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A Quantitative Analysis of Intermediate Forms within Astarte from the Atlantic Coastal Plain

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A QUANTITATIVE ANALYSIS OF INTERMEDIATE FORMS WITHIN *ASTARTE* FROM THE ATLANTIC COASTAL PLAIN

A Thesis
Presented to
The Faculty of the Department of Geosciences
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In Partial Fulfillment
of the Requirements for the Degree
of Master of Science

by
Randal Philip Roberson
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ABSTRACT

The Atlantic Coastal Plain has long been recognized as a natural laboratory useful for testing hypotheses about various environmental and ecological effects on marine fauna. For studies such as these to continue being conducted in a rigorous and easily repeatable manner, a reliable taxonomy must be established for genera within this physiographic province. The bivalve genus, *Astarte*, is a cosmopolitan genus that is commonly found within the Atlantic Coastal Plain. This genus has many formally recognized species, even though it lacks many features that would encourage diversification, marking it as a taxonomic group in need of potential revision. The complexity of bivalve shells, such as *Astarte*, yield numerous possible landmarks, making them great candidates for a study using geometric morphometrics to discriminate species.

A morphometric analysis of 918 shells representing ten different taxa from the Pliocene of the Atlantic Coastal Plain was conducted. A total of nine homologous landmarks and five pseudo-landmarks were collected from scaled digital photographs. Procrustes transformation and Principal Components Analysis (PCA) were performed on the collected dataset. PCA was also performed on allometric residuals and outline harmonics to fully understand the variability of morphologies present.

All PCA results show large amounts of overlap between all species. *Astarte concentrica* and *Astarte undulata* exhibit the most morphological variation and encompass all possible shape variants present within this study. These two species were most likely “trash bins” in which unknown specimens have been dumped throughout the years and suggest there are species within *Astarte* that should be synonymized.

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INTRODUCTION

The range of environments and diverse faunal assemblages, both fossil and extant, recorded by Atlantic Coastal Plain sediments has allowed this physiographic province to be used as a natural laboratory by paleontologists. The latitudinal extent of the Atlantic Coastal Plain, which stretches along the East Coast of the United States from New York to Florida, means the physiographic province experiences a large range of climate variability, both in the recent and throughout its geologic past. In addition to its latitudinal range, this area of the early Atlantic Ocean was heavily influenced by numerous environmental disturbances, such as the expansion of continental glaciers in the Late Pliocene (Shackleton et. al., 1984; Stanley, 1986) or the emergence of the Central American Isthmus and subsequent changes in ocean circulation (Allmon, 2001; Lessios, 2008). These environmental disturbances and the episodes of biotic turnover which they caused have been used to test a wide range of hypotheses about various environmental and ecological effects. For example, Saupe et. al. (2014) measured the response of economically important shellfish to climate change and tested for niche evolution in the form of expanded thermal tolerances, while others have evaluated biotic interactions between predators and prey in order to determine their influence on evolutionary dynamics (Kelley and Hansen, 2006; Casey et. al. 2015). However, to make use of the wide ranging environmental circumstances the Atlantic Coastal Plain provides, paleontologists need reliable taxonomies to tackle evolutionary and ecological questions in a rigorous and reliable manner (Cavender-Bares et. al., 2009)

One taxonomic group in potential need of taxonomic revision is the bivalve genus *Astarte*. *Astarte* appears mostly in Mio-Pliocene age (2.5-5.3 Ma) sediments within the Atlantic Coastal Plain but does have extant species found in higher latitudes (Saleuddin, 1965). *Astarte* are commonly recognized by their concentric ridges along the external shell surface which helped to sustain their life position from potential disruption. Depending on their symmetry, these ridges allowed the bivalve to grip the sediment to prevent backward rotation and re-burrow rapidly after becoming exposed or helped to reduce scour of sand around the burrow if the bivalve became partly exposed (Stanley, 1981). The ridges were likely exapted (*sensu* Gould and Vrba, 1982) to defend against predatory drilling and durophagous predators (Klompmaker and Kelley, 2015). *Astarte* is a non-siphonate, shallow infaunal, filter-feeder, with only a single point of fusion separating the inhalant and exhalant currents (Stanley, 1968). This mode of life places them directly adjacent to the sediment-water interface (Figure 1). These primitive features relegate *Astarte* to subtidal environments, as they could not handle high-energy conditions that are typical within the intertidal zone (Stanley, 1968).

Stanley (1968) noted this lack of adaptations kept the genus from diversifying extensively. Despite this apparent lack of diversification, numerous species have been formally named. The morphologically similar Pliocene-aged specimens are often reported as separate species, while anecdotal evidence suggests these species lack any true morphological distinction. Chrpa and Oleinik (2015) reported variants within living and Pliocene fossil populations of *Astarte borealis* that show gradational morphological variation, with numerous intermediate forms that are not necessarily distinct species. Glassburn (1995) examined the temporal shape variation of eight Early to Late Miocene bivalve species, three of which were *Astarte*. Within *Astarte*, there was a shift from cuneiform (wedge) shapes, where the length from anterior to posterior was larger than the width from the beak to the commissure, to trigonal (triangular) shapes, where the width from beak to commissure was slightly larger than the length from anterior to posterior, with a range of intermediate forms between the two end members.

Smith (1994) stated that species within paleontology are typically named by "minimal morphological clusters of individuals...". This means most paleontological species are merely "morphospecies" and do not always match the kind of taxonomic resolution that can be achieved with molecular data. However, Kowalewski et. al. (1997) demonstrated taxonomic resolution similar to that achieved with molecular data is possible using geometric morphometrics, even in the absence of morphological complexity. The authors examined lingulide brachiopods, which lack many morphological landmarks. They could correctly identify species using morphometric methods that closely matched species characterized with molecular data. In comparison to these biometric simpletons, *Astarte* yields numerous landmarks, making the genus a great candidate for a study using geometric morphometric analysis to reliably identify morphospecies.

