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ORIGINAL ARTICLE

Description of the first juvenile stage of *Dilocarcinus septemdentatus* (Herbst, 1783) (Crustacea, Decapoda, Trichodactylidae)

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ABSTRACT

A total of 38 freshwater brachyuran species occur in Brazil, of which 79% are distributed in the northern region. However, for only two species of freshwater crabs are descriptions available for their juveniles. The importance of these studies lies in understanding of life-cycle aspects as well the potential elucidation of phylogenetic relationships within the group because the characters are usually solely based on adult specimens. The morphology of the first juvenile stage of the *Dilocarcinus septemdentatus* (Herbst, 1783) is described and illustrated for the first time based on specimens hatched by an ovigerous female collected in the northeastern region of the Brazilian Amazon. Juveniles of *Dilocarcinus pagei* Stimpson, 1861 and *D. septemdentatus* have one flagellar segment on the exopod of the first maxilliped while the only described juvenile of an unidentified species of *Trichodactylus* Latreille, 1828 has two. *Dilocarcinus septemdentatus* differs from other congeneric species mainly in the number of setae on the antennae and number of segments of the mandibular palp. Variations in the number of segments and

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aesthetascs enable the comparison between the juveniles of *D. septemdentatus* with those of other Brachyuran species previously studied and suggest possible adaptations to freshwater environments.

Key words
Brachyura, juvenile development, aesthetascs, freshwater crab, morphology.

Introduction

Freshwater crabs are Brachyura Heterotremata that reproduce exclusively by direct development with the larval stages occurring inside the egg and newly hatched juveniles exhibiting characteristics similar to those of the adults (sensu Williamson, 1969; Cumberlidge and Ng, 2009). This group includes more than 1,280 species in 220 genera in the Neotropical, Afrotropical, Palearctic, Oriental and Australasian regions (Cumberlidge and Ng, 2009). A total of 43% of all Brazilian freshwater decapod fauna occur in the Amazon basin (Magalhães, 2003).

Sternberg *et al.* (1999) separated the freshwater crabs into two monophyletic groups, the first one with five families and the other one consisting of the family Trichodactylidae H. Milne-Edwards, 1853, but this classification is controversial. Bott (1970), Cumberlidge (1999) and Martin and Davis (2001) included the Trichodactylidae in the superfamily Portunoidea Rafinesque, 1815, but Števčić (2005) transferred it to the superfamily Trichodactyloidea H. Milne-Edwards, 1853, which was followed by Ng *et al.* (2008), Cumberlidge and Ng (2009), and De Grave *et al.* (2009). The family has two subfamilies, Dilocarcininae Preztmann, 1978, consisting of 12 genera and 33 species, and Trichodactylinae H. Milne Edwards, 1853, encompassing 3 genera and 16 species (De Grave *et al.*, 2009). In Brazil, Trichodactylidae is represented by 10 genera and 29 species that occur in all of the river basins in the country, excluding the temporary rivers of the semiarid northeastern region, but are primarily distributed in the Amazon basin (Magalhães, 2003). These animals are found in streams, lakes, wetlands, backwaters and swamps, where they occupy various microhabitats, including submerged leaf litter, branches and logs, as well as aquatic vegetation, marginal pits and cracks under and between riverbed stones (Magalhães, 2000; 2003).

According to Magalhães and Türkay (2008), *Dilocarcinus* H. Milne Edwards, 1853 comprises of *Dilocarcinus pagei* Stimpson, 1861, *Dilocarcinus septemdentatus* (Herbst, 1783) and *Dilocarcinus truncatus* Rodríguez, 1992. *Dilocarcinus septemdentatus* is found in Suriname, French Guiana and Brazil (Acre, Amazonas, Goiás, Maranhão, Pará and Maranhão), where it inhabits rivers and lakes in marginal areas with ravines as well as inside burrows, in shallow areas and in association with floating macrophyte roots (Magalhães, 2003; Magalhães and Türkay, 2008). The species is listed as "Least Concern" in the IUCN Red List of Threatened Species (Cumberlidge, 2008).

