JOURNAL OF CRUSTACEAN BIOLOGY, 29(3): 364-372, 2009

FIRST ZOEAL STAGE AND MEGALOPA OF *UCA (UCA) MARACOANI* (DECAPODA: BRACHYURA), WITH COMMENTS ON THE LARVAL MORPHOLOGY OF SOUTH-AMERICAN SPECIES OF OCYPODIDAE

Maria L. Negreiros-Fransozo, Gustavo L. Hirose, Adilson Fransozo, and Eduardo A. Bolla, Jr.

(MLN, correspondence, mlnf@ibb.unesp.br; GLH; AF; EAB) Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, 18618-000 Botucatu, São Paulo, Brasil

ABSTRACT

On the Brazilian coast, ten species of fiddler crabs occur in the estuaries and mangrove systems. The larval development of only five of these species is completely known. Here we describe the first zoeal stage and megalopa of *Uca* (*Uca* s. str.) *maracoani*. Ovigerous females and megalopae were obtained at Jabaquara Beach, Paraty, state of Rio de Janeiro, Brazil. The first zoeal stage was obtained from ovigerous females in the laboratory, and the megalopae directly from the field. Both zoeae and megalopae were raised in laboratory conditions. The megalopae survived until the eighth juvenile stage, when they could be identified to species. The larval morphology was analyzed and compared with the species already known for the Brazilian coast, and some other species, such as the southeast Atlantic fiddler crab, *Uca tangeri*. The comparison showed that *U. maracoani* has some characteristics that are more similar to *U. tangeri* than the previously studied species from the Brazilian coast. This is the first description of the zoea and megalopa morphology of a member of the genus *Uca* from the southwest Atlantic, of which the adult has a narrow front sensu Crane (1975), and it is helpful for taxonomic, systematic and ecological purposes.

KEY WORDS: Brazilian coast, fiddler crab, larval morphology, Ocypodidae, *Uca*

DOI: 10.1651/08-3087.1

INTRODUCTION

The superfamily Ocypodoidea, according to Števčić (2005) and Ng et al. (2008), consists of eight families (Captamdriidae, Dotillidae, Heloeciidae, Macrophthalmidae, Mictyridae, Ocypodidae, Ucididae, and Xenophthalmidae). Only Ocypodidae and Ucididae are represented on the Brazilian coast, by members of the genera *Uca* Leach, 1814 and *Ocypode* Weber, 1795 of the former family, and *Ucides* Rathbun, 1897 of the latter family.

Ten species of the genus *Uca* Leach, 1814 occur along the Brazilian coast. They can be arranged in distinct subgenera, and classified in two groups: narrow-fronted fiddler crabs (one subgenus) and broad-fronted fiddler crabs (two subgenera) (Bott, 1973; Crane, 1975). These species of *Uca* are: *U.* (*Uca* s. str.) *maracoani* (Latreille, 1802–1803), with a narrow front (sensu Crane, 1975); *U. (Minuca) thayeri* (Rathbun, 1900), with apparently an intermediate front but classified as broad front; and *U. (Minuca) rapax* (Smith, 1870), *U. (Minuca) vocator* (Herbst, 1804), *U. (Minuca) mordax* (Smith, 1870), *U. (Leptuca) leptodactylus* Rathbun, 1898, *U. (Leptuca) uruguayensis* (Nobili, 1901), *U. (Leptuca) cumulanta* Crane, 1943, *U. (Minuca) burgersi* Holthuis, 1967, and *U. (Minuca) victoriana* von Hagen, 1987, with a wide front (sensu Crane, 1975). This subdivision, established by Crane (1975), has been contested by some authors, who have used new techniques in order to evaluate and reorganize the groupings; for instance, Levinton et al. (1996) used ADNr 16s base sequences, and Rosenberg (2001) carried out a morphological phylogenetic analysis based on 236 discrete characters. More recently, Beinlich and von Hagen (2006) proposed a new subdivision, adopted here, recognizing eight subgenera for *Uca* (*Australuca*, *Tubuca*, *Gelasimus*, *Uca* s. str., *Cranuca*, *Paraleptuca*, *Leptuca*, and *Minuca*).

The larval development of ocypodid crabs is well known for several species worldwide. The larval development of *Ocypode quadrata* (Fabricius, 1787) was completely described by Díaz and Costlow (1972). There are also five species of the genus *Uca* occurring in Brazil for which the complete larval development is described: *U. thayeri* by Anger et al. (1990); *U. vocator*, *U. uruguayensis*, *U. mordax*, and *U. burgersi* by Rieger (1996, 1997, 1998, 1999). Additionally, the first zoeae of *U. leptodactylus* and *U. rapax* were described by Batistelli (2003).

In a pioneer paper, Hyman (1920) studied the post-embryonic development of three fiddler-crab species: *Uca (Leptuca) pugilator* (Bosc, 1802), *U. (Minuca) minax* (Le Conte, 1855), and *U. (Minuca) pugnax* (Smith, 1870). She obtained several juvenile stages of *U. pugilator* and was also able to identify the sex by means of the secondary sexual characters of the individuals raised. Subsequent to her work, other authors treated the larval development of ocypodid species, such as Rabalais and Cameron (1983), Pasupathi and Kannupandi (1988), and Jang et al. (1991).

In the present study, we describe the morphology of the zoea I and the megalopa of *U. maracoani* (Latreille, 1803), the only 'narrow front' species occurring on the Brazilian coast. We compare the larvae of other species of Ocypodidae (sensu Ng et al., 2008) previously described for the South Atlantic, in order to offer data for new studies on phylogeny, biogeography, and planktology.

