

# Ontogenetic trajectories in *Callinectes danae* (Crustacea: Brachyura): sex and age polymorphism

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*We analysed the morphological variations through geometric morphometric approaches of the dorsal and ventral views of growing male and female Callinectes danae Smith 1869, based on the hypothesis that swimming crabs present polymorphism during growth. Our research identified six instars for females, seven instars for males and one instar for unsexed individuals (young). The sixth instar of females and the seventh instar of males were composed of adults. We identified 20 landmarks from the dorsal view, and 16 landmarks from the ventral view. Based on canonical analysis and Procrustes distance, we observed the formation of clearly separated instars (both views), indicating a significant change during ontogeny, not only in the pubertal moult. The most prevalent changes occurred in the abdomen, with males thinning and females broadening the abdomen during growth. In the dorsal view, we observed a displacement of anterolateral spines to the posterior region throughout the growth period and that the anterolateral and frontal teeth of juveniles were more ornate than those of adults. The ontogenetic trajectories for males and females have similar origins and follow different directions over the instars, with maximum distance after the pubertal moult ( $P < 0.05$ ).*

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## INTRODUCTION

The use of geometric morphometrics has been applied to solve problems not captured by classical morphometry. This change has occurred due to the importance of identifying the full shape, instead of pairs of linear measurements. Distance measures gave rise to geometrical methods (Rohlf & Marcus, 1993), where images are obtained in two or three dimensions, and after the removal of the effects of translation, scaling and rotation, it is possible to quantify the change within landmark coordinates (Rohlf & Marcus, 1993). In this context, Klingenberg (2016) defines allometry as a covariation of size with a distinction of size and shape, in which the main interest has usually been to separate size and shape per se, rather than to remove the allometric consequences of variation in size.

In general, there are three types of allometry: static allometry, that reflects individual variation within a population and age class; evolutionary allometry is the result of phylogenetic variation among taxa; and ontogenetic allometry is due to growth processes (Klingenberg, 2016). Ontogenetic allometry is based on the fact that specimens may closely resemble each other during early stages of morphogenesis, diverging thereafter or they may differ substantially early in development

then come to resemble each other later in development. When there are several modifications of ontogeny, we can quantify how much each modification would contribute to a disparity between juveniles and adults and then how changes interact with each other (Sheets & Zelditch, 2013). In this context, Adams & Nistri (2010) described that is possible to quantify phenotypic trajectories from many ecological and evolutionary processes, whose data encode multivariate characterizations of the phenotype, including: phenotypic plasticity, ecological selection, ontogeny and growth, local adaptation and biomechanics.

Crustaceans are a suitable group for the use of geometric morphometrics and ontogenetic trajectories because of their hard exoskeleton and the easy identification of homologous landmarks. These qualities are ideally exhibited among Portunids (crabs) due to their suitably flattened body, reducing the distortion of the depth (third dimension) of the images. In addition, the crustaceans show sudden changes in growth that indicate critical stages during ontogeny, for example, the pubertal moult (Hartnoll, 1969), drastically changing growth trajectory. However, the application of this technique in crustaceans has not yet been adequately explored (Rufino *et al.*, 2009).

The genus *Callinectes* is characterized by having an abdomen which is locked to its thoracic sternites until the pubertal moult when the individuals become adults (Van Engel, 1990), exposing the copulatory organ and making copulation possible. However, there are no reports of a

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change in the shape of the carapace of individuals, with only visual changes of the abdomen of adult females having been reported.

Among studies of decapod crustaceans involving geometric morphometrics, Rosenberg (1997) pioneered studying the shape differences between chelipeds of *Uca pugnax*. Thereafter, a few dozen studies have been developed, mainly of the *Aegla* genus (e.g. Barriá *et al.*, 2011; Hepp *et al.*, 2012; Marchiori *et al.*, 2015). Silva & Paula (2008) used the format of the chela as a means of comparison between Brachyura; Silva *et al.* (2010) observed population differentiation of *Carcinus maenas*; Buckup & Rossi (1977) and Duarte *et al.* (2014) used geometric morphometrics for differences in claw shape showing the effect of exposure to adult conspecific cues and early heterochely; Alencar *et al.* (2014) and Marochi *et al.* (2016) analysed the sexual dimorphism of the mangrove crab *Ucides cordatus* and the *Hepatus pudibundus*, respectively; and Fujiwara & Kawai (2016) studied the mechanical advantages of pinching and disarticulation of the chela. However, there is a lack of information in many genera and families, including changes during the growth.