Studies of the juvenile stage of the Decapoda are important because all the characters used to identify species are exclusively based on adult morphology, which complicates their identification when they are juvenile. According to Martin *et al.* (1984), juvenile morphological studies may also help to clarify the phylogenetic relationships within Brachyura and facilitate their taxonomic identification. Considering the large number of brachyuran species in Brazil, there is little knowledge about the juvenile development of crabs. Juvenile development has only been described for three freshwater crabs: the trichodactylids *Trichodactylus* sp. by Müller (1892) and *D. pagei* by Vieira *et al.* (2013), and the pseudothelphusid *Kingsleya ytupora* Magalhães, 1986 by Wehrtmann *et al.* (2010). However, the latter authors described only the carapace of the first and second juvenile stages.

In this study we aim to provide the full description of the first juvenile stage of *D. septemdentatus* as well as to highlight the main differences in comparison with other Brazilian species from different habitats already described.

Material and Methods

One ovigerous female of *D. septemdentatus* was collected using a 3-mm mesh sieve on the banks of the Rio Preto creek (00°59'59.2"S 47°06'53.7"W) in Primavera, state of Pará, Brazil. The juveniles began hatching while still in the field and were preserved in 70% alcohol.

The juveniles were counted and dissected in the laboratory. The appendages were fixed in a 96% alcohol and glycerin mixture (ratio of 1:1) and drawn in dorsal view using a Zeiss microscope equipped with a camera lucida. The dorsal and ventral views of the juveniles were photographed using a Leica M205A stereomicroscope equipped with a DFC420 camera, and the setae were counted for ten individuals. Measurements were made using an ocular micrometer. Descriptions are reported from the proximal to the distal segments, following Clark *et al.* (1998), and setae classified as simple or plumose.

Female and juveniles are deposited in the Museu Paraense Emilio Goeldi (MPEG) under catalog number MPEG 1174.

Results

A total of 101 juveniles hatched from the eggs. The female had a carapace width of 35 mm. The juveniles had a mean carapace width of 1.62 mm (range: 1.43 –1.75 mm) and a mean carapace length of 1.57 mm (range: 1.23–1.71 mm).

Similar to the adults, the carapace of the first juvenile stage of *Dilocarcinus septemdentatus* are wider than long, the abdomen extends beyond the first transverse suture of the thoracic sternum (fourth sternite), and the chelipeds have spines in the merus and carpus.

Dilocarcinus septemdentatus (Herbst, 1783)

Description of the first juvenile stage.

Carapace (Fig. 1A) slightly wider than long, subquadrangular, posterior margin wider than anterior one, convex in anteroposterior direction; front bilobed, slightly deflected. Dorsal region convex with simple and plumose setae sparsely; early differentiation of the gastric, cardiac, intestinal and branchial regions. Anterolateral margin with minute spine. Small red and brown spots over the entire dorsal region of carapace. Sternum (Fig. 1B) without setae.

Abdomen (Fig. 1C) attached to sternum, with six somites wider than long, extending beyond transverse suture of fourth sternite. Ventrally with four pairs of pleopodal buds from second to fifth somite.

Telson subtriangular, with small simple and plumose setae scattered on dorsal region.

Antennule (Fig. 2) with the basal segment well-developed with 8–11 simple and 12–15 plumose setae. Peduncle two-segmented, first segment smooth, second segment with 4 simple setae. Endopod (ventral flagellum) two-segmented, proximal segment with 1 subterminal simple seta, distal segment with 4 simple setae (2 subterminal and 2 terminal). Exopod (dorsal flagellum) 3-segmented; first segment smooth; second segment with 1 simple seta and 4 aesthetascs ending in a globose tip with a sharp point; third segment with 2 simple setae and 4 aesthetascs ending in a globose tip with a sharp point.

Antenna (Fig. 3) with peduncle three-segmented; first segment with 2 simple and 1 plumose setae; second segment with 3 simple setae; third segment with

