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Population genetics and evolutionary demography of *Ucides cordatus* (Decapoda: Ocypodidae)

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Abstract

Variation in a fragment of the mitochondrial control region was investigated to assess the population history of the mangrove land crab, *Ucides cordatus* L., based on 100 individuals from five locations throughout the Brazilian coast. There was considerable variability in the studied fragment, with every individual showing a distinct haplotype. When regions of ambiguous alignment were removed, 90 haplotypes were still recognized, of which only 1 was shared among locations. There was no statistically significant evidence for geographical structure in the pattern of genetic variability based on a nested clade analysis, even though the geographical distances among the farthest collection sites exceeded 3000 km. Moreover, the mismatch distribution of pairwise differences showed a smooth unimodal distribution that is consistent with a recent population expansion of *U. cordatus*, either when each location was analysed in isolation or when all samples were combined. Interestingly, the estimates for the duration of such expansion vary latitudinally, suggesting that the expansion of the population of *U. cordatus* proceeded in a southward direction. These results indicate a possible relationship between the growth in the population of the mangrove land crab and the dynamics of mangrove ecosystems during the Quaternary.

Problem

The increasingly larger number of analytical and conceptual tools for the study of genetic variability has revealed a remarkable variety of patterns of gene flow and historical demography of marine organisms (Graves 1998; Shaw *et al.* 1999; Weber & Levy 2000; Knutsen *et al.* 2003; Roman & Palumbi 2004; Bay *et al.* 2006; Santos *et al.* 2006). Even among closely related species, one can find drastically different degrees of geographical structure and genetic diversity, as recently observed in two closely related penaeid shrimp species (McMillen-Jackson & Bert 2003), as well as several species of *Callinectes* crabs (Weber & Levy 2000; McMillen-Jackson & Bert 2004; Pfeiler *et al.* 2005). However, there is still no comprehensive picture of how physiographical and historical events have shaped the patterns of genetic diversity of marine species since the beginning of the Quaternary. Such information would be instrumental, not only to understand the diversification process of marine taxa, but also to establish conservation strategies that maintain the long-term evolutionary potential of these species (Palumbi 2004).

A marine crustacean of particular importance in Brazilian mangrove areas is the mangrove land crab *Ucides cordatus* L. It is considered a keystone species in mangroves of the western Atlantic for its role in processing decaying plant material and nutrient cycling in those

environments (Nordhaus *et al.* 2006). In addition, it is among the most important fishery resources in northeastern Brazil, particularly among underprivileged coastal communities (Diele *et al.* 2005). A combination of overexploitation (Ministério do Meio Ambiente 2004; Amaral & Jablonski 2005) and an emerging infectious disease (the Lethargic Crab Disease, Boeger *et al.* 2005) has caused severe depressions in natural stocks of *U. cordatus* (Alves & Nishida 2003), leading to an urgent necessity to develop efficient management strategies to maintain the genetic integrity of local populations. The first genetic study of this species was carried out by Oliveira-Neto *et al.* (2007) using RAPD and PCR-RFLP of the mitochondrial control region (CR) and showed no evidence for genetic structure in this species. However, further studies using sequence data and a broader geographical range are necessary to establish these findings firmly.

Changes in the size of a population tend to leave recognizable signatures in its patterns of genetic variability. In particular, the distribution of pairwise sequence differences in a sample (known simply as the mismatch distribution) can contain information on the history of a population (Rogers & Harpending 1992). Given that the genealogy of a population of constant size is expected to have long deep branches, mutations occurring along these branches will be shared by several lineages, resulting in an irregular or ragged mismatch distribution. Conversely, the genealogy of a population that has substantially grown in size has long terminal branches, and the mutations that have occurred along these branches will be specific to single lineages. Under these conditions, a unimodal mismatch distribution is expected, whose mean, under an infinite-sites mutation model, increases as a function of the time elapsed after population growth. Mismatch distribution methods are used in the present study to infer the population history of the mangrove land crab, *U. cordatus*, through the investigation of the patterns of variation in a fragment of the mitochondrial DNA CR among locations along the Brazilian coast. The observed results are consistent with the expansion of *U. cordatus* populations, which seems to have occurred from the northernmost locations into higher latitudes.

