = 43$, $p = 0.392$) or as a group (Wilcoxon Rank Sum test, $n_1 = n_2 = 14$, $W = 111$, $p = 0.547$). The relationship between taxon age and morphological variation at the time of the Plio-Pleistocene extinction was also nonsignificant (Spearman rank correlation test, $n = 28$, $\rho = -0.171$, $p = 0.383$). Although a detailed analysis of the relationships between taxon age, morphological variation, and survivorship is beyond the scope of the current study, these results suggest that the observed relationship between variation and survivorship is not the result of differences in taxon age within pairs.

Discussion

Overall, species that survived the Plio-Pleistocene extinction tended to have greater morphological variation than related species

that became extinct. Although results varied somewhat among scales of comparison, survivors had greater variation than victims in the majority of cases regardless of the protocol, and in many cases this difference was statistically significant. Morphological variation may therefore play a significant role in governing a species' likelihood of becoming extinct.

Recent work has indicated that intraspecific morphological variation can govern clade history in a number of ways. Morphological variation can affect the direction and rate of adaptive responses to selective pressures (Schluter 1996; Renaud et al. 2006), and evolutionary transitions can be concentrated in features for which morphological variation is the greatest (Hunt 2007). Evidence from trilobites suggests that intraspecific morphological variation may also promote speciation and diversification (Webster 2007). With respect to extinction, morphological variation may decrease extinction risk; a study by Liow (2007) found that species described qualitatively as "highly variable" had taxon longevity twice the length of species that were not. Although traits that promote survivorship during background levels of extinction frequently do not overlap with those promoting survivorship during mass extinctions (Jablonski 1986), our study suggests that the advantages of morphological variation may also extend to larger events on the scale of a regional mass extinction.

Previous studies have examined several other factors relating to extinction selectivity in bivalves during the Plio-Pleistocene event. Endemic species had a significantly lower survival rate than species that occupied more than one biogeographic province, and many ecological groups dominated by endemic taxa experienced higher rates of extinction than groups with lower percentages of endemic taxa (Stanley 1986; Vermeij and Petuch 1986). Stanley (1986) observed that the extinction selectively removed stenothermal tropical species, while a larger percentage of eurythermal species survived, suggesting that climate change may have played a role in the extinction. Morphological evidence suggests that changes in nutrient availability and

productivity also played a role in the extinction: data from chionine and corbulid bivalves from the western Atlantic indicate that body size decreased from the early Pliocene to the Pleistocene (Roopnarine 1996; Anderson 2001), and some evidence suggests that the extinction may also have been selective against highly armored, sculptured mollusks that presumably required high-productivity conditions (Vermeij and Petuch 1986; however, see also Hansen et al. 1999). Although the results of our study do not speak directly to the cause of the Plio-Pleistocene event, they do provide further insight into the processes that control extinction dynamics.

The positive association between morphological variation and extinction survivorship could result from several mechanisms. First, high morphological variation may reflect high levels of underlying, heritable additive genetic variation (Strauss 1991; Yezerinac 1992), which contribute directly to survivorship by facilitating adaptation to changing environmental conditions. Elementary quantitative genetics predicts that the rate of evolution by natural selection is proportional to additive genetic variance (Lande 1976; Falconer and Mackay 1996), and models suggest that increased genetic variance can greatly reduce extinction risk in the face of sustained environmental change (Lande and Shannon 1996). The interval encompassing the Plio-Pleistocene extinction was marked by numerous environmental changes, and, if morphological variation or some fraction thereof is heritable, the ability to adapt to these changing conditions may therefore have conferred a benefit to species with high morphological variation. It is also possible that species benefit by exhibiting multiple morphological forms among their populations at any given point in time, as some forms might survive or thrive during environmental changes that hinder or cause the extinction of other conspecific morphological forms (Liow 2007). Finally, even if differences in variation have an environmental, rather than genetic basis, phenotypic plasticity can itself be adaptive (Via et al. 1995) and confer a survival advantage (Lande 2009). In each of

these scenarios, morphological variation directly causes differences in survivorship.

