


Morphometric analysis of selected claw traits in *Tubuca forcipata* (Ocypodidae) from Southern Vietnam

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ABSTRACT. A total of 233 specimens of the fiddler crab *Tubuca forcipata* (189 males and 44 females) were collected monthly from intertidal mudflats in Dam Doi and Hoa Binh, Ca Mau Province, Southern Vietnam, from July to October 2025. Selected morphometric traits, comprising the carapace width left-to-right (CW_{L-R}), the carapace width right-to-left (CW_{R-L}), the manus widths ($MW2$ and $MW3$), the pollex width ($PW5$), and the dactyl width ($DW7$), were measured to 0.01 mm. Generalized linear models with a gamma distribution and log link were used for trait comparisons; cheliped traits were analyzed with sex and the carapace width (CW_{L-R} or CW_{R-L}) as predictors. The carapace width did not differ by sex ($p > 0.05$), whereas $MW2$, $MW3$, $PW5$, and $DW7$ were significantly larger in males after adjusting for the carapace width ($\beta_{sex} = 0.156-0.257$; rate ratios (RR) = 1.17–1.29; $p < 0.001$). The carapace width had strong positive effects on all cheliped traits ($\beta_{CW} = 0.054-0.070$; RR $\approx 1.06-1.07$; $p < 0.001$). Model diagnostics showed $\chi^2/df < 1$, indicating no overdispersion. These results demonstrate pronounced sex-linked functional dimorphism in the chelae of *T. forcipata* despite similar overall body size, providing a quantitative morphometric baseline for ecological and evolutionary studies of mangrove crabs in the Mekong Delta.

Keywords: dactyl width, manus width, Mekong Delta, pollex width, *Tubuca forcipata*

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1. Introduction

Fiddler crabs (family Ocypodidae) are among the most ecologically influential organisms in tropical and subtropical intertidal ecosystems, acting as key bioturbators and bioindicators of habitat condition (Rosenberg, 2020). They typically occupy distinct intertidal zones within mangrove forests, exhibiting strong habitat preferences and high adaptability to microenvironmental variations (Zolkhiflee et al., 2021). In Vietnam, the diversity and distribution of fiddler crabs, including species of the genus *Tubuca*, were extensively recorded along coastal regions (Shih et al., 2022). Within this context, the Mekong Delta, particularly Ca Mau Province, represents an ecologically important area where populations of *Tubuca* species have recently attracted increasing scientific interest (Tran et al., 2025b).

The species *Tubuca forcipata* (Adam & White, 1849) constitutes an integral component of mangrove

faunas throughout Southeast Asia (Auliaputri et al., 2023). Accurate identification of this species, previously classified within the genus *Uca*, often requires a combination of morphological and molecular approaches to resolve its phylogenetic relationships (Andriyono et al., 2019). Fiddler crabs, in general, have a complex and dynamic taxonomic history that continues to be revised through modern morphometric and phylogenetic analyses (Rosenberg, 2001). Recent systematic updates have reclassified several species from *Uca* (sensu lato) into *Tubuca*, reflecting clearer evolutionary lineages (Rosenberg, 2019).

A defining feature of *Tubuca* species is their marked sexual dimorphism, first described in classical works (Crane, 1975). Males possess a characteristically enlarged major claw, while females have two smaller symmetrical claws (Tran and Dinh, 2025). The male claw, a hallmark of sexual selection, exhibits substantial variation in shape and mechanical structure among species (Swanson et al., 2013). Even subtle differences

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in claw morphology can serve as diagnostic features for distinguishing closely related or cryptic taxa within the genus (Shih et al., 2018).

Ecologically, fiddler crabs contribute to sediment aeration, nutrient cycling, and overall mangrove ecosystem functioning through their burrowing and mound-building activities (Pardo et al., 2020). Consequently, the composition and diversity of fiddler crab assemblages, including *T. forcipata*, are often regarded as reliable indicators of mangrove ecosystem health and resilience (Ashton and Macintosh, 2024).

Most previous studies on fiddler crabs focused on aspects of reproductive biology, population dynamics, and environmental influences, including gonadal development (Castiglioni et al., 2007), breeding seasons (Andriyono et al., 2019; Cobo and Fransozo, 2003), sex ratios, and maturity sizes (Oshiro, 1999; Silva and Oshiro, 2002). Furthermore, recent phylogeographic analyses have enhanced understanding of the historical dispersal and isolation of *Tubuca* species across Southeast Asia (Shih et al., 2022).

