

Paleobiogeographical variation of Cretaceous
Mecaster batnensis and *Mecasterourneli* (Echinoidea:
Spatangoida)

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For my sister,
Chelsea Layne Sorensen
May 23, 1990 – Dec 21, 2012

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ABSTRACT

Spatangoids are the echinoid group best represented in the South American Cretaceous fossil record. This study analyzed two Cretaceous spatangoid species of the genus *Mecaster* (*M. batnensis* (Coquand, 1862) and *M. fourneli* (Agassiz, 1847)) found in South America as well as Africa, North America, Asia and possibly Europe (Smith and Bengtson 1991, Smithsonian Collection). This study assessed the paleobiogeographical variation of these species. Specimens from at least eight widely spaced localities were measured for morphometric analysis. Initial observations using length, width, and height data of *M. batnensis* and *M. fourneli* populations indicate regional differences in growth trajectories. A comparative morphometric analysis including traditional two-dimensional measurements using calipers and three-dimensional landmark measurements obtained with a laser scanner was performed. Principal component analysis and other multivariate methods identified the extent of variation between localities.

PREFACE

While pursuing this thesis project, I have frequently contemplated the sources of material for this and future projects. I have reflected on the need to mitigate sampling biases in the fossil record. I have sought information on collections that lay untouched in museums. I have learned about the value, and challenges, of collaboration. And I have even contemplated, as part of my future career, the potential of educating my own network of future collaborators from regions where little work has been done.

Echinoids have a dense fossil record and generally are well preserved; however, because of geographic sampling bias, the known fossil record of echinoids mostly records North American and European patterns (Smith 2007). The simple solution to correcting this bias is to collect samples in under represented areas, but to do so one must navigate the politics of local law and local academic climates. Many foreign samples previously collected are not currently located in the originating country, but rather in museums in Europe and North America. In starting this study I found that often fossils from many South American countries are not found in museums within the country of origin but at foreign institutions (personal communication del Rio 2012) - the Smithsonian Institution National Museum of Natural History (USNM) being one of these “foreign” institutions. In some conversations with curators of museums in various countries there was evident resentment that type specimens from their countries were not part of their collections, but were rather parts of collections outside of their countries.

For this current project I have used the collections at the Smithsonian Institution National Museum of Natural History (USNM). The samples come from many sources. Some were collected by curators of the museum; others were donated by collectors; while further

samples were initially sent in as inquiries from assorted businesses and government agencies regarding identity and later donated. One set of samples used in this study were from the Harvey Bassler collection of Peruvian fossils. The samples were collected by Bassler in excursions up and down Amazonian tributaries through the rain forests of Peru in the 1920's (Willard 1966). He donated the collection to Lehigh University upon his death, and later Lehigh University donated the collection to the USNM. Other than the volume describing the general contents and collection localities of the Bassler collection (Willard 1966), I am unaware of any other published use of echinoderm specimens from this collection until this current study.

The Bassler collection is not the only collection sitting in drawers in museums not being studied. Personal conversations with curators at other museums have informed me of collections from under represented regions that have yet to be processed, and literature searches have led me to knowledge of echinoid collections that have only cursorily been identified as either regular or irregular (e.g., Weidemeyer 2007). In future research I hope to utilize these unused resources, but for now, as part of this thesis project, I am pleased to utilize the general USNM collection and a portion of the Bassler collection.

Many countries have in recent decades enacted or begun to enforce legislation to preserve their paleontological and archeological heritage. While some of these laws prove problematic to navigate, collaboration with local scientists can ease the process and has potential to be fruitful. A recent field excursion with my advisor, Colin Sumrall, to Argentina demonstrated to me the potential of such collaboration. We went to an area that has been thoroughly studied by stratigraphers over the past 150 years, and experts on trilobites, brachiopods, and sponges have regularly published on fauna, including new species, from the area. Echinoderms, on the other

hand, were little known and only mentioned in a few publications - and generally in passing. The few echinoderm workers in Argentina focus on other time periods and/or crinoids, so Colin's expertise was desirable to his collaborators. Collaboration with a local expert on sponges, Marcelo Carrera, allowed us to go to localities that otherwise would have been challenging to find and understand. The paleontological success or failure of the trip is Colin's to report in the future; however, the collaborative success of the trip set a precedence that I hope to follow in my future research.

This thesis project is the start of a career that I hope includes much more research, but I hope my career is also filled with educating future paleontologists. As I pursue my goals in research I hope that some of those paleontologists who I may have the opportunity to educate are students from regions where understanding of the fossil record needs to improve. While somewhat idealized, if these opportunities do occur, I hope that work in those regions of the world results in local pride of both the individuals involved in the research as well as preservation of the local paleontological heritage.

The full extent of these issues will not be resolved through the work of this study alone, but I hope this study is an acceptable contribution. Through this study I seek to improve the knowledge and understanding of the African and South American fossil records in conjunction with the record of North America. In so doing I utilize a new application of three-dimensional landmark morphometrics in paleobiogeography of some spatangoid echinoids (Chapter II), and consider how these techniques may allow the testing of larger evolutionary hypotheses in future research (Chapter III).

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CHAPTER I INTRODUCTION AND GENERAL INFORMATION

Introduction

This thesis project seeks to increase understanding of the Cretaceous record of South American and African fossil echinoids by assessing morphometric change in echinoid morphospace relative to the proximity of basins during a vicariance event (i.e., the break-up of Pangea). Spatangoid echinoids of the genus *Mecaster* are ideal for this study because they are common fossils that occupied the continental shelves of North America, South America, Africa, India, and Europe during the Late Cretaceous - a time of vast global changes in the positioning of the continents. *Mecaster batnensis* and *M.ourneli* are found in a subset of these continents from the Cenomanian through the Campanian (100 Ma - 72.1 Ma). The change in shape of these two species will be assessed using traditional two-dimensional morphometrics and a new application of three-dimensional landmark morphometrics.

General Background

Echinoids - sea urchins, sand dollars, heart urchins, sea cookies, and sea biscuits - are a clade of echinoderms that are common components of marine faunas since the Ordovician. The group crossed the Permo-Triassic extinction (251 Ma), and the surviving lineage diversified greatly during the Jurassic. Eventually 174 families of echinoids descended from within this post-Paleozoic lineage (Kroh and Smith 2010). The Jurassic diversification of echinoids coincided with the break-up of Gondwana, and further diversification, especially within the spatangoids continued during the Cretaceous.

Break-up of Gondwana in the Cretaceous

The Cretaceous was a time of vast global changes. New basins and seaways opened up as the continents separated and sea levels increased (Néraudeau and Mathey 2000). These changes provided opportunities for the isolation of species and other opportunities for species to spread; in both cases new species could evolve. Echinoids are one group of marine organisms that took advantage of these new pathways and basins. At the start of the Cretaceous Laurasia was fully separated from Gondwana because the Tethys Ocean on the eastern portion of Pangea had spread across the rifting boundaries of Gondwana and Laurasia during the Triassic. By 180 Ma, in the Jurassic, the western portion of Laurasia had separated from Gondwana forming what would become the North Atlantic Ocean, and Antarctica and Australia, moving as one unit, had separated from Gondwana. The separation of South America and Africa occurred in the Cretaceous over a span of 40 Myr beginning with the opening of the South Atlantic at the Alulhas Basin around 142 Ma (Néraudeau and Mathey 2000). India pulled away from the eastern margin of Africa around 120 Ma providing more direct pathways from the Tethys Ocean to the widening South Atlantic.

Echinoids from the Tethys Seaway made their way into the growing South Atlantic by circling Africa and passing between Africa and Madagascar (Néraudeau and Mathey 2000). The connection between South Atlantic and equatorial Atlantic water did not occur until the Late Albian (~100 Ma) (Eagles 2007), allowing western Tethyan fauna to spread into the South Atlantic (Néraudeau and Mathey 2000; Figure 1A). Along the western seaboard of South America there was flooding at various intervals forming epicontinental seas over Colombia, Ecuador, and Peru; the Andean Basin over part of Chile, Bolivia, and western Argentina; and the Magallanes Basin over Patagonia. Echinoid taxa occupied the epicontinental seas throughout the

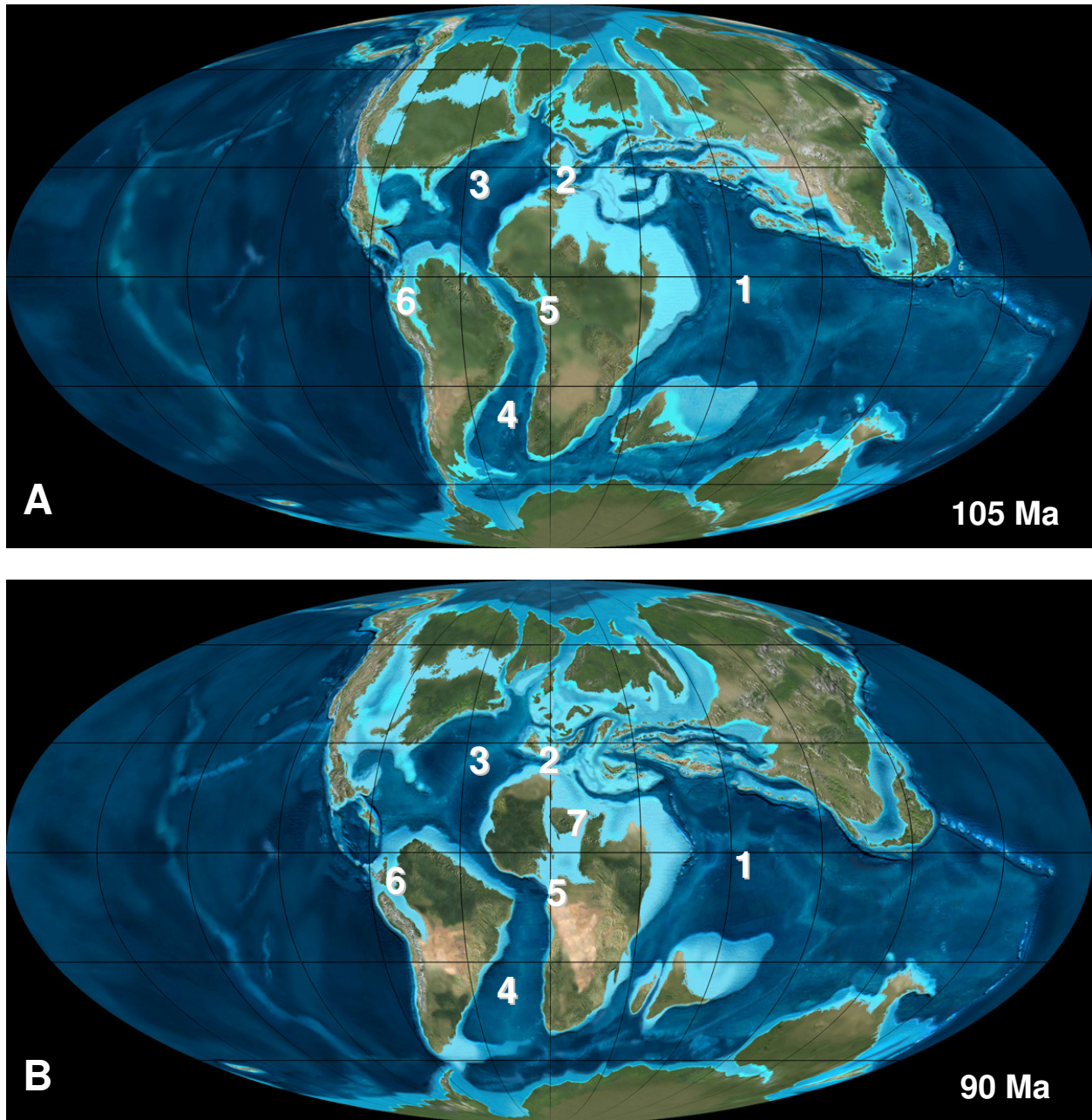


Figure 1. Global maps of the late Early Cretaceous and Late Cretaceous.

The locations of features discussed in the text include the Tethys Ocean (1), Tethys Seaway (2), Western Tethys (3), South Atlantic (4), Benue Trough (5), South American epicontinental seas (6), and the trans-Saharan seaway. Note the absence of the trans-Saharan seaway in the late Early Cretaceous (Figure 1A) and the presence of the seaway in the Late Cretaceous (7; Figure 1B). The trans-Saharan seaway was open during the late Cenomanian and early Turonian. It closed by the mid-Turonian and reopened in the Maastrichtian. (Maps from Ron Blakey, NAU Geology)

Aptian and the rest of the Late Cretaceous. The failed third branch of the rifting between South America and Africa formed the Benue Trough which completed the connection of the trans-Saharan seaway with the South Atlantic. Following the opening of the Equatorial Atlantic Gateway in the late Albian, the South Atlantic was connected to the Western Tethys via the trans-Saharan seaway and the Benue Trough during the late Cenomanian and early Turonian (Néraudeau and Mathey 2000). The trans-Saharan connection to the Mediterranean Tethys closed up by the mid-Turonian and reopened in the Maastrichtian.

Spatangoids

Echinoids are divided into two groups - regular echinoids which generally have pentaradiate symmetry, large spines, and the periproct (or anus) positioned atop the test within the apical system, and irregular echinoids in which the test has a superimposed bilateral symmetry, small spines, and the periproct positioned on the side of the test outside the apical system (Smith and Kroh 2011). As a whole, regular echinoids are epifaunal grazers, whereas irregular echinoids are infaunal deposit feeders or occasionally suspension feeders.

Within the irregular echinoids, spatangoids are part of the clade Atelostomata, diagnosed by a generally small peristome lacking buccal notches and ambulacra with differentiated tube-feet and pore-pairs which can form both phylodes and petals (Smith and Kroh 2011).

Atelostomates also have the posterior interambulacral zone on the oral surface differentiated into a plastron (Smith and Kroh 2011). Spatangoids are differentiated from other atelostomates by having an amphisternous plastron - where the labral plate is followed by an enlarged pair of sternal plates, and ocular plates II and IV are exsert such that the four genital plates abut (Smith and Kroh 2011). Other differences in the plastron and apical system are used in classifying clades within Spatangoida. Petal length is used to further differentiate genera and species in

current classifications. Spatangoids evolved as burrowers (Kier 1982), and as such acquired various shapes for burrowing, including the wedge shape found in hemiasterids (Kanazawa 1992) and in the genus *Mecaster*.

Spatangoids are thought to have originated from a circum-Mediterranean center (Smith 1984). From this “center of endemism” they spread at different times to South America and Africa. Some species came to South America after establishing themselves in the Western Tethys; thus many species in South Atlantic basins of Africa and South America are found in the Caribbean and in North America. Other species came directly from the Mediterranean via pathways through and around Africa. Zoeke (1951) demonstrated regional differences in Hemiasterid echinoids relating to regional environments. *Hemiaster fourneli* (= *Mecaster fourneli*) and *Hemiaster similis* exhibited differences in petal length and number of ambulacral pores in direct relationship to the climate of the region these species inhabited. *Hemiaster fourneli* inhabited the warmer circum-Mediterranean region and had more ambulacral pores and longer petals, while *H. similis* inhabited the cooler Northern Europe region and has fewer ambulacral pores and shorter petals. Variation in the *Micraster* group spatangoids was sufficient to allow Stokes (1975) to establish faunal provinces throughout Europe. Furthermore, in the South American fossils of the genus *Mecaster* changes in test roundness and pore pair density in the ambulacra allowed for potential stratigraphic correlation of samples from unknown stratigraphic position (Smith and Bengtson 1991).

Spatangoids are common during the Late Cretaceous, are well preserved, and are known across a broad geographic range, making them ideal for use in this study. In a synthesis of Cretaceous fossil echinoids from South America (Roney et al. 2012) distinct trends in distribution and preservation of echinoids were identified. All echinoid groups show a temporal

trend toward high diversity in the mid-Cretaceous. Spatangoid apparent diversity is consistently higher than in other clades (Figure 2). South American basins almost always have spatangoid species (Appendix 1A), and individual spatangoid species are also frequently known in more localities outside South America than species of other groups (Column 3, Appendix 1B).

The relatively dense spatangoid record probably results from the greater likelihood of preservation of irregular echinoids over regular echinoids. Kier (1977) reasons that regular echinoids, which are epifaunal, are poorly preserved because their tests are exposed to currents and scavengers, whereas irregular echinoids, and especially spatangoids, are typically infaunal and already buried at death. Further aiding irregular echinoid preservation is the smaller apical system which is more tightly sutured to the test than with regular echinoids. Irregular echinoid deposit feeding life mode causes the gut to be filled with sediment at death and keeps the test from floating out of the sediment in which it is buried. Furthermore, the sediment fill in the gut provides postmortem structural stability as sediment deposits build up on top of the buried tests (Kier 1977). Finally, regular echinoids typically live in environments of active erosion, while irregular echinoids, as deposit feeders, live in locations of active deposition, further increasing the likelihood of burial and preservation (Smith 1984).

Background on the genus *Mecaster*

The group chosen for this study is the spatangoid genus *Mecaster*. This group was chosen based on its prevalence in the fossil record (e.g. Roney et al. 2012), the numerous affinities of *Mecaster* species with Africa, North America and Europe (Maury 1936, Manso 2006, Smith and Bengtson 1991, Néraudeau and Mathey 2000, Manso and Andrade 2008, Benavides-Caceres 1956, Willard 1966), and the availability of a large collection of *M. batnensis* and *M. fourneli* at

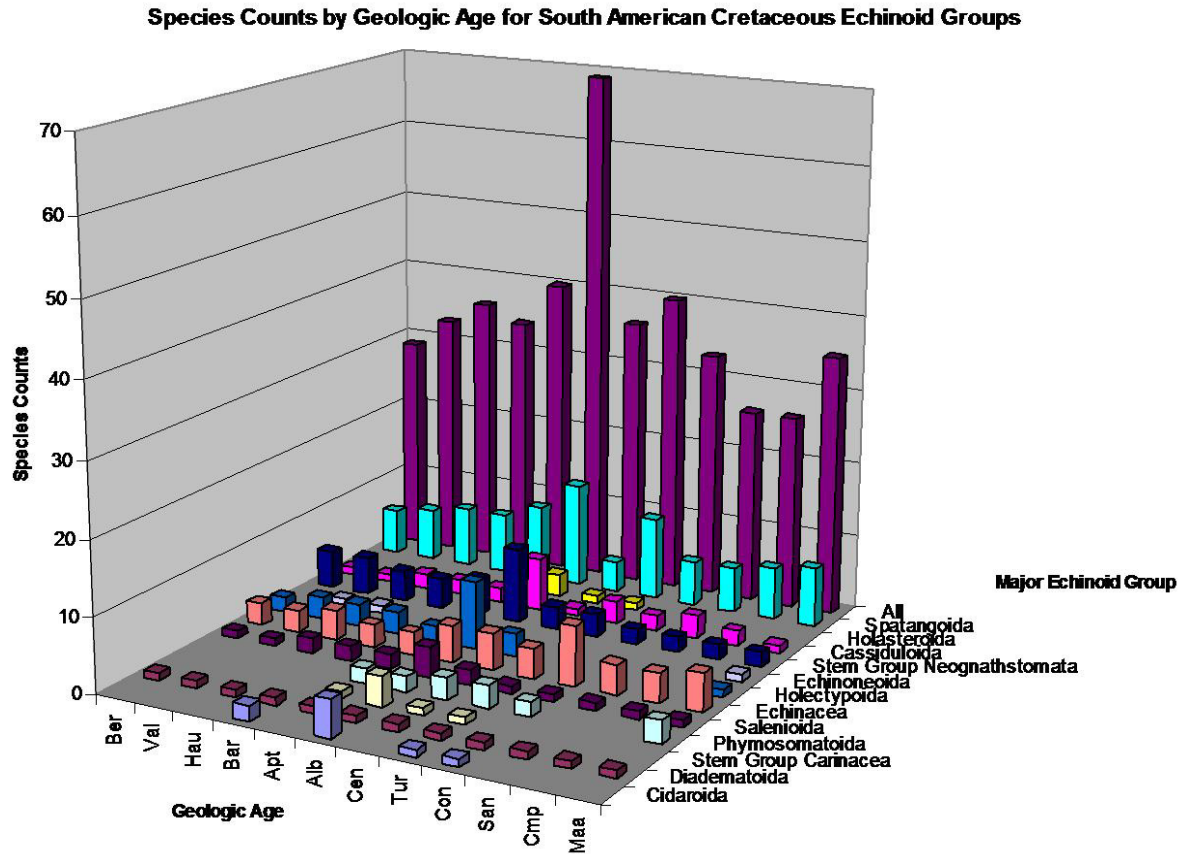


Figure 2. Echinoid Species Richness in South America during the Cretaceous.

Total number of named species for each major echinoid group in each geologic age was tallied. These counts do not reflect synonymies and thus could be lower. Species diversity throughout the Cretaceous averaged around 30 species in each geologic age, except during the Albian when total diversity was over 60. Almost all groups reflect a gradual increase in diversity prior to a spike in apparent diversity during the Albian. This was followed by a decrease in diversity in most groups. Salenioids; however, had peak diversity in the Coniacian. Spatangoids maintained higher diversity than almost all other groups in any geologic Age. Irregular echinoids in general present higher diversity throughout the Cretaceous. Taphonomy could be a factor influencing this pattern (See discussion on future research in Chapter III). (Graph from Roney et al. 2012)

the Smithsonian Institution National Museum of Natural History (USNM). The genus *Mecaster* was originally included in the Hemiasteridae, but was separated from the family due to unique characteristics such as angular interambulacra, a concave posterior face, and the formation of subanal fascioles in fine substrates (Néraudeau 1990, Néraudeau and David 1990). *Mecaster* is also no longer thought to be directly related to the *Hemiaster*, but rather part of an *incertae sedis* family that is sister to Hemiasteridae (Néraudeau 1994). In a later study of spatangoid phylogeny (Villier et al. 2004), *Mecaster* was represented by *M. batnensis* and the analysis again excluded the genus from the family Hemiasteridae. Currently *Mecaster* is still listed within the family Hemiasteridae on the Echinoid Directory (Smith and Kroh 2011), and the relationship of *Mecaster* to the other hemiasterids has yet to be fully resolved.

Conclusion

Based on the abundant spatangoid fossil record in South America, and the affinities of various species with North America and Africa, spatangoids of the genus *Mecaster* have been chosen for study. Occurrences of *Mecaster batnensis* and *Mecaster fourneli* across three continents provide an opportunity to evaluate variation between the different populations of these species. The study presented in Chapter II uses traditional two-dimensional morphometrics and three-dimensional landmark morphometrics to determine if these *Mecaster* species vary geographically; if they do vary, to what extent, and does this have implication as to their respective species classification and for possible patterns of migration or speciation?

CHAPTER II

PALEOBIOGEOGRAPHICAL VARIATION OF CRETACEOUS *MECASTER BATNENSIS* AND *MECASTER FOURNELI*

Introduction

Landmark morphometric analysis has been used to assess taxonomic richness and morphological diversity in atelostomate echinoids (Eble 2000) and spatangoids (Villier and Eble 2004). The same techniques have been used to discriminate between species in blastoids of a single locality (Atwood and Sumrall 2012). In this study these techniques will be used to evaluate morphologic variation between populations of two spatangoid species of the genus *Mecaster* from different global localities.

Background

Echinoids of the genus *Mecaster* are readily diagnosed as spatangoids by their bilateral symmetry, small peristome lacking buccal notches, the presence of both petals and phylodes on the ambulacra, the oral surface of interambulacrum 5 differentiated into a plastron, and ocular plates II and IV being exsert (Smith and Kroh 2011). The genus *Mecaster* was originally included in the Hemiasteridae based on the globular shape, high test, and anterior notch, which are diagnostic of members of *Hemiaster*. The petals of *Mecaster* are subequal (Smith and Bengtson 1991), whereas the posterior petals in *Hemiaster* are shorter than the anterior petals, and the apical system in *Mecaster* is not ethmophract (Figure 3A), which is a diagnostic feature of Hemiasteridae (Smith and Kroh 2011). The apical system of *Mecaster* species is either ethmolytic (Figure 3C) - meaning the madreporite separates the entire posterior portion of the

apical system, or semi-ethmolytic (Figure 3B) - where the madreporite separates the posterior genital pore plate, leaving only the posterior oculars in contact. *Mecaster* was separated from Hemiasteridae by Néraudeau (1990) and Néraudeau and David (1990) due to unique characteristics such as angular interambulacra, concave posterior face, and the formation of subanal fascioles in fine substrates. Consequently, it is no longer thought to be directly related to *Hemiaster* (Néraudeau 1994). In a later study of spatangoid phylogeny (Villier et al. 2004), *Mecaster* was represented by *M. batnensis* and the analysis again indicated a relationship outside Hemiasteridae.

Currently *Mecaster* is still listed within the family Hemiasteridae on the Echinoid Directory (Smith and Kroh 2011), and the relationship of *Mecaster* to hemiasterid taxa has yet to be fully resolved. Smith and Bengtson (1991) placed species of *Mecaster* into four generalized groups. While these groups were not systematically defined, they do summarize the major similarities within *Mecaster* and create a framework upon which one can assess similarities in a

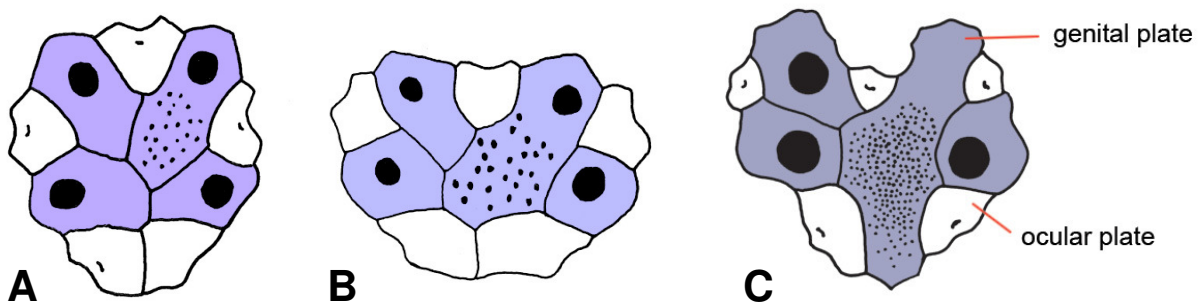


Figure 3. Apical system plate arrangements.

These are not the apical systems of the specific species discussed in this study, but the plates of the apical systems in *Hemiaster* and *Mecaster* are arranged in the same relationships. An apical system is defined as ethmophract (A) when the posterior genital plates are in contact with each other. When the posterior genital plates are separated by the madreporite, but the posterior ocular plates are not separated, an apical system is semi-ethmolytic (B). When the madreporite separates both ocular plates and the posterior ocular plates an apical system is ethmolytic (C). Images from the Echinoid Directory glossary (Smith and Kroh 2011).

genus that has over 50 named taxa and numerous synonyms. Included within the species groups are various hemiasterid species which have previously been misclassified.

Recently the genus *Hemiaster* has undergone a major taxonomic revision. Various *Hemiaster* species, including *H. fourneli*, *H. africanus*, and *H. batnensis*, have been reassigned to the genus *Mecaster* (Smith and Bengtson 1991). Likewise, *H. jacksoni* found in Brazil and other parts of South America has also been reported from Texas, USA (Cooke 1955), Arizona, USA (Kirkland 1996), New Mexico, USA (Hook et al. 1983), Mexico (Cooke 1953, Buitron 1968) and possibly France (Smith and Bengtson 1991) and has been synonymized with *M. batnensis*. In one instance a Brazilian occurrence of *H. jacksoni* was synonymized with *H. proclivus* (Smith and Bengtson 1991); however, the majority of Brazilian occurrences were synonymized with *M. batnensis* or *M. fourneli* (Smith and Bengtson 1991). The number of localities of *M. batnensis* and *M. fourneli* has increased as a result of the generalized classification scheme put forth by Smith and Bengtson (1991) and the accompanying revisions to *Hemiaster* and *Mecaster* phylogeny. These synonyms can be used to evaluate patterns of variation within the two species.

***Mecaster batnensis* (Coquand, 1862)**

Mecaster batnensis, as well as *M. fourneli*, can be identified by apomorphic character traits. *M. batnensis* is diagnosed by bearing a semi-ethmolytic apical system, meaning the madreporite separates the posterior genital plates, but not the ocular plates (Figure 3B). The anterior and posterior petals (ambulacra I, II, IV, and V) are subequal and broad, while the anterior ambulacrum (ambulacrum III) has relatively few pore-pairs between the apex and the peripetalous fasciole (Smith and Bengtson 1991). The features of the apical system in samples used in this study were generally distinguishable. Synonymies to this species include some occurrences of *Hemiaster batnensis* Coquand, 1862; *Hemiaster cristatus* Stolizcka?, 1887;

Hemiaster delgadoi de Loriol, 1888; *Hemiaster jacksoni* Maury, 1925; and *Hemiaster cedroensis* Maury, 1937 (Smith and Bengtson 1991). Specimens of *M. batnensis* and its synonyms have been identified in the United States (Arizona, New Mexico, Texas), Mexico, Venezuela, Brazil, Algeria, Tunisia, Egypt, Palestine, and Portugal (Maury 1936, Benavides-Caceres 1956, Willard 1966, Zaghib-Turki 1987, Smith and Bengtson 1991, Néraudeau and Mathey 2000, Manso 2006, Manso and Andrade 2008). Samples of *M. batnensis* used in this study come from Palestine, Egypt, Algeria, Brazil, Mexico, Texas, New Mexico and Arizona (Figures 4 & 5).

***Mecasterourneli* (Agassiz & Desor, 1847)**

Mecasterourneli is thought to form an “evolutionary lineage” with *M. batnensis* (Smith and Bengtson 1991) as a direct descendant. This species is diagnosed by an ethmolytic apical system, meaning the madreporite fully separates the posterior genital and ocular plates, and the interradial suture between sternal plates on the plastron reaching the labrum subcentrally (Figure 3C) (Smith and Bengtson 1991). Features of the apical system are generally easy to distinguish in samples used for this study, but the plating structure of the plastron is only infrequently visible. Occurrences of *Hemiasterourneli* Agassiz and Desor, 1847 and *Hemiaster jacksoni* Maury 1925 have been synonymized with *M.ourneli* (Smith and Bengtson 1991). Specimens of *M.ourneli* have been identified in Colombia, Ecuador, Peru, Bolivia, Brazil, Algeria, Egypt, Cameroon, Nigeria, and Gabon (Maury 1936, Benavides-Caceres 1956, Willard 1966, Smith and Bengtson 1991, Néraudeau and Mathey 2000, Manso 2006, Manso and Andrade 2008). Samples of *M.ourneli* used in this study come from Algeria and Peru (Figure 4 & 5).

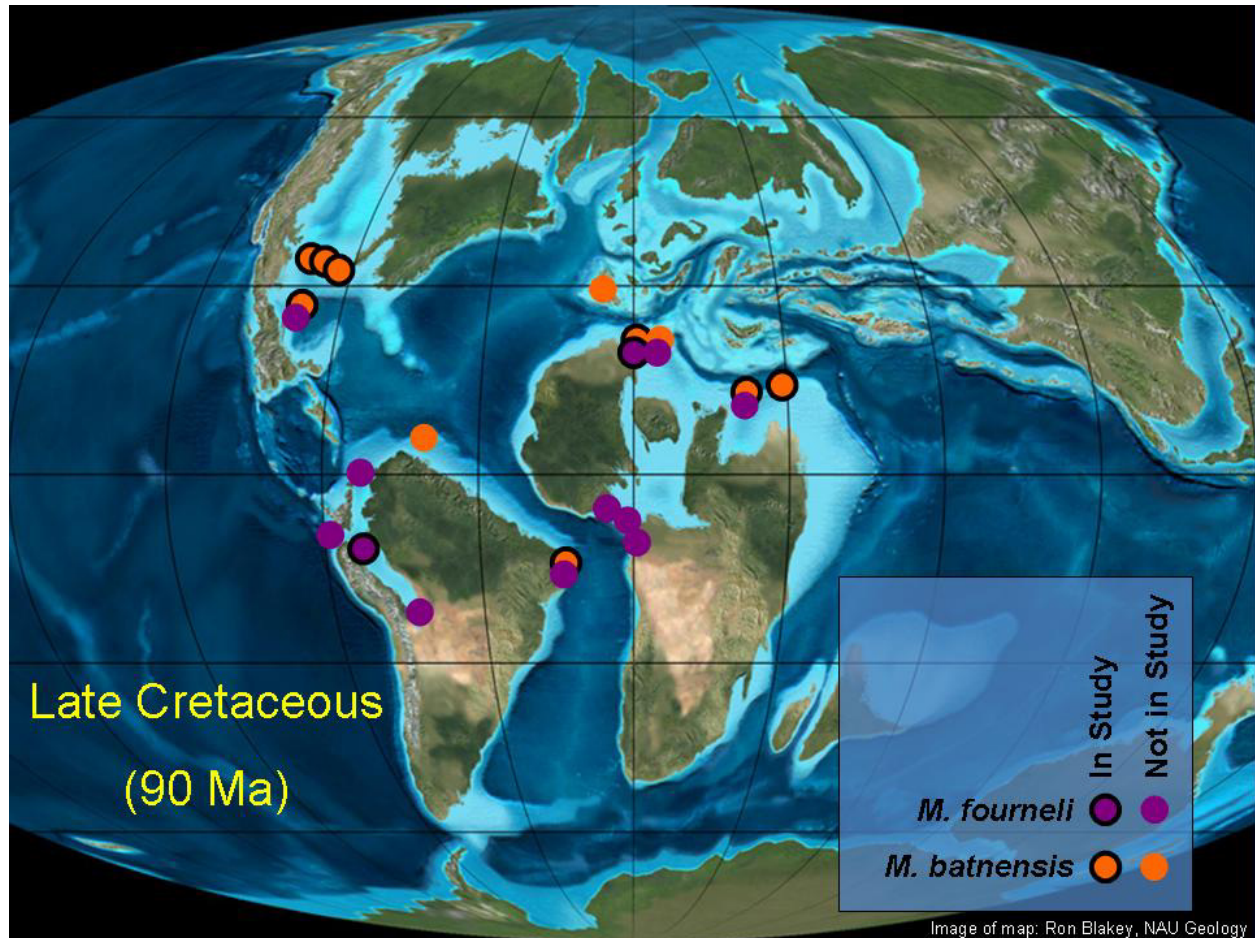


Figure 4. Known localities of *M. batnensis* and *M. fourneli* on a global map of the Late Cretaceous (90 Ma).

Orange circles indicate locations of *M. batnensis* and purple circles represent locations of *M. fourneli*. Circles outlined in bold black are the locations represented in this study. Overlapping circles of both species are the same location, they are shifted in order to show the presence of both species and not different neighboring localities. (Map from Ron Blakey, NAU Geology)

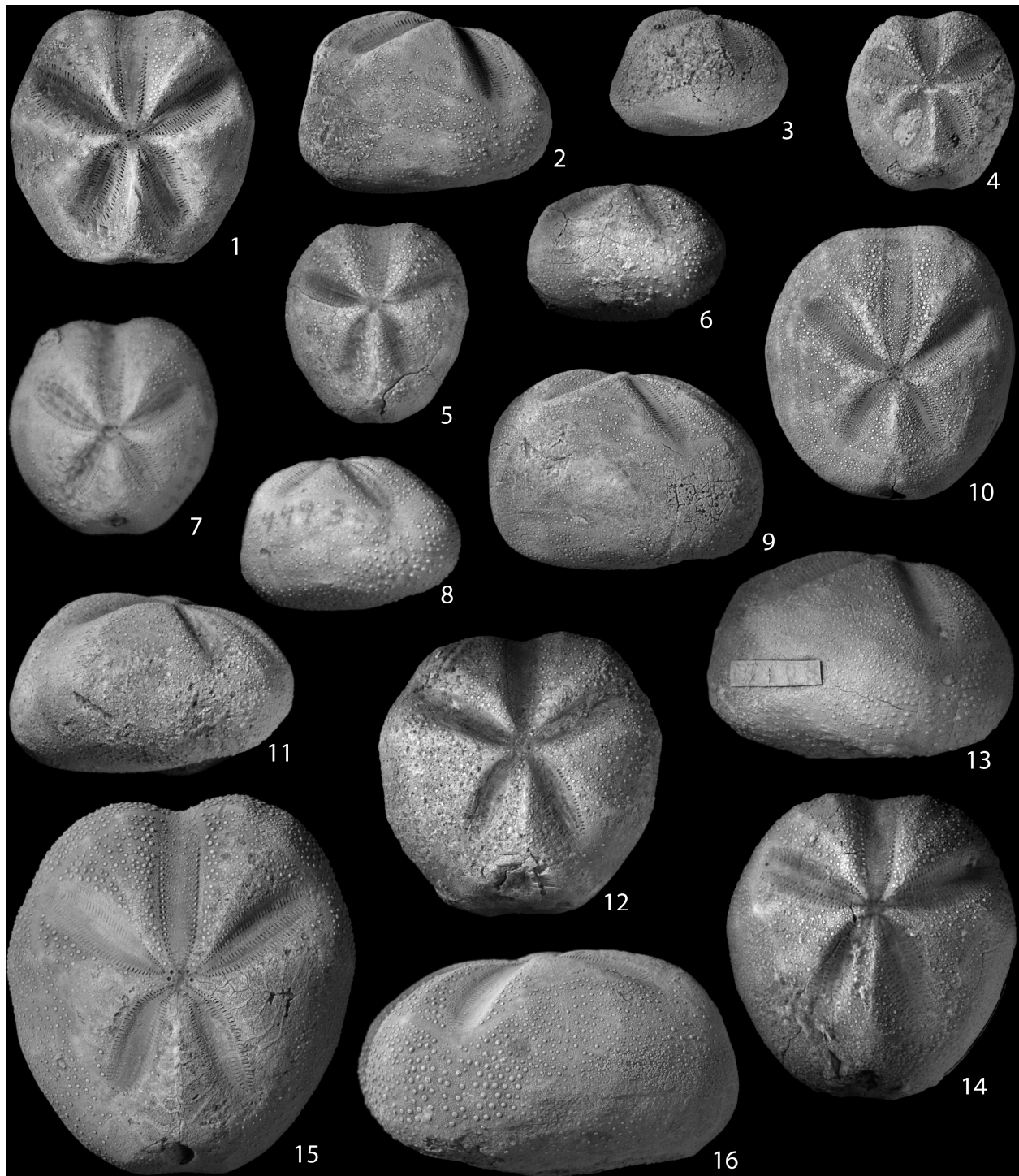


Figure 5. *M. batnensis* and *M. fourneli* from localities used in this study.

M. batnensis from Texas (1 & 2; USNM 468877); Mexico (3 & 4; Acq. Num. 231242 batch J68); Arizona (3 & 6; USNM 468554); Brazil (7 & 8; USNM 449388); Egypt (9 & 10; USNM 468944); Algeria (11 & 12; USNM 31102); and New Mexico (13 & 14; USNM 468535). *M. fourneli* from Algeria (15 & 16; USNM 29246). *M. fourneli* from Peru not pictured. All images 2x actual size.

Table 1. Localities and Geologic Ages of Samples.

AGE	<i>Mecaster batnensis</i>	<i>Mecasterourneli</i>
Campanian (83.5 Ma – 70.6 Ma)		AL (1), PE*
Santonian		AL (6), PE*
Coniacian (89.3 Ma – 85.8 Ma)		AL (19), PE*
Turonian (93.5 Ma – 89.3 Ma)	TX (12), BR**	AL (1)
Cenomanian (99.6 Ma – 93.5 Ma)	NM (6), EG (2), PA (1), BR (10), AL (1), MX (1)	

Localities in this study are listed by species according geologic age. The ages of samples are known for Algeria (AL), Egypt (EG), Palestine (PA), Brazil (BR), New Mexico (NM), and Texas (TX). The ages of samples from Arizona (AZ) are not constrained. The numbers of samples per locality used in the three-dimensional landmark analysis are in parentheses. Row heights are equivalent to the duration of each age. Further information regarding sample specimens used in this study is found in Appendix 10.

* Peru samples were only constrained to the Senonian which describes a time period from the Coniacian through the Campanian. **Samples of *M. batnensis* are known from Brazil in the Turonian, but were not part of this study.

Stratigraphy

Minimal stratigraphic information for the sample localities is available. The majority of samples are constrained to geologic Age (Table 1), and a few samples have information on the stratigraphic formations from which they originate. In most cases further specific information regarding age or more detailed stratigraphic range is not available. *Mecaster batnensis* has a known stratigraphic range from the Cenomanian to the Turonian (Smith and Bengtson, 1991, and USNM specimens in this study). The majority of *M. batnensis* samples are Cenomanian in age except for the Texas samples collected from the Turonian aged Eagle Ford Shale. New Mexico and Arizona populations are most likely from units of the Mancos Shale (Hook et al. 1983;

Kirkland 1996), and the Mexico population originates from the Early Cenomanian Indidura Formation (Buitron 1968). Detailed information constraining sample location to position within stratigraphic layers is not available for most specimens, and as such, specific information regarding sediment type and size cannot be used to correlate any possible variation in shape to environment. Samples of *M. fourneli* cover time periods from the Turonian to the Campanian with highest abundance in the Coniacian to the Santonian (Smith and Bengtson, 1991, and USNM specimens in this study). Similarly, the specific details regarding location were not available for specimens of *M. fourneli*.

Preliminary Analysis of populations

Initial observations of specimens of *Mecaster batnensis* and *Mecaster fourneli* repositied at the Smithsonian Institution National Museum of Natural History (USNM) include measurements of test length (L), test width (W), and test height (H) (Appendix 2A). Length was measured longitudinally from the posterior of the organism to the anterior, width laterally between the extreme of each side of the organism, and height was the distance measured from the extremes of the oral and aboral surfaces. Specimens of *M. batnensis* were measured from Palestine (n=14), Egypt (n=2), Algeria (n=5), Brazil (n=21), Mexico (n=71), Texas (n=60), New Mexico (n=73) and Arizona (n=45), for a total of 291 specimens. Specimens of *M. fourneli* were measured from Algeria (n=20) and Peru (n=57) for a total of 77 specimens. Specimens were visually assessed for taphonomic distortion, and all specimens with all three axes undeformed were measured.

To test if species show a significant difference in the slopes of growth trajectory between populations an analysis of variation (ANOVA) of the linear regressions of the data on each population compared to the regression line of one of the populations in that species results in an

analysis of covariation (ANCOVA). In the majority of populations the three measurements had sufficiently normal distributions for use in this type of analysis. An ANCOVA can confirm if there is a difference in general shape between the populations, and in which set of parameters this difference is manifest. Each measurement parameter was compared to the other measurements resulting in three analyses for each species (W vs. L; H vs. L; and W vs. H; Appendices 2B and 2C). In each ANCOVA the standardized coefficients with 95% confidence intervals of each population were calculated and plotted (Figures 6 & 7).

The analysis of W vs. L (F-ratio, 0.850; and p-value, 0.546; Figure 6A) of the eight populations of *M. batnensis* shows no significant difference between the populations. The 95% confidence intervals are wide and there is a large amount of overlap of each population. This suggests the test outline of each population has very little variation between populations. The analysis of H vs. W (F-ratio, 8,128 and p-value, <0.0001; Figure 6B) shows significant variation between populations. Arizona and New Mexico have similar confidence intervals that do not overlap with the confidence intervals of Algeria, Brazil, Mexico, and Palestine. The variation between populations is most significant in the analysis of H vs. L (F-ratio, 13,090 and p-value, <0.0001; Figure 6C). The same groupings of populations seen in the analysis of H vs. W are seen in the analysis of H vs. L; however, the confidence intervals tighten and the separation between populations widens. Thus, height appears to be the parameter with the greatest variation between populations.

The comparison of *Mecaster founeli* populations is simpler as there are only two populations (Figure 7). Both populations are different by standardized coefficients of less than 0.1 in all comparisons. The differences between these populations are largest, though not significant, in the outline of the test as reflected by length and width (F-ratio, 0.464; p-value,

0.498; Figure 7A). The next greatest difference is height and length (F-ratio, 0.250; p-value, 0.619; Figure 7B), with the lowest reflected in height and width (F-ratio, 0.077; p-value, 0.783; Figure 7C). Therefore, of the three axes measured, length appears to contain the greatest amount of variation between the two populations of *M. fourneli*; however, these two populations do not appear to be significantly different.

Two-dimensional and Three-dimensional Morphometrics

To further evaluate the variation between populations of these species additional observations are needed. In this study two different morphometric measurement schemes were used to assess variation between the populations of *M. batnensis* and *M. fourneli*. The results of the different morphometric schemes will be compared and differences assessed for how well the measurement schemes discriminated among populations. The techniques used are analysis of traditional two-dimensional measurements and three-dimensional landmark analysis.

Traditional morphometric measurements consist of linear measurements of the shapes and features of specimens. Such measurements generally create a dependency upon the size of the organism. When it is desirable to remove the effect of size in linear measurements it is common to use ratios between two different measurements, though the use of ratios can result in confounding errors. The techniques used in this study are discussed below. In this study all linear measurements were made with digital calipers (error: +or- .02mm). (See Figure 8)

Three-dimensional landmark morphometrics utilizes points located on or along certain features to make a measure of shape change and/or translocation of features. Bookstein (1991) defines landmarks as points of juxtaposition of tissue on an organism, maxima or curves of various surfaces, or extremal points. Points of juxtaposition, such as the point of contact of

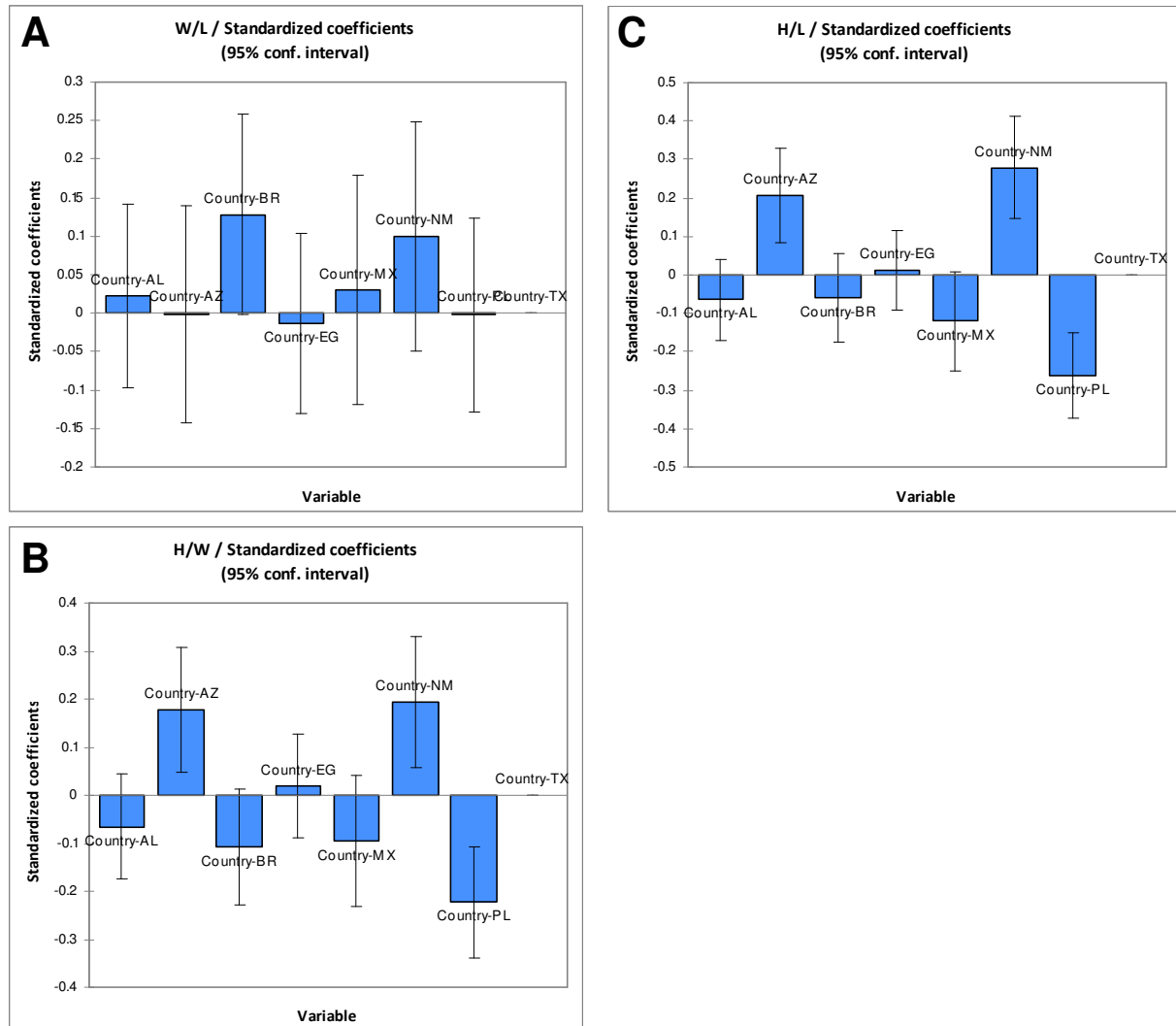


Figure 6. Standardized coefficients, with 95% confidence intervals, from ANCOVAs of initial large sampling of *M. batnensis* populations.

Test width (W) vs. test length (L) (A), test height (H) vs. test width (W) (B), and test height vs. test length (C) are compared between populations. When confidence intervals overlap localities are similar; if they do not overlap localities have more variation between them. Note that the Texas (TX) population is the one to which all other populations have been compared creating the baseline from which the bars for the other populations plot. ($n_{\text{total}}=291$)

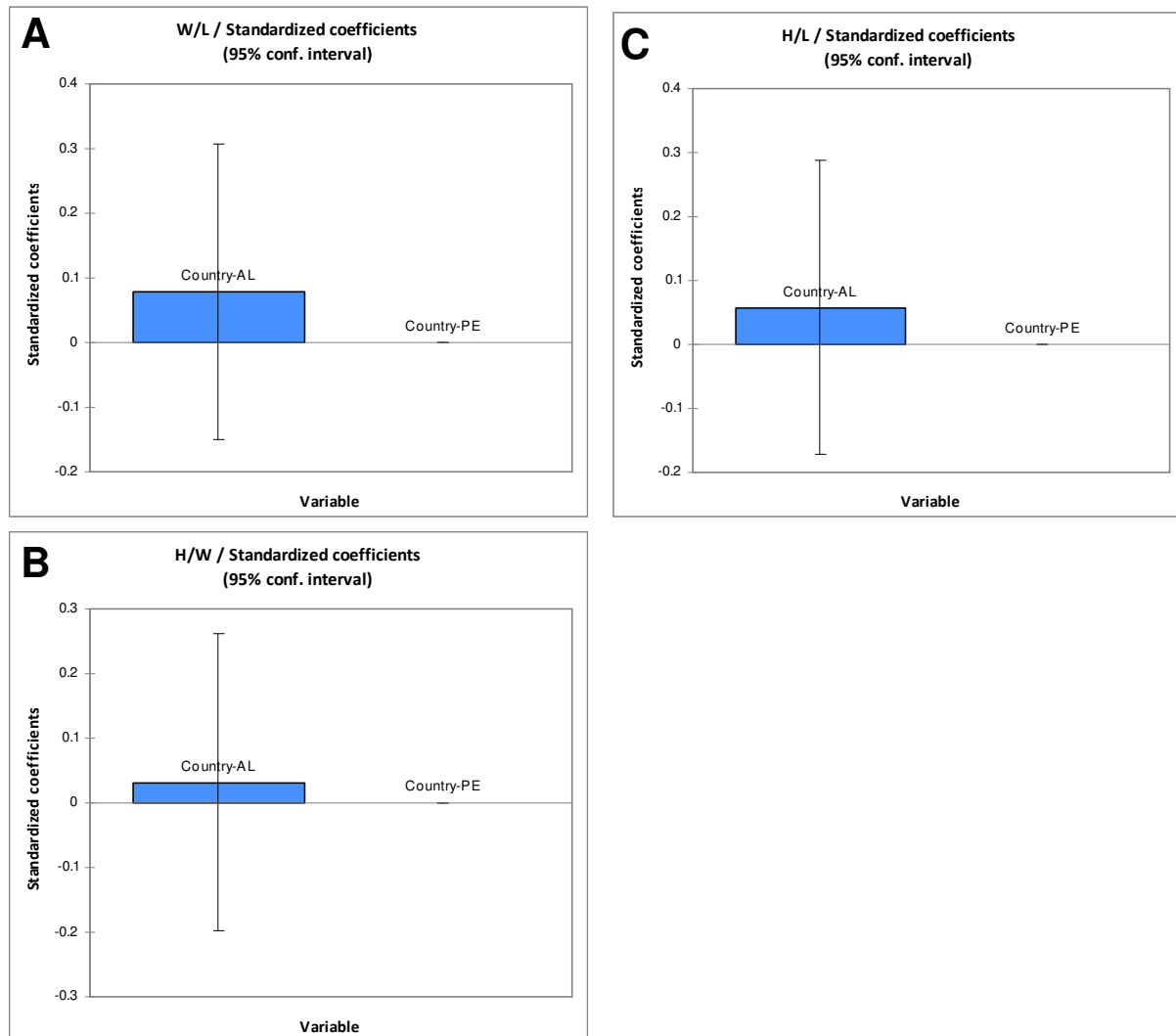


Figure 7. Standardized coefficients, with 95% confidence intervals, from ANCOVAs of initial large sampling of *M. furneli* populations.

Test width (W) vs. test length (L) (A), test height (H) vs. test width (W) (B), and test height vs. test length (C) are compared between populations. No distinct difference is found between populations as the confidence interval for Peru crosses the baseline in each comparison, but the largest standardized coefficient was found in the comparison between test width and test length. Note that the Peru (PE; n=57) population is the one to which the Algeria (AL; n=20) population has been compared. ($n_{\text{total}}=77$)

three plate boundaries on echinoid tests, are most preferable, and are called Type 1 landmarks. Maxima or curves, such as extent of labral plate toward the peristome (Figure 9), are Type 2 landmarks. Extremal points, such as the points used to define maximum length of an organism, are Type 3 landmarks, also called semi-landmarks, and may not even be true landmarks (Zelditch et al. 2012). More recently, further semi-landmark types have been identified and classified (Weber and Bookstein 2012). They are subsets of the original definition of Type 3 landmarks; however, the biologic use of such landmarks is frequently debated as their use becomes more prevalent.

The importance of a landmark is found after analysis and not determined *a priori* (Zelditch et al. 2012); thus the challenge is to select landmarks which will capture potential variation in shape. A potential template for identifying landmarks on spatangoids is Eble's (2000) study on disparity and diversity in heart urchins. In this study a three-dimensional landmark based morphometrics measurement scheme was used. Eble (2000) selected locations which he felt best captured test architecture. Eighteen specific landmarks representing 38 different variables were identified in his study (Figure 9). The same scheme was also used by Villier and Eble (2004) to assess the sensitivity of disparity estimates in varying protocols and analyses. This present study will use 10 landmarks, the majority of which are Type 1 landmarks (Figure 9). The landmarks excluded in this study which were included in Eble's (2000) study are mostly Type 3 landmarks and not deemed sufficiently repeatable.

Methods and Procedures

Material for this study consisted of samples from the Smithsonian Institution National Museum of Natural History (USNM). Type fossils, where available, and general collection

samples were included in the measured sample set. No field collecting was done. The USNM collection contains samples of *M. batnensis* from Arizona, New Mexico, Texas, Mexico, Brazil, Algeria, Egypt and Palestine, and samples of *M. fourneli* from Algeria and Peru. Samples of *M. fourneli* from Brazil are also known (Smith and Bengtson 1991) but were not borrowed for logistical reasons; however, available data regarding these samples will be compared with the results of this study.

All samples from the USNM collection with at least nine of the ten three-dimensional morphometric landmarks were used in this study. The criteria for specimen inclusion once identified to a species level are 1) quality of preservation – including preservation of landmarks and 2) preservation of shape by not having any visible taphonomic deformation. In order to eliminate ontogenetic effects in this study, specimens selected for analysis are mature. The overwhelming majority of available specimens are adults with gonopores fully opened. As most *Mecaster* juveniles develop in different localities than adults (Néraudeau 1991) the available specimens rarely include any juveniles; in fact, of 12 specimens that are obviously juvenile, none satisfied the criteria for quality and would not have been selected for inclusion in this study even if juveniles were intended for inclusion. *Mecaster* species also do not generally express sexual dimorphism, so differences between sexes are not an effect on this study as they could potentially be with a number of *Hemiaster* species (Néraudeau 1993).

Two-Dimensional Measurement Scheme

Selected samples of *M. batnensis* and *M. fourneli* were measured with digital calipers. The measurement scheme used in this study consisted of 22 linear measurements and three feature counts (Figure 8). The measurements in this study are the same as those used in both Villier and Eble (2004) and Smith and Bengtson (1991) (Table 2) allowing for comparisons of

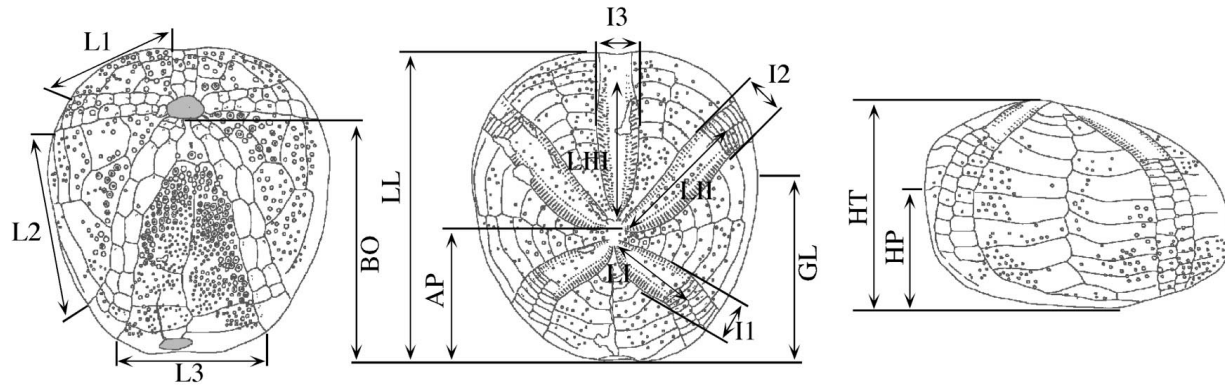


Figure 8. Two-dimensional measurement scheme.

Measurements made in Villier and Eble (2004). Further measurements in the two-dimensional scheme of this study include measurements of peristome and periproct length and width, distances of the peristome and apical system to the anterior margin, and pore counts of petals I, II, and III.

those studies with this study. Measurements made include length, width, and height of the test; lengths of petals I, II, and III; pore counts of petals I, II, and III; lengths and widths of the periproct and peristome; measurements of locations of the peristome and apical system in relation to the anterior and posterior margins of the test; and height of the periproct from the base of the test. All measurements are recorded to 1/100mm except in the case of one measurement discussed below to 1/10mm (Appendix 3A).

The length, width, and height of each specimen were measured with length being the longitudinal distance measured from the posterior of the test to the anterior, width being the lateral length measured between the extreme of each side of the organism, and height being the measure of distance from the extremes of the oral and aboral surfaces. In many echinoids, height is a measure from the peristome (or area immediately adjacent) to the apical system, but in many spatangoids, including the two species used in this study, due to the wedge shape of the test the lowest part of the test is actually on the plastron, posterior to peristome, while the highest point on the test is generally posterior to the apical system along the middle of interambulacra 5.

Lengths of petals I, II, and III are measured from the first pore-pair adjacent to the ocular plate in the apical system to the last pore-pairs at the extreme of the petal. In the case of petal three the extreme of this petal is located where the peripetalous fasciole crosses the ambulacra. Width of these petals was measured between the outer edge of the pore-pairs and not the edge of the ambulacral plates because the plate edges were not always distinguishable. The number of pore-pairs in petals I, II, and II were counted using the greatest number of pore-pairs on either side of the petal.

In measuring the length and width of the peristome and periproct, length in both instances was defined as the measurement parallel to the longitudinal axis of the test, while width was the measurement perpendicular to the longitudinal axis of the test. This causes the width of the peristome to actually be the longer measurement in the instance of these species; however, this measurement scheme would keep such measurements consistent between different species of other groups of echinoids. The location of the apical system on the test was measured by the distance from the ocular plate adjacent to petal III to the anterior edge of the test and from the same ocular plate to the posterior edge of the test. The location of the peristome was measured from the contact of ambulacra III with the peristome to the anterior edge of the test and from the lip of labral plate to the posterior edge of the test. The location of the periproct was measured from the base of the test to the base of the periproct.

The widths of interambulacra 3, 4, and 5 were measured along the ambitus at the suture lines between the measured interambulacrum and its neighboring ambulacra. In instances where this was not possible for interambulacra 3 or 4 a measurement was taken at interambulacra 2 or 1 respectively; however, even that was not always possible, so this measurement is lacking in a small number of specimens used in this study. Using these replacement measurements assumes a

level of symmetry that has not been tested, but is biologically reasonable. There is no alternate measurement available when this measurement is not possible in interambulacrum 5 as it sits across the line of bilateral symmetry of the test.

The final measurement is the length from the widest part of the test (i.e., where the test width measurement is taken) to the posterior of the organism. This is the most difficult measurement to constrain, and is the measurement with the most potential error. In order to eliminate some of this error, this measurement was taken three or more times and recorded as a simple average to 1/10 mm.

Three-Dimensional Landmark Scheme

Selection of landmarks to measure was based on observations specific to *M. batnensis* and *M. fourneli* and the scheme used in Eble (2000) (Figure 9). Ten landmark points have been selected (Figure 9), the majority of which are Type 1 landmarks. Five points define the distal tips of petals I, II, III, IV, and V near where the ambulacral plates meet the peripetalous fasciole. These points were marked along the perradial suture at the juncture of the last two pore-pair bearing ambulacral plates with the first ambulacral plate that is not part of the petal. Two points along the perinterradial suture record the top and bottom of the periproct where the plates of interambulacrum 5 meet the periproct. One point records the plate junctures where ambulacral plates from ambulacrum III meet the peristome. Another point, a Type 2 landmark, records the farthest extent of the labral plate of the plastron, which forms a lip over the peristome. The last point is a Type 3 landmark; here the general position of the apical system is marked by a point midway between the two anterior genital pores. While this is a Type 3 landmark, this point is very well constrained due to the small size of the apical system and short distance between the two genital pores.

Table 2. Comparison of Measurements used in this Study and prior Studies.

Definition	Villier & Eble 2004	Smith & Bengtson 1991	This Study
<i>Test Length</i>	LL	Test Length	L
<i>Test Width</i>		Test Width	W
<i>Test Height</i>	HT	Test Height	H
<i>Length Petal I</i>	LI	Length Posterior Petal	PI
<i>Length Petal II</i>	LII	Length Anterior Petal	PII
<i>Length Petal III</i>	LIII		PIII
<i>Pore Count, Petal I</i>		Number of Pores in Posterior Petal	Pores I
<i>Pore Count, Petal II</i>		Number of Pores in Anterior Petal	Pores II
<i>Pore Count, Petal III (up to peripetalous fasciole)</i>		number of pores in amb III adapical of fasciole	Pores III
<i>Apical System to Anterior Margin</i>		apical disc to anterior border	AS-AM
<i>Apical System to Posterior Margin</i>	AP		AS-PM
<i>Peristome Length</i>			PS L
<i>Peristome Width</i>			PS W
<i>Periproct Length</i>			PP L
<i>Periproct Width</i>			PP W
<i>Height to Periproct</i>	HP	Height to Periproct	H to PP
<i>Peristome to Anterior Margin</i>		Peristome to Anterior Border	PS-AM
<i>Peristome to Posterior Margin</i>	BO		PS-PM
<i>Maximum width to Posterior Margin</i>	GL		MaxW-PM
<i>Width Petal I</i>	I1		WI
<i>Width Petal II</i>	I2		WII
<i>Width Petal III</i>	I3		WIII
<i>Width Interambulacrum 3</i>	L1		I3
<i>Width Interambulacrum 4</i>	L2		I4
<i>Width Interambulacrum 5</i>	L3		I5

Villier and Eble (2004) used 15 measurements; Smith and Bengtson (1991) used 11. There was overlap of only 5 measurements between the two schemes making a total of 21 measurements which were also used in this study. Four measurements used in this study were unique to this study making the total of 25 measurements.

