On sexual maturity in male fiddler crab, *Gelasimus hesperiae* (Crane, 1975) (Brachyura: Ocypodidae)

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ABSTRACT: Determining the sexual maturity of male fiddler crabs based on morphological observations is a challenging task. In this study, we attempted to determine the onset of sexual maturity in the male fiddler crab, *Gelasimus hesperiae*, by considering body morphometry and the morphological and histological characteristics of the reproductive system. Crabs with carapace lengths (CL) from 2.0 to 22.0 mm were randomly sampled from the field and measured for carapace widths (CW) and major propodus lengths (MPL). The onset of morphological sexual maturity (CL_{50}) was determined to be CL 11.0 mm using a Lysack's model, and accordingly, those crabs below CL 11.0 mm were designated as immature. Allometric growth estimation and regression analysis between the body morphometry of the immature and mature groups revealed a positive allometry between CL and MPL. Since, the reproductive system is not visible in immature stage 1 crabs (with CL < 7.0 mm), they were not considered for the analysis of physiological sexual maturity. Between the immature stage 2 (CL 7.1–11.0 mm) and mature groups (CL > 11.0 mm), there was a significant difference ($p < 0.05$) in the width of the testes, length and width of vas deferens, and length and width of the tubules of accessory sex gland. However, principal component analysis (PCA), revealed no discrete cluster formation between these groups, especially for the immature stage 2 crabs (CL 8.0–11.0) close to CL_{50}. Further, histologically, the testes of these immature stage 2 crabs showed signs of spermatogenesis and spermiogenesis similar to that found in mature crabs, indicating the fulfilment of physiological sexual maturity. Overall, our results indicate that the commencement of physiological sexual maturity in male *G. hesperiae* precedes morphological sexual maturity, and hence, the external morphology cannot be considered as the sole criterion for determining the sexual maturity in this species.
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KEY WORDS: *Gelasimus hesperiae*, morphometry, allometry, sexual maturity, male reproductive system.

О половом созревании самцов манящего краба, *Gelasimus hesperiae* (Crane, 1975) (Brachyura: Ocypodidae)

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РЕЗЮМЕ: Определение стадии полового созревания самцов манящего краба по морфологическим признакам является сложной задачей. Мы предприняли попытку выявить надежные признаки достижения половозрелости самцов манящего краба *Gelasimus hesperiae* на основе морфометрии туловища и гистологических исследований половой системы. Крабы с длиной карапакса (CL) от 2,0 до 22,0 мм были собраны в полевых условиях, у особей были проведены промеры ширины карапакса (CW) и длины проподуса большей клешни (MPL). Наступление морфологической половой зрелости (CL 50) наступало при CL 11,0 мм по модели Лайсака, крабы с CL менее 11,0 мм были неполовозрелыми. Аллометрическая оценка роста и регрессионный анализ между морфометрией тела неполовозрелых и зрелых групп выявили положительную аллометрию между CL и MPL. Половая система не обнаруживалась в крабах первой неполовозрелой стадии, (CL < 7,0 мм). Между крабами второй неполовозрелой стадии (CL 7,1–11,0 мм) и половозрелыми крабами (CL > 11,0 мм) были обнаружены достоверные различия ($p < 0,05$) в ширине семенников, длине и ширине семяпровода, и длине и ширине протока придаточной половой железы. Однако, анализ главных компонентов (PCA) не выявил образования дискретных кластеров для этих групп, особенно для неполовозрелых крабов стадии 2 (CL 8,0–11,0), близких к CL50. Гистологическое исследование семенника неполовозрелых крабов второй стадии выявило признаки сперматогенеза и спермиогенеза, схожи с таковыми у взрослых крабов, показывающее наступление физиологической половой зрелости. Таким образом, наши результаты показывают, что физиологическая половая зрелость у самцов *G. hesperiae* наступает раньше морфологической половой зрелости, и внешнее строение не может быть единственным критерием для определения наступления половой зрелости самцов этого вида.
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КЛЮЧЕВЫЕ СЛОВА: *Gelasimus hesperiae*, морфометрия, аллометрия, половое созревание, репродуктивная система самца.

Introduction

Sexual maturity refers to the morphological and physiological changes that occur when a juvenile organism attains the ability to produce gametes and reproduce (Mantelatto, Fransozo, 1996). Studies on sexual maturity are crucial for determining population kinetics and understanding geographic variance (Hines, 1989; Voje, 2016). Sexual maturity in crustaceans is generally determined by growth-related changes in the morphology of secondary sexual characteristics and reproductive organs. The allometric approach used to estimate the size at the commencement of sexual maturity reveals information about the species' reproductive characteristics (Vaninni, Gherardi, 1988; Sampedro *et al*., 1999; Corgos, Freire, 2006; Manchado *et al*., 2021).

The morphological maturity of brachyuran crabs can be determined by observing changes in the relative growth of their various body sections (Hartnoll, 1974; Conan *et al*., 2001; Corgos, Freire, 2006; Manchado *et al*., 2021). In the paddle crab, *Ovalipes trimaculatus* (De Haan, 1833), and the freshwater crab, *Goyazana castelnaui* (H. Milne Edwards, 1853), the functional and anatomical properties of female and male reproductive systems determine physiological maturity (Vallini *et al*., 2014; Freita *et al*., 2021).

The size of sexual maturity varies in *Hemigrapsus oregonensis* (H. Milne-Edwards, 1853) and *Scyra acutifrons* Dana, 1851, which are dispersed in different geographic regions (Hines, 1989). This variation might be influenced by the food supply, population density, and ecosystem of these different regions (Hines, 1989; De Grande *et al*., 2021). Variations have also been reported in the age at which a population of the same or distinct species reaches sexual maturity (Fontelles-Filho, 1989). Many researchers have

provided morphological data as one of the criteria to determine the size for the commencement of sexual maturity (Masunari, Swiech-Ayoub, 2003; Benetti, Negreiros-Fransozo, 2004; Masunari, Dissenha, 2005; Masunari *et al*., 2005).

In brachyuran crabs, the study of physiological sexual maturity has been conducted through macro- and microscopic observations of the gonad (Fontelles-Filho, 1989). In the crab *Uca rapax* (Smith, 1870), physiological sexual maturity is attained when it releases gametes for reproduction, shortly after the critical puberty molt (Castiglioni, Negreiros Fransozo, 2006). In the case of male crabs, physiological sexual maturity hardly determined from the morphological maturity as it doesn't serve to trace proper gonad development (Sastry, 1983; Conan, Comeau, 1986; Choy, 1988). This situation necessitates the accurate estimation of the morphological as well as physiological sexual maturity to understand the organism's reproductive capability (Hines, 1982). A combined approach considering the external (body) morphology and the physiology of gonad development has been adopted by researchers to estimate the sexual maturity in crabs such as *Hepatus pudibundus* (Herbst, 1785), *Liocarcinus depurator* (Linnaeus, 1758), *Cyrtograpsus angulatus* Dana, 1851, *Perisesarma guttatum* (A. Milne-Edwards, 1869) (Reigada, Negreiros-Fransozo, 1999; Muiño *et al*., 1999; Castiglioni, Santos, 2000; Flores *et al*., 2002).