The purpose of this study is to use geometric morphometrics to evaluate the hypothesis that there is a lack of true morphological separation between species within the genus *Astarte*. The lack of diversification and reported gradational forms within the genus suggests it likely only possesses a few legitimate species, and much of the variability that has been interpreted as separate species is gradational variation within only a few species. The hypothesis will be supported if large amounts of overlap are present between species within the PCA-defined morphospace. Morphospace refers to the display of potential shapes on a resulting graph, where each point within the morphospace represents an individual specimen. However, if there is separation between species, the hypothesis will be rejected. This will offer a clearer understanding of definable species within the genus, as well as highlight easily identifiable characters to aid in the identification of valid species or suggest possible taxonomic revisions.

METHODS

Scaled photographs of *Astarte* from collections within the Florida Museum of Natural History were taken for the analysis. The geometric morphometric methodology similar to Kowalweski et. al. (1997) was followed. Landmark data were collected for each *Astarte* specimen using ImageJ ver. 1.50i (Schneider et. al., 2012). Landmarks are commonly used in geometric morphometrics since they are “specific points on a biological form that are chosen according to some rule” (MacLeod, 2013). MacLeod (2013) described three types of landmarks. Type I landmarks are those which are chosen based on homology provided by biologically unique patterns (e.g., juxtaposition of two or more features). Type II landmarks are points chosen based on homology provided only by geometric criteria, and Type III landmarks are those which are “deficient” because their location is dependent on the location of other landmarks. Nine geometric landmarks (Type II) were chosen because they are homologous within all specimens of *Astarte*. Five pseudo-landmarks (Type III) were chosen along the outline of the specimens (Figure 2). To make landmark collection more robust and easily repeatable between all specimens, three lines were added to each individual shell image. Line A starts with landmark 1 and was extended to the ventral margin bisecting the space defined by landmarks 3 and 4. Line B also begins at landmark 1 but is extended straight down to the ventral margin to capture variation along the anterior of the margin. The resulting angle created by the two lines beginning at landmark 1 measures 20°. These lines were used to define the location of landmarks 13 and 14. Line C is defined by landmarks 6 and 8 and was extended to the lateral margins to identify the location of landmarks 11 and 12. The landmarks were collected on both left and right valves, but to maintain uniformity all right valves were mirrored before landmarks were collected.

Procrustes transformation was performed on the resulting landmark data, which aligns and resizes all specimens using translation, rotation, and uniform scaling to be directly comparable. Since it allows for the projection and analysis of a multivariate dataset down to a few dimensions in a way that preserves as much variance as possible, Principal Components Analysis (PCA) was then ran on the resulting Procrustes transformed coordinates. To assess the impact of allometry, PCA was also performed on residuals calculated from a linear regression analysis that used the centroid size provided by the Procrustes transformation and the Procrustes transformed X-Y coordinates. All analyses were performed with R 3.4.0 (R Core Team, 2017) using R Studio 1.1.423 (RStudio Team, 2016).

An outline analysis was performed on all specimens using SHAPE ver. 1.3, a software package for Quantitative Evaluation of Biological Shapes Based on elliptical Fourier descriptors (Iwata and Ukai, 2002). The variation in outline shape is characterized by Elliptic Fourier descriptors (EFDs), which were created by decomposing a curve into a sum of harmonically related ellipses (Kuhl and Giardina, 1982). The EFDs were used to find the principal components of shape variation. Following the procedure in Iwata and Ukai (2002), the coefficients of the EFDs were calculated such that the score for any principle component is equal to +2 or -2 times the standard deviation from the mean. These coefficients were used to create contour shapes to visually represent the data. The visual output is useful in interpreting the variation associated with each principle component.

Convex hulls (the smallest shape that contains all points within a subset of data) were used on all PCA results to approximate the area occupied by each species. Separate images were created for each convex hull within the three PCA graphs. These images were then used to calculate the overall percentage of morphospace occupied by each species. Pairwise Mahalanobis distances were also calculated for all PCA results (Table 1). Mahalanobis distances calculate the centroid of each species' distribution, then measure the distance between the calculated centroids of each distribution. This allows a comparison of each pairwise set while maintaining the variance of each variable and the covariance between variables, allowing the distance between species' morphospaces to be measured while still accounting for the multidimensional space and scale being measured within PCA.

RESULTS

A total of 918 individual valves were measured. All specimens of *Astarte* were Pliocene-aged and collected from five states within the Atlantic Coastal Plain (Virginia, North Carolina, South Carolina, Georgia, and Florida; Figure 3). The specimens represent ten different taxa, including one sub-species (*A. concentrica, A. deltoidea*, *A. floridana, A. floridana leonensis*, *A. glenni*, *A. leonensis, A. perplana*, *A. symmetrica, A. undulata*, *A. vaughani*; Table 2*)*. Principal Component (PC) 1 and PC 2 resulting from the landmark-only PCA analysis account for 51.5% of the overall variation (Figure 4). Typically, in a study such as this, PC 1 would capture any variation due to size. However, Procrustes transformation removes any size influence, so the variation noted is variation in shape only. The resulting graphs display the range of morphologies exhibited by the species studied. Each axis corresponds to a combination of variables that numerically describes the shape of the organism.

Astarte concentrica and *Astarte undulata* occupy 69.6% and 59.4% of the total morphospace respectively, with some overlap. These two species have the highest intraspecific shape variation. The other species, especially *A. floridana, A. deltoidea, A. floridana leonensis,* and *A. leonensis* fall within the broad overlapping species-morphospace of *A. concentrica* and *A. undulata.* These species show a smaller intraspecific variation than what is present in *A. concentrica* and *A. undulata*. *A. floridana* and *A. deltoidea* only occupy 33.7% and 32.9% of the total morphospace respectively, showing there is a large division between those species with high intraspecific shape variation and those with low intraspecific shape variation. None of the remaining species occupy more than 30% of the overall morphospace. Mahalanobis distance values (Table 1) show very small distances between all of these various species. Results of the PCA performed on linear regression residuals yielded similar results (Figure 5). The smallest individual species morphospaces increased in size, thus increasing the amount of overlap of all species. For example, *A. floridana* only occupied 33.7% of the total morphospace from the landmark-only PCA results, but then increased to occupy 90.4% of the total morphospace from the linear regression PCA.

