Paleobiology

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Testing the "Plus ça change" model: a comparison of nuculid bivalve evolution across contrasting broadscale climatic regimes

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Article

Cite this article: Slattery, J. S., P. J. Harries, M. B. Jarrett, and A. L. Sandness (2025). Testing the "Plus ça change" model: a comparison of nuculid bivalve evolution across contrasting broadscale climatic regimes. *Paleobiology*, 1–18. https://doi.org/10.1017/pab.2025.10046

Received: 10 April 2023
Revised: 02 May 2025
Accepted: 09 May 2025

Handling Editor:
Ms. Jessica Kastigar and Dr. Erin Saupe

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Guest Editor:
Linda Ivany

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Abstract

Documenting patterns of evolution and stasis has been a major focus of paleobiology. However, despite substantial knowledge gleaned on this topic, many questions related to the underlying environmental processes that determine the dynamics of evolution and stasis remain unresolved. Therefore, this study focuses on examining these evolutionary patterns framed within an environmental context. Specifically, we test Sheldon's "Plus ça change" model, which predicts that morphological change is associated with more stable environments, such as in tropical latitudes or greenhouse climates, whereas stasis is linked to less stable environments, like those found in temperate latitudes or during icehouse climates. We examine the role that broadscale climatic variation exerts on evolutionary dynamics by documenting morphological change among nuculid bivalves in shallow-shelf settings from three different climate regimes: (1) the stable Late Cretaceous greenhouse climate; (2) the moderately stable Neogene transitional climate; and (3) the less stable Quaternary icehouse climate. Morphological changes over time were assessed using both bivalve size and outline shape. Comparison among changes in size and outline-shape patterns for Late Cretaceous and Neogene–Quaternary *Nucula* indicates that morphological change over time and stasis, respectively, dominated these different time intervals. In all cases, morphological change over time coincided with the more stable and less climatically variable greenhouse conditions, whereas stasis was associated with the more variable regimes characteristic of icehouse climates. These data provide strong support for the need to consider broad environmental factors—in this case climate—when assessing evolutionary modes. Furthermore, they point to the relevance of the Plus ça change model to explain patterns of evolution and stasis.

Non-technical Summary

This study explores how changes in the environment affect the way species evolve or remain morphologically unchanged over time. Although scientists have long studied evolution and stasis (the tendency of species to stay the same morphologically), many questions remain about what environmental factors drive these patterns. In this study, we examine these patterns within the context of climate change. We tested the "Plus ça change" model, which suggests that species are more likely to evolve when the environment is stable (e.g., tropical latitudes or greenhouse climates) and more likely to stay the same when the environment is unstable (e.g., temperate latitudes or icehouse climates). To investigate this, we looked at the evolution of nuculid bivalves during three different climate intervals: the stable Late Cretaceous greenhouse climate, the moderately stable Neogene transitional climate; and the less stable Quaternary icehouse climate. We measured changes in the size and shape of these bivalves over time. Our findings show that nuculid bivalves evolved more during stable climate intervals and remained mostly unchanged during unstable ones. These results suggest that the stability of the climate plays a significant role in whether species evolve or stay the same morphologically. The study supports the idea that broad environmental factors, such as climate, must be considered when examining how species change morphologically over time and highlights the relevance of the Plus ça change model in explaining these patterns.

Introduction

Eldredge and Gould (1972) argued that the dominant evolutionary pattern through time is not akin to Darwin's (1859) notion of gradual change—that is, phyletic gradualism—but instead is characterized by what they termed "punctuated equilibrium." Their idea would lead to a significant reevaluation of the nature of evolutionary patterns observed in the fossil record as

https://doi.org/10.1017/pab.2025.10046 Published online by Cambridge University Press

well as the mechanisms responsible for both prolonged periods of morphological stasis and sudden bursts of evolutionary change (e.g., Erwin and Anstey 1995; Gould 2002; Hunt 2006, 2007). Despite the substantial knowledge gleaned on this topic, many questions related to the processes that drive different patterns remain unresolved (e.g., Lieberman et al. 1995; Lieberman and Dudgeon 1996; Eldredge et al. 2005). This gap in understanding reflects the focus of most evolutionary studies on documenting the legitimacy and frequency of different evolutionary patterns, while largely ignoring their underlying environmental context and potential controls (e.g., Kelley 1984; Stanley and Yang 1987; Erwin and Anstey 1995).

Considerable debate currently surrounds the analyses of mechanisms controlling patterns of evolution and stasis, with some researchers emphasizing environmental factors (Sheldon 1996, 1997), whereas others focus on intrinsic factors, such as genetic constraints or developmental processes (Lieberman and Dudgeon 1996; Gould 2002; Eldredge et al. 2005). In paleobiology, most studies examining the relationship between physical environmental change and evolution have typically utilized compilations, such as the Paleobiology Database (www.paleodb.org), to investigate broadscale controls on macroevolutionary patterns of diversification over large spans of geological time (e.g., Alroy et al. 2000; Cárdenas and Harries 2010; Cárdenas-Rozo and Harries 2016). This lack of focus on the environmental context or controls on microevolutionary processes and patterns is due to the assumption that evolutionary responses to environmental change almost always result in adaptive evolutionary changes in traits or the extinction of species (McKinney 1993). In contrast, morphological stasis has been thought to be controlled by intrinsic mechanisms, including developmental constraints and genetic homeostasis, or extrinsic controls, such as habitat tracking, stabilizing selection, or metapopulation dynamics (Hecht et al. 1974; Lieberman and Dudgeon 1996; Gould 2002; Eldredge et al. 2005).

Sheldon's (1996) "Plus ça change" model, which conceptually translates to "the more things change, the more they stay the same," challenges the notion that environmental factors and their variability plays a minor, if any, role in determining patterns of evolution and stasis. From an evolutionary perspective, this model hypothesizes that rapid and pronounced environmental variability will result in morphological stasis until an environmental threshold is breached, which triggers rapid speciation (i.e., punctuated equilibrium); whereas reduced environmental variability, particularly when it approximates the rate of adaptation in a given clade, will drive more gradual morphological changes (i.e., phyletic gradualism). In this model, short-term and frequent physical environmental changes limit the amount of time phenotypic change can accumulate in response to a given set of environmental parameters before those conditions vary to the extent that any accumulated morphological response is overprinted by subsequent morphological changes. Thus, stabilizing selection dominates, and morphological stasis is maintained. With slower and more consistent environmental change, phenotypic evolution increases due to the longer intervals of relative environmental stability, resulting in gradual morphological change. In this model, lineages that persist in a changing environment over geological timescales are those that are relatively unaffected by each environmental shift, whereas, susceptible lineages that are unable to adapt to these environmental shifts are filtered out through extinction. Furthermore, this model predicts that species inhabiting more unstable environmental settings, such as shallow shelves and temperate or high-latitude regions, are more likely to display stasis, whereas settings with more stable environments, characteristic of the deep sea and the tropics, are more likely to display gradualism (Sheldon 1996; 1997).

These predictions for the environmental context of different evolutionary patterns inherent in the Plus ça change model should also be associated with the well-documented, broadscale climatic trends through the Phanerozoic. These trends depict the long-term oscillation between two end-members: ice- and greenhouse climatic regimes, which are predominantly controlled by the interplay of plate tectonics and orbital forcing (Frakes et al. 1992; Zachos et al. 2001; De Vleeschouwer et al. 2017). Icehouse climates show the greatest amount of short-term environmental fluctuations largely within the Milankovitch frequencies, whereas greenhouses display dampened variation. There are also transitional states characterized by intermediate conditions with generally cooler intervals punctuated by shorter ice- and greenhouse phases (Wolfe and Upchurch 1987; Frakes and Francis 1990; Wright 1992; Steuber et. al. 2005; Crippa et al. 2016; Herbert et al. 2016). Despite evolutionary tempo and mode being important for understanding both micro- and macroevolution, limited attention has been given to examining them within a broadscale climatic context. Harries and Allmon's (2007) reanalysis of the various studies contained within Erwin and Anstey (1995) revealed that all examples of gradual change, with or without stasis, are limited to greenhouse climate regimes, which highlighted the need to reassess evolutionary patterns within an environmental context.

The primary goal of this study is to deepen our understanding of evolutionary patterns by examining their environmental context and specifically testing predictions from Sheldon's (1996) Plus ça change model. This study focuses on evolutionary patterns during intervals dominated by the two most common broadscale climate regimes: greenhouses and icehouses. By investigating morphological changes in various species of the marine bivalve *Nucula* Lamarck, 1799, across these contrasting climate regimes, we aim to clarify the climatic influences on different evolutionary patterns.

Background

Broadscale Climatic Setting

To test the Plus ça change model's prediction that reduced environmental variability promotes evolutionary change, this study traces morphological change within the infaunal bivalve *Nucula* through the late Late Cretaceous, which is characterized by a greenhouse climate (Fig. 1). This interval is distinguished by elevated atmospheric pCO_2 levels, forced by increased magmatism at mid-ocean ridges and associated subduction-derived volcanism (Arthur et al. 1985; McKenzie et al. 2016). Due to greenhouse conditions, the effects of higher-order (10^4 to 10^5 years) Milankovitch-controlled climate and sea-level changes were dampened as compared with cooler climatic intervals resulting in stable environmental conditions (i.e., little change in marine shelf areas or temperature) over long intervals (Wolfe and Upchurch 1987; Frakes and Francis 1990; Wright 1992; Steuber et al. 2005; Slattery et al. 2015).

To test the Plus ça change model's prediction that elevated environmental variability limits net evolutionary change, this study also examines the evolution of *Nucula* through the Neogene–Quaternary (Fig. 2). The Neogene transitional regime was dominated by two 6.0 to 8.0 Myr long, moderately cool intervals that were

