



Intraspecific variation in carapace morphology among fiddler crabs (Genus *Uca*) from the Atlantic coast of Brazil

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ABSTRACT: Isolation due to geographical barriers should promote genetic and morphological divergence among populations. Marine currents flowing in opposing directions along landmasses can constitute barriers that isolate populations dependent upon aquatic dispersal. The distribution of fiddler crabs (genus *Uca*) is regulated primarily by the oceanic transport of their planktonic larvae and by available adult habitat. Along the Brazilian coast of eastern South America, the flow of 2 major oceanic currents separates northern from southern *Uca* populations, which may promote intraspecific divergence in 'trans-Brazilian' species. Populations of 10 *Uca* species were sampled at 64 locations north and south of the Ponta do Calcanhar, Rio Grande do Norte, Brazil. Carapace shape was assessed using geometric morphometrics to analyze 12 surface landmarks in 1319 female crabs. Carapace shape differs significantly in each species. In morphospace, the carapace forms of the 10 species appear to separate into traditional subgeneric clusters. Within the 8 species exhibiting trans-Brazilian distributions, northern and southern populations show distinct carapace differences. Depending on species, either the hepatic or the branchial region is larger in northern populations. Since significant genetic variability among such populations has not been confirmed, divergence in carapace shape suggests significant ecological modulation of phenotype within each species. Apparently, environmental differences between northern and southern localities exert a greater impact on carapace morphology than impeded gene flow. The drivers underpinning diversification of carapace shape remain unknown, however.

KEY WORDS: Brachyura · Fiddler crab · *Uca* · Structural variation · Landmark analysis · Isolation · Ecophenotypy

INTRODUCTION

The coast of Brazil constitutes a composite of 5 contiguous tropical and subtropical biomes, stretching from above the Amazon River in the north to the border with Uruguay in the south (Thurman et al. 2013). Two of these biomes occur along the northern coast, and 3 along the southern coast, where they are separated by the Ponta do Calcanhar in Rio Grande do Norte state. At the Ponta do Calcanhar, the westward flow of the Central South Equatorial Current (CSEC)

splits into the North Brazil/Guiana Current (NBC) and the South Brazil Current (SBC) (see Fig. 1) constituting a significant biogeographical barrier for species with planktonic larval stages (Briggs 1974, Shanks 2009, Weersing & Toonen 2009). Further to the north, the freshwater outflows of the Amazon and Orinoco Rivers form a substantial barrier to the distribution of littoral and shallow-water marine species into the southern Caribbean via the North Brazil Current (Rocha 2003). In contrast, the South Brazil Current that flows along the 3 southern biomes appears

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to be unimpeded by significant freshwater outflow. To illustrate, molecular studies have shown littoral populations of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) between Ponta do Calcanhar and São Paulo to be genetically homogeneous, implying a high degree of connectivity and panmixia among populations (Oliveira-Neto et al. 2007).

Fiddler crabs are fossorial, semi-terrestrial crustaceans that live primarily in the littoral zone of protected bays, estuaries and lagoons, and particularly in mangroves (Crane 1975). Twenty species of *Uca* are known from the shores of the western Atlantic, Gulf of Mexico and the Caribbean Sea (Beinlich & von Hagen 2006). The geographical range of the adult crabs appears to be partly dependent on the dispersal of planktonic larvae carried by ocean currents and tides (Epifanio et al. 1988, Christy 2011, López-Duarte et al. 2011, Shih 2012). Of the 10 species inhabiting the coastline of the western South Atlantic Ocean, 8 occupy both the northern and the southern coasts of Brazil (Melo 1996, Bezerra 2012, Thurman et al. 2013) and represent 4 subgenera. When adult females along the northern coast release zoeae into estuarine or coastal waters, the larvae are transported toward the Amazon River and the Caribbean or out into the mid-Atlantic Ocean. In contrast, larvae released along the southern coast are transported in the opposite direction toward Cabo Frio and Uruguay (Boltovskoy et al. 1999, Psuty & Mizobe 2005).

While the geographical distribution of *Uca* (sensu lato) in Brazil is influenced primarily by regional hydrology, geomorphology and climate (Thurman et al. 2013), ocean current patterns help regulate larval dispersal and thus direct gene flow and affect connectivity. Connectivity in turn can influence intraspecific variation both within and among marine populations (Kelly & Palumbi 2010, Sanford & Kelly 2011, Ituarte et al. 2012). The division of the major currents at the Ponta do Calcanhar, in particular, may significantly control gene exchange between the northern and southern populations of individual fiddler crab species. Should this be the case, we would expect to see divergence among northern and southern populations.

By the early Miocene (22 million years ago), fiddler crabs were genetically distinct from other Ocypodidae (Levinton et al. 1996, Sturmbauer et al. 1996), and all Pacific and North American clades of *Uca* were genetically distinct by the late Miocene (17 million years ago). Rosenberg (2001) analyzed the phylogeny of 88 species of *Uca* using 236 morphological traits, providing results similar to those previously reported in molecular studies. Nevertheless, the pre-

vailing view holds that speciation in *Uca* from the western Atlantic has proceeded without significant morphological divergence (Salmon et al. 1979, Levinton 2001). Crane (1975) reported difficulty in distinguishing among females of 3 sympatric Brazilian species belonging to the subgenus *Leptuca*. She felt that the females of *U. leptodactyla* Rathbun, 1898, *U. cumulanta* Crane, 1943 and *U. uruguayensis* Nobili, 1901 differed only in relative proportions. However, very few studies have quantitatively addressed intraspecific phenotypic variation in *Uca* over a wide geographical area. Silva et al. (2010) found the widespread species *U. annulipes* (Milne-Edwards, 1837) from southeast Africa to exhibit very little morphological or genetic structure, suggesting that populations distributed over 3300 km between Mikindani, Kenya, and Mlalazi, Republic of South Africa, are sufficiently connected by high larval transport to maintain panmixia. In contrast, along 13 500 km of coastline in the USA and Mexico, several endemic *Uca* species show detectable morphological variation (Hopkins & Thurman 2010) even though the widespread species do not necessarily exhibit greater variation than species with smaller ranges.

In this study, we examine the impact of the major oceanic currents along the eastern coast of South America on phenotypic variation in several species of fiddler crabs from Brazil. Specifically, we address 2 questions: (1) Based on carapace structure, are the various *Uca* species morphologically distinct? (2) Does the Ponta do Calcanhar constitute a significant geographical feature coincident with phenotypic diversification within each *Uca* species? After collecting and preserving specimens from numerous locations, we performed geometric morphometric analyses to quantify variation in carapace shape both within and among the 10 *Uca* species from Brazil. We expanded Rosenberg's (2001) phylogenetic analysis to include all the Brazilian species, finding that morphological variation largely corresponds to the known phylogenetic relationships. Further, the 8 trans-Brazilian species exhibited morphological differences between their northern and southern populations, suggesting that the Ponta do Calcanhar might represent a biogeographical feature that underpins intraspecific divergence. In general, as carapace width broadens, length shortens when comparing specimens from northern to southern populations. The greatest variation occurs in the branchial and hepatic regions. However, given available genetic information for *Uca* species from Brazil, such differentiation does not appear to correlate with underlying genetic structure (Wieman et al. 2013).