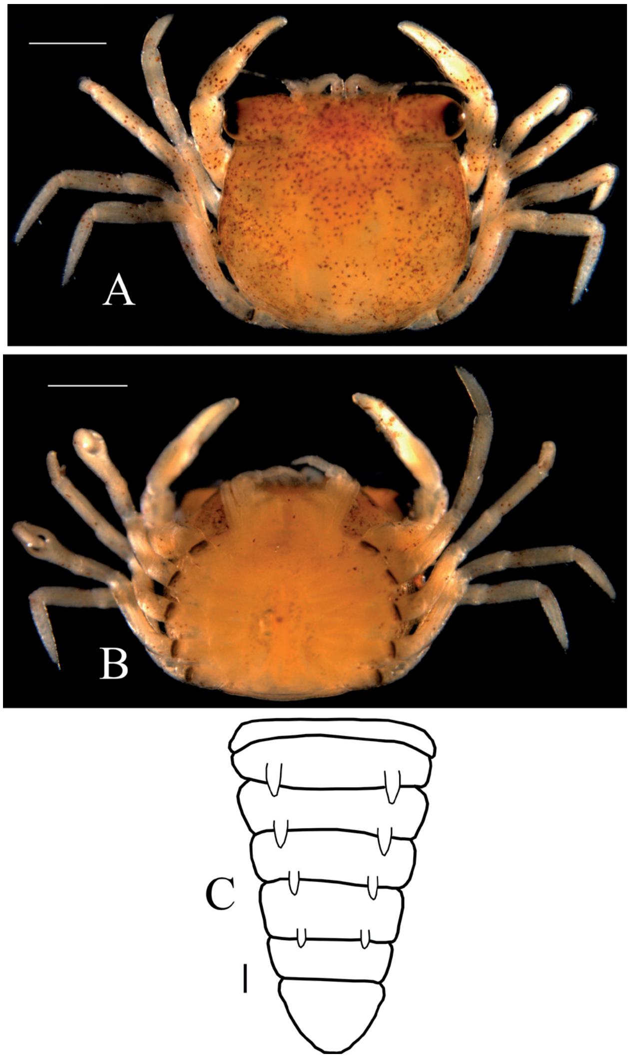

Figure 1. *Dilocarcinus septemdentatus* (Herbst, 1783), first juvenile stage. A, dorsal view; B, ventral view; C, ventral view of abdomen with pleopods. Scale bars: A, B = 1.0 mm; C = 0.1 mm.

1 simple seta. Antennal flagellum with 5 segments bearing 0, 0, 3, 2, 3, simple setae, one of which extremely long.

Mandible (Fig. 4) with cutting blade and three segmented palp with 0, 2, 10 plumose setae.

Maxillule (Fig. 5) with coxal endite with 10–13 plumose setae. Basal endite with 1–2 simple and 19–23 plumose setae. Endopod unsegmented, with 2 terminal plumose setae. Protopod with 2 long plumose setae.

Maxilla (Fig. 6) with coxal endite bilobed, proximal lobe without setae and distal lobe with 1 plumose seta. Basal endite bilobed with 3–4 simple and 8 plumose setae on the proximal lobe; distal lobe with 4–6 simple and 5 plumose setae. Endopod unsegmented with 1 plumose seta. Exopod (scaphognathite) with 82–90 marginal plumose setae and 8–12 simple setae on the dorsal surface.

First maxilliped (Fig. 7) with coxal endite with 14–17 plumose setae. Basal endite with 28–34 plumose setae. Endopod unsegmented with 0–1 proximal plumose seta and 6–8 distal plumose setae. Exopod two-segmented with 6–13 plumose setae on the proximal segment and 4 long terminal plumose setae on the distal segment. Epipod with 8–12 proximal plumose setae, and 16–24 median and terminal plumose setae. No gills present.

Second maxilliped (Fig. 8) with protopod smooth. Endopod with five segments. Ischium with 1–2 simple and 5–9 plumose setae. Merus with 1–2 simple and 3–4 plumose setae. Carpus with 0–1 plumose seta. Propodus with 2 simple and 8–10 plumose setae. Dactylus with 10–14 plumose setae. Exopod two-segmented, proximal segment with 12–16 plumose setae; distal segment with 4 long terminal plumose setae. Epipod with 9–14 plumose setae. Podobranch rudimentary.

Third maxilliped (Fig. 9) protopod with 6–9 simple and 22–31 plumose setae. Endopod five-segmented. Ischium with 12–17 simple and 12–11 plumose setae. Merus with 7–9 simple and 5–7 plumose setae. Carpus with 3–4 simple and 3–4 plumose setae. Propodus with 2–4 simple and 4–6 plumose setae. Dactylus with 5–7 plumose setae. Exopod two-segmented with 3–5 plumose setae on proximal segment and 4 long terminal plumose setae on distal segment. Epipod with 24–34 plumose setae. Arthrobranch rudimentary.