In Vietnam, emerging research has begun to document morphological variations among *Tubuca* species in the Mekong Delta, for instance, interprovincial differences in *T. paradussumieri* (Tran et al., 2025a) and claw and leg morphometrics in *T. rhizophorae* (Tran and Dinh, 2025). Dao et al. (2024) further reported significant sexual and spatial differences in *T. rhizophorae* populations from Bac Lieu and Ca Mau. However, detailed morphometric data for *T. forcipata* in Ca Mau remain scarce, creating a critical knowledge gap regarding its sexual dimorphism, allometric scaling, and ecological role within mangrove ecosystems of the Mekong Delta.

In this study, we test the hypothesis that males of *T. forcipata* possess disproportionately larger cheliped components (manus, pollex, and dactyl) than females of equivalent body size. Specifically, we predict that: (i) the carapace width left-to-right (CW_{L-R}), the carapace width right-to-left (CW_{R-L}) (does not differ significantly between sexes, indicating comparable overall body size; and (ii) functional claw traits ($MW2$, $MW3$, $PW5$, and $DW7$) are significantly larger in males after accounting for the carapace width, reflecting sex-linked allometric investment in chela development. By quantitatively assessing these relationships using generalized linear models (GLMs), this study aims to clarify the extent and scaling of sexual dimorphism in *T. forcipata*,

providing essential baseline data for future ecological and evolutionary investigations of mangrove crabs in Southern Vietnam.

2. Materials and methods

2.1. Sample collection and morphometric measurements

Specimens of *T. forcipata* (Fig. 1) were collected manually from intertidal mudflats along the Dam Doi and Hoa Binh coastlines, Ca Mau Province, Southern Vietnam, during low tide from July to October 2025 (Fig. 2). Sampling was conducted monthly, yielding a total of 233 individuals (189 males and 44 females). Crabs were captured by hand or using baited traps, then preserved in 70% ethanol for transport to the laboratory.

In the laboratory, individuals were identified based on external morphological characteristics consistent with the descriptions of *Tubuca* species in the Indo-Pacific region. Each specimen was sexed by observing the abdominal shape—males possess a narrow, triangular abdomen, whereas females have a broad, rounded one.

Morphometric characteristics were analyzed following the procedures described by Dao et al. (2024), including the carapace width from left to right (CW_{L-R}), the carapace width from right to left (CW_{R-L}), the manus width ($MW2$ and $MW3$), the pollex width ($PW5$), and the dactyl width ($DW7$) (Fig. 3). All measurements were taken using a digital caliper (Model: MOORMW-110-15DIP) with a precision of 0.01 mm.

2.2. Data analysis

All statistical analyses were conducted using jamovi v2.6.44 (the jamovi project, 2024) with the GAMLj module. Prior to model fitting, the normality of each variable was assessed using the Shapiro–Wilk test. Results indicated that both CW_{L-R} and CW_{R-L} slightly deviated from normality ($p < 0.05$), whereas all other variables ($MW2$, $MW3$, $PW5$, and $DW7$) were strongly right-skewed. Consequently, all variables were analyzed using generalized linear models (GLMs) with a gamma distribution and log-link function, which appropriately handle skewed continuous data.

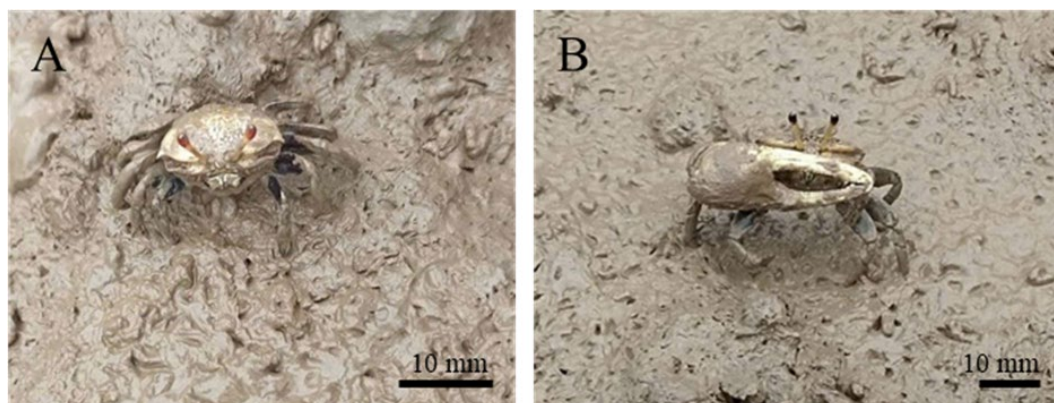


Fig.1. *Tubuca forcipata* (A: female; B: male).