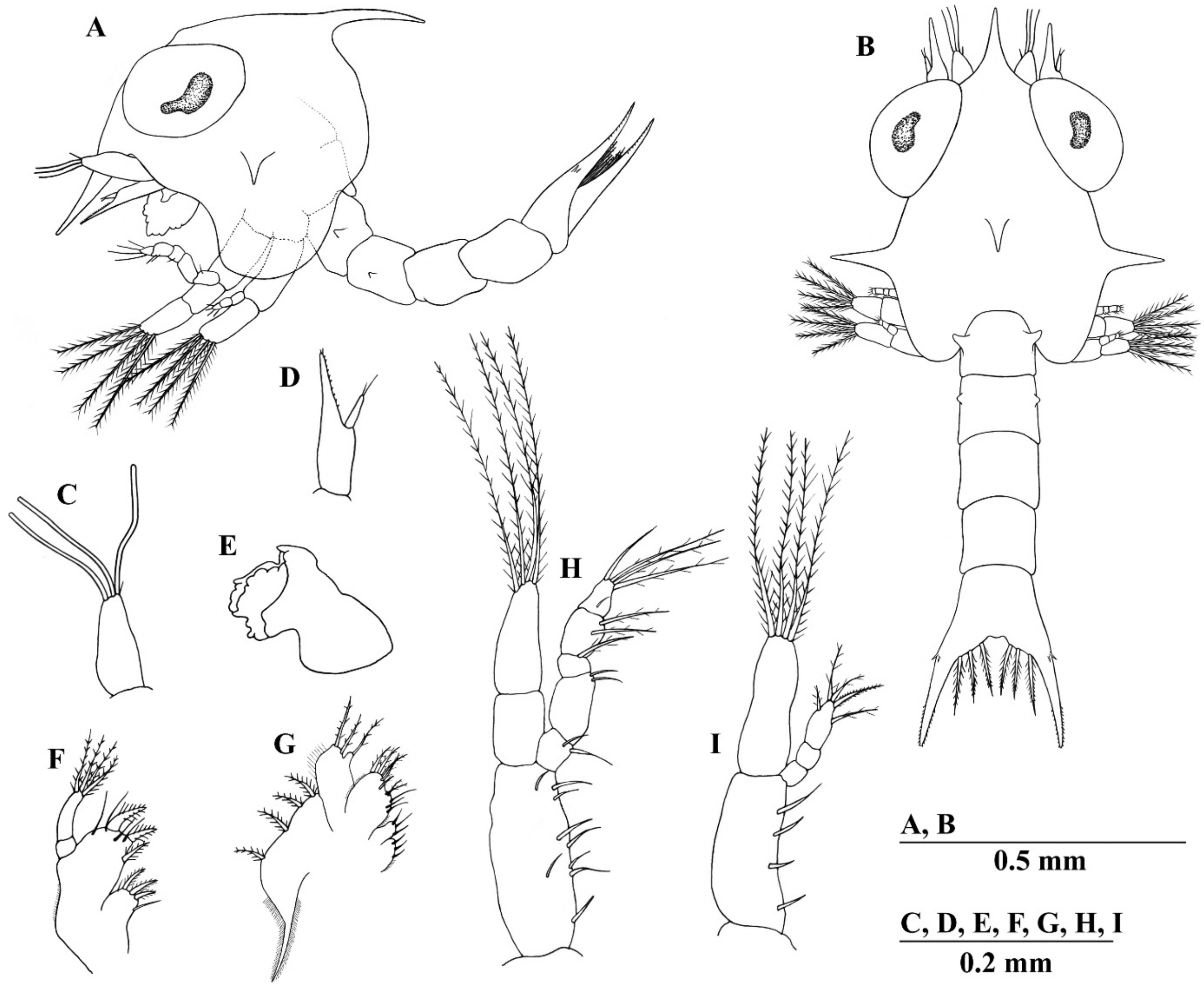

Fig. 1. *Uca (Uca) maracoani*. Zoea I: A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped.

Material and Methods

The fiddler crab *U. maracoani* is distributed in the Western Atlantic, in the Antilles, Venezuela, Guyanas, and Brazil (from the states of Maranhão to Paraná), according to Melo (1996). Specimens of the fiddler crab *Uca cumulanta* Crane, 1943 could also be found living near the mud flat where *U. maracoani* was obtained. Ovigerous crabs and megalopa larvae were collected at a mud beach named Jabaquara, in Paraty, state of Rio de Janeiro, Brazil, during low-tide periods. The larvae (zoea I) were obtained from ovigerous females maintained in the laboratory until their eggs hatched. The megalopae specimens were captured with small coffee spoons and immediately transferred to plastic containers with water from the collecting site.

In the laboratory, the megalopae were placed in individual containers and received an identification number. As soon as they molted and reached more advanced stages (juveniles), we were able to identify them to species level with confidence by checking carapace shape and front size. Both megalopa and early juvenile stages of *U. maracoani* are larger than *U. cumulanta*, the other species that was raised up to juvenile stages. The remaining specimens of other species were kept in the scientific collection for further studies.

All the containers were inspected daily for the presence of molts and to record the changes of stages. Both zoea and megalopa larvae were fed with newly hatched *Artemia* sp. nauplii and had their water renewed daily. No zoea I molted to the next stage. In short, the larvae were reared as described by Negreiros-Fransozo et al. (2007).

The exuviae and the dead crabs were conserved in the scientific collection of the NEBECC (Study Group on Crustacean Biology, Ecology and Culture) with their respective data on rearing.

Drawings were made with the aid of a camera lucida. Measurements were made under an optical microscope (Axioskop 2, Zeiss) provided with an image system (Axiovision, Zeiss). Dimensions measured on each zoea were: (CL) carapace length from between the eyes to the posterior margin of the carapace; (CW) maximum width of the carapace in a frontal view, without the spines; (CWS) maximum width of the carapace in frontal view, including the spines; (RS) rostral spine length; and (DS) dorsal spine length. Dimensions measured on each megalopa were: (CL) carapace length from the tip of the rostrum to the posterior margin of the carapace; and (CW) maximum width of the carapace.

The figures were prepared based on at least 10 specimens of each stage studied, and followed literature recommendations (see Clark et al., 1998 and Pohle et al., 1999). Setae terminology also follows Garm (2004).

Results

Description of the zoea I (Fig. 1)

CL = 0.396 ± 0.011 mm; CW = 0.276 ± 0.008 mm; CWS = 0.459 ± 0.013 mm; RS = 0.19 ± 0.012 mm; DS = 0.192 ± 0.010 mm).

