

Comparative morphology of the first zoea of twelve brachyuran species (Crustacea: Decapoda) from the Amazon region

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ABSTRACT. The laboratory-hatched first zoeal stage of twelve brachyuran species collected in the estuarine area of the Caeté River in the Amazonian region are described and illustrated in the present study: *P. americanus* Saussure, 1857, *Eurytium limosum* (Say, 1818), *Sesarma curacaoense* De Man, 1892, *S. rectum* Randall, 1840, *Armases rubripes* (Rathbun, 1897), *Aratus pisonii* (H. Milne Edwards, 1837), *Ocypode quadrata* (Fabricius, 1787), *Uca rapax* (Smith, 1870), *U. maracoani* (Latreille, 1802), *U. thayeri* Rathbun, 1900, *Ucides cordatus* (Linnaeus, 1763) and *Pachygrapsus gracilis* (Saussure, 1858). Through intraspecific comparisons of the respective larval stage, an identification key was generated and provided. Most of the studied species presented morphological differences (e.g. type and presence or absence of setae) when compared to the same species previously described in the literature.

KEY WORDS. Decapod crabs; identification; larval morphology; zooplankton.

Brachyuran crabs are among the most important groups of crustaceans in coastal ecosystems, and one of the most abundant macroinvertebrate groups that inhabit tropical mangroves and tidal flats (CLARK & PAULA 2003). The taxonomic classification of brachyuran crabs is still mostly based on the morphological characteristics of the adults. However, it has been hypothesized that adults share many convergent adaptations to their specific benthic environment (FLORES *et al.* 2003, CLARK 2009). A valuable, but frequently overlooked alternative to adult characters is larval morphology (CLARK 2009). Taxonomically useful characters found in larvae are believed to be less problematic, because immature forms inhabit a planktonic environment with relatively uniform characteristics (RICE 1980). Phylogenetic studies on brachyuran crabs show that larval morphology is more congruent with molecular data than with adult morphology (HULTGREN *et al.* 2009).

Larval morphology can be used in ecological studies to evaluate species diversity and reproductive period (KORNIENKO & KORN 2009), population estimates, spatial and temporal distribution, dispersal, recruitment and other ecological aspects (ANGER *et al.* 1995, QUEIROGA *et al.* 1994, CLARK & PAULA 2003). Such studies depend on the availability of taxonomic identification tools such as identification keys (HART 1971, MARTIN 1984, PAULA 1996, BÁEZ 1997, FRANZOZO *et al.* 1998, PESSANI *et al.* 1998, SCHUBART & CUESTA 1998, POHLE *et al.* 1999, ANOSOV 2000, GONZÁLEZ-GORDILLO *et al.* 2000, KO & YANG 2003, DOS SANTOS & GONZÁLEZ-GORDILLO 2004, RICE & TSUKIMURA 2007, LEE & KO 2008, GONZALES *et al.* 2009, KORNIENKO & KORN 2009, KORN & KORNIENKO 2010, VIEIRA & CALAZANS 2010). Alternatively, and to get the most up to date knowledge,

one would have to consult the publications where larvae of individual species are described. However, with many crab larvae still unknown, such resources are presently limited.

Larval morphology may also prove useful in phylogenetic studies within and among taxonomic groups (RICE 1980, 1983, CLARK & WEBBER 1991, MARQUES & POHLE 1998, 2003, SANTANA *et al.* 2003, 2004a, b, ANGER 2006, KORNIENKO & KORN 2009) helping us to understand species evolution (BÁEZ 1997).

According to CLARK *et al.* (1998), detailed, standardized descriptions of larvae obtained in the laboratory are necessary in many kinds of studies. As an example, the patterns of setae on the appendages can be used in systematic analyses because they are very conservative (FLORES *et al.* 2003, VIEIRA & CALAZANS 2010).

Studies based on larval morphology facilitate direct comparison and help to discern consistent morphological patterns among taxa. However, some old descriptions need to be revised, as they sometimes lack the necessary details (SCHUBART & CUESTA 1998). The aim of the present study is to investigate the larval diversity of crustaceans that inhabit an estuary of the Amazon region. We describe the morphology of the first larval stage of the following species: *P. americanus* Saussure, 1857, *Eurytium limosum* (Say, 1818), *Sesarma curacaoense* De Man, 1892, *S. rectum* Randall, 1840, *Armases rubripes* (Rathbun, 1897), *Aratus pisonii* (H. Milne Edwards, 1837), *Ocypode quadrata* (Fabricius, 1787), *Uca rapax* (Smith, 1870), *U. maracoani* (Latreille, 1802), *U. thayeri* Rathbun, 1900, *Ucides cordatus* (Linnaeus, 1763) and *Pachygrapsus gracilis* (Saussure, 1858), and provide an identification key for them.

MATERIAL AND METHODS

Field-collecting was conducted in different localities along the mangrove estuary of the Caeté River (Pará, Brazil). Ovigerous females were captured manually and later taken to the laboratory. Next, two females of each species were carefully washed and identified according to RODRIGUEZ (1980) and MELO (1996). Species and their locations, as well as their time of hatching, are shown in Table I.

Table I. Collecting locality and hatching date of species obtained at the Caeté River estuary, Pará, Brazil.

Species	Collecting locality	Hatching date
Panopeidae		
<i>Panopeus americanus</i>	Furo Grande (00°50'421"S, 046°38'398"W)	Jan. 2011
<i>Eurytium limosum</i>	Ilha de Canela (00°46'571"S, 046°43'524"W)	Aug. 2010
Sesarmidae		
<i>Sesarma curacaoense</i>	Furo da Ostra (00°53'494"S, 046°39'387"W)	Aug. 2010
<i>S. rectum</i>	Furo Grande (00°50'421"S, 046°38'398"W)	Jan. 2011
<i>Armases rubripes</i>	Furo da Ostra (00°53'494"S, 046°39'387"W)	Jan. 2011
<i>Aratus pisonii</i>	Furo do Meio (00°52'470"S, 046°39'008"W)	Feb. 2010
Ocypodidae		
<i>Ocypode quadrata</i>	Praia de Ajuruteua (00°49'751"S, 46°36'248"W)	Jul. 2010
<i>Uca maracoani</i>	Ilha de Canela (00°46'571"S, 046°43'524"W)	Apr. 2010
<i>U. rapax</i>	Furo do Café (00°50'752"S, 046°38'892"W)	Mar. 2010
<i>U. thayeri</i>	Canal de Chavascal (00°48'963"S, 46°36'974"W)	Apr. 2010
Ucididae		
<i>Ucides cordatus</i>	Furo da Ostra (00°53'494"S, 046°39'387"W)	Mar. 2009
Grapsidae		
<i>Pachygrapsus gracilis</i>	Furo do Taíci (00°58'138"S, 046°44'264"W)	Dec. 2010

The females were isolated and stored in 5 L-tanks containing seawater (salinity = 30) with constant aeration, and subjected to an artificial photoperiod of 12/12 hours until the larvae hatched.