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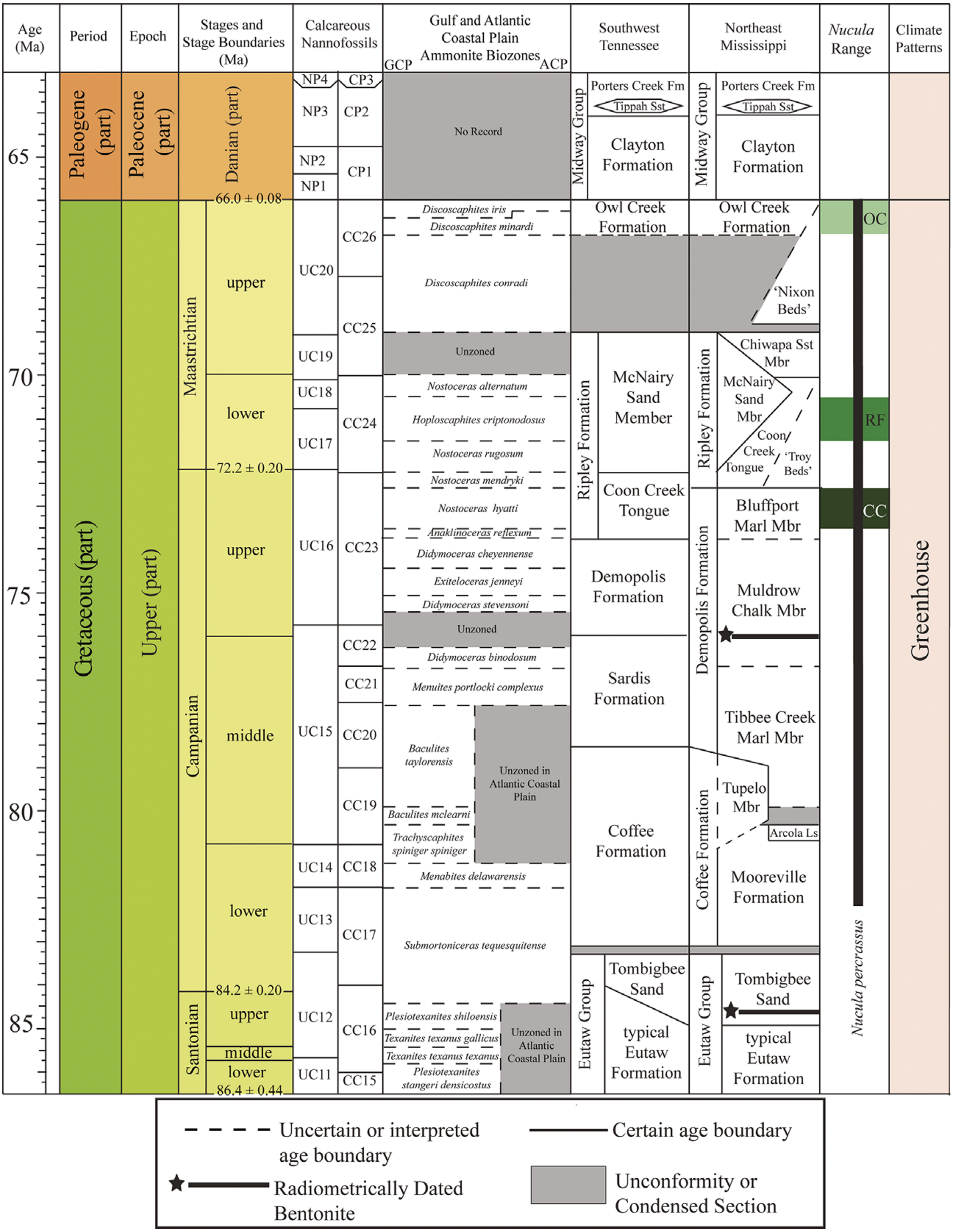

Figure 1. Stratigraphic interval of Cretaceous *Nucula percrassa* Conrad, 1858 samples from the Gulf Coastal Plain used in study (see Fig. 3 for geographic distribution), total range of Cretaceous *N. percrassa*, and broadscale climate patterns (modified from Wingard and Sohl 1990; Frakes et al. 1992; Singer et al. 2024; Slattery et al. in press). Colored intervals on range chart correspond to time intervals and geological units sampled for this study. Abbreviations: GCP, Gulf Coastal Plain; ACP, Atlantic Coastal Plain; CC, Coon Creek; RF, Ripley Formation; OC, Owl Creek Formation.

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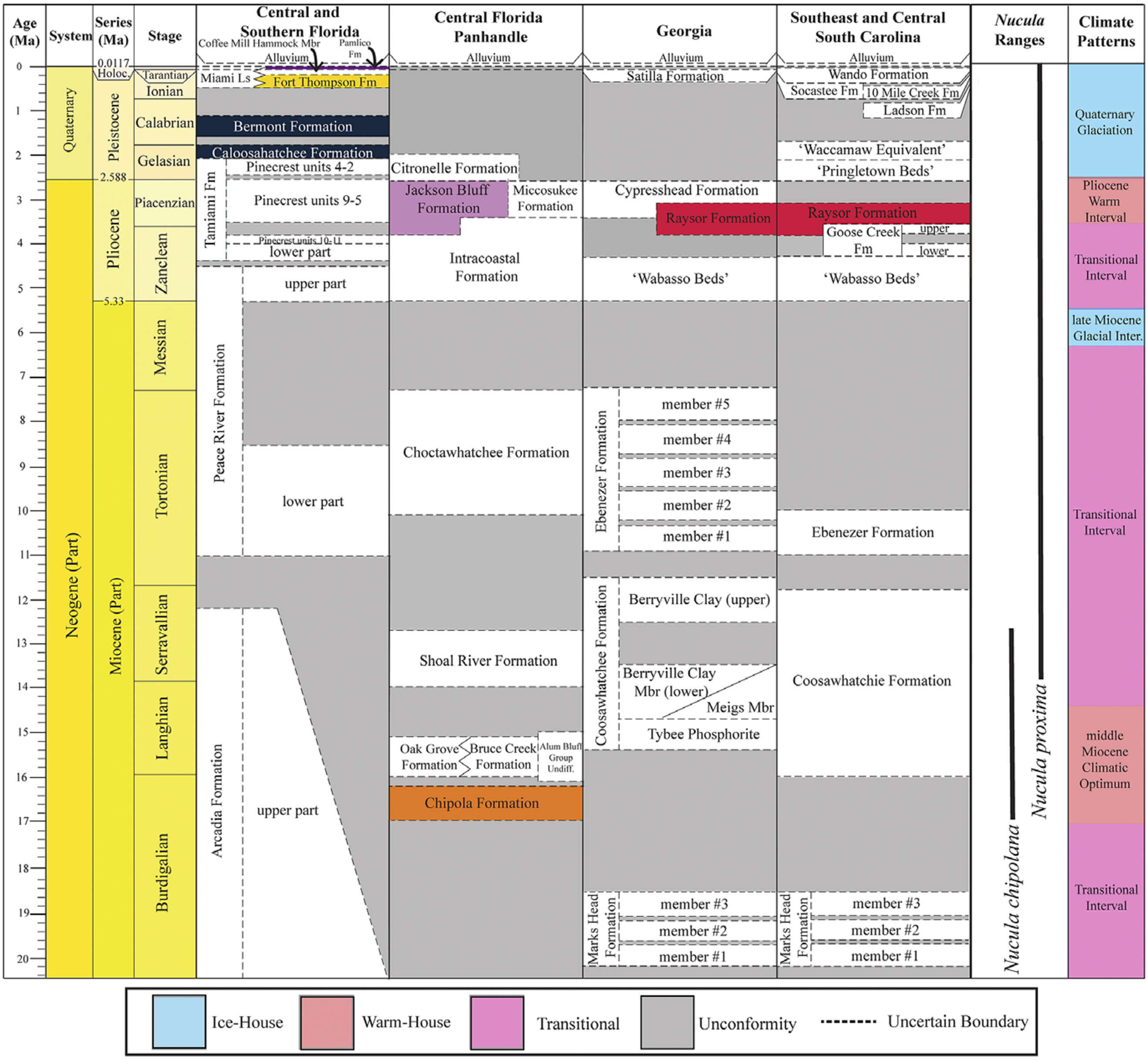

Figure 2. Stratigraphic interval of Neogene–Quaternary *Nucula* samples from the U.S. Atlantic and Gulf Coastal Plains used in study (see Fig. 3 for geographic distribution), total ranges of *Nucula* species, and broadscale climate patterns (modified from Huddlestun 1984; Weems and Edwards 2001; Zachos et al. 2001; Weems and Lewis 2002; Weems et al. 2004; Edwards et al. 2005; Weems and George 2013; Saupe et al. 2014; Powars et al. 2015; Hastings and Dooley 2017; Slattery et al. 2024).

interrupted by shorter (~0.4 to 2.7 Myr) cooler as well as warmer intervals (Fig. 2). Neogene temperatures and sea levels were higher than those in the Quaternary, but were declining due to a decrease in pCO_2 levels (Zachos et al. 2001; Miller et al. 2005; De Vleeschouwer et al. 2017). Temperature and sea-level fluctuations were still moderate during the Neogene and were, for the most part, influenced by the 41 kyr obliquity band of Milankovitch variations (Zachos et al. 2001; Miller et al. 2005).

Temperature decline and sea-level oscillations accelerated in the Quaternary in association with the initiation of permanent Northern Hemisphere glaciation, which resulted in the greater expression of Milankovitch-scale variations that modulated the glacial–interglacial cycles characteristic of this interval (Zachos et al. 2001; Miller et al. 2005). By the middle Pleistocene (~950 ka), there was a significant shift in the amplitude and frequency of the glacial–interglacial cycles from the lower-amplitude 41 kyr (obliquity) variations to the higher-amplitude 100 kyr (eccentricity) changes (Zachos et al. 2001). The middle Pleistocene climate shift resulted in a change from more temporally symmetrical glacial–interglacial cycles to more asymmetrical cycles with very long, cold glacial periods punctuated by short, warmer interglacials (Mudelsee and Schulz 1997; Zachos et al. 2001; Tziperman and Gildor 2003). Overall, the Pleistocene is characterized by an increase in variance in the climatic spectrum (Frakes et al. 1992).

Geological Setting

Cretaceous and Neogene–Quaternary *Nucula* specimens were collected from the passive-margin settings of the U.S. Atlantic and Gulf Coastal Plains (Fig. 3). Cretaceous localities sampled in this

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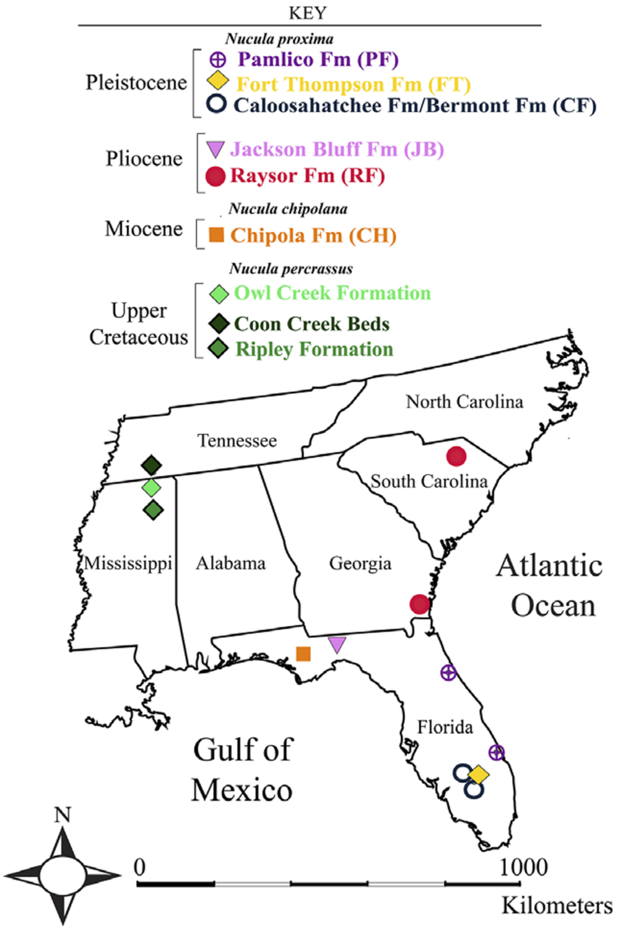

Figure 3. Cretaceous and Neogene–Quaternary *Nucula* localities in the U.S. Atlantic and Gulf Coastal Plains sampled for this study.

study are characterized as sandy clay-rich units with well-preserved aragonitic shells, which were deposited in shallow, lower shoreface to proximal offshore-transitional shelf settings. Neogene–Quaternary formations sampled in this study were deposited during highstands and are separated by substantially longer intervals that are recorded in lowstand unconformities. Neogene–Quaternary localities are represented by sandy, shell-rich units with well-preserved aragonitic shells deposited in shallow, upper shoreface to proximal offshore-transitional shelf settings (Allmon 1992, 1993; Slattery et al. 2024; Gomes et al. 2025).

