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ANIMAL SCIENCE

Ontogenetic variation of the *Goyazana castelnaui* H. Milne-Edwards, 1853 (Brachyura, Trichodactylidae), crab in the semiarid region of Brazil

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Abstract: In order to know the morphological variations of *Goyazana castelnaui*, we conducted an ontogenetic study from the first crab stage to the adult stage using geometric morphometry. We studied 36 females, 43 males and 162 juveniles collected in the Pajeú River, Brazil. We photographed crabs' carapace, pleon and right cheliped with they arranged parallel to the plane, afterwards landmarks and semi-landmarks were strategically distributed in the images. Through principal components analysis, we observed that the variation occurred mainly in the frontal and posterior region of the carapace. The pleon presented marked variations in the posterior and anterolateral region, while chelipeds presented greater variations at the base of the fixed finger. The canonical variation between sexes and between juveniles and adults ($p<0.05$) varied significantly. Correct allocations obtained by discriminant analysis ($p<0.05$) varied between 89.3% and 100.0%. The carapace shows a constant dimorphism along the ontogenetic trajectory, and both sexes reach similar centroid sizes ($p>0.05$). While the pleon and the cheliped, both sexes are similar when juvenile, diverging along the trajectory and reaching different centroid sizes ($p<0.05$). Females have a larger pleon and males a larger cheliped, corroborating the monophyletic theory of Brachyura.

Key words: Freshwater crab, ontogenetic polymorphism, semiarid, sexual dimorphism.

INTRODUCTION

The growth of Brachyura occurs through consecutive molts (ecdysis). They are characterized by physiological, morphological, chemical, and behavioral changes. The period between molts can be influenced by biotic and abiotic factors, as well as individual size and ability to obtain and store resources for the next molt (Aiken & Waddy 1992, Lima & Oshiro 2006, Schram & Castro 2015). Successive molts lead to the appearance of patterns of body growth that allow these organisms to develop specific functional behaviors typical for each sex, such as male cheliped and female pleon positive allometry, mainly at the pre-pubertal phase (Hartnoll 1974), thus generating dimorphic characteristics (Marochi et al. 2016) in a same species.

The study of morphological patterns has been improving over the years. Such studies have replaced techniques related to classical morphometry through geometric morphometry in order to understand an organism as a whole. They provide knowledge of how an individual's shape can be formed by complex interactions between genetic factors and the environment (Klingenberg 2010). Due to the rigid exoskeleton and an easy identification of anatomical

landmarks, crustaceans are ideal organisms for geometric morphometry analyses (Rufino et al. 2004). Their growth can be identified through an ontogenetic trajectory.

Some studies carried out using geometric morphometry in crabs have aimed to ascertain variations in the shape of specimens considering the differentiation between populations from different locations (Trevisan & Masunari 2010, Scalici et al 2013, Deli et al. 2015, Pramithasari et al. 2017) in order to differentiate individuals with regard to sexual dimorphism (Alencar et al. 2014, Marochi et al. 2016), as well as variations in ontogenetic trajectory (Shinozaki-Mendes & Lessa 2017), which consists of variations associated with growth processes. For the species *Goyazana castelnaui*, only the study by Silva et al. (2018) has used geometric morphometry to identify the existence of sexual and age dimorphism for sexed young and adult individuals. However, this work did not include juveniles in the first crab stage or cheliped analyses; only individuals recruited to fishing were included.

The present study aims to analyze the morphological variations of the dorsal (carapace), ventral (pleon) and right chelipeds of *G. castelnaui* along the ontogenetic trajectory. The purpose is to ascertain age and sexual polymorphism of this species during growth using geometric morphometry techniques.

MATERIALS AND METHODS

Study area and laboratory procedures

Crabs of the species *Goyazana castelnaui* were collected (SISBIO license 63227-4) along the Pajeú River in the semiarid region of Brazil from February 2011 to September 2016. The approximate coordinates are 08°38' S and 038°35' W (Figure 1). The collections were carried out in the twilight and in the night using shrimp nets. In laboratory, the specimens were cryo-anesthetized, identified, and sexed according to Magalhães (2003). Females had a wide semicircular pleon with four pairs of pleopods, and males had a triangular and narrow pleon. 79 free-living individuals (36 females - F, and 43 males - M) and 162 non-sexed juveniles (J) were collected in the incubation chambers of females at the first crab stage, since there were no traces of ecdysis.

