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Minuca panema (Coelho, 1972): Resurrection of a Fiddler Crab Species from Brazil Closely Related to *Minuca burgersi* (Holthuis, 1967) (Crustacea, Decapoda, Brachyura, Ocypodidae)

Carl. L. Thurman¹, Hsi-Te Shih^{2,}*, and John C. McNamara^{3,4}

¹Department of Biology, University of Northern Iowa, 1227 West 27th St., Cedar Falls, IA 50614-0421, USA. E-mail: thurman@uni.edu (Thurman). Tel: +1 319 273-2276

²Department of Life Science and Research Center for Global Change Biology, National Chung Hsing University, Taichung 402, Taiwan. *Correspondence: E-mail: htshih@dragon.nchu.edu.tw (Shih). Tel/Fax: 886-4-22856496

³Departamento de Biologia, FFCLRP, Universidade de São Paulo, Ribeirao Preto 14040-901, Brazil. E-mail: mcnamara@ffclrp.usp.br (McNamara). Tel: +55 16 3315 3687

⁴Centro de Biologia Marinha, Universidade de São Paulo, 11600-000 SP, Brazil

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We redescribe a species of fiddler crab, Minuca panema (Coelho, 1972), from the Atlantic coast of South America. It is closely related to M. mordax (Smith, 1870), and until now, the taxon has been considered to be synonymous with another closely related species Minuca burgersi (Holthuis, 1967). However, we found that two clades of *M. burgersi sensu lato* were restricted to the Caribbean Basin. This distribution differs from than that of *M. panema*, which occurs primarily along the eastern coast of South America, ranging from the island of Trinidad to Praia da Armação, Santa Catarina, Brazil. Based on our field studies, the geographical boundary between *M. burgersi* sensu stricto and *M. panema* is the Tobago Basin, north of Trinidad. Since the two species diverged only 3 to 4 million years ago, as dated from the phylogeny of the genus Minuca Bott 1954, there are few reliable morphological features that can be used to distinguish them clearly. In live crabs, there is a striking difference in coloration between the cherryred South American M. panema and the rusty-red Caribbean M. burgersi sensu lato. In males, the pattern of tubercles on the inner surface of the major cheliped varies between the two species. In females, the vulva is slightly larger in *M. burgersi* sensu stricto. Ocean tides and currents together with siltation owing to freshwater outflow from the Amazon and Orinoco rivers most likely have driven the divergence of these species. In the Caribbean, small tidal amplitudes have minimized long-distance gene flow in M. burgersi sensu stricto from isolated insular lagoons. In contrast, large tidal amplitudes and exposed habitats on riverbanks along the eastern Atlantic coast of South America have enabled long-distance dispersal in M. panema. DNA analysis reveals that haplotypes of cytochrome c oxidase subunit 1 are not shared between the species. Since natural selection and/or genetic drift have yet to produce extensive morphological divergences between M. panema and M. burgersi sensu stricto, we speculate that changes in the genes regulating mitochondrial DNA functions have led to speciation at the molecular level. According to the mitonuclear compatibility concept, we propose that mitochondrial DNA may be at the forefront of speciation events and that co-evolved mitonuclear interactions are responsible for some of the earliest genetic incompatibilities arising among isolated populations.

Key words: Morphology, 16S rDNA, 28S rDNA, Cytochrome c oxidase subunit I (COI), Biogeography

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BACKGROUND

Fiddler crabs are common inhabitants of intertidal and supratidal regions around the world. Found along most temperate and tropical shores, these brachyurans exhibit substantial species diversity. Currently, there are 107 identified species of fiddler crabs (Shih et al. 2016 2018 2019a; Shih and Poupin 2020). Previously, all fiddler crabs were classified within a single genus, Uca Leach, 1814 (Rathbun 1897 1918; Crane 1975). Based on mitochondrial and nuclear DNA, Shih et al. (2016) accepted 11 genera of fiddler crabs as valid, supported further by mitogenomics (Conrad et al. 2021; Liu and Shih 2022) and larval morphology (Kumar and Al-Aidaroos 2022; Zhang and Shih 2022). This proposal has been adopted by most investigators and by the World Register of Marine Species (WoRMS) (Shih and Chan 2022).

Along the shores of the western Atlantic Ocean, from Cape Cod, Massachusetts to Buenos Aires, Argentina, 20-21 species are currently recognized (Shih et al. 2016). Until 1939, only 14 species could be identified with certainty across regions in the western Atlantic (Rathbun 1918). At that time, Oliveira (1939) added three new taxa from the southeastern Brazilian coast near Rio de Janeiro: Uca olympioi, Uca salsisitus and Uca pugnax brasiliensis. Crane (1943) described Uca cumulanta from the Gulf of Paria near Capure, Pedernales, Venezuela. In 1967, Holthuis described Uca burgersi (= Minuca burgersi) (Fig. 1) specifically from Curaçao but acknowledged that the species was common throughout the Caribbean, from Florida to Mexico and south to Trinidad and Tobago. A related taxon, Uca panema Coelho, 1972, from Brazil was proposed five years later. In the northern Gulf of Mexico, three new species were described: Uca virens

Salmon & Atsaides, 1968, *Uca longisignalis* Salmon & Atsaides, 1968 and *Uca panacea* Novak & Salmon, 1974. On the eastern coast of Mexico, *Uca marguerita* Thurman, 1981 was distinguished from the older, established taxa, *U. burgersi*, *Uca mordax* (Smith, 1870), *Uca rapax* (Smith, 1870) and *Uca spinicarpa* Rathbun, 1900. The last species described in the region based on morphology was *Uca victoriana* von Hagen, 1987 from southeastern Brazil.

In Crane's monograph (1975), taxonomic revisions were proposed for some species in the western Atlantic. In particular, the three species of Oliveira (1939) were found to be junior synonyms of older taxa. Crane considered U. olympioi and U. pugnax brasiliensis to be Uca uruguavensis Nobili, 1901 and U. rapax, respectively. Later, Tavares and de Mendonça (2003) questioned the validity of U. salsisitus as a species since the type specimens consisted of both U. rapax and Uca vocator (Herbst, 1804). Regarding "Ciecie Panema" in Marcgrave (1648: 185), Herbst (1782: 81) considered the species to be Cancer vocans minor Herbst, 1782 (= Gelasimus annulipes H. Milne Edwards, 1837; see Shih et al. 2021). However, the identity of the species was uncertain (Lemos de Castro 1962; Tavares 1993). Coelho (1972) provided a preliminary description of a new species, Uca panema, collected from Itamaracá Island, Pernambuco, Brazil, for Marcgrave's (1648) "Ciecie Panema". In her monograph, Crane (1975) reported M. burgersi to range from Florida, the Yucatan Peninsula, Belize, Guatemala, Panama and throughout the Caribbean islands to Venezuela. For the first time, she added specimens of M. burgersi sensu lato from Fortaleza (USNM 138509), Rio de Janeiro (USNM 136511) and São Sebastião (USNM 1136004, 138510), Brazil. Crane's treatment led to the recognition of U. panema as a junior synonym of M. burgersi in Brazil.



Fig. 1. A: *Minuca panema* (Coelho, 1972) and B: Male *Minuca burgersi* (Holthuis, 1967). A: From the South Atlantic Ocean – Brazil, São Paulo state, Caraguatatuba, Praia da Enseada (23.726°S, 45.419°W) (ZMUSP 20835). B: From type location, Caribbean – The Netherlands Antilles, Curaçao, Westpunt, Grote Knip, salt pond (12.352°N, 69.15122°W) (UNI 721). Scale bar = 10 mm.

In 1980, von Hagen examined specimens of U. panema and wrote to Coelho that they were identical to U. burgersi, suggesting they were synonymous (pers. com., Jesser Fidelis de Souza Filho, Oceanography Museum, Federal University of Pernambuco (MOUFPE)). Coelho persisted in acknowledging the species (Coelho and Coelho-Filho 1993). However, Coelho dropped the name and began using M. burgersi instead (Coelho 1995; Almeida and Coelho 2008; Coelho et al. 2008; Almeida et al. 2010). Neither the designated type specimen nor the paratypes for U. panema as stipulated by Coelho (1972) are currently available at MOUFPE. Melo (1996) published a guide to the brachyurans of the western Atlantic and indicated that *M. burgersi* is distributed from Florida and the Gulf of Mexico to northern South America. There is no mention of U. panema. Melo reported U. burgersi to be absent from Guyana, Suriname and French Guiana as well as from locations in Brazil north of the Amazon estuary. Minuca burgersi appears again along the Brazilian coast from São Luis, Maranhão to Cabo Frio near Rio de Janeiro. Consequently, the species' range is not continuous but is disrupted by the silty freshwater outflow from the Amazon and Orinoco Rivers.