Material and Methods

Samples of *U. cordatus* were obtained from several locations throughout the Brazilian coast (Fig. 1). Muscle tissue from one of the pereiopods was removed, preserved in EDTA-DMSO buffer (Seutin *et al.* 1991), and maintained at −20 °C. Genomic DNA was extracted using the DNeasy kit (Qiagen) according to the manufacturer's instructions. The primers 12SUCAF3 (5′-CCA GTA NRC CTA CTA TGT TAC GAC TTA T-3′) and ILEUCAR3 (5′-GCT AYC CTT TTA AAT CAG GCA C-3′) were used for the amplification of an ≈1.6 kb fragment including the complete CR of *U. cordatus* (Oliveira-Neto *et al.* 2007). The CR is a non-coding fragment of the mitochondrial genome. In crustaceans, the CR is usually flanked on its 5′ end by the 12S ribosomal gene and on its 3′ end by the isoleucine-tRNA. Each 25 μl PCR included the following final concentrations: 6 mM of $MgCl_2$, 0.25 mM of each dNTP, 0.1 U μl^{-1} of Taq polymerase, 1X buffer, 2 μM of each primer, and 1.2 ng μl^{-1} of template DNA. Thermocycling conditions included an initial denaturation at 95 °C for 2 min, followed by 35 cycles at 95 °C for 20 s, 56 °C for 30 s, and 72 °C for 90 s, and a final extension at 72 °C for 2 min. A 2 μl aliquot of each PCR product was electrophoresed in a 1.5% agarose gel, stained with ethidium bromide and visualized under UV light. Successfully amplified products were purified using a MinElute kit (Qiagen). Sequencing reactions were carried out using internal primers (DL.USSA.R1: 5′-GGTTAGAGAGA AGGTTAGAGGAC-3′, and DL.USSA.F1: 5′-GTATA ACCGCGAATGCTGGCAC-3′), which generate a fragment that could be reliably sequenced in a single reaction, including 112 bp of the 5′-flanking 12S gene and approximately 400 bp into the CR (actual size varied due to indels). Cycle sequencing in 10 μl solutions included the following final concentrations: 5 ng μl^{-1} of template DNA, 0.16 μM of primer, 0.15X of reaction buffer, and 0.5 μl of BigDye (Applied Biosystems). The final product was purified using Sephadex G50 and processed on a ABI3130 automatic sequencer. Forward and reverse strands were reconciled using the Staden package (Staden 1996). Sequences were aligned using Clustal W (Thompson *et al.* 1994), as implemented in BioEdit (Hall 1999). Regions with ambiguous alignment were omitted from further analyses.

The existence of geographical structure in the pattern of genetic variability among populations of *U. cordatus* was tested using nested clade analysis (NCA), as implemented in the program GeoDis (Posada *et al.* 2000) according to the methods of Templeton *et al.* (1995). This program calculates the clade distances D_c (average distance between the location of the members of the clade and the geographical center of the clade), and the nested clade distances D_n (the average spatial distance between the members of each clade and the geographical centre of the entire nesting clade). Additionally, the measures of average distance between tip and interior clades within the nested group $(\text{Int-Tip})_c$, and the tip to interior distance for the nesting clade $(\text{Int-Tip})_n$ are estimated. The assessment of whether any of these distances is significantly smaller or larger than expected by chance was carried out by 10,000 permutation resamplings. Interpretation of the

