



Homochely in males of *Minuca vocator* (Herbst, 1804) (Brachyura: Ocypodidae: Gelasiminae)

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Abstract. This study evaluates the frequency of the abnormal homochelic male morphotype in a population of *Minuca vocator* (Herbst, 1804) inhabiting the mangroves of the Itanhaém River (SP), Brazil, which differs from the typical heterochelic pattern observed in Gelasiminae males. Out of 382 specimens captured (232 males and 151 females), only two males exhibited homochelic small chelipeds, accounting for 0.86% of the male population. This low percentage may be genetically determined or could result from differential cheliped loss, depending on the developmental phase, which permanently affects this condition after regeneration. Although males with both abnormal hypertrophied morphotypes have been observed in other fiddler crab species, this phenomenon was not confirmed in this population. These abnormal conditions could confer either disadvantages or advantages to the individuals, warranting specific ethological experiments to investigate potential implications for trophic and behavioral interactions.

Keywords: Fiddler crabs, Itanhaém, malformation, mangrove, morphology.

Resumo. Machos homoquelos de *Minuca vocator* (Herbst, 1804) (Brachyura: Ocypodidae: Gelasiminae). Este estudo avalia a frequência do morfotipo anormal de macho homoquelo em uma população de *Minuca vocator* (Herbst, 1804) no manguezal do Rio Itanhaém (SP), Brasil, que difere do padrão heteroquelo típico observado em machos Gelasiminae. Dos 382 espécimes capturados (232 machos e 151 fêmeas), apenas dois machos exibiram quelípodos pequenos homoquelos, representando 0,86% da população masculina. Essa baixa porcentagem pode ser determinada geneticamente ou pode resultar da perda diferencial de quelípodos, dependendo da fase de desenvolvimento, que afeta permanentemente essa condição após a regeneração. Embora machos com ambos os morfotipos hipertrofiados anormais tenham sido observados em outras espécies de chama-marés, esse fenômeno não foi confirmado nesta população. Essas condições anormais podem conferir desvantagens ou vantagens aos indivíduos, sendo necessário experimentos etológicos específicos para investigar potenciais implicações para interações tróficas e comportamentais.

Palavras-chave: Chama-marés, Itanhaém, malformações, manguezal, morfologia.

Abnormal morphotypes, or anomalies, can occur naturally or randomly during ontogeny (Araújo & Calado, 2012, Silva & Shinozaki-Mendes 2018). These anomalies are commonly reported in arthropods, particularly in locomotor appendages (Nickerson & Gray, 1967, Flandroit *et al.*, 2024). Such anomalies may involve the suppression or repetition of elements in certain appendages, as well as their atrophy or hypertrophy. In general, decapod crustaceans (e.g., crabs) exhibit one cheliped that is more hypertrophied and stronger than the other, with the position of the major chela (right or left) referred to as laterality or handedness (see Yosef *et al.*, 2021, Rozaimi *et al.*, 2023). These abnormalities are rare in crustaceans, as are structural malformations, although they have been well-documented in crab species, primarily affecting the locomotor appendages (Pinheiro & Toledo, 2010, Lira *et al.*, 2012, Rady, 2022). This rarity is understandable, given that chelipeds are the last structures to be released from the old exoskeleton during molting (Lira *et al.*, 2012, Zambrano, 2017).

Fiddler crabs (Ocypodidae) represent a taxonomic group comprising 11 genera and 107 species worldwide (Crane, 1975, Shih & Chan, 2022). Among these, only 9.3% (n = 10) are documented in Brazil, ranging from the state of Amapá to Rio Grande do Sul, with *Leptuca uruguayensis* extending as far as Uruguay and

Argentina (Thurman *et al.*, 2013, Rosenberg, 2020). Male fiddler crabs are easily recognizable by their unequal chelae (heterochely), where one is hypertrophied and distinctly shaped or ornamented, used in agonistic behaviors such as male-male combat, while the other chela is markedly reduced and used for feeding. In contrast, females, according to Crane (1966, 1975), possess small chelae of similar shape and size (homochely).