In the outline analysis, PC1 and PC2 account for a combined 66.5% of overall variation (Figure 6). *A. concentrica* and *A. undulata* once again show little to no separation and occupy 63.8% and 74.4% of the total morphospace respectively. As in the previous analyses, the remaining species fall within the overlapping convex hulls of *A. concentrica* and *A. undulata.* However, several of the species with small total morphospace occupation show separation from one another. For example, *A. floridana leonensis* shows no overlap with *A. deltoidea* nor *A. symmetrica.* However, there are no species that fall outside of the morphospace occupation defined by the convex hull overlap of *A. concentrica* and *A. undulata*.

DISCUSSION

There is evidence of extensive morphological overlap between all species analyzed. The small Mahalanobis distances between taxa, large amounts of overlap of the convex hulls, and high intraspecific variation present in each analysis support the hypothesis that *Astarte* lacks true morphological separation between species. *Astarte concentrica* and *A. undulata* possess the highest amounts of morphological variation indicating that they have many morphological variants, showing not only intermediate forms between species, but also showing specimens with very similar shapes to all the other named species. The species of *Astarte*, excluding *A. concentrica* and *A. undulata*, have been seen as different enough to be named as separate species. These remaining eight species have much lower intraspecific variation and some morphological separation as indicated by the smaller, non-overlapping convex hulls present in the outline PCA analysis (Figure 6). This difference in outline shape may mean that they represent true monophyletic groups; although, whether those monophyletic groups represent species or sub-species remains to be determined.

Diagnosable morphological characteristics have always been used to recognize and differentiate species (Sokal & Crovello, 1970). Within paleontology, empirical observations of phenotypic traits (morphology) have been the only practical method for identifying species (Smith, 1994). Individuals within a single species can often have varying morphologies. These different appearances are commonly driven by environmental stressors, causing the individuals to develop ecophenotypes, or morphologies that result as a function of their environment. Ecophenotypic variation usually results in several intermediate morphologies being represented within a single species. In particular, paleontologists rely on these intermediate morphologies within co-occurring taxa to identify different morphotypes as belonging to a single species, in an effort to achieve a similar resolution to true biological species (Benton and Pearson, 2001). Outline shape and external ridge structure are often used to describe specimens within *Astarte* (Conrad, 1834). Subtle differences in outline shape were revealed between the low-intraspecific taxa examined in this study. Seeing variation in outline shape, previous studies identified each variant as a new species instead of assigning them to an already established taxon, even where abundant intermediate forms were present. However, the presence of numerous intermediate morphologies calls these taxonomic divisions into question.

The outline PCA results do show some separation between species, however, none are outside the range of morphospace occupation of *A. concentrica* and *A. undulata*. This means some of the species with low intraspecific variation (specifically those showing some separation within the outline PCA morphospace) are likely monophyletic groups. The fact all eight of the low intraspecific variation taxa fall within the portion of the morphospace where *A. concentrica* and *A. undulata* overlap suggests that these groups may represent monophyletic sub-species within *A. concentrica* or *A. undulata* rather than separate species. If this is the case, all species would need to be synonymized to a small number of taxa (~1-3 species). However, it is also possible that *A. concentrica* and *A. undulata* have been used as trash-bin taxa, a species that serves as a safe taxonomic designation for unknown specimens, due to their high amounts of intraspecific variation that basically encompass every shape of *Astarte* measured. If this were the case, the small intraspecific variation species may be valid and the specimens within *A. concentrica* and *A. undulata* would need to be redistributed into the species of *Astarte* with which they share a morphology. In that case, only the two “trash-bin” species would need to be synonymized, but they would by synonymized with a range of 6-7 species. If the small intraspecific variation groups are valid sub-species within only one or two legitimate species, we would expect the convex hulls for the smaller groups to fall obviously within the broader convex hulls of the formal species to which they belong. However, if the monophyletic groups represent different species, we would expect to see clear separation of groups, and any trash-bin taxa present would exhibit all possible ranges of morphology.

A. concentrica and *A. undulata* have likely been used as trash-bins to assign unknown specimens due to their broad range of morphological variation and their presence as intermediate forms between other separate groups. These two taxa most likely need to be redistributed into the small monophyletic groups that do exhibit some separation. The Mahalanobis values for the outline PCA (Table 1) support the separation of these smaller groups. For example, *A. glenni* and *A. floridana leonensis* show higher distance values, relative to scale, within the outline PCA results than they do within the other results. When *A. concentrica* and *A. undulata* are removed from the outline PCA results it is clear the remaining taxa show some separation (Figure 7). Looking at only these results objectively it is easy for one to claim these species as different enough from one another to be legitimate species. However, it is important to remember that even though they are not present in Figure 7, *A. concentrica* and *A. undulata* still occupy the total morphospace. So, even though separation is present within the outline analysis, it is not present for any species form these two overbearing taxa.

It is possible these results could be influenced by small sample size and the addition of the external sculpture to the analysis. *Astarte concentrica* and *A. undulata* have the largest sample sizes (Table 2), which could contribute to their high intraspecific variation. The species with the lowest sample sizes do exhibit the lowest amounts of intraspecific variation and occupy the least amounts of the total morphospace. If the smallest groups were to retain low amounts of intraspecific variation with the addition of new specimens, the redistribution of *A. concentrica* and *A. undulata* would be supported. If the amounts of intraspecific variation were to increase with added specimens, we would no longer support these taxa as separate groups, but would instead support *Astarte* only possessing one or two legitimate species. Due to species within *Astarte* being hard to distinguish, it is unlikely larger numbers of these species exist. Some collections, such as those at The Virginia Museum of Natural History, are not even identified past genus, so if larger collections of these species exist, they are not currently identified. The external sculpture of *Astarte* is often used to further discriminate species but is not present in this analysis. It is possible that the external sculpture could increase the separation among groups once added. However, within a single species of *Astarte* the external sculpture usually shows as much variation as the other features included within this analysis. For example, specimens of *A. undulata* exhibit the various types of external shell sculpture present within the species pool evaluated (Figure 8). For this reason, it seems unlikely that the addition of external shell morphology characteristics would substantially change the results present herein.