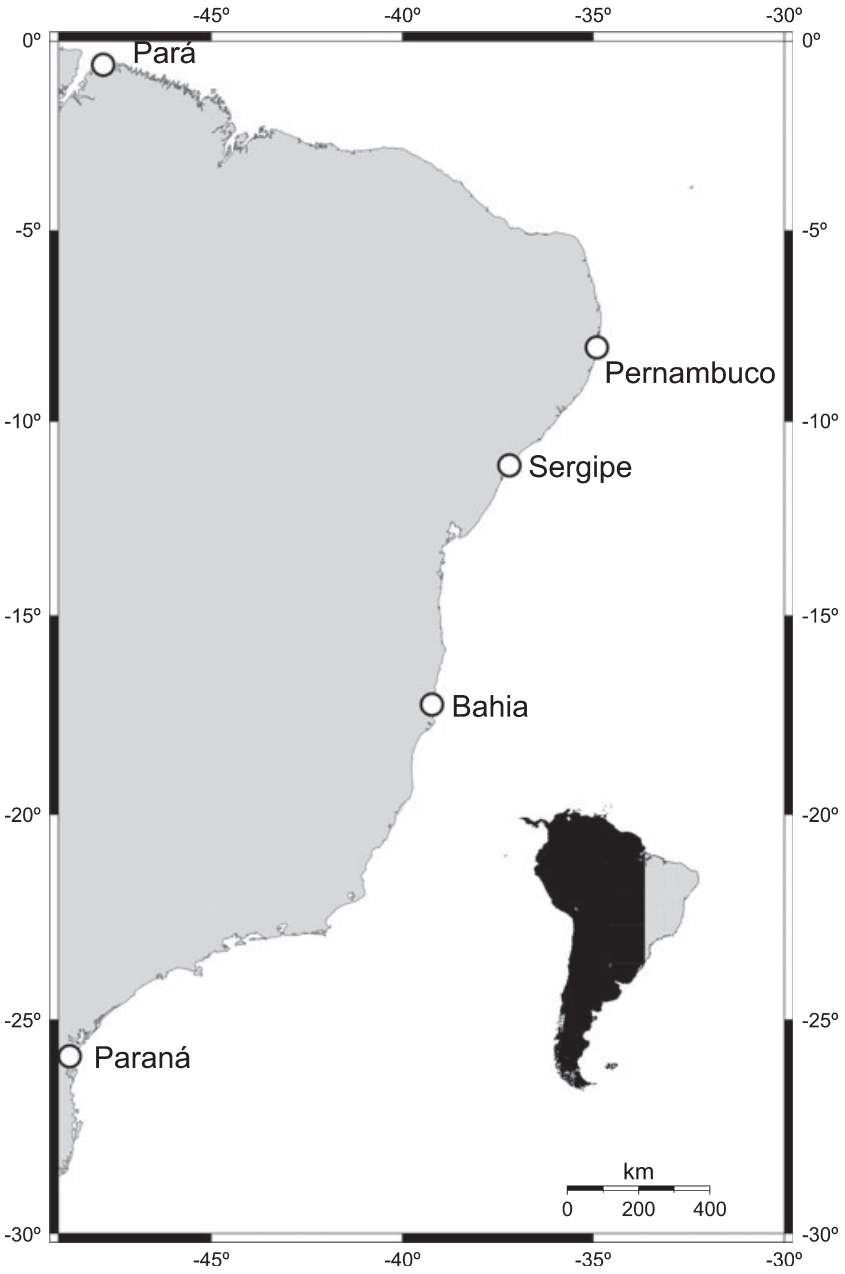

Fig. 1. Map of the coast of Brazil indicating the sampled locations. Detailed coordinates of each location can be obtained from the authors upon request.

results followed the method given in Templeton *et al.* (1995).

Inferences on past demographic history were assessed using the mismatch distribution analysis (Slatkin & Hudson 1991; Rogers & Harpending 1992). Three parameters are estimated using Rogers & Harpending's (1992) model: $\theta_0 = 2N_0u$, $\theta_1 = 2N_1u$, and $\tau = 2ut$, where an initial population of effective size N_0 is assumed to grow rapidly to a new size of N_1 at a time t generations before the present, and u is the per-generation probability that a mutation strikes a particular nucleotide in the region under study. These parameters were estimated using the generalized nonlinear least-square approach developed by Schneider & Excoffier (1999). Also, the degree of approximation between the observed mismatch distribution and that expected under population growth was tested using Harpending's (1994) raggedness statistic.