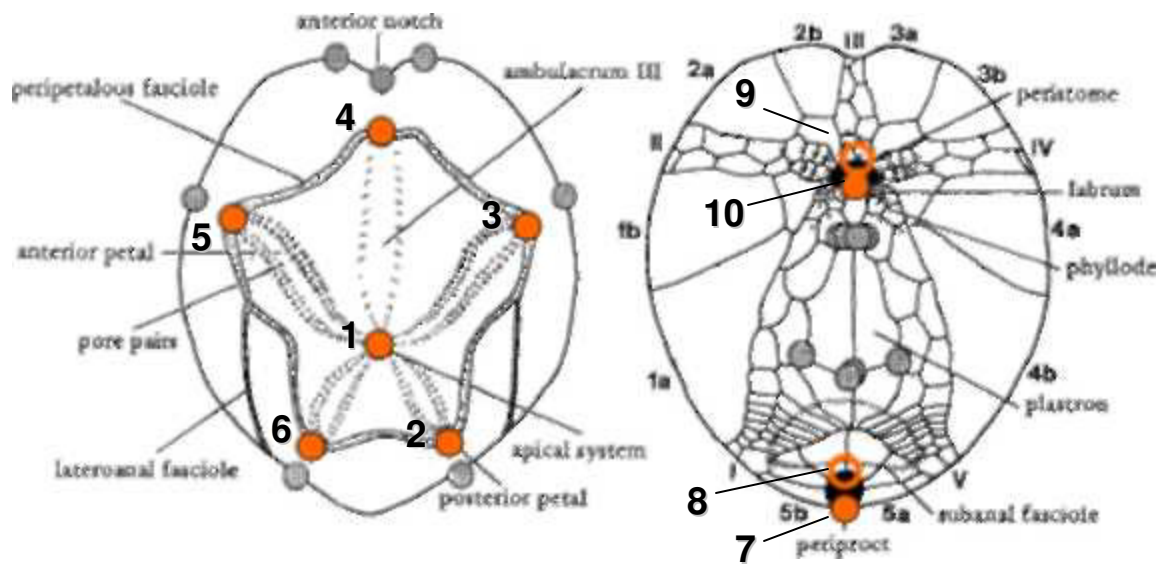


Figure 9. Three-dimensional landmark morphometrics measurement scheme.

Landmarks used by Eble (2000) are solid circles. Measurements made in this study are in orange. Open circles are landmarks in this study not used by Eble (2000). Landmarks are numbered according to the labels used throughout this study. Landmarks 2 – 9 are Type 1 landmarks, landmark 10 is a Type 2 landmark, and landmark 1 is a Type 3 landmark. (Image modified from Eble 2000)

All points were marked with a 0.5 mm pencil so that any markings made could easily be removed. Because of the size of the pencil tip, markings were made with the side of the pencil tip and to the side of the landmark so that the edge of the marking in a known direction was the desired landmark.

The points not included in this scheme which were included in Eble's (2000) scheme are mostly Type 3 landmarks, such as the location of the ambulacra along the test margin - also called the ambitus, and the forward points of the test on either side of the sulcus. A few Type 1 landmarks on the plastron were also not included as they are rarely visible on available specimens. Type 3 landmarks on the ambitus were not used for two reasons. The first, and most important to this study, is the lack of repeatability of marking these landmarks. Secondly, while these points are mathematically homologous, they do not necessarily mark biologically

homologous structures (Zelditch et al. 2012), hence the biologic significance of these points is suspect and requires separate analysis which is beyond the scope of this study. This issue is discussed further in chapter 3.

Scanning

Scans were completed using the NextEngine desktop scanner. The scanner uses reflected laser light to generate a three-dimensional mesh recording the surface shape of an object. With each scan, a digital photographic image is made of the object allowing the image to be overlain on the resultant three-dimensional mesh. Samples were analyzed in five different overlapping scans covering a full 360°. Two scan sets were made of each sample to cover the entire surface of the specimen. For the first scan set, the test of each sample was oriented with the axis of the stage rotation going through interambulacrum 2 and ambulacrum V. The second scan set was made with the axis of stage rotation positioned through the forward portions of interambulacra 1 and 4 near ambulacra II and IV at the widest part of the test. Scans were made at the highest resolution possible of 160,000 points per square inch, which equates to a point every 0.0635mm. This allows for precision to 0.127mm.

The resultant scan sets were trimmed to remove components unrelated to the specimen such as the scan stage and frame. The pair of cleaned scan sets of each sample were then aligned to each other using a minimum of three common points. Alignment was made to a tolerance of 0.025mm. Following alignment, the two scan sets were then fused together to a tolerance of 0.06mm. These tolerances, when achieved, minimized the introduction of error into the resulting three-dimensional mesh. If at any point these tolerances were not achieved alignment and fusing was processed a second time. A few instances required complete rescanning of the sample. The

fused scan sets were then exported as object files (.obj) which are readable by numerous computer programs to observe and manipulate three-dimensional meshes.

Collecting Landmark Points

The three-dimensional meshes derived from the laser scans were imported into MeshLab (Cignoni et al., 2008) where the location of each marked landmark was recorded by the points marked on the samples in pencil and by comparison with the physical sample. Each landmark point was then “pinned” on the mesh using the PickPoints tool. This resulted in sets of Cartesian coordinates (x,y,z) for each point (Appendix 3B). Points were picked in the same sequence on each sample to ensure proper export of the resulting coordinates for use in the analysis. To test for error in selecting data points, point data for a single specimen was collected multiple times (10 replicates) for later analysis.

Data and Analysis

Of over 500 available specimens of *Mecaster batnensis* only 38 were complete and clean enough and reasonably undamaged for use in this study. Samples came from the eight previously listed localities - Palestine (n=1), Egypt (n=2), Algeria (n=1), Brazil (n=10), Mexico (n=1), Texas (n=12), New Mexico (n=6), and Arizona (n=5). Of over 100 available specimens of *Mecaster fourneli* only 36 were in similar usable condition. Samples came from Algeria (n=27) and Peru (n=9). These numbers are far smaller than the 291 *M. batnensis* and 77 *M. fourneli* specimens measured in the preliminary assessment, but the specimens in that assessment only needed to have a test that was intact without regard to visibility or preservation of detailed features.

The process of standardization for the three-dimensional data was different than the

scheme used by Eble (2000) where the origin of the coordinate system was centered between the frontal genital pores of the apical disc. Rather, differences in location, scale, and orientation were removed using a full Procrustes superimposition leaving only differences in shape to be analyzed (Bookstein 1991, Zelditch et al. 2004; Figure 10; Appendix 6). Three-dimensional data were analyzed in the program MorphoJ (Klingenberg 2011), while two-dimensional data were analyzed using the statistical program JMP. Three-dimensional data were processed twice - once without any symmetry defined and a second time with the bilateral symmetry of the echinoids defined and the appropriate landmarks for petals I, II, IV, and V paired. The Procrustes superimposition (called the Procrustes fit in MorphoJ), as well as many analyses in MorphoJ, generate lollipop shape change graphs with vectors (the stick of the “lollipop”) indicating the direction of change for a given landmark projecting from the point (the candy of the lollipop) that indicates the average location of said landmark. These graphs will be used here to illustrate the results of analyses and to characterize species populations.

Data collected under each measurement scheme were analyzed using various multivariate statistical methods. Principle component analysis (PCA) and canonical variate analysis (CVA) of the data were used to evaluate variation in and between populations of the two *Mecaster* species (Bookstein 1991, Zelditch et al. 2004, Quinn and Keogh 2002). PCA maximizes similarities between observations, and indicates which data most influences the overall pattern of observations. On the other hand, CVA maximizes the differences between observations, and allows any patterns of population difference to be discerned. In the case of CVA, observations are placed into categories (localities in the case of this study) which are defined *a priori*. If groups can be discriminated they are separated by the CVA and plotted apart on the canonical plot, but if they are not discriminated they will plot together. Discriminate

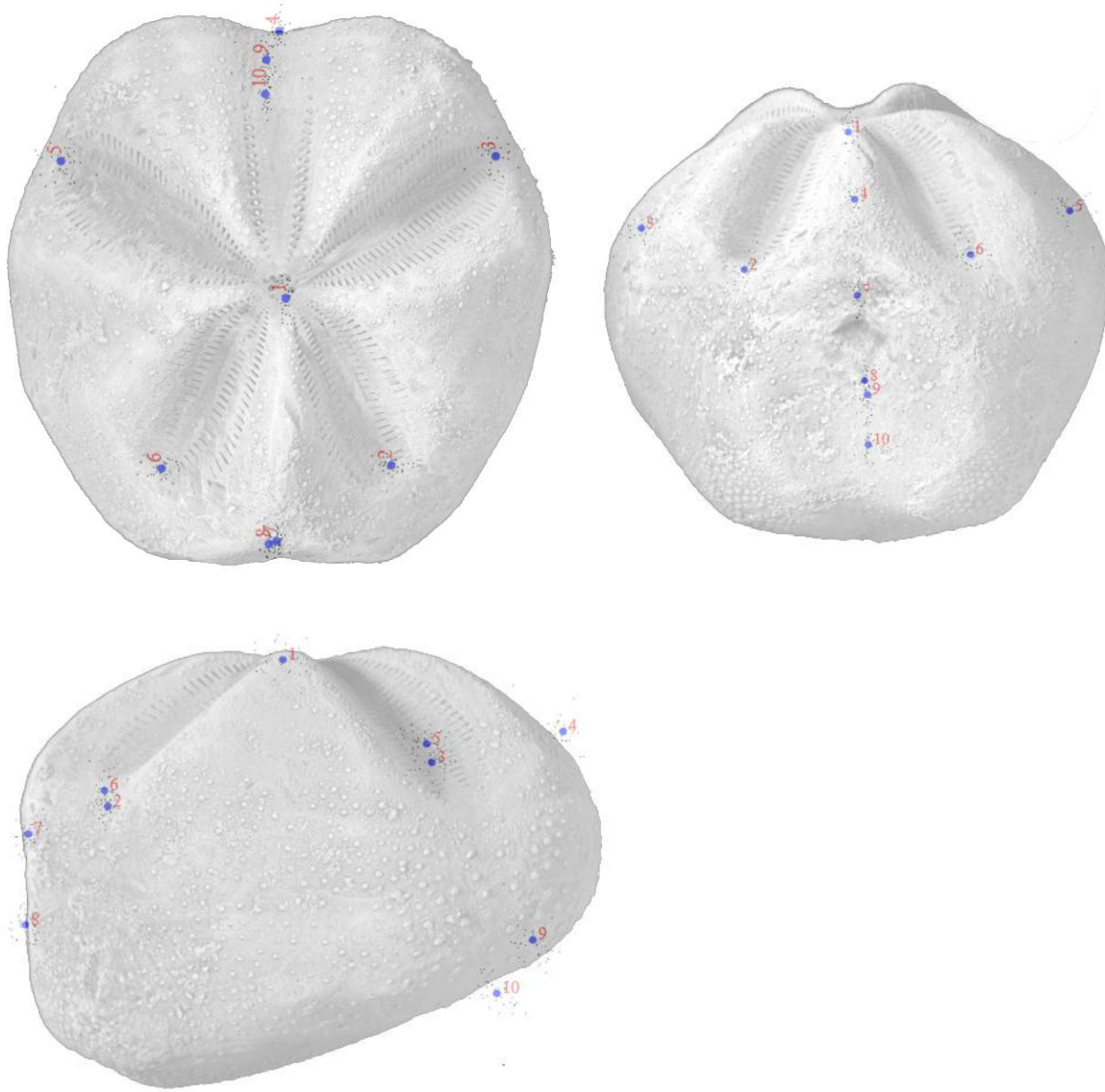


Figure 10. Procrustes Fit of *M. batnensis* imposed on image of a specimen.

The ten landmarks used in this study are shown in three orientations: aboral view, posterior view, and side view. The larger point indicating each landmark (accompanied by a number labeling which landmark) is the average location of the landmark as found in the full Procrustes fit of all specimens of *M. batnensis*. The “cloud” of smaller points around each of the landmarks is made up of the actual landmark location for each specimen. Because the larger points are the average position of each landmark, the image imposed on each view will not touch all of the averaged landmarks, but the positions of the landmarks on the specimen are within the cloud of points. Sample Specimen: USNM 468877 from Texas. (Appendix 6A)

function analysis (DFA) also uses predefined qualifiers, but in this case it maximizes the probability of correctly assigning observations to their predetermined group (Quinn and Keough 2002), thus indicating whether populations are different enough to distinguish the origin of a given specimen.

Results

Two-Dimensional Analysis

In a PCA using the row-wise estimation method of both species and all localities combined (Figure 11), the first 3 principal components (PCs) accounted for 86.7% of the total variance in the data. The loadings on PC1 (75.1% variance; p-value, <0.001) with component scores >0.90 are largely measurements related to size - length, width, height, width of interambulacra 3 and 4, and length of petal II. The width of the periproct, width of petal III, and the number of pores in petal III load on PC2 (7.6% variance; p-value, 0.001) with component scores between 0.48 and 0.53. The number of pores in petal I has the highest loading on PC3 (4.0% variance; p-value, <0.001) with a component score of 0.52. The next highest measurements to load on PC3 are the pores of petals II and III and the periproct length and width with component scores between 0.27 and 0.33. In a plot of PC2 versus PC3 the two species visibly separate along PC2, while localities remain mostly interspersed. This means the two species differ most in where the peripetalous fasciole crosses ambulacra III, the pore count on ambulacra III, and the width of the periproct.

Running additional PCAs by species (Figures 12 & 13), results in 86.1% of the variance in *M. batnensis* and 92.0% of the variance in *M. fourneli* being explained in the first three PCs. In each instance PC1 is loaded by measurements related to size. For *M. batnensis* PC1 (73.7%

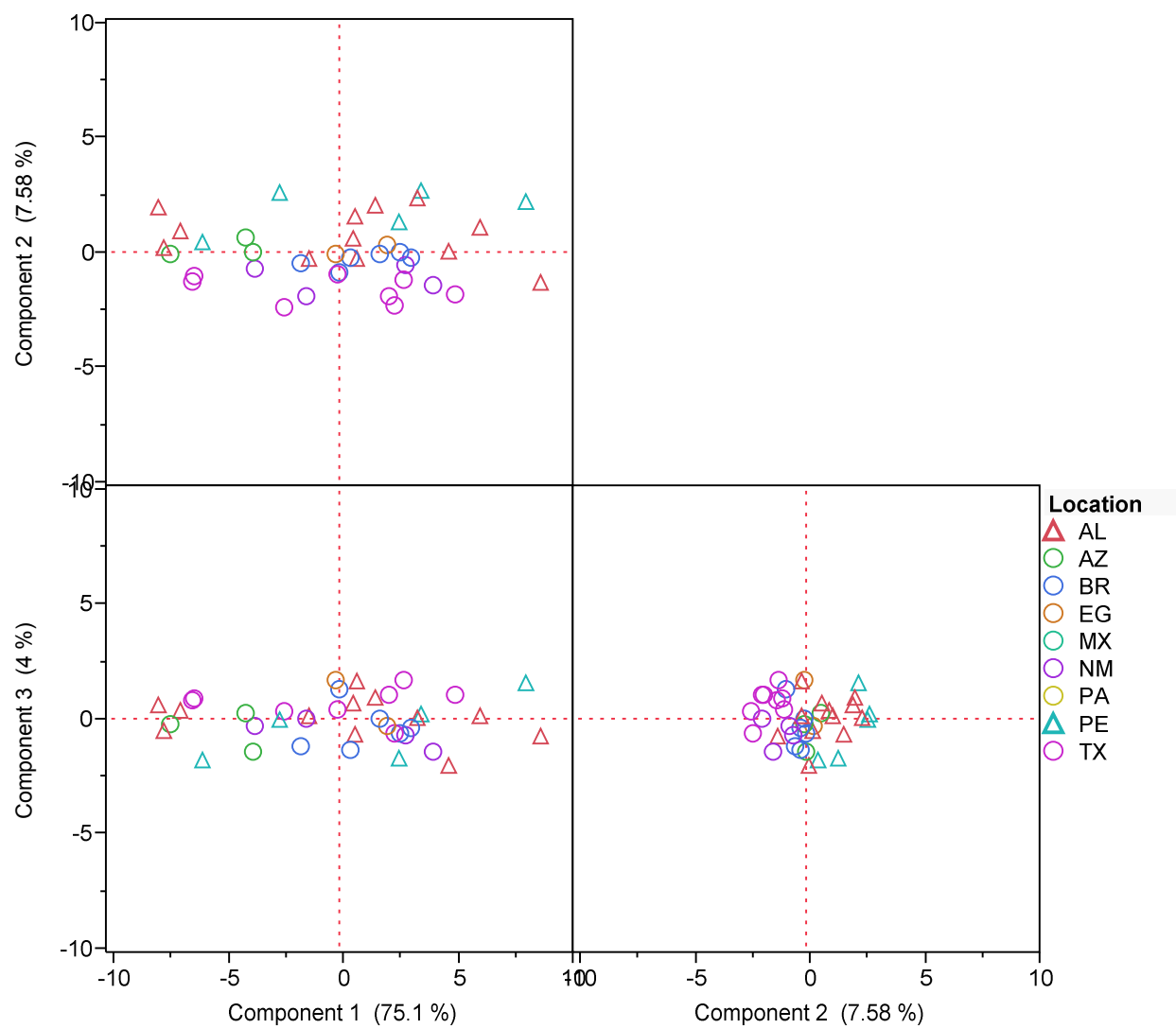


Figure 11. Score Plots of two-dimensional Principal Component Analysis of Both Species Combined. (see also Appendix 4A)

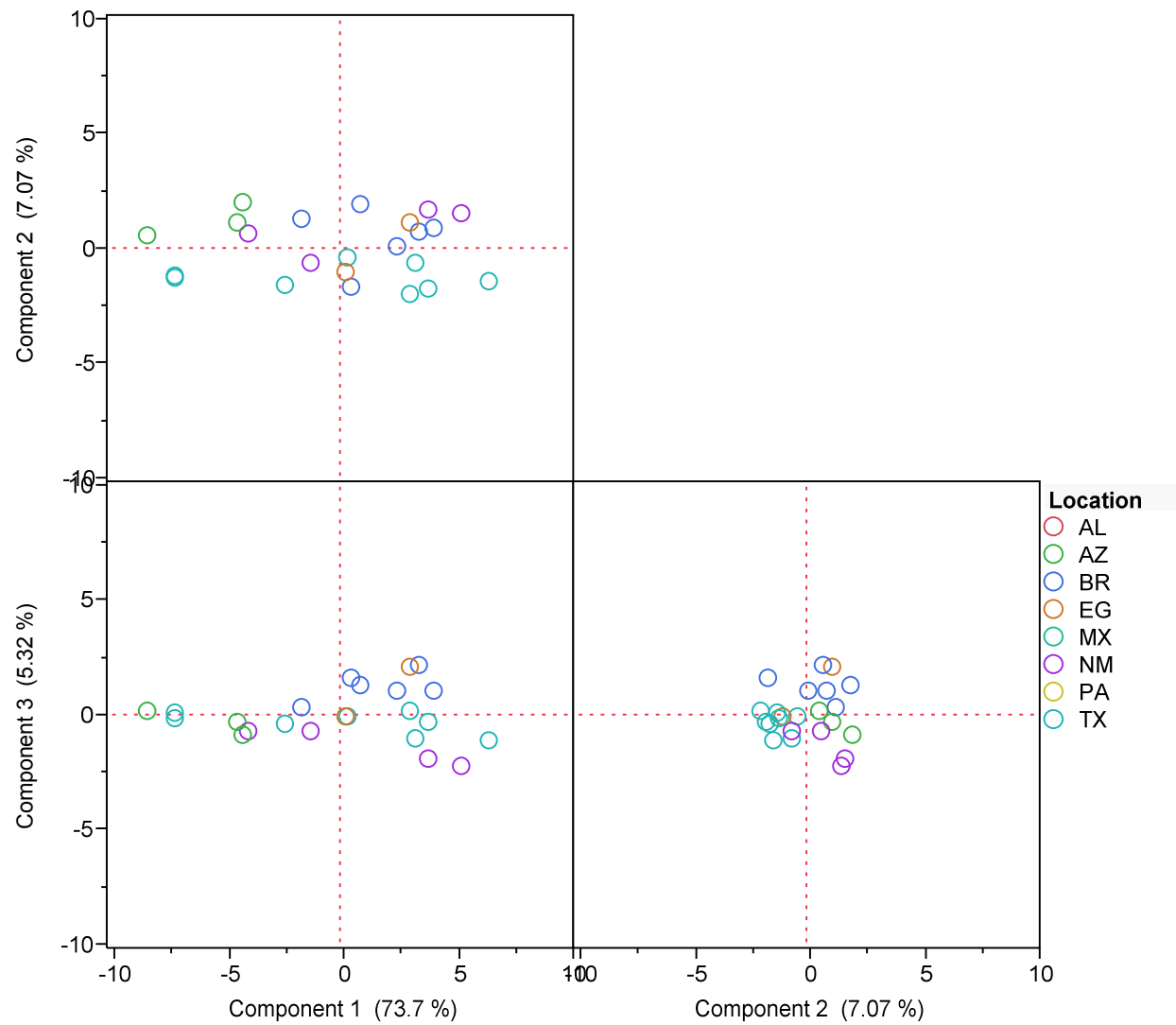


Figure 12. Score Plots of two-dimensional PCA of *M. batnensis*. (See also Appendix 4B)

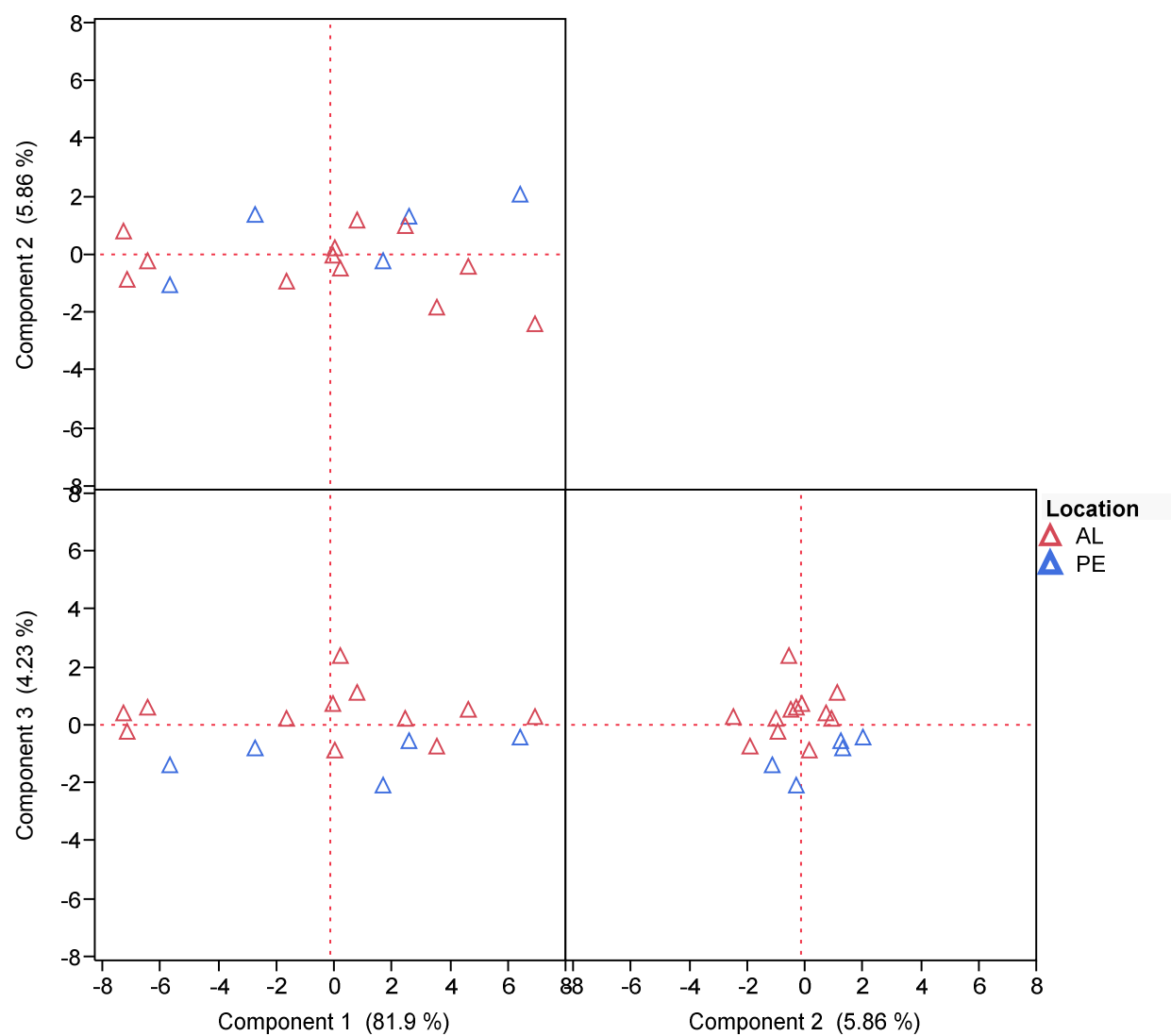


Figure 13. Score Plots of two-dimensional PCA of *M. furneli*. (see also Appendix 4C)

variance; p-value, <0.001) is controlled by length, width, height, petal lengths, and relation of the peristome to the posterior margin, which load with component scores > 0.90. In the case of *M. fourneli*, PC1 (81.9% variance; p-value, <0.001) loads with every component related to size and no measurement loading with a score smaller than 0.69.

The loadings on PC2 and PC3 are more specific with each species. The pores of petal I (component score, -0.58) and width of petal III (0.53) load on PC2 (7.07% variance; p-value, <0.001) for *M. batnensis*; and pore count of petal II (0.51) and peristome width (0.46) are the main controls on PC3 (5.32% variance; p-value, <0.001). Periproct width (-0.62) and length (-0.43) along with ambulacrum III width (0.46) load on PC2 (5.86% variance; p-value, <0.001) for *M. fourneli*; and pore counts for petal I (0.59) and petal III (0.47) with length of petal III (-0.43) load on PC3 (4.23% variance; p-value, <0.001).

Plots of PC2 versus PC3 in each instance show a separation of populations within the plotted grouping of all populations. The Texas, New Mexico, and Arizona populations of *M. batnensis* separate by their scores along PC2, thus they differ in pore counts in petal I and the width of ambulacrum III. These three populations of *M. batnensis* are divided from the Brazil population by their scores along PC3, indicating a difference based on the pores in petal II and the width of the peristome. The two populations of *M. fourneli* show little to no overlap in the way their scores plot and largely separate along PC3, therefore the populations differ in petals I and II pore counts and in the length of petal III.

Canonical plots in both CVA and DFA of two-dimensional data of all populations of both species were initially run prior to running separate analyses by species. The resultant canonical plots were nearly identical, so the more informative DFA will be discussed. The DFA of the two-dimensional data (Figure 14) resulted in no specimens being misclassified. The first two

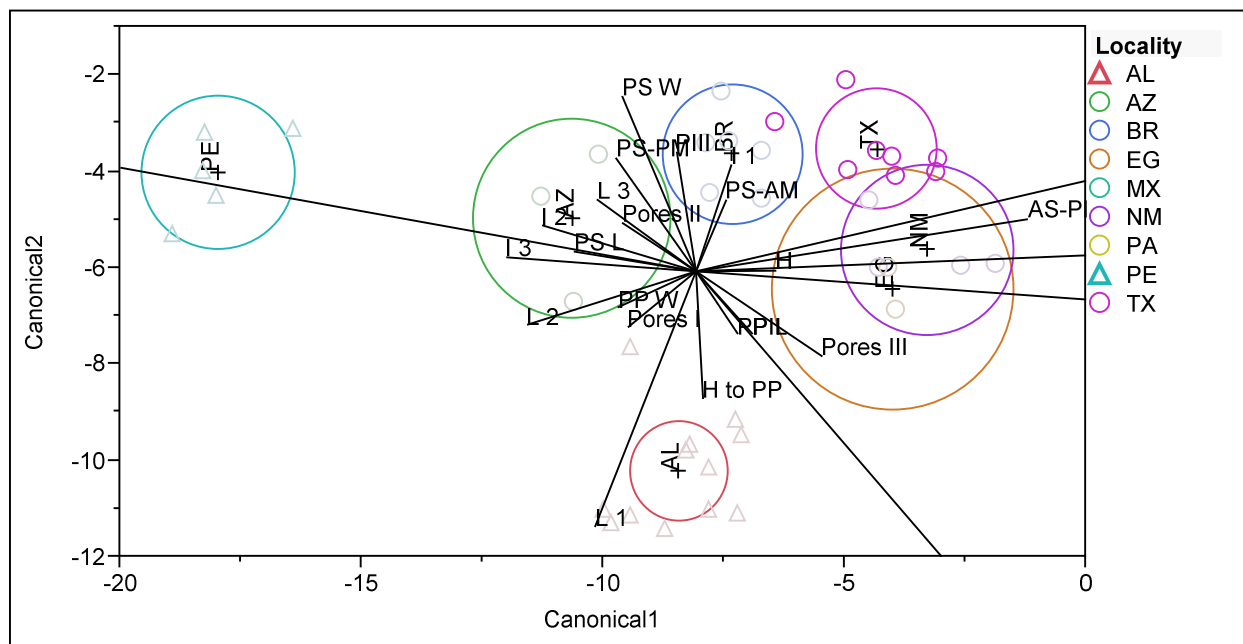


Figure 14. Canonical Plot from two-dimensional analysis of Both Species. (See also Appendix 5A)

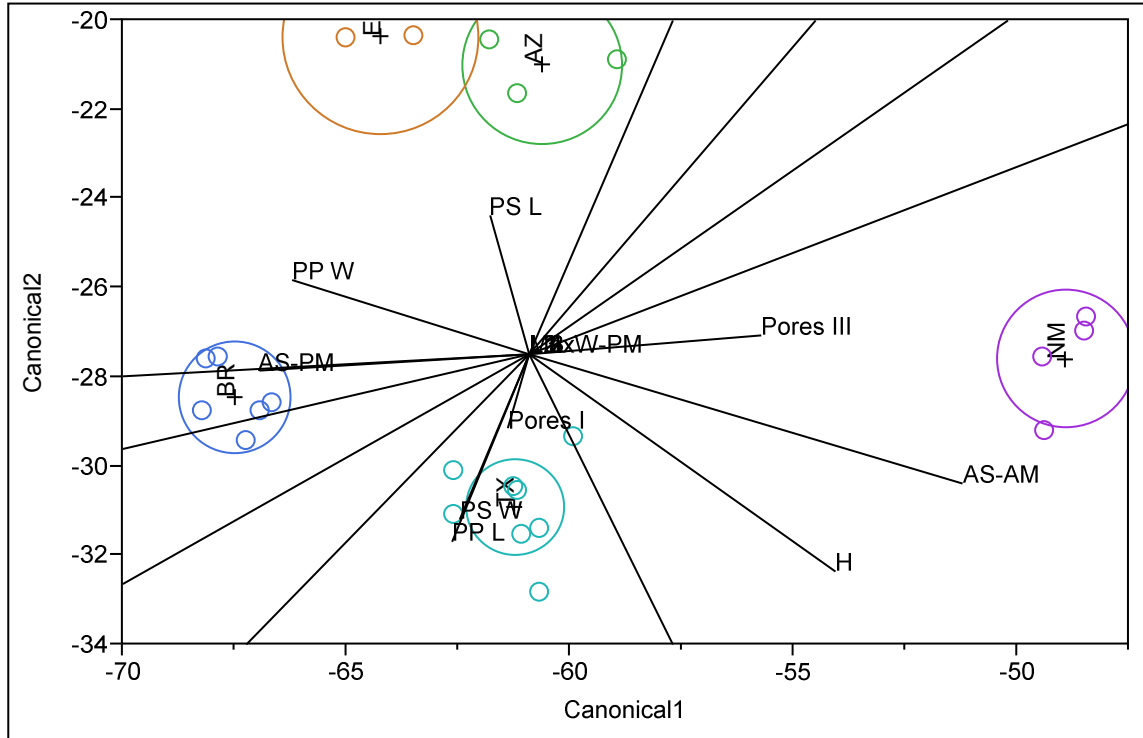


Figure 15. Canonical Plot from two-dimensional analysis of *M. batnensis*. (See also Appendix 5B)

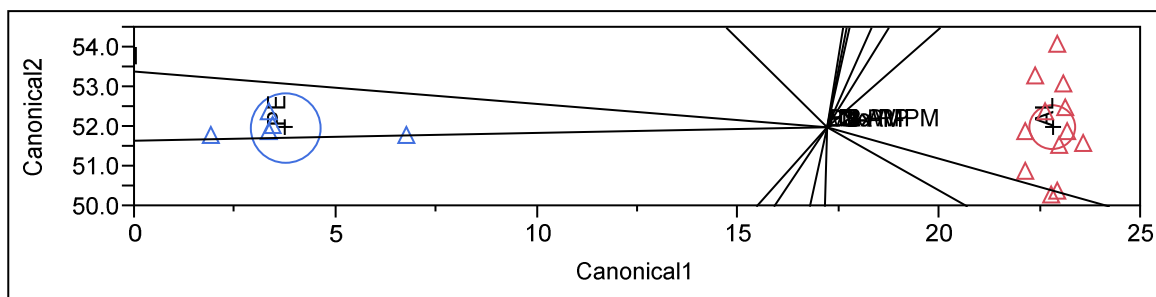


Figure 16. Canonical Plot from two-dimensional analysis of *M. fourneli*. (See also Appendix 5C)

canonical axes explain 72% of the model. The p-values of all canonical axes were greater than 0.2, thus the difference of all populations was not significant. This is most likely a result of genus level similarities between the populations of both species.

In the DFA of *M. batnensis* populations (Figure 15), again, no groups were misclassified. The first two canonical axes explain 81.8% of the model, and all canonical axes had p-values less than 0.0001, falsifying the null hypothesis that the populations are the same. The same analysis of *M. fourneli* (Figure 16) had no misclassifications, and was fully explained in two canonical axes with p-values below 0.0001, again falsifying the hypothesis that these populations are the same.

Three-Dimensional Analysis

Procrustes fit - Each population of *M. batnensis* is characterized by specific deviations from the Procrustes fit of all samples of the species. Average Procrustes fits by population (Figure 17 and Appendix 6G) show variation in location of tips of anterior and posterior petals, the apical system, peristome, peripetalous fasciole along ambulacrum III, and the periproct. The Arizona population is characterized by anterior petals that are shorter than average, posterior petal tips that are closer together and slightly higher than average, apical system and peripetalous fasciole located near average, periproct slightly smaller than average, and an increase in overall height as shown by a lower position of the peristome.

The New Mexico population of *M. batnensis* is characterized by anterior position of the apical system and anterior petal tips. The angle between the tips of the anterior petals is wider, and the posterior petals are slightly closer to each other. The periproct is positioned further down with no change in size, while the location of the peripetalous fasciole on ambulacrum III is lower. The peristome is longer with the anterior angled slightly more upward. The Texas

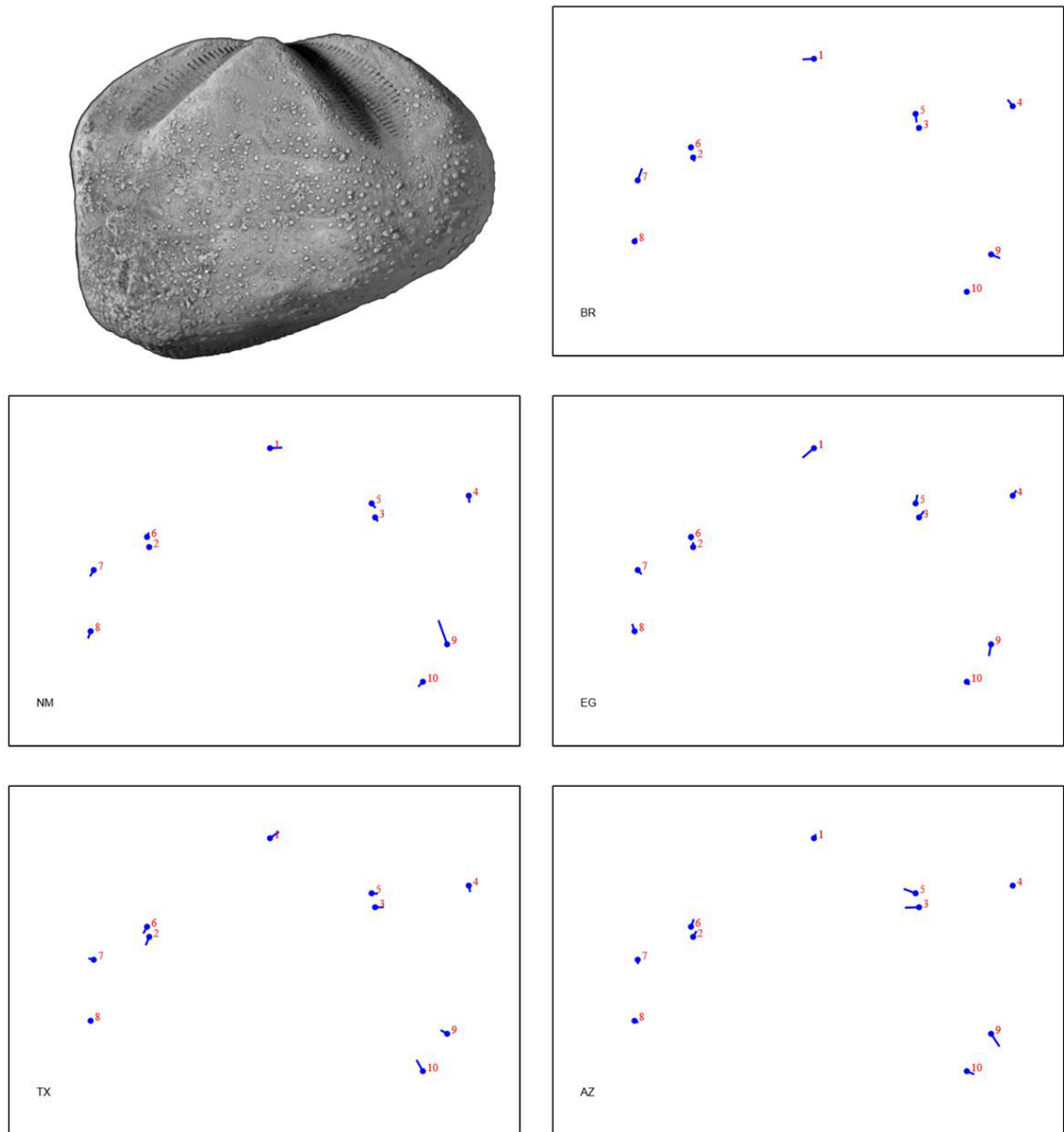
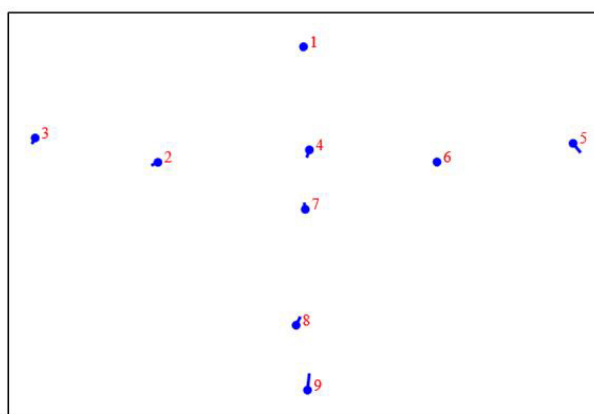
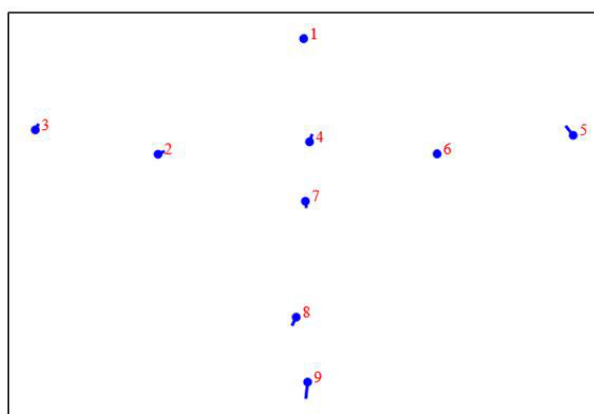
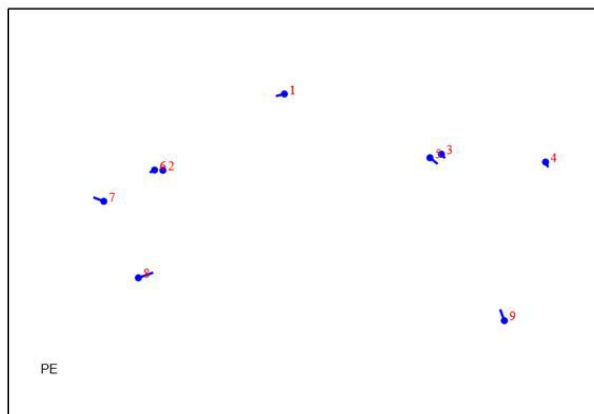
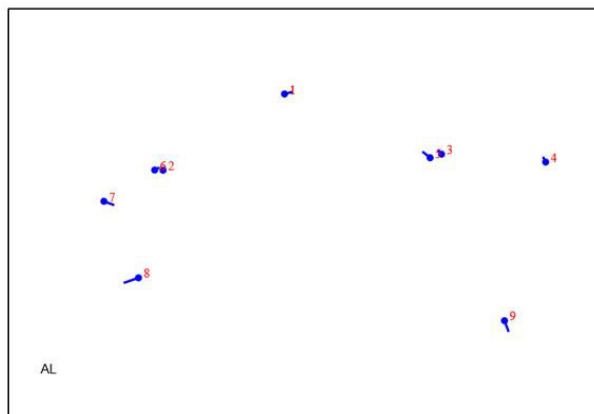
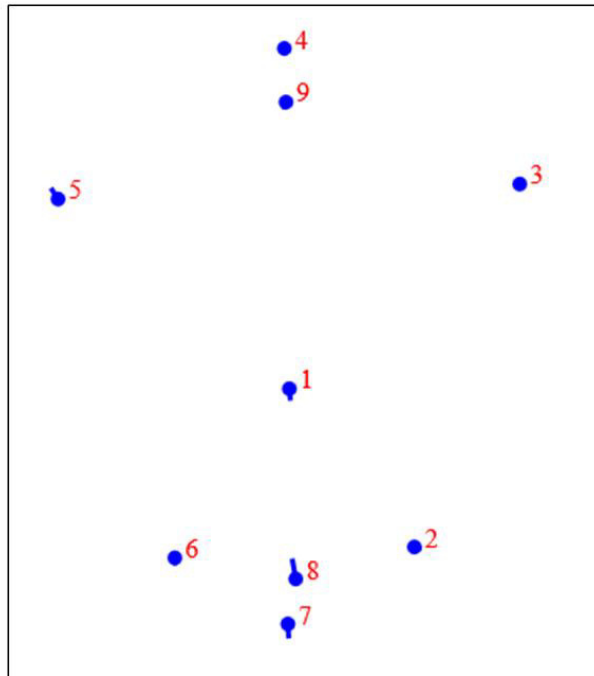
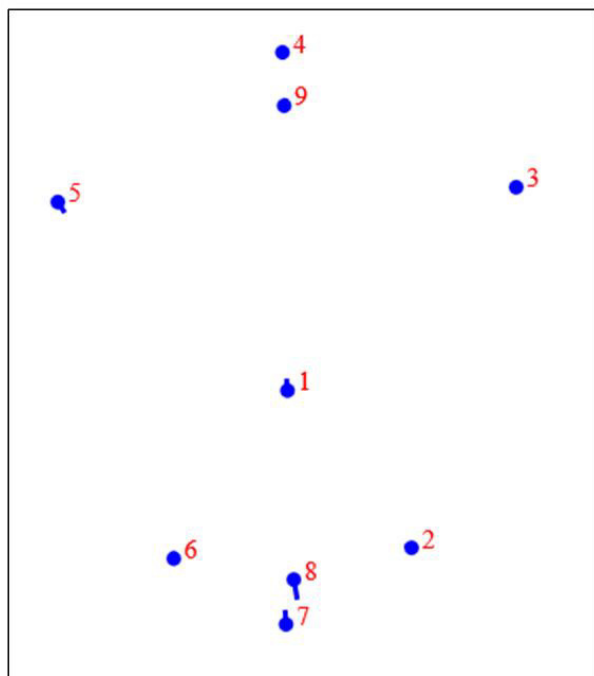


Figure 17. Procrustes fit of *M. batnensis* averaged by locality.

Side view orientation of lollipop diagrams indicating differences between populations from Brazil (BR), New Mexico (NM), Egypt (EG), Texas (TX), and Arizona (AZ). The “candy” marking each landmark is the average shape calculated in the full Procrustes fit. The “stick” radiating from each “candy” indicates the direction and extent of difference of each population’s average shape from the overall average. The majority of variation between these populations is visible in this orientation; other orientations can be found in Appendix 6C.

Figure 18. Procrustes Fit of *M. fourneli* averaged by locality. (Appendix 6D)

All orientations (aboral, side, posterior) of lollipop diagrams indicating differences between the average shape of Peru (PE) and Algeria (AL) populations. The “candy” at each landmark is the average shape of both populations combined. The “stick” radiating from each “candy” indicates the direction and extent of difference of each population’s average shape from the overall average.



population presents similar differences from the average as the New Mexico population in anterior petal tips, apical system, and location of the peripetalous fasciole on ambulacrum III. The posterior petal tips of the Texas population are lower and positioned more toward the posterior. The periproct is angled closer to vertical at landmark 7, and the peristome is closer to the center of the body and is slightly smaller.

The Brazil population is characterized by an apical system which is more posterior, a larger periproct, and a larger peristome which is further out from the average position. The posterior petals are slightly longer and more separated, the anterior petal tips extend further down, and the peripetalous fasciole crosses ambulacrum III further back, though the difference in location of the peripetalous fasciole almost corresponds equally to the difference in posterior position of the apical system.

The small sample sizes of the Egypt and Mexico populations limit the reliability of their characterization. Even so, the population from Egypt appears to have longer anterior petals than average. The tips of the anterior petals are positioned forward while the apical system is positioned more toward the posterior. The peristome is smaller and the periproct is angled away from vertical, and there is little deviation from average of the location of the posterior petals. The Mexico sample is only characterized in the analysis with symmetry (Appendix 6K) and the apical system is more anterior and higher, while the anterior petals are closer. The periproct is lower, but the angle remains the same as average; and the peristome is at a slightly more horizontal angle due to positioning of landmark 10 toward the center of the test.

The average Procrustes fit of *M. fourneli* (Figure 18) shows the Peru population to have longer anterior petals than the Algeria population. The periproct is more vertical in the Peru population, while the peristome is farther from the center in the Algeria population. The apical

system of the Peru population is more to the posterior while the location of the peripetalous fasciole is more anterior resulting in a longer distance between the two features on ambulacrum III than is found in the Algeria population. Despite the differences in the anterior portions of the test, there is no difference in the posterior petal landmarks.

Principal component analysis -PCA of all specimens of both species combined explains 67.6% of the variance in the first three principal components. Principal Component 1 explains 34.5% of the variance, PC2 explains 24% of the variance, and PC3 9.2%. The two species separate largely along PC2 (Figure 19) with little overlap of groupings, though they fit together in one large overall group which can be interpreted to confirm generic relationship.

Principal Component Analysis of *Mecaster batnensis* results in 70.2% of the variance being explained in the first three principal components. Principal Component 1 explains 34% of the variance. Along PC1 the Texas and New Mexico populations lie to the side of all other populations. The plot of PC2 (22.8% of variance) with PC3 (13.4% of variance) shows the majority of samples from individual localities grouping mostly by locality within the overall grouping. A sample from Brazil and one from New Mexico lie outside the main grouping of this PCA. Upon assessing the samples further one shows evidence of taphonomic effects with separation of plates along the perinterradial suture of interambulacrum 5, and the other is a misidentified specimen upon evaluation of its pseudo-triangular test shape.

Rerunning the analysis with these two samples removed results in a 64% of the variance being explained in the first three PCs (Figure 20). This time all groups except Egypt separate with some overlap in a plot of PC1 (32.9% of variance) and along PC2 (17.2% of variance). Principal Component 3 (14.3% of variance) also divides the populations, but with more overlap of populations.

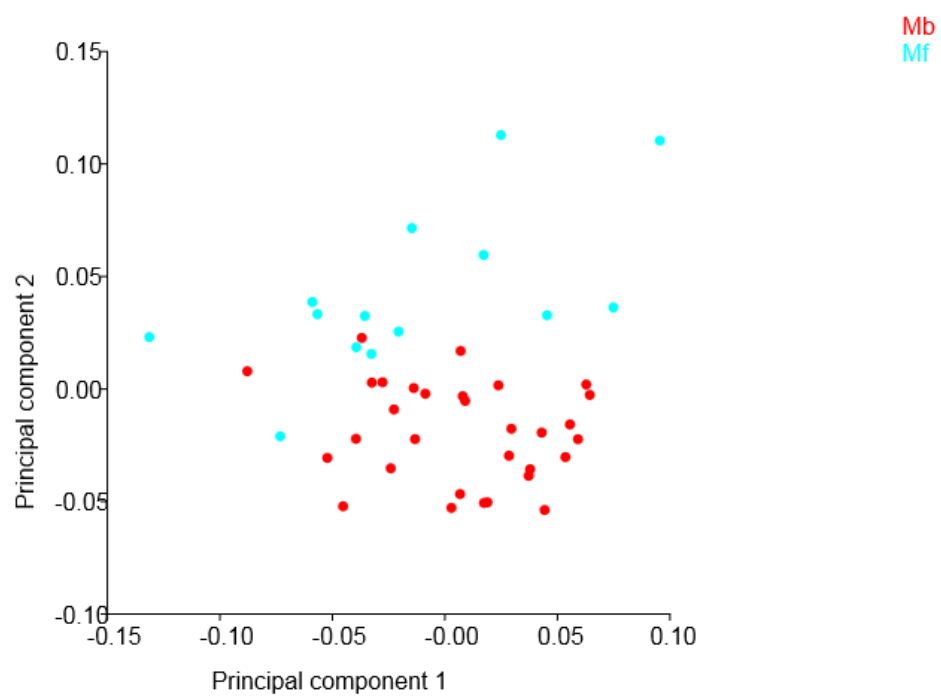
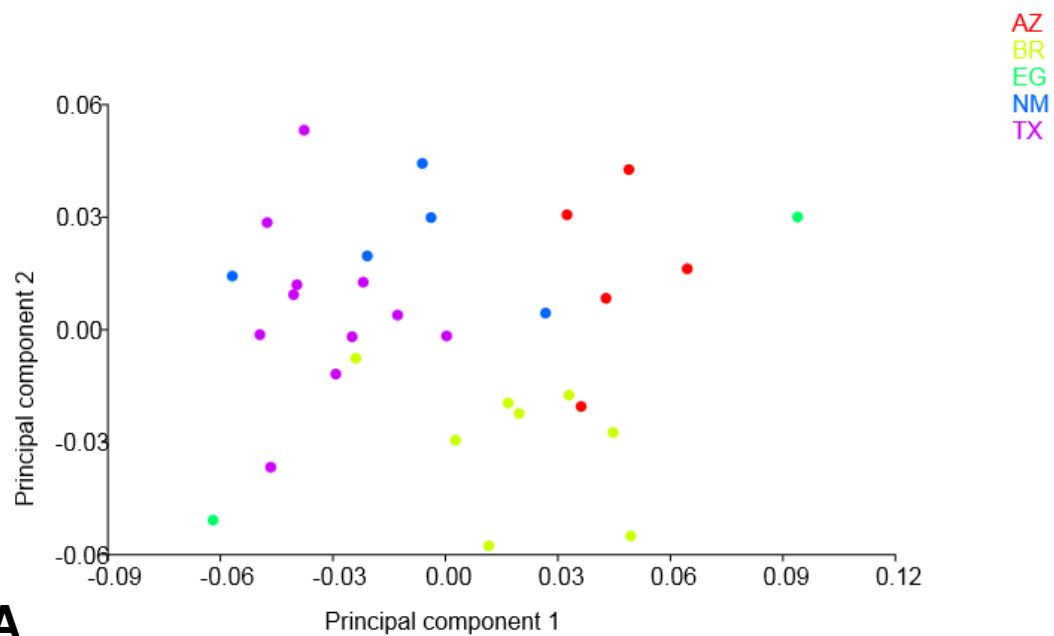


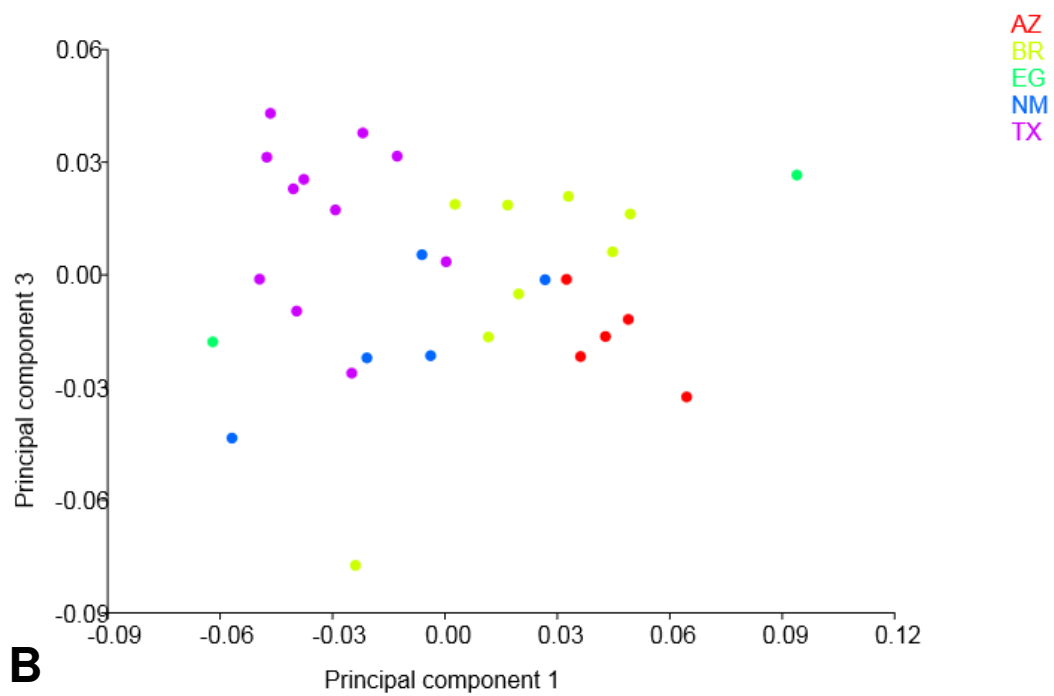
Figure 19. PCA of three-dimensional data for both species combined. (Appendix 7A)

Figure 20. PCA of *M. batnensis* three-dimensional data.

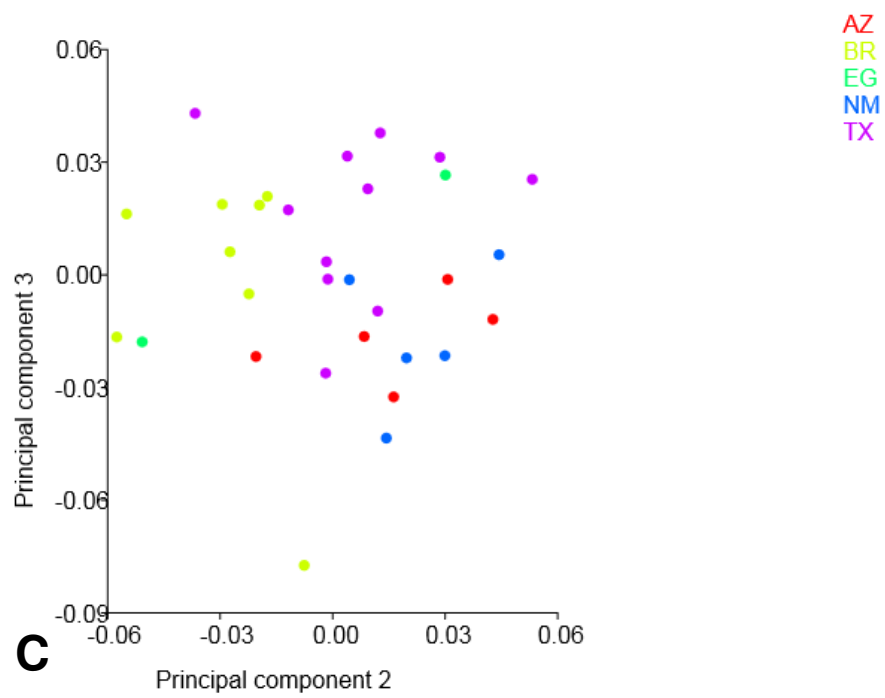
The first three PCs are compared to each other. All axes are scaled equally. (See also Appendix 7B)



A



B

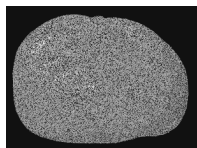


The x component (Cartesian coordinate of landmarks in Procrustes units) of landmark 1, which represents the location of the apical system, is a major factor of PC1 (PC Coefficient, -0.28) and PC2 (PC Coefficient, 0.41). The y component of landmark 1 is a large component of PC3 (PC Coefficient, 0.45). The x component of landmarks 3 and 5 (anterior petal tips) is the largest factor of PC1 (PC Coefficients, -0.35 and -0.36), and the z component of the same landmarks contribute to PC3 (PC Coefficients, -0.38 and 0.50) nearly equally as the y component of landmark 1. The y component of landmarks 2 and 6 (posterior petal tips) is a factor on both PC1 and PC2 (PC Coefficients, >|0.22|). And the x and y components of landmarks 9 and 10 (the peristome) (PC Coefficients, >|0.28|) factor nearly as much landmarks 3 and 5 on PC1. The y component of landmarks 7 and 8 (the periproct; PC Coefficients, -0.46 and -0.35) is the largest factor of PC 2. These coefficients represent variation in the length of the posterior and anterior petals, the more downward position of the peristome (possibly indicating a change in overall height), and positioning of the apical system toward the posterior in PC1 (Figure 21A); variation in the posterior petals, the apical system, the location of the peripetalous fasciole, and the location of the periproct in PC2 (Figure 21B); and lengthening of the anterior petals and an upward position of the apical system in PC3 (Figure 21C).

The first three principal components of a PCA of *Mecaster fourneli* explain 89.4% of variance (Figure 22A). The Algeria population groups tightly, while the Peru population lies loosely along one side of the Algeria grouping. Four samples from Algeria and one from Peru lie outside of the main grouping. Further evaluation of the outer samples confirm correct identification of four and misidentification of one specimen with a rounder flatter test shape. The four correctly identified samples had various taphonomic issues that were not identified in initial

Figure 21. Lollipop diagrams for Principal Components of PCA of *M. batnensis*.

The vectors at each landmark indicate the direction and extent of the variance between localities explained in the Principal Component indicated. e.g., Landmark 1 in PC1 explains the posterior positioning of the apical system as represented by the landmark (A). While PC2 of the same landmark explains the anterior and upward positioning (B), and, lastly, PC3 explains the posterior and upward positioning of the landmark (C).



1

53

4

62

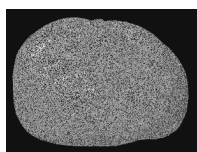
7

8

A PC1

9

10



1

53

4

62

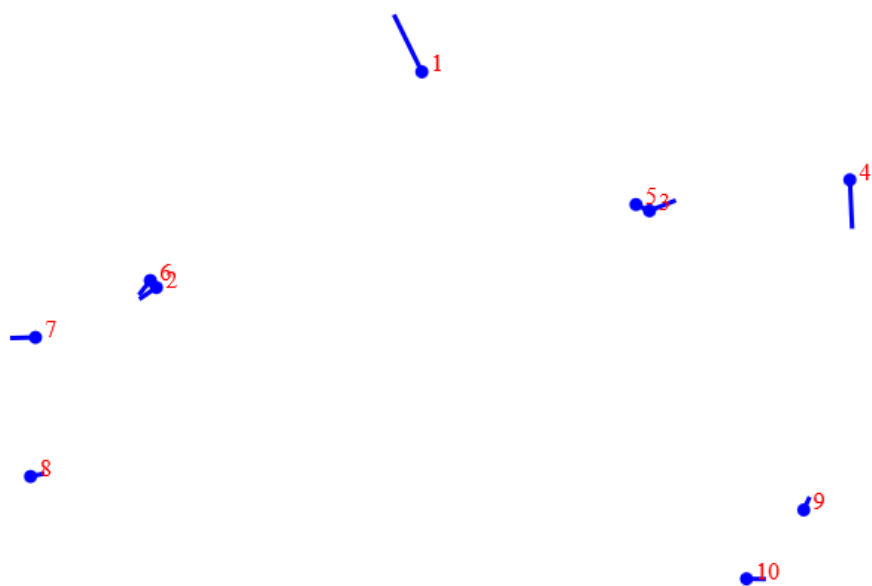
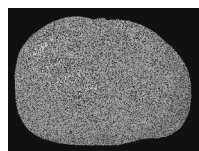
7

8

B PC2

9

10



C PC3

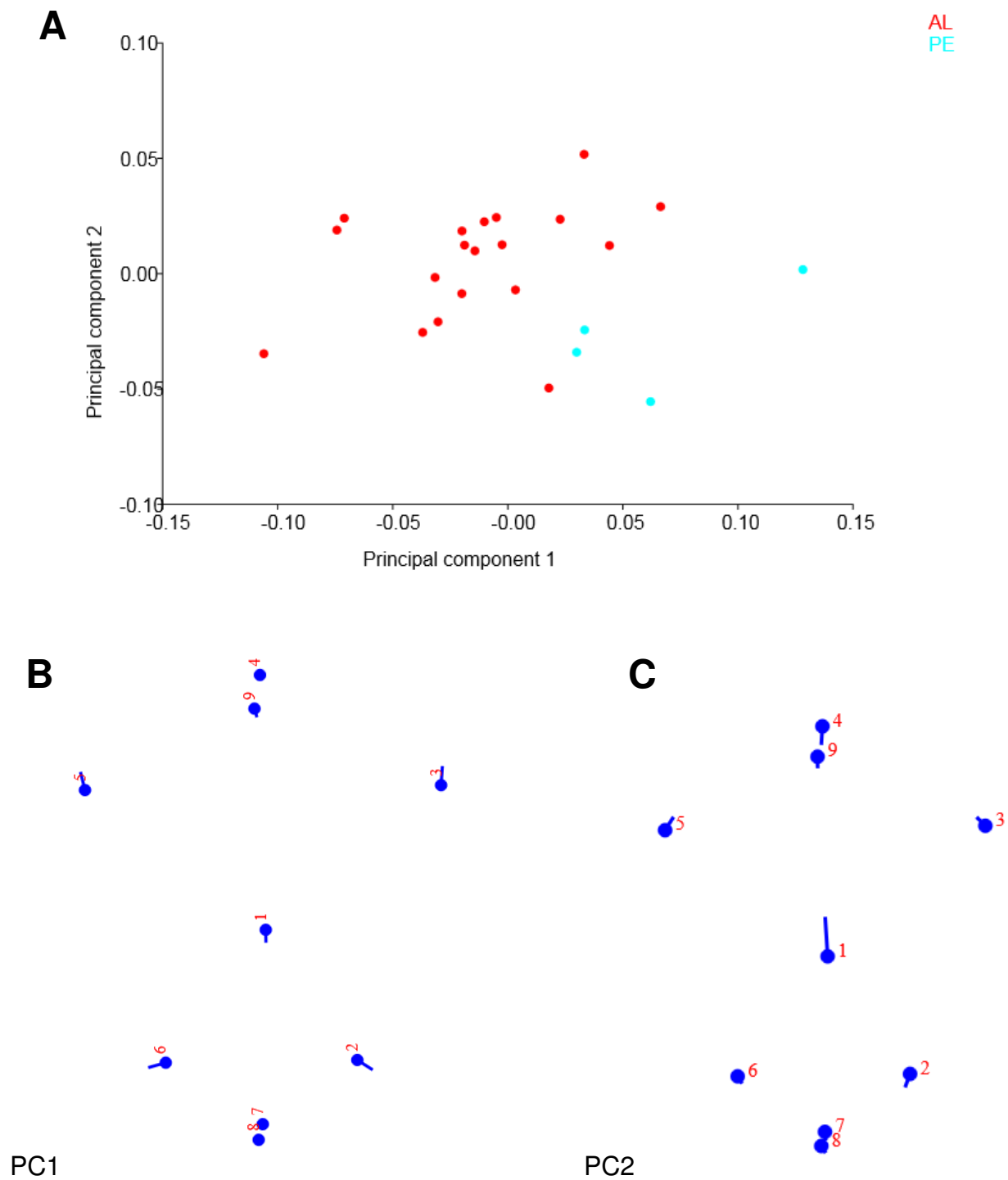


Figure 22. PCA of *M. furneli*. (see also Appendix 7C)

specimen preparation. The new PCA results in 76.2% of the variance explained in the first three PCs.

