SOCIEDADE BRASILEIRA DE CARCINOLOGIA 30

Sexual dimorphism in *Aegla marginata* (Decapoda: Anomura)

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Abstract

A study on sexual dimorphism in *Aegla marginata* was conducted using geometric morphometric methods. The carapace of 47 females and 75 males and the left and right cheliped propodus of 29 females and 40 males were analyzed. Eighteen landmarks were established in the carapace and 10 in the cheliped propodus. A Generalized Procrustes Analysis based on landmark configurations was used to separate the components of size and shape. A Student t-test was used to determine whether statistically significant sexual dimorphism was shown by the carapace and the cheliped propodus. The variation in the shape of the structures was evaluated with a discriminant analysis. Our results show that there is no sexual dimorphism in the carapace of *A. marginata*. However, the size of the propodus differed statistically between the sexes. The carapace shape differed between the sexes: the females showed a wider posterior area and a narrower anterior area than the males. The shape of the cheliped propodus also differed between the sexes: overall, the females had a longer and narrower cheliped propodus than the males. The variations in the carapace shape found in this study confirm the results of other studies on aeglid morphology; however, the information presented by this study regarding variation in the shape of the cheliped propodus is new to the literature. The geometric morphometric approach applied in this study provided useful tools for achieving the proposed objectives.

Keywords: Aeglidae, carapace, cheliped, geometric morphometrics, sexual size dimorphism, sexual shape dimorphism.

Introduction

Sexual dimorphism is widely known in the animal kingdom (Shine, 1989). Many studies have attempted to use a conventional metric analysis with linear measurements to demonstrate or to provide hypotheses about the adaptive significance of morphological differences between sexes (Gould, 1974; Slatkin, 1984; Hedrick and Temeles, 1989; Katsikaros and Shine, 1997; Abraham, 1998; Green, 2000; Walker and Fell, 2001). Currently, techniques based on geometric morphometric allow the use of landmarks or contours to generate multiple variables that can be used to test the variation in body shape shown by different groups, such as species, populations or sexes (Rohlf and Marcus, 1993; Adam *et al.*, 2004; Hepp *et al.*, 2012).

These techniques have been used in different animal groups, including mammals (Klingenberg and Leamy, 2001; Cordeiro-Estrela *et al.*, 2006; Fornel *et al.*, 2010; Gonzalez *et al.*, 2011), reptiles (Claude *et al.*, 2004), amphibians (Adams and Rohlf, 2000), fishes (Clabaut *et al.*, 2007), insects (Monteiro *et al.*, 2002), mollusks (Rufino *et al.*, 2006a), and crustaceans (Rosenberg, 1997; Rufino *et al.*, 2006b; Silva and Paula, 2008). Because decapod crustaceans have a hard exoskeleton with many spines and sutures, they are considered to represent an interesting group for evaluating the shape of the body with geometric morphometric techniques (Rosenberg, 1997; Clark *et al.*, 2001). In aeglids, this technique was used to study interspecific variation, ontogenetic variation and sexual dimorphism (Giri and Collins, 2004; Collins *et al.*, 2008; Giri and Loy, 2008; Barría *et al.*, 2011; Hepp *et al.*, 2012).

The family Aeglidae Dana, 1852 is currently composed of 72 species (Santos *et al.*, 2012). These species occur in southern South America between São Paulo and Minas Gerais states (in Brazil), to the Duque de York Islands (Chile) (Oyanedel *et al.*, 2011).

Aegla marginata Bond-Buckup and Buckup, 1994 occurs in Brazil from southern São Paulo State to northwestern Santa Catarina State, including the eastern portion of Paraná State (Bond-Buckup and Buckup, 1994). Despite its relatively wide distribution, little information about the species is currently found in the literature. The available information is related to differences in pigmentation (Morachioli, 1994), the occurrence of populations in both epigean and subterranean environments in Parque Estadual Intervales (PEI), Iporanga city, southeastern Brazil (Rocha and Bueno, 2004) and the external abnormalities found in a cave population (Fernandes *et al.*, 2010).

The objective of this study was to analyze the sexual dimorphism in the size and shape of the carapace and the chelipeds through geometric morphometric techniques in a population of *A. marginata* from the Taquaral River in eastern Paraná State, Brazil, to determine whether statistically significant sexual dimorphism occurs. In addition to the carapace, which suitable structures for defining anatomical landmarks, the chelipeds were selected for this study because they represent a secondary sexual character in several groups of crustaceans (Hartnoll, 1978 and 1982; Flores *et al.*, 2002; Castiglioni and Negreiros-Fransozo, 2004; Castiglioni and Coelho, 2011).