MATERIALS AND METHODS

Sampling

Over 7000 fiddler crab specimens were collected from habitats along 9600 km of the Brazilian coast between 2009 and 2010 (Thurman et al. 2013). Field collections, authorized by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA, permit nos. 2009/18559-1 and 2010/23976-1) were made at 64 localities between the states of Amapá (AP) and Santa Catarina (SC) (Fig. 1). Fifty-four of these locations were sampled between Pernambuco (PE) (Itapissuma, Ilha de Itamaracá, and northernmost point) and SC (Palhoça, Barra da Passagem, and Rio Massambu) from June to November 2009. The remaining 10 localities were sampled from AP (Calçoene, Rio Cacoal) to Ceará (CE) (Fortaleza, Rio Cocó) between June and August 2010. These sites were not randomly chosen but constitute convenient points of access to littoral habitats by road, track or boat; the collections may be biased for particular or rare species. The habitat character (salinity, substrate), species composition and precise location of the sites are provided in Table S1 in the Supplement (available at www.int-res.com/articles/suppl/b020p053_supp.pdf).

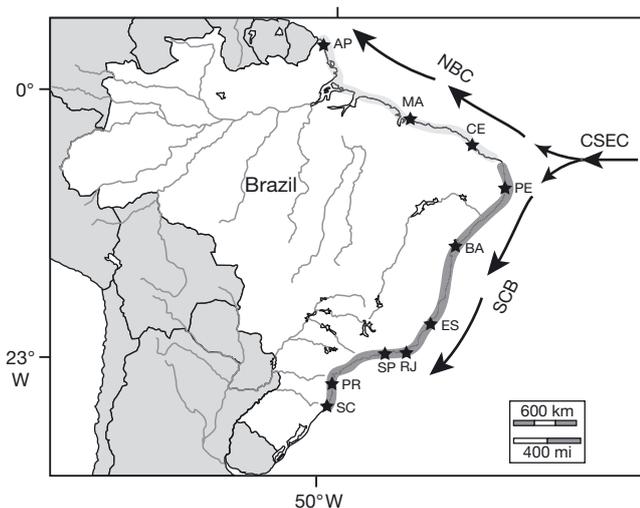


Fig. 1. *Uca* spp. General sampling localities for fiddler crabs along the coast of Brazil (AP = Amapá, MA = Maranhão, CE = Ceará, PE = Pernambuco, BA = Bahia, ES = Espírito Santo, RJ = Rio de Janeiro, SP = São Paulo, PR = Paraná, SC = Santa Catarina). Light gray shading denotes northern localities; dark gray shading denotes southern localities. Pertinent surface ocean currents are indicated by arrows (CSEC = Central South Equatorial Current, SBC = South Brazil Current, NBC = North Brazil Current). See Table S1 in the Supplement (available at www.int-res.com/articles/suppl/b020p053_supp.pdf) for site details

Species identification

The 10 species of fiddler crabs collected during this study were identified using traditional morphological characteristics. Since 5 of the species occur in North America, details of their morphologies have been described elsewhere (Barnwell & Thurman 1984). A dichotomous key (Melo 1996) was used to identify the Brazilian fiddler crabs, together with supplementary descriptions of the more cryptic species (Crane 1943, Holthuis 1967, Chase & Hobbs 1969, Coelho 1972, von Hagen 1987, Tavares & de Mendonça 2003, Bedê et al. 2007). Although there is some overlap between the morphological characters used to discriminate among species and those captured by the landmark data (see below), specimens were assigned to species prior to digitizing landmarks. Thus, the character set used to identify specimens and that used to estimate variation are not coincident. Further, species were identified largely by one investigator (C.L.T.) while morphometric analysis was performed by others (M.J.H., K.R.H.).

The 10 Brazilian species are divided among 4 subgenera (Melo 1996): (1) subgenus *Uca* (sensu stricto) (*U. maracoani* (Latreille, 1802–1803)); (2) subgenus *Boboruca* (*U. thayeri* Rathburn, 1900); (3) subgenus *Leptuca* (*U. cumulanta* Crane, 1943, *U. leptodactyla* Rathburn, 1898, and *U. uruguayensis* Nobili, 1901); and (4) subgenus *Minuca* (*U. burgersi* Holthuis, 1967, *U. mordax* (Smith, 1870), *U. rapax* (Smith, 1870), *U. victoriana* von Hagen, 1987, and *U. vocator* (Herbst, 1804)). For simplicity, subgenus is incorporated into the species' name throughout (e.g. *Uca Minuca victoriana* or *U. (M.) victoriana*).

Eight of the 10 species (*U. Minuca burgersi*, *U. Leptuca cumulanta*, *U. (L.) leptodactyla*, *U. (U.) maracoani*, *U. (M.) mordax*, *U. (M.) rapax*, *U. Boboruca thayeri*, and *U. (M.) vocator*) are distributed both north and south of the Ponta do Calcanhar. Two species, *U. (L.) uruguayensis* and *U. (M.) victoriana*, do not extend north of the Ponta do Calcanhar to any great degree. Consequently, only 8 species, here termed 'trans-Brazilian' species, could be examined for intraspecific morphological variation relative to the prevailing oceanic currents along the Atlantic coast of Brazil.

Phylogenetic analysis

A phylogenetic reconstruction for the 10 species of *Uca* from Brazil was created based on a parsimony

analysis of morphological characters. A scored list of 236 characters for each of 11 species was taken from Rosenberg (2001). A character list for *U. Minuca victoriana* was developed from preserved specimens taken at the type locality in Vitoria, Espírito Santo by H. O. von Hagen (Table S2 in the Supplement). Since a close taxonomic relationship seemed likely between *U. (M.) rapax*, *U. (M.) victoriana* and *U. (M.) marguerita* Thurman, 1981, *U. (M.) marguerita* was also included to clarify and assess the *rapax*–*victoriana* relationship (von Hagen 1987). Two maximum parsimony trees were found employing PAUP software, version 4.0b10 (Swofford 2000) and the PaupUp, version 1.0.3.1 graphical interface (Calendini & Martin 2005), using the Branch-and-Bound search algorithm and *U. Afruca tangeri* (Eydoux, 1835) as the out-group (see Rosenberg 2001). All characters were unordered and equally weighted (121 parsimony-informative characters, 66 constant characters). Multi-state taxa were considered polymorphic. A bootstrap tree was constructed from 500 pseudo-replicates and using a full heuristic search (Fig. 2). The final tree is a strict consensus. Excluding *U. (M.) marguerita*, all tree branches were equal in length from one node and no bootstrap values were greater than 50%. Consequently, this working phylogeny with 12 species is tentative, and we have chosen not to rename any taxa, although the subgenera *Minuca* and *Leptuca* may be paraphyletic.

