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COMBINING MORPHOMETRIC AND PALEOECOLOGICAL ANALYSES: EXAMINING SMALL-SCALE DYNAMICS IN SPECIES-LEVEL AND COMMUNITY-LEVEL EVOLUTION

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ABSTRACT

By combining two powerful types of quantitative techniques—landmark morphometric and paleocommunity analyses—we can examine the role of ecology in evolutionary processes by determining whether major morphological changes co-occur with significant changes in paleocommunity structure. Whereas morphological changes using landmark morphometric analysis indicate evolutionary changes within a lineage, changes in paleocommunity metrics such as abundance and dominance can be used to indicate ecological changes and identify species of special interest.

This preliminary study documents both major ecological and morphological changes within the scallop *“Pecten” thompsoni* from two closely spaced stratigraphic horizons of the Neogene marine sequence of the Dominican Republic. Ecologically, the abundance and dominance of this species differs dramatically between the two samples. Morphometrically, while size does not change significantly, the two populations exhibit statistically different shapes. In addition, there appears to be a shift in ontogenetic patterns where initially an allometric pattern exists but then changes to an isometric growth relationship. These different morphological patterns are consistent with changes in paleoenvironmental conditions. We suggest that a coupled approach of morphometric and paleocommunity analyses may focus future studies on intervals and taxa where evolutionary change may be directly correlated to concomitant ecological changes.

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INTRODUCTION

The fossil record clearly documents both changes in taxonomic lineages and community composition. However, it is unclear how closely related the processes and patterns of species evolution and community changes may be. The evidence to suggest that the role of biotic interactions shape the evolutionary paths of lineages remains controversial (e.g., Valentine 1973; Kitchell 1985; Gould 2001; Vermeij 2004).

Among neontologists, however, local ecological interactions between species have been cited as a major influence on speciation and evolution. The geographic mosaic theory of co-evolution has provided a new way of considering the role of local ecology and biotic interactions in allopatric speciation processes and evolutionary patterns. For example, in examining the interactions between a species of moth and a plant in western US states, Thompson (1997, 1999) documented that there existed mutualistic, commensalistic, or even antagonistic relationships between the two species depending on the presence or absence of other insect species. These differences in biotic interactions can be correlated with different genetic populations (Thompson 1999) and thus, can drive speciation through time (Forde et al. 2004). Another implication of these observations and interpretations is that within small geographic areas, “[I]nteractions may show selection mosaics, such that different traits and outcomes are favored by natural selection in different communities” (Thompson 1999).

In a paleontological context, the geographic mosaic theory of co-evolution suggests that paleocommunity composition and biotic interactions may vary geographically and temporally even at small scales, and that these differences may result in evolutionary changes. This theoretical framework may, therefore, bridge the fields of evolutionary biology and paleoecology as well as neoecology and population genetics. In this paper, we explore the potential of using quantitative morphometric and paleocommunity composition data to examine whether correlations exist between community-level and species-level patterns. Quantitative morphometrics allows for the evaluation of species-level microevolutionary changes whereas the analysis of paleocommunity composition provides a first-level proxy for evaluating biotic interactions and ecological fluctuations. If evolutionary changes within lineages as evidenced by morphological change are concurrent with major changes in community structure, it would allow us to seriously reconsider the role of biotic interactions in determining patterns of species evolution in the fossil record.

In order to investigate the relationship between ecological and evolutionary processes, one must have appropriate depositional systems and fossil samples which will allow for robust quantitative analyses. One such depositional system is in the Neogene marine sequences of the Cibao Valley of the northern Dominican Republic. This system has become a major focal point of many important paleobiological studies for many good reasons. The fossils have been studied since the mid 1800s with much modern study based on collections made by E. and H. Vokes and the Naturhistorisches Museum of Basel, Switzerland, since the 1970s (see Jung 1986 for review of molluscan studies and NMITA web site, http://porites.geology.uiowa.edu/). The marine sequences exposed in river gorges in the north central highlands are very fossiliferous and are believed to represent fairly continuous deposition in a gradually deepening basin (Saunders et al. 1986).

Many paleontologists around the world have been involved in examining the Dominican Republic Neogene fauna. Experts in taxonomic groups have systematically surveyed the samples collected by the Naturhistorisches Museum of Basel (many monographs have been published in *Bulletins of American Paleontology*). Given the long history of taxonomic study, the alpha taxonomy and basic identification of fossils found in these rocks is comparatively good even if higher level taxonomic reorganizations have not yet been completed for most of the groups. In addition, paleobiologists have long used this system to examine patterns of evolution, including documenting rates of change and investigating the role of heterochrony in speciation processes (e.g., Anderson 1994; Cheetham et al. 1994; Nehm and Geary 1994).