Geometric morphometry and statistics

Initially, we took photographs of the crabs' carapace (28 F, 43 M, and 162 J), pleon (28 F, 43 M, and 162 J) and the dorsal (external) view of the right propodi (36 F, 33 M, and 40 J). The images of individuals with malformation or injuries were discarded from analyses. For linear morphometry, the specimens were measured using the software UTHSCSA *ImageTool* 3.0 (Wilcox et al. 1996). Carapace width (CW), pleon length (PL), and the right chelate propodus length (CL) were measured.

Males and females were photographed using a digital camera attached to a tripod with 50-mm focal length lens (Canon Inc 2012). The subjects were arranged parallel to the plane. The juveniles were photographed with a camera attached to a stereoscopic microscope (Bel Photonics 2014).

The photos showed four landmarks and seven semi-landmarks in the carapace, three landmarks and ten semi-landmarks in the pleon, and three landmarks and seven semi-landmarks in chelipeds (Figure 2). They were strategically distributed for better obtaining the animal's shape using the software TPSDig version 2.10 (Rohlf 2006).

To align the coordinates of landmarks and semi-landmarks with the centroid, the generalized Procrustes analysis (GPA) was performed using the software MorphoJ,

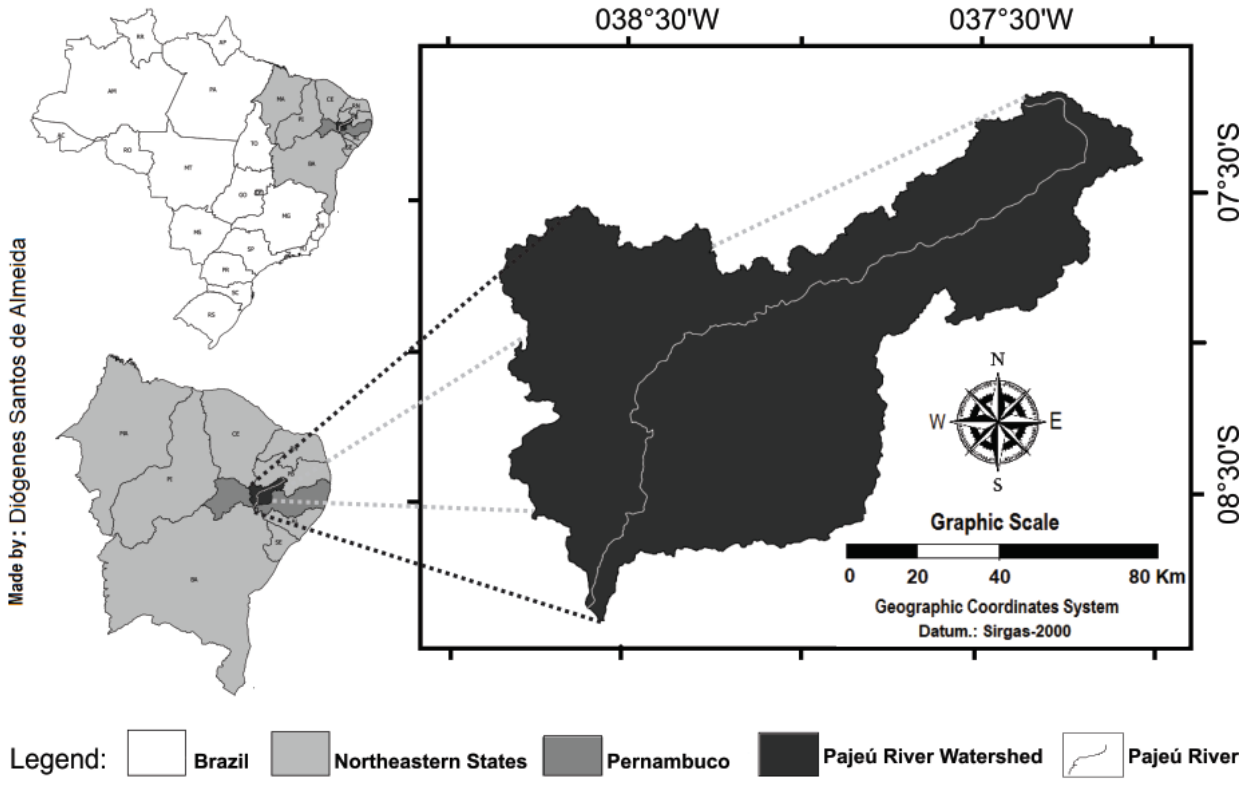

Figure 1. Geographic location of the collection area of *Goyazana castelnaui* in Pajeú River, Pernambuco, Brazil.