Brachyuran crabs inhabit diverse ecosystems and are a major ecologically significant macrofauna playing a vital role in trophic food webs. Among them, fiddler crabs, which inhabit the intertidal zones of estuaries, are highly copious and support higher trophic levels by consuming producers, primary consumers, and detritus (Koch, Woiff, 2002; McLusky, Elliott, 2004; Hogarth, 2007). *Gelasimus hesperiae* (Crane, 1975), commonly known as the spiny wristed fiddler crab, is distributed along the geographic range of the Indo-West Pacific coast and has both ecological and geographical importance (Crane, 1975). Most of the studies found on this species are female-focused (Cannicci *et al*., 1999; Jaroensutasinee *et al*., 2002; Dyson, 2008; Rosenberg, 2013, 2014; Shih Hsi-Te *et al*., 2016; Wazed *et al*., 2016; Fratini *et al*., 2017; Peer, Nasreen *et al.*, 2018), and very few consider the male. This prompted us to assess the sexual maturity of the male population of *G. hesperiae* inhabiting the intertidal zone of the Muzhupilangad estuary (Kerala, India). For this purpose, we adopted a combined approach, considering the body morphometry (Carapace length [CL], Carapace width [CW] and Major propodus length [MPL]) as well as the morphometry and histological details of the reproductive system. In this study, we attempt to establish a relationship between morphological and physiological maturity, thereby providing a measuring scale to determine sexual maturity in the male population of *G. hesperiae.*

Material and methods

BODY MORPHOMETRY. 643 male fiddler crabs, *G. hesperiae*, were randomly collected from the intertidal zone of the Muzhupilangad estuary (11º46′48″N 75º27′36″E) in Kerala, India. For the collection, catch per unit effort (CPUE: 30 minutes of crab collection per surveyor in a fortnight during the low tide) was applied (Castiglioni, Negreiros Fransozo, 2006). The crabs were taxonomically identified using keys (Crane, 1975; Shih *et al.*, 2016) and DNA barcoding (Accession number MW857280).

The morphometric measurements of carapace length (CL), carapace width (CW), and major propodus length (MPL) were recorded in millimetres (mm), using a 0.01 mm digital calliper. CL was measured from the mid-anterior end to posterior end of the carapace along the central axis of the body of the crab, and CW was measured between the anterolateral spines. MPL was measured from the tip of the propodus fixed finger to the base of the major propodus of the enlarged chelae, usually found on the crab's right hand (Crane, 1975). The minimum, maximum, and mean values (± standard deviation) of each variable were calculated.

DETERMINATION OF THE ONSET OF MORPHOLOGICAL SEXUAL MATURITY (CL_{50}). Considering carapace length (CL) as the determining variable, the onset of sexual maturity (CL_{50}) of the male population of *Gelasimus hesperiae* was assessed using a logistic fit curve. This was performed by employing the non-linear Lysack's model $PL = 1/1+e^{-d\,(CL50\,-\,CL)}$, where PL is the "proportion mature" at carapace length (CL). "Proportion mature" is defined as the proportion obtained from the frequency of mature and immature crabs under each length categories. The values for the immature and mature individuals ranged from 0 to 1. CL_{50} is the size at which 50% of crabs are mature, where d is the rate at which maturity is attained.

MATURITY CATEGORIZATION BASED ON CL_{50}. Based on the results of CL_{50}, a preliminary

level attempt was made to categorize the male population into two groups: (1) immature (CL < 11.0 mm) and (2) mature (CL > 11.0 mm). In the immature group, those having CL < 7.0 mm and showing no sign of a morphologically visible reproductive system (after removing the carapace), were categorized as immature stage 1 (CL < 7.0 mm), and that showed a visible reproductive system were grouped as immature stage 2 (CL 7.1–11.0 mm). For the morphometric and histological analyses of the reproductive system, the immature stage 1 was excluded and only immature stage 2 was considered.

REGRESSION ANALYSIS AND ESTIMATION OF ALLOMETRIC GROWTH. The biometric data (derived from the morphometric measurements of CL, CW and MPL) of all the immature and mature groups were subjected to statistical analysis as described by Sampedro *et al*. (1999). The data were log-transformed, and analysed using a K-means clustering analysis, followed by bivariate discriminant analysis. The regression analysis was also performed between all the growth stages (immature and mature) using the respective biometric data. The relative growth was estimated by adopting the allometric technique, $y = ax^b$ (Huxley, 1950). For the purpose, CL was considered to be the independent variable (x) and CW and MPL to be the dependent variables (y). 'a' represents the intercept of the y value at x = 0, and 'b' is the slope of the regression line formed according to the observational points. The 'b' value was used to predict the growth pattern of the plotted variables: b>1: Positive allometry; b=1: Isometry; b<1: Negative allometry (Hartnoll, 1982). The statistical significance of the b value was tested using Student's t test. The regression coefficients (b) and intercepts (a) among the groups were subjected to an analysis of covariance (ANCOVA) (Zar, 1996).

DETERMINATION OF THE ONSET OF PHYSIOLOGICAL SEXUAL MATURITY. MORPHOMETRY OF THE REPRODUCTIVE SYSTEM. The anaesthetized crabs were kept immersed in 0.9% saline, and the carapace was carefully removed. The exposed reproductive system was carefully dissected out, and its paired functional regions such as testes, vas deferens, and accessory sex glands were quickly identified (Krol *et al*., 1992). The tissue was then immediately fixed in 3% neutral formaldehyde for the morphometric analysis. The testes and vas deferens were carefully separated from the fixed tissue and placed on a microscopic slide. The curved regions were carefully lineated, and their length was measured on a mm scale using a Vernier calliper. From the photomicrographic images, the width of the testes and vas deferens, and the length and width of the tubules of the accessory sex gland were measured. The number of testes lobules and tubules of the accessory sex glands were counted under the microscope, and the obtained data were subjected to unpaired t-test and one-way ANOVA.

