Redescription of the megalopa of the fiddler crab *Uca uruguayensis* (Decapoda, Brachyura, Ocypodidae) with special emphasis on its setae

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Abstract
The megalopa stage of the fiddler crab endemic to the Neotropical region, *Uca uruguayensis*, is redescribed, measured and illustrated from 216 specimens collected at Channel 1, Samborombón Bay, Argentina, the southernmost permanent population of the species. Special attention is given to the description of the types of setae, which are compared to those cited for *U. uruguayensis* and other fiddler crab megalopae reared in the laboratory. The differences are given in the outline of the carapace, the plumose spines of the telson, and also in the following appendages: antennule, antenna, mandible, maxillule, maxilla, first, second and third maxillipeds. These cited differences could be due to: the origin of the organisms, caught in the field from their settlement area versus reared in the laboratory, and/or the sampling locality. The purpose of the present paper is to provide a detailed description of the megalopa that may allow resolution of taxonomic and phylogenetic relationships within this complex genus.

Keywords: Fiddler crab, megalopa, *Uca uruguayensis*

Introduction
The fiddler crab, *Uca uruguayensis* (Nobili, 1901), is recorded in the temperate biogeographic region of the south-western Atlantic Ocean. It is an endemic species that is distributed from Río de Janeiro (Brazil) to Río Quequén (Buenos Aires, Argentina), where it occupies the high levels of the silty or silt-sandy intertidal ecosystem, building burrows (Spivak et al. 1991; Spivak 1997a, 1997b).

The megalopa represents a transitional stage between the planktonic zoeas and the benthic first crab stage. The mouthpart structures and pereiopods are similar to those found in adults, the abdomen is well developed and the pleopods are natatory organs (Menu-Marque 1970; Boschi 1981). Although the megalopae are frequently found in plankton samples, they tend to have a more benthic habit. They constitute the final pelagic larval stage before metamorphosis to the benthic first crab stage occurs. They settle in the
intertidal areas occupied by older conspecifics, so are mainly responsible for recruitment to adult populations. In the Ocypodidae, and particularly in *Uca* species, the development encompasses, in general, five zoeal and one megalopal stages, except for those species with abbreviated development, as in the case of *U. subcylindrica* (Rabalais and Cameron 1983).

The megalopal stage of different brachyuran species (Crane 1940; Boschi et al. 1967; Menu-Marque 1970; Diaz and Costlow 1972; Sclero and Lichtschein de Bastida 1978; Iorio 1983; Bacardit 1985; Martin et al. 1985; Montú et al. 1988; Pereyra Lago 1988; Hernández et al. 2000; among others) as well as *Uca* species (Hyman 1920; Rabalais and Cameron 1983; Anger et al. 1990; Rodríguez and Jones 1993; Rieger 1996, 1998) have been described, but mainly from individuals reared in the laboratory.

Although Rieger (1996) described the megalopa of *U. uruguayensis*, his work dealt with organisms reared in the laboratory. In this paper, the megalopa stage of this species is re-described but from individuals caught from the parental habitat in their settlement areas, at their southernmost extreme of distribution. In this work special emphasis is given to the morphology of their setae, which will help to clarify the taxonomic and phylogenetic relationships of the fiddler crab species and to allow the identification of their larvae in field studies on larval ecology and distribution.

**Material and methods**

**Study area**

The Samborombón Bay includes the so-called “Depresión del Río Salado” that extends from Punta Piedras (35°30′S, 56°45′W) to Cabo San Antonio (36°22′S, 57°23′W). This bay is a depocenter of significant magnitude, formed by sediments from the sea and the Uruguay and Paraná rivers, generating coastal plains with large marshes (Violante et al. 2001). The coast of the bay is bathed by salty waters of variable salinity belonging to the estuarine area of the Río de la Plata river (Boschi 1988). The sediments are clayish, with medium to low values of organic carbon, and organic matter with reference to soils following Folk (1954; César et al. forthcoming). In the alluvial plain the vegetation is predominantly herbaceous with “esparillo” grasslands (*Spartina alterniflora* Loisel. and *S. densiflora* (Brong.)), “pasto salado” (*Distichlis scoparia* (Kth.) Arech. and *D. spicata* (L.) Greene) and “cortadera” (*Cortaderia selloana* (Schult.) Asch. et Graebn.). Little vegetation is found on the floodable and very clayish soils of the area due to exposure, salinity and erosion, as well as to the sediment depositions that give rise to “jume” meadows (*Salicornia ambiguа* Michx.) (Vervoort 1967). Dense populations of *Uca uruguayensis* and *Chasmagnathus granulatus* Dana, 1851 (42 and 52 individuals per m², respectively) develop in this habitat, giving the landscape a special physiognomy called “cangrejal” (César et al. forthcoming).