version 1.06 (Klingenberg 2008). Differences in orientation, position, and scales were removed (Rohlf & Marcus 1993, Bookstein 1996, Adams et al. 2004). From the matrix of residues generated in the GPA, a principal components analysis (PCA) was performed to determine the main characteristics of shapes. Later, a canonical variance analysis (CVA) was performed with 10,000 permutations to find the shape characteristics that best distinguish and separate groups using the Procrustes distance (Dist. Proc.).

Before the main analysis, landmark and semi-landmark measurements were taken twice for carapace, pleon and right cheliped by the same researcher with the images in random orders. Then, the two groups (original and repetition) were compared using the Hotelling test (T^2) ($p<0.05$) for discriminant analysis. In case of difference between groups, a third measurement was taken until no significant difference has been identified.

A multivariate analysis of variance was performed (MANOVA) with probability fitting for Bonferroni multiple comparisons (Fornel & Cordeiro-Estrela 2012) in order to identify possible differences in shape (Carapace, Pleon and Cheliped) and the centroid size. For these analyses, the software Past, version 3.07, was used (Hammer et al. 2001).

To test the existing differences between the shapes of each group and calculate the percentages of its characteristics, a discriminant function analysis was performed (DA) together with permutation test with 10,000 permutations to validate the crossing between groups (Viscosi & Cardini 2011). The Hotelling test (T^2), with Bonferroni fitting ($p<0.05$), was used to determine correct allocations in each DA group.