Departures from mutation–drift or mutation–selection equilibrium were tested using Tajima's D and Fu's F_s. In Tajima's (1989) test, the parameter θ is independently estimated twice, once from the number of polymorphic sites and once from the average mismatch of the sample. Differences between the two estimates are then attributed to selection or to the demographic history of the population

studied. Similarly, Fu's (1997) F_s statistic compares the observed number of alleles in a sample with the number of alleles expected if the population has kept a constant size. The significance of D and F_s was tested by randomization. D and F_s are calculated for each simulated data set to obtain an empirical null distribution of these statistics and hence the probability of the observed D and F_s under the hypothesis of demographic stationarity. A recent population expansion would produce negative values for both statistics. Unless otherwise stated, all analyses were carried out as implemented in ARLEQUIN 3.1 (Excoffier *et al.* 2005).

Results

Genetic variation

A 600-bp fragment of the mitochondrial DNA was bidirectionally sequenced for 100 individuals of *U. cordatus*. There was considerable variability in the study fragment, with every individual showing a distinct CR haplotype. When regions of ambiguous alignment were removed, 505 segregating sites were observed to define 90 haplotypes, of which only 1 was shared among locations and 10 were found in more than one individual. There was no clear latitudinal trend in the number of haplotypes, the average number of differences, and the nucleotide diversity among the studied sites, with the statistics being high along the Brazilian coast (Table 1). Sequences for these haplotypes are deposited in GenBank under the accession numbers EU057729–EU057828.

Population structure

There was no statistically significant geographical structure in the pattern of genetic variability among the studied locations according to the NCA (Table 2). This result is evident from the haplotype network (Fig. 2), in which there is no apparent relationship between the location where a given sample was located and its genetic relationship with the other haplotypes. This result indicates that knowing the haplotype of a given individual cannot be used to predict the location where it was collected. The lowest observed P-value was 0.035, which is not statistically significant after using any correction to control for the multiple statistical tests involved in an NCA analysis such as the Bonferroni method.

Past population expansion

Estimates of Tajima's D and Fu's F were negative in all locations, although the associated probabilities did not reach statistical significance in most cases (Table 1). In addition, the distribution of pairwise nucleotide differences showed a smooth unimodal pattern characteristic of population expansion, either when each location was analysed individually or when all samples were combined

Table 1. Molecular characterization of the studied populations. See text for details on the calculated statistics.

	entire data set	Pará	Pernambuco	Sergipe	Bahia	Paraná
number of individuals	100	20	20	20	20	20
number of haplotypes	90	17	19	19	18	17
number of unique haplotypes	88	17	19	18	18	16
average number of differences	16.17	18.32	16.71	14.84	16.17	15.6500
nucleotide diversity (SD)	0.035 ± 0.017	0.041 ± 0.021	0.035 ± 0.018	0.033 ± 0.017	0.036 ± 0.018	0.032 ± 0.016
Tajima's D	−1.472	−1.036	−0.811	−1.215	−1.227	−0.6
P_D	0.045	0.149	0.209	0.088	0.091	0.315
Fu's F_s	−24.01	−2.03	−5.63	−6.01	−5.52	−2.97
P_F	<0.001	0.188	0.018	0.019	0.018	0.106
Θ_0 (95% CI)	0 (0–3.15)	0.035 (0–3.69)	0.028 (0–3.99)	1.526 (0–5.15)	2.7 (0–8.62)	0 (0–3.67)
Θ_1 (95% CI)	191.56 (120–∞)	∞ (178.8–∞)	300.46 (126.19–∞)	187.18 (92.06–∞)	184.06 (82.5–∞)	73.91 (37.75–∞)
τ (95% CI)	16.62 (12.29–18.44)	20.73 (16.22–22.96)	18.65 (13.16–21.40)	16.12 (11.84–20.93)	16.85 (12.53–23.62)	12.18 (7.42–14.88)
raggedness index r	0.001	0.034	0.007	0.012	0.007	0.011
P_r	0.991	0.017	0.854	0.528	0.871	0.731

Table 2. Nested clade analysis of the variation in the control region of the mitochondrial DNA of *Ucides cordatus*.

