



e-ISSN 2358-2936

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This article is part of the special series offered by the Brazilian Crustacean Society in honor to **Nilton José Hebling** in recognition of his dedication and contributions to the development of carcinology in Brazil.



ORIGINAL ARTICLE

First zoeal stage of the crab *Domecia acanthophora* (Desbonne, in Desbonne & Schramm, 1867) (Decapoda, Brachyura) and revision of the larval morphology of superfamily Trapezioidae

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SUBMITTED 24 February 2016
ACCEPTED 13 July 2016
PUBLISHED 21 November 2016

Guest Editors
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DOI [10.1590/2358-2936e2016021](https://doi.org/10.1590/2358-2936e2016021)

Nauplius, 24 e2016021

ABSTRACT

The morphology of the first zoeal stage of *Domecia acanthophora* (Desbonne, in Desbonne & Schramm, 1867) was described from laboratory-hatched material obtained from ovigerous females collected at Vitória Island on the southeastern Brazilian coast. We compared the larval morphology

(zoea I) of fourteen species of the superfamily Trapezoidea, which *Domecia glabra* Alcock, 1899 is the only congeneric representative of the species described in this study. The morphological characteristics of the first zoea that distinguish *D. acanthophora* from *D. glabra* are: three aesthetascs on the exopod antennule; three pairs of lateral spines on carapace; bilobed basial endite of maxilla, with four plumodenticulate setae on each lobe; and telson furcae distally spinulated. It also provides information that may enhance some phylogenetic hypotheses within Trapezoidea crabs.

KEY WORDS

Domeciidae, larval description, southeastern Brazil, Tetraliidae, Trapeziidae.

INTRODUCTION

The most recent Brachyura classification (Ng *et al.*, 2008; De Grave *et al.*, 2009; Ahyong *et al.*, 2011) recognizes the superfamily Trapezoidea Miers, 1886, which consists of three families: Domeciidae Ortmann, 1893, Tetraliidae Castro, Ng & Ahyong, 2004 and Trapeziidae Miers, 1886. Crabs of the family Domeciidae are grouped into four genera: *Domecia* Eydoux & Souleyet, 1842, *Jonesius* Sankarankutty, 1962, *Maldivia* Borradaile, 1902 and *Palmyria* Galil & Takeda, 1986. The species *Domecia acanthophora* (Desbonne, in Desbonne & Schramm, 1867) has a wide geographical distribution in the Western Atlantic, extending from North Carolina, Bermuda, Florida, the Gulf of Mexico, the Antilles, northeastern South America and Brazil (St. Peter and St. Paul Archipelago, Rocas Atoll, Fernando de Noronha, and from states of Ceará and Pernambuco to São Paulo) (Alves *et al.*, 2006; Coelho-Filho, 2006; Melo, 1998).

In recent decades, several studies about the morphology of larval stages have been used to elucidate the taxonomic status of these crabs, of which there is still no consensus with respect to the superfamily Trapezoidea (*e.g.*, Clark and Guerao, 2008; Clark and Ng, 2010). About 60 species of the superfamily Trapezoidea are known (see Ng *et al.*, 2008), but the morphology of the first zoeal stage is described only for 14 species (see Tab. 1).

Considering the morphology of the first larval stage is unknown for most species of the superfamily Trapezoidea, new descriptions could contribute with knowledge of the relationship within this taxon. Thus, we provided here a detailed description of the first zoea of the crab *D. acanthophora*, hatched in the laboratory. Additionally, we reviewed and compared the larval morphology (zoea I) of Trapezoidea species (*sensu*

Ng *et al.*, 2008) in a comparative table, in order to facilitate the identification of these larvae.

MATERIAL AND METHODS

Two ovigerous females of *D. acanthophora* were collected in September 2006 by scuba divers at Vitória Island ($23^{\circ}44'04''S$ $45^{\circ}01'35''W$) in the southeastern of the São Paulo State, Brazil. The crabs were kept isolated in aquaria filled with seawater from the collecting site, at constant temperature ($24 \pm 1^{\circ}\text{C}$), salinity (35 ± 1) and moderate aeration, until the larvae hatched. Newly hatched zoeae were preserved in a 1:1 mixture of 70% ethyl alcohol and glycerin. For detailed examination, the larvae and appendages were dissected under a Zeiss Stemi 200C trinocular stereomicroscope and prepared on semi-permanent slides with glycerin.