PRINCIPAL COMPONENT ANALYSIS (PCA). Crabs from the immature stage 2 and mature groups were divided into four size classes each (CL 7.1–8.0 mm, CL 8.1–9.0 mm, CL 9.1–10.0 mm and CL 10.1–11.0 mm for immature stage 2; CL 11.1–12.0 mm, CL 12.1–13.0 mm, CL 13.1–14.0 mm and CL 14.1–15.0 mm for mature groups); decimal value 0.1 represented as its non-integer in the figure and table. Principal component analysis was performed between the carapace length (CL) and the morphometry of the testes, vas deferens and accessory gland. The derived data (correlation and covariance matrix of the transformed data) were interpreted to distinguish and display the valid components among the variables, establish correlation among the variables and expose the cluster between the immature stage 2 and mature groups. To obtain an appropriate number of valid components and eliminate inappropriate results, the PCA analysis was performed multiple times with the data set. Derived data from each of the four size classes (for both immature stage 2 and mature groups) were plotted as points in space created according to the first two PCA axes.

HISTOLOGY OF THE MALE REPRODUCTIVE SYSTEM. The reproductive system from immature stage 2 and mature crabs was dissected out and fixed in Bouin's fluid for 24 hours at room temperature. Subsequently, it was dehydrated using a gradient ethanol series (50, 70, 90, 100% — 1 hour each). The tissues were xylene exposed, wax embedded, microtome sectioned (with thickness 3 to 4 μm), double-stained (hematoxylin-eosin), mounted with DPX and observed under the microscope.

DOCUMENTATION. Microscopic images of the morphological and histological details of the reproductive system were taken using a Leica ICC50 camera attached to a Research Microscope (Leica-DM-750) and the images were analysed using the software LAS EZ, Leica Application Suite-Version 1.7.0.

STATISTICAL ANALYSIS. t-test and ANCOVA were performed for regression and allometric growth analysis using GraphPad Prism 8. The morphometric data of the reproductive system, based on the CL of immature stage 2 and mature crabs, were subjected to an unpaired t-test, one-way ANOVA and Post hoc Tukey's test using GraphPad Prism 8. Principal component analysis on the data (CL, CW, MPL) and reproductive system was performed using PAST 4.03 software. For the estimation of sexual maturity, curve fitting (CL_{50}) was performed using Origin Pro 2020b.

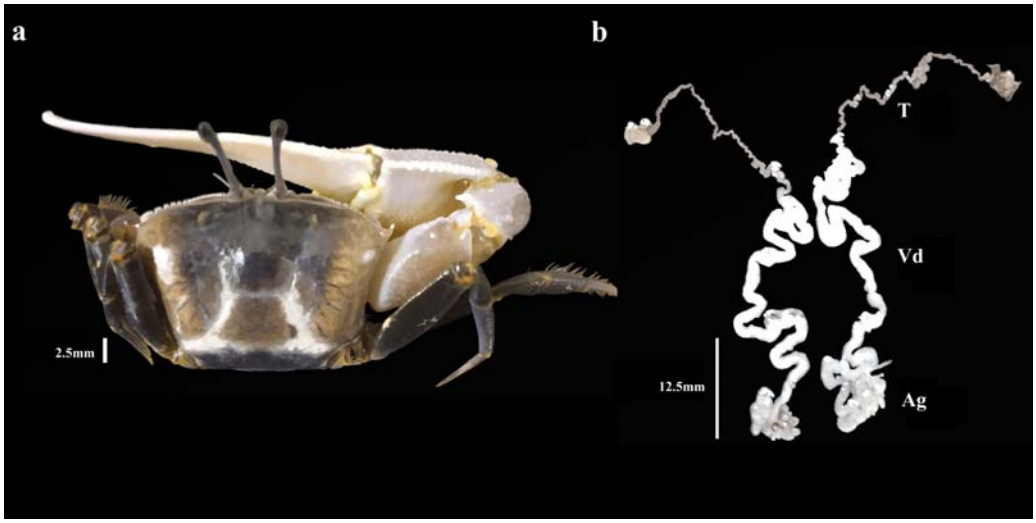

Fig. 1. Male fiddler crab *Gelasimus hesperiae*: a — general appearance; b — photo micrograph of the reproductive system. T — testis, Vd — vas deferens, Ag — accessary sex gland.
Рис. 1. Самец манящего краба *Gelasimus hesperiae*: a — общий вид; b — репродуктивная система самца. T — семенник, Vd — спермодукт, Ag — дополнительная половая железа.

Results

Morphological sexual maturity in male *Gelasimus hesperiae*

BODY MORPHOMETRY. Photo images of the male fiddler crab, *Gelasimus hesperiae*, and the reproductive system are shown in Figure 1. The measured carapace lengths (CL) of the randomly sampled 643 crabs during the present study ranged from 2.0–22.0 mm. The carapace widths (CW) and major propodus lengths (MPL) ranged from 8.5–26.0 mm, and 12.0–42.0 mm, respectively.

CL_{50} AND CATEGORIZATION OF IMMATURE AND MATURE CRABS. The CL_{50} of the male crabs was found at CL 11.0 mm (Fig. 2). Out of the 643 crabs sampled for the study, 217 crabs showed CLs below 11.0 mm and 426 crabs showed CLs above 11.0 mm. Since the onset of morphological sexual maturity lies at CL 11.0 mm, the crabs with CL < 11.0 mm were initially grouped as immature and those with CL > 11.0 mm were considered mature. Those immature crabs with CL < 7.0 mm were considered to be immature stage 1, since their reproductive systems were not visible, even under the microscope (Table 1). Those immature crabs with CLs ranging between 7.1–11.0 mm showed thin strands of testes, vas deferens, and accessory gland were considered to be immature stage 2. In this immature group, the reproductive system showed a proportional increase with the increase of CL. The crabs in the mature group showed highly coiled testes and vas deferens, and distinct tubules of the accessory gland.

While 66% (426 out of 643) of crabs belonged to the mature group (CL < 11.0 mm), 31% (200 out of 643) of the crabs wherein immature stage 2 and 3% in immature stage 1 (17 out 643) group (Fig. 3).