Chelipeds (Fig. 1A, B) symmetrical, covered with simple and plumose setae. Presence of small red and

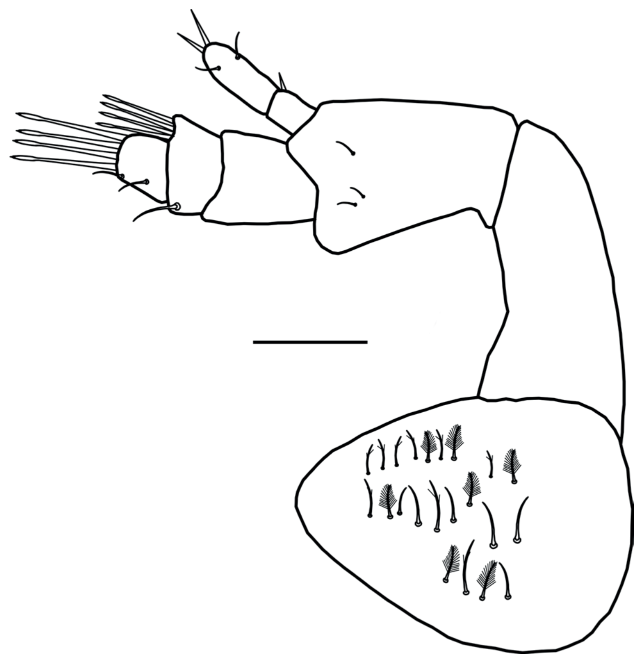

Figure 2. *Dilocarcinus septemdentatus* (Herbst, 1783). Lateral view of right antennule. Scale bar = 0.1 mm.

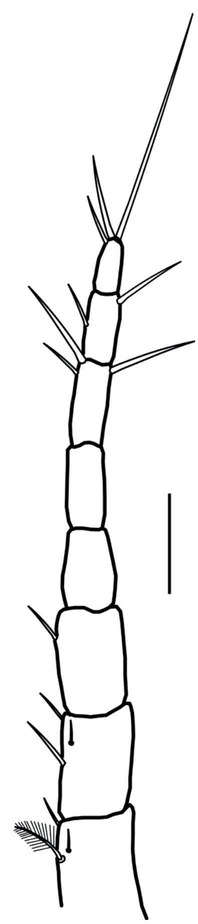

Figure 3. *Dilocarcinus septemdentatus* (Herbst, 1783). Dorsal view of right antenna. Scale bar = 0.1 mm.

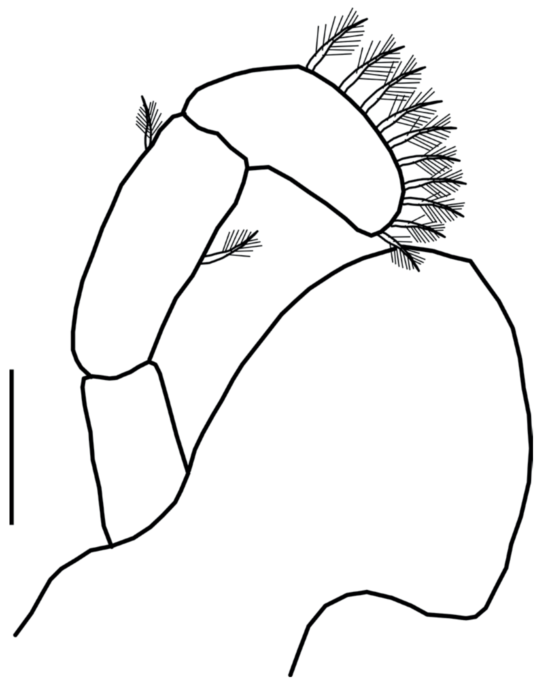

Figure 4. *Dilocarcinus septemdentatus* (Herbst, 1783). Dorsal view of left mandible. Scale bar = 0.1 mm.

Figure 5. *Dilocarcinus septemdentatus* (Herbst, 1783). Dorsal view of right maxillule. Scale bar = 0.1 mm.