**Sampling methods and material treatment**

Megalopae were collected on 14 February 2003 at the mouth of Channel 1 (36°16′S, 57°06′W) at the Refugio de Vida Silvestre Bahía Samborombón, Argentina. They were collected from the sediment surface at the intertidal of the southern embankment (site 1), at a little higher location with an *S. ambiguа* meadow (sites 2 and 3), and at another location just at the mouth of the channel (site 4), where there is a notable exposure to tides. Physico-chemical variables were measured in the surrounding water: temperature
(°C), pH and conductivity (Table I). Megalopae were collected by hand, kept in plastic bags and frozen. In the laboratory, the organisms were thawed at room temperature, fixed in 10% formalin, and preserved in 70% ethanol, so chromatophores could not be observed.

A total of 216 megalopae were collected and examined, and 65 individuals were measured with an ocular micrometer. Carapace width (CW) was measured at the greatest distance across the carapace, carapace length (CL) was measured from the rostrum to the posterior margin, and total length (TL) from the rostrum to the posterior margin of the telson. The material collected has been deposited in the Museo de Ciencias Naturales de La Plata (no. 25809).

Drawings of the whole organism were made using a stereoscopic microscope equipped with a camera lucida. Appendages were dissected using a stereoscopic microscope and drawn under a binocular microscope with a drawing tube. Details of the appendages were observed at 400 x and 1000 x with a compound microscope. The nomenclature for the different types of setae is that proposed by Stuck and Truesdale (1988). In the illustrations the secondary setation is frequently omitted for clarity.

**Descriptions**

Megalopae of *Uca uruguayensis* have both cephalothorax and abdomen flattened dorso-ventrally (Figure 1). The rostrum is rounded, the cephalothorax is smooth, oval with small simple setae and other sparsely plumose setae longer than the former ones dispersed on the dorsal surface. The carapace has sparsely plumose setae regularly distributed on lateral and posterior margins. The abdomen (as in most brachyurans) comprises six segments and the telson, with small simple setae and some sparsely plumose setae on the dorsal surface. The fifth somite of the abdomen has posterolateral projections. The telson is subquadrate with rounded angles and bears four (rarely five) plumose spines on the posterior margin, and 8–10 simple setae on its dorsal surface. The cuticle, as in other species of the genus but contrary to that of *Ocypode*, is not noticeably thick and hard. Sizes of the individuals measured are listed in Table II.

**Table I.** Physical and chemical variables of water measured at sites sampled on Channel 1, Samborombón Bay.

| Site | T (°C) | Conductivity (μS cm⁻¹) | Salinity (mg l⁻¹) | pH  |
|------|--------|------------------------|------------------|-----|
| 1    | 29.6   | 3670                   | 3.303            | 8.68|
| 2 and 3 | 26.6 | 7490                   | 6.741            | 8.47|
| 4    | 29.2   | 3210                   | 2.889            | 8.09|

The salinity values were obtained after multiplying the conductivity by 0.9.

**Table II.** Sizes of *Uca uruguayensis* megalopae (n=65) collected in Channel 1, Samborombón Bay.

|                  | Total length (mm) | Carapace length (mm) | Carapace width (mm) |
|------------------|-------------------|----------------------|---------------------|
| Mean             | 2.488             | 1.323                | 1.097               |
| Standard deviation | 0.084           | 0.065                | 0.069               |
| Range            | 2.284–2.830       | 1.047–1.476          | 0.952–1.261         |
Appendages

Antennule (Figure 2a). Comprises a basal segment, followed by other three segments, bearing two simple setae in the medial segment and one in the distal segment. Exopodite four-segmented, with 9–11 aesthetascs (three, three, and three to five in each segment, respectively) and two sparsely plumose setae on the outer margin (Figure 2b). Endopodite unsegmented with three terminal simple setae and one simple seta subterminally.

Antenna (Figure 2c). Peduncle with three segments (basal, medial and distal), bearing one, one, and two simple setae, respectively. Flagellum with seven segments, with two to three short simple setae on the third one, one long sparsely plumose seta on the fourth segment, two long sparsely plumose and one short simple setae on the fifth, two long sparsely plumose setae on the sixth and three to four setae (short simple and long sparsely plumose) on the seventh segment.

Mandible (Figure 3a). Molar process with a straight cutting edge, mandibular palp three-segmented, with seven to nine setae on distal segment, two sparsely plumose setae externally and five to seven multidenticulate setae internally (Figure 3b).
Maxillule (Figure 3c). Endopodite two-segmented, with four setae (simple and sparsely plumose) on distal segment and one sparsely plumose on proximal segment. Basal endite unilobate, with 18–20 setae (10 stout simple setae, surrounded by eight stout cuspidate setae and one sparsely plumose seta). Coxal endite also unilobate, with eight stout multidenticulate setae, and another 4–11 sparsely plumose and simple setae.