REGRESSION ANALYSIS AND ALLOMETRIC GROWTH. The regression analysis based on the morphometric data on CL, CW and MPL derived from the immature and mature crabs showed a positive correlation. Morphometries exhibiting positive correlations include CL vs. CW ($r = 0.80$), and CL vs. MPL ($r = 0.70$) (Table 2). Assessment of the allometry between the morphometric variables of mature and immature crabs showed a positive relationship between CL and MPL, based on their b values (1.21 for immature group and 1.20 for mature group). In both mature and immature groups, the differences between the pairs of CL vs CW and CL vs MPL were statistically significant ([CL vs CW: $t = 35.50$; $p < 0.001$ for immature group and $t = 36.27$; $p < 0.001$ for

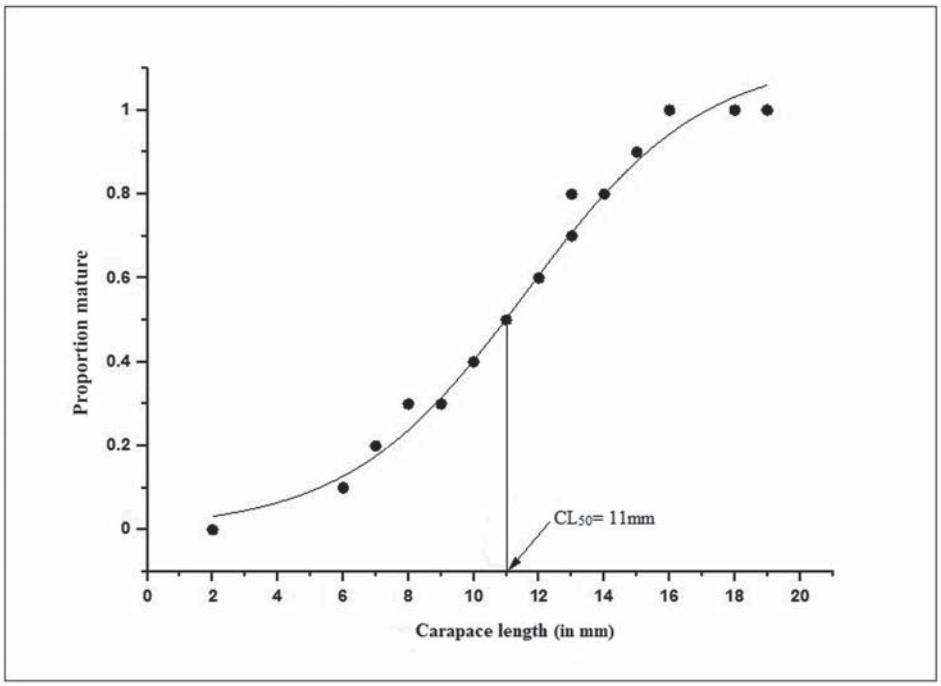

Fig. 2. Logistic fit curve for determining the onset of morphological sexual maturity in *Gelasimus hesperiae*.
Рис. 2. Логистическая сглаженная кривая для определения наступления морфологической половой зрелости у *Gelasimus hesperiae*.

Table 1. Categorization of immature and mature stages in the male *Gelasimus hesperiae* based on carapace length (CL) and visible features of reproductive system.
Таблица 1. Характеристика неполовозрелых и взрослых самцов *Gelasimus hesperiae* на основании длины карапакса (CL) и строения репродуктивной системы.

Maturity stages		**Carapace length (mm)**	**Macroscopic features of the reproductive system**
Immature	Stage 1	<7	Testes, vas deferens, accessory glands-Invisible
	Stage 2	7–11	Testes, vas deferens, accessory glands — thin and delicate structure; size increase proportional with carapace length increase
Mature		11–15 (>11)	Highly coiled testes; coiled, swelled vas deferens; accessory sex gland with swelled tubules

mature group]; [CL vs MPL: $t = 31.72$; $p < 0.001$ for immature group and $t = 36.27$; $p < 0.001$ for mature group]). ANCOVA analysis also showed significant differences ($p < 0.05$) while considering CL vs CW and CL vs MPL (Table 2).

Physiological sexual maturity in male *Gelasimus hesperiae*

MORPHOMETRY OF THE REPRODUCTIVE SYSTEM. The morphometry of testes (T), vas deferens (Vd) and accessory sex gland (Ag) of immature stage 2 and mature crabs are

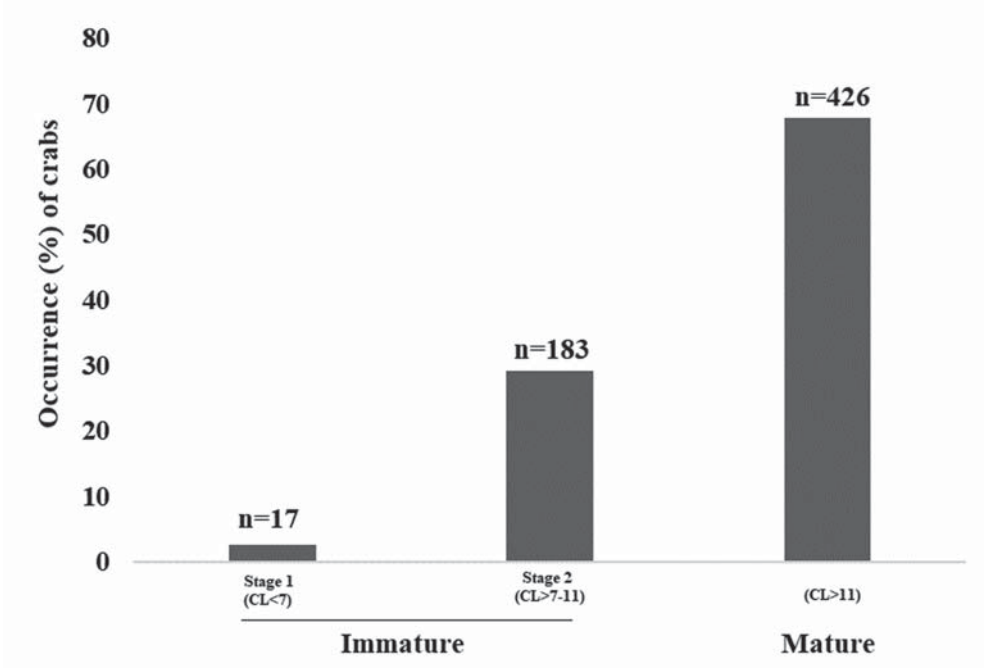

Fig. 3. Proportion (%) of the sampled morphologically mature and immature crabs of *Gelasimus hesperiae* (n — number of crabs).
Рис. 3. Соотношение (%) отобранных морфологически взрослых и неполовозрелых крабов *Gelasimus hesperiae* (n — количество особей).

shown in Figure 4. Based on the data, the immature stage 2 crabs did not show any significant difference in the lengths of the testes ($t = 0.69$; $p = 0.511$) nor the number of testes lobules ($t = 0.58$; $p = 0.57$), compared with the data derived from the mature group (Fig. 4a, b). Further, the numbers of tubules of accessory sex gland derived from both groups (immature stage 2 and mature) were also found to be comparable ($t = 0.42$; $p = 0.68$) (Fig. 4b). However, the width of the testes, length and width of vas deferens, and length and width of tubules of the accessory sex gland showed significant differences ($p < 0.05$) (Fig. 4c).