The species *Callinectes danae* Smith, 1869 is distributed from Florida (USA) to Rio Grande do Sul state (Brazil) (Melo, 1996). It is the most abundant portunid in many regions, for example in Venezuela (Carmona-Suárez & Conde, 2002), northern Brazil (Nevis *et al.*, 2009) and South-east Brazil (Severino-Rodrigues *et al.*, 2001), being widely captured and marketed by the artisanal fishermen of these regions. So, due to the economic relevance, in addition to the unquestionable ecological importance, a clear understanding about ontogenetic development can support the sustainability of fishery activity through conservation actions.

The aim of the present study was to analyse the morphological variations and the ontogenetic trajectories through geometric morphometric approaches of the dorsal and ventral views of male and female *Callinectes danae* Smith, 1869 during growth, based on the hypothesis that the swimming crab presents polymorphism during growth, and not just at a specific age (juveniles and adults, due to the pubertal moult) and sex dimorphism (males and females).

## MATERIALS AND METHODS

Brachyurans were caught in the Santa Cruz Canal (08°43'00"S–08°49'00"S and 034°51'00"W–034°54'00"W) on the coast of the state of Pernambuco, Brazil. Samples were collected from March 2009 to March 2010, using beach seine and baited lines (for a full description, see Shinozaki-Mendes *et al.*, 2012a). Specimens of *Callinectes danae* (N = 175) were identified at the taxonomic level using the guidelines proposed by Williams (1974) and Melo (1996).

The sex and maturity were determined from the shape and adherence of the abdomen. Juveniles have an abdomen locked distally to the thoracic sternites, whereas in adults this abdomen becomes unlocked. The male's abdomen has an 'inverted T' shape, and the female abdomen has a triangular or semi-circular abdomen (Van Engel, 1990). The small specimens, whose sex could not be identified by the shape of the abdomen, were classified as unsexed (NI) first crabs with zero-age.

Our research utilized the age groups (instars) proposed by Shinozaki-Mendes *et al.* (2012b) for males (seven instars) and

females (six instars) (Table 1). These values were obtained using the Bhattacharya method (Gayanilo *et al.*, 2005) and were validated by performing experimental cultivation, as cited in this paper. The classification of specimens with intermediate sizes between instars becomes inaccurate since the authors only provided mean values and standard deviations (Table 1). Additionally, variations in the size at which moults occur for each individual can result in misclassification. For this reason, we selected 10 to 15 specimens with a CW close to the average of each instar of males, females and unsexed individuals, totalling 175 specimens, to place the landmarks.

Images (telephoto lens; 2816 × 2112 pixels) from the dorsal and ventral view of each individual were obtained using a digital camera with a tripod parallel to the lens plane. Although the information about geometric morphometrics of *C. danae* is unexplored, the landmarks were chosen to allow a comparison with classical morphometry. Twenty landmarks were determined from the dorsal view, while 16 landmarks were determined from the ventral view (Figure 1).

Once the animals attain bilateral symmetry, only the landmarks on the left portion must be selected to avoid symmetry issues (Rufino *et al.*, 2009; Klingenberg, 2015). The landmarks were digitized using the program TPSDig, authored by Rohlf (2006), and the Procrustes superimposition (Kendall, 1984) was performed for translating, rotating and scaling the images.

A covariance matrix containing factors related to sex and the age groups (instars) was created. We applied a principal component analysis (PCA) in order to identify the variation within a sample and to characterize the main features of shape variation. The Canonical Variate Analysis (CVA), with 999 permutations, was used to find the shape features that best distinguish among instars, which were determined a priori. Discriminant function analysis (DFA) allowed us to analyse the degree of separation of the groups and Hotelling's  $T^2$  test was performed with 999 permutations. The thin-plate spline functions were applied for juveniles and adults, as well as for males, females and unsexed individuals. For these steps, we used the program MorphoJ (Klingenberg, 2008).

To test the hypothesis that male and female differ in their allometric trajectories, adapted from Sheets & Zelditch (2013), we performed a resampling MANCOVA of shape on centroid size and group (CV1) followed by an angle pairwise test.

**Table 1.** Mean value of cephalothorax widths (CW) ± standard deviation (SD) for each supposed age group (instar) of females and males (proposed by Shinozaki-Mendes *et al.*, 2012b) for unsexed juveniles (NI) of *Callinectes danae*.