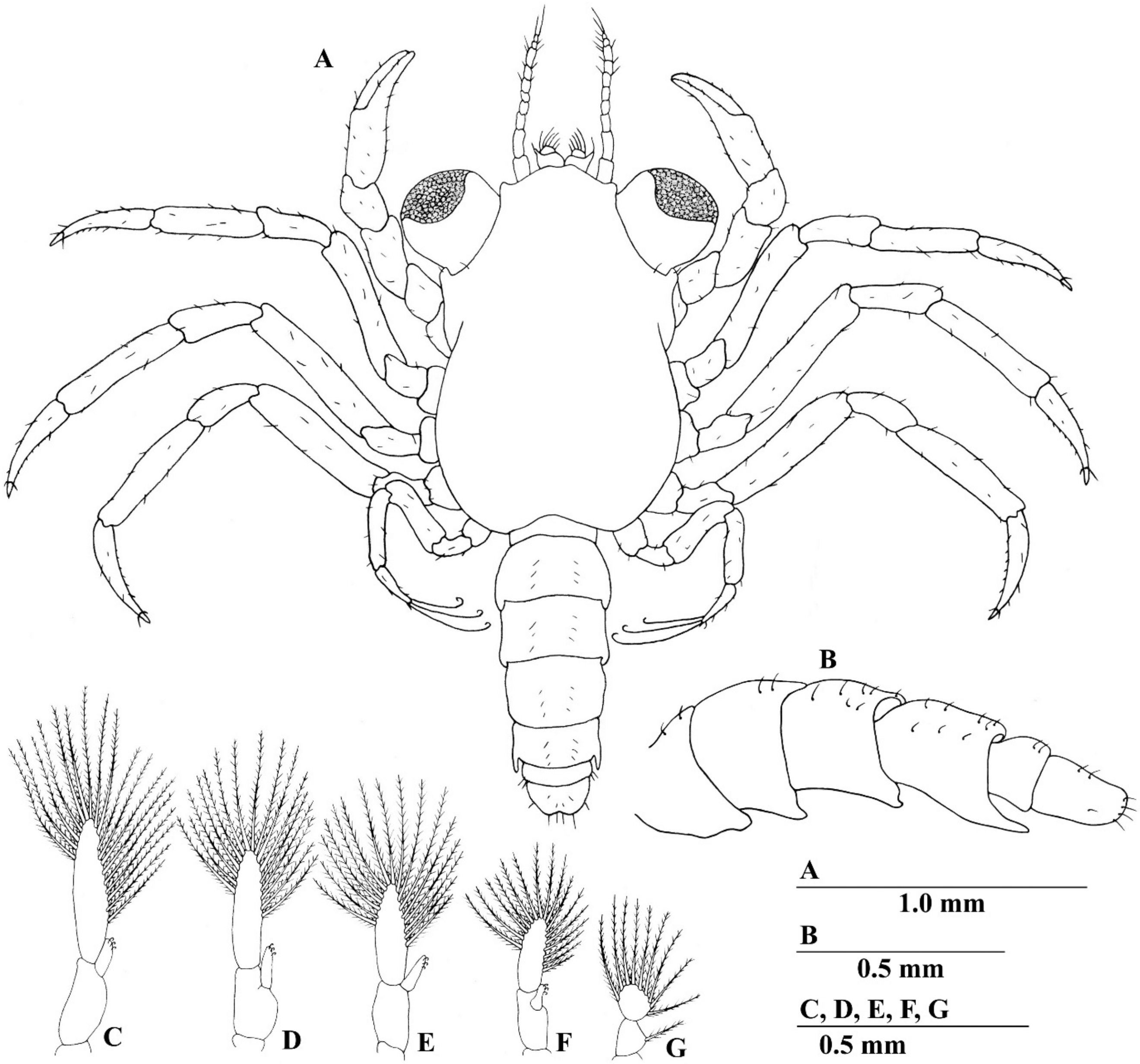

Fig. 2. *Uca (Uca) maracoani*. Megalopa: A, dorsal view; B, lateral view of pleon; C-F, pleopods from second to fifth abdominal segments; G, uropod.

The carapace (Fig. 1A, B) is round, and is provided with 1 rostral, 1 dorsal, and 2 lateral spines. The eyes are sessile.

The antennule (Fig. 1C) is unsegmented, and has 3 long aesthetascs and simple setae.

The antenna (Fig. 1D) protopod has 2 opposite rows of very small denticles; the exopod is small (around 1/4 to 1/5 of the protopod), with 2 simple setae.

Mandible (Fig. 1E) with molar and incisive process.

Maxillule (Fig. 1F) with the endopod two-segmented, with 3 terminal plumose setae; coxal endite with 3 strong setae and 2 simple setae; basal endite with 3 cuspidate setae and 4 simple setae. It was not possible to observe microtrichae on the maxillule. Exopodal setae absent.

Maxilla (Fig. 1G) with the endopod unsegmented, bearing 2 terminal plumose setae and 1 subterminal seta, as well as several microtrichae on the external margin; exopod with 4 plumose marginal setae and a plumose apical process; coxal endite bilobed with 6 simple setae, and basal endite bilobed with 5(7) simple setae on the proximal lobe and 2(3) simple setae and 2 serrate setae on the distal lobe.

First maxilliped (Fig. 1H) with basis bearing 9 simple setae arranged 3+2+3+1; endopod five-segmented with 0(2), 0(2), 1, 2, and 4 (5) plumose setae (but with a very few setules); exopod two-segmented, with 4 long plumose setae on its tip.

Second maxilliped (Fig. 1I) with basis bearing 4 simple setae arranged 1 + 1 + 1 + 1; endopod three-segmented with 0, 0, and 4 plumose setae (with very few setules) and 1 serrate seta; exopod unsegmented, with 4 long plumose setae.

There is no evidence of a rudimentary third maxilliped, or rudimentary pereiopods.

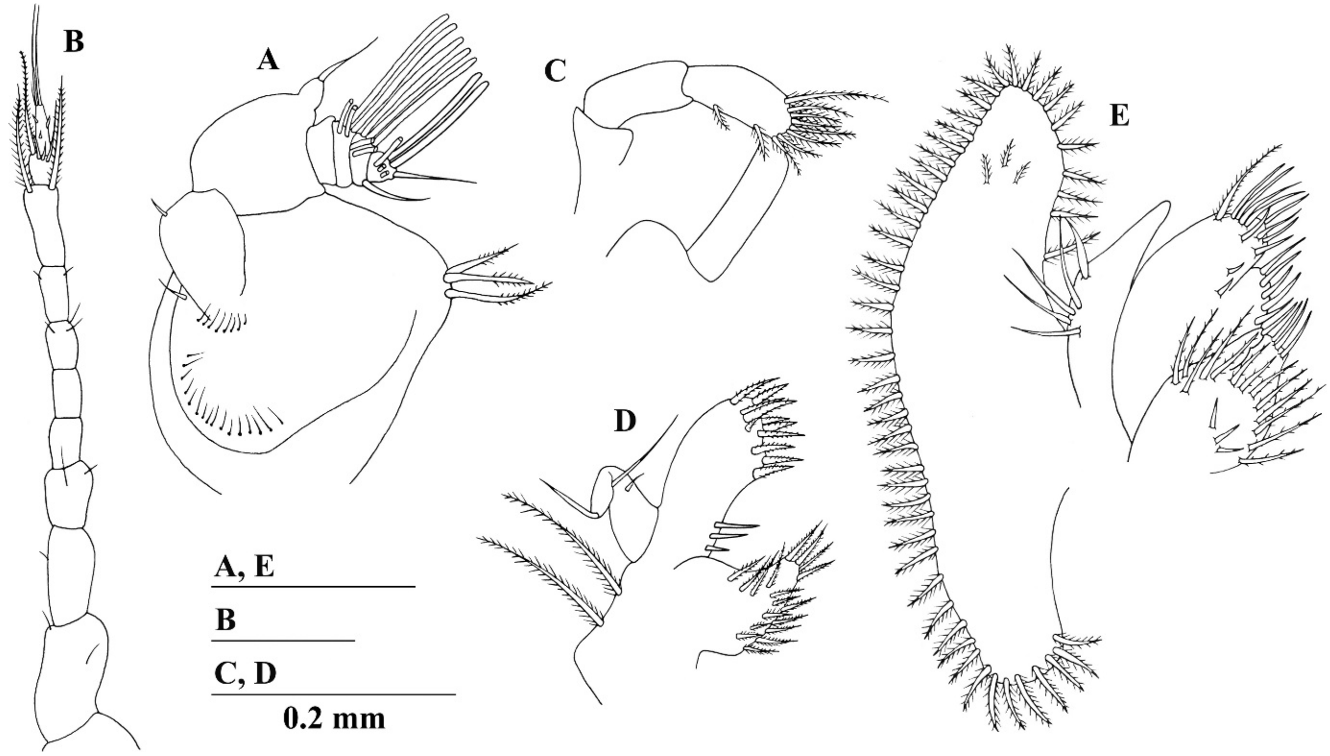

Fig. 3. *Uca (Uca) maracoani*. Megalopa: A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla.

