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Latitude and environmental pressure: their impact on carapace morphology in three species of fiddler crabs (genus *Uca*) across the Atlantic Ocean

Katherine Susannah Mary Thomas
University of Northern Iowa

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LATITUDE AND ENVIRONMENTAL PRESSURE:
THEIR IMPACT ON CARAPACE MORPHOLOGY IN THREE SPECIES OF FIDDLER
CRABS (GENUS *UCA*) ACROSS THE ATLANTIC OCEAN

A Thesis Submitted
in Partial Fulfillment
of the Requirements for the Designation
University Honors with Distinction

Katherine Susannah Mary Thomas

University of Northern Iowa

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ABSTRACT

Among semi-terrestrial fiddler crabs, three species from the subgenus *Uca* (*sensu stricto*) appear to be basal in the phylogeny of the genus: *Uca major* (Herbst 1782-1804), *Uca maracoani* (Latreille 1802-1803) and *Uca tangeri* (Eydoux 1835). These species evolved vicariantly as tectonic plates separated to form the Atlantic Ocean. Currently, the three species, found in Africa, South America, and the Caribbean, exhibit a high affinity for their respective tectonic plates. Inter- and intra-specific variation in carapace shape was assessed using geometric morphometrics to analyze 12 surface landmarks in the three species. In 314 female specimens, surficial coordinates were superimposed, standardized, and subjected to canonical variance (CVA) and principal component (PCA) analysis, after which the three species form distinct clusters. Within each species, there are clear differences among populations from northern to southern latitudes. In *Uca maracoani*, there is a significant correlation between carapace shape and certain environmental factors, such as biotope, salinity, and substrate. As it has not been demonstrated that there is extensive, structured geographic variation in the population genetics for *Uca*, this polymorphism is likely a result of environmental pressures, i.e., ecophenotypy.

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INTRODUCTION

Fiddler crabs (genus *Uca*) are crustaceans found world-wide in habitats along the coast line of most temperate and tropical regions (Crane 1975). Planktonic larval stages consisting of several zoea and megalopae reside in bays and coastal oceans until they reach maturity (Hyman 1922). Then the juveniles seek an appropriate environment to settle and transform into small crabs (O'Connor and Judge 2004, Behum et al. 2004, Borgianini et al. 2012). Adults occupy burrows on sand or muddy beaches, marshes, and mangroves. In the temperate-tropical Atlantic Ocean alone there are 21 described species (Bienlich & von Hagen 2006), including *Uca major* (Herbst 1782), *Uca maracoani* (Latreille 1802), and *Uca tangeri* (Eydoux 1835).

Since the drift of tectonic plates over many millions of years can drive the isolation of populations within a single species (Cox and Moore 2010), ancestors are expected to have diverged as they separated and experienced different environmental pressures or genetic drift (i.e. vicariant evolution). "Narrow-fronted" fiddler crabs, including species studied here, of the Atlantic Ocean may have evolved from a common ancient progenitor (Strumbauer et al. 1996, Rosenberg 2001). In addition, they appear limited in distribution to different tectonic plates (Figure 1). *U. major* (Figure 2A) is found in the Caribbean Sea and overlaps marginally with *U. maracoani* (Figure 2B), which is found along the eastern South American coast from Venezuela to southern Brazil (Thurman et al. 2013). In the eastern Atlantic, *U. tangeri* (Figure 2C) ranges from southern Portugal to Angola. Across their ranges, remote populations of each species live in a wide variety of environments with very different physical and biological composition. It is generally appreciated that variation in biological structure is a product of both genetic and environmental factors. Alone, the impact of environmental pressure(s) on shape or morphology is known as ecophenotypic variation.

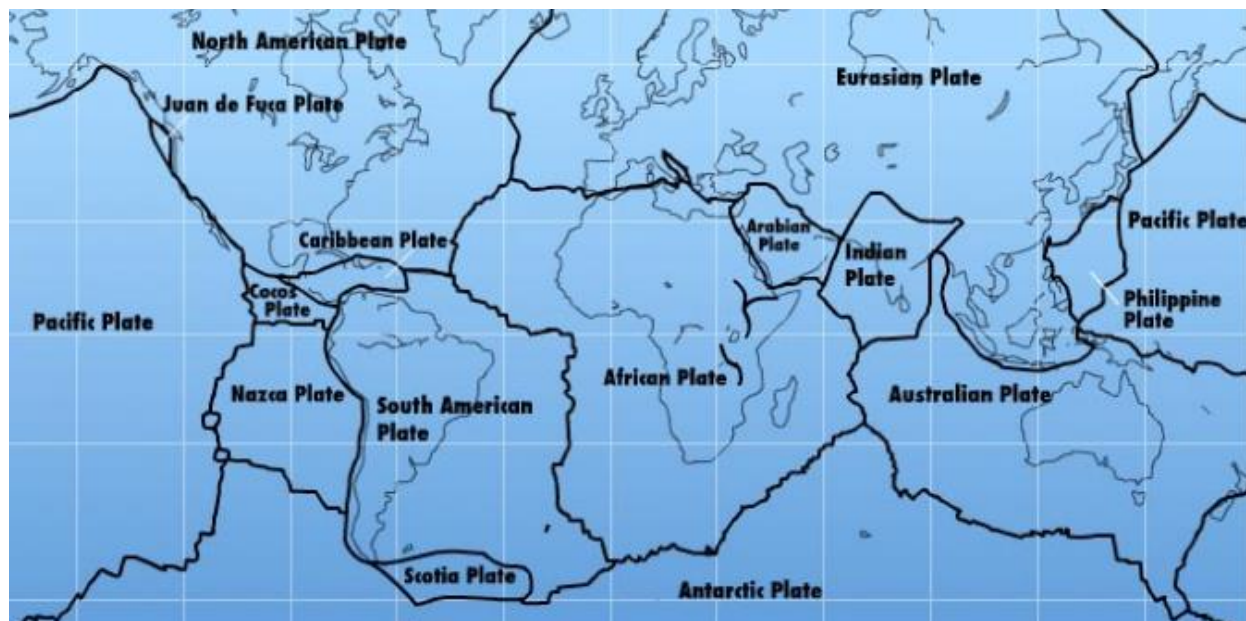


Figure 1. A map of current tectonic plate positions.



Figure 2A. *Uca major*



Figure 2B. *Uca maracoani*



Figure 2C. *Uca tangeri*

“Ecophenotypy” is a likely cause of carapace variance across geographically separated populations in several species of fiddler crabs (Hopkins and Thurman 2010, Hampton et al. 2014, Wieman et al. 2014).

The object of this study was to analyze carapace shape in the narrow-fronted fiddler crab species from the Atlantic Ocean using geometric morphometrics. Using only females, carapace shape was compared among three closely-related species from the subgenus *Uca* (*sensu stricto*); *U. major*, *U. maracoani*, and *U. tangeri*. In addition, variation was examined across the geographic distribution in each species. Specimens of *U. major* were compared from populations in Mexico, the Bahamas, Jamaica, Colombia, and Trinidad and Tobago. Additionally, *U. maracoani* specimens from Trinidad and Tobago, Guyana, and Brazil were used in this analysis. Specimens of *U. tangeri* originated in populations from Portugal, Nigeria, and Angola. Based on carapace shape analysis, all three species were morphologically distinct, indicating significant interspecific variation. Although some degree of variation within each species is related to size (i.e. allometric variation), most intraspecific divergence correlated with latitude in the three species (i.e. environmental variation). In the case of *U. maracoani*, habitat data describing salinity, substrate, and biotope were available for each site of collection in Brazil. In part, morphological divergence among *U. maracoani* populations appears to be associated with specific environmental pressures. Since genetic variation among populations in several species of fiddler crabs (including *U. maracoani*) is known to be very low and geographically unstructured (Silva et al. 2010, Wieman et al. 2014), variation observed within species is most likely related to habitat pressure.

LITERATURE REVIEW

Fiddler crabs (genus *Uca* Leech 1814) have been studied extensively. Based on a Google Scholar search there are more than 11,300 articles and books describing various aspects of these crabs. Currently, approximately 100 species are known to inhabit protected bays, lagoons, and riverbanks around the world. Crabs of this genus are considered amphibious because the adult and larval stages are spent in different habitats. After fertilization, female fiddler crabs carry the developing embryos on their abdomen (Hyman 1922). The zoea larvae are released into a bay or ocean during high tides and carried away by coastal and oceanic currents. After a few weeks in the plankton, the zoeae transform into shrimp-like megalopae. The megalopae return to the estuary seeking an appropriate habitat where they become young crabs and grow into adults. Most frequently, the juveniles mature in environments inundated daily by the tides (Forward et al. 2001; Borgianini et al. 2012). Consequently, parents and their immediate offspring are not likely to occupy the same location.

Several conflicting phylogenies exist for genus *Uca* (*sensu lato*). Sturmbauer et al. (1996) place *U. tangeri* at the base of the *Uca* phylogeny. Levinton et al. (1996) agreed that subgenus *Uca* and subgenus *Afruca* (i.e. *U. tangeri*) are the most ancestral clades and rejected an Indo-Pacific center of origin theory, proposed by Crane (1975). Later, Rosenberg (2001) also placed *U. tangeri* at the base of the phylogeny, with *U. major* and *U. maracoani* being more closely related. He moved *U. tangeri* into the subgenus *Uca* (*sensu stricto*) eliminating the subgenus *Afruca*. Using the fossil record, Dominguez-Alonso (2008) also supports a basal position of *U. tangeri*. Nine subgenera represent all species in the genus *Uca* (*sensu lato*) (Rosenberg 2001). Historically, the genus is considered to be divided among two forms based on carapace shape (Rathbun 1918). If the intraocular distance (between eyestalks) is less than

25% of the carapace width, the species is considered “narrow-fronted”. On the other hand, if the intraocular distance is greater than 25%, the species is called “broad-fronted”. Among the subgenera, the subgenus *Uca (sensu stricto)* appears to have the most archaic species (Rosenberg 2001; Dominguez-Alonso 2008) three of which are endemic to tropical shores of the Atlantic.

Jocelyn Crane (1975) described the three species from the subgenus *Uca (sensu stricto)* in her extensive tome on the genus *Uca (sensu lato)*. For fiddler crabs in the Atlantic Ocean, *Uca major*, found across the Caribbean and Mexico (Barnwell and Thurman 1984, Utrera-López and Capistrán-Barradas 2013), appears to be “uncommon,” and no large population of the species has ever been recorded. This narrow-fronted species ranges across the West Indies, Panama, Venezuela, and, perhaps, French Guiana living just above the low tide mark on substrates ranging from muddy sand to sandy mud. It is usually found on salt flats that are nearly cut off from open water (Crane 1975). The description of this species is credited to Herbst in 1782. Another species, *Uca maracoani*, is also narrow-fronted but is found predominately along the Brazilian coastline in low-tide mud near mangroves. *U. maracoani* was first described by Latreille in 1802. The third narrow-fronted Atlantic species, *Uca tangeri*, is found along the eastern Atlantic coastline from southern Spain and Portugal to Angola. It has recently been reported in the Canary Islands (Castro 2012). This species lives near mouths of streams and rivers on muddy sand. It is the only member of the genus found in Europe and West Africa. The first accurate description of this fiddler crab originates from Eydoux in 1835.

The description and naming of the three narrow-fronted fiddler crabs cannot go without comment. Although these are among the oldest fiddler crabs known to taxonomists, their history is fraught with error and confusion. The first described species called *Cancer vocans major* by Herbst (1782) was considered by Leech (1814) as the type species for the genus *Uca (sensu*

lato). Their descriptions were based, in part, on an illustration of a specimen called *Cancer Uka una, Brasiliensibus* published by Seba in 1759 (*Locupletissimi Rerum Naturalium Thesauri* 3: 44, pl. 18, fig. 8). Later, Bott (1973) argued effectively that the figures of Seba are not *Uca major* as the early carcinologist believed but rather *Uca tangeri* from the Atlantic coast of Africa. The origin of the Seba specimen, Brazil, was apparently a clerical error perpetuated by the museum curators. Since the original specimens of both Seba and Herbst have been lost to science, Holthuis (1979) designated an “appropriate” specimen at the Muséum National d’Histoire Naturelle (MNHN), Paris, as the new type-example for the species (neotype) for *U. major*. Unfortunately, the specimen was allegedly collected at Cayenne, French Guiana, in 1837 where *U. major* is not known to occur at the present. In 1648, Marcgrave presented a drawing of *Cancer palustris cunicolas, maracoani* from the northeast coast of Brazil in a manuscript on his 1638-1644 expedition to South America. Later Latreille (1802-1803) described it as what we now call *Uca maracoani* which is distributed only along the Atlantic coast of South America. Coincidentally, the type specimen at MNHN was also collected at Cayenne in 1837. The original illustration and location for this species are clearly accurate, but previous reports of the species in Jamaica (Sloane 1725, Rathbun 1918) appear to be misidentified *U. major* (Barnwell 1986). And finally, due to the original misidentification of the Seba specimen, *Uca tangeri* should actually be known as *Uca major*. Thankfully, this confusing situation was resolved by Holthuis (1979) and the current status of *U. major* and *U. tangeri* was established by the International Commission on Zoological Nomenclature, London (1983). Obviously, it has been difficult even for professional taxonomists to correctly distinguish preserved specimens of the three narrow-fronted species from each other.

Based on analysis of 16s ribosomal DNA, Strumbauer et al. (1996) found the subgenus *Uca (sensu stricto)* to be the most ancestral clad among the nine subgenera proposed by Crane (1975). Due to the degree of genetic divergence of *U. tangeri* from the other “American” members of the subgenus, trans-Atlantic migration of American species to Africa by plankton in the ocean currents seems unlikely. Thus based on the current global distribution of the subgenus, the authors suggested that the ancestors of all fiddler crabs probably arose in the “proto-Atlantic” and their descendants separated by continental drift. Since the oldest fossils of *Uca (sensu lato)* are from strata in the Americas (Rathbun 1926, Brito 1993, Dominguez-Alonso 2008), their hypothesis is supported by paleontology. Further, the derived clads (subgenera) appear to have diverged from the ancestral subgenus *Uca (sensu stricto)* by the Early Miocene, more than 25 million years ago (MYA). The more recently derived American-Indo-Pacific clades appear to have split from each other by the middle Miocene, 17 MYA. Consequently, the first fiddler crabs probably appeared as a component in primitive mangrove communities appearing during the early Eocene, about 58 MYA. Fossil records for close relatives to the fiddler crabs are known from Paleocene, 65-60 MYA (Beinlich and von Hagen 2006). We suspect, over sufficient time, ancestral populations on different plates could diverge into distinct species if gene flow is limited or blocked (i.e. evolution by vicariance). Beinlich and von Hagen (2006) postulate a primary center of dispersal as a combination of the Indo-West Pacific region, the Tethys Sea and proto-Atlantic Ocean from the Upper Mesozoic to Lower Miocene (Salmon and Zucker 1987), and the Americas (Levinton et al. 1996 and Strumbauer et al. 1996). Consequently, patterns of evolution among the early *Uca (sensu lato)* in the proto-Atlantic may be related to the separation and spread of continental plates.

An understanding of tectonic movement is essential to predicting evolutionary trajectories among the *Uca* (*sensu stricto*). Formation of the Atlantic Ocean began around 140 million years ago (Rayment and Tait 1972). Formation of the Atlantic Ocean via seafloor spreading between the American and African/Eurasian tectonic plates (Figure 1) began around 185 million years ago. According to Keigwin (1982), the “salinity of the Caribbean surface waters began increasing four million years ago... in concert with changing tectonic, climatic, and biogeographic patterns.” This correlates with Ibaraki’s (1997) assertion that the closing of the Central American Seaway 3.7-3 million years ago caused an increase in coastal upwelling in the Southeast Pacific and an abrupt cooling of Ecuador’s coastal surface waters. In addition, the slow closing of the Panamanian seaway seems to have stimulated an increase in mollusk diversity on the Caribbean plate as opposed to a mass extinction as previously proposed (Jackson et al. 1993). These high extinction rates were balanced by accelerated evolutionary rates following the Pliocene era (Allmon et al. 1993). Others have suggested that the seaway closure caused staggered or progressive isolation rather than an instantaneous isolation of trans-Panamanian biota. This has been confirmed by genetic analysis (Knowlton et al. 1993).

There is an extensive literature on size variation in *Uca* (*sensu lato*). Fiddler crabs have been studied morphologically since 1901 when Robert Yerkes published a study on *Gelasimus pugilator* (now known as *Uca* (*Leptuca*) *pugilator* Bosc). Male fiddler crabs are characterized by their asymmetry between their major and minor claws. As such, much of the earlier research revolves around claw variation. Thomas Morgan published numerous papers about secondary characteristics and asymmetrical variation in fiddler crabs (1920, 1923a, 1923b). In this same time period, Julian Huxley was also writing about variation within species (1924). This was instrumental in the development of Huxley’s famous allometric equation ($y = kx^a$). Nearly fifty

years later, Miller (1973) continued to study fiddler crab asymmetry. In 1997, Michael Rosenberg described the evolutionary differences between the major and minor claws in fiddler crabs and found that the larger claw is not simply an allometric projection of the smaller claw. He proposed that the major cheliped was a product of sexual-selection to enhance courtship and combat effectiveness.

One source of variation in any population may be derived from genetics. The few available papers on this subject relevant to fiddler crabs reject this hypothesis. Using molecular techniques, Silva et al (2010) determined that there appeared to be “extensive gene flow among mangroves along the coast” resulting in low gene diversity and a lack of genetic structure across populations of *U. annulipes* in east Africa. More recently, Laurenzano (2012, 2013) found a similar lack of gene diversity and phylogeographic structure in two species of fiddler crabs (*Uca Minuca rapax* and *Uca Leptuca uruguayensis*) from the Atlantic coast of South America. However, Caribbean populations of *Uca rapax* diverged genetically from South American populations. In an extensive molecular study of *U. maracoani*, Wieman et al. (2013) found little genetic diversity across its geographic range in Brazil. Consequently, genetic diversity does not appear to contribute significantly to geographic variation in any species of fiddler crab.

Few published studies have addressed intraspecific morphological variation in fiddler crabs. Rosenberg (1997) studied variation in cheliped shape in a population of *Uca Minuca pugnax* from New England. Silva et al (2010) examined carapace and cheliped shape along with molecular genetic variation in *Uca Austrauca annulipes*. They found no significant intraspecific variation across the species’ range in east Africa. On the other hand, Hopkins and Thurman (2010) studied carapace morphology in eight species of fiddler crabs from the Gulf of Mexico. They found different species to display various degrees of intraspecific variation. In a more

recent study, Hampton et al. (2013) found distinct intraspecific differences in carapace shape for population along the northern and southern coast of Brazil. Consequently, *Uca (sensu stricto)* from the Atlantic Ocean appear to be an excellent species for both studies of interspecific and intraspecific phylogeographic patterns of variation.