Principal Component 1 (50.1% of variance) is most influenced by the z component of landmark 9 (PC Coefficient, 0.58). The next highest loadings are <0.29 and include components of the landmarks 2, 3, 5, 6, and 8. The differences represented by PC1 include more posterior position of the apical system, upward position of the peristome, more anterior position of the anterior petal tips, more posterior position of the posterior petal tips, and upward position of the periproct and peristome with a change in shape of the peristome to be smaller (Figure 22B). The populations begin to mix more in PC2 (14.8% of variance) and continue to mix through later PCs. The highest component of PC2 is the z component of landmark 4 (PC Coefficient, 0.34) where there is a more downward position to where ambulacrum III reaches the peripetalous fasciole (Figure 22C). The same component contributes to PC3 (10.7% of variance) with nearly the same PC Coefficient (0.32); however, the x component of landmark 9 (PC Component, 0.53) is the highest contributing variable.

Canonical Variate Analysis - CVA of three-dimensional landmark data for *Mecaster batnensis* results in the first two canonicals explaining 96.1% of the variance among populations of *M. batnensis*. In a plot of CV1(88.9% variance) with CV2 (7.2% variance; Figure 23) the population from Brazil plots in the center with the Egypt population separated far to the left along CV1 and the Arizona, New Mexico, and Texas populations plotting to the right along CV1. The variance in CV1 is explained by the peristome being positioned more toward the interior of the test and an upward and anterior difference in location of the apical system (Figure 24a). The three populations from Arizona, New Mexico and Texas are separated along CV2, which is a result of

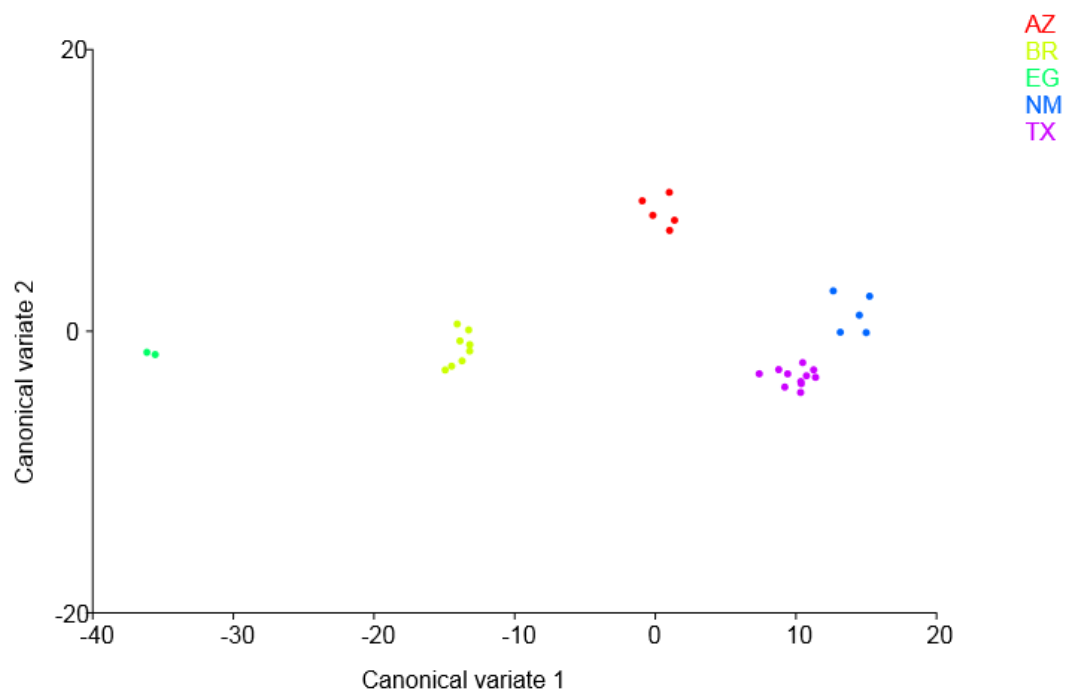


Figure 23. CVA of *M. batnensis* three-dimensional data with outliers removed. (see also Appendix 8A)

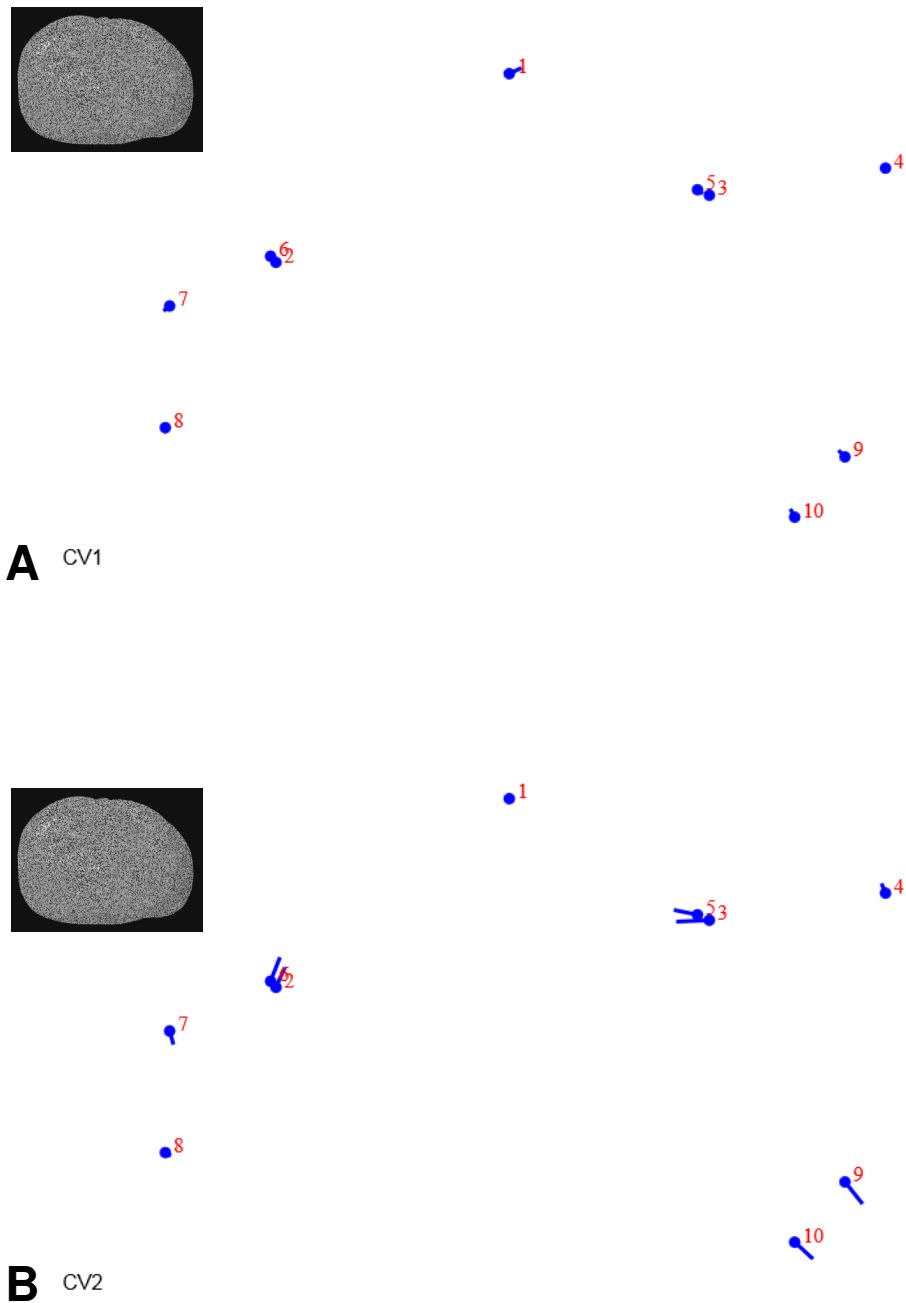


Figure 24. CV2 of CVA by locality of *M. batnensis*.

The vectors at each landmark indicate the direction and extent of variation between localities explained in Canonical 1 (**A**) and Canonical 2 (**B**). Note the small length of these vectors; they are scaled up by a factor of 4 in order to make them more visible. (see also Appendix 8A).

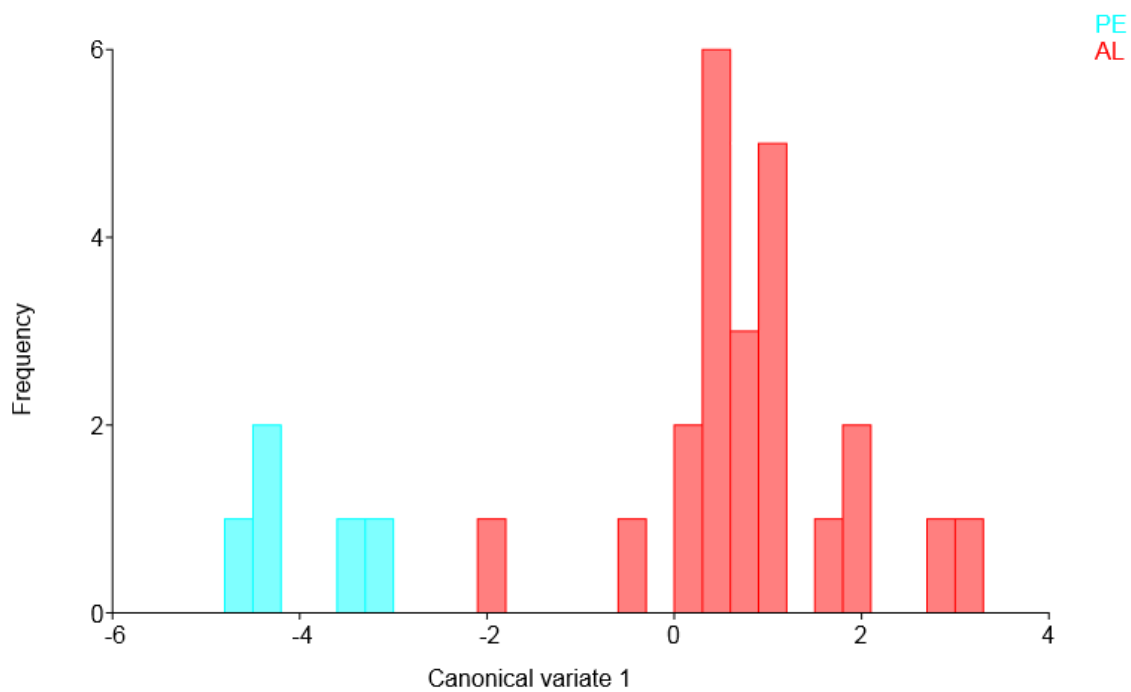


Figure 25. CVA of *M. furneli* three-dimensional data.

As only two populations were compared in this analysis there is only one canonical. (For lollipop diagrams associated with this analysis see Appendix 8B)

large difference in the location of the peristome and variation in anterior and posterior petals. (Figure 24b). The differences between populations on CV3 (2.7% of variance) and CV4 (1.2% of variance) are small relative to CV1 and CV2. Differences in the peristome and periproct size along with differences in the location of the apical system are manifest on CV3 while CV4 reflects variation on almost every landmark.

The same analysis on three-dimensional data for *Mecaster fourneli* explains the variance completely along CV1 with no overlapping of the populations (Figure 25). The variation between these two populations is explained by an upward position of the peristome, a posterior positioning of the apical system, more anterior position of anterior petal tips, and positioning of the anterior edge of the peristome anteriorly and upward.

Discriminate Function Analysis - DFA of three-dimensional data for *M. batnensis* results in no misclassifications. Mahalanobis distances between populations of *M. batnensis* ranged from 0.897 to 9.54. Using the T-square statistic to run a permutation test (1000 runs) the p-values for Procrustes distances and T-square statistics are 0.001, or less, for all comparisons except Arizona and New Mexico classifications and any comparison made with the Egypt population (n=2). While the DFA between Arizona and New Mexico populations reports no misclassifications between the two populations, the Procrustes distance p-value is 0.0130 and the T-square statistic p-value is 0.075, failing to reject the hypothesis that the Arizona and New Mexico populations are different. DFA of three-dimensional data for *M. fourneli* run with a permutation test (1000 runs) using the T-square statistic reports no misclassifications and a p-value of <0.0001 for the Procrustes distance, but only a p-value of 0.3020 for the T-square statistic. The Mahalanobis distance between these two populations is 13.2122.

Analysis of Error

Repeated measures of landmarks were performed on the 3D mesh of a single specimen. Principal component analysis was performed to compare other specimens of the same species (Figure 26). User error is minor especially with respect to the variation seen within the species. Smaller, darker markings would make identifying landmarks on the 3d mesh easier and possibly further remove error.

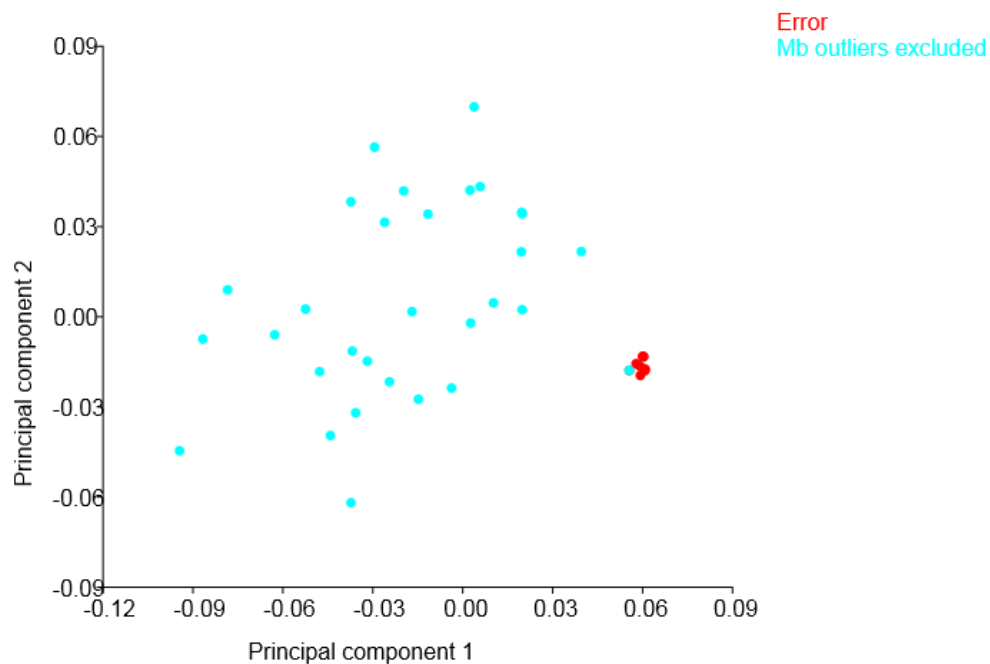


Figure 26. PCA of *M. batnensis* and Error measurements for three-dimensional data.

Repeated measures of landmark points for a single specimen were collected and plotted with all of the measurements of that species. User error is minor, but could be improved by better markings on specimens; however, markings could not be permanent, which eliminated finer marking tools so a mechanical pencil was used.

Discussion

Sampling size

Sampling size turned out to be less than ideal in most localities and essentially unusable in a few. Sample sizes of $n=1$ eliminated the Palestine, Algeria, and Mexico populations of *Mecaster batnensis* from being included in most analyses. The two samples from Egypt fit in with the larger group of *M. batnensis* samples, but any conclusions made regarding these two samples may in fact not reflect the actual Egypt population. The Brazil and Texas populations ($n=10$ and $n=12$) are near the general ideal threshold for minimum sample size ($n=10$), while the New Mexico and Arizona populations ($n=6$ and $n=5$) are just large enough to begin to be informative. The Algeria population of *M. fourneli* is the largest sampling of any one population ($n=27$) though the usable number dropped to $n=23$ when taphonomically damaged or deformed samples were identified and removed. This sample size increases the precision of any conclusions regarding this population, and a solid baseline upon which to compare the smaller sampling of the Peru population ($n=9$). The Peru sample of *M. fourneli* turned out to be less robust than the 9 measured when only 4 samples had complete information and could be used in the three-dimensional analysis. Again this smaller sampling is just sufficient to be informative.

Patterns of variation in M. batnensis and M. fourneli

The results of the two- and three-dimensional analyses confirm a pattern of paleobiogeographic variation. Some components of the patterns involved confirm the preliminary hypotheses that height is a major factor of variation in *M. batnensis*, and other components of analysis indicate features beyond general test size that are varying. In the Peru population of *M. fourneli* the two-dimensional analysis indicates petal II is longer as compared to

the Algeria population. Pore density in petal II also decreases with this change. This change is also seen in the three-dimensional data as the petal tips marked by landmarks 2, 5, 3, and 6 stay in the average location on a Procrustes fit and the apical system is located more toward the posterior. There is no change in petal I pore density so an increase in both the average length and width of the Peru population accommodates this change in shape. The other difference between the Algeria and Peru populations of *M. fourneli* is in the width of ambulacra III, which is relatively wider (by 10%) in the Algeria population when compared to the width of the test. The three-dimensional landmark scheme could not measure this type of change, though points used in Eble(2000) on the ambitus could have identified any changes in the sulcus. The scheme used in this present study identified in the Peru population a more anterior position in where the peripetalous fasciole crosses ambulacrum III. This positioning may only be a function of the location of the fasciole relative to the length of the anterior petals. Corresponding with this difference in shape is the location of the peristome. It is located more anteriorly in the Algeria population. Not all differences between populations are limited to the anterior of the test. The periproct in the Algeria population is closer to vertical, while the periproct in the Peru population is less vertical. These differences combined make the Peru population slightly more wedge shaped than the Algeria population.

In the populations of *M. batnensis* the peristome varies in width. Interestingly, the width of ambulacrum III varies in a similar pattern, but in the inverse of the variation in peristome width. Thus, the Brazil population with the widest peristome has the narrowest ambulacrum III, and the Arizona population, the narrowest peristome and the widest ambulacrum. The pore densities of petals I and II usually differ by 0.2 - 0.4 pores per mm between the petals of the test in each population; however, the pore densities of petals in each population differed into two

groupings. Brazil and Arizona populations have pore densities of 3.6 and 3.7 pores per mm on petal I and pore densities of 3.5 and 3.3 pores per mm on petal II, while the same densities on the New Mexico and Texas populations are 3.01 and 3.1 pores per mm on petal I and 2.7 and 3.1 pores per mm on petal II. This lower pore density in the Brazil and Arizona populations corresponds with the shorter petal lengths in petals I and II. The patterns of shape change found in the three-dimensional analysis correspond with these observations from the two-dimensional data. The Procrustes fit lollipop diagrams of each population (Appendix 6C) characterize the reasons for differences in petal length. The Brazil population has shorter posterior petals that reflect a more posterior position of the apical system, rather than the petal being shorter at the tip. The Arizona does not have any change in posterior petal length, but the petals do close in the angle between each other. The posterior petals in the new Mexico population also have the angle closed in between them, but the petals are longer by the more anterior position of the apical system. The anterior petals shorten in the Arizona population, while they lengthen in the New Mexico population. In the Texas population all of the petals are longer. These differences in petals between populations are reflected in the three-dimensional analysis - both the PCA and the CVA.

Relationship of variation to Ontogeny

In order to eliminate the possibility that the variation identified between populations is merely an ontogenetic effect the centroid size¹ of each specimen can be compared to the first principal component from the analysis of the two-dimensional data for the same specimens. As PC1 is mostly a function of size it can be considered a proxy for the age of specimens. If there is

¹ Calculated as the square root of the summed squared distances of each landmark from the centroid of the three-dimensional landmark configuration (Zelditch et. al. 2012)

an ontogenetic effect and/or sampling of specimens only representative of a certain size, then the populations from each locality will group separately along the regression line of this comparison; however, if there is no effect then the specimens of all populations will be interspersed along the regression line. In the case of the comparison of the centroid size and PC1 of the *M. batnensis* specimens (Figure 27), the later is mostly the case, save for the Arizona population which only has smaller samples on one end of the regression line, however the Arizona population is interspersed with the smaller samples from Texas and New Mexico. Thus, in general there appears to have been little to no ontogenetic effect in sampling of the populations of *M. batnensis*. Results are similar for the two populations of *M. fourneli*, though specimens in the Algeria population range both smaller and larger than specimens of the Peru population.

Biologic interpretation of Paleobiogeographical variation in M. batnensis and M. fourneli

Variation and speciation in echinoids have been related to sediment types (e.g. Ciampaglio 2007 and the clypeasteroid *Periarchus lyelli* in the Southeastern and South-Central United States), or to climate (eg. Stokes 1975 and the genus *Mecaster* in Europe). Spatangoids evolved as burrowers (Kier 1982), and, as mentioned earlier in this text, the wedge shape found in hemiasterids (Kanazawa 1992) is one such development. The shape of spatangoid tests have been correlated to sediment type - species with flat type tests and globular type tests are found in sandier sediment, while wedge shaped tests are found in muddy sediments (Kanazawa 1992). The tests of *M. batnensis* are more globular than *M. fourneli* which is more wedge shaped, but the difference between the two species is not so extreme. The globular shape has been correlated to deeper burrowing (Kanazawa 1992), so any variation in relative height of the test may be related to burrowing depth in *M. batnensis*. One interesting feature of the *Mecaster* test is the angled

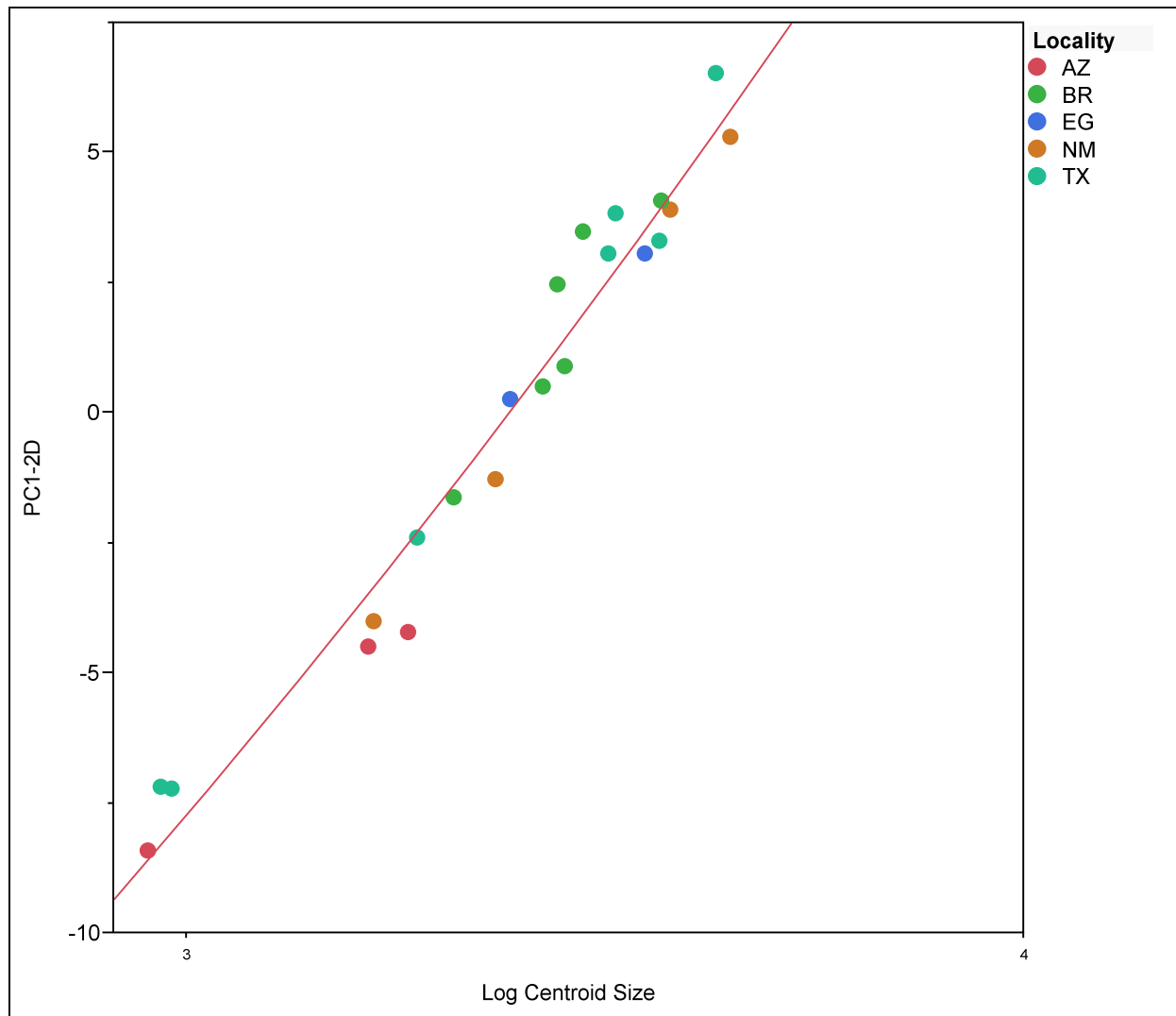


Figure 27. Log Centroid Size vs. PC1 for *M. batnensis*.

The log centroid size of the three-dimensional data, used in performing the full Procrustes Fit for *M. batnensis*, compared to the first Principal Component of the PCA performed on the two-dimensional data for *M. batnensis* ($R^2=0.96213$).

flattened surface surrounding the periproct. Though the only functional difference in that region of the test that has been shown to be related to sediment size is the presence of a subanal fasciole in *M. fourneli* in finer muddy sediment. None of the specimens in this study possessed this feature.

The morphologic variation identified in this study between the two populations of *M. fourneli* was in the overall wedge shape of the test. The different profiles of the tests in each population may be a result of adaptation to the sediment in the respective basins of each population. The Peru population being more wedge shaped presumably lived in finer sediment than the Algeria population.

The greatest variation in populations of *M. batnensis* was found in the location of the apical system and in lengths of the petals. With these variations came differences in pore densities. Differences in climate cannot explain the difference as Arizona was in the same latitude as New Mexico and Texas and it groups with Brazil which was in tropical latitudes. The similarity between the Arizona and Brazil populations is that the basins are closer to exposed land, while the New Mexico and Texas basins are in more open water. Perhaps sediment input from the continents affected oxygen levels and a few more tube-feet facilitated better breathing. Likewise, sediment could explain the differences in peristome width and the width of ambulacrum III, but confounding a unified answer to these variations between populations is the fact that the Arizona population matches with Brazil in one variation, but is the complete opposite in the other. Specific information regarding the sediment in which specimens were found would assist in making an interpretation relating sediment to test size, though as discussed earlier this information was not available with the specimens in the USNM collection.

Conclusion

This study demonstrated the utility of three-dimensional landmark morphometrics in distinguishing variation between localities of the same species. Both two-dimensional and three-dimensional schemes identified similar patterns of variation. The information provided by each analysis overlapped, but each scheme provides different information in ways which are unique to the scheme. The most variation in the two-dimensional scheme came out of the pore counts on petals, most likely because all other measurements were so intimately tied to size. Thus, due the way in which three-dimensional landmark analysis removes size effects information regarding shape is able to emerge.

Two-dimensional analysis can provide sufficient results to identify patterns of variation and identify specific causes for said patterns. The robustness of three-dimensional analysis was demonstrated here when the three-dimensional PCA identified two misclassified specimens (one from each species data set), and five taphonomically altered specimens. When the data for these specimens were removed from the three dimensional analysis the groupings on the PCA plots became more evident, and in the CVA of the three-dimensional data, the population groupings separated completely from each other. When these data were removed from the two dimensional analysis little change was noted on a PCA of both species combined and one of just *M. batnensis*. Only the data set for *M. fourneli* presented a demonstrably visible change, though the information gleaned from this change was simply further confirmation of a previously visible pattern. Three-dimensional landmark analysis allows for more specific understanding of variation; however, such analysis produces at least a three-fold increase in analytic output to be evaluated. The amount of time to gather three-dimensional data and the time needed to handle all of the analytic output is a cost one must consider when weighing the benefits of doing such an

analysis.

Three-dimensional analysis characterizes the whole shape of an organism insofar as the landmarks are properly selected. It would be interesting to see what variation in shape occurs around the ambitus, but better techniques to repeatably mark these points need to be created. This study would have benefited greatly from more quality specimens from each locality. Beyond more specimens from localities, more localities from which specimens are sampled would better characterize the global patterns of variation in these species. Further improvement in understanding could also be gained from stratigraphically located samples, improving the resolution on patterns within localities as well as identifying more complicated patterns between localities. In the future these techniques can be used to build a better phylogenetic hypothesis of the genus *Mecaster* or to better understand patterns of speciation. A more complete morphometric scheme could capture the morphospace of all echinoids more fully.

CHAPTER III FUTURE WORK

Introduction

While completing the research comprising Chapters I and II, a number of ideas for further research came to mind. The current research explored paleobiogeography of two *Mecaster* species. Further similar research could be done on the entire genus, and may identify larger evolutionary patterns. The three-dimensional morphometric scheme used in this study was simplified, and an improved three-dimensional morphometric scheme could better capture variation in echinoid test shape. Such a measurement scheme may prove useful in understanding test shape in larger clades of echinoids or even all post-Paleozoic echinoids. Lastly, the apparent patterns of diversity mentioned in Chapter I, which were cited as reasons for focusing on a fossil spatangoid genus, may be an indication of a larger taphonomic pattern in spatangoid preservation. An evaluation of the overall fossil record of echinoids may identify reasons for this apparent pattern of preservation.

Future work

Phylogeny and Paleobiogeography

Most research on spatangoids has been limited to European and North American occurrences with minor consideration of African populations. This project sought to build knowledge on two species found in South America, North America, and Africa. The two spatangoid species chosen as the focus of this study (*Mecaster batnensis* and *Mecaster fourneli*) are only a small subset of *Mecaster* and *Hemiaster* species which can be studied to better understand the echinoid family Hemiasteridae. Hemiasteridae comprises a monophyletic group

derived from *Hemiaster* (Néraudeau 1994), leaving *Mecaster* in an *incertae sedis* family with the genus *Palhemiaster*, a sister clade to Hemiasteridae. Combining the data from this study with similar data from other *Mecaster* and *Hemiaster* species could result in a better, more complete, phylogenetic hypothesis of the two groups and facilitate further study of paleobiogeographic relationships of related species.

With a more complete phylogenetic hypothesis, evolutionary trends related to environmental and/or stratigraphic differences may be identified. Rather than species radiating from a center of origin (Smith 1984), the perceived center of origin may instead be a center of alpha diversity, or rather an area where multiple regions of diversity overlap creating a locality of highest diversity. Smith (1992) analyzed the biogeography of echinoids through the brief time span of the Cenomanian (~4.5 million years of time). In his study he found the distribution patterns were suggestive of overlapping geographic ranges and not discrete provinces. In future research I would test patterns of speciation, and narrow the focus to spatangoids, or even hemiasterids (including sister taxon *Mecaster*), and widen the observed timeline to include the entire Cretaceous and the Paleocene.

Toward the end of this study it was also learned that samples of *Hemiaster jacksoni* (the species synonymized by Smith (Smith and Bengtson 1991) with *Mecaster batnensis*) from throughout Texas are held at the Texas Memorial Museum at the University of Texas - Austin. As these come from the same region as samples of *H. jacksoni*/*M. batnensis* held at the USNM they could contribute to further evaluation beyond this current study.

Morphometrics

Samples with all landmarks were sought for use in this study; however, use of symmetry in the analysis of landmark data could allow for the inclusion of more samples in the study.

Missing landmarks at the end of petals I, II, IV, or V can be substituted for by their symmetrically paired landmark. The fact that a majority of landmarks in the scheme used in this study lie along the line of bilateral symmetry limits the opportunity for substitution of missing landmarks. Other potential landmarks that may allow better capture of echinoid test shape include the use of semilandmarks. These more advanced three-dimensional morphometric techniques involve the use of sliders on curves and a concept called bending energy to define points for semi-landmarks on curved surfaces (Weber and Bookstein 2011).

As mentioned in Chapter II the biologic significance of landmark points on the ambitus of a spatangoid is suspect and requires separate analysis outside the scope of this study. This is a consequence of the landmarks not necessarily marking a biologically homologous structure (Zelditch et al. 2012). Were this a study of clypeasteroids, the ambitus is an obvious anatomical feature that is easily, repeatably marked, and is presumably biologically homologous. Even so, one could evaluate if the clypeasteroid ambitus occurs along the same plate junctions, and similar consideration to the ontogeny of other echinoid groups could define the ambitus in regard to specific plate junctions along the interradial and perinterradial sutures. In clypeasteroids, and a few other groups, even without considering the location of plate junctures, the ambitus is within a single plane and creates a distinct sub-angular to sub-rounded ridge that is the reason these urchins are called sand dollars and sea cookies. In some spatangoids, such as *Mecaster* spp. from this study, the ambitus is not along a plane, but is curved. Rather than arbitrarily mark a poorly constrained landmark along the curve of the perradial sutures of the test, the use of semilandmarks could allow Type 1 landmarks to be marked along the perradial and perinterradial sutures, and curves along the test between these landmarks can be used to define semi-landmarks on the echinoid test.

While marking samples in this study and looking over other echinoid clades in the USNM collection a potential scheme for measuring echinoid morphospace using landmarks and semi-landmarks became evident. The basic post-Paleozoic test shape is near spherical. This led to thinking of this primitive state as a sphere or globe with longitudinal divisions along sutures that intersect at “poles” located at the apical system and peristome. The ambitus then becomes the “equator” of this scheme. Changes in peristome shape and position gets recorded, as does the location and shape of the apical system. As test shapes differ, and petal shapes vary, the longitudinal lines along the sutures will capture the variation in shape. And even the location and size of the periproct can be defined by a gap in semi-landmarks in the “longitudinal” semi-landmark curve along the perinterradial suture of interambulacrum 5. The “equatorial” semi-landmark curve marking the ambitus, found using minimized bending-energy, will capture any variation, including all of the notches found on some clypeasteroids. Lunules can be captured in this morphometric scheme the same way the location of the periproct is recorded - by gaps of semi-landmarks on the semi-landmark curves. The “longitudinal” semilandmarks would also capture petal shape as well as petal depth (or height in some species). Given the rapid improvements of scanners, an automated process is not beyond the realm of reason. A clade such as Clypeasteroida would be good to use in developing this scheme, but ultimately the goal would be to characterize the entirety of used and potential echinoid morphospace in this scheme.

Echinoid Taphonomy

The Paleobiology Database (PBDB) contains 1205 records of echinoids throughout the world in the Cretaceous. Six hundred and twenty-one of these records are of spatangoid species. There is obviously some form of taphonomic bias related to test preservation. This bias was discussed in Chapter I in regard to only South American echinoids (Roney et al. 2012), but it

appears that this pattern may be global. Kier(1977) highlighted echinoid species counts from the Miocene and Recent. Clypeasteroids have the best record in the Miocene (408 species), and spatangoids come in a close second (348 species). Cassiduloids are not as well preserved, but are still better preserved than any of the remaining groups of echinoids (157 species).

The reasons supporting why the spatangoid record is better in South America were stated in Chapter I, but interestingly the record of related cassiduloids - also irregular echinoids – is not as good. The cassiduloid record seems lower than should be expected, as the group lives in environments similar to those of clypeasteroids and spatangoids. Evaluation needs to be made of the biases which exist in environment and sedimentation that could affect preservation, and burrowing depth needs to be evaluated as a possible factor in preservation.

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APPENDICES

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Appendix 1 – Part A

Cretaceous Echinoids of South America

There are 147 named species in total, less (~120) when synonymies and generic level identification are taken into account. The country (or countries) where each species has been found is marked (with an **X**) as well as the geologic Age for each find. The markings for geologic age are indicate with an **X** when the age is certain, an **I** along a possible range, and a **V** at the most probable time period when uncertain. In instances where the time of finds differs in multiple countries the two letter abbreviation for the country name is used. Abbreviations used for countries are AR for Argentina, BR for Brazil, VE for Venezuela, CO for Columbia, EC for Ecuador, PE for Peru, BO for Bolivia, and CL for Chile. Only South American countries with Cretaceous basins are listed on the table. References for all information in this table are in Part C of Appendix 1.

	Species	Location South America								Geologic Age of South American Samples											
										Early Cretaceous						Late Cretaceous					
		AR	BR	VE	CO	EC	PE	BO	CL	Ber	Val	Hau	Bar	Apt	Alb	Cen	Tur	Con	San	Cmp	Maa
CIDAROIDA	? <i>Prionocidarissp.</i>		X														X	X			
	<i>Cidaris branneri</i>		X												X						
	<i>Prionocidarissp.</i>																				
	<i>Temnocidarissp.</i> (<i>Stereocidarissp.</i>) <i>malheiroi</i> (De Loriol)		X												X						
	<i>Rhabdocidarissp.</i> <i>brasiliensis</i>		X												X						
	<i>Phalacrocidaris branneri</i> (White)		X												X						
	<i>Cidarissp.</i>		X	X			X						X		X						
	<i>Cidarissp. californicus</i>			X									X								
DIADEMATOIDA	<i>Diadema sp.</i>						X			I	I	I	I	I	I	I	I	I	I	I	I
Stem Group CARINACEA	<i>Orthopsis titacacana</i>						X										X				
	<i>Orthopsis miliaris</i>		X												X	X					
	<i>Pseudodiadema grangeri</i>		X												X						
	<i>Orthopsis gr. miliaris</i>		X				X								X						
	<i>Pseudodiadema texanum</i> Roemer						X						X	X							
PHYMOSOMATOIDA	<i>Cyphosoma riograndensis</i> (SUBSPECIES: <i>Cyphosoma riograndensis parahybensis</i>)		X																		X
	<i>Phymosoma parahybensis</i>		X																		X
	<i>Gomphechinus aff. selim</i>		X																		X

Appendix 1 – Part A continued

	Species	AR	BR	VE	CO	EC	PE	BO	CL	Ber	Val	Hau	Bar	Apt	Alb	Cen	Tur	Con	San	Cmp	Maa
PHYMOSOMATOIDA	<i>Cyphosoma schlagintweiti</i>						X											X			
	<i>Phymosoma</i> aff. <i>major</i>		X														X	X			
	<i>Phymosoma baylei</i> Cotteau		X														X				
	<i>Phymosoma major</i> Coquand																X				
	<i>Tetragramma</i> sp.			X			X									X					
	<i>Tetragramma</i> ? <i>variolare</i>		X													X					
	<i>Tetragramma deshayesi</i>		X													X					
	<i>Phymosoma binexilis</i> White		X												X						
	<i>Phymosoma texanum</i>						X								X						
	<i>Phymosoma tinocoi</i>		X											X							
	<i>Phymosoma mollense</i> Paulcke								X					X							
	<i>Tetragramma malbosii</i> (Agassiz)		X	X	X		X							X							
	<i>Phymosoma</i> sp. (cf. <i>Cyphosoma</i>)						X			I	I	I	I	I	I	I	I	I	I	I	I
	<i>Cyphosoma</i> sp.						X			I	I	I	I	I	I	I	I	I	I	I	I
SALENIODA	<i>Leptosalenia sergipensis</i> (White)		X												X	X					
	<i>Salenia sergipensis</i>		X												X						
	<i>Salenia similis</i>		X												X						
	<i>Holosalenia</i> sp.		X											X							
	<i>Leptosalenia prestensis</i> (Desor)	X										X	X								
	<i>Salenia</i> sp.						X			I	I	I	I	I	I	I	I	I	I	I	I
ECHINACEA	<i>Codiopsis castroi</i> (Maury)		X																		X
	<i>Goniopygus durandi</i>		X															X			
	<i>Goniopygus hemiscidariformis</i>						X											X			
	<i>Goniopygus superbus</i>						X											X			
	<i>Rosadosoma riograndensis</i>		X															X			

Appendix 1 – Part A continued

	Species	AR	BR	VE	CO	EC	PE	BO	CL	Ber	Val	Hau	Bar	Apt	Alb	Cen	Tur	Con	San	Cmp	Maa
ECHINACEA	<i>Coelopleurus castroi</i>		X				X										X	I	I	I	X
	<i>Cottaldia</i> aff. <i>benettiae</i>		X													X					
	<i>Micropedina</i> <i>olisoponensis</i>		X													X					
	<i>Cottaldia australis</i>		X												X						
	<i>Cottaldia</i> gr. <i>benettiae</i> (Koenig)		X												X						
	<i>Codechinus</i> Desor	X										X									
	<i>Goniopygus</i> sp.						X			I	I	I	I	I	I	I	I	I	I	I	I
	" <i>Codiopsis</i> " sp. (cf. <i>Cidaris</i>)						X			I	I	I	I	I	I	I	I	I	I	I	I
	<i>Micropedina</i> sp.						X			I	I	I	I	I	I	I	I	I	I	I	I
HOLECTYPOIDA	<i>Coenholectypus</i> <i>subcrassus</i> Peron & Gauthier		X																		X
	<i>Coenholectypus</i> sp.		X													X					
	<i>Coenholectypus castilloi</i>			X		X									X	X					
	<i>Coenholectypus</i> <i>neocomiensis</i>		X												X	X					
	<i>Holectypus</i> (<i>Caenholectypus</i>) <i>castilloi</i> Cotteau				X										X						
	<i>Holectypus</i> (<i>Caenholectypus</i>) <i>planatus aponensis</i> Cooke			X											X						
	<i>Holectypus</i> (<i>Caenholectypus</i>) <i>planatus</i> Roemer				X										X						
	<i>Holectypus pennanus</i>		X												X						
	<i>Coenholectypus planatus</i>		X	X	X	X	X								X						
	<i>Coenholectypus planatus</i> Romer var. <i>numismalis</i> (Gabb)	X					X				AR	AR	AR	PE	PE						
	<i>Holectypus planatus</i> Roemer						X			I	I	I	I	X	X						
	<i>Pygaster gerthi</i> Weaver	X								I	I	I	I								

Appendix 1 – Part A continued

	Species	AR	BR	VE	CO	EC	PE	BO	CL	Ber	Val	Hau	Bar	Apt	Alb	Cen	Tur	Con	San	Cmp	Maa
ECHINONEOIDA	<i>Pyrina parahybensis</i>		X																		X
	<i>Pygopyrina gerthi</i> (Weaver)	X									X	X									
Stem Group NEOGNATHSTOMATA	<i>Clypeopygus daglensis</i> Gauthier (1889)		X														X				
	<i>Phyllobrissus angustatus</i> (Clark)				X										X	X					
	<i>Acriaster sergipensis</i>		X												X						
	<i>Colliclypeus nettoanus</i> (White)		X												X						
	<i>Conoclypeus nettoanus</i>		X												X						
	<i>Catopygus aequalis</i>		X												X						
	<i>Nucleolites freitasi</i>		X												X						
	<i>Phyllobrissus freitasii</i>		X	X											X						
	<i>Echinobrisus subquadratus</i>						X								X						
	<i>Phyllobrissus zulianus</i> Cooke			X										X							
	<i>Pygurus jagueyanus</i> Cooke				X		X							X							
	<i>Pygurus tinocoi</i> Beurelen		X											X							
	<i>Clypeopygus robinaldus</i> (d'Orbigny)	X								I	X	X	I								
	<i>Pygurus (Pygurus) sp.</i>	X								X	X										
	<i>Pygurus (Mepygurus) sp.</i>	X								I	I	I	I	I	I	I	I	I	I	I	I
	<i>Echinobrisus sp.</i>						X			I	I	I	I	I	I	I	I	I	I	I	I
	<i>Pygurus colombianus</i> (Orbigny)				X					I	I	I	I								
CASSIDU- LOIDA	<i>Petalobrissus aff.</i> <i>setifensis</i>		X																X	X	
	<i>Hardouinia clypeus</i> Cooke				X														X		
	<i>Petalobrissus cubensis</i>		X															X			

Appendix 1 – Part A continued

	Species	AR	BR	VE	CO	EC	PE	BO	CL	Ber	Val	Hau	Bar	Apt	Alb	Cen	Tur	Con	San	Cmp	Maa
CASSIDULOIDA	<i>Petalobrissus aff. setifensis</i>		X														X				
	<i>Petalobrissus cubensis</i>		X														X				
	<i>Nucleopygus gr. atlanticus</i>		X				X								X						
	<i>Faujasia rancheriana</i> Cooke		X		X										X						
	? <i>Parapygus</i> sp.		X												X						
	<i>Parapygus</i>			X											X						
	<i>Arnaudaster colombianus</i> Cooke				X										X						
	<i>Bothropygus</i> sp.						X								X						
	<i>Faujasia araripensis</i> Beurlen		X											X							
	<i>Pygorhynchus obovatus</i> (Agassiz)	X										X	X								
	<i>Bothropygus compressus</i> Gabb						X			I	I	I	I	I	I	I	I	I	I	I	I
HOLASTEROIDA	<i>Cardiaster batnensis</i>		X														X				
	<i>cf. Pseudholaster tricarinatus</i>		X												X	X					
	<i>Pseudholaster tricarinatus</i> Lambert		X												X						
	<i>Pseudananchys</i> sp. <i>indet.</i>			X											X						
SPATANGOIDA	<i>Hemiaster ?delawarensis</i>		X																		X
	<i>Linthia variabilis</i>		X																		X
	<i>cf. Periaster</i> sp.						X													X	
	<i>Linthia romani</i> Brito		X																X	I	I
	<i>Hemiaster pullus</i>	X																	X	I	I
	<i>Hemiaster cristatus</i>	X																	X	I	I
	<i>Mecaster texanum</i>		X															X			
	<i>Hemiasterourneli</i> Deshayes		X				X											X			
	<i>Mecasterourneli</i> (Deshayes)		X		X	X	X	X									X	X	X	X	
	<i>Hemiaster cedroensis</i>		X														X				

Appendix 1 – Part A continued

SPATANGOIDA	Species	AR	BR	VE	CO	EC	PE	BO	CL	Ber	Val	Hau	Bar	Apt	Alb	Cen	Tur	Con	San	Cmp	Maa
	<i>Mecaster africanus</i>		X														X				
	<i>Mecaster latigrunda</i> (Péron & Gauthier)		X		X	X	X	X									X				
	<i>Mecaster texanum</i>		X				X										X				
	<i>Hemiaster steinmanni</i>						X										X				
	<i>Hemiaster texanus</i> Roemer					X										I	I	I	I	I	I
	<i>Mecaster batnensis</i>		X													X	X				
	<i>Hemiaster jacksoni</i>		X												X		X				X
	<i>Mecaster calvini</i>			X											X						
	<i>Mecaster proclivus</i>		X												X						
	<i>Hemiaster proclivus</i>		X												X						
	<i>Hemiaster cranium</i>		X																		
	<i>Wishitaster bravoensis</i> (Boese)			X	X		X	X							X	X					
	<i>Macraster boipebensis</i>		X												X						
	<i>Enallaster (wishitaster)</i> <i>bravoensis</i> Böse			X	X										X						
	<i>Enallaster peruanus</i>						X								X						
	<i>Enallaster</i> sp.						X								X						
	<i>Heteraster obliquatus</i>						X								X						
	<i>Heteraster roseheni</i>						X								X						
	<i>Heteraster</i> sp.						X								X						
	<i>Hemiaster</i> sp.		X	X			X							X			X	X			
	<i>Mecaster elegans</i> <i>washitae</i> (Lambert)	X			X									X							
	<i>Epiaster</i> sp.		X											X							
	<i>Heteraster texanus</i> Roemer	X												X							
	<i>Toxaster ?collegni</i>		X											X							
	<i>Toxaster</i> cf. <i>colombianus</i>		X											X							
	<i>Wishitaster roscheni</i> Richards				X		X							X							
	<i>Epiaster whitei</i> Clark			X						I	I	I	I	V	I						
	<i>Heteraster cesarensis</i> Cooke				X								V								
	<i>Toxaster roulinae</i>				X							X									

Appendix 1 – Part A continued

SPATANGOIDA	Species	AR	BR	VE	CO	EC	PE	BO	CL	Ber	Val	Hau	Bar	Apt	Alb	Cen	Tur	Con	San	Cmp	Maa
	<i>Toxaster colombianus</i> (Lea)		X		X		X				X	X	X	X							
	<i>Mecaster wayensis</i> (Larrain, 1985)								X	I	I	I	I								
	<i>Mecaster? cascajalensis</i> (Cooke)						X			I	I	I	I								
	<i>Washitaster cesarensis</i> (Cooke)				X					I	I	I	I								
	<i>Heteraster chilensis</i> (Philippi)								X	I	I	I	I								
	<i>Enallaster texanus</i> Roemer						X			I	I	I	I	I	I	I	I	I	I	I	I

Appendix 1 – Part B

Global affinities and synonymies of Cretaceous Echinoids of South America

Localities where named species are known outside South America and related taxa. Notes on synonymies are in brackets in order to differentiate from notes on related taxa. Affinities reflect the changes occurring to ocean basins which occurred throughout the Cretaceous. Not all taxa from Appendix 1 – Part A are listed; those listed here are kept in the same order as found on Appendix 1 – Part A. References are found in Appendix 1 – Part C.

	Echinoids	Other Localities	Possible Related taxa and notes
CIDAROIDA	<i>Temnocidaris</i> (<i>Stereocidaris</i>) <i>malheiroi</i> (De Loriol)	Angola	
	<i>Phalacrocidaris</i> <i>branneri</i> (White)	Angola	
Stem Group CARINACE	<i>Orthopsis</i> gr. <i>miliaris</i>	Angola	[<i>Orthopsis titicacana</i> Cooke (1949)]
PHYMOSO-MATOIDA	<i>Cyphosoma riograndensis</i> (SUBSPECIES: <i>Cyphosoma riograndensis parahybensis</i>)		Regarding the name <i>Cyphosoma</i> Unavailable name (non Mannerheim, 1837); = <i>Phymosoma</i> Haime, 1853. (EDB)
	<i>Phymosoma parahybensis</i>		Related to <i>Gomphechinus selim</i> Peron & Gauthier [<i>Gomphechinus collignoni</i> by Lambert (1933)] of Algeria and Madagascar
	<i>Cyphosoma schlagintweiti</i>		(= <i>Phymosoma</i>)
	<i>Phymosoma baylei</i> Cotteau	Algeria	
	<i>Phymosoma major</i> Coquand	Mediterranean - Tethyan, Angola	related to <i>P. tinocoi</i>
	<i>Phymosoma binexilis</i> White	endemic	
	<i>Phymosoma tinocoi</i>		related to <i>P. major</i> , and <i>Phymosoma</i> sp. of Angola
	<i>Tetragramma malbosii</i> (Agassiz)	Texas, Mexico, Honduras, France	Other Names: ' <i>Echinus</i> ' <i>bolivarii</i> Orbigny, <i>Tetragramma taffi</i> Cragin, <i>Tetragramma texanum</i> (Roemer).
SALENIOIDA	<i>Leptosalenia sergipensis</i> (White)	Angola	
	<i>Leptosalenia prestensis</i> (Desor)	Mediterranean	<i>Leptosalenia sergipensis</i> (White)
ECHINACEA	<i>Codiopsis castroi</i> (Maury)		<i>Codiopsis stephensoni</i> Cooke of Texas and a cast in Senegal
	<i>Goniopygus durandi</i>	Algeria	
	<i>Cottaldia</i> gr. <i>benettiae</i> (Koenig)	Angola, Texas, France, GB	[<i>Cottaldia rotula</i> Clark and Twitchell (1915)]

Appendix 1 – Part B continued

ECHINACEA continued	Echinoids	Other Localities	Possible Related taxa and notes
	<i>Codechinus</i> Desor		Specimens of the same genus found in North Africa and Europe (Smith 2006) from the Aptian to the Eocene
	<i>Micropedina</i> sp.		per citation in Echinoid Directory - subjective junior synonym of <i>Cottaldia</i> Desor, 1856
HOLECTYPOIDA	<i>Coenholectypus subcrassus</i> Peron & Gauthier	North Africa	
	<i>Holectypus</i> (<i>Caenholectypus</i>) <i>castilloi</i> Cotteau	Texas, Mexico	
	<i>Holectypus</i> (<i>Caenholectypus</i>) <i>planatus aponensis</i> Cooke	Texas	
	<i>Holectypus</i> (<i>Caenholectypus</i>) <i>planatus</i> Roemer	Texas	
	<i>Coenholectypus planatus</i>	Mexico, Texas, Gabon	Similar forms also in Mexico and Texas: <i>Coenholectypus adkinsi</i> (Smiser), <i>C. castilloi</i> (Cotteau), <i>Coenholectypus engenerrandi</i> (Lambert), <i>Coenholectypus transpecoensis</i> (Cragin)
	<i>Coenholectypus planatus</i> Romer var. <i>numismalis</i> (Gabb)		Genus <i>Coenholectypus</i> known in Europe, North America, Central America, North Africa, Middle East (Iran, Turkey, and the Arabic Penninsula) (Aguirre-Urreta et al. 2008)
	<i>Pygaster gerthi</i> Weaver		last K representative, bearing no relation to European forms
ECHINONIOIDA	<i>Pygopyrina gerthi</i> (Weaver)	endemic	
Stem Group NEOGNATH- STOMATA	<i>Clypeopygus daglensis</i> Gauthier (1889)	Tunisia, Cuba, Mexico, Texas, Egypt	Synonymous with <i>P. cubensis</i> (Weisbord) and <i>P. brasiliensis</i> (Beurlen) of Cuba and Brazil, <i>Clypeopygus waltheri</i> Gauthier (1905) in Mexico Texas and Egypt
	<i>Phyllobrissus angustatus</i> (Clark)	Texas	
	<i>Acriaster sergipensis</i>	endemic	
	<i>Colliclypeus nettoanus</i> (White)	endemic	
	<i>Phyllobrissus freitasii</i>	Angola	
	<i>Echinobrisus subquadratus</i>		(= <i>Nucleolites</i>)
	<i>Pygurus jagueyanus</i> Cooke	Caribbean	related to <i>P. tinocoi</i>

Appendix 1 – Part B continued

	Echinoids	Other Localities	Possible Related taxa and notes
Stem Group NEOGNATH- STOMATA continued	<i>Pygurus tinocoi</i> Beurelen		related to <i>P. jagueyanus</i> , <i>distinct from Pygurus africanus</i> of West Africa
	<i>Clypeopygus robinaldus</i> (d'Orbigny)	Europe (Kier 1962, Smith and Wright 2000)	
	<i>Pygurus (Pygurus) sp.</i>		<i>Pygurus (Pygurus) andinus</i> Larrain and Biro'-Bago'czky from the Tithonian of central Chile (Larrai'n and Biro'-Bago'czky 1985)
	<i>Echinobrisus sp.</i>		(= <i>Nucleolites</i>)
	<i>Pygurus colombianus</i> (Orbigny)		Could be descendant of <i>Pygurus andinus</i> Larrain & BiroBagoczky which is related to <i>Pygurus depressus somalensis</i> Currie and <i>Pygurus smelliei</i> Currie of Somalian Jurassic
CASSIDULOIDA	<i>Petalobrissus</i> aff. <i>setifensis</i>		<i>Petalobrissus setifensis</i> (Coquand) of North Africa
	<i>Hardouinia clypeus</i> Cooke	Alabama	
	<i>Nucleopygus</i> gr. <i>atlanticus</i>	Congo, DRC, Zululand	[<i>Nucleopygus</i> cf. <i>similis</i> Orbigny in Smith and Bengtson 1991, <i>Echinobrisus</i> sp. in Benavides 1956] <i>Nucleopygus angutior</i> of Algeria is probably same morphological group
	? <i>Parapygus</i> sp.	endemic	similar to <i>Parapygus</i> of Venezuela
	<i>Parapygus</i>		similar to ? <i>Parapygus</i> sp. of Brazil
	<i>Arnaudaster colombianus</i> Cooke		Kier (1962, p. 105) thought this species should be referred to <i>Pygorhynchus</i> (EDB)
	<i>Bothropygus</i> sp.		nom. null.; <i>Botriopygus</i> d'Orbigny, 1856, p. 344; junior synonym of <i>Pygorhynchus</i> L. Agassiz, 1839 (EDB)
HOLASTEROIDA	<i>Pygorhynchus obovatus</i> (Agassiz)		type species of genus. genus known in Europe, Africa, North America (Kier 1962, Smith 2006)
	<i>Cardiaster batnensis</i>	Algeria	
SPATANGOIDA	<i>Pseudholaster tricarinatus</i> Lambert	Angola, Zululand, Madagascar	
	<i>Hemiaster</i> ? <i>delawarensis</i>	West Europe, North America	<i>Hemiaster (Bolbaster) delawarensis</i>
	<i>Linthia variabilis</i>		related to <i>Linthia brodermanni</i> Sanchez Roig of Cuba, and <i>L. romani</i>
	<i>Linthia romani</i> Brito		related to <i>Linthia brodermanni</i> Sanchez Roig of Cuba

Appendix 1 – Part B continued

SPATANGOIDA continued	Echinoids	Other Localities	Possible Related taxa and notes
	<i>Hemiasterourneli</i> Deshayes		(= <i>M.ourneli</i>)
	<i>Mecasterourneli</i> (Deshayes)	Egypt, Nigeria, Gabon, Cameroon, Mexico, and Texas	[<i>Mecasterriopanensis</i> (Brito 1981), <i>Hemiasterteilhardi</i> (Basse 1928), <i>Hemiastersteinmanni</i> (Neumann 1907; Benavides 1956)] Related to <i>H.</i> <i>pullus Stolicka</i> and <i>H. cristatus</i> <i>Stolicka</i> , and <i>Mecastermessai</i> Peron & Gauthier of Senegal.
	<i>Mecasterlatigrunda</i> (Péron & Gauthier)	Egypt, Nigeria, Gabon, Cameroon, Mexico, and Texas	In Neraudeau and Mathhey (2000) is discussed along with <i>M.ourneli</i>
	<i>Mecastertexanum</i>	Egypt, France, Jordan, Nigeria,	
	<i>Hemiastersteinmanni</i>		(= <i>M.ourneli</i>)
	<i>Hemiastertexanus</i> Roemer	Texas	
	<i>Mecasterbatnensis</i>	Egypt, Jordan	
	<i>Hemiasterjacksoni</i>	Texas, Mexico	Has been grouped with <i>M. batnensis</i> . Some records have been grouped with <i>H. proclivus</i> .
	<i>Mecastercalvini</i>	Mexico, Texas	Related to <i>Mecasterhourcqi</i> (Lambert) of Madagascar
	<i>Mecasterproclivus</i>	Angola	[<i>Mecasterreinecke</i> (Haughton) in Darteville (1953)] also found in variety <i>M. calvini</i> Clark. Related to <i>Mecasterhourcqi</i> (Lambert) of Madagascar
	<i>Wishitasterbravoensis</i> (Boese)	Mexico, Texas, but not Atlantic of S.A.	[<i>Heterasterlorioli</i> Harrington, <i>Heterasterperuanas</i> (Gabb), <i>Heterastertschudii</i> Desor] similar to <i>W. roscheni</i> of Aptian of Peru
	<i>Macrasterboipebensis</i>		[<i>Epiaster</i> in Brito 1964, <i>Heteraster</i> in Brito 1974] Similar to <i>Macraster</i> groups found in Texas as well as species from Angola, Nigeria, and Madagascar per Neraudeau and Mathey (2000)
	<i>Enallaster</i> (<i>wishitaster</i>) <i>bravoensis</i> Böse	Mexico, Texas	
	<i>Mecasterelegans</i> <i>washitae</i> (Lambert)	Caribbean	
	<i>Epiaster</i> sp.		[<i>Hemiaster</i> sp. in Brito 1981] related to <i>Epiasterdartoni</i> Cooke from Mexico
	<i>Heterastertexanus</i> Roemer	Caribbean	

Appendix 1 – Part B continued

SPATANGOIDA continued	Echinoids	Other Localities	Possible Related taxa and notes
	<i>Toxaster</i> cf. <i>colombianus</i>		close to <i>T. colombianus</i> and Tethyan <i>Toxaster collegnoi</i>
	<i>Wishitaster roscheni</i> Richards	Caribbean	
	<i>Epiaster whitei</i> Clark	Texas	
	<i>Toxaster colombianus</i> (Lea)	Caribbean	invalid designation <i>Toxaster roulini</i> Agassiz. Texas ' <i>Epiaster</i> ' <i>whitei</i> , ' <i>Pliotoxaster</i> ' <i>whitei</i> . <i>Pygurus collegnoi</i> Sismonda North Tethyan regions.
	<i>Mecaster?</i> <i>cascajalensis</i> (Cooke)		<i>Mecaster whitei</i> Clark), <i>M. wayensis</i> (Larrain) (<i>Macraster</i> in Clark (1893))
	<i>Washitaster</i> <i>cesarensis</i> (Cooke)		<i>Heteraster</i> of America and Tethys

Appendix 1 – Part C

References for Appendix 1

The references for any of the information listed Appendix 1 – Parts A and B are listed here. Rather than list species by clade and by age as was done in Parts A and B, species are listed alphabetically.