MATERIALS

Appropriate samples for rigorous, quantitative analyses of both morphological and paleoecological change were collected by one of the authors (CT) during an expedition to the Rio Gurabo and Rio Cana of the Dominican Republic in the summer of 2000. Bulk fossil sampling was employed where matrix and fossil materials were collected together without discrimination along restricted vertical and lateral intervals. Five sub-samples were taken at each locality; collectively these are referred to as one bulk fossil sample. These sampling localities are closely aligned to sampling localities of the

Naturhistorisches Museum of Basel collection (Saunders et al. 1986).

By restricting the lateral extent from which the samples were collected, we minimize as much as possible the effect biological and taphonomic patchiness may have on assemblage composition. The average lateral extent of the samples was 1.02 m (median = 0.87 m); 26% of the samples extended less than 0.50 m horizontally. Similarly, by restricting vertical thicknesses, the time averaging represented within samples was minimized as much as possible. For the 31 bulk fossil samples collected from the Dominican Republic in 2000 (each with five sub-samples), the average thickness of samples was 0.156 m with the maximum thickness at 0.23 m.

The taphonomic condition of the fossil material is another proxy often used to assess time averaging (Best and Kidwell 2000). In all of the fossil samples we collected, there is little evidence of post-mortem boring or encrusting, thus suggesting that the fossils did not spend much time on the seafloor surface before being buried; virtually all borings in the samples are predatory borings, (Tang 2002). Not uncommonly, articulated corbulid bivalves are found and in several cases, very delicate spines (for example, on spondylid bivalves) and thin tubes of scaphapods and vermetid gastropods are present, again suggesting limited amounts of post-mortem exposure on the seafloor as well as limited transport. Preserved color patterns have been observed in associated Dominican Republic fossil samples (Costa et al. 2001). Thus, we interpret these fossil assemblages to be para-authochthonous, or representative of disturbed neighborhood assemblages (in this paper we will refer to these as “paleocommunities”).

The two samples analyzed for this paper—060700-2A and 052500-1C—were collected from the Rio Gurabo section. Our fieldwork indicates that these samples are roughly equivalent to samples 18189 and 15907 of Saunders et al. (1986) respectively, in both stratigraphic and geographic location. Based on close correlation with the stratigraphic section prepared by Saunders et al. (1986), the samples are estimated to be separated by approximately 9 m vertically, with 060700-2A located at approximately 136 m in the section and 052500-1C at 127 m. Both are from within the NN 11 zone of the Late Miocene Cercado Formation. All specimens and unwashed sub-samples are deposited at the California Academy of Sciences Department of Invertebrate Zoology and Geology collections (San Francisco, California, USA).

The two samples analyzed are composed of skeletal grains in a matrix of poorly cemented siliciclastic grains. This type of muddy tropical depositional environment is considered to have minimal time averaging due to a higher rate of sedimentation and minimal physical reworking (Best and Kidwell 2000). Sample 060700-2A comes from blue-grey muddy sandstone horizons that contained thin shell beds, which were laterally continuous and traceable for some distance. The foraminifera *Amphistigena* was common in this sample as observed in the field, and it was also noted to contain medium to large bivalves, scaphapods, and gastropods. Sample 052500-1C was collected from a horizon containing an amalgamated, densely packed shell bed. In the field, it was noted that the siliciclastic and fossil components did not appear to be well size-sorted and that delicate molluscs were well preserved. Both samples appear to be storm-deposited shell beds and have similar lithological and taphonomic properties.

One complete sample bag from each sample analyzed was washed over a 2 mm sieve; most of the materials are fairly unconsolidated although occasional soaking and rewashing was necessary to disaggregate some portions of some samples. To clean individual fossils for accurate identification and morphometric analyses, specimens were soaked overnight in water and a sharp thin pick used to gently remove matrix particles.

METHODS

Initially, all fossils and fossil fragments were picked from the > 2 mm aliquot. For this analysis, all complete bivalve fossils and fragments that were (1) at least two-thirds complete and (2) were identifiable to at least a generic level were counted. Because almost all of the bivalves are disarticulated into two valves, this counting method estimates the maximum abundance of bivalves present in the assemblage. Furthermore, because this study is based exclusively on bivalves, there was no attempt made at this juncture to convert these maximum counts of bivalve individuals into a number that can be used to compare bivalve abundances to those of gastropods, scaphopods, solitary corals or other taxa, nor with colonial organisms like bryozoans.