Maxilla (Figure 3e). Flattened exopodite (scaphognathite) bearing 46–49 plumose fringing setae around outer margin. Endopodite reduced, unsegmented, with one to two plumose setae proximally. Basal endite composed of two lobes, with seven to nine and 9–12 multidenticulate setae, respectively. Coxal endite also bilobate, with two to three and 14–15 sparsely plumose setae on each lobe, respectively.

First maxilliped (Figure 3g). Protopod bilobed, basal endite with 14–16 cuspidate setae and one sparsely plumose seta externally; coxal endite with 10–11 multidenticulate setae. Endopodite three-segmented bearing two simple setae on medial segment and one on distal segment. Exopodite is two-segmented, with three plumose setae on basal segment and five sparsely plumose on distal one. Epipod showing a triangular form, bearing nine long sparsely plumose setae.

Second maxilliped (Figure 3h). Protopod unilobate. Endopodite with five segments, showing the following setation from the proximal segment: one, one, one (all of them sparsely
plumose setae), five to six setae (sparsely plumose and plumodenticulate) and seven to eight setae (cuspidate, sparsely plumose and plumodenticulate). Exopodite two-segmented, bearing one seta on proximal segment and five sparsely plumose setae on distal one. Epipod bears two sparsely plumose setae terminally.

Third maxilliped (Figure 3j). Protopod with 15–21 multidenticulate setae. Endopodite five-segmented: ischium bearing 11–12 sparsely plumose setae (nine internally and two externally); merus with 10–11 sparsely plumose setae (six internally and four externally); carpus with four to six setae (two short simple setae and the other long plumodenticulate setae); propodus bearing five to eight setae (as the last segment, with two short simple setae and plumodenticulate setae), and dactylus with six to eight plumodenticulate setae. Exopodite two-segmented, bearing one to two simple setae on proximal segment and four
Figure 3. *Uca uruguayensis* megalopa: (a) mandible; (b) detail of palp showing multidenticate and sparsely plumose setae; (c) maxillule; (d) detail of cuspidate seta; (e) maxilla; (f) detail of marginal setae of scaphognathite; (g) first maxilliped; (h) second maxilliped; (i) detail of plumodenticulate seta; (j) third maxilliped. Scale bar: 300 μm (a, c, e, g, h, j); 75 μm (b, d, f, i).
to five setae (four sparsely plumose and one simple) on distal segment. Epipod elongate, well developed, with some 17 long setae, very sparsely plumose distally and some 14 sparsely plumose setae proximally. It bears lamellae of a differentiated arthrobranch.

Pereiopods (Figure 4). Chelipeds are equal and well developed, they are large and functional as pincers, and also in crawling. They have a robust chela with the inner margin of the propodus bearing small teeth as shown. When closed, the chelae keep their ends intercrossed. Chelipeds bear simple setae on all of their segments. Pereiopods 2–4 are long and thin, with their ends “hooked”, and they also have setae on all of their segments. Pereiopods 3 and 4 bear a cuspidate spine on the propodus. The fifth pereiopod is small, five-segmented and has three long modified hooked serrate setae (“brachyuran feelers”) on the last segment (dactylus).

Pleopods (Figure 5). Present on abdominal segments 2–6, they are large and well-developed swimming organs. The first four pairs are biramous (bearing exopodite and endopodite), the exopodites are well developed, with flattened lobes, and 15, 16, 15, and 14 plumose setae on each one, respectively. A reduction in size from the first to the fourth pairs of pleopods is noticed. The endopodites are reduced and show three hooked setae on distal end. The fifth pair (uropods) is small, bisegmented and lacking endopodite, with eight plumose setae (a few individuals collected showed seven or nine setae) on exopodite.

Discussion

The fiddler crabs (*Uca*, Ocypodidae) live as adults on intertidal substrata in estuaries and other protected coastal bodies of water, but their planktonic larvae develop in the coastal ocean. Megalopae, their final larval stage, may return to adult habitats either slowly, via transport by residual currents near the bottom, or rapidly, by riding nocturnal flood tides (Christy 1989). The megalopa is the first post-zoeal phase and is characterized by the transfer of the locomotory role from the thoracic appendages to the abdominal pleopods. In the brachyurans, where the abdomen is greatly reduced or otherwise modified in the adult, the metamorphosis between the megalopa and the first crab is almost as dramatic as that between the terminal zoea and the megalopa. In these crustaceans the megalopa stage is morphologically intermediate between the pelagic zoea and the benthic juvenile, and although the megalopa possesses a combination of features found in both the zoeal and juvenile phases, it also has some unique characters which might provide clues to crab relationships which are not available in either of the other two phases (Rice 1981). The anatomy of adult organisms frequently displays complex structures that constitute adaptations to the habitat. These structures often obscure the phylogenetic relationships between organisms, but early stages of development may help to clarify them. All *Uca* species known at present can be distinguished in all of their larval stages, if a combination of morphological characters is used (Anger et al. 1990).