Thurman's et al. (2021) molecular study revealed three clades showing minor morphological differences within the Minuca burgersi species complex. "Clade 3" includes samples from the type locality of Uca burgersi Holthuis, 1967 (Grote Knip, Westpunt, Curaçao) which should be considered the true *M. burgersi*. "Clade 1" is distributed along the Atlantic shores of South America and includes the type locality of Uca panema Coelho, 1972 (Itamaracá Island, Pernambuco, Brazil). Although Uca panema has been synonymized as Uca burgersi since 1995 (e.g., Coelho 1995; Almeida and Coelho 2008; Coelho et al. 2008), the minor morphological differences are now supported by molecular evidence (Thurman et al. 2021) and the species can be considered a pseudocryptic species (e.g., Ragionieri et al. 2009; Shih et al. 2018; Fratini et al. 2019; Prema et al. 2022). In this article we redescribe in detail the characters of Uca panema Coelho, 1972 as a species closely related to both M. mordax and M. burgersi sensu lato. Because the holotype of Uca panema cannot be located (see above) and the species is similar to M. burgersi and M. mordax, it is necessary to designate a neotype to resolve issues of doubtful identity and to maintain nomenclatural stability (see ICZN 1999: Art. 75, Art. 75.3, Art. 75.3.4). We have selected a neotype male specimen from the Rio Maracaípe, Pernambuco, Brazil (latitude $\approx 8.5^{\circ}$ S), which is near the original type locality (Itamaracá Island, Pernambuco, Brazil; latitude $\approx 7.8^{\circ}$ S) (see ICZN 1999: Art. 75.3.6). Here, we distinguish Minuca panema from M. burgersi sensu stricto in the southeast Caribbean (Fig. 2). *Minuca* aff. *burgersi* will be analyzed in a forthcoming publication.

MATERIALS AND METHODS

Sampling

A total of 1,060 preserved specimens from 39 locations along the shores of the western Atlantic Ocean between the Bahamas and southern Brazil (Table S1) was examined. Based on previous observations (Thurman et al. 2021), the specimens were separated into two geographical groups (see below) depending upon whether they were collected north or south of the Tobago Strait (11.000°N latitude). For the northern locations, 504 specimens were collected from 19 sites across the Bahamas, Puerto Rico, U.S. Virgin Islands, Netherlands Leeward Islands, Barbados, Netherlands Antilles and Tobago ("Clade 3" in Thurman et al. 2021). For the southern populations ("Clade 1" in Thurman et al. 2021), 556 specimens of *M. burgersi*-like crabs were examined from 20 locations along the Atlantic coast of South America. Specimens were captured from Trinidad, and the coastal states of Brazil (Ceará, Paraíba, Pernambuco, Bahia, Espírito Santo, Rio de Janeiro, Paraná and Santa Catarina) (Table S1).

Freshly collected crabs were frozen, preserved in 80% ethanol and deposited into the collections housed at the Department of Biology, University of Northern Iowa (UNI) or at the Zoological Museum, University of São Paulo (ZMUSP). Voucher specimens of M. burgersi were examined at the National Museum of Natural History, Washington, DC, USA (USNM), the Zoological Museum, University of São Paulo, São Paulo, Brazil, and the Rijks Museum, Leiden, the Netherlands (RMNH) to authenticate the morphological characteristics of the specimens. Additional materials from zoological collections held at the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); Senckenberg Museum, Frankfurt am Main, Germany (SMF); Museo Zoológico de la Universidad de Costa Rica, San José (UCR); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC) were included in the molecular study.

Morphology

Previously we provided a morphometric examination of U. *burgersi* from the Caribbean and South America (Thurman et al. 2021). All measurements taken to the nearest 0.01 mm were obtained with



Fig. 2. Geographical distribution of *Minuca burgersi* (Holthuis, 1967) (blue; distributed Bahamas, Curaçao, Barbados), *M.* aff. *burgersi* (green; distributed Florida, Virgin Islands, Belize) and *M. panema* (Coelho, 1972) (red; Atlantic coast of South America: Trinidad Island to Florianópolis, Santa Catarina, Brazil). Modified from Thurman et al. (2021).

digital calipers (Fowler Sylvac, Switzerland). The terminology of Crane (1975) was used to describe the anatomical structures of the crabs. Characteristics of the male first gonopod (G1), vulva, carapace, thoracic sternum, cheliped and ambulatory legs were examined in detail with an Olympus ST-SZ binocular dissecting microscope (Olympus Corporation, Tokyo, Japan). Macroscopic structures were photographed with a Nikon D40 digital camera and a zoom micro-lens (Nikkor AF-S, F1:2.8G). Structural details were recorded using a Zeiss Stemi 305 digital microscope and Jenoptik GRYPHAX (V2.1.0.725) software (Carl Zeiss Gmbh, Jena, Germany). Adobe Photoshop CC 2020 was used to process the digital images. An ocular micrometer was used to estimate the size of microscopic structures.

Molecular analyses

To analyze mitochondrial 16S and cytochrome *c* oxidase subunit 1 (*COI*) haplotypes, crabs were collected from 12 locations in the eastern Caribbean and 12 locations in Brazil (see Thurman et al. 2021: Table 1; Fig. 2). Additional 16S and *COI* sequences for *M. marguerita* were obtained with primers 16H10, 16L29, LCO1490 and HCO2198 (see Schubart 2009). The nuclear 28S sequences were obtained from *M. argillicola* (Crane, 1941), *M. burgersi*, *M. aff. burgersi*, *M. marguerita* and *M. panama* with the primers 28L4

Table 1. Haplotypes of 16S rDNA, COI and 28S rDNA markers for species of Minuca and related outgroups

	Locality	Catalogue # NCHUZOOL . (unless indicated)	Access. # for 16S	Access. # for COI	Access. # for 28S
M. argillicola	Ecuador: Puerto Morro	SMF 34737	LC150346	FN430701	FN430713
	Brazil: Rio de Janeiro	13956	LC150347	LC150407	LC150476
M. burgersi	Puerto Rico: Río de la Plata	UNI 2729	MW310201	MW311060	OQ476644
	Barbados: St. Lucy: Maycocks Bay	UNI 3345	MW310199	MW311063	
	Curaçao: Charo	UNI 3276	MW310204	MW311060	
M. aff. burgersi	USA: Florida	UNI 486	MW310192	MW311051	
	Bahamas: San Salvador: Salt Pan	ZRC	LC087920	LC087950	
M. ecuadoriensis	Ecuador: Puerto Morro	SMF 34740	LC150348	FN430704	FN430716
M. galapagensis	Ecuador: Puerto Morro	SMF 34741	LC150349	FN430705	FN430717
	Peru: Tumbes	SMF 13151	LC150348	FN430704	FN430716
M. herradurensis	Panama: Diablo Heights mangroves	13580	AB813664	AB813680	AB813709
"M. longisignalis"	Texas, USA: Ingleside Cove, Corpus Christi	13938	LC087922	LC087952	LC087979
M. marguerita	Mexico: L. La Mancha, Veracruz	15166	OQ456151	OQ456152	OQ476645
M. minax	Virginia, USA: Chesapeake Bay	13939	LC087921	LC087951	LC087978
	Florida, USA	13957	LC150350	LC150408	LC150477
M. mordax	Brazil: São Paulo	13940	LC087923	LC087953	LC087980
M. osa	Costa Rica: Golfo Dulce	UCR 2620-01	LC150351	FN430711	FN430722
M. panema	Trinidad and Tobago: Maracas Bay Village	UNI A3464	MW310187	MW311039	OQ476647
	Brazil: Ceará: Fortaleza	UNI 2401	MW310189	MW311043	OQ476648
M. pugnax	(#1) Maryland, USA: Assateague I.	13941	LC087924	LC087954	LC087981
	(#2) Maryland, USA: Assateague I.	13941	LC087925	LC087955	LC087982
M. rapax	Jamaica: Trelawny	13942	LC087926	LC087956	LC087983
	British Virgin: Paraquita Bay	13943	LC087927	LC087956	LC087984
	Panamá: Bocas del Toro	13944	LC087928	LC087957	LC087984
M. victoriana	Brazil: Bahia	13945	LC087929	LC087958	LC087985
M. virens	(#1) Texas, USA: Ingleside Cove, Corpus Christi Bay	13584	AB813665	AB813681	AB813710
	(#2) Texas, USA: Ingleside Cove, Corpus Christi Bay	13584	LC087930	AB813681	LC087986
	Florida, USA: Money Bayou, Gulf County	13946	AB813665	AB813681	LC087984
M. vocator	Brazil: Ceará	13948	LC087931	LC087959	LC087987
	Trinidad	SMF 34745	LC150352	FN430709	FN430720
M. zacae	El Salvador	SMF 2104a	LC150353	FN430710	FN430721
Outgroups					
Leptuca pugilator	South Carolina, USA: Georgetown	13586	AB813662	AB813678	AB813707
Petruca panamensis	Panamá: Culebra I.	USNM 1294205 (neotype)	LC087917	LC087943	LC087975