clades	D_c	D_n	clades	D_c	D_n	clades	D_c	D_n
2-1	0	1930						
2-2	1600	2639	3-1	2660.7	1714.9			
2-3	0	3100						
1-T	960	893.5						
2-4	0	2000						
2-5	0	1000	3-2	1600	1534			
2-6	0	1000						
1-T	0	−1000						
2-7	0	1291				4-1	1692.2	1642
2-8	0	1748.1	3-3	1984.2	1714.9			
2-9	0	1575						
2-10	1600	2311.7						
2-11	4600	2875						
2-12	450	1318.7	3-4	2031.6	1671.0			
2-13	0	1262.5						
2-14	0	566.6						
2-15	0	1100	3-5	763.6	1269.4			
2-16	0	680						
2-17	0	450						
2-18	0	450	3-6	450	881.2			
1-T	0	0				4-3	776.5	1308.2
			3-7	0	683.3			
			1-T	−450	−197.9			
2-19	0	2300	3-8	3066	2472			
2-20	4600	3450						
			1-T	490	572.4			
			3-9	0	1472	4-2	2186.1	1953.3
2-21	0	1350						
2-22	0	1350	3-10	1350	1500			
1-T	0	0						
2-23	0	1225						
2-24	0	1225	3-11	1960	1431.2			
2-25	0	2450						
1-T	0	612.5						
2-26				0	727.3			
2-27	2150	1733.3	3-12			4-4	1262.2	1443.2
2-28	0	1220		1500	1211.6			
1-T	2150	513.3						
			3-13	0	847.6			
			3-14	0	1261.9			
2-29	1080	1481.25						
2-30	0	2150	3-15	1663.6	1786			
1-T	−1080	668.75						
2-31	0	3700	3-16	3700	2683	4-5	2189.5	1858.7
2-32	0	3700						
2-33				0	1650			
			1-T	−2369.1	−923.7			

into a single analysis (Fig. 3). Harpending's raggedness index was uniformly low in all cases, confirming the good fit of the data to a unimodal distribution. The sample from Pará had a relatively low associated probability ($P = 0.017$), which becomes non-significant after controlling for multiple comparisons.

Estimates of θ_0 and θ_1 indicate that populations increased from a very small size (close to 0 in some cases) to very large, with the 95% confidence interval (CI) including infinity in all cases (Table 1). Interestingly, there was a steady decrease in τ from the north ($\tau = 20.7$ in Pará) to south ($\tau = 12.18$ in Paraná), suggesting that the expan-

Table 2. Continued.

clades	D_c	D_n	clades	D_c	D_n	clades	D_c	D_n
2-34	0	540						
2-35	0	450	3-17	900	1762			
2-36	0	1350						
2-37	0	2000						
2-38	0	2000	3-18	2000	2369.4			
1-T	0	0						
2-39	0	3075						
2-40	0	1625	3-19	2316.7	1900.9			
2-41	0	2250						
2-42	0	1170.6				4-6	1922.1	1743.7
2-43	4600	2655.5						
2-44	0	1105.5						
2-45	0	1827.8						
2-46	0	977.7	3-20	1616.2	1661.4			
2-47	0	977.7						
2-48	0	977.7						
2-49	0	977.8						
1-T	1022.2	524.3						
			1-T	0.4	282			
2-50	0	1650						
2-51	0	4100						
2-52	0	1885.7	3-21	2635.2	2106.9			
2-53	0	2150						
1-T	0	747.6						
			3-22	0	1979.3			
2-54	4600	3066						
2-55	0	1683.3	3-23	2375	1924.1	4-7	2046.9	1899.3
2-56	0	1683.3						
1-T	−4600	−1383.3						
			3-24	0	1410			
2-57	0	716.6						
2-58	0	716.6	3-25	681.8	1600			
2-59	0	950						
2-60	0	416.6						
						1-T	38.1	−68.7

sion of the population of *U. cordatus* proceeded in a southward direction ($r^2 = 0.89$, $P = 0.016$, Fig. 4).