Morgan (1920) described two male specimens of the fiddler crab *Leptuca pugilator* (Bosc, 1801) with abnormal chelipeds: one with both chelipeds large (termed "double-clawed") and the other with both chelipeds small (termed "intersex"). However, Morgan did not provide information about the total number of specimens analyzed. Similar abnormal specimens, exhibiting either both small or both hypertrophied chelipeds, have been reported in other fiddler crab species (Ahmed, 1976, 1978, Zou & Fingerman, 2000, Benetti & Negreiros-Fransozo, 2003, Lira *et al.*, 2006, Vale *et al.*, 2015, Silva & Shinozaki-Mendes, 2018).

This study aims to evaluate the frequency of abnormal male specimens of *Minuca vocator* based on the occurrence of homochelic chelipeds (either smallest or hypertrophied) in a population well-established in the mangroves of the Itanhaém River (SP), Brazil, and to spec-

ulate on the potential causes of these anomalies.

Two field expeditions were conducted in July 2022 and January 2023 in a mangrove area of the Itanhaém River (24°09'36" S, 46°48'19" W) in the municipality of Itanhaém, São Paulo, Brazil (Figure 1 A-B-C). A total of 407 specimens of *Minuca vocator* (255 males and 152 females) were collected as part of this study. Specimens were manually gathered using spatulas, either directly from their burrows or while active on the sediment surface. After collection, the individuals were transported to the laboratory and identified using the taxonomic keys provided by Bezerra (2012) and Masunari *et al.* (2020). Only specimens confirmed to belong to the target species were retained for analysis.

The sex of each specimen was determined based on abdominal morphology and the number of pleopod pairs: males were identified by their triangular abdomen and two pairs of pleopods, while females were distinguished by their semi-ovate abdomen and four pairs of pleopods. Each specimen then under-

went structural biometry under a magnifying glass connected to a Computer Image Analysis System (KS-300, Zeiss®), which recorded the following measurements: carapace width (CW) and propodus length of both chelipeds (PL_R: right; PL_L: left). Juvenile specimens whose sex could not be determined, as well as adults missing one or both chelipeds, were excluded from the analysis, resulting in a final sample of 232 males and 151 females (n = 382).

Among the specimens analyzed, only two males of *Minuca vocator* exhibited abnormal cheliped morphotypes, representing 0.86% of the male population. These individuals displayed homochely with small chelae, a condition that deviates from the typical male morphotype (Fig. 2 A-B) and more closely resembles the female morphotype (Figure 2 C-D). Specifically, Male #1 measured 20.6 mm in carapace width (CW) with chelae measuring 7.9 mm (right) and 7.7 mm (left), while Male #2 measured 15.2 mm CW with chelae measuring 6.4 mm (right) and 6.0 mm (left). These specimens have been deposited in the Crustacean Collection at the Zoology Museum of the Uni-



Figure 1. Itanhaém River mangrove. **A)** Location of Itanhaém city, São Paulo, within the Metropolitan Region of Baixada Santista on the coast of São Paulo state, Brazil; **B)** Close-up of the city of Itanhaém, São Paulo; **C)** Urban area of Itanhaém, showing the lower part of the river basin, with the Itanhaém River indicated in blue, mangrove forests in green, and the collection site highlighted with a red dot.



Figure 2. Comparison between a homochelous male (body: 20.6 mm CW; chelae: 7.9 mm PLR and 7.7 mm PLL) and a heterochelous male (body: 20.0 mm CW; chelae: 7.7 mm PLR and 23.8 mm PLL) of *Minuca vocator*. **A)** Heterochelous male, dorsal view; **B)** Heterochelous male, ventral view; **C)** Homochelous male, dorsal view; **D)** Homochelous male, ventral view. Scale bars = 10 mm. Photographs by Nicholas Kriegler.

iversity of São Paulo (MZUSP #43773 - Lots 5 and 6).