Instar	Females CW ± SD	Males CW ± SD
0 NI	1.27 ± 0.15	
1st	2.99 ± 0.33	2.10 ± 0.24
2nd	4.02 ± 0.29	3.23 ± 0.27
3th	5.07 ± 0.39	4.57 ± 0.32
4th	6.05 ± 0.54	6.37 ± 0.32
5th	7.05 ± 0.14	8.43 ± 0.25
6th	8.05 ± 0.43	10.35 ± 0.38
7th	–	11.05 ± 0.26

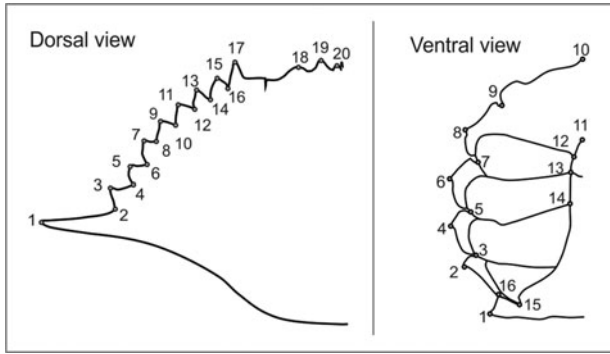


Fig. 1. Location of the landmarks used in the geometric morphometrics of the dorsal and ventral views of *Callinectes danae*.

RESULTS

We analysed 14 unsexed specimens (NI), 80 females and 80 males with cephalothorax widths (CW) ranging from 0.99 to 1.19 cm, from 2.86 to 9.71 cm and from 2.17 to 12.45 cm, respectively.

The first component of the principal component analysis (PCA1) represented 67.28% of the variance in the ventral view and 61.39% of the variance in the dorsal view. The second component (PCA2) represented 10.15% and 7.87% from ventral and dorsal views, respectively.

In the dorsal view, PCA1 was mainly composed by lateral spine variation (landmark 1), some anterolateral teeth (landmarks 11–17) and frontal teeth (landmarks 19 and 20) and PCA2 by lateral spine and all anterolateral teeth (landmarks 3–17) (Figure 2). In the ventral view PCA1 was mainly composed by landmark 14, located laterally to the abdomen, and PCA2 by the anterior extremity of thoracic sternites (landmark 10) (Figure 2).

The first canonical variable affected the separation of instars in the dorsal view, in which male instar 7 loads at a lower axis value, followed by other instars in sequence of increasing values until instar 1, which is positioned at the opposite end of the axis (Figure 3A). This same distribution was observed for females, but at higher values of the axis. The unsexed instar was different from the others, totally separated at the highest axis values. The influence of the second canonical variable on distribution points was more

subtle with a lower range of values and less evident group separation.

When analysing the changes that occurred in the dorsal view between two consecutive moults we observed that the females did not differ significantly between ♀<sub>4</sub> and ♀<sub>5</sub> and that the males did not differ significantly between ♂<sub>1</sub> and ♂<sub>3</sub> (Table 2). There was a statistically significant change in shape during other moults. Visually, progressive displacement of anterolateral spines to the posterior region is noticeable when consecutive moults were analysed (Figure 4). We also observe that the teeth at landmarks 11, 13, 15 and 17 presented a progressive displacement to the anterior region while the teeth at landmarks 3, 5 and 7 displaced to the posterior region.

When observing the total variation during ontogeny (Figure 5) we noted that the anterolateral and frontal teeth of juveniles were more ornate than those of adults. Additionally, males had larger dorsal regions as compared with females (Figure 5).

Differentiation was more evident for the canonical variables in the ventral view (Figure 3A) than in dorsal view. The females exhibited a wide variation in the function of the first variable. Adult females (instar 6) loaded at lower axis values, at the opposite end from all other instars. The males were more influenced by the second variable, with adult males (instar 7) loading at lower axis values and instar 1 loading at the opposite end, close to the unsexed instar (Figure 3A).