For this project, carapace structural variation was analyzed in three narrow-fronted fiddler crabs from the subgenus *Uca (sensu stricto)* using geometric morphometrics. Specimens were obtained from several locations across the geographic range of each species in the Atlantic Ocean. From this study, each *Uca* is clearly distinct in morphospace. The structural relation among the three species appears to be predicted by phylogeny. Within each species, allometric variation due to size and/or growth could be distinguished from variation associated with distribution. Since a complete series of environmental measurements is available for *U. maracoani*, carapace shape appears to vary with certain physical factors in this species. This is the first study to document quantitatively both intra- and inter-specific variation in the basal clade of fiddler crabs from the Atlantic Ocean.

MATERIALS AND METHODS

SAMPLING

According to the literature, *Uca major* is known to range throughout the Caribbean into the southern Gulf of Mexico (Crane 1975, Barnwell and Thurman 1984, Utera-Lopez and Capistran-Barradas 2013). *Uca maracoani* is a South American species, with some overlap with *U. major* in Venezuela and Trinidad in the north (von Hagen 1970), and throughout Brazil along the eastern coastline of the continent. *Uca tangeri* is found on the West African coast as far north as Spain and Portugal to as far south as Angola. To represent the distributions of the three species, crab specimens were collected from twenty-six localities along the coasts of Brazil, Mexico, Angola, Nigeria, Portugal, and the Caribbean (Figure 3). Field work in Brazil was authorized by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA, permit nos. 2009/185559-1 and 2010/23976-1) for localities between Amapá (AP) and Santa Catarina (SC). Fifteen locations were sampled across the states of Amapá, Bahia (BA), Ceara (CE), Espirito Santo (ES), Maranhão (MA), Paraná (PR), Pernambuco (PE), Rio de Janeiro (RJ), and São Paulo (SP). Sites were chosen by convenience of littoral habitats by road, track, or boat, which may allow for sampling bias. Additionally, habitat characteristics were recorded at time of collection (salinity and substrate).

Samples were also borrowed from the Smithsonian Institution National Museum of Natural History (Table 1). Localities for *U. major* were Trinidad, Campeche Bay, and Kingston. *U. maracoani* samples from the Smithsonian came from Trinidad and Georgetown, while specimens of *U. tangeri* came from Angola, Nigeria, and Portugal. Additional samples of *Uca major* (Isla San Andres, Colombia), *U. tangeri* (Spain and Morocco) and *U. maracoani* (Pará and BA, Brazil) provided by Frank H. Barnwell, University of Minnesota (Table 1).

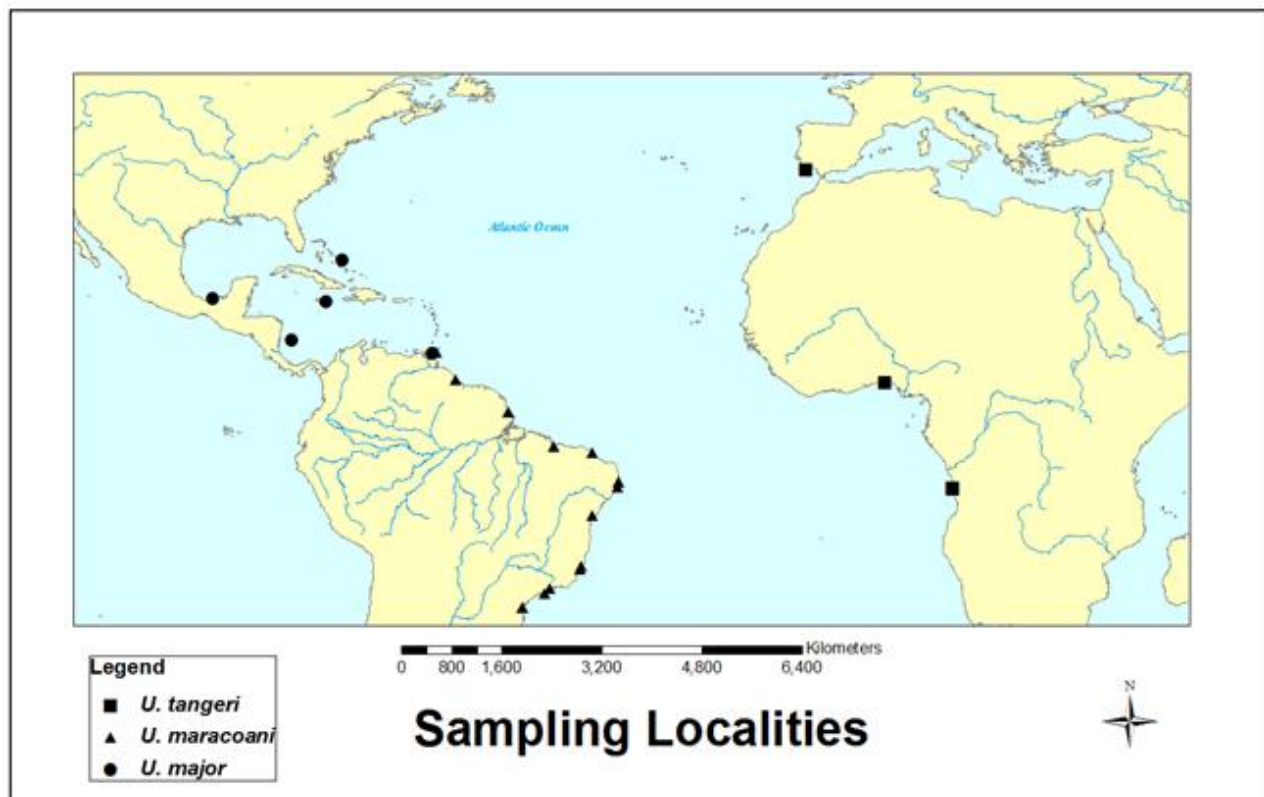


Figure 3. Map of the Atlantic Ocean showing the collection sites for samples utilized in this study.

Species	Collection	Location	Country	Latitude	Longitude	N
USMN						
Major	137748	Trinidad, Diego Martin River, Holes in Tidal mud flats	Trinidad	10.674	-61.559	1
Major	180184	Campeche Bay, Puerto Ceiba, Rio Seco, near Coconut grove	Mexico	18.422	-93.169	1
Major	210461	Kingston, St. Albans, S Causeway, E Side, Tidal Flat	Jamaica	17.9705	-76.8461	3
Maracoani	138579	Trinidad, Cocorite	Trinidad	10.7812	-60.9466	16
Maracoani	138581	Georgetown, Foot of Kitty Village	Guyana	6.8211	-58.1656	13
Tangeri	138109	Luanda, Samba	Angola	-8.829	13.214	25
Tangeri	138111	Luanda, Ilya de Caba	Angola	-8.778	13.247	25
Tangeri	138107	Lagos, Tarkwa Bay, Behind Breakwater	Nigeria	6.399	3.393	14
Tangeri	138105	Faro, Algarve	Portugal	36.99	-7.903	40
USP-ZM						
Maracoani	23190	Amapa 4	Brazil	2.1364	-50.69782	1
Maracoani	23192	Amapa 6	Brazil	2.13643	-50.69782	11
Maracoani	20977-80	Bahia, Madre Deus	Brazil	-12.73657	-38.60433	7
Maracoani	23188	Ceara, Rio Ceara	Brazil	-3.70214	-38.5965	18
Maracoani	20927	Espirito Santo, San Antonio	Brazil	-20.30778	-40.35543	2
Maracoani	20981-2	Espirito Santa, Santa Cruz	Brazil	-19.9532	-40.16842	10
Maracoani	23183	Maranhao, Rio Munin	Brazil	-2.77549	-44.06629	26
Maracoani	20929	Parana, Baxio Mirim	Brazil	-25.873875	-48.60771	9
Maracoani	20973-76	Parana, Garcinhas	Brazil	-25.87136	-48.63449	10
Maracoani	20726	Parana, Rio Fundo	Brazil	-25.8403	-48.58309	4
Maracoani	NA	Pernambuco, Maracaipe	Brazil	-8.53787	-35.008	1
Maracoani	20967	Pernamubuco, Orange Creek	Brazil	-7.81045	-34.84285	6
Maracoani	20983-85	Pernambuco, Rio Santa Cruz	Brazil	-7.81853	-34.86131	25
Maracoani	20968-72	Rio de Janerio, Paraty	Brazil	-23.20164	-44.7219	18
Maracoani	20926	Sao Paulo, Araca	Brazil	-23.81261	-45.40833	1
Major	Thurman	San Salvador, Bahamas	Bahamas	23.981	-74.484	26
Major	Barnwell	Isla San Andres	Colombia	12.525	-81.729	1

Table 1. A list of locations, latitude, and number of specimens per site for each species. The Smithsonian number is included where relevant.

SPECIES IDENTIFICATION

Each specimen was identified to species before landmark digitization. The three species of fiddler crabs analyzed in this study were identified using traditional morphological characteristics (Rathbun 1918, Chase and Hobbs, 1969). Specimens were identified by one investigator (C.L.T.), photographed by another (M.J.H.), while analysis was performed by yet another (K.S.T.).

SPECIMEN PREPERATION

Brazilian samples of *U. maracoani*, after collection, were transported to a laboratory at the Centro de Biologia Marinha (CEBIMar/USP), Sao Sebastiao, Sao Paulo, Brazil, for use in physiological experiments. Following this, crabs were quickly euthanized by chilling and preserved in 80% ethanol (Rufino et al. 2004). Species were divided into lots based on location and stored at the Museu de Zoologia of the Universidade de São Paulo (Table 1). Male carapaces are often asymmetric because of a biomechanical response to the single large cheliped. For methodological reasons, the asymmetric component of variation must be analyzed separately from the symmetrical component. As this study focused only on the symmetric component, it was limited to females (Bookstein 1996, Klingenberg et al. 2002). Though there is asymmetrical variation within individuals, such as that which results from developmental instability, the symmetrical component reveals shape variation among individuals. Only female specimens (n=314) were used to focus our study of geographic variation rather than sexual selection.

Each specimen was photographed individually, oriented so that the carapace was horizontal in frontal view and its anterior- and posterior-most edges lay on the same horizontal plane. Error due to orientation and digitization were assessed by repeatedly mounting and

digitizing a single random specimen of each species (Hopkins & Thurman 2010). All photographs were taken by a single investigator while all digitization was performed by another.

DATA COLLECTION

Twenty one landmarks, as well as two on a ruler for size comparison, were identified on each photograph and digitized using the program tpsDig (Rohlf 2010). The landmarks were specifically chosen because they accurately summarize the general carapace shape, as well as internal features of the individual crab. Landmark positions can be viewed in Figure 4 (Hopkins & Thurman 2010). The last two for size were placed one centimeter apart on the photograph in the ruler to scale each configuration.

Statistical analyses were performed with Integrated Morphometrics Package (IMP) software by Sheets (2001-2007). Paired landmarks were averaged across the 1-3 center line and then averaged, as they are not independent and the carapace is symmetrical. The superimposition reduces the number of landmarks to eleven, as shown in Figure 5. Data were compiled into a single file, which was processed by the PCAGEN6 program to check for outliers.

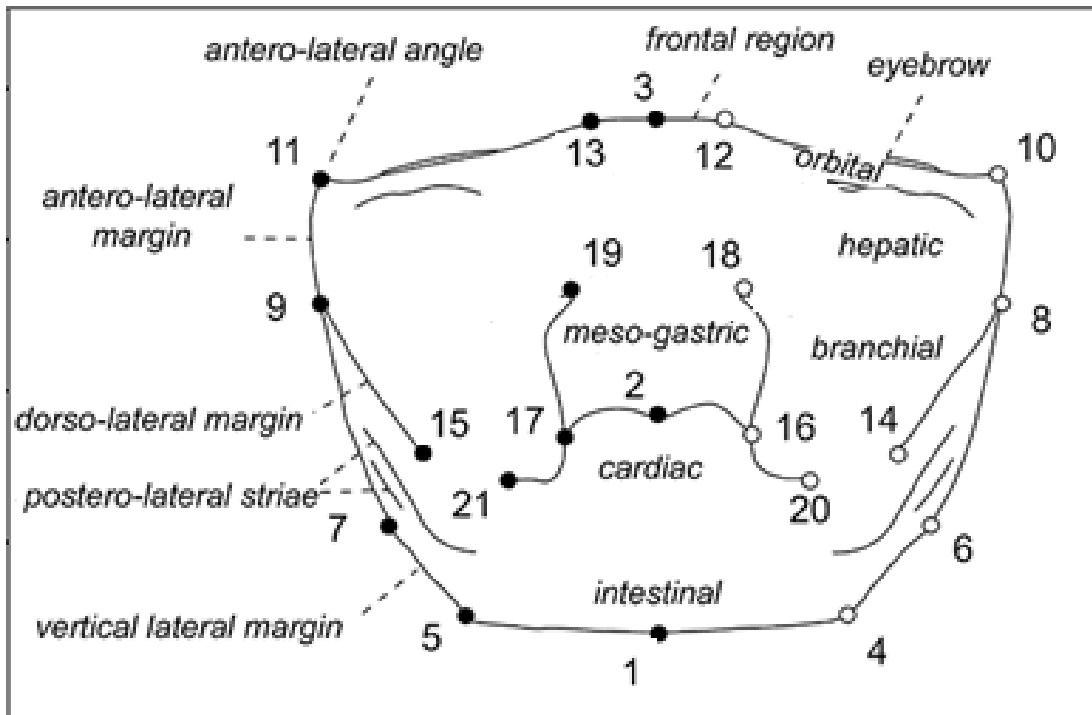


Figure 4. A representation of anatomical regions and locations of 21 landmarks on the female carapace. Closed circles show the configuration of landmarks after averaging across the midline (points 1, 2, and 3), while open circles indicate original landmark points.

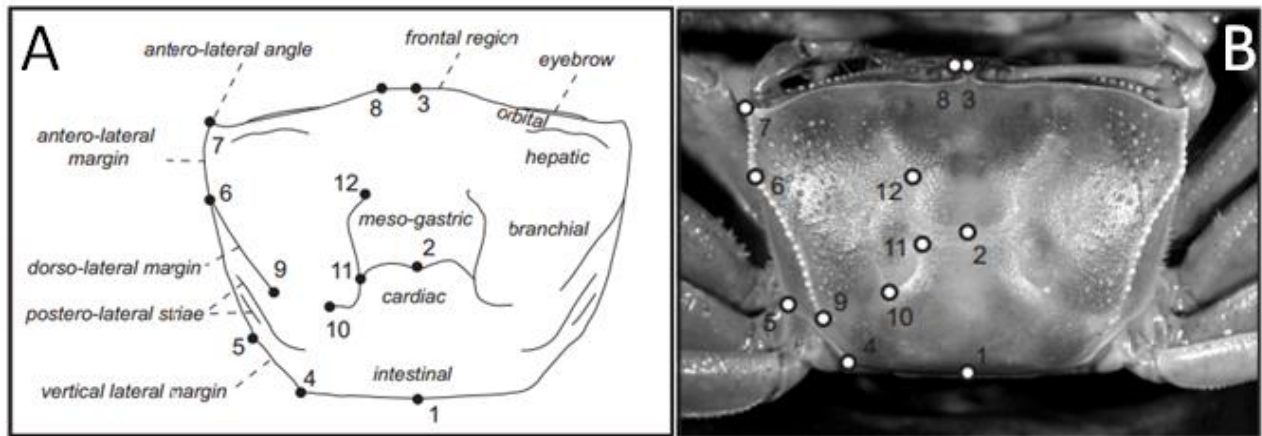


Figure 5. (A) A representation of anatomical regions after averaging across the midline, resulting in 12 total landmarks. (B) Landmarks represented on the crab carapace itself as performed on the 314 samples.

HABITAT/ENVIRONMENTAL GROUPING

Using the latitude of collection (Table 1), specimens each three species were divided into northern and southern populations. In addition Brazilian samples of *U. maracoani* specimens were also divided into groups according to high/low salinity (i.e. above or below 620 mosm/Kg H₂O), substrate (muddy or sandy), and biotope (Thurman et al. 2013). Based on hydrology and climate, the Brazilian shore between AP and SC can be divided into four distinct biomes: I - humid tropical, II - mixed, dry, tropical, III - humid, tropical, and IV – subtropical. The geographic distribution of these habitat parameters (Table 2) were used to localized the factors promoting carapace variation.

State	Site designation (municipality/feature)	Georeference (latitude, longitude)	Habitat osmolality (mosm/kg H ₂ O)	Habitat type
AP	Calçoene, Goiabal, river	02.59653, -50.84833	105	sandy-mud
	Amapá, Amapá R.	02.14724, -50.69581	463	open mud flat, mngv
	Amapá, Amapá R.	02.13643, -50.69782	270	clay flat
	Amapá, Amapá R.	02.08035, -50.76265	75	low tide bar
MA	Raposa, Caêma R.	-02.41575, -44.10077	930	exposed sand
	São José do Ribamar	-02.56377, -44.05370	825	exposed sandy mud
	Icatu, Munim R.	-02.77549, -44.06629	80	humus, mngv
CE	Fortaleza, Ceará R. mouth	-03.70214, -38.59650	590	mngv, open
	flat Fortaleza, upper Cocó R.	-03.76818, -38.45075	60	mngv mud
PE	Itamaracá, Sta. Cruz R. channel	-07.81853, -34.86131	716	open sand-mud flat
	Itamaracá, Ft. Orange Creek	-07.81045, -34.84285	960	mngv mud
BA	Madre de Deus, Baía Santos	-12.73657, -38.60433	951	open sand/mud
	Maragogipe, Iguape bay	-12.78070, -38.90875	827	sand, mngv
	Salvador, Aratu bay, marina	-12.81383, -38.45294	675	mngv, humus mud
ES	Santa Cruz, Sta. Cruz R.	-19.95320, -40.16842	791	mngv mud
	Vitória, Joana D'arc	-20.28357, -40.31325	675	mngv mud
	Vitória, Santo Antônio	-20.30778, -40.35543	675	open mud flat
	Rio de Janeiro, Guaratiba	-23.02868, -43.56275	33	sandy mud
	Paraty, Jabaquara beach	-23.20164, -44.72115	800	mngv, mud
SP	São Sebastião, Araçá beach	-23.81261, -45.40833	1010	sand beach, mngv
PR	Guaratuba, bay, Ilha Garcinhas	-25.87136, -48.63449	328	mngv roots, mud
	Guaratuba, bay, Baixio-mirim	-25.87388, -48.60798	650	sand flat
	Guaratuba, bay, Rio Fundo	-25.84030, -48.58309	715	shelly sand

Table 2. Site localities and principal habitat characteristics for *Uca* collected along the Atlantic coast of Brazil between May 2009 and August 2010. Habitat abbreviations: mangrove - mngv.

