PROCEEDINGS OF THE TWENTY-SIXTH ANNUAL KECK RESEARCH SYMPOSIUM IN GEOLOGY

April 2013
Pomona College, Claremont, CA

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ISSN# 1528-7491

The Consortium Colleges The National Science Foundation ExxonMobil Corporation

KECK GEOLOGY CONSORTIUM
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Funding Provided by:
Keck Geology Consortium Member Institutions
The National Science Foundation Grant NSF-REU 1062720
ExxonMobil Corporation

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KECK Geology Consortium
Learning Science Through Research
Published by Keck Geology Consortium
Short Contriubtions
26th Annual Keck Symposium Volume
6 April, 2013
ISBN: 1528-7491

LINEAR AND LANDMARK-BASED MORPHOMETRIC COMPARISON OF TWO POPULATIONS OF CAMPELOMA, SP. ACROSS THE K-PG BOUNDARY

GARY LINKEVICH, Vassar College
Research Advisor: Stephanie Peek

INTRODUCTION

In the three decades since Alvarez et al. (1980) published crucial evidence for a bolide impact as the primary cause of the Cretaceous-Paleogene (K-Pg) extinction, research interests have focused more on environmental conditions before and after the event. Some of the best records of these conditions are available in the Mesozoic and early Cenozoic sediments of the western United States, particularly the late-Cretaceous Hell Creek and early-Paleogene Fort Union formations. Similarly-motivated studies of these strata have explored a wide range of available information, from sedimentology and paleobotany to isotopic analysis of invertebrate shells. The richness and concentration of fossil beds in these formations also allows for anatomically-driven studies in morphometrics and population statistics.

Gastropods have been the subject of numerous morphometric studies over the past few decades due to their taxonomic diversity, consistent presence throughout the Phanerozoic, and excellent preservation potential. Much of this research has been dedicated to quantifying and systematizing morphometric analysis. Kohn and Riggs (1975) analyzed linear measurements of specimens and photographs to characterize the *Conus* shell and noted the need for precise, objective methods in "selecting characters, coding character states, and evaluating the similarity of character states among individuals." As technological advances offered newer ways of obtaining data, landmark-based geometric morphometric analyses became possible and quickly surpassed manual morphometrics in popularity among gastropod studies (Johnston et al., 1991; McShane et al., 1994; Chiu et al., 2002; Queiroga et al., 2011; and Cruz et al., 2012 to name a few).

This study utilizes both manual linear measurements and landmark-based geometry, to morphometrically compare two populations of the freshwater gastropod *Campeloma sp.*, one from before and one from after the K-Pg boundary.

METHODS

All specimens were collected in the Williston Basin, Montana, in mid-July of 2012. Cretaceous specimens were obtained from a fossil-rich exposure of the Hell Creek Formation at 47.753°N, 106.499°W (elev. 784 m) (Hartman site L6867), with most specimens selected from float, some extracted from a large consolidated block that had recently rolled down from the conglomerated shell-bearing layer, and a few collected in situ. Paleogene specimens were obtained from a series of broad promontories composed of unconsolidated mudstone and sporadic red sandstone, representing the Tullock member of the Paleogene Fort Union Formation, at 47.312°N, 106.769°W (elev. 798 m) (Hartman site L6978).

MANUAL MORPHOMETRICS

The initial stage of data acquisition for this study relied on manual measurements. All 53 originally collected Paleogene specimens, and a diverse selection of the Cretaceous specimens, were measured with a caliper (to the nearest 0.1 mm) and goniometer (to the nearest integer) for height, maximum major and minor diameters, last whorl height, low-whorl angle (LWA, defined as the angle formed by the intersection

of the lines tangent to either side of the shell's spire at the last 2 whorls), and 'modified aperture height' (MAH), defined as the height from the bottom of the shell to the shoulder immediately above the aperture (landmark 5 in Figure 2). Some of these measurements were then utilized to determine compound parameters, including maximum cross-sectional area (MXSA) and cross-sectional ellipticity (XSE). MXSA is an effective indicator of overall shell size, while XSE captures a combination of fossil deformation and terminal aperture growth rate, since the end-of-life value of the rate at which the width of the aperture increases throughout the shell determines how extreme the aperture width / shell width ratio becomes. All of the manual morphometric data were then analyzed in PAST (Palaeontological Statistics) (Hammer & Harper 2001).