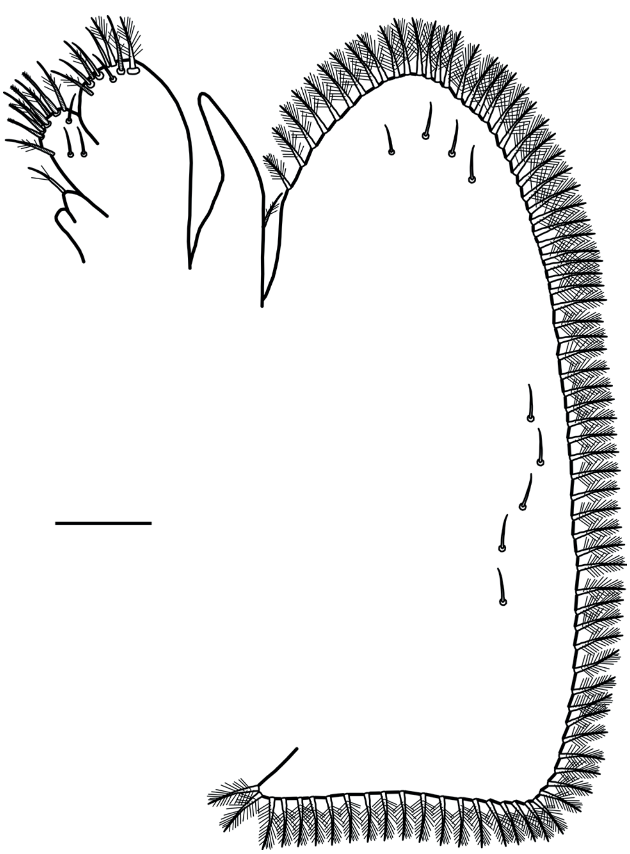

Figure 6. *Dilocarcinus septemdentatus* (Herbst, 1783). Dorsal view of right maxilla. Scale bar = 0.1 mm.

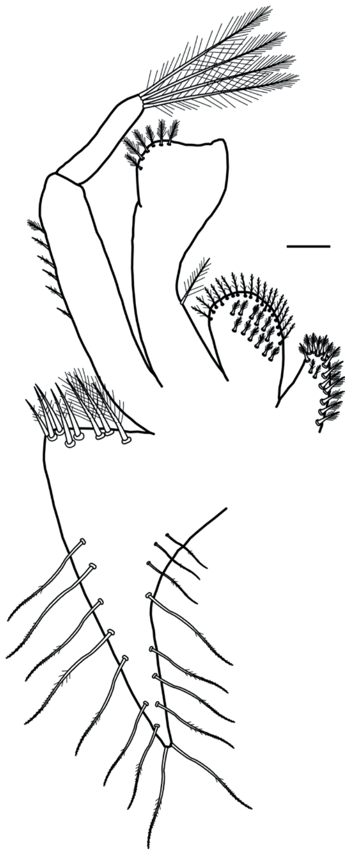

Figure 7. *Dilocarcinus septemdentatus* (Herbst, 1783). Dorsal view of left first maxilliped. Scale bar = 0.1 mm.

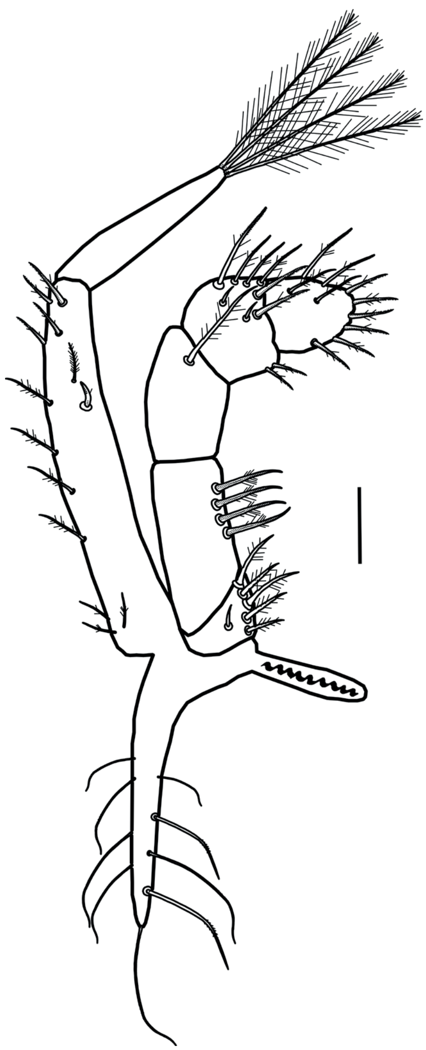

Figure 8. *Dilocarcinus septemdentatus* (Herbst, 1783). Dorsal view of left second maxilliped. Scale bar = 0.1 mm.