and 28H4 (Ragionieri et al. 2009) (Table 1) following Shih et al. (2016). Other 28S sequences for *Minuca* species were taken from Shih et al. (2016) and are included in table 1. A phylogeny for 16 species of *Minuca* collected from 31 locations in the Gulf of Mexico, the western Atlantic Ocean and the Pacific Ocean was constructed employing DNA sequences from 16S, *COI* and 28S genes, with *Leptuca pugilator* (Bosc, 1802) and *Petruca panamensis* (Stimpson, 1859) serving as the outgroups.

For the combined 16S, *COI* and 28S dataset, the best-fitting models for sequence evolution of individual datasets were determined using PartitionFinder (vers. 2.1.1, Lanfear et al. 2017) selected by using the Bayesian information criterion (BIC). The best models for the three individual datasets were all GTR+G+I and were subsequently employed for Bayesian inference (BI) analysis. The BI was performed with MrBayes (vers. 3.2.6, Ronquist et al. 2012). The search was run with four chains for 10 million generations and four independent runs, trees being sampled every 1,000 generations. The convergence of chains was determined by the average standard deviation of split frequency values below the recommended 0.01 (Ronquist et al. 2020); the first 800 trees were discarded as the "burn-in".

RESULTS

TAXONOMY

Family Ocypodidae Rafinesque, 1815 Subfamily Gelasiminae Miers, 1886 Genus *Minuca* Bott 1954

Minuca panema (Coelho, 1972) (Figs. 1, 3–7)

Ciecie panema Marcgrave 1648: 185 (list; Brazil).

- Cancer vocans minor Herbst 1782: 81 (= Gelasimus annulipes H. Milne Edwards, 1837; see Shih et al. 2021) (not Gelasimus annulipes H. Milne Edwards, 1837).
- Uca panema Coelho, 1972: 42 [Pernambuco, Paraíba]; Coelho and Coelho-Filho 1993: 48 [key; Brazil]; Coelho 1995: 139 [list]; Shih et al. 2016: 154 [list]; Questel 2019: 28 [list].
- Uca (Minuca) burgersi Crane 1975: 168–172, 604 [part, list; Brazil]; Almeida et al. 2010: 354 [Brazil]; Bezerra 2012: 216–219 [part, list; Brazil]; Thurman et al. 2013: 6, 8, 9, fig. 1 [list; Brazil].
- Uca burgersi von Hagen 1983: 230 [part; Brazil]; von Hagen 1984: 205 [Trinidad]; Almeida and Coelho 2008: 207 [Brazil].
- *Minuca burgersi* Shih et al. 2016: 143, 154, fig. 3; Thurman et al. 2017: 247–250, tables 1–5, figs. 3, 5, 6, [Brazil]; Rosenberg 2019: 735 [list]; Thurman et al. 2021: 1–28 [South America].

Material examined: Minuca panema (Table S1): Neotype: male 11.55 × 8.24 mm (MZUSP 42510), Brazil, Pernambuco, Rio Maracaípé. Others: Trinidad: (RMNH 23040), Blanchisseuse (USNM 138505), L. Ebranche River (RMNH 23040, UNI 722), Burro River, Invader's Bay (UNI 721, 720), Cocorite Swamp (USNM 137745); Brazil: Pará, Curuçá (MZUSP 12313); Maranhão, Icatú (MZUSP 23176); Ceará, Fortaleza (USNM 138509) (MZUSP 23179); Paraíba, Mamanguape (MZUSP 13255); Pernambuco, Rio Maracaípé (MZUSP 20838 and 20841); Bahia, Itaparica (USNM 138510), Madre de Deus: Plataforma Lobato (MZUSP 20834, 20844); Espírito Santo: Conceição (MZUSP 18650), Anchieta (MZUSP 18638), Santa Cruz: Bairro Joana D'Arc: Guarapari (MZUSP 20837, 20840, 20842, 20990, 20991); Rio de Janeiro: Ilha do Pinheiro (USNM 138511), Ilha de Paquetá (USNM 19971), Itacuruçá (MZUSP 17201), Barra de Guaratiba (MZUSP 20839); São Paulo: Ilhabela (USNM 136004), Santos (USNM 138512), São Sebastião, Bertioga (USNM 1136004, MZUSP 20834, 20835, 20839, 23177, 23178); Paraná: Baía de Guaratuba: Ponta de Venda (ZMUSP 42511), Baía de Guaratuba (MZUSP 20833); Santa Catarina: Rio Itajaí-Mirim: Balneário Daniela: Barra da Lagoa: Praia da Armação (MZUSP 20828, 20829, 20830, 20831, 20832).

Comparative material: Minuca burgersi (Holthuis, 1967) (Table S1): Netherlands Antilles: Curaçao: Grote Knip (RMNH 23012 (holotype); USNM 121099 (paratype), 7577; UNI 719); Aruba (USNM 138503); Leeward Islands: Sint Maarten (USNM 138497, 138498); Tobago: Pigeon Point (USNM 138504); Barbados, St. Peter's Bay, Maycock's Bay, Graeme Hall (UNI 716, 717, 718).

Description (Fig. 3): Carapace trapezoidal, surface strongly convex, smooth and glossy with numerous small pits. Front angled from midline to lateral margin about 16°. Eyebrows barely visible (Fig. 3A: a). Length of carapace 68% width in females (n = 108)and 66% in males (n = 401). H-depression deep with some pubescence and two large central pores in sulcus. Frontal region compared to carapace width 37.1% or greater (n = 10). Sulcus posterior to orbits deep (Fig. 3A: b). Lower orbital margin with rectangular dentals (Fig. 3F: c). Anterolateral angles (Fig. 3A: d, Fig. 3B: d) sharp, pointed inward toward medial line. Hepatic area swollen and rounded behind angle. Anterior edge of lateral line almost straight forming smooth, obtuse angle with posterior lateral line (Fig. 3B: e). Two posterolateral striae (Fig. 3B: f) present. Dorsal striae long and fragmented into two parts. Second more ventral and shorter. Patch of pubescence (Fig. 3B: g) between striae and ventral edge of carapace. Outer surface of major cheliped with dorsal ridge on manus. Large tubercles on upper manus decreased in size to ventral margin (Fig. 3C). Dactyl articulation joint (Fig. 3C: h) with row of tubercles. Base of pollex at manus forming smooth triangular sulcus (Fig. 3C: i). Pollex (Fig. 3C: j) and dactyl (Fig. 3C: k) horizontally compressed, blade like with smooth surfaces. Three rows of tubercles in gap. End of pollex trifurcated with three tooth-like tubercles. Dactyl with two larger tubercles (Fig. 3C: k, Fig. 4A: a); one proximal and the other distal. Pollex with large tubercle on distal half followed by second smaller tubercle (Fig. 3C: j). Inner surface of major cheliped with carina of tubercles lining dorsal edge of carpal cavity (Fig. 3D: l). Carina often ending in a patch of tubercles with upper row pointed to dactyl. A smooth triangular area above the carina terminus. Lower edge of carpal cavity with apex of tubercles at proximal end of oblique ridge (Fig. 3D: m). Distally oblique ridge across palm undeveloped. Dactyl joint with row of 5–8 tubercles (Fig. 3D: o). Lines of tubercles on predactyl and articulating ridges not parallel. Predactyl ridge