Systematic and Evolutionary Overview among Nucula *Analyzed in Study*

This study examined one Cretaceous and two Neogene–Quaternary species of *Nucula* (Figs. 1–4). These species were selected because of their excellent aragonitic preservation, abundance, and long stratigraphic ranges. The Cretaceous portion of this study is focused on *N. percrassa* Conrad, 1858 (Fig. 4A), which ranges from the lower Campanian up to the Cretaceous/Paleogene (K/Pg) boundary (Speden 1970; Wingard and Sohl 1990; Fig. 1). The Neogene–Quaternary component of this analysis includes two taxa: *N. chipolana* Dall, 1898 and *N. proxima* Say, 1822 (Fig. 4B,C). The former ranges from the Burdigalian to Serravallian (Dall 1898; Gardner 1926; Portell et al. 2006; Fig. 2), whereas the latter ranges from the Serravallian to Holocene (Richard and Harbison 1942; Gardner and Mansfield 1943; Edwards et al. 2005; Portell et al. 2006; Mikkelsen and Bieler 2007; Fig. 2).

The evolutionary relationships among the *Nucula* species analyzed in this study are poorly known. A major contributing factor to this lack of understanding is the absence of comprehensive phylogenetic analysis of both fossil and living species within this group. The challenge is further compounded by the numerous homoplasies observed within the clade and, due to their simple shell morphology, the limited availability of morphological characters suitable for robust phylogenetic reconstructions. Despite having a relatively similar biogeographic range, the Cretaceous species are separated in time from the Neogene–Quaternary species by ~40 Myr. Therefore, it is unclear whether the latter are descendants of the former or whether the latter represent an unrelated, smaller-sized lineage.

The two Neogene–Quaternary species are likely from one lineage and are possibly the same species based on their pronounced morphological similarity, including shape outline, inflation, hinge line, and relative shell thicknesses (see Fig. 4B,C). The most distinguishing contrast between the two species is their size, with *N. chipolana* and *N. proxima* typically having mean lengths of 3–4 mm and 10 mm, respectively. They also overlap in their biogeographic range, and the last appearance of the former species overlaps with the first appearance of the latter species in the lower Serravallian (see Fig. 2). This stratigraphic range overlap possibly represents a speciation event or possibly misidentification of one of the taxa at this stratigraphic level.

Methods

Sample Localities

Cretaceous *Nucula* specimens used in this study were collected from three localities in the Gulf Coastal Plain (Figs. 1, 3): the Upper Campanian Coon Creek Tongue of the Ripley Formation at Coon Creek, Tennessee, the lower Maastrichtian Ripley Formation at Blue Springs, Mississippi, and the upper Maastrichtian Owl Creek Formation at Owl Creek, Mississippi. The ages of these localities are constrained by ammonite and inoceramid biostratigraphy; however, due to their condensed biostratigraphic records and the extended age ranges of Gulf Coastal Plain ammonite biozones, many of these localities span relatively long intervals of time (i.e., >1–2 Myr; also see Slattery et al., in press). The Coon Creek locality is the oldest site and correlates with the *Nostoceras hyatti* Biozone (73.5–72.6 Ma). The Blue Springs locality correlates with the *Hoploscaphites criptonodosus* Biozone (71.7–70.5 Ma). The Owl Creek locality is the youngest Cretaceous site and correlates with the *Discoscaphites minardi* and *D. iris* Biozones (66.8–66.0 Ma). Therefore, the samples studied here range across ~7.5 Myr from the late Campanian to the late Maastrichtian.

Neogene–Quaternary *Nucula* specimens analyzed in this study come from six formations and seven localities (Figs. 2, 3). The age ranges of these formations are derived from micro- and macrofossil biostratigraphy, isotopic dating, and relative stratigraphic relationships (Huddlestun 1984; Weems and Edwards 2001; Zachos et al. 2001; Weems and Lewis 2002; Weems et al. 2004; Edwards et al. 2005; Weems and George 2013; Saupe et al. 2014; Powars et al. 2015; Hastings and Dooley 2017; Slattery et al. 2024). These formations span ~17 Myr; however, this record is clearly discontinuous, as these formations are all bounded by hiatuses or unconformities, which span from tens of millions to hundreds of thousands of years. *Nucula chipolana* specimens were collected

https://doi.org/10.1017/pab.2025.10046 Published online by Cambridge University Press

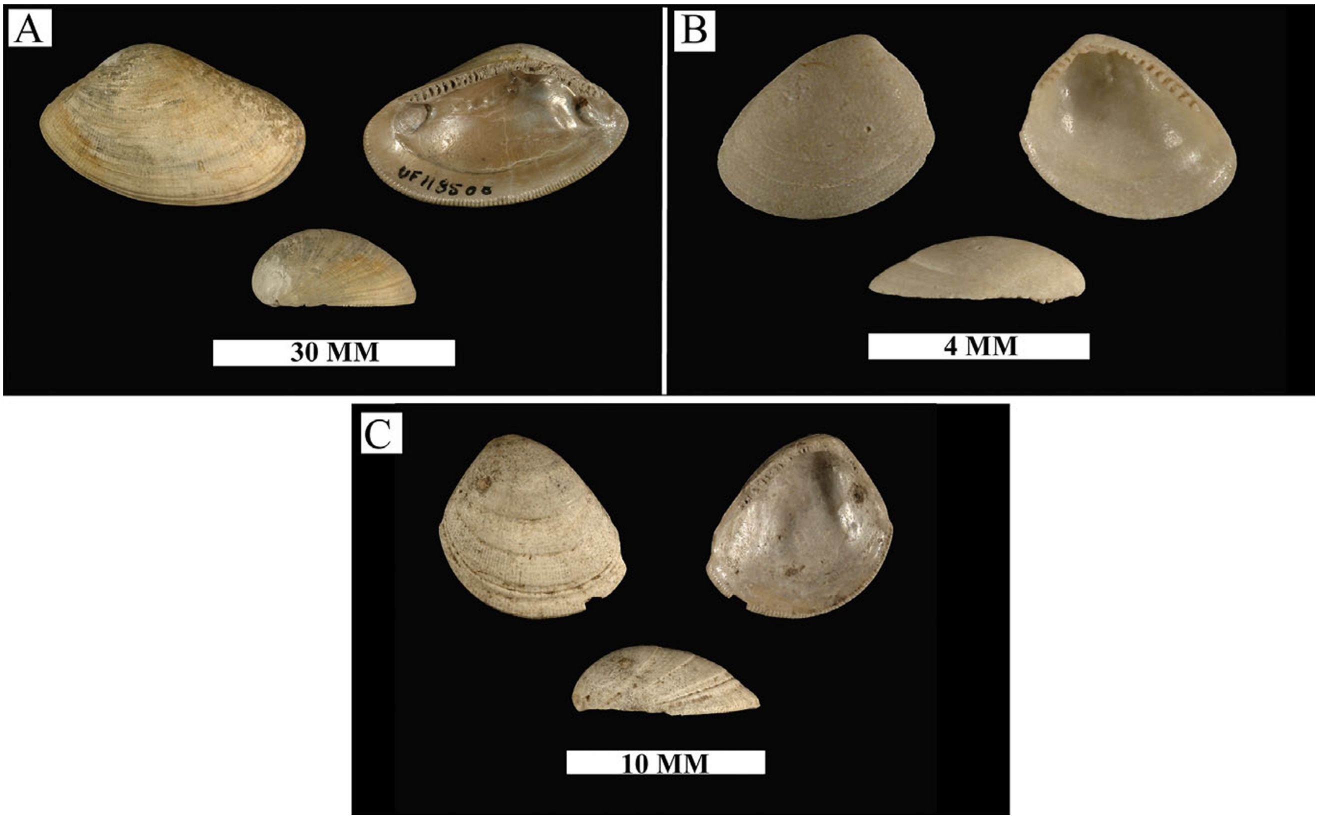

Figure 4. Examples of *Nucula* species examined in this study, including: **(A)** Cretaceous *N. percrassa* Conrad, 1858 (UF118500); **(B)** Miocene *N. chipolana* Dall, 1898 (UF133012); and **(C)** Pliocene to Holocene *N. proxima* Say, 1822 (UF267837). Photos courtesy of R. Portell, Florida Museum of Natural History, University of Florida.

from the middle Miocene Chipola Formation (17–16.3 Ma) at a single locality in Florida. These samples are separated by a ~12.5 Myr gap in the *Nucula* record ranging from the middle Miocene Chipola Formation to the Pliocene Raysor and Jackson Bluff formations (16.3–3.6 Ma; see also Fig. 2). This gap in the *Nucula* record reflects a lack of available material due to numerous and relatively long unconformities that span >1 Myr as well as relatively poor preservation of fossil mollusks in the existing deposits (i.e., steinkern preservation). The Pliocene to Pleistocene *N. proxima* record ranges from 3.6 to 0.04 Ma and is more complete due to both the better representation of specimens from different intervals in museum collections and the shorter time intervals represented by unconformities as well as better preservation. Pliocene specimens come from individual localities in Florida, Georgia, and South Carolina, whereas the Quaternary specimens are all derived from six sites in Florida.

Samples

A total of 887 pooled right and left valves of Cretaceous and Neogene–Quaternary *Nucula* specimens were analyzed for this study (Table 1; Supplementary Table 1). Out of these, 141 are

Table 1. Number of *Nucula* specimens used in study along with their ages and repositories. MMNS, Mississippi Museum of Natural Science; UF, Florida Museum of Natural History, University of Florida; YPM, Yale Peabody Museum of Natural History.

Species	Formation	Age	Ma	Source	Total valves
Nucula proxima Say, 1820	Pamlico Fm	Pleistocene	0.13	UF	73
Nucula proxima Say, 1820	Fort Thompson Fm	Pleistocene	0.35	UF	197
Nucula proxima Say, 1820	Caloosahatchee Fm/Bermont Fm	Pleistocene	2	UF	170
Nucula proxima Say, 1820	Jackson Bluff Fm	Pliocene	3.2	UF	140
Nucula proxima Say, 1820	Raysor Fm	Pliocene	3.4	UF	105
Nucula chipolana Dall, 1898	Chipola Fm	Miocene	16.6	UF	61
Nucula percrassa Conrad, 1856	Owl Creek Fm	Cretaceous	66.4	MMNS	46
Nucula percrassa Conrad, 1856	Ripley Fm	Cretaceous	69.2	MMNS	68
Nucula percrassa Conrad, 1856	Coon Creek Tongue	Cretaceous	72.8	UF and YPM	27
				Total:	887

https://doi.org/10.1017/pab.2025.10046 Published online by Cambridge University Press

Cretaceous *N. percrassa* valves and 746 are Neogene–Quaternary *Nucula* valves (Table 1). These specimens are reposited in the collections at the Mississippi Museum of Natural Science (MMNS), Florida Museum of Natural History, University of Florida (UF), and Yale Peabody Museum of Natural History (YPM). All associated data for these specimens are available through the Dryad Digital Repository (https://doi.org/10.5061/dryad.sqv9s4ndb).

Morphometric and Quantitative Analysis

We document the evolutionary patterns among *Nucula* lineages during contrasting climatic regimes using two elements: size measurements and outline shapes. The morphometric techniques used in this study were chosen to accurately capture the true biological patterns of size and shape change, minimizing distortion or bias that could arise from measurement or analytical methods.