Material and Methods

Samplings

Aegla marginata were sampled from the Taquaral River, located in the Coastal Basin of Paraná State (Maack, 1968; Bigarella, 1978) within the limits of Marumbi State Park (25°26'24"S - 48°55'12"W), in Morretes municipality. The animals were fixed in 4% formalin and preserved in 75% ethanol.

Morphometric data were obtained from the carapace of 122 adults (47 females and 75 males) and from the major and minor cheliped propodus of 69 adults (29 females and 40 males).

Geometric morphometrics

Images of the carapaces and cheliped propodus in dorsal view were obtained with a Dino-Lite Pro AM413 digital microscope (AnMo Electronics Corporation, Hsinchu, Taiwan; www.dino-lite.com) with 1.3 mega pixels resolution. Eighteen two-dimensional landmarks were established for the images of the carapace and 10 for the images of the cheliped propodus (Fig. 1).

Landmarks were digitized twice by the same researcher on different days with TPS Dig2 software, version 2.16 (Rohlf, 2010; available in: http://life.bio.sunysb.edu/morph). A Generalized Procrustes Analysis (GPA) was performed for each body part

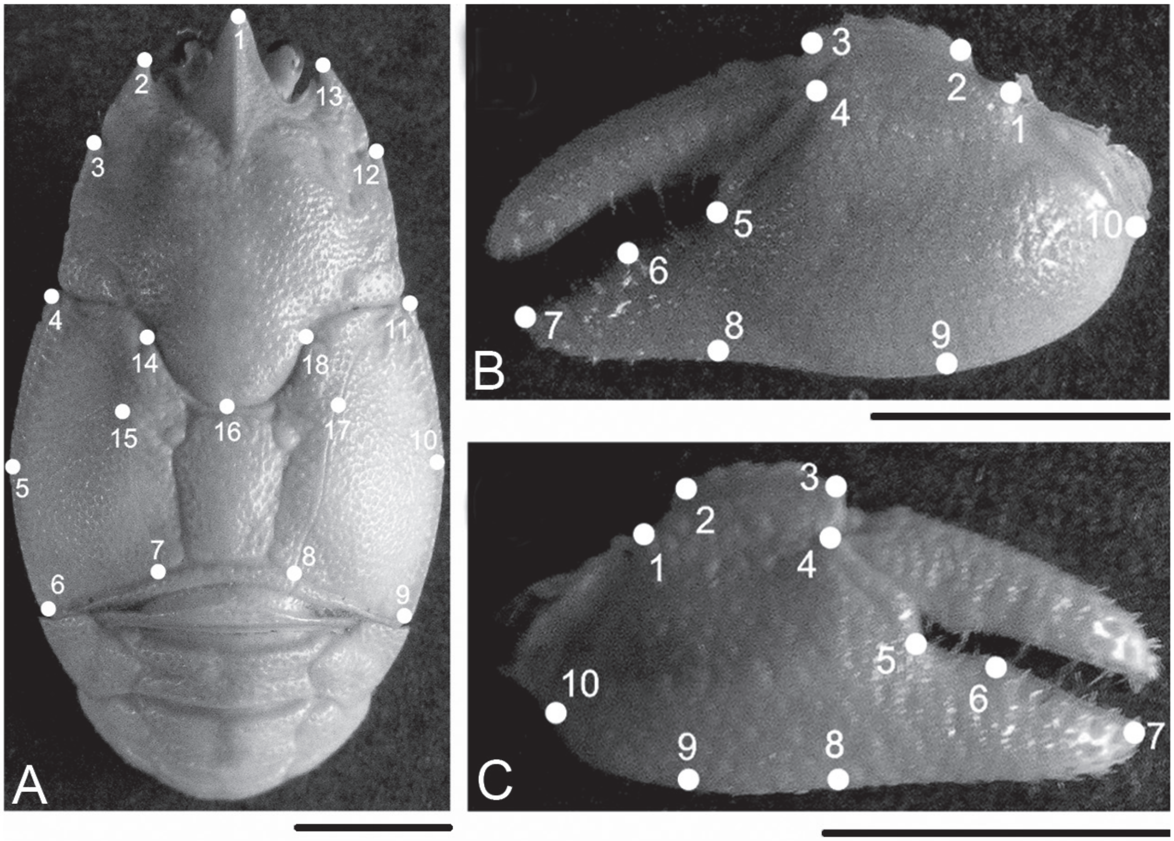

Figure 1. *Aegla marginata*. (A) Position of the morphological landmarks on the carapace; (B) left cheliped propodus; (C)right cheliped propodus. Scale: 5mm. (A) 1: Tip of the rostrum; 2 and 13: Tip of antero-lateral spines; 3 and 12: Intersection between the first and second hepatic lobe; 4 and 11: Intersection between the third hepatic lobe and epibranchial tooth; 5 and 10: Intersection between posterior branchial line and posterior "linea aeglica lateralis"; 6 and 9: Posterior vertex of carapace; 7 and 8: Posterior extreme of the longitudinal dorsal line; 14 and 18: Cervical groove;15 and 17: Anterior extreme of the intersection between branchial line and "linea aeglica dorsalis"; 16: Center-anterior vertex of aureole; (B and C) 1: Inner base of the articulation carpo-propodus; 2: Proximal tip of the cheliped "crista palmar"; 3: Distal tip of the cheliped "crista palmar"; 4: Suture in the intersection between "pré-dactilar" lobe and the base of cheliped "crista palmar"; 5: Base of the fixed finger of the cheliped; 6: Lobular tooth; 7: Tip of the fixed finger of the cheliped; 8: Vertical line through the base of the fixed finger; 9: Vertical line through the proximal base proximal of cheliped "crista palmar"; 10: Outer base of the articulation carpo-propodus.

(carapace, right and left cheliped propodus) to separate the size and shape components of the landmark configuration. GPA is applied by representing landmark configurations by a centroid (the center of mass of a configuration), by calculating the size of the centroid of each configuration for the value one, and by then rotating the landmark configurations to obtain a least squares fit to the corresponding anatomical landmarks (Adams *et al.*, 2004).