The pleon (Fig. 1B) is constituted by 5 somites, without appendages, and the first somite is partly or totally covered by the cephalothorax. In the median region of each of the second and third pleomeres there is a pair of dorsolateral processes. The telson (Fig. 1A, B) has a pair of small outer lateral spines on each furca, and 6 terminal processes arranged 3 by 3 on each side of the small median notch.

Description of the megalopa (Figs. 2 to 4)

CL = 0.777 ± 0.019 mm; CW = 1.226 ± 0.018 mm.

Carapace (Fig. 2A) subquadrate, convex dorsally, with few small simple setae sparsely distributed on its surface, those on the orbital region being the most evident. Eyes pedunculate. The pereiopods, pleopods and uropod appear differentiated at this stage.

The antennule (Fig. 3A) has the proximal segment well developed, with 3 plumose setae, 1 simple seta near the peduncle, and two rows of simple setae, the first row near the peduncle and the other in the marginal region of the proximal segment. The peduncle is two-segmented, with 1 simple seta on the proximal segment. Endopod with 1 simple seta. Exopod four-segmented, with the proximal segment smooth, the second segment with 4 aesthetascs, the third segment with 5 aesthetascs and 1 simple seta, and the distal segment with 5 aesthetascs and 1 simple seta.

The antenna (Fig. 3B) has a three-segmented peduncle, with 2, 1, 2 simple setae. Antennal flagellum composed of 7 segments, with 0, 0, 3, 2 simple setae from the first to the fourth segment; 2 plumose setae on the fifth segment; 1 plumose seta and 3 simple setae on the sixth segment; and 3 simple setae on the seventh segment.

Mandible (Fig. 3C) with a well-chitinized blade, palp two-segmented with 10 plumose setae on the distal segment.

Maxillule (Fig. 3D) with protopod bearing 2 plumose setae (exopodal and epipodal). Unsegmented endopod with 2 simple subdistal setae and 1 terminal seta. Coxal endite with 18 plumose setae. Basal endite with 11 cuspidate setae and 3 simple setae.

Maxilla (Fig. 3E) with unsegmented endopod bearing 5 simple setae. Scaphognathite (exopod) with 51(54) marginal plumose setae and 3 setae on blade surface. Coxal endite with 1 and 5 simple setae on distal lobe; 8 plumose setae and 6 simple setae, of which 3 are proximal and 3 are distal, on the proximal lobe. Basal endite bearing 11 simple setae and 1 plumose seta on the distal lobe, and 5 simple setae on the proximal lobe.

First maxilliped (Fig. 4A) with unsegmented endopod bearing 5 simple setae. Exopod two-segmented, with 3 plumose setae on proximal segment and 4 plumose setae on distal segment. Coxal endite bearing 13 simple setae, and basal endite with 11 simple setae. Epipod with 11 simple setae.

Second maxilliped (Fig. 4B) with endopod four-segmented, bearing 1 simple setae on proximal segment, 1 plumose and 1 simple seta on second segment, 5 serrate setae and 1 simple seta on third segment, and 9 serrate setae on distal segment. Exopod two-segmented, with 2 plumose setae on the proximal segment and 5 plumose setae on the distal segment. Epipod reduced, with 1 distal plumose seta.

Third maxilliped (Fig. 4C) with protopod smooth. Endopod five-segmented, with 12 simple setae on proximal

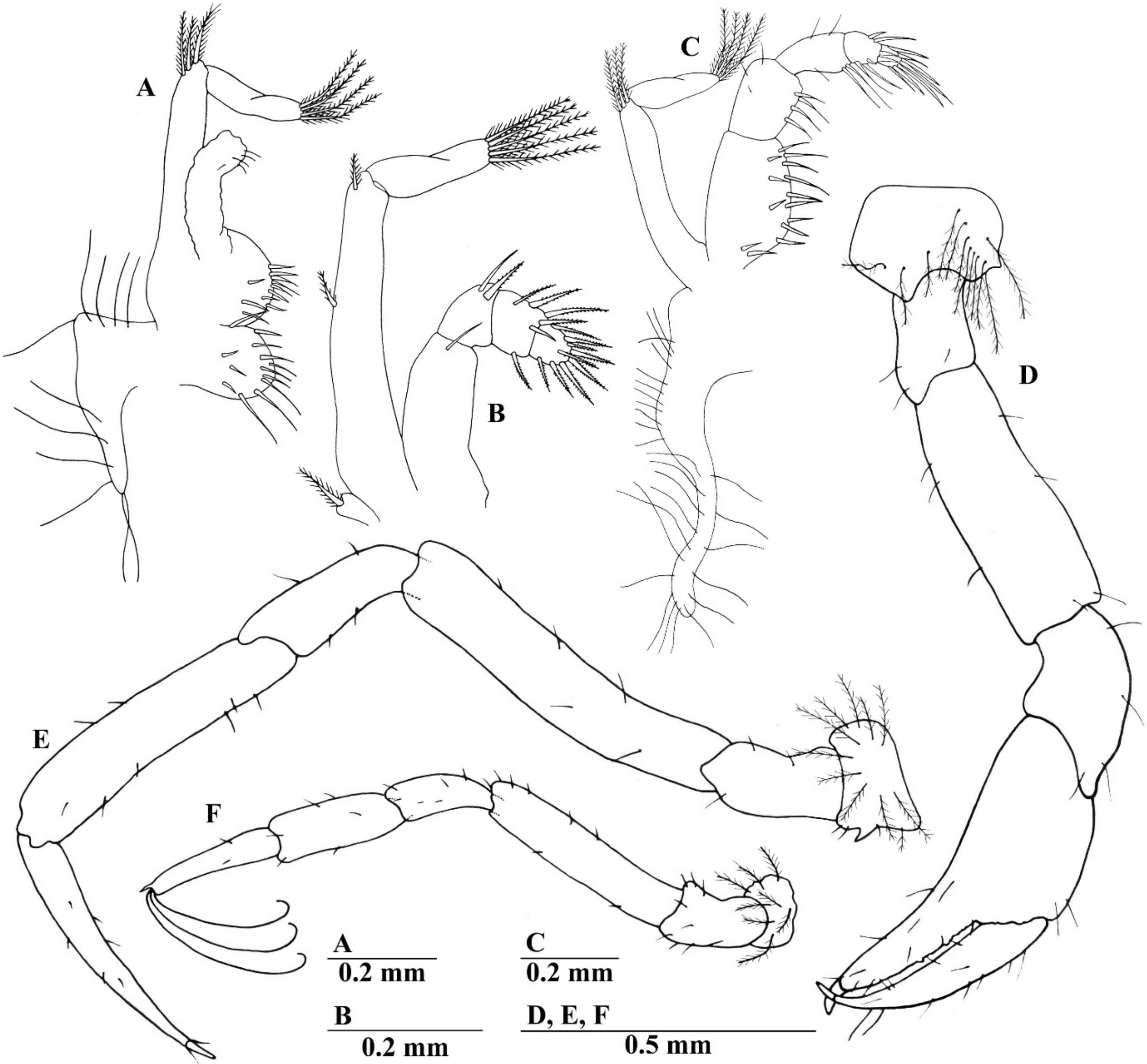

Fig. 4. *Uca (Uca) maracoani*. Megalopa: A, first maxilliped; B, second maxilliped; C, third maxilliped; D, cheliped; E, third pereiopod; F, fifth pereiopod.

segment, 7 simple setae on second segment, 5 simple setae on third segment, and 7 simple setae on each of fourth and fifth segments. Exopod two-segmented, with 3 plumose setae on proximal segment and 4 plumose setae on distal segment. Epipod with 27 simple setae.