<i>"Codiopsis" sp. (cf. Cidaris)</i>	Willard 1966
<i>?Parapygus sp.</i>	Smith and Bengtson 1991, Néraudeau and Mathey 2000
<i>?Prionocidarissp.</i>	Smith and Bengtson 1991
<i>Acriaster sergipensis</i>	Smith and Bengtson 1991, Néraudeau and Mathey 2000
<i>Arnaudaster colombianus</i> Cooke	Néraudeau and Mathey 2000
<i>Bothropygus compressus</i> Gabb	Willard 1966
<i>Bothropygus sp.</i>	Néraudeau and Mathey 2000
<i>Cardiaster batnensis</i>	Smith and Bengtson 1991
<i>Catopygus aequalis</i>	Maury 1936
<i>cf. Periaster sp.</i>	Mourier et al. 1988
<i>cf. Pseudholaster tricarinatus</i>	Smith and Bengtson 1991
<i>Cidaris aff. californicus</i>	PBDB, von der Osten 1957
<i>Cidaris branneri</i>	Maury 1936
<i>Cidaris sp.</i>	Maury 1936, von der Osten 1957, Willard 1966
<i>Clypeopygus daglensis</i> Gauthier (1889)	Néraudeau and Mathey 2000
<i>Clypeopygus robinaldus (d'Orbigny)</i>	Néraudeau and Mathey 2000, Aguirre-Urreta et al. 2008
<i>Codechinus</i> Desor	Aguirre-Urreta et al. 2008
<i>Codiopsis castroi</i> (Maury)	Smith and Bengtson 1991
<i>Coelopleurus castroi</i>	Maury 1930, Willard 1966
<i>Coenholectypus castilloi</i>	Néraudeau and Mathey 2000
<i>Coenholectypus neocomiensis</i>	Smith and Bengtson 1991
<i>Coenholectypus planatus</i>	Néraudeau and Mathey 2000, Hillebrant 1970, Benavides-Caceres 1956
<i>Coenholectypus planatus</i> Romer var. <i>numismalis</i> (Gabb)	Néraudeau and Mathey 2000, Aguirre-Urreta et al. 2008, Sommermeier 1913
<i>Coenholectypus sp.</i>	Smith and Bengtson 1991
<i>Coenholectypus subcrassus</i> Peron & Gauthier	Smith and Bengtson 1991
<i>Colliclypeus nettoanus</i> (White)	Smith and Bengtson 1991, Néraudeau and Mathey 2000
<i>Conoclypeus nettoanus</i>	Maury 1936
<i>Cottaldia aff. benettiae</i>	Smith and Bengtson 1991

<i>Cottaldia australis</i>	Maury 1936
<i>Cottaldia</i> gr. <i>benettiae</i> (Koenig)	Néraudeau and Mathey 2000
<i>Cyphosoma riograndensis</i> (SUBSPECIES: <i>Cyphosoma riograndensis parahybensis</i>)	Maury 1930
<i>Cyphosoma schlagintweiti</i>	Benavides-Caceres 1956
<i>Cyphosoma</i> sp.	Willard 1966
<i>Diadema</i> sp.	Willard 1966
<i>Echinobrisus</i> sp.	Willard 1966
<i>Echinobrisus subquadratus</i>	PBDB, Benavides-Caceres 1956
<i>Enallaster (wishitaster) bravoensis</i> Böse	Cooke 1955, Cooke 1961
<i>Enallaster peruanus</i>	Benavides-Caceres 1956
<i>Enallaster</i> sp.	Benavides-Caceres 1956
<i>Enallaster texanus</i> Roemer	Willard 1966
<i>Epiaster</i> sp.	Néraudeau and Mathey 2000
<i>Epiaster whitei</i> Clark	Cooke 1961
<i>Faujasia araripensis</i> Beurlen	Néraudeau and Mathey 2000
<i>Faujasia rancheriana</i> Cooke	Néraudeau and Mathey 2000
<i>Gomphechinus</i> aff. <i>selim</i>	Smith and Bengtson 1991
<i>Goniopygus durandi</i>	Smith and Bengtson 1991, EDB
<i>Goniopygus hemiscidariformis</i>	Benavides-Caceres 1956
<i>Goniopygus</i> sp.	Willard 1966
<i>Goniopygus superbus</i>	Benavides-Caceres 1956
<i>Hardouinia clypeus</i> Cooke	Cooke 1955
<i>Hemiaster</i> ? <i>delawarensis</i>	Smith and Bengtson 1991, Manso and Andrade 2008
<i>Hemiaster cedroensis</i>	Maury 1936
<i>Hemiaster cranium</i>	Brito
<i>Hemiaster cristatus</i>	Néraudeau and Mathey 2000
<i>Hemiaster fourneli</i> Deshayes	Benavides-Caceres 1956, Willard 1966
<i>Hemiaster jacksoni</i>	Maury 1930, 1936, Smith and Bengtson 1991
<i>Hemiaster proclivus</i>	Smith and Bengtson 1991
<i>Hemiaster pullus</i>	Néraudeau and Mathey 2000
<i>Hemiaster</i> sp.	Benavides-Caceres 1956, Cooke 1961, Néraudeau and Mathey 2000, Robert and Bulot 2005
<i>Hemiaster steinmanni</i>	Kummel 1948
<i>Hemiaster texanus</i> Roemer	
<i>Heteraster cesarensis</i> Cooke	Cooke 1955

<i>Heteraster chilensis</i> (Philippi)	Néraudeau and Mathey 2000
<i>Heteraster obliquatus</i>	Robert and Bulot 2005
<i>Heteraster roseheni</i>	Robert and Bulot 2005
<i>Heteraster</i> sp.	Robert and Bulot 2005
<i>Heteraster texanus</i> Roemer	Néraudeau and Mathey 2000
<i>Holactypus</i> (<i>Caenholactypus</i>) <i>castilloi</i> Cotteau	Cooke 1955
<i>Holactypus</i> (<i>Caenholactypus</i>) <i>planatus aponensis</i> Cooke	Cooke 1961
<i>Holactypus</i> (<i>Caenholactypus</i>) <i>planatus</i> Roemer	Cooke 1955
<i>Holactypus pennanus</i>	Maury 1936
<i>Holactypus planatus</i> Roemer	Benavides-Caceres 1956, Willard 1966
<i>Holosalenia</i> sp.	Smith and Bengtson 1991
<i>Leptosalenia prestensis</i> (Desor)	Aguirre-Urreta et al. 2008
<i>Leptosalenia sergipensis</i> (White)	Smith and Bengtson 1991, Néraudeau and Mathey 2000
<i>Linthia romani</i> Brito	Néraudeau and Mathey 2000
<i>Linthia variabilis</i>	Smith and Bengtson 1991
<i>Macraster boipebensis</i>	Néraudeau and Mathey 2000
<i>Mecaster africanus</i>	Smith and Bengtson 1991
<i>Mecaster batnensis</i>	Smith and Bengtson 1991, Manso and Andrade 2008
<i>Mecaster calvini</i>	Néraudeau and Mathey 2000
<i>Mecaster elegans washitae</i> (Lambert)	Néraudeau and Mathey 2000
<i>Mecasterourneli</i> (Deshayes)	Maury 1936, Manso 2006, PBDB, Smith and Bengtson 1991, Néraudeau and Mathey 2000, Manso and Andrade 2008, Benavides-Caceres 1956, Willard 1966
<i>Mecaster latigrunda</i> (Péron & Gauthier)	Smith and Bengtson 1991, Manso and Andrade 2008
<i>Mecaster proclivus</i>	Néraudeau and Mathey 2000
<i>Mecaster texanum</i>	Smith and Bengtson 1991
<i>Mecaster texanum</i>	Manso 2006
<i>Mecaster wayensis</i> (Larrain, 1985)	Néraudeau and Mathey 2000
<i>Mecaster? cascajalensis</i> (Cooke)	Néraudeau and Mathey 2000
<i>Micropedina olisoponensis</i>	Smith and Bengtson 1991
<i>Micropedina</i> sp.	Willard 1966
<i>Nucleolites freitasi</i>	Maury 1936
<i>Nucleopygus</i> gr. <i>atlanticus</i>	Néraudeau and Mathey 2000
<i>Orthopsis</i> gr. <i>miliaris</i>	Néraudeau and Mathey 2000
<i>Orthopsis miliaris</i>	Smith and Bengtson 1991

<i>Orthopsis titacacana</i>	Benavides-Caceres 1956
<i>Parapygus</i>	Néraudeau and Mathey 2000
<i>Petalobrissus</i> aff. <i>setifensis</i>	Smith and Bengtson 1991
<i>Petalobrissus</i> aff. <i>setifensis</i>	Manso 2006
<i>Petalobrissus cubensis</i>	Smith and Bengtson 1991
<i>Petalobrissus cubensis</i>	Manso and Andrade 2008, Manso 2006
<i>Phalacrocidaris branneri</i> (White)	Smith and Bengtson 1991, Néraudeau and Mathey 2000
<i>Phyllobrissus angustatus</i> (Clark)	Cooke 1955
<i>Phyllobrissus freitasii</i>	Smith and Bengtson 1991
<i>Phyllobrissus zulianus</i> Cooke	Cooke 1961
<i>Phymosoma</i> aff. <i>major</i>	Smith and Bengtson 1991, Manso 2006
<i>Phymosoma baylei</i> Cotteau	Smith and Bengtson 1991, Néraudeau and Mathey 2000, Manso and Andrade 2008
<i>Phymosoma binexilis</i> White	Smith and Bengtson 1991, Néraudeau and Mathey 2000
<i>Phymosoma major</i> Coquand	Néraudeau and Mathey 2000
<i>Phymosoma mollense</i> Paulcke	Néraudeau and Mathey 2000
<i>Phymosoma parahybensis</i>	
<i>Phymosoma</i> sp. (cf. <i>Cyphosoma</i>)	Willard 1966
<i>Phymosoma texanum</i>	Benavides-Caceres 1956
<i>Phymosoma tinocoi</i>	Néraudeau and Mathey 2000
<i>Prionocidaris</i> sp.	
<i>Pseudananchys</i> sp. <i>indet.</i>	Cooke 1961
<i>Pseudholaster tricarinatus</i> Lambert	Smith 1992
<i>Pseudodiadema grangeri</i>	Maury 1936
<i>Pseudodiadema texanum</i> Roemer	
<i>Pygaster gerthi</i> Weaver	Néraudeau and Mathey 2000
<i>Pygopyrina gerthi</i> (Weaver)	Aguierre-Urreta et al. 2008
<i>Pygorhynchus obovatus</i> (Agassiz)	Aguierre-Urreta et al. 2008
<i>Pygurus</i> (<i>Mepygurus</i>) sp.	Aguierre-Urreta et al. 2008
<i>Pygurus</i> (<i>Pygurus</i>) sp.	Aguierre-Urreta et al. 2008
<i>Pygurus colombianus</i> (Orbigny)	Néraudeau and Mathey 2000
<i>Pygurus jagueyanus</i> Cooke	Néraudeau and Mathey 2000
<i>Pygurus tinocoi</i> Beurelen	Néraudeau and Mathey 2000
<i>Pyrina parahybensis</i>	Maury 1930
<i>Rhabdocidaris brasiliensis</i>	Maury 1936
<i>Rosadosoma riograndensis</i>	Smith and Bengtson 1991

<i>Salenia sergipensis</i>	Maury 1936
<i>Salenia similis</i>	Maury 1936
<i>Salenia</i> sp.	Willard 1966
<i>Temnocidaris (Stereocidaris) malheiroi</i> (De Loriol)	Smith and Bengtson 1991, Néraudeau and Mathey 2000
<i>Tetragramma ?variolare</i>	Smith and Bengtson 1991
<i>Tetragramma deshayesi</i>	Smith and Bengtson 1991
<i>Tetragramma malbosii</i> (Agassiz)	Smith and Bengtson 1991, Néraudeau and Mathey 2000, Cooke 1955
<i>Tetragramma</i> sp.	Benavides-Caceres 1956, Cooke 1961.
<i>Toxaster ?collegni</i>	Smith and Bengtson 1991
<i>Toxaster</i> cf. <i>colombianus</i>	Néraudeau and Mathey 2000
<i>Toxaster colombianus</i> (Lea)	Cooke 1955, Néraudeau and Mathey 2000
<i>Toxaster roulinae</i>	PBDB, Bürgli 1960, Cooke 1955
<i>Washitaster cesarensis</i> (Cooke)	Néraudeau and Mathey 2000
<i>Wishitaster bravoensis</i> (Boese)	Néraudeau and Mathey 2000
<i>Wishitaster roscheni</i> Richards	Néraudeau and Mathey 2000

Appendix 2 – Part A

Length (L), width(W), and height (H) measurements of *Mecaster batnensis* and *Mecaster founeli* Basic size measurements of 291 samples of *Mecaster batnensis* and 77 samples of *Mecaster founeli* from the Smithsonian National Museum of Natural History (USNM) Springer Collection. Measurements were made during visits to USNM in May and August 2012. Samples of *M. batnensis* come from Algeria (AL, n=5), Arizona (AZ, n=45), Brazil (BR, n=21), Egypt (EG, n=2), Mexico (MX, n=71), Palestine (PL, n=14), New Mexico (NM, n=73), and Texas (TX, n=60). Samples of *M. founeli* come from Algeria (AL, n= 20) and Peru (PE, n=57). Catalogue numbers are included with the first specimen from a set of specimens. All measurements are in mm. In the case Mexico samples USNM acquisition numbers are followed by locality identifications associated with the samples. Peru samples come from the Bassler Collection

Mecaster batnensis:

Sample #	Country	L	W	H
46880	MX	29.3	26.5	20.3
	MX	29.8	25.6	21.2
	MX	21.8	20.0	15.1
	MX	17.4	16.8	10.4
	MX	27.1	25.8	17.7
No ID R29C14D2	MX	23.5	23.4	17.2
	MX	26.4	24.4	17.5
	MX	28.1	25.9	18.1
	MX	28.3	28.0	18.1
	MX	31.1	31.2	21.9
	MX	33.2	30.4	22.3
10599	MX	36.7	33.5	25.2
1018	MX	42.0	39.9	26.6
	MX	37.6	37.6	21.4
	MX	33.7	33.6	23.4
232124 (j68)	MX	12.5	12.0	9.4
	MX	20.0	19.3	13.9
	MX	20.5	19.3	14.7
	MX	20.8	19.6	12.0
	MX	18.4	16.8	12.4
	MX	15.7	15.1	11.0
	MX	20.9	18.3	12.0
	MX	17.8	17.2	10.5
	MX	19.9	20.0	12.0
	MX	17.2	15.5	12.0
	MX	23.5	21.3	15.6
	MX	20.2	18.9	14.0
	MX	18.6	17.9	13.2
	MX	14.8	13.7	10.3
	MX	17.7	15.9	12.8
	MX	24.7	24.4	17.4
	MX	16.6	15.5	11.7

Sample #	Country	L	W	H
	MX	29.8	28.4	18.9
	MX	25.1	24.5	16.2
	MX	17.5	15.9	11.0
2321242 (K69)	MX	12.9	11.5	8.7
	MX	23.2	21.6	14.2
	MX	16.7	21.6	14.2
	MX	16.7	15.2	11.1
	MX	14.7	13.8	10.1
	MX	23.3	20.9	16.1
	MX	29.2	29.4	19.2
	MX	31.2	28.4	20.6
	MX	26.5	24.6	16.0
	MX	25.7	22.1	14.6
	MX	21.0	19.5	15.1
	MX	24.3	22.8	16.2
	MX	22.4	20.5	15.7
	MX	23.3	21.4	16.1
	MX	14.3	13.9	9.7
	MX	22.8	20.8	14.0
	MX	20.4	19.0	14.3
	MX	20.8	18.5	13.4
	MX	13.3	12.6	9.4
	MX	16.3	18.7	11.6
	MX	16.9	18.6	12.9
2321242 (K127)	MX	23.0	20.6	12.2
	MX	26.1	17.6	26.1
	MX	25.5	23.3	17.4
	MX	30.2	26.7	20.1
	MX	19.0	18.0	12.1
	MX	17.9	16.6	12.8
	MX	23.4	19.4	12.5
	MX	22.9	20.5	12.3

Appendix 2 – Part A continued: *M. batnensis*

Sample #	Country	L	W	H	Sample #	Country	L	W	H
	MX	26.4	23.2	17.8	468944	EG	22.1	20.8	14.7
2321242 (J44)	MX	25.3	22.4	15.1		EG	26.1	23.8	18.9
	MX	26.3	24.1	15.0	468877	TX	24.4	23.0	17.7
	MX	17.9	16.3	12.3		TX	27.7	24.7	18.6
	MX	26.5	25.4	14.9		TX	23.3	22.3	16.8
	MX	20.4	18.2	13.0		TX	19.9	18.7	13.4
	MX	12.2	11.6	7.1		TX	22.8	20.9	17.0
468879	BR	22.5	21.0	15.6		TX	17.6	15.9	13.5
	BR	21.9	20.9	15.3		TX	16.1	15.1	10.7
	BR	19.4	18.0	12.6	108396	TX	26.6	26.5	16.9
	BR	20.1	19.3	14.8	468876	TX	20.5	19.9	14.7
	BR	20.7	20.1	13.1		TX	20.6	19.7	12.9
	BR	27.1	25.8	16.1		TX	27.6	24.5	16.7
	BR	17.3	16.1	12.1		TX	20.6	19.4	14.2
	BR	23.8	22.8	14.9		TX	23.2	21.8	16.6
	BR	25.5	24.0	18.1		TX	22.4	21.1	14.3
	BR	17.9	17.1	10.8		TX	14.0	12.9	10.0
108395	BR	26.7	24.8	18.0		TX	19.0	17.4	13.3
449382	BR	24.7	23.9	16.4		TX	18.6	17.5	10.4
449383	BR	23.6	22.9	17.0		TX	23.7	22.9	17.4
449385	BR	24.5	25.3	16.0		TX	19.0	17.1	13.5
449386	BR	19.6	18.7	14.9		TX	32.8	29.2	20.1
449388	BR	21.2	20.4	14.5		TX	24.6	24.0	15.2
12681	BR	20.7	20.2	14.9		TX	21.9	20.7	15.9
12682	BR	28.3	25.5	19.5		TX	22.5	21.5	15.9
468966	BR	23.6	23.0	14.2		TX	21.5	20.4	14.8
	BR	23.7	21.3	12.9		TX	20.2	18.7	13.5
no id R29C13D13	BR	31.5	32.6	21.7		TX	17.8	17.0	12.7
468939	PL	21.5	20.6	13.1		TX	17.5	16.8	12.0
	PL	23.4	21.3	17.0		TX	15.6	14.6	11.1
	PL	26.1	25.5	17.2		TX	16.6	15.3	11.1
	PL	26.4	24.9	15.3	46883	TX	15.2	13.1	9.4
	PL	26.0	27.0	19.5		TX	24.9	23.1	16.9
	PL	28.8	26.0	16.8		TX	15.2	13.9	9.5
	PL	28.4	26.8	17.0		TX	15.1	14.8	11.6
	PL	30.3	27.2	17.0		TX	15.9	14.4	10.7
	PL	34.0	32.5	17.9		TX	17.2	15.2	10.9
	PL	37.7	31.1	23.2		TX	17.5	15.5	12.1
	PL	38.0	34.4	24.3		TX	17.8	17.7	12.1
	PL	41.5	38.4	23.9		TX	19.1	18.0	12.9
	PL	37.6	35.9	19.5		TX	19.5	18.2	14.1
	PL	40.4	37.7	22.9		TX	22.7	22.0	16.3
S 6358	AL	31.5	28.9	20.7		TX	11.5	10.6	7.6
19600	AL	23.4	23.1	16.3		TX	14.4	13.3	9.6
S 6359	AL	25.3	22.6	17.2		TX	14.9	14.6	10.2
31102	AL	24.6	24.7	16.1		TX	17.1	15.5	10.7
131039	AL	47.8	43.3	27.3		TX	17.6	16.8	12.2

Annendix 2 – Part A continued: *M. batnensis*

Sample #	Country	L	W	H	Sample #	Country	L	W	H
	TX	18.0	16.8	12.4		NM	29.1	27.2	20.8
	TX	20.0	19.5	12.1		NM	31.3	30.3	23.4
	TX	22.2	21.8	15.4	468564	NM	18.3	17.5	13.5
	TX	24.9	23.0	17.8		NM	19.4	19.1	13.0
	TX	26.7	24.3	16.9		NM	21.0	19.5	14.2
	TX	30.7	27.1	21.2		NM	21.4	20.3	15.5
46881	TX	11.9	10.6	8.0		NM	26.3	24.8	19.1
	TX	12.0	11.0	9.1		NM	27.4	26.0	16.0
	TX	12.7	11.7	9.2	468558	NM	24.3	23.0	17.3
	TX	15.0	14.9	11.2		NM	30.3	28.3	22.0
	TX	20.6	19.5	15.6		NM	28.8	28.9	23.4
	TX	23.0	21.3	15.1	468531	NM	31.5	30.5	24.2
	TX	24.3	22.2	17.2	468532	NM	21.0	19.8	16.9
468884	TX	24.4	23.0	18.7	468537	NM	19.7	17.4	14.5
468885	TX	12.9	12.0	7.1	468563	NM	12.5	11.5	8.3
468566	NM	13.3	11.9	10.1		NM	16.7	15.8	11.8
	NM	14.2	13.7	9.1		NM	16.9	16.3	11.6
	NM	15.1	14.2	9.5		NM	18.7	18.1	13.9
	NM	19.7	18.0	14.6		NM	17.3	16.6	12.7
	NM	20.9	20.6	15.2		NM	18.6	18.4	15.2
	NM	21.7	19.7	16.6		NM	19.3	17.5	14.2
46882	NM	20.2	19.1	15.0		NM	17.1	16.6	12.8
468864	NM	20.7	20.3	15.1		NM	20.7	19.7	14.7
468551	NM	13.3	11.9	8.9		NM	19.8	18.5	13.4
	NM	13.0	12.2	9.5		NM	20.1	19.7	14.3
	NM	14.7	13.7	11.7		NM	21.1	20.6	14.0
	NM	16.3	14.9	12.8		NM	21.8	21.0	15.5
	NM	15.6	14.1	11.0	468536	NM	18.9	18.7	14.0
	NM	16.5	14.4	11.1	468542	NM	18.4	17.3	13.5
	NM	15.6	14.0	11.4	468543	NM	22.4	21.3	15.2
	NM	19.2	17.4	13.5	468538	NM	16.5	15.5	11.8
	NM	21.0	20.3	17.4	468539	NM	16.2	15.5	11.8
468562	NM	12.1	11.6	9.1	468528	NM	22.0	20.8	13.5
	NM	11.7	11.4	8.6	468533	NM	23.0	22.4	15.7
	NM	14.5	13.7	10.1	468529	NM	23.1	21.5	17.1
	NM	14.2	13.5	10.3	468540	NM	17.8	16.1	12.5
468561	NM	11.4	10.5	9.2	468544	NM	20.1	18.5	14.1
468556	NM	23.8	22.6	17.4	468541	NM	20.0	19.1	15.3
	NM	24.5	22.6	17.8	468535	NM	28.9	27.5	19.6
	NM	23.9	23.8	17.6	468534	NM	22.5	21.5	16.7
	NM	25.3	24.1	15.6	468530	NM	22.7	21.5	14.9
	NM	25.2	24.9	20.3	468547	AZ	19.1	17.5	14.3
	NM	28.9	27.4	21.1	468552	AZ	20.8	20.0	14.9
468559	NM	18.1	16.3	13.0	468546	AZ	15.6	14.5	10.7
	NM	19.1	18.0	14.9	468553	AZ	16.1	14.9	11.8
	NM	19.5	17.8	15.7	468545	AZ	13.7	12.6	9.5
	NM	18.9	18.0	13.9	468549	AZ	24.9	24.0	18.7

Appendix 2 – Part A continued: *M. batnensis*

Sample #	Country	L	W	H
468554	AZ	18.8	17.3	13.2
468555	AZ	20.4	18.4	13.7
468548	AZ	20.6	19.7	14.9
468551	AZ	19.2	18.0	14.3
468871	AZ	21.0	19.6	15.6
	AZ	21.4	20.2	15.4
468873	AZ	20.5	19.1	15.1
	AZ	19.9	18.5	14.4
	AZ	19.5	17.8	13.8
468866	AZ	12.1	11.1	8.4
	AZ	13.7	12.5	9.5
	AZ	15.8	15.1	10.9
	AZ	16.3	15.8	12.3
	AZ	19.5	18.6	14.0
	AZ	20.3	17.9	12.6
468865	AZ	12.9	11.6	9.3
	AZ	19.5	17.4	14.6
	AZ	22.1	20.2	15.3
468869	AZ	10.1	9.4	7.7
	AZ	11.2	9.7	8.4

Sample #	Country	L	W	H
	AZ	11.1	10.1	8.0
	AZ	12.4	11.6	9.0
	AZ	13.3	12.9	10.2
	AZ	13.1	11.9	9.5
	AZ	12.7	11.9	9.2
	AZ	12.9	12.0	9.6
	AZ	12.8	12.1	8.9
	AZ	13.3	12.6	9.7
	AZ	15.7	14.7	10.7
468872	AZ	18.8	17.4	13.7
	AZ	18.9	18.4	13.6
	AZ	19.8	18.3	13.9
	AZ	19.7	19.1	14.5
468868	AZ	13.2	13.0	9.4
	AZ	14.4	13.7	9.6
	AZ	14.2	12.9	9.8
	AZ	19.3	18.7	14.0
	AZ	19.8	19.2	15.1
	AZ	19.7	18.8	14.3

Mecastera fourneli:

Sample #	Country	L	W	H
468897	AL	41.3	40.2	22.6
	AL	41.0	38.8	22.7
29246	AL	36.1	33.1	21.7
468891	AL	25.2	22.2	17.2
468888	AL	31.5	28.9	20.3
468893	AL	37.6	35.6	
468894	AL	36.8	33.9	21.7
	AL	40.5	39.3	24.9
	AL	33.1	30.5	29.8
468898	AL	26.3	25.0	18.3
	AL	22.9	21.5	15.4
	AL	28.3	26.3	18.0
	AL	29.9	27.5	19.9
468899	AL	41.3	37.2	25.6
	AL	41.4	39.0	26.9
	AL	43.2	36.8	
	AL	32.0	29.9	22.6
	AL	32.8	30.0	20.8
	AL	24.8	22.6	15.7
	AL	18.5		12.5
Hanguirilla	PE	43.8	40.2	26.2
	PE	26.1	23.1	19.6
	PE	21.7	19.8	19.0
	PE	23.9	21.4	15.3
	PE	26.5	24.7	15.6
	PE	27.4	24.8	18.0
	PE	21.2	19.4	13.5
	PE	17.7	17.5	11.5
Bayana	PE	40.8	35.9	24.3
	PE	35.0	31.1	20.8
	PE	31.8	31.2	21.0
	PE	32.2	31.3	20.6
	PE	29.7	26.7	17.1
	PE	30.8	28.3	18.6
	PE	30.8	30.1	21.2
	PE	30.2	28.0	18.1
Rio Pupturita to Marañon	PE	38.8	36.1	18.9
	PE	31.2	28.4	20.3
Chasuta	PE	29.3	28.0	19.0

Sample #	Country	L	W	H
Chinchipe	PE	35.0	33.0	21.7
Chipanta	PE	36.3	33.9	22.9
A. Ucayali	PE	34.8		20.3
Q. Cocani	PE	29.3	27.2	20.2
Pachitea	PE	37.7	32.6	20.2
	PE	25.1	24.2	16.0
	PE	25.2	24.8	19.4
Rio San Jose, Biobab Basin	PE	42.0	36.9	24.5
	PE	26.5	24.1	16.5
	PE	21.7	19.3	14.4
Hondo Cuesta	PE	33.3	31.6	20.2
	PE	27.8	26.7	17.8
	PE	26.4	23.2	17.1
	PE	23.3	20.7	12.5
Manseriche	PE	40.4	37.4	23.6
	PE	34.0	31.2	20.2
	PE	29.7	26.5	18.7
	PE	30.3	28.6	17.6
	PE	22.3	20.2	14.3
Chamoya	PE	35.0	30.9	23.9
	PE	34.5	30.5	23.3
	PE	33.1	29.1	21.3
	PE	32.4	28.6	20.4
Chamoya	PE	32.7	31.6	22.6
	PE	30.3	29.4	19.9
	PE	29.8	25.7	20.0
	PE	33.3	31.2	21.1
	PE	25.6	24.4	16.0
	PE	30.1	28.3	16.8
	PE	27.5	25.6	18.2
	PE	25.3	24.0	16.4
	PE	26.0	25.4	17.7
	PE	23.4	21.2	19.5
	PE	26.7	25.3	16.3
	PE	23.5	21.7	14.7
	PE	21.8	19.7	13.7
	PE	17.3	15.7	10.1
	PE	15.6	14.5	9.7

Appendix 2 – Part B

ANCOVA graphs and tables for Mecaster batnensis

Analysis of covariation done on regression lines of data listed in Appendix 2 – Part A.

Summary
statistics:

Variabl e	Observ ations	Obs. with missing data	Obs. without missing data	Minimu m	Maxim um	Mean	Std. deviatio n
W/L	291	0	291	0.674	1.292	0.939	0.045
H/L	291	0	291	0.517	1.001	0.689	0.062
H/W	291	0	291	0.542	1.486	0.735	0.077

Variabl e	Categor ies	Frequencies	%
Countr y	AL	5	1.718
	AZ	45	15.464
	BR	21	7.216
	EG	2	0.687
	MX	71	24.399
	NM	73	25.086
	PL	14	4.811
	TX	60	20.619

Correlation matrix:

Variabl es	Country -AL	Country-AZ	Country-BR	Countr y-EG	Countr y-MX	Countr y-NM	Country- PL	Countr y-TX
Countr y-AL	1.000	-0.057	-0.037	-0.011	-0.075	-0.077	-0.030	-0.067
Countr y-AZ	-0.057	1.000	-0.119	-0.036	-0.243	-0.247	-0.096	-0.218
Countr y-BR	-0.037	-0.119	1.000	-0.023	-0.158	-0.161	-0.063	-0.142
Countr y-EG	-0.011	-0.036	-0.023	1.000	-0.047	-0.048	-0.019	-0.042
Countr y-MX	-0.075	-0.243	-0.158	-0.047	1.000	-0.329	-0.128	-0.290
Countr y-NM	-0.077	-0.247	-0.161	-0.048	-0.329	1.000	-0.130	-0.295
Countr y-PL	-0.030	-0.096	-0.063	-0.019	-0.128	-0.130	1.000	-0.115
Countr y-TX	-0.067	-0.218	-0.142	-0.042	-0.290	-0.295	-0.115	1.000
W/L	0.008	-0.050	0.107	-0.023	-0.023	0.069	-0.027	-0.057
H/L	-0.079	0.202	-0.092	0.005	-0.216	0.316	-0.297	-0.050
H/W	-0.073	0.191	-0.129	0.014	-0.153	0.232	-0.245	-0.024

Multicollinearity statistics:

Statistic	Country-AL	Country-AZ	Country-BR	Country-EG	Country-MX	Country-NM	Country-PL	Country-TX
Tolerance	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
VIF	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Regression of variable W/L:

Goodness of fit statistics (Variable W/L):

Observations	291.000
Sum of weights	291.000
DF	283.000
R ²	0.021
Adjusted R ²	-0.004
MSE	0.002
RMSE	0.045
MAPE	3.053
DW	1.824
Cp	8.000
	-
AIC	1796.764
	-
SBC	1767.378
PC	1.035

Analysis of variance (Variable W/L):

Source	DF	Sum of squares	Mean squares	F	Pr > F
Model	7	0.012	0.002	0.850	0.546
Error	283	0.573	0.002		
Corrected Total	290	0.585			

Computed against model $Y = \text{Mean}(Y)$

Model parameters (Variable W/L):

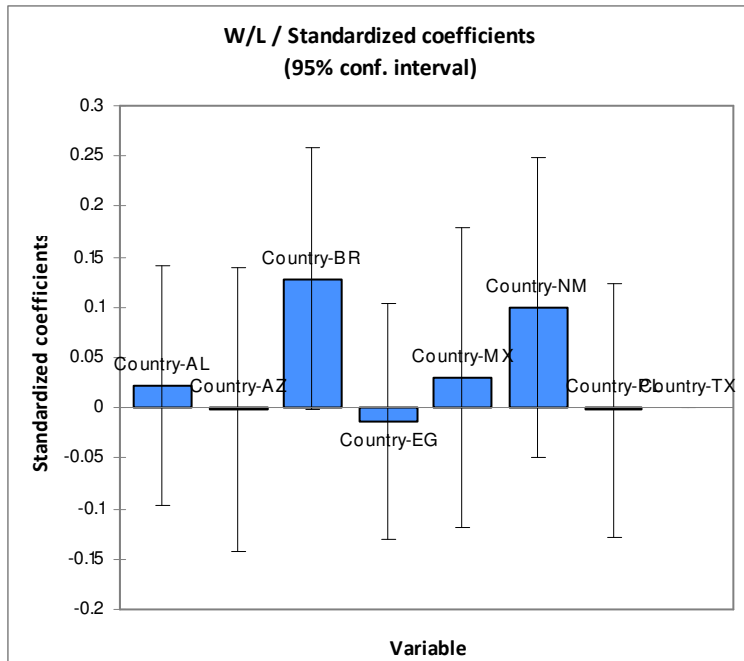
Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Intercept	0.934	0.006	160.731	0.0001	0.923	0.945
Country-AL	0.008	0.021	0.370	0.712	-0.033	0.049
Country-AZ	0.000	0.009	-0.032	0.975	-0.018	0.017
Country-BR	0.022	0.011	1.947	0.053	0.000	0.045
Country-EG	-0.007	0.032	-0.223	0.823	-0.071	0.056
Country-MX	0.003	0.008	0.404	0.686	-0.012	0.019
Country-NM	0.010	0.008	1.320	0.188	-0.005	0.026
Country-PL	0.000	0.013	-0.034	0.973	-0.027	0.026
Country-TX	0.000	0.000				

Equation of the model (Variable W/L):

W/L = 0.934057315335454+7.74722322583347E-03*Country-AL-2.82884012427702E-04*Country-AZ+0.022215939606276*Country-BR-7.22678678273138E-03*Country-EG+3.19079937332956E-03*Country-MX+1.03570555512727E-02*Country-NM-4.5621026635944E-04*Country-PL

Standardized coefficients (Variable W/L):

Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Country-AL	0.022	0.061	0.370	0.712	-0.097	0.142
Country-AZ	-0.002	0.072	-0.032	0.975	-0.143	0.139
Country-BR	0.128	0.066	1.947	0.053	-0.001	0.258
Country-EG	-0.013	0.060	-0.223	0.823	-0.131	0.104
Country-MX	0.031	0.076	0.404	0.686	-0.118	0.179
Country-NM	0.100	0.076	1.320	0.188	-0.049	0.249
Country-PL	-0.002	0.064	-0.034	0.973	-0.128	0.123
Country-TX	0.000	0.000				



Regression of variable H/L:

Goodness of fit statistics (Variable H/L):

Observations	291.000
Sum of weights	291.000
DF	283.000
R ²	0.245
Adjusted R ²	0.226
MSE	0.003
RMSE	0.054
MAPE	5.792
DW	2.051
Cp	8.000
AIC	1687.415
SBC	1658.028
PC	0.798

Analysis of variance (Variable H/L):

Source	DF	Sum of squares	Mean squares	F	Pr > F
Model	7	0.270	0.039	13.090	< 0.0001
Error	283	0.835	0.003		
Corrected Total	290	1.105			

Computed against model Y=Mean(Y)

Model parameters (Variable H/L):

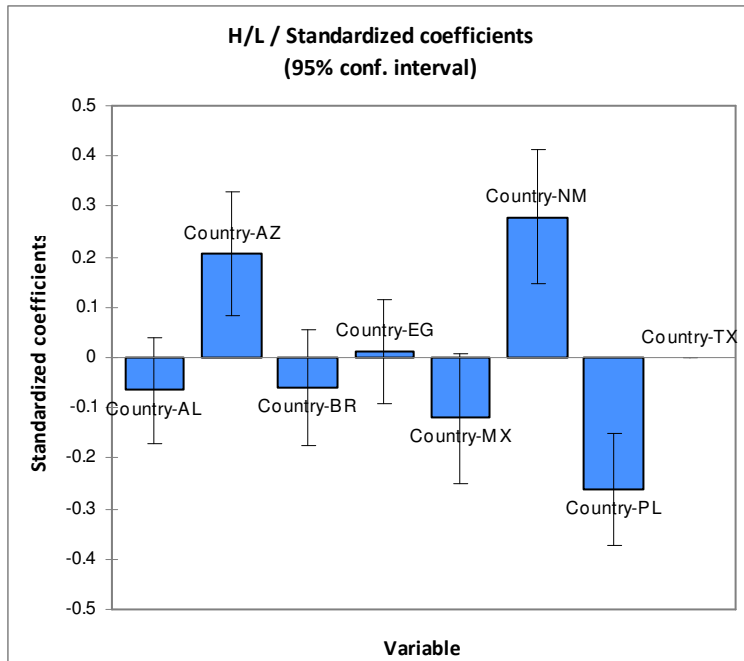
Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Intercept	0.683	0.007	97.402	0.0001	0.669	0.697
Country-AL	-0.031	0.025	-1.224	0.222	-0.081	0.019
Country-AZ	0.035	0.011	3.285	0.001	0.014	0.056
Country-BR	-0.014	0.014	-1.034	0.302	-0.041	0.013
Country-EG	0.010	0.039	0.250	0.803	-0.067	0.087
Country-MX	-0.017	0.010	-1.819	0.070	-0.036	0.001
Country-NM	0.040	0.009	4.201	0.0001	0.021	0.058
Country-PL	-0.075	0.016	-4.671	0.0001	-0.107	-0.044
Country-TX	0.000	0.000				

Equation of the model (Variable H/L):

H/L = 0.683027469645799-3.09355206615274E-02*Country-AL+3.51836270744452E-02*Country-AZ-1.42436732229973E-02*Country-BR+9.74675245065662E-03*Country-EG-1.73294823292235E-02*Country-MX+3.97668876136718E-02*Country-NM-7.53007956763856E-02*Country-PL

Standardized coefficients (Variable H/L):

Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Country-AL	-0.065	0.053	-1.224	0.222	-0.170	0.040
Country-AZ	0.206	0.063	3.285	0.001	0.083	0.330
Country-BR	-0.060	0.058	-1.034	0.302	-0.174	0.054
Country-EG	0.013	0.052	0.250	0.803	-0.090	0.116
Country-MX	-0.121	0.066	-1.819	0.070	-0.251	0.010
Country-NM	0.280	0.067	4.201	0.0001	0.149	0.411
Country-PL	-0.261	0.056	-4.671	0.0001	-0.372	-0.151
Country-TX	0.000	0.000				



Regression of variable H/W:

Goodness of fit statistics (Variable H/W):

Observations	291.000
Sum of weights	291.000
DF	283.000
R ²	0.167
Adjusted R ²	0.147
MSE	0.005
RMSE	0.071
MAPE	6.042
DW	2.042
Cp	8.000
AIC	1532.961
SBC	1503.574
PC	0.880

Analysis of variance (Variable H/W):

Source	DF	Sum of squares	Mean squares	F	Pr > F
Model	7	0.285	0.041	8.128	< 0.0001
Error	283	1.420	0.005		
Corrected Total	290	1.705			

Computed against model Y=Mean(Y)

Model parameters (Variable H/W):

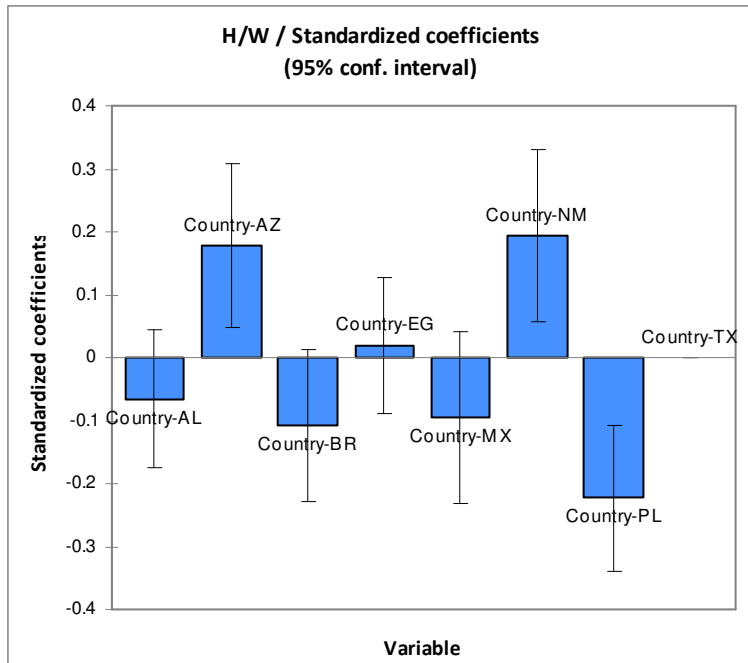
Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Intercept	0.732	0.009	80.020	0.0001	0.714	0.750
Country-AL	-0.039	0.033	-1.169	0.243	-0.103	0.026
Country-AZ	0.038	0.014	2.706	0.007	0.010	0.065
Country-BR	-0.032	0.018	-1.772	0.078	-0.067	0.004
Country-EG	0.017	0.051	0.325	0.746	-0.084	0.117
Country-MX	-0.017	0.012	-1.380	0.169	-0.042	0.007
Country-NM	0.034	0.012	2.768	0.006	0.010	0.058
Country-PL	-0.080	0.021	-3.803	0.000	-0.121	-0.039
Country-TX	0.000	0.000				

Equation of the model (Variable H/W):

H/W = 0.731690805874703-3.85440107979872E-02*Country-AL+3.77947786461975E-02*Country-AZ-3.18135659561286E-02*Country-BR+1.65219150618216E-02*Country-EG-1.71345173563104E-02*Country-MX+3.41689309951289E-02*Country-NM-7.99561277023031E-02*Country-PL

Standardized coefficients (Variable H/W):

Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Country-AL	-0.065	0.056	-1.169	0.243	-0.176	0.045
Country-AZ	0.179	0.066	2.706	0.007	0.049	0.308
Country-BR	-0.108	0.061	-1.772	0.078	-0.227	0.012
Country-EG	0.018	0.055	0.325	0.746	-0.090	0.126
Country-MX	-0.096	0.070	-1.380	0.169	-0.233	0.041
Country-NM	0.194	0.070	2.768	0.006	0.056	0.331
Country-PL	-0.224	0.059	-3.803	0.000	-0.339	-0.108
Country-TX	0.000	0.000				



Appendix 2 – Part C

ANCOVA graphs and tables for Mecaster fourneli

Analysis of covariation done on regression lines of data listed in Appendix 2 – Part A.

Summary statistics:

Variable	Observations	Obs. with missing data	Obs. without missing data	Minimum	Maximum	Mean	Std. deviation
W/L	77	0	77	0.852	0.986	0.924	0.032
H/L	77	0	77	0.487	0.900	0.639	0.066
H/W	77	0	77	0.524	0.977	0.692	0.074

Variable	Categories	Frequencies	%
Country	AL	20	25.974
	PE	57	74.026

Correlation matrix:

Variables	Country-AL	Country-PE	W/L	H/L	H/W
Country-AL	1.000	-1.000	0.078	0.058	0.032
Country-PE	-1.000	1.000	-0.078	-0.058	-0.032
W/L	0.078	-0.078	1.000	0.077	-0.253
H/L	0.058	-0.058	0.077	1.000	0.945
H/W	0.032	-0.032	-0.253	0.945	1.000

Multicollinearity statistics:

Statistic	Country-AL	Country-PE
Tolerance	0.000	0.000
VIF	0.000	0.000

Regression of variable W/L:

Summary of the variables selection (Variable W/L):

No. of variables	Variables	MSE	R ²	Adjusted R ²	Mallows' Cp	Akaike's AIC	Schwarz's SBC	Amemiya's PC
1	Country	0.001	0.006	-0.007	2.000	-526.366	-521.678	1.020

The best model for the selected selection criterion is displayed in blue

Goodness of fit statistics (Variable W/L):

Observations	77.00
Sum of weights	0
DF	75.00

	0
R ²	0.006
Adjusted R ²	-
MSE	0.001
RMSE	0.032
MAPE	2.871
DW	2.038
Cp	2.000
	-
AIC	526.366
	-
SBC	521.678
PC	1.047

Analysis of variance (Variable W/L):

Source	DF	Sum of squares	Mean squares	F	Pr > F
Model	1	0.000	0.000	0.464	0.498
Error	75	0.079	0.001		
Corrected Total	76	0.079			

Computed against model $Y = \text{Mean}(Y)$

Model parameters (Variable W/L):

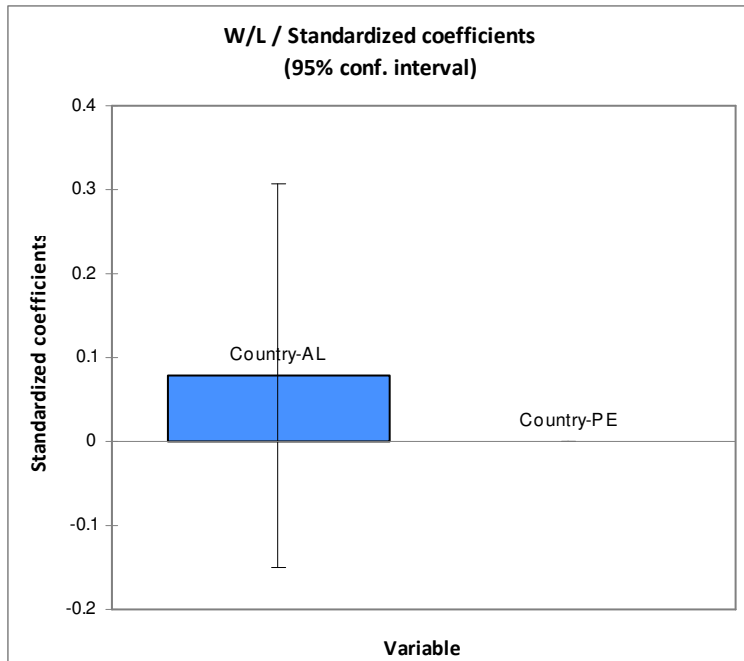
Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Intercept	0.922	0.004	215.155	0.0001	0.914	0.931
Country-AL	0.006	0.008	0.681	0.498	-0.011	0.022
Country-PE	0.000	0.000				

Equation of the model (Variable W/L):

$W/L = 0.922249239176292 + 5.72653363058527E-03 * \text{Country-AL}$

Standardized coefficients (Variable W/L):

Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Country-AL	0.078	0.115	0.681	0.498	-0.151	0.308
Country-PE	0.000	0.000				



Regression of variable H/L:

Summary of the variables selection (Variable H/L):

No. of variables	Variables	MSE	R ²	Adjusted R ²	Mallows' Cp	Akaike's AIC	Schwarz's SBC	Amemiya's PC
1	Country	0.004	0.003	-0.010	2.000	-415.997	-411.310	1.023

The best model for the selected selection criterion is displayed in blue

Goodness of fit statistics (Variable H/L):

Observations	77.00
Sum of weights	77.00
DF	75.00
R ²	0.003
Adjusted R ²	-
MSE	0.004
RMSE	0.066
MAPE	6.726
DW	1.724
Cp	2.000
	-
AIC	415.997

	-
	411.3
SBC	10
PC	1.050

Analysis of variance (Variable H/L):

Source	DF	Sum of squares	Mean squares	F	Pr > F
Model	1	0.001	0.001	0.250	0.619
Error	75	0.329	0.004		
Corrected Total	76	0.330			

Computed against model $Y = \text{Mean}(Y)$

Model parameters (Variable H/L):

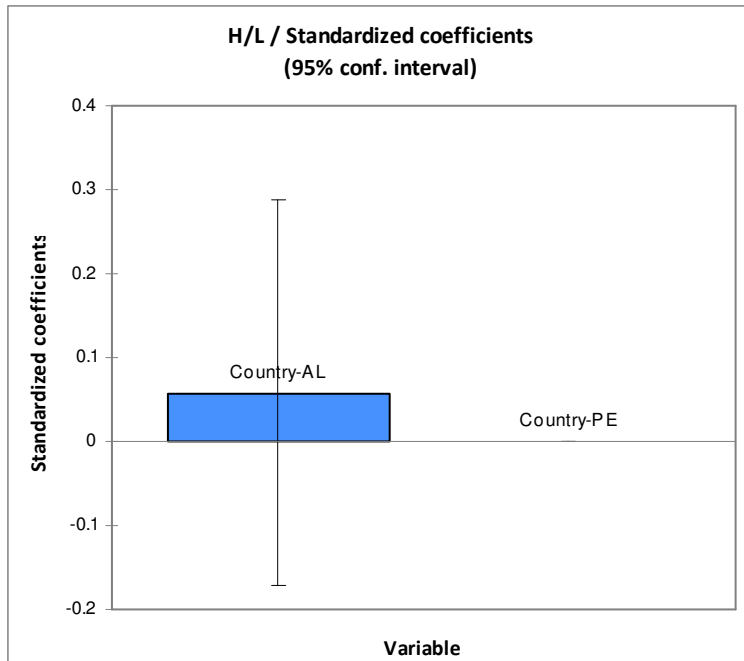
Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Intercept	0.637	0.009	72.545	0.0001	0.619	0.654
Country-AL	0.009	0.017	0.500	0.619	-0.026	0.043
Country-PE	0.000	0.000				

Equation of the model (Variable H/L):

$$H/L = 0.636731221596575 + 8.61083663791333E-03 * \text{Country-AL}$$

Standardized coefficients (Variable H/L):

Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Country-AL	0.058	0.115	0.500	0.619	-0.172	0.287
Country-PE	0.000	0.000				



Regression of variable H/W:

Summary of the variables selection (Variable H/W):

No. of variables	Variables	MSE	R ²	Adjusted R ²	Mallows' Cp	Akaike's AIC	Schwarz's SBC	Amemiya's PC
1	Country	0.006	0.001	-0.012	2.000	-398.012	-393.324	1.025

The best model for the selected selection criterion is displayed in blue

Goodness of fit statistics (Variable H/W):

Observations	77.00
Sum of weights	77.00
DF	75.00
R ²	0.001
Adjusted R ²	-
MSE	0.012
RMSE	0.006
MAPE	0.074
DW	6.975
Cp	1.685
	2.000
	-
AIC	398.012
	12

	-
	393.3
SBC	24
PC	1.052

Analysis of variance (Variable H/W):

Source	DF	Sum of squares	Mean squares	F	Pr > F
Model	1	0.000	0.000	0.077	0.783
Error	75	0.416	0.006		
Corrected Total	76	0.416			

Computed against model $Y = \text{Mean}(Y)$

Model parameters (Variable H/W):

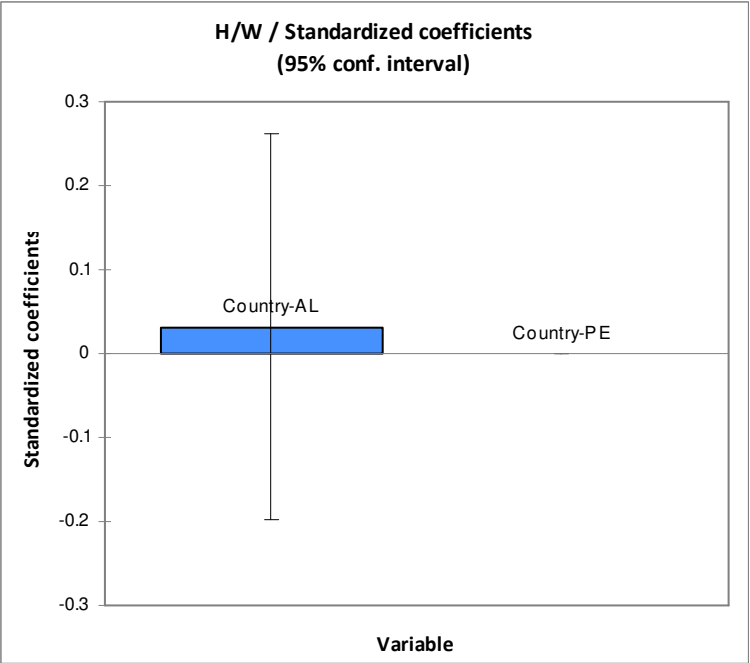
Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Intercept	0.691	0.010	70.048	0.0001	0.671	0.711
Country-AL	0.005	0.019	0.277	0.783	-0.033	0.044
Country-PE	0.000	0.000				

Equation of the model (Variable H/W):

$$H/W = 0.690975259207058 + 5.35836737227134E-03 * \text{Country-AL}$$

Standardized coefficients (Variable H/W):

Source	Value	Standard error	t	Pr > t	Lower bound (95%)	Upper bound (95%)
Country-AL	0.032	0.115	0.277	0.783	-0.198	0.262
Country-PE	0.000	0.000				



Appendix 3 – Part A

Two-dimensional measurements

Linear measurements in mm. Pores I, II, and III are counts. Columns are defined in Table 2 of main text.

	Country	Species	L	W	H	PI	PII	PIII	Pores I	Pores II	Pores III	AS-AM	AS-PM	PS L	PS W	PP L	PP W	H to PP	PS-AM	PS-PM	MaxW-PM	WI	WII	WIII	I3	I4	I5
108395_1	BR	Mb	26.7	24.8	18.0	9.6	12.2	11.0	30	37	24	13.4	14.6	2.0	4.2	3.7	3.1	11.1	6.1	20.3	15.5	3.5	4.0	3.5	9.7	15.7	13.2
108396_1	TX	Mb	26.6	26.7	16.9	9.7	10.9	12.0	30	32	17	11.9	14.3	1.8	3.1	4.1	3.0	11.6	7.4	18.8	15.7	4.0	4.6	3.0	9.0	14.1	13.1
29246_1	AL	Mf	36.2	33.2	21.9	12.5	14.5	16.1	36	41	31	18.0	20.5		4.5	4.8	3.3	15.6	9.7		21.5	4.1	4.6	4.1	13.5	21.2	13.9
308812-1-2	PE	Mf	27.8	24.5	16.1	8.0	12.9	14.9	28	43	27	16.1	12.6	2.5	3.6	3.2	2.4	10.8	6.6	20.2	16.9	3.5	3.7	4.4	9.3	15.9	15.6
308812-1-3	PE	Mf	32.5	28.5	19.1	11.2	16.2	17.6	34	45	29	18.2	14.9	2.7	3.9	3.4	2.5	13.9	5.5	24.8	19.3	4.8	5.8	4.6	10.5	20.4	17.3
308812-1-5	PE	Mf	27.8	24.5	17.0	8.1	12.3	15.2	28	40	25	15.9	13.0			2.9	2.2	11.8		21.0	16.8	3.6	4.2	4.3	9.0	15.7	15.5
308812-1-6	PE	Mf	26.3	24.2	16.1	8.1	12.9	13.7	27	42	28	15.0	12.3			3.3	2.3	10.5		20.0	16.3	3.9	4.0	4.6	8.7	16.1	14.7
308812-1-7	PE	Mf	21.1	19.1	12.8	5.8	10.0	12.0	23	35	23	11.9	9.1	1.7	2.8	2.8	1.8	7.9	4.1	15.2	12.2	2.9	3.1	3.7	7.6	12.6	11.1
308812-2-4	PE	Mf	17.2	16.1	11.2	4.6	7.2	8.5	17	26	18	8.0	9.3	2.0	2.6	3.1	2.4	6.6	4.3	11.4	9.5	2.2	2.6	3.0	6.1	9.6	8.3
308812-3-1	PE	Mf	33.6	30.3	19.7	9.6	14.6	17.8	31	46	33	16.6	17.6			4.0	2.4	13.2	8.1		20.2	4.2	4.4	4.8			
308812-5-1	PE	Mf	27.5	26.3	17.6	7.1	12.0	14.6	23	37	20	14.7	12.6	2.3	3.3	3.8	2.5	11.3	6.0	19.2	15.6	3.6	4.0	4.0	10.4	13.7	14.7
31097_1	AL	Mf	27.4	25.7	16.9	9.6	11.8	13.2	33	39	19	12.5	15.2		3.1	3.8	3.1	13.8	7.6		17.1	3.4	3.7	4.3	9.1	15.1	13.1
31102_1	AL	Mb	24.7	24.7	16.0	8.3	9.9	10.4	30	34	16	11.4	15.5	1.9	3.3		2.7		7.1	17.5	15.3	3.2	3.3	2.9	9.2	15.5	11.5
449382_1	BR	Mb	24.8	23.9	15.4	8.4	10.5	11.8	28	38	26	12.9	13.1	2.3	3.5	3.9	2.6	10.6	6.8	16.8	14.0	3.6	4.3	3.1	8.7	13.7	12.3
449383_1	BR	Mb	23.6	22.9	16.8	7.8	10.3	12.0	28	34	21	12.1	13.1	2.0	4.5	3.5	2.7	10.3	5.8	17.1	13.6	3.1	3.4	2.9	9.4	13.8	7.8
449385_1	BR	Mb	24.7	25.4	16.0	8.3	11.1	11.5	31	39	24	15.0	12.4	2.5	4.5	4.0	3.2	9.1	6.3	17.4	14.4	3.7	4.0	3.4	9.6	14.1	12.6
449388_1	BR	Mb	21.2	20.4	14.6	7.1	8.7	10.6	26	31	19	12.1	11.5	2.2	3.1	3.6	2.6	10.3	5.6	14.9	11.7	2.9	3.2	2.9	8.0	11.4	8.7
468531_1	NM	Mb	31.6	30.6	24.2	11.9	14.6	15.7	31	34	23	13.9	19.3	2.7	4.4	4.5	3.5	14.8	7.3	23.7	21.4	4.2	4.6	4.4	13.0		
468535_1	NM	Mb	28.9	27.5	19.7	10.8	12.0	12.8	29	30	21	12.5	17.1	2.3	3.5	4.2	2.9	12.0	7.5	19.8	15.8	4.0	4.3	4.0	10.5	15.5	11.1
468546_1	AZ	Mb	15.6	14.5	10.7	5.4	6.2	7.0	24	24	18	6.2	9.1	1.5	2.1	2.4	2.2	7.2	4.0	11.3	9.1	1.9	2.1	2.7	5.3	9.6	6.8
468547_1	AZ	Mb	19.1	17.6	14.2	6.8	8.6	9.4	22	29	16	9.2	12.1	1.8	2.7	3.1	2.3	9.2	4.8	14.2	10.5	2.1	3.1	3.5	7.5	9.5	8.3
468548_1	AZ	Mb	20.7	19.8	15.0	7.5	9.0	10.2	26	30	19	10.8	11.6	2.1	3.2	2.9		9.2	5.1	15.2	11.2	2.9	3.1	3.1	8.5	11.2	8.3
468554_1	AZ	Mb	18.8	17.3	13.1	6.7	7.8	8.9	27	30	18	9.0	11.3	2.2	2.7	2.3	1.8	8.6	4.8	14.1	11.5	2.4	2.8	3.4	7.1	10.0	7.8
468564-1	NM	Mb	27.4	26.0	16.0	9.3	11.0	11.4	30			12.0	18.3	2.3	3.2	3.2	2.9	10.7	7.4	19.2	14.9	4.1	4.1	3.4	9.8	14.9	13.2
468564-2	NM	Mb	26.2	25.0	19.0	10.6	11.8	11.9	28	32	22	13.0	15.9	2.5	3.1	3.5	2.8	12.2	6.4	20.0	14.6	3.7	4.3	4.1	10.3	14.6	9.9

Two-dimensional measurements continued

	Country	Species	L	W	H	PI	PII	PIII	Pores I	Pores II	Pores III	AS-AM	AS-PM	PS L	PS W	PP L	PP W	H to PP	PS-AM	PS-PM	MaxW-PM	WI	WII	WIII	I3	I4	I5
468564-3	NM	Mb	21.4	20.4	15.5	8.2	10.0	9.2	28	30	21	9.0	13.3	2.0	2.5	3.6	2.8	9.9	6.6	13.8	11.8	3.3	3.8	2.6	7.5	11.5	8.0
468564-4	NM	Mb	18.3	17.6	13.7	7.0	8.3	7.8	25	28	20	8.5	12.4	1.7	2.5	3.3	2.3	8.1	5.1	13.2	10.4	3.1	3.2	3.2	7.3	11.6	6.7
468873_1	AZ	Mb	20.5	19.1	15.1	7.4	9.4	10.3		30	18	10.3	13.4	1.8		3.5	2.4	8.6	4.6	14.1	12.1	2.1	2.6	3.8	7.7	11.2	8.5
468876-14	TX	Mb	15.5	14.6	11.1	6.4	6.7	6.9	26	29	16	6.0	9.9	1.5	2.3	2.6	1.9	7.2	4.9	10.4	10.4	2.6	3.1	2.2	5.6	8.7	8.8
468876-3	TX	Mb	23.1	21.9	16.6	9.6	11.7	11.1	28	35		10.1	12.9	2.4	3.1	3.3	2.5	9.5	5.5	16.3	15.8	4.1	4.3	3.0	7.9	13.7	10.5
468876-5	TX	Mb	18.9	17.4	13.4	7.7	8.6	8.9	29	30		7.6	12.4	1.4	2.5	3.0	2.1	8.0	5.1	11.7	12.3	3.4	3.8	2.9	6.9	10.2	9.0
468876-6	TX	Mb	22.0	20.7	15.9	9.5	9.6		33	29		8.7	13.8	2.2	3.1	4.2	2.3	8.4	6.9	14.4	14.1	3.7	4.4	2.9	7.1		
468877-1	TX	Mb	22.8	20.9	17.0	8.6	10.2	11.0	29	34	20	10.4	13.6	2.0	3.2	3.3	2.5	9.6	6.0	15.5	14.4	3.5	4.1	2.9	7.7	13.0	10.4
468877-2	TX	Mb	16.1	15.2	10.7	6.1	7.0	6.4	26	27	17	7.0	10.3	1.6	2.1	2.7	2.0	7.6	4.5	10.6	9.0	3.0	3.2	2.1	5.6	9.0	7.0
468877-3	TX	Mb	24.4	23.0	17.7	10.3	11.9	11.0	33	37	22	10.5	13.8	2.3	3.1	3.6	3.3	11.0	6.4	17.6	14.4	4.1	4.5	2.9	7.8	14.0	13.4
468877-4	TX	Mb	19.9	18.7	13.4	8.4	8.4	9.1	30	31	16	8.4	13.0	1.6	2.5	3.4	3.0	8.1	5.9	14.2	12.1	3.3	3.8	2.5	7.4	10.9	10.1
468877-5	TX	Mb	23.2	22.4	16.8	9.5	10.3	12.2	29	33		9.7	14.4	2.2	3.6	3.4	2.8	11.3	6.5	16.5	13.5	3.7	4.4	2.7	8.8	13.6	11.0
468878_1	TX	Mb	27.7	25.3	20.4	11.0	12.1	13.0	35	36	25	12.0	17.2	2.5	3.2	4.0	3.1	12.8	7.3	20.1	16.8	4.6	5.1	3.5	8.9	16.0	14.2
468879-2	BR	Mb	17.8	17.0	10.9	5.0	6.8	6.9	22	31	18	7.8	10.6	2.0	3.1	3.3	2.3	6.2	4.9	10.7	9.8	2.1	2.5	2.4	7.5	9.3	
468879-3	BR	Mb	25.5	24.1	18.1	8.4	11.1	11.6	28	36		12.9	13.8	2.2	3.8	3.8	2.7	9.5	6.8	17.0	15.1	3.5	3.8				
468879-4	BR	Mb	21.9	20.9	15.4	7.1	9.5	10.5	26	34	21	10.1	12.1	2.0	4.0	4.3	3.6	7.7	4.7	14.8	12.8	3.2	3.6	2.8	8.1		
468879-5	BR	Mb	22.5	21.0	15.7	8.7	10.4	10.5	33	38	23	10.8	12.4	2.0	3.1	3.3	3.0	7.5	5.4	15.2	13.3	3.7	3.9	2.8	8.1	12.9	12.3
468879-6	BR	Mb	20.1	19.3	14.3	6.4	8.3	8.8	26	31	21	8.9	10.8	1.9	3.3	3.3	2.3	8.0	4.0	13.3	13.1	3.0	3.5	2.5	7.7		
468883-1	TX	Mb	24.9	23.1	17.8	10.5	12.1	12.4	33	36	25	10.8	15.2	2.5	3.0	3.2	2.6	13.3	6.6	17.4	14.5	4.3	4.4	2.9	8.4	15.8	14.1
468889-1	AL	Mf	28.8	26.9	18.6	8.9	12.7	14.4	29	34	25	15.5	15.3	2.5	3.8	4.4	3.5	12.8	7.0	20.4	16.8	3.2	3.5	3.9	10.7	16.6	14.7
468889-2	AL	Mf	30.5	26.9	19.6	9.5	12.3	15.8	33	43	30	16.9	16.4	2.7	3.4	3.4	3.1	12.9	8.0	22.3	18.3	3.2	3.9	3.7	11.4	17.5	15.0
468889-3	AL	Mf	27.7	25.3	17.8	8.5	11.7	14.4	28	38	25	14.6	14.5		3.7	3.8	2.4	11.0	6.4		15.1	3.2	3.5	4.5	10.6	16.5	12.0
468889-4	AL	Mf	24.1	22.5	15.8	6.7	11.1	13.1	25	37	24	14.5	12.1	1.9	2.9	3.3	2.4	12.6	5.6	17.7	14.3	3.3	3.2	3.7	9.2	12.8	12.1
468891-2	AL	Mf	15.7	14.8	11.1	4.8	6.1	7.2	21	24	18	6.9	8.1	1.2	2.1	2.5	1.8	8.0	4.4	11.1	9.0	1.8	2.2	2.2	5.8	9.3	7.5
468895_1	AL	Mf	13.7	12.4	9.3	3.4	5.0	7.0	19	26	19	7.7	7.9	1.4	1.8	2.3	1.5	6.2	3.6	9.1	8.2	1.5	1.6	2.4			
468896-1	AL	Mf	21.9	21.4	15.0	7.2	9.7	11.0	27	34	23	11.1	11.4		3.4	4.0	2.6	9.3		16.5	12.9	2.8	3.2	3.8	7.6	13.2	11.2
468896-2	AL	Mf	16.8	15.8	10.6	4.8	6.3	7.5	23	28	19	8.2	9.6		2.6	2.8	1.9	7.5	3.8		10.5	1.8	2.1	2.7	6.5	8.5	7.7
468897-4	AL	Mf	38.1	34.0	23.2	12.8	15.8	19.0	32	39	28	17.7	20.3	3.4	5.1	4.0	2.9	16.3	8.4	27.2	23.6	4.3	5.1	4.8	13.6		
468897-6	AL	Mf	23.6	21.2	16.3	7.5	9.9	11.4	27	35	25	10.8	12.2		2.8	3.1	2.1	11.2	6.0		14.8	2.8	3.2	3.5	8.6	14.2	10.8
468898-1	AL	Mf	36.1	33.5	22.3	12.4	16.3	18.4	36	45	31	16.9	18.1	2.5	4.3	5.0	3.4	14.8	9.3	25.8	22.1	4.8	5.1	6.3			
468898-10	AL	Mf	24.8	22.3	16.2	8.3	11.0	14.1	31	41	31	13.0	12.1	1.7	3.1	3.5	2.1	9.5	6.7	17.4	15.5	3.0	3.7	4.1	9.5	13.4	11.9
468898-3	AL	Mf	33.0	30.8	21.5	11.8	13.6	14.2	36	40	26	16.0	18.6	2.7	4.1	4.6	3.9	13.7	7.6	25.6	19.3	4.2	4.5	3.6	12.5	19.4	17.7
468898-4	AL	Mf	32.9	30.2	22.8	11.3	15.7	15.4	33	48	35	18.4	16.9	3.1	3.8	4.7	3.8	15.3	7.2	25.8	20.7	4.9	5.2	4.9	10.6		