Fig. 3. *Minuca panema* (Coelho, 1972) (ZMUSP 20833). A: Dorsal view. B: Lateral carapace view on side of minor cheliped. C: Outer surface of major cheliped. D: Inner surface of major cheliped. E: Second ambulatory leg. F: Oral view of carapace. a. eyebrow, b. postorbital sulcus, c. dental on suborbital margin, d. anterolateral angle, e. posterolateral line, f. posterolateral striae, g. pubescence, h. articulation ridge, i. pre-pollex depression, j. pollex, k. dactyl, l. superior carpal cavity carina, m. apex of oblique ridge, n. pre-dactyl ridge, o. articulation ridge, p. manus-pollex ridge, q. pubescence, r. setae. Scale bar = 10.0 mm.

forming crescent arch initially extending toward palm but returns to articulation (Fig. 3D: n). Keel on lower edge of manus and ventral pollex. Exterior surface of minor cheliped smooth. Long ridge from manus to end of pollex. Dactyl with faint ridge from articulating junction to terminus. Pollex and dactyl with 6-8 sawtooth tubercles in gap. Distal tips of dactyl and pollex with sharp, chitinized edge. On inner surface of pollex and dactyl, distal end with regularly arranged comb-like setae covering about one-third of pollex length. Width of merus on ambulatory legs 1-3 of minor side (Fig. 3E) approximately 37% of length (n = 10). Dorsal and lateral surfaces of carpus and manus on ambulatory legs 1-3 of with pubescence (Fig. 3E: q). Dorsal surface of dactyl without pubescence. No pubescence on ventral surface of manus, carpus or dactyl. Long setae (Fig. 3E: r) plentiful on manus but sparse on merus. Distal end of G1 with long setae (Fig. 5A: a, b; Fig. 5B, C). Proximal group few in number but long (0.5 to 0.75 mm) (Fig. 5C). A few setae near terminal flange. Flange with pronounced cusp (Fig. 6A: a; Fig. 6B: a). In females, operculum of vulvae small and protruding, no tubercle (Fig. 7A).

Remarks (Figs. 4, 7; Table 2): The relationship of *M. panema* to other species in the *Minuca* genus is addressed in the "DISCUSSION" section. Since they are geminate species, here, we focus on the subtle anatomical landmarks distinguishing *M. panema* from *M. burgersi* sensu stricto (Table 2). For males, there are two or three large tubercles (Fig. 4A: a) at the distal end of the cheliped pollex in M. panema. In M. burgersi sensu stricto, there is usually only one tubercle (Fig. 4B: a) on the pollex. Minuca panema has a prominent smooth sulcus on the lateral surface of the major cheliped at the pollex-manus junction (Fig. 4A: b). Tubercles on the lateral surface of the manus form a distinct pre-dactyl ridge (Fig. 4A: c) in M. panema. In M. burgersi, the ridge is weak (Fig. B: c). On the medial inner surface of cheliped, oblique tubercle ridges are more clearly defined in M. panema (Fig. 4C: d). The carina (Fig. 4C: e) along the lower edge of the carpal cavity are more distinct in M. panema. The carina along the upper edge of the carpal cavity terminates in a tubercle field (Fig. 4C: f) that expands to the medial predactyl ridge. The pre-dactyl ridge (Fig. 4C: g) arches strongly and intersects with the tubercle ridge on the swelling of at the articulating joint in M. panema. In M. burgersi, the oblique ridge (Fig. 4D: d) is less developed and the inferior carpal carina has only a few tubercles (Fig. 4D: e). The field of tubercles at the distal end of superior carpal carina (Fig. 4D: f) does not extend to the pre-dactyl ridge. This area is usually smooth.

Figures 5 and 6 are images of the right G1 from *Minuca panema* and *M. burgersi*. In figure 5, the former, G1 is ornamented with setae that have been removed in figure 6. In *M. panema*, setae near G1 tip (Fig. 5A–C)



Fig. 4. Comparison of male major cheliped between *Minuca panema* (Coelho, 1972) (A, C; MZUSP 20833) and *M. burgersi* (Holthuis, 1967) (B, D; UNI 719). A, B: outer surface, C, D: inner surface. a. tubercle at distal end of pollex, b. sulcus at pollex-manus junction, c. lateral predactylar tubercle ridge, d. oblique palmar tubercle ridge, e. anterior of carpal cavity, f. tubercle field, g. medial predactylar ridge. Ruler with 1 mm divisions at upper edge of figure 5A, B.

Characters	M. burgersi	M. panema		
Eye orbits	From dorsal view, ocular cavities angled to posterior. Eyebrows visible. Dorsal carina lightly beaded, lower strongly beaded.	Ocular cavities not strongly angled. Eyebrows visible. Upper and lower carina almost smooth.		
Carapace surface	Surface finely granular with pits. Post-orbital sulcus deep. Medially with tubercle. Laterally curved to intersect dorsal lateral margin. H-depression deep. Interocular lobe formed about $34.0 \pm 1.3\%$ of carapace width. Eyestalks short with 25% retina. From front, carapace arched.	Surface finely granular with pits. Post-orbital sulcus deep. Medial end curving toward H-depression. Large tubercle at antero- and medial sulcus. H-depression shallow. Interocular lobe $37.8 \pm 3.0\%$ carapace width. Eyestalks like <i>M. burgersi</i> . From front carapace flat.		
Orbital floor	Floor smooth. Lateral ends with 3-sharp tubercles surround by short setae. Lower edge with rectangular dentals. Setae behind dentals.	Floor smooth. Lateral ends with 2-tubercles. Lower edge with rectangular dentals. Setae behind line of dentals.		
Anterolateral angle	Anterolateral angles pointed forward but converging toward body midline.	Same as <i>M. burgersi</i> .		
Anterolateral, dorsolateral and vertical lateral margins	Anterolateral margins intersecting with dorsolateral margin at widest portion of carapace. Lines almost smooth. 2 posterolateral striae present. Anterolateral margins diverging into vertical lateral margin. This terminating between 3rd and 4th ambulatory legs.	Margin lines strongly tuberculated. Otherwise margins very similar.		
outer surface	Outer surface: Dorsal surface with two parallel ridges of tubercles. Outer upper surface with large tubercles decreasing in size ventrally. Ventral margin with a tubercle ridge.	Parallel tubercle ridges on dorsal surface weakly developed. Sulcus at pollex-manus junction.		
predactylar ridge	Predactylar articulation joint weakly developed.	No tubercles on predactylar joint.		
pollex	Pollex face smooth with pits. One tooth about 2/3 distance of pollex. Terminus with 3 teeth. 3 rows of teeth on dorsal edge of pollex.	Teeth on dorsal edge of pollex same as <i>M. burgersi</i> .		
dactyl	Dactyl blade-like with variable number of teeth in gap and no grooves. Rows of tubercles on anterior and posterior edge. Random teeth between.	Dactyl blade-like and smooth. Others same as <i>M. burgersi</i> .		
inner dactyl	At articulation, 2 predactylar ridges diverging dorsally. Surface smooth.	2 diverging predactylar ridges. Surface smooth.		
inner palm surface	Dorsal carina completely outlining carpal cavity. Tubercle ridge diverging point to dactyl. Triangle above carina smooth. Palm with high tubercle ridge running obliquely.	Carpal carina ending in a patch of 10–20 large tubercles above apex of oblique ridge. Few tubercles connecting apex and carina.		
Minor chela	 Dorsal surface with ridge. Outer surface smooth. Depression below dactyl articulation. Strong line on pollex. Teeth in gap small. Distal 3–4 largest. Distal end of minor claw ridged and sharp. Inner surface smooth. 4–5 long setae on distal end of pollex. Carpus with numerous vertical lines of tubercles on posterior face. Merus with numerous rows of vertical tubercles on posterior surface. 	Outer surface smooth. Dorsal surface of dactyl with small ridge. Pollex with Ridge. 3–5 teeth in gap. Tip of pollex and dactyl rigid and sharp. Inner palm smooth. Long setae on inner faces of both dactyl and pollex. Carpus smooth. Merus with short row of tubercles.		
stridulation ridges on 1st ambulatory leg	Face of adjacent 1st ambulatory leg without stridulating apparatus.	No obvious stridulation apparatus on 1st ambulatory leg.		
Ambulatory legs	Manus and carpus with pubescence and long setae on dorsal surface. Merus and ischium with short setae. Longer setae on ventral surface. Merus width about 1/3 segment length.	Dorsal surface of manus and carpus wit pubescence and long setae. No pubescence on 4th ambulatory leg. Ventral surface smooth with long setae. Proximal merus with short setae.		
G1 (Crane 1975: fig. 66F)	G1 with setae near terminus. Terminal flange dark and semi- cylindrical. Pre-terminal palp present.	Few long setae. Deep cusp in flange.		
Vulva (Crane 1975: fig. 54G)	Sternal opening covered by bulging plate. No protruding tubercle.	Sternal opening covered by bulging plate. No protruding tubercle.		
carapace	Dorsal carapace surface purple to brown. H-depression large, red- brown. Lower carapace dark chocolate brown.	Dorsal surface gray with white spots. H-depression thin, bright red. Lower carapace cherry red-brown.		
cheliped	Cheliped dark red-orange. Fingers off-white.	Cheliped yellow-orange. Fingers light in color.		
ambulatory legs	Legs brown, carpus and manus banded.	Legs proximally red, distally light brown tan.		