PRINCIPAL COMPONENT ANALYSIS. Data on the morphometry of the reproductive system (including the testes length, width and number of lobules, vas deferens length and width, and accessory gland length, width and number of tubules related to the CL of both immature stage 2 and mature) were subjected to a PCA. For the analysis, an input of four CL ranges each, from the immature stage 2 (CL 7.1–8.0, 8.1–9.0, 9.1–10.0 and 10.1–11.0 mm) and the mature group (CL 11.1–12.0, 12.1–13.0, 13.1–14.0 and 14.1–15.0 mm) was given. The principal components, PC1 and PC2, were interpreted from the data extracted from PC1–PC7 of both groups (immature stage 2 and mature). The value of variance & covariance was deduced as 99.47% and the correlation was 58.07% (Table 3).

The Biplot derived from the PCA components (PC1 [eigenvalue 4.65] and PC2 [eigenvalue 1.64]) correlated the morphometric variables of the reproductive system in immature stage 2 and mature groups. The zone-wise correlations (between the parameters) are represented as follows: 1. From the zone division, there existed a correlation in crabs in the mature group having two CL ranges (12.0–13.0 & 13.0–14.0 mm) with testes width, length and width of vas deferens, accessory sex gland tubules length and width. In the next zone, though members of the immature stage 2 (CL 10.0–11.0 mm) and mature (CL 14.0–15.0 mm) groups were found, no correlation with the parameters existed. In the third zone, the immature stage 2 (CL 7.0–

Table 2. Regression and allometric analysis of the body morphometries of *Gelasimus hesperiae*.
Таблица 2. Регрессионный и аллометрический анализы морфометрии тела *Gelasimus hesperiae*.

Stages of male *G. hesperiae*	Morphometric relationships	Inflection point	N	Linearized equation log y=log a+b logx	r	ANCOVA F value		t test b	Allometric growth
						a	b		
Immature	CL vs CW	11.47	220	log CW = –0.0373 + 0.9176 log CL	0.80	15.37	9.62*	35.60*	–
Mature			406	log CW = –0.72033 + 0.8320 log CL	0.80			36.27*	–
Immature	CL vs MPL	12.00	220	log MPL = –1.1249 + 1.210 log CL	0.70	4.85	264.1*	31.72*	+
Mature			406	log MPL = 0.08691 + 1.201 log CL	0.70			38.70*	+

CL — carapace length; CW — carapace width; MPL — major propodus length; r — coefficient of correlation * — significant result (á<0.05); + — positive allometric growth; – — negative allometric growth.

8.0 mm) correlated with the number of accessory gland tubules in the next sector. In the last zone, the immature stage 2 with CL (8.0–9.0 and 9.0–10.0 mm) correlated with the length and the number of lobules number in the testes (Fig. 5a). According to the correlation loading plot, the highest influence of testes width, vas deferens length, width and accessory sex gland tubules length and width was predominant in all CL ranges of mature group. Negative correlation was also observed in the length of the testes and number of lobules in the testes and the number of accessory gland tubules in all size classes of immature stage 2 and one size classes (11.0–12.0 mm) in the mature group (Fig. 5b). The correlation loading plot of principal component 2 was influenced positively by the morphometric variables (testes width, length and width of vas deferens, accessory sex gland tubules length and width), but with the number of accessory sex gland tubules, influence was found negative (Fig. 5c). Over all data derived from the PCA suggest that there is no demarcation between immature stage 2 and mature groups while considering the morphometric characters of the reproductive system, particularly for those close to the CL_{50}.

HISTOLOGY. Histology of the reproductive system of the immature stage 2 and mature groups are represented in Figure 6. The presence of spermatocytes and spermatozoa were obvious in the testis of both groups, indicating active spermatogenesis. However, the distinct zonal differentiation and density of spermatozoa are more prominent in the mature group (Fig. 6a, b). Vas deferens also contained spermatozoa in both groups, but its multitude in the mature group was much more as evidenced from the histological sections (Fig. 6c, d). In both groups, accessory sex glands were shown to be secretory, but the nature of the secretory materials seemed to be different judged from the histological sections (Fig. 6e, f).

Discussion

The ontogenetic changes in crustaceans can be seen through the differential growth of their body parts, such as the changed appearance of secondary sexual characters after