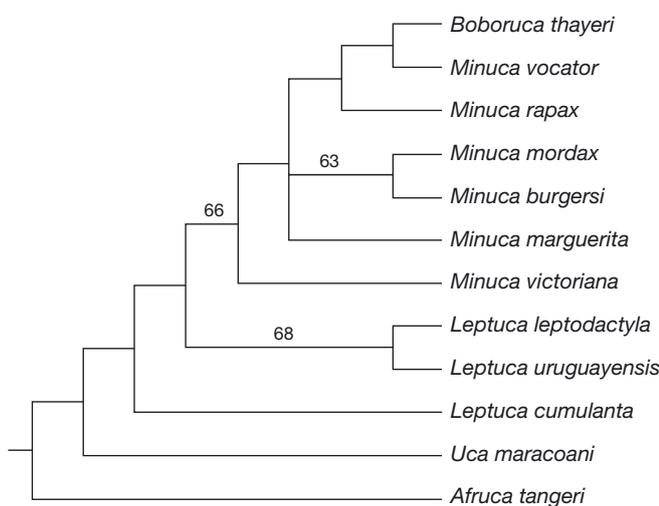


Fig. 2. *Uca* spp. Strict consensus tree of Brazilian *Uca* species obtained by maximum parsimony analysis of 236 morphological characters in each species using PAUP. Bootstrap values after 500 pseudo-replicates

Specimen preparation

After collection, live specimens were transported by air or car to a laboratory at the Centro de Biologia Marinha (CEBIMar/USP), São Sebastião, São Paulo, Brazil, where they were used in physiological experiments. Subsequently, the crabs were quickly killed by chilling and preserved in 80% ethanol (Rufino et al. 2004). Lots labeled by location for each species were deposited at the Museu de Zoologia of the Universidade de São Paulo. Since male fiddler crabs have one greatly enlarged cheliped, their carapace shape may be distorted as a structural response to claw asymmetry (Yerkes 1901, Duncher 1903, Huxley 1971, Miller 1973). Given statistical considerations, the asymmetrical component of variation within largely bilaterally symmetric organisms must be analyzed separately from the symmetrical component (Bookstein 1996, Klingenberg et al. 2002). While the asymmetrical component is frequently of interest in studies of variation within individuals (e.g. that due to developmental instability), the symmetrical component represents the shape variation among individuals. Since we were interested in this aspect of variation, and in changes related to biogeography rather than sexual selection, only female specimens ($n = 1319$) were used, and only the symmetrical component of variation was analyzed here.

Specimens were oriented for photography so that the carapace was horizontal in frontal view and its anterior- and posterior-most edges lay in the same horizontal plane in lateral view (Fig. 3). Orientation and digitization error was assessed by repeatedly mounting and digitizing a single random specimen for each species analyzed (Hopkins & Thurman 2010). A single investigator (M.J.H.) performed all photography, and all digitization was carried out by another (K.R.H.). Error was quantified by comparing disparity in the error samples with that in the species data using DisparityBox6i (Sheets 2001–2007). The disparity in each error sample was less than an order of magnitude smaller than that for the entire species; thus, measurement error was deemed negligible.

Morphometric analysis

Morphological variation was examined using geometric morphometric techniques (Bookstein 1991, Zelditch et al. 2004). A total of 21 landmarks were chosen to capture the overall shape of the carapace using the program 'tpsdig2' (Rohlf 2010). The landmarks utilized here reflect the 3-dimensional nature

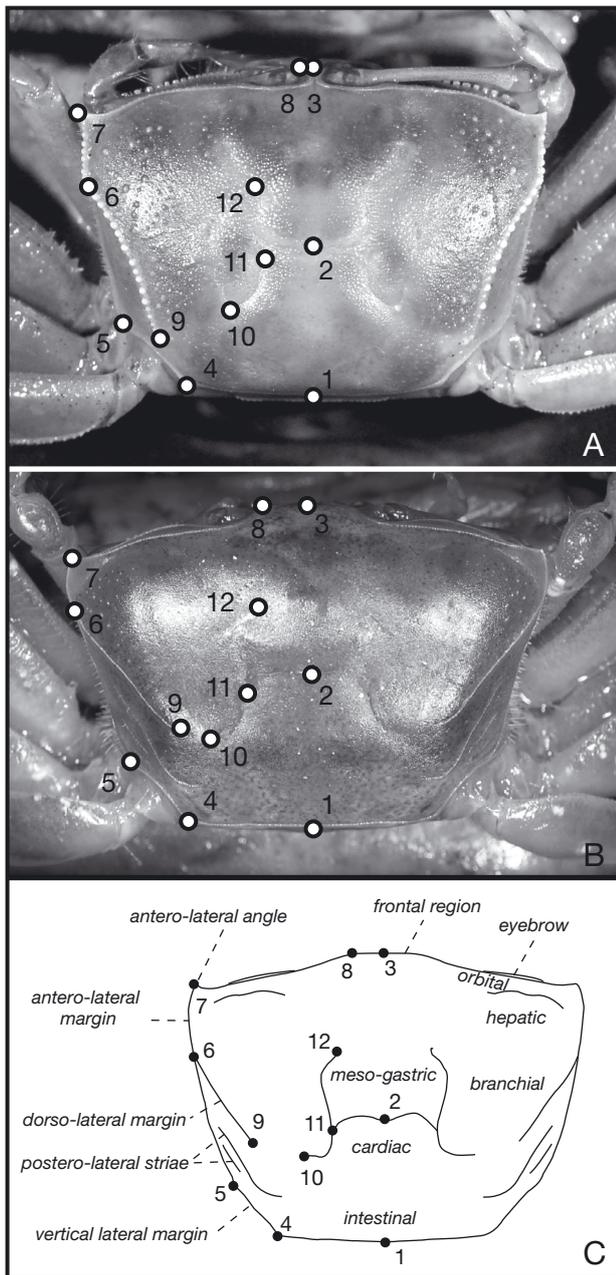


Fig. 3. *Uca* spp. Anatomical regions and location of landmarks on carapace. Circles show configuration of landmarks after averaging. (A) Female *U. maracoani* with 12 landmarks. (B) Female *U. Minuca mordax* with 12 landmarks. (C) Anatomical regions of carapace relative to landmark positions

of the carapace and its underlying structures (Hopkins & Thurman 2010; see Fig. S1 in the Supplement). As paired landmarks represent redundant information regarding the symmetric component of variation, we reflected the landmarks across the midline, leaving 12 landmarks for analysis (Fig. 3). The

landmark data were standardized using Standard6 (Sheets 2001–2007) to eliminate variation due to allometric growth (Fig. S1) and were transformed using thin-plate spline decompositions; the resulting partial and uniform warp scores were then used to perform statistical analyses (Rohlf 1990, Bookstein 1991, Zelditch et al. 2004). Partial warps describe the same variation as Procrustes residuals; each can be transformed into the other by rotation of the coordinate system.

Variation among and within species was evaluated using a principal components analysis (PCA) of the warp scores (Zelditch et al. 2004). The morphometric shape data were mapped onto the phylogeny using unweighted squared-change parsimony to reconstruct values at internal nodes from the shape averages of the species at the terminals (Maddison 1991, Klingenberg & Gidaszewski 2010). Phylogenetic signal in the morphological data was assessed using a permutation test. The morphological shape data are randomly swapped between terminals and the resulting tree lengths calculated. When phylogenetic signal is absent from the shape data, randomly swapping these data is equally likely to produce a greater or smaller tree length. If phylogenetic signal is present, then randomly swapping the shape data should result in a greater tree length. Thus, the null hypothesis holds that the shape data show no phylogenetic signal, and the empirical p-value for the test is the proportion of the permuted data sets in which the sum of squared changes is shorter or equal to the value obtained for the original data (Klingenberg & Gidaszewski 2010). Both analyses were performed using MorphoJ (Klingenberg 2011).