Photography and Image Editing

To obtain measurements and outline shapes, *Nucula* were photographed against a clean, low-reflectivity, black surface using an Olympus Stylus Tough camera set to macro and mounted onto an adjustable copy stand under four-point lighting. Each *Nucula* specimen was photographed concave down with the umbo oriented toward the bottom of the image. These methods provide high-quality images that reduce potential motion blur. The adjustable copy stand allows the standardization of the working distance between the specimens and the lens, which, if varied between photographs, could impact the scale of the image for collection of size data.

Images sampled for shape data were uploaded into the GNU Image Manipulation Program (GIMP) (Solomon 2009). In GIMP, images were converted to grayscale, and their contrast or threshold was adjusted to produce a black-and-white silhouette, which facilitated the extraction of shape data. Images were then cleaned to remove small specks (e.g., loose sediment) surrounding the valves, which could result in the capture of inaccurate shape outlines.

Outline Shape and Size Data Extraction and Analysis

The National Institutes of Health shareware program FIJI (a modified version of ImageJ; Schindelin et al. 2012) was used to collect outline-shape data. Edited images were imported into FIJI, where the shells were selected using the Wand Tracing Tool to replicate the outline. Once the shell outline was demarcated, the xy-coordinates (>10,000 coordinates per specimen) were extracted.

To extract size data, centroid sizes were calculated by summing the squared distances between all landmarks on *Nucula* specimens and the centroid (Webster and Sheets 2010). A 10 mm scale included with *Nucula* images was used as a reference to calculate centroid sizes in metric units (Bookstein 1989, 1997; Rohlf and Bookstein 2003; Frieß 2003; Jonke et al. 2003; Hammer and Harper 2006; Webster and Sheets 2010).

Preparation of Outline Data and Elliptical Fourier Analysis of Outlines

Elliptical Fourier analysis (EFA) was used to quantitatively describe *Nucula*'s morphological form. This mathematical method was specifically developed by Kuhl and Giardina (1982) to quantitatively describe closed outline shapes.

Before Fourier analysis, the outline data from the right and left valves were pooled, smoothed, and aligned on their centroids to increase sample sizes and eliminate artifacts caused by variations in raw xy-coordinate position, size, translation, rotation, and starting position, which could influence the outcome of EFA. To pool the outline data, *Nucula* right-valve semi-landmarks were mirrored on the y-axis. The xy-coordinates defining the outline shapes of the bivalves were smoothed through 100 iterations to remove digitization noise and then interpolated to 400 evenly spaced points using methods discussed by Claude (2008). The outlines were scaled to the same centroid size (i.e., all centroid sizes = 1) and rotated using an unpublished, point-independent method of outline rotation developed by Jarrett (2016) with an R script (R Development Core Team 2015). Smoothed and interpolated outlines were compared with the original configurations to ensure that the outline was not significantly affected by these processes. The rotation methods used in this study involve determining the angle of the first Fourier ellipse relative to the horizontal plane by utilizing its two extreme points (Supplementary Fig. 1A). The angle required to align this line horizontally is then calculated, and the shape is rotated by this angle. Jarrett's (2016) approach results in a more accurate outline rotation as compared with the commonly used Procrustes methods (Supplementary Fig. 1B,C). Finally, a standardized starting position for the outline trace was calculated using the function *setstart*, which places the starting position of the outlines at a point that is the most morphologically similar among all outlines. This is important, because EFA is sensitive to the starting position and could, without correction, reflect variation in starting position rather than shape (Haines and Crampton 2000). EFA was used to calculate Fourier coefficients from the corrected xy-coordinates using methods provided by Claude (2008). This decomposition method was employed to reduce the dimensionality and remove redundant information from the cleaned xy-coordinates. To decompose the data, EFA uses harmonically related trigonometric curves (i.e., progressively higher sine and cosine functions), that are summed to replicate open or closed outlines (Davis 1986). This approach was selected because it effectively recreates specimens or characters with relatively simple shapes (e.g., roughly ovate outlines shapes), such as the outlines of bivalves and brachiopods (Crampton 1995; Haines and Crampton 2000). Computational details of EFA are described in more detail in Kuhl and Giardina (1982), Ferson et al. (1985), and Crampton (1995). EFA methods have been criticized because returned harmonics are not independent of each other. Notably, Haines and Crampton (2000) posit that this non-independence may result in "spurious correlations." However, the methods applied here were tested by Jarrett (2016) on extant *Chione elevata* (Say 1822). Results show correct separation and grouping based on ecophenotype as well as separability of subtle morphological differences between right and left valves.

Evolutionary Analysis

To examine changes in size over time, centroid size data were visualized by time interval using: (1) box-and-whisker plots and (2) ridgeline plots. As size measurements varied across several orders of magnitude, size data were log transformed so that they could be plotted on a proportional scale to make them more comparable, as recommended by Hunt and Carrano (2010).

To examine changes in shape over time, Fourier coefficients of *Nucula* were analyzed in R using principal component analysis (PCA). PCA—a statistical technique that has typically been used to examine the variance among specimens (e.g., Mitteroecker and

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Bookstein 2011; Zelditch et al. 2012)—is an eigenvalue-eigenvector analytical method that sorts variation in multivariate datasets along two or more independent (uncorrelated) axes, which are ranked in order of decreasing importance (Zelditch et al. 2012). Here, we examine only the first three axes of the PCA plots, referred to as PC 1, PC 2, and PC 3. These axes explain 68.3%, 12.6%, and 5.9% of the morphological variation, respectively. Cumulatively, these axes reflect 86.5% of the total morphological variation. Additional PCA axes were not examined for this study because they explain progressively smaller amounts of the variation, thus yielding diminishing explanatory power. The mean PCA scores were plotted along each axis with 95% confidence ellipsoids for comparison.

The time-series analysis R package paleoTS (Hunt 2015) was used to examine the magnitudes of morphological changes over time among *Nucula*. This was done by applying sample covariance and likelihood-based methods to both size data as well as PC 1 and PC 2 results. To measure the magnitude of morphological change over time between samples, among sample variation (omega) was computed using the *fitSimple* function available in paleoTS by fitting the stasis model to both Cretaceous and Neogene–Quaternary samples, respectively, without pooling the data. Specific evolutionary patterns (e.g., unbiased random walk, generalized random walk) for size and shape data were not evaluated using Akaike support in the R package paleoTS due to the limited number of time bins; in the Cretaceous and Neogene–Quaternary there were three and six, respectively. This is based on Hunt's (2012, 2015) analysis, which showed that a minimum of seven time bins are necessary to undertake a robust determination of evolutionary patterns using Akaike support.

The geomorph package in R was used to calculate morphological disparity (Procrustes variance). These data were bootstrapped by culling 25 specimens at random from each sample and computing the disparity 100 times each, which allowed for the calculation of standard error for disparity.

Allometry

To ensure that morphological patterns reflect changes in shape over time rather than changes in shape with ontogeny, *Nucula* PCA axes 1 to 3 scores were compared with centroid sizes (Bookstein 1989, 1997; Rohlf and Bookstein, 2003; Freissias 2003; Jonke et al. 2003; Hammer and Harper 2008). If the shape variation, as primarily explained in PCA axes 1 to 3 scores, correlates with centroid size (i.e., allometric growth), then the primary element being compared in the analysis is size dependent and thus reflects ontogenetic variation within populations rather than variation in shape over geological time and must be corrected. However, if the shape variation reflected by PCA scores does not correlate with centroid size, then the primary shape element being compared in the analysis is size independent and thus reflects variation in shape over geological time.

Results

Size Change

Cretaceous *Nucula* decrease in mean log centroid size over the 7.5 Myr interval in the late Campanian (log centroid size = 0.22)

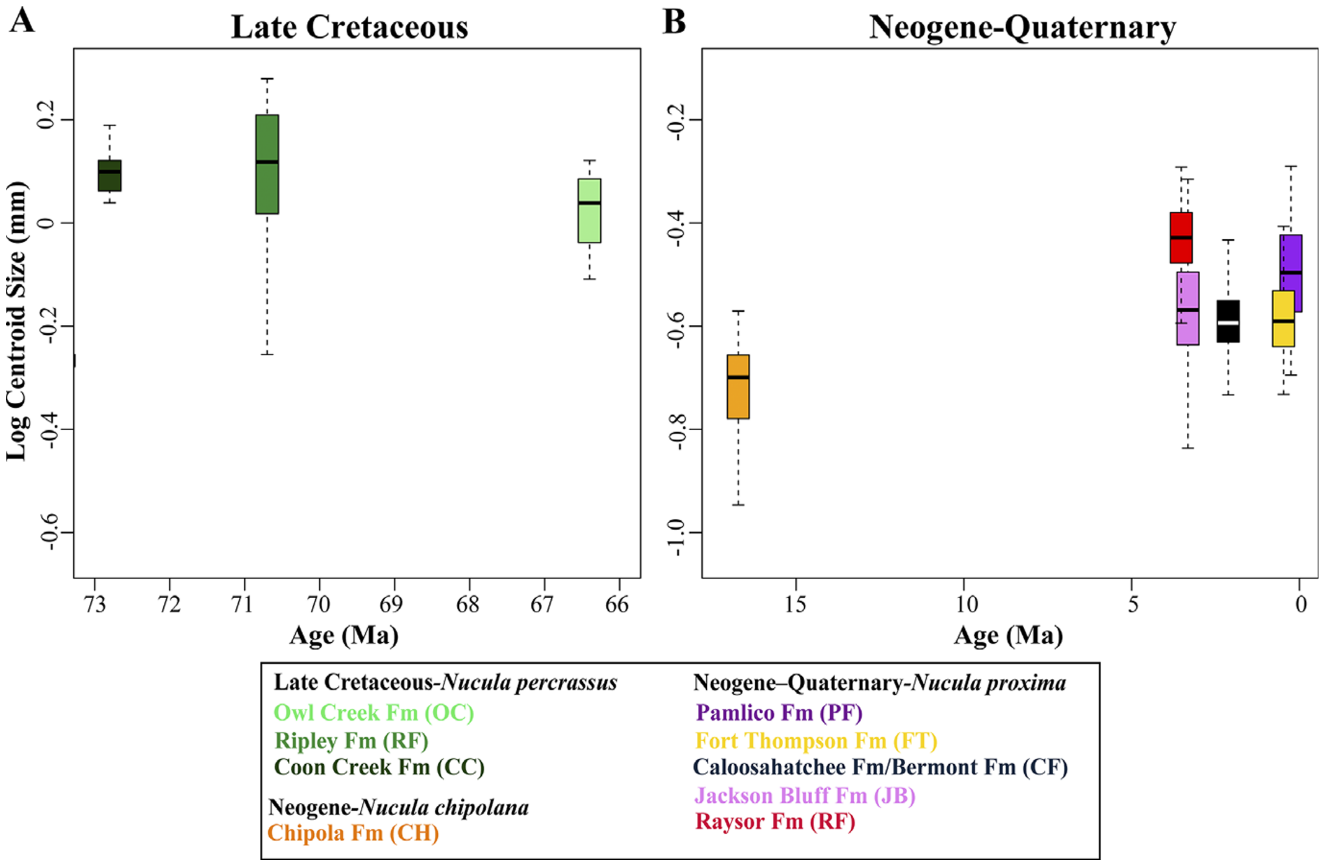

Figure 5. Box plots showing log centroid sizes of Late Cretaceous **(A)** and Neogene–Quaternary **(B)** *Nucula.*