Symmetrical chelipeds (Fig. 4D) with segments provided with small simple setae; the basis has a small spine and 12 to 14 plumose setae; inner propodus margin with 2 small teeth. Second to fourth pereiopods (Fig. 4E) have similar shapes, covered by small simple setae; on the basis of the third pereiopod is a small spine; and 8 to 10 plumose setae on their basis. Fifth pereiopod (Fig. 4F) has 3 hooked setae and an acute spine on the distal portion of the dactyl.

The pleon (Fig. 2B) corresponds to 4/5 of the carapace length. The fifth pleomere has a postero-lateral projection on each side that reaches the middle of the sixth somite. The telson is rounded, and bears some small simple setae on its surface and posterior border.

There are 4 pairs of pleopods (Fig. 2C to F) located ventrally on the pleon from the second to the fifth somites. They decrease in size from the first pair to the last one. The exopod has respectively, 18, 16, 16, 16 plumose setae from the second to the fifth somites, and all the endopods have 3 cincinnuli each.

The uropod (Fig. 2G) is located ventrally on the sixth pleomere, and is smaller than the pleopods. The uropod has 9 plumose setae on the exopod, and 1 plumose seta on the protopod.

Discussion

The number of zoeal stages in the development of ocypodid crabs from the Brazilian coast ranges from 4 to 6 in *U.*

Table 1. Comparison of morphologic characters of the first zoeal stage in Ocypodidae previously described from Brazilian coast. s = segment; p = proximal; d = distal; ss = simple setae; pl = plumose setae; sr = serrate setae; sp = spine; pd = plumodenticulate setae; * = obtained from original figures.

Structure	Characters	*Ocypode quadrata*	*Uca rapax*	*Uca mordax*	*Uca burgersi*	*Uca thayeri*	*Uca vocator*	*Uca leptodactylus*	*Uca uruguayensis*	*Uca maracoani*
References		Diaz and Costlow (1972)	Batistelli (2003)	Rieger (1997)	Rieger (1998)	Anger et al. (1990)	Rieger (1999)	Batistelli (2003)	Rieger (1996)	Present paper
Carapace	Lateral spines	present	absent	absent	absent	absent	absent	absent	absent	present
Pleon	Lateral Process 5th somite	absent	absent	present	absent	absent	present	absent	absent	absent
Telson	Lateral spines	absent	absent	absent	absent	absent	absent	absent	absent	2 small
Antennule	Number of simple setae	2	1	1,2	1	1	1(2)	1	1 (2)	1
	Number of aesthetascs	2	3	2 (3)	2 (3)	2	2	3	3	3
Antenna	Exopod	2ss	2 ss and 1 sp	3 ss	3 ss	3 ss	3 ss	absent	3 ss	2 ss
Maxillule	Endopod	2s: 0,4 pl	2s: 0, 4 pd	2s: 0,4 pl	2s: 0,4 pl	2s: 0,4 pl	2s: 0,4 pl	2s: 1, 5 pd	2s: 0,4 pl	2s: 0,3 pl
	Basial endite	5 sr	5 pd	5 pl	5 pl	4sr* + 1pl	5 pl	5 pd	5 pl	2 sp, 5ss
	Coxal endite	5 sr	5 pd	5 pl	5 pl	4 sr*	5 pl	6 pd	5 pl	6 ss
Maxilla	Endopod	3 pl	3 pd	3 pl	3 pl	3 ss	3 pl	4 pd	3 pl	3 pl
	Exopod	4 pl	4 pl	5 pl	5 pl	4 pl	5 pl	4 pl	5 pl	4 pl
	Plumose Apical process	absent	present	absent	absent	absent	absent	absent	absent	present
	Basial endite: p,d	5, 4 pl	5; 4 pd	5; 4 pl	4; 4 pl	3, 5 pl	5(4); 4 pl	5; 4 pd	5; 4 pl	5 ss; 2 sr, 3ss
	Coxal endite: p,d	3, 3 pl	3; 3 pl	3(4); 3 pl	3; 3 pl	3, 3 pl	3; 3 pl	3; 5 pl	3; 3 pl	3; 3 ss
First Maxilliped	Endopod	5s: 2,2,1,2,5 ss	5s: 2,2,1,2, 5 pd	5s: 2,2,1,2,5 ss	5s: 2,2,1,2,5 ss	5(4)s: 0,1,1,2,4 (5) ss	5s: 2,2,1,2,5 ss	5s: 1,2,1,2,5 pd	5s: 2,2,1,2,5 ss	5s: 2ss, 2ss,1pl, 2pl, 2ss + 3pl
	Exopod	2s: 0, 4 pl	1s: 4 pl	2s: 0,4 pl	2s: 0,4 pl	2s: 0,4 pl	1s: 4 pl	1s: 4 pl	2s: 0,4 pl	2s: 0,4 pl
	Basipod	8 pl	9 pd	9 ss	9 ss	6 ss	9 ss	8 pd	9 pl	9 ss
Second Maxilliped	Endopod	3s: 0, 0, 5 ss	3s: 0,0,5 pd	3s: 0,0,1pl + 4ss	3s: 0,0,1pl + 4ss	3s: 0,0,4 ss	3s: 0,0,1pl + 4ss	3s: 0,1,5 pd	3s: 0,0,1pl + 4 ss	3s: 0,0,1ss + 4pl
	Exopod	4 pl	4 pl	4 pl	4 pl	4 pl	4 pl	4 pl	2s: 0,4 pl	4 pl
	Basipod	4 pl	4 pd	4 ss	4 ss	4 ss	4 ss	4 pd	4 pl	4 ss

Table 2. Comparison of the morphologic characters of the megalopa of Ocypodidae previously described from Brazilian coast. s = segment; p = proximal; d = distal; ss = simple setae; pl = plumose setae; sr = serrate setae; pd = plumodenticulate setae; ae = aesthetascs * = obtained from original figures.