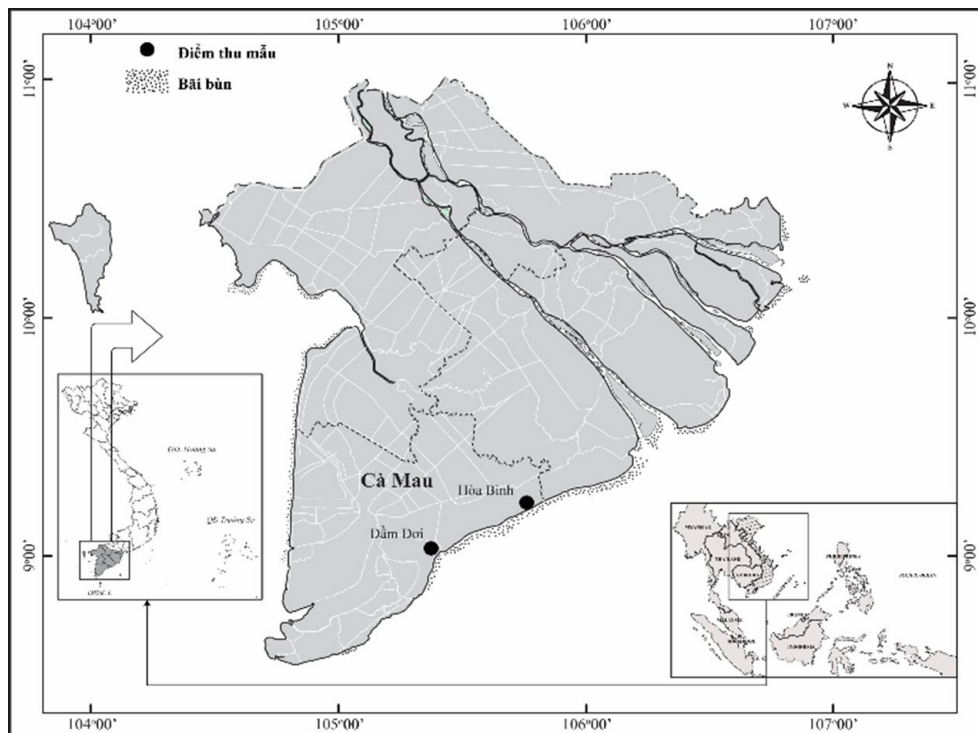


Fig.2. Sampling sites map in Cau Mau (modified from Dinh (2018)).

Separate GLMs were fitted for each response variable following the general structure: $Y \sim \text{Sex} + CW_{L-R}/CW_{R-L}$, where Y denotes each morphometric trait (MW2, MW3, PW5, and DW7), and Sex is a categorical factor with two levels (male and female). Carapace-width covariates were mean-centered before analysis to enhance model interpretability. For each model, parameter estimates ($\beta \pm \text{SE}$), Wald z-values, p-values, and rate ratios ($\text{RR} = e^{\beta}$) were extracted. Significance was set at $p < 0.05$. Positive $\beta(CW)$ coefficients indicate that the trait increases with body size. To assess model adequacy, the Akaike information criterion (AIC), the Bayesian information criterion (BIC), deviance, and the chi-squared-to-df ratio (χ^2/df) were examined; values of $\chi^2/\text{df} < 1$ were interpreted as evidence of good model fit without overdispersion. Estimated marginal means (EMMs) for each sex were obtained from the fitted GLMs to provide adjusted means and confidence intervals on the response scale. These adjusted values are reported in tables and figures of the Results to facilitate interpretation of sex-related differences while accounting for variation in body size.

3. Results

Descriptive statistics and normality

A total of 233 individuals of *T. forcipata* (189 males and 44 females) were analyzed. Descriptive statistics for all morphometric variables are summarized in Table 1. Mean carapace widths were 18.74 ± 0.22 mm (CW_{L-R}) and 18.44 ± 0.22 mm (CW_{R-L}). The Shapiro–Wilk test indicated significant deviations from normality for most variables ($p < 0.05$), except for MW(3) ($p = 0.0844$). Because both carapace-width variables also deviated slightly from normality (CW_{L-R} , $p = 0.0179$; CW_{R-L} , $p = 0.0441$), all traits were analyzed using gamma-log GLMs to ensure consistent treatment of skewed data.