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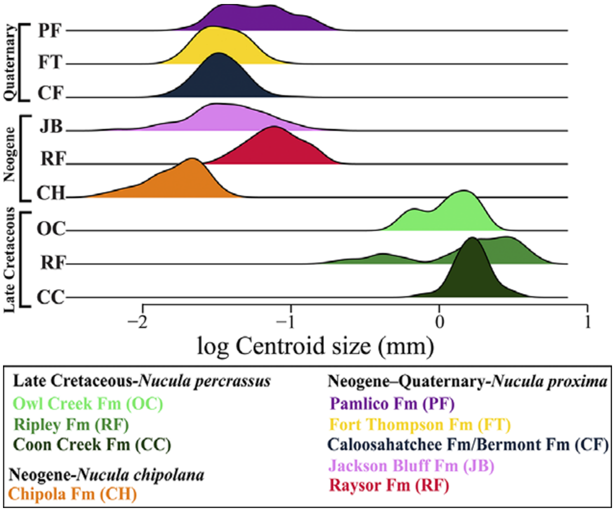

Figure 6. Ridgeline plot showing changes in log centroid sizes for *Nucula* during the Late Cretaceous and Neogene–Quaternary.

to late Maastrichtian (log centroid size = 0.09) (Figs. 5A, 6, 7A, Supplementary Table 2). The mean log centroid size of Late Campanian *Nucula* are 18% and 72% larger than early and late Maastrichtian age specimens, respectively. However, the median sizes of late Campanian and early Maastrichtian age specimens are similar. The difference in mean sizes is primarily due to the presence of small specimens in the early Maastrichtian age Ripley Formation. In addition, the early Maastrichtian Ripley Formation and, to a lesser degree, the late Maastrichtian age Owl Creek Formation *Nucula* show bimodal distributions in size, which is not apparent for the late Campanian Coon Creek *Nucula*.

Cenozoic *Nucula* show changes in mean log centroid size during the Neogene and then little change from the late Pliocene through latest Pleistocene (Figs. 5B, 6, 7B, Supplementary Table 2). *Nucula* increase 37% in size from the middle Miocene to middle Pliocene and then decrease by 29% in mean log centroid size from the middle to late Pliocene. Their mean log centroid size remains identical (i.e., ~—1.46 mm) from the late Pliocene to middle Pleistocene and then increases by 15% into the latest Pleistocene. The middle

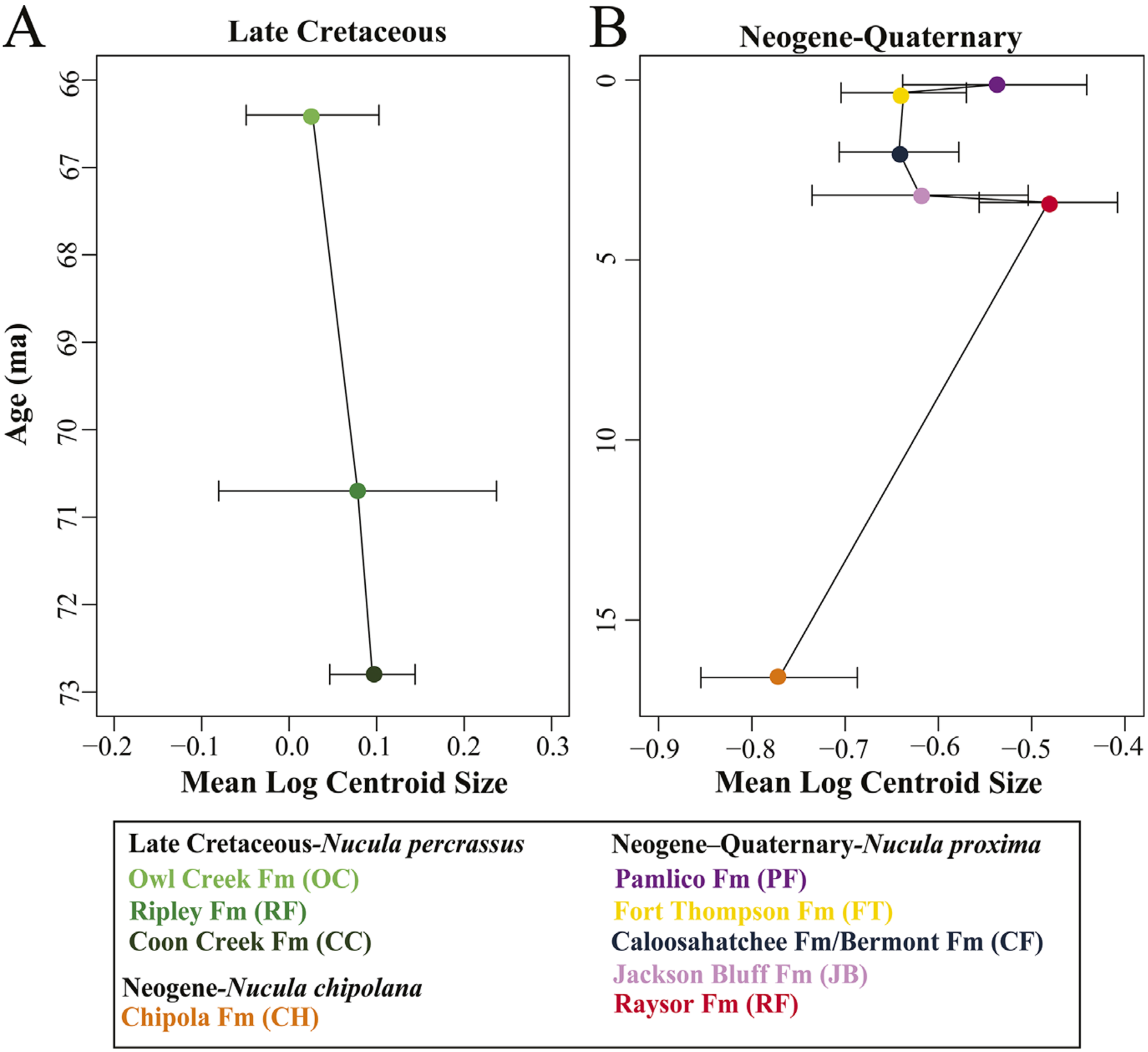

Figure 7. Time series showing changes in mean log centroid size of Late Cretaceous **(A)** and Neogene–Quaternary **(B)** *Nucula.*

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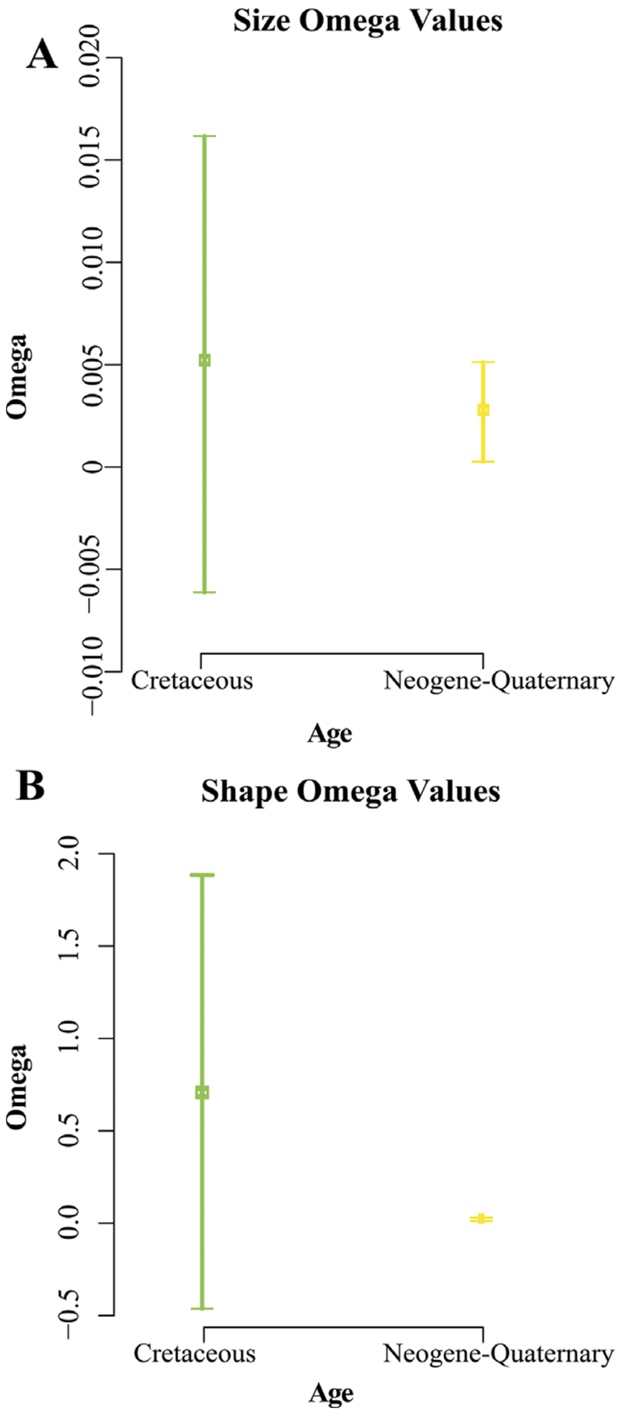

Figure 8. Comparison of omega values for changes in the magnitude of size **(A)** and shape **(B)** for Late Cretaceous and Neogene–Quaternary *Nucula.*

Pliocene Raysor Formation and latest Pleistocene Pamlico Formation *Nucula* have the largest mean centroid sizes and are the only samples from the Atlantic Coastal Plain.

The omega values based on mean log centroid size are greater for the Cretaceous *Nucula percrassa* compared with the Neogene–Quaternary *Nucula chipolana–proxima* lineage (Fig. 8A, Table 2). The omega value for the Cretaceous *Nucula* is 0.005, whereas the Neogene–Quaternary specimens have a value of 0.003. Thus, the omega value for size data in the Cretaceous *Nucula* is approximately 1.9 times greater than in the Neogene–Quaternary specimens. The broader confidence limits for Cretaceous *Nucula* compared with Neogene–Quaternary forms are likely due to the smaller sample sizes for the older nuculids (Fig. 8A, Table 2).

Table 2. Omega values for determining the magnitude of size and shape changes for Cretaceous and Neogene–Quaternary *Nucula.*

Omega values for size				
Time interval	Upper bound	Median	Lower bound	Time bins
Neogene–Quaternary	0.005	0.003	0.0002	6
Cretaceous	0.016	0.005	−0.006	3
Omega values for shape				
Neogene–Quaternary	0.017	0.008	−0.001	6
Cretaceous	1.87	0.697	−0.476	3

Shape Changes

PC 1 to PC 3 scores for *Nucula* reveal pronounced shape similarities among Neogene–Quaternary specimens, but reduced morphological similarities among Cretaceous specimens (Figs. 9–11, Supplementary Table 3). This is despite the Neogene–Quaternary specimens spanning almost twice the time interval (i.e., 16.5 Myr vs. 7.5 Myr) compared with the Cretaceous specimens. PC 1 scores of Cretaceous and Neogene–Quaternary *Nucula* explain 68.3% of the observed shape variation, whereas PC2 and PCS explain 12.6% and 3.5% of the observed shape variation, respectively. The variation along PC 1 primarily reflects changes in shell length, whereas variation along PC 2 reflects differences in umbo shape and prominence. Along PC 1, Neogene–Quaternary *Nucula* exhibit negative scores, whereas Late Cretaceous *Nucula* exhibit positive scores. Along PC 2, both Neogene–Quaternary and Cretaceous *Nucula* have scores that vary around the zero-axis line. All 95% confidence intervals around mean scores for Neogene–Quaternary *Nucula* specimen closely overlap along both PC 1 and PC 2. In contrast, Cretaceous *Nucula* specimen 95% confidence intervals around mean scores from the different intervals show reduced overlap (Fig. 9).