The carapace is symmetrical, but its shape can be partitioned into symmetric and asymmetric components (Klingenberg *et al.*, 2002). To analyze sexual dimorphism, only symmetrical components of the carapace shape were used in this study. The size of each body part was estimated as the size of the centroid, defined as the square root of the sum of the squared distances of the constituent points from the centroid of the selected group, in units of millimeters (mm).

Data analysis

A Student t-test was used to determine whether statistically significant sexual dimorphism was shown by the carapace and cheliped propodus. The analyses were performed with R software (R Development Core Team, 2011; available in: www.R-project.org).

To evaluate the occurrence of sexual dimorphism in shape, a principal component analysis (PCA) was performed on the variance-covariance matrix of the residuals from the GPA. The principal component scores were used as new variables to characterize the shape. This approach allowed the scores to be used as independent variables and served to reduce the dimensionality of the data (Klingenberg and Monteiro, 2005; Fornel *et al.*, 2010). Differences in shape between the sexes were tested with a discriminant analysis (DA) in conjunction with a permutation test. This analysis computed the classification percentages and performed a cross-validation between the groups (Viscosi and Cardini, 2011). The analyses were performed with the MorphoJ program (Klingenberg, 2011; available in: http://www.flywings.org.uk)

Results

Sexual size dimorphism in carapace and cheliped propodus

The carapace size did not differ significantly between male and female *A. marginata* (t = -1.84, $P = 0.068$, mean ± SD: females = 26.6 ± 4.1 mm, males = 27.9 ± 3.8 mm). However, the size of the left cheliped propodus (t = -2.96, $P < 0.01$) and the right cheliped propodus (t = -4.62, $P < 0.01$) differed significantly between the sexes. The cheliped propodus on both sides was larger in the males than in the females (left cheliped propodus: females = 11.6 ± 2.1 mm, males = 13.3 ± 2.4 mm; right cheliped propodus: females = 10.7 ± 2.0 mm, males = 13.5 ± 2.9 mm).

Sexual dimorphism in the shape of the carapace and cheliped propodus

The shape of the carapace differed significantly between the males and the females (Procrustes distance = 0.020, $P < 0.001$; Mahalanobis distance = 3.71, $P < 0.001$), with a percentage of correct classification of 90.2%. The *Sexual shape dimorphism* of the carapace was related primarily to the variation in landmarks 6 and 7 and in the corresponding homologous landmarks (8 and 9) at the posterior margin of the carapace (Fig. 2). The females showed a wider posterior margin than the males. In contrast, the anterior area in the females was slightly narrower than that in the males due to the small difference in the anterior contour related to the variation in landmarks 2, 3, and 4 and their homologous landmarks (13, 12, and 11). The tip of the rostrum was slightly longer (landmark 1) and the carapace was slightly shorter (landmark 16) in the females than in the males (Fig. 2).