Discussion

The results of an NCA of the genetic variation in *U. cordatus* did not show any evidence of geographical structure, even though the distances among the farthest locations exceeded 3000 km. This result corroborates a previous study on the same species over a smaller geographical range and using other genetic methods (Oliveira-Neto *et al.* 2007). Although such a lack of population differentiation is also found in other species [*e.g. Pachygrapsus crassipes* (Cassone and Boulding 2006) and *Callinectes sapidus* (McMillen-Jackson & Bert 2003)], it is certainly not shared by all estuarine crustaceans. Indeed, a spectrum of population differentiation levels has been recorded that may range from weak to very strong (Weber & Levy 2000; Roman & Palumbi 2004; Diniz *et al.* 2005; Remerie *et al.* 2006; Ricklefs *et al.* 2006). Such differences are probably because of interspecific variation in larval biology, in which larval retention/exportation would be associated with varying levels of gene flow among estuaries. Indeed, larvae of *U. cordatus* are known to be exported into shelf waters given their tidal phenology and the high dispersal capacity (Diele 2001), a strategy that is consistent with an expected low geographical differentiation. A considerable level of genetic variability was observed in *U. cordatus* populations, as commonly observed in marine crustaceans (*e.g.* McMillen-Jackson & Bert 2003, Diniz *et al.* 2005, Cassone and Boulding 2006). A high level of haplotype diversity is usually interpreted as the result of a combination of high mutation rates and large effective population sizes (McMillen-Jackson & Bert