DATA ANALYSIS

Visualizations of morphological variation were created with principal components analysis (PCA) and canonical variates analysis (CVA) of the partial warp scores (Figure 6). In PCA, all of the images are superimposed and standardized, then rotated in multivariate space to express the most variations on a few axes, ignoring any group affiliation. While CVA is similar, it transforms data to maximize the variation between the groups. Each specimen is given a score for each axis, first on the horizontal axis (PC1 and CV1, respectively) which explains the most variance while each latter axis explains less and less variance. The distribution of specimens or groups in morphospace may be visualized by plotting the first two axes against one another in a bivariate plot.

Morphological differences between specimens along these axes may be visualized using deformation plots. These deformation plots use a grid combined with vectors to show not only the extent of the variance, but also the direction and location on the carapace. As differences do occur among groups, a resampled F-Test which used the Procrustes coordinates was used to determine significance (Sheets 2001-2007). This resulted in two values, including the distance between the means, which indicates space between a pair of samples in morphospace. This reveals which groups have more common morphology and which groups have more differences. The p-value was also generated, which is the probability that the differences between groups could occur by pure chance. In this study, p-values less than 0.05 were determined to be significant.

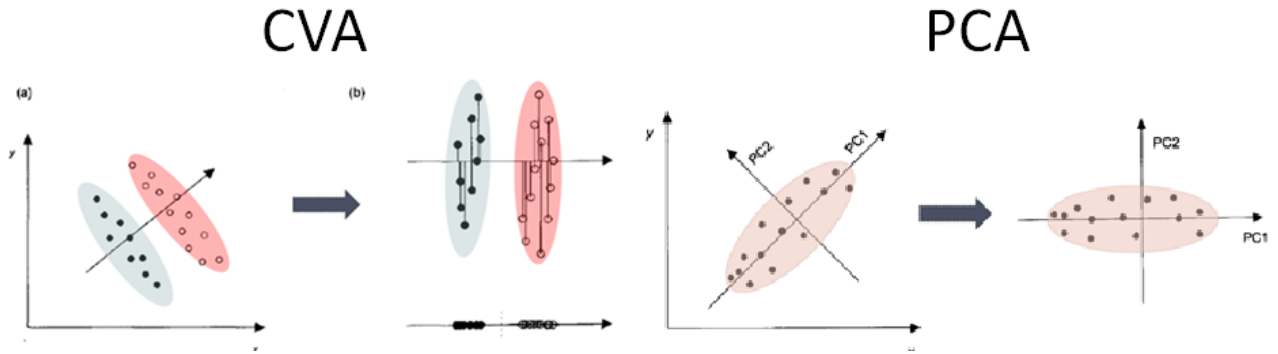


Figure 6. Visual representation of Canonical Variance and Principal Components Analyses. Both analyses rotate the data to maximize differences between groups and reduce the number of variables to study. CVA alters data and is based on an assumption of equal variance while PCA does not alter the original data.

RESULTS

ALLOMETRIC VARIATION

From geometric morphometric analysis of the fiddler crab carapace, the twelve surficial landmarks can be used to calculate centroid position and size based on the square root of the summed squared distance from the centroid to each landmark. Since size is a major component of morphological variation, allometric growth of the carapace was examined in the three fiddler crab species. Figures 7, 8, and 9 illustrate the relationship between log centroid size and distance in morphospace for each species, respectively. Morphological distance on the Y axis is partial Procrustes distance between the mean of the smallest three specimens sampled and each of the other specimens for that species. "Partial Procrustes distance" refers to the method of superimposition. The mean value of the smallest three specimens can be thought of as the "expected" most-juvenile form. The distances represent the difference in shape between the expected juvenile form and each of the larger specimens.

Significant positive allometry is expressed as a result of carapace enlargement in all three *Uca (sensu lato)*. As the carapace centroid size (logarithm) increases from 2.75 to 3.4 in *U. major* (n = 32), the Procrustes distance increases from 0.025 to 0.060 (Figure 7). Likewise, in *U. maracoani* (n = 178) as the logarithm of centroid size increases from 2.30 to 3.70, the Procrustes distance increases from 0.025 to 0.093 (Figure 8). For *U. tangeri*, as the logarithm centroid increases from 2.4 to 3.8 (n = 104), the Procrustes distance increases from 0.020 to 0.145 (Figure 9). For subsequent analysis, allometric growth was removed by regressing shape against centroid size using Regress (Sheets 2001-2007).

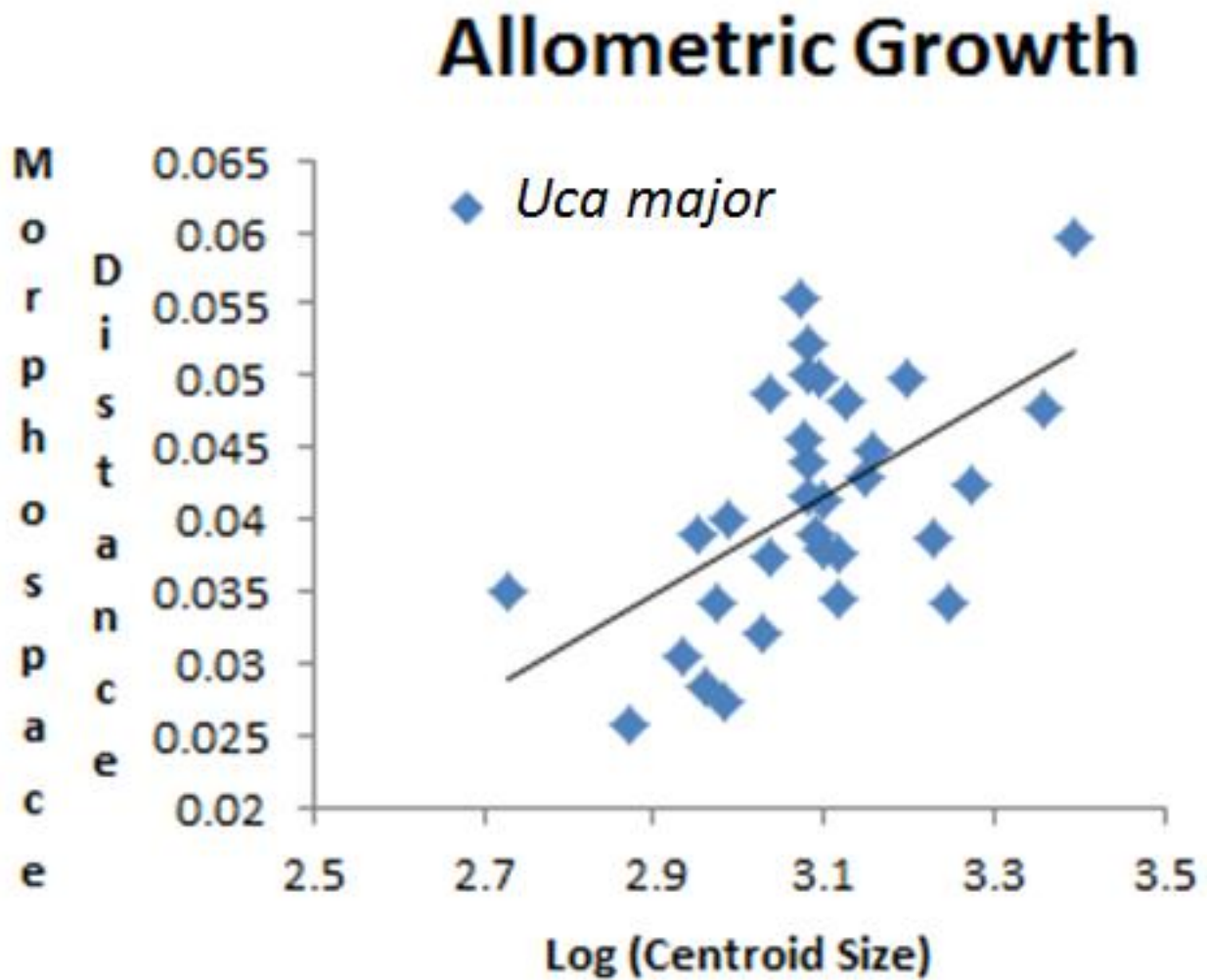


Figure 7. Regression analysis of allometric growth in *Uca major* (N=32). Morphospace distance is estimated by averaging the smallest three specimens of each species and comparing the rest of the samples against them. The equation of the regression line is $Y = 0.034x + 0.064$; correlation coefficient 0.55 ($r^2 = 0.3025$) where x is the log of the centroid size and y is the distance in morphospace.

Allometric Growth

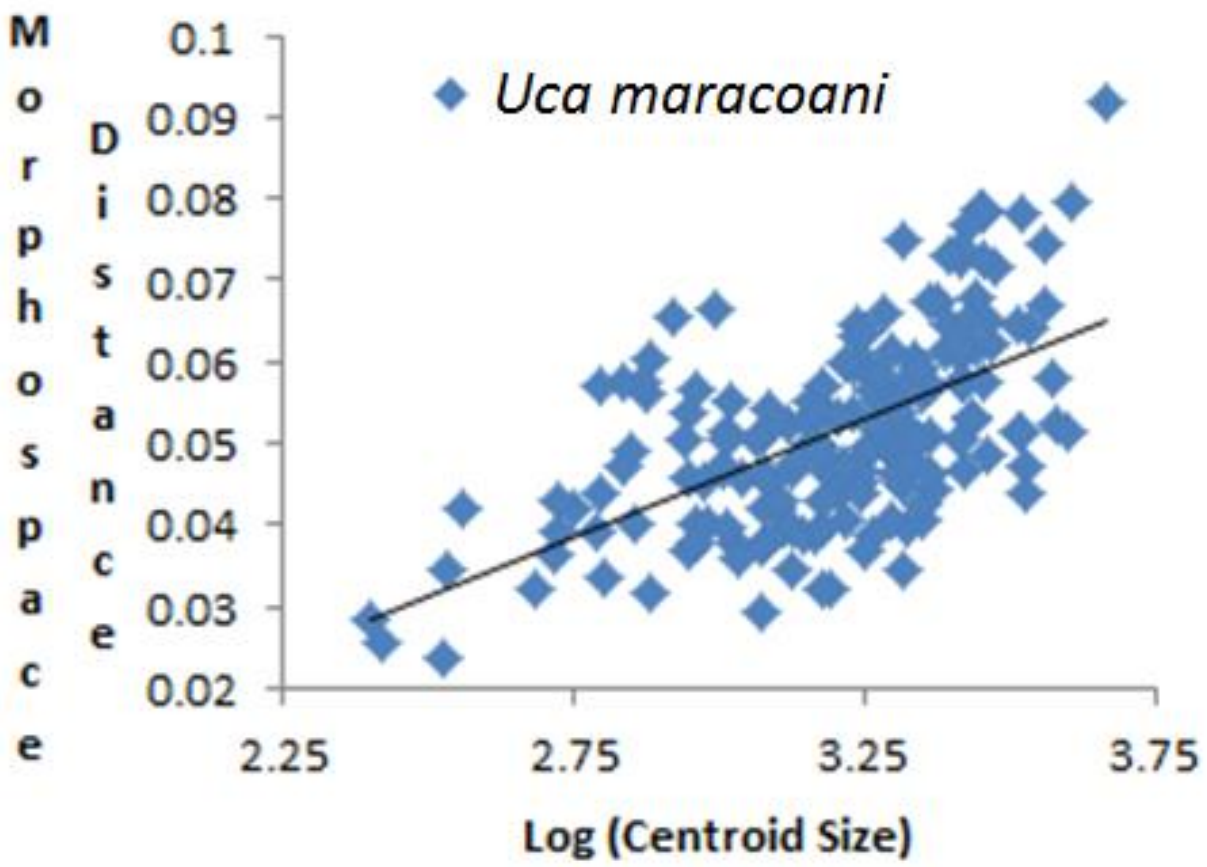


Figure 8. Regression analysis of allometric growth in *Uca maracoani* (N = 178). Morphospace distance is estimated by averaging the smallest three specimens of each species and comparing the rest of the samples against them. The equation of the regression line is $Y = 0.029x - 0.041$; correlation coefficient 0.59 ($r^2 = 0.3481$) where x is the log of the centroid size and y is the distance in morphospace.

Allometric Growth

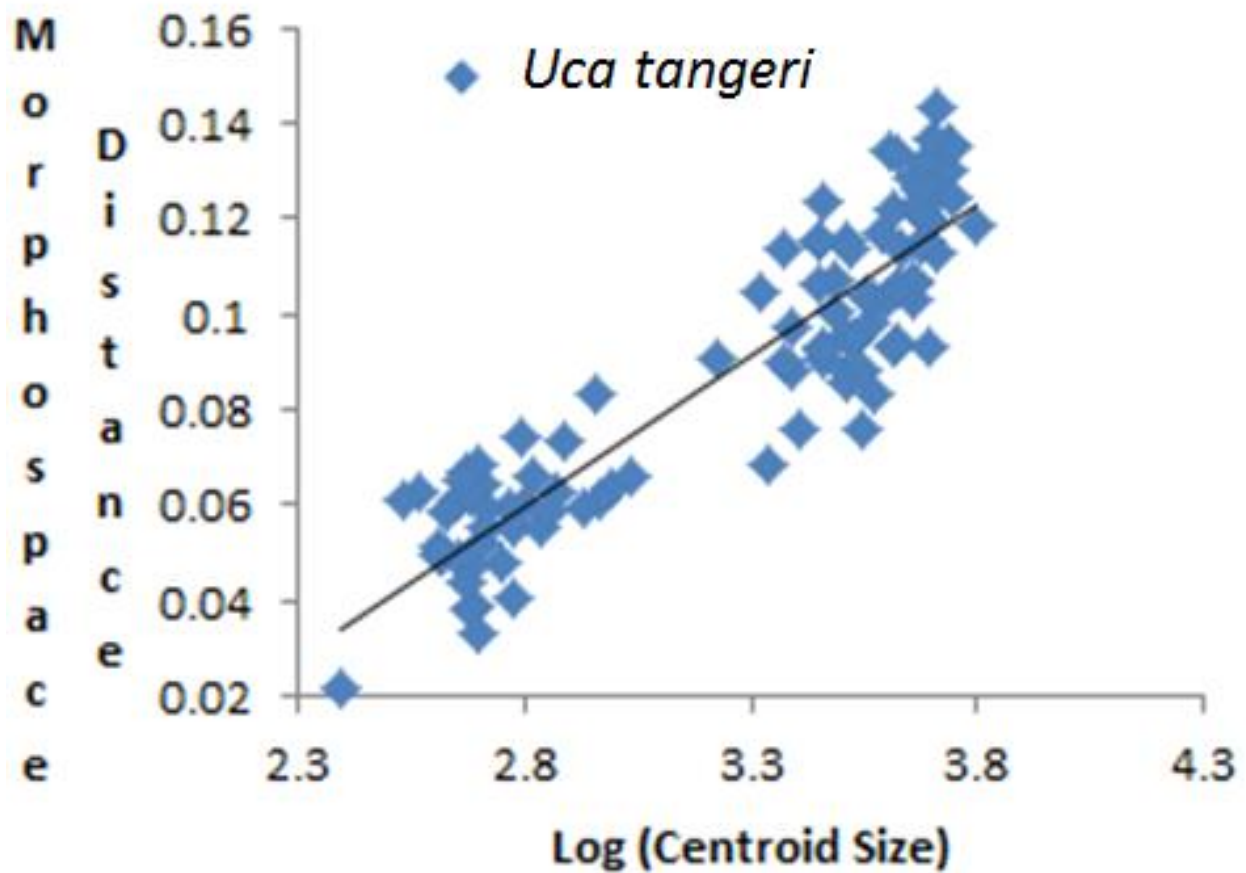


Figure 9. Regression analysis of allometric growth in *Uca tangeri* (N = 104). Morphospace distance is estimated by averaging the smallest three specimens of each species and comparing the rest of the samples against them. The equation of the regression line is $Y = 0.063x - 0.12$; correlation coefficient 0.91 ($r^2 = 0.8281$) where x is the log of the centroid size and y is the distance in morphospace.

INTERSPECIFIC VARIATION

After removing allometric variation, PCA reveals that 57.51% of carapace variation is associated with PC1 and 10.11% with PC2. Together the two account for 67.62% of the variation. Using either CVA or PCA, the three species exhibit no overlap in morphospace (Figure 10, Figure 11, Table 3). Based on PC1 and PC2, each species is distinct in morphospace (Fig 10). Using the canonical variates analysis, CV1 shows some separation between *U. tangeri* and *U. maracoani* while *U. major* is more distinct, and CV2 shows more equal distances between the three species (Figure 11). From Table 3, *U. major* and *U. tangeri* are separated by the largest mean partial Procrustes distance of 0.155 while *U. major* and *U. maracoani* are separated by a mean partial Procrustes distance of 0.150. Carapace shape in *U. tangeri* and *U. maracoani* are more similar with a mean partial Procrustes distances of 0.070. By resampled Goodall's F-test, the carapace shapes of all three species are statistically significant (Table 3; $P \leq 0.0001$).