This study is the first to document homochelic male specimens with small chelae in *M. vocator*. However, similar cases have been reported in males of two other congeneric species: *Minuca panema* (Coelho, 1972), previously referred to as *Minuca burgersi* (Holthuis, 1967) (Thurman *et al.*, 2023) and *M. rapax* (Smith, 1870). In the case of *M. panema*, Benetti & Negreiros-Fransozo (2003) documented six males with abnormal chelipeds: four with small homochelous chelae (1.3% of the males analyzed) and two with hypertrophied homochelous chelae (0.6% of the males). For *M. rapax*, Vale *et al.* (2015) and Silva & Shinozaki-Mendes (2018) each reported a single male with hypertrophied homochelous chelae. Across species, these abnormalities consistently occur in males at frequencies of $\leq 1.3\%$, ranging from 0.6% to 1.3%.

Crane (1975) suggested that the laterality of the major chela in male fiddler crabs typically follows a consistent pattern. However,

some species deviate from the expected 1:1 (right:left) ratio (Johnson, 2003, Jaroensutasinee & Jaroensutasinee, 2004). Vernberg & Costlow (1966) conducted experiments indicating that the laterality of the major cheliped is genetically determined. However, Yamaguchi's (1977) experiments led to the conclusion that laterality occurs randomly, with males acquiring chelae asymmetry when one cheliped is lost during the symmetrical or early juvenile phase. In such cases, the remaining cheliped develops into the hypertrophied chela, while the lost cheliped regenerates as a smaller one. Yamaguchi confirmed this through natural loss or artificial removal of a cheliped during the last larval instar (megalopa) or juvenile stage. He also noted that if both chelipeds are lost, they regenerate as small chelae. Conversely, if neither cheliped is lost, both develop into hypertrophied chelae. It is widely accepted that once the chelar morphotype is established, it remains unchanged, regardless of whether the individual exhibits heterochely or homochely (Vernberg & Costlow, 1966, Yamaguchi, 1977, Ahmed, 1978).

In populations where the laterality of the hypertrophied cheliped follows a specific heterochelous pattern, the determination may be genetically influenced, with cheliped loss during the symmetrical phase potentially inducing asymmetry (Yamaguchi, 1977). In this study, the ratio of right-handed (51%) to left-handed (48%) individuals in *M. vocator* remained close to 1:1 ($X^2 = 0.43$; $p > 0.05$), suggesting that the laterality of the hypertrophied chela is likely random. This finding implies that the homochelous individuals recorded may have lost both chelipeds during the symmetrical phase, leading to the permanent establishment of this condition.

Larger chelipeds play a critical role in various behaviors related to intra- and interspecific social interactions, resource competition, territorial defense, and visual signaling during courtship and copulation (Crane, 1966, Callander *et al.*, 2012). Consequently, males with small homochelous chelae may be at a disadvantage in reproductive interactions (Gadgil, 1972). Females typically prefer to mate with heterochelous males, especially those with larger chelae (Oliveira & Custódio, 2010, Callander *et al.*, 2012), although males with small homochelous chelae have been observed to reproduce under laboratory conditions (Yamaguchi, 1977).

Maintaining a hypertrophied chela imposes a high energy cost, with males lacking a hypertrophied chela exhibiting lower oxygen consumption compared to those with a hypertrophied chela (Allen & Levinton, 2007, Gadgil, 1972). Overall, the scarcity of studies on this subject makes it difficult to determine the causes and potential implications of these abnormal specimens within the population. Further investigation is required to clarify these issues.