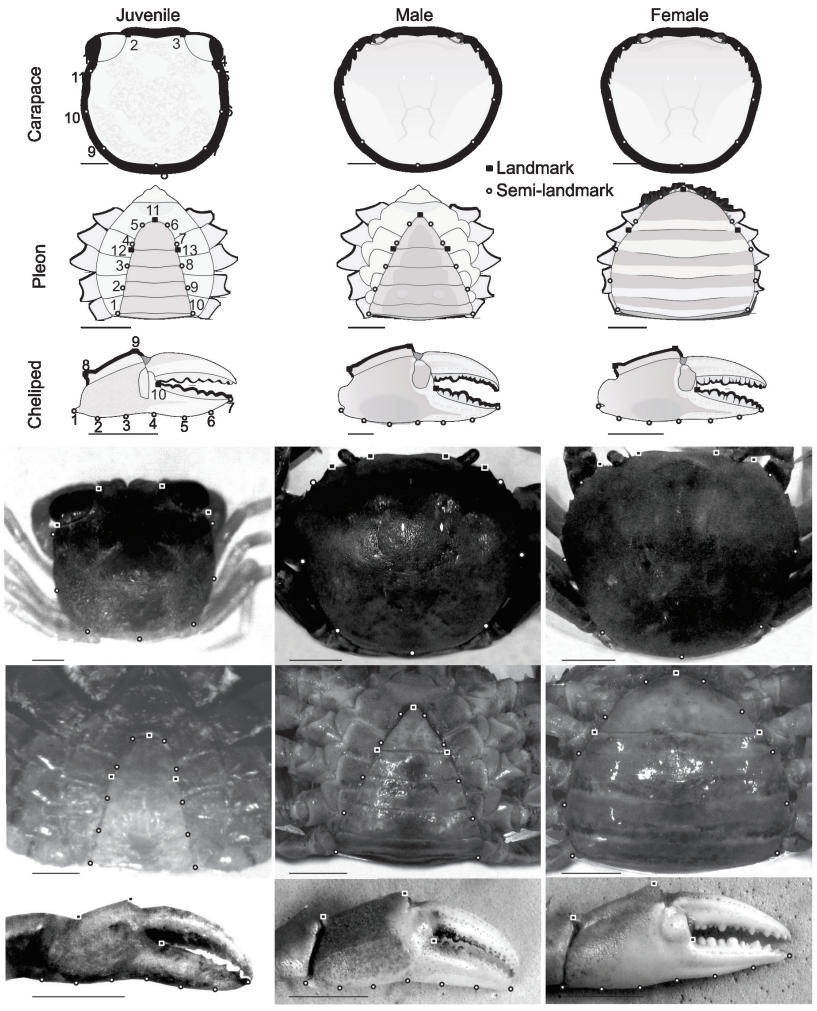

Figure 2. Schematic drawing and images of specimens of juvenile, males, and females of *Goyazana castelnaui* showing the location of anatomical landmarks and semi-landmarks on the carapace, pleon, and right cheliped. Carapace: 1 and 4, exorbital tooth ends; 2 and 3 - lobes on the frontal margin of the carapace; 5 and 11, second exorbital tooth ends. Start and end point of the allocation of semi-landmarks (6 to 10) which surround the carapace with equal distance. Pleon: 1 and 10, posterior end of the II abdominal somite. Start and end point of the allocation of semi-landmarks (2 to 9) which border the pleon with equal distance; 11, apex of the telson; 12 and 13, posterior end of the telson. Right cheliped: 1, tip of the lower tooth close to the carpus-propodus. Starting point for the allocation of semi-landmarks (2 to 6) which border the propodus with equal distance to semi-landmark 7; 7 - Distal end of the fixed finger; 8, tip of the upper tooth close to the carpal-propodus joint; 9, distal end of the crest of the propodus; 10, proximal base of the first tooth of the fixed finger. Scales: juvenile 0.5 mm; male and female 10.0 mm.

In order to statistically evaluate possible differences in carapace, pleon, and cheliped sizes along the ontogenetic trajectory of specimens of *G. castelnaui*, regression graphs were plotted using the distribution of CVA scores (dependent variable) according to centroid size (independent variable).

RESULTS

Juveniles presented CW ranging between 2.2 and 2.6 mm, females between 35.2 and 52.2 mm, and males between 36.1 and 50.8 mm. The PL varied between 0.8 and 1.20 mm (juveniles), 22.9 and 37.6 mm (females), and 18.4 and 28.0 mm (males). The CL of juveniles varied between 1.1 and 1.2 mm, of females between 14.3 and 34.4 mm, and of males between 9.6 and 59.6 mm.

Initially, the repeatability of the measurements was attested, with no significant difference between the original measurement and the repetition for all analyzes (p-value ranging from 0,9743 to 0,9999), with no need for third analyzes.

In principal components analyses of the variation of carapace landmarks, the PC1 represented 94.3% of the variance and the PC2 only 1.9% (Figure 3). In PC1, the negative values of the x-axis comprised only juveniles, with a marked a distancing of this group from the others (F and M), especially regarding the frontal (landmarks 1, 2, 3 and 4) and posterior region (semi-landmarks 7, 8 and 9). The PC2 separated