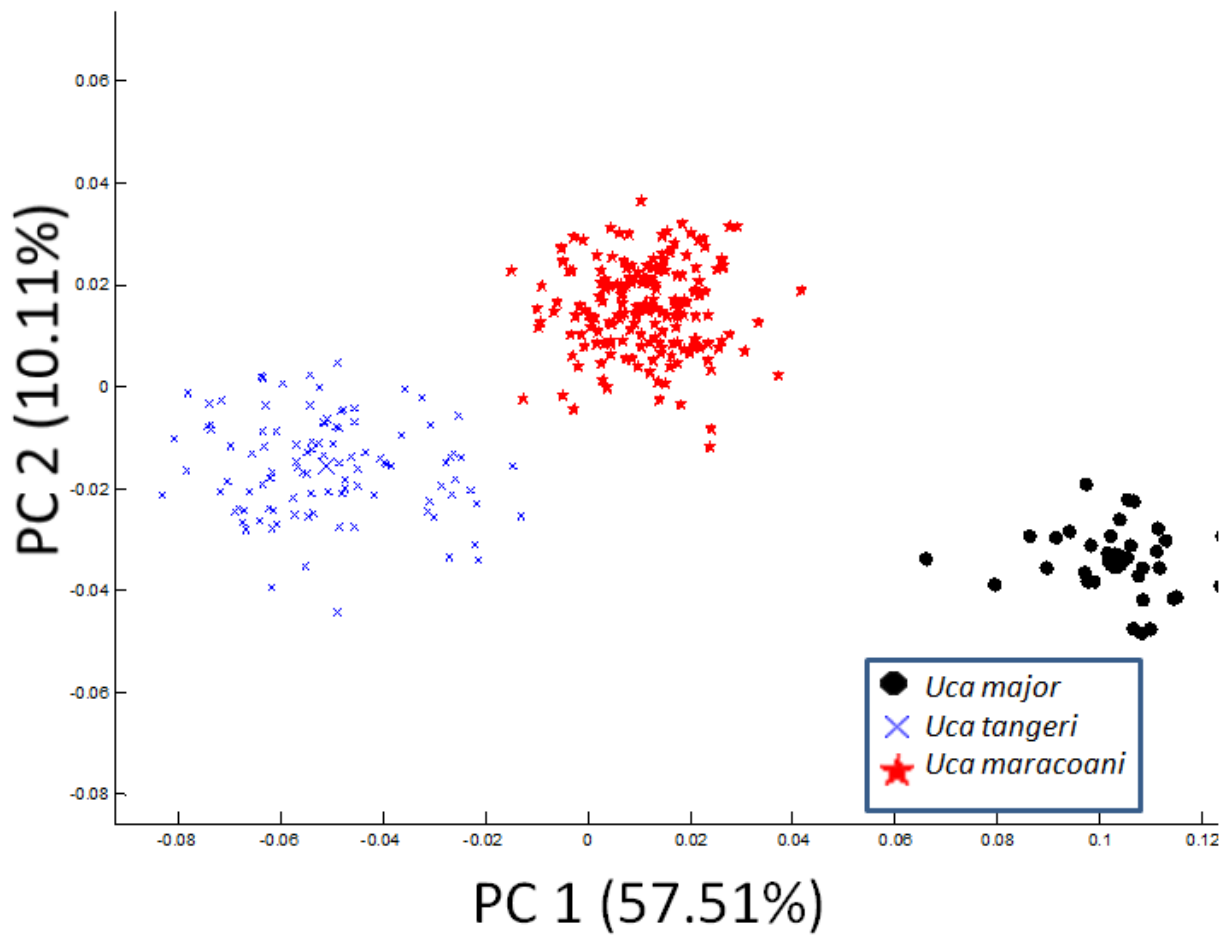


Figure 10. Principal components analysis of all 314 specimens. Symbol colors indicate different species. PC1 and PC2 scores denote variance accounted for by that axis. All three species are clearly distinct on the horizontal PC1 axis, but are less distinct when viewed on the vertical PC2 axis.

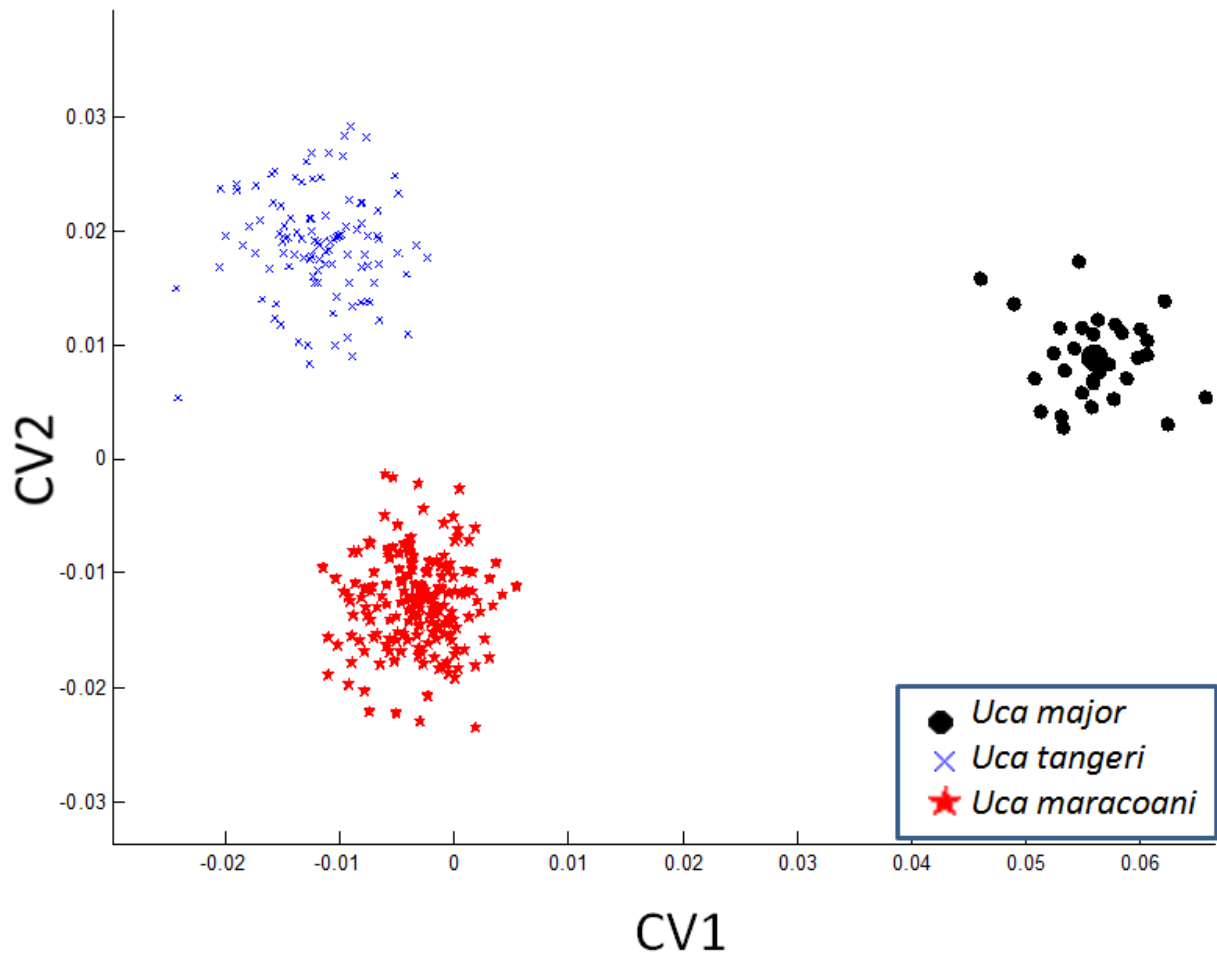


Figure 11. Canonical variance analysis plot (CV1 vs CV2) of all 314 specimens of *U. major*, *U. maracoani*, and *U. tangeri*. When viewed on the horizontal CV1 axis, *U. tangeri* and *U. maracoani* are quite close together while *U. major* is quite isolated. When viewed on the vertical CV2 axis, *U. major* is more closely placed between the two continental species.

Comparison	F-score	p value	Distance Between Means
U. major - U. maracoani	247.52	<0.0001	0.105
U. major - U. tangeri	348.87	<0.0001	0.1555
U. maracoani - U. tangeri	220.75	<0.0001	0.07

Table 3. Goodall's F-test comparison from Procrustes coordinates of landmark data, which compares the difference in mean shape between two samples relative to the shape variation found within the samples. All three comparisons yielded highly significant results, with $p < 0.001$. The distances between the means of *U. major* and *U. tangeri* were the greatest.

INTRASPECIFIC VARIATION

IMPACT OF LATITUDE ON CARAPACE SHAPE IN SUBGENUS UCA

For museum specimens, little information on habitat other than location of collection is available. Consequently, carapace variation was analyzed in regards to latitudinal distribution. On the other hand, since *U. maracoani* were collected specifically for this project (Thurman et al. 2013), carapace variation in this species can be correlated with latitude, soil type, salinity and biotope (Table 2).

Northern and southern populations of all three species were compared in morphospace and subjected to statistical analysis. *U. major* was divided into northern or southern populations based on country of origin (Bahamas were defined as north with a latitude of 22° degrees north, all others were south). The Ponta do Calcanhar in Brazil divided *U. maracoani* at a latitude of 7° degrees, while the equator divided the populations of *U. tangeri* at a latitude of 0° degrees. Deformation plots were used to analyze variation with latitude when comparing all three species. These plots illustrate which regions of the carapace are experiencing morphological distortion. The most significant area of morphological variation in the carapace, shown in the Procrustes deformation plots, differed among the species. In *U. major*, the largest variation was seen in the branchial region (Figure 12). The frontal and hepatic regions showed the most variation in *U. maracoani* (Figure 13). *U. tangeri* had the most variation in the meso-gastric and hepatic regions (Figure 14). Procrustes deformation plots from Canonical Variates Analysis (CVA) showed more diverse variation throughout many regions of the carapace than seen after PCA. Discrepancies are due to the innate differences of the two programs and how they rotate the data.

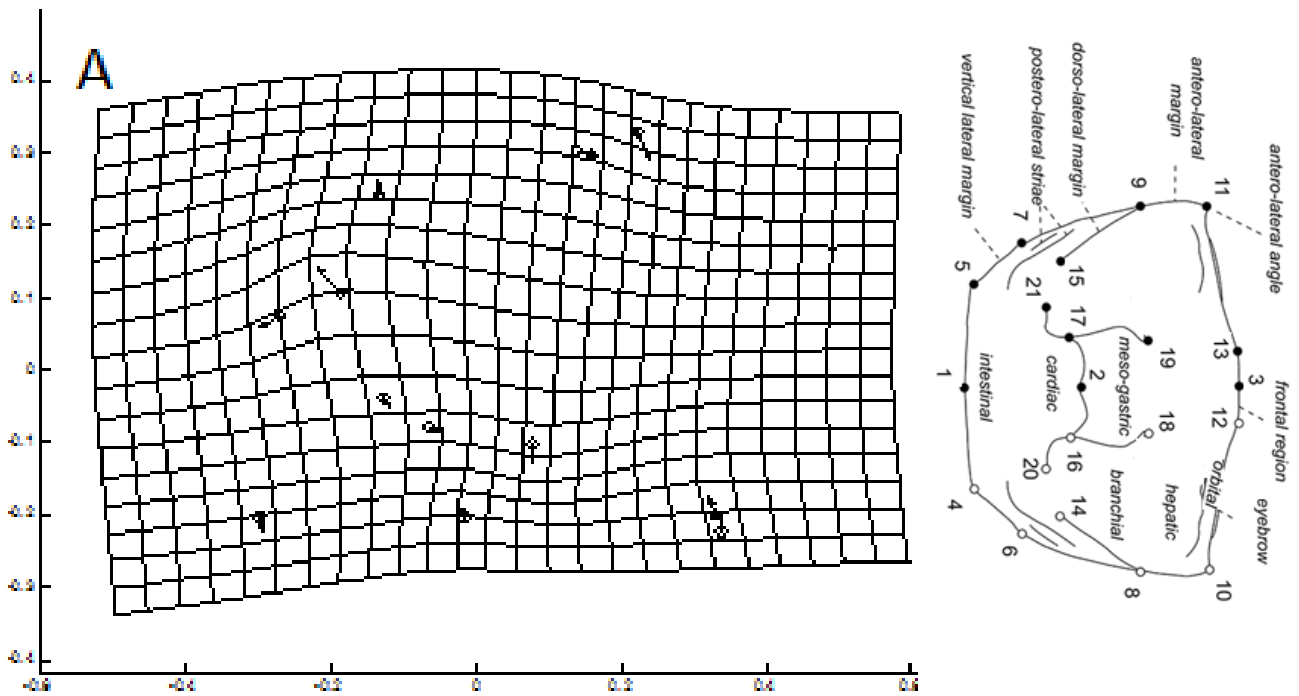


Figure 12. CV1 Procrustes deformation plot due to latitude. Most variation is seen in the branchial and frontal regions in *U. major*.

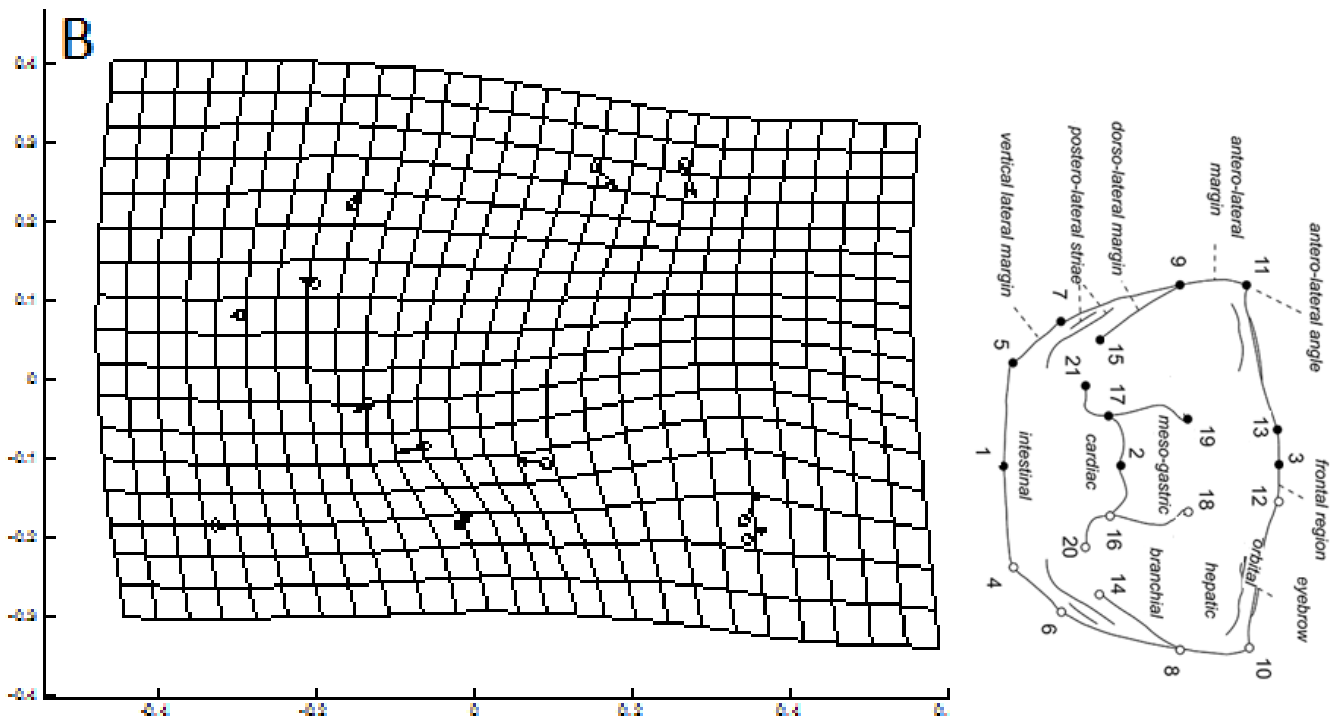


Figure 13. CV1 Procrustes deformation plot due to latitude. The frontal and hepatic regions had the most variation in *U. maracoani*.

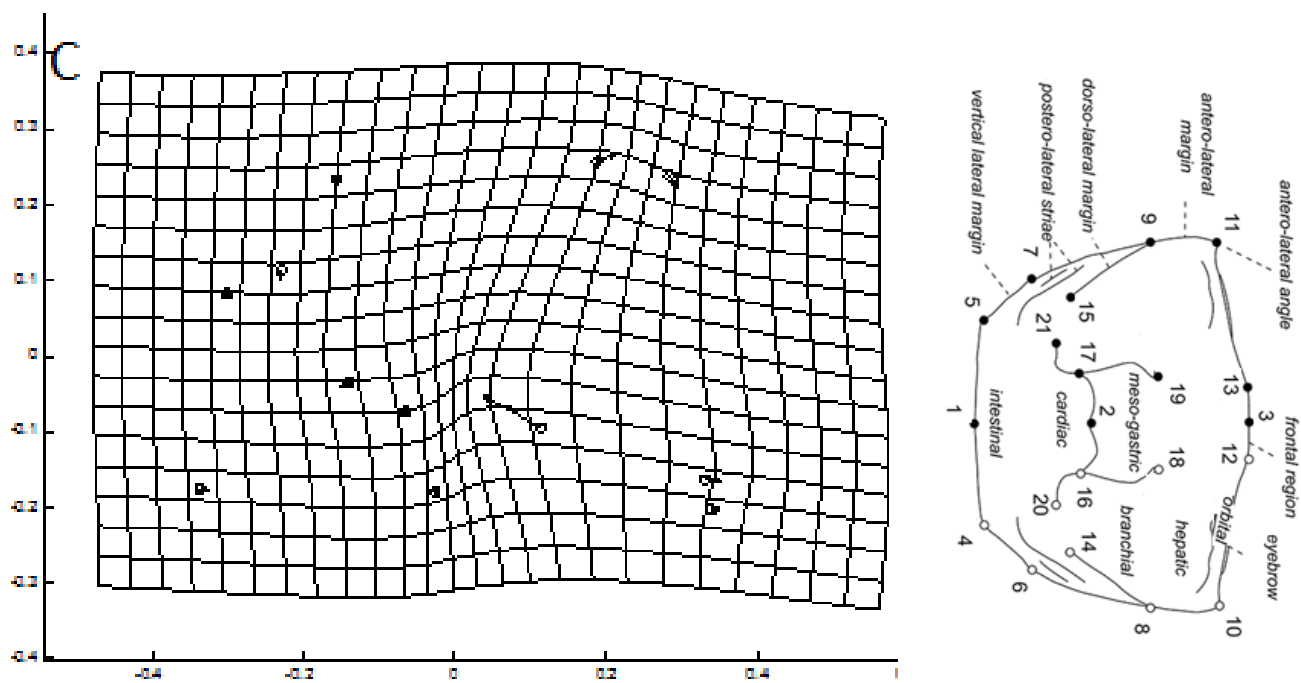


Figure 14. CV1 Procrustes deformation plot due to latitude. In *U. tangeri*, most variation is displayed in the meso-gastric and hepatic regions.

In *U. major*, the specimens collected from the Bahamas were compared by PCA and CVA with those from Jamaica, Colombia, Mexico, and Trinidad. Specimens from the Bahamas clustered together in PCA, as seen in Figure 15. Although only a few specimens were used (n=32), intraspecific variation is clearly evident based on PC1. On the PC1 axis, 26.56% of the variation is represented. Specimens from northern populations show similarity in the variation captured by the PC1 axis compared to specimens from southern populations. Since overlap in groups sorted by latitude on the PC2 axis is considerable, it is not useful for documenting population variation. Canonical variance analysis (CVA) produces similar results, though separation is seen more clearly (Figure 18). The F-score, statistical significance, and the distance between the means can be seen in Table 4.

The degree of variation in *U. maracoani* is broader (Figures 16 and 19). The PC1 axis accounts for 20.80% of the variation (Figure 16). Populations can be clearly distinguished by the variation represented by PC1. On the other hand, variation in PC2 is similar across all populations regardless of latitude, so variation represented by PC2 is unhelpful in discriminating populations. Populations from each region cluster together, but there is a great deal of overlap. The mean shapes of the two latitudinal groups are separated by a mean partial Procrustes distance of 0.0175 in morphospace (Table 4). Again, CV1 produces better separation than PC1.