When visually analysing the changes that occurred at each moult (Figure 4), change is noticeable for both sexes (NI-♀<sub>1</sub> and NI-♂<sub>1</sub>) only at the first moult, and additionally for females at the pubertal moult (♀<sub>6</sub>-♀<sub>7</sub>). Females did not show statistical variations in ventral view between ♀<sub>1</sub> and ♀<sub>2</sub> and between ♀<sub>4</sub> and ♀<sub>5</sub>, while males only showed statistical differentiation in the pubertal moult (♂<sub>6</sub>-♂<sub>7</sub>) (Table 2). When comparing males and females, there was a significant difference in the initial (♀<sub>1</sub> vs ♂<sub>1</sub>) and final (♀<sub>6</sub> vs ♂<sub>7</sub>) stages (Table 2 and Figure 5).

During ontogeny, the females showed a wide variation in landmark 14 of the ventral view and a noticeable change in the remaining landmarks. Males showed more subtle variation that was more noticeable in landmarks 1, 10 and 15 (Figure 5). Males had narrower abdomens as compared with females (landmark 14) and sternites larger than those found for females (landmarks 2–6) (Figure 5).

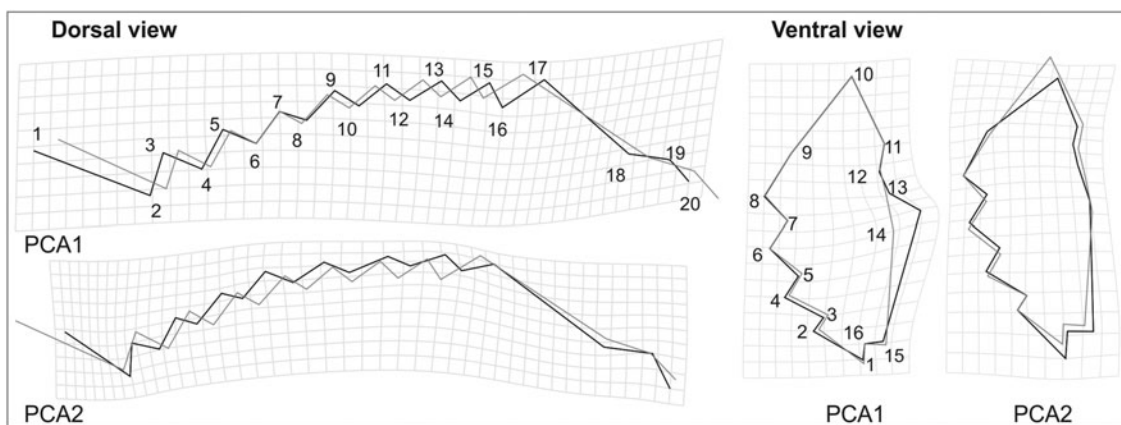
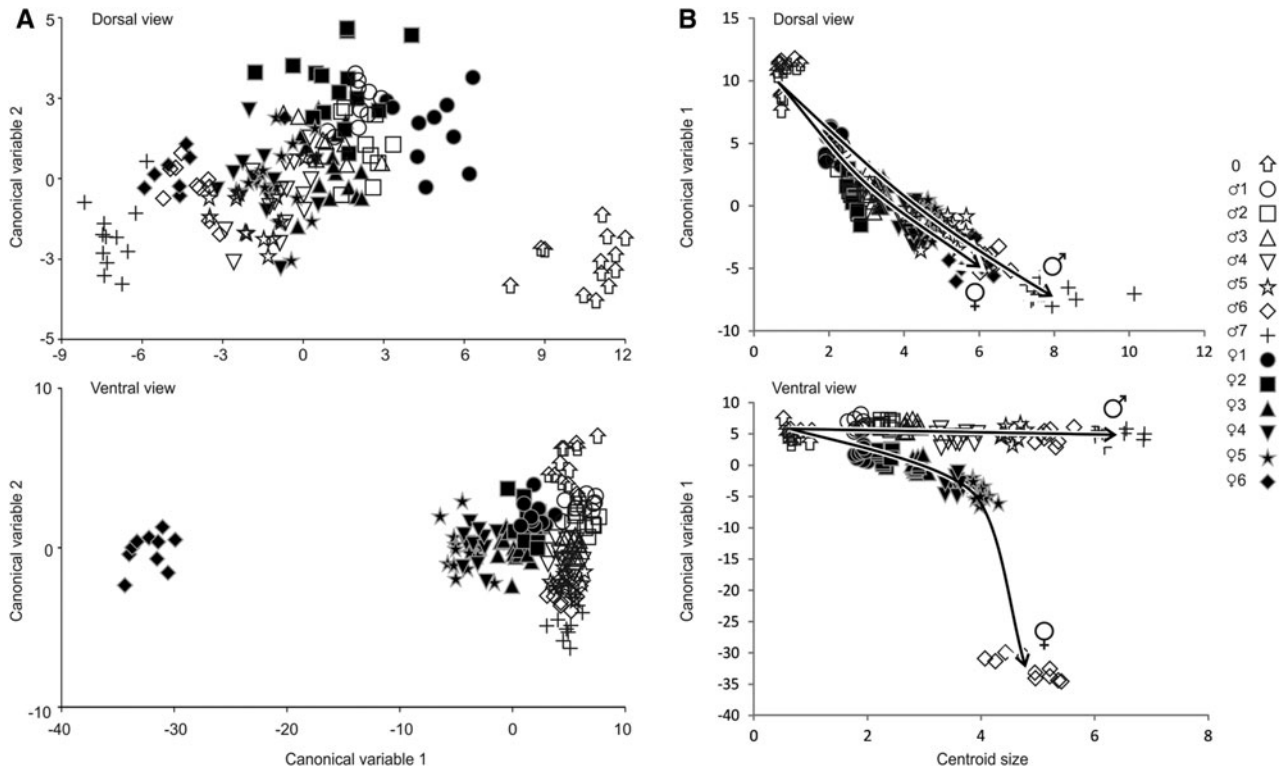