After hatching, individuals of the first larval stage displaying active swimming were preserved in glycerine + 70% ethanol (1:1). Larvae were dissected with fine needles, measured, and then illustrated using a Coleman microscope equipped with *camera lucida* and a Zeiss Axioskop 40 compound microscope, both with a micrometer eyepiece. For improved visualization some structures were stained using methylene blue (0.5%).

Morphometric data and illustrations are based on about 10 larvae of each species. Carapace length (CL) was obtained by measuring from the base of the rostral spine to the posterior margin of the carapace; dorsorostral length (DRL) was obtained by measuring from the tip of the rostral spine to the tip of the dorsal spine. Mean values and standard deviation were calculated for each species (Table II).

Table II. Measurements of zoea I of the species described in this study.

Species	Dorsorostral length (DRL) ± SD (mm)	Carapace length (CL) ± SD (mm)
<i>P. americanus</i>	1.36 ± 0.01	0.50 ± 0.01
<i>E. limosum</i>	1.73 ± 0.01	0.58 ± 0.01
<i>S. curacaoense</i>	1.39 ± 0.02	0.81 ± 0.01
<i>S. rectum</i>	1.16 ± 0.01	0.66 ± 0.01
<i>A. rubripes</i>	0.73 ± 0.01	0.43 ± 0.01
<i>A. pisonii</i>	0.70 ± 0.01	0.43 ± 0.01
<i>O. quadrata</i>	1.28 ± 0.15	0.63 ± 0.01
<i>U. maracoani</i>	0.69 ± 0.02	0.41 ± 0.01
<i>U. rapax</i>	0.58 ± 0.01	0.36 ± 0.01
<i>U. thayeri</i>	0.62 ± 0.01	0.39 ± 0.01
<i>U. cordatus</i>	1.01 ± 0.02	0.49 ± 0.01
<i>P. gracilis</i>	0.73 ± 0.01	0.35 ± 0.005

The illustrations and morphological characteristics were used to construct a dichotomous key. Characters in the key are based mainly on external characters that can be viewed without dissection. The terminology used in the descriptions follows FACTOR (1978), POHLE & TELFORD (1981), CLARK *et al.* (1998), RIEGER & SANTOS (2001), GARM (2004), HORN & BUCKUP (2004). Samples of larvae and females were deposited in the Museum Emilio Goeldi (Pará, Brazil) under the following catalog numbers: *P. americanus* 1108, *E. limosum* 1109, *S. curacaoense* 1110, *S. rectum* 1111, *A. rubripes* 1112, *A. pisonii* 1113, *O. quadrata* 1114, *U. maracoani* 1115, *U. rapax* 1117, *U. thayeri* 1116, *U. cordatus* 1118 and *P. gracilis* 1119.

RESULTS

Panopeidae

Panopeus americanus Saussure, 1857

Carapace (Fig. 1). Globose, smooth, with a pair of posterodorsal simple setae. Small protuberance medially in the anterior and posterior regions. Dorsal spine present, long and distally curved. Lateral spines present, with about 1/4 of the antennal length and projected perpendicularly. Rostral spine as long as antennal protopod. Eyes sessile. **Antennule** (Fig. 2). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 3 (1 smaller) simple setae. **Antenna** (Fig. 3). Protopod well

developed armed distally with rows of spines. Exopod minute, with 1 terminal simple seta. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with about seven small and two teeth arranged separately on the inner margin. Molar process with a large tooth in the base and circular regions provided of small and irregular teeth. **Maxillule** (Fig. 4). Coxal endite with 6 plumodenticulate setae (5 terminal and 1 lateral subterminal) and 1 simple subterminal lateral seta. Basial endite with 2 cuspidate and 3 plumodenticulate (1 subterminal) setae. Endopod 2-segmented, with 1 sparsely plumose seta in proximal segment and 6 (2 subterminal) sparsely plumose setae in distal segment. **Maxilla** (Fig. 5). Coxal endite bilobed with 4 (2 subterminal) + 4 (2 subterminal) plumose setae. Basial endite bilobed with 5 (1 plumodenticulate and 2 subterminal plumose) setae + 4 (1 subterminal) plumose setae. Endopod bilobed with 3 (1 subterminal) + 5 sparsely plumose setae. Scaphognathite with 4 marginal densely plumose setae and a long posterior process with microtrichias. **First maxilliped** (Fig. 6). Basis with 2, 2, 3, 3 sparsely plumose setae in the inner margin. Endopod 5-segmented with 3, 2, 1, 2 and 5 (1 subterminal simple seta + 4 terminal) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Second maxilliped** (Fig. 7). Basis with 1, 1, 1, 1 sparsely plumose setae in the inner margin. Endopod 3-segmented with 1, 1 (denticulate), 5 (1 denticulate + 2 simple) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Abdomen** (Fig. 8). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Somites 3-5 with a pair of long posterolateral spines. Telson bifurcated, dorsally curved with 2 small unequal lateral spines and 1 dorsal spine. Inner margin with 6 (3+3) plumodenticulate setae separated by a medial arch.

Eurytium limosum (Say, 1818)

Carapace (Fig. 9). Globose, smooth, with a pair of posterodorsal simple seta. Small protuberance in the anterior and posterior regions. Dorsal spine present, long and distally curved. Rostral spine as long as antennal protopod. Lateral spines present, small, about 1/10 antennal length and projected perpendicularly. Eyes sessile. **Antennule** (Fig. 10). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 2 simple setae. **Antenna** (Fig. 11). Protopod well-developed, armed distally with rows of spines. Exopod small, with 1 terminal simple seta.