Some groups of bivalves were identified to generic and species levels based on descriptions by Maury (1917). While we recognize that there has been some systematic revisions and synonimization of these taxa, this preliminary study was more concerned with the identification of species-level groupings rather than on their taxonomic revision. Although some bivalves were not identified to the generic level, they were still counted so that we

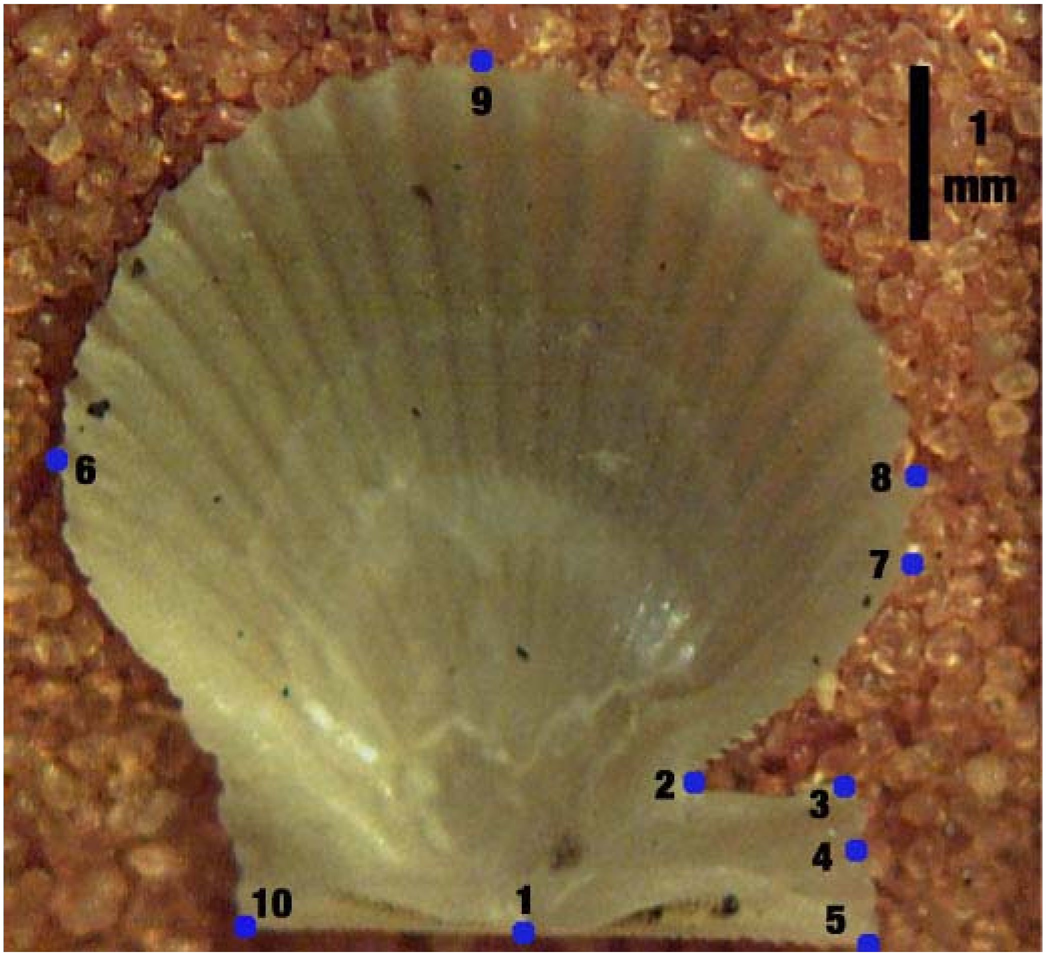

Figure 1. "*P.*" *thompsoni* valve and landmarks used in this study; numbered landmarks correspond to those in Figure 6.

could obtain a snapshot of the entire bivalve paleocommunity and examine dominance patterns.

All 22 individuals of *"Pecten" thompsoni* were selected for morphometric analysis from Sample 052500-1C while 21 individuals were randomly selected for analysis from Sample 060700-2A. Specimens were imaged with either a Kodak MDS100 digital camera mounted on a Wild M400 dissecting microscope or a high- resolution flatbed scanner. Digital images were then imported as jpeg files into TnImage 3.0.6 (Linux) where 10 specimen landmarks were digitized (Figure 1).

The raw landmark data were used to calculate specimen size and describe the shape of the shell. Size was calculated as centroid size, which can be described independently of shape (Bookstein 1991), and bears the advantage of being uncorrelated with measures of shape in the absence of allometry.

Shape was described using principal warp analysis (Bookstein 1991), which summarizes shape as a transformation relative to a common reference form. Specimens were first scaled to unit centroid size and rotated to maximum interspecimen alignment using a Procrustes iterative alignment. Each specimen, or its map of landmarks, may then be represented in a special "shape space," relative to the common reference form, with each unique landmark configuration occupying a unique position in the shape space. This resulting Kendall shape space (Kendall 1986; actually, the small portion occupied by the distribution of specimens) is then projected onto a tangential Euclidean space where the axes correspond to the major dimensions of specimen distribution (variation) in the curved shape space (principal warps) (Rohlf 1996), with specimen coordinates on these axes (partial warp scores) summarizing specimen shape. Procrustes alignment and principal warp analyses were performed with tpsRelw (Rohlf 2002).