Fig. 2. Flexion of thin plates in the dorsal and ventral views associated with values of the first (PCA1) and second (PCA2) components from the principal component analysis of *Callinectes danae*.



**Fig. 3.** Canonical analysis (A) and ontogenetic trajectories (B) based on geometric morphometrics of the dorsal and ventral views for males ( $\sigma$ , seven instars), females ( $\varphi$ , six instars) and unsexed juveniles (NI, one instar) of *Callinectes danae*.

The correct allocation of most individuals into their group (instar) of origin (Table 2) is a good indication of the conspicuous changes that occur during ontogeny in dorsal and in ventral view.

The ontogenetic trajectory from CV1 vs centroid size (Figure 3B) showed different directions in dorsal view ( $P$ -value from pooled regression = 0.0217) and ventral view ( $P = 0.0101$ ). By analysing the pairwise in ventral view, males presented statistical equality ( $P > 0.05$ ) in CV1 while females showed a statistical difference, most evident in the 6th instar

( $P = 0.0127$ ). In the dorsal view, the variation of both sexes was less abrupt (Figure 4) with no statistical difference in values ( $P > 0.05$ ).

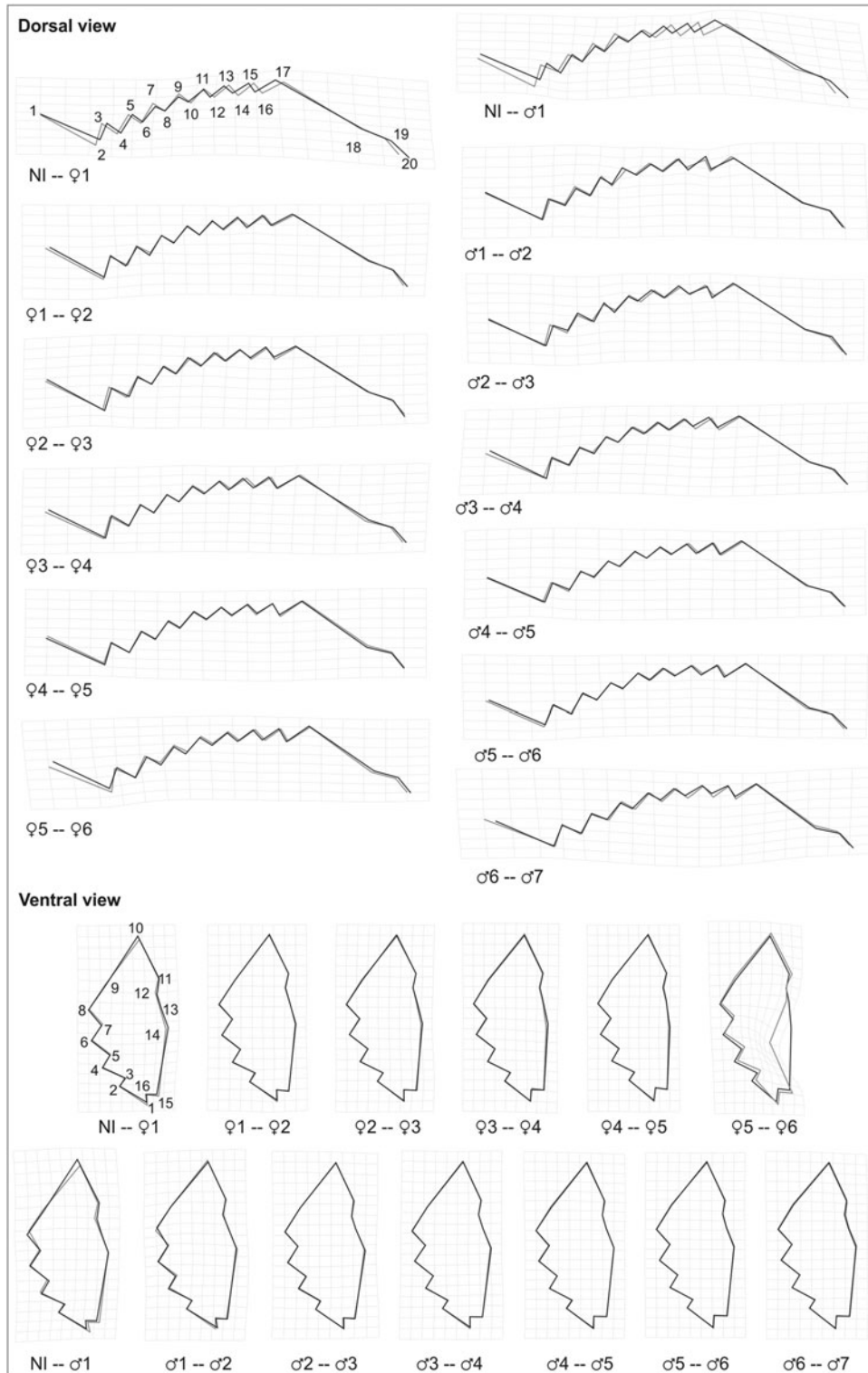
## DISCUSSION

The measures of the mean size, standard deviation of size and variance of shape used in geometric morphometrics studies have been found to be fairly accurate, even in relatively

