



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

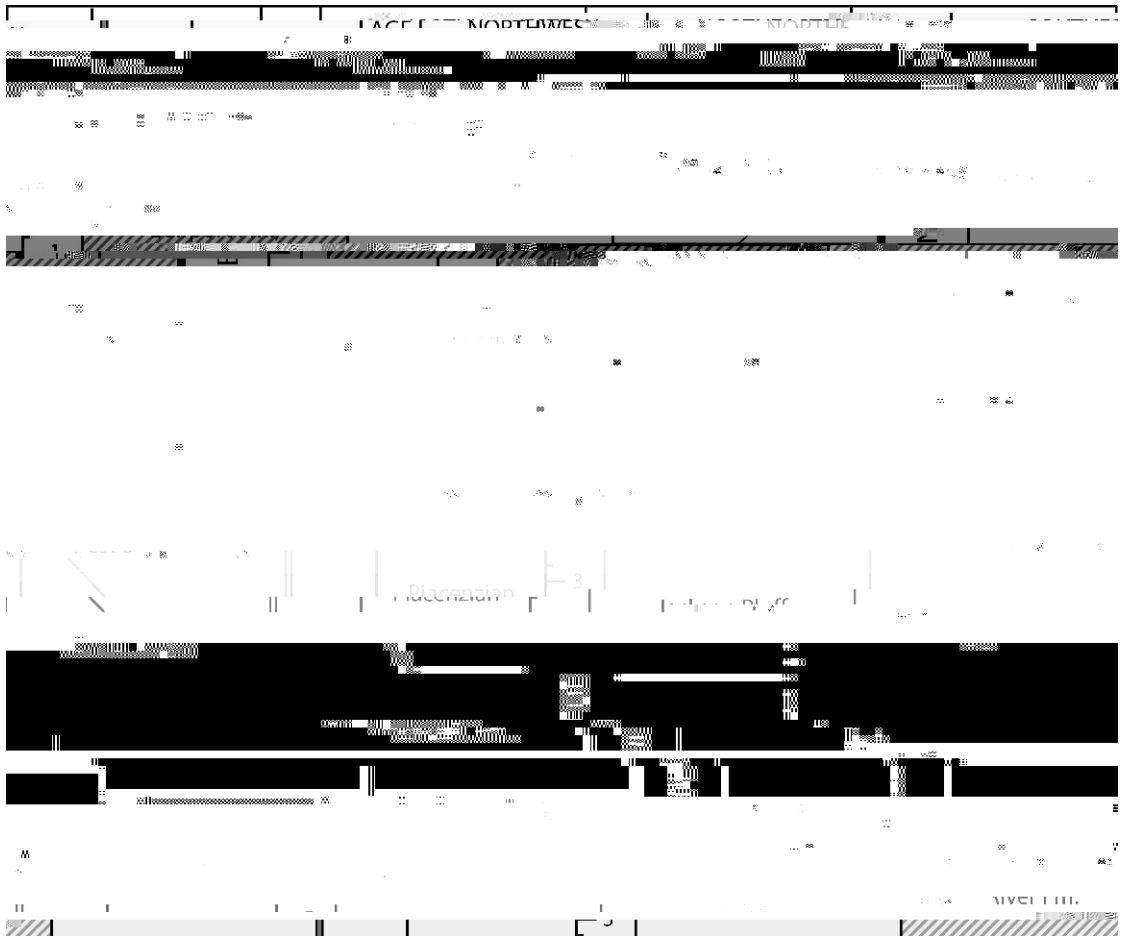


FIGURE 1. Generalized correlation chart of Pliocene and Pleistocene deposits in Florida (based on Akers 1972; Akers and Koepfel 1973; Huddleston 1988; Otvos 1988, 2005; Rupert 1990; DuBar et al. 1991; Jones et al. 1991; Lyons 1991; Allmon 1992; McCartan et al. 1995; and Missimer 2001a,b). The units sampled 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 Koepfel 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

**K<sub>7</sub> i**—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,

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



1998). A mean form is calculated during GPA by averaging the x and y coordinates of each of the fitted landmark points (Rohlf 1990). Pro-



variation, including average within-locality variation, the PCA-based measure of morphological variation produced results that were similar to those obtained using 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 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



within-locality variation and locality-con-

—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-

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



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