Structure	Characters	*Ocypode quadrata*	*Uca mordax*	*Uca burgersi*	*Uca thayeri*	*Uca uruguayensis*	*Uca vocator*	*Uca maracoani*
References		Diaz and Costlow (1972)	Rieger (1997)	Rieger (1998)	Anger et al. (1990)	Rieger (1996)	Rieger (1999)	Present paper
Pleon	Presence of lateral process	Not mentioned	5th somite	2nd, 3rd, 4th, 5th somites	absent	4th, 5th somites	2nd, 3rd, 4th, 5th somites	5th somite
Telso	Number of setae	17 pl + 10 ss	4 pl	Several ss	9 ss	2 pl + several ss	6 ss*	4 ss
Antennule Number of setae	Basial segment	14 pl	3 (2) pl	5 pl	Not mentioned	5 pl	1 pl	3 pd + 25 ss
	Peduncle	2s: 9, 8 pl	2s: 1 pl	2s: 2, 0 pl	1 ss*	2s: 2, 0 pl	2s: 2, 0 pl	2s: 1, 0 ss
	Endopod	3 pl	2 pl	2 pl	Not mentioned	2 pl	2 pl	1 ss
	Number of aesthetascs on exopod	3s: 11, 8, 6 ae	3s: 0, 8(7), 5(4) ae	3s: 0, 8(7), 4(3) ae	3s: 0, 7, 3 ae*	3s: 0, 7, 5 ae	3s: 0, 6(5), 5(6) ae	4s: 0, 4, 5, 5 ae
	Exopod	3s: 0, 4 + 1, 2 pl	3s: 0, 0, 1ss	3s: 0, 0, 1 ss	3s: 0, 0, 2ss*	absent	absent	4s: 0,0,1,1 ss
Antenna	Peduncle	3s: 1, 2, 3 ss	3s: 1, 1, 1ss	3s: 1, 1, 2 ss	3s: 1, 1, 1 ss	3s: 0, 1, 1 ss	3s: 1, 1, 2 ss	3s: 0,0,2 ss
	Flagellum	7s: 0, 0, 5, 2, 6, 3, 3 ss	7s: 0, 1(0), 1(0), 1(2), 4(3), 2(1), 2(3) ss	7s: 0, 0, 3(2), 0, 4(3), 1(2), 2 ss	7s: 0, 0, 2, 1, 3, 1, 3 ss	7s: 0, 0, 2, 0, 3, 1, 3 ss	7s: 1, 0, 2, 0, 3, 1, 2 ss	7s: 0, 0, 3ss, 2ss, 2 pl, 1 pl + 3ss, 6ss
Mandible	Palp	2s: 2, 18 pd	2s: 0, 4 pl	2s: 0, 4 pl	1s: 4 ss	2s: 0, 4 pl	2s: 0, 4 pl	2s: 0, 10pl
Maxillule	Endopod	4 pl	2s: 1(0) ss, 1 pl	2s: 1, 2(1) pl	1 ss	1 pl + 1ss	2s: 0, 1(2) pl	3 ss
	Basial endite	16 pd + 16 sr	19(18) pl	20(18,19) pl	14 sr* + 5 pl	18 pl	16 (17, 18) pl	11 sr + 3ss
	Coxal endite	8 sr + 16 pd + 25pl	15(14) pl	16(15-17) pl	12 pl	14 pl	13(14, 15) pl	18 pl
	Protopod	3 pl	2 pl	2 pl	1 pl	2 pl	2 pl	2 pl
Maxilla	Endopod	7 pl	Setae absent	2pl	Setae absent	Setae absent	2 (0, 1) pl	5 ss
	Exopod	Several pl	43-49 pl	47(44-46,48) pl	35 pl*	43-49 pl	32-39 pl	51-54 pl + 3ss
	Basial endite: p;d	Total of 30 pl	7 pl; 8(7) pl	9(10); 8 pl	8; 8 pl*	7; 7 pl	7 (8) pl; 6 (7) pl	5 ss; 11 ss + 1 pl
	Coxal endite: p;d	Total of 40 pl	14(12-13); 7(6) pl	Total of 20(19,21) pl	4; 6 pl*	12; 6 pl	Total of 14 (15, 16, 17) pl	6 ss + 8 pl; 1 ss + 5 pl
First Maxilliped	Coxal endite	25-30 pl	6-9 pl	8(7-9) pl	6 ss*	7(8) pl	7 (6) pl	13 ss
	Basial endite	25-30 pl	7-9 pl	7(8) pl	6 ss*	7(6) pl	8 (9) pl	11 ss
	Endopod	8 pl	4pl + 1ss	5(4) pl + 1ss	2 ss*	4(5) pl	4 (3) pl	5 ss
	Exopod	2s: 4, 3 pl	2s: 3, 3 pl	2s: 2, 3 pl	2s: 2, 4 pl*	2s: 2, 3 pl	2s: 2, 3 pl	2s: 3,4 pl
	Epipod	20 pl	6 ss	7 ss	7 ss*	6 (7) ss	5 (3, 4) ss	11 ss
Second Maxilliped	Endopod	4s: 8, 3, 10, 10 pl	4s: 0, 1, 4, 6(7,8) pl	3s: 1, 4, 7 pl	3s: 1 pl*, 4 pl*, 6 sr*	3s: 1, 4, 7 pl	3s: 1(2), 3(4,5), 7(6) pl	4s: 1ss, 1ss + 1sr, 5sr + 1ss, 9sr
	Exopod	2s: 12, 2 pl	2s: 1 ss, 4 pl	2s: 1, 4 pl	2s: 0, 4 pl*	2s: 1, 4 pl	2s: 1, 4 pl	2s: 2, 5 pl
	Epipod	10 pl	1 pl	1 pl	Not mentioned	1 pl	Not mentioned	1 pl
Third Maxilliped	Endopod	5s: several pd or pl	5s: 12(11), 6(7), 2(3), 5(4,6), 6 pl	5s: 11(10,12), 6(5), 3(4), 6, 6(5-7) pl	5s: 6, 2, 1, 3, 5 ss*	5s: 12(11), 7(6,8), 3, 6, 6 pl	5s: 8(6,7,10), 3(4,5), 4(2,3), 4(3,5), 6(7) pl	5s: 12, 7, 5, 7, 7 ss
	Exopod	2s: 2, 3 pl	2s: 0(1), 4 pl	2s: 1(2), 4 pl	2s: 1ss*, 1 ss* + 4 pl*	2s: 1, 4 pl	2s: 2, 4 pl	2s: 3, 4 pl
	Protopod	Not mentioned	5(6) pl	6(7) pl	Not mentioned	6(5,7,8) pl	3(4) pl	absent
	Epipod	Several pd or pl	6(5) pl + 13-15 ss	4(5) pl + 13ss	16 ss	6(5) pl + 11(12,13) ss	4(3,6) pl + 9 (7,8) ss	27 ss
Pleopod	Number of plumose setae on exopod	46; 44; 38; 33	16(17); 15(16); 14(15); 13(12,14)	17(16); 16(15); 15(16); 14	14; 14; 11; 14	16(17); 15(16); 14-16; 12-14	14(15,13); 13(12); 12(13,11); 10(12)	18;16;16;16
Uropod	Number of plumose setae	6 + 26 = 32	1 + 7(8) = 8(9)	1 + 8 = 9	1 + 7 = 8	1 + 7 = 8	1 + 6 = 7	1 + 9 = 10

uruguayensis, *U*. *mordax*, *U*. *burgersi*, and *U*. *vocator*. Consistently 5 zoeal stages are found in *O*. *quadrata* and *U*. *thayeri*. Such variation in the zoeal number is not common among brachyurans, but it has been reported for some crabs, mainly estuarine intertidal species (Spivak and Cuesta, in press).