Two-dimensional measurements continued

	Country	Species	L	W	H	PI	PII	PIII	Pores I	Pores II	Pores III	AS-AM	AS-PM	PS L	PS W	PP L	PP W	H to PP	PS-AM	PS-PM	MaxW-PM	WI	WII	WIII	I3	I4	I5
468898-5	AL	Mf	21.1	19.6	14.3	6.6	8.3	10.3	26	33	26	10.9	11.7	2.5	3.5	2.8	2.3	10.5	4.9	15.3	14.2	2.4	3.1	3.0	6.8	13.0	
468898-6	AL	Mf	14.6	13.6	9.5	4.3	6.4	7.8	24	27	23	8.1	7.5	1.3	2.0	2.2	1.5	6.0	3.2	10.3	9.4	2.1	1.8	2.8	6.4	8.2	7.8
468898-7	AL	Mf	27.0	25.4	17.6	8.9	11.9	13.6	28	40	32	13.2	13.3	2.4	3.7	4.0	2.3	11.3	4.8	20.0	17.1	3.5	3.8	4.4	9.8	15.0	13.8
468899-1	AL	Mf	32.3	30.3	20.6	9.9	12.8	15.5	34	40	31	15.7	17.2			4.5	3.1	14.1	7.0		19.2	3.7	4.4	4.1	11.5	18.9	16.3
468899-10	AL	Mf	24.5	21.6	16.1	8.9	10.2	3.4	34	38	27	10.9	14.5	2.1	3.5	3.4	2.2	10.1	6.2	16.4	15.0	3.2	3.7	3.6	8.5	13.8	11.1
468899-12	AL	Mf	24.4	22.6	16.7	8.3	9.9	11.8	32	36	24	11.9	13.9	2.1	3.1	3.2	2.3	9.8	5.5	15.6	15.2	3.0	3.5	3.6	8.7	13.9	11.4
468899-2	AL	Mf	15.4	14.6	11.3	4.9	6.3	7.5	25	30	21	7.3	8.1	1.5	2.3	2.6	2.0	6.4	3.7	9.6	10.6	1.7	2.1	2.5	5.9	10.2	8.2
468899-5	AL	Mf	28.5	27.3	19.5	9.5	12.2	13.7	33	40	31	13.4	14.8	2.0	3.6	4.3		10.5	6.0	20.3	17.5	3.5	4.1	4.4	10.3		
468899-6	AL	Mf	22.3	21.4	14.6	6.3	9.0	11.1	25	34	21	11.4	12.1	2.1	3.1	3.3	2.4	8.8	4.9	16.8	13.6	3.3	3.8	4.0	8.5	15.4	
468899-8	AL	Mf	21.3	19.4	14.9	6.4	8.6	10.0	27	33	24	10.0	11.2	1.9	3.1	3.6	2.7	9.3	5.1	15.0	14.7	3.9	3.3	2.8	7.3	12.8	10.0
468899-9	AL	Mf	25.6	23.6	17.3	8.0	10.2	12.4	30	36	26	12.8	13.7	2.3	3.7	4.0	2.7	10.6	6.0	18.6	16.0	3.2	4.0	3.7	8.5	15.6	
468939-4	PA	Mb	26.4	24.9	15.3	9.5	11.9	11.9	34	37	28	11.8	14.6			3.8	2.6	9.1		18.5	15.8	3.8	4.0	3.8	9.5	17.0	12.5
468944-1	EG	Mb	22.1	20.8	14.6	8.3	10.8	10.2	31	40	21	10.6	13.8	2.2	2.3	2.9	2.2	9.9	6.7	15.0	14.0	3.8	3.5	3.4	7.9	12.8	11.4
468944-2	EG	Mb	26.1	23.8	18.8	7.9	10.8	13.7	30	38	26	14.5	13.9	1.5	3.7	3.2	2.9	13.1	7.0	19.4	14.8	3.2	3.2	2.8	9.4	15.5	11.2
J68	MX	Mb	16.7	15.8	11.8	6.6	7.8	6.6	25	30	16	8.0	10.3	2.0	2.9	2.5	2.0	7.9	4.1	11.8	10.0	3.3	3.4	2.3	5.7		

Appendix 3 – Part B

Three-dimensional measurements

ID	x1	y1	z1	x2	y2	z2	x3	y3	z3	x4	y4	z4
108395_1	23.2273	-70.3328	-0.38172	20.5567	-75.5644	-8.75377	16.5307	-62.3048	-6.08276	16.8979	-62.6921	3.48453
108396_1	25.1837	-72.121	-0.10798	22.5235	-64.2483	-6.67145	19.448	-65.6057	7.59337	18.2091	-76.6724	8.57371
29246_1	24.8304	-65.6267	0.056956	22.987	-73.4077	-10.0587	19.448	-54.1492	-7.74448	16.7045	-53.0739	6.12211
308812_1_1	27.6701	70.1693	-8.15397	25.3062	-72.2724	-16.4983	21.5081	-56.6022	-10.4111	20.0237	-57.864	1.55833
308812_1_2	26.3532	-71.0666	-5.99693	25.0424	-74.4802	-14.2246	21.0621	-59.6126	-10.1059	18.6266	-59.8866	-0.0641
308812_1_3	28.966	-68.3317	-6.05146	25.0539	-73.6995	-16.1584	20.2984	-54.7832	-11.2891	19.4266	-55.2831	0.892607
308812_1_5	26.5876	-70.2703	-4.41826	24.7517	-72.9092	-12.99	20.4281	-59.3956	-7.78595	18.5913	-59.9424	2.95122
308812_1_6	25.3275	-71.7303	-4.26346	21.652	-65.3263	-9.73828	18.8862	-63.8065	4.81074	19.117	-73.5	7.68698
308812_1_7	23.9368	-74.0113	-3.98778	22.5642	-76.1715	-9.63297	18.9641	-65.3664	-6.68344	17.2451	-65.6386	1.79
308812_2_4	23.859	-74.6173	-2.60212	23.1716	-76.257	-7.8477	19.9002	-68.4593	-5.18681	18.0985	-69.725	1.26261
308812_3_1	30.354	-66.3564	-6.77011	28.7165	-70.4266	-16.6476	23.2497	-53.6422	-12.4881	20.2475	-53.9983	-0.10172
308812_5_1	25.7401	-69.8605	-5.448	25.613	-74.11	-12.5736	19.9446	-60.0016	-11.6571	16.6152	-59.4632	-0.66364
31097_1	19.9955	-72.5264	-0.74018	17.5114	-67.322	-9.31042	14.6434	-63.051	5.54755	13.4663	-72.7657	10.4175
31102_1	20.9189	-69.5086	1.54098	20.8457	-73.9356	-6.45143	16.8626	-61.9696	-4.06577	14.0449	-62.6256	5.13466
449382_1	19.0314	-72.1909	-0.80452	16.5297	-75.3534	-8.34354	14.2162	-63.5379	-4.50557	13.0634	-64.3332	5.45107
449383_1	25.489	-73.8764	0.938948	23.1217	-68.7096	-6.13131	20.1945	-65.8734	5.74938	18.7211	-74.6787	10.2378
449385_1	19.9719	-72.2977	-2.67682	16.2848	-67.1731	-9.06074	15.0615	-63.5884	3.29621	15.3617	-72.8351	7.97204
449388_1	21.0209	-74.8878	-5.07088	17.4394	-70.4038	-10.6728	16.9141	-68.2293	-0.26757	16.5319	-75.8424	4.33765
468531_1	22.155	-68.977	5.00205	17.5368	-64.4352	-6.73859	13.0788	-56.8444	9.27891	12.2085	-69.3566	16.9952
468535_1	26.1786	-71.1585	2.64135	23.8293	-65.5696	-7.7375	19.2927	-61.9001	7.09895	17.8757	-72.0751	12.1776
468546_1	22.3094	-77.6971	-1.29613	21.0448	-74.751	-5.93577	19.1668	-73.1432	1.30346	18.5563	-78.8545	4.0954
468547_1	14.3371	-76.0535	7.14583	12.5602	-74.3386	0.389348	9.26731	-69.0745	8.16901	8.64868	-75.496	14.4526
468548_1	20.6202	-73.3016	-0.39543	19.8542	-77.0723	-7.77835	16.0696	-66.9126	-4.85819	13.7426	-67.7614	3.78844
468554_1	23.05	-75.997	2.28617	21.4143	-72.7131	-4.44601	17.6966	-69.5008	4.54677	17.4978	-77.0808	8.65607
468564_1	21.9962	-68.3141	-5.65205	22.1318	-74.8993	-13.6706	17.1913	-60.8654	-13.3085	15.1119	-59.8771	-2.30879
468564_2	24.0482	-70.282	-2.33597	21.3645	-76.224	-11.2222	17.0032	-62.9168	-9.1339	15.7936	-62.7055	2.80342
468564_3	21.506	-72.9385	-2.58781	20.2329	-76.7274	-10.3788	16.6462	-65.305	-6.9359	15.0952	-67.7121	2.1874
468564_4	21.7028	-73.2196	-1.09901	21.6316	-77.0294	-8.02383	16.2999	-68.2337	-5.3181	15.4914	-69.8214	2.31064
468873_1	9.93887	-74.777	7.06473	6.62226	-70.3776	1.39138	4.06674	-68.8741	11.6454	3.97328	-77.3033	14.9323
468876_14	22.3018	-65.1234	-11.4568	21.3403	-62.3651	-17.3611	18.3244	-59.5938	-9.71157	17.967	-65.0996	-6.33323

Three-dimensional measurements continued

ID	x1	y1	z1	x2	y2	z2	x3	y3	z3	x4	y4	z4
468876_3	24.6868	-61.5568	-12.0143	21.0606	-56.5688	-20.2592	17.1114	-53.5653	-7.86705	16.8385	-63.0515	-4.37033
468876_5	23.3224	-63.8123	-13.9229	20.9777	-60.7731	-21.2604	18.6898	-57.2947	-11.5499	16.9995	-63.6917	-7.1966
468876_6	25.0507	-63.0659	-11.7557	22.3	-58.7236	-20.9483	19.7873	-55.3153	-8.39034	18.4108	-63.0957	-5.00186
468877_1	23.165	-71.8997	-2.42433	21.1431	-77.2958	-9.57401	17.0942	-65.2655	-7.9183	15.4141	-64.86	0.838278
468877_2	18.8501	-75.5617	0.899154	18.9103	-78.7275	-4.76904	15.7127	-70.7138	-2.81107	14.477	-71.704	3.2447
468877_3	22.7711	-70.752	-0.71807	20.0436	-75.1974	-10.2008	15.5438	-62.7276	-5.17022	15.5568	-64.5597	4.68106
468877_4	21.4302	-73.3102	-0.08746	20.197	-77.9698	-7.70973	17.0168	-67.2243	-5.19012	15.5213	-67.4498	3.17659
468877_5	15.7835	-70.7455	0.568397	13.4092	-75.364	-8.64934	9.03534	-63.4123	-3.74804	6.54499	-64.9647	6.0334
468878_1	26.0399	-71.8366	-2.30412	23.7438	-66.3318	-12.4708	18.5845	-63.2457	2.16977	17.0208	-73.0053	7.04977
468879_2	21.6467	-64.7726	-14.0628	20.9335	-62.1317	-19.7926	18.7912	-58.0295	-12.5872	18.4678	-64.3859	-7.78986
468879_3	25.1264	-60.6399	7.48994	21.0464	-54.8144	0.239158	18.9475	-53.1294	14.3184	-9999	-9999	-9999
468879_4	24.7821	-61.6351	13.5036	20.79	-56.9551	8.24279	19.0976	-55.8214	19.8599	19.1404	-64.1093	22.4909
468879_5	24.6261	-60.9882	-6.08578	22.2382	-64.373	-14.6236	19.1311	-52.5053	-10.4997	18.0754	-53.8699	-1.20114
468879_6	21.4245	-61.1784	-5.64589	19.5309	-65.222	-11.3708	17.3793	-54.9371	-10.0997	15.9098	-54.2459	-2.69062
468883_1	17.7469	-68.1243	0.337886	15.5247	-73.6746	-9.55448	9.58221	-61.395	-5.62016	7.75868	-62.5127	4.4007
468889_1	20.46	-69.6845	-1.16144	19.6255	-74.098	-9.37155	15.5049	-59.4928	-5.16879	12.4457	-60.3487	6.31441
468889_2	24.0883	-69.5522	-2.45618	21.583	-75.3099	-10.1624	18.4708	-59.7253	-8.44796	16.0441	-57.7597	3.99863
468889_3	24.6464	-71.3731	-1.6393	22.8924	-75.6563	-9.40819	18.7006	-61.1938	-6.38631	16.6893	-61.2762	4.74058
468889_4	22.8146	-73.0622	-0.75267	21.3677	-73.9493	-7.63853	17.6995	-63.1308	-3.02784	15.4524	-65.1449	6.37851
468891_2	23.115	-74.9681	-3.89515	23.1118	-78.3193	-8.0482	20.0986	-70.2223	-7.59343	18.3835	-70.0692	-1.25911
468895_1	16.0318	-77.7542	-0.36165	15.6886	-79.0884	-3.28813	13.7559	-73.6645	-1.96354	12.3026	-73.5684	2.96767
468896_1	21.2393	-73.5737	3.69876	20.5587	-76.934	-3.46035	16.9244	-65.7422	-0.63691	14.5839	-66.4334	7.96435
468896_2	19.9667	-75.4735	1.69886	19.5803	-78.9751	-2.37045	17.2383	-70.9058	-1.86269	15.6914	-70.3863	4.2719
468897_4	28.5337	-52.4871	-6.39941	25.5796	-59.8875	-17.8595	21.0176	-40.0938	-15.1517	17.6009	-38.1753	0.114083
468897_6	21.5054	-59.6168	-5.65879	20.0681	-63.6498	-12.5662	15.8917	-51.5865	-9.53935	14.3184	-52.3902	0.002728
468898_1	27.5714	-55.7789	-11.2153	24.1607	-47.8845	-22.593	19.1961	-44.068	-2.69408	18.8932	-56.2824	3.40799
468898_10	26.2297	-62.4024	-18.0694	23.4243	-57.6351	-25.5629	17.8421	-61.9942	-6.56227	20.5444	-70.2537	-12.3218
468898_3	33.9308	-64.1797	-30.8562	33.1232	-51.1455	-30.5951	29.8066	-46.865	-13.0151	28.7031	-57.5685	-7.71545
468898_4	27.2706	-56.6171	-11.5099	21.3906	-50.0133	-20.496	20.0477	-47.32	-1.00504	22.7094	-58.4698	3.00953
468898_5	10.7457	-55.0435	-16.4688	9.47616	-51.7403	-22.7364	7.04372	-48.2023	-12.4154	6.78882	-54.9336	-8.02577
468898_6	18.3305	-66.0217	-9.06428	17.6135	-62.8284	-12.35	15.2113	-61.5854	-5.26101	13.6812	-66.9639	-3.38306
468898_7	26.3733	-59.454	-12.8046	24.6212	-54.218	-19.9819	20.7825	-50.9751	-5.48486	18.9753	-61.052	-0.81342
468899_1	23.6011	-55.4966	-6.56251	22.1026	-61.6588	-15.7828	18.6002	-44.7806	-13.2446	14.9489	-44.0992	-0.20536
468899_10	25.9091	-69.5741	-5.23793	-9999	-9999	-9999	20.0212	-63.152	-11.6596	17.6883	-61.0667	-2.88813

Three-dimensional measurements continued

ID	x1	y1	z1	x2	y2	z2	x3	y3	z3	x4	y4	z4
468899_12	25.6394	-72.1387	-9.31194	21.9741	-68.1368	-17.1407	21.1793	-64.6281	-3.05959	20.0594	-73.1083	0.933124
468899_2	19.1949	-63.719	-7.75749	18.768	-66.5941	-12.5573	15.5154	-58.9466	-11.0977	13.9749	-59.0432	-4.4156
468899_5	22.0411	-56.378	-8.30066	21.2865	-63.5982	-15.7706	17.1253	-48.3451	-16.9509	12.9991	-45.9993	-6.62581
468899_6	20.6981	-60.8865	-5.05355	20.0119	-64.5242	-11.0807	17.4001	-53.3918	-10.4011	13.8635	-52.2427	-2.09211
468899_8	26.0919	-73.7597	-6.66393	24.1974	-70.2527	-12.1941	21.9228	-67.5183	-1.93377	20.8357	-74.6537	2.10225
468899_9	22.4623	-58.7668	-5.76493	20.4258	-62.0468	-14.3855	17.3892	-49.4381	-8.20457	14.6294	-51.959	0.839205
468939_4	21.6483	-57.8763	-11.1945	19.7794	-63.5407	-20.3529	16.1602	-48.7409	-17.2598	15.0506	-49.091	-6.68832
468944_1	12.893	-75.2209	5.97849	10.8796	-70.8813	-1.49019	7.80779	-66.7053	10.3512	7.62444	-74.8117	14.6241
468944_2	12.327	-72.4159	1.83284	9.19027	-68.0799	-4.87729	7.29415	-65.251	8.02359	6.89945	-73.6255	14.0978
J68	12.7022	-74.66	-1.53895	11.8582	-78.355	-7.57239	8.06335	-69.3714	-5.2316	8.21844	-70.8761	1.58279

Highlighted sample numbers in gray indicate missing data on only one landmark. Red highlights indicate more than one landmark with missing data. Landmarks with missing data have coordinates of -9999 so that MorphoJ recognizes them as missing data points.

Three-dimensional measurements continued

ID	x5	y5	z5	x6	y6	z6	x7	y7	z7	x8	y8	z8
108395_1	6.67078	-70.431	8.16533	20.4149	-80.4199	0.191307	20.971	-80.9127	-6.1086	17.474	-82.3829	-6.53345
108396_1	20.7247	-82.6888	-0.66301	23.2313	-73.5913	-10.8352	22.8188	-67.2373	-12.207	19.7236	-67.4537	-13.8696
29246_1	18.9357	-64.5551	13.7259	23.5147	-78.2336	0.588218	23.2476	-80.0846	-6.87816	19.0588	-82.2646	-7.89042
308812_1_1	22.7424	-68.6268	5.34856	26.1651	-79.3263	-7.20837	25.2083	-78.8742	-14.1179	21.9288	-80.1449	-14.6583
308812_1_2	20.3128	-68.6474	5.14572	24.8339	-79.5662	-4.56094	25.4307	-80.5274	-10.7797	22.576	-81.5523	11.6686
308812_1_3	19.9972	-64.8557	8.48372	25.3899	-79.735	-3.69319	26.8385	-79.4378	-11.6318	23.3188	-80.9109	-12.2555
308812_1_5	20.9369	-69.5586	6.99483	25.417	-79.2289	-3.90966	25.8253	-78.5614	-10.2567	23.6691	-79.983	-10.9441
308812_1_6	20.7842	-82.1691	2.13577	23.122	-76.7795	-11.2685	23.3704	-70.5502	-13.9218	20.1349	-70.2732	-15.4248
308812_1_7	19.4627	-72.9688	5.44934	23.1395	-80.2159	-2.49366	23.2637	-80.4219	-7.54334	20.8509	-81.8521	-8.11609
308812_2_4	20.0078	-75.7655	4.16259	23.5286	-79.7331	-6.25281	21.7086	-81.6474	-7.53439	14.4086	-72.4804	-0.60757
308812_3_1	23.9223	-65.1467	6.19443	28.8022	-76.7571	-5.7064	29.3218	-76.3006	-12.6898	26.4146	-78.6328	-14.0289
308812_5_1	19.2203	-68.818	6.04447	25.3796	-78.4862	-3.70366	25.3602	-79.7285	-10.1761	22.0464	-81.4856	-10.6514
31097_1	15.7224	-81.4973	4.84003	17.9192	-78.1512	-9.16951	18.5099	-72.4145	-12.1504	15.2065	-72.558	-14.1779
31102_1	16.4587	-70.5805	10.4406	20.8374	-78.3905	1.5727	21.4839	-78.9213	-3.62778	-9999	-9999	-9999
449382_1	14.4334	-73.7862	8.78451	16.7943	-80.7226	-0.81368	16.8938	-80.4842	-6.43124	13.4081	-82.0799	-7.23447
449383_1	20.5428	-82.2773	3.71329	23.338	-77.9468	-6.99901	23.4284	-72.9284	-9.33577	20.1367	-72.9171	-10.9693
449385_1	15.6297	-82.4183	2.41032	16.4542	-78.0928	-9.16134	16.0062	-72.6202	-11.7793	12.4645	-72.8628	-12.7186
449388_1	18.3421	-82.4879	-1.44945	18.0321	-79.0344	-11.6466	18.0453	-74.5561	-13.1325	14.777	-74.9091	-14.0573
468531_1	15.6573	-81.9963	9.82371	19.3149	-74.7438	-6.14829	16.6877	-70.3244	-11.2296	12.4115	-71.0988	-12.4786
468535_1	20.2767	-81.8071	5.32856	24.4752	-76.2231	-8.21705	23.2592	-70.477	-13.0038	19.744	-70.558	-14.7867
468546_1	20.1736	-83.6649	0.039647	21.5578	-79.8421	-6.6873	21.1987	-77.0921	-8.68551	19.631	-77.2133	-9.5478
468547_1	11.0159	-83.5428	10.95	13.5475	-80.5938	1.30865	12.3605	-78.1316	-2.06485	9.94762	-77.9857	-3.15125
468548_1	15.3889	-76.9369	7.02139	19.7812	-81.5639	-2.00465	19.1439	-82.3073	-7.2696	16.0354	-83.0579	-7.71592
468554_1	19.7193	-83.3714	4.21669	22.5135	-78.8244	-4.25137	22.4824	-75.2378	-6.55384	20.5926	-75.5265	-8.14566
468564_1	16.3854	-69.0437	5.79634	22.1489	-79.0188	-4.20538	22.14	-80.8042	-10.3534	19.6272	-82.7521	-11.129
468564_2	18.1272	-72.4861	7.82972	21.7635	-80.7941	-2.83069	21.3037	-81.9284	-9.22623	18.6023	-83.328	-9.61455
468564_3	16.1482	-75.9345	6.0868	20.0495	-81.8915	-4.10895	19.9478	-81.3732	-9.35302	16.7735	-82.3627	-10.5967
468564_4	17.9296	-76.6767	6.15655	22.7641	-80.8406	-2.16343	22.365	-81.031	-6.94122	19.8706	-82.8904	-7.62743
468873_1	6.23556	-83.6684	8.83066	7.78513	-77.8591	-0.27832	5.79391	-73.8164	-2.58642	2.92071	-73.4728	-3.66873
468876_14	20.1275	-70.9936	-9.65099	22.4496	-68.3332	-16.8627	22.138	-65.165	-18.8764	20.0842	-65.6938	-20.2724
468876_3	18.6066	-70.4321	-9.90355	22.0996	-65.1381	-20.482	22.394	-60.9081	-23.3208	19.4128	-60.7215	-25.1208
468876_5	19.5796	-70.5237	-10.4962	21.7606	-67.9899	-20.9986	20.6863	-64.632	-24.0749	18.462	-65.1714	-25.1743
468876_6	19.5247	-70.8382	-8.69569	22.3336	-66.9991	-21.234	22.6899	-62.7533	-24.0813	19.239	-62.9422	-24.6763

Three-dimensional measurements continued

ID	x5	y5	z5	x6	y6	z6	x7	y7	z7	x8	y8	z8
468877_1	17.5843	-71.9005	6.18312	-9999	-9999	-9999	20.761	-82.349	-7.58158	17.7858	-83.7267	-7.90134
468877_2	15.2258	-77.1592	6.07381	18.6255	-82.2539	0.009624	19.3191	-82.089	-3.66723	17.4943	-83.3823	-4.46797
468877_3	16.6671	-73.5444	8.87488	21.032	-81.5864	-1.84205	20.2542	-81.1359	-8.4666	16.419	-82.1061	-8.57057
468877_4	16.9977	-74.8323	7.45885	20.1612	-82.1646	-0.58401	20.8452	-82.1398	-5.27444	17.9138	-83.1096	-5.88205
468877_5	10.2695	-73.735	9.64309	14.0491	-81.3882	-1.30854	13.8571	-80.8751	-6.47701	10.8137	-82.072	-7.23561
468878_1	19.7028	-82.323	1.52922	25.0997	-77.5238	-12.6605	24.8049	-71.9268	-16.7228	21.4711	-72.361	-18.3724
468879_2	19.0859	-70.8283	-11.0429	20.9	-68.1959	-19.5983	21.0761	-65.1055	-21.5288	19.1306	-65.3224	-23.4696
468879_3	20.1782	-70.2325	10.5985	21.6648	-64.2153	-1.32365	21.24	-58.9033	-3.52479	17.6529	-58.8218	-4.85571
468879_4	20.725	-70.636	16.5178	21.8824	-64.867	6.38592	21.3742	-60.4814	4.84964	17.3348	-60.8559	3.54012
468879_5	18.6282	-62.3938	2.17907	21.496	-69.9021	-7.24454	22.4211	-69.3761	-12.5216	19.4069	-70.5667	-13.3956
468879_6	16.9324	-60.6362	1.60265	19.057	-68.2873	-5.03852	19.6475	-69.0505	-9.41068	17.0126	-70.3905	-9.94928
468883_1	10.3086	-70.6641	9.44137	15.9554	-79.3169	0.398956	17.5425	-78.7756	-6.22221	14.8575	-80.6469	-6.90956
468889_1	15.6371	-70.3304	10.1419	19.8205	-79.0897	-1.90105	3.15559	-67.3719	2.45757	15.3962	-81.4167	-7.8913
468889_2	19.234	-67.975	9.83285	22.4909	-79.8369	-0.49525	21.3436	-81.387	-6.79818	17.8608	-83.2767	-7.14088
468889_3	18.7793	-71.1715	9.52156	22.8254	-80.6728	-1.31197	22.0641	-81.313	-7.22502	19.0079	-82.6643	-7.90952
468889_4	17.7191	-73.8486	9.53103	21.4068	-80.8953	0.027178	21.5064	-79.5781	-5.59521	18.7794	-81.3595	-6.748
468891_2	19.9623	-75.8854	1.78921	23.144	-80.4325	-4.43225	23.0322	-80.8433	-7.35382	21.407	-82.1609	-7.77593
468895_1	14.1058	-78.3525	4.75502	15.9355	-81.3801	-0.42348	15.7373	-81.779	-2.9525	14.137	-83.0951	-3.37512
468896_1	16.3133	-73.8931	12.2737	20.2323	-81.5663	3.71412	20.4313	-81.369	-1.54379	17.1493	-83.2142	-2.01211
468896_2	17.2651	-75.6123	7.56113	19.684	-80.8685	1.90743	19.4681	-82.1275	-1.1527	17.1724	-83.8101	-1.82719
468897_4	19.0086	-51.2475	7.92943	24.0654	-66.5032	-4.71627	24.4738	-67.5348	-13.4532	21.0475	-69.4658	-14.7007
468897_6	17.3545	-60.5289	4.13494	21.0572	-68.0252	-5.9825	20.526	-68.5478	-10.8241	18.3382	-70.0933	-11.3318
468898_1	20.3692	-69.1901	-3.22291	25.5328	-62.6692	-21.9874	25.3683	-55.3595	-26.7931	20.5342	-55.7293	-28.851
468898_10	23.3948	-66.8478	-25.1332	23.1332	-62.2479	-28.233	20.2749	-62.6213	-29.8578	12.0976	-61.9616	-11.2931
468898_3	30.3118	-67.9594	-13.1567	34.0942	-58.0682	-34.1264	30.3354	-58.6869	-36.6579	18.9299	-58.2381	-11.8203
468898_4	21.4847	-68.98	-2.70949	22.4343	-63.1546	-21.6989	20.9987	-56.0702	-25.2507	16.6955	-56.4538	-26.1955
468898_5	7.97714	-61.8559	-11.7073	9.98462	-59.4616	-22.2068	9.67561	-55.4309	-24.973	7.04259	-55.759	-26.4666
468898_6	16.3125	-71.0139	-6.6545	18.1527	-67.7437	-13.2464	17.8768	-65.1124	-14.6546	16.2107	-64.9051	-15.6777
468898_7	21.8131	-69.4728	-6.57595	25.3408	-64.0814	-20.2924	25.1807	-58.6921	-23.2368	9.65866	-59.8188	-7.28368
468899_1	17.2587	-54.6337	6.11488	22.037	-66.7317	-6.03308	21.7575	-67.6297	-12.876	18.2069	-69.8402	-13.9757
468899_10	19.8437	-68.0494	3.72726	23.8925	-79.2398	-2.9428	24.0674	-81.0599	-8.46124	-9999	-9999	-9999
468899_12	-9999	-9999	-9999	-9999	-9999	-9999	21.5379	-72.4392	-20.5061	18.4311	-72.5234	-21.4123
468899_2	16.326	-64.3193	-2.00403	19.1259	-69.4362	-8.20521	18.3757	-69.8693	-11.5114	16.5643	-71.0375	-12.1256
468899_5	14.8984	-53.3577	1.46075	20.3548	-66.7114	-5.72667	20.5158	-68.8379	-11.9675	16.9671	-70.7333	-12.7886

Three-dimensional measurements continued

ID	x5	y5	z5	x6	y6	z6	x7	y7	z7	x8	y8	z8
468899_6	15.8715	-59.6239	3.15404	19.5145	-67.4611	-4.17544	19.4213	-68.9937	-8.8901	16.3208	-70.5692	-9.7613
468899_8	23.1108	-80.8519	-2.64746	24.8749	-77.6025	-12.5887	24.573	73.5121	-14.8853	21.8235	-73.702	-16.7579
468899_9	17.2448	-60.8234	3.73668	20.6783	-67.7645	-7.81128	20.8029	-66.9936	-13.2336	17.7859	-68.8855	-14.4455
468939_4	16.4337	-57.853	-0.72006	20.4565	-68.1438	-11.1412	20.6901	-68.6419	-16.7985	17.6165	-70.3955	-17.8303
468944_1	8.45048	-83.6718	10.9217	10.9172	-80.9168	-1.52289	11.5815	-75.8223	-3.57678	9.35576	-76.0574	-5.28548
468944_2	9.32005	-80.8974	7.07519	10.1381	-76.8864	-5.05388	7.0053	-72.3748	-9.15926	4.31409	-72.6425	-10.0407
J68	9.38035	-76.5266	4.4962	12.4186	-81.5444	-2.50874	12.0947	-81.5786	-6.31644	10.0314	-82.5641	-6.77886

Three-dimensional measurements continued

ID	x9	y9	z9	x10	y10	z10
108395_1	7.14585	-65.3189	2.27869	6.36569	-66.8812	1.23705
108396_1	10.681	-75.189	4.55144	9.64149	-74.7458	2.92664
29246_1	6.79949	-57.6841	4.29474	-9999	-9999	-9999
308812_1_1	-9999	-9999	-9999	12.1561	-62.3848	-1.34841
308812_1_2	-9999	-9999	-9999	11.273	-64.8692	3.00483
308812_1_3	12.8092	-58.8111	-0.49362	11.2426	-60.8993	-1.48586
308812_1_5	-9999	-9999	-9999	11.5893	-64.7671	-0.13294
308812_1_6	-9999	-9999	-9999	11.4314	-73.8528	3.89363
308812_1_7	13.1319	-68.2364	0.351242	12.3091	-69.6505	-0.49468
308812_2_4	13.3497	-73.8526	-1.76785	23.3519	-79.8894	-2.63363
308812_3_1	12.6309	-59.7332	-2.95056	-9999	-9999	-9999
308812_5_1	11.388	-63.9936	-2.92624	10.2291	-65.7937	-3.60907
31097_1	5.65261	-72.9022	5.61572	-9999	-9999	-9999
31102_1	8.19108	-67.1332	2.78752	7.19073	-68.9456	1.71253
449382_1	5.4734	-67.9845	3.19603	4.47323	-69.5533	1.77724
449383_1	11.1365	-74.0064	6.23836	9.96817	-73.9468	4.39958
449385_1	7.16294	-73.0178	6.15314	6.07115	-73.0497	4.25453
449388_1	9.79449	-76.3748	2.48551	8.16171	-76.5494	0.524332
468531_1	17.4267	-70.2273	13.3571	0.251336	-71.1154	9.59417
468535_1	9.86181	-72.2857	6.5177	8.32635	-72.0664	3.74602
468546_1	13.5868	-79.222	1.38409	13.0242	-78.9531	0.226264
468547_1	2.30056	-75.9832	11.0133	1.44591	-76.1709	9.44423
468548_1	7.05701	-71.393	0.70806	6.5067	-72.6383	-0.48118
468554_1	11.6596	-77.6442	5.03869	10.8154	-77.6232	3.36102
468564_1	8.9795	-65.4143	-4.67417	8.13917	-67.5503	-5.45842
468564_2	7.89398	-66.8281	0.571219	6.46585	-68.5991	-0.49757
468564_3	8.86479	-71.1376	-0.96166	7.89936	-72.4757	-2.33667
468564_4	10.3272	-74.5309	0.223388	10.254	-75.5339	-0.4703
468873_1	-2.72864	-77.8298	11.6993	-3.05313	-77.8065	10.1107
468876_14	14.0273	-66.1146	-9.67161	13.6969	-66.3173	-11.0544
468876_3	10.8271	-63.177	-8.6384	9.76751	-62.8774	-10.9609
468876_5	12.6426	-64.4443	-11.3278	12.1957	-64.6502	-12.4182
468876_6	12.1905	-62.9535	-9.23806	10.9789	-63.125	-11.0722

Three-dimensional measurements continued

ID	x9	y9	z9	x10	y10	z10
468877_1	9.64347	-69.1321	-0.82183	8.76764	-71.0445	-1.34609
468877_2	10.4277	-74.5654	0.715657	10.046	-75.6452	0.209999
468877_3	8.86775	-67.9405	2.91078	8.03498	-69.4967	1.52696
468877_4	10.2959	-71.4807	1.01006	10.0649	-72.6553	-0.00462
468877_5	1.51822	-69.2774	3.16183	0.444178	-70.9474	2.00673
468878_1	9.93813	-73.3169	1.75641	8.39768	-73.1827	-0.54039
468879_2	13.2113	-64.2833	-11.5929	12.5703	-64.5453	-13.4712
468879_3	9.09938	-62.5453	13.501	8.08447	-62.3227	11.2557
468879_4	12.4042	-64.195	19.9465	10.9189	-63.8885	17.541
468879_5	10.5615	-56.881	-3.95883	9.69112	-58.3394	-5.12843
468879_6	9.65982	-56.8983	-3.81992	8.55404	-58.8183	-5.09418
468883_1	2.455	-67.4234	1.70925	1.44237	-69.3844	0.389102
468889_1	4.89442	-63.7034	3.90524	3.43458	-66.2584	2.22991
468889_2	7.57822	-62.4832	1.9803	5.87151	-64.2878	1.48506
468889_3	9.4166	-65.0706	2.33084	-9999	-9999	-9999
468889_4	9.04337	-67.9694	3.84553	8.27285	-69.4872	2.52768
468891_2	-9999	-9999	-9999	13.1963	-73.6613	-3.48912
468895_1	7.84316	-76.0243	2.18197	7.49818	-76.9674	1.40472
468896_1	-9999	-9999	-9999	7.66066	-71.0555	5.12112
468896_2	10.7998	-73.1633	3.36872	-9999	-9999	-9999
468897_4	9.24833	-44.1632	-2.5794	7.47884	-46.7022	-3.91866
468897_6	8.42014	-57.1799	-2.08658	-9999	-9999	-9999
468898_1	10.0939	-56.8582	-2.67437	9.10013	-57.286	-4.69558
468898_10	10.9734	-61.9309	-13.3964	-9999	-9999	-9999
468898_3	17.3945	-58.1713	-14.3397	36.0781	-57.7777	-20.0711
468898_4	10.0191	-58.9251	1.86418	-9999	-9999	-9999
468898_5	-0.6161	-55.86	-9.79895	-2.3293	-56.142	-11.904
468898_6	10.0617	-66.9376	-6.29634	9.71924	-66.8204	-8.03818
468898_7	11.0308	-61.2769	-4.66839	9.64128	-61.737	-6.98937
468899_1	6.03431	-48.8646	-3.30479	-9999	-9999	-9999
468899_10	12.1098	-65.9948	-4.23445	11.3586	-67.8271	-4.84131
468899_12	12.6725	-73.7088	-2.24585	10.8604	-73.9112	-3.94244
468899_2	8.982	-62.3233	-6.46281	8.62343	-63.5208	-6.99398
468899_5	4.92858	-50.621	-8.82772	3.36292	-52.5503	-9.59147

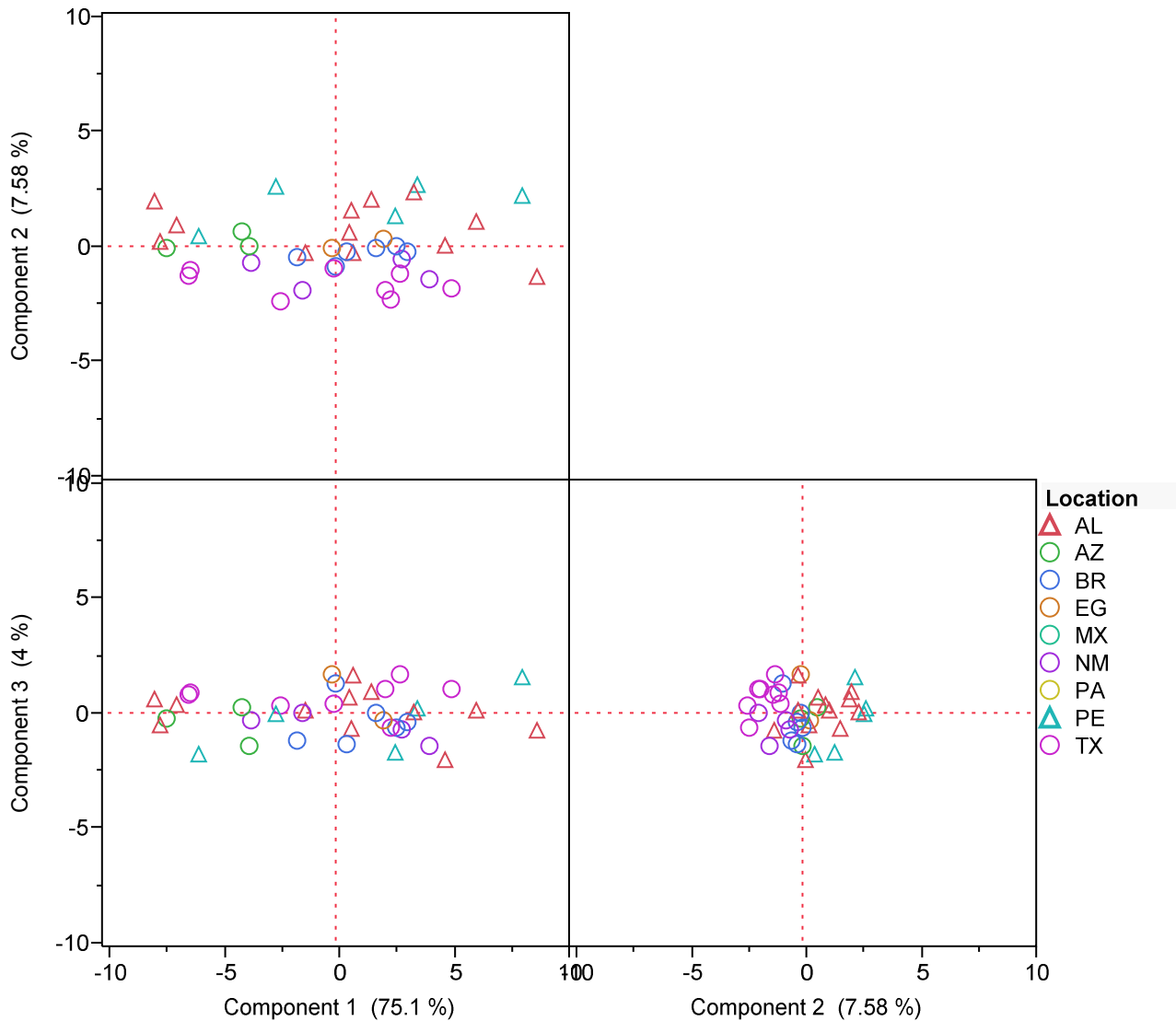
Three-dimensional measurements continued

ID	x9	y9	z9	x10	y10	z10
468899_6	8.10979	-55.3122	-3.89189	6.73596	-56.6678	-4.66695
468899_8	14.2667	-75.1203	-0.88362	12.9806	-75.2866	-2.32079
468899_9	7.76373	-54.89	-1.7884	6.48483	-56.3494	-2.99055
468939_4	-9999	-9999	-9999	8.18353	-54.7743	-8.62568
468944_1	0.949952	-75.6526	9.88673	0.123413	-75.6451	8.11114
468944_2	-2.40125	-74.5419	10.573	-3.7934	-74.855	9.31953
J68	2.76958	-75.0469	-0.93478	-9999	-9999	-9999

Appendix 4 – Part A

Principal Components: on correlations; both species combined

Score Plot

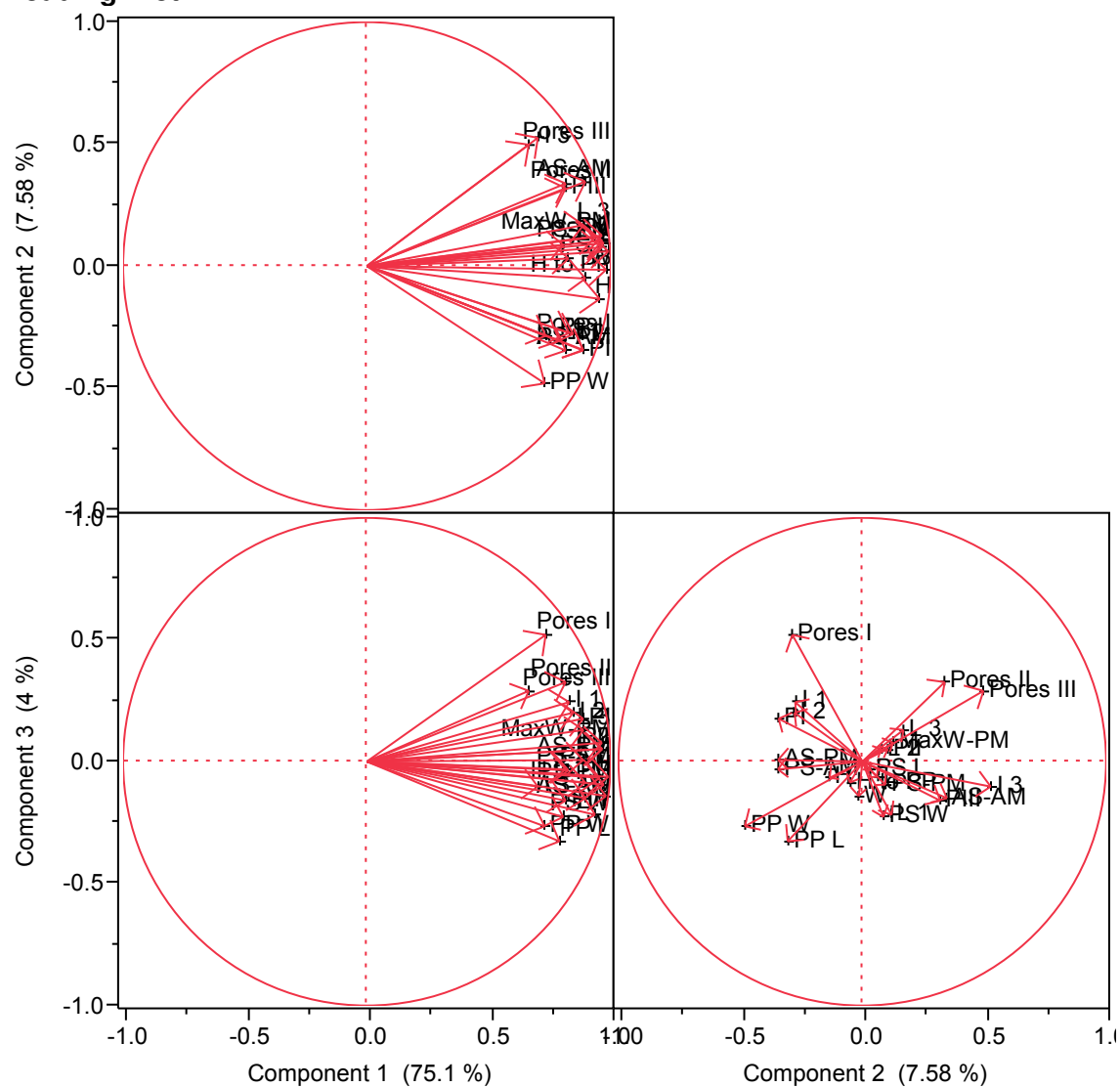


Open circles are specimens of *M. batnensis*. Open triangles are specimens of *M. fourneli*.

Eigenvalues

Number	Eigenvalue	Percent	Percent	Cum Percent	ChiSquare	DF	Prob>ChiSq
1	18.7870	75.148		75.148	3764.70	282.419	<.0001*
2	1.8960	7.584		82.732	1861.92	293.382	<.0001*
3	1.0007	4.003		86.735	1504.54	272.421	<.0001*
4	0.6762	2.705		89.440	1293.70	250.694	<.0001*
5	0.4993	1.997		91.437	1138.39	229.327	<.0001*

Loading Plot



Loading Matrix

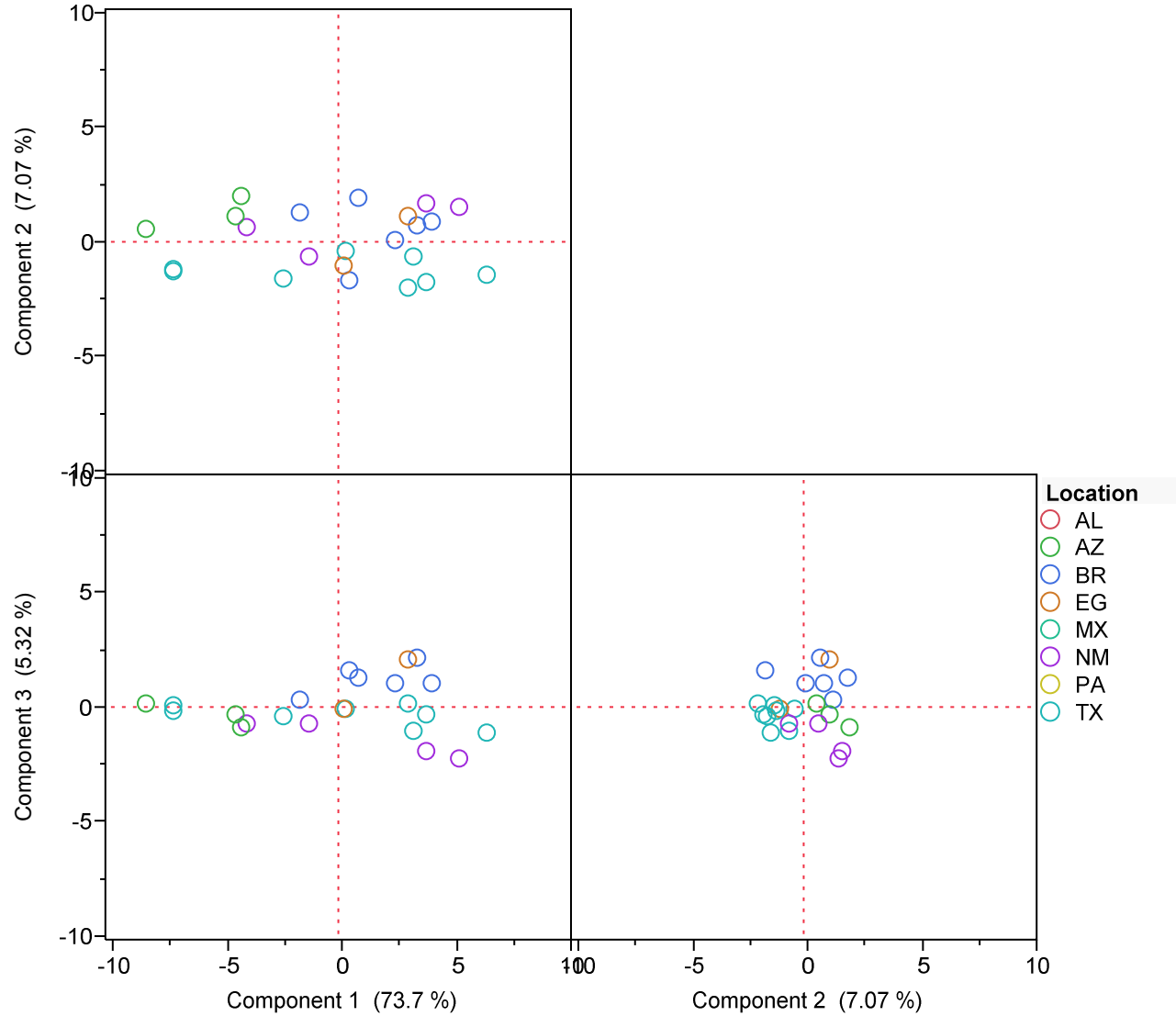
	Prin1	Prin2	Prin3
L	0.98976	0.06001	-0.06255
W	0.98051	-0.01496	-0.14113
H	0.95513	-0.13477	-0.06682
PI	0.88759	-0.34366	0.17547
PII	0.96563	0.10397	0.05127
PIII	0.81484	0.31985	-0.15980
Pores I	0.73314	-0.28643	0.51936
Pores II	0.81498	0.33841	0.32645
Pores III	0.66450	0.49740	0.29025
AS-AM	0.89614	0.34636	-0.14925
AS-PM	0.88683	-0.34646	0.00668
PS L	0.82744	0.03134	-0.03563
PS W	0.80540	0.08661	-0.22720

	Prin1	Prin2	Prin3
PP L	0.78927	-0.30613	-0.32742
PP W	0.72969	0.48160	-0.26559
H to PP	0.89597	-0.05084	-0.08534
PS-AM	0.81505	-0.34591	-0.03142
PS-PM	0.97116	0.09408	-0.09425
MaxW-PM	0.96437	0.12604	0.07670
I 1	0.83001	-0.27485	0.24445
I 2	0.84610	-0.27788	0.19974
I 3	0.70059	0.52578	-0.10202
L 1	0.93571	0.11983	-0.21783
L 2	0.96353	0.07690	0.05194
L 3	0.88779	0.16798	0.12940

Appendix 4 – Part B

Principal Components: on correlations; Mecaster batnensis

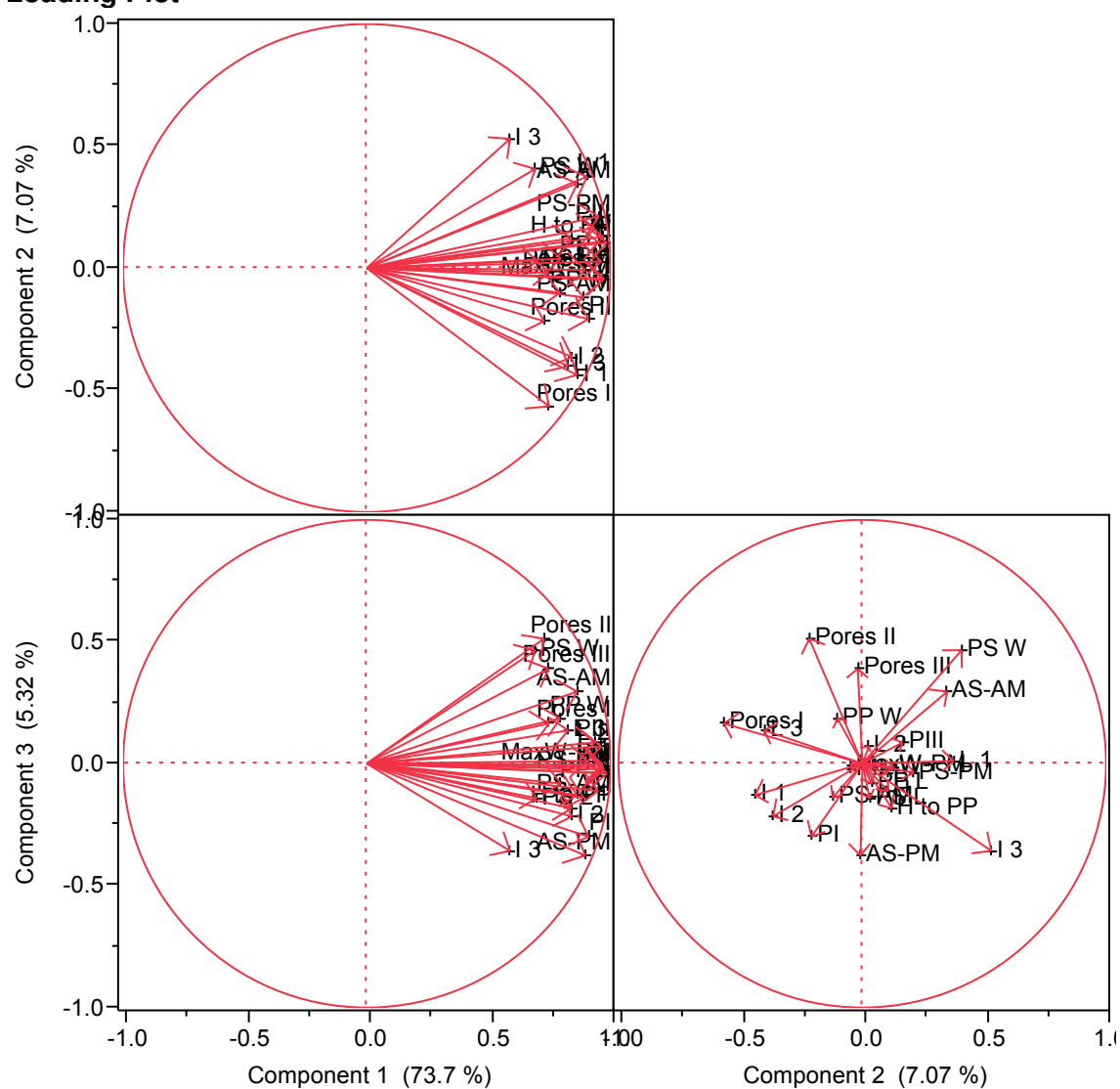
Score Plot



Eigenvalues

Number	Eigenvalue	Percent	Percent	Cum Percent	ChiSquare	DF	Prob>ChiSq
1	18.4273	73.709		73.709	3602.65	282.840	<.0001*
2	1.7667	7.067		80.776	2725.91	293.124	<.0001*
3	1.3297	5.319		86.095	2541.56	271.964	<.0001*
4	0.9775	3.910		90.005	2364.63	250.769	<.0001*
5	0.7314	2.926		92.931	2197.70	229.806	<.0001*

Loading Plot



Loading Matrix

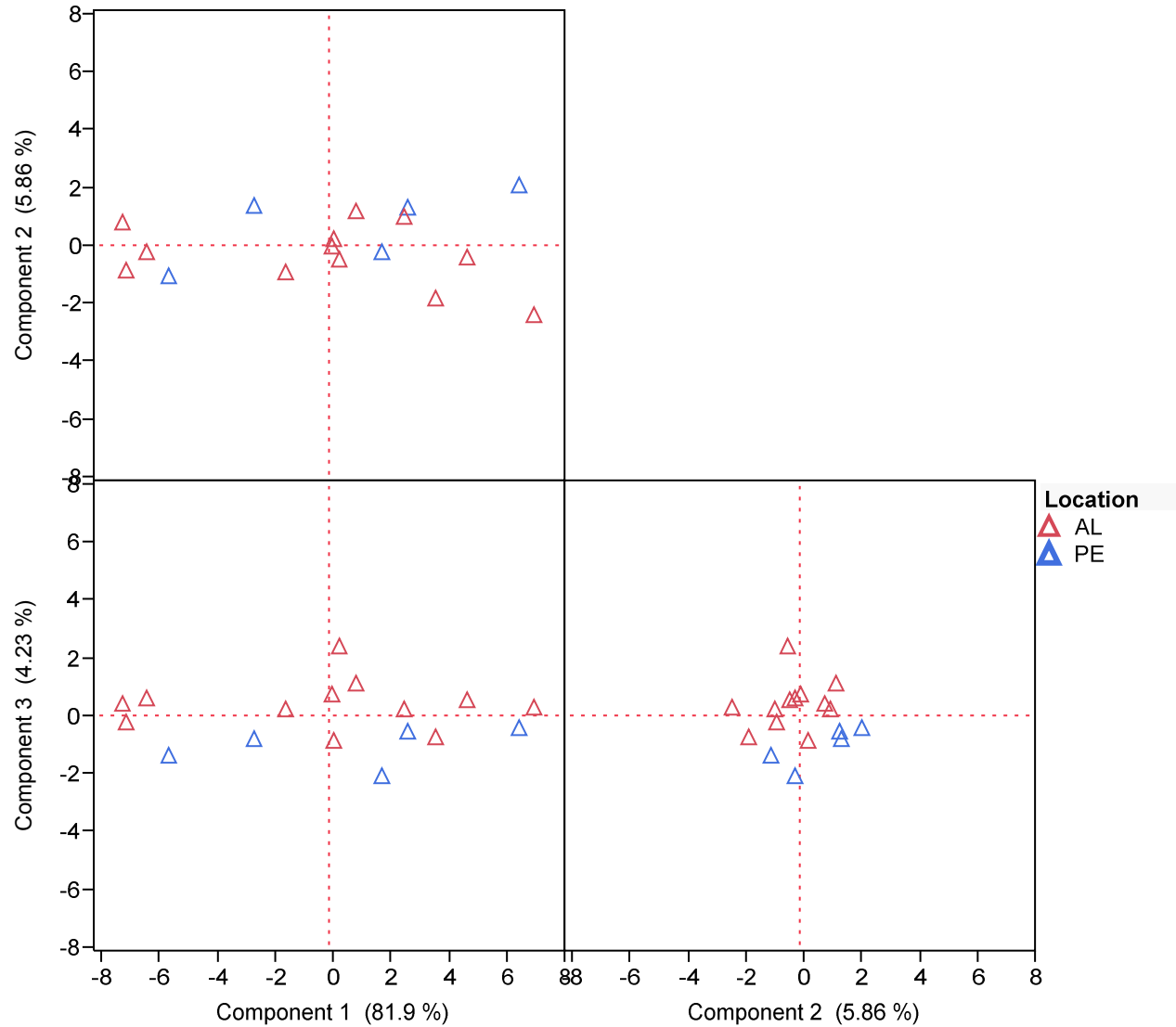
	Prin1	Prin2	Prin3
L	0.98492	0.10321	-0.04098
W	0.97038	0.12847	-0.01435
H	0.94907	0.10607	-0.11279
PI	0.90936	-0.20918	-0.29925
PII	0.97300	-0.04417	-0.02377
PIII	0.93306	0.16490	0.08672
Pores I	0.74731	-0.56750	0.16488
Pores II	0.72645	-0.21800	0.51197
Pores III	0.74421	-0.01916	0.38945
AS-AM	0.86275	0.34757	0.29583
AS-PM	0.89663	-0.00752	-0.37740
PS L	0.69591	0.03044	-0.14233
PS W	0.69112	0.40656	0.46454

	Prin1	Prin2	Prin3
PP L	0.79549	0.03826	-0.08184
PP W	0.79220	-0.10174	0.18480
H to PP	0.84002	0.12126	-0.18275
PS-AM	0.89023	-0.12093	-0.13976
PS-PM	0.95135	0.21154	-0.03661
MaxW-PM	0.96849	-0.04920	-0.00420
I 1	0.86175	-0.43907	-0.12899
I 2	0.84187	-0.36595	-0.21645
I 3	0.58684	0.52906	-0.35779
L 1	0.90292	0.37498	0.01020
L 2	0.96204	0.02718	0.07133
L 3	0.82601	-0.40266	0.13670