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References

- AHMED, M. 1976. A study of the normal and aberrant sexual types of the Venezuelan fiddler crabs *Uca cumulanta* and *Uca rapax*. Bull. Mar. Sci. 26(4): 499-505. Available at: <<https://www.ingentaconnect.com/content/umrsmas/bullmar/1976/00000026/00000004/art00008?crawler=true>>. Accessed on: Aug. 26, 2024.
- AHMED, M. 1978. Development of asymmetry in the fiddler crab *Uca cumulanta* Crane, 1943 (Decapoda, Brachyura). Crustaceana. 34(3): 29-300. Available at: <<https://www.jstor.org/stable/20103284>>. Accessed on: Aug. 26, 2024.
- ALLEN, B. J. & LEVINTON, J. S. 2007. Costs of bearing a sexually ornamental weapon in a fiddler crab. Funct. Ecol. 21(1): 154-161. Available at: <<https://link.springer.com/article/10.1007/s00442-014-3002-y>>. Accessed on: Aug. 26, 2024.
- ARAÚJO, M. S. L. C. & CALADO, T. C. S. 2012. New record of malformation in the true crab *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Decapoda, Ucididae), at Brazilian coast. Rev. Nordestina Zool. 6(1): 15-19. Available at: <https://www.researchgate.net/publication/259802223_New_record_of_malformation_in_the_true_crab_Ucides_cordatus_Linnaeus_1763_Crustacea_Decapoda_Ucididae_at_Brazilian_coast>. Accessed on: Aug. 26, 2024.
- BENETTI, A. S. & NEGREIROS-FRANSOZO, M. L. 2003. Symmetric chelipeds in males of the fiddler crab *Uca burgersi* Holthuis, 1967 (Decapoda, Brachyura, Ocypodidae). Nauplius. 11(2): 141-144. Available at: <<http://>>