The Procrustes distance between species' means was used to evaluate relatedness of groups in morphospace, and a resampled Goodall's *F*-test was performed on the standardized data to test for statistically significant differences between the northern and southern populations. A canonical variates analysis (CVA) was used to describe the morphological variation between northern and southern populations. To assess the proportion of original specimens from the northern or southern populations matching the CVA discrimination, a jack-knife assessment test was performed *a posteriori* within each species. The better the assignment matches the original grouping, the better the CVA is able to discriminate between the 2 populations. A 2-way multivariate analysis of variance (MANOVA) was also conducted to test for differences in carapace shape within species and among localities (northern versus southern populations), and for any species–locality interaction. Finally,

shape trajectories between northern and southern populations were compared in terms of magnitude (vector length) and direction (angular difference between vectors). Differences were tested using a permutation test where the null hypothesis is that the difference is greater than expected from random pairs of vectors (Collyer & Adams 2007, Adams & Collyer 2009) as implemented using the trajectory analysis function in the geomorph package for R (Adams & Otarola-Castillo 2013). All effects and differences were considered significant at $p \leq 0.05$.

RESULTS

Interspecific distinctions

Principal components (PC) 1 and 2 account for 63.2% of variation across all the *Uca* (sensu lato) species examined (Fig. 4). Each species is statistically distinct from its congeners (Table 1), and species considered to be members of the same subgenus cluster closely together in morphospace (Fig. 4). The working phylogeny was projected onto the species' distributions described by the PCA and displayed in morphospace (Fig. 5). Each point represents the mean shape of the species. The morphometric data show significant phylogenetic signal ($p \leq 0.0002$ after 10 000 permutations). In the reconstruction, clear divergence is seen along the first principal component axis between species in the subgenera *Minuca* and *Leptuca*. Divergence between *U.*

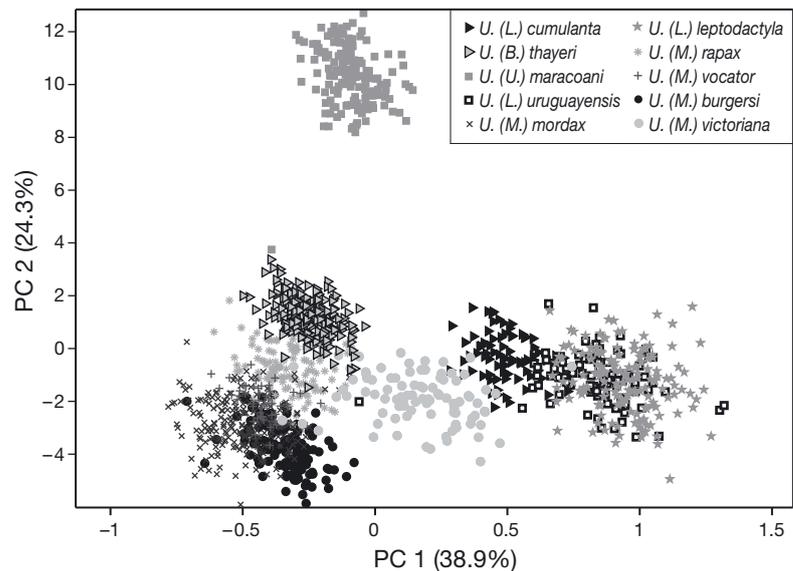


Fig. 4. *Uca* spp. Principal components analysis (PCA) for *Uca* (sensu lato) examined in the present study. The subgenus *Uca* (*U.*) occupies the upper left quadrant and is thus distinguished from the other clades along PC 2. Subgenera *Boboruca* (*B.*), *Minuca* (*M.*) and *Leptuca* (*L.*) overlap, sharing a larger total portion of morphospace, and clustering in the lower-central and middle-right regions of the plot. Subgenera *Minuca* and *Leptuca* are most clearly discriminated along PC 1. The subgenus *Boboruca* is separated from the subgenus *Minuca* along PC 2

(*U.*) *maracoani* and all other species is clearly evident along the second principal component axis. Within the subgenus *Minuca*, there is clear divergence of species along both the first and second principal components axes (lower left portion of Fig. 5).

In general, the distribution in morphospace of the 10 species of Brazilian fiddler crabs is consistent with the older evolutionary relationships suggested by Crane (1975), and supported by Rosenberg (2001) and Beinlich & von Hagen (2006). Differences among

Table 1. *Uca* spp. Species comparison among Brazilian fiddler crabs. Partial Procrustes distances between species means at lower left and in italics; resampled Goodall's *F*-test at upper right. Higher *F*-values imply greater morphological separation. Each pairwise comparison is statistically significant ($p < 0.0001$). Parentheses: species sample size (i.e. *N*) used in comparison test. Subgenera are *Leptuca* (*L.*), *Minuca* (*M.*), *Boboruca* (*B.*) and *Uca* (*U.*)

		1	2	3	4	5	6	7	8	9	10
1	<i>U. (L.) leptodactyla</i> (158)	x	171.17	90.06	361.39	290.68	700.21	951.21	643.48	1056.67	936.97
2	<i>U. (L.) cumulanta</i> (80)	<i>0.0833</i>	x	60.52	348.47	60.35	412.26	545.35	309.99	390.16	662.3
3	<i>U. (L.) uruguayensis</i> (94)	<i>0.0614</i>	<i>0.0507</i>	x	331.1	131.66	511.99	738.22	486.54	709.38	761.2
4	<i>U. (M.) vocator</i> (50)	<i>0.1438</i>	<i>0.1134</i>	<i>0.135</i>	x	128.07	56.26	34.73	117.03	293.12	485.26
5	<i>U. (M.) victoriana</i> (99)	<i>0.1065</i>	<i>0.0484</i>	<i>0.0768</i>	<i>0.0796</i>	x	201.4	301.88	114.02	236.63	641.27
6	<i>U. (M.) burgersi</i> (142)	<i>0.1383</i>	<i>0.1059</i>	<i>0.1268</i>	<i>0.0441</i>	<i>0.0762</i>	x	77.16	229	526.43	1027.79
7	<i>U. (M.) mordax</i> (210)	<i>0.1467</i>	<i>0.1205</i>	<i>0.1445</i>	<i>0.0356</i>	<i>0.0888</i>	<i>0.0375</i>	x	198.75	569.44	1074.49
8	<i>U. (M.) rapax</i> (119)	<i>0.1383</i>	<i>0.0911</i>	<i>0.1261</i>	<i>0.0615</i>	<i>0.0583</i>	<i>0.0692</i>	<i>0.0625</i>	x	161.58	754.45
9	<i>U. (B.) thayeri</i> (217)	<i>0.1395</i>	<i>0.0858</i>	<i>0.1235</i>	<i>0.0846</i>	<i>0.0684</i>	<i>0.0853</i>	<i>0.0839</i>	<i>0.0483</i>	x	988.02
10	<i>U. (U.) maracoani</i> (150)	<i>0.1578</i>	<i>0.1346</i>	<i>0.1538</i>	<i>0.1312</i>	<i>0.1354</i>	<i>0.1435</i>	<i>0.1387</i>	<i>0.1255</i>	<i>0.1162</i>	x