Appendix 4 – Part C

Principal Components: on correlations; Mecaster fourneli

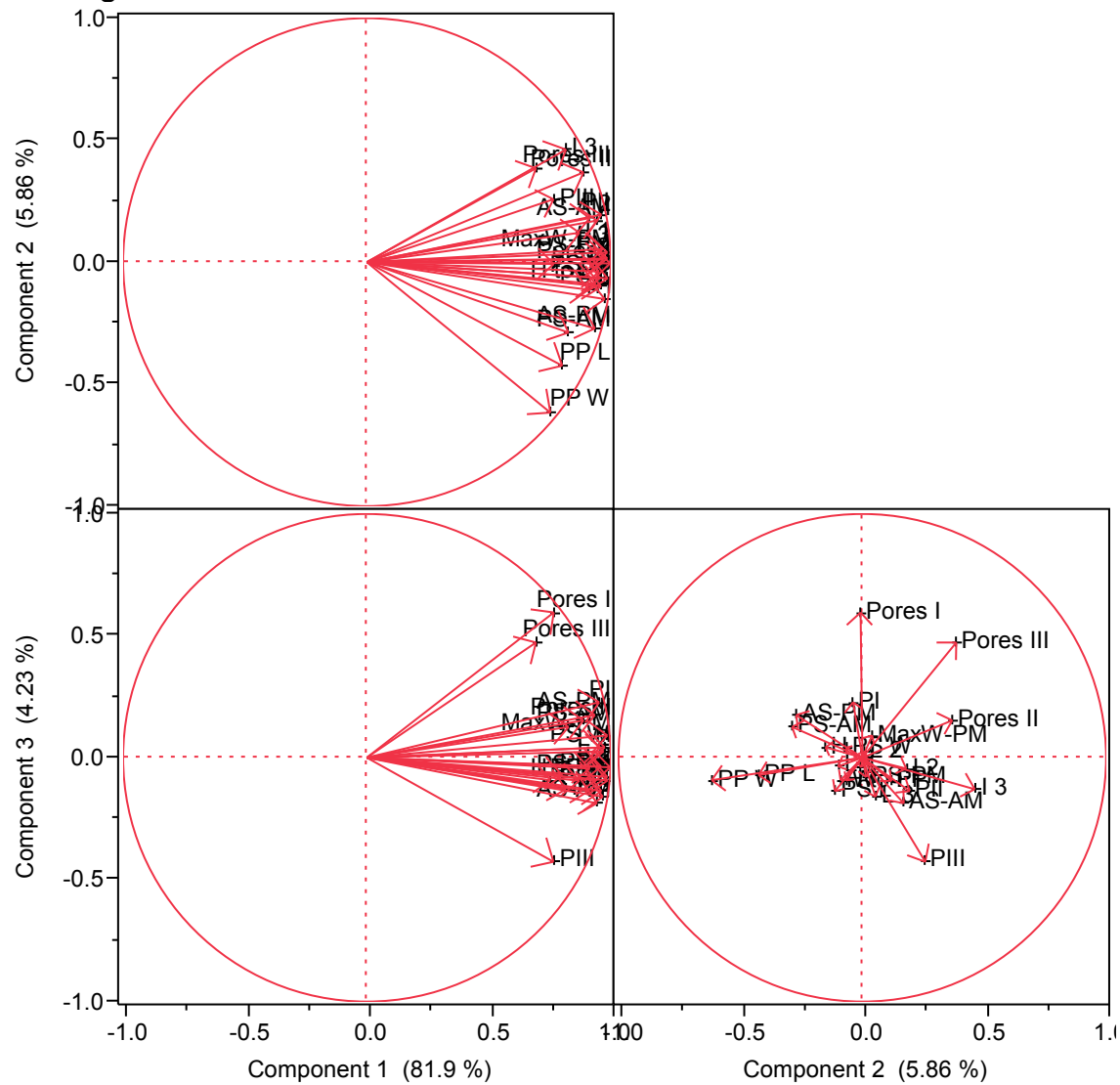
Score Plot



Eigenvalues

Number	Eigenvalue	Percent	Percent	Cum Percent	ChiSquare	DF	Prob>ChiSq
1	20.4822	81.929		81.929	3513.62	280.704	<.0001*
2	1.4641	5.856		87.785	2490.24	294.953	<.0001*
3	1.0581	4.232		92.017	2277.81	273.167	<.0001*
4	0.5549	2.220		94.237	2065.56	251.497	<.0001*
5	0.3823	1.529		95.766	1913.87	230.027	<.0001*

Loading Plot



Loading Matrix

	Prin1	Prin2	Prin3
L	0.99682	-0.00493	-0.03967
W	0.98769	-0.06686	-0.09392
H	0.97622	-0.15079	0.04210
PI	0.95288	-0.03854	0.22706
PII	0.96188	0.19449	-0.13645
PIII	0.76564	0.25780	-0.42682
Pores I	0.76685	-0.00760	0.59481
Pores II	0.88797	0.36803	0.15317
Pores III	0.69402	0.38460	0.47170
AS-AM	0.94344	0.17004	-0.18674
AS-PM	0.93418	-0.27203	0.17522
PS L	0.90861	-0.11232	-0.13706
PS W	0.95654	-0.06497	0.04101

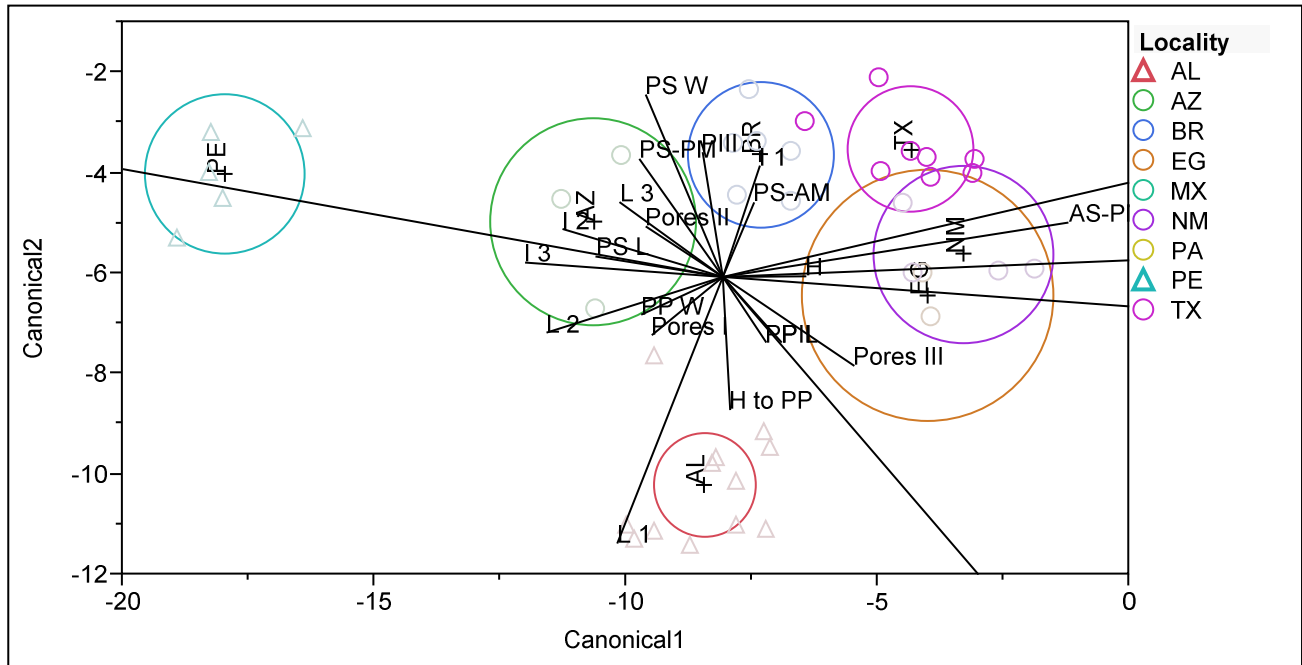
	Prin1	Prin2	Prin3
PP L	0.80125	-0.42520	-0.07201
PP W	0.75205	-0.61736	-0.09267
H to PP	0.93859	-0.08967	-0.09263
PS-AM	0.82667	-0.28853	0.12612
PS-PM	0.98528	0.01526	-0.07903
MaxW-PM	0.98574	0.03997	0.09169
I 1	0.87178	0.12019	-0.09417
I 2	0.91400	0.18066	-0.04415
I 3	0.81661	0.46121	-0.12890
L 1	0.96022	-0.09978	-0.03552
L 2	0.97085	0.01067	0.02584
L 3	0.96844	0.05429	-0.15958

Appendix 5 – Part A

Discriminant Analysis: both species combined

Discriminant Method: Linear

Canonical Plot



Eigenvalue	Percent	Cum Percent	Canonical Corr	Likelihood Ratio	Approx. F	NumDF	DenDF	Prob>F
24.2508939	49.9401	49.9401	0.97999869	1.12071e-5	1.1908	200	69.23	0.2008
10.3097768	21.2310	71.1711	0.95476747	0.00028299	0.9178	168	65.424	0.6729
5.94351156	12.2395	83.4106	0.92519222	0.00320055	0.7331	138	60.281	0.9297
4.10097809	8.4452	91.8557	0.8966377	0.02222305	0.5744	110	53.778	0.9926
2.18611074	4.5019	96.3576	0.8283343	0.11335929	0.4018	84	45.898	0.9999
1.76873907	3.6424	100.0000	0.79926514	0.36117524	0.2484	60	36.636	1.0000

Test	Value	Approx. F	NumDF	DenDF	Prob>F
Wilks' Lambda	0.0000112	1.1908	200	69.23	0.2008
Pillai's Trace	4.8568807	0.8653	200	112	0.8123
Hotelling-Lawley	48.56001	1.4202	200	13.774	0.2335
Roy's Max Root	24.250894	13.5805	25	14	<.0001*

Discriminant Scores

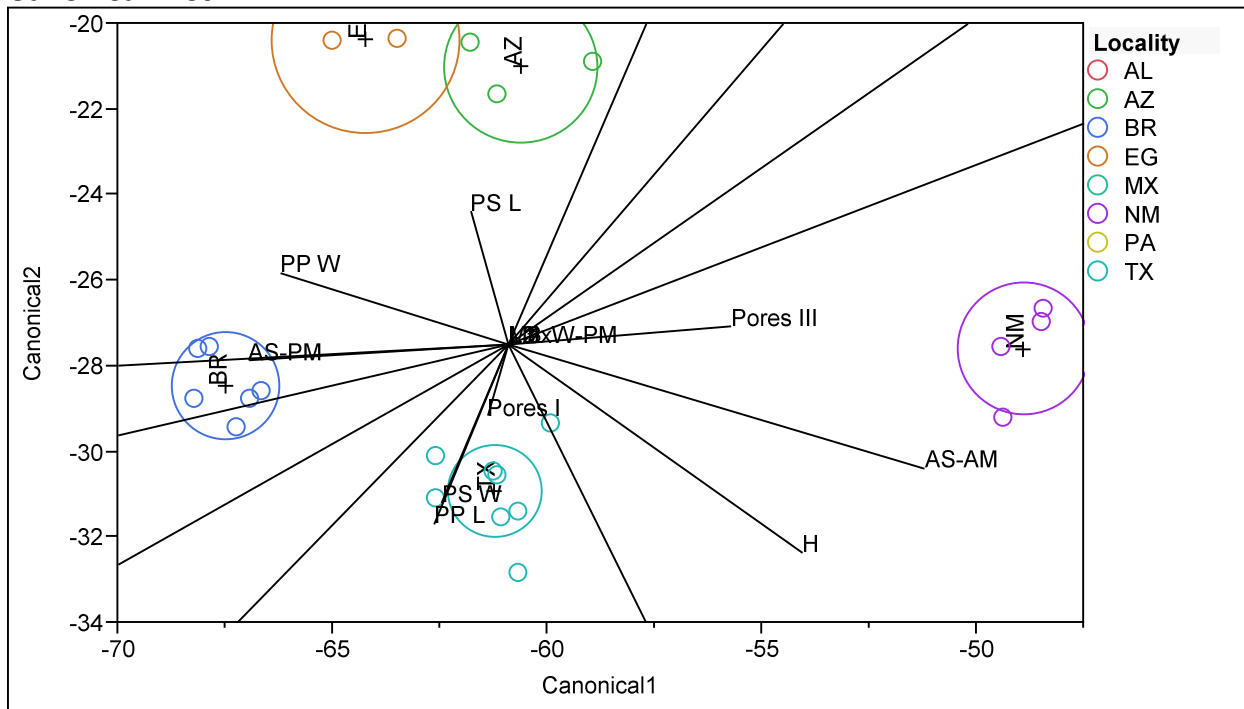
	Training
Number Misclassified	0
Percent Misclassified	0
-2LogLikelihood	0.017

Appendix 5 – Part B

Discriminant Analysis: Mecaster batnensis

Discriminant Method: Linear

Canonical Plot



Eigenvalue	Percent	Cum Percent	Canonical Corr	Likelihood Ratio	Approx. F	NumDF	DenDF	Prob>F
57.2536541	59.2462	59.2462	0.99137969	1.1864e-5	-1.2243	175	-49.29	<.0001*
21.8362357	22.5962	81.8423	0.97785988	0.00069112	-0.6675	144	-38.86	<.0001*
14.4445248	14.9472	96.7895	0.96708435	0.01578257	-0.3410	115	-29.51	<.0001*
3.10249075	3.2105	100.0000	0.86962385	0.24375436	-0.1036	88	-21.25	<.0001*

Test	Value	Approx. F	NumDF	DenDF	Prob>F
Wilks' Lambda	1.1864e-5	.	175	-49.29	.
Pillai's Trace	3.6305414	.	175	-21	.
Hotelling-Lawley	96.636905	.	175	-75	.
Roy's Max Root	57.253654	.	25	-3	.

Discriminant Scores

	Training
Number Misclassified	0
Percent Misclassified	0
-2LogLikelihood	0

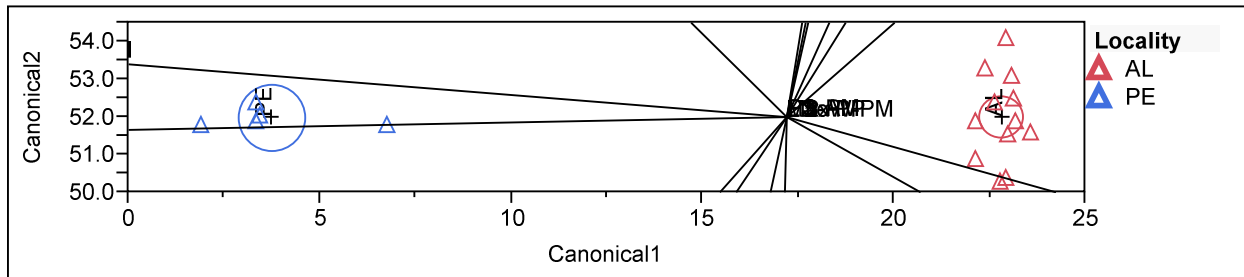
Regularization was needed due to singular within-covariance matrix

Appendix 5 – Part C

Discriminant Analysis: Mecaster fourneli

Discriminant Method: Linear

Canonical Plot



Eigenvalue	Percent	Cum Percent	Canonical Corr	Likelihood Ratio	Approx. F	NumDF	DenDF	Prob>F
85.5235817	100.0000	100.0000	0.99420443	0.01155754	-30.7885	25	-9	<.0001*

Test	Value	Exact F	NumDF	DenDF	Prob>F
Wilks' Lambda	0.0115575	.	25	-9	.
Pillai's Trace	0.9884425	.	25	-9	.
Hotelling-Lawley	85.523582	.	25	-9	.
Roy's Max Root	85.523582	.	25	-9	.

Discriminant Scores

	Training
Number Misclassified	0
Percent Misclassified	0
-2LogLikelihood	0

Regularization was needed due to singular within-covariance matrix

Appendix 6 – Part A

Procrustes Fit : Mecaster batnensis

10 landmarks in 3 dimensions.

The dataset contains 38 observations, of which 33 are included for analyses.

Average shape:

Lmk.	Axis 1 (x)	Axis 2 (y)	Axis 3 (z)
1	-0.02135763	-0.01368089	0.19658632
2	-0.23814034	-0.15023895	0.01500380
3	0.16320926	-0.28523508	0.06958823
4	0.32589673	-0.00522689	0.10782192
5	0.15710419	0.27721393	0.09263033
6	-0.24227450	0.14713874	0.03477124
7	-0.33649399	-0.00187092	-0.01897859
8	-0.34024782	0.00792665	-0.13137809
9	0.28854481	0.01130968	-0.14990188
10	0.24375928	0.01266374	-0.21614330

Procrustes sums of squares: 0.3195419085392288

Tangent sums of squares: 0.3042730264024231

Data matrices in this dataset:

- Mb, Raw coordinates
- Mb, centroid size
- Mb, Procrustes coordinates

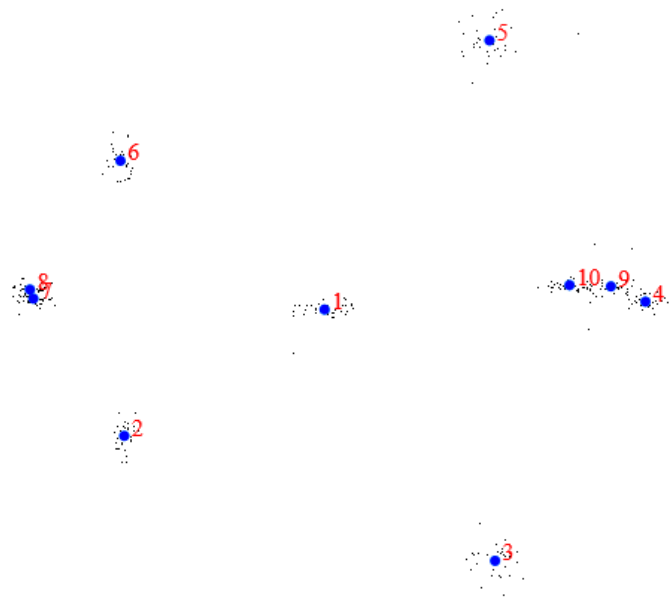
Missing data by landmark:

Lmk	Number missing
1	0
2	0
3	0
4	1
5	0
6	1
7	0
8	1
9	1
10	1

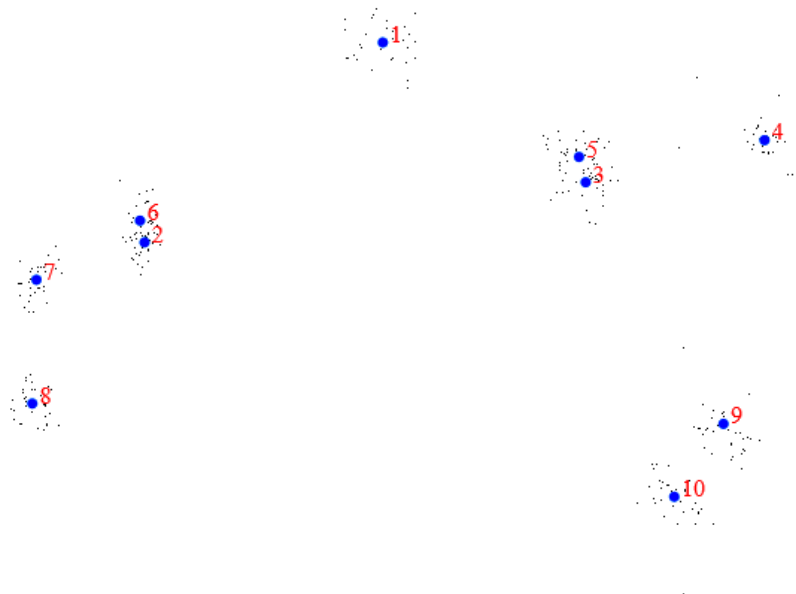
Samples excluded from analysis:

31102_1, 468877_1, 468879_3, 468939_4, J68

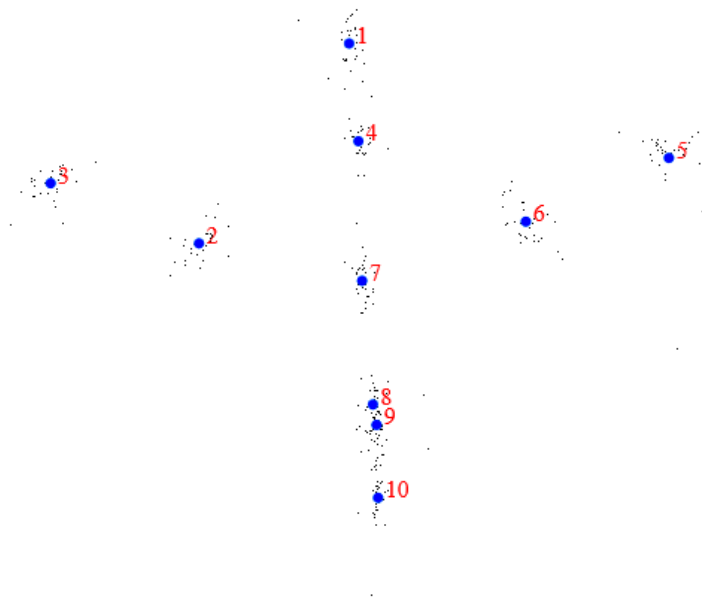
***M. batnensis* – Axis 1 vs. Axis 2**



***M. batnensis* – Axis 1 vs. Axis 3**



***M. batnensis* – Axis 2 vs. Axis 3**



Appendix 6 – Part B

Procrustes Fit: Mecasterourneli

9 landmarks in 3 dimensions.

The dataset contains 36 observations, of which 28 are included for analyses.

Average shape:

Lmk.	Axis 1 (x)	Axis 2 (y)	Axis 3 (z)
1	-0.03035086	0.00146916	0.16087064
2	-0.23890581	-0.15549231	0.03412222
3	0.22037670	-0.29240446	0.06244405
4	0.39435070	0.00882337	0.05043652
5	0.19703999	0.29245942	0.05892821
6	-0.25013397	0.14763852	0.03489706
7	-0.32879943	0.00334844	-0.02277329
8	-0.29572848	-0.00987586	-0.15110230
9	0.33215116	0.00403371	-0.22782310

Procrustes sums of squares: 2.037984996760159

Tangent sums of squares: 1.35985357022626

Data matrices in this dataset:

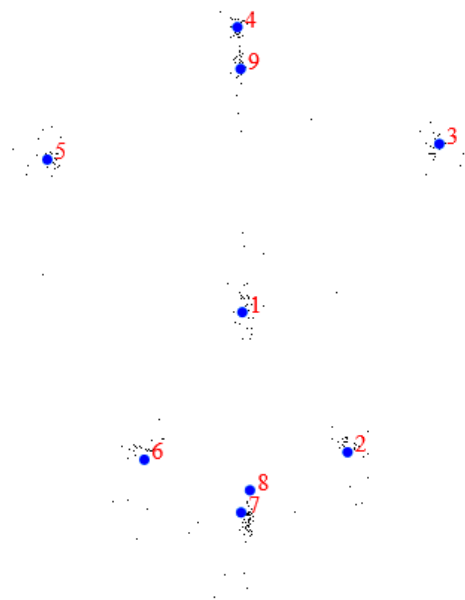
- Mf only, no 10, raw data
- Mf only, no 10, centroid size
- Mf only, no 10, Procrustes coordinates

Missing data by landmark:

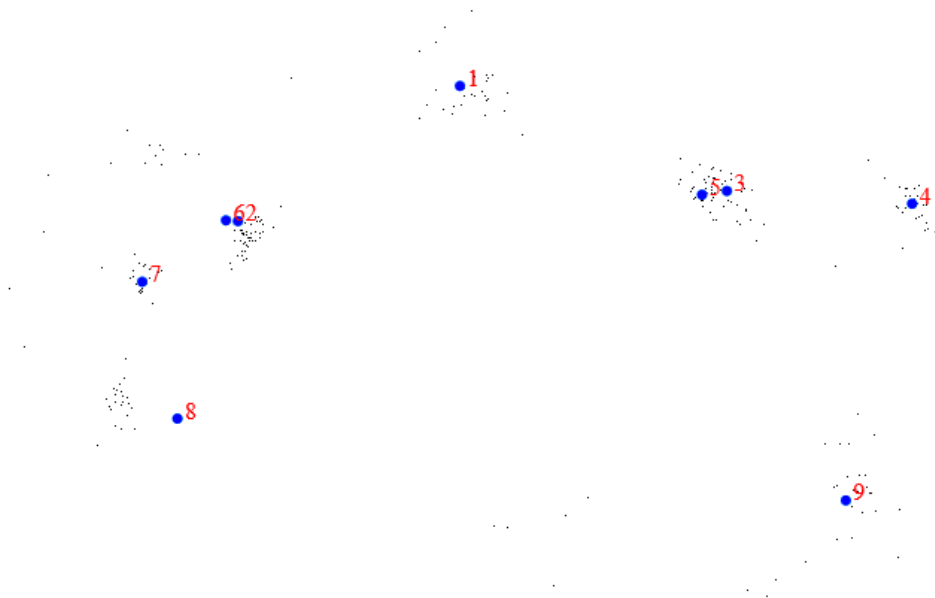
Lmk	Number missing
1	0
2	1
3	0
4	0
5	1
6	1
7	0
8	1
9	6

Samples excluded from analysis:

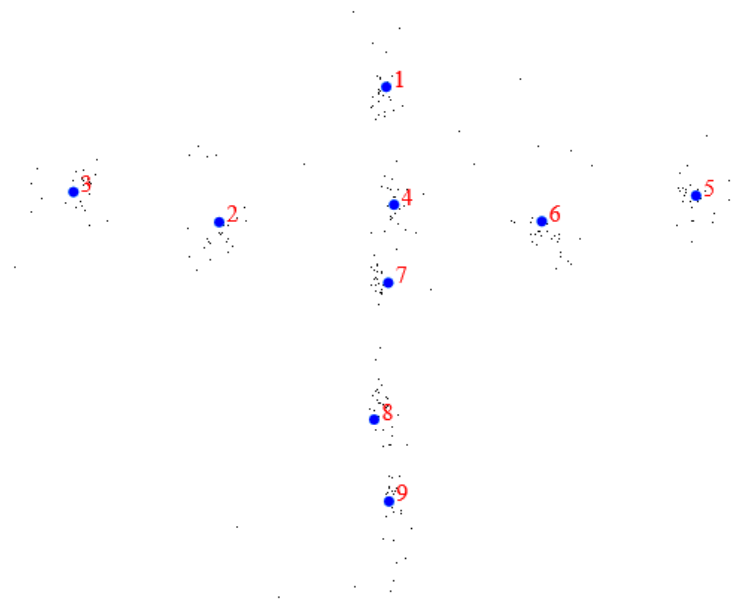
***M. fourneli* – Axis 1 vs. Axis 2**



***M. fourneli* – Axis 1 vs. Axis 3**



***M. fourneli* – Axis 2 vs. Axis 3**



Appendix 6 – Part C

Procrustes Fit: Mecaster batnensis, averaged by locality

10 landmarks in 3 dimensions.

The dataset contains 5 observations, of which 5 are included for analyses.

Observations include: Arizona, Brazil, Egypt, New Mexico, Texas

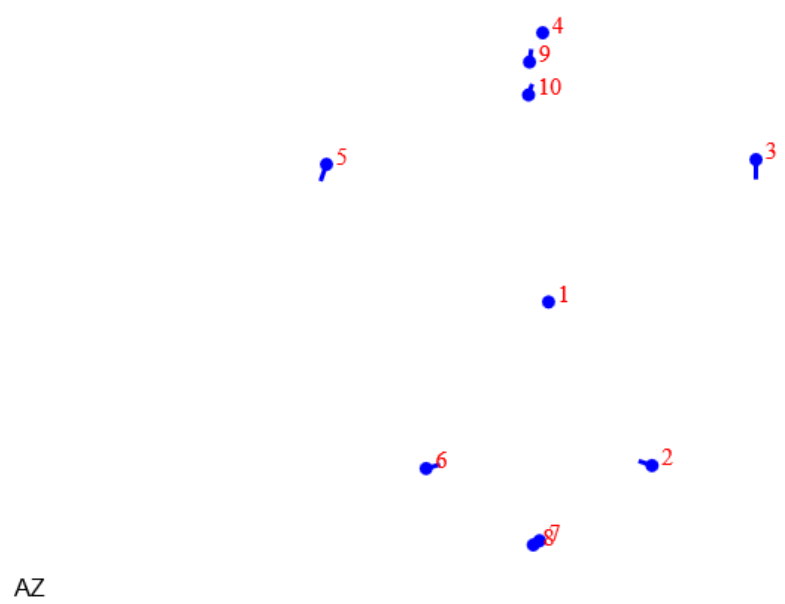
Average shape:

Lmk.	Axis 1 (x)	Axis 2 (y)	Axis 3 (z)
1	-0.02404624	-0.01339122	0.19337110
2	-0.23731988	-0.14852822	0.01857381
3	0.16156508	-0.28424502	0.07102204
4	0.32692390	-0.00573929	0.10937614
5	0.15539777	0.27648997	0.09581157
6	-0.24116133	0.14643242	0.03648967
7	-0.33526467	-0.00164167	-0.02198746
8	-0.34075456	0.00649577	-0.13013650
9	0.28875812	0.01143199	-0.15314396
10	0.24590180	0.01269528	-0.21937641

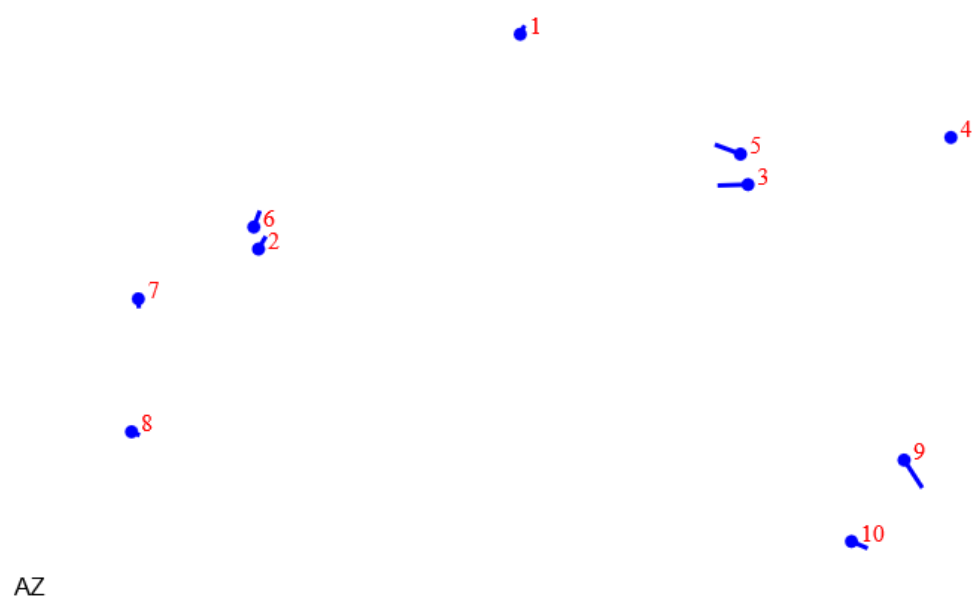
Data matrices in this dataset:

- Mb, centroid size
- Mb, Procrustes coordinates

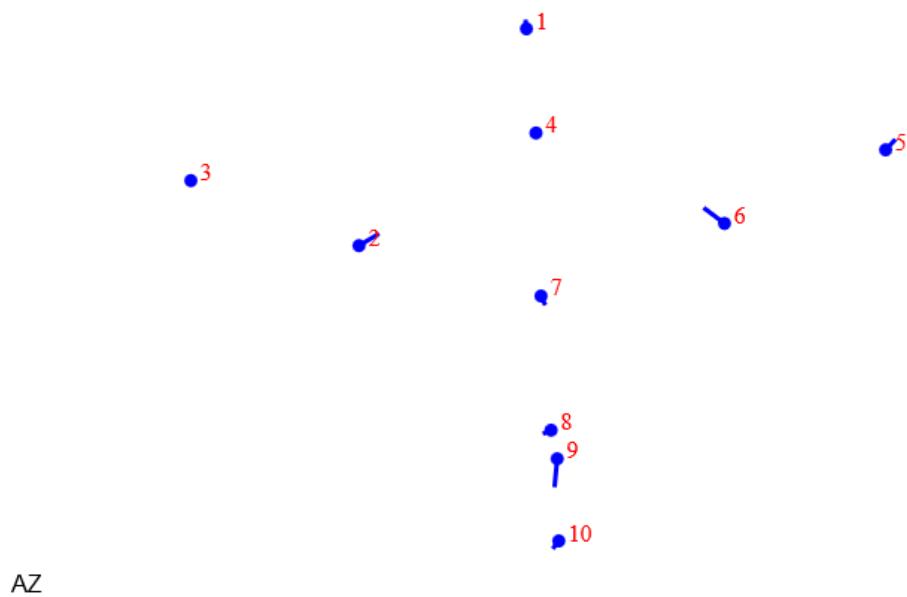
***M. batnensis* – Arizona – Axis 1 vs. Axis 2**



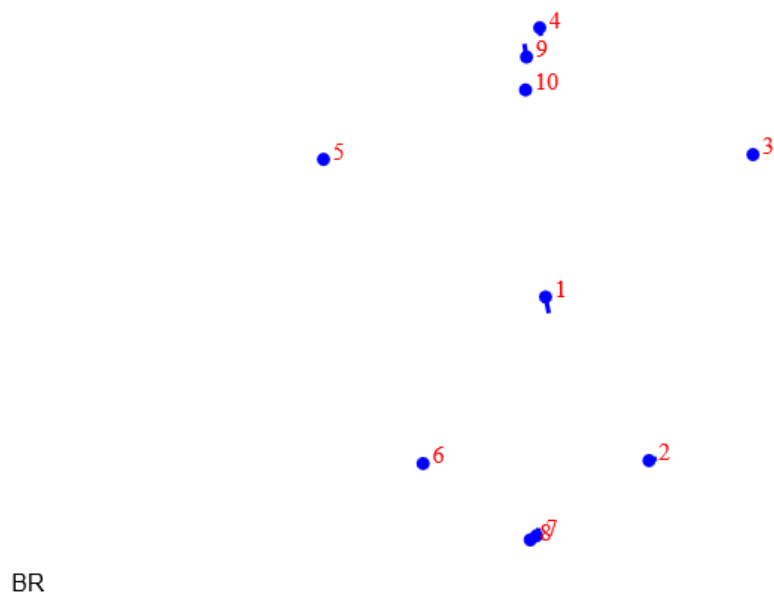
***M. batnensis* – Arizona – Axis 1 vs, Axis 3**



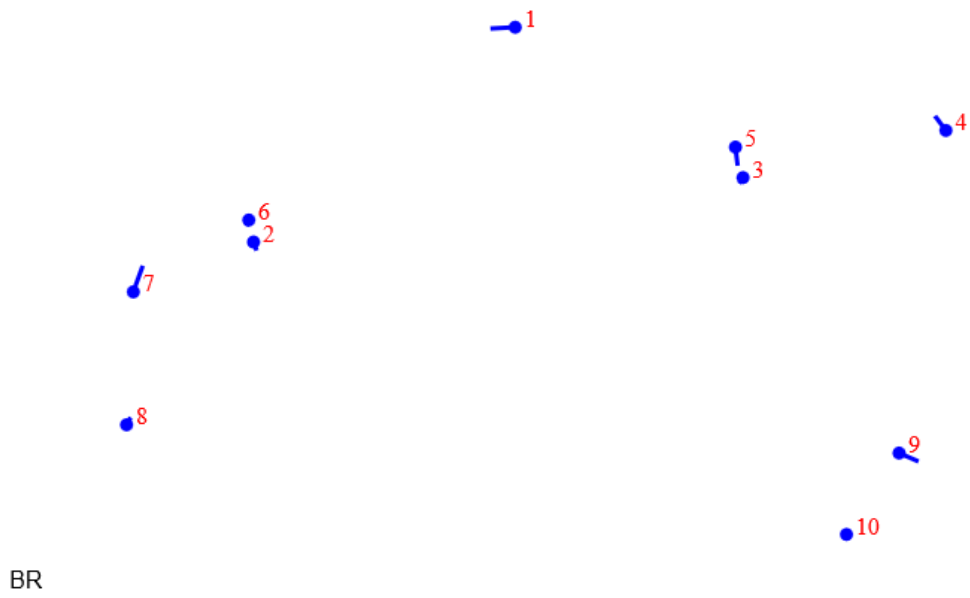
***M. batnensis* – Arizona – Axis 2 vs. Axis 3**



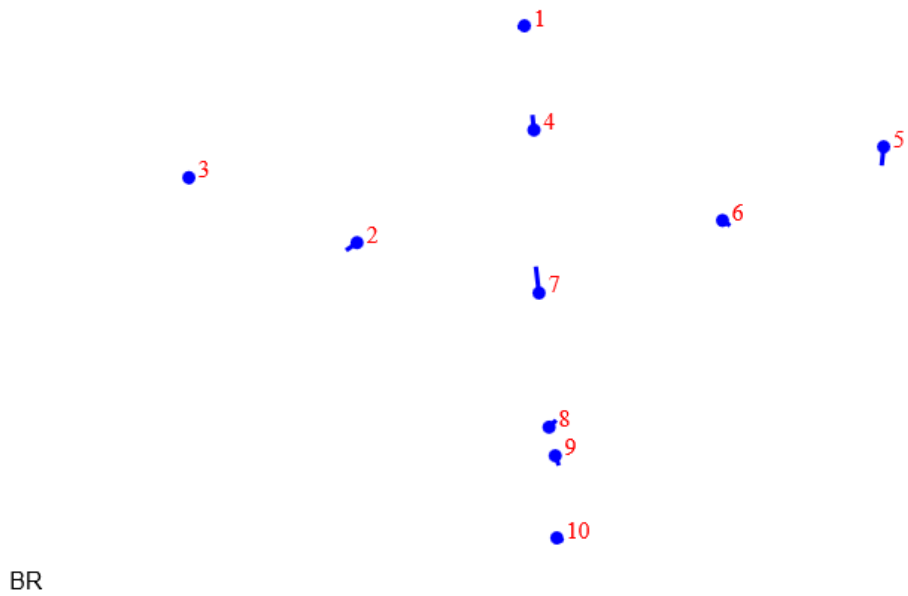
***M. batnensis* – Brazil – Axis 1 vs. Axis 2**



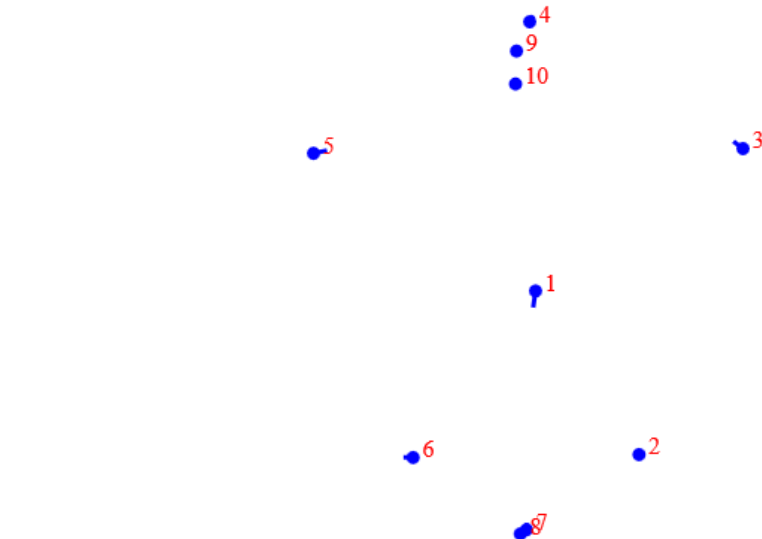
***M. batnensis* – Brazil – Axis 1 vs. Axis 3**



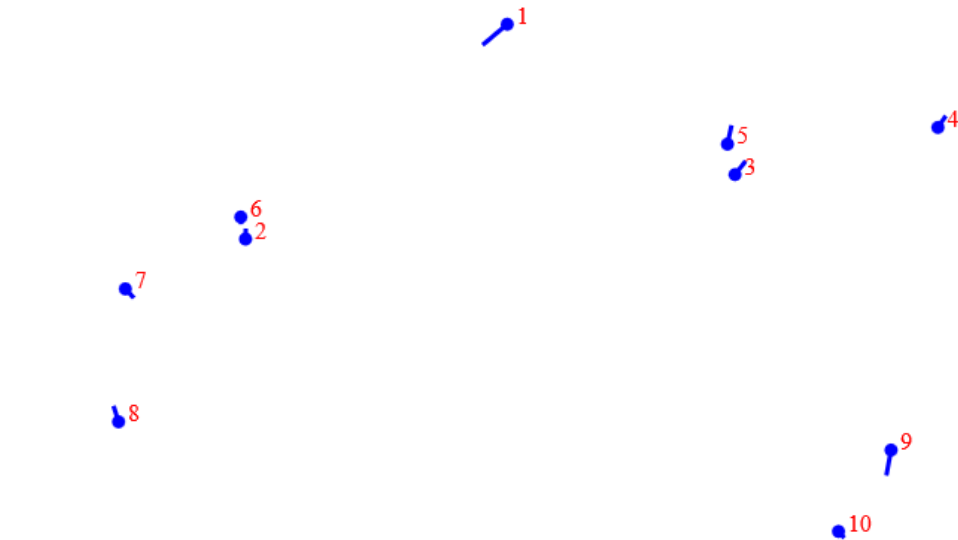
***M. batnensis* – Brazil – Axis 2 vs. Axis 3**



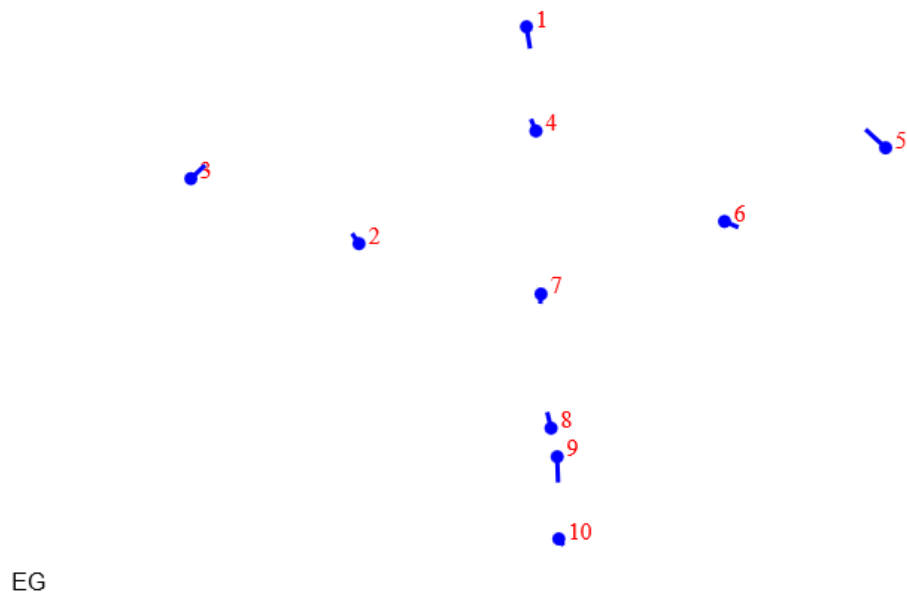
***M. batnensis* – Egypt – Axis 1 vs Axis 2**



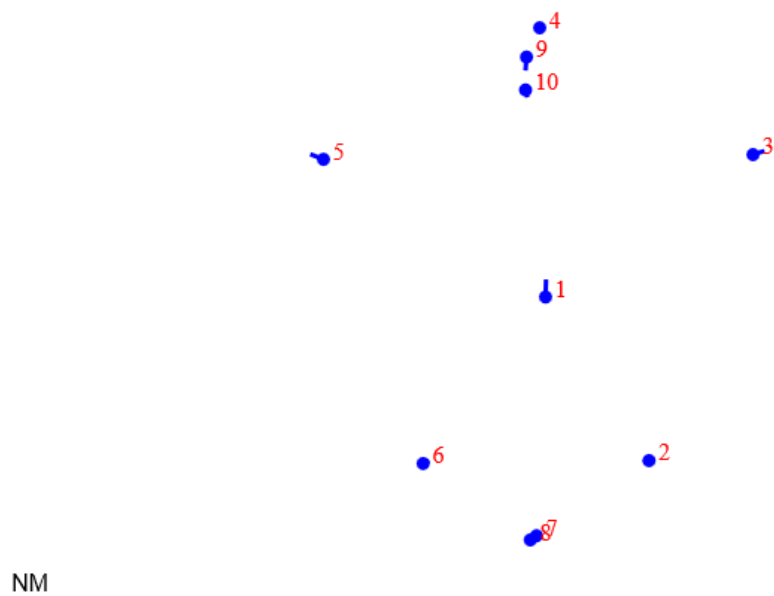
***M. batnensis* – Egypt – Axis 1 vs. Axis 3**



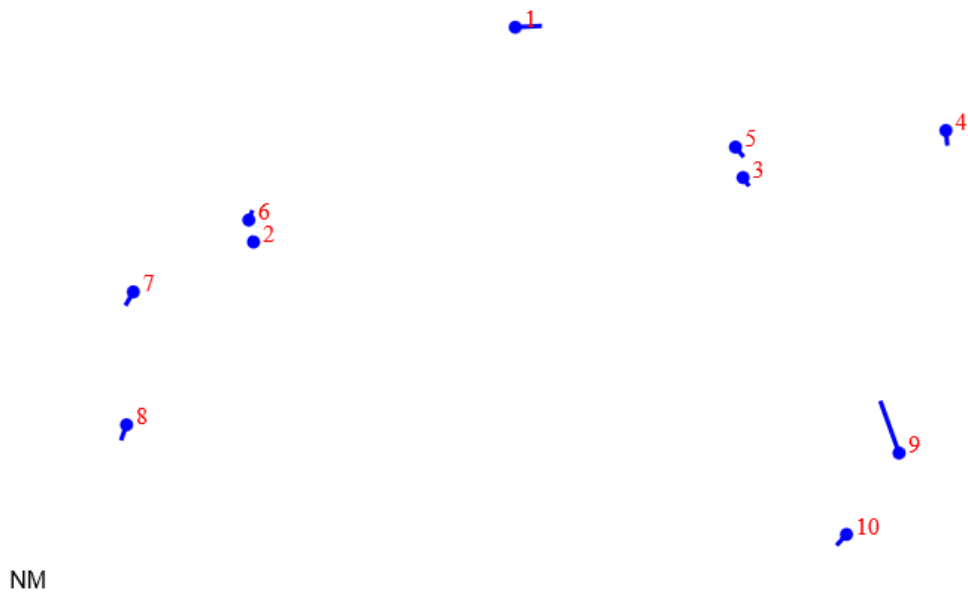
***M. batnensis* – Egypt – Axis 2 vs. Axis 3**



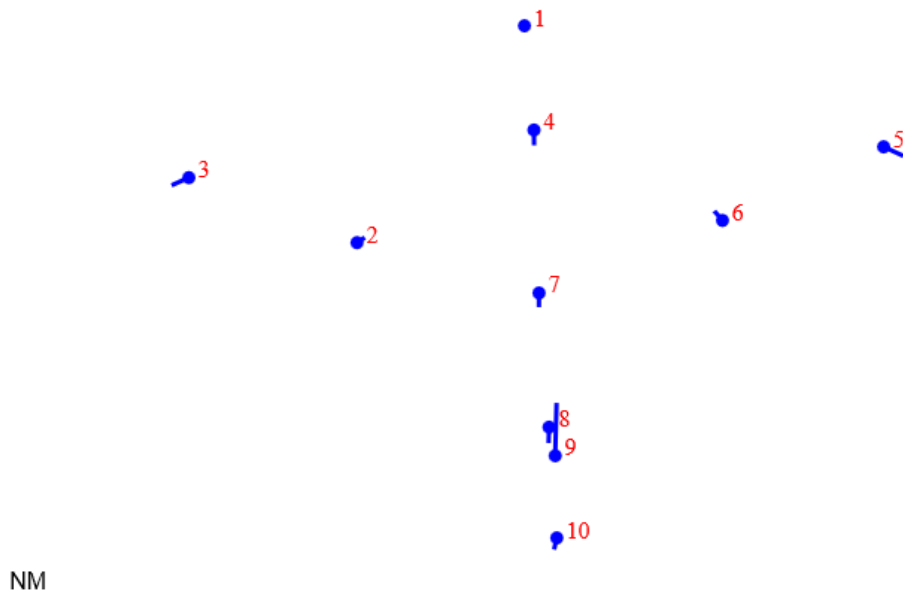
***M. batnensis* – New Mexico – Axis 1 vs. Axis 2**



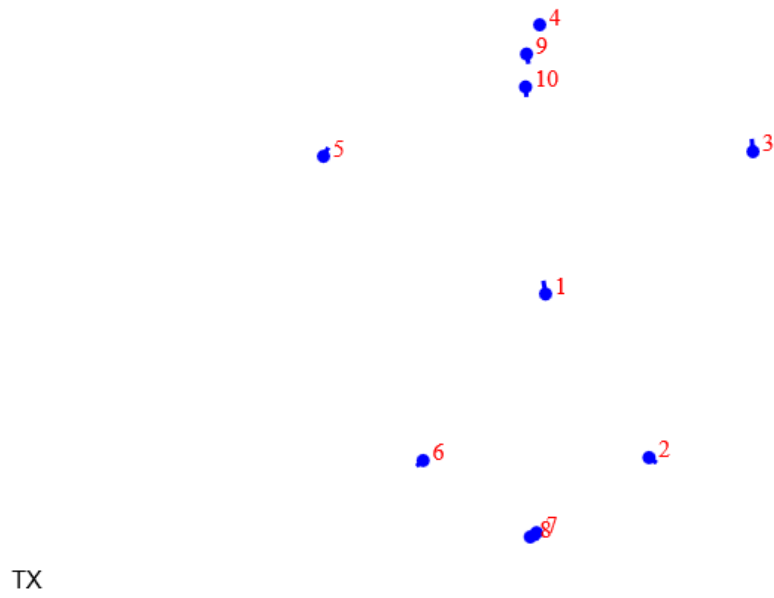
***M. batnensis* – New Mexico – Axis 1 vs. Axis 3**



***M. batnensis* – New Mexico – Axis 2 vs. Axis 3**



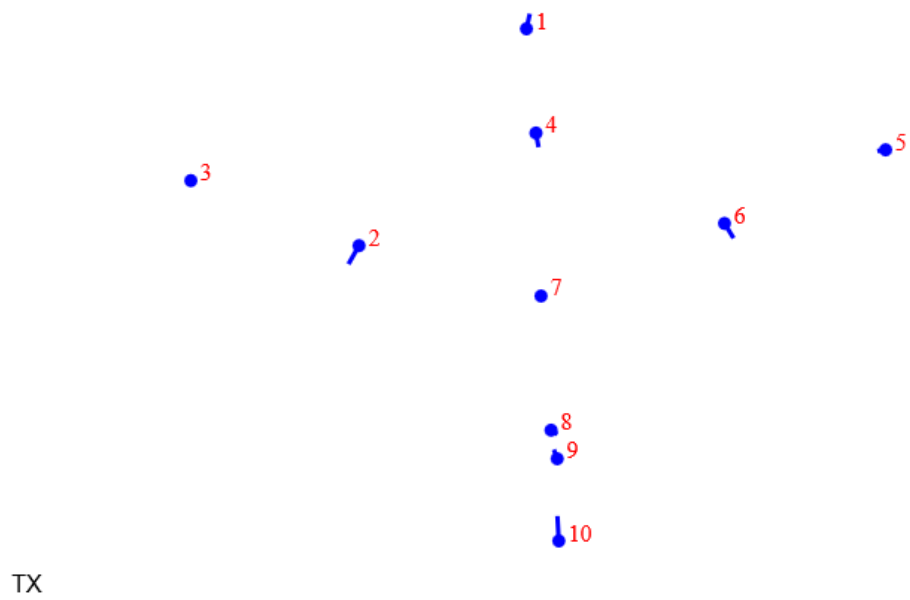
***M. batnensis* – Texas – Axis 1 vs. Axis 2**



***M. batnensis* – Texas – Axis 1 vs. Axis 3**



***M. batnensis* – Texas – Axis 2 vs, Axis 3**



Appendix 6 – Part D

Procrustes Fit: Mecasterourneli, averaged by locality

9 landmarks in 3 dimensions.

The dataset contains 2 observations, of which 2 are included for analyses.

Observations include Algeria and Peru

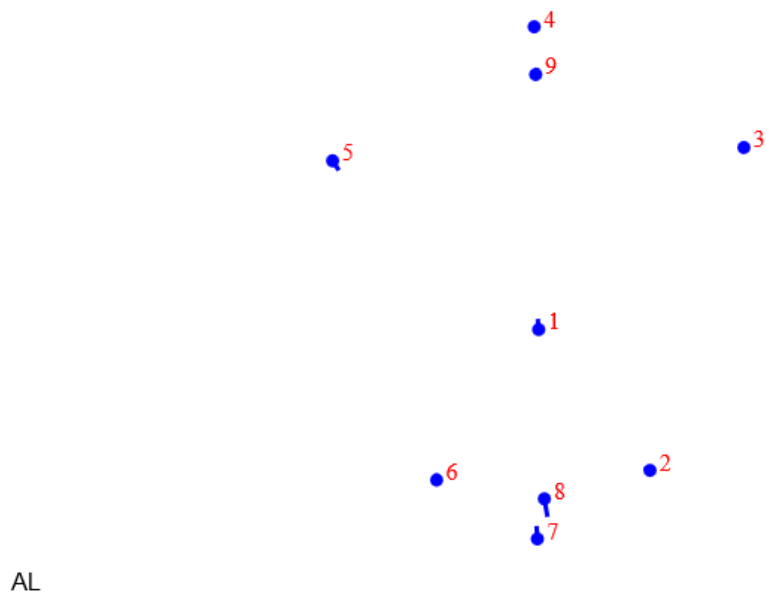
Average shape:

Lmk.	Axis 1 (x)	Axis 2 (y)	Axis 3 (z)
1	-0.03808938	0.00082631	0.15888037
2	-0.24026337	-0.15923791	0.03236192
3	0.22331098	-0.29420858	0.05904965
4	0.39663010	0.00728523	0.04599048
5	0.20425047	0.29713950	0.05311339
6	-0.25415407	0.14754998	0.03275051
7	-0.33867924	0.00276582	-0.01909328
8	-0.28111229	-0.00732929	-0.14600041
9	0.32810680	0.00520894	-0.21705263

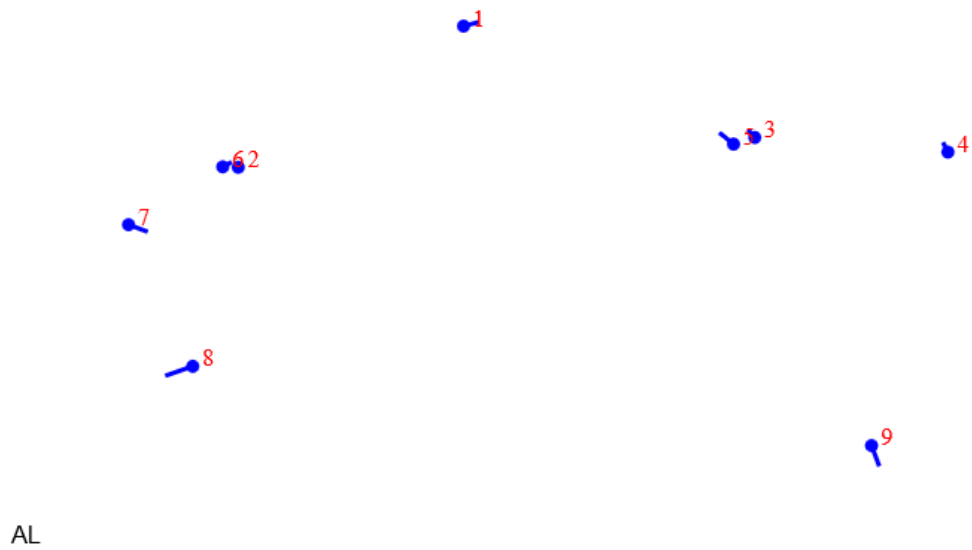
Data matrices in this dataset:

- Mf only, no 10, centroid size
- Mf only, no 10, Procrustes coordinates

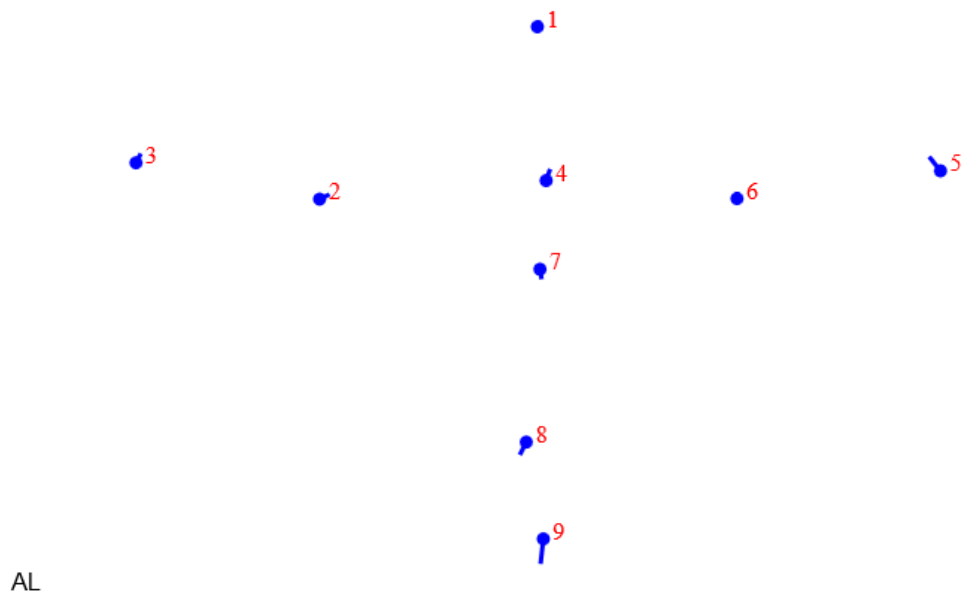
***M. fourneli* – Algeria – Axis 1 vs, Axis 2**



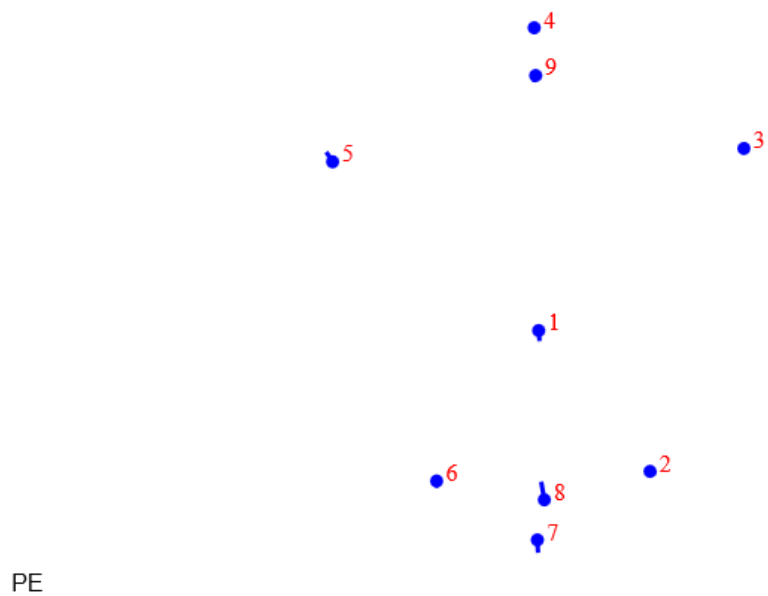
***M. fourneli* – Algeria – Axis 1 vs, Axis 3**



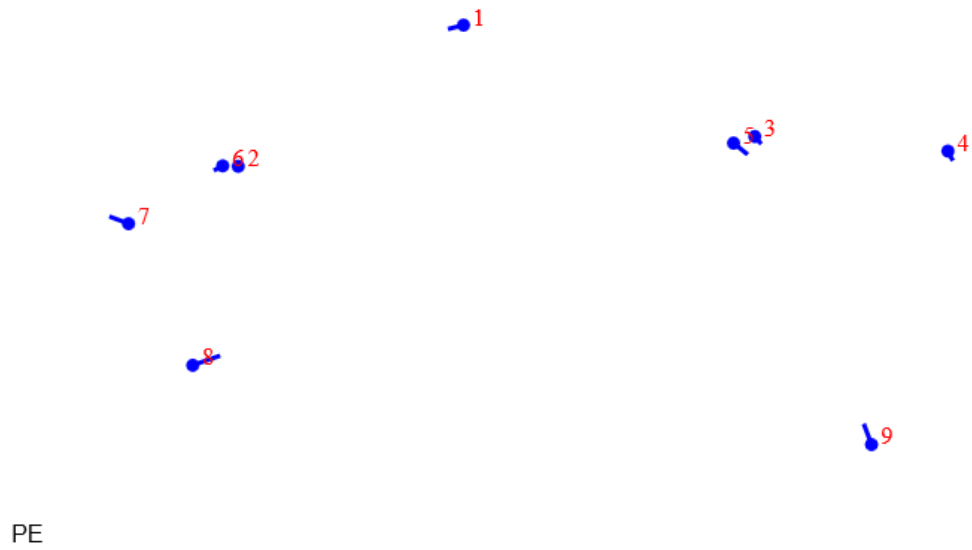
***M. fourneli* – Algeria – Axis 2 vs, Axis 3**



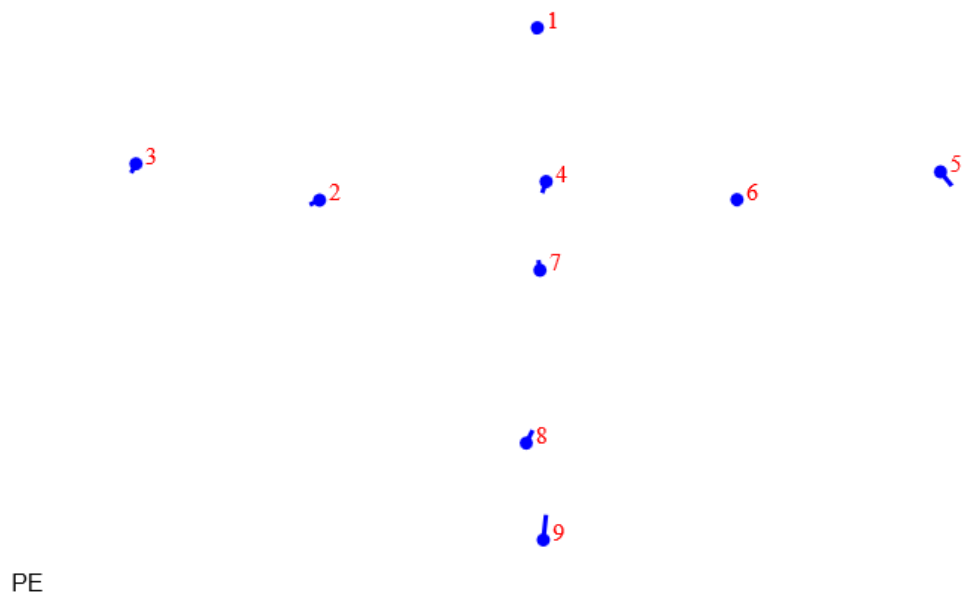
***M. fourneli* – Peru – Axis 1 vs, Axis 2**



***M. fourneli* – Peru – Axis 1 vs, Axis 3**



***M. fourneli* – Peru – Axis 2 vs, Axis 3**



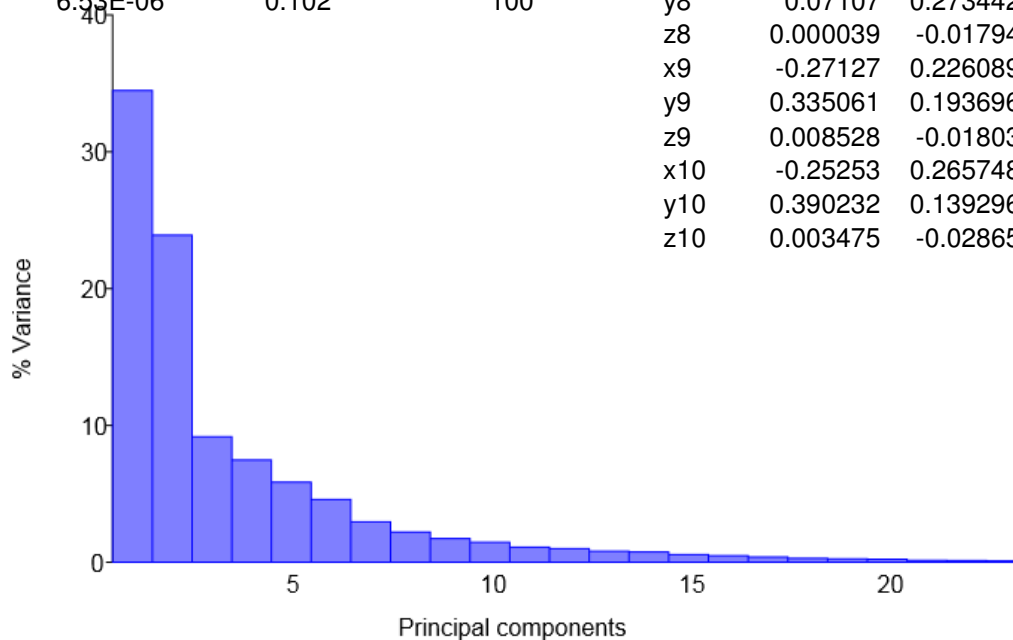
Appendix 7 – Part A

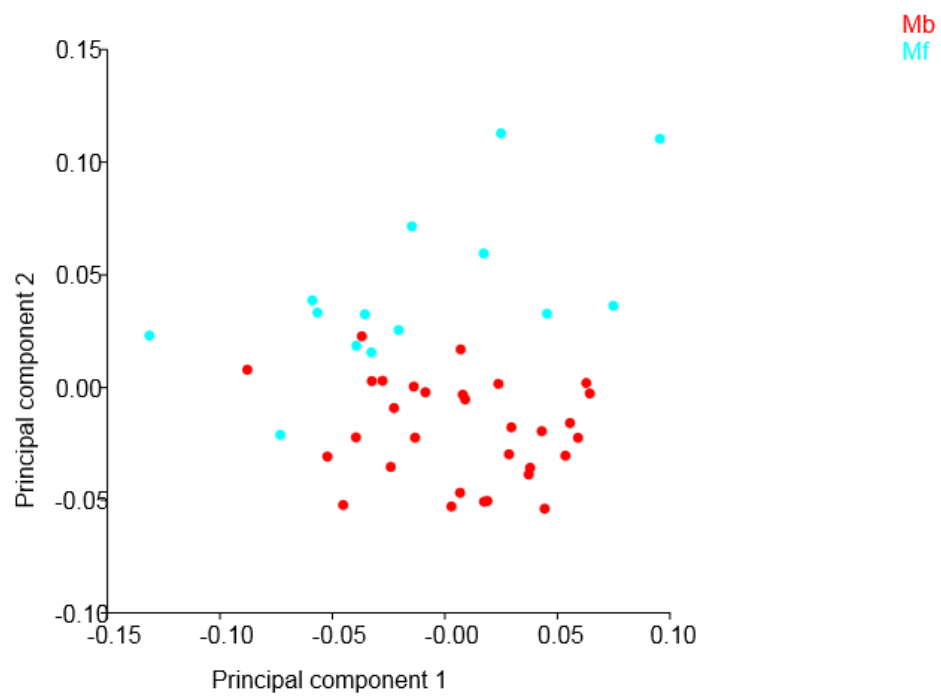
Principal Component Analysis: Both Species, outliers removed

For more on the outliers see Parts B and C of this Appendix.