- crustacea.org.br/wp-content/uploads/2014/02/nauplius-v11n2a10.BenettiNegreiros-Fransozo.pdf>. Accessed on: Aug. 26, 2024.
- BEZERRA, L. E. A. 2012. The fiddler crabs (Crustacea: Brachyura: Ocypodidae: genus *Uca*) of the South Atlantic Ocean. *Nauplius*. 20(2): 203-246. Available at: <<https://www.scielo.br/j/nau/a/TgvFVjS7kqH3RTRbbYzHxvk/>>. Accessed on: Aug. 26, 2024.
- CALLANDER, S., JENNIONS M. D. & BACKWELL P. R. Y. 2012. The effect of claw size and wave rate on female choice in a fiddler crab. *J. Ethol.* 30: 151-155. Available at: <<https://link.springer.com/article/10.1007/s10164-011-0309-6>>. Accessed on: Aug. 26, 2024.
- CRANE, J. 1966. Combat, display and ritualization in fiddler crabs (Ocypodidae, genus *Uca*). *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 251(772): 459-472. Available at: <<https://royalsocietypublishing.org/doi/10.1098/rstb.1966.0035>>. Accessed on: Aug. 26, 2024.
- CRANE, J. 1975. *Fiddler Crabs of the World*. Ocypodidae: Genus *Uca*. Princeton, NJ: Princeton University Press, 736 p.
- FLANDROIT, A., SIMON, L & CAULIER, G. 2024. Description of limb anomalies resulting from molt irregularities in *Ammothea hilgendorfi* (Pycnogonida: Ammotheidae). *Arthropoda*. 2: 156-168. Available at: <<https://doi.org/10.3390/arthropoda2020012>>. Accessed on: Aug. 26, 2024.
- GADGIL, M. 1972. Male dimorphism as a consequence of sexual selection. *Am. Nat.* 106 (951): 574-580. Available at: <<https://doi.org/10.1086/282797>>. Accessed on: Aug. 26, 2024.
- JAROENSUTASINEE, M. & JAROENSUTASINEE, K. 2004. Morphology, Density, and Sex Ratio of Fiddler Crabs from Southern Thailand (Decapoda, Brachyura, Ocypodidae). *Crustaceana*. 77(5): 533-551. Available at: <<https://www.jstor.org/stable/20105738>>. Accessed on: Aug. 26, 2024.
- JOHNSON, P. T. J. 2003. Biased sex ratios in fiddler crabs (Brachyura, Ocypodidae): A review and evaluation of the influence of sampling method, size class, and sex specific mortality. *Crustaceana*. 76(5): 559-580. Available at: <<https://www.jstor.org/stable/20105595>>. Accessed on: Aug. 26, 2024.
- LIRA, C., BOLAÑOS, J., HERNÁNDEZ, G. & HERNÁNDEZ, J. 2006. Un caso de hipertrofia bilateral de quelas en el cangrejo violinista *Uca cumulanta* (Decapoda: Ocypodidae). *Ver. Biol. Trop.* 54(3): 117-119. Available at: <https://www.scielo.sa.cr/scielo.php?pid=S0034-77442006000600016&script=sci_arttext>. Accessed on: Aug. 26, 2024.
- LIRA, C., BOLIVAR, N., OLIVEIRA, A. & BOLAÑOS, J. 2012. A case of leg malformation in the atlantic ghost crab *Ocypode quadrata* (Decapoda, Brachyura, Ocypodidae). *Crustaceana*. 85(14): 1787-1791. Available at: <<https://www.jstor.org/stable/41720812>>. Accessed on: Aug. 26, 2024.
- MASUNARI, S., MARTINS, S. B. & ANACLETO, A. F. M. 2020. An illustrated key to the fiddler crabs (Crustacea, Decapoda, Ocypodidae) from the Atlantic coast of Brazil. *ZooKeys*. 943: 1-20. Available at: <<https://doi.org/10.3897/zookeys.943.52773>>. Accessed on: Aug. 26, 2024.
- MORGAN, T. H. 1920. Variations in the secondary sexual characters of the fiddler crab. *Am Nat.* 54(632), 220-246. Available at: <<https://doi.org/10.1086/279753>>. Accessed on: Aug. 26, 2024.
- NICKERSON, R. B. & GRAY, G. W. 1967. Abnormalities of king crab pereopods (Decapoda, Anomura, Lithodidae). *Crustaceana*. 12(1): 9-12. Available at: <<https://www.jstor.org/stable/20102808>>. Accessed on: Aug. 26, 2024.
- OLIVEIRA, R. F. & CUSTÓDIO, M. R. 2010. Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*. *Ethol. Ecol. Evol.* 10(3): 241-251. Available at: <<https://doi.org/10.1080/08927014.1998.9522855>>. Accessed on: Aug. 26, 2024.
- PINHEIRO, M. A. A. & TOLEDO, T. R. 2010. Malformation in the crab *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ocy-