Table 2. Comparison of morphological landmarks between Minuca panema and Minuca burgersi sensu stricto

are few in number but very long. In *M. burgersi* (Fig. 5D–F), the setae are shorter and form a wide, brushlike structure. When the setae are removed (Fig. 6), the apical flange and "thumb" are easier to see. Both Chase and Hobbs (1969: p 210, fig. 71a, b) and Crane (1975: p 380, fig. 66 F) provided drawings of the naked tip. In *M. panema*, the terminal edge of the flange (a) is deeply incised with a cusp (Fig. 6A, B) while the indentation is shallow in *M. burgersi* (Fig. 6C, D). Both species have a

surface of G1. For females, the vulvae are similar (Fig. 7A, B). A cover or operculum bulges outward slightly but with no prominent tubercle (Fig. 7A, B). A small posterior rim is present in both species. In females of similar carapace widths, diameter of vulva is about 0.20 mm for *M. burgersi* but smaller in *M. panema* (about 0.12–0.15 mm).

thumb-like palp (Fig. 6B: b, Fig. 6D: b) on the anterior

Etymology: The specific name honors the original

designation by Marcgrave (1648) in reference to the species' common name at that time, "Ciecie Panema" or "Cranguersinho des Manges".

Geographical range (Fig. 2): Eastern coast of South America from Trinidad Island to Praia da Armação, Santa Catarina, Brazil.

Color in life: Anterior portion of carapace mottled in smudgy gray or blue gray (Fig. 1A). Posterior carapace "crimson" or "cherry" red. Major cheliped in male ochre-orange with pollex and dactyl near white. Proximal portion of ambulatory legs "crimson-red" with distal regions brown.

Habitat: Near the mouths of rivers, islands and estuaries. Most frequently colonizing red-brown clay to silty sand or sandy clay in the upper or supratidal zone. Habitats are oligo- to mesohaline (0.6 to 36.3 psu; 18 to 1,037 mOsm kg⁻¹ H₂O) with a modal value of 7.7 psu (220 mOsm kg⁻¹ H₂O) and a mean of 12.2 ± 2.7 psu (349 ± 79 mOsm kg⁻¹ H₂O). Found near mangroves



Fig. 5. Male right G1 tip with setae from *Minuca panema* (Coelho, 1972) (A, B, C; MZUSP 20833) and *M. burgersi* (Holthuis, 1967) (D, E, F; UNI 719). A, D, posterior view, B, E, anterior view, C, F, lateral view of tip. a. terminal setae, b. terminal flange. Scale bar = 0.5 mm.



Fig. 6. Male right G1 from *Minuca panema* (Coelho, 1972) (A, B: MZUSP 20833) and *M. burgersi* (Holthuis, 1967) (C, D: UNI 719). a. apical flange, b. "thumb" or palp. Scale bar = 0.5 mm.

(*Rhizophora* sp. and *Laguncularia* sp.) (Coelho, 1972) but very common in open or low vegetation such as *Batis maritima*, *Samolus* sp., *Salicornia* sp. and *Disticilis* sp. (Thurman et al. 2013 2017).

Molecular analysis: The pairwise nucleotide divergences of COI with K2P distances and bp differences for Minuca panema, M. burgersi sensu stricto, M. aff. burgersi and M. mordax are given in table 3. The intraspecific and interspecific divergences of *COI* are $\leq 2.81\%$ (18 bp) and $\geq 4.61\%$ (29 bp), respectively. The phylogenetic tree based on combined 16S, *COI* and 28S sequences (Fig. 8) shows that the Neotropical species forming the genus *Minuca* are monophyletic. *Minuca brevifrons* (Stimpson, 1860) appears as a basal species. Three taxa, *M. burgersi*, *M. panema* and *M.* aff. *burgersi* cluster together with



Fig. 7. Female vulva in *Minuca panema* (Coelho, 1972) (A: MZUSP 20833) and *M. burgersi* (Holthuis, 1967) (B: UNI 719). Arrow indicates left gonopore. Scale bar = 1.0 mm.



Fig. 8. Molecular phylogeny based on mitochondrial 16S and COI, as well as nuclear 28S for 19 species in the genus Minuca. The outgroups are Leptuca pugilator (Bosc, 1802) and Petruca panamensis (Stimpson, 1859).

Table 3. Matrix of percentage pairwise nucleotide divergences with Kimura 2-parameter (K2P) distances and number of base pair differences based on cytochrome c oxidase subunit I (*COI*) within and between *Minuca panema*, *M. burgersi*, *M.* aff. *burgersi* and *M. mordax* from the eastern Americas. In the right half, lower-left values are K2P distances and upper-right values are base pair differences. Ranges are shown in parentheses

	Intraspecif	ic	Interspecific			
	Nucleotide divergence	bp difference	M. panema	M. burgersi	M. aff. burgersi	M. mordax
M. panema	0.84	5.49		39.57	33	38.66
	(0-1.39)	(0–9)		(35–44)	(29–38)	(35–42)
M. burgersi	0.43	2.79	6.4		41.42	50.29
	(0-1.39)	(0–9)	(5.62-7.17)		(37–49)	(48–53)
M. aff. burgersi	1.16	7.51	5.28	6.71		41.3
	(0-2.81)	(0-18)	(4.61–6.13)	(5.95-8.04)		(38–47)
M. mordax	0.38	2.5	6.2	8.24	6.65	
	(0–0.76)	(0–5)	(5.58–6.77)	(7.84–8.73)	(6.08–7.63)	

M. mordax forming a clade of related species. Three additional clades of related species appear within the genus *Minuca*: 1) *zacae*, 2) *vocator-ecuadoriensis-osa*, 3) *pugnax-argillicola-victoriana-marguerita-minax-longisignalis-herradurensis-galapagensis-rapax-virens*.

DISCUSSION

From accurate surveys of species' diversity and distributions, M. burgersi sensu lato was previously thought to range from Veracruz, Mexico and eastern Florida in North America south to Florianópolis, Santa Catarina in Brazil (Barnwell and Thurman 1984; Thurman et al. 2010 2013). The species also occurs in Trinidad and Tobago (Holthuis 1967; von Hagen 1970; Crane 1975) but is absent to the south along the coasts of eastern Venezuela, Guyana, Suriname, French Guiana and the state of Amapá in Brazil (Holthuis 1959; Melo 1996; Thurman et al. 2013 2021). An initial, albeit superficial, indication of intraspecific divergence within *M. burgersi* was noted as a color difference between specimens from the Caribbean and Brazil (Fig. 1; Thurman et al. 2013: p. 14, table 4). Despite the color difference and geographical disjunction, the osmoregulatory capabilities of the two groups are similar (Thurman et al. 2017). Recently, allometric and geometric morphometrics have been used together with molecular analyses to estimate intraspecific variation among clades of *M. burgersi* sensu lato (Thurman et al. 2021). Although specimens from the Caribbean are larger than those from Brazil, most allometric relationships are very similar for specimens from both regions. Based on geometric analysis of carapace shape, four distinct patterns emerge. Each is associated with a geographical region: 1) Mexico to Florida, 2) Caribbean, 3) northern Brazil, and 4) southern Brazil (Hampton et al. 2014; Thurman et al. 2021). The crabs in the clade from Brazil have a more swollen branchial chamber than do the Caribbean crabs, which correlates more with geographical region than with either salinity or substrate. Molecular data from 16s rDNA and cytochrome oxidase subunit I reveal three distinct clades (Thurman et al. 2021): two clades are from the Caribbean and the other is from the Atlantic coast of South America (Fig. 2). Clade 1 crabs, M. panema, are from 12 locations between Trinidad and Florianópolis, Brazil. Clade 2 specimens, M. aff. burgersi, are from populations in the northern Caribbean, Florida and Belize. Clade 3 contains samples of M. burgersi sensu stricto from the type locality at Grote Knip, Westpunt, Curaçao; the Netherlands Antilles; and other areas in the southern and eastern Caribbean. Clades 2 and 3 are sympatric in the Bahamas and the US Virgin Islands.