LANDMARK MORPHOMETRICS

For the landmark-based component of this study, all 622 specimens were photographed using a Canon XSi digital camera and 28-135mm Ultrasonic lens. Photographs were kept consistent by using modeling clay to hold each specimen in the same position, a spotlight to provide steady lighting, and a tripod and external remote to minimize camera movement and vibration (Fig. 1).

Photographs were then evaluated by four parameters: presence of an intact bottom edge, visibility of the aperture, presence of a leading aperture edge, and presence of a complete apex. Most specimens failed in one or two of these criteria, but 141 of them failed in all four due to their poor preservation; these (photographs) were discarded. The remaining photographs were digitized using the tps software suite (Rohlf 2005). Landmarks were placed at some combination of 15 generally well-preserved locations on each specimen, as shown in Figure 2 (that is, some landmarks were omitted for some specimens if they lacked the physical features to allow for such landmark placement). Landmark locations were chosen after consideration of consistently preserved shell features as well as landmarks utilized by numerous other studies (Kohn and Riggs, 1975; Chiu et al., 2002; Cruz et al., 2011; and Queiroga et al., 2011; to name a few).

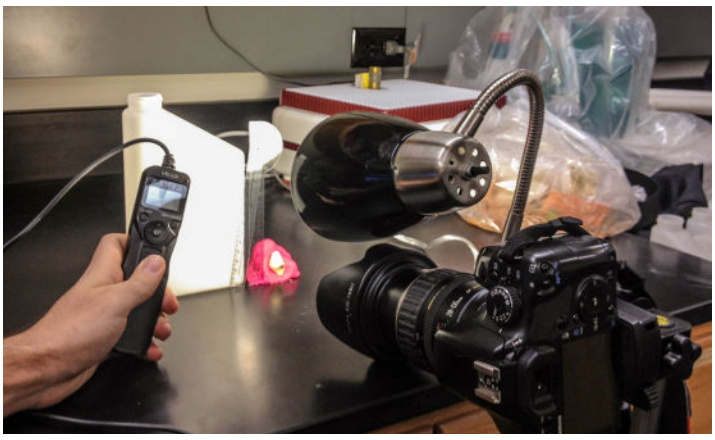

Figure 1. The setup used to photograph every specimen used in this study. Photograph by Min Chen (Vassar College).

The cumulative data obtained were then optimized to create the best possible database of complete but accurate information. There were no Paleogene specimens analyzed with natural (non-reconstructed) apex data, so for comparative purposes, apex data from the Cretaceous specimens were discarded. Marginal specimens and those with limited sets of data were likewise disregarded, for the sake of robust statistical comparison. This produced a final sample population of 30 Paleogene and 128 Cretaceous specimens (Fig. 3).