According to Anger (2001), the additional zoeal stages in crabs have been associated with unfavorable combinations of temperature and salinity. Nevertheless, some species of *Uca* showed variations even when they were reared under favorable conditions (Rieger, 1996, 1997, 1998). This suggests another cause for long pathways: we could suppose that some estuarine species have larval adaptations to some environmental factors (tidal regime, for instance), in order to extend their development to await a better occasion for settling.

In a comparative analysis of existing morphological descriptions for zoea I among Ocypodidae, some features can be used to distinguish the larvae of *O*. *quadrata* and *U*. *maracoani* from other *Uca* species: both have lateral spines on the carapace (Table 1). This character is helpful in the southwestern Atlantic ocypodid larvae identification, because only the first zoeae of *O*. *quadrata* and *U*. *maracoani* have lateral spines on the carapace. Additionally, the zoea I of *U*. *maracoani* has two small lateral outer spines on each telson furca (Table 1), which is not observed in any other zoea of the genus *Uca* that occurs in the same area. Recently, Spivak and Cuesta (2009) found 3 small lateral spines on each telson furca of the zoea I of *U*. *tangeri* (Eydoux, 1835), which occurs only in the southeastern Atlantic.

Additional characters that identify the zoea of *Uca* can be found in the number of setae on the maxilla (basal lobe) and the first maxilliped (endopod) (Table 1).

With respect to the megalopa stage, the morphological features obtained for *U*. *maracoani* are also useful to distinguish the larvae of the genus *Uca* from other Ocypodidae that are described from the South Atlantic. Differentiation is mainly by the presence of a spine on the basis of the chelipeds and third pereiopod, which do not occur in any of the ocypodid species described until now, or in *U*. *tangeri* from the southeast Atlantic. With these characters, which are easy to check, one can differentiate the megalopa of *U*. *maracoani* from those of the subgenera *Leptuca* and *Minuca*, or the genus *Ocypode*. An additional feature can assure a more-confident identification, such as the number of segments of the antennular exopod. Differences among other structures are listed in Table 2. Crane (1940) noted certain differences in the number of setae on the exopod of the fifth pleopod for the separation of *Ocypode* and *Uca*. Similar differences were observed in this study: *U*. *maracoani* has only 16 plumose setae on the exopod of the fifth pleopod (Table 2).

Comments on Larval Morphology and *Uca* Relationships

The morphological features of the first zoea and megalopa of *U*. *maracoani* do not resemble any other *Uca* species previously described for the American species. The only species described for the genus *Uca* worldwide, whose morphological larval features agree with those of *U*. *maracoani*, is *U*. *tangeri*, which was described by Rodrigues and Jones (1993) and re-described by Spivak and Cuesta (in press).

According to Rice (1983), the study of the zoeae can indicate phylogenetic lines, depending on the identification of the basal and derived characters. This author also asserted that the evolutionary tendencies in the eubrachyuran zoeae indicate that the most advanced larvae show reductions of spines, setae, and segmentation compared to the most primitive ones. Both *U*. *maracoani* and *U*. *tangeri* have lateral spines on the carapace and telson, which have not been observed in any other zoea of the genus *Uca*. This feature could indicate a basal character for the subgenus *Uca* s. str., to what the above-mentioned species belong.

The relationships among the subgenera of *Uca* have often been discussed, based on taxonomy and morphology (Crane, 1975; Rosenberg, 2001), molecular biology (Levinton et al., 1996), and reproduction (Salmon and Zucker, 1987; Christy and Salmon, 1991; Murai et al., 1995). Taking into account our results, some evidence from larval morphology (presence of lateral spines on the carapace and telson) supports a link between a species from the southwest Atlantic (*U*. (*Uca* s. str.) *maracoani*) and another from the southeast Atlantic (*U*. (*Uca* s. str.) *tangeri*), both narrow-front species. Obviously, we assume here that previous larval descriptions of other *Uca* species did not overlook these spines.

We also consider the evidence of a fossil record from the Lower Miocene, reported by Brito (1993), who found a specimen identified as *U*. *maracoani*; this is the oldest fossil of a fiddler crab. This finding suggests that this fossil is an ancestor of the subgenus *Uca* s. str. Additionally, the results obtained by Levinton et al. (1996) suggest that *Uca* s. str. (*Uca* + *Afruca*, sensu Crane, 1975) arose within a proto-Atlantic realm, perhaps before the differentiation of the great Tethyan Sea that formerly connected tropical marine biotas from the Pacific to the Caribbean.

Considering that there is no molecular study including *U*. *maracoani* in the analysis, we must still use caution in splitting or grouping any subgenus of fiddler crabs as suggested by Spivak and Cuesta (2009).

Acknowledgements

The authors thank to the "Fundação de Amparo à Pesquisa do Estado de São Paulo - Fapesp" (04/15194-6) for financing this research; to NEBECC members for their help during field work; to José A. Cuesta for his helpful comments on the manuscript; and to Janet W. Reid for English corrections. The samplings were performed according to State and Federal laws concerning wild animals.

References

Anger, K., M. Montú, C. de Bakker, and L. L. Fernandes. 1990. Larval development of *Uca thayeri* Rathbun, 1900 (Decapoda, Ocypodidae) reared in laboratory. Meeresforschung 32: 276-294.

Batisteli, N. M. 2003. Descrição morfológica e aspectos evolutivos larvais em Ocypodoidea e grupos relacionados (Decapoda: Brachyura). Master of Science Dissertation - Instituto de Biociências de Botucatu, Universidade Estadual Paulista, Botucatu, São Paulo, ix+134 pp.

Beinlich, B., and H. O. von Hagen. 2006. Subdivision of the genus *Uca* Leach. Zoologische Mededelingen 80(2): 9-32.

Bosc, L. A. G. 1802. Histoire naurelle des Crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature. Paris 1: 1-258, pl.1-8.

Bott, R. 1973. Die verwandtschaftlichen Beziehungen der *Uca*-Arten (Decapoda: Ocypodidae). Senckenbergiana Biologica 54: 315-325.

Clark, P. F., D. K. Calazans, and G. W. Pohle. 1998. Accuracy and standardization of brachyuran larval descriptions. Invertebrate Reproduction and Development 33(2–3): 127-144.

Crane, J. 1940. Eastern Pacific expeditions of the New York Zoological Society, XVIII. On the post-embryonic development of brachyuran crabs of the genus *Ocypode*. Zoologica 25: 65-82.

———. 1943. Crabs of the genus *Uca* from Venezuela. Zoologica 28: 33-44, 1 pl.

———. 1975. Fiddler crabs of the world. Ocypodidae: Genus *Uca*. Princeton University Press, Princeton, New Jersey. 736 pp.

Díaz, H., and J. D. Costlow Jr. 1972. Larval development of *Ocypode quadrata* (Brachyura: Crustacea) under laboratory conditions. Marine Biology 15: 120-131.

Eydoux, F. 1835. Nouvelle espèce de *Gélasime*. Magazine de Zoologie 5, cl.7; 4 pp.

Fabricius, J. C. 1787. Mantissa insectorum sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specifis, emendationibus, observationibus I: i-xx, 1-348. Hafniae.