Geometric morphometrics has been shown to work well when identifying congeneric species of bivalves and taxa with extremely simple morphologies. Kowalewski et. al. (1997) were able to reliably reconstruct species distinctions between groups of brachiopods that matched groupings derived from molecular data. In spite of the brachiopod’s very simple morphologies, morphometric groupings showed clear separation. *Astarte* has many more complex features than the lingulide brachiopods studied by Kowalewski et. al. (1997), so if there was morphological separation between the species in this genus these methods should provide us with a clear indication of such. Similarly, other bivalve studies have reliably distinguished species from one another when they all fall within the same genus (i.e., show minimal morphological differences). For example, Rufino et. al. (2006) were able to distinguish congeneric bivalve species reliably using outline shape. Both studies were able to show separation between species when using similar methods to this study. However, there is no separation of *Astarte* species that is exhibited in any PCA morphospace in this study, meaning the taxa within this study are not likely valid species within *Astarte*.

CONCLUSION

A clean taxonomy allows paleontologists to better understand and answer evolutionary and ecological questions (Cavender-Bares et al., 2009). The Atlantic Coastal Plain is often used as a natural laboratory for paleontologists (Kelley and Hansen, 2006; Saupe et al., 2014; Casey et al. 2015), and such studies could greatly benefit from a clean taxonomy. The overall lack of morphological separation between *Astarte* species in each morphospace analysis shows that *Astarte* needs to be taxonomically revised. The slight amounts of separation present within the outline PCA suggest some of the species with low intraspecific variation are likely sub-species within the larger "bins" of *Astarte concentrica* and *A. undulata*. A taxonomic revision of *Astarte* would allow any study using *Astarte* to be conducted in a more rigorous and easily repeatable manner.

Larger sample sizes for species with low intraspecific variation would allow a fuller understanding of sub-species variation within this genus. If the large division between species with high intraspecific variation (such as *A. concentrica*) and the species with low intraspecific variation (such as *A. glenni*) is robust to the addition of new material, then we know those smaller species should remain as sub-species. However, if that pattern does not hold, we know we only have a few legitimate species within this genus that exhibit high amounts of variation within their morphology.

TABLES

Table 1. Pairwise Mahalanobis distance values. Shaded area represents outline PCA results (multiplied by 1000); unshaded area represents landmark-only PCA results.

	A. con	*A. delt*	*A. flor*	*A. flor. leo*	*A. glen*	*A. leo*	*A. perp*	*A. symm*	*A. und*	*A. vaugh*
A. concentrica		6.70	2.70	9.80	4.10	2.80	3.00	8.90	1.90	1.70
A. deltoidea	4.62		3.90	8.50	9.80	4.60	5.70	3.80	2.20	6.00
A. floridana	3.39	1.52		3.20	9.90	0.20	3.00	11.00	0.80	2.00
A. flor. leonensis	6.37	3.32	1.40		22.40	3.80	9.90	20.70	6.50	8.50
A. glenni	6.11	6.44	6.35	9.94		9.50	7.00	7.30	5.90	6.50
A. leonensis	5.95	2.75	0.92	2.94	7.48		2.50	12.10	1.00	2.30
A. perplana	3.42	1.68	0.69	2.05	5.46	2.03		11.30	2.30	2.00
A. symmetrica	4.70	5.06	6.92	11.92	10.54	7.59	6.29		6.70	11.00
A. undulata	3.38	0.64	0.81	1.82	5.25	2.54	0.85	6.46		1.60
A. vaughani	2.83	2.54	0.80	2.53	4.22	1.69	1.20	7.14	1.23	

Table 2. Specimen counts by formation and state found.

	A. con	*A. delt*	*A. flor*	*A. flor. leo*	*A. glen*	*A. leo*	*A. perp*	*A. symm*	*A. und*	*A. vaugh*
Yorktown - VA	19							19	92	
Duplin - NC	73								2	
Yorktown - NC	31							5		
Duplin/Raysor – SC					13					
Duplin/Raysor – GA									68	
Jackson Bluff – FL			117	6		19			39	
Tamiami – FL	332		25				3			2
Unknown		34					4	10	2	3
Total	455	34	142	6	13	19	7	34	203	5

FIGURES

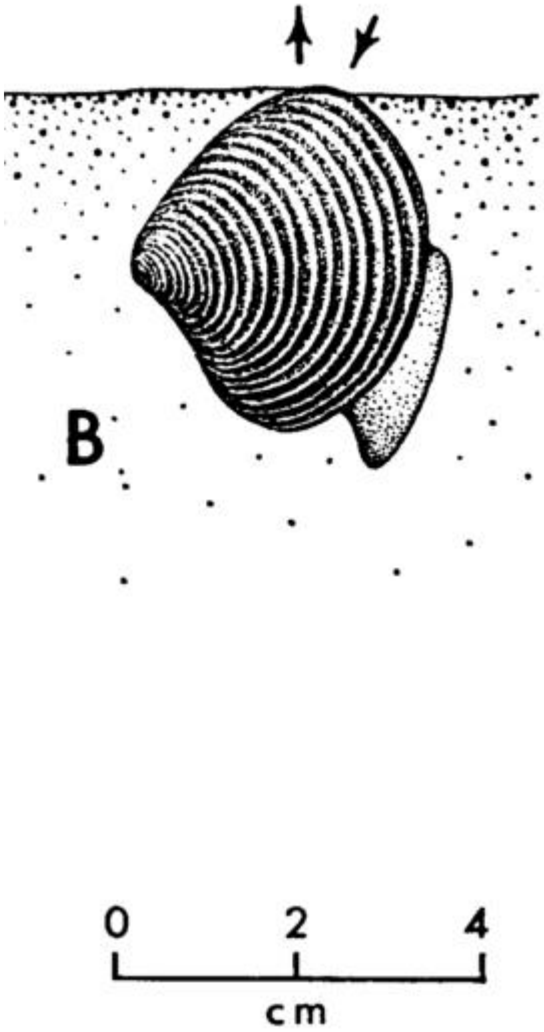

Figure 1. Inferred life position of *Astarte*. Modified from Stanley, 1968.