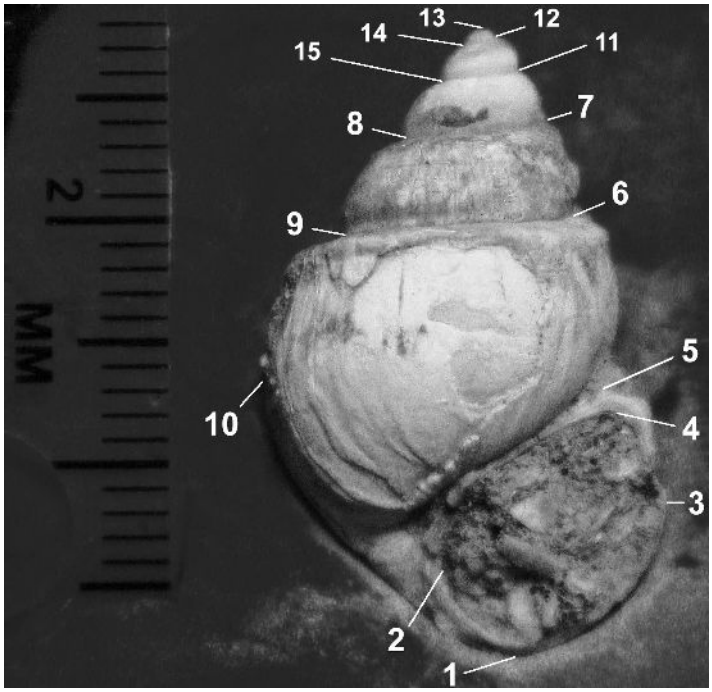

Figure 2. Landmarks used in this study, plotted on a well-preserved Cretaceous specimen. Definitions for the landmark locations are as follows: 1) Bottom edge of shell; 2) Innermost edge of aperture; 3) Outermost edge of aperture; 4) Uppermost edge of aperture; 5) Joint between the shoulder above the aperture and the wall of the last whorl; 6-15) Further joints between each whorl and the shoulder of the next whorl, with the exception of: 10) Furthest-left point on the shell when the central axis is positioned vertically; and 13) Apex.