The shape of the cheliped propodus also differed between the sexes on the left side (Procrustes distance = 0.030, $P < 0.001$; Mahalanobis distance = 3.26, $P < 0.001$) and on the right side (Procrustes distance = 0.039; $P < 0.001$; Mahalanobis distance = 3.92, $P < 0.001$). The left cheliped propodus showed a percentage of correct classification of 87.0%.

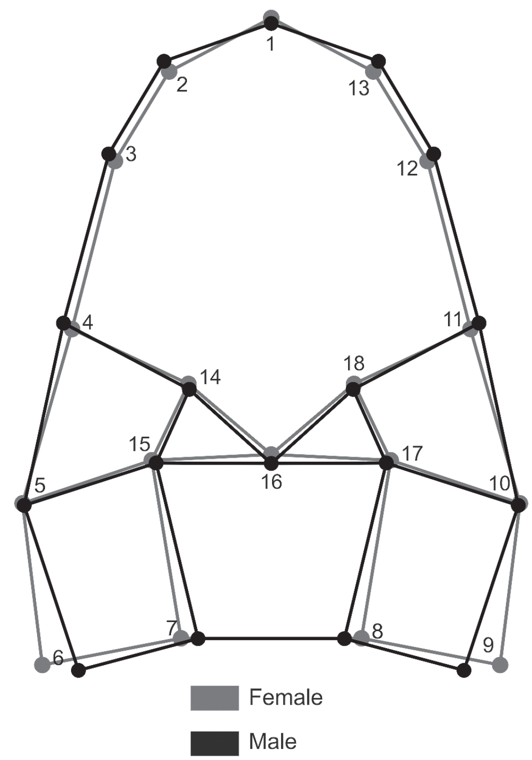

Figure 2. *Aegla marginata*. Sexual dimorphism in the shape of carapace. Deformations magnified 3 times.