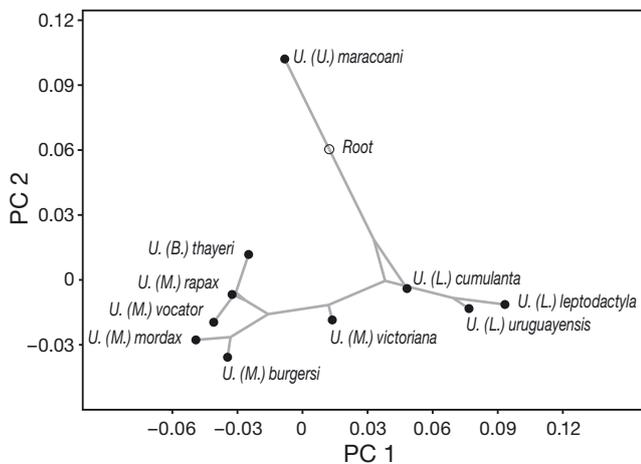


Fig. 5. *Uca* spp. Phylogeny of 10 *Uca* spp. from Brazil projected into a morphospace circumscribed by principal component 1 (PC 1) and PC 2. (●) Mean shape for a species, (○) root (outgroup = *U. Afruca tangeri*). Positions of the internal nodes were reconstructed by unweighted squared-change parsimony using the tree shown in Fig. 2. See Table 1 for subgenus abbreviations

clades are due primarily to intraocular distance and the shape of the branchial and hepatic carapace regions. Thus, proximity in morphospace (Figs. 4 & 5) implies, by and large, evolutionary relatedness rather than convergence in carapace structure. The subgenus *Uca* is clearly very divergent and constitutes the most distinct clade both evolutionarily and morphologically. Within the subgenus *Leptuca*, *U. (L.) leptodactyla* and *U. (L.) uruguayensis* are most similar, and form a monophyletic group. Both are distinct and distant from *U. (L.) cumulanta*. Based on spatial proximity within the morphospace and phylogenetic analysis, *U. Boboruca thayeri* most closely resembles *U. Minuca rapax*. Three species in the subgenus *Minuca*, *U. (M.) burgersi*, *U. (M.) mordax* and *U. (M.) vocator*, appear very similar based on PC 1 and PC 2. However, it is surprising that *U. (M.) victoriana* does not lie closer to *U. (M.) rapax* on the tree or in morphospace, since these species have been considered taxonomically similar (von Hagen 1987).

Intraspecific variation

Based on the CVA, each of the 8 species with a trans-Brazilian distribution exhibits morphological divergence between populations from the northern and southern coasts. Variation is due primarily to the relative size and shape of the hepatic and branchial regions of the carapace (Fig. 6). Intraspecific differ-

ences are statistically significant in each of the 8 species (resampled Goodall's *F*-test, Table 2). The 2-way MANOVA also confirmed significant differences between species ($F = 279.496$, $df = 140$, 7265.3 , $p < 0.0001$) and between northern and southern populations ($F = 17.527$, $df = 20$, 1092.0 , $p < 0.0001$) with a significant interaction between the 2 factors ($F = 4.585$, $df = 140$, 7265.3 , $p < 0.0001$), suggesting that all species exhibit a significant morphological shift from northern to southern sites. Based on the difference between means, populations of *Uca Minuca mordax* are the most divergent while those of *U. Boboruca thayeri* differ least.

In general, southern populations are broader in the antero-lateral ridge and shorter in carapace length than are the northern populations (Fig. 6). Variation in the hepatic and branchial regions manifests as a swelling and broadening of the carapace. However, there are differences in the patterns of divergence between northern and southern populations among the 8 species. For example, *Uca Minuca mordax*, *U. (M.) burgersi*, and *U. Leptuca leptodactyla* show primary swelling in the hepatic region (Fig. 6L,N,P). *U. (M.) vocator* and *U. (M.) rapax* show an enlargement of the branchial region (Fig. 6I,J). *U. (L.) cumulanta* and *U. Boboruca thayeri* show generalized swelling of the carapace (Fig. 6K,O). Finally, *U. (U.) maracoani* differs from all other species in showing enlargement of both the hepatic and branchial regions (Fig. 6M). As a result, a number of species show significant differences in magnitude and direction of shape change between their northern and southern populations (Table 3). Notably, magnitude differs far more frequently than direction, suggesting that species differ mostly in the degree to which they have diverged across this geographical boundary. These differences may be due to different rates of divergence over time, to different lengths of time during which divergence has taken place, or to different degrees of plasticity among the species.

The jack-knife assignment test indicated that individuals initially 'assigned correctly' to a region were frequent but not remarkable (Table 4). In each of the 8 cases, this might be expected since the 2 populations belong to the same species. While some differences are present, the populations overlap morphologically. Again, the populations of *Uca Minuca mordax* appear to express the greatest degree of intraspecific divergence while those of *U. Boboruca thayeri* and *U. (M.) vocator* show the least divergence. However, the latter case may derive from the small number of specimens used (N, north = 34, N, south = 16).