**Table 2.** Pairwise iteration of the geometric morphometric of the dorsal and ventral view of the unsexed individuals, males (seven stages) and females (six stages) of *Callinectes danae*.

Pair	$P$	Dorsal			$P$	Ventral		
		$P$ -value*	%A**	%C**		$P$ -value*	%A**	%C**
NI- $\varphi_1$	0.0539	<0.0001	100	87.50	0.0345	0.0010	100	50
$\varphi_1$ - $\varphi_2$	0.0214	0.0250	100	96.00	0.0102	0.4960 <sup>ns</sup>	100	60
$\varphi_2$ - $\varphi_3$	0.0206	0.0050	100	55.17	0.0131	0.0090	100	68.97
$\varphi_3$ - $\varphi_4$	0.0228	<0.0001	100	73.33	0.0213	<0.0001	100	55.17
$\varphi_4$ - $\varphi_5$	0.0126	0.0850 <sup>ns</sup>	100	65.52	0.0104	0.2070 <sup>ns</sup>	100	53.33
$\varphi_5$ - $\varphi_6$	0.0281	<0.0001	100	78.26	0.1332	<0.0001	100	100
NI- $\sigma_1$	0.0741	0.0010	100	100	0.0487	0.1520 <sup>ns</sup>	100	80
$\sigma_1$ - $\sigma_2$	0.0227	0.9780 <sup>ns</sup>	66.67	33.33	0.0257	0.7100 <sup>ns</sup>	60	40
$\sigma_2$ - $\sigma_3$	0.025	0.2760 <sup>ns</sup>	100	81.82	0.0149	0.6930 <sup>ns</sup>	69.23	23.08
$\sigma_3$ - $\sigma_4$	0.0253	<0.0001	100	58.33	0.0110	0.1520 <sup>ns</sup>	100	56
$\sigma_4$ - $\sigma_5$	0.0155	0.0070	92.59	62.96	0.0099	0.1810 <sup>ns</sup>	100	70.37
$\sigma_5$ - $\sigma_6$	0.0174	0.0010	95.45	68.18	0.0100	0.2170 <sup>ns</sup>	95.45	50
$\sigma_6$ - $\sigma_7$	0.0368	<0.0001	100	90.91	0.0149	0.0020	100	63.64
$\varphi_1$ - $\sigma_1$	0.0368	0.0110	80	66.67	0.0313	0.0080	100	84.62
$\varphi_6$ - $\sigma_7$	0.0368	<0.0001	100	100	0.1777	<0.0001	100	100