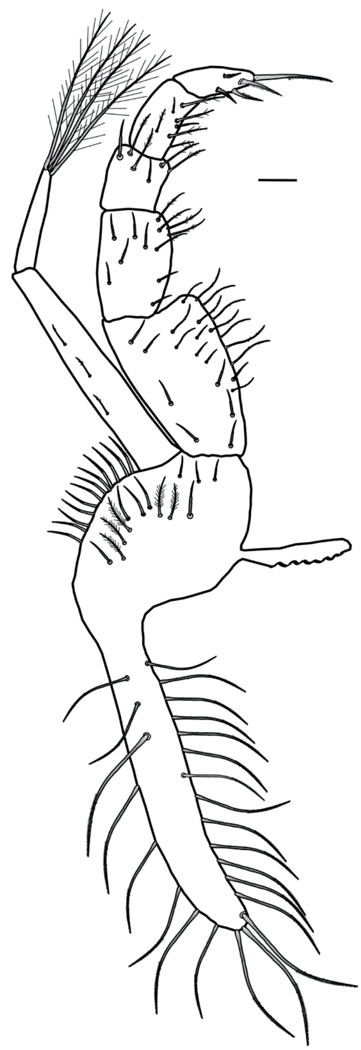

Figure 9. *Dilocarcinus septemdentatus* (Herbst, 1783). Dorsal view of left third maxilliped. Scale bar = 0.1 mm.

brown dorsal spots on all chelipeds segments. Ischium with conspicuous dark pigmentation in ring format. Merus with prominent spine on anterolateral region. Carpus with distal spine on dorsolateral inner portion, near articulation with propodus.

Pereopods 2–5 (Fig. 1A, B) similar, with simple and plumose setae. Presence of small red and brown dorsal spots along pereopods. Ischium of all pereopods with conspicuous dark pigmentation in ring format.

Discussion

Direct development in Decapoda results from secondary embryogenesis of the ancestral larval stages (zoea and megalopa), with these phases occurring inside the egg (Felder *et al.*, 1985). The main morphological differences between adults and juveniles of *D. septemdentatus* are: adults have 6–7 acute teeth on the anterolateral margin of the carapace whereas this margin is smooth in juveniles; adults have abdominal somites III–VI fused whereas they are free in juveniles; and the presence of four pairs of rudimentary pleopods on abdominal somites II–V in the juveniles (adult males have only the first and second pairs modified as gonopods, and adult females have all the four pairs of pleopods). In none of the juvenile specimens analyzed, it was possible to define the sex because there is no conspicuous modification in the pleopods. In *D. pagei* the sex differentiation begins at the second juvenile stage (Vieira *et al.*, 2013), likely the same in *D. septemdentatus*.

The juveniles of *D. septemdentatus* (present study) and *D. pagei* (Vieira *et al.*, 2013) are very similar morphologically and can only be differentiated through a combination of characters. *D. septemdentatus* has an antenna consisting of 8 segments and 3 setae on the sixth segment; the mandibular palp is 3-segmented; the basal endite of the maxillule has 20–24 setae; the basal endite of the first maxilliped has 28–34 setae; the exopod flagellum of the second maxilliped has 1 segment; and the protopodite of the third maxilliped has 28–40 setae. For the same characteristics, *D. pagei* has 8 segments on the antenna and the sixth segment has 4 setae; the mandibular palp is 2-segmented; the basal endite of the maxillule has 25–28 setae; the basal endite of the first maxilliped has 33–37 setae; the exopodal flagellum of the second maxilliped has 2 segments; and the protopodite of the third maxilliped has 41 setae (Vieira *et al*., 2013). In general, *D. septemdentatus* has fewer setae than *D. pagei*.

Juveniles of *Trichodactylus* sp. (Trichodactylinae) described by Müller (1892) differ from *D. septemdentatus* and *D. pagei* (Dilocarcininae) mainly because the exopod of the antennule consists of 2 segments instead 3; the antenna consists of 9 segments instead of 8; and the exopodal flagella of the first and third maxillipeds have 2 segments instead of 1. Other variations among the Trichodactylidae species that had their first juvenile stage described are outlined in Tab. 1.