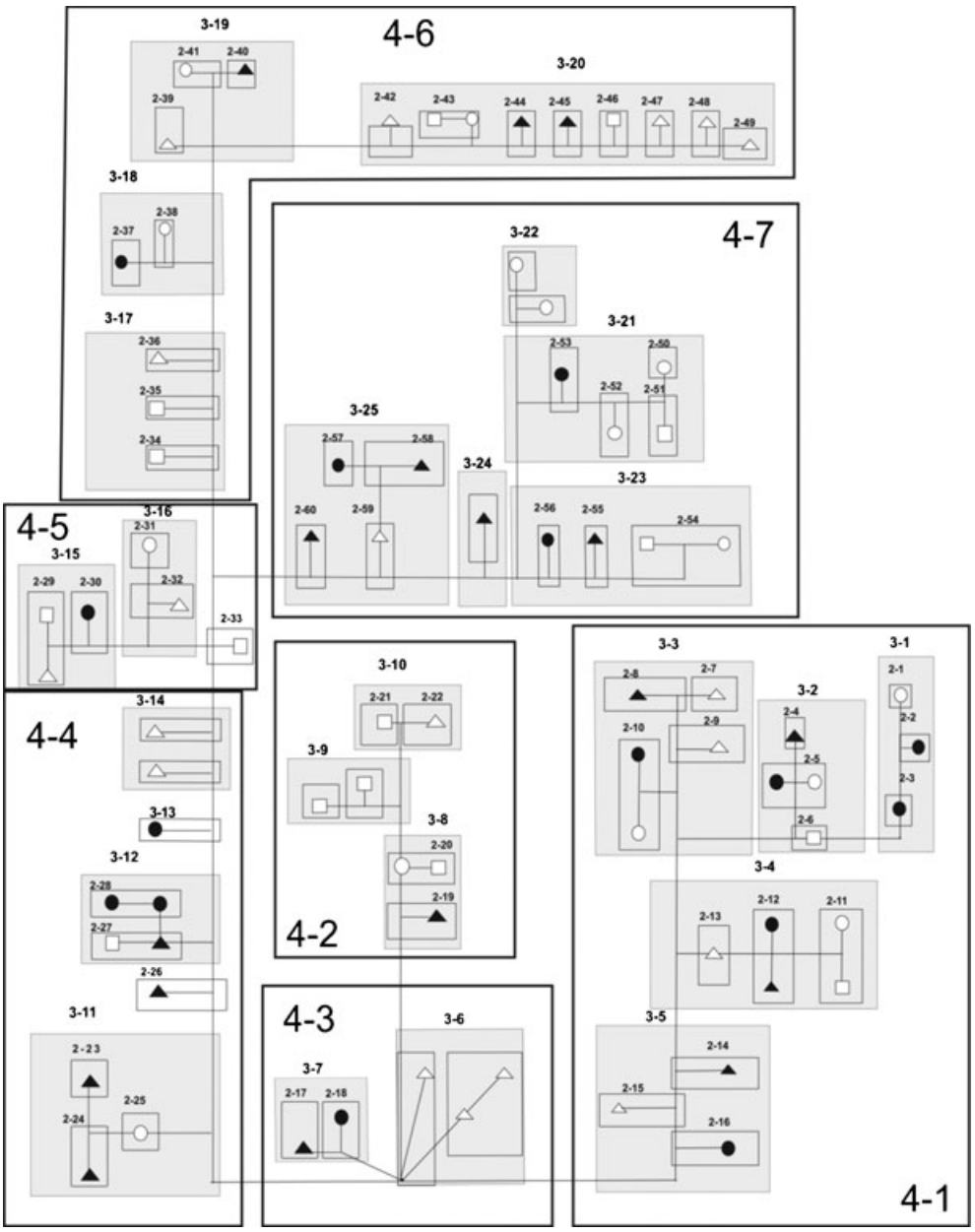

Fig. 2. The nesting design inferred from the cladogram estimation of 90 haplotypes detected for *Ucides cordatus*. Level 1 clades were omitted. The number inside each square represents haplotypes. Sampling locations are indicated by their respective symbols: (white triangle) Pernambuco; (white square) Pará; (black triangle) Sergipe; (white circle) Paraná; (black circle) Bahia.

2003; Diniz *et al.* 2005; Cassone and Boulding 2006; Ricklefs *et al.* 2006).

Population size changes leave particular footprints that may eventually be detected in DNA sequence data (Slatkin & Hudson 1991; Rogers & Harpending 1992). The mismatch distributions observed in the studied data set are clearly unimodal, a result that is consistent with a recent demographic expansion (Slatkin & Hudson 1991; Rogers & Harpending 1992) or through a range of expansion with high levels of migration between neighboring demes (Ray *et al.* 2003; Excoffier 2004). The observed mismatch distributions might also explain the observed high haplotype diversity, given that population expansions cause the number of generated haplotypes to be higher than the number of haplotypes that are lost by drift (Avise *et al.* 1984). It is important to note that, even though the high genetic variability in the studied fragment probably violates the infinite-sites assumption of mis-