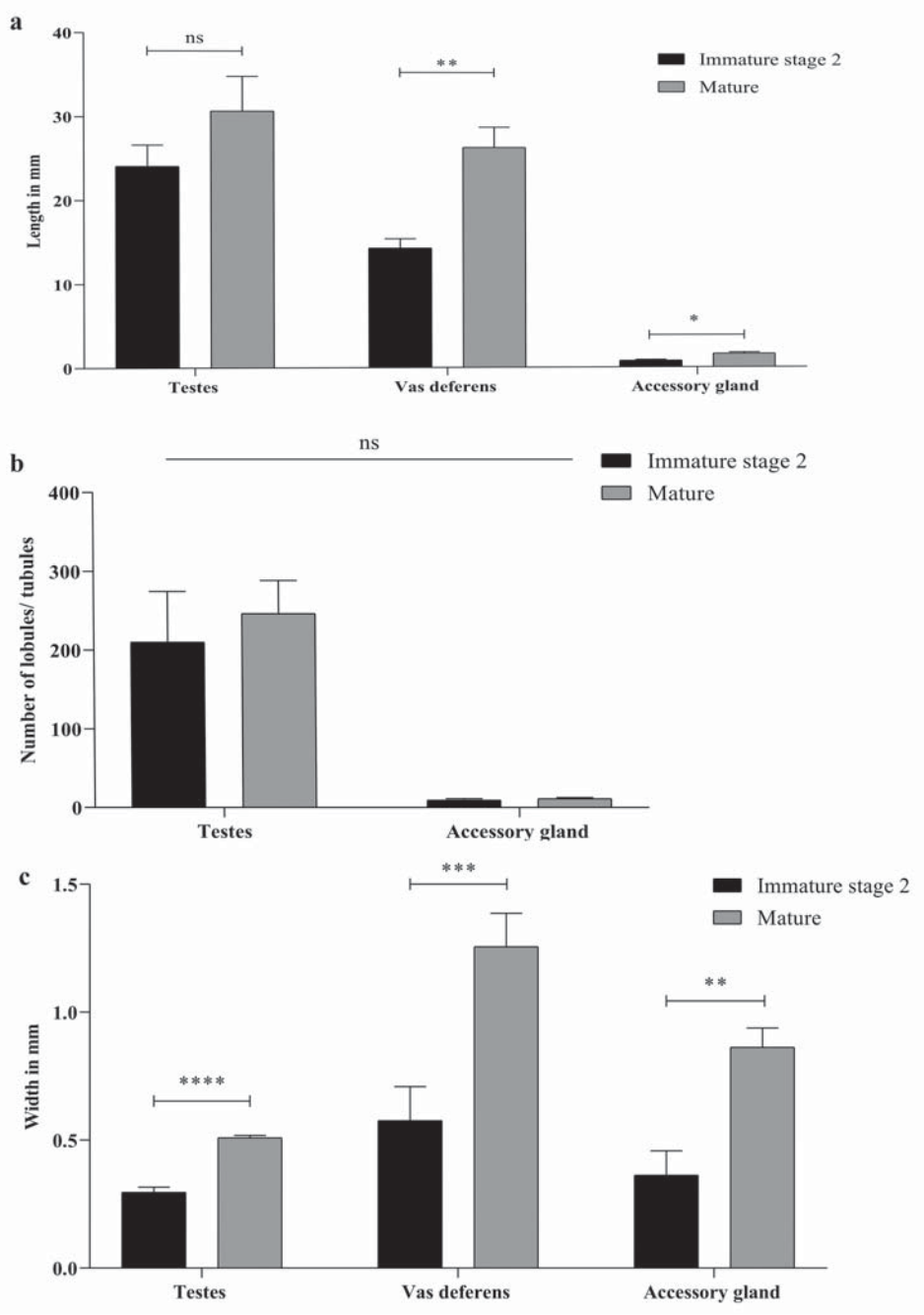

Fig. 4. Morphometry of the reproductive system in *Gelasimus hesperiae* (a — length of the structure; b — its number and c — width). Mean ± SE; n = 40. ns — insignificant ($p > 0.05$); *significant ($p < 0.05$), statistical tool: one-way ANOVA (Tukey test result), unpaired t-test.

Рис. 4. Морфометрия репродуктивной системы самцов *Gelasimus hesperiae* (a. длина структуры; b — ее число, c — ее ширина). Среднее ± стандартное отклонение; n = 40. ns — недостоверно ($p > 0,05$); *достоверно ($p < 0,05$), статистический метод: однофакторный дисперсионный анализ ANOVA (результат теста Тьюки), непарный t-критерий.

Table 3. Eigenvectors for principal component analysis (PCA) ordination.
Table 3. Характеризующие векторы для ординации методом анализа главных компонентов (PCA).

	Principal components correspond to the morphometry of the reproductive system						
	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7
IM (7–8)	–2.223	–2.579	–0.214	0.100	0.341	0.022	–0.059
IM (8–9)	–2.761	0.489	0.115	0.103	–0.241	–0.108	0.259
IM (9–10)	–0.711	1.067	0.513	–1.316	0.272	0.350	–0.036
IM (10–11)	1.948	–0.831	0.332	–1.030	–0.490	–0.326	–0.039
M (11–12)	–1.710	1.509	–1.089	0.341	–0.099	–0.190	–0.184
M (12–13)	2.896	0.419	–0.495	0.183	0.673	–0.188	0.100
M (13–14)	0.555	0.336	1.758	1.112	–0.025	0.018	–0.074
M (14–15)	2.005	–0.411	–0.919	0.505	–0.430	0.421	0.034
Eigenvalues	4.645	1.637	0.829	0.636	0.162	0.070	0.017
Variance (%)	58.072	20.469	10.363	7.961	2.034	0.877	0.223
Cumulative (%)	58.072	78.541	88.904	96.865	98.900	99.777	100

The principal components (PCs) are made up of the coefficients of the linear combinations for the 8 morphometric variables of the reproductive system of male immature stage 2 and mature *Gelasimus hesperiae* (testes length, testes width, testes lobules number, vas deferens length, vas deferens width, accessory sex gland tubules length, accessory sex gland tubules width, accessory gland tubules number).

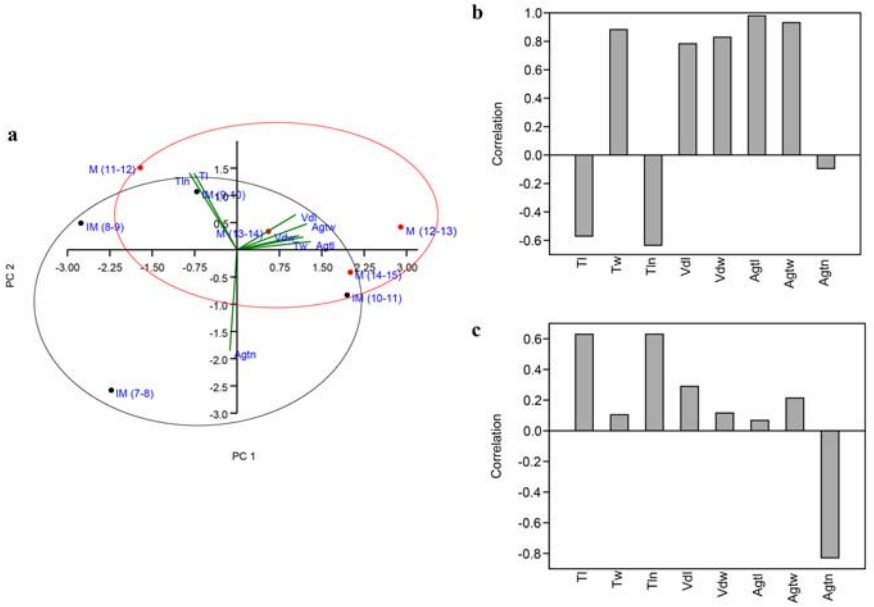

Fig. 5. Principal component analysis (PCA) ordination plot of 8 morphometric variables of the reproductive system in *Gelasimus hesperiae* for immature (black dots) and mature (red dots) groups of male. 5a — the plot was built using the first two components (PC1 and PC2); 5b, c — loading plots of PC1 and PC2.
Tl — testes length, Tw — testes width, Tln — testes lobules number, Vdl — vas deferens length, Vdw — vas deferens width, Agtl — accessory sex gland tubules length, Agtw — accessory sex gland tubules width, Agtn — accessory gland tubules number.

Рис. 5. Ординация восьми морфометрических переменных репродуктивной системы *Gelasimus hesperiae* методом главных компонент (PCA) для неполовозрелых (черные точки) и половозрелых (красные точки) групп самцов. 5а — диаграмма, построенная с использованием первых двух компонентов (PC1 и PC2); 5b, c — диаграммы распределения нагрузки на компоненты PC1 и PC2.
Tl — длина семенников, Tw — ширина семенников, Tln — количество лопастей семенника, Vdl — длина семяпровода, Vdw — ширина семяпровода, Agtl — длина трубочек приадточной железы, Agtw — ширина трубочек придаточной железы, Agtn — количество трубочек придаточной железы.