Drawings and measurements were done using a Leica DM750 microscope equipped with camera lucida. The illustrations and measurements were based on at least 10 specimens. The carapace length (CL) was considered from the eyes (base of the rostrum) to the posterolateral cephalothorax margin, and the rostrrodorsal length (RDL) was considered from the tip of the rostral spine to the tip of the dorsal spine. The long terminal plumose natatory setae on distal exopod segments of the first and second maxillipeds were drawn truncated.

Larval description and terminology of setae are based on Clark *et al.* (1998) and Garm (2004). The parental females of *D. acanthophora* were deposited in the crustacean collection of the Museum of Zoology of the University of São Paulo (MZUSP-16705). The larvae of *D. acanthophora* were deposited in the scientific collection of the Marine Biology Laboratory of the University of Taubaté (UNITAU-201237).

Table 1. Comparison of some larval characters of the first zoeal stage of *Domecia acanthophora* (Desbonne, in Desbonne & Schramm, 1867) and other species of the superfamily Trapezoidea.

Species/original larval description	Domeciidae Ortmann, 1893		Tetralidae Castro, Ng & Ah Yong, 2004		Calocarctiniae Števčić, 2005		Quadrellinae Števčić, 2005		Trapeziidae Miers, 1886		Trapeziidae Miers, 1886		
	<i>Domecia acanthophora</i> (Desbonne, in Desbonne & Schramm, 1867) ¹	<i>Domecia glabra</i> Alcock, 1899 ²	<i>Tetralia cavimana</i> Heller, 1861 ³	<i>Tetralia glaberrima</i> (Herbst, 1790) ⁴	<i>Tetralia rubridactyla</i> Garth, 1971 ⁵	<i>Calocarctinus africanus</i> Calman, 1909 ⁶	<i>Quadrilla maculosa</i> Alcock, 1898 ⁷	<i>Quadrilla serrei</i> Galil, 1986 ⁸	<i>Trapezia cymodoce</i> (Forska, 1775) ⁹	<i>Trapezia digitalis</i> (Herbst, 1801) ¹⁰	<i>Trapezia heterata</i> Latreille, 1828 ¹¹	<i>Trapezia rufopunctata</i> (Herbst, 1799) ¹²	<i>Trapezia septata</i> Dana, 1852 ¹³
Carapace													
Rostral	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)
Dorsal	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)	1sp (smooth)
Lateral	6sp (3 pairs) (with 2 spinules) (with 1 spinule)	4sp (2 pairs) (with 4sp (2 pairs) (with 1 spinule))	4sp (2 pairs) (with 4sp (2 pairs) (with 1 spinule))	4sp (2 pairs) (with 6sp (3 pairs) (with 1 spinule))	4sp (2 pairs) (with 6sp (3 pairs) (with 1 spinule))	4sp (2 pairs) (with 6sp (3 pairs) (with 1 spinule))	4sp (2 pairs) (with 6sp (3 pairs) (with 1 spinule))	4sp (2 pairs) (with 6sp (3 pairs) (with 1 spinule))	4sp (2 pairs) (with 6sp (3 pairs) (with 1 spinule))	2sp (1 pair) (spinulate)	2sp (1 pair) (spinulate)	2sp (1 pair) (spinulate)	2sp (1 pair) (spinulate)
Antennule	3a+1s	4a+1s	4a+1s, 1sp	2a+2s*	4a+1s	5a+1s*	4a+1s	4a+1s	3a+1s	4a+1s, 1sp	2a+3s	4a+1s	2a+3s
Exopod													