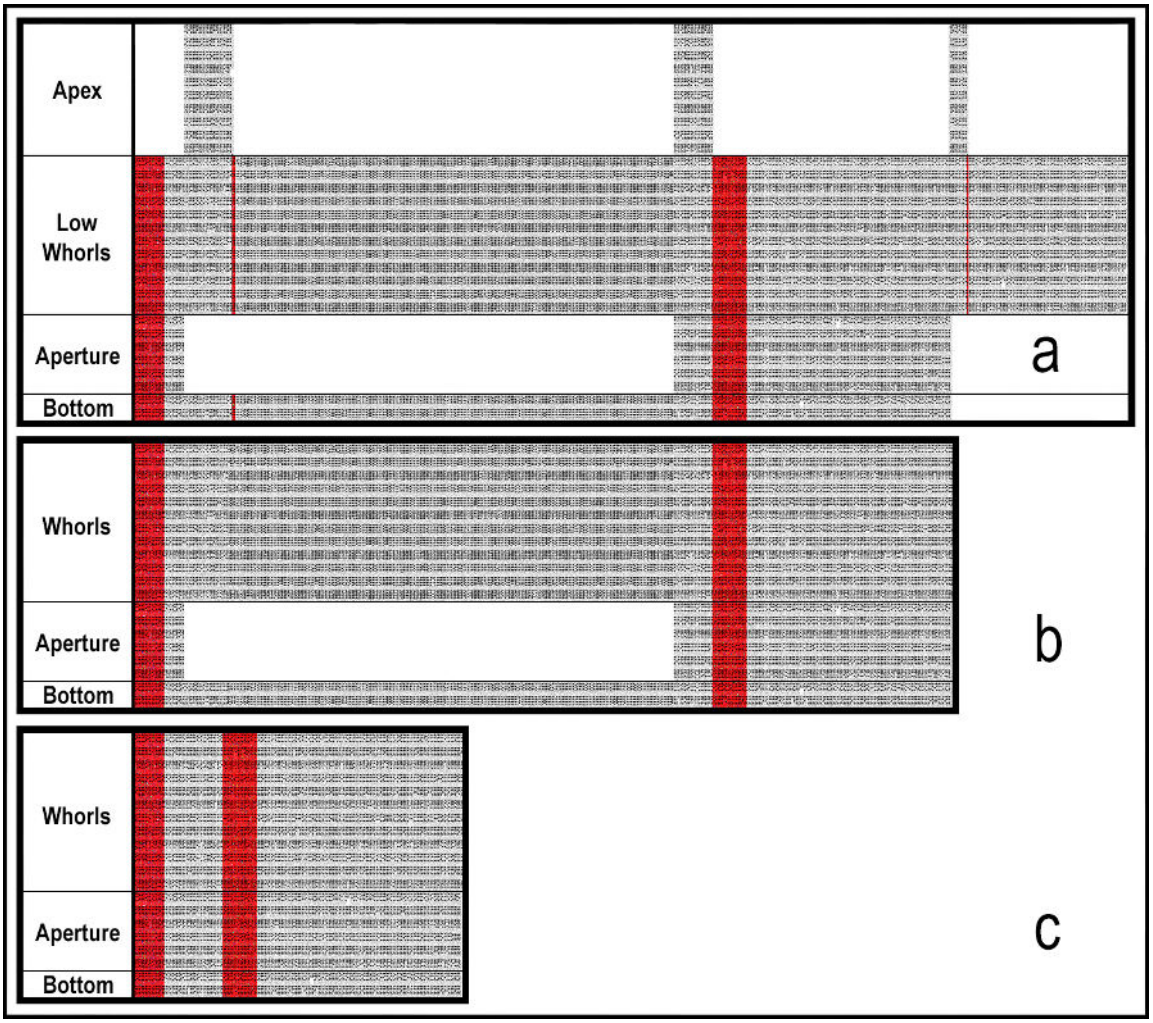

Figure 3. Visual representation of landmark data obtained from all specimens, created by visually condensing the Microsoft Excel spreadsheet containing the data. Data from Paleogene specimens are highlighted in red; all other data come from Cretaceous specimens. Blanks indicate missing data (data that could not be collected from a particular specimen). (a) Cumulative initial data; (b) Total data after the removal of apex data, marginal Paleogene specimens, and morphometrically poor Cretaceous specimens; (c) Final data used for all statistical comparisons.

Various measurements derived from the data were used to establish ten parameters of variation: 1) aperture area; 2) aperture elongation (with values > 1 signifying a taller, rather than wider, ellipse); 3) shell width (the horizontal distance between landmarks 3 and 10 in Figure 2); 4) ratio of aperture width to shell width; 5) height of the last whorl; 6) height of the last 2 whorls; 7) ratio of parameters 5 and 6; 8) θ_{low} (synonymous to LWA in the manual measurements); 9) θ_{mid} (synonymous to θ_{low}, but using the next 2 whorls); and 10) $\Delta\theta$, defined as the difference between parameters 8 and 9. For principal components analysis, the $\log_{10}$ of parameters 8-10 was used instead of the original value due to the difference in magnitude of discrepancies (as compared to parameters 1-7).

RESULTS

MANUAL MORPHOMETRICS

A principal components analysis of manually-obtained linear data showed a high degree of separation between the two groups of specimens, with only a small amount of overlap (Fig. 4a). PC1 consists of a strong positive correlation between shell height and MXSA, as well as a weaker positive correlation between MAH and last whorl height; XSE and log(LWA) are statistically irrelevant (Fig. 4b). PC2 is overall very similar to PC1, with the exception that MXSA is negatively correlated with the axis (and log(LWA) contributes slightly more than in PC1). PC1 and PC2 captured ~95% of the variation between the two groups (Fig. 4d).