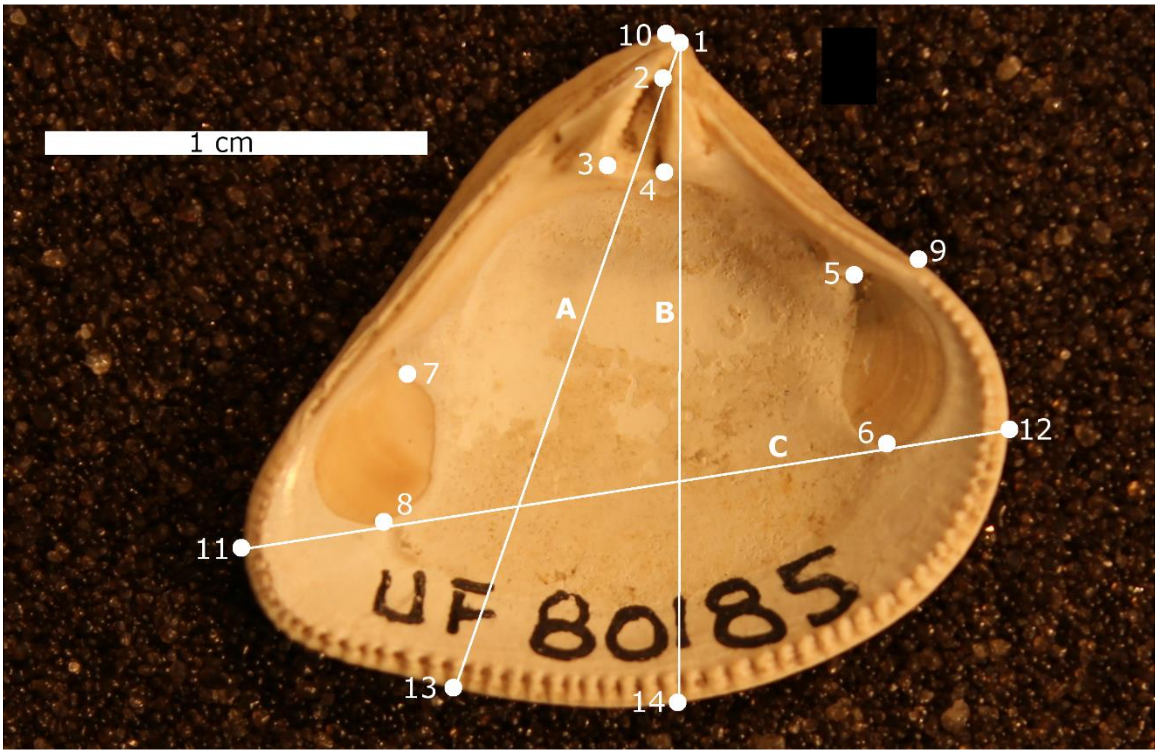

Figure 2. Landmarks used in this analysis. Homologous landmarks (1-9): 1. Beak, 2. Top of cardinal teeth/socket, 3. End of posterior cardinal teeth, 4. End of anterior cardinal teeth, 5. Top of anterior adductor muscle scar, 6. Junction of anterior adductor scar and pallial line, 7. Top of posterior adductor muscle scar, 8. Junction of posterior adductor scar and pallial line, 9. End of lunule. Pseudo-landmarks (10-14): 10. Dorsal maxima, 11. Posterior end of Line C, 12. Anterior end of Line C, 13. End of Line A, 14. End of Line B.