Like the other two species, PC1 in *U. tangeri* shows distinct clustering of populations based on latitude regions. The PC1 axis represents 35.82% of the shape variation in cara pace morphology (Figures 17 and 20). The mean partial Procrustes distance between the northern and southern populations is 0.027 (Table 4) and is statistically significant ($p = 0.0011$). On the other hand, the variance on the PC2 axis among specimens from both regions overlap considerably and would not be useful in distinguishing their origin (Figure 17).

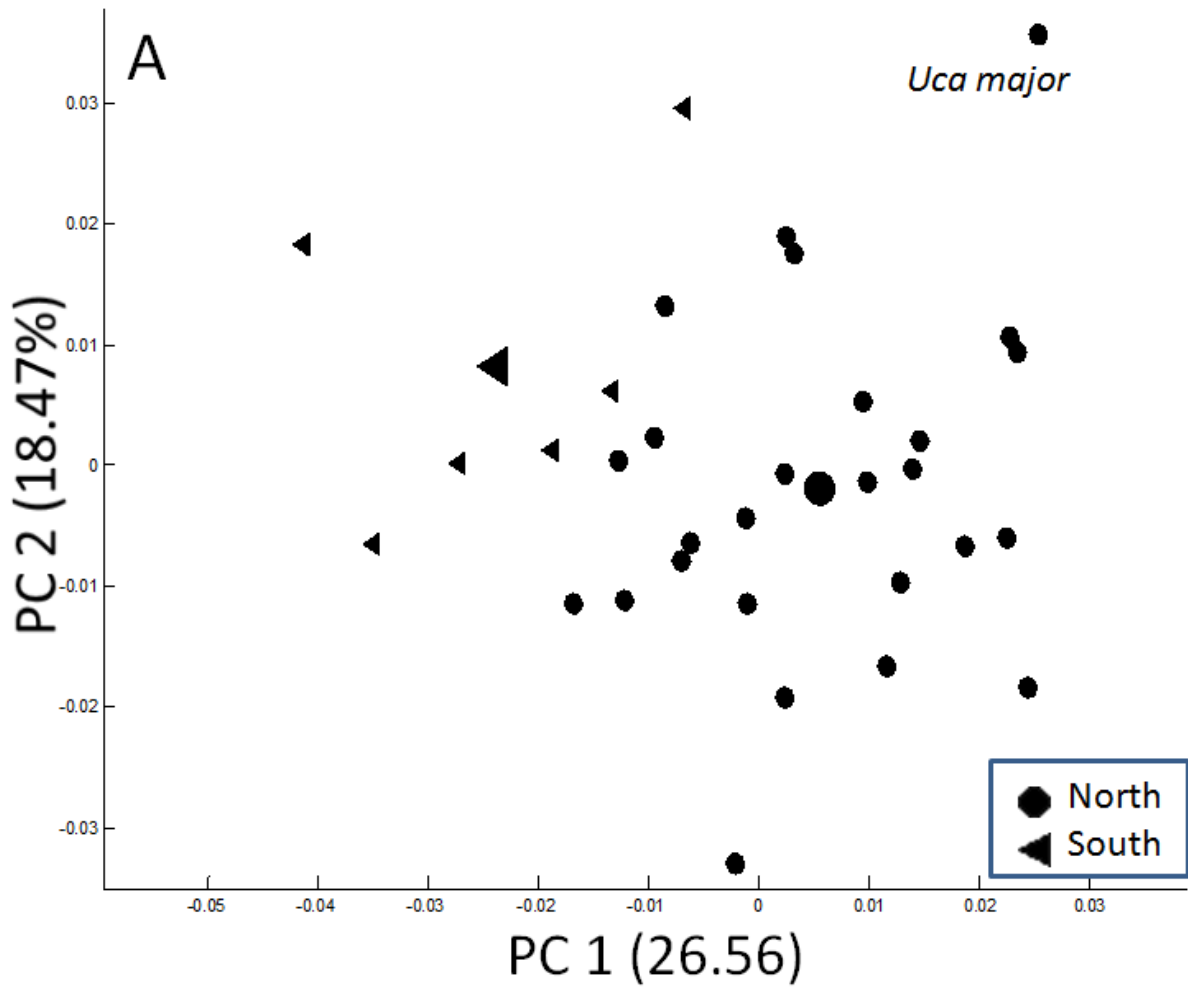


Figure 15. Principal components analysis comparing northern and southern populations *U. major*. Populations are very distinct on the PC1 axis and moderately separate on the PC2 axis. Northern populations originated in the Bahamas, while the southern populations originated from Colombia, Trinidad, Jamaica, and Mexico. There is not much separation on either the PC1 or PC2 axes.

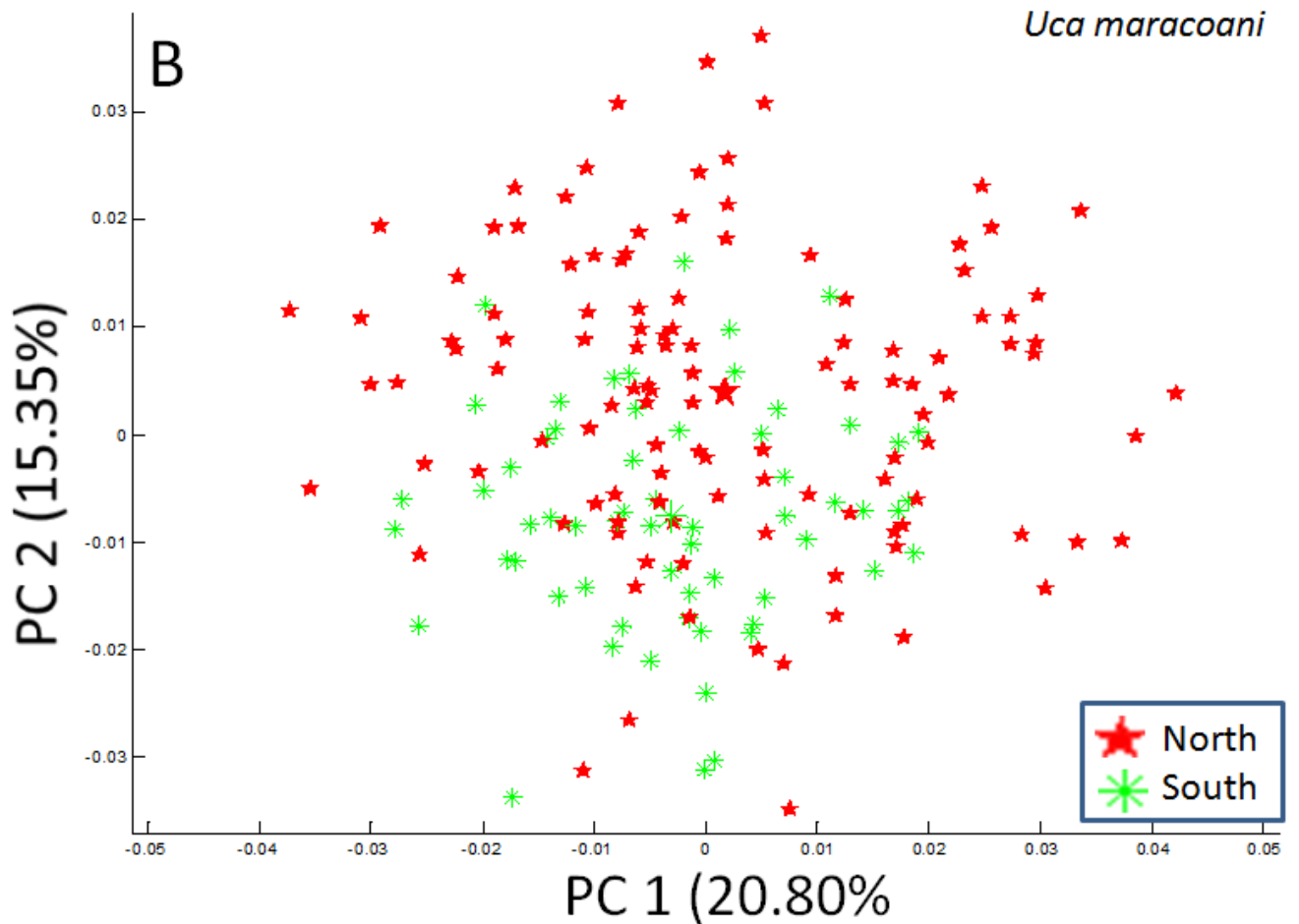


Figure 16. Figure 12. Principal components analysis comparing northern and southern populations *U. maracoani*. Populations display overlap extensively on the PC1 axis, and to a lesser amount on the PC2 axis. Northern and southern populations were divided by the Ponta do Calcanhar. There is not much separation on either the PC1 or PC2 axes.

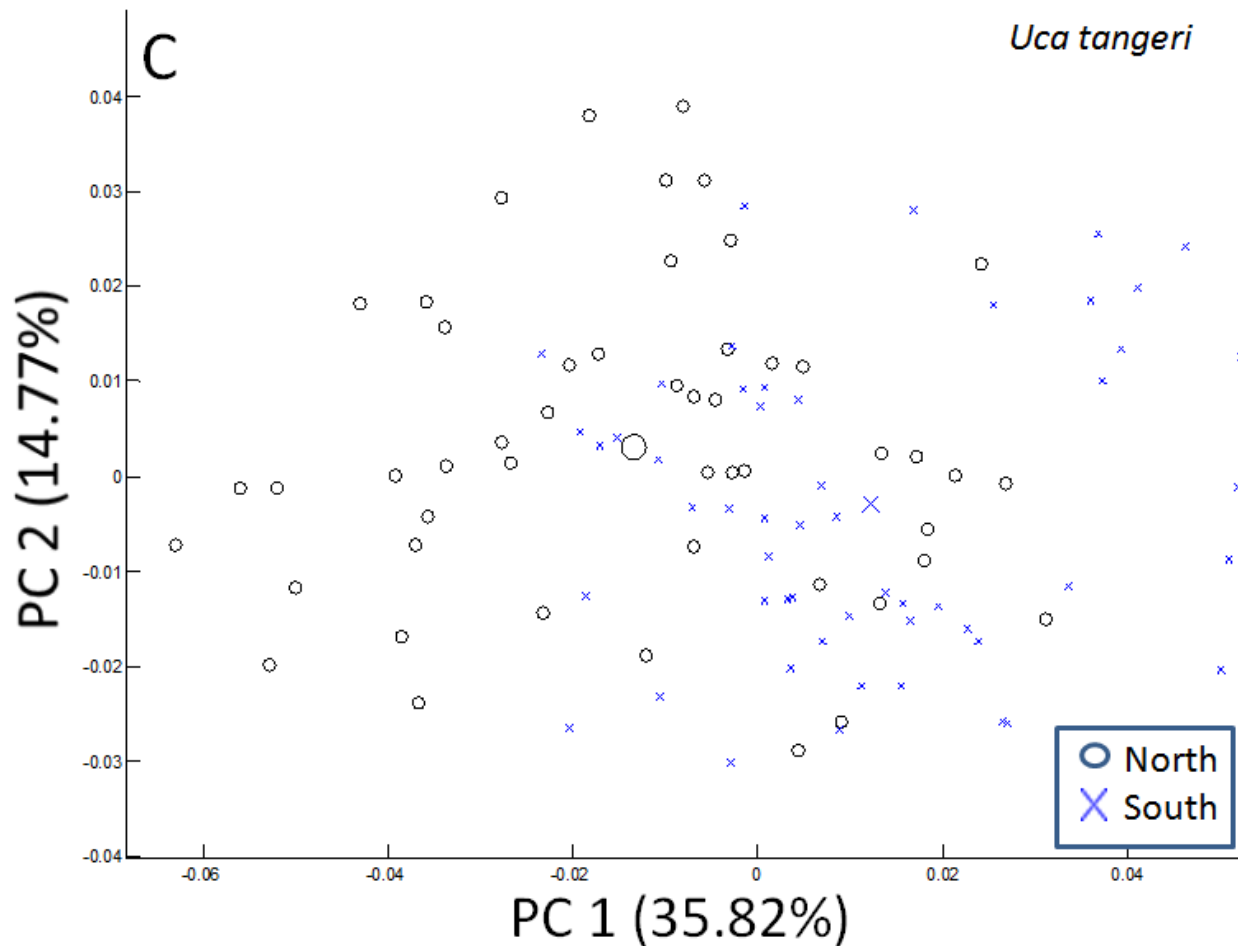


Figure 17. Principal components analysis comparing northern and southern populations *U. tangeri*. Populations display some separation on the PC1 axis and overlap on the PC2 axis. Northern and southern populations were divided by the Equator. There is not much separation on either the PC1 or PC2 axes.

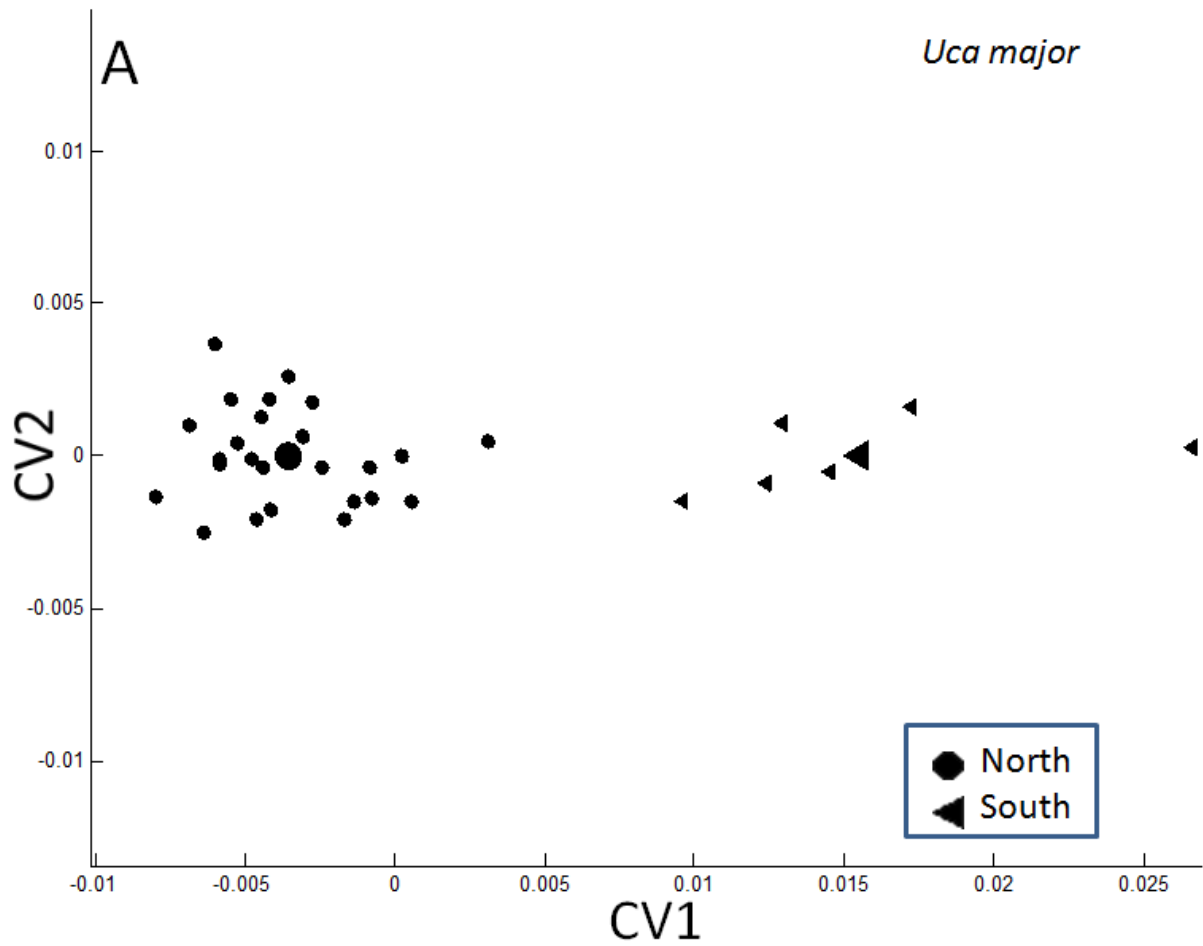


Figure 18. Canonical variates analysis comparing northern and southern populations in *U. major*. Populations are quite distinct on the CV1 axis. Northern populations originated in the Bahamas, while the southern populations originated from Colombia, Trinidad, Jamaica, and Mexico. There is clear separation on the CV1 axis.

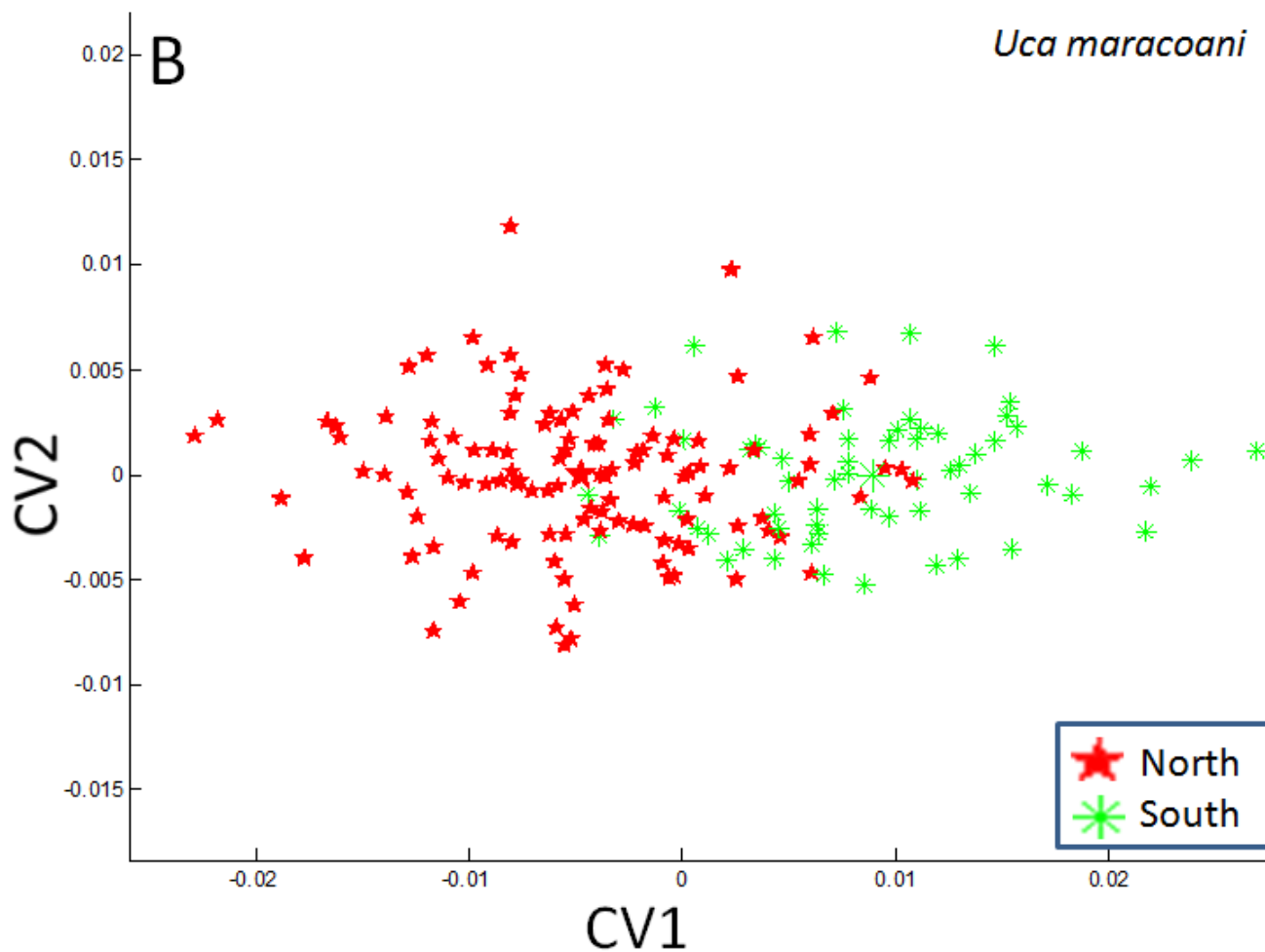


Figure 19. Canonical variates analysis comparing northern and southern populations in *U. maracoani*. It is mostly separated on the CV1 axis. Northern and southern populations were divided by the Ponta do Calcanhar. There is clear separation on the CV1 axis.