Antenna													
Exopod	3s	3s	3s	3s	3s	3s	3s+1sp	3s	3s	3s	3s	3s	3s
Protopod													
Maxillule													
Coxal endite	(1s+5pd)	(2+5)p*	(2+5)p?	(2+5)p	(2+5)p*	(1+6)p*	(2+5)p*	(2+5)p*	(2+5)p*	(2+5)p*	(2+5)p*	(2+5)p*	(2+5)p*
Basal endite	(2+5+3pd)m	(3+7)p*	(4+6)*-12	(5p+2c)	(4+6)*-12	(3pd+2c)*	(4c+1p)*	(4c+1p)*	(3pd+2c)*	(3c+2c)*	(3p+2c)*	(3p+2c)*	(3p+2c)*
Endopod	0, (3pd+1s)	0, 4p*	1s, (1+4)p	1p (1+4)p	1p (1+4)p	1pd*, (2+4)p*d	1p (2+4)p*	1p (2+4)p*	1s, (1+4)p*	1s, (1+4)p*	1s, (1+4)p*	1s, (1+4)p*	1s, (1+4)p*
Maxilla													
Coxal endite	(4+3)pd, 1sp	(4+3)*, 1sp	(4+3)*, 1sp	(4+3)*, 1sp	(4+3)*, 1sp	(6+4)p*	(5+3)p*, 1sp	(5+3)p*, 1sp	(5+3)p*, 1sp	(5+3)p*	(5+3)p*	(5+3)p*	(5+3)p*
Basal endite	(4+4)pd, m	(5+3)p*	(4+4)pd	(4+4)pd	(4+4)pd	(4p, sp+4p)*	(5+4)p*	(5+4)p*	(5+4)p*	(4+4)p*	(4+4)p*	(4+4)p*	(4+4)p*
Endopod	(1pd, 1s+2pd, 1s)	(3+2)p*	(2+3)?	(2+3)?	(2+3)?	(2+3)p*	(3+5)p*	(3+5)p*	(3+5)p*	(3+2)p*	(3+2)p*	(3+2)p*	(3+2)p*
First maxilliped													
Coxa	no seta	1p*	?	1p*	1p*	no seta	no seta	?	?	?	?	?	no seta
Basis	(2+2+3+2)s	(2+2+3+2)p*	(2+2+3+3)?	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*	(2+2+3+3)p*
Endopod	1s, (1s+1pd), 0, 2pd, (2+2)pd	1p, 2p, 0, 2p, (4+1)p*	2?; 2?; 1?; 2? (4+1)?	2p, 2p, 1s, 2s, (4p+1s)*	2p, 2p, 1s, 2s, (4p+1s)*	(1s+2p), 2p, 1p, 2p, (4+1)p*	3p, 2p, 1p, 2p, (4p+1s)*	3p, 2p, 1p, 2p, (4p+1s)*	2s, 2s, 1s, 2s, (4p+1s)*	2s, 2s, 1s, 2s, (4p+1s)*	2p, 2p, 1p, 2p, (4p+1s)*	2s, 2s, 1s, 2s, (4p+1s)*	2s, 2s, 1s, 2s, (4p+1s)*
Second maxilliped													
Basis	(1+1+1)s	(1+1+1)p*	(1+1+1)?	(1+1+1)s*	(1+1+1)s*	(1+1+1)p*	(1+1+1)p*	(1+1+1)p*	(1+1+1)p*	(1+1+1)p*	(1+1+1)p*	(1+1+1)p*	(1+1+1)p*
Endopod	0, 0, (2+2)p	0, 0, (2+2)p*	1?, 1?; 1?; (1+3)?	1s, 1s, (2p+2s)*	1p, 1p, (2p+2s)*	1p, 1p, (2s+3s)*	1p, 1p, (2s+3s)*	1p, 1p, (2s+3s)*	0, 1s, (1c+2s)*	0, 1s, (1c+2s)*	0, 1s, (2p+1s)*	0, 1s, (2p+2s)*	0, 1s, (1p+3s)*
Telson													
Furcae	4sp (2 pairs)	smooth	smooth	spindle	smooth	spindle	smooth	spindle	smooth	smooth	smooth	smooth	smooth
Spine 2	absent	vestigial	absent	absent	absent	developed	developed	developed	vestigial	vestigial	vestigial	vestigial	absent
Abdomen													
Dorsolateral process on somites 4 and 5	absent	absent	absent	absent	absent	present	present	4 present 5 absent	absent	absent	absent	absent	absent

a = aesthetasc; s = simple seta; p = plumose seta; c = cuspitate seta; pd = plumodenticulate seta; sp = spine; spp = spinule; m = microtrichia. References: ¹Present study; ²Clark and Ng (2010); ³Clark and Guerao (2008); ⁴Al-Aidarous (1992); ⁵The author did not mention the setae type. ⁶Data from figures observation. ⁷Galil (1988); ⁸Shikatani and Shokita (1990); ⁹Clark and Ng (2006); ¹⁰Clark and Guerao (2008); ¹¹Galil & Lewinsohn, 1985¹²; ¹²Levitin, 1985¹³; ¹⁴Souleyet, 1842?