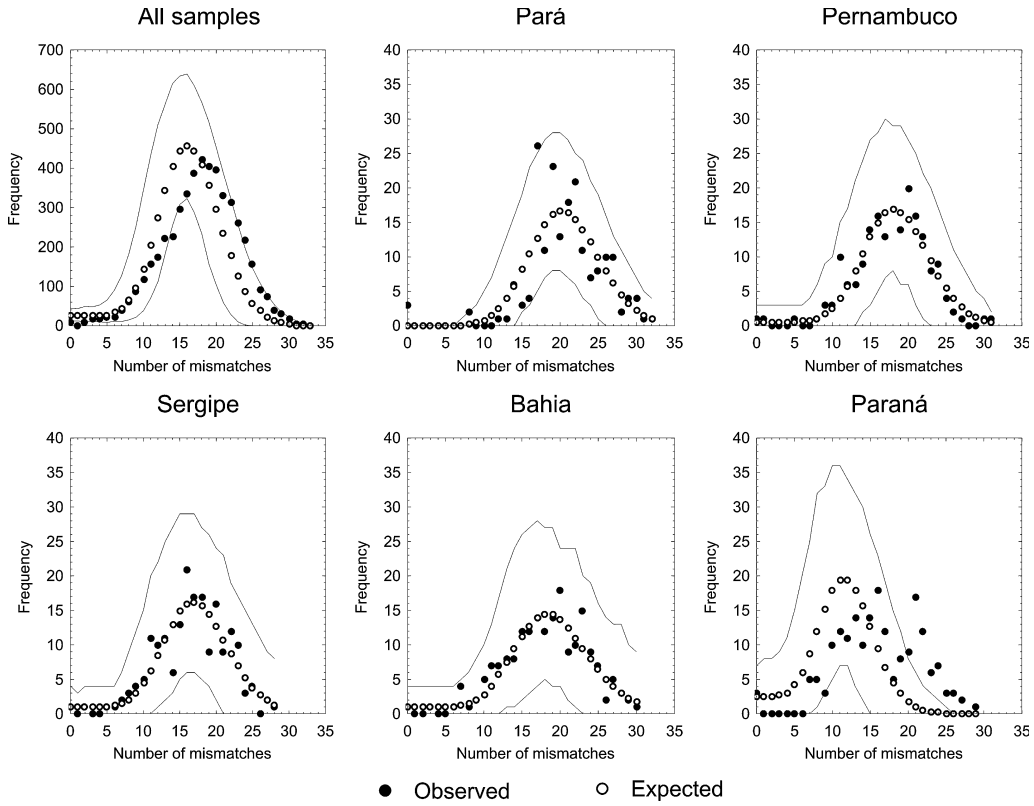

Fig. 3. Mismatch distributions of all samples combined, as well as each location separately, indicating the observed (closed circles) and expected (open circles) mismatch patterns. The latter are complemented by the respective 95% confidence intervals.

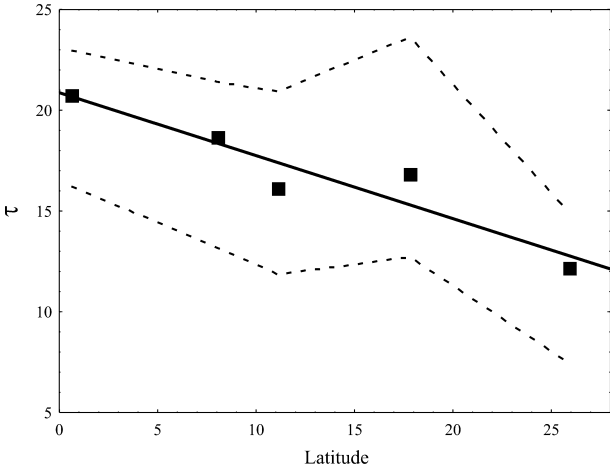

Fig. 4. Relationship between the parameter τ of each study location and their respective latitude. The regression is significant (r^2 = 0.8906, P = 0.0159).

match distribution analysis, simulation studies have shown that parameter estimates are robust to such violations, even when site-specific mutation rates follow a gamma distribution (Rogers *et al.* 1996).

A remarkable aspect of the observed mismatch distributions is their systematic change in τ, indicating a possible latitudinal range expansion. If one assumes that the mutation rate is constant among locations, the northernmost studied population (τ = 20.7) is almost twice as old as the southernmost population (τ = 12.18). Given the strong link between the ecology of *U. cordatus* and mangrove forests, this expansion might indicate a corresponding increase in the availability of mangrove areas along the Brazilian coast. Mangroves are thought to have originated in Southeast Asia and gradually dispersed throughout Old World and New World locations over the Tertiary and Quaternary (Woodroffe & Grindrod 1991). Studies of the palynological record during the Quaternary have shown that the distribution dynamics of mangrove environments was a highly dynamic process, particularly in response to sea-level fluctuations (Woodroffe & Grindrod 1991; Ellison 1996). In particular, mangrove expansion has been linked to periods of marine transgression, which cannot be simply associated with periods of dry/humid climate (Grinrod *et al.* 1999). This hypothesized expansion in mangrove environments along the Brazilian coast could be indicative of the formation of

well-developed tidal estuaries, as suggested by Grinrod *et al.* (1999) for the Australian tropics.

The results of the present study suggest that such expansion might have left its signature in the pattern of genetic variation of the mangrove land crab, possibly also experiencing a southward expansion of mangrove habitats. Unfortunately, to the best of our knowledge, no comparable data sets of mangrove crustaceans (or other animals and plants) are currently available to determine the extent to which this pattern is robust. However, at least an additional sympatric crab species showed highly concordant genetic patterns (*Cardisoma guanhumi*, Oliveira-Neto *et al.*, unpublished data). Studies estimating the absolute rate of mutation using calibration points such as the formation of the Isthmus of Panama might be particularly revealing to uncover the timeframe for this expansion.

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