Shape variation was tested with multivariate analysis of variance (MANOVA) of partial warp scores and subsequent classification of specimens performed using canonical variates analysis (CVA). Intrasample allometry was tested by regression of relative warp scores on centroid size. Relative warps are factors (principal components of partial warp scores) which themselves summarize the major vectors of shape variation within samples. Because relative warps are independent components decomposing shape, a proper depiction of allometry is the multiple regression of size on all relative warps, or the individual regression of relative warps on size. The latter approach is used here. All statistical analyses were performed with SYSTAT 10 (Windows) and Stata 8.0 (Linux).

RESULTS

Bivalve paleocommunity composition

The number of counted bivalve specimens was similar for both samples with 501 individuals in Sample 52500-1C and 511 in Sample 060700-2A. Paleocommunity differences are often assessed either with presence/absence data or with census data. We have compared our two samples using these two different metrics, and the results indicate that census data conclusions differ from those obtained from presence/absence data alone. Since not all groups were identified in this initial study and since substantive taxonomic revisions need to be undertaken for the groups, we report initial comparisons for some bivalve groups here only to provide evidence for major paleocommunity differences between these two samples.

Arcids made up 19.2% of the bivalve individuals in Sample 52500-1C and 12.7% of Sample 060700-2A bivalves. There are five different arcid species present in Sample 52500-1C and nine different species in Sample 060700-2A. One of those species is *Scapharca hispaniolana,* and it shows marked differences of abundance between the two samples. In Sample 52500-1C, *S. hispaniolana* comprised 18.4% of all bivalves counted and 95.8% of all the arcids whereas in Sample 060700-2A, it comprised only 0.6% of all bivalves and 4.6% of the arcids. Another arcid species, *Scapharca cibaoica*, is not found at all in Sample 52500-1C but comprised 4.7% of bivalves and 36.9% of arcids in Sample 060700-2A.

In another example, pectinids are only 10.4% of Sample 52500-1C but make up 61.8% of Sample 060700-2A. But this significant difference between samples is not reflected in the number of species present: Sample 52500-1C has eight different pectinid species while the other sample has nine. They have seven species in common. “*Pecten” thompsoni* is one of those species but its abundance varies greatly between samples. In Sample 52500-1C, “*P.” thompsoni* comprised 59.6% of pectinid individuals and only 6.2% of all bivalves. However in Sample 060700-2A, this species was 90% of pectinids and 50.7% of bivalves.

Morphology

Given the disparity in paleocommunity numerical composition between the two samples, the morphological results can be used to determine if paleoecological changes are correlated with phenotypic differences.

“Pecten” thompsoni was selected because of its contrasting abundance in one of the samples and its relatively smaller role in the other assemblage. This taxon is also easy to recognize due to the distinctive protuberances near its byssal notch. The distinctive nature of the species eliminates any errors, which may occur due to taxonomic misidentifications. In addition, valves of *“P.” thompsoni* are not highly convex and allow for digital image capture using a flatbed scanner for larger individuals rather than on a conventional microscope-digital camera setup. This combination of factors makes it an ideal candidate for morphometric work.

Centroid size does not differ statistically between the two samples (t-test, p = 0.2283), although the variance is slightly greater in Sample 060700-2A (but not statistically significant, F-test, p = 0.2765) (Figure 2). Relative warps analysis of the two samples does, however, indicate differences in shape (Figure 3), though there is considerable overlap. Multivariate analysis of variance and subsequent CVA of partial warp scores confirms that the samples differ significantly in shape (Wilks' Lambda , p < 0.0001) (Figure 4), with 97.7% of specimens correctly identified by the discriminant function.

Allometric development was measured for each sample by examining the correlation between centroid size and relative warp factors, revealing that there is an allometric relationship apparent in one population but not in the other. In Sample 060700-2A, there is no shape change through the different size classes. Correlations between relative warps I, II, and IV are not significant (Figure 5A; linear regression of relative warp I on centroid size, F-ratio, p = 0.4811). A significant relationship between relative warp III and size (Pearson's correlation coefficient = -0.4563, p = 0.0376) is the spurious result of a single outlying specimen and is not considered further.

The first relative warp of Sample 052500-1C displays significant allometry (Pearson's correlation coefficient = -0.4676, p = 0.0282), but a plot of this warp and centroid size (Figure 5B) shows very clearly that the relationship between size and