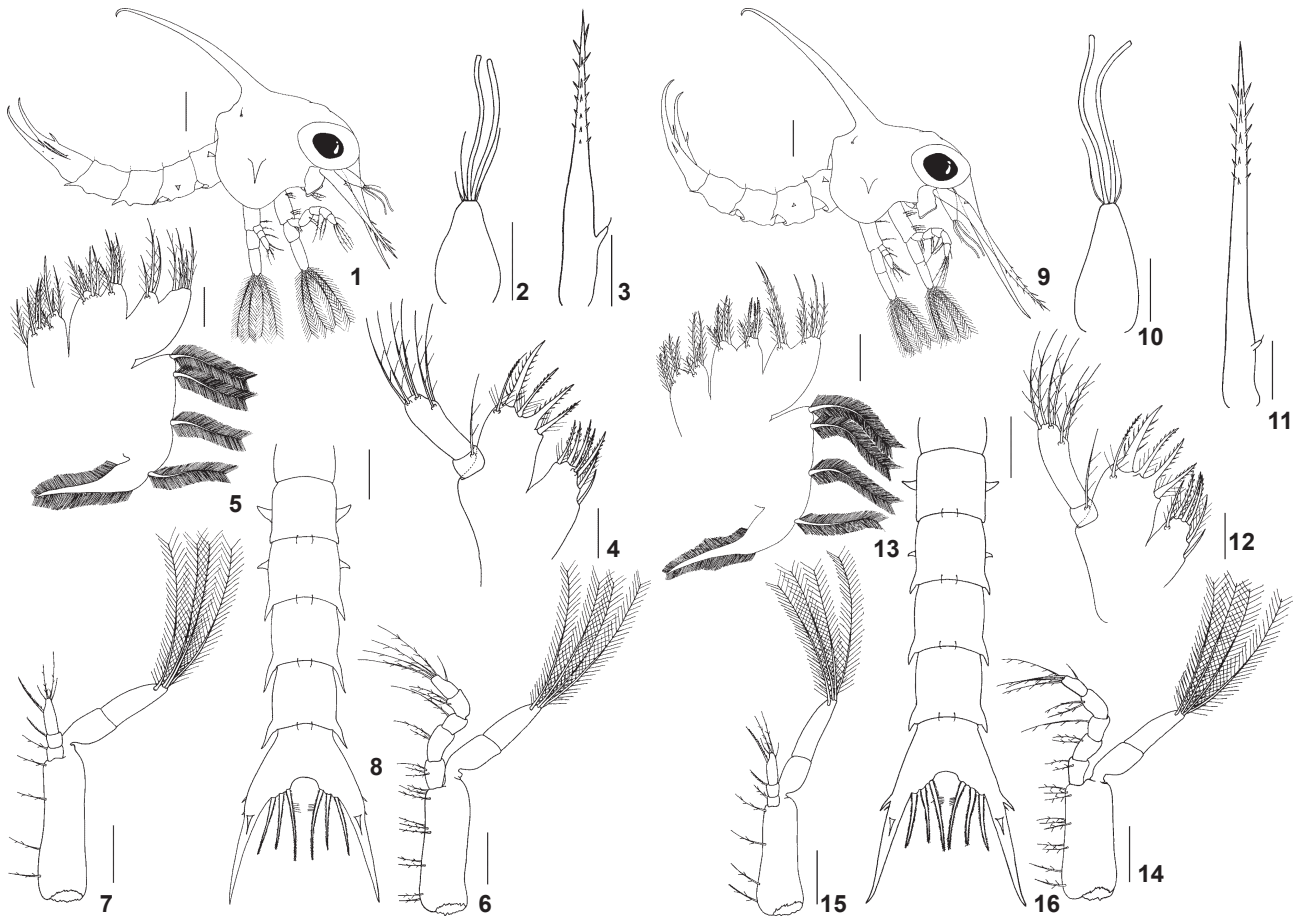
Mandible. Symmetric, palp absent, incisor process with a prominent distal tooth and two teeth arranged separately on the inner margin. Molar process with a large tooth in the base and circular regions provided of small and irregular teeth. **Maxillule** (Fig. 12). Coxal endite with 3 plumodenticulate, 1 subterminal plumose and 2 subterminal (1 plumose + 1 simple) lateral setae. Basial endite with 2 cuspidate setae and 3

plumodenticulate (1 subterminal) setae. Endopod 2-segmented, with 1 sparsely plumose seta in the proximal segment and 6 (2 subterminal) sparsely plumose setae in the distal segment. **Maxilla** (Fig. 13). Coxal endite bilobed with 4 + 4 (2 subterminal, 1 similar to hamate) plumose setae. Basial endite bilobed with 5 (1 subterminal) + 4 (1 subterminal plumose + 3 plumodenticulate) setae. Endopod bilobed with 3 (1 subterminal) + 5 (1 subterminal) plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 14). Basis with 2+2+3+3 sparsely plumose setae in the inner margin. Endopod 5-segmented with 2, 2, 1, 2, 5 (1 subterminal lateral simple setae + 4 terminal) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Second maxilliped** (Fig. 15). Basis with 1+1+1+1 sparsely plumose setae in the inner margin. Endopod 3-segmented with 1, 1 (denticulate), 5 (1 denticulate + 2 simple) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Abdomen** (Fig. 16). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Somites 3-5 with a pair of posterolateral spines. Telson bifurcated, dorsally curved with 2 (1 fine spine) unequal lateral and 1 dorsal spines. Inner margin with 6 (3+3) plumodenticulate setae separated by a medial arch.

Sersarmidae

Sesarma curacaoense De Man, 1892

Carapace (Fig. 17). Globose, smooth, with a small protuberance on anterior region, 1 pair of posterodorsal simple setae and 2 pairs of anterodorsal simple setae. Pereiopods present. Dorsal spine present and distally curved. Lateral spines absent. Rostral spine slightly smaller than antenna. Eyes sessile. **Antennule** (Fig. 18). Uniramous conical-shaped and unsegmented with 3 aesthetascs and 2 distal simple seta. **Antenna** (Fig. 19). Protopod well-developed longer than rostral spine, armed with 2 rows of unequal spines. Exopod with 2 simple setae of different sizes terminally. Endopod present and extending beyond the half of exopod. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with about 7 small teeth. Molar process with prominent terminal dentiform. **Maxillule** (Fig. 20). Coxal endite with 5 setae (4 plumodenticulate + 1 subterminal plumose) and 2 plumose subterminal lateral setae. Basial endite with 2 cuspidate and 3 plumodenticulate (1 subterminal) setae. Endopod 2-segmented, with 1 simple seta on the proximal segment, distal segment with 1 simple medial and 4 terminal sparsely plumose setae. **Maxilla** (Fig. 21). Coxal endite bilobed with 5 plumose setae (2 subterminal) + 4 plumose setae (2 subterminal + 1 similar to hamate). Basial endite bilobed with 5 setae (2 plumose, 1 subterminal + 1 denticulate + 1 plumodenticulate + 1 simple) + 4 setae (2 plumose, 1 subterminal + 2 plumodenticulate). Endopod bilobed with 2 (1 subterminal) + 3 sparsely plumose