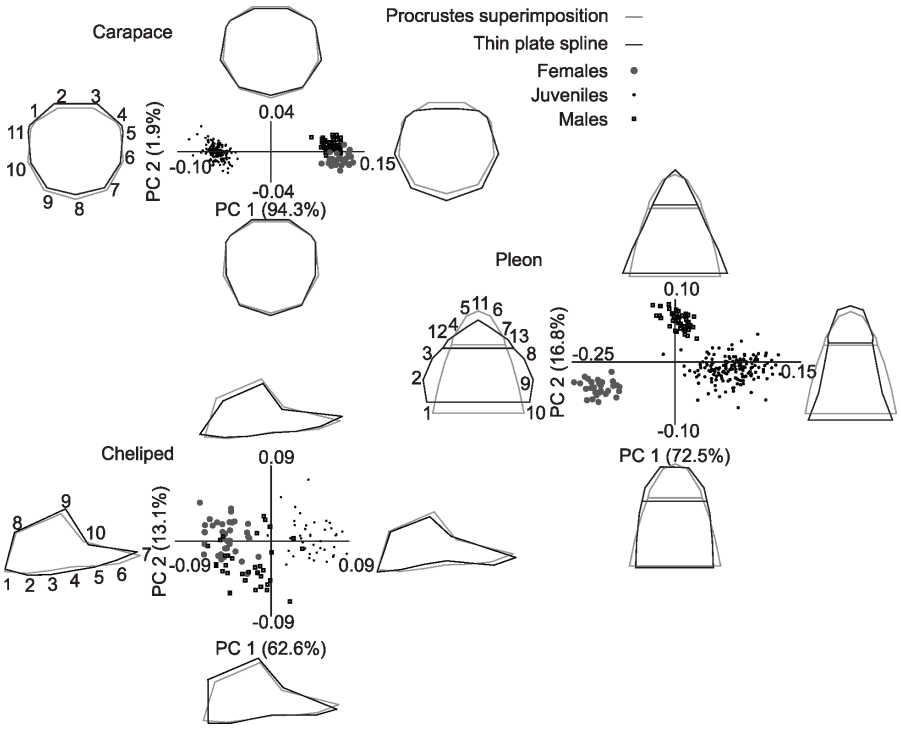

Figure 3. Carapace, pleon and cheliped Thin Plate Splines associated with variations in the analysis of the first (PC1) and second (PC2) principal components of *G. castelnaui*. The thin gray plates correspond to the overlap of Procrustes (mean values) and the black plates represent deformities. Scores of females are represented by gray circles, juveniles by black circles, and males by squares.

the group F from group M. The scores of females were distributed mainly on the negative y-axis and that of the males on the positive axis, while juveniles showed dispersion along the axis. The main variations occurred in the posterior (8) and lateral (6 and 10) semi-landmarks.

The PC1 of the pleon explained 72.5% of variation, with noticeable changes in all points, mainly in the posterior and anterolateral regions. The scores of the female group were dispersed at the end of the negative x-axis, in contrast to the juveniles, whose scores were dispersed along the positive axis; males remained in the central region of the axis closest to the origin. The PC2 accounted for 16.8% of the variation mainly at the base of the pleon (in the posterior semi-landmarks 1, 2 and their counterparts); at the apex of telson (landmark 11) and on the sides of telson (in the previous semi-landmarks 4, 5 and their counterparts). In the y-axis, the extreme negative values were represented by the group of females, the juveniles were dispersed in the central region of the axis, and the males were distributed along the positive axis (Figure 3).

The PC1 of the cheliped showed 62.6% of variation. Distortions were mainly in the lower region of the fixed finger, corresponding to semi-landmarks 3, 4, 6 and 7, in the distal end of the crest of the cheliped and in the proximal base of the first tooth of the fixed finger in anatomical landmarks 9 and 10, respectively. The scores of the female group were dispersed at the end of the negative x-axis, in contrast to the juveniles, whose scores dispersed mainly along the positive x-axis; males remained in the central region of the axis, mostly in the negative axis.

In PC2, there was a 13.1% variation mainly at the tip of the lower tooth close to the carpus-propodus (semi-landmark 1), at the end of the fixed finger (semi-landmark 7), at the tip of the upper tooth close to the carpus-propodus (landmark 8), and at the distal end of the cheliped crest (landmark 9). Along the y-axis, the values were dispersed for the three groups. Males presented most values on the negative

axis, and females presented most values on the positive axis, thus not evidencing a noticeable separation between juveniles and the others (Figure 3).