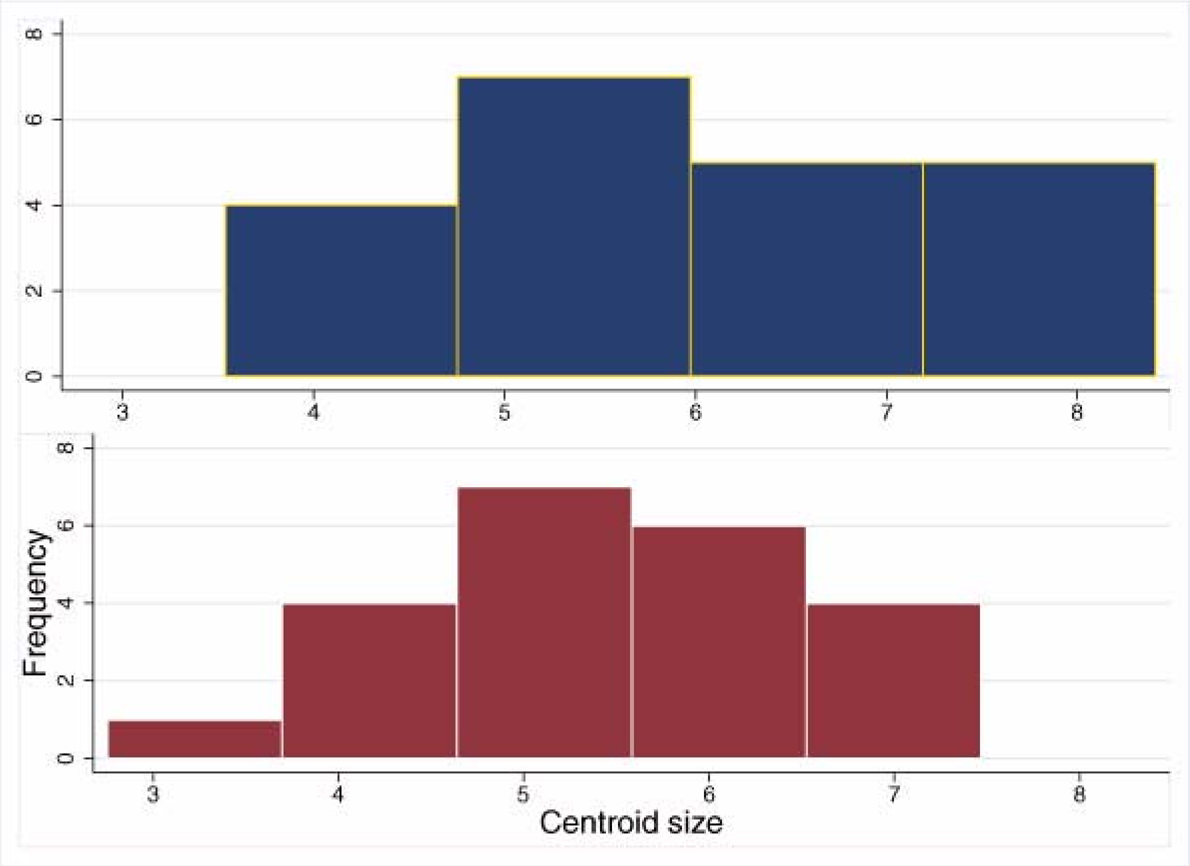

Figure 2. Histograms of centroid sizes in 060700-2A (upper graph) and 052500-1C (lower graph). There is no statistical difference between the two populations (t-test, p = 0.2283).

shape is not linear. There is an obvious change in the relationship when specimens attain a centroid size of approximately 5.5 mm. A regular (first order) linear regression of relative warp I on size, while statistically significant (F-ratio, p = 0.0282), produces highly irregular residuals. A better regression relationship is found with a second order polynomial regression (F-ratio, p = 0.0069), which produces normally distributed residuals.

An examination of specimens from Sample 052500-1C suggests that the allometric development is due mainly to a widening of the byssal notch and a change in the shape of the anterior auricle. This change is confirmed by thin-plate spline visualization of the allometry, which was done by constructing splines of predicted specimen shapes, on relative warp I, at two centroid sizes, 4 and 7 mm (Figure 6). The shapes were predicted using the regression functions of relative warp I on centroid size. Figure 6 illustrates the shape changes that occur in specimens, from both Samples 060700-2A and 052500-1C, in this size range. Specimens from the former sample develop isometrically, whereas specimens from Sample 052500-1C exhibit a displacement largely localized

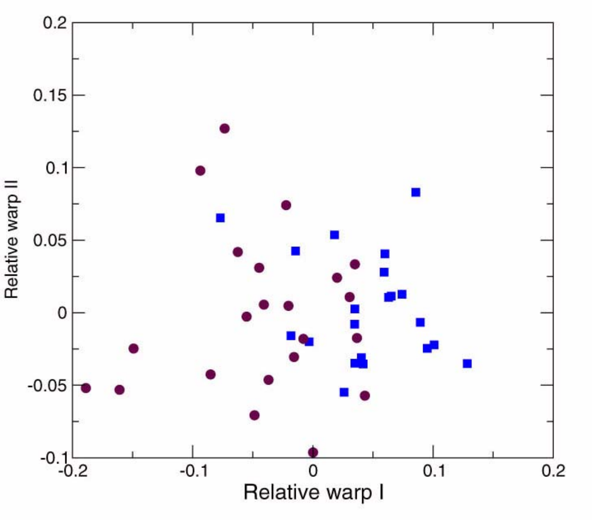

Figure 3. Plot of relative warp scores (I and II) of 060700-2A in blue squares and 052500-1C in red circles. Although overlap does occur between the two populations, they differ from one another statistically.