Alternatively, morphological variation may contribute to survivorship by permitting species to occupy a wider range of environmental and geographic settings, increasing the spatial range of the species, which would reduce extinction risk. This possibility is supported by recent studies indicating that high morphological variation promotes invasive behavior (Tomeček et al. 2007; Záhorská et al. 2009). Numerous studies have demonstrated that a large geographic or environmental range size confers resistance to extinction (Lloyd and Gould 1993; Payne and Finnegan 2007; Jablonski 2008). Morphological variation has also been correlated with niche breadth in several cases (Van Valen 1965; Findlay and Black 1983; Bolnick et al. 2007); if highly variable species act as generalists they may be more robust to environmental changes (Kammer et al. 1997). These explanations posit an indirect but nevertheless causal relationship between variation and extinction: variation causes geographic or ecological breadth, which in turn promotes survivorship.

Conversely, species that inhabit a wide geographic and environmental range may develop high morphological variation because of their broad distribution. A species that occupies many selectively distinct environments may have different optimal forms across its range, and gene flow across locations means that the morphologies found in a given population can be a highly variable compromise among these different optima (Yeaman and Jarvis 2006). In this case, the relationship between variation and survivorship is not causal; both are governed by geographic or ecological breadth. Modern studies indicate that shifts in morphology and morphological variation can be related to expansions in geographic range caused by other factors, such as habitat and food availability, thereby supporting the plausibility of this third scenario (Alisauskas 1998).

Conclusions

Consistent with our initial hypothesis, veneroid bivalve species that survived the

regional Plio-Pleistocene extinction in Florida were more variable morphologically in a significant number of cases when compared with closely related counterparts that did not survive the event. Previous research indicates that a variety of environmental factors fluctuated over short time scales during the Plio-Pleistocene extinction. High-variation species may have benefited from a broader range of adaptations, which caused them to be less sensitive to these rapid environmental and ecological changes, or from a greater ability to respond to these stresses. Alternatively, the relationship between variation and survivorship may have been indirect, mediated through factors such as geographic and ecological range.

Acknowledgments

We thank R. Portell and L. Ward for facilitating access to museum collections, and H. Packard, B. Stackhouse, B. Leatherman, and E. Gnass for providing assistance in data collection. M. Webster and an anonymous reviewer provided valuable comments that greatly improved the manuscript. This project was made possible by a Chappell Research Fellowship and Student Travel Grant from the Charles Center of the College of William and Mary, and by a travel grant from the Southeastern Section of the Geological Society of America. Acknowledgment is made to the Donors of the American Chemical Society Petroleum Research Fund for partial support of this research.