In the comparison of shapes, as well as in CVA, there was a significant difference between all groups, with p-values lower than 0.01. The results obtained by the DA through the T^2 test with Bonferroni correction also showed a significant difference in shape between the groups ($p<0.01$) as for carapace and pleon. In chelipeds, there was a significant difference between the groups F and J and M and J ($p<0.01$). Between the groups F and M there was no significant difference ($p=0.68$), with greater distances in pleon analyses for all groups.

By analyzing the correct allocation in groups, the pleon of juveniles, males and females obtained a 100% correct classification, whereas for carapace there was a variation between 89.30% (of females allocated in the group of females, in comparison with males) and 100%, and for chelipeds between 90.91% (of males allocated correctly compared to females) and 100% (Table I).

Based on the regression scores of CVA1 with CVA2 in function of centroid size (CS), we noted that juveniles were separated from the other groups by centroid size, varying between positive and negative regression scores for carapace and pleon and remaining only on the positive axis in the cheliped analysis (Figure 4).

The carapace shows a constant dimorphism along the trajectory. Juveniles dispersed along the y-axis, males on the positive axis, and females on the negative axis. Both sexes reached similar centroid sizes ($p=0.53$), differing from juveniles ($p<0.01$). As for the pleon and the cheliped, both sexes are similar when juvenile, diverging along the trajectory and reaching different centroid sizes. Females have a larger pleon ($p<0.01$) and males a larger cheliped ($p=0.02$).

DISCUSSION

Sexual dimorphism is a notoriously and historically recorded aspect of *Brachyura* as secondary sexual characters, mainly in the regions of the pleon and chelipeds. However, variations in carapace shape have rarely been associated with dimorphism. In the present study, non-sexed juveniles showed an ontogenetic trajectory of the carapace and a tendency to sexual dimorphism due to varying positive (male) and negative (female) regression scores. This dimorphism at the early juvenile stages was also recorded for *Dilocarcinus pagei* (Stimpson, 1861), whose variation is evident from the second juvenile stage; at the third stage, the carapace becomes wider than longer, similar to what occurs in adults (Vieira et al. 2013), corroborating the variation observed in the present study.

Table I. Results of discriminant function analysis of carapace, pleon, and cheliped, and the correct allocation of groups in pair interactions with males (M) females (F) and juveniles (J) of *Goyazana castelnaui*.

	Correct allocation of groups (%)			
	F - J	**F – M**	**M - J**	**p-value (T^2)**
Carapace	100 - 100	89.30 - 95.30	100 - 100	< 0.01
Pleon	100 - 100	100 - 100	100 - 100	< 0.01
Cheliped	100 - 100	94.44 - 90.91	100 - 100	< 0.01

Allometry is the morphometric variation related to one or more characteristics of organisms that change with growth due to different biological phenomena. There are static, ontogenetic, and evolutionary allometries (Klingenberg 1996). Sexual dimorphism can cause allometric variations in the body structure of organisms because of pressures of natural or sexual selection (Adam et al. 2018). The ontogenetic variation of *G. castelnaui* (shown in PC1) is more evident than sexual dimorphism (shown in PC2) related to the shape of carapace, pleon, and cheliped. This corroborates the statement that changes in morphological characteristics among individuals of a same species can occur throughout development or only in adulthood, and that growth and allometric level can influence dimorphism and ontogenetic trajectories (Marochi et al. 2018).

In linear morphometry, juveniles of *G. castelnaui* presented the narrowest frontal region. This may be related to the shape and size of eyes because, compared to adult individuals, the eyes are proportionally larger following the relation between carapace and eye. Marochi et al. (2018) stated that ecological factors demand such ocular adaptations, which gradually become more proportional to body size and its functions in the environment.