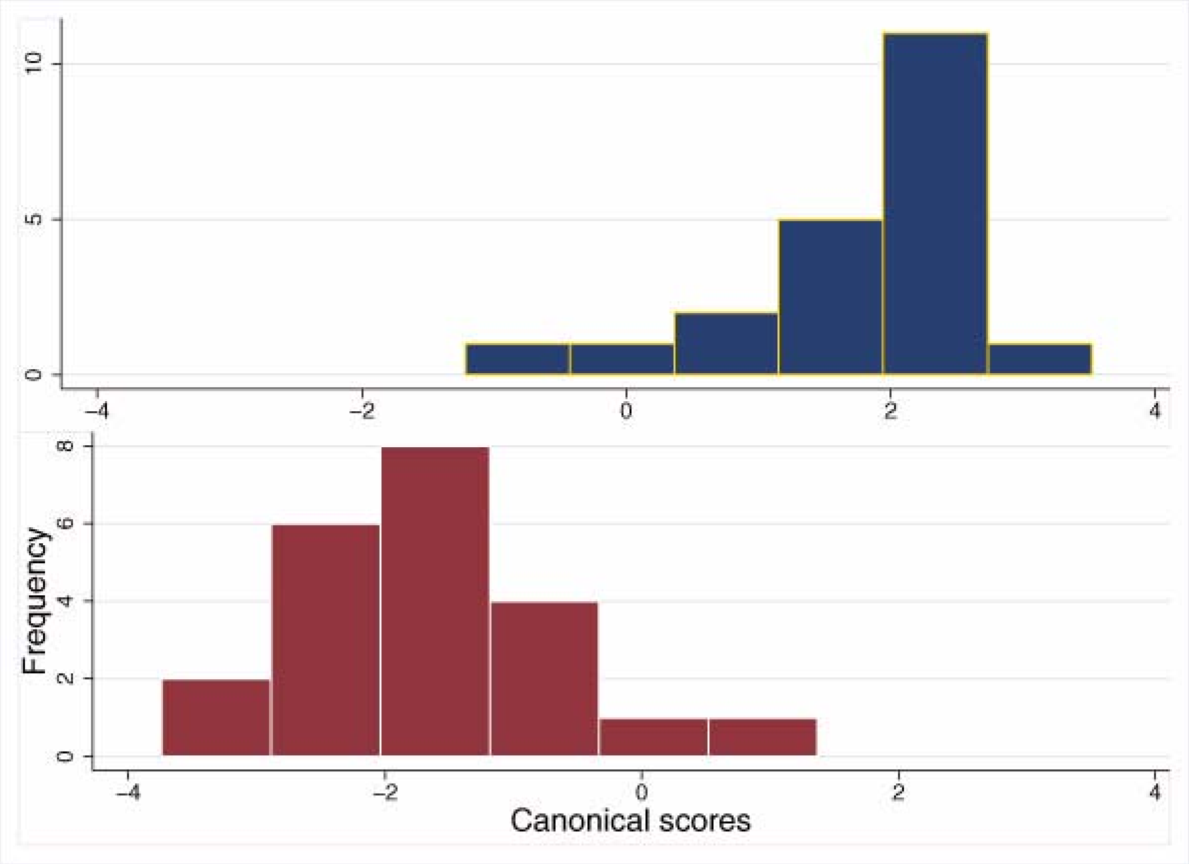

Figure 4. Distributions of canonical variate scores in 060700-2A (upper graph) and 052500-1C (lower graph). There is a highly significant difference between the two populations (Wilks' Lambda, $p < 0.0001$).

between landmarks 3 and 7. This displacement is the area of the byssal notch.

DISCUSSION

In this preliminary paleoecological analysis, the abundance of one bivalve family, the arcids, exhibited little difference between two samples while another bivalve family, the pectinids, exhibited great variability in dominance. However, the presence and absence of species within the arcids and their individual abundances did vary greatly between samples. Among pectinids, the species presence/absence data alone would not have differentiated the two samples but the species abundances would have been informative. Thus, these different data sets may provide non-overlapping lines of evidence for subtle differences in paleocommunity structure. In this case, the differences in species compositions and abundances between samples in stratigraphic proximity may not have clear significance in terms of the reconstruction of food webs or paleoecological roles but the differences may suggest subtle paleoenvironmental or paleoecological conditions useful for reconstructing the context for evolutionary change. In addition, the paleocommunity analysis allows for the identification of species that may be sensitive to ecological changes over short time intervals and thus may warrant additional evolutionary analysis. Other proxies examined in Dominican Republic Rio Gurabo samples have suggested similar paleoecological differences between other closely spaced stratigraphic samples (Tang et al. 2003; Chan et al. 2003).