$P$ : Procrustes distance; \*:  $P$ -value of  $P$  for 999 iterations; <sup>ns</sup>: not statistically significant ( $P > 0.05$ ); \*\*: % of individuals allocated to the correct group (instar) in discriminant analysis (%A) and on cross-validation (%C).



**Fig. 4.** Flexion of thin plates of the dorsal and ventral view associated with values of the discriminant function for males (♂, seven instars), females (♀, six instars) and unsexed juveniles (NI, one instar) of *Callinectes danae*. The thin plate from the initial form is indicated in black and the final form is indicated in grey below the illustration.

small samples (Cardini & Elton, 2007). However, Cardini & Elton (2007) also noted that the mean shapes and angles between static allometric trajectories are strongly affected by sampling error. Thus, it is important to note that the results found here may show a bias due to the sample for each instar being kept close to each instar's mean value (available

in Table 1) which was done to ensure the correct selection by avoiding the sizes that occur at the superimposition of classes, as described by Sparre & Venema (1997).

In the classical morphometry of portunids, the measures used in the dorsal view are the linear distance between landmarks 1, 2 and 20 and their opposite sides, which is called

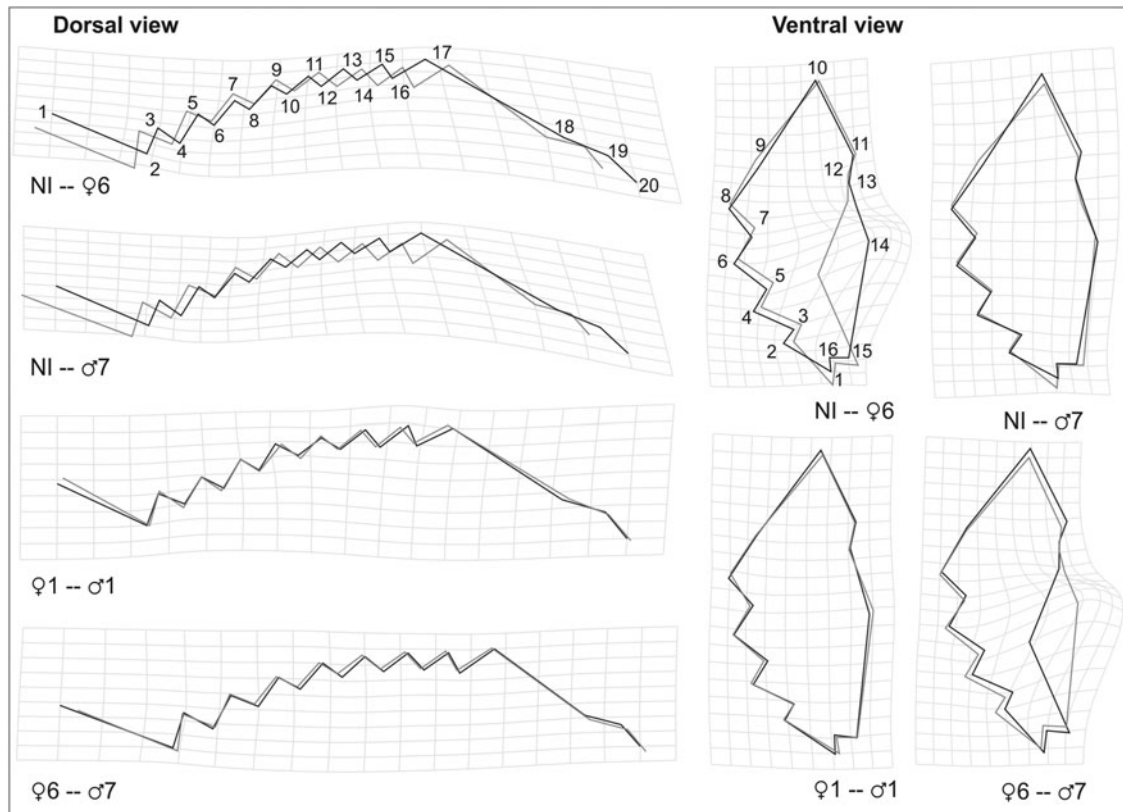


Fig. 5. Flexion of thin plates of the dorsal and ventral view associated with extreme values of the discriminant function for males ( $\sigma^7$ ), females ( $\text{♀}$ ) and unsexed juveniles (NI) of *Callinectes danae*. The thin plate from the initial form is indicated in black and the final form is indicated in grey below the illustration.