We observed in the analysis of variation in the ontogenetic trajectory and in the linear morphometry that, for the species *G. castelnaui*, both sexes reached similar centroid sizes for the carapace. This characteristic may be directly related to copulation, since in some *Brachyura*,

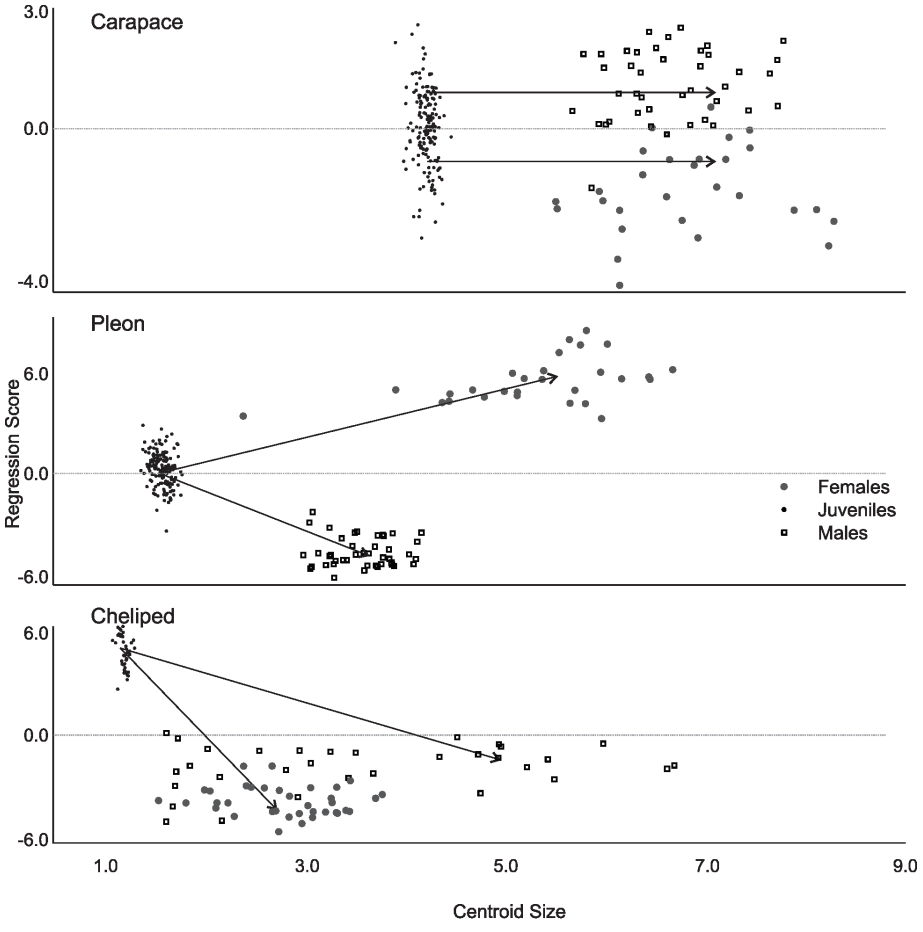

Figure 4. Ontogenetic trajectory of *Goyazana castelnaui* in relation to regression scores of the canonical variation coefficients 1 and 2 in function of centroid size based on geometric morphometry of the carapace, pleon, and chelipeds of females (large gray circles), juveniles (small black circles), and males (white squares).

the male holds the young female until the moment of pubertal molt (such as *Callinectes danae*, (Shinozaki-Mendes & Lessa 2018), while *G. castelnaui* presents a gonopore open and copulation can occur without relation to the period of ecdysis (personal observation).

Alencar et al. (2014) reported for the species *Ucides cordatus* (Linnaeus, 1763) that the carapace shape of females shows a slight reduction of lateral points, and in males the posterolateral region of the carapace is more rounded, as could be observed for *G. castelnaui* in the present study. In agreement with Rufino et al. (2004), who commented on this shape being also present in males of *Liocarcinus depurator* (Linnaeus, 1758), the situation coincides with the area of fitting of pereopods and chelipeds. They can thus be related to a stronger muscle in this region, which can be used for agonistic behaviors.

The study on sexual and age dimorphism carried out by Silva et al. (2018) also demonstrated for *G. castelnaui* an increase in the posterior region of the carapace in adult females, suggesting that this characteristic may be associated with the accommodation of gonads within the cephalothorax, as proposed by Alencar et al. (2014) for *U. cordatus* females. According to Marochi et al. (2018), another factor that can cause allometric growth of the posterior margin of the carapace is pleon growth because, as it is a part of a surrounding structure of the carapace, it can thus be affected in females.