Our preliminary paleocommunity analysis suggested that "*P.*" *thompsoni* may be a good candidate for looking at morphological differences, which may occur when paleoecological conditions change significantly. In the stratigraphically lower sample, "*P.*" *thomsponi* comprised only 6.2% of the total bivalves present whereas in the upper sample, it comprised 50.7% of the total bivalves counted. This difference suggests a significant change in ecological conditions as well as a significant change in the ecological role for "*P.*" *thompsoni,* making this species a good candidate for investigating whether there are measurable morphological responses correlated with these paleoecological changes.

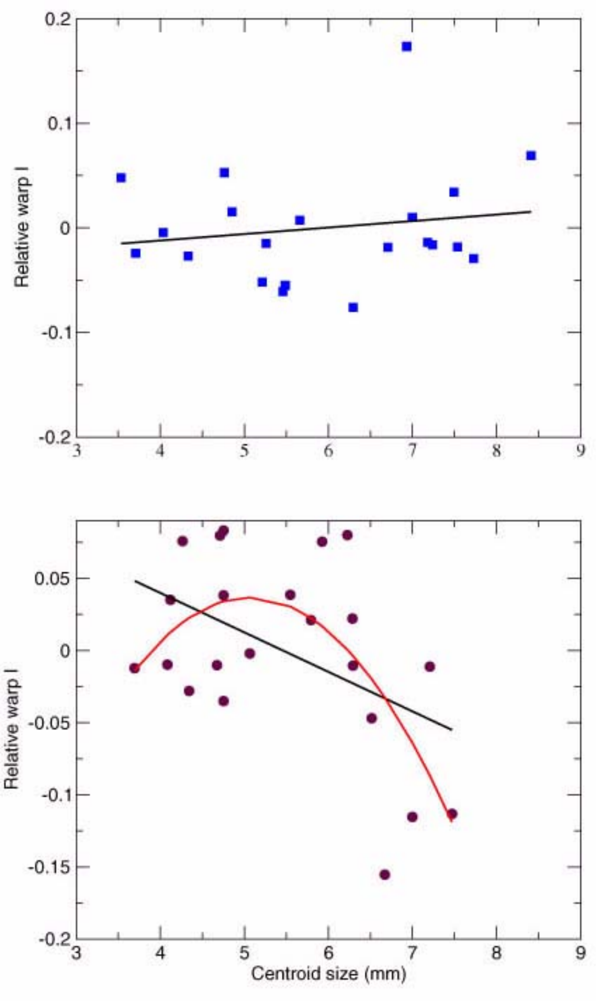

Figure 5. Plots of shape (relative warp score I) and size in 060700-2A (A; upper graph) and 052500-1C (B; lower graph). A. Linear regression indicates no change in shape with increasing sizes. B. A second-order polynomial regression indicates an allometric relationship with shape changing with size and is a better fit than a linear regression.

The results indicate that there is a significant difference in morphological patterns between the two samples. Although there is no size difference between the two populations of *"P." thompsoni*, detailed landmark analysis indicates marked differences of shape between the samples and more surprisingly, a change in growth patterns as well. In the lower interval, we documented a clear difference between smaller and larger individuals whereas in the upper sample, there is no allometric growth signal.

Whereas it is impossible without further study to determine the selection pressures that may have led to the different morphologies of these two *"P." thompsoni* populations, the shape changes are consistent with biomechanical interpretations of the paleoenvironmental conditions of the two samples. The analysis suggests that both the shape difference and the allometry are related to morphological landmarks surrounding the byssal notch. Bivalves pass bundles of byssal threads through the byssal notch to attach to hard substrates, and these morphological structures are related to life habits (such as swimming in pectinids), water energy, and even substrate composition (Waite et al. 2002). Based on sedimentary information, it does appear that sample 052500-1C—which is an amalgamated shell bed—would have experienced higher energy levels than the other sample. This interpretation is consistent with the hypothesis that the byssal notch is wider in 052500-1C so that individuals have a larger bundle of byssal threads as holdfasts attached to the substrate.

This difference in hydraulic energy regimes between the two paleoenvironments may also explain the significant change in growth patterns exhibited by the two populations. While it is difficult to differentiate between genetically based differences and ecophenotypic variation in fossil populations, the difference in growth patterns strongly suggests a genetic or developmental change. In pectinids, byssal threads are usually lost during ontogeny so that adults are free-lying on the sea floor, although given "*P.*" *thompsoni*'s small size, the byssus might have been retained throughout life. The fact that there are differences in the byssal notch between small and large individuals in sample 052500-1C suggests that there are size- or age-dependent factors reflecting a greater need for physical attachment to a hard substrate at larger size. Perhaps larger individuals in this sample with higher water energy were subjected to disproportionately greater hydrodynamic forces than in the other population and hence required relatively denser byssal bundles, with greater surface areas of attachment (Vogel 1988). Also suggestive is the fact that this species was much less abundant in 052500-1C where hydraulic energy is inferred to be higher.