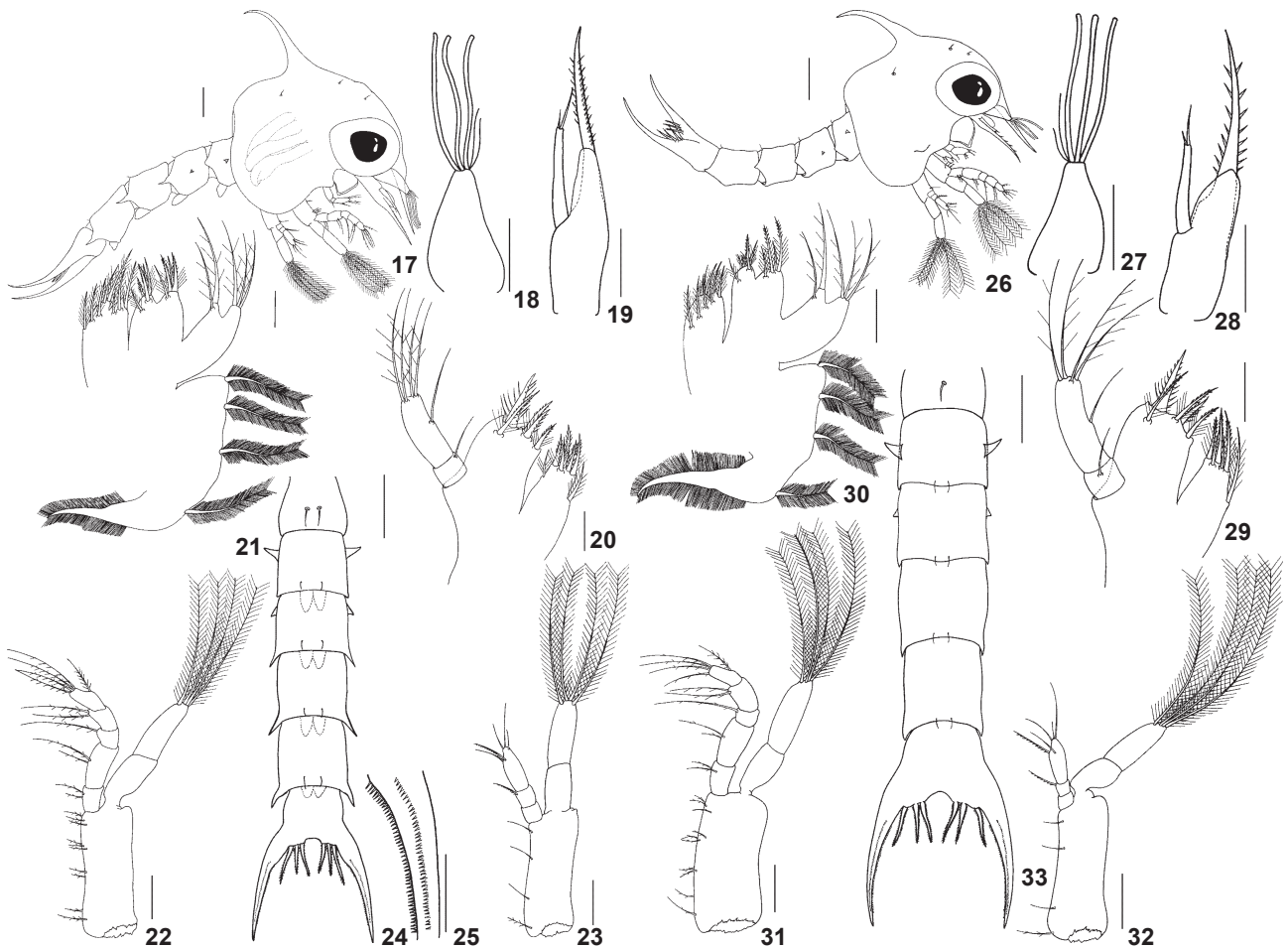
Figures 1-16. (1-8) *Panopeus americanus*: lateral view (1); antennule (2); antenna (3); maxillule (4); maxilla (5); first maxilliped (6); second maxilliped (7); abdomen and telson (8). (9-16) *Eurytium limosum*: lateral view (9); antennule (10); antenna (11); maxillule (12); maxilla (13); first maxilliped (14); second maxilliped (15); abdomen and telson (16). Scale bars: 1, 9, 16 = 0.13 mm; 2, 6, 7 = 0.08 mm; 10 = 0.06 mm; 3, 8, 11, 14, 15 = 0.1 mm; 4, 5, 12, 13 = 0.03 mm.

setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 22). Basis with 2+2+3+3 sparsely plumose setae on the inner margin. Endopod 5-segmented with 2,2,1,2 and 5 (4 sparsely plumose terminal setae + 1 subterminal lateral plumose seta) from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Second maxilliped** (Fig. 23). Basis with 1 (sparsely plumose)+ 1+1+1 simple setae on the inner margin. Exopod 3-segmented with 0,1 (denticulate), 5 (1 denticulate) simple setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Abdomen** (Fig. 24). With 5 somites and telson. First somite with 2 simple medial setae. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Somites 3-5 with a pair of posterolateral spines. Pleopods (under developing) present on somites 2-5. Telson bifurcated, with inner margin with 6 (3+3) plumodenti-

culate setae separated by a medial arch. Each furca with 2 long rows of minute spines (Fig. 25).

Sesarma rectum Randall, 1840

Carapace (Fig. 26). Globose, smooth with 2 pairs anterodorsal and 1 pair of posterolateral setae. Dorsal spine present and curved. Rostral spine only slightly longer than antenna. Mediolateral inferior region with a small protuberance. Lateral spines absent. Eyes sessile. **Antennule** (Fig. 27). Uniramous, conical-shaped and unsegmented with 3 aesthetascs and 2 unequal simple setae. **Antenna** (Fig. 28). Protopod well-developed, armed with 2 rows of unequal spines. Endopod present, longer than half of exopod. Exopod reaching half distance of the protopod, bearing 2 unequal simple setae. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with five small and two teeth arranged sepa-



Figures 17-33. (17-25) *Sesarma curacaoense*: lateral view (17); antennule (18); antenna (19); maxillule (20); maxilla (21); first maxilliped (22); second maxilliped (23); abdomen and telson (24); furca (25); (26-33) *Sesarma rectum*: lateral view (26); antennule (27); antenna (28); maxillule (29); maxilla (30); first maxilliped (31); second maxilliped (32); abdomen and telson (33). Scale bars: 17, 33 = 0.13 mm; 18, 19, 27, 28 = 0.1 mm; 20, 21, 29, 30 = 0.03 mm; 22, 23, 31, 32 = 0.08 mm; 24, 26 = 0.2 mm; 25 = 0.05 mm.

rately on the inner margin. Molar process with a large tooth in the base and circular regions provided of small and irregular teeth. **Maxillule** (Fig. 29). Coxal endite with 5 setae (3 plumodenticulate + 2 simple, 1 subterminal) and 1 plumose subterminal lateral seta. Basal endite with 2 cuspidate setae and 3 plumodenticulate (1 subterminal). Endopod 2-segmented, with 1 simple seta in the proximal segment, distal segment with 1 simple medial seta and 4 sparsely plumose terminal setae. **Maxilla** (Fig. 30). Coxal endite bilobed with 5 (3 subterminal) plumose setae + 4 (1 subterminal + 1 similar to hamate) plumose setae. Basal endite bilobed with 5 (1 plumodenticulate + 4 plumose, 1 subterminal) setae + 4 (2 plumodenticulate + 1 simple + 1 plumose subterminal) setae. Endopod bilobed with 2 (1 subterminal) + 3 sparsely plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped**

(Fig. 31). Basis with 2+2+3+3 sparsely plumose setae in the inner margin. Endopod 5-segmented with 2,2,1,2,5 (4 terminal + 1 plumose subterminal lateral) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Second maxilliped** (Fig. 32). Basis with 1 (sparsely plumose)+1+1+1 simple setae in the inner margin. Endopod 3-segmented with 0,1(denticulate), 5 (4 simple + 1 denticulate) setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Abdomen** (Fig. 33). With 5 somites and telson. The first somite with 1 simple seta. Somites 2 and 3 with a pair of dorsolateral spine. Somites 2-5 with a pair of small simple posterodorsal setae. Telson bifurcated, with inner margin with 6 (3+3) plumodenticulate setae separated by a medial arch. Each furca with 2 rows of minute spines on the inner margin.