Speciation

In a recent study, we demonstrated that M. burgersi sensu lato is a complex of three regionallydefined clades (Thurman et al. 2021: figs. 17, 18). Here, we propose that "Clade 1" be recognized as Minuca panema. Since there are few differentiating morphological features between "Clade 1" and "Clade 3" (= M. burgersi sensu stricto), we have used additional molecular characteristics to support the resurrection of M. panema from eastern South America. Interspecific divergence in COI sequences between the two species is $\geq 5.62\%$ (Table 3). In semi-terrestrial and freshwater crabs, this degree of molecular divergence is usually sufficient to recognize independent species (Chu et al. 2015). For example, the minimum interspecific distance in some ocypodid Gelasiminae is 3.78% between Tubuca urvillei (H. Milne Edwards, 1852) and T. alcocki Shih, Chan & Ng, 2018 (Shih et al. 2018); 3.81% between Minuca rapax and M. virens (Thurman et al. 2018); and 4.59% between Austruca citrus Shih & Poupin, 2020 and A. perplexa (H. Milne Edwards, 1852) (Shih and Poupin 2020). Additionally, interspecific distance is 1.49% between Leptarma liho (Koller, Liu & Schubart, 2010) and L. paucitorum (Rahayu & Ng, 2009) (Sesarmidae) (Shih et al. 2019b); 3.2% between Sesarmops imperator Ng, Li & Shih 2020 and S. impressus (H. Milne Edwards, 1837) (Sesarmidae) (Ng et al. 2020); 5.63% between Tortomon gejiu Huang, Wang & Shih 2020 and T. puer Huang, Wang & Shih 2020 (Potamidae) (Huang et al. 2020); and 6.11% between Tiwaripotamon pingguoense Dai & Naiyanetr, 1994 and T. xiurenense Dai & Naiyanetr, 1994 (Potamidae) (Do et al. 2016). Consequently, at the molecular level, Minuca panema and M. burgersi sensu stricto are sufficiently distinct to be considered separate species.

Previously we proposed that several geological events and hydrographical barriers to larval flow along the northeastern coast of South America and Central America have contributed to the genetic disparity between M. panema and M. burgersi sensu stricto without substantial morphological distinction (Thurman et al. 2021). We estimated that the two species shared a common ancestor about 4 to 5 million years ago (Mya) (Thurman et al. 2021) and are currently in the process of diverging. Diversification of semi-terrestrial crabs commenced approximately 110 Mya during the middle Cretaceous (Tsang et al. 2014). The western tectonic plate of the Gondwana supercontinent began to rotate clockwise, opening a rift that became the proto-South Atlantic Ocean (Reyment and Tait 1972; Perez-Diaz and Eagle 2017). By the Santonian in the Late Cretaceous (85 Mya), the South Atlantic Oceanic Basin stretched

from the equator to the South Pole. As the young South Atlantic Ocean became deeper and wider during the Late Cretaceous (75 to 65 Mya), the seaway initially flowed southward from the Central Atlantic Basin of the Tethys Sea (Perez-Diaz and Eagles 2017). The South American Plate began moving northwestward about 35 Mya (Late Eocene to Early Oligocene), and the ocean floor between South America and Africa widened. As the Nazca Plate began to subduct under the northwestern edge of the South American Plate, the northern Andes began to rise. The near-shore currents of Brazil flowed northward as the mid-oceanic South Atlantic current continued in a southerly direction. The South Atlantic cyclonic gyre was located east of Argentina. During the Neogene (7 to 23 Mya), the gyre moved northward and the equatorial current system was established. By the Late Miocene (6 to 11 Mya), the Equatorial Current contributed to both the North and South Brazilian Currents across the Ponto de Calcanhar, Touros, Rio Grande do Norte, Brazil (Thurman et al. 2013). At that time, the coastal currents along southeastern Brazil started to flow south. Around 8 to 12 Mya in the Middle Miocene-Early Pliocene, the northeastern edge of the South American Plate collided with the eastward moving Caribbean Plate thrusting up the Cordillera de Mérida mountain range along the coast of Venezuela (Audemard 2003). Then, approximately 4.3 Mya, seismic activity in northeastern Venezuela and Trinidad produced the Columbus Channel and Bocas del Dragón, enhancing the tectonic disjunction of the Caribbean and the South American plate (Comeau 1991). Around 3 Mya, the Isthmus of Panama was established and the northward flow of the Gulf Stream commenced (O'Dea et al. 2016; Jaramillo et al. 2017). The recent geological events of 3-5 Mya are particularly relevant to the genesis of Minuca panema and M. burgersi.

Molecular studies of fiddler crabs indicate that species diversification is often synchronous with geological events. The first "fiddler crabs" arose in the Americas during the Oligocene or Miocene Epochs (16–28 Mya) (Levinton et al. 1996; Sturmbauer et al. 1996). The Tethys Sea provided a connection from the proto-Atlantic to the proto-Indian Ocean across northern Africa and southern Europe (Steininger and Rögl 1984). From the Eocene (65 Mya) until the early Miocene 20 Mya the east-west Tethys portal closed gradually (Bialik et al. 2019). This event coincided with the genetic divergence of the ancestral fiddler crab taxa (e.g., Uca and Afruca) from other ocypodid crabs 22-23 Mya (Sturmbauer et al. 1996). The oldest fossils for ghost crab relatives are from the lower Miocene of Argentina from 20-23 Mya (Casadío et al. 2005). Currently, fossil Uca and Afruca are known from the Miocene of Spain, Brazil, Honduras and Panama (Brito 1972; Artal 2008; de Gilberta et al. 2013; Domínguez 2013; Luque et al. 2018; Lima et al. 2020). As the Tethys connection disappeared approximately 17 Mya in the middle Miocene, ancestral taxa of Neotropical species (e.g., Minuca, Leptuca and Pertuca) diverged from the progenitors of the Indo-West Pacific species (e.g., Tubuca, Xeruca, Gelasimus, Cranuca, Paraleptuca and Austruca) (Stumbauer et al. 1996; Shih et al. 2016). With the rise of the Isthmus of Panama 2.8 to 3.1 Mya, ancestral forms of some Neotropical genera (i.e., Minuca, Leptuca and Uca) on opposite sides of the land bridge became distinct geminate species (Sturmbauer et al. 1996; Lessios 2008; O'Dea et al. 2016; Jaramillo et al. 2017). Within the genus Minuca (Fig. 8), three groups appear as trans-isthmic cohorts: 1) herradurensis-galapagensis-rapax-virens, 2) vocatorecuadoriensis-osa, 3) marguerita-victoriana-argillicola. In the Eastern Pacific, M. brevifrons (Smith 1860) appears to be basal in the molecular phylogeny. More recently, other species-pairs or trios evolved within the Western Atlantic basin: 1) virens-rapax, 2) minaxlongisignalis, 3) marguerita-victoriana, and 4) mordaxburgersi-panema-aff. burgersi. Based on geology, we suspect that the separation of an ancestral taxon of the mordax-burgersi sensu stricto-panema complex occurred in the Late Miocene-Pliocene (3-7 Mya) after the closure of the Panamanian sea portal.

Based on nucleotide substitution rates, the "mordax-burgersi-aff. burgersi-panema" complex began diverging approximately 4.3 ± 0.5 Mya (Thurman et al. 2021). The divergence time of the "burgersi-aff. *burgersi-panema*" complex occurred 4.1 ± 0.5 Mya, implying that the three arose simultaneously. This speciation event was assumed to be influenced by increased sedimentation and outflow volume of the Amazon River due to continental uplift 5-7 Mya (Latrubesse et al. 2010; van Soelen et al. 2017). As a result, coastal habitats north of the Amazon River discharge became dilute and silt-rich during the Pliocene. This habitat is ideal for *M. mordax* but not for M. burgersi which is adapted to sandy-clay (Thurman et al. 2013). During the same period, seismic activity in eastern Venezuela continued along the rift as the South American plate subducted under the Caribbean plate creating the isle of Trinidad and the Tobago Trough (Comeau 1991). As the North American and Cocos plate collided with it in the west, the lighter Caribbean plate was uplifted 2.6 Mya producing an island-ringed plateau covered by a shallow sea (Meschede and Frisch 2002; Feuillet et al. 2011). As a result, today, tidal amplitudes and near-shore currents are significantly reduced across the Caribbean plate when compared to those on the eastern or western coast of South America. The longdistance larval dispersal of *M. panema* appears to originate in estuarine habitats inundated by strong semidiurnal tides of 2 to 4 m amplitudes along the eastern coast of South America (Thurman et al. 2021). In contrast, tides across the Caribbean islands are smaller in amplitude (0.34 to 0.85 m) and their currents are weaker. The tenuous tides of the Caribbean are known to alter seasonal reproduction in fiddler crabs (Morgan and Christy 1994). The diameter of ova in M. burgersi sensu lato from Barbuda is 50% greater than in most other fiddler crabs (Gibbs 1974), which suggests that reproduction in land-locked lagoons and dry estuaries on Caribbean islands is autochthonous with limited larval dispersal, *i.e.*, breeding and development take place locally. Our observation (Fig. 7) that the vulva of female *M. burgersi* sensu stricto is slightly larger than that of *M. panema* supports the notion of autochthonous development in the Caribbean. The smaller ova and larger clutch sizes in M. panema suggest that the species uses a long-distance dispersal strategy (Gray 1942; Reiger 1998). Similar strategies are found in other semiterrestrial thoracotreme crabs living in xeric habitats (Thurman 1985; Schubart et al. 1998).