As this study has shown, morphological change need not be interpreted solely as a species-level phenomenon, but can and should be considered in a paleocommunity context. The geographic mosaic theory of co-evolution suggests that microevolutionary variation is influenced by local conditions and biotic interactions, and the Dominican Republic material represents a prime opportunity to test this assertion. A major direction of further research should therefore be the characterization of morphological evolution in multiple co-occurring lineages, for example among pectinids

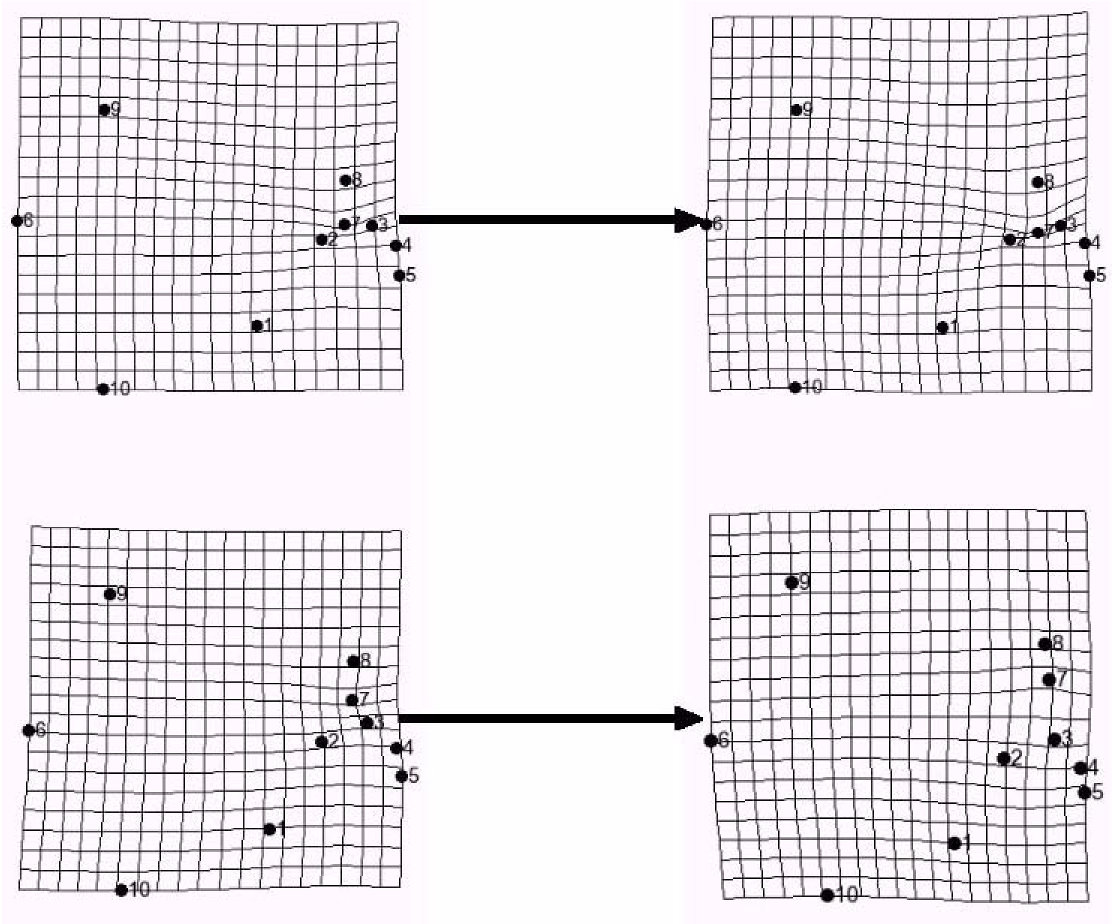

Figure 6. Thin-plate spline diagrams of predicted specimen shapes (relative warp I) at centroid size 4 mm and 7 mm for sample 060700-2A (upper diagram) and 052500-1C (lower diagram). Note the lack of significant changes in 060700-2A and the difference around landmarks 3 and 7 for sample 052500-1C. Pixelation of the figure is a function of the analysis routine's output.

and arcids, coupled with increased study of the potential direct and indirect biotic interactions among those lineages. The use of both quantitative morphometric techniques to evaluate population-level differences and quantitative paleoecological techniques to evaluate community-level differences can provide a powerful approach for characterizing these linkages within the context of evolutionary paleoecology.

CONCLUSIONS

1. Paleocommunity analysis at the family, species, and abundance levels yielded different patterns of paleoecological information.
2. Among populations that are closely spaced stratigraphically, significant differences in shape and growth patterns were detected in *"P." thompsoni* using landmark morphometrics. These differences are consistent with changes in paleoenvironmental conditions.
3. Simple morphological analysis (for example, size only) would not have been sufficient to detect the morphological differences documented between samples.
4. Paleocommunity analysis complements morphological studies of microevolutionary processes by (a) providing a context for evolutionary change and (b) indicating species that are ideal candidates for examining how paleoecological changes may be reflected in morphology.

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