Armases rubripes (Rathbun, 1897)

Carapace (Fig. 34). Globose, smooth with 1 pair of anterodorsal simple setae and 1 pair of posterodorsal simple setae. Dorsal spine present and curved, with some minute spines randomly arranged on the anterior surface. Mediolateral inferior region with a small protuberance. Lateral spines absent. Rostral spine slightly shorter than antenna. Eyes sessile. **Antennule** (Fig. 35). Uniramous, conical-shaped, unsegmented with 3 aesthetascs and 2 unequal simple setae. **Antenna** (Fig. 36). Protopod well-developed, armed with 2 rows of unequal spines. Exopod about 1/3 protopod size, with 2 simple unequal terminal setae. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with five small teeth. Molar process with a prominent tooth and circular region provided of small and irregular teeth. **Maxillule** (Fig. 37). Coxal endite with 5 (3 plumodenticulate + 2 simple, 1 subterminal) setae and 1 plumose subterminal lateral seta. Basial endite with 2 cuspidate and 3 plumodenticulate (1 subterminal) setae. Endopod 2-segmented, with 1 simple seta in the proximal segment, distal segment bearing 1 simple medial seta and 4 sparsely plumose terminal setae.

Maxilla (Fig. 38). Coxal endite bilobed with 5 (3 subterminal) plumose setae + 4 (2 subterminal + 1 similar to hamate) plumose setae. Basial endite bilobed with 5 (1 subterminal) plumose setae + 4 (1 subterminal) plumose setae. Endopod bilobed with 2 (1 subterminal) + 3 sparsely plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 39). Basis with 2+2+3+3 sparsely plumose setae in the inner margin. Endopod 5-segmented with 2,2,1,2,5 (4 terminal + 1 lateral subterminal) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Second maxilliped** (Fig. 40). Basis with 1 (sparsely plumose) + 1+1+1 simple setae in the inner margin. Endopod 3-segmented with 0,1(denticulate), 6 (5 simple + 1 denticulate) setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Abdomen** (Fig. 41). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Somites 3-5 with a pair of small posterolateral spine. Telson bifurcated with inner margin with 6 (3+3) plumodenticulate setae separated by a medial arch. Each furca with two rows of minute spines on the inner margin.

Aratus pisonii (H. Milne Edwards, 1837)

Carapace (Fig. 42). Globose, smooth with 1 pair of posterodorsal simple setae and 2 pairs of anterodorsal simple setae. Dorsal spine present and curved, with some minute spines on the anterior surface. Mediolateral inferior region with a distinct protuberance. Lateral spines absent. Rostral spine length equal to antennal protopod. Eyes sessile. **Antennule** (Fig. 43). Uniramous, conic-shaped and unsegmented with 3 aesthetascs and 2 simple setae of different sizes. **Antenna** (Fig. 44). Protopod

well-developed armed with 2 rows of unequal spines. Exopod with 2 unequal simple setae and 2-minute terminal spines. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with four small and two teeth arranged separately on the inner margin. Molar process with a large tooth in base and circular region provided of small and irregular teeth.

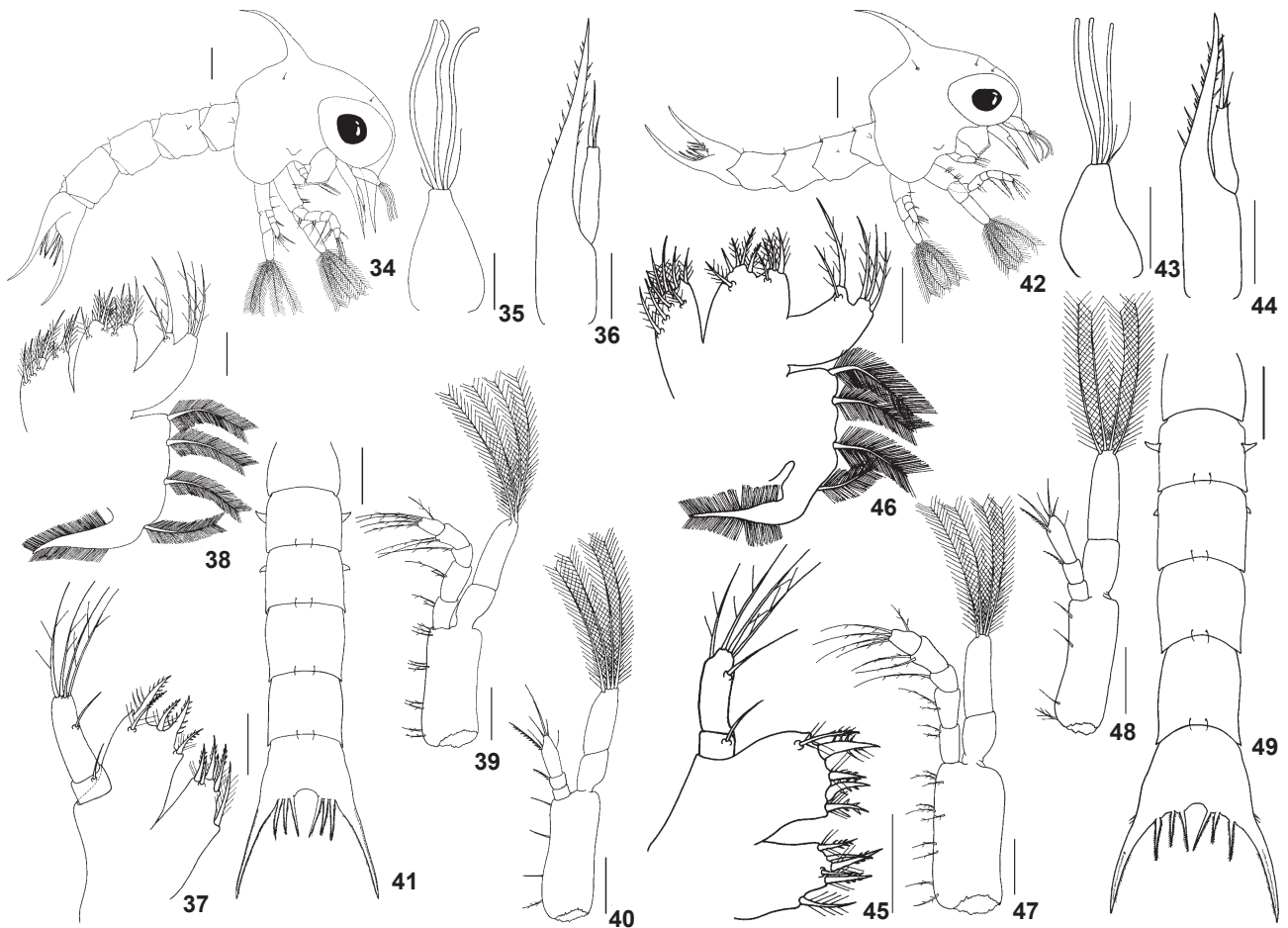
Maxillule (Fig. 45). Coxal endite with 5 (3 plumodenticulate + 2 simple, 1 subterminal) setae and 1 plumose subterminal lateral seta. Basial endite with 2 cuspidate and 3 plumodenticulate (1 subterminal) setae. Endopod 2-segmented with 1 simple seta on proximal segment, distal segment with 1 simple median seta and 4 sparsely plumose terminal setae. **Maxilla** (Fig. 46). Coxal endite bilobed with 5 (3 subterminal) plumose setae + 4 (1 subterminal + 1 similar to hamate) plumose setae. Basial endite bilobed with 5 (3 plumose, 1 subterminal + 1 plumodenticulate + 1 simple) setae + 4 (1 subterminal) plumose setae. Endopod bilobed with 2(1 subterminal) + 3 sparsely plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 47). Basis with 2+2+3+3 sparsely plumose setae in the inner margin. Endopod 5-segmented with 2,2,1,2,5 (4 terminal + 1 lateral subterminal) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Second maxilliped** (Fig. 48). Basis with 1 (sparsely plumose seta) + 1+1+1 simple setae in the inner margin. Endopod 3-segmented with 0,1 (denticulate), 6 (5 simple + 1 denticulate) setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Abdomen** (Fig. 49). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Somites 3-5 with a pair of short posterolateral spines. Telson bifurcated, inner margin with 6 (3+3) plumodenticulate setae (inner margin of the setae of the central pair lacking plume) separated by a medial arch. Each furca with 2-minute lateral spines and 2 rows of minute spines on the inner margin.