Carapace width (CW_{L-R} and CW_{R-L})

No significant sex-related differences were detected for either CW_{L-R} or CW_{R-L} ($p > 0.05$). Estimated marginal means (EMMs) were nearly identical between males and females (Table 1), confirming the first hypothesis that overall body size does not differ significantly between sexes.



Fig.3. Illustration of morphometric measurements in *Tubuca forcipata* (carapace width (CW), manus width (MW2, MW3), pollex length (PW5), and dactyl length (DW7)).

Functional morphometric traits (MW2, MW3, PW5, and DW7)

When the carapace width was included as a covariate, all cheliped traits (MW2, MW3, PW5, and DW7) were significantly affected by sex (all $p < 0.001$), supporting the second hypothesis. Males exhibited markedly larger adjusted means for each trait compared with females (Table 3).

Across all gamma-log models, sex coefficients ranged from $\beta = 0.156$ to 0.257 , corresponding to rate ratios (RR) = 1.17 – 1.29 , which indicated that male chela components were 17–29% larger than those of females at equivalent carapace widths. Both CW covariates had significant positive effects ($\beta = 0.054$ – 0.070 ; $p < 0.001$; $RR \approx 1.06$ – 1.07), indicating that a 1-mm increase in the carapace width resulted in an approximately 6–7% increase in cheliped size.

Model diagnostics confirmed a good fit, with all $\chi^2/df < 1$ and no indication of overdispersion. The inclusion of CW_{L-R} or CW_{R-L} as covariates yielded consistent results, demonstrating the robustness of these effects (Table 2).

The adjusted means (EMMs) for each trait by sex (Table 3) clearly illustrate the magnitude of sexual dimorphism. Males averaged 5.34 ± 0.13 mm for MW2, 7.13 ± 0.13 mm for MW3, 3.16 ± 0.07 mm for PW5, and 2.75 ± 0.06 mm for DW7. Corresponding female means were 4.57 ± 0.14 mm, 5.66 ± 0.14 mm, 2.45 ± 0.07 mm, and 2.23 ± 0.07 mm, respectively. These results confirm a consistent pattern of functional dimorphism in chela components, while overall body size (as measured by carapace width) remains statistically equivalent between sexes. These findings demonstrate that *T. forcipata* exhibits sex-linked functional dimorphism localized to the chelae, rather than generalized body enlargement.

4. Discussion

This study provides quantitative evidence of sex-related morphometric differentiation in *T. forcipata* from the Dam Doi and Hoa Binh estuaries, Ca Mau Province. The two tested hypotheses were fully supported: the carapace width did not differ significantly between sexes, whereas all functional cheliped traits,

Table 1. Estimated marginal means of carapace width (mm) by sex from GLMs

Parameter	Sex	n	Mean \pm SE	p
CW_{L-R} (mm)	Female	44	18.10 ± 0.48	0.155
	Male	189	18.89 ± 0.24	
CW_{R-L} (mm)	Female	44	17.89 ± 0.50	0.233
	Male	189	18.57 ± 0.25	

Note: Carapace width from left to right (CW_{L-R}); carapace width from right to left (CW_{R-L}).

including the manus width (MW2 and MW3), the pollex width (PW5), and the dactyl width (DW7), were significantly larger in males after adjusting for body size. These findings confirm that sexual dimorphism in *T. forcipata* is primarily functional rather than structural, reflecting differential allocation of growth to the claws rather than general body enlargement.

The present analysis also revealed that neither the carapace width nor the morphometric traits of the minor chela (MW2, MW3, PW5, and DW7) differed significantly between males and females, even after controlling for body size. This outcome indicates that the minor chela in both sexes develops proportionally, consistent with its shared role in sediment manipulation and feeding rather than in reproductive signaling or territorial competition (Crane, 1975; Zeil and Hemmi, 2006).