- podidae), in São Vicente, State of São Paulo, Brazil. *Revi. CEPSUL - Biod. Conserv. Mar.* 1 (1): 61-65. Available at: <<https://doi.org/10.37002/revistacepsul.vol1.29961-65>>. Accessed on: Aug. 26, 2024.
- RADY, A. 2022. First record of morphological malformations in the blue swimming crab, *Portunus segnis* (Portunidae: Brachyura) from the Timsah Lake, Suez Canal, Egypt. *Egypt J. Aquat. Biol. Fish.* 26(2): 877-888. Available at: <<https://doi.org/10.21608/ejabf.2022.279078>>. Accessed on: Aug. 26, 2024.
- ROSENBERG, M. S. 2020. A fresh look at the biodiversity lexicon for fiddler crabs (Decapoda: Brachyura: Ocypodidae). Part 2: Biogeography. *J. Crust. Biol.* 40(4), 364–383. Available at: <<https://doi.org/10.1093/jcbiol/ruaa029>>. Accessed on: Aug. 26, 2024.
- ROZAIMI, R., SHU-CHIEN, A. C., WANG, Y., SUTIKNO, S., IKHWANUDDIN, M., SHI, .X, AZMIE, G., FAZHAN, H. & WAIHO, K. 2023. Heterochely and handedness in the orange mud crab *Scylla olivacea*: implication for future culture practice optimization. *PeerJ*. Available at: <<https://doi.org/10.7717/peerj.15143>>. Accessed on: Aug. 26, 2024.
- SHIH, H. & CHAN, B. K. K. 2022. Systematics and Biogeography of fiddler crabs – a special issue in *Zoological Studies*. *Zool. Stud.* 61: 64. Available at: <<https://doi.org/10.6620/ZS.2022.61-64>>. Accessed on: Aug. 26, 2024.
- SILVA, L. N. S. & SHINOZAKI-MENDES, R. A. 2018. A case of bilateral hypertrophy in the chelae of a male specimen of *Minuca rapax* (Smith, 1870) (Decapoda, Brachyura, Ocypodidae). *Nauplius*. 26: e2018032. Available at: <<https://doi.org/10.1590/2358-2936e2018032>>. Accessed on: Aug. 26, 2024.
- THURMAN, C. L., FARIA, S. C. & MCNAMARA, J. C. 2013. The distribution of fiddler crabs (*Uca*) along the coast of Brazil: implications for biogeography of the western Atlantic coast. *Mar. Biodivers.* 6: 1-21. Available at: <<https://doi.org/10.1017/S1755267212000942>>. Accessed on: Aug. 26, 2024.
- THURMAN, C. L., SHIH, H. & MCNAMARA, J. C. 2023. *Minuca panema* (Coelho, 1972): Resurrection of a fiddler crab species from Brazil Closely Related to *Minuca burgersi* (Holthuis, 1967) (Crustacea, Decapoda, Brachyura, Ocypodidae). *Zool. Stud.* 62:45. Available at: <<https://doi.org/10.6620/ZS.2023.62-45>>. Accessed on: Aug. 26, 2024.
- VALE, V. F., ALENCAR, C. E. R. D., MORAES, S. A. S. N. & FREIRE, F. A. M. 2015. First record of bilateral hypertrophy in chelas of *Uca rapax* male specimen (Crustacea, Decapoda, Ocypodidae) on the Brazilian coastline. *Biol. Assoc. UK.* 8(52): 1-5. Available at: <<https://doi.org/10.1017/S1755267215000299>>. Accessed on: Aug. 26, 2024.
- VERNBERG, F. J. & COSTLOW, J. D. 1966. Handedness in fiddler crabs (Genus *Uca*). *Crustaceana.* 11(1): 61-64. Available at: <<https://www.jstor.org/stable/20102765>>. Accessed on: Aug. 26, 2024.
- YAMAGUCHI, T. 1977. Studies on the handedness of the fiddler crab, *Uca lactea*. *Biol. Bull.* 152(3): 424-436. Available at: <<https://doi.org/10.2307/1540430>>. Accessed on: Aug. 26, 2024.
- YOSEF, R., DARABY, M., SEMIONOVICH, A. & KOSICKI, J. Z. 2021. Individual Laterality in Ghost Crabs (*Ocypode saratan*) Influences Burrowing Behavior. *Symmetry*, 13: 1512. Available at: <<https://doi.org/10.3390/sym13081512>>. Accessed on: Aug. 26, 2024.
- ZAMBRANO, R. 2017. First record of malformations in males of *Ucides occidentalis* (Brachyura, Ocypodidae) in the Gulf of Guayaquil, Ecuador. *Crustaceana*, 90(5): 631-638. Available at: <<https://www.jstor.org/stable/44250217>>. Accessed on: Aug. 26, 2024.
- ZOU, E. & FINGERMAN, M. 2000. External features of an intersex fiddler crab, *Uca pugilator* (Bosc, 1802) (Decapoda, Brachyura). *Crustaceana*, 73(4): 417-423. Available at: <<https://www.jstor.org/stable/20106302>>. Accessed on: Aug. 26, 2024.