Ocypodidae

Ocypode quadrata (Fabricius, 1787)

Carapace (Fig. 50). Globose, smooth with 1 pair of posterodorsal simple setae. Anterior region with a small protuberance. Dorsal spine present and curved, bearing minute spines randomly arranged on anterior surface. Rostral spine about length twice of antennal size. Lateral spines present, long and curved downward. **Antennule** (Fig. 51). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 2 simple setae of different sizes.

Antenna (Fig. 52). Protopod well-developed with 2 rows of small spines. Exopod about 1/5 of protopod length, bearing 2 unequal simple setae and 2 minute terminal spines. **Mandible**. Symmetric, palp absent, incisor process with two prominent teeth separated by four small and two teeth arranged separately on the inner margin. Molar process with a large tooth in base and



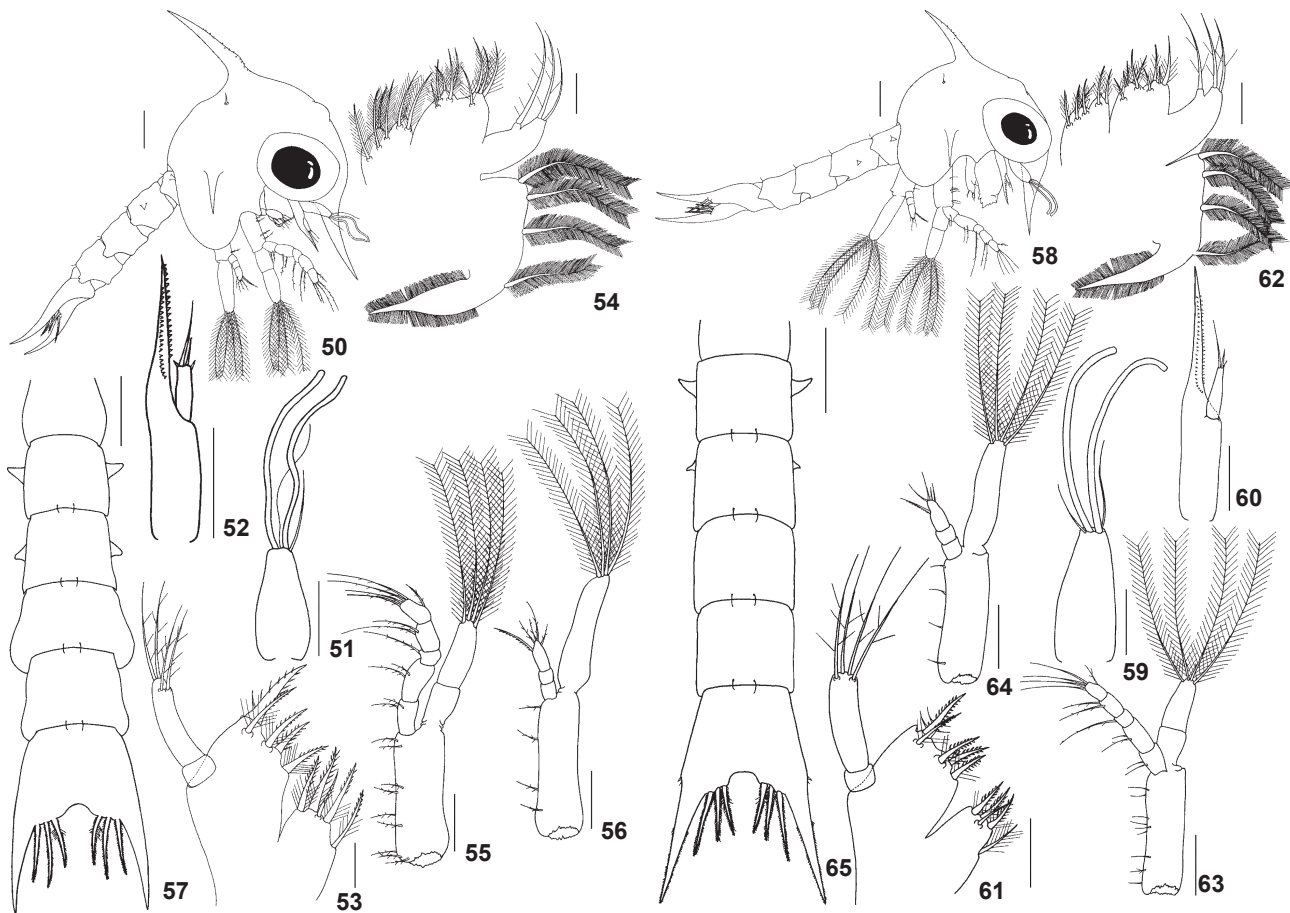
Figures 34-49. (34-41) *Armases rubripes*: lateral view (34); antennule (35); antenna (36); maxillule (37); maxilla (38); first maxilliped (39); second maxilliped (40); abdomen and telson (41); (42-49) *Aratus pisonii*: lateral view (42); antennule (43); antenna (44); maxillule (45); maxilla (46); first maxilliped (47); second maxilliped (48); abdomen and telson (49). Scale bars: 34 = 0.08 mm; 35-38 = 0.03 mm; 39, 40, 47, 48 = 0.06 mm; 43-46 = 0.05 mm; 41, 42, 49 = 0.1 mm.