The analyses carried out in this study highlighted the pleon shape and size mainly of *G. castelnaui* females compared to that of males and juveniles. Females present a semicircular pleon that in adulthood becomes larger and covers the entire thoracic sternite. Silva et al. (2018) observed this when describing the development of these structures compared to young females. This is possibly because females have more space to accommodate eggs and juveniles. Although this characteristic is common to all *Brachyura*, on the one hand, freshwater crabs have larger eggs than marine crabs and have a direct (epimorphic) development (Pinheiro & Taddei 2005); on the other hand, in marine crabs, eggs hatch in a more primitive phase (zoea) and females have a high fertility rate. Thus, freshwater species have evolved towards a more prolonged development and a greater parental care for their offspring (Mansur & Hebling 2002, MClay & Becker 2015). The expansion of the pleon is essential for reproductive success.

The male and juvenile pleon are triangular and their apex comprise the telson that extends through the thoracic sternites, partially covering them. Apparently, the shape of the male pleon corresponds only to the protection of gonopods in the first abdominal somite (Hartnoll 1974). However, it was not possible to determine visually the sex of juveniles at the first crab stage by observing the pleon. According to Vieira et al. (2013), the sex of *D. pagei* is identified by the pleon from the second juvenile stage. Santos & Vieira (2017) suggested that this also happens with another freshwater species: *Dilocarcinus septemdentatus* (Herbst, 1783).

Males of *G. castelnaui* stand out for the more robust shape of the right chelipeds and for their size, corroborating what was found for the species *Hepatus pudibundus* (Herbst, 1785). This species shows that the chelipeds of males reach greater lengths and the centroid sizes are larger than those of females along the ontogenetic trajectory, as well as presenting the fixed finger and the widest propodus (Marochi et al. 2016). Still according to Marochi et al. (2016), the females of *H. pudibundus* not only presented larger dimensions in the posterior region of the carapace, but also a greater increase in the posterior part of the fixed finger of chelipeds,

which may be associated with parental care. The females of *G. castelnaui* showed elongation in the distal portion of the fixed finger, which can facilitate the handling of the offspring.

The juveniles of *G. castelnaui* differed from male and female chelipeds along the ontogenetic trajectory, not so much for their structural components, but for the more elongated shape, whereas in sexed individuals, the chelipeds tended to become more robust along the trajectory and equal as for shape. However, the males of *G. castelnaui* invest more in cheliped growth along the ontogeny compared to females, which invest more in the pleon. The growth of the carapace is similar, thus reflecting this intersexual difference, as Gherardi & Micheli (1985) also observed for the freshwater crab *Potamon potamios palestinians* (Bott, 1967). One can also relate the growth of organs with the extent to which they will interact for optimal functioning, in addition to minimizing the waste of resources. For example, the decrease in the growth of the female's pleon after the pubertal molt is also limited by sternum size (Hartnoll 1974). Male chelipeds are different. They continue to grow (Hartnoll 1974) as they can continue to be useful for defense, reproduction, search for food, and demarcation of territory, according to reports for *Uca leptodactyla* (Rathbun, 1898) (Masunari & Swiech-Ayoub 2003).

Although there are important works on dimorphism, already mentioned in the previous paragraphs, as well as works that compare juveniles and adults (e.g., Silva et al. 2018), the absence of ontogenetic comparisons that include first crab stages limit the perception of real amplitudes of growth variations, which notoriously also occur in the first ecdysis and not only in the pubertal molt, as has been reported for several *Brachyura* (e.g., Hartnoll 1978, Tsuchida & Fujikura 2000, Masunari & Dissenha 2005, Corgos et al. 2007).

Finally, we highlight that the present work has a low "n" sample due to the low abundance of the species in several rivers, accentuated by the degradation of the natural environment (personal observation). However, there was no impairment to the analyses since statistical differences are marked. With this publication, it is now possible to advance knowledge about the biology of this species, whose data corroborate the monophyletic theory of *Brachyura* (Scrham 1986).

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