Total variance: 0.00643352

	Eigenvalues	% Variance	Cumulative %		PC1	PC2	PC3
1	0.002218	34.482	34.482	x1	0.175684	-0.60787	-0.06269
2	0.001538	23.909	58.391	y1	0.083827	-0.38642	-0.20607
3	0.00059	9.175	67.565	z1	-0.00199	0.022053	-0.02023
4	0.000481	7.469	75.035	x2	-0.09901	-0.05354	0.0959
5	0.000377	5.854	80.888	y2	-0.25194	0.002966	-0.12559
6	0.000295	4.589	85.477	z2	0.207534	0.094383	0.130055
7	0.00019	2.958	88.435	x3	0.325457	0.101011	-0.1298
8	0.000142	2.2	90.635	y3	-0.1916	-0.04359	-0.15958
9	0.000111	1.733	92.368	z3	0.139499	-0.12649	0.342602
10	9.36E-05	1.455	93.823	x4	0.00426	0.08791	-0.1895
11	7.08E-05	1.1	94.923	y4	-0.05079	-0.24941	0.401913
12	6.4E-05	0.995	95.918	z4	0.008024	-0.00938	-0.00529
13	5.17E-05	0.804	96.722	x5	0.315042	0.098864	-0.18249
14	4.83E-05	0.751	97.473	y5	-0.2122	-0.13262	-0.02058
15	3.57E-05	0.555	98.028	z5	-0.1549	0.159727	-0.34904
16	3.1E-05	0.482	98.51	x6	-0.06606	-0.02985	0.093469
17	2.48E-05	0.386	98.896	y6	-0.2093	-0.00999	-0.18631
18	1.81E-05	0.282	99.178	z6	-0.21566	-0.0872	-0.20721
19	1.55E-05	0.24	99.418	x7	-0.08874	0.00662	0.268895
20	1.43E-05	0.223	99.641	y7	0.035642	0.212638	0.357574
21	8.55E-06	0.133	99.774	z7	0.005449	0.01152	0.027248
22	8.01E-06	0.124	99.898	x8	-0.04285	-0.09498	0.045372
23	6.53E-06	0.102	100	y8	0.07107	0.273442	0.201134
				z8	0.000039	-0.01794	0.031599
				x9	-0.27127	0.226089	0.142831
				y9	0.335061	0.193696	-0.08493
				z9	0.008528	-0.01803	0.006858
				x10	-0.25253	0.265748	-0.08198
				y10	0.390232	0.139296	-0.17756
				z10	0.003475	-0.02865	0.043404





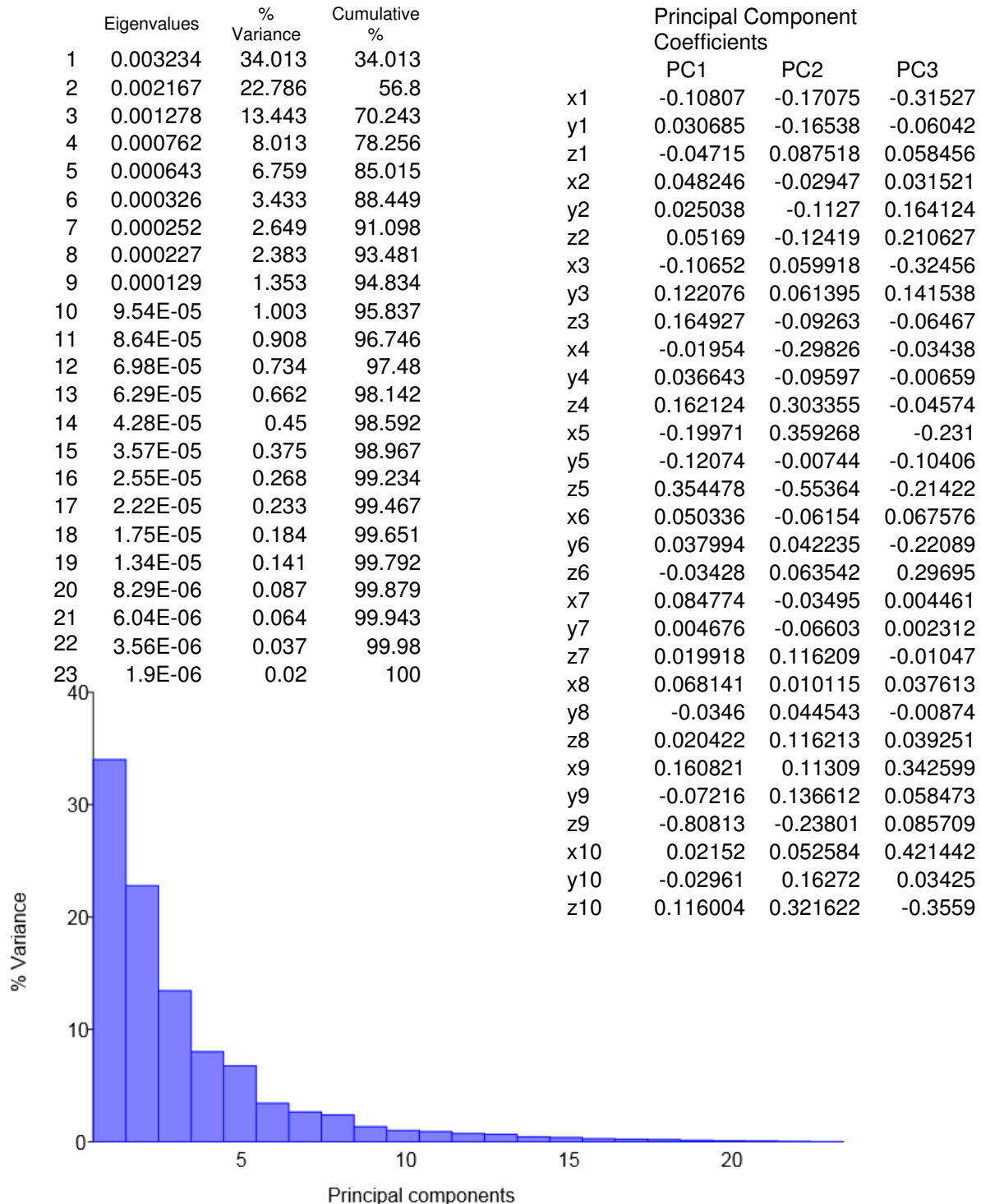
Appendix 7 – Part B

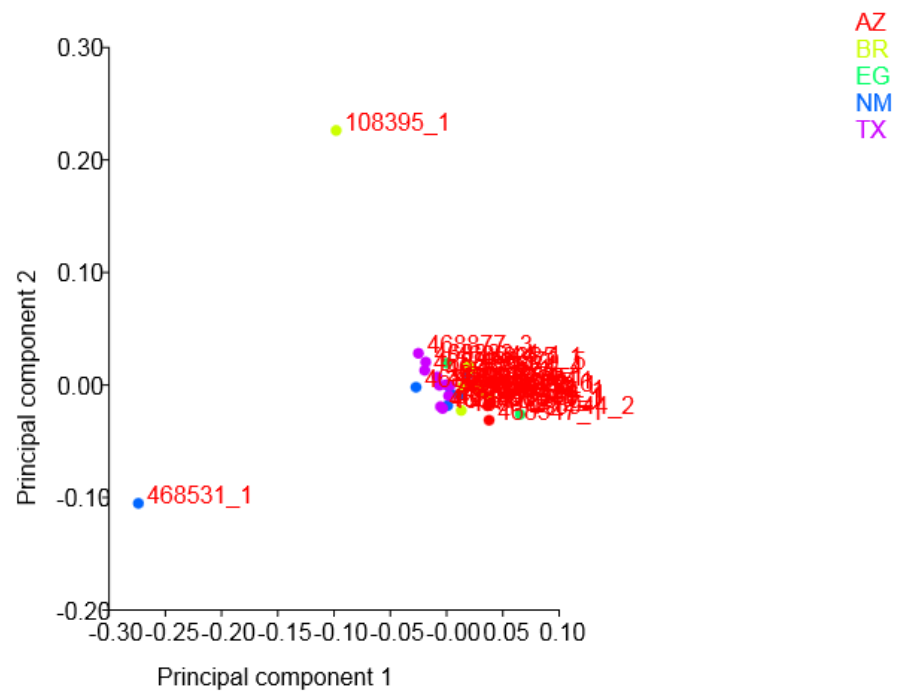
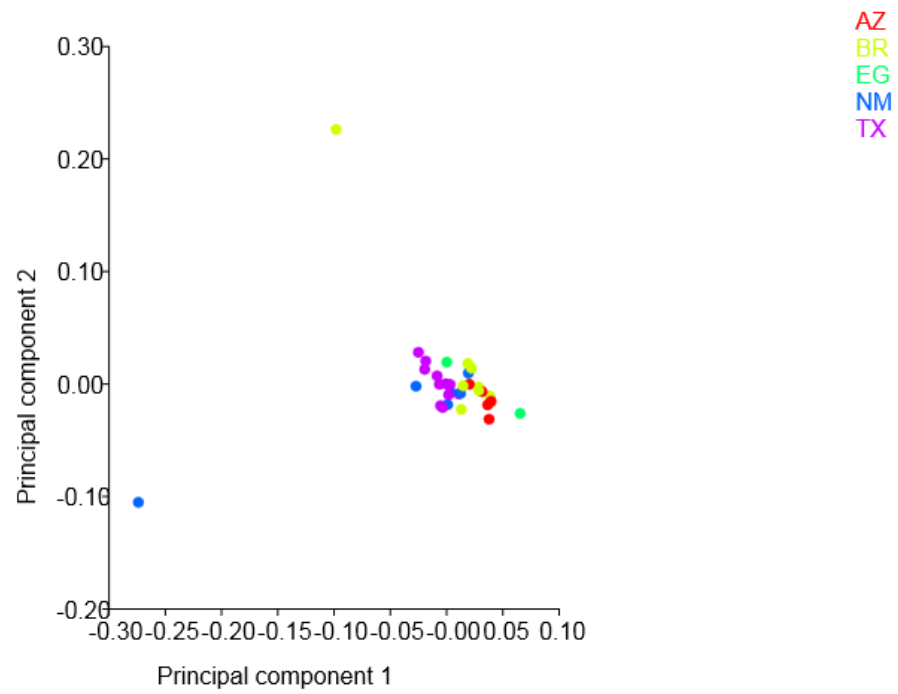
Principal Component Analysis: Full data set Mecaster batnensis

For the analysis with outliers removed go to page 157

The dataset contains 38 observations, of which 33 are included for analyses.

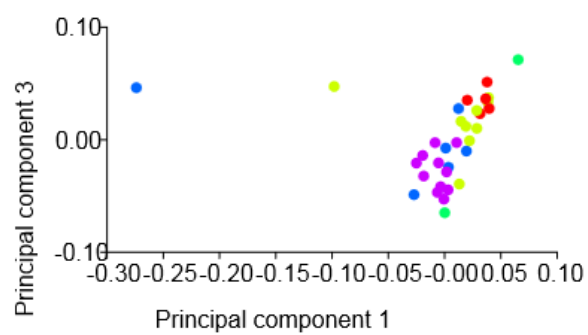
Total variance: 0.00950853



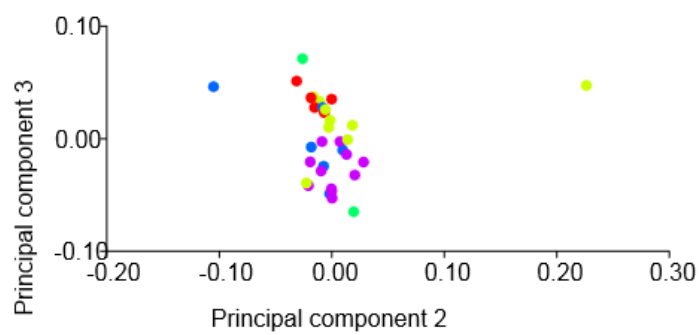


This plot identifies outliers in the populations.

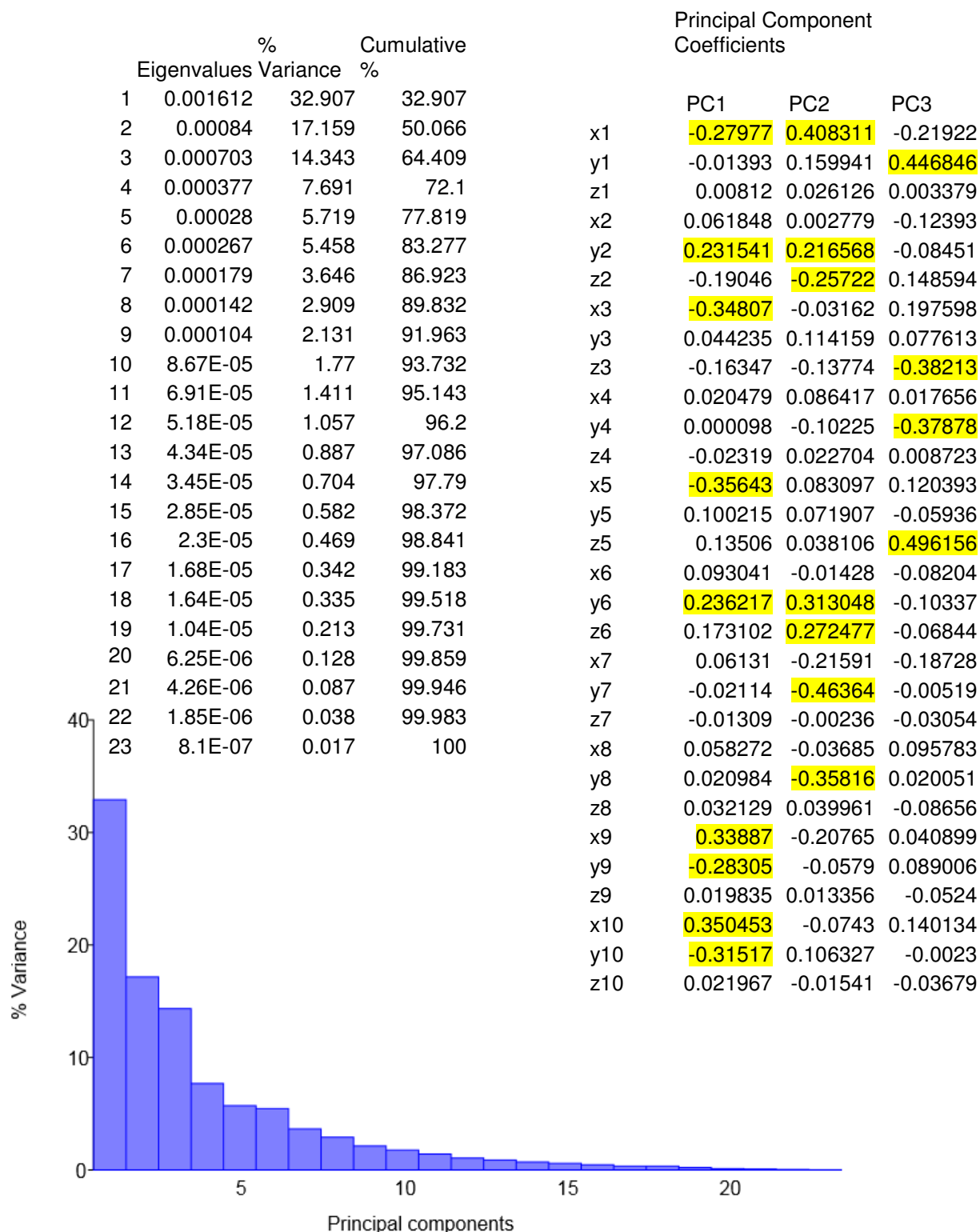
AZ
BR
EG
NM
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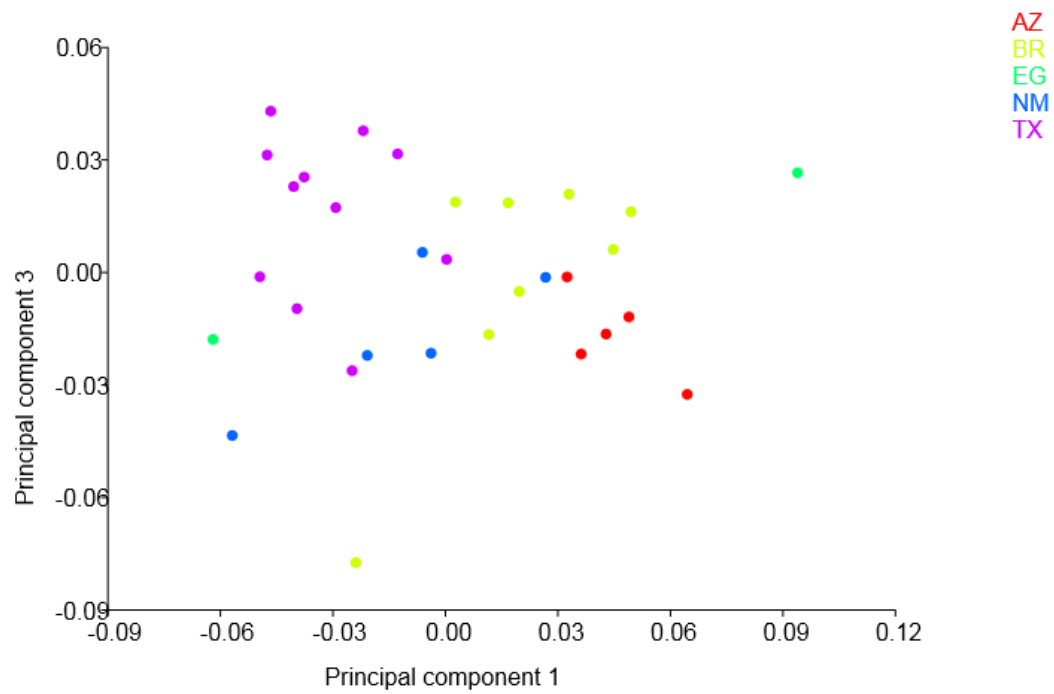
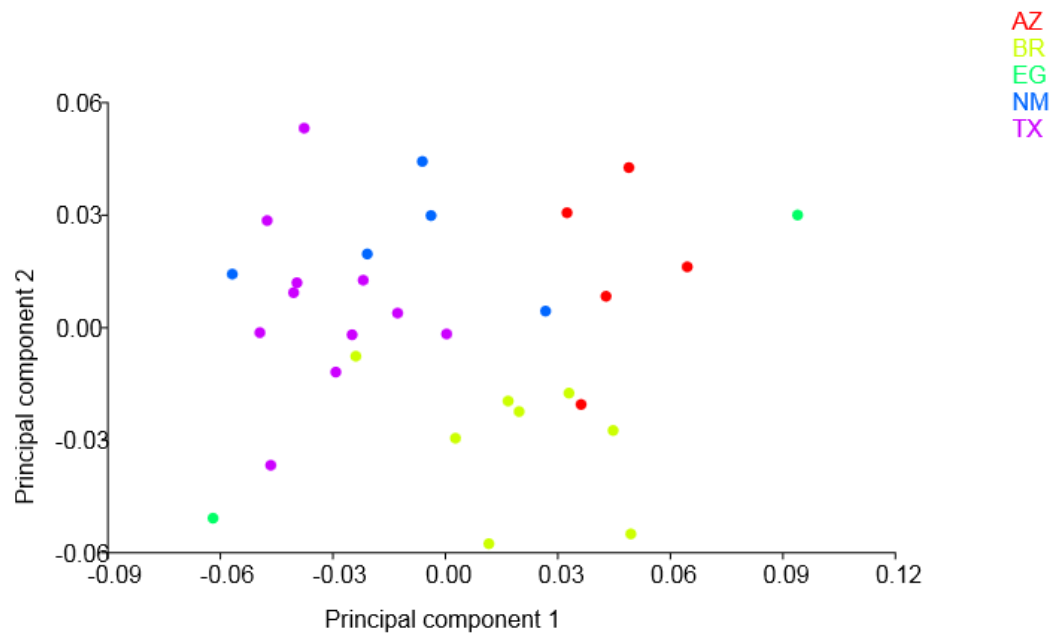


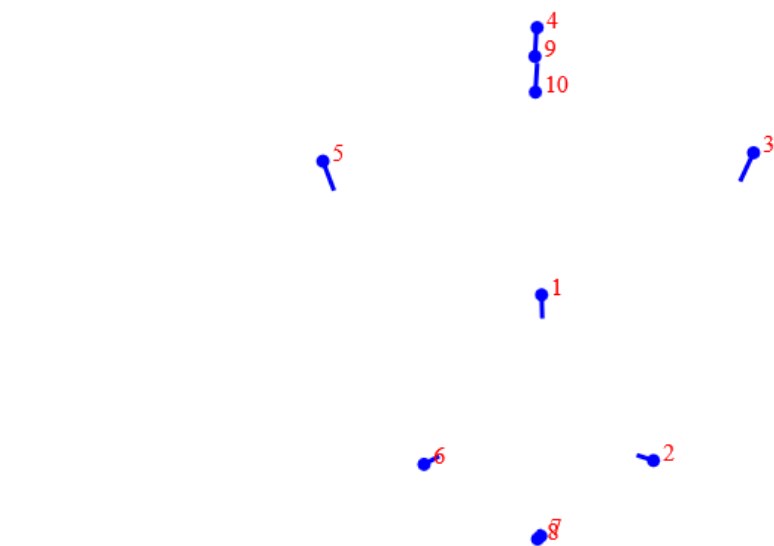
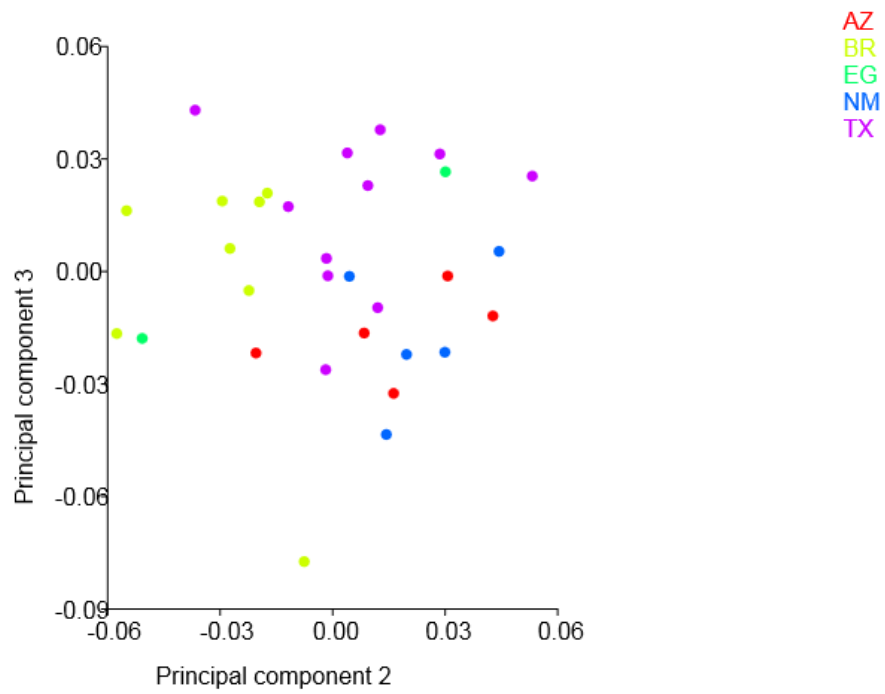
AZ
BR
EG
NM
TX



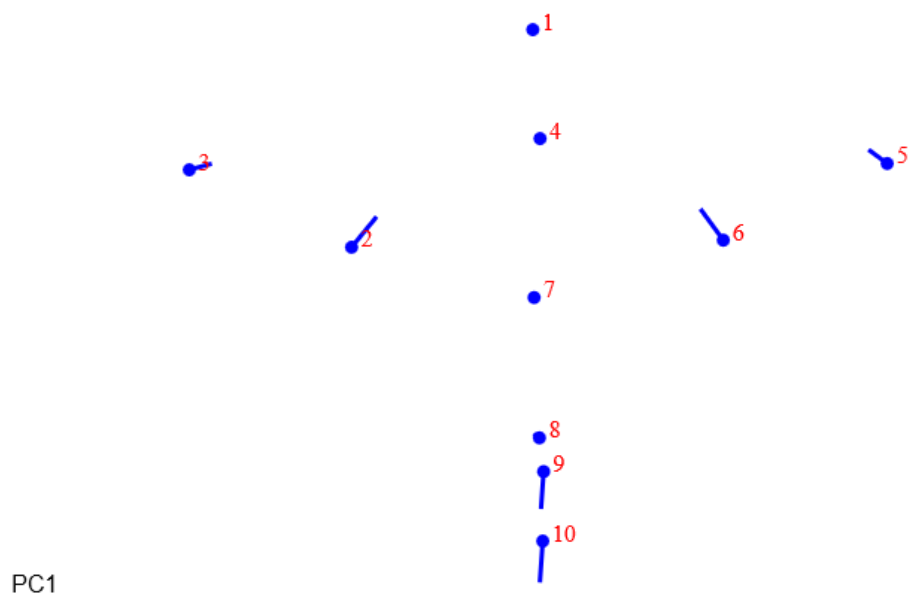
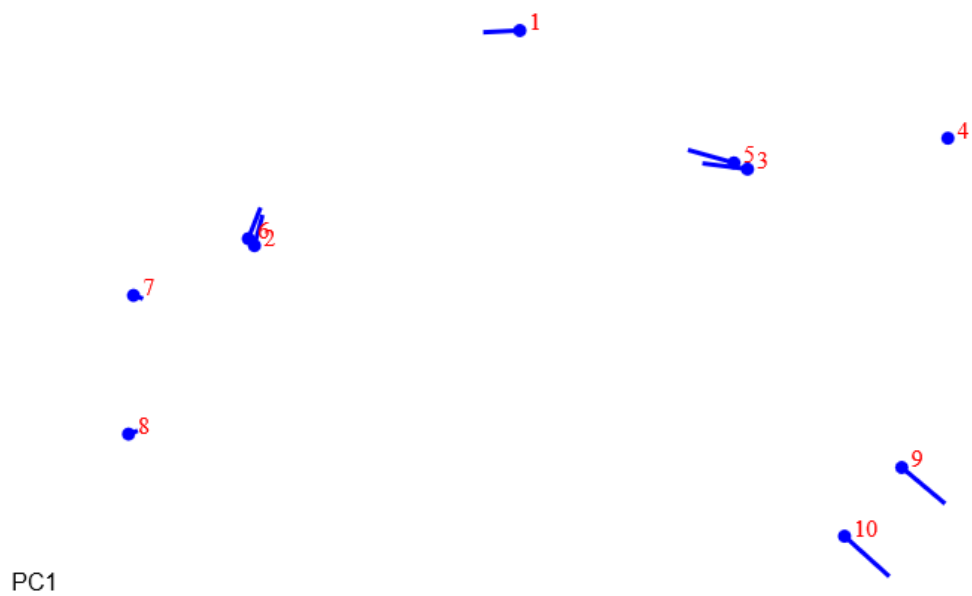
Principal Component Analysis: PCA: CovMatrix, PCA outliers excluded, Procrustes coordinates
 31 observations included in analysis
 Total variance: 0.00489793

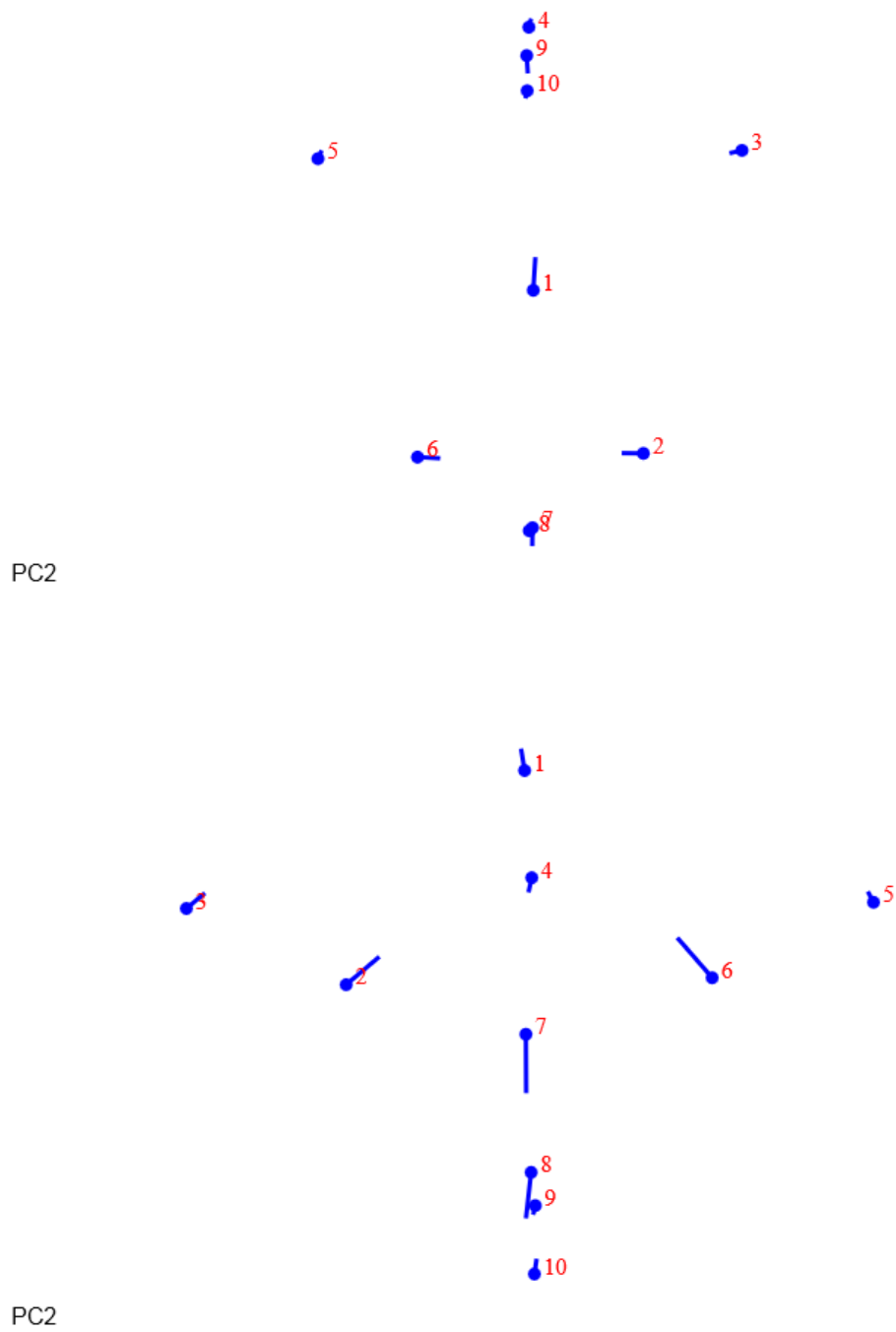


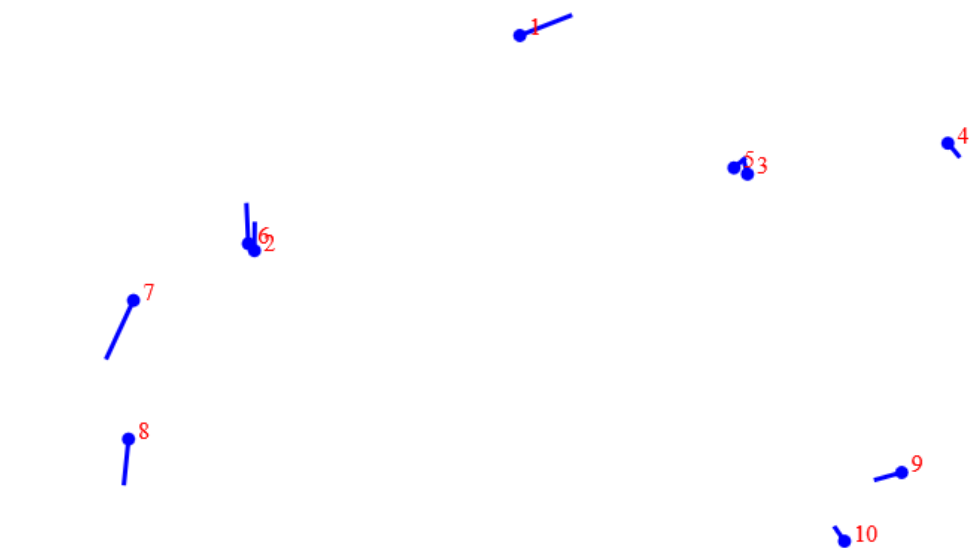




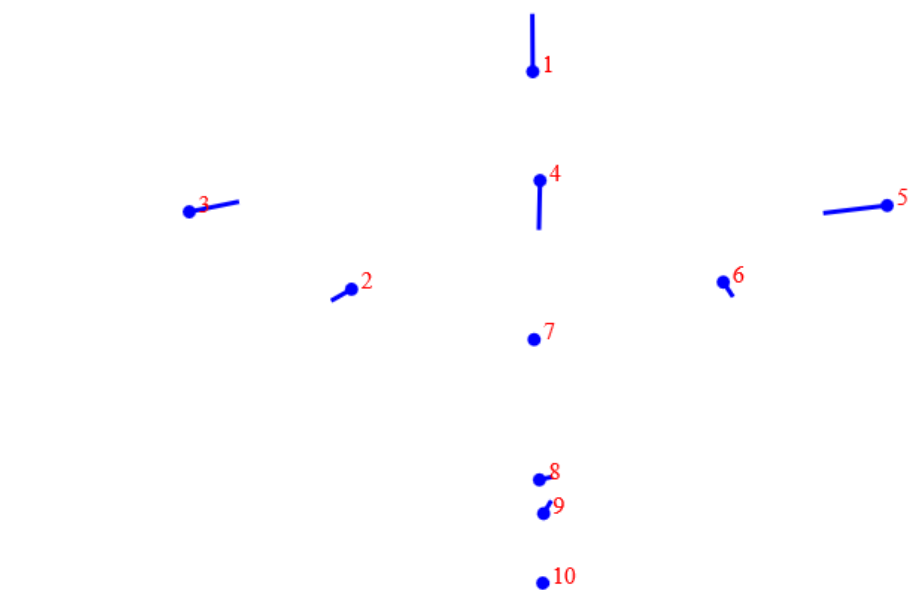
PC1



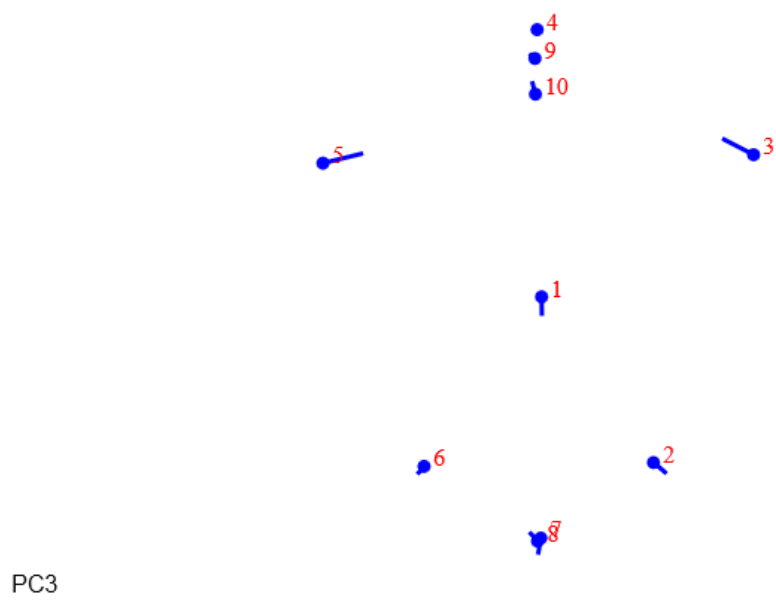
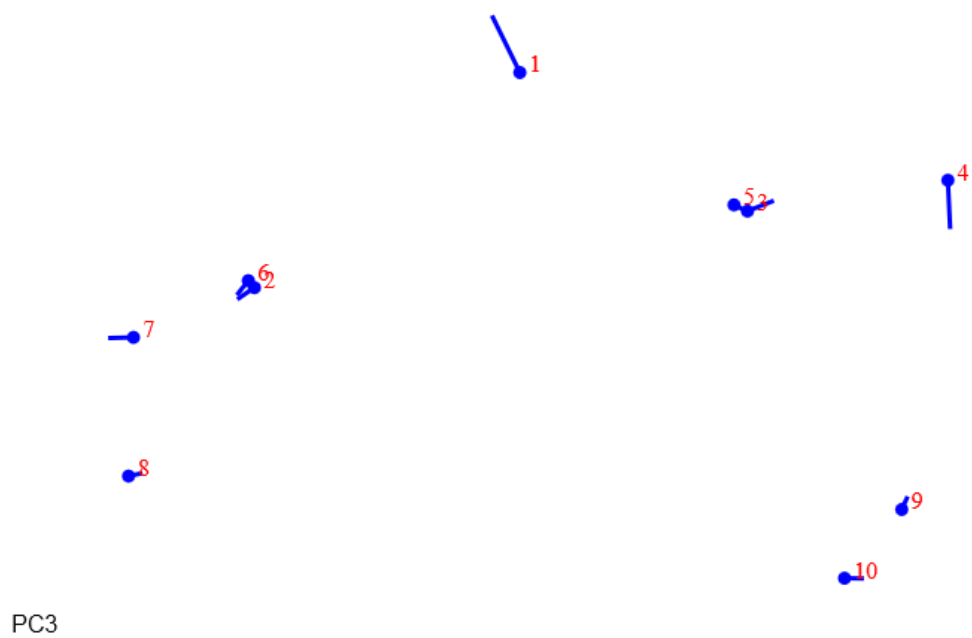




PC2



PC3



Appendix 7 – Part C

Principal Component Analysis: PCA: CovMatrix, Mf, Procrustes coordinates

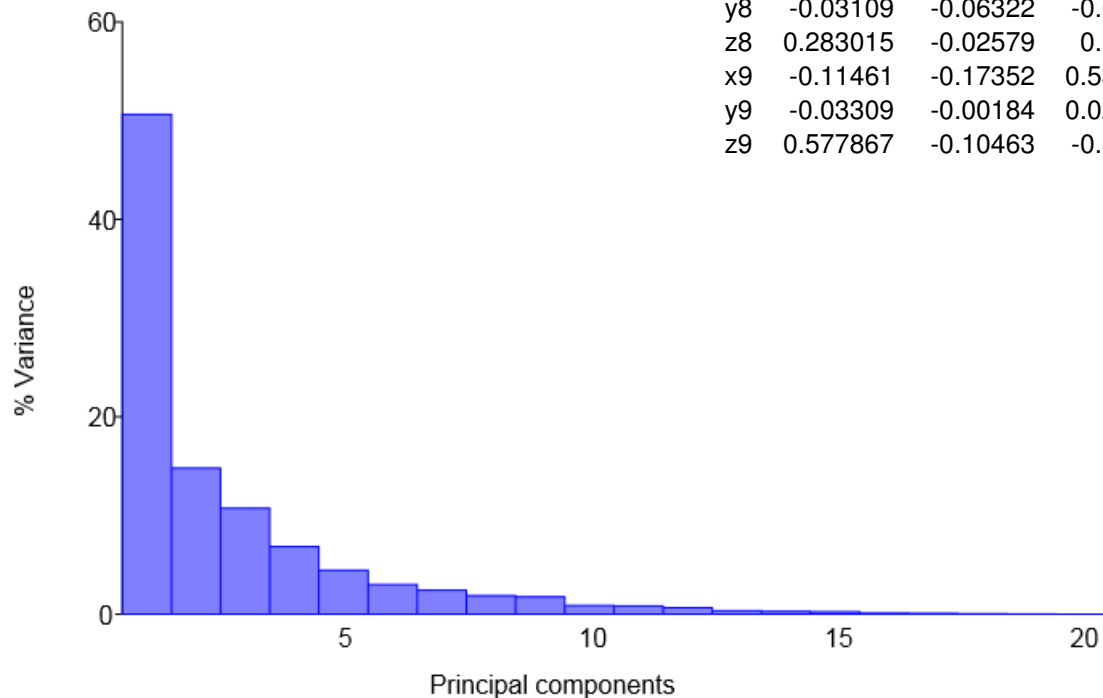
Total variance: 0.05036495

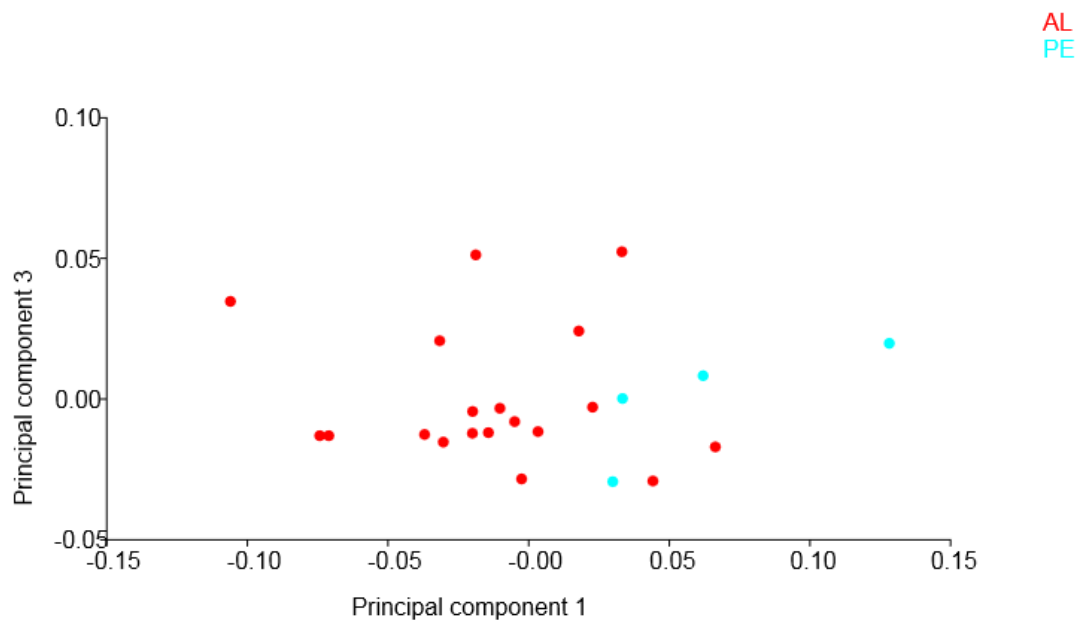
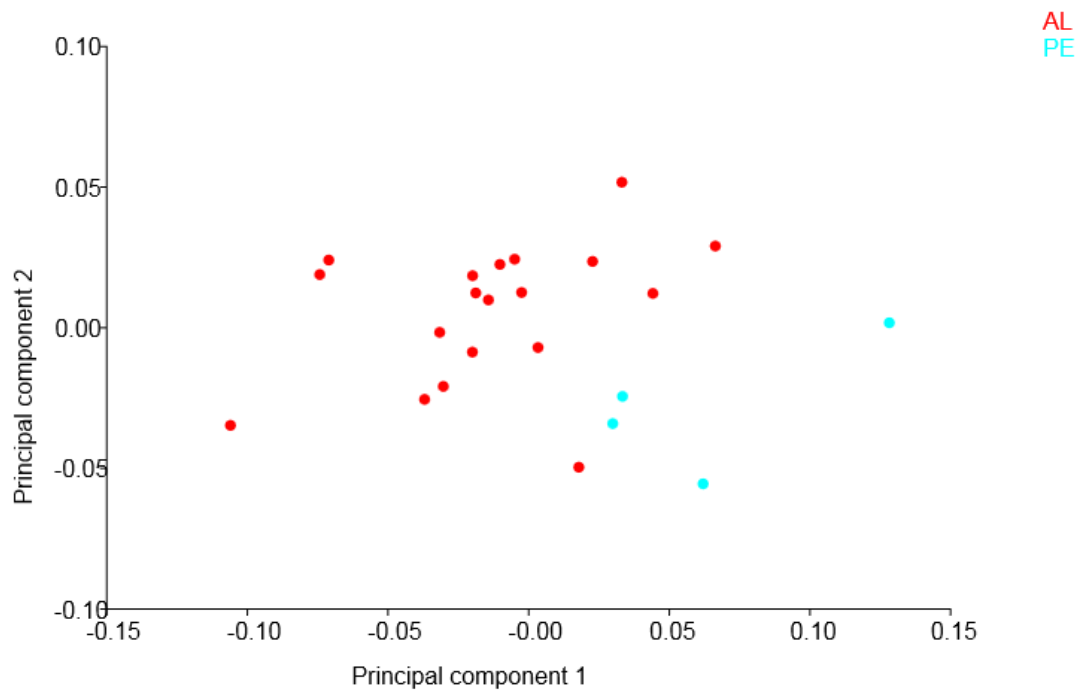
	Eigenvalues	% Variance	Cumulative %		Principal Component Coefficients		
					PC1	PC2	PC3
1	0.032633	64.794	64.794				
2	0.008255	16.391	81.185				
3	0.00413	8.199	89.384	x1	0.115318	0.037069	0.339702
4	0.002007	3.986	93.37	y1	-0.06574	0.039781	-0.25077
5	0.001029	2.043	95.413	z1	-0.0883	-0.14753	0.082664
6	0.000877	1.742	97.155	x2	0.130808	0.20717	-0.03433
7	0.000477	0.947	98.102	y2	-0.01967	-0.02979	0.266025
8	0.000263	0.523	98.625	z2	-0.13117	-0.2118	-0.08128
9	0.000242	0.48	99.105	x3	-0.03448	-0.02606	0.23457
10	0.000121	0.24	99.345	y3	0.089211	0.118601	-0.00224
11	0.000112	0.223	99.567	z3	0.046717	-0.01474	-0.14424
12	6.15E-05	0.122	99.69	x4	-0.02524	-0.05787	-0.00125
13	5.74E-05	0.114	99.804	y4	0.004506	-0.03996	0.096711
14	3.55E-05	0.071	99.874	z4	0.044494	0.042379	0.124302
15	0.000024	0.048	99.922	x5	0.05651	0.18101	-0.46594
16	1.82E-05	0.036	99.958	y5	-0.05332	-0.07272	-0.07204
17	1.12E-05	0.022	99.98	z5	-0.0343	-0.09438	0.128705
18	6.09E-06	0.012	99.992	x6	0.174833	0.205022	0.145159
19	2.94E-06	0.006	99.998	y6	0.045536	0.003986	0.253416
20	9.6E-07	0.002	100	z6	-0.13888	-0.20061	-0.11335
				x7	0.242125	-0.65295	-0.13129
				y7	-0.11641	-0.16655	0.285776
				z7	-0.11609	0.474695	0.120487
				x8	-0.81287	0.020033	-0.08973
				y8	0.066128	0.076941	-0.32541
				z8	0.247198	-0.03807	-0.08318
				x9	0.152989	0.086573	0.003116
				y9	0.049756	0.069706	-0.25148
				z9	0.170321	0.190049	-0.0341

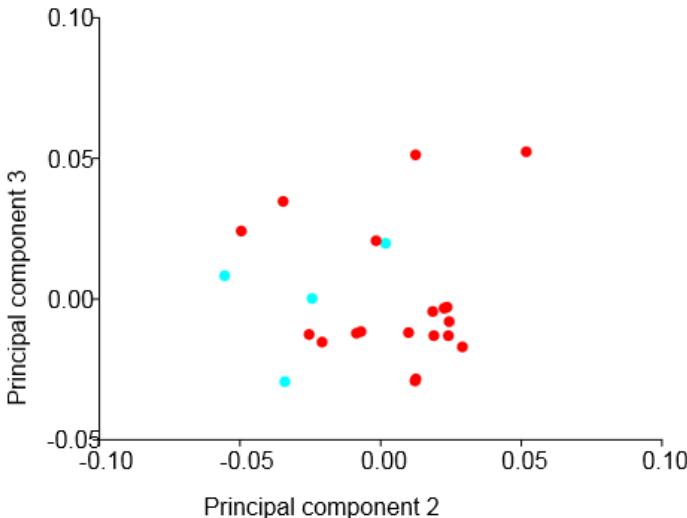
Principal Component Analysis: PCA: CovMatrix, PCA outliers excluded, Procrustes coordinates
Total variance: 0.00513375

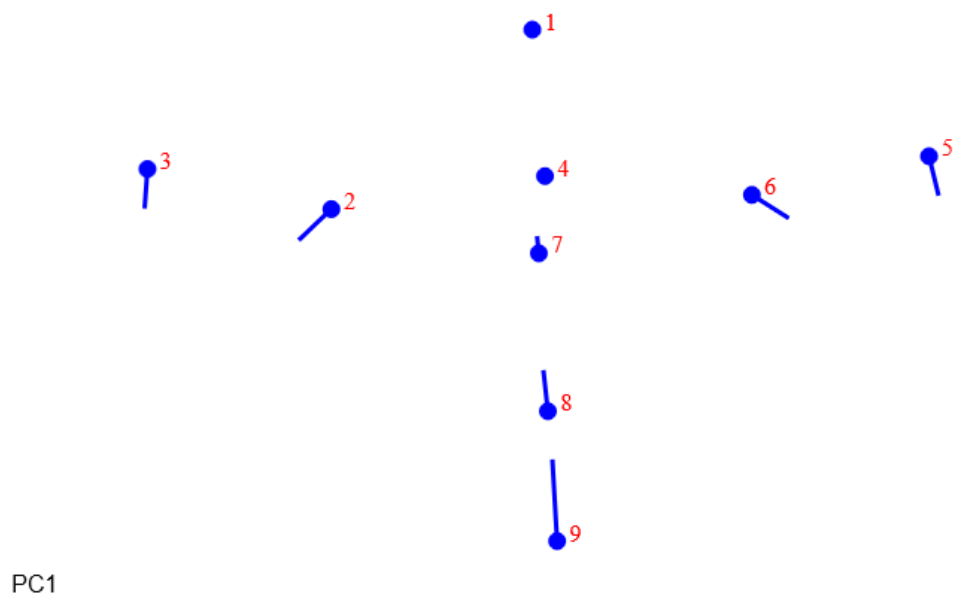
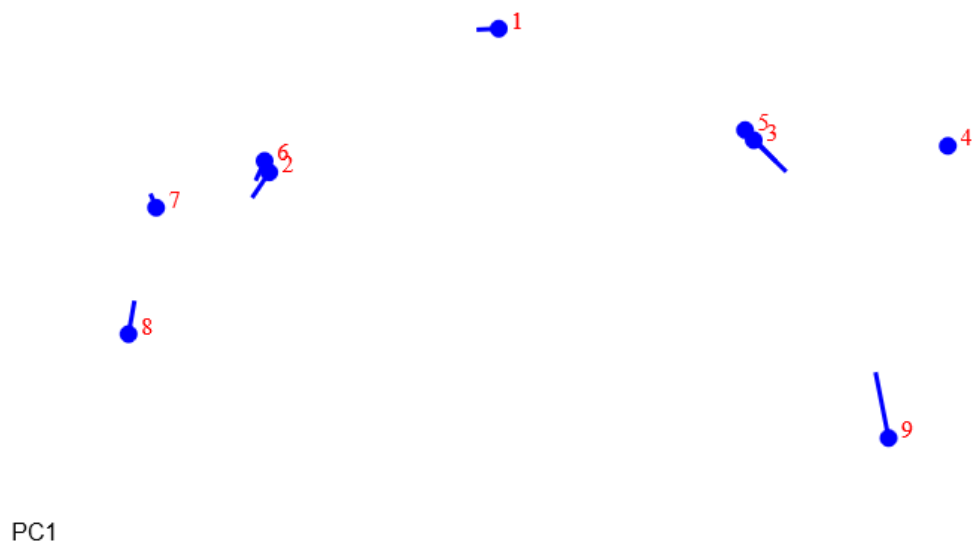
	Eigenvalues	% Variance	Cumulative %	Principal Component Coefficients			
1	0.002599	50.632	50.632				
2	0.00076	14.806	65.438		PC1	PC2	PC3
3	0.000551	10.728	76.166	x1	-0.18133	0.667931	-0.27611
4	0.000351	6.833	82.999	y1	-0.00309	0.042127	-0.0654
5	0.000228	4.447	87.446	z1	-0.00841	0.259823	-0.0851
6	0.000154	2.991	90.437	x2	-0.14453	-0.21001	0.019028
7	0.000125	2.426	92.863	y2	-0.22571	0.07605	-0.08445
8	9.64E-05	1.877	94.741	z2	-0.21481	-0.16671	-0.02127
9	9.01E-05	1.756	96.497	x3	0.281452	0.13075	-0.0054
10	4.54E-05	0.884	97.381	y3	-0.01939	0.133817	0.248924
11	4.25E-05	0.829	98.209	z3	-0.27217	-0.08008	-0.11477
12	3.38E-05	0.659	98.868	x4	-0.04255	-0.29904	-0.36381
13	1.82E-05	0.355	99.223	y4	0.001755	0.018864	-0.03615
14	1.48E-05	0.288	99.512	z4	-0.0405	0.335595	0.317419
15	1.28E-05	0.249	99.76	x5	0.267533	0.207864	0.062569
16	5.38E-06	0.105	99.865	y5	0.066083	-0.13323	-0.17574
17	3.77E-06	0.073	99.938	z5	-0.27136	-0.05914	-0.12194
18	2.02E-06	0.039	99.978	x6	-0.07252	-0.10244	0.007578
19	6.8E-07	0.013	99.991	y6	0.255609	-0.06214	0.178697
20	4.8E-07	0.009	100	z6	-0.16194	-0.10146	-0.05306
				x7	-0.0439	-0.1229	0.065095
				y7	-0.01107	-0.01044	-0.07385
				z7	0.108306	-0.05762	0.265492
				x8	0.050452	-0.09864	-0.04061
				y8	-0.03109	-0.06322	-0.02184
				z8	0.283015	-0.02579	0.15855
				x9	-0.11461	-0.17352	0.531662
				y9	-0.03309	-0.00184	0.029801
				z9	0.577867	-0.10463	-0.34532

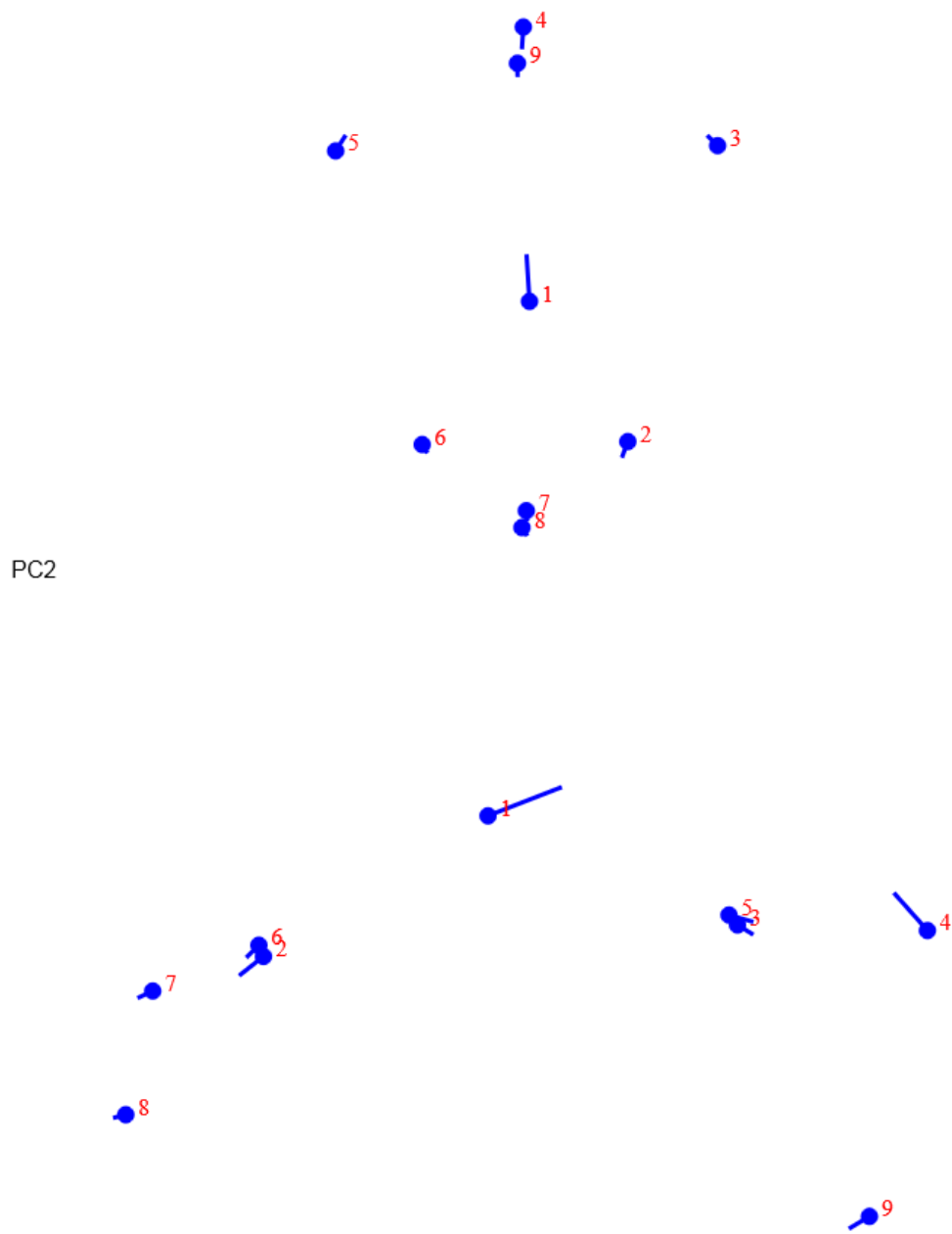
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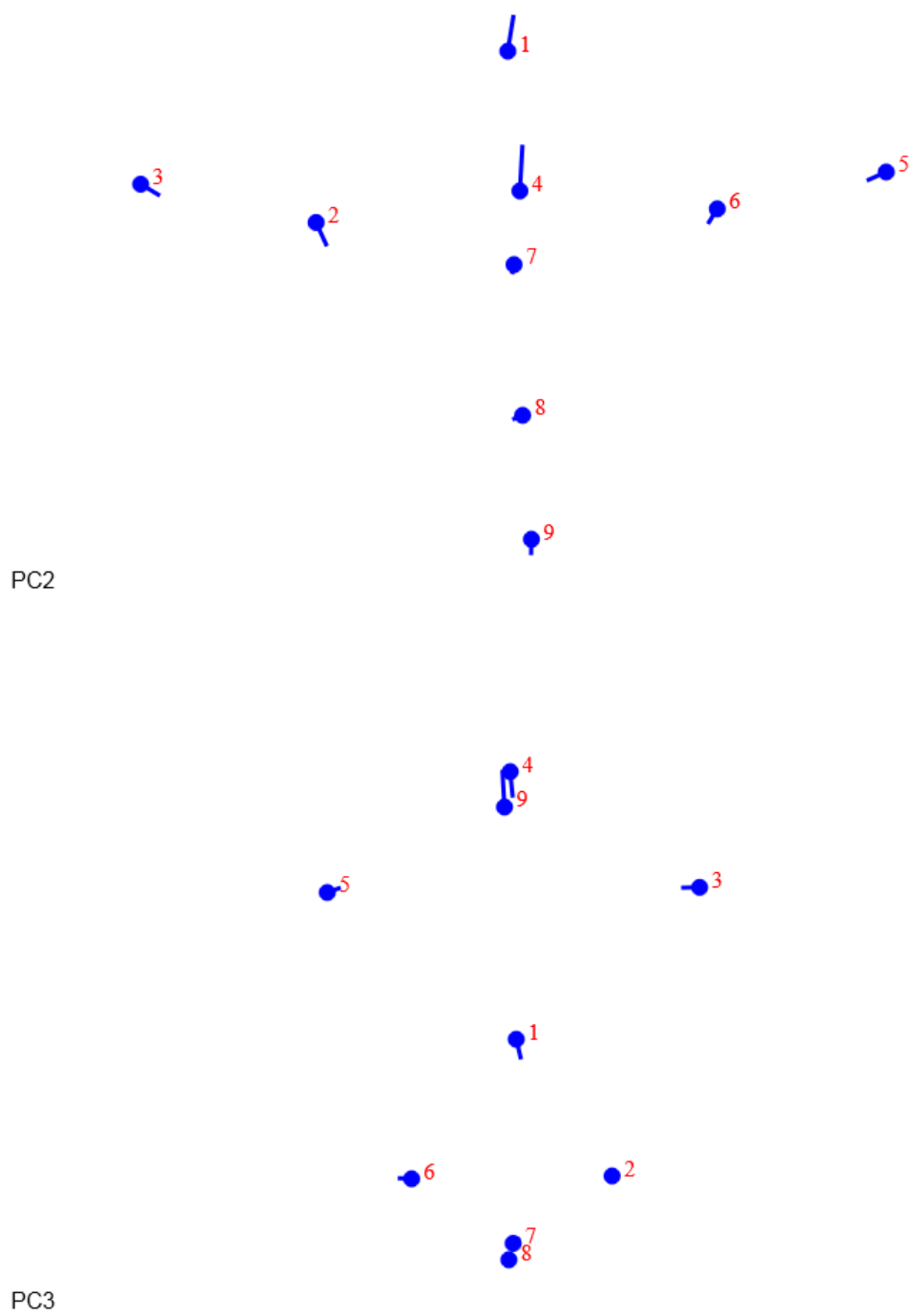


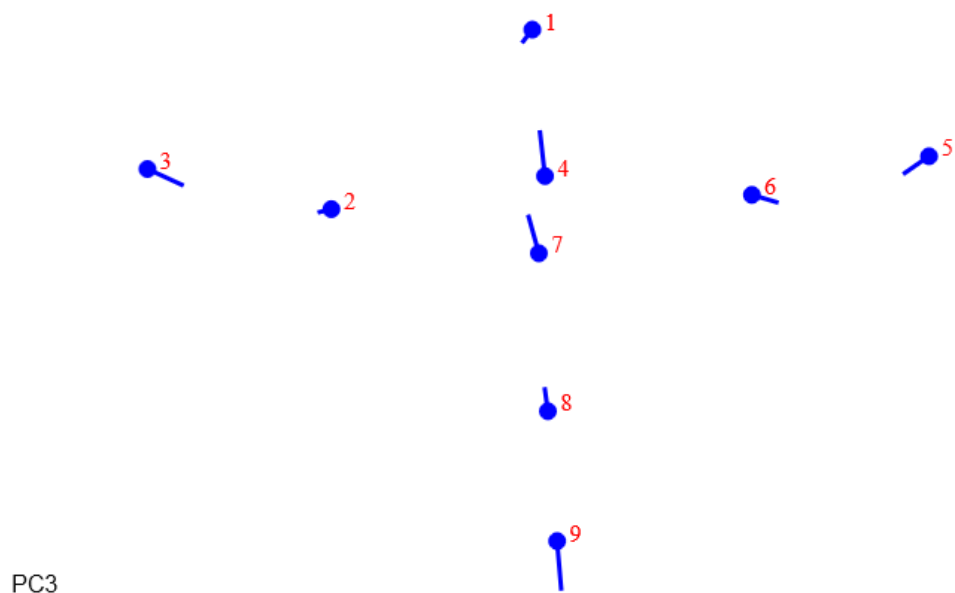


AL
PE









Appendix 8 – Part A

Canonical Variate Analysis – Mecaster batnensis by location

Groups		Observations
1.	AZ	5
2.	BR	9
3.	EG	2
4.	NM	6
5.	TX	11

Variation among groups, scaled by the inverse of the within-group variation

	Eigenvalues	% Variance	Cumulative %
1.	58.09258501	78.882	78.882
2.	8.44392524	11.466	90.348
3.	6.03686017	8.197	98.545
4.	1.07134846	1.455	100.000

Mahalanobis distances among groups:

	AZ	BR	EG	NM
BR	10.3898			
EG	22.5501	15.8372		
NM	5.5905	11.5166	23.8219	
TX	9.2102	13.1072	26.1678	5.4251

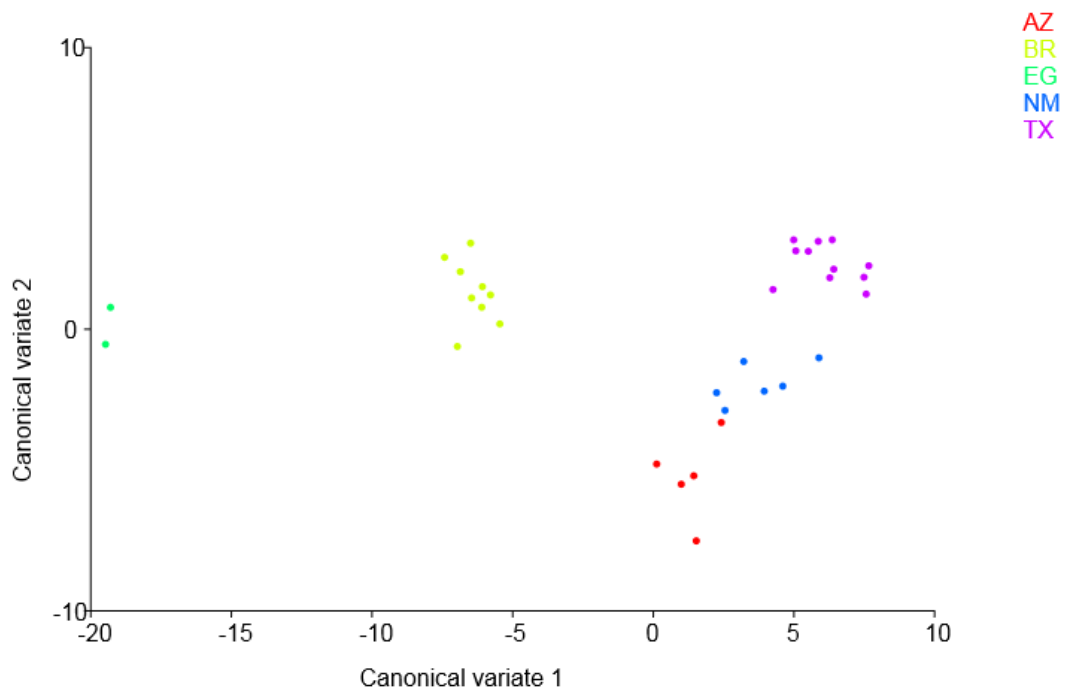
Procrustes distances among groups:

	AZ	BR	EG	NM
BR	0.0677			
EG	0.0719	0.0564		
NM	0.0883	0.0863	0.0954	
TX	0.0856	0.0657	0.0709	0.0630

Canonical coefficients:

	CV1	CV2	CV3	CV4
x1	297.8038	9.6299	-35.7988	47.6154
y1	-324.8928	8.3334	137.9270	-106.0258
z1	82.0546	-31.7096	-55.0598	-8.4430
x2	-178.7965	-136.5900	23.5286	-191.9861
y2	39.6109	-90.3064	28.1479	-57.6591
z2	-127.0644	-21.9993	-108.1928	43.3712
x3	-108.1833	44.6110	85.4908	13.7403

y3	136.5747	-0.5171	-175.9662	59.5527
z3	39.7764	10.2726	104.7781	15.1696
x4	-78.9131	21.6312	-21.3501	-59.2449
y4	142.6066	153.2154	52.7718	73.3069
z4	-180.1565	9.8966	-12.3793	-2.0973
x5	-72.6410	10.8252	19.4477	13.6611
y5	117.0943	-101.5568	-117.3629	35.7368
z5	4.9195	-25.4168	-13.5781	12.0042
x6	235.9471	-30.2650	-96.5938	82.1654
y6	9.3350	-12.7244	77.2626	-15.9904
z6	-70.9381	44.5434	197.4048	-2.9077
x7	-86.8393	113.0922	-27.6889	151.2695
y7	89.2799	-22.2557	9.8950	-13.3508
z7	235.1850	22.9240	-246.0858	-13.5266
x8	-140.2675	-22.0063	110.8385	-75.6936
y8	-124.1910	126.5316	-46.5867	50.3785
z8	-200.0609	-40.0705	188.5133	-37.0723
x9	69.7570	27.5784	15.6587	37.2199
y9	-101.2281	-53.6215	35.1811	-8.0356
z9	35.5286	11.5734	-6.5512	20.1188
x10	62.1328	-38.5066	-73.5328	-18.7471
y10	15.8105	-7.0985	-1.2695	-17.9131
z10	180.7557	19.9862	-48.8492	-26.6168



Canonical Variate Analysis: CVA ...