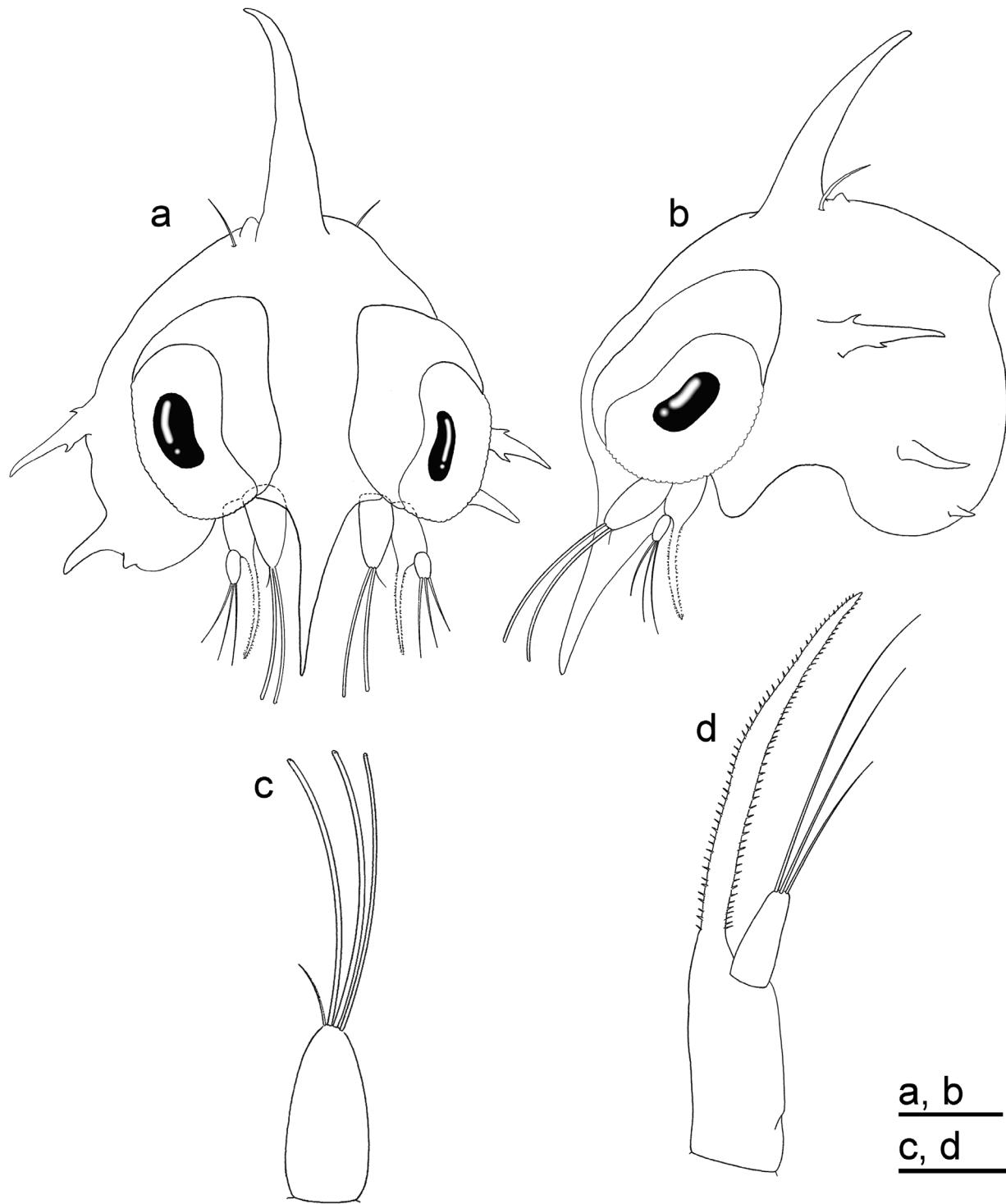


Figure 1. *Domecia acanthophora* (Desbonne, in Desbonne & Schramm, 1867), Zoea I. a. Cephalothorax, frontal view; b. Cephalothorax, lateral view; c. Antennule; d. Antenna (scale bars: a, b = 0.1 mm; c, d = 0.05 mm).

RESULTS

Description of first zoea of *D. acanthophora* (Figs. 1–3).

Dimensions: CL: 0.38 ± 0.01 mm; RDL: 0.76 ± 0.02 mm ($n = 10$).