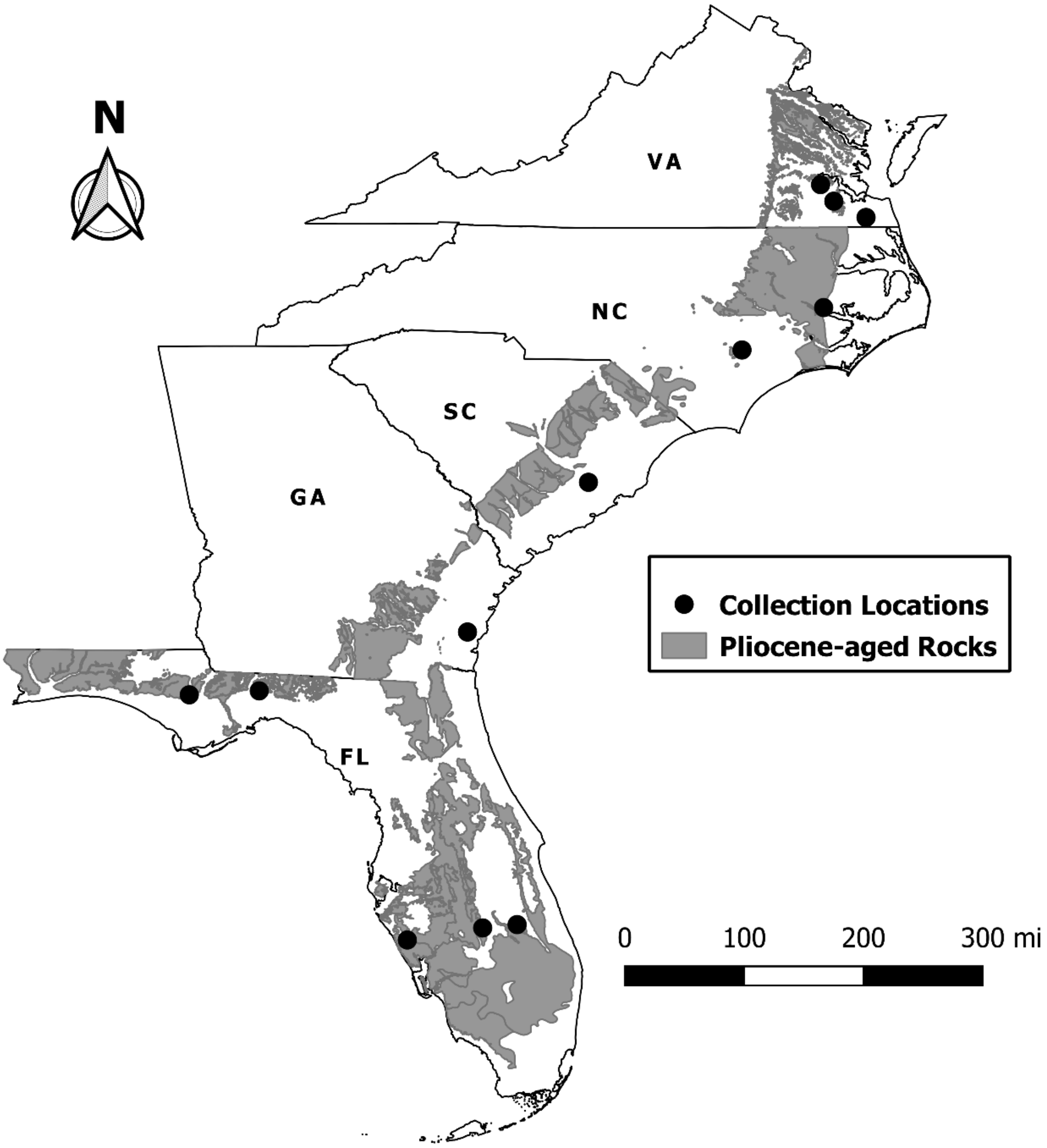

Figure 3. Map of states within the Atlantic Coastal Plain used within this study. All formations shown are Pliocene-aged. All locations marked are where specimens used in this study were originally collected.

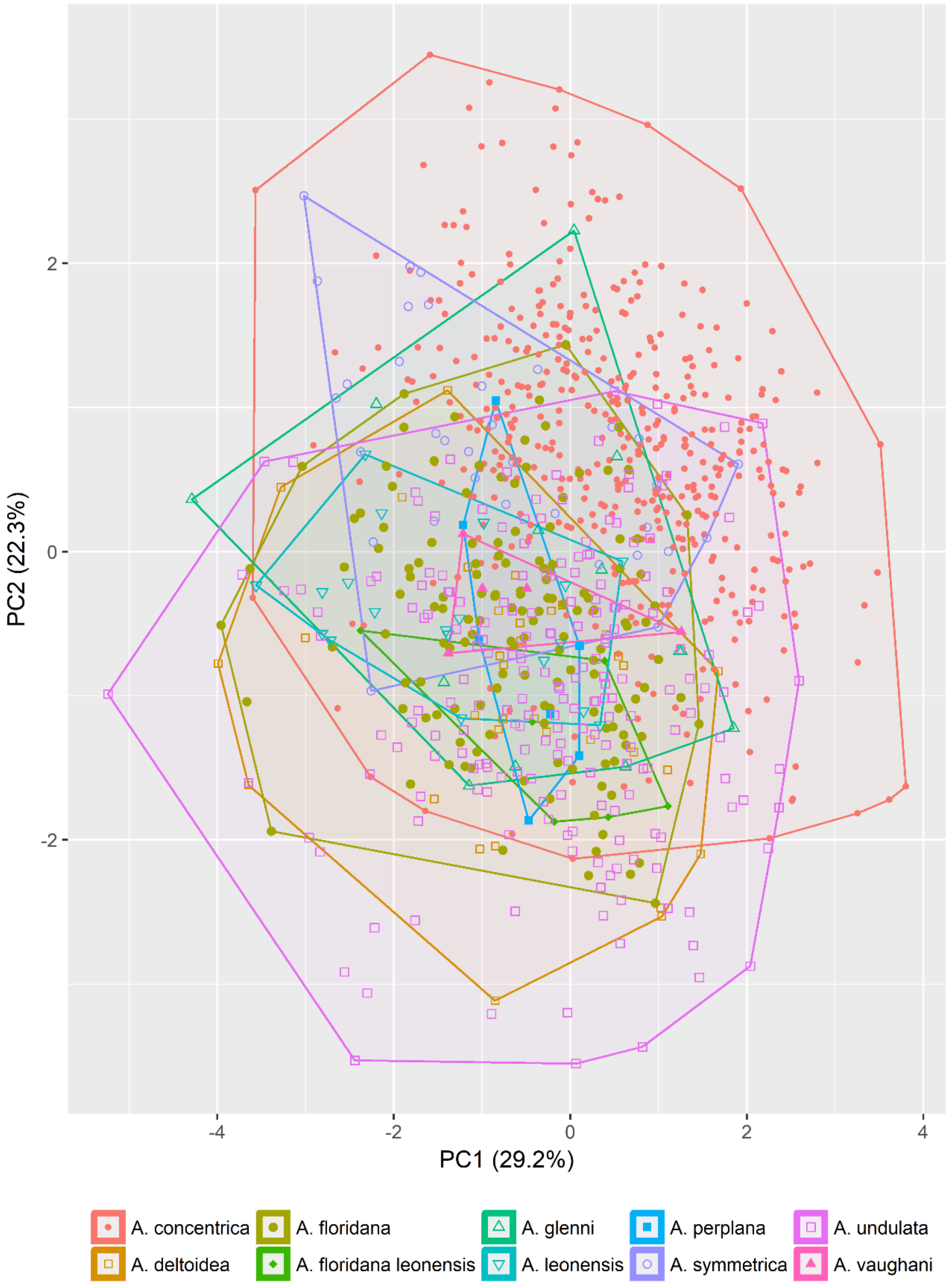

Figure 4. PCA results of landmark-only analysis. Each point represents an individual specimen. The individual species' morphospace is marked with a convex hull.