Literature Cited

- Akers, W. H. 1972. Planktonic foraminifera and biostratigraphy of some Neogene formations, northern Florida and Atlantic Coastal Plain. *Tulane Studies in Geology and Paleontology* 9:1-139.
- , and P. E. Koepfel. 1973. Age of some Neogene formations, Atlantic Coastal Plains, United States and Mexico. Pp. 80-93 in L. A. Smith and J. Hardenbol, eds. *Proceedings of symposium on calcareous nannofossils*. Gulf Coast Section, Society of Economic Paleontologists and Mineralogists, Houston.
- Alisauskus, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent Lesser Snow Geese. *Auk* 115:851-862.
- Allmon, W. D. 1992. Whence southern Florida's Plio-Pleistocene shell beds? In T. M. Scott and W. D. Allmon, eds. *The Plio-Pleistocene stratigraphy of southern Florida*. Florida Geological Survey Special Publication 36:1-20.
- . 1993a. Age, environment, and mode of deposition of the densely fossiliferous Pinecrest Sand (Pliocene of Florida): implications for the role of biological productivity in shell bed formation. *Palaaios* 8:183-201.
- . 1993b. Do Florida's Plio-Pleistocene shell beds have large-scale paleobiological significance? In V. Zullo, W. Harris, T. Scott, and R. Portell, eds. *The Neogene of Florida and adjacent regions*. Proceedings of the third Bald Head Island conference on coastal plain geology. Florida Geological Survey Special Publication 37:67-72.
- . 2001. Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166:9-26.
- Allmon, W. D., S. D. Emslie, D. S. Jones, and G. S. Morgan. 1996. Late Neogene oceanographic change along Florida's west coast: evidence and mechanisms. *Journal of Geology* 104:143-162.
- Anderson, F. M. 1929. Marine Miocene and related deposits of North Colombia. *Proceedings of the California Academy of Sciences* 18:73-213.
- Anderson, L. C. 2001. Temporal and geographic size trends in Neogene Corbulidae (Bivalvia) of tropical America: using environmental sensitivity to decipher causes of morphological trends. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166:101-120.
- Berggren, W. A., D. V. Kent, C. C. Swisher III, and M.-P. Aubry. 1995. A revised Cenozoic geochronology and chronostratigraphy. *Society for Sedimentary Geology Special Publication* 54:129-364.
- Bolnick, D. I., R. Svanback, M. S. Araujo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences USA* 104:10075-10079.
- Budd, A. F., K. G. Johnson, and T. A. Stemann. 1996. Plio-Pleistocene turnover and extinctions in the Caribbean reef-coral fauna. Pp. 168-204 in Jackson et al. 1996a.
- Chapman, R. E. 1990. Conventional Procrustes approaches. In F. J. Rohlf and F. L. Bookstein, eds. *Proceedings of the Michigan morphometrics workshop*. University of Michigan Museum of Zoology Special Publication 2:251-267.
- Cronin, T. M. and H. J. Dowsett. 1996. Biotic and oceanographic response to the Pliocene closing of the Central American Isthmus. Pp. 76-104 in Jackson et al. 1996a.
- Doran, N. A., A. J. Arnold, W. C. Parker, and F. W. Huffer. 2006. Is extinction age dependent? *Palaaios* 21:571-579.
- Dryden, I. 2006. Shapes: statistical shape analysis. R package, Version 1.1-1. <http://www.maths.not.ac.uk/~ild/shapes>
- Dryden, I. L., and K. V. Mardia. 1998. *Statistical shape analysis*. Wiley, Chichester, U.K.
- DuBar, J. R., R. Jules, T. E. Ewing, E. L. Lundelius Jr., E. G. Otvos, and C. D. Winker. 1991. Quaternary geology of the Gulf of Mexico coastal plain. Pp. 583-610 in R. B. Morrison, ed. *Quaternary nonglacial geology; conterminous United States*. Geology of North America, Vol. K-2. Geological Society of America, Boulder.
- Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Addison-Wesley, Essex, U.K.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1-15.
- Findlay, J. S., and H. Black. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* 64:625-630.
- Finnegan, S., J. L. Payne, and S. C. Wang. 2008. The Red Queen revisited: reevaluating the age selectivity of Phanerozoic marine genus extinctions. *Paleobiology* 34:318-341.
- Foote, M. 1993. Contributions of individual taxa to overall morphological disparity. *Paleobiology* 19:403-419.