Disparity (i.e., morphological variance) among Cretaceous *Nucula* is greater, with a range between 0.73 and 1.26, compared with Neogene–Quaternary species, which vary between 0.32 and 0.44 (Fig. 11A, Supplementary Table 3). During the late Campanian to early Maastrichtian age, *Nucula* disparity increased from 1.05 to 1.25 and then decreased during the early to late Maastrichtian to 0.73 (Fig. 11A). Morphological disparity remained the same through the Neogene and then varied over a narrow range during the Quaternary (Fig. 11B, Supplementary Table 3). Disparity among *Nucula* decreased from 0.35 in the Miocene down to 0.33 during the late Pliocene. It then varied between 0.36 to 0.32 from the early and middle Pleistocene to late Pleistocene.

The omega values based on PCA of shape are greater for the Cretaceous *N. percrassa* compared with the Neogene–Quaternary *N. chipolana–proxima* lineage (Fig. 8B, Table 2). Specifically, the omega value for the Cretaceous *Nucula* is 0.697, whereas the Neogene–Quaternary specimens have a substantially lower value of 0.008. Therefore, the omega value for the Cretaceous *Nucula* is approximately 3.81 times greater than that of the Neogene–Quaternary *Nucula.* As noted earlier, the larger confidence limits for Cretaceous versus Neogene–Quaternary *Nucula* are due to the smaller sample size for the former group (Fig. 8B, Table 2).

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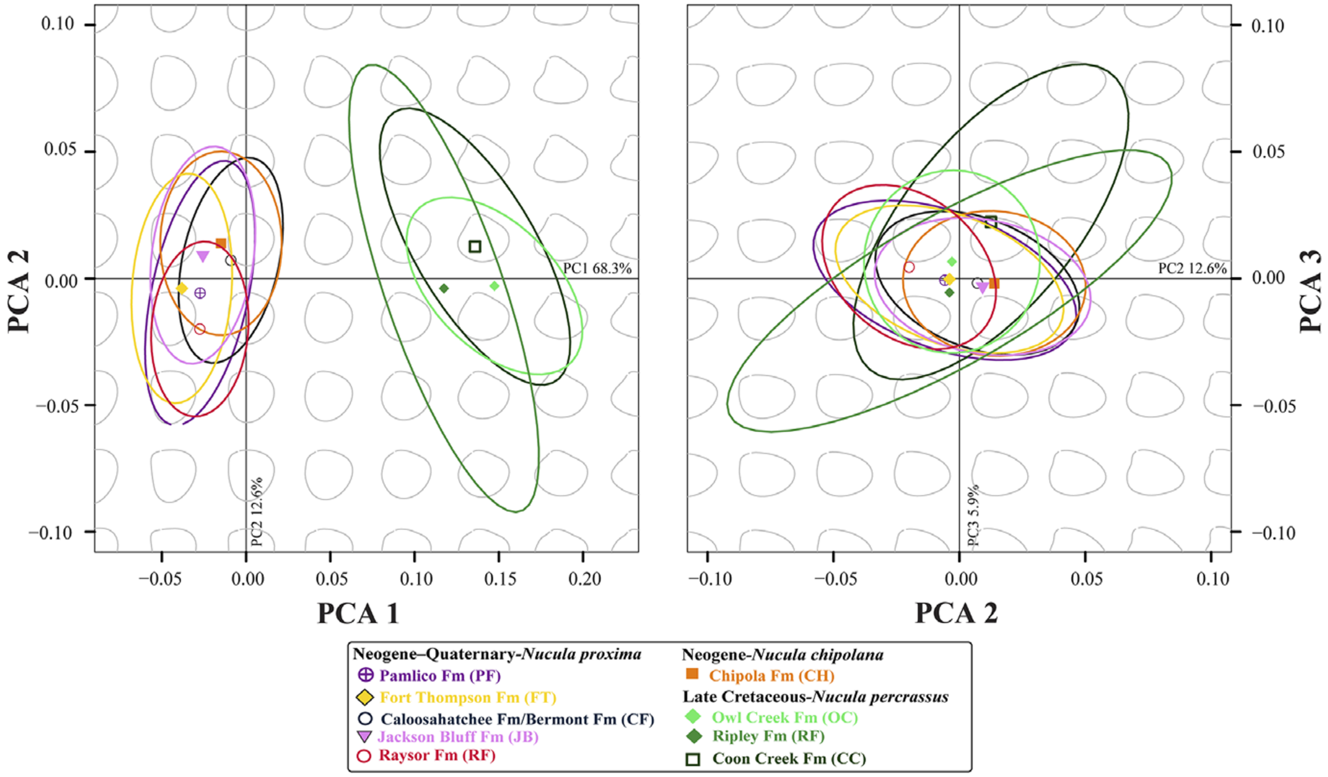

Figure 9. Principal component analysis (PCA) axes 1 to 3 scores for Late Cretaceous and Neogene–Quaternary *Nucula*. Back-transformed shapes (gray) in background show *Nucula* outline shape variation in morphospace. Ellipses represent 95% confidence intervals around mean PCA scores.

Allometry

The relationship between size and shape (i.e., allometry) for the Cretaceous and Neogene–Quaternary *Nucula* shows limited correlation for PCA axes 1 to 3 scores (Fig. 12, Table 3). The trend between principal components (i.e., a measure of shape) and centroid sizes (i.e., a measure of size) of Cretaceous *Nucula* as well as the Neogene–Quaternary *Nucula* have small R^2 values (see Fig. 12).

Discussion

Size Trends

Box, ridgeline, and time-series plots as well as omega values for Cretaceous *Nucula* reveal a size decrease over time (Figs. 5A, 6, 7A, Table 2). This trend is related to either progressively shorter life spans through the latest Cretaceous or heterochronic changes in development (e.g., see Haveles and Ivany 2010; McNamara 2012; McKinney and McNamara 2013). The former explanation requires a decrease in longevity through time, whereas the latter explanation involves a progressive reduction in the timing of maturity. Both factors would have been driven by changes in extrinsic environmental factors through the latest Cretaceous. To determine the efficacy of these potential mechanisms, a combination of detailed stratigraphic refinement in environmental proxies and sclerochronologic approaches are required to determine if this decrease in size was driven by either ecologic or evolutionary factors.

The bimodal size distributions of *Nucula* from the early Maastrichtian age Ripley Formation and the late Maastrichtian age Owl Creek Formation have several possible explanations (Fig. 6). These specimens, representing different time intervals, were collected from closely spaced localities within the eastern Mississippi Embayment (Fig. 3), making geographic differences an unlikely cause for the bimodal size distribution. The most parsimonious explanation is that the bimodal size distributions result from the preferential collection of certain size classes or sampling from different stratigraphic horizons in the Ripley Formation and Owl Creek Formation, which contain *Nucula* of different sizes.

The *N. chipolana–proxima* lineage shows an increase in mean centroid size from the middle Miocene to the Pliocene (Figs. 5B, 6, 7B). This size increase occurred during a progressive global cooling trend from the middle Miocene climatic optimum to the beginning of the Pliocene warm interval (Zachos et al. 2001). Similar patterns of late Neogene size increase have been observed in other Western Atlantic bivalves and clades across the Gulf and Atlantic Coastal Plains (e.g., Gardner 1926; Thompson 2001; Slattery 2019). Several non-mutually exclusive factors could explain this trend, including: (1) Bergmann's rule, which posits that species are larger in colder climates (Hunt and Roy 2006; Crouch and Clarke 2019); (2) Cope's rule, which suggests that organisms increase in size over time (Cope 1887, 1896; Newell 1949; Stanley 1973; Jablonski 1997; Alroy 1998); (3) increased longevity over time; (4) higher growth rates due to increased productivity (Haveles and Ivany 2010); or (5) heterochronic changes in development (Haveles and Ivany 2010; McNamara 2012; McKinney and McNamara 2013).

Determining the specific drivers of this size change is challenging due to gaps in the stratigraphic record that limit our ability to constrain the timing of morphological shifts and their relationship

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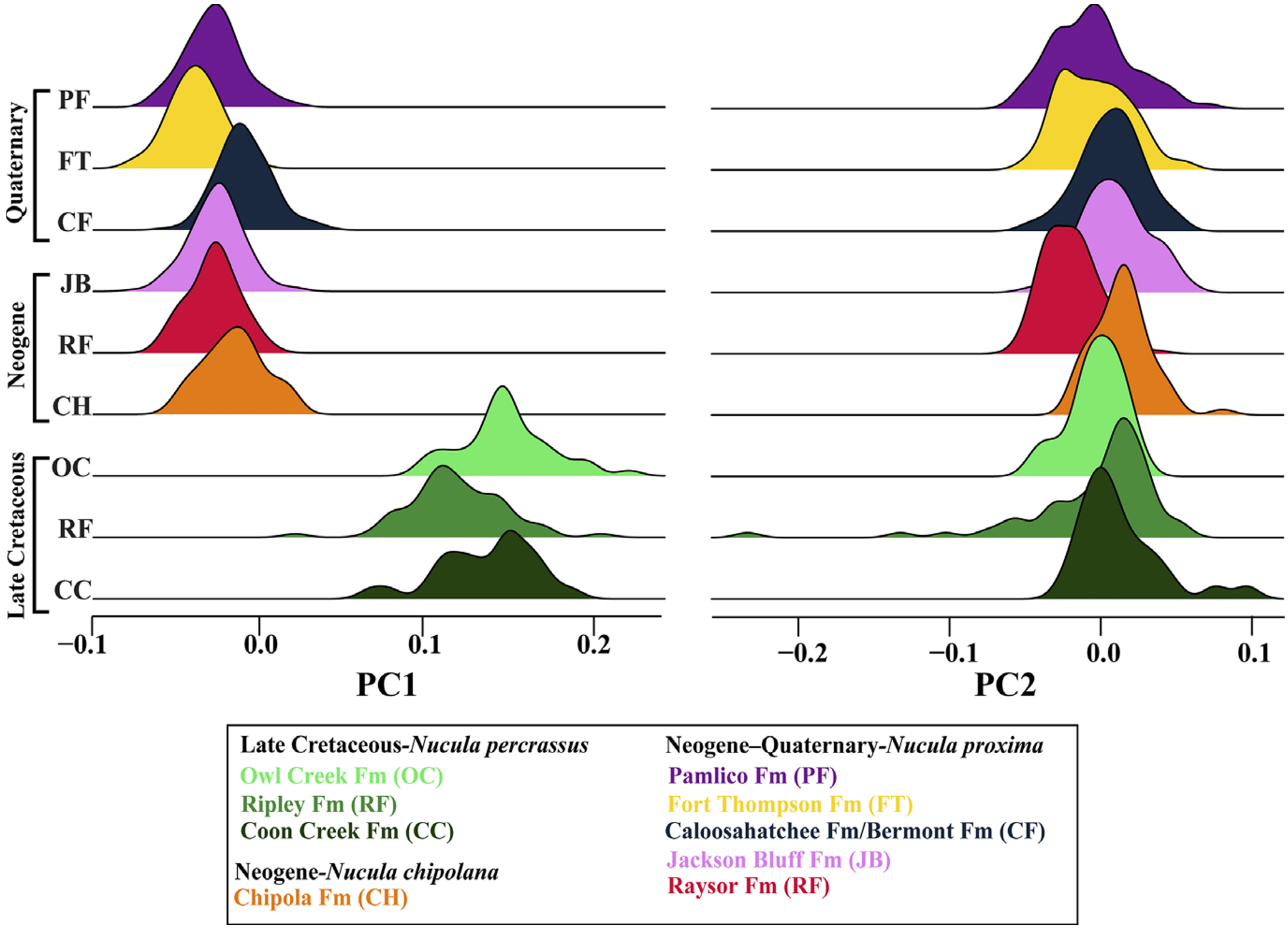

Figure 10. Ridgeline plots showing changes in *Nucula* principal component analysis (PCA) axes 1 and 2 scores for the Late Cretaceous and Neogene–Quaternary.

to environmental changes. To determine the driver of this size change, higher-resolution stratigraphic sampling of *Nucula* through this interval, combined with sclerochronological analysis of shell growth rates and improved chronostratigraphic data, would enable more precise correlations with environmental changes documented in continuous stratigraphic successions (i.e., data documented from deep-sea cores).