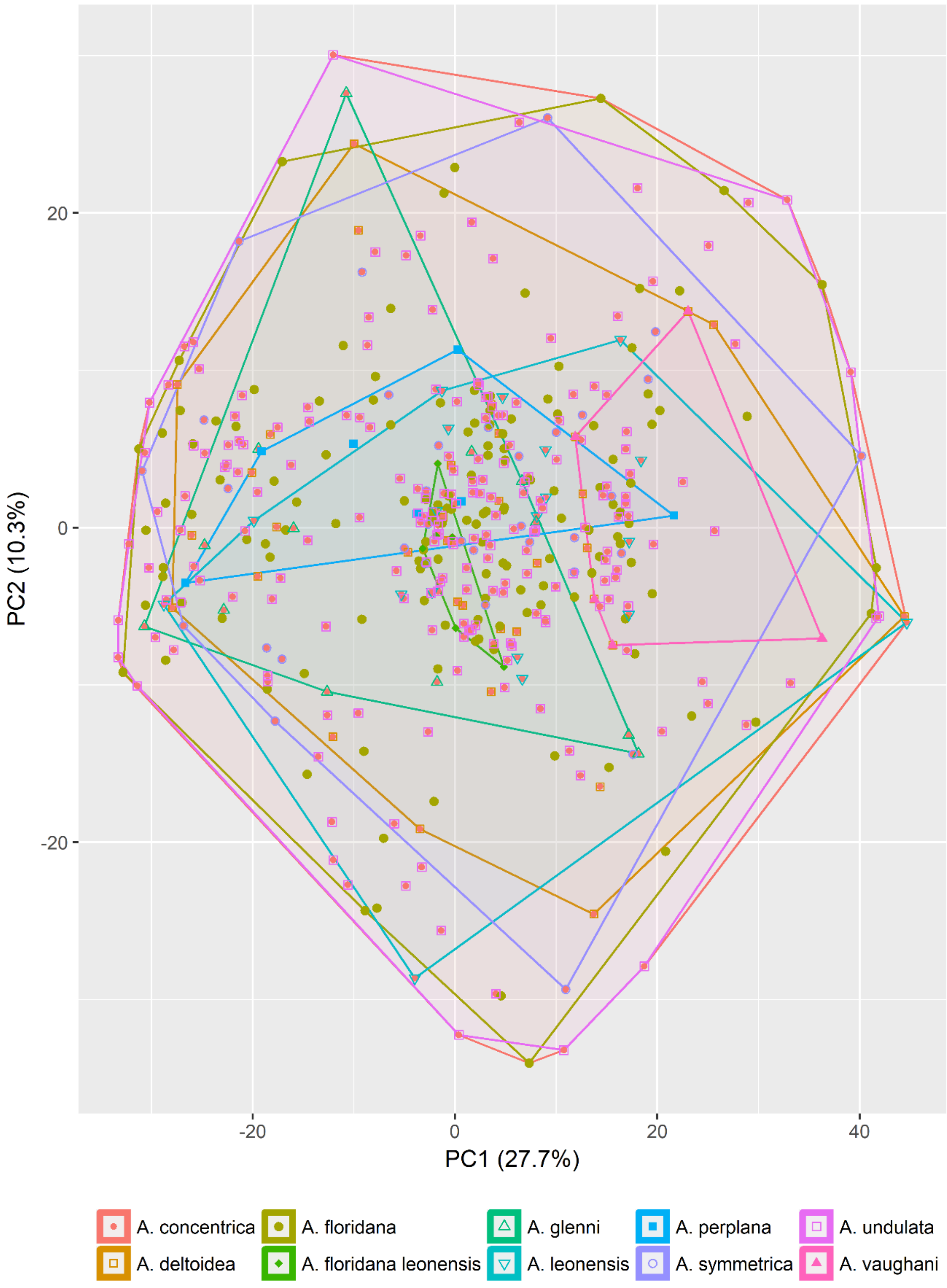

Figure 5. PCA results of allometric residuals. Each point represents and individual species, and the individual species' morphospace is represented by convex hulls.