With populations along the Atlantic coast of South America disconnected reproductively from those in the Caribbean (Thurman et al. 2021), genetic divergence without morphological distinction must have evolved quickly (i.e., 3-4 Mya). Traditionally, we rely on natural selection by environmental conditions or genetic drift in small groups to explain significant alterations in allelic frequencies among the populations of a species (Levins 1968). Since larval distribution throughout populations of *M. panema* among coastal colonies is mostly likely random, the inter-populational genetic variance in South America is expected to be low. In Caribbean populations where gene flow is limited, inter-populational genetic variation would be greater. Further, intra-populational genetic variation also would be low since the frequency of inbreeding is higher. Because of selection and mutation pressures, we anticipate greater allelic variation among populations of *M. burgersi* sensu lato in the Caribbean than in *M. panema* in South America. The geological rift between their respective tectonic plates re-enforces this distinction. We have considered environmental factors such as salinity, substratum and temperature that could lead to genetic and phenotypic divergence among the three clades, and now between two species (Thurman et al. 2021). Recently, the "mitonuclear compatibility species concept" was advanced to explain rapid evolution at the molecular level (Hill 2016). Co-evolution can lead rapidly to divergences in coadapted mitochondrial and nuclear gene sets whenever gene flow among populations is disrupted. Mitochondrial gene products often interact with nuclear mRNAs and proteins. A change in the mitogenomic code may disrupt general cellular function (Hill 2017) and such a mutation could exert selective pressure on the nuclear genome to maintain proper metabolic function. With mutations accumulating rapidly in both the mitochondrial and nuclear genomes, isolated populations would drift apart genetically. Eventually, the mitogenome of one population could become incompatible with the nuclear genes of a different population, leading to reproductive isolation (Callier 2019). Since mitochondria are inherited through the maternal lineage, some paternal nucleogenes may be unresponsive to epistatic mitogenomic regulation, driving sympatric genetic divergence. Although this mechanism is speculative, it is attractive and awaits future investigation in fiddler crabs.

Taxonomic distinction among local Minuca species

Species in the genus *Minuca* are often sympatric and difficult to distinguish. *M. panema* is sympatric with *M. mordax* (Smith, 1870) (see von Hagen 1983 1984) (Fig. 9A), *M. rapax* (Smith, 1870) (Fig. 9B), *M. victoriana* von Hagen, 1987 (Fig. 9C) and *M. vocator* (Herbst, 1804) (Fig. 9D). Coelho and Coelho-Filho (1993: p. 47–48) published an early identification key for these species. More recently, Masunari et al. (2020) produced an illustrated identification key. Here we provide descriptions and images of other sympatric *Minuca* for practical comparisons with *M. panema*.

Minuca mordax (Smith, 1870) (Fig. 10). Front angle from midline to lateral margin about 14°. Eyebrows (Fig. 10A: a) visible. Carapace finely tuberculated and pitted. Carapace length 65% of width. H-depression shallow with sparse pubescence in lateral sulci. Frontal region > 34.5% carapace width. Postorbital sulcus (Fig. 10B: b) short and not connect to H-depression. Lower orbital margin (Fig. 10F: c) without tubercles (mostly setae). Anterolateral angles sharp (Fig. 10A: d; Fig. 10 B: d), pointed forward or inward. Hepatic region near anterolateral surface with larger tubercles in a cluster. Transition from antero- to posterolateral lines (Fig. 10B: e) smoothly curving. Posterolateral striae (Fig. 10B: f) long. Dorsal cheliped surface with ridge. External surface with large tubercles. Ventral surface smooth without manuspollex ridge. Dactyl articulation joint (Fig. 10C: h) without row of tubercles. Gap wide. Pollex (Fig. 10C: i) with one central large tubercle, distal end with three tubercles. On inner surface of claw, carina (Fig. 10D: 1) on dorsal edge of carpal cavity extending toward dactyl. Prominent knob of large tubercles (Fig. 10D: m) at proximal end of oblique ridge. Distal end of oblique ridge inconspicuous. Area between carpal carina and oblique ridge with large tubercles. Predactyl ridge (Fig. 10D: n) in palm with low, smooth tubercles not easily visible. Very short row of tubercles on dactyl articulation (Fig. 10D: o). Dactyl (Fig. 10C: k) with moderate-sized tubercles in gap but no large "tooth". Carpus and manus of ambulatory legs 1–3 covered with pubescence and long setae (Fig. 10E: q, r). Pubescence on dorsal, lateral and ventral merus and manus surfaces (Fig. 10E). Width of merus from ambulatory legs 1–3 on minor side approximately 30% of length. Ventral surface of ambulatory legs 1–3, fine pubescence (Fig. 10E). G1 in Crane (1975: p. 381, fig. 67F). Female with small tubercle on operculum of vulva.

Minuca rapax (Smith, 1870) (Fig. 11). Angle of front from midline to lateral margin about 14°. Eyebrows (Fig. 11A: a) visible. Carapace surface rough appearing with small tubercles but no pits. Carapace length 63% of width. H-depression very shallow. Frontal region 32.5% carapace width (n = 10). Post-orbital depression (Fig. 11A: b) shallow, no tubercles but shows a channel to H-depression. Margin of lower orbital lined with prominent rectangular dentals (Fig. 11F: c). Two small teeth along lateral edge of orbit. Anterolateral angles (Fig. 11B: d) pointed inward slightly. Intersection of anterolateral and posterolateral (Fig. 11B: e) lines forming smooth curve. Upper posterolateral striae (Fig. 11B: f) long. Second striae, just above ventral carapace margin, shorter (Fig. 11B: f). Major cheliped with ridge on dorsal surface. Tubercles on outer face decreasing in size to ventral manus. Manus with ventral keel (Fig. 11C: p) extending to pollex. Pollex (Fig. 11: j) with midlength large tubercle and terminus with 3-4 tubercles. Dactyl (Fig. 11C: k) with 3-4 larger tubercles proximal to articulation. Gap wide. Inner surface of cheliped with carpal carina (Fig. 11D: 1) terminating abruptly in palm. Predactyl ridge (Fig. 11D: n) parallel to row of tubercles on dactyl articulating joint (Fig. 11D: o) (clearly not curved toward palm and carpal cavity). Oblique ridge simple line of tubercles running from lower carpal cavity to ventral edge of manus. Proximal apex (Fig. 11D: m) not prominent. On ambulatory legs, dorsal and lateral surfaces with pubescence and long setae (Fig.



Fig. 9. Other sympatric *Minuca* from the south Atlantic coast of South America. A: *Minuca mordax* (Smith, 1870), B: *Minuca rapax* (Smith, 1870), C: *Minuca victoriana* von Hagen, 1987. D: *Minuca vocator* (Herbst, 1804). Adult males, scale bar \approx 10 mm. Specimens not catalogued.