Box, ridgeline, and time-series plots as well as omega values reveal that *N. proxima* maintained a relatively similar mean size from the Pliocene into the late Pleistocene (see Figs. 5B, 6, 7B). Limited size change suggests that *N. proxima* was under stasis for a minimum of 3.6 Myr. The potential maximum duration of stasis could be considerably longer, but the lack of latest Miocene and early Pliocene age stratigraphic successions from which to collect additional well-preserved specimens prohibits the inclusion of nuculids from this interval.

During the Pliocene and latest Pleistocene, *N. proxima* exhibited a decrease and increase in size, respectively (Figs. 5B, 6, 7B). These patterns reflect either an evolutionary response to ocean–climate shifts or geographic size differences between *N. proxima* populations along the Atlantic and Gulf of Mexico margins. For example, the size decrease and increase correlate with the Pliocene warm interval and with global cooling following the middle Pleistocene climatic transition, respectively. While it could be argued that these patterns reflect evolutionary changes in response to climate, they are more likely due to geographic factors. The larger *N. proxima* specimens come from the Pliocene age Raysor Formation and the latest Pleistocene age Pamlico Formation of the Atlantic Coastal Plain, where bivalves are generally larger than those in the Gulf Coastal Plain (Slattery 2019). The variation in *N. proxima* sizes between these regions is likely influenced by a combination of factors, including Bergmann's rule, geographic differences in longevity, or variation in growth rates due to differences in productivity between the Western Atlantic and Gulf of Mexico shelves. Identifying the cause of this variation is beyond the scope of this study and requires both sclerochronological approaches and geochemical datasets to investigate the environmental context of these size changes/differences.

Shape Trends

PCA and omega values of outline shapes indicate greater morphological differences over time for Cretaceous *Nucula.* These differences are shown by a decreased overlap in PCA 95% confidence intervals and changes in morphological distributions over time (Figs. 9–11). The larger omega values for Cretaceous *Nucula* support a greater magnitude of morphological change from the latest Campanian to the latest Maastrichtian (Fig. 8B, Table 2).

In contrast, the greater overlap of PCA 95% confidence intervals and morphological distributions over time, along with smaller omega values, support stasis for *Nucula* during the Neogene–Quaternary (Figs. 9–11). The pronounced overlap in shape outlines

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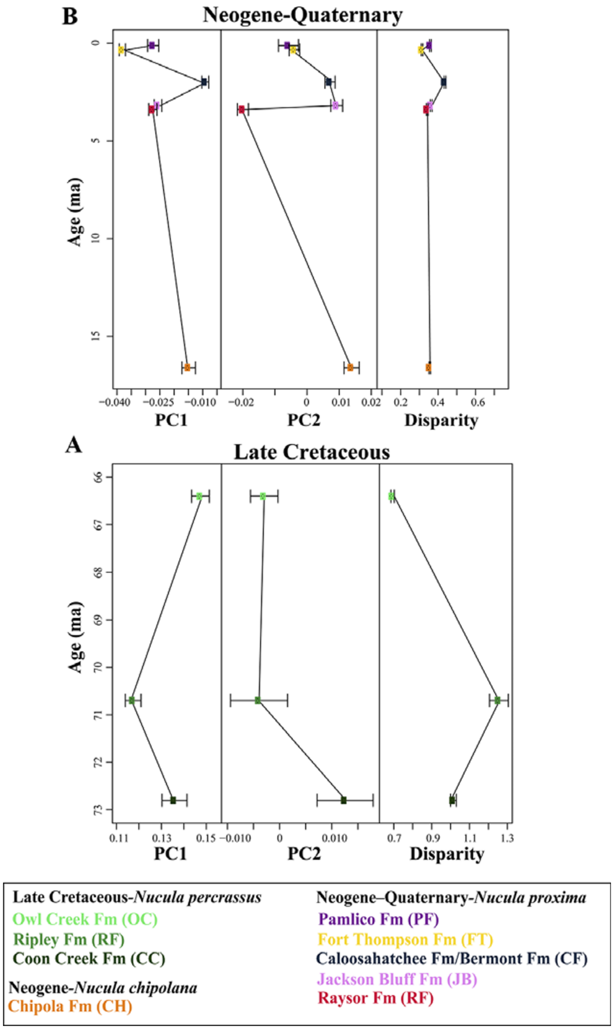

Figure 11. Time series showing changes in *Nucula* mean morphology and disparity during the Late Cretaceous **(A)** and Neogene–Quaternary **(B)**.

indicates minimal morphological change for the *N. chipolana–proxima* lineage from the middle Miocene through the Pleistocene and supports the interpretation that *N. chipolana* and *N. proxima* are the same species. However, a broader range of characters needs to be analyzed to rigorously evaluate whether these are the same species.

As compared to Neogene–Quaternary specimens, Cretaceous *Nucula* exhibit broader morphological distributions on ridgeline plots and larger disparity values (Figs. 10, 11), which indicate greater morphological variability and, consequently, more raw phenotypic variation for natural selection among Cretaceous species (e.g., West-Eberhard 1989, 2003; Lloyd and Gould 1993; Sheldon 1993; Day and McPhail 1996; Yacobucci 2004). The specific mechanism(s) driving this variability are still debated, but it is likely related to the timing and duration of relative environmental stability, ecological interactions, environmental change, and potential interactions between these components (Simpson 1944; Parsons 1987; Ayala et al. 1975; Sheldon 1993; Pigliucci 2001, 2005; Pigliucci et al. 2006; Yacobucci 2004). However, there remains considerable debate around the conditions and environments that drive increases in phenotypic variability. Parsons (1987) suggests that high phenotypic variability is characteristic of high-stress environments, as greater variability would be advantageous for adaptation. Conversely, Ayala et al. (1975) and Sheldon (1993) hypothesize that high phenotypic variability is more likely to occur in stable environments, as these conditions provide greater opportunities for phenotypic experimentation and the accumulation of directional change. A more stable environment allows taxa to evolve along various trajectories throughout their biogeographic range without environmental change “resetting” those trends. The greater shape variability in Cretaceous *Nucula* suggests that the more stable environments of this interval allowed this evolutionary response that is reflected in increased morphological variation. In contrast, the limited morphological variability in Neogene–Quaternary *Nucula* suggests that more frequent and pronounced environmental changes did not allow sufficient time for the expression of morphological variation in the group. Reduced variability is supported by the decrease in morphological disparity from the stable early Neogene to the increasingly unstable late Neogene (Fig. 11B).

Allometric Effects on Shape

Allometric effects must be considered in shape analysis, as morphological differences might reflect ontogenetic stage rather than changes over time. Many species exhibit allometric effects, where shape proportions change through ontogeny (Bonner 2006). However, the weak correlation between size and shape for Cretaceous and Neogene–Quaternary *Nucula* indicates that size plays a limited role in controlling specimen shape (Fig. 12, Table 3). The weak correlation suggests that *Nucula* species grow isometrically, with all shell dimensions expanding at identical rates. Therefore, the shell characteristics of large individuals are indistinguishable from those of small individuals. Isometric growth indicates that the observed patterns in *Nucula* shape reflect true changes over time and are not being confounded by ontogenetic changes.

Implications for the Plus ça Change Model

The empirical data presented here support the Plus ça change model, which predicts that environmental stability during different climatic regimes is linked to varying evolutionary patterns. The results, which are derived from a single genus to avoid potential confounding issues associated with taxonomic variation, also indicate that morphological disparity is related to environmental stability over geological timescales. Furthermore, the analysis suggests that ocean–climate interactions play a significant role in shaping environmental stability, and, consequently, selection pressures.

The changes in size and shape documented here for Cretaceous *Nucula* support the Plus ça change prediction that reduced environmental variability is associated with directional evolutionary responses. During greenhouse intervals, the amplitudes and rates of environmental variation are sufficiently reduced that they do not substantially alter marine habitats over the long term. This fosters greater ecological stability, providing marine faunas more time to adapt to both environmental shifts and non-environmental selection pressures. Thus, the slowly changing environment of the Late Cretaceous greenhouse reduced environmental selection pressures and led to more consistent biotic interactions over geological timescales, permitting *Nucula* to evolve in response to non-environmental pressures, such as competition or escalation. These conditions also allowed for reduced environmental selection pressures to promote greater phenotypic variation which, in turn, provided more raw material for natural selection among the Cretaceous species, potentially resulting in gradual phyletic evolution over the long term.