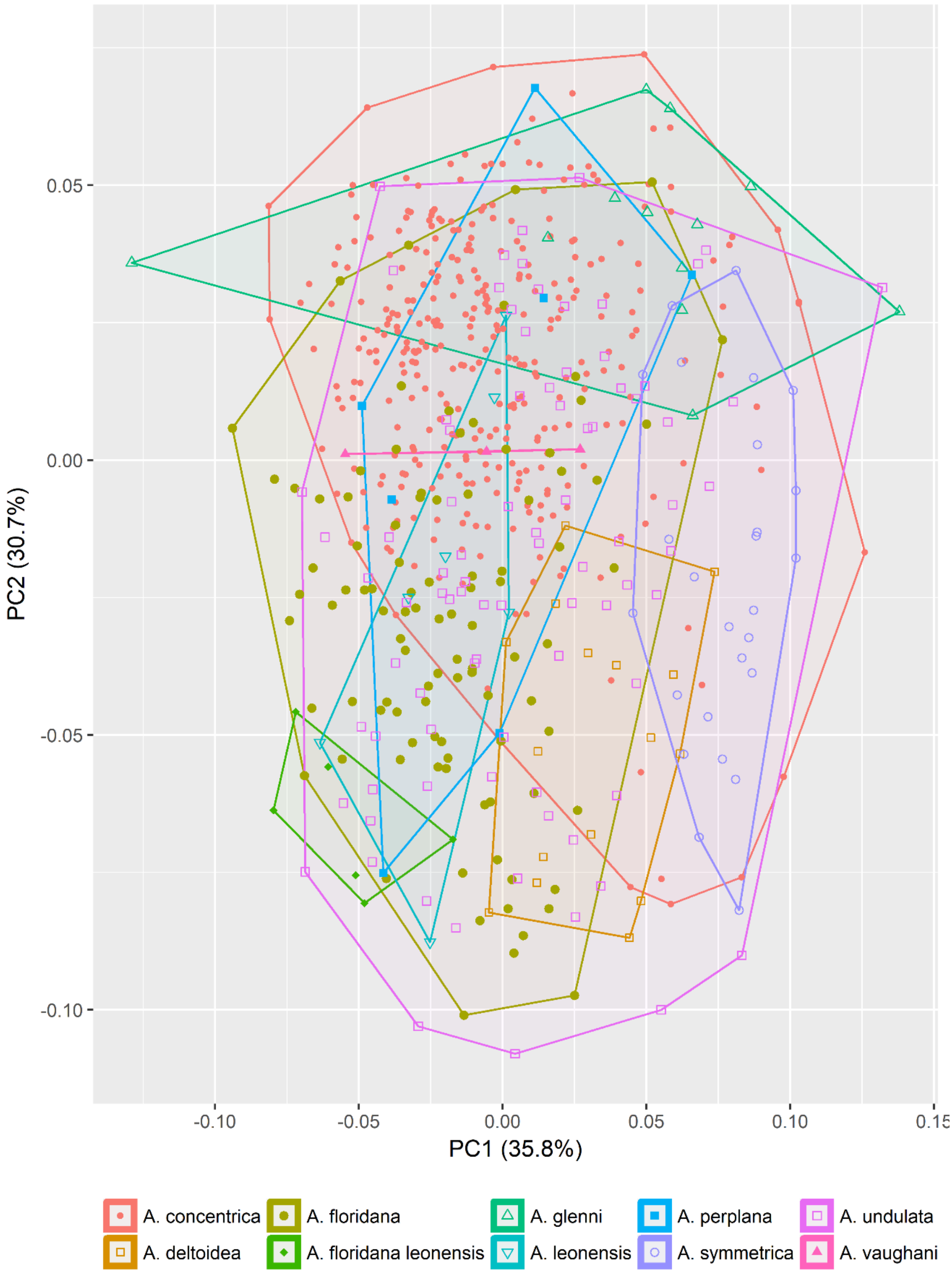

Figure 6. PCA results of outline harmonics. Each point represents an individual specimen. The individual species’ morphospace is represented with convex hulls.

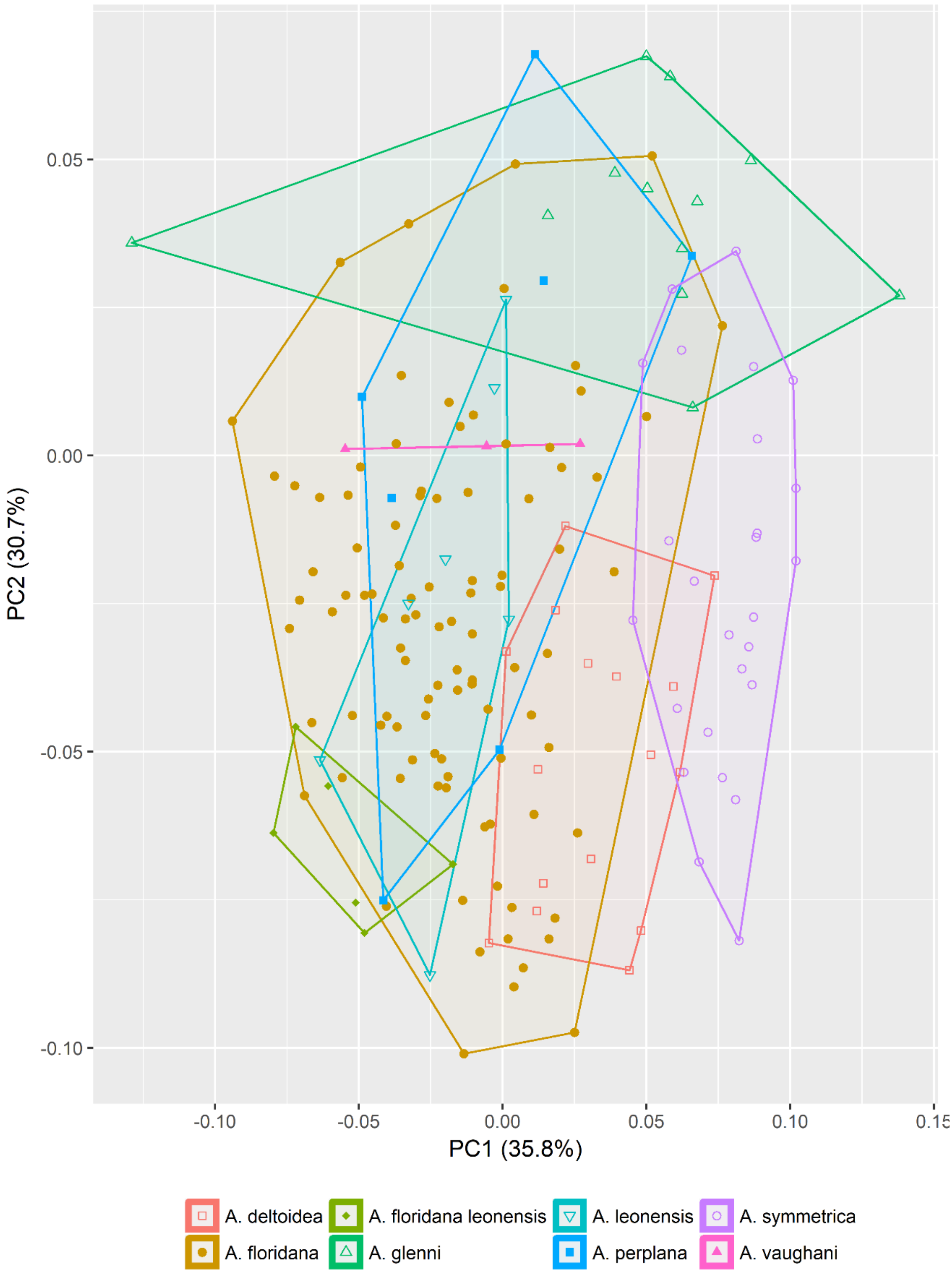

Figure 7. PCA results of outline harmonics. Each point represents an individual specimen. *Astarte concentrica* and *Astarte undulata* have been removed from the total morphospace to better illustrate the separation between the remaining taxa.

Figure 8. Four specimens of *Astarte undulata*. These four exhibit various types of external shell sculpture.

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