Cephalothorax (Fig. 1a, b): dorsal spine smooth,

gently curved backward distally, almost equal in length to rostral spine. Pair of posterodorsal simple seta near the basis of the dorsal spine, posterodorsal protuberance present. Three pairs of lateral spines: dorsal pair curved ventrally, with one ventral and one

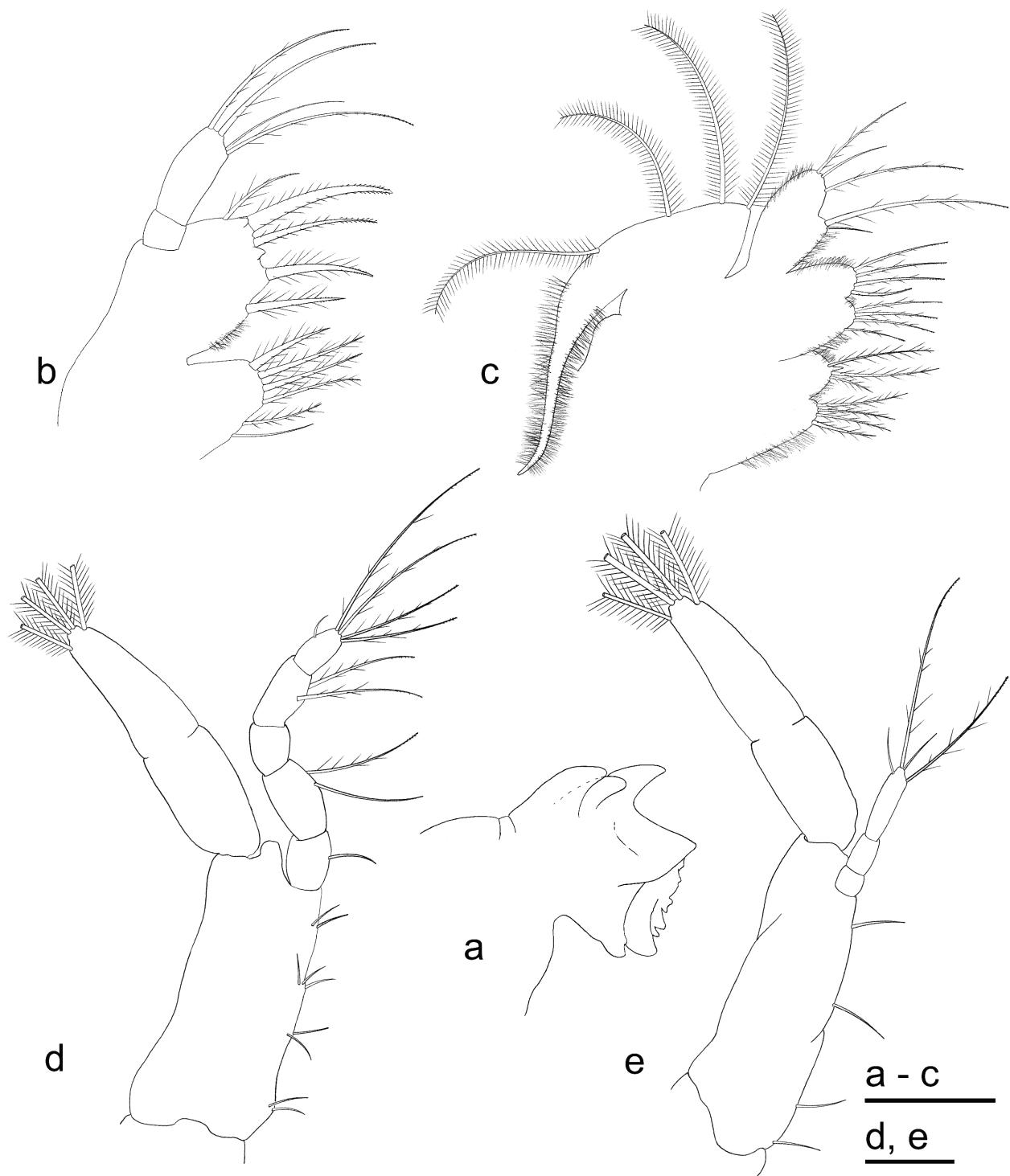


Figure 2. *Domecia acanthophora* (Desbonne, in Desbonne & Schramm, 1867), Zoea I. a. Mandible; b. Maxillule; c. Maxilla; d. First maxilliped; e. Second maxilliped (scale bars: a–e = 0.05 mm).