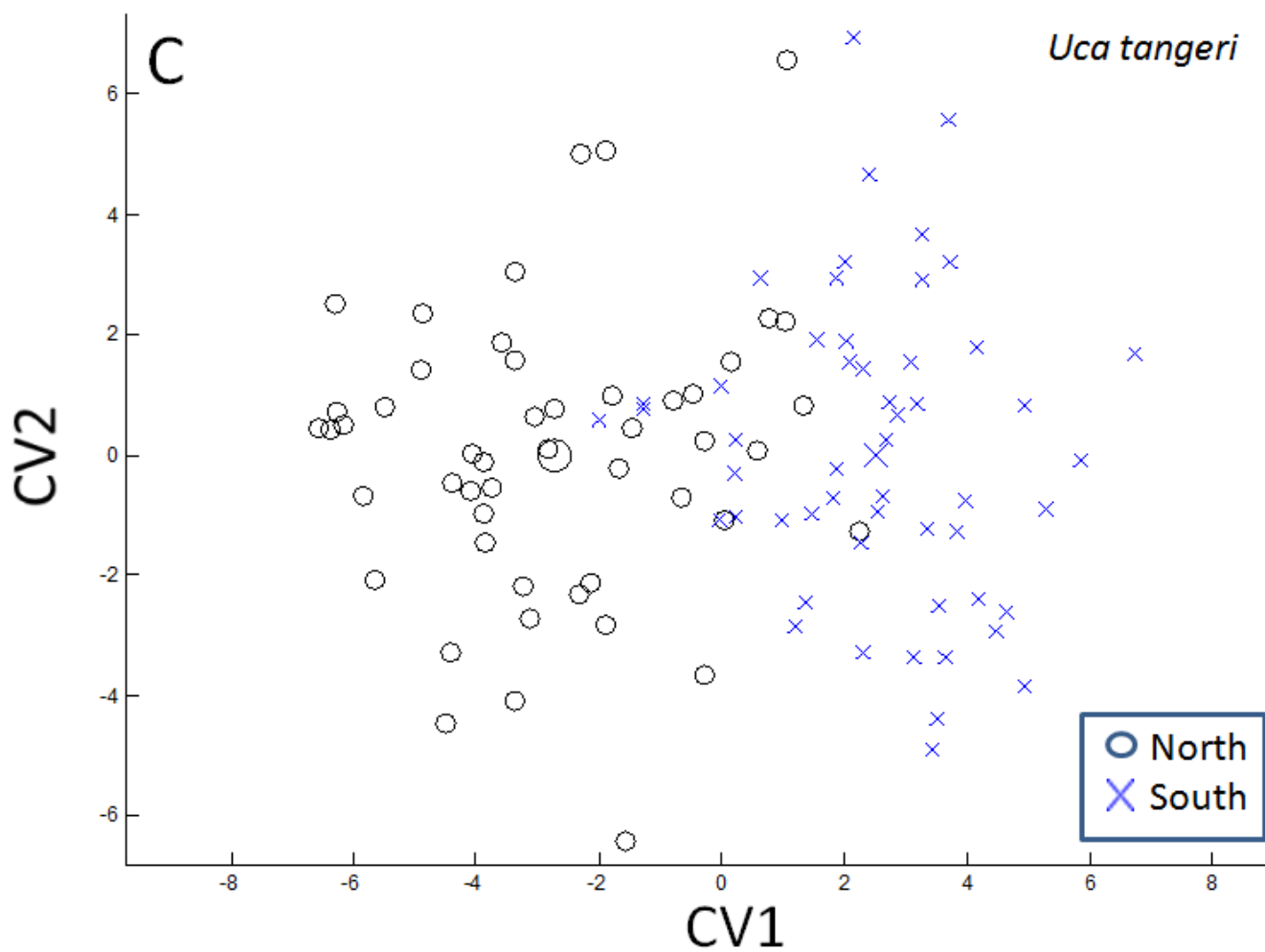


Figure 20. Canonical variates analysis comparing northern and southern populations *U. tangeri*. There is minor overlap on the CV1 axis. There is clear separation on the CV1 axis.

Latitude	F-score	p value	Distance Between Means
U. major	5.68	0.0011	0.0336
U. maracoani	10.54	0.0011	0.0175
U. tangeri	11.19	0.0011	0.027

Table 4. Goodall's F-test comparison from Procrustes coordinates of landmark data contrasting northern and southern populations in each of the three species. All three resulted in statistically significant values, $p \leq 0.0011$ in all species. Distances between the means of northern and southern populations varied the most in *U. major*.

IMPACT OF BIOTOPE REGION ON *U. MARACOANI*

U. maracoani lives in four of Brazil's five recognized Biotopes (Thurman et al. 2013). Principal component and canonical variance analyses are shown in Figures 21 and 22, respectively. The PC1 axis represents 21.22% of the carapace shape variance in this species, while 16.19% is represented on the PC2 axis. Based on CVA, CV1 can distinguish crabs originating in Biotope 2 and Biotope 4 while CV 2 distinguishes crabs from Biotope 1 from those collected in Biotopes 2, 3, and 4 (Fig 22). Based on CV1, crabs from Biotope 2 are intermediate in structure between those from Biotope 2 and 4. Table 5 shows the statistical analyses done for biotope, including a bootstrapped F-test and the distance between the means. Goodall's F-test compares the difference in mean shape between two samples relative to the shape variation found within the samples. Figure 23 shows the Procrustes deformation plot for biotope, showing that the area of greatest deformation is constriction in the antero-latero margin and constriction of the postero-lateral margin.

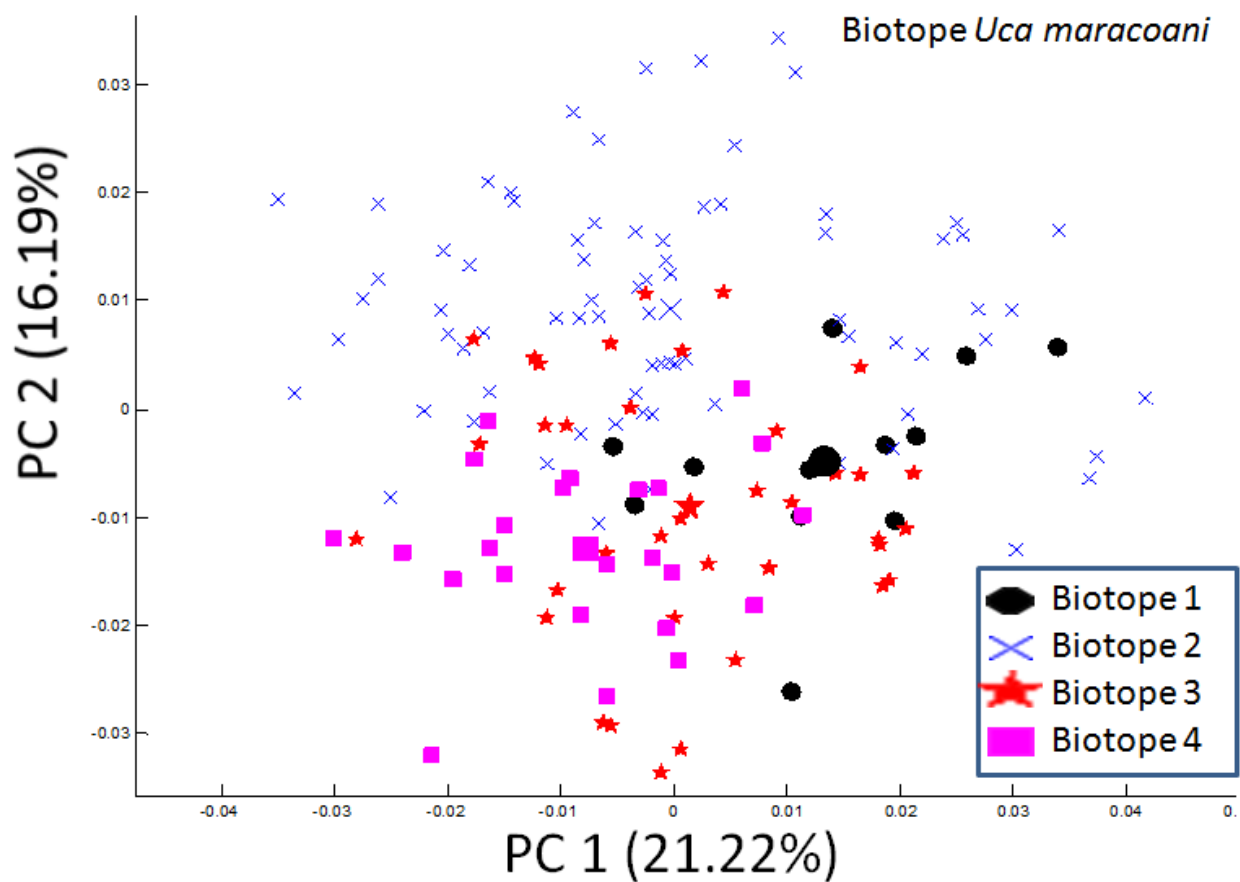


Figure 21. Principal components analysis of all *U. maracoani* samples from Brazil. Symbol colors indicate different species. PC1 and PC2 scores denote variance accounted for by that axis.

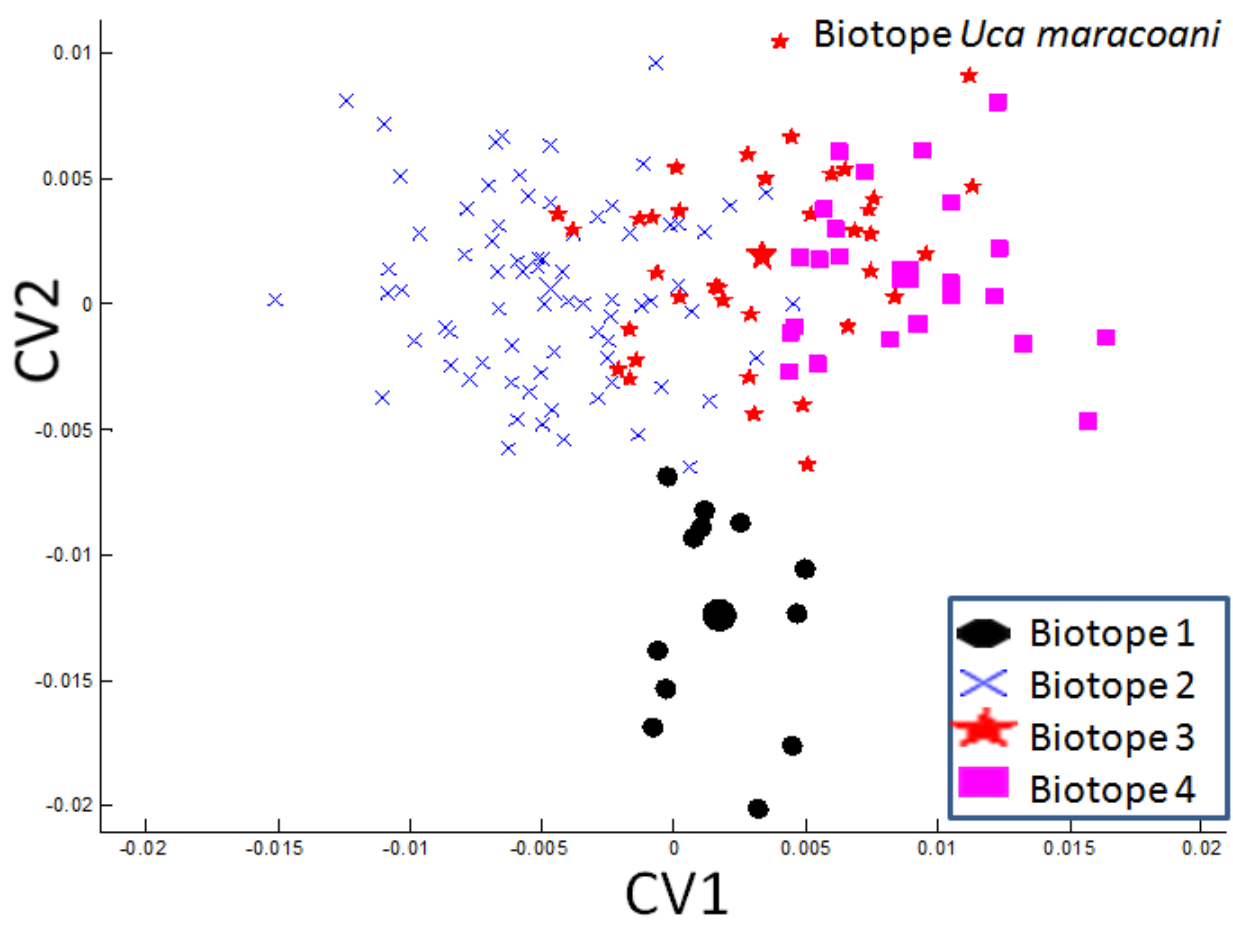


Figure 22. Canonical variance analysis plot (CV1 vs CV2) of all Brazilian samples of *U. maracoani*. When viewed on the horizontal CV1 axis, Biotopes 2, 3, and 4 are a gradient while Biotope 1 overlaps with Biotope 3. When viewed on the vertical CV2 axis, Biotope 1 is isolated from the overlap in Biotopes 2, 3, and 4.

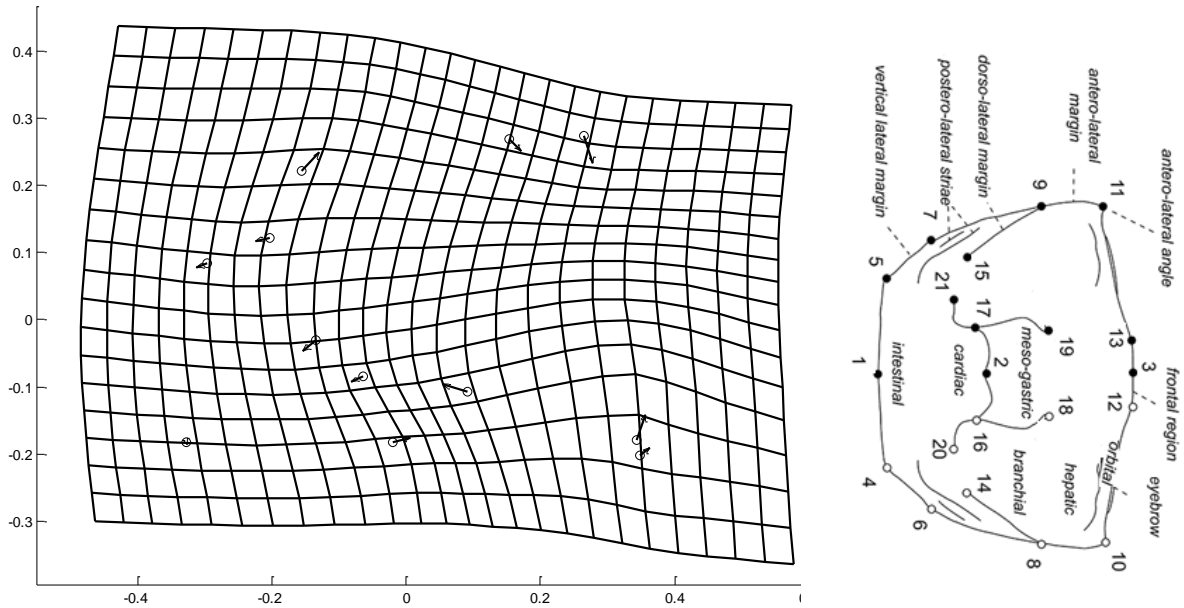


Figure 23. CV1 Procrustes deformation plot due to different biotopes. Most variation is seen in the antero-lateral margin and the postero-lateral margin.

Biotope	F-Score	p value	Distance Between Means
Biotope 1-2	7.41	0.0011	0.0287
Biotope 2-3	8.53	0.0011	0.0196
Biotope 3-4	3.04	0.0011	0.0138
Biotope 1-4	8.89	0.0011	0.0319
Biotope 1,2 - 3,4	12.93	0.0011	0.0201

Table 5. Goodall's F-test comparison from Procrustes coordinates of landmark data contrasting four biotopes in *Uca maracoani*. All comparisons resulted in statistically significant values, $p \leq 0.0011$ in all biotopes. Distances between the means of biotopes 1 and 4 were the greatest and the means were smallest between biotopes 3 and 4.

IMPACT OF HABITAT SALINITY ON *U. MARACOANI*

After principal components analysis, CV1 in these specimens form cohesive groups based on salinity regime (either above or below $600 \text{ mOsm kg}^{-1} \text{ H}_2\text{O}$), supporting the notion that osmolality may impact carapace shape (Figure 24). PC1 and PC2 represent 37.41% of the variation in the dataset (Figure 25). Consequently canonical variates analysis (CVA) provides a clearer view distinguishing the two salinity groups. However, overlap is still visible in the CVA plot (Figure 24). A resampled F-test (Table 6) yielded a statistically significant value, $p = 0.0011$. Figure 26 is the Procrustes deformation plot for salinity, which reveals that the greatest areas of plasticity are similar to those seen due to biotope. The antero-lateral margin of the carapace is constricted and the postero-lateral margin is enlarged.