Dataset: PCA outliers excluded

Classification criterion: Location

Groups	Observations
1. AZ	5
2. BR	8
3. EG	2
4. NM	5
5. TX	11

Variation among groups, scaled by the inverse of the within-group variation

	Eigenvalues	% Variance	Cumulative %
1.	238.30236777	88.945	88.945
2.	19.25896153	7.188	96.134
3.	7.13290692	2.662	98.796
4.	3.22551660	1.204	100.000

Mahalanobis distances among groups:

	AZ	BR	EG	NM
BR	17.5581			
EG	38.3583		23.8446	
NM	16.4935		28.6654	50.3149
TX	15.1153		24.1461	46.3434
				8.1951

P-values from permutation tests (10000 permutation rounds) for Mahalanobis distances among groups:

	AZ	BR	EG	NM
BR	0.0007			
EG	0.0481		0.0011	
NM	0.0001		0.0002	0.0071
TX	<.0001		<.0001	0.0023
				<.0001

Procrustes distances among groups:

	AZ	BR	EG	NM
BR	0.0604			
EG	0.0720		0.0477	
NM	0.0607		0.0657	0.0671
TX	0.0856		0.0677	0.0710
				0.0452

P-values from permutation tests (10000 permutation rounds) for Procrustes distances among groups:

	AZ	BR	EG	NM
BR	0.0014			
EG	0.2149	0.6192		
NM	0.0157	0.0037	0.3085	
TX	0.0002	<.0001	0.1395	0.0066

Canonical coefficients:

	CV1	CV2	CV3	CV4
x1	520.7265	-0.7454	-55.0839	-9.9107
y1	137.4769	142.3388	-72.0403	8.4951
z1	186.8113	329.5352	-271.6471	99.7167
x2	-71.9024	146.9336	104.8613	2.4853
y2	529.3447	3.8474	171.2093	-363.0614
z2	88.8720	-257.2792	42.3072	-128.8405
x3	-271.3743	-148.9923	57.2146	40.1153
y3	-344.3567	-44.8907	-36.0528	196.1804
z3	-182.3461	-199.8011	174.3658	53.6251
x4	-141.9797	122.3884	-37.3379	36.7788
y4	-393.2928	143.6890	-30.9512	27.8160
z4	431.4670	290.2126	175.0066	-214.2151
x5	-150.0976	-4.0537	14.4137	7.3712
y5	106.9235	-194.0839	54.9021	-90.5387
z5	-423.1190	-195.1022	22.5330	130.8232
x6	721.0867	-83.9012	26.3987	-200.4164
y6	-666.0500	-144.8346	-9.7549	276.0455
z6	246.3967	-15.9454	16.3032	-149.0188
x7	-385.8191	-15.8538	-92.7331	5.3956
y7	982.9814	57.7751	-47.1880	-299.2387
z7	-355.8618	26.6769	-52.5933	57.2050
x8	-400.0727	-42.9882	51.4756	126.5379
y8	-945.3126	49.0212	-20.2166	320.9776
z8	371.4804	159.8423	67.2550	17.8835
x9	-1032.5443	-36.3353	-342.0699	397.6196
y9	721.0720	-56.1808	192.0586	-244.7176
z9	-370.7881	3.9580	-213.2975	186.5923
x10	1211.9770	63.5478	272.8610	-405.9765
y10	-128.7864	43.3183	-201.9661	168.0417
z10	7.0875	-142.0969	39.7671	-53.7714

Dataset 'CVA ..., scores'

10 landmarks in 3 dimensions.

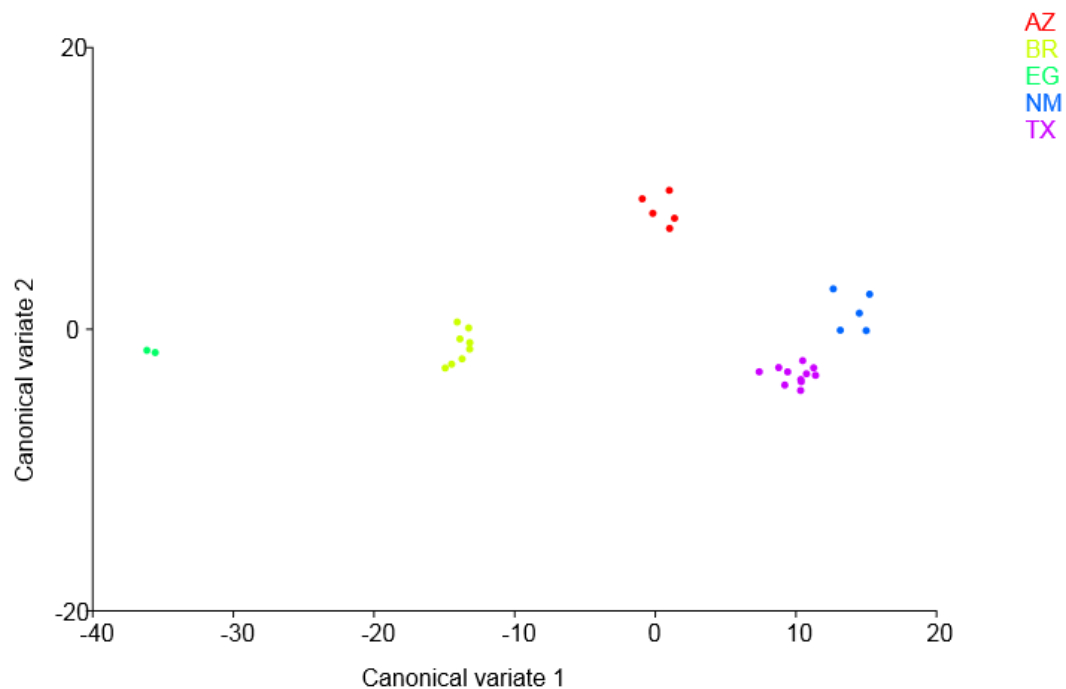
The dataset contains 38 observations, of which 31 are included for analyses.

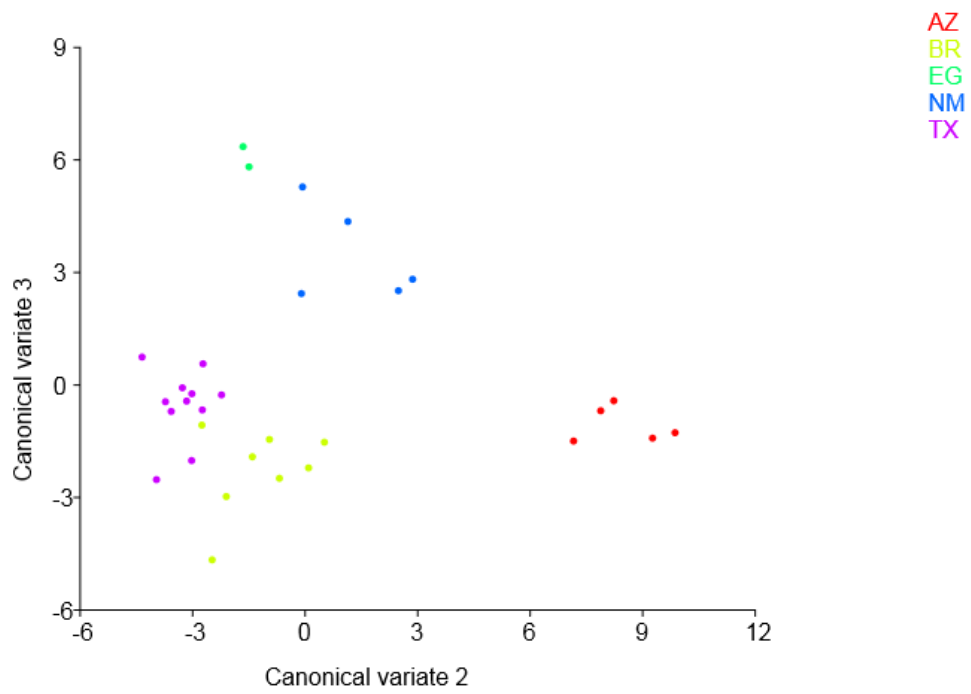
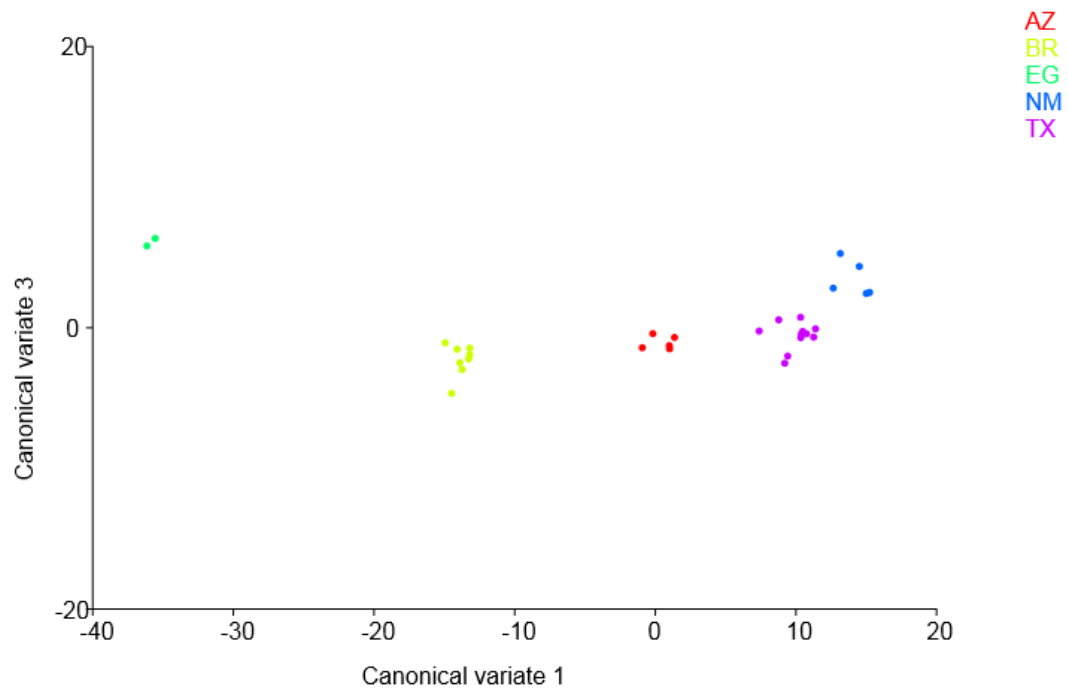
Average shape:

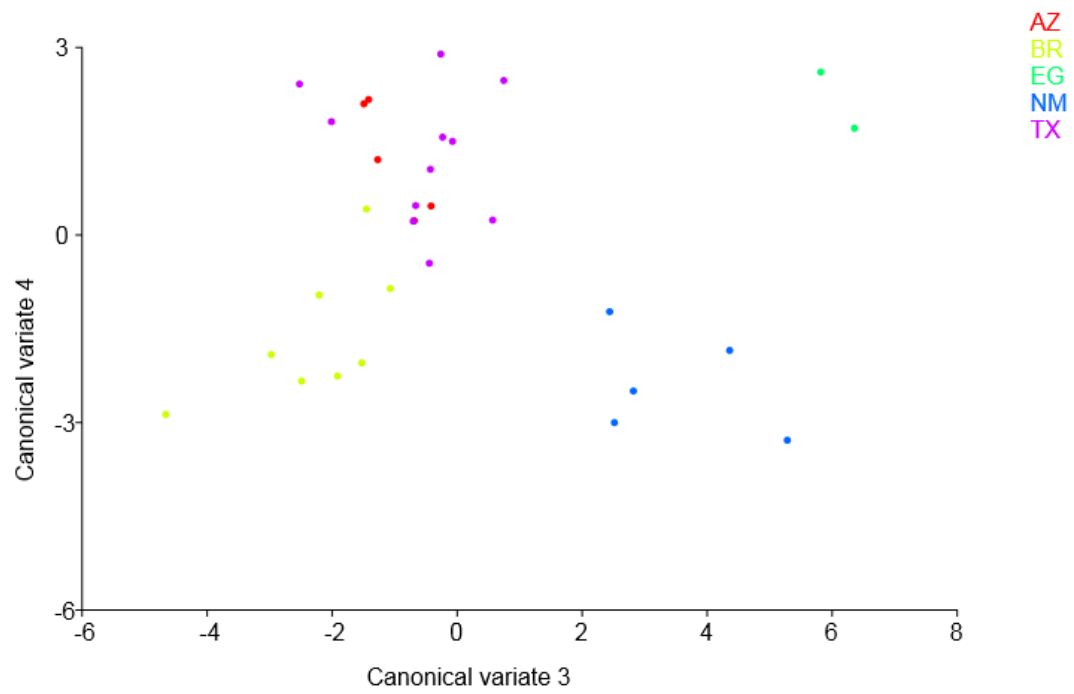
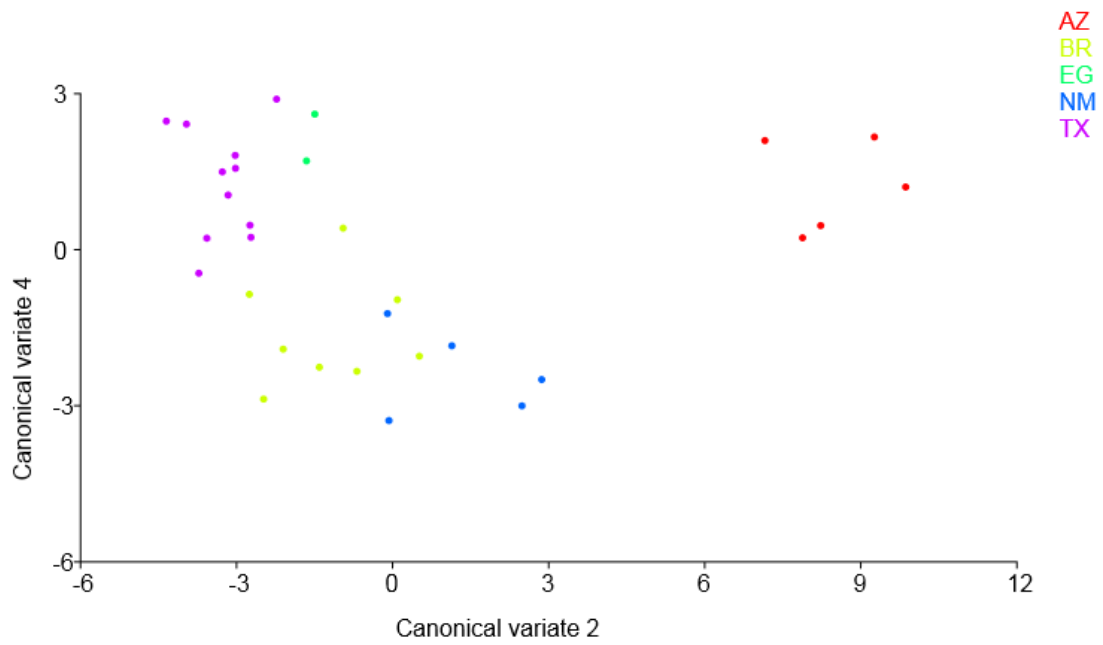
Lmk.	Axis 1 (x)	Axis 2 (y)	Axis 3 (z)
1	-0.02125879	0.19618010	0.00451246
2	-0.23709701	0.02127968	0.15020508
3	0.16377212	0.08350661	0.28062831
4	0.32673849	0.10861463	-0.00132459
5	0.15279535	0.08856505	-0.28034588
6	-0.24203471	0.02694411	-0.14862360
7	-0.33541544	-0.01916211	0.00345594
8	-0.33938294	-0.13193152	-0.00079971
9	0.28919321	-0.15906584	-0.00419961
10	0.24268970	-0.21493071	-0.00350839

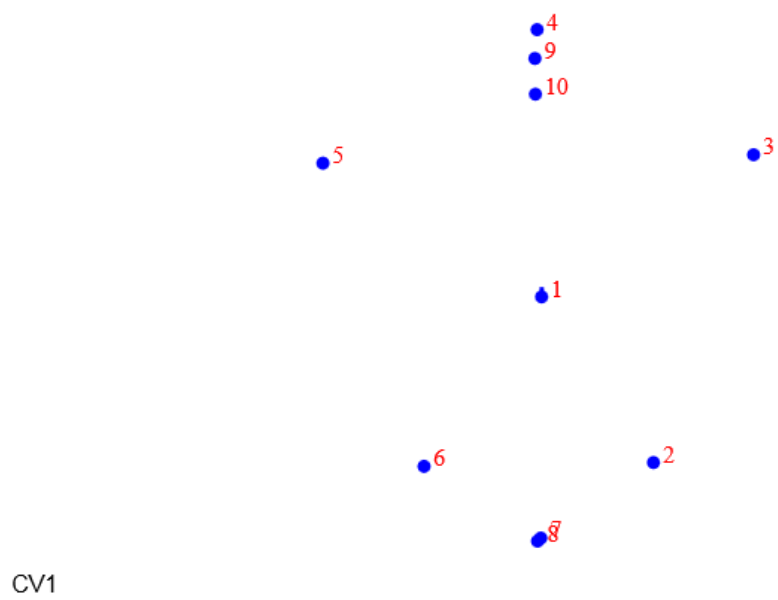
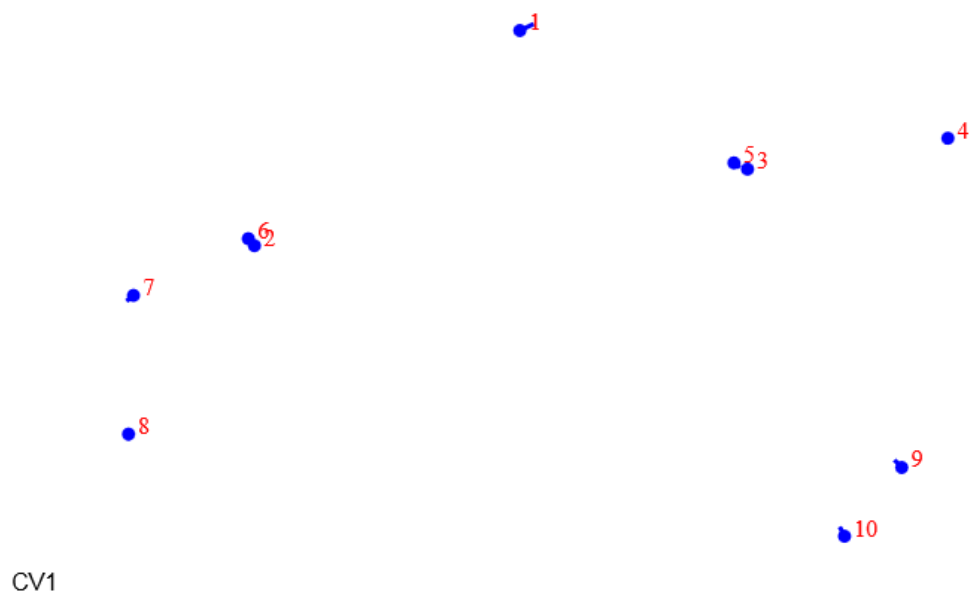
Data matrices in this dataset:

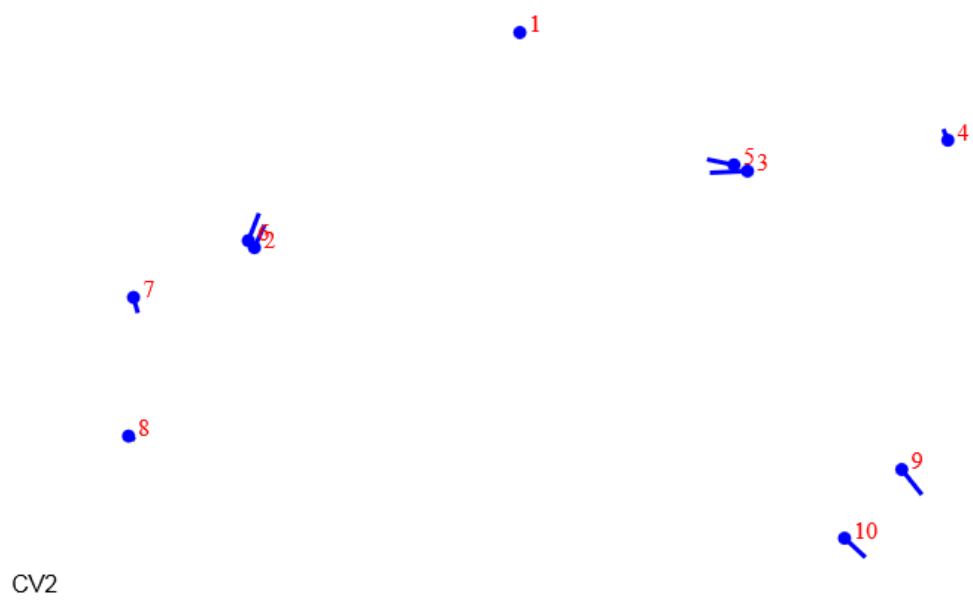
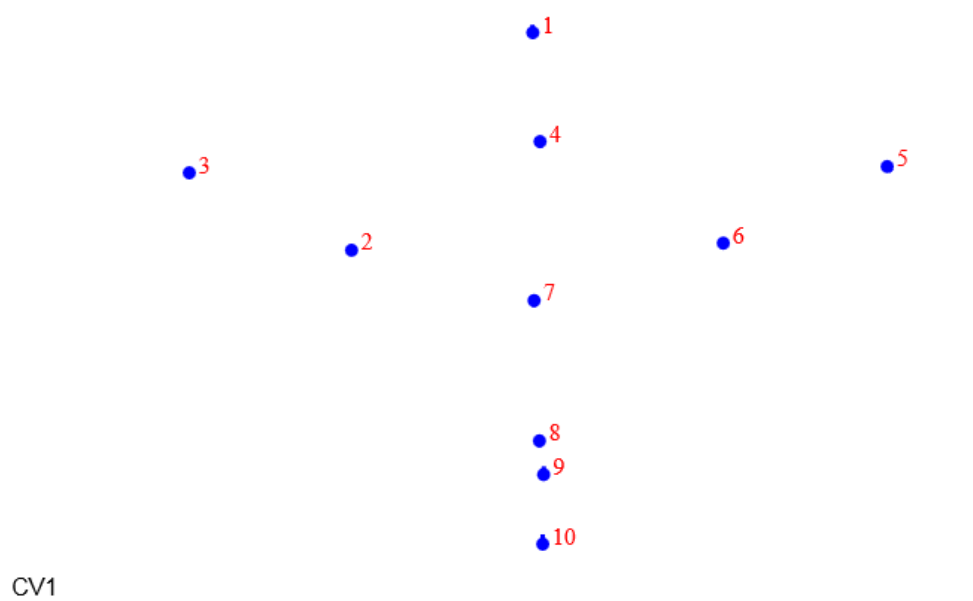
- CVA ..., scores
-

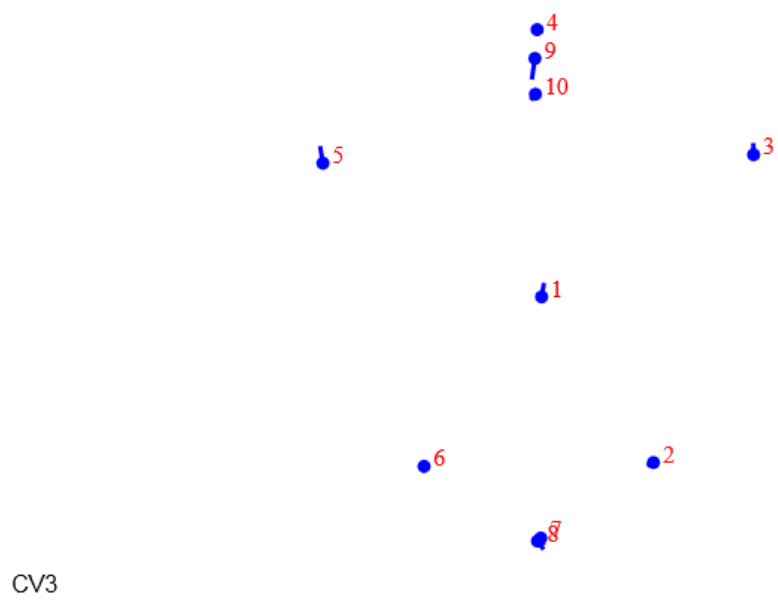
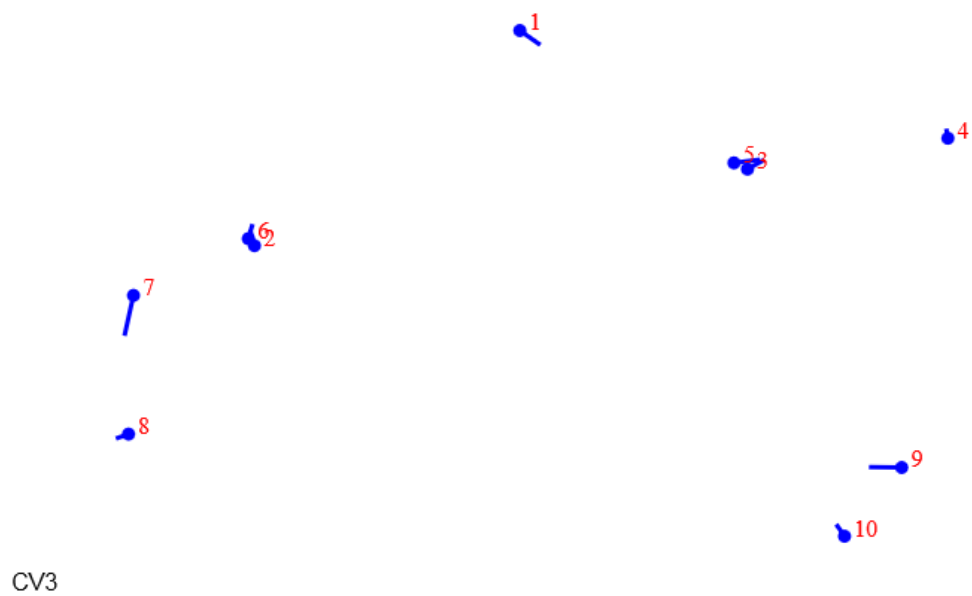


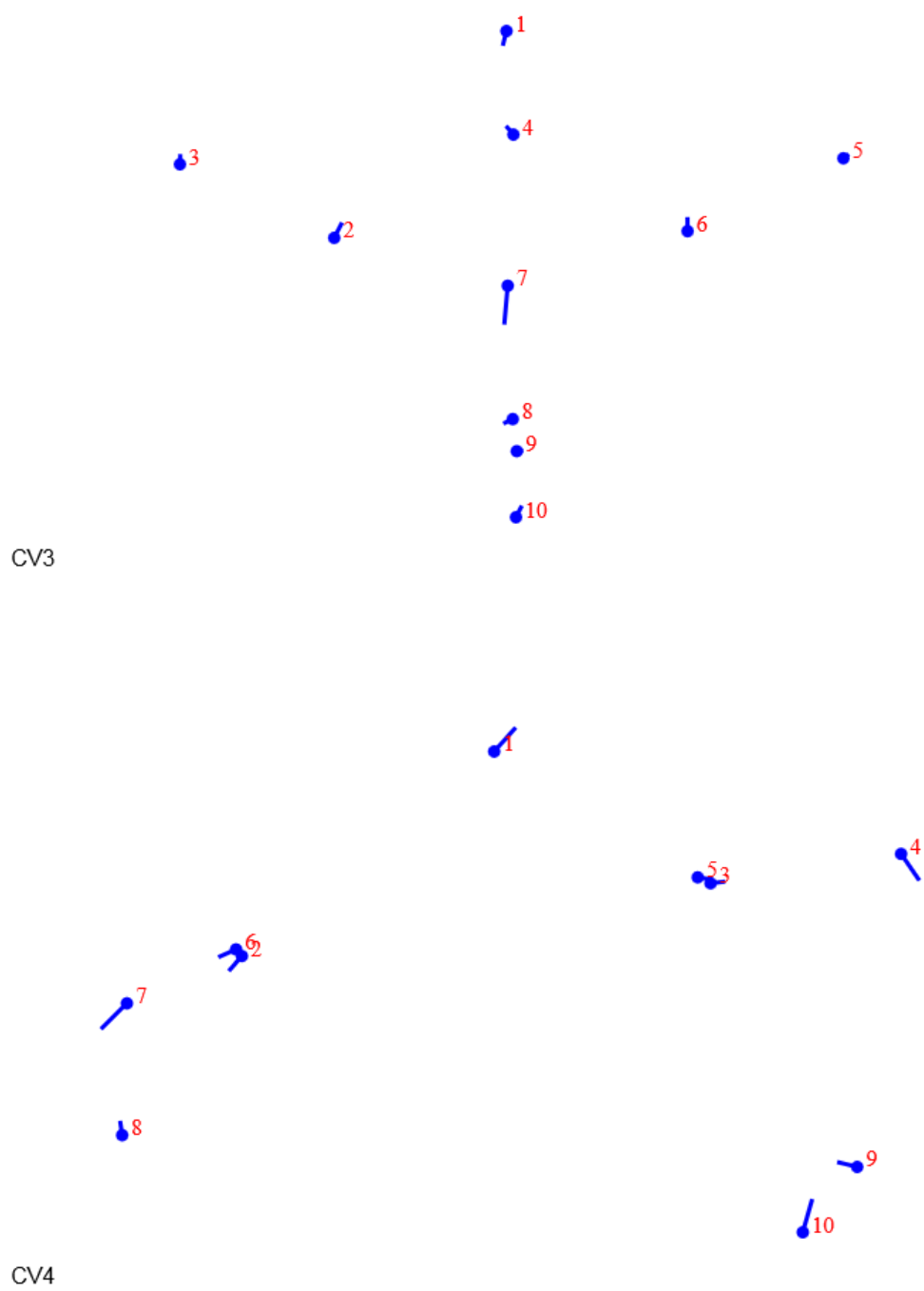


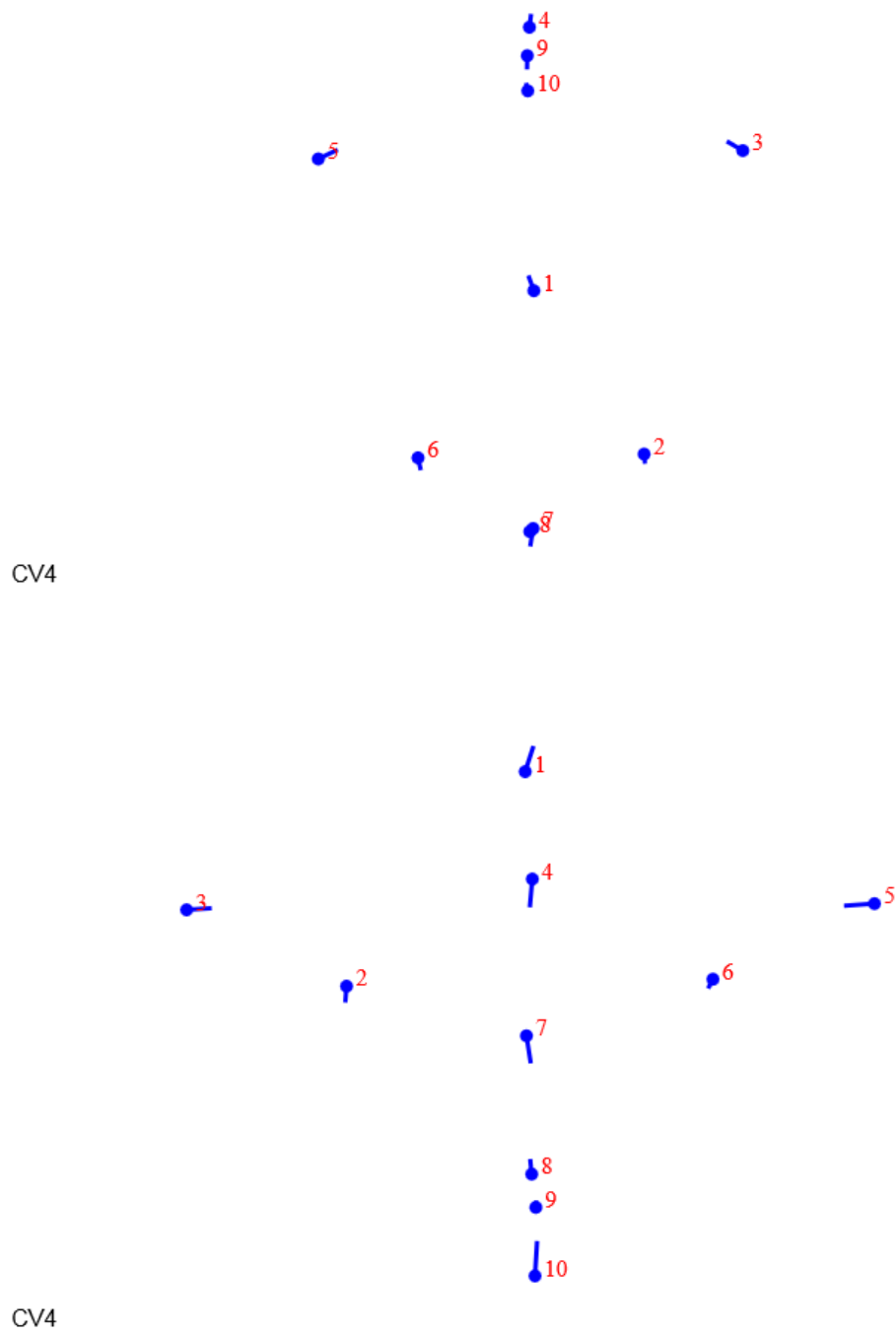












Appendix 8 – Part B

Canonical Variate Analysis – Mecaster fourneli by location

9 landmarks in 3 dimensions.

The dataset contains 36 observations, of which 28 are included for analyses.

Average shape:

Lmk.	Axis 1 (x)	Axis 2 (y)	Axis 3 (z)
1	-0.03035086	0.00146916	0.16087064
2	-0.23890581	-0.15549231	0.03412222
3	0.22037670	-0.29240446	0.06244405
4	0.39435070	0.00882337	0.05043652
5	0.19703999	0.29245942	0.05892821
6	-0.25013397	0.14763852	0.03489706
7	-0.32879943	0.00334844	-0.02277329
8	-0.29572848	-0.00987586	-0.15110230
9	0.33215116	0.00403371	-0.22782310

Data matrices in this dataset:

- CVA ..., scores

Groups	Observations
1. AL	23
2. PE	5

Variation among groups, scaled by the inverse of the within-group variation

	Eigenvalues	% Variance	Cumulative %
1.	3.66637347	100.000	100.000

Mahalanobis distances among groups:

	AL
PE	4.8176

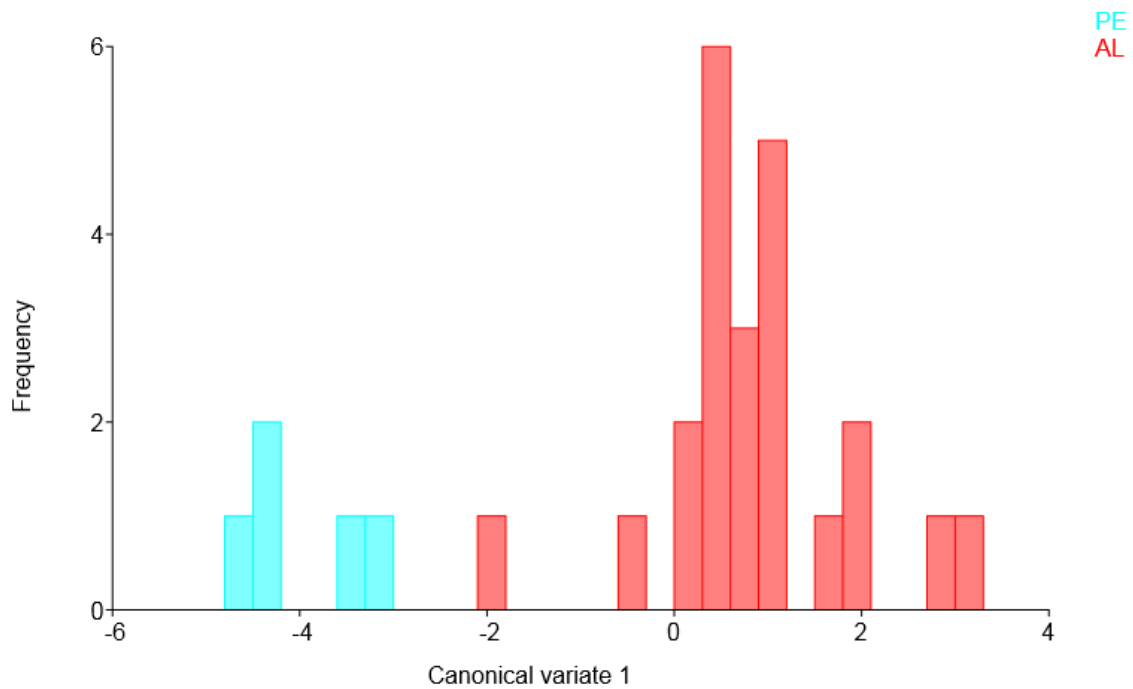
Procrustes distances among groups:

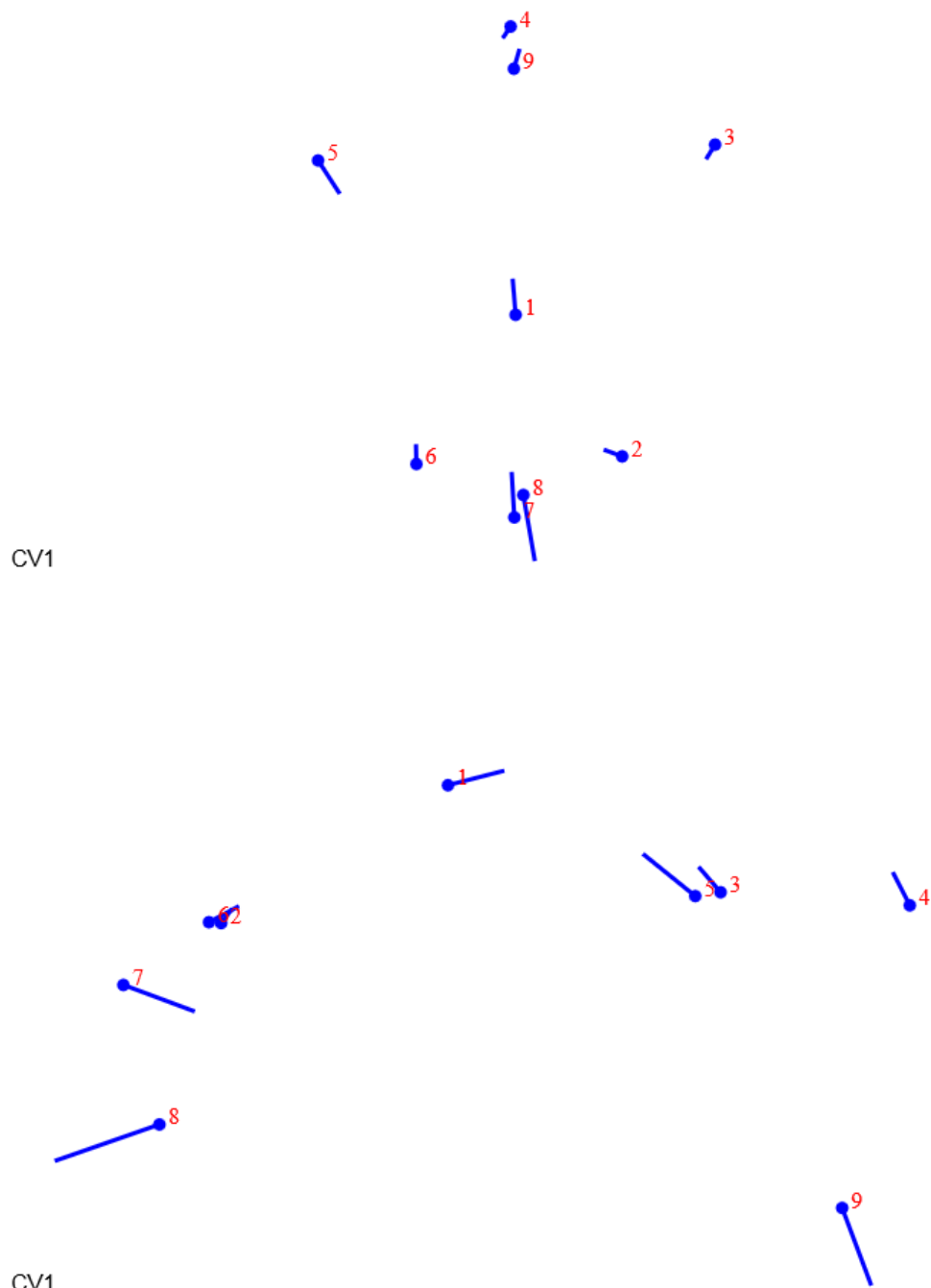
	AL
PE	0.0854

Canonical coefficients:

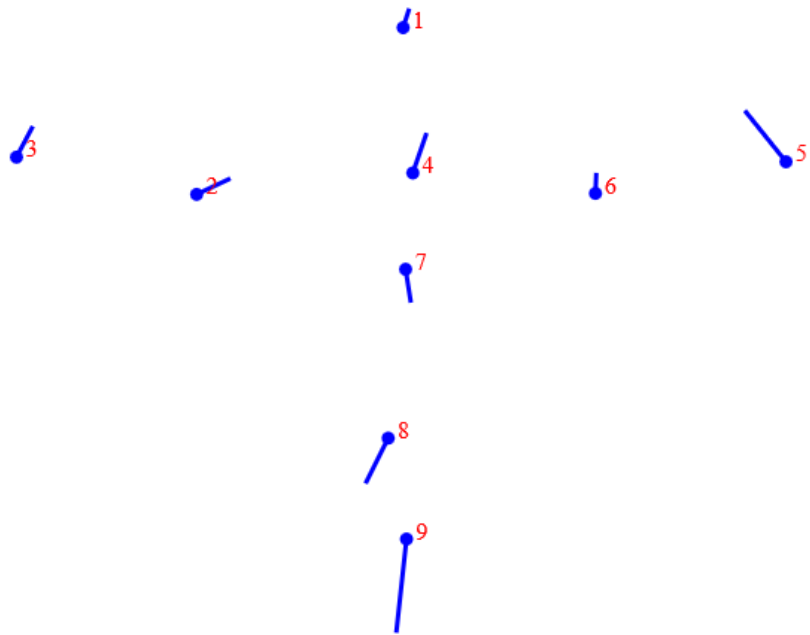
	CV1
x1	-4.8878
y1	77.5431
z1	102.4274

x2	50.1897
y2	-12.2938
z2	-217.2619
x3	-17.7541
y3	-120.0044
z3	108.8928
x4	-22.6725
y4	20.8648
z4	44.0814
x5	-60.5071
y5	-92.4713
z5	-150.4387
x6	97.5231
y6	104.8455
z6	227.6542
x7	-36.1891
y7	-12.6311
z7	-72.2393
x8	9.1981
y8	-64.0179
z8	18.6045
x9	-14.9003
y9	98.1651
z9	-61.7204





CV1



Appendix 9 – Part A

Discriminate Function Analysis : Mecaster batnensis

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- BR

Difference between means:

Procrustes distance: 0.06041257

Mahalanobis distance: 5.7786

T-square: 102.7464, P-value (parametric): 0.6990

Classification/misclassification tables

Group 1: AZ

Group 2: BR

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	8	8

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	3	2	5
Group 2	1	7	8

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- EG

Difference between means:

Procrustes distance: 0.07195478

Mahalanobis distance: 2.1432

T-square: 6.5617, P-value (parametric): 0.8916

Classification/misclassification tables

Group 1: AZ

Group 2: EG

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	4	1	5
Group 2	0	2	2

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	3	2	5
Group 2	2	0	2

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- NM

Difference between means:

Procrustes distance: 0.06066091

Mahalanobis distance: 3.0977

T-square: 23.9893, P-value (parametric): 0.8590

Classification/misclassification tables

Group 1: AZ

Group 2: NM

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	5	5

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	1	4	5

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- TX

Difference between means:

Procrustes distance: 0.08557926

Mahalanobis distance: 9.5400

T-square: 312.8543, P-value (parametric): 0.5581

Classification/misclassification tables

Group 1: AZ

Group 2: TX

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	11	11

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	11	11

Discriminant Function Analysis 'Discriminant function ...'

Comparison: BR -- EG

Difference between means:
 Procrustes distance: 0.04774167
 Mahalanobis distance: 2.5311
 T-square: 10.2505, P-value (parametric): 0.9630

Classification/misclassification tables

Group 1: BR

Group 2: EG

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	6	2	8
Group 2	0	2	2

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	3	8
Group 2	2	0	2

Discriminant Function Analysis 'Discriminant function ...'

Comparison: BR -- NM

Difference between means:
 Procrustes distance: 0.06565779
 Mahalanobis distance: 3.6026
 T-square: 39.9344, P-value (parametric): 0.8904

Classification/misclassification tables

Group 1: BR

Group 2: NM

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	8	0	8
Group 2	0	5	5

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	6	2	8
Group 2	2	3	5

Discriminant Function Analysis 'Discriminant function ...'

Comparison: BR -- TX

Difference between means:
 Procrustes distance: 0.06767306
 Mahalanobis distance: 9.1169
 T-square: 384.9654, P-value (parametric): 0.6017

Classification/misclassification tables

Group 1: BR

Group 2: TX

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	8	0	8
Group 2	0	11	11

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	6	2	8
Group 2	2	9	11

Discriminant Function Analysis 'Discriminant function ...'

Comparison: EG -- NM

Difference between means:
 Procrustes distance: 0.06709199
 Mahalanobis distance: 0.8972
 T-square: 1.1499, P-value (parametric): 0.9945

Classification/misclassification tables

Group 1: EG

Group 2: NM

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	1	1	2
Group 2	2	3	5

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	0	2	2
Group 2	1	4	5

Discriminant Function Analysis 'Discriminant function ...'

Comparison: EG -- TX

Difference between means:
 Procrustes distance: 0.07096129
 Mahalanobis distance: 4.5034
 T-square: 34.3203, P-value (parametric): 0.9128

Classification/misclassification tables

Group 1: EG

Group 2: TX

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	2	0	2
Group 2	0	11	11

From cross-validation:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	0	2	2
Group 2	2	9	11

Discriminant Function Analysis 'Discriminant function ...'

Comparison: NM -- TX

Difference between means:

Procrustes distance: 0.04521140

Mahalanobis distance: 4.9547

T-square: 84.3857, P-value (parametric): 0.8502

Classification/misclassification tables

Group 1: NM

Group 2: TX

From discriminant function:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	5	0	5
Group 2	0	11	11

From cross-validation:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	4	1	5
Group 2	1	10	11

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- BR

Difference between means:

Procrustes distance: 0.06041257

Mahalanobis distance: 5.7786

T-square: 102.7464, P-value (parametric): 0.6990

P-values for permutation tests (1000 permutation runs):

Procrustes distance: 0.0010

T-square: 0.0010

(Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: AZ

Group 2: BR

From discriminant function:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	5	0	5
Group 2	0	8	8

From cross-validation:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	3	2	5
Group 2	1	7	8

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- EG

Difference between means:

Procrustes distance: 0.07195478

Mahalanobis distance: 2.1432

T-square: 6.5617, P-value (parametric): 0.8916

P-values for permutation tests (1000 permutation runs):

Procrustes distance: 0.2090

T-square: 0.1090

(Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: AZ

Group 2: EG

From discriminant function:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	4	1	5
Group 2	0	2	2

From cross-validation:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	3	2	5
Group 2	2	0	2

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- NM

Difference between means:

Procrustes distance: 0.06066091

Mahalanobis distance: 3.0977

T-square: 23.9893, P-value (parametric): 0.8590

P-values for permutation tests (1000 permutation runs):

Procrustes distance: 0.0130

T-square: 0.0750

(Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: AZ

Group 2: NM

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	5	5

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	1	4	5

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AZ -- TX

Difference between means:

Procrustes distance: 0.08557926

Mahalanobis distance: 9.5400

T-square: 312.8543, P-value (parametric): 0.5581

P-values for permutation tests (1000 permutation runs):

Procrustes distance: <.0001

T-square: 0.0010

(Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: AZ

Group 2: TX

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	11	11

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	11	11

Discriminant Function Analysis 'Discriminant function ...'

Comparison: BR -- EG

Difference between means:

Procrustes distance: 0.04774167

Mahalanobis distance: 2.5311

T-square: 10.2505, P-value (parametric): 0.9630

P-values for permutation tests (1000 permutation runs):

Procrustes distance: 0.6300

T-square: 0.6350

(Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: BR

Group 2: EG

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	6	2	8
Group 2	0	2	2

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	5	3	8
Group 2	2	0	2

Discriminant Function Analysis 'Discriminant function ...'

Comparison: BR -- NM

Difference between means:

Procrustes distance: 0.06565779

Mahalanobis distance: 3.6026

T-square: 39.9344, P-value (parametric): 0.8904

P-values for permutation tests (1000 permutation runs):

Procrustes distance: 0.0040

T-square: 0.0040

(Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: BR

Group 2: NM

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	8	0	8
Group 2	0	5	5

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	6	2	8
Group 2	2	3	5

Discriminant Function Analysis 'Discriminant function ...'

Comparison: BR -- TX

Difference between means:
 Procrustes distance: 0.06767306
 Mahalanobis distance: 9.1169
 T-square: 384.9654, P-value (parametric): 0.6017
 P-values for permutation tests (1000 permutation runs):
 Procrustes distance: <.0001
 T-square: <.0001
 (Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: BR

Group 2: TX

From discriminant function:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	8	0	8
Group 2	0	11	11

From cross-validation:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	6	2	8
Group 2	2	9	11

Discriminant Function Analysis 'Discriminant function ...'

Comparison: EG -- NM

Difference between means:
 Procrustes distance: 0.06709199
 Mahalanobis distance: 0.8972
 T-square: 1.1499, P-value (parametric): 0.9945
 P-values for permutation tests (1000 permutation runs):
 Procrustes distance: 0.3430
 T-square: 0.9680
 (Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: EG

Group 2: NM

From discriminant function:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	1	1	2
Group 2	2	3	5

From cross-validation:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	0	2	2

Group 2 1 4 5

Discriminant Function Analysis 'Discriminant function ...'

Comparison: EG -- TX

Difference between means:
 Procrustes distance: 0.07096129
 Mahalanobis distance: 4.5034
 T-square: 34.3203, P-value (parametric): 0.9128
 P-values for permutation tests (1000 permutation runs):
 Procrustes distance: 0.1560
 T-square: 0.0450
 (Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: EG

Group 2: TX

From discriminant function:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	2	0	2
Group 2	0	11	11

From cross-validation:

True Group	Allocated to		Total
	Group 1	Group 2	
Group 1	0	2	2
Group 2	2	9	11

Discriminant Function Analysis 'Discriminant function ...'

Comparison: NM -- TX

Difference between means:
 Procrustes distance: 0.04521140
 Mahalanobis distance: 4.9547
 T-square: 84.3857, P-value (parametric): 0.8502
 P-values for permutation tests (1000 permutation runs):
 Procrustes distance: 0.0080
 T-square: 0.0090
 (Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: NM

Group 2: TX

From discriminant function:

True Group	Allocated to
------------	--------------

Group	Group 1	Group 2	Total
Group 1	5	0	5
Group 2	0	11	11
From cross-validation:			

True	Allocated to		Total
Group	Group 1	Group 2	
Group 1	4	1	5
Group 2	1	10	11

Appendix 9 – Part B

Discriminate Function Analysis – Mecasterourneli

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AL -- PE

Difference between means:

Procrustes distance: 0.08484301

Mahalanobis distance: 13.2122

T-square: 576.8129, P-value (parametric): 0.3006

Classification/misclassification tables

Group 1: AL

Group 2: PE

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	19	0	19
Group 2	0	4	4

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	13	6	19
Group 2	3	1	4

Discriminant Function Analysis 'Discriminant function ...'

Comparison: AL -- PE

Difference between means:

Procrustes distance: 0.08484301

Mahalanobis distance: 13.2122

T-square: 576.8129, P-value (parametric): 0.3006

P-values for permutation tests (1000 permutation runs):

Procrustes distance: <.0001

T-square: 0.3020

(Note: The permutation test using the T-square statistic is equivalent to a test using Mahalanobis distance.)

Classification/misclassification tables

Group 1: AL

Group 2: PE

From discriminant function:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	19	0	19
Group 2	0	4	4

From cross-validation:

True	Allocated to		
Group	Group 1	Group 2	Total
Group 1	13	6	19
Group 2	3	1	4

Appendix 10

Information Regarding Sample Specimens used in this Study

Samples used in this study are listed by USNM sample number or USNM acquisition numbers (in gray). Species identifications, locations (country, state, and county or city), geologic time period, stratigraphic formation or locality are information from the USNM databases, except for the geologic time period for the Peru samples which comes from Willard 1966. The number of samples used is listed; however, these numbers do not reflect the total number of available samples in the USNM collection.

USNM	Species	Country	State	County or City	Time Period	Stratigraphy or Locality	Number of Samples Used
108395	<i>M. batnensis</i>	Brazil	Sergipe		Cenomanian	Bom Jesus	1
108396	<i>M. batnensis</i>	United States	Texas			Woodbine Group: Eagle Ford Shale	1
29246	<i>M. fourneli</i>	Algeria		Tamarins	Senonian		1
308812	<i>M. fourneli</i>	Peru			Senonian	Huanguerilla	6
308812	<i>M. fourneli</i>	Peru			Senonian	Chamoya	1
308812	<i>M. fourneli</i>	Peru			Senonian	Manseriche	1
308812	<i>M. fourneli</i>	Peru			Senonian	Pachitea	1
31097	<i>M. fourneli latigranda</i>	Algeria		Tebessa	Turonian		1
31102	<i>M. batnensis lorioli</i>	Algeria*			Cenomanian		1
449382	<i>M. batnensis</i>	Brazil	Sergipe		Cenomanian	Bom Jesus	1
449383	<i>M. batnensis</i>	Brazil	Sergipe		Cenomanian	Bom Jesus	1
449385	<i>M. batnensis</i>	Brazil	Sergipe		Cenomanian	Bom Jesus	1
449388	<i>M. batnensis</i>	Brazil	Sergipe		Cenomanian	Bom Jesus	1
468531	<i>M. batnensis</i>	United States	New Mexico	Valencia	Upper Cenomanian	Mancos Shale	1
468535	<i>M. batnensis</i>	United States	New Mexico	Valencia	Upper Cenomanian	Mancos Shale	1
468546	<i>M. batnensis</i>	United States	Arizona				1
468547	<i>M. batnensis</i>	United States	Arizona				1
468548	<i>M. batnensis</i>	United States	Arizona				1
468554	<i>M. batnensis</i>	United States	Arizona				1
468564	<i>M. batnensis</i>	United States	New Mexico	McKinley	Upper Cenomanian		4
468873	<i>M. batnensis</i>	United States	Arizona				1
468876	<i>M. batnensis</i>	United States	Texas		Upper/Late Turonian	Woodbine Group: Eagle Ford Shale	4
468877	<i>M. batnensis</i>	United States	Texas		Upper/Late Turonian		5
468878	<i>M. batnensis</i>	United States	Texas		Upper Turonian	Woodbine Group: Eagle Ford Shale	1
468879	<i>M. batnensis</i>	Brazil	Sergipe		Cenomanian		5
468883	<i>M. batnensis</i>	United States	Texas				1

Sample specimen list continued

468889	<i>M. fourneli</i>	Algeria			Upper Santonian		4
468891	<i>M. fourneli</i>	Algeria			Upper/Late Campanian		1
468895	<i>M. fourneli</i>	Algeria			Upper/Late Coniacian		1
468896	<i>M. fourneli</i>	Algeria			Upper/Late Coniacian		2
468897	<i>M. fourneli</i>	Algeria			Upper/Late Santonian		2
468898	<i>M. fourneli</i>	Algeria			Upper/Late Coniacian		7
468899	<i>M. fourneli</i>	Algeria			Upper/Late Coniacian		8
468939	<i>M. batnensis</i>	Palestine			Upper/Late Cenomanian		1
468944	<i>M. batnensi cf.</i>	Egypt		Sinai	Upper/Late Cenomanian		2
231242	<i>M. batnensis</i>	Mexico			Lower Cenomanian	J68 – Indidura Fm.	1

VITA

Ryan Oliver Roney was born in 1979 in Boise, Idaho. He attended Cross Keys High School in Atlanta, Georgia and graduated from Collin's Hill High School in Suwanee, Georgia in 1997. He was a missionary in Fortaleza, Brazil from 1998 to 2000. He earned a Bachelor's of Arts in Spanish from the University of West Georgia in 2007 and a Bachelor's of Science in geology from Georgia Southwestern State University in 2011. He is currently a candidate for a Master's of Science in geology from the University of Tennessee, and will begin PhD studies at the University of Tennessee immediately upon completion of the Master's program. Ryan is married, and, at the time of this publication, is the father of 1.5children.