11E: q, r). Ventral surface no pubescence or long setae. Merus width on ambulatory legs 1–3, 37% length (Fig. 11E). G1 in Crane (1975: p. 381, fig. 67C). Female vulvar operculum with large tubercle. See Crane (1975: p. 371, fig. 54F). *Minuca victoriana* (von Hagen, 1987) (Fig. 12). Front angle from midline to lateral margin about 20°. Eyebrow (Fig. 12A: a) visible. Surface of carapace smooth, shiny and finely granular. Carapace length 59% of width. H-depression deep with pubescence in lateral



Fig. 10. *Minuca mordax* (Smith, 1870), collected from Belize (UNI 47). A: Dorsal view of entire crab. B: Lateral carapace view on side of minor cheliped. C: Outer surface of major cheliped. D: Inner surface of major cheliped. E: Second ambulatory leg. F: Oral view of carapace. a. eyebrow, b. postorbital sulcus, c. suborbital margin, d. anterolateral angle, e. posterolateral line, f. posterolateral striae, h. articulation ridge, j. pollex, k. dactyl, l. superior carpal cavity carina, m. apex of oblique ridge, n. pre-dactyl ridge, o. articulation ridge, q. pubescence, r. setae.

sulcus. Frontal region 33% carapace width (n = 10). Post-orbital sulcus shallow (Fig. 12A: b). Ventral margin of orbit with rectangular dentals (Fig. 12F: c). Carapace surface irregular near anterolateral margin (Fig. 12: d, e). Anterolateral angles (Fig. 12B: d) pointing outward. Intersection of lateral and posterolateral (Fig. 12B: e) lines forming sharp obtuse angle. Posterolateral striae very long (Fig. 12B: f). On major cheliped, dorsal surface with ridge. Moderate-size tubercles decreasing in size toward ventral manus. Short keel on ventral manus extending to pollex (Fig. 12C: p). A triangular depression (Fig. 12C: i) with pubescence (Fig. 12C:



Fig. 11. *Minuca rapax* (Smith, 1870), collected from Puerto Rico (UNI 421). A: Dorsal view of entire crab. B: Lateral carapace view on side of minor cheliped. C: Outer surface of major cheliped. D: Inner surface of major cheliped. E: Second ambulatory leg. F: Oral view of carapace. a. eyebrow, b. postorbital sulcus, c. dental on suborbital margin, d. anterolateral angle, e. posterolateral line, f. posterolateral striae, h. articulation ridge, j. pollex, k. dactyl, l. superior carpal cavity carina, m. apex of oblique ridge, n. pre-dactyl ridge, o. articulation ridge, p. manus-pollex ridge, q. pubescence, r. setae.

g) just dorsal to origin of pollex (Fig. 12C: j). Dactyl articulation (Fig. 12C: h) without tubercles. Pollex (Fig. 12C: j) with one large tubercle in gap. Gap wide. Dactyl (Fig. 12C: k) with several larger tubercles proximal to articulation in gap with a single large distal tubercle. On

inner surface, dorsal carina (Fig. 12D: l) of carpal cavity with elongate tubercles. Carina extends around distal cavity margin to prominent tubercles at proximal end of oblique ridge (Fig. 12D: m). Structure sharply defined with clearly separate tubercles. Predactyl tubercle ridge



Fig. 12. *Minuca victoriana* (von Hagen, 1987), collected from Vitória, Brazil (UNI 168). A: Dorsal view of entire crab. B: Lateral carapace view on side of minor cheliped. C: Outer surface of major cheliped. D: Inner surface of major cheliped. E: Second ambulatory leg. F: Oral view of carapace. a. eyebrow, b. postorbital sulcus, c. dental on suborbital margin, d. anterolateral angle, e. posterolateral line, f. posterolateral striae, g. pubescence, h. articulation ridge, i. pre-pollex depression, j. pollex, k. dactyl, l. superior carpal cavity carina, m. apex of oblique ridge, n. pre-dactyl ridge, o. articulation ridge, p. manus-pollex ridge, q. pubescence, r. setae.

parallel to dactyl articulation (Fig. 12D: n, o). Tubercles on dactyl articulation fused. Dorsal surface of carpus in cavity with no large teeth. On ambulatory legs (1–3), dorsal manus and carpus with pubescence and long setae (Fig. 12E: q, r). No setae or pubescence on ventral merus of ambulatory legs. Merus width of ambulatory legs 1–3 about 29% length (Fig. 12E). G1 illustrated in von Hagen (1987: p. 86, fig. 3A–C). Female vulvar operculum flat, without tubercle.

Minuca vocator (Herbst, 1804) (Fig. 13). Front



Fig. 13. *Minuca vocator* (Herbst, 1804), collected from Curaçao (UNI 713). A: Dorsal view of entire crab. B: Lateral carapace view on side of minor cheliped. C: Outer surface of major cheliped. D: Inner surface of major cheliped. E: Second ambulatory leg. F: Oral view of carapace. a. eyebrow, b. postorbital sulcus, c. dental on suborbital margin, d. anterolateral angle, e. posterolateral line, f. posterolateral striae, g. pubescence, h. articulation ridge, i. pre-pollex depression, j. pollex, k. dactyl, l. superior carpal cavity carina, m. apex of oblique ridge, n. pre-dactyl ridge, o. articulation ridge, p. manus-pollex ridge, q. pubescence, r. setae.

angled from midline to lateral margin about 16°. Evebrow visible (13A: a). Carapace length 68% of width. Dorsal surface of central carapace smooth with pubescence on lateral hepatic regions (Fig. 13A: g). H-depression shallow with pubescence. Frontal region 37% carapace width (n = 10). Post-orbital sulcus shallow (Fig. 13A: b). Lower orbital margin without rectangular dentations (Fig. 13F: c). Anterolateral angles (Fig. 13B: d) pointed inward. Anterolateral lines curved. Junction with posterolateral (Fig. 13B: e) line forming curve. Dorsolateral lines with pubescence in sulcus (Fig. 13B: d, e). Posterolateral striae (Fig. 13B: f) heavily pubescent. Pubescence between striae and ventral margin of carapace (13B: g). Dorsal ridge on male cheliped almost flat. Tubercles on outer face small, visible only with magnification. Ventral manus with prominent keel (Fig. 13C: p) extend to pollex. Predactyl ridge (Fig. 13C: h) smooth. No tubercles on dactyl articulation. Base of pollex with shallow oblong depression (Fig. 13C: i). Pollex (Fig. 13: j) smooth. Gap wide. Few tubercles in gap, largest at mid-length. Pollex (Fig. 13C: j) terminus with three tubercles. Dactyl smooth, few larger "teeth" at proximal end (Fig. 13C: k). Inner face of cheliped with a prominent knob of tubercles (Fig. 13D: m) protruding into carpal cavity. Carina of superior carpal cavity formed from fused tubercles (Fig. 13D: 1). Carina ends in patch of larger tubercles extending to predactyl ridge (Fig. 13D: n). Predactyl ridge with large, widely-space tubercles. Few tubercles on dactyl articulation (Fig. 13D: o). Lower palm smooth. A cluster of 5-8 large tubercles (Fig. 13D: m) on lower edge of carpal cavity. Oblique ridge poorly developed. Large smooth sulcus (Fig. 13D: i) between oblique ridge and predactyl ridge. Heavy pubescence (Fig. 13E: q) on dorsal and ventral surfaces on ambulatory legs 1-3, but none on lateral surface of manus and carpus. Merus width of third ambulatory legs about 40% of length (Fig. 12E). Dorsal surface of merus with heavy pubescence (Fig. 12E: q). Ventral surface of merus without pubescence or setae. G1 in Crane (1975: p. 380, fig. 66D). Female with extremely large tubercle on vulvar operculum.

CONCLUSIONS

We describe a species of fiddler crab related to *M. burgersi* sensu stricto. Three closely related clades in the *M. burgersi* species complex occur across its range in the western Atlantic Ocean. The southern-most clade ("Clade 1" in Thurman et al. 2021) was considered to be *M. burgersi* sensu stricto. Specimens from this clade collected along the Atlantic coast of South America between the Island of Trinidad and Santa Catarina,

Brazil are now recognized as *Minuca panema* (Coelho, 1972). We offer molecular and morphological evidence to distinguish the species from *M. burgersi* sensu stricto. Based on a molecular clock, the "*burgersi-aff. burgersi-panema*" complex diverged from a common ancestor 4.1 Mya as a result of changing geology and hydrology along the coast of northeastern South America.

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Supplementary materials

Table S1. Latitudinal distribution of the specimens examined of *Minuca burgersi* Holthuis 1967 sensu stricto and *M. panema*. UNI = University of Northern Iowa; USNM = National Museum of Natural History (Smithsonian), Washington, D.C.; ZMUSP = Zoological Museum, University of São Paulo, São Paulo, Brazil; RMNH = Naturalis Biodiversity Center, Leiden, the Netherlands. *- type , ** - paratype, ***- neotype specimen. See figure 2 for geographical location of species. (download)