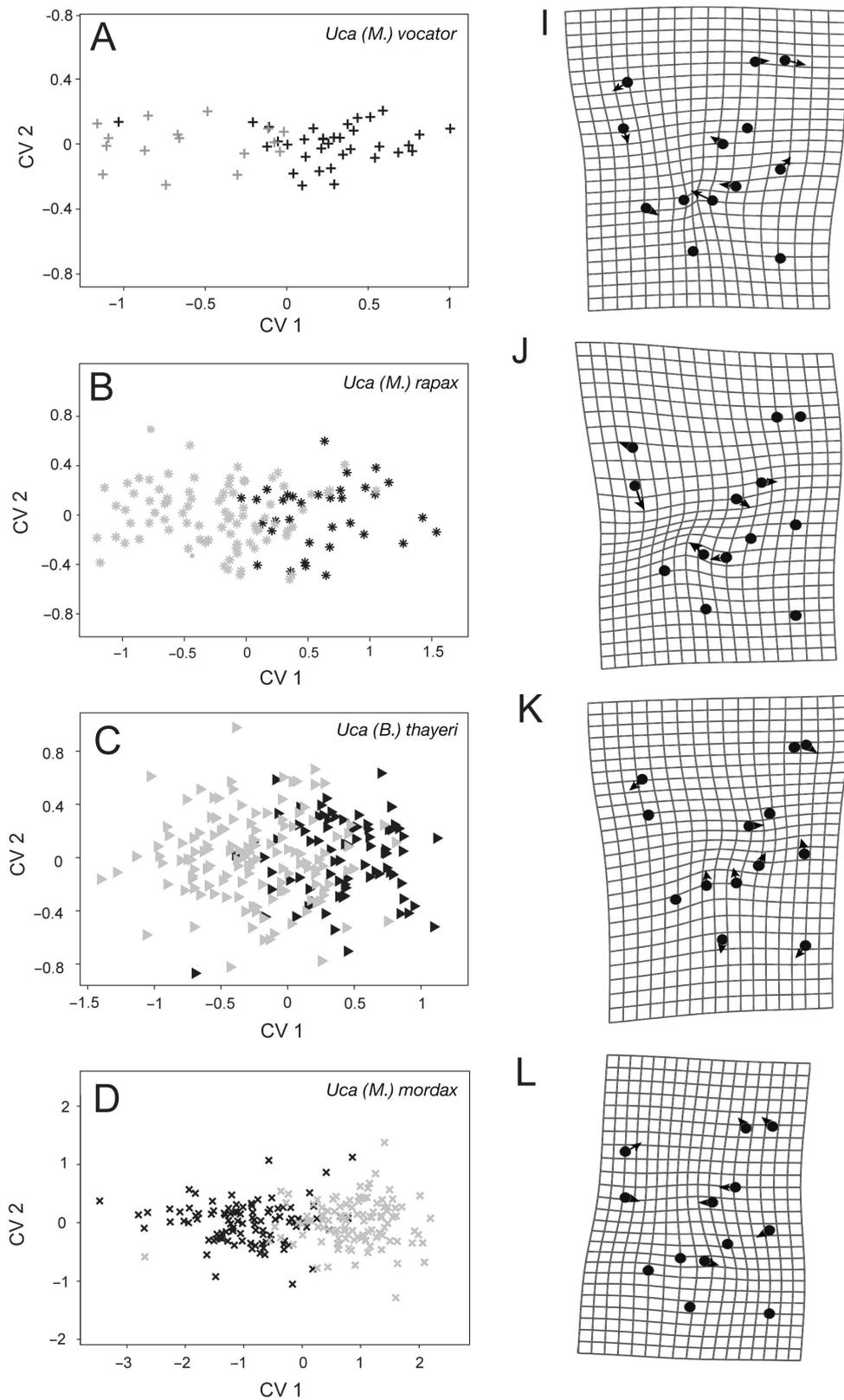


Fig. 6. *Uca* spp. Canonical variates analyses (CVA) for each species (A–H) and corresponding Procrustes deformation plots for the first canonical variate (I–P). Specimens from northern populations are represented by black points and specimens from southern populations are represented by gray points. On deformation plots, circles show typical landmark configuration for a specimen with a low CV 1 score while the arrows point to a typical landmark configuration for a specimen with a high CV 1 score. CV axes $\times 10^{-2}$. (A, I) *U. Minuca vocator*, (B, J) *U. (M.) rapax*, (C, K) *U. Boboruca thayeri*, (D, L) *U. (M.) mordax*, (E, M) *U. (U.) maracoani*, (F, N) *U. Leptuca leptodactyla*, (G, O) *U. (L.) cumulanta*, (H, P) *U. (M.) burgersi*

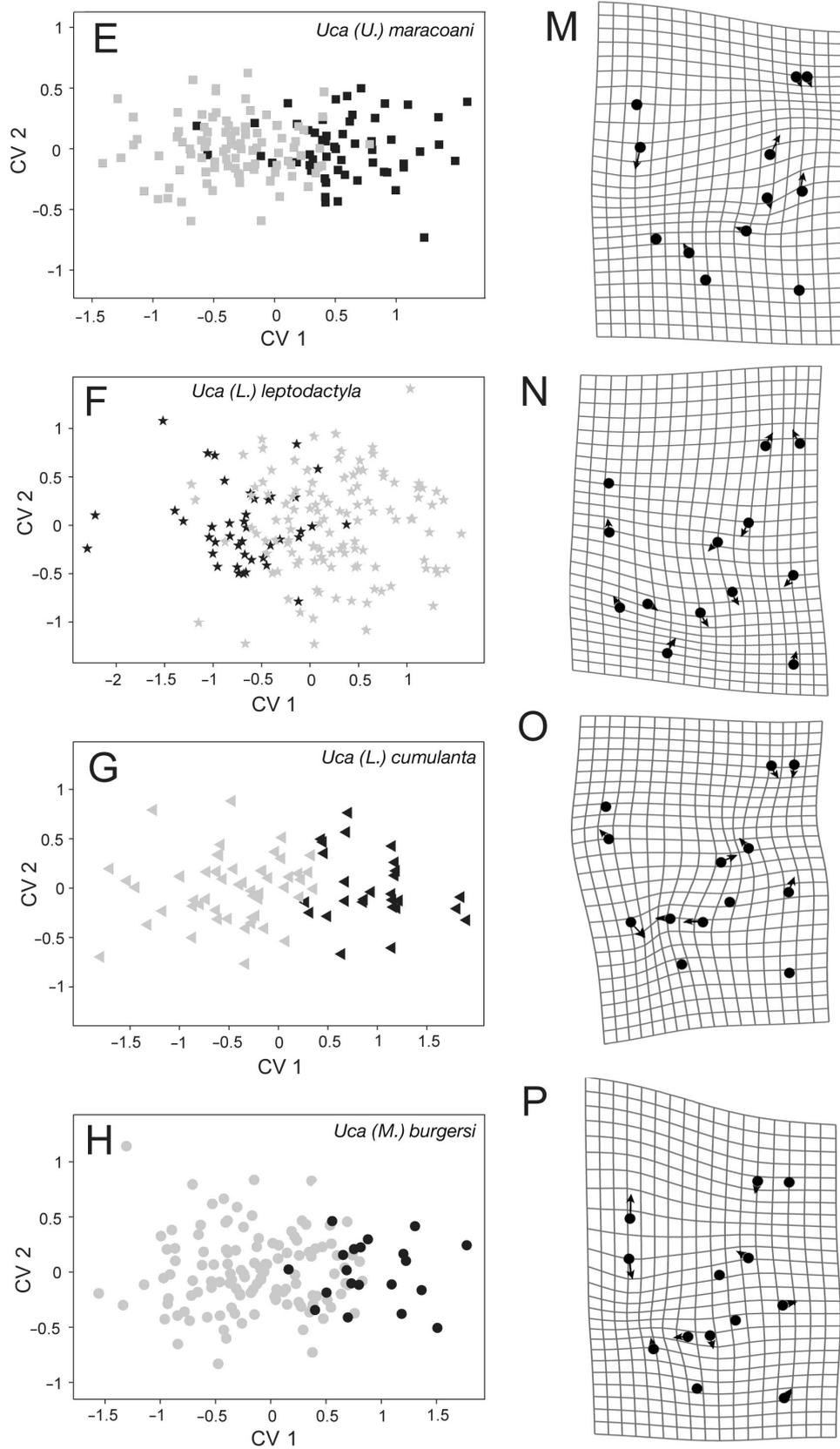


Fig. 6 (continued)

Table 2. *Uca* spp. Results from resampled Goodall's *F*-test. N = number of specimens from northern populations; S = number of specimens from southern populations. Total = total number of specimens. See Table 1 for subgenus abbreviations

Species	Goodall's <i>F</i>	p	Distance between means	N/S	Total
<i>Uca</i> (<i>U.</i>) <i>maracoani</i>	7.37	0.0011	0.0173	55/95	150
<i>Uca</i> (<i>M.</i>) <i>mordax</i>	23.21	0.0011	0.0255	99/111	210
<i>Uca</i> (<i>M.</i>) <i>rapax</i>	3.60	0.0011	0.0135	37/85	119
<i>Uca</i> (<i>B.</i>) <i>thayeri</i>	7.02	0.0011	0.0118	80/137	217
<i>Uca</i> (<i>M.</i>) <i>vocator</i>	4.49	0.0011	0.0180	34/16	50
<i>Uca</i> (<i>M.</i>) <i>burgersi</i>	4.30	0.0011	0.0187	20/122	142
<i>Uca</i> (<i>L.</i>) <i>cumulanta</i>	8.91	0.0011	0.0244	27/53	80
<i>Uca</i> (<i>L.</i>) <i>leptodactyla</i>	3.83	0.0044	0.0177	42/116	158

DISCUSSION

Interspecific variation

Our presumptive phylogeny for the 10 *Uca* (sensu lato) species from Brazil is in consonance with that proposed for fiddler crabs from Trinidad by Albrecht & von Hagen (1981). However, neither *U. Leptuca uruguayensis* nor *U. Minuca victoriana* were included in the latter phylogeny, and *U. (U.) major* (Herbst, 1804) was not incorporated in the present scheme since it is not ecologically relevant for Brazil. Here, all 10 *Uca* species are morphologically distinct to varying degrees (Figs. 4 & 5). We found *U. (L.) leptodactyla* to be very similar morphologically to both *U. (L.) cumulanta* and *U. (L.) uruguayensis* (Fig. 5, Table 4). Also, *U. (M.) vocator* and *U. (M.) burgersi* were similar to *U. (M.) mordax*, implying a close evolutionary relationship. Although closely resembling both *U. (M.) rapax* and *U. (M.) marguerita*, a sibling species from Mexico, *U. (M.) victoriana*, does not appear to be closely related but rather is intermediate between species in the subgenera *Minuca* and *Leptuca* (Fig. 5).