In most fiddler crabs, the major chela, which is found only in males, is highly exaggerated and acts as a sexually selected structure for waving displays, visual communication, and combat (Crane, 1975; Swanson et al., 2013). In contrast, the minor chela serves as the principal feeding appendage and remains morphologically similar between sexes. The morphological stability of this structure in *T. forcipata* supports its interpretation as a functional trait that is shaped predominantly by natural rather than sexual selection. Comparable results were reported for other *Tubuca* species, such as *T. rhizophorae* and *T. paradussumieri*, in which the minor chela shows minimal sexual variation, whereas the major claw exhibits marked dimorphism under strong sexual selection (Dao et al., 2024; Tran and Dinh, 2025; Tran et al., 2025a).

Table 2. Gamma-log GLM results for effects of sex and carapace width on functional traits

Parameter	Controlled variable	β (sex) \pm SE	z	p	RR	Sex effect	β	p	AIC
MW2	CW_{L-R}	-0.049 ± 0.038	-1.28	0.2003	0.95	♂ 5% smaller	0.041	< 0.001	219.47
	CW_{R-L}	-0.057 ± 0.039	-1.46	0.1442	0.94	♂ 6% smaller	0.036	< 0.001	233.84
MW3	CW_{L-R}	-0.030 ± 0.023	-1.30	0.1936	0.97	♂ 3% smaller	0.052	< 0.001	95.15
	CW_{R-L}	-0.038 ± 0.027	-1.40	0.1601	0.96	♂ 4% smaller	0.045	< 0.001	150.93
PW5	CW_{L-R}	-0.014 ± 0.121	-0.11	0.910	0.99	♂ \approx ♀	0.060	< 0.001	185.50
	CW_{R-L}	-0.009 ± 0.124	-0.07	0.944	0.99	♂ \approx ♀	0.045	0.0015	202.78
DW7	CW_{L-R}	-0.062 ± 0.045	-1.38	0.167	0.94	♂ 6% smaller	0.059	< 0.001	-75.49
	CW_{R-L}	-0.067 ± 0.048	-1.41	0.158	0.94	♂ 6% smaller	0.050	< 0.001	-53.52

Note: Carapace width from left to right (CW_{L-R}) and carapace width from right to left (CW_{R-L}); manus width (MW2 and MW3), pollex width (PW5), and dactyl width (DW7).

The strong positive association between carapace width and all minor-chela dimensions in this study reflects isometric to slightly positive allometric growth, indicating that as individuals grow, the feeding appendages scale proportionally with body size. Such relationships are typical of *Tubuca* species and are linked to their benthic lifestyle, where coordinated development of the body and appendages facilitates sediment processing and burrow maintenance (Pardo et al., 2020; Zolkhiflee et al., 2021).

Overall, the results suggest that sexual dimorphism in *T. forcipata* is localized to the major chela and is absent in the minor chela, which remains functionally conserved across sexes. This pattern reflects an evolutionary trade-off between maintaining feeding efficiency and developing energetically costly display structures. The minor chela thus represents a morphologically stable component, which is constrained by ecological function, while the major claw evolves more dynamically under the pressures of sexual selection. These findings add new quantitative insight into structure-specific sexual dimorphism within *Tubuca*, emphasizing that morphological divergence in fiddler crabs arises from a balance between sexual and ecological selection forces.

5. Conclusion

This study on *T. forcipata* from Ca Mau Province, Mekong Delta, found no significant sex-related differences in the carapace width (CW_{L-R} , CW_{R-L}) or in minor chela traits ($MW2$, $MW3$, $PW5$, and $DW7$) after accounting for body size, with male characteristics only slightly larger (3–6%, $p=0.14–0.91$). The carapace width strongly predicted chela trait sizes ($\beta=0.036–0.060$; $p<0.001$), indicating proportional scaling between body and appendage growth. Sexual dimorphism in this species is thus limited to the major chela, while the minor chela remains functionally conserved across sexes. These findings provide essential morphometric data for future ecological and evolutionary studies of fiddler crabs in the Mekong Delta.

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Conflict of Interest

The authors declare no conflicts of interest.

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Table 3. Estimated marginal means of functional traits (mm) by sex from Gamma–log GLMs

Parameter	Sex	Mean ± SE
MW2	Female	1.62 ± 0.06
	Male	1.70 ± 0.03
MW3	Female	2.06 ± 0.04
	Male	2.13 ± 0.02
PW5	Female	0.91 ± 0.10
	Male	0.92 ± 0.05
DW7	Female	0.76 ± 0.03
	Male	0.81 ± 0.02

Note: Manus width (MW2 and MW3), pollex width (PW5), and dactyl width (DW7)

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