Garm, A. 2004. Revising the definition of the crustacean seta and setal classification systems based on examinations of the mouthpart setae of seven species of decapods. Zoological Journal of the Linnean Society 142: 233-252.

Hagen, H. O. von. 1987. Morphologie und Winkbalz einer neuen *Uca*-art (Crustacea: Brachyura) aus dem Staat Espirito Santo (Brasilien). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 84: 81-94.

Herbst, J. F. W. 1782-1804. Versuch einer naturgeschichte der krabben und krelse nebst einer systematischen beschreibung iher verscheidenen arten. Vol. 1-3. Gottlieb August Lange, Berlin & Stralsund. 515 pp, 62 pls.

Holthuis, L. B. 1967. On a new species of *Uca* from the West Indian region (Crustacea: Brachyura: Ocypodidae). Zoologische Mededelingen 42: 51-54.

Hyman, O. W. 1920. The development of *Gelasimus* after hatching. Journal of Morphology 33: 485-525.

Jang, K., C. H. Kim, and D. R. Fielder. 1991. The complete larval development of *Ilyoplax pingi* Shen, 1932 (Decapoda, Brachyura, Ocypodidae) reared in the laboratory. Crustaceana 60: 123-138.

Latreille, P. A. 1803. Histoire naturelle, générale et particulière des crustacés et des insects. Ouvrage faisant suit aux Oevres de Leclerc de Buffon, et partie du Cours complete d'Histoire naturelle rédigé par C. S. Sonnin, membre de plusié Société savantes Paris, Dufart. V. 5, 1-407, vol. 6, 1-391.

Le Conte, J. 1855. On a new species of *Gelasimus*. Proceedings of the Academy of Natural Sciences of Philadelphia 7: 402-403

Leach, W. E. 1814. Crustaceology, In, D. Brewster (ed.), The Edinburgh Encyclopedia 7: 383-437, pl. 221.

Levinton, J., C. Stumbaker, and J. Christy. 1996. Molecular and biogeography: resolution of a controversy over evolutionary history of a pan-tropical group of invertebrates. Journal of Experimental Marine Biology and Ecology 203: 117-131.

Linnaeus, C. 1763. Centuria insectorum quam, praeside. D. D. Car von Linné, proposuit Boas, Calmariensis, In, C. Linnaeus, Amoenitates Academicae, seu dissertations variae, physicae, medicae, botanicae, antehac seorsim editae, nunc collectae & auctae 6: 384-415.

Melo, G. A. S. 1996. Manual de Identificação dos Brachyura (Caranguejos e Siris) do Litoral Brasileiro. São Paulo, Ed. Plêiade. 603 pp.

Negreiros-Fransozo, M. L., E. L. Wenner, D. M. Knott, and A. Fransozo. 2007. The megalopa and early juvenile stages of *Calappa tortugae* Rathbun, 1933 (Crustacea, Brachyura) reared in the laboratory from South Carolina neuston samples. Proceedings of the Biological Society of Washington 120: 469-485.

Ng, P. K. L., D. Guinot, and P. J. F. Davie. 2008. Systema Brachyurorum: part 1: an annotated checklist of extant brachyuran crabs of the world. The Raffles Bulletin of Zoology 17: 1-286.

Nobili, G. 1901. Decapodi raccolti dal Dr. Fillipo Silvestri nell'America meridionale. Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Universita di Torino 16: 1-11.

Pasupathi, K., and T. Kannupandi. 1988. Larval development of *Macrophthalmus erato* De Man, 1887 (Brachyura Ocypodidae). Hydrobiologia 169: 327-338.

Pohle, G. W., F. L. M. Mantelatto, M. L. Negreiros-Fransozo, and A. Fransozo. 1999. Decapod larvae, pp. 1281-1351. In, D. Boltovskoy (ed.). South Atlantic Zooplankton., 1st ed., vol. 2. Balkema Books, The Netherlands.

Rabalais, N. N., and J. N. Cameron. 1983. Abbreviated development of *Uca subcylindrica* (Stimpson, 1859) (Crustacea, Decapoda, Ocypodidae) reared in the laboratory. Journal of Crustacean Biology 3: 519-541.

Rathbun, M. J. 1897. A revision of the nomenclature of the Brachyura. Proceedings of the biological society of Washington 11: 153-167.

———. 1898. The Brachyura collected by U. S. Fish commission steamer Albatross on the voyage from Norfolk, Virginia to San Francisco, California, 1887-1888. Proceedings of the United States National Museum 21: 567-616, pls 41-44.

———. 1900. Results of the Branner-Agassiz Expedition to Brazil. I. The Decapod and Stomatopod Crustacea. Proceedings of the Washington Academy of Sciences 2: 133-156.

Rice, A. L. 1983. Zoeal evidence for brachyuran phylogeny, pp. 313-329. In, F. R. Schram (ed.). Crustacean Issues. I. Crustacean Phylogeny. A. A. Balkema Publishers, Rotterdam.

Rieger, P. J. 1996. Desenvolvimento larval de *Uca (Celuca) uruguayensis* Nobili, 1901 (Decapoda: Ocypodidae), em laboratório. Nauplius 4: 73-103.

———. 1997. Desenvolvimento larval de *Uca (Minuca) mordax* (Smidth, 1870) (Crustacea, Decapoda, Ocypodidae), em laboratório. Trabalhos Oceanográficos da Universidade Federal de Pernambuco UFPE 25: 227-267.

———. 1998. Desenvolvimento larval de *Uca (Minuca) burgersi* Holthuis, 1967 (Crustacea, Decapoda, Ocypodidae), em laboratório. Revista Brasileira de Zoologia 15: 727-756.

———. 1999. Desenvolvimento larval de *Uca (Minuca) vocator* (Herbst, 1804) (Crustacea, Decapoda, Ocypodidae), em laboratório. Nauplius 7: 1-37.

Rodríguez, A., and D. A. Jones. 1993. Larval development of *Uca tangeri* (Eydoux, 1835) (Decapoda: Ocypodidae) reared in the laboratory. Journal of Crustacean Biology 13: 309-321.

Rosenberg, M. S. 2001. The systematic and taxonomy of fiddler crabs: a phylogeny of the genus *Uca*. Journal of Crustacean Biology 21: 839-869.

Smith, S. I. 1870. Notes on American Crustacea, no. 1, Ocypodoidea. Transactions of the Connecticut Academy of arts and sciences 2: 113-176.

Spivak, E. D., and J. A. Cuesta. 2009. The effect of salinity on larval development of *Uca tangeri* (Eydoux, 1835) (Brachyura: Ocypodidae) and new findings of the zoeal morphology. Scientia Marina 73: 297-305.

Števčić, Z. 2005. The reclassification of Brachyuran crabs (Crustacea, Decapoda, Brachyura). Fauna Croatica 14: 1-159.

Weber, F. 1795. Nomenclator entomologicus secundum entomologicum systematicam ill. Fabricii adjectis speciebus recens detectis et varietatibus. Chilonii & Hamburgi. Vii+ 171 pp.

Received: 29 August 2008.
Accepted: 24 November 2008.