In traditional classification schemes, species of the genus *Uca* can be separated into 2 morphological groups consisting of the 'narrow-fronted' and the 'broad-fronted' species (Rathbun 1918, Bott 1954). Crane (1975) divided the genus into 9 subgenera creating a unique subgenus, *Boboruca*, for *U. thayeri* and *U. umbratila* Crane, 1941. Owing to cheliped armature, lethargy and form of waving display, she considered *Boboruca* to be related to the Indo-Pacific subgenera *Paraleptuca* Bott (= *Amphiuca* Crane) and *Tubuca* Bott (= *Deltuca* Crane). Crane's classification system was modified recently by Rosenberg (2001) and Beinlich & von Hagen (2006), and *Boboruca* was incorporated into the subgenus *Minuca*.

Some findings support Crane's supposition that the subgenus *Boboruca* is distinct. Salmon (1987) compared courtship behavior, reproductive biology and ecology of *Uca (B.) thayeri* to broad-fronted (*U. Leptuca pugilator* (Bosc, 1802)) and narrow-fronted (*U. Gelasimus vocans* (Linnaeus, 1758)) species. Inter-tidal ecology, habitat usage and female behaviors (burrow defense, incubation and mate selection) were most similar to the subgenus *Gelasimus*. However, female reproductive physiology (opercula decalcification, receptivity and clutch periodicity) was more similar to the subgenus *Leptuca*. Emphasizing distinctness, the ultrastructure of spermatozoa from *U. (B.) thayeri* is unique for the genus (Benetti et al. 2008). Salmon & Zucker (1987) thus offered an alternative hypothesis that *U. (B.) thayeri* is a broad-fronted species demonstrating convergence in behavior, ecology and physiology with species in the narrow-fronted subgenera, arguing that *U. (B.) thayeri* is not derived from the subgenus *Minuca* but

is not derived from the subgenus *Minuca* but

Table 3. *Uca* spp. Comparison of shape vectors between northern and southern populations among species. Differences in magnitude (vector length) shown at upper right; differences in direction (angular difference between vectors) shown at bottom left. Although the angles between vectors are large, only a few are significant. This is likely due to the degree of within-group variation relative to the orientation of angles between vectors. **p* < 0.05, ** *p* < 0.01, *** *p* < 0.001 based on permutation test (1000 iterations). See Table 1 for subgenus abbreviations

	1	2	3	4	5	6	7	8
1 <i>U. (M.) burgersi</i>	0	0.024***	0.011*	0.011	0.032***	0.001	0.012	0.008
2 <i>U. (L.) cumulanta</i>	76.00	0	0.013	0.013	0.008	0.024***	0.012	0.016*
3 <i>U. (U.) maracoani</i>	53.05*	53.72	0	>0.001	0.021***	0.011	0.001	0.003
4 <i>U. (L.) leptodactyla</i>	70.81	106.90	106.75	0	0.021**	0.011	0.001	0.003
5 <i>U. (M.) mordax</i>	93.44	118.89	119.46	71.49	0	0.032***	0.020	0.024***
6 <i>U. (B.) thayeri</i>	69.50*	102.12	71.61*	102.38	96.27	0	0.013	0.009
7 <i>U. (M.) rapax</i>	115.53	100.85	123.29	86.21	59.64	118.34	0	0.004
8 <i>U. (M.) vocator</i>	110.69	118.34	130.80	60.56	72.47	113.43	72.74	0

Table 4. *Uca* spp. Findings from the jack-knife assessment test. Original groupings from northern (N) and southern (S) populations along rows; groupings based on canonical variates analysis (CVA) along columns. Within each species matrix, diagonal scores indicate the number of specimens correctly assigned to the north and south populations while the off-diagonal scores indicate incorrectly assigned specimens. Percentages indicate the proportion of specimens correctly assigned to both the northern and southern populations based on CVA scores

<i>U. burgersi</i>			<i>U. cumulanta</i>		
73 %	N	S	78 %	N	S
N	13	7	N	21	6
S	31	91	S	12	41
<i>U. leptodactyla</i>			<i>U. maracoani</i>		
68 %	N	S	80 %	N	S
N	28	14	N	47	9
S	36	80	S	21	74
<i>U. mordax</i>			<i>U. rapax</i>		
88 %	N	S	65 %	N	S
N	86	13	N	23	11
S	13	98	S	31	54
<i>U. thayeri</i>			<i>U. vocator</i>		
74 %	N	S	68 %	N	S
N	63	17	N	34	0
S	39	98	S	16	0

represents an independent, converging evolutionary trajectory. Additionally, employing a multivariate analysis of 12 meristic characteristics in 6 species, Diniz-Filho (1990) sorted adult male *Uca* from Brazil into 3 distinct clusters along PC 1 (size) and PC 2 (shape) axes. Specimens from the subgenera *Uca* and *Leptuca* were clearly distinct from those of the subgenera *Minuca* and *Boboruca*. Although *U. (B.) thayeri*, *U. (M.) vocator* and *U. (M.) rapax* formed a central cluster on a graphic projection of the PCA, the subgenera *Boboruca* and *Minuca* were morphologically distinct. Diniz-Filho found *U. (M.) rapax* and *U. (M.) vocator* to be more closely related and concluded that, although *U. (B.) thayeri* and *U. (M.) rapax* are similar cladistically, the relationship was not supported by morphometric analysis.

Results from molecular phylogenetic analyses are contradictory. Using DNA or 16S ribosomal RNA, Sturmbauer et al. (1996) and Levinton et al. (1996) found that *Uca Boboruca thayeri* is most closely related to several species in the subgenus *Leptuca*. Landstorfer & Schubart (2010) compared *U. (B.) umbratila* to 9 other tropical *Minuca* species from the Pacific shores of Costa Rica. Their parsimony network analysis of a 619 bp DNA sequence for 28S ribosomal

RNA from species in the subgenus *Boboruca* revealed marked differences compared to those of the 9 species of the subgenus *Minuca*. However, analysis of the relationships among the species using Bayesian Inference of 658 bp DNA sequences for a cytochrome oxidase subunit (COX-1) suggests that *U. (B.) umbratila* is most closely related to *U. Minuca brevifrons* (Stimpson, 1860), a sibling species of *U. (M.) mordax*. Based on these molecular studies, the exact relation of *U. (B.) thayeri* to other New World 'broad-fronted' *Uca* remains unresolved.