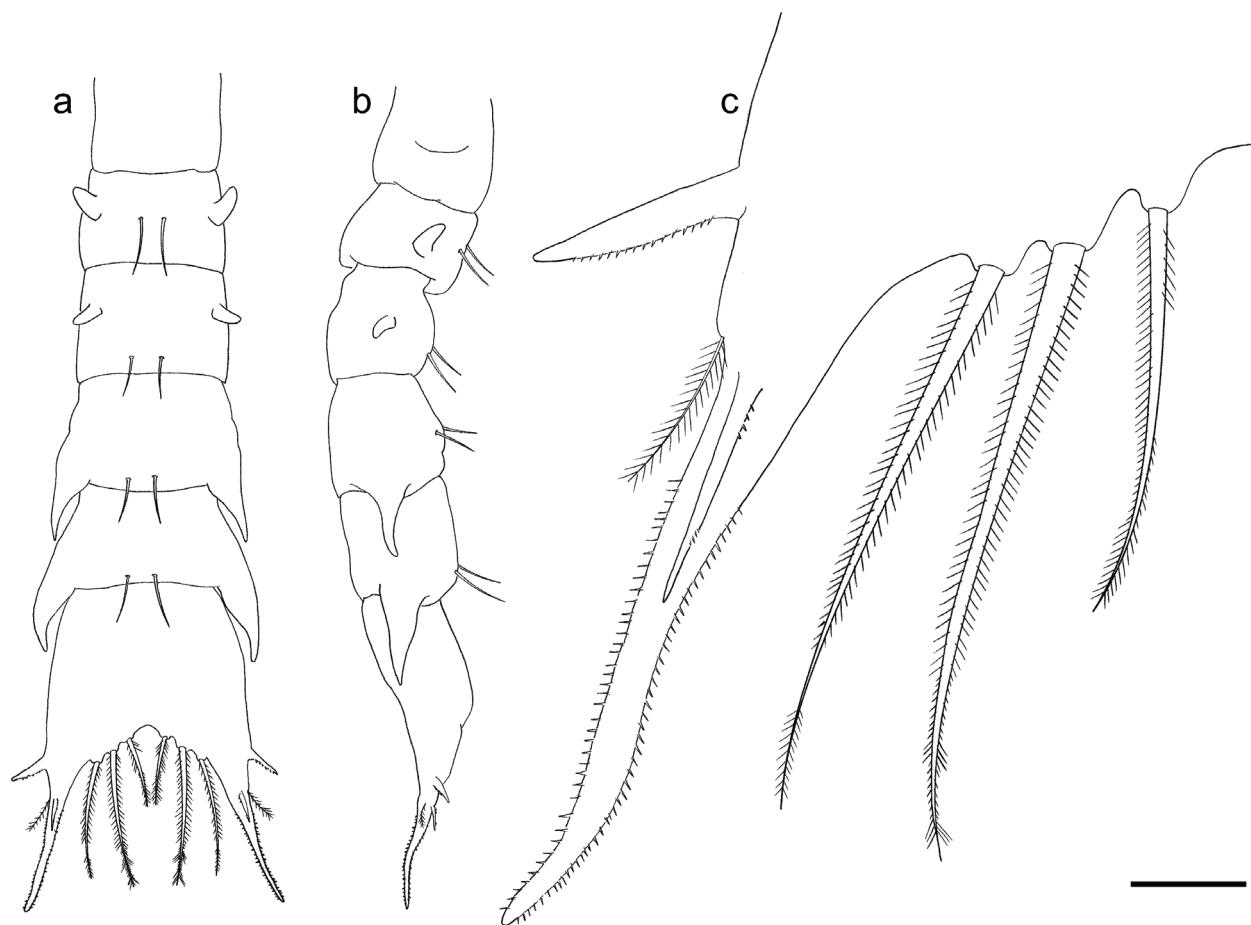


Figure 3. *Domicia acanthophora* (Desbonne, in Desbonne & Schramm, 1867), Zoea I. a. Pleon, dorsal view; b. Pleon, lateral view; c. Detail of spinulation of the telson furcae (scale bars: a, b = 0.1 mm; c = 0.02 mm).

dorsal spinules; second pair smaller, smooth, slightly curved ventrally; third pair smallest and smooth near carapace margin. Sessile eyes.