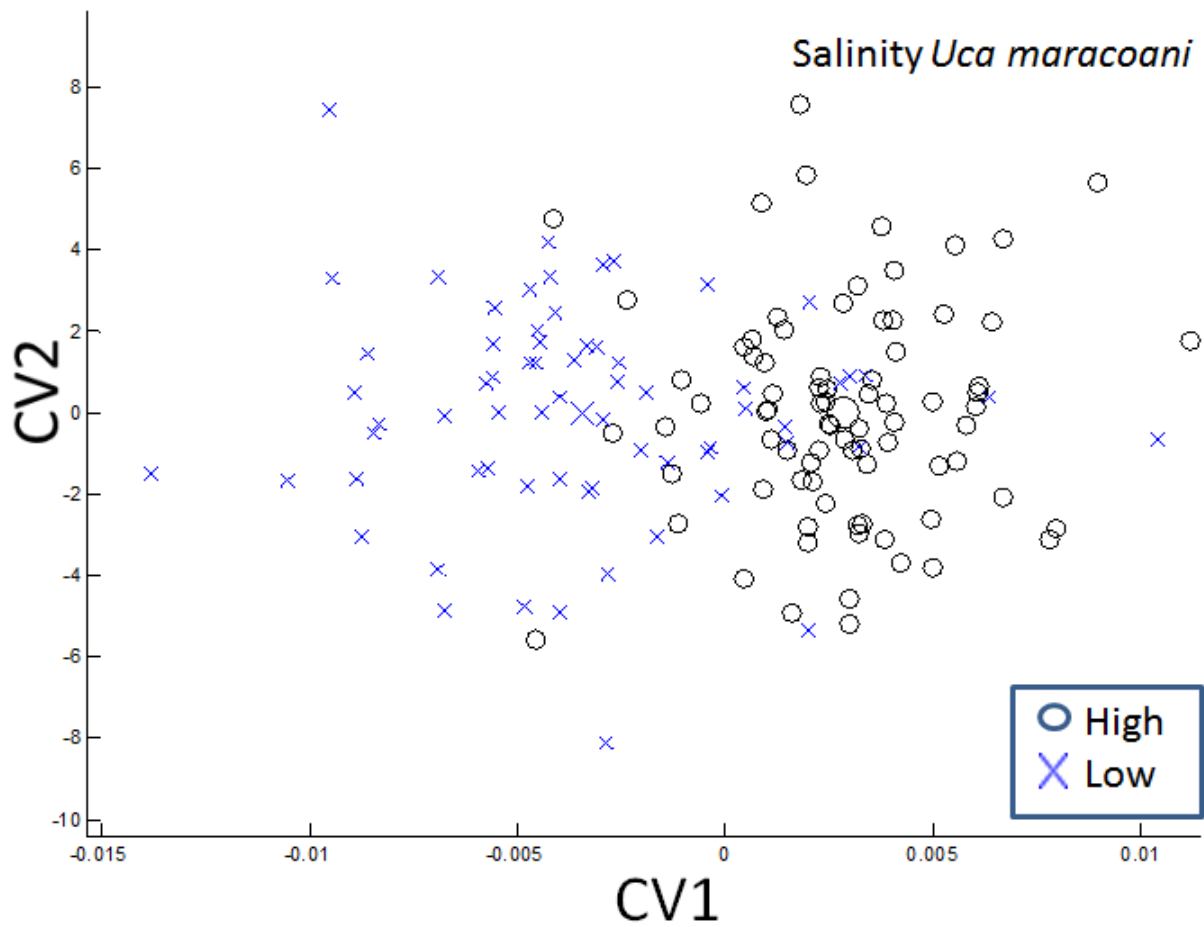


Figure 24. Canonical variance analysis plot (CV1 vs CV2) of all Brazilian samples of *U. maracoani*. When viewed on the horizontal CV1 axis, low and high salinity have marginal overlap.

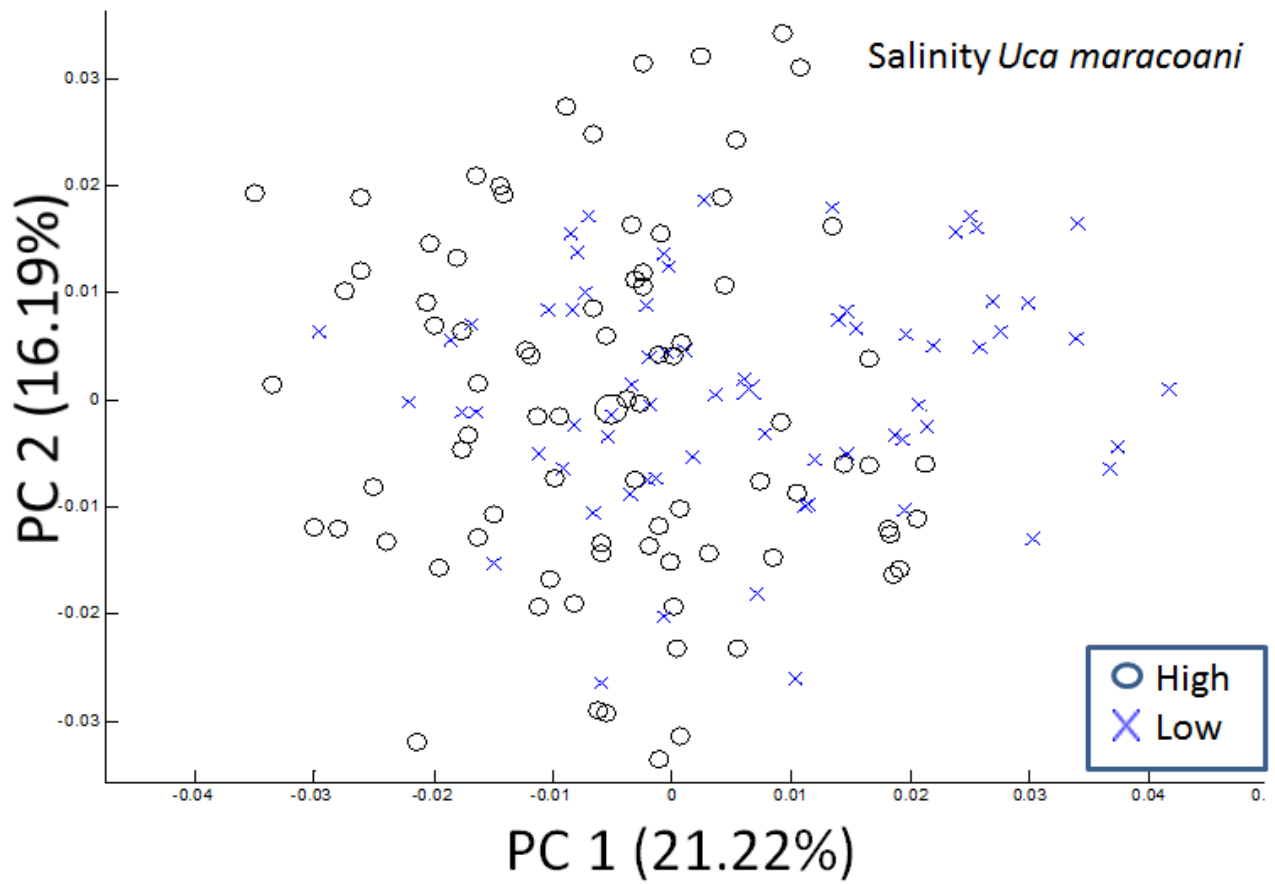


Figure 25. Principal components analysis of all *U. maracoani* samples from Brazil based on high or low salinity. Symbol colors indicate different species. PC1 and PC2 scores denote variance accounted for by that axis.

Salinity	F-score	p value	Distance Between Means
High/Low	7.48	0.0011	0.0154

Table 6. Goodall's F-test comparison from Procrustes coordinates of landmark data contrasting high and low salinity in Brazilian *Uca maracoani*. The comparison resulted in a statistically significant value, $p \leq 0.0011$. Distances between the means were 0.0154.

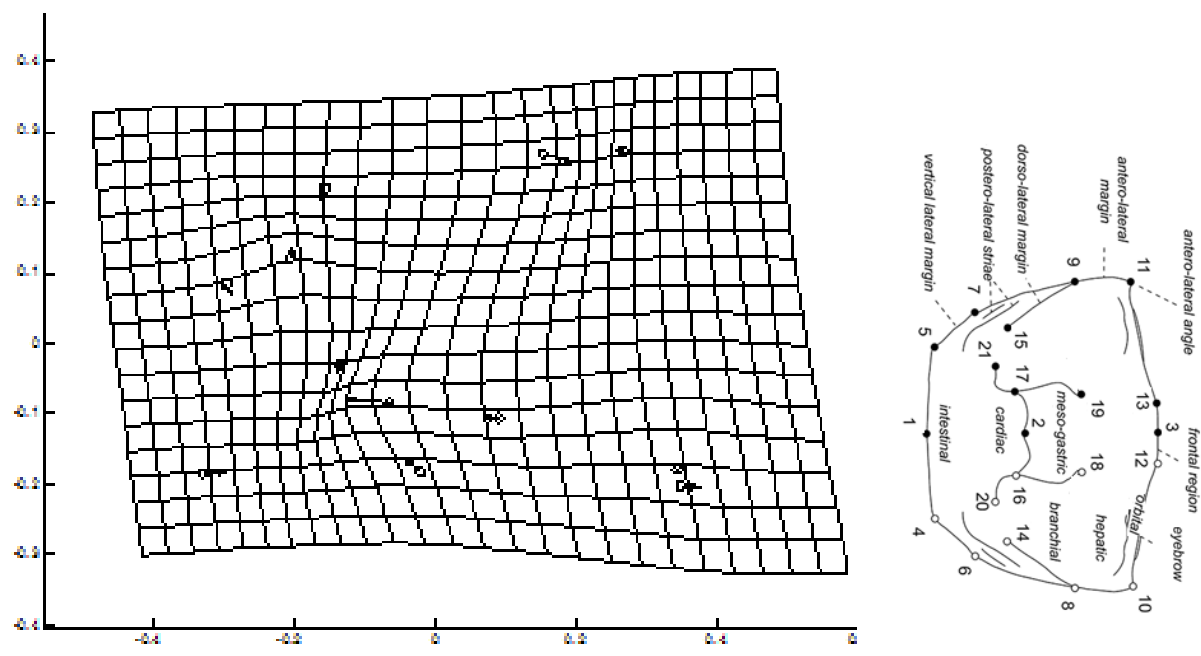


Figure 26. Procrustes deformation plot from CV1 for salinity. Most variation is seen in the antero-lateral margin and the postero-lateral margin.

IMPACT OF HABITAT SUBSTRATE ON *U. MARACOANI*

Like salinity, substrate (sand or mud), 21.22% of variation is represented on the PC1 axis, Figure 27. While PC1 illustrates considerable overlap among populations from sandy or muddy areas, the morphology of crabs from the different substrates do differ significantly (Figure 28). The canonical variates analysis gives similar results, though with a larger degree of separation, but with quite a few outliers from each substrate. Bootstrapped F-tests (Table 7) show that while the distance is significant, the mean partial Procrustes distance between the means is only 0.0133. Figure 29 illustrates the areas of greatest plasticity as seen in the Procrustes deformation plots from CV1, which are a narrowing of the rostrum and an increase of the antero-lateral margin.

Although we are limited to detailed analysis in only one species, it appears that morphological variation in all three species varies with latitude. Based on our analysis of *U. maracoani*, environmental factors such as climatology (Biotope), salinity and substrate have a decided influence on carapace shape. Apparently muddy substrates in high salinity habitats produce crabs with a shape differing from those living (or developing) in sandy habitats with lower salinity. Exactly how this influences development awaits exploration.

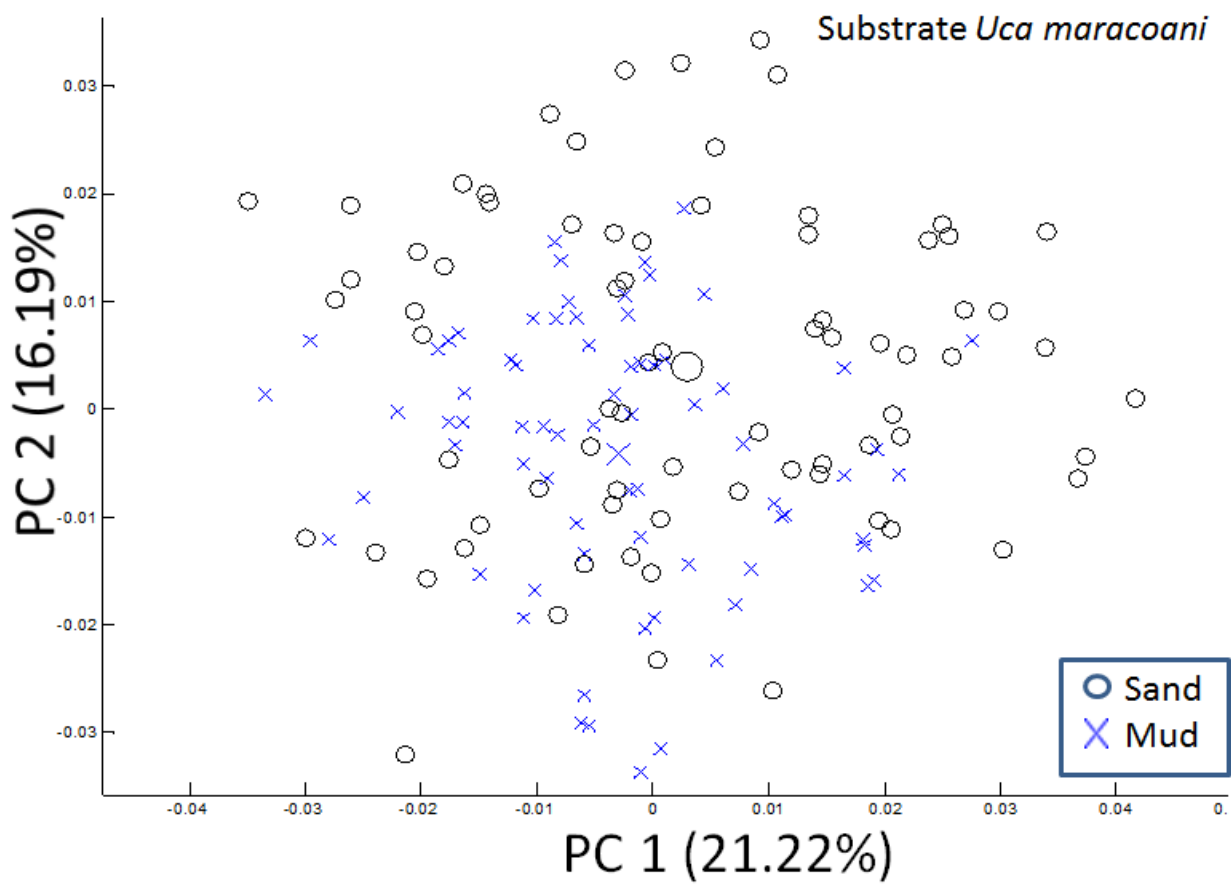


Figure 27. Principal components analysis of all *U. maracoani* samples from Brazil based on sandy or muddy substrate. Symbol colors indicate different species. PC1 and PC2 scores denote variance accounted for by that axis.

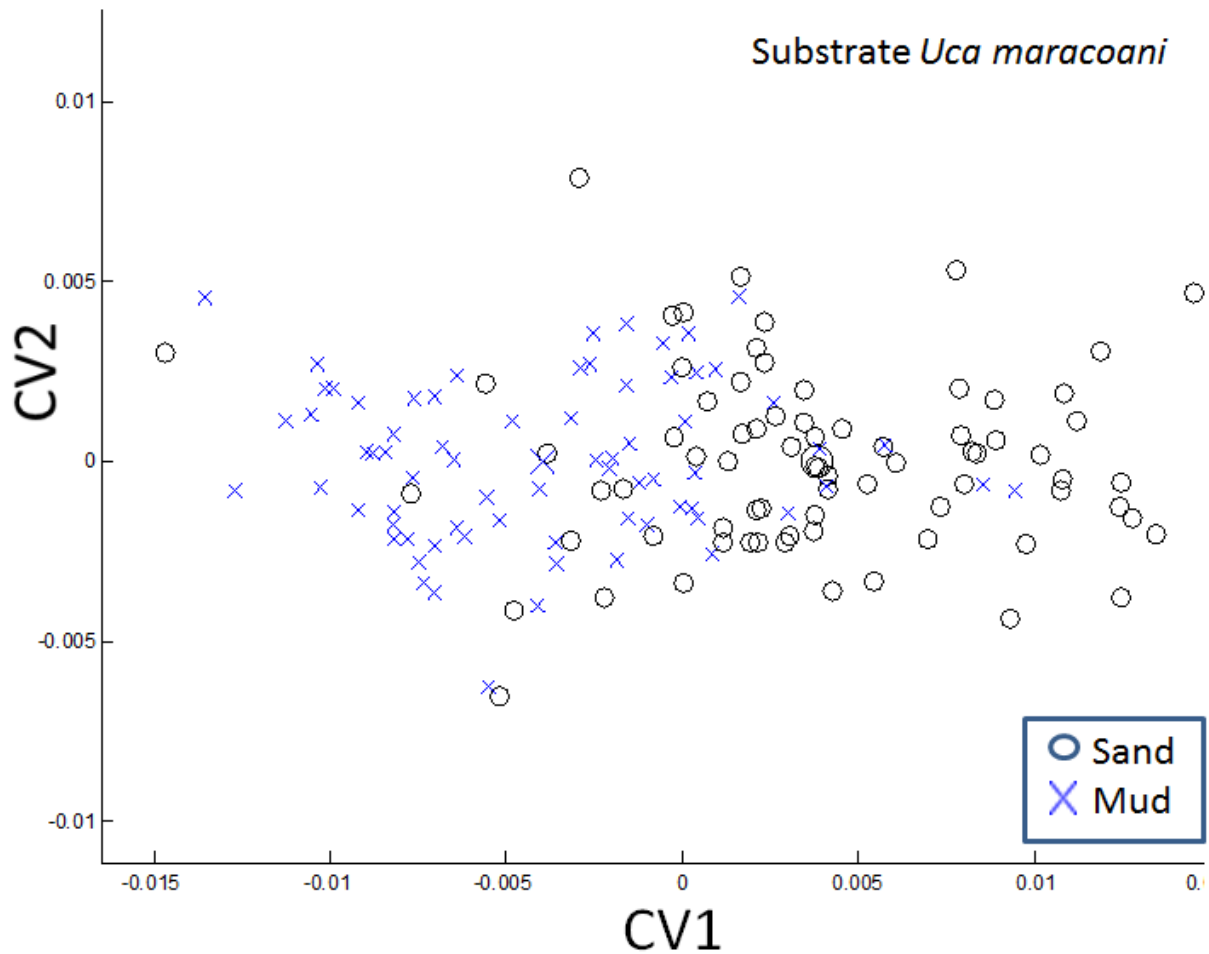


Figure 28. Canonical variance analysis plot (CV1 vs CV2) of all Brazilian samples of *U. maracoani*. When viewed on the horizontal CV1 axis, different substrates display some overlap. When viewed on the vertical CV2 axis, there is complete overlap between various substrates.