In the present study, the 10 Brazilian species generally form subgeneric clusters in morphospace, supporting previously hypothesized evolutionary relationships (Crane 1975, Rosenberg 2001, Beinlich & von Hagen 2006). *Uca (U.) maracoani* is distinct in morphospace from the *Minuca* and *Leptuca* clades. The *Uca* (sensu stricto) clade is thought to be basal in the phylogeny to both the subgenera *Minuca* and *Leptuca* (Rosenberg 2001), which share a more recent relationship (Albrecht & von Hagen 1981, Sturmbauer et al. 1996). Our findings also support Albrecht & von Hagen's (1981) suggestion to abandon the subgenus *Boboruca* and incorporate its member species (*U. thayeri* and *U. umbratila* Crane, 1941) into the subgenus *Minuca*. The New World fiddler crabs would then form 3 clades (Beinlich & von Hagen 2006): subgenus *Uca* (narrow-fronted), subgenus *Minuca* (broad-fronted) and subgenus *Leptuca* (broad-fronted). The frontal (interocular) width is approximately 20% of carapace width in the subgenus *Boboruca*, 10% in the subgenus *Uca*, and between 30% and 40% in the subgenera *Minuca* and *Leptuca*. Interestingly, in terms of its osmotic physiology, *U. (B.) thayeri* exhibits the regulatory pattern seen in members of the subgenus *Uca* (i.e. *U. (U.) major* and *U. (U.) maracoani*) rather than in species from the subgenera *Minuca* or *Leptuca* (Lin et al. 2002, Thurman 2005, Thurman et al. 2010, Faria et al. 2011). *U. (B.) thayeri* has an elevated hemolymph isosmotic concentration and does not osmoregulate well in low or high salinities, unlike most *Leptuca* and *Minuca*. Thus, there may be some convergence in osmotic physiology between *Boboruca* and *Uca*.

Intraspecific variation

The 8 species with trans-Brazilian distributions exhibit significant intraspecific variation in carapace morphology. These findings contrast with a study from the east coast of Africa in which Silva et al. (2010) found a lack of both morphological and

genetic variation across very remote, isolated populations of *Uca (Leptuca) annulipes* (Milne-Edwards, 1837) in the western Indian Ocean. However, the present findings are consistent with those of Hopkins & Thurman (2010) for fiddler crabs along the eastern shore of North America, where similar patterns of morphological variation were found in geographically separated populations in the Gulf of Mexico and Atlantic Ocean. The differing results for the American and African studies may derive from the choice of landmarks, since those used by Silva et al. (2010) allowed analysis of carapace perimeter but not of the dorsal surface. However, the findings most likely differ due to the spatial scale assessed: the coastlines sampled by Hopkins & Thurman (2010), and here, are much longer (~13500 and ~7500 km, respectively) than the African coastline (~3300 km) sampled by Silva et al. (2010).

Divergent carapace morphology in the 8 trans-Brazilian species suggests that the Ponta do Calcanhar may be a disruptive geographical barrier. It bisects the coast of Brazil into 2 regions where conspecific crabs differ significantly in carapace shape. Intraspecific variation is localized primarily in 2 anatomical regions: branchial and hepatic. As the specific site of carapace variation is not unique to subgenus or species, there may be a relationship between carapace shape and environmental factors. For example, habitat differences in humidity may affect gene expression and morphological variation via an unidentified epigenetic mechanism. The branchial region of the carapace overlying the gill chambers assures water conservation. Thus, enlarging the branchial chambers would likely serve as a safeguard against desiccation (Jones 1941). Fiddler crab species from arid regions in the western Gulf of Mexico show similar adaptations (Thurman 1998, Hopkins & Thurman 2010). A detailed examination of the relationship between various environmental factors and carapace shape in several species is currently in progress. Beyond latitude, we expect these studies to demonstrate that various components of shape variation are related to habitat salinity and substrata grain size.

Climate along the northeastern Brazilian coast between Pernambuco (PE) and São Luis (Maranhão, MA) is arid, while the southern coast is more humid (Espenshade & Morrison 1974, Boltovskoy et al. 1999, Psuty & Mizobe 2005). However, this may not account for morphological variation within species. For example, among the 8 trans-Brazilian species, only *Uca Boboruca thayeri* and *U. Leptuca cumulanta* show similar salinity and substrate preferences

(Thurman et al. 2013), and they exhibit equivalent variation in branchial and hepatic carapace regions. No other pairs or group of species exhibiting ecological similarities display a common pattern of morphological variation. *U. (L.) leptodactyla* and *U. Minuca burgersi* both live on coarse sandy substrates and express variation in the hepatic carapace region; however, *U. (L.) leptodactyla* inhabits eusaline waters while *U. (M.) burgersi* occurs in oligosaline habitats. *U. (M.) rapax* and *U. (M.) vocator* both exhibit variations primarily in the branchial carapace, but *U. (M.) rapax* tolerates a very broad spectrum of salinities while *U. (M.) vocator* is more restricted to meso- to oligosaline habitats. *U. (M.) rapax* prefers a medium-grained substrate while *U. (M.) vocator* inhabits fine-grained substrates. In general, variation in a specific carapace region does not correlate with differences in salinity or substrate preference among the species. Also, there appears to be no obvious difference in habitat vegetation that might influence divergence among the northern and southern crab communities (Thurman et al. 2013, Table S1 in the Supplement).

Presently, no known factor appears to drive morphological variation in populations of Brazilian *Uca* (sensu lato). In fiddler crabs, gene flow is promoted by larval transport on oceanic currents and tides (Epifanio et al. 1988, Neethling et al. 2008, Weersing & Toonen 2009, López-Duarte et al. 2011), and larvae of long planktonic duration are expected to disperse over greater distances (Grantham et al. 2003, Lester et al. 2007, Shanks 2009). This should promote extensive communication among populations, maintaining uniformity in morphology and genotype across the species' range. Morphological divergence among populations should be either random and unstructured or related to environmental differences between localities (Sanford & Kelly 2011). However, several studies have found genetic structure and dispersal potential to be uncorrelated (Weersing & Toonen 2009). Further, population networks of small effective population size may receive little or no influx of novel genes, and eventually diverge through inbreeding and drift (Fisher 1958, Dobzhansky 1959, Wright 1969). Thus, genotypic diversity among isolated populations may increase as variation within each population declines. At each location across the range, environmental factors may act selectively on phenotypes, altering genotype frequencies or even producing unique genotypes. Finally, certain habitat conditions can produce a variety of phenotypes from a single genotype (Miner et al. 2005, Vogt et al. 2008). Consequently, depending upon habitat–organism interac-

tions, both genetic variability and phenotypic plasticity can drive diversity.

Historically, low intraspecific genetic diversity is a hallmark in fiddler crabs. Felder & Staton (1994) reported minimal divergence in several allozyme systems among 8 trans-Floridian populations of *Uca Minuca minax* (LeConte, 1855). Like east African *U. annulipes* (Silva et al. 2010), no genetic structure has yet been found across coastal populations of fiddler crabs in Brazil. Wieman et al. (2013) found little genetic variation in the DNA sequences of cytochrome oxidase-1 haplotypes in *U. (U.) maracoani* distributed between Amapá (AP) and Paraná (PR). Studies on other crab species also suggest that marine populations along the southern coast of Brazil are intimately connected by gene flow (Oliveira-Neto et al. 2007, Laurenzano et al. 2012, 2013). However, other brachyuran species along this coast may exhibit strong genetic differentiation in patterns that indicate isolation-by-distance over about the same length of coastline (Ituarte et al. 2012). For fiddler crabs, at least, the absence of demonstrated genetic structure across populations implies that intraspecific variation results from phenotypic plasticity attributed to either epigenetic change (Miner et al. 2005, Vogt et al. 2008), variation at other genetic loci, or currently unknown variables.

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