circular regions provided of small and irregular teeth. **Maxillule** (Fig. 53). Coxal endite with 4 (3 plumodenticulate + 1 simple) setae and 1 lateral subterminal plumodenticulate seta. Basal endite with 2 cuspidate and 3 plumodenticulate (1 subterminal) setae. Endopod 2-segmented, proximal segment lacking setae and distal segment with 4 sparsely plumose setae. **Maxilla** (Fig. 54). Coxal endite bilobed with 4 (3 subterminal) + 3 (1 similar to hamate) plumose setae. Basal endite bilobed with 5 (3 subterminal) + 4 (1 subterminal) plumose setae. Endopod bilobed with 1 sparsely plumose + 2 (1 sparsely plumose + 1 simple) setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 55). Basis with 3+2+2+2 sparsely plumose setae in the inner margin. Endopod 5-segmented, with 2,2,1,2,5 (4 terminal + 1 lateral subterminal) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. Sec-

ond maxilliped (Fig. 56). Basis with 1+1+1+1 sparsely plumose setae in the inner margin. Endopod 3-segmented with 0,0,5 (1 denticulate, 4 sparsely plumose) setae from proximal to distal segment. Exopod unsegmented with 4 long plumose natatory terminal setae. **Abdomen** (Fig. 57). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Posterior margin of the 4th somite laterally enlarged. Telson bifurcated with inner margin with 6 (3+3) plumodenticulate setae separated by a medial arch.

Uca maracoani (Latreille, 1802)

Carapace (Fig. 58). Globose, smooth with 1 pair of posterodorsal simple setae. Anterior region with a small protuberance. Dorsal spine present and curved, bearing minute spines randomly arranged on the anterior surface. Lateral spines



Figures 50-65. (50-57) *Ocyropsis quadrata*: lateral view (50); antennule (51); antenna (52); maxillule (53); maxilla (54); first maxilliped (55); second maxilliped (56); abdomen and telson (57); (58-65) *Uca maracoani*: lateral view (58); antennule (59); antenna (60); maxillule (61); maxilla (62); first maxilliped (63); second maxilliped (64); abdomen and telson (65). Scale bars: 50, 57 = 0.13 mm; 51, 52, 58, 63, 64 = 0.08 mm; 53, 54, 59-62 = 0.3 mm; 55, 56, 65 = 0.1 mm.

present, slightly curved downward. Rostral spines slightly curved. Eyes sessile. **Antennule** (Fig. 59). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 2 unequal simple setae. **Antenna** (Fig. 60). Protopod well-developed, with 2 rows of minutes spines. Exopod with 3 unequal simple setae. **Mandible**. Symmetric, palp absent, incisor process with four prominent and two teeth arranged separately on the inner margin. Molar process with a large tooth in base and circular regions provided of small and irregular teeth. **Maxillule** (Fig. 61). Coxal endite with 4 (3 plumodenticulate + 1 subterminal simple) setae and 1 subterminal lateral plumose seta. Basial endite with 2 cuspidate and 3 plumodenticulate (2 subterminal) setae. Endopod 2-segmented, proximal segment lacking setae, distal segment with 4 sparsely plumose setae. **Maxilla** (Fig. 62). Coxal endite bilobed with 4 (3 subterminal) + 3 (1 subterminal + 1 similar to hamate) plumose setae. Basial endite with 5 (2 subterminal) + 4 (1 subterminal) plumose setae.

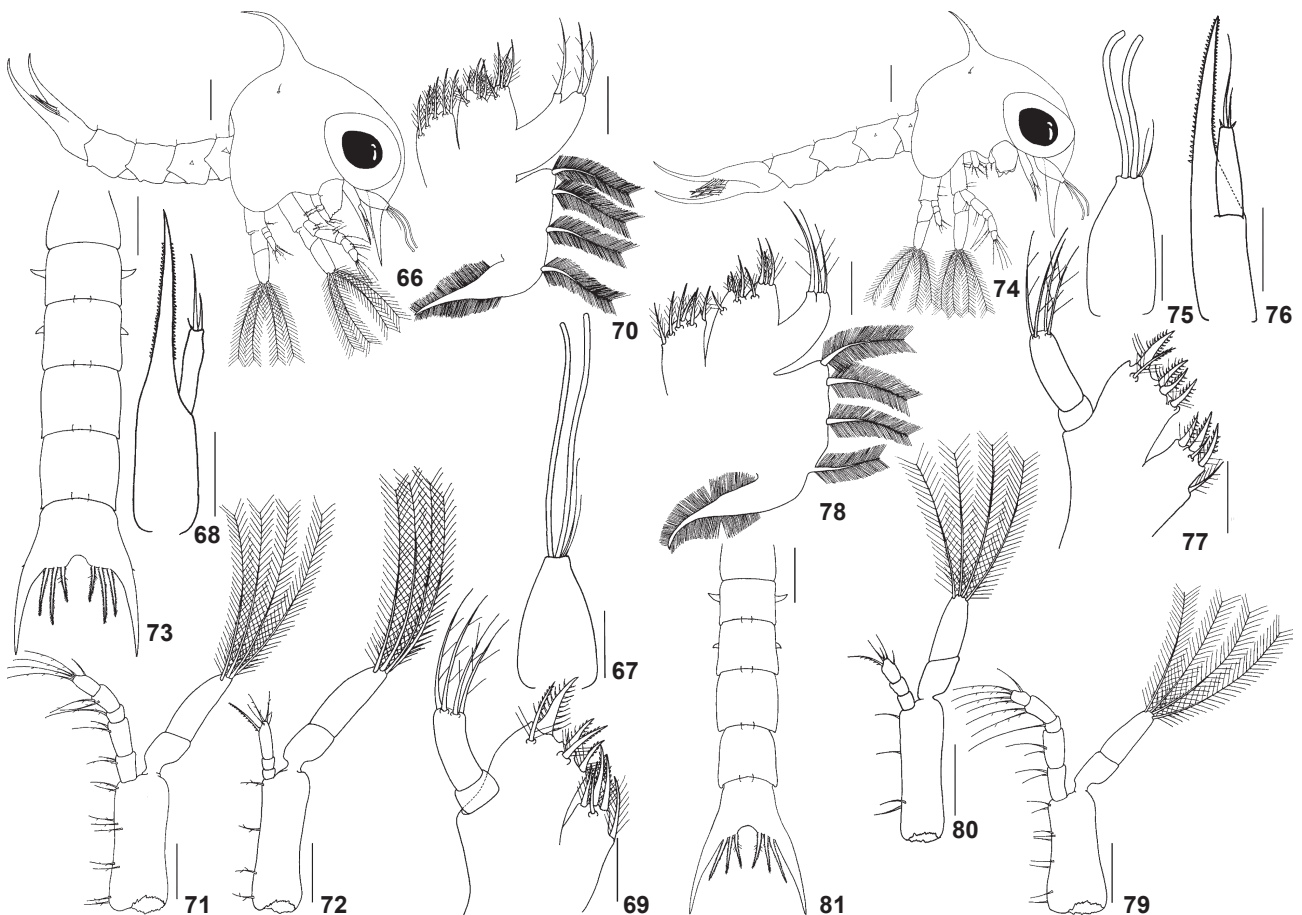
Endopod bilobed with 1 + 2 sparsely plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 63). Basis with 1+1 (sparsely plumose)+1+4+2, simple setae in the inner margin. Endopod 5-segmented with 0 (2), 1 (2), 1, 2, 1 (5) setae, sparsely plumose, from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Second maxilliped** (Fig. 64). Basis with 1+1+1+1 simple setae in the inner margin. Endopod 3-segmented with 0,0,5 (4 simple + 1 denticulate) setae from proximal to distal segment. Exopod unsegmented with 4 long plumose natatory setae. **Abdomen** (Fig. 65). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Telson bifurcated with inner margin with 6(3+3) plumodenticulate setae separated by a medial arch. Each furca with 2-minute lateral spines and 2 rows of minute marginal spines.