Substrate	F-score	p value	Distance Between Means
mud-sand	5.59	0.0011	0.0133

Table 7. Goodall's F-test comparison from Procrustes coordinates of landmark data contrasting muddy and sandy substrates in Brazilian *Uca maracoani*. The comparison resulted in a statistically significant value, $p \leq 0.0011$. Distances between the means were 0.0133.

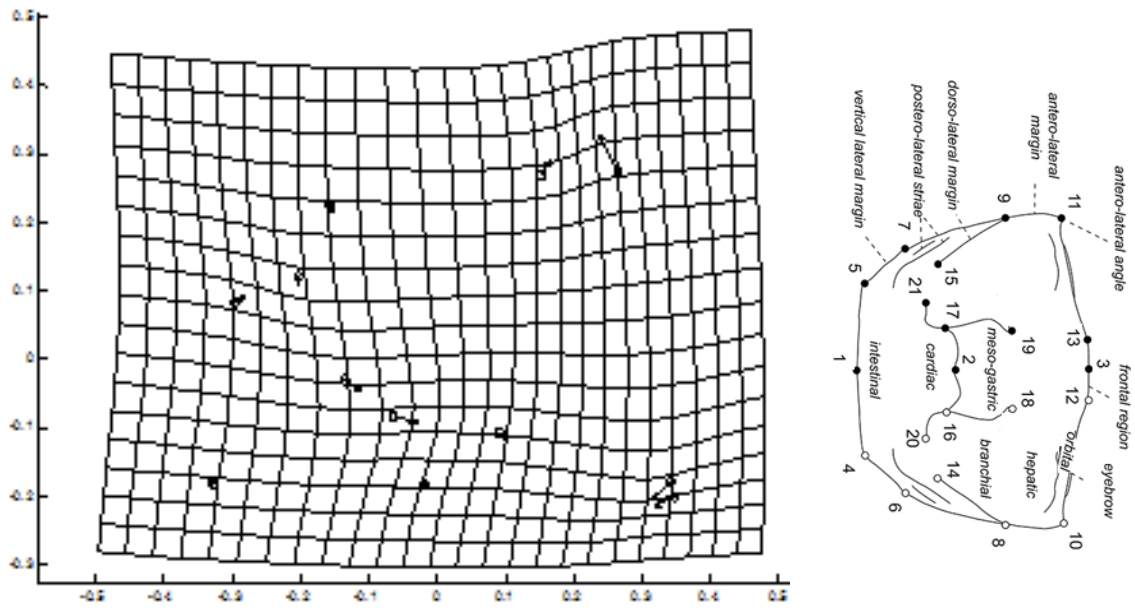


Figure 29. Procrustes deformation plot from CV1 for substrate. Most variation is seen in the rostrum and the antero-lateral margin.

DISCUSSION

Morphological variation may be related to the influence of several different forces working simultaneously on an organism (Williams 1966). Differences among or within species may be the consequence of disruptive natural selection acting on different populations. On the other hand, variation may be due to random variation and bottle necks in communication (migration) among those populations. Within a species, variation may be linked on both habitat and genetic diversity. In this study, interspecific variation appears to have resulted from the divergence of *Uca major*, *U. maracoani*, and *U. tangeri* over the last forty to fifty million years. Intraspecific variation across the latitudes was significant in all three species. In the case of *U. maracoani*, where they are known, biotope, salinity, and substrate were examined in detail across populations in Brazil to determine which factors impact carapace morphometrics. It appears that intraspecific variation in carapace form, in part, can be related with specific environmental conditions, particularly biotope region. Since it has been established that morphometric variation occurs without genetic distinction (Miner et al. 2005), these results suggest phenotypic plasticity plays a major role in anatomical acclimation to new habitats.

DISTRIBUTION IN RELATION TO DISPERSAL POTENTIAL

The distribution of each of the three species studied here is clearly associated with their respective tectonic plates (Figures 2 and 3). Since their zoeae and megalopae spend two to three months offshore in the plankton (Hyman 1922), this would imply they are susceptible to transport by the oceanic currents. Based on this potential for long-distance dispersal (Palumbi 1994), it is surprising that these ancient, basal species are not more widely distributed. In the western Atlantic, the oceanic current flows from northern South America into the Caribbean. *U.*

maracoani, in particular, has the potential for ranging from the Ponta do Calcanhar to the Yucatan and southern Mexico (Thurman et al. 2013). However, except for a single specimen from the Dominican Republic (Crane 1975), the species' boundary is only as far north as Venezuela and Trinidad-Tobago (von Hagen 1970, Crane 1975). On the other hand, based on hydrography, it is unlikely that *U. major* would be found in northern South America since the prevailing current flows north. Its present distribution lies from Trinidad north to Mexico and the Bahamas (von Hagen 1970, Thurman et al. 2010, Utrera-López and Capistrán-Barradas 2013). It appears to be mostly an insular species.

Across the Atlantic, *U. tangeri* is the only fiddler crab species along the western shores of African continent and southwestern Europe. Due to cold currents converging on the Equator from the north and south, this species is not expected at higher latitudes. In the north, larvae are distributed southward from Portugal and Spain toward the Equatorial Current, while in the south the current brings larvae from Angola north toward the equator. Furthermore, *U. tangeri* does not occur frequently off-shore of islands in the eastern Atlantic (i.e. Azores, Madeira, Cape Verde, Príncipe, Tinhosa Pequena, Tinhosa Grande, São Tome, Annobón and St. Helena). Based on a rare specimen, it has only recently been documented on Gran Canaria in the Canary Islands (Castro 2012). Like the *Uca (sensu lato)* in Brazil, the current range of *U. tangeri* is not explained by a combination of oceanographic hydrology and long-distance dispersal potential. In spite of their potential, the three species from the subgenus *Uca (sensu stricto)* are not distributed by ocean currents far beyond their “home” tectonics.

By contrast, some members of the recently evolved “broad-fronted” subgenera (i.e. *Leptuca* and *Minuca*) clearly demonstrate a long-distance dispersal potential using the ocean current. Although several species within each subgenus are endemic to various tectonic plates in

the western Atlantic (i.e. North American, Caribbean and South American), five are distributed across all three plates: *U. burgersi* Holthuis 1967, *U. rapax* (Smith 1870), *U. vocator* (Herbst 1804), *U. leptodactyla* (Rathbun 1898) and *U. thayeri* (Rathbun 1900). The other thirteen, including *U. maracoani* and *U. major*, are restricted in distribution to location on each of the three plates (Thurman et al. 2013). Lopez-Duarte et al. (2011) discovered that zoeae of some fiddler crabs can adjust their pattern of vertical migration to either catch or avoid select tides. This appears to be a behavioral mechanism for regulating dispersal. If the larvae choose to enter the water column on an ebb tide, they will be dispersed over a greater distance than individuals selecting to ride the flood tides and remain in the local nursery. Apparently, the species with more cosmopolitan distributions select ebb tides to assure long distance dispersal. On the other hand, species with limited distributions selected flood tides to remain in the estuary inhabited by their parents. Since the duration of larval development does not vary widely between narrow-fronted and broad-fronted species, the ability for larvae to independently navigate flood or ebb tide transport may be a key propensity in long-range dispersal. It appears to be better developed in the more recently evolved taxa than the ancient-basal species.

INTERSPECIFIC VARIATION

In general, closely-related species resemble each other, superficially. From Rosenberg's study of 88 species and 236 discrete morphological characters, the subgenus *Uca* (*sensu stricto*) is basal in the phylogeny of the genus (2001; fig 4; Figure 30). *Uca tangeri*, *U. major* and *U. maracoani* are literally proximal to each other near the bottom of the tree implying morphological similarity. When projected in morphospace the three form quite distinct and separate clusters (Figures 10 and 11). Assuming these species are monophyletic with a common

origin on a single tectonic plate, it is likely that time drove their ancestor on at least three separate evolutionary trajectories. As the present tectonics have drifted apart for the last 140 million years, the distinctness of each species is the result of a vicariant evolutionary processes (Cox and Moore 2010). Since larval dispersal potential in the basal species is limited, over time natural selection and genetic drift have produce three species from their progenitor(s) on different tectonic plates. Their morphological distinctness is supported by the statistically significant Partial Procrustes distances of the means between the species (Table 3). In spite of their relatedness and similarity, there is little basis for confusing the three taxa as was the case historically (Bott 1973, Holthuis 1979). Currently, these species have been adequately re-described and there is little chance of taxonomic confusion.

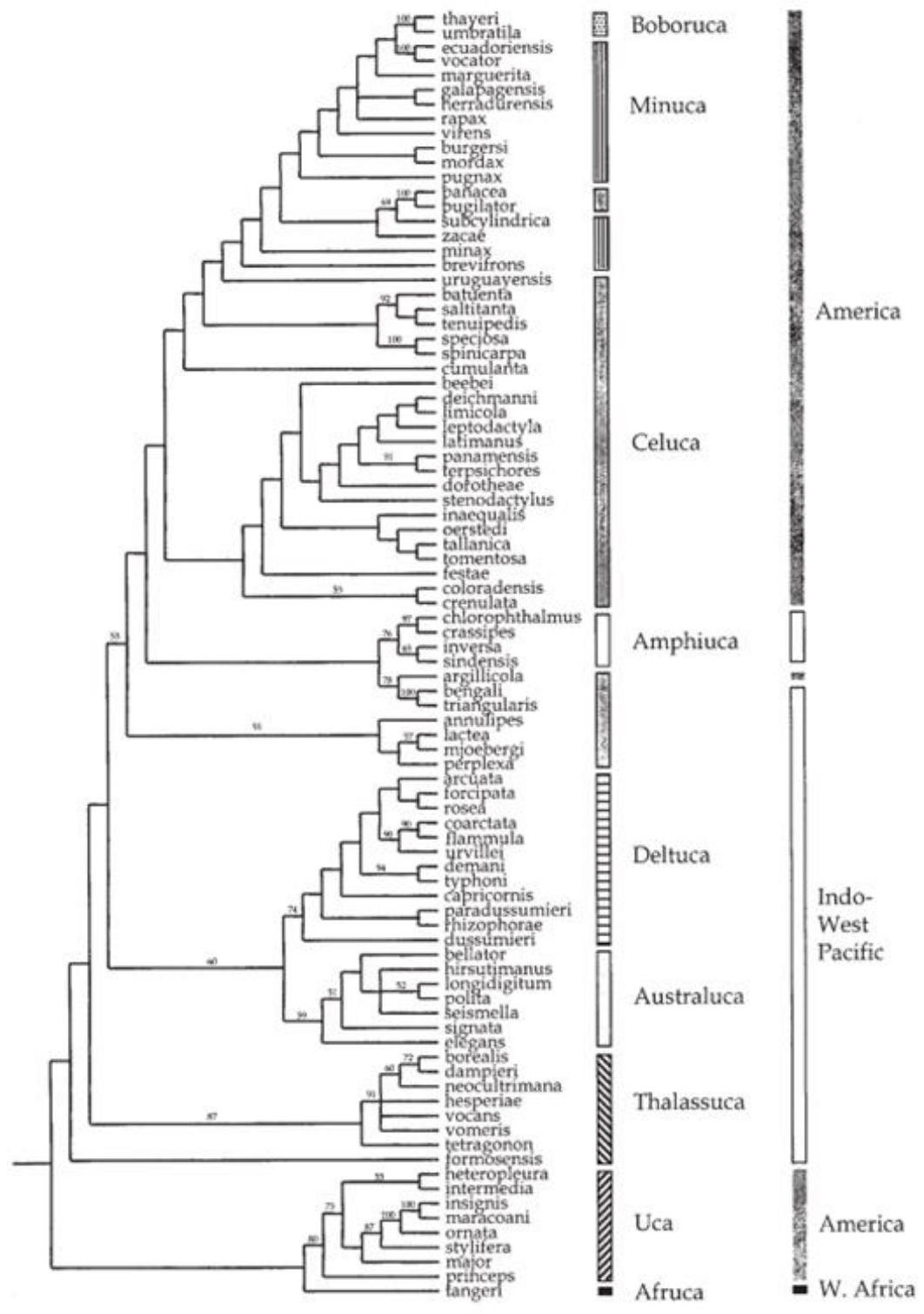


Figure 30. Phylogeny of *Uca* from Rosenberg (2001) "Strict consensus of 12 most-parsimonious trees (length = 1,517, CI = 0.161, RI = 0.660) from unconstrained analysis. Numbers above branches are bootstrap values."

INTRASPECIFIC VARIATION IN THE THREE SPECIES

In the absence of large temperature gradients in the tropics, several other environmental factors are known to regulate carapace form in fiddler crabs (Hopkins and Thurman 2010, Hampton et al. 2014). From both CV and PC analyses, all three species studied here exhibit distinct latitudinal patterns in shape variation (Table 4). Among the three, the greatest extent of divergence is seen in *U. major* and the least in *U. maracoani*. The area with the largest degree of variation was the branchial region. In southern populations of *U. major*, the frontal region is more swollen while the branchial region is compressed. The areas of greatest deformation in *U. maracoani* are the frontal and hepatic regions. Southern populations have a narrower hepatic and broader frontal region than northern populations, overall. In *U. tangeri*, the meso-gastric region is more swollen in southern populations, and the hepatic region broader. Although there is significant variation in carapace structure with latitude in each species, the nature of the transforming vector is unknown in this analysis. Alone, latitude has no direct influence. Rather, the analysis implies either gradients in environmental factors or genetic structure to be associated with global position. Among the three Atlantic species from the subgenus *Uca* (*sensu stricto*), we have genetic and environmental data only for *U. maracoani*. From this it is possible to examine how carapace shape variation is correlated with each factor. Using a mitochondrial loci for cytochrome oxidase (COX1) and amplified fragment length polymorphisms (AFLP) analysis, the populations of *U. maracoani* along the coast of Brazil exhibit little or no genetic variation and structure (Wieman et al. 2014). Consequently, carapace shape is a result of ecophenotypic variation.

Ecophenotypic plasticity is apparent in the fiddler crabs of Brazil. Using the Ponto do Calcanhar as a barrier to gene flow via oceanic currents, Hampton et al. (2014) found significant

variation in the carapace shape of eight “trans-Brazilian” species of *Uca* (*sensu lato*) including *U. maracoani*. In the present study, factors such as biotope, salinity and substrate were found influence carapace morphology in *U. maracoani*. Both biotope and salinity appear to have similar impacts on the morphology of a carapace in female crabs (Tables 5 and 6). Both are associated with constriction of the antero-lateral and the postero-lateral margins. Substrate, however, appears to have a different influence on morphology in that it narrows the rostrum and increases the antero-lateral margin in populations found on sandier substrates. Consequently, it is reasonable to suspect that other environmental factors change in a systematic fashion across latitudes. From a morphometric perspective, this possibility remains to be investigated in most species.

Geometric morphometrics have been used to study the carapace in several different crustaceans including crabs. Rufino et al (2006) found the carapace of the crab *Liocarcinus depurator* to vary along the Mediterranean coast of Spain. They attributed this plasticity to differences in currents along the shore. Across the Mediterranean Sea, Black and Spanish Atlantic Ocean, the crab *Xantho poressa* was found to vary in carapace color and shape (Reuschel and Schubart 2007). Since neither feature correlated with genetic differences in COX1 among populations, it appears that phenotype variation is due to different habitats across the range in the species. Recently, Lezcano et al. (2012) found the crab *Cyrtograpsus affinis* from two different estuaries on the South Atlantic coast of Argentina to differ significantly in carapace shape. The authors attributed variation to the aquatic variables turbidity, temperature and salinity. On Reunion Island in the Indian Ocean, the carapace of the freshwater prawn *Macrobrachium austral* varies between lentic and lotic stream habitats (Zimmermann et al. 2012). Since the island is small and spawning occurs in saltwater, the adults migrate up island

streams. The rostrum grows longer in slower running streams. In another crab from Argentina, *Cyrtograpsus angulatus*, Idaszkin et al. (2013) found that the carapace is more slender in specimens from rock habitats and longer in those from muddy salt marshes. The authors proposed that the slender shape was a modification necessary for living in small spaces along the rocky shore. In fiddler crabs from the Gulf of Mexico, the aridity of the local habitat has a greater impact on carapace shape than other environmental factors (Hopkins and Thurman 2010). In crabs from sub-arid coastal habitats, the carapace appears to be swollen as a method for water conservation preventing desiccation. Consequently, the impact of salinity and substrate on carapace shape of *U. maracoani* in the absence of genetic variation is not unanticipated. These environment pressures apparently promote structural variation in carapace shape among several species of *Uca*. Although similar habitat data is unavailable for *U. tangeri* and *U. major*, ecophenotypic variation in these species is probably associated with one or more habitat variables as in *U. maracoani*.

LIMITATIONS

One of the limitations of this study was the lack of data for environmental factors for all specimens other than *U. maracoani* from Brazil. For all other samples, only latitude was available for comparison. Additionally, temperature gradients could have been another environmental factor worth studying.

Furthermore, information on genotypic variation is not readily available, which would provide details about gene flow in fiddler crabs. Phenotypic variation is readily influenced by many environmental factors as well as genetic factors.

Lastly, female specimens were very limited for *Uca major*, with only one specimen each coming from Colombia, Mexico, and Trinidad, and only three from Jamaica. Our largest sample population came from the Bahamas, and contained only 26, giving a total sample size of 32 individuals of *U. major*. Small sampling sizes may not reflect the morphology of crabs from this region accurately. A larger sample size may provide a better representation of the region for comparison with other species.

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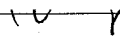
This study by: Katherine Thomas

Entitled: Latitude and Environmental Pressure: Their Impact on Carapace Morphology in
Three Species of Fiddler Crabs (Genus *Uca*) Across the Atlantic Ocean

has been approved as meeting the thesis or project requirement for the Designation University
Honors with Distinction.


5/5/2014

Date


Dr. Carl Thurman, Honors Thesis Advisor, Biology Department


5/1/14

Date


Dr. Melanie Hopkins, American Museum of Natural History

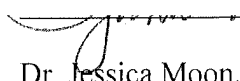
5/5/14

Date


Dr. David Saunders, Ph.D. Chair and Head of Biology Department

5/5/14

Date


Dr. Jessica Moon, Director, University Honors Program