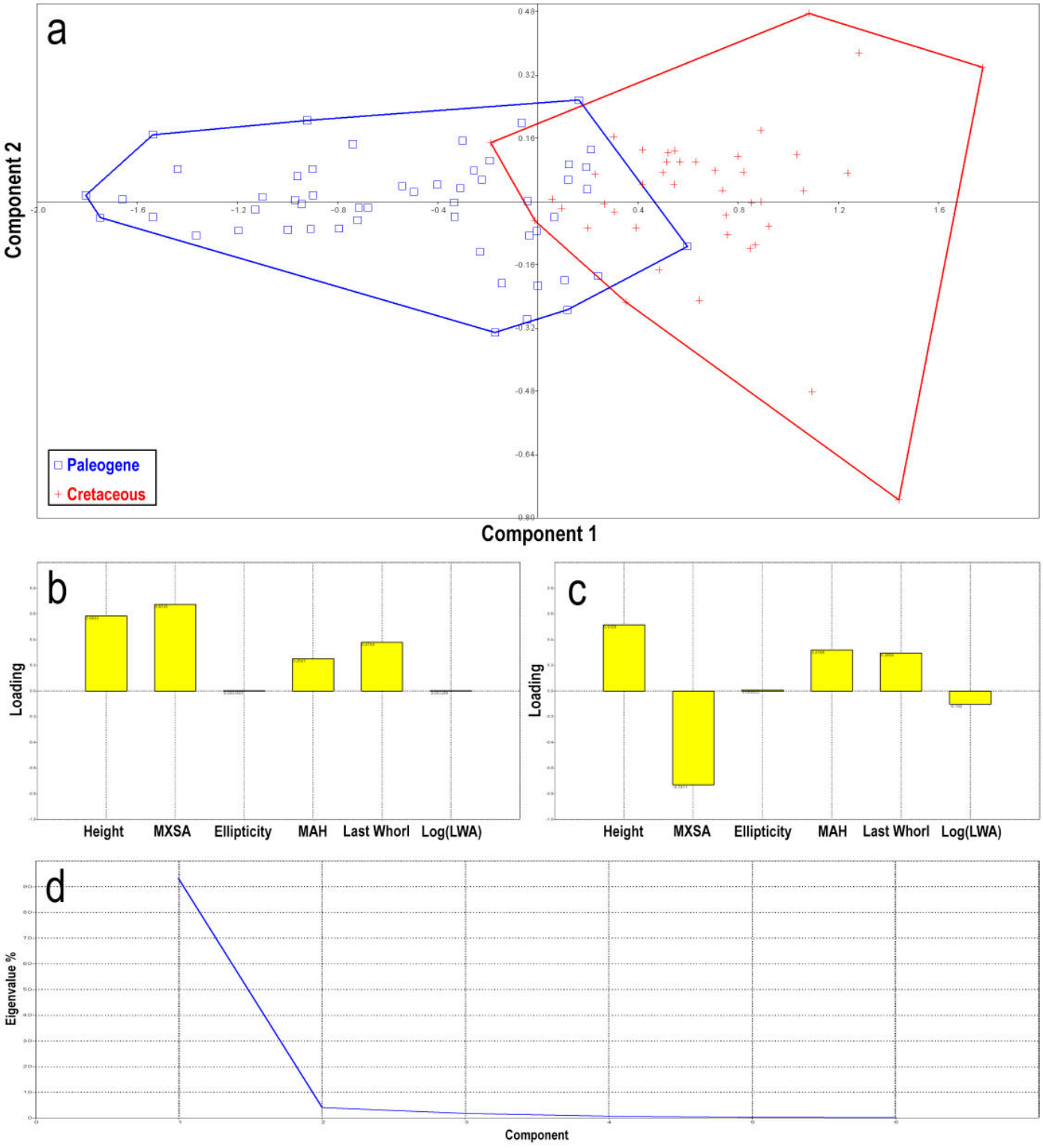

Figure 4. Principal components analysis of manually obtained morphometric data. (a) Scatter plot; (b-c) Loadings for PC1 and PC2 (respectively); (d) Scree plot showing the additional amount of variation captured by each successive PC. All figures created in PAST and edited in Adobe Photoshop CS6.

LANDMARK MORPHOMETRICS

Landmark-obtained morphometric data showed far less separation between the two groups, with a great majority of the data in overlap (Fig. 5a). PC1 consists of a positive correlation with aperture area, shell width, the height of the last 1 and last 2 whorls, and log(Δθ), a very weak negative correlation with aperture elongation, log(θ_{low}), and log(θ_{mid}), and almost no contribution from the aperture/shell width ratio or last 1 / last 2 whorl ratio (Fig. 5b). PC2 is almost entirely controlled by a positive correlation with log(Δθ), with little and mostly negative influence from all other parameters. PC1 and PC2 captured ~80% of the variation between the two groups (Fig. 5d).