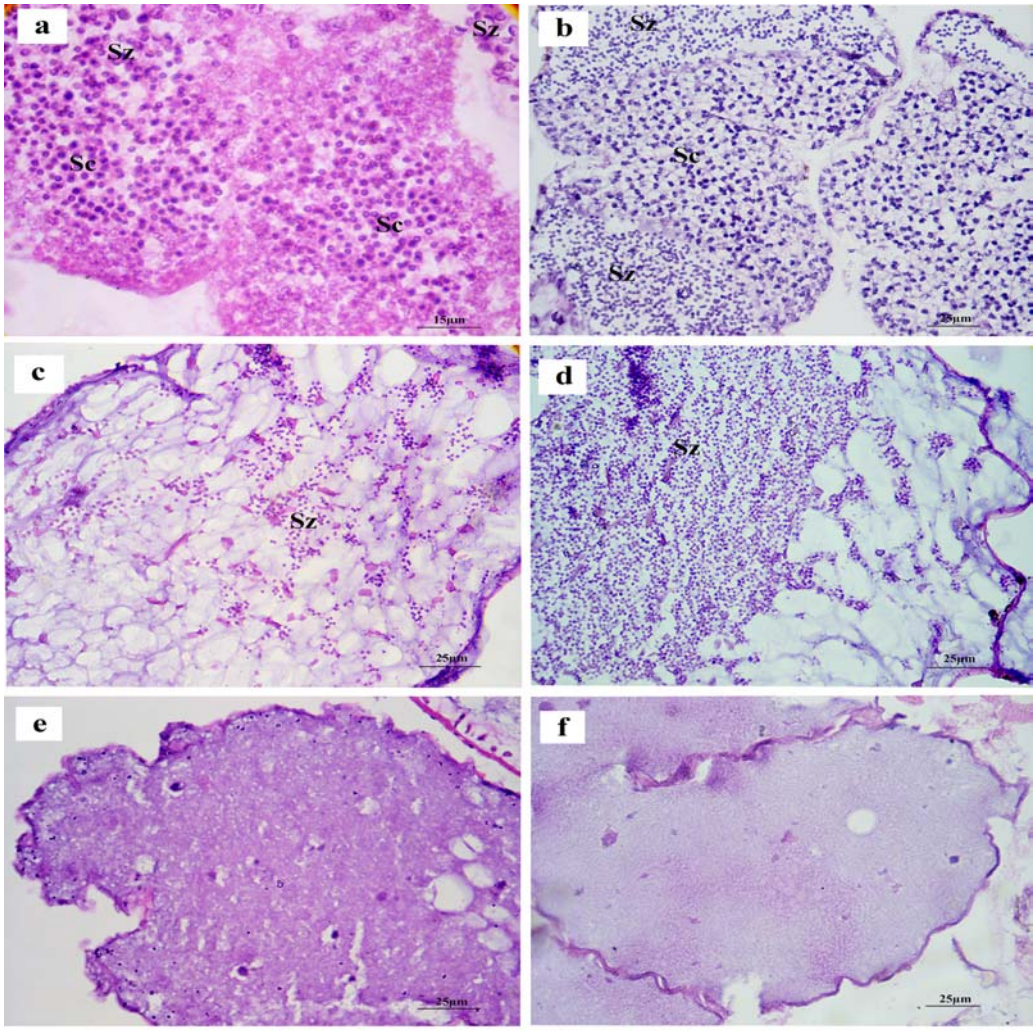

Fig. 6. Histology of the reproductive system in *Gelasimus hesperiae*. Immature crab (CL 8.0 mm, a, c, e), mature crab (CL 11.0 mm, b, d, f): a — testes (1000x), b — testes (400x), c, d — vas deferens (400x), e, f — accessory sex gland (400x).
Spermatocytes (Sc); Spermatozoa (Sz).
Рис. 6. Гистологическое строение репродуктивной системы *Gelasimus hesperiae*. Неполовозрелый краб (CL 8,0 мм, a, c, e), половозрелый краб (CL 11,0 мм, b, d, f): a — семенник (1000x), b — семенник (400x), c, d — семяпровод (400x), e, f — придаточная половая железа (400x).
Sc — сперматоциты, Sz — сперматозоиды.

metamorphosis, including the cheliped, abdomen, and pleopods found in both sexes (Hartnoll, 1974, 1978). In brachyurans, the external morphometries of carapace length (CL), carapace width (CW) and major propodus length (MPL) change over their lifespans (Pralon, Negreiros-Fransozo, 2008). These morphometric variables, however, are not always synchronized in all species. In *G. hesperiae* (present study), there was a positive correlation between carapace length and major propodus length irrespective of the stage of maturity. In *G. hesperiae*, the coefficient of determination was less (0.70), than the r-value (of CL vs. MPL) in other male fiddler crabs such as *Uca thayeri* Rathbun, 1900, *U. uruguayensis* (Nobili, 1901), *U. cu-*

mulanta Crane, 1943, *U. burgersi* Holthuis, 1967 (Negreiros-Fransozo *et al*., 2003; Benetti, Negreiros-Fransozo, 2004; Pralon, Negreiros-Fransozo, 2008; Hirose *et al.*, 2013). In brachyuran morphometric studies, carapace length is considered as the independent variable (x) (Pralon, Negreiros-Fransozo, 2008). In male *G. hesperiae*, CL vs CW exhibited negative allometry in both immature and mature groups, but positive allometry with respect to CL vs MPL, agreeing with reports on other fiddler crabs such as *U. rapax*, *U. thayeri*, and *U. burgersi* (Negreiros-Fransozo *et al*., 2003; Castiglioni, Negreiros-Fransozo, 2004; Benetti, Negreiros-Fransozo, 2004). According to other reports on brachyuran crabs (e.g., *Portunus spinimanus* Latreille, 1819, *Eriphia gonagra* (Fabricius, 1781), *Sesarma rectum* Randall, 1840 and *Panopeus austrobesus* Williams, 1983, when carapace length and carapace width are correlated, no changes occur during ontogeny because of the isometric growth (Santos *et al.*, 1995; Mantelatto, Fransozo, 1999; Negreiros-Fransozo, Fransozo, 2003). The present observation in male *G. hesperiae* agrees with the view of previous investigators regarding the inadequacy of considering CW as a morphometric variable, since, in this species, CL vs CW exhibited negative allometry in both immature and mature groups.