Antennule (Fig. 1c): uniramous, smooth. Endopod absent; exopod unsegmented, with three long terminal aesthetascs and one simple seta.

Antenna (Fig. 1d): biramous; well-developed and long protopod, with one row of short, equal spines in each lateral margin of similar sizes. Endopod absent. Exopod unsegmented, with three unequal terminal simple setae, the longest almost equal in length to exopod.

Mandibles (Fig. 2a): incisor and molar processes as illustrated; palp absent.

Maxillule (Fig. 2b): coxal endite with 1 (subterminal) simple and 5 (1 subterminal and 4 terminal) plumodenticulate setae. Basial endite with 5 plumodenticulate setae and 2 small protuberances, microtrichia on proximal margin. Endopod 2-segmented, proximal segment without seta; distal

segment with 3 (1 subterminal, 2 terminal) sparsely plumodenticulate setae, 1 shorter subterminal simple seta. Exopod seta absent.

Maxilla (Fig. 2c): coxal endite bilobed, with 4 plumose setae on proximal lobe, 3 plumose setae and 1 terminal small spine on distal lobe. Basial endite bilobed, with 4 plumodenticulate setae on each lobe. Unsegmented endopod bilobed, with 2 (1 plumodenticulate, 1 simple) setae on proximal lobe, 3 (1 subterminal, 2 terminal) setae on distal lobe. Exopod (scaphognathite) margin with 4 plumose setae and a long distal process. Microtrichia on both proximal and distal margins of coxal and basial endites, endopod and distal process of the scaphognathite.

First maxilliped (Fig. 2d): coxa without setae. Basis with 9 simple setae arranged 2+2+3+2. Endopod 5-segmented with 1 simple seta on first segment; 2 (1 simple, 1 plumodenticulate) setae on second segment; no seta on third segment; 2 plumodenticulate setae on fourth segment; 4 (2 subterminal, 2 terminal)

plumodenticulate setae and one subterminal simple seta on distal segment. Exopod slightly 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 2e): coxa without setae. Basis with 4 simple setae arranged 1+1+1+1. Endopod 3-segmented, with 0, 0 and 4 (2 simple, 2 long sparsely plumodenticulate) setae, respectively. Exopod slightly 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Pleon (Fig. 3a, b): five somites. First somite smooth. Second to fifth somites with one pair of posterodorsal simple seta. Second and third somites with one pair of dorsolateral processes. Fourth and fifth somites with long and acute posterolateral processes; pleopods absent.

Telson (Fig. 3a–c): telson furcae distally spinulated and slightly curved outward, with 1 pair of well-developed lateral spines (spinulated only on the posterior margin), 1 pair of plumose setae posteriorly to the well-developed spines, and one pair of dorsal spines (spinulated only on the proximal inner margin); inner margin with 3 pairs of plumose setae.

DISCUSSION

According to Clark and Ng (2010), the characters that separate the early stages of zoeae of the species of superfamily Trapezoidea are: the spinulation of the antennal protopod, the terminal setation of the antennule, the setation of the maxillule, maxilla, first and second maxillipeds, and medial and dorsolateral processes of the abdominal somites (see Tab. 1). The antennal morphology of *D. acanthophora* follows that observed for the other genera of the superfamily Trapezoidea (Tab. 1). However, the distal spinulation of the antennal protopod in these genera is variable. The antennal protopod and its distal spinulation of *D. acanthophora* is similar to that of *Domecia glabra* Alcock, 1899 and *Calocarcinus africanus* Calman, 1909, which is formed by two rows of similar size spines. Other trapezioids have a distinct spinulation of the antennal protopod: *Quadrella maculosa* Alcock, 1898 and *Quadrella serenei* Galil, 1986 show an antennal protopod distally multispinulated (Clark and Ng, 2006); *Tetralia cavimana* Heller, 1861 and *Tetralia*

rubridactyla Garth, 1971 present two rows of variable size distal spines (Clark and Galil, 1988; Clark and Ng, 2006); *Trapezia cymodoce* (Herbst, 1799) and *Trapezia richtersi* Galil & Lewinsohn, 1983 present two rows of distal spines arranged sparsely (Clark and Galil, 1988; Shikatani and Shokita, 1990; Al-Aidaroos, 1992; Clark and Ng, 2006).