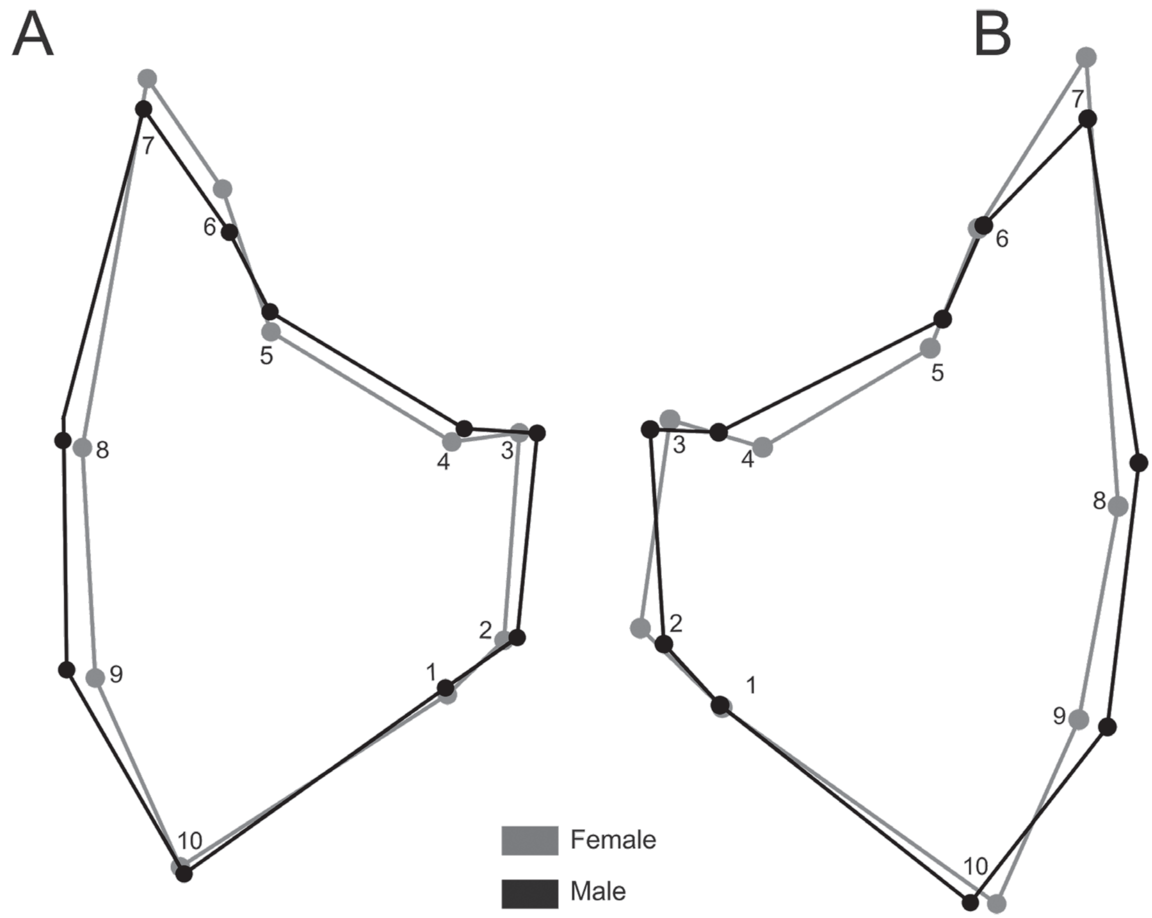

Figure 3. *Aegla marginata*. Sexual dimorphism in the shape of left (A) and right (B) propodus. Deformations magnified 3 times.

This result showed that the sexes could be accurately distinguished based on the shape of the cheliped. The margin of insertion of the mobile finger (between landmarks 4 and 5) was more concave in the females than in the males. The fixed finger was narrower and longer in the females than in the males (Fig. 3A). The same patterns of variation were observed for the right cheliped propodus (percentage of correct classification, 87.0%), except for the margin of articulation with the carpus (between landmarks 1 and 10), which was wider in the females than in the males (Fig. 3B). Overall, the shape of the cheliped propodus was longer and narrower in the females than in the males.

Discussion

In this study, we found no sexual dimorphism in the size of the carapace of *A. marginata*, although the carapace shape differed between the males and the females. However, both the size and the shape of the right and left cheliped propodus differed between the sexes. We consider that the dimorphism of carapace shape and the size and shape of the cheliped are related to the separate reproductive roles of the sexes.

The size difference between the larger males and the smaller females is the most common feature of aeglid populations from southeastern and southern Brazil: *Aegla laevis laevis* Latreille, 1818 (Bahamonde and López, 1961), *Aegla paulensis* Schmitt, 1942 (López, 1965; Cohen *et al.*, 2011), *Aegla perobae* Hebling and Rodrigues, 1977 (Rodrigues and Hebling, 1978), *Aegla castro* Schmitti, 1942 from Paraná State (Swiech-Ayoub and Masunari, 2001) and from São Paulo State (Fransozo *et al.*, 2003), *Aegla leptodactyla*

Buckup and Rossi, 1977 (Noro and Buckup, 2003), *Aegla longirostri* Bond-Buckup and Buckup, 1994 (Colpo *et al.*, 2005), *Aegla franciscana* Buckup and Rossi, 1977 (Gonçalves *et al.*, 2005), *Aegla schmitti* Hobbs III, 1979 (Teodósio and Masunari, 2009) and *Aegla manuinflata* Bond-Buckup and Santos, 2009 (Trevisan and Santos, 2011). The sole exception to this pattern is *Aegla platensis* Schmitti, 1942 from Rio Grande do Sul State (Bueno *et al.*, 2000).

The absence of a statistical difference in carapace size between the sexes in *A. marginata* can be explained in terms of several factors, including differential migration and/or mortality between the sexes and geographical isolation. These factors may act in conjunction with natural and sexual selection to produce the observed size similarity between the sexes (Giesel, 1972; Montague, 1980; Fairbairn and Preziosi, 1994; Fairbairn and Preziosi, 1996). Nutritional status, food availability and genetic factors may also cause this similarity (Tzeng, 2004; Anastasiadou *et al.*, 2009).