- Hansen, T. A., P. H. Kelley, V. D. Melland, and S. E. Graham. 1999. Effect of climate-related mass extinctions on escalation in molluscs. *Geology* 27:1139–1142.
- Hopkins, M. J., and M. Webster. 2009. Ontogeny and geographic variation of a new species of the corynexochine trilobite *Zacanthopsis* (Dyeran, Cambrian). *Journal of Paleontology* 83:524–547.
- Hunt, G. 2007. Evolutionary divergence in directions of high phenotypic variance in the ostracode genus *Poseidonamicus*. *Evolution* 61:1560–1576.
- Huddlestone, P. F. 1988. A revision of the lithostratigraphic units of the coastal plain of Georgia, the Miocene through the Holocene. *Georgia Geologic Survey Bulletin* 104:1–154.
- International Commission on Stratigraphy. 2009. International stratigraphic chart. www.stratigraphy.org
- Jablonski, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* 231:129–133.
- . 2008. Extinction and the spatial dynamics of biodiversity. *Proceedings of the National Academy of Sciences USA* 105:11528–11535.
- Jablonski, D., and G. Hunt. 2006. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *American Naturalist* 168:556–564.
- Jackson, J. B. C., P. Jung, A. G. Coates, and L. S. Collins. 1993. Diversity and extinction of tropical American mollusks and the emergence of the Isthmus of Panama. *Science* 260:1624–1626.
- Jackson, J. B. C., A. F. Budd, and A. G. Coates, eds. 1996a. *Evolution and environment in tropical America*. University of Chicago Press, Chicago.
- Jackson, J. B. C., P. Jung, and H. Fortunato. 1996b. Paciphilia revisited: transisthmian evolution of the *Strombina* group (Gastropoda: Columbellidae). Pp. 234–270 in Jackson et al. 1996a.
- Jones, D. S., B. J. MacFadden, S. D. Webb, P. A. Mueller, D. A. Hodell, and T. M. Cronin. 1991. The integrated geochronology of a classic Pliocene fossil site in Florida: linking marine and terrestrial biochronologies. *Journal of Geology* 99:637–648.
- Kammer, T. W., T. K. Baumiller, and W. I. Ausich. 1997. Species longevity as a function of niche breadth: evidence from fossil crinoids. *Geology* 25:219–222.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- . 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology* 22:1435–1446.
- Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50:434–437.
- Liow, L. H. 2007. Does versatility as measured by geographic range, bathymetric range, and morphological variability contribute to taxon longevity? *Global Ecology and Biogeography* 16:117–128.
- Lloyd, E. A., and S. J. Gould. 1993. Species selection on variability. *Proceedings of the National Academy of Sciences USA* 90:595–599.
- Lyons, W. G. 1991. Post-Miocene species of *Latirus* Montfort, 1810 (Mollusca: Fasciolaridae) of southern Florida, with a review of regional marine biostratigraphy. *Bulletin of the Florida Museum of Natural History* 35:131–208.
- Lockwood, R. 2004. The K/T event and infaunality: morphological and ecological patterns of extinction and recovery in veneroid bivalves. *Paleobiology* 30:507–521.
- Maddison, W. P. 2000. Testing character correlation using pairwise comparisons on a phylogeny. *Journal of Theoretical Biology* 202:195–204.
- Mansfield, W. C. 1932. Miocene pelecypods of the Choctawatchee Formation of Florida. *Florida State Geological Survey Bulletin* 8:1–240.
- McCartan, L., S. D. Weedman, G. L. Wingard, L. E. Edwards, P. J. Sugarman, M. D. Feigenson, M. L. Buursink, and J. C. Libarkin. 1995. Age and diagenesis of the upper Floridan aquifer and the intermediate aquifer system in southwestern Florida. *U.S. Geological Survey Bulletin* 2122:1–26.
- McGhee, G. R. 1995. Geometry of evolution in the biconvex Brachiopoda: morphological effects of mass extinction. *Neues Jahrbuch für Geologie und Paläontologie* 197:357–382.
- Missimer, T. M. 2001a. Late Neogene geology of northwestern Lee County, Florida. In T. M. Missimer and T. M. Scott, eds. *Geology and hydrology of Lee County, Florida* (Durward H. Boggess Memorial Symposium). Florida Geological Survey Special Publication 49:21–34.
- . 2001b. Late Paleogene and Neogene chronostratigraphy of Lee County, Florida. In T. M. Missimer and T. M. Scott, eds. *Geology and hydrology of Lee County, Florida* (Durward H. Boggess Memorial Symposium). Florida Geological Survey Special Publication 49:67–90.
- Ogg, J. G., G. Ogg, and F. M. Gradstein. 2008. *The concise geologic time scale*. Cambridge University Press, Cambridge.
- Olsson, A. A. 1961. *Mollusks of the tropical eastern Pacific, particularly from the southern half of the Panamic-Pacific Faunal Province (Panama to Peru), Part I. Panamic Pacific Pelecypoda*. Paleontological Research Institution, Ithaca, N.Y.
- Otvos, E. G. 1988. Pliocene age of coastal units, northeastern Gulf of Mexico. *American Association of Petroleum Geologists Bulletin* 72:1119–1120.
- . 2005. Numerical chronology of Pleistocene coastal plain and valley development; extensive aggradation during glacial low sea-levels. *Quaternary International* 135:91–113.
- Payne, J. L., and S. Finnegan. 2007. The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences USA* 104:10506–10511.
- Petuch, E. J. 1982a. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37:277–312.
- . 1982b. Notes on the molluscan paleoecology of the Pinecrest Beds at Sarasota, Florida with a description of *Pyrullia*, a stratigraphically important new genus (Gastropoda: Melongenidae). *Proceedings of the Academy of Natural Sciences of Philadelphia* 134:12–30.
- Purvis, A. 2008. Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics* 39:301.
- R Core Development Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.
- Renaud, S., J.-C. Auffray, and J. Michaux. 2006. Conserved phenotypic variation patterns, evolution along the lines of least resistance, and departure due to selection in fossil rodents. *Evolution* 60:1701–1717.
- Richards, H. G., and A. Harbison. 1942. Miocene invertebrate fauna of New Jersey. *Proceedings of the Academy of Natural Sciences of Philadelphia* 94:167–250.
- Rohlf, F. J. 1990. Rotational fit (Procrustes) methods. In F. J. Rohlf and F. L. Bookstein, eds. *Proceedings of the Michigan morphometrics workshop*. University of Michigan Museum of Zoology Special Publication 2:227–236.
- . 2006. tpsDIG, version 2.05, available at <http://life.bio.sunysb.edu/morph>.
- Roopnarine, P. D. 1996. Systematics, biogeography, and extinction of chionine bivalves (Bivalvia: Veneridae) in tropical America: early Oligocene–Recent. *Malacologia* 38:103–142.