The morphology of the larval stages of decapod crustaceans is used in studies to evaluate phylogenetic questions (e.g. Marques et al., 2003; Barros-Alves et al., 2013; Guerao et al., 2014). According to phylogenetic analysis, Clark and Ng (2010) suggested that the genera *Domecia*, *Quadrella* Dana, 1851, *Tetralia* Dana, 1851 and *Trapezia* Latreille, 1828 are nested in one clade that is defined by the absence of seta 3.5 and seta 3.4 on the third endopodal segment of the second maxilliped (for details, see Clark and Guerao, 2008), and should be according to a synapomorphy defines the *Domecia + Tetralia + Trapezia* clade: the presence of one subterminal seta on the distal endopod segment of the maxillule (*vs.* two subterminal setae). Other synapomorphies define the sister group *Domecia + Tetralia*, including: the absence of a subterminal seta on the distal endopod lobe of the maxilla; and the absence of dorsolateral process on abdominal somites fourth and fifth (Clark and Ng, 2010). However, *D. acanthophora* presents two subterminal seta on the distal endopod segment of the maxillule and one subterminal seta on the distal endopod lobe of the maxilla. Thus, these features contradict the synapomorphies mentioned above, since they differ from observed by Clark and Ng (2010).

As previously discussed by Clark and Guerao (2008) and Clark and Ng (2010), *Calocarcinus* Calman, 1909 appears not to be related to the trapezioids. However, a similar morphological characteristic was observed for *C. africanus* and *D. acanthophora*: the presence of three pairs of lateral spines on the carapace. Therefore, the presence of this structure seems to be evidence that supports *Calocarcinus* relationship with the trapezioids (see Tab. 1), but further analysis is needed about this relationship.

Clark and Ng (2010) suggested, as autapomorphic features of *D. glabra*, the absence of setae on the proximal endopod segment of the maxillule, four terminal setae and one subterminal seta on the distal endopod segment of the maxillule, the basial setation

of the first maxilliped arranged as 2, 2, 3, 2, the first endopod segment of the first maxilliped bearing only one seta, and the endopod of the second maxilliped with only four (two subterminal and two terminal) seta in the distal segment. These characters were also observed for the first zoea of *D. acanthophora* in this study, except the number of subterminal seta on the distal endopod segment of the maxillule (two for *D. acanthophora* vs. one for *D. glabra*). Thus, we suggest that other characters could be synapomorphies of the genus *Domecia*.

Some characters of the first zoeal stage that could be used to distinguish *D. acanthophora* and *D. glabra* are: the number of aesthetascs in the antennula exopod (three and four, respectively); the number of spines in the lateral carapace (three pairs and two pairs, respectively), wherein the lower pair is not ventrally deflected as in *D. glabra*; the number of setae in the basial endite of maxilla (4+4 and 5+3, respectively); the pairs of spines on the telson (two and three, respectively); and furcae distally spinulate in *D. acanthophora* and smooth in *D. glabra* (see Tab. 1).

The first zoeal stage of *D. acanthophora* exhibits some characters that differ from the other Trapezioidae species, such as the presence of simple setae at the basis of the first maxiliped (*vs.* plumose setae); the presence of only two pairs of spines on the telson furcae (*vs.* three pairs); and telson furcae with one pair of plumose setae posteriorly to the well-developed spines (*vs.* absent) (see Tab. 1). Thus, these characters can be considered as autapomorphy of *D. acanthophora*. Therefore, to prove this hypothesis, it is necessary further zoea I descriptions for the remaining species of the superfamily Trapezioidae.

The current study expands the number of species with first zoeal morphology known in Trapezioidae. Thus, we assert in favor of future studies to increase the number of larval descriptions, and to improve larval culture techniques in the laboratory, enabling the culture of larval stages for the species that the cultivation techniques currently used not guarantee survival and complete larval development, thereby enabling knowledge of a greater number of stages for larval species. This would certainly help to solve taxonomic and phylogenetic problems in the infraorder Brachyura.

ACKNOWLEDGEMENTS

The authors are indebted to Dr. Maria Lucia Negreiros-Franozo, who gave us valuable suggestions for improving the manuscript. DFRA is grateful to CNPq - Conselho Nacional de Desenvolvimento Científico e Tecnológico (134950/2007-0) for his Master of Science fellowship. JAFP thanks Capes for a PhD scholarship. RCC is grateful to CNPq (PQ 305919/2014-8). We thank the “Omni Mare” Dive Center for the facilities provided during fieldwork. All sampling was conducted in accordance with applicable Brazilian state and federal laws with respect wild animals.

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