As Rodríguez (1992), Sternberg and Cumberlidge (2003) and Daniels *et al*. (2006) suggested that Trichodactyloidea might have a marine origin and affinities with the Portunoidea, we performed a comparison with the first juvenile stage of *Callinectes sapidus* Rathbun, 1896 (see Barutot *et al*., 2001), *Callinectes ornatus* Ordway, 1863 (see Bolla Junior *et al*., 2008), *D. pagei*, *D. septemdentatus*, and *Trichodactylus* sp. (Tab. 2). Only the number of segments in the endopodite of the antennule is the same across the five species. While the species of *Callinectes* Stimpson, 1860 have 7 segments in the exopod of the antennule and the antenna have 10 or 11 segments, *Dilocarcinus* and *Trichodactylus* species have, at most, 3 segments in the exopod of the antennule, and the antenna has 8 or 9 segments. There are also variations in the number, size and shape of the aesthetascs and setae of the cephalic and thoracic appendages, with *Dilocarcinus* and *Trichodactylus* having a lower number. These variations might be adaptations to the freshwater environment in order to reduce the area of contact with the external environment, which is a key factor for maintaining osmotic balance. According to Lockwood (1962), marine species tend to be characterized by a high surface permeability to ions and water to sustain the blood concentration and, in general, freshwater species have a less permeable area than estuarine species. With the reduction of body surface, freshwater can promote further restriction of the permeability favoring the process of osmotic regulation (Lockwood, 1962).

Table 1. Morphological characters that allow the differentiation and identification of the first juvenile stages of *Dilocarcinus septemdentatus* (Herbst, 1848), *Dilocarcinus pagei* Stimpson, 1871 and *Trichodactylus* sp.

	D. septemdentatus	*D. pagei*	*Trichodatylus* sp.
Reference	Present study	Vieira *et al.* (2013)	Müller (1892)
Antennule	+	+	-
Articles on exopod	3	3	2
Aesthetascs on exopod	0+4+4	0+4+3(4)	3+3
Antenna			
Number of article	3+5	3+5	4+5
Mandible			
Articles on palp	3	2	3
Maxillule			
Articles on endopod	1	1	2
First maxilliped			
Articles on flagellum of exopod	1	1	2
Second maxilliped			
Articles on flagellum of exopod	1	2	2
Third maxilliped			
Articles on flagellum of exopod	1	1	2

Table 2. Diagnostic characters that allow differentiation of the first juvenile stages of Brachyura species that occur in Brazilian waters for which the juvenile development is known.

	Reference	Article on endopod of antennule	Article on exopod of antennule	Number of aesthetascs	Article on antenna	Article on palp of mandible	Article on Endopod of maxillule
Trichodactylidae							
Dilocarcinus septemdentatus	Present study	2	3	8	3+5	3	1
Dilocarcinus pagei	Vieira *et al.* (2013)	2	3	7–8	3+5	2	1
Trichodactylus sp.	Müller (1892)	2	2	6	4+5	3	2
Aethridae							
Hepatus pudibundus	Hebling and Rieger (2003)	2	8	31	3+7	2	1
Inachidae							
Stenorhynchus seticornis	Yang (1976)	2	4	13	3+5	2	2
Inachoididae							
Pyromaia tuberculata	Luppi and Spivak (2003)	3	4	14	3+5	2	2
Mithracidae							
Mithraculus sculptus	Rhyne *et al.* (2006)	2	4	13 a 16	3+6	2	1
Parthenopidae							
Parthenope serrata	Yang (1971)	2	5	?	3+7	2	2
Portunidae							
Callinectes ornatus	Bolla Junior *et al.* (2008)	2	7	32	3+10(11)	3	2
Callinectes sapidus	Barutot *et al.* (2001)	2	7	15 a 18	3+8	3	2
Panopeidae							
Eriphia gonagra	Fransozo and Negreiros-Fransozo (1987)	3	6	26–28	4+8	2	2
Eurypanopeus abbreviatus	Fransozo and Negreiros-Fransozo (1987)	2	3	10	4+7	3	1
Eurytium limosum	Guimarães and Negreiros-Fransozo (2005)	2	5	15	3+7	2	1
Menippe nodifrons	Fransozo *et al.* (1988)	2	8	36	3+9	2	2
Panopeus herbstii	Hebling *et al.* (1982)	2	4	14 a 15	3+7	2	2
Grapsidae							
Pachygrapsus transversus	Flores *et al.* (1998)	3	6	18	3+8	3	2
Sesarmidae							
Armases rubripes	Diaz and Ewald (1968)	Absent	?	4	3+5	2	2
Metopaulias depressus	González-Gordillo *et al.* (2010)	Absent	2	4	2+6	2	1
Sesarma rectum	Fransozo (1986/87)	Absent	2	3	3+5	2	2
Varunidae							
Cyrtograpsus angulatus	Rieger and Beltrão (2000)	2	4	11–16	3+7(6)	3	2
Neohelice granulata	Rieger and Nakagawa (1995)	2	4	12	3+7	2	2
Ocypodidae							
Uca burgersi	Vieira *et al.* (2010)	1	3	9–11	3+6	3	2