- Rupert, F. R. 1990. Geology of Gadsden County, Florida. Florida Geological Survey Bulletin 62:1–61.
- Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50:1766–1774.
- Schmidt, W. 1984. Neogene stratigraphy and geologic history of the Apalachicola Embayment, Florida. Florida Geological Survey Bulletin 58:1–146.
- Smith, J. T., and K. Roy. 2006. Selectivity during background extinction: Plio-Pleistocene scallops in California. *Paleobiology* 32:408–416.
- Stanley, S. M. 1986. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the Western Atlantic bivalve fauna. *Palaos* 1:17–36.
- . 1988. Adaptive morphology of the shell in bivalves and gastropods. Pp. 105–141 in E. R. Trueman and M. R. Clark, eds. *The Mollusca*, Vol. 11. Academic Press, New York.
- . 1990. Delayed recovery and the spacing of mass extinctions. *Paleobiology* 16:401–414.
- Stanley, S. M., and L. D. Campbell. 1981. Neogene mass extinction of Western Atlantic mollusks. *Nature* 293:457–459.
- Strauss, R. E. 1991. Correlations between heterozygosity and phenotypic variability in *Cottus* (Teleostei: Cottidae): character components. *Evolution* 45:1950–1956.
- Todd, J. A., J. B. C. Jackson, K. G. Johnson, H. M. Fortunato, A. Heitz, M. Alvarez, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London B* 269:571–577.
- Tomeček, J., V. Kováč, and S. Katina. 2007. Biological flexibility of pumpkinseed, a successful coloniser throughout Europe. Pp. 307–336 in F. Gherardi, ed. *Freshwater bioinvaders: profiles, distribution, and threats*. Springer, Dordrecht.
- Van Valen, L. 1965. Morphological variation and width of ecological niche. *American Naturalist* 99:377–390.
- Vermeij, G. J. 1990. Tropical Pacific pelecypods and productivity: a hypothesis. *Bulletin of Marine Science* 47:62–67.
- Vermeij, G. J., and E. J. Petuch. 1986. Differential extinction in tropical American mollusks. Endemism, architecture, and the Panama land bridge. *Malacologia* 27:29–41.
- Via, S., R. Gomulkiewicz, G. Dejong, S. M. Scheiner, C. D. Schlichting, and P. H. Vantienderen. 1995. Adaptive phenotypic plasticity—consensus and controversy. *Trends in Ecology and Evolution* 10:212–217.
- Ward, L. W. 1992. Diagnostic mollusks from the APAC Pit, Sarasota, Florida. In T. M. Scott and W. D. Allmon, eds. *The Plio-Pleistocene stratigraphy and paleontology of southern Florida*. Florida Geological Survey Special Publication 36:161–166.
- Webster, M. 2007. A Cambrian peak in morphological variation within trilobite species. *Science* 317:499–502.
- Willard, D. A., T. M. Cronin, S. E. Ishman, and R. J. Litwin. 1993. Terrestrial and marine records of climatic and environmental changes during the Pliocene of subtropical Florida. *Geology* 21:679–682.
- Woodring, W. P. 1966. The Panama land bridge as a sea barrier. *Proceedings of the American Philosophical Society* 110:425–433.
- Yeaman, S., and A. Jarvis. 2006. Regional heterogeneity and gene flow maintain variance in a quantitative trait within populations of lodgepole pine. *Proceedings of the Royal Society of London B* 273:1587–1593.
- Yezerinac, S. M., S. C. Loughheed, and P. Handford. 1992. Morphological variability and enzyme heterozygosity: individual and population level correlations. *Evolution* 46:1959–1964.
- Záhorská, E., V. Kováč, I. Falka, S. Katina, G. H. Copp, and R. E. Gozlan. 2009. Morphological variability of the Asiatic cyprinid, topmouth gudgeon *Pseudorasbora parva*, in its introduced European range. *Journal of Fish Biology* 74:167–185.
- Zelditch, M. L., D. L. Swiderski, H. D. Sheets, and W. L. Fink. 2004. *Geometric morphometrics for biologists: a primer*. Elsevier Academic Press, San Diego.