cephalothorax/carapace width (CW); CW without lateral spines; and cephalothorax/carapace length. In the ventral view, the distance between landmarks 14 and 15 and their opposite sides are called the width of the 5th and 4th abdominal segment, respectively (e.g. Pinheiro & Fransozo, 1993).

The largest variation found in the thin plates of the ventral view of the 14th landmark is an indication that this region of the body is involved in reproductive activity and is a characteristic of sexual and age polymorphism. In other words, the female abdomen becomes larger in order to accommodate the incubation of eggs (Hartnoll, 1969). This variation is also evident in other Brachyuran species, such as *Ucides cordatus* (Alencar *et al.*, 2014), *Liocarcinus depurator* (Rufino *et al.*, 2009) and some species from the *Aegla* genus (Giri & Loy, 2008; Barría *et al.*, 2011).

The adults showed the greatest change in the ventral view, as opposed to the dorsal view. A similar result was found for *Liocarcinus depurator* (Linnaeus, 1758), in which males had a larger carapace with more conspicuous spines. Following Rufino *et al.* (2009), this peculiarity can be associated with defence against predators and to protect females.

Although there have been several studies regarding the relative growth of *C. danae* (e.g. the relationship between weight and size (Branco & Thives, 1991; Baptista-Metri *et al.*, 2005) or the growth function (Branco & Masunari, 1992), studies of the geometric relationship are lacking.

Among the studies using linear morphometrics of *C. danae*, Fúria *et al.* (2008) in North-eastern Brazil examined the relationship between the width and length of the cephalothorax for individuals from 4.3 to 12.5 cm for the different sexes. For the same population studied here, Shinozaki-Mendes *et al.*

(2012b) separated males from females and juveniles from adults showing relationships between cephalothorax width and both abdomen width and chela length. While all of these relationships were significantly different, the classification 'juvenile' included the female stages 1–5 and the male stages 1–6 as defined here.

As can be observed from the studies mentioned above, without geometric morphometrics, only the separation between the sexes or based on pubertal changes were examined. However, the present study shows that the changes are progressive at each moult, and it is crucial to understand these changes for better knowledge of the dynamics and growth of the species.

The variation in the geometry of the dorsal view during the moult cycle was evident for both sexes. The variation in the position of the anterolateral teeth during ontogeny can be directly attributed to the hydrodynamics of the specimens, since *C. danae* is a swimming crab and swimming is an important resource for escaping predators. One hypothesis for this change would be due to the natural abrasion of the extremity, which eventually has a rounding effect due to friction with the substrate. This feature was also noted by Giri & Collins (2004), who compared two sympatric species of Aegliidae. However, as these are two different species, this does not constitute an intraspecific character. These authors noted that the variation in spines can be associated with an evolutionary response.

The similarity between male and female juveniles can be explained by the ontogeny of Brachyura, where juveniles at the first stage after assessment are very similar, including in their abdomen sizes (Johnson, 1980). The most evident variation that is generally not noticed in research with linear

morphometry, but was identified in the present work, is the size at which sex differentiation occurs, i.e. individuals in the first stage are not yet identifiable by abdomen shape, differentiating after a single moult.

Ontogenetic changes have already been evidenced for some species, and may be considered a standard for Brachyura, such as pubertal moult (Hartnoll, 1982). However, these changes occur progressively at each instar, highlighting the age polymorphism for both sexes, culminating in pubertal moult. In this context, Hartnoll & Bryant (2001) cite that the modifications that occur in each moult vary according to the amount of energy expended for other purposes during life cycle.

This is the first contribution to use geometric morphometrics and ontogenetic trajectories to differentiate the moult stages in crustaceans. Based on the results found here, it is evident that the ontogenetic trajectories for males and females have similar origins and follow different directions over the instars, with maximum modification at first moult in which differentiation of the abdomen begins as well as at the pubertal moult in which secondary sexual characters become evident.

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