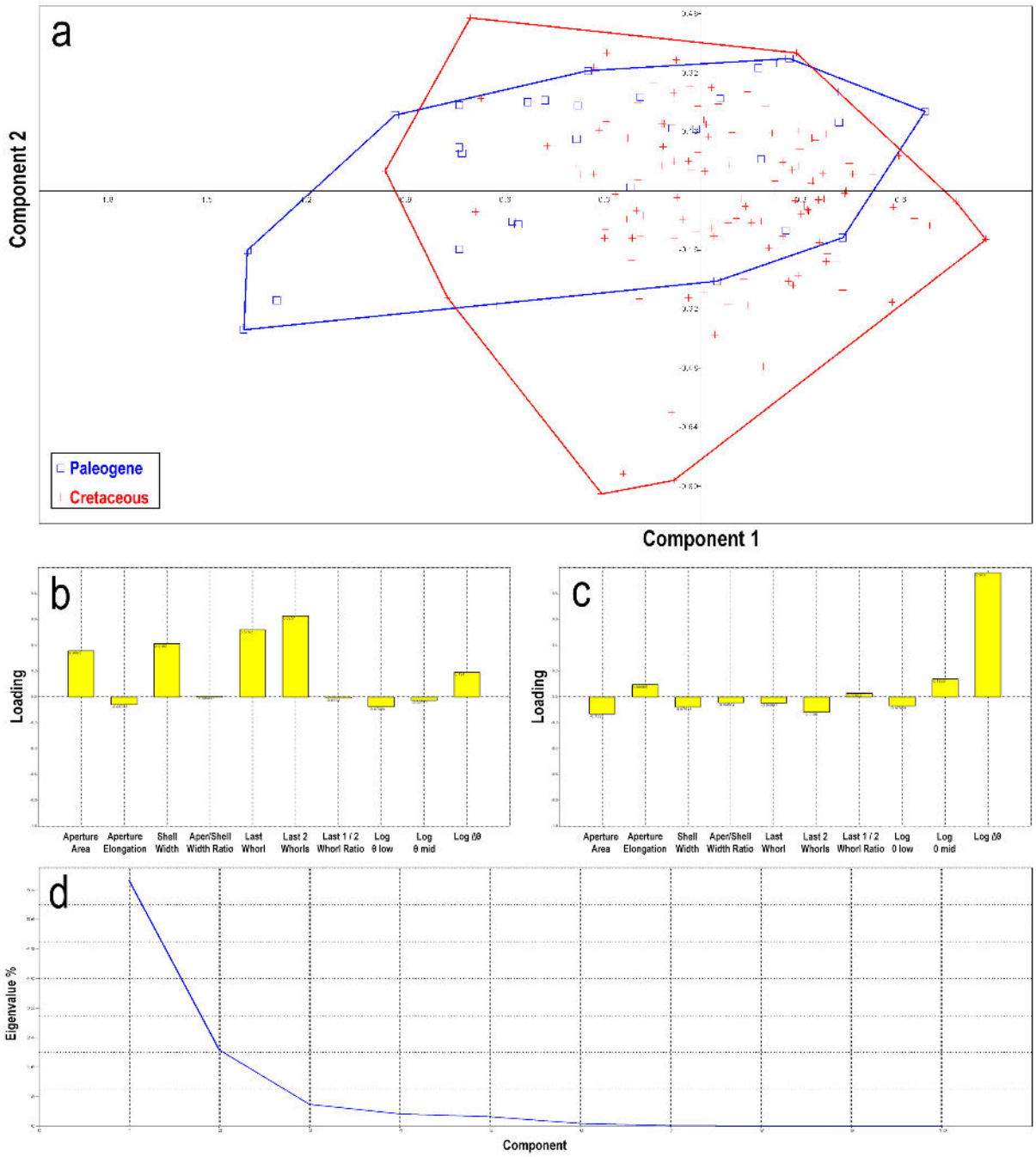

Figure 5. Principal components analysis of landmark-based morphometric data. (a) Scatter plot; (b-c) Loadings for PC1 and PC2 (respectively); (d) Scree plot showing the additional amount of variation captured by each successive PC. All figures created in PAST and edited in Adobe Photoshop CS6.