*Uca uruguayensis* is the only fiddler crab species distributed in Argentina (Spivak 1997a), the southernmost permanent population inhabits Samborombón Bay (Spivak et al. 1991; César et al. forthcoming), however, some intermittent populations are found in Mar Chiquita coastal lagoon (Spivak et al. 1991). This species probably exports larvae to the ocean and re-invades the estuary as megalopae (Anger et al. 1994) and in Mar Chiquita their megalopae are found only sporadically and in individual burrows (Valero et al. 1999).
Figure 4. *Uca uruguayensis* megalopa: (a) right cheliped; (b) detail of chela teeth; (c) pereiopods 2–4; (d) detail of cuspidate spine of pereiopods 3–4; (e) fifth pereiopod; (f) modified hooked serrate seta of fifth pereiopod. Scale bar: 500 μm (a, c, e); 75 μm (b, d, f).
This was not the case in Samborombón Bay, where the individuals collected were abundant and sharing the habitat with older conspecifics.

In *U. uruguayensis* megalopae the cuticle was not noticeably thick and hard, as in other species of the genus, probably due to adaptations to life in protected marshes and lagoons, contrary to that of *Ocypode* species that have a very robust megalopa usually adapted to
inhabit beaches fully exposed to heavy surf (Crane 1940). The feeding appendages, mandible, maxillule, maxilla, and maxillipeds, were notably more setose with a greater variety of setae, a condition more typical of a first crab, than other Uca megalopae (e.g. U. burgeri Holthuis, 1967, U. thayeri Rathbun, 1900) (Anger et al. 1990; Rieger 1998).

Rieger (1996) described the larval development of U. uruguayensis reared in the laboratory, comprising four to six zoeal stages and a megalopa. He described the megalopa stage, but unfortunately, he did not mention the size of the individuals, or the variety of setae described in the present paper. He only mentioned two types of setae: simple and plumose, whereas in the present description, following Stuck and Truesdale (1988), reference to eight from 11 of the types proposed by the cited authors is made.

The more obvious differences in both descriptions are: the outline of the carapace, which in the megalopae collected in Samborombón Bay is much more oval and elongated; the telson bears four (rarely five) plumose spines, contrary to the two plumose setae cited by Rieger (1996). There are also differences in the following appendages: antennule (number of segments, number and types of setae); antenna (number and types of setae); mandible (number of segments in the palp and number of setae); maxillule (number of segments and setae in the endopodite, setation of basal and coxal endites); maxilla (setation of endopodite, basal and coxal endites); first maxilliped (number and types of setae of epipodite; number of segments, types and number of setae of endopodite; and number of setae of protopodite); second and third maxillipeds (number and types of setae). The megalopae collected in Samborombón Bay showed cuspidate spines on pereiopods 3 and 4, not described by Rieger (1996), and eight plumose setae on the uropods in most of the individuals, but all of them on the exopodite. These cited differences could be due to: the origin of the organisms, caught in the field from their settlement area versus reared in the laboratory, and/or the sampling locality. In the first case a population was sampled from the extreme southernmost distribution of the species (Provincia de Buenos Aires, Argentina) while in the other case the megalopae were reared in the laboratory from ovigerous females collected at Rio Grande do Sul, Brazil, at the northern range of the distribution.

Megalopae of U. uruguayensis collected in the present study showed sizes similar to those of U. lactea (De Haan, 1835), similar or larger than those measured in U. tangeri (Eydox, 1835) (Rabalais and Cameron 1983; Rodriguez and Jones 1993), larger than U. annulipes (Milne-Edwards, 1837), U. triangularis (Milne-Edwards, 1873), U. panacea Novak and Salmon, 1974, U. pugnax (Smith, 1870), and U. thayeri, but smaller than U. subcylindrica (Stimpson, 1859) (Rabalais and Cameron 1983; Anger et al. 1990). However, most of the cited species were reared in laboratory. As a consequence of its abbreviated development the megalopa of U. subcylindrica is considerably larger than other previously recorded Uca species (Rabalais and Cameron 1983). Uca subcylindrica would represent an extreme departure from normal larval morphology of Uca, and these features are clearly affected by the abbreviated development in this species (Rodriguez and Jones 1993).

The purpose of the present paper was to provide a detailed description of this megalopa that may allow resolution of taxonomic and phylogenetic relationships within this complex genus.

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