In *D. septemdentatus*, *D. pagei* and some Grapsoidea species from estuarine and semiterrestrial habitats the antenna has one simple and extremely long seta located on the last and penultimate segments (see Diaz and Ewald, 1968; Fransozo, 1986/87; Rieger and Nakagawa, 1995; Flores *et al*., 1998; Rieger and Beltrão, 2000), this simple seta is presumably sensorial (Bauer and Caskey, 2006). Others types of setae have mechanical functions in Decapoda. Plumose, serrate and plumodenticulate setae are adapted for particle retention and the promotion of water flow, scrape and brush other setae and surfaces or to release food from substrates (Thomas, 1970; Farmer, 1974; Felgenhauer and Abele, 1983; Alexander and Hindley, 1985; Martin and Felgenhauer, 1986; Watling, 1989; Garm, 2004).

Aesthetascs are structures found on the terminal end of the outer flagellum of antennules in decapods; they have a chemoreceptor function and are involved in the detection of sex pheromones (Meusy and Payen, 1988). A striking characteristic of decapods is the variation in the number and morphology of aesthetascs that occur among marine, estuarine, freshwater and semiterrestrial species (Tab. 2). Marine species with juvenile development already described belonging to Aethridae Dana, 1851, Inachidae MacLeay, 1838, Inachoididae Dana, 1851, Mithracidae MacLeay, 1838, Parthenopidae MacLeay, 1838, Portunidae Rafinesque, 1815 (*Callinectes ornatus*) and Panopeidae Ortmann, 1893 have 13–32 long aesthetascs (Yang, 1971; 1976; Hebling *et al*., 1982; Fransozo and Negreiros-Fransozo, 1987; Fransozo *et al*., 1988; Hebling and Rieger, 2003; Luppi and Spivak, 2003; Rhyne *et al*., 2006; Bolla Junior *et al*., 2008). Meanwhile, estuarine species, including Portunidae (*C. sapidus*), Grapsidae MacLeay, 1838, Varunidae H. Milne Edwards, 1853, Panopeidae [*Eurypanopeus abbreviatus* (Stimpson, 1860) and *Eurytium limosum* (Say, 1818)] and Ocypodidae Rafinesque, 1815 have 10–18 aesthetascs usually shorter than those of marine species (Tab. 2) (Fransozo and Negreiros-Fransozo, 1987; Rieger and Nakagawa, 1995; Flores *et al*., 1998; Rieger and Beltrão, 2000; Barutot *et al*., 2001; Guimarães and Negreiros-Fransozo, 2005; Vieira *et al*., 2010).

Compared to marine species, the number of aesthetascs is lower in juveniles of Trichodactylidae (6 to 8) and larger than in juveniles of semiterrestrial species of Sesarmidae Dana, 1851, with only up to 4 aesthetascs (see Müller, 1892; Diaz and Ewald, 1968; Fransozo 1986/87; González-Gordillo *et al*., 2010; Vieira *et al*., 2013). According to Shenoy *et al*. (1993), the aesthetascs of marine species present thin cuticles that are pointed or uniformly rounded and, in the estuarine species, the aesthetacs are short and robust. The morphological changes in the aesthetascs from marine to semiterrestrial species occur as reduction of number and size a well ass thickening trends. These modifications likely facilitate the conservation of water and sodium ions and have the function to prevent against the wear to which aesthetascs of freshwater and semiterrestrial species are subjected (Edmondson, 1929; Shenoy *et al*., 1993).

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