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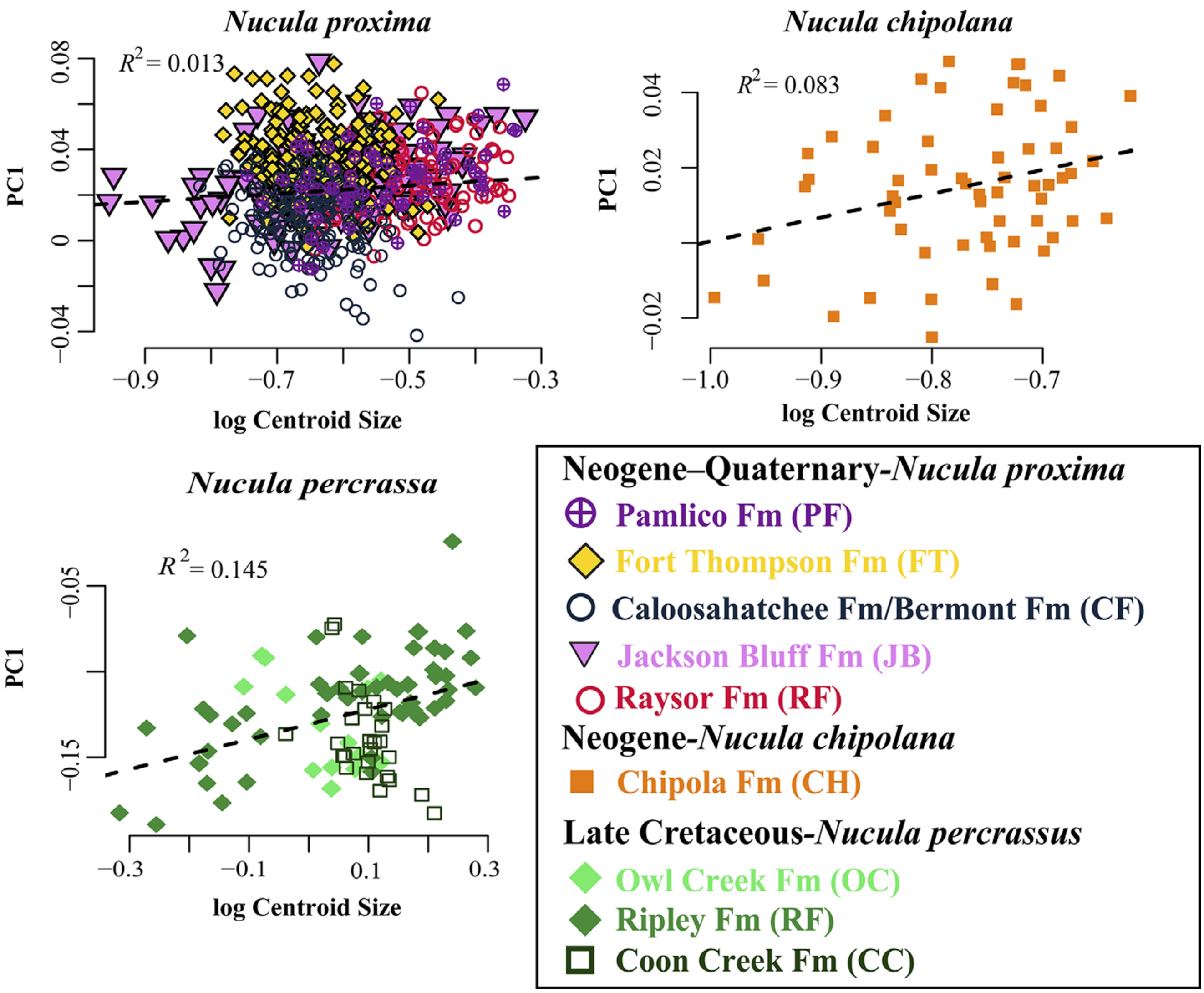

Figure 12. Allometric test of principal component analysis (PCA) axis 1 scores (i.e., a measure of shape) and centroid sizes (i.e., a measure of size) of Late Cretaceous *Nucula percrassa* Conrad, 1858, Miocene *N. chipolana* Dall, 1898, and Pliocene to Holocene *N. proxima* Say, 1822.

Table 3. R^2 values for Cretaceous and Neogene–Quaternary *Nucula* centroid sizes versus principal component analysis (PCA) axes 1 to 3 scores.

	R^2 values for centroid size vs. PCs		
	N. proxima	*N. chipolana*	*N. percrassa*
PC 1	0.013	0.083	0.164
PC 2	0.15	0.075	0.005
PC 3	0.014	0.036	0.036

The limited size and shape changes observed in Miocene to Pleistocene *Nucula* further support the Plus ça change hypothesis, which predicts that increased environmental variability, such as that characteristic of climate variation during the late Cenozoic, is more likely to be associated with morphological stasis. During transitional and icehouse regimes, environmental fluctuations due to the pronounced impact of Milankovitch band variation are rapid and reduce overall stability, leading to fluctuating selection pressures on marine species (Roy et al. 1996). These rapidly fluctuating conditions and changing selection pressures in transitional and icehouse climates promote stasis through four possible, non-mutually exclusive mechanisms: (1) limited time available for species to adapt to rapidly changing conditions, (2) reduced phenotypic disparity, (3) coordinated stasis, and (4) change in morphological traits tracking and constrained by the boundaries of climatic fluctuations.

The first mechanism suggests that environmental fluctuations drive species to track shifting habitats, resulting in populations fragmenting and reforming over time (Potts 1983; Pease et al. 1989). This process is akin to a reticulate evolutionary model (sensu Sylvester-Bradley 1977) but occurs over time intervals that are too short for new species or lineages to originate, as they are recombined before sufficient evolutionary differentiation can occur to produce genetic isolates (Futuyma 1987; Liebermann et al. 1995; Eldredge et al. 2005). Over the long term, this short-term instability reduces the ability of species to produce an evolutionary response before the dynamic environmental system changes again (Roy et al. 1996). Under these conditions, organisms do not display evolutionarily significant morphological variation over geological

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timescales and accommodate most changes ecologically through habitat tracking.

The second mechanism suggests that the amplitude and rapidity of environmental changes reduce morphological disparity, as exemplified by the Neogene–Quaternary *Nucula*. This decrease in disparity limits the raw phenotypic variation available for natural selection, restricting the ability of *Nucula* to evolve a broader range of forms. As a result, the limited size and shape changes documented during this interval are a consequence of this constrained phenotypic variation.

A third mechanism that may explain stasis during transitional and icehouse regimes is coordinated stasis. This model posits that, despite environmental and climatic fluctuations, stable habitats persist over time, which species track (Brett et al. 1996; Ivany et al. 2009; Brett 2012). In this context, morphological stasis is promoted when multiple coexisting species undergo minimal evolutionary change. Limited morphological change across many coexisting species reinforces stasis in each species, as minimal change in one species reduces selective pressures on the others. This dynamic helps maintain a steady ecological assemblage over time, with each species preserving relatively constant forms within the community. Coordinated stasis should also operate under greenhouse conditions, when stable habitats may be more prevalent. However, the data presented here suggest that morphological change is associated with less variable environmental conditions. Therefore, while coordinated stasis is a plausible mechanism, it fails to account for the lack of stasis during greenhouse regimes.

The final mechanism, first proposed by Hunt et al. (2015), suggests that rather than accumulating morphological changes over time, traits track temperatures bounded by glacial–interglacial cycles. These fluctuating traits enable species to adapt and maintain stability during each cycle, resulting in dynamic stasis—a pattern of minor evolutionary changes without significant net change. According to this model, the short-term nature of climate variation during icehouse regimes, compared with a species' total temporal range, ensures that morphological characters remain within the bounds of glacial–interglacial cycles. As a result, traits exhibit stasis, fluctuating within these boundaries. Although this model explains how stasis can occur during environmental change, it also predicts that morphological variation should be greater during icehouse regimes than during greenhouse periods, because the environmental variation (or bounds) are more pronounced in the former over an identical time interval. Based on this prediction and our morphological data, we infer that bounded climatic fluctuations likely played a minimal role in promoting stasis among *Nucula*, as the morphological variation in Neogene–Quaternary species was smaller than that observed in the Cretaceous examples.

Paleobiological Implications

While this study supports the Plus ça change model, it represents just one analysis that explicitly examines the influence of extrinsic controls on morphological change over time. Since Sheldon's (1996) hypothesis was published, only a limited number of studies have explicitly tested the hypotheses inherent in this concept (e.g., Kim et al. 2009). The limited number of case studies testing the Plus ça change model underscores the need for further research to elucidate how the duration and types of stability influence evolutionary responses of various clades. This is particularly important, because most studies on evolutionary processes emphasize biological/ecological agents over broader environmental factors (e.g., Palmer 1979; Dietl 2003; Audino et al. 2020; Pigot et al. 2020), creating a critical gap in understanding how large-scale environmental changes impact evolution.

As Gould, Eldredge, and others have emphasized, the debate over contrasting evolutionary patterns are not about whether different tempos and modes exist, but rather their relative frequencies throughout geological time. Understanding these frequencies is crucial for uncovering how species respond to environmental changes, identifying the drivers of biodiversity, and clarifying the mechanisms that shape life's evolutionary history. More case studies explicitly testing the relationship between evolutionary tempo and mode and paleoenvironmental context—particularly those employing standardized methods and analyzing multiple traits within well-constrained lineages and settings—are needed to provide deeper insights into how environmental variables shape evolutionary patterns and processes.

Conclusions

Understanding the processes driving evolutionary change is a major challenge in paleobiology. Despite its significance, much of the discourse in the field has centered on theoretical debates, with relatively few empirical studies directly documenting the morphological change inherent in species, lineages, or groups. Most evolutionary tempo and mode studies using the fossil record focus on identifying different evolutionary patterns, often neglecting the underlying processes that drive them. Furthermore, in the rare examples where underlying processes are considered, biological/ecological agents typically receive more attention than broader environmental factors, leaving an important gap in our understanding of how large-scale environmental changes influence evolution.

This study demonstrates that the bivalve *Nucula* underwent morphological change during the Cretaceous greenhouse, while remaining in stasis during the Neogene–Quaternary transitional and icehouse climate intervals. These findings align with the predictions of Sheldon's (1996) Plus ça change model, which posits that increased environmental variability, such as during transitional and icehouse intervals, fosters stasis, whereas reduced variability, such as during greenhouse intervals, allows for the accumulation of progressive morphological change. By linking evolutionary patterns to distinct climatic regimes, this study provides deeper insights into how environmental processes have the potential to shape evolutionary outcomes over geological timescales.

The limited number of case studies testing the Plus ça change model underscores the need for further research to document the prevalence of different evolutionary patterns in their environmental and climatic contexts over geological time. Rather than debating the existence of different evolutionary patterns, the focus should shift to their relative frequencies and the mechanisms driving them to better understand morphological change, speciation, and diversification. To advance our understanding of evolutionary processes, future studies must integrate paleoenvironmental contexts, use standardized methodologies, and examine multiple traits within well-defined lineages and settings. Such efforts will not only enhance our understanding of evolutionary patterns but will also shed light on the underlying processes behind them.

Acknowledgments. We sincerely thank E. Saupe and J. Kastigar for their invaluable support in shepherding our manuscript through the review process. Thanks to G. Hunt, L. Ivany, B. Andres, N. Landman, M. Meyer, K. Minor, M. Puckett, R. Ostrander, and M. Olney for their helpful suggestions and critical

https://doi.org/10.1017/pab.2025.10046 Published online by Cambridge University Press

input on this paper. We acknowledge A. and B. Carroll (Mississippi), M. Gibson (University of Tennessee Martin), W. Creel (Pink Palace Museum), and P. Broadbent (Coon Creek Science Center) for their assistance in accessing localities. We also thank R. Portell (Florida Museum of Natural History), G. Phillips (Mississippi Museum of Natural Science), K. McKinney (United States Geological Survey), S. Butts (Yale Peabody Museum of Natural History), and J. Utrup (Yale Peabody Museum of Natural History) for help accessing and photographing museum specimens. Partial funding for this research has been provided by National Science Foundation through Grant EAR 1053517 to P.J.H. Funding was also provided to J.S.S. by the Tampa Bay Fossil Club Louis Villei Memorial and Research grants, St. Petersburg Shell Club Research Grant, University of South Florida School of Geosciences Richard A. Davis Jr. Endowed Fellowship in Geology Research Award, Paleontological Research Institute J. Thomas Dutro Jr. Student Award in Systematic Paleontology, Association of Applied Paleontological Services Rene M. Vandervelde Research Grant, American Museum of Natural History Lerner Gray Fund for Marine Research and Collection Study Grant, Geological Society of America Student Research Grant, Florida Paleontological Society Gary S. Morgan Award, Gulf Coast Association of Geological Societies Student Grant Program, Yale Peabody Museum of Natural History Schuchert and Dunbar Grant in Aid Program, and Sigma-Xi Grants-in-Aid-of-Research.

Competing Interests. The authors declare that they have no competing interests.

Data Availability Statement. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sqv9s4ndb.

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