Variation in the chelate leg sizes of male and female crabs is thought to be caused by the modification of its feeding options and range of expansion (Williner *et al*., 2014). In male crabs, a larger chelate leg could be an advantage when it comes to consuming a varied diet adult crabs consume more plant debris and large sized invertebrates than young crabs, which in turn fulfil the requirement for the production of gametes (Nagaraju, 2011; Williner, Collins, 2013; Williner *et al*., 2014). In male fiddler crabs, the cheliped, as a secondary sexual character become larger instantly after maturity (Hartnoll, 1982). Male ocypodid crabs usually have asymmetrical chelipeds, with one perceptibly larger claw and another smaller claw, which is used to feed (Castiglioni, Negreiros-Fransozo, 2004). Certain specific behaviours associated with cheliped growth benefit the organism during intra and inter specific struggle, combative activity, territory defence, and courtship (Christy, Salmon, 1984; Castiglioni, Negreiros-Fransozo, 2004). For instance, during courtship behaviour, the cheliped is used for the waving that attracts a receptive mate as well as handling them during copulation (Salmon, 1987; Latruffe *et al.*, 1999). Thus, the allometry of MPL is a reliable parameter for detecting sexual maturity. According to previous reports, immature and mature *Uca cumulanta*, *U. burgersi*, *Uca mordax*, *U. thayeri* and *Ucides cordatus* (Linnaeus, 1763) displayed positive allometry with respect to CL and MPL (Negreiros-Fransozo *et al*., 2003; Benetti, Negreiros-Fransozo, 2004; Masunari, Dissenha, 2005; Pralon, Negreiros fransozo, 2008; Castiglioni *et al*., 2011; Araujo *et al*., 2012). The present study on *G. hesperiae*, also showed a positive allometry between CL and MPL, irrespective of their maturity, as evidenced from the b value (1.20). Thus, both CL and MPL could be considered to be appropriate morphometric variables for the detection of morphological sexual maturity in *G. hesperiae.*

Size at the onset of sexual maturity is considered to be a key life history parameter which reflects the longevity and life-time investment in reproduction of a species (Anger, Moreira, 1998). According to the present logistic fit curve (CL_{50}), the size at which the onset of morphological sexual maturity occurs in the male *G. hesperiae* is 11 mm. The size of sexual maturity is different in two male populations of *U. thayeri* found in two different geographical regions of Brazil. The population inhabiting the Ariquindá River attain maturity at 11.80 mm while those inhabiting the Mamucabas River attain maturity at 12.10 mm (Araujo *et al*., 2012). Different populations of *U. rapax*, inhabiting two different mangrove system of Brazil also showed different sizes for the onset of sexual maturity (CW_{50} 14.8 and 13.6 mm) (Castiglioni, Negreiros-Fransozo, 2006). In male *Uca vocans* (Linnaeus, 1758), the estimated size is 23.88 mm, while in females it is 23.27 mm (Litulo, 2005). The onset of sexual maturity in male *Austruca iranica* (Pretzmann, 1971) (Ocypodidae) inhabiting two different regions in Pakistan has also been reported at different sizes (CW_{50} at 6.65 and 8.2 mm) (Saher *et al*., 2019). In the case of male *Opusia indica* (Alcock, 1900), another ocypodid, the size at which 50% population attained sexual maturity was 5.51 mm (Saher *et al*., 2016). According to Costa *et al*., 2021, 50% of male *Uca maracoani*

(Latreille, 1803) is sexually mature at CW 13.8 mm. Masunari *et al*. (2005), Hirose *et al*. (2007) and Silva *et al*. (2016), however, found a different value of onset sexual maturity (CW_{50}%) in the population of *U. maracoani* at different latitudes from Brazil.

Variation in the size in the onset of sexual maturity reported, even in the same species of Ocypodid crabs, is presumably due to diverged environmental conditions (Pralon, Negreiros-Fransozo, 2008; Araujo *et al*., 2012; Hirose *et al*., 2013).

Gonadal morphometric measurements are also important to precisely assess sexual maturity in crabs (Negreiros-Fransozo *et al*., 2002; Benetti *et al*., 2007; Castiglioni, Negreiros-Fransozo, 2004). The reproductive system of *G. hesperiae* includes the testes, vas deferens, and accessory sex gland. According to the unpaired t-test and one-way ANOVA, the majority of the morphometric variables of the reproductive system showed a considerable increase ($p < 0.05$) from the immature to mature stages. This finding was also supported by the results of the principal component analysis. The data reveals the importance of including 'morphometry of the reproductive system' as an important criterion for assessing physiological sexual maturity in fiddler crabs. All the morphometric variables used in this study, except the number of accessory sex gland tubules, could be considered as physiological sexual maturity indicators. Our study reveals that, the onset of morphological sexual maturity is at CL 11.0 mm, while the onset of physiological sexual maturity could be attained much earlier, at CL 8.0 mm, as evidenced from the histological details of the reproductive system (Fig. 6).

Several studies report the synchrony of morphological and physiological sexual maturity in crabs (Hartnoll, 1965; Negreiros-Fransozo, Flores, 1999). However, exceptions have been reported in *Cancer irroratus* Say, 1817, *Ovalipes stephensoni* Williams, 1976, *Liocarcinus holsatus* (Fabricius, 1798), *Liocarcinus puber* (Linnaeus, 1767) and males of *Arenaeus cribrarius* (Lamarck, 1818) in which no synchrony exists between morphological and physiological maturity (Campbell, Eagles, 1983; Haefner, 1985; Pinheiro, Fransozo, 1998). In male *G. hesperiae*, the existence of partial synchrony between the morphological and physiological sexual maturity could be suggested, based on the data from the present study. However, there is still a possibility that physiological sexual maturity could commence much earlier than the onset of morphological sexual maturity in this species.

Conclusions

According to our logistic fit curve (CL_{50}), the size for the onset of sexual maturity in the fiddler crab, *Gelasimus hesperiae*, is CL 11.0 mm. *G. hesperiae* exhibit a positive correlation and positive allometric growth between carapace length (CL) and major propodus length (MPL), irrespective of their stage of maturity. Supporting this, there was also a significant difference in the gonad morphometry between these groups. The principal component analysis, however, did not show any distinct cluster to confirm this difference. Obviously, the testes in immature crabs, especially those with carapace length close to CL_{50}, appear to be active in spermatogenesis, possibly indicating the onset of physiological sexual maturity much earlier than the onset of morphological sexual maturity. Thus, external morphology cannot be considered the sole criterion for determining the sexual maturity in this species.

We presume that, the physically immature male *G. hesperiae* are involved in reproduction to supply a high proportion of individuals year-round as a survival strategy. Further study involving molecular tools is highly warranted to confirm this hypothesis.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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