It is possible that the variation in carapace shape between the sexes of *A. marginata* occurred as a consequence of relative growth in their body proportions. This growth process is completed in adulthood (Hartnoll, 1974; 1978). The enlarged posterior carapace in females corresponds to the enlargement of the incubatory space and serves to accommodate a large egg mass. This assumption is based on previous studies of relative growth and size at the onset of morphometric maturity in aeglids. These studies include morphological analyses and analyses involving the geometric morphometric of the carapace (Giri and Collins, 2004; Colpo *et al.*, 2005; Viau *et al.*, 2006; Collins *et al.*, 2008; Giri and Loy, 2008; Oliveira and Santos, 2011; Hepp *et al.*, 2012; Trevisan and Santos, 2012). The enlargement of the posterior carapace is a sexually related process that occurs specifically among aeglids. As a result of this process, the abdomen is bent at its midpoint (i.e., the anterior half of the abdomen remains on the dorsal side).

Sexual dimorphism in the width of the abdomen is not found in other groups of Anomura (e.g., hermit crabs). In studies that discuss issues related to relative growth in Anomura, changes in the rates of allometric growth of the cheliped are the most frequently used markers of the average size at the onset of morphological sexual maturity (Mantelatto and Martinelli, 2001). However, the average length of the abdomen is greater in the females than in the males is some members as the porcelain crab *Petrolisthes armatus* Gibbes, 1850, in which positive allometric growth of this structure occurs between the juvenile and adult stages (Miranda and Mantelatto, 2010), as in several species of Aeglidae.

The chelipeds are modified pereiopods. They have attracted considerable attention from carcinologists, not only because of their peculiar morphology but also because of their importance in feeding, sexual behavior, and agonistic activities (Hartnoll, 1982; Mariappan *et al.*, 2000). The chelipeds, like the female abdomen, exhibit allometric growth in several crustacean groups. The allometric growth of the chelipeds is generally positive in males and is highly variable in females, with cases of positive allometry, negative allometry and isometry (for a complete review, see Finney and Abel, 1981; Muino *et al.*, 1990; Garvey and Stein, 1993; Pinheiro and Fransozo, 1993; Grandjean *et al.*, 1997; Mariappan *et al.*, 2000; Trevisan and Santos, 2012).

The finding by this study that both propods are larger in the males of *A. marginata* than in the females suggests the possible functions cited above. It is generally observed in studies of the relative growth of aeglids that the males show greater growth in the cheliped after the transition to adulthood. This difference is one of the factors that produces sexual dimorphism in the group (Colpo *et al.*, 2005; Viau *et al.*, 2006; Oliveira and Santos, 2011; Trevisan and Santos, 2012). This pattern of ontogenetic development is most likely related to variation in the size and shape of the *A. marginata* chelipeds.

Unfortunately, most previous studies of the growth of the chelipeds in aeglids involved comparisons between the left and right sides of the same individual (e.g., previous studies of *A. paulensis*, *A. perobae* and *A. uruguayana*). Assessments of the sexual dimorphism of the chelipeds are scarce for this family. For this reason, interspecific comparisons of this interesting pattern of intraspecific variation are difficult (López, 1965; Rodrigues and Hebling, 1978; Viau *et al.*, 2006). In *Aegla franca* Schmitt, 1942, both chelipeds show a high degree of sexual dimorphism. In all carapace-length size classes in which both males and females were represented, the males had larger and more robust chelipeds than the females (Bueno and Shimizu, 2009).

The *Sexual shape dimorphism* of the cheliped propods, in conjunction with the similar carapace size of males and females, indicates the need by the males for a wider palm and palmar region between the crest and the base of the fixed finger. The result of this characteristic is that the fixed finger is shorter and stronger in the males than in the females. The extension of the cheliped propod may be related to the insertion of different muscles in the region of the cheliped palm. A shorter and rugged fixed finger can provides to males with the strength needed to perform agonistic behaviors related to females or territories or to guard the females after copulation, as observed in the males of *A. platensis* (Almerão *et al.*, 2010). Moreover, the thinner and more delicate fixed finger of the females can be used to assist in the process of self-cleaning of the abdominal camera and sensory structures after egg laying (Almerão *et al.*, 2010).

Although few studies using the technique of geometric morphometric are available for aeglid species (Giri and Collins, 2004; Collins *et al.*, 2008; Giri and Loy, 2008; Barría *et al.*, 2011; Hepp *et al.*, 2012), this technique has provided robust results and has allowed a precise interpretation of sexual dimorphism in shape and size in *A. marginata*.

Acknowledgments

We are grateful to the editor and three anonymous reviewers for their insightful comments, which greatly improved the manuscript. The authors thank the Postgraduate Programs in Zoology and in Entomology, Federal University of Paraná for providing all the laboratory facilities for this study. This research was supported by grants from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

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Submitted 09 May 2012
Accepted 31 July 2012