DISCUSSION

MANUAL MORPHOMETRICS

The four parameters comprising PC1 (height, MXSA, MAH, and last whorl) (Fig. 4b) are all fundamentally synonymous to the organism's overall age and size, and their mutual positive correlation supports the basic notion that all of them increase steadily over the course of the organism's lifespan, as well as the secondary notion that all of the information they represent could therefore be represented by any one of them. This supports the findings of McShane et al. (1994), who concluded that shell height alone among 61 populations of abalone (*Haliotis iris*) captured over 70% over the variation in other parameters covarying with specimen length. It was an expected result that cross-sectional ellipticity (XSE) and low-whorl angle (log(LWA)) have no correlation with these basic parameters of shell size. That MXSA has a negative correlation with the other three size-related parameters in PC2 (Fig. 4c) was not anticipated, and its cause is not yet understood. Based on the loadings for PC1 and PC2, the largest specimens should appear in Quadrant I of the scatter, and the smallest in Quadrant III. This corresponds with the distribution of K and Pg specimens in Figure 4a. This distribution also shows that PC1 (the vertical axis) mostly captures variation between individuals within each group, while PC2 (horizontal) much more effectively captures the variation between the two groups. Furthermore, since PC1 and PC2 capture ~95% of the variation in the data (Fig. 4d), Fig. 4a is an effective representation of the differences between the two populations and their individual members. Based on these observations, the key distinguishing parameter (not directly related to size) of the Pg specimens appears to be a greater cross-sectional area at any particular height of the shell and last whorl.

LANDMARK MORPHOMETRICS

Similarly to the manual morphometric results, the primary factors controlling the axis of greatest variation (PC1) are all directly related to the organism's size: aperture area, shell width, and the heights of the last 1 and last 2 whorls (Fig. 5b). There is almost no contribution to PC1 (and little to PC2) from the ratios of aperture width : shell width or last 1 : last 2 whorls, which suggests that these ratios are fairly consistent throughout all specimens. The reason that PC2 (Fig. 5c) is controlled almost exclusively by $\log(\Delta\theta)$ – more than all other parameters combined – has not yet been identified, but is most likely a result of simple inconsistency; accurate angle measurements were difficult to achieve with the landmarks and software used, evidently introducing an underestimated degree of error. More importantly, neither PC1 (effectively, size) nor PC2 (effectively, change in θ with height) offer any distinguishable trend of variation between the two groups; the vast majority of the data are in overlap (Fig. 5a). Furthermore, given their lack of clarity, that PC1 and PC2 capture only ~80% of the variation in the data (Fig. 5d) suggests that the remainder of the information (which is not represented in Fig. 5a) offers even less distinction between the two populations.

CONCLUSION

Taken together, the manual and landmark data suggest that the two populations of *Campeloma sp.* are anatomically similar to each other in most respects, with the primary distinguishing characteristic of the Paleogene organisms being a greater cross-sectional area given a comparable height and width. This implies a more bulbous shell shape that would be able to accommodate a larger body given its internal volume. This suggests that the ecologically poor environment after the K-Pg extinction event may have allowed the few surviving genera to dominate and flourish. It should be noted that the greatest distinction between the manual and landmark-based analyses used in this study is in the proportion of Paleogene to Cretaceous specimens, due to availability at the time of measurement (1.26:1 in manual, 0.23:1 in landmark). Future studies incorporating a synthesis of these two methods may achieve clearer results by using a consistent balance of specimens, if possible.

ACKNOWLEDGMENTS

This research was made possible by funds from the Keck Geology Consortium, Vassar College Environmental Research Institute, and Vassar College Earth Science Dept. My utmost gratitude goes to David P. Gillikin (Union College) and David Goodwin (Denison University) for my participation in this project, and for their irreplaceable guidance; to Joseph

H. Hartman (Univ. of North Dakota) and Art Bogan (North Carolina Museum of Natural Sciences) for their invaluable expertise and generosity; and to Stephanie L. Peek (Vassar College) for her continued patience, support, and multiple revisions of this paper. Special thanks also go to Lois Horst, Rick Jones, Alexandra Dadon and Min Chen for their endless logistical assistance in and out of the lab.

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