Uca rapax (Smith, 1870)

Carapace (Fig. 66). Globose, smooth, with 1 pair of posterodorsal simple setae. Dorsal spine present and strongly curved. Lateral spines absent. Rostral spine slightly curved, extending beyond antenna. Eyes sessile. **Antennule** (Fig. 67). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 2 simple unequal setae. **Antenna** (Fig. 68). Protopod well-developed with 2 rows of small equal-sized spines. Exopod about $\frac{1}{4}$ of protopod length, with 3 unequal simple setae. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with three small teeth of unequal size and two teeth arranged separately on the inner margin. Molar process with a large tooth in base and circular regions provided of small and irregular teeth.

Maxillule (Fig. 69). Coxal endite with 4 (2 plumodenticulate + 1 simple subterminal + 1 plumose) setae and 1 plumose

subterminal lateral seta. Basial endite with 2 cuspidate setae and 3 (2 subterminal) plumodenticulate setae. Endopod 2-segmented with proximal segment without setae and 4 sparsely plumose terminal setae on the distal segment. **Maxilla** (Fig. 70). Coxal endite bilobed with 4 (3 subterminal) + 3 (1 similar to hamate) plumose setae. Basial endite bilobed with 5 (1 subterminal) + 4 (1 subterminal) plumose setae. Endopod bilobed with 1 + 2 sparsely plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 71). Basis with 2+2+3+2 sparsely plumose setae in the inner margin. Endopod 5-segmented with 2,2,1,2,5 (1 simple lateral seta) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Second maxilliped** (Fig. 72). Basis with 1+1+1+1 sparsely plumose setae in the inner margin. Endopod 3-segmented with 0,0,5 (2 simple + 2 sparsely



Figures 66-81. (66-73) *Uca rapax*: lateral view (66); antennule (67); antenna (68); maxillule (69); maxilla (70); first maxilliped (71); second maxilliped (72); abdomen and telson (73); (74-81) *Uca thayeri*: lateral view (74); antennule (75); antenna (76); maxillule (77); maxilla (78); first maxilliped (79); second maxilliped (80); abdomen and telson (81). Scale bars: 66, 73, 74, 79, 80 = 0.08 mm; 67, 68, 75-78 = 0.03 mm; 69, 70 = 0.025 mm; 71, 72 = 0.06 mm; 81 = 0.1 mm.

plumose + 1 denticulate) setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Abdomen** (Fig. 73). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Telson bifurcated with 1 minute lateral spine. Inner margin with 6(3+3) plumodenticulate setae separated by a medial arch.

Uca thayeri Rathbun, 1900

Carapace (Fig. 74). Globose, smooth with 1 pair of posterodorsal simple setae. Dorsal spine present and curved, bearing minute spines randomly arranged on the anterior surface. Lateral spines absent. Rostral spine slightly curved, extending beyond antenna. Eyes sessile. **Antennule** (Fig. 75). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 2 simple setae. **Antenna** (Fig. 76). Protopod well-developed with 2 rows of small marginal spines. Exopod with 2 simple setae of different sizes and 2 small spines. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with two small teeth of unequal size and two teeth arranged separately on the inner margin. Molar process with a large tooth in the base and circular regions provided of small and irregular teeth. **Maxillule** (Fig. 77). Coxal endite with 4 apical setae (3 plumodenticulate + 1 simple subterminal) and 1 lateral plumose seta. Basial endite with 2 cuspidate and 3 plumodenticulate (1 subterminal) setae. Endopod 2-segmented, proximal segment lacking setae, 4 sparsely plumose terminal setae on the distal segment. **Maxilla** (Fig. 78). Coxal endite bilobed with 4 setae (2 subterminal) + 3 setae (1 similar to hamate) sparsely plumose. Basial endite bilobed with 5 setae (2 subterminal) + 4 setae (1 subterminal) sparsely plumose. Endopod bilobed with 1+2 sparsely plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 79). Basis with 2+2+3+2 simple setae in the inner margin. Endopod 5-segmented with 0(2),0(2),0(1),2,4(5) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Second maxilliped** (Fig. 80). Basis with 1+1+1+1 simple setae in inner margin. Endopod 3-segmented with 0,0,5 (4 simple + 1 denticulate) simple setae from proximal to distal segment. Exopod 2-segmented with 4 long plumose natatory terminal setae. **Abdomen** (Fig. 81). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with a pair of small simple posterodorsal setae. Telson bifurcated, with inner margin with 6 (3+3) plumodenticulate setae separated by a medial arch.

Ucididae

Ucides cordatus (Linnaeus, 1763)

Carapace (Fig. 82). Globose, smooth with 1 pair of posterodorsal simple setae. Dorsal spine present, sloped posteriorly. Lateral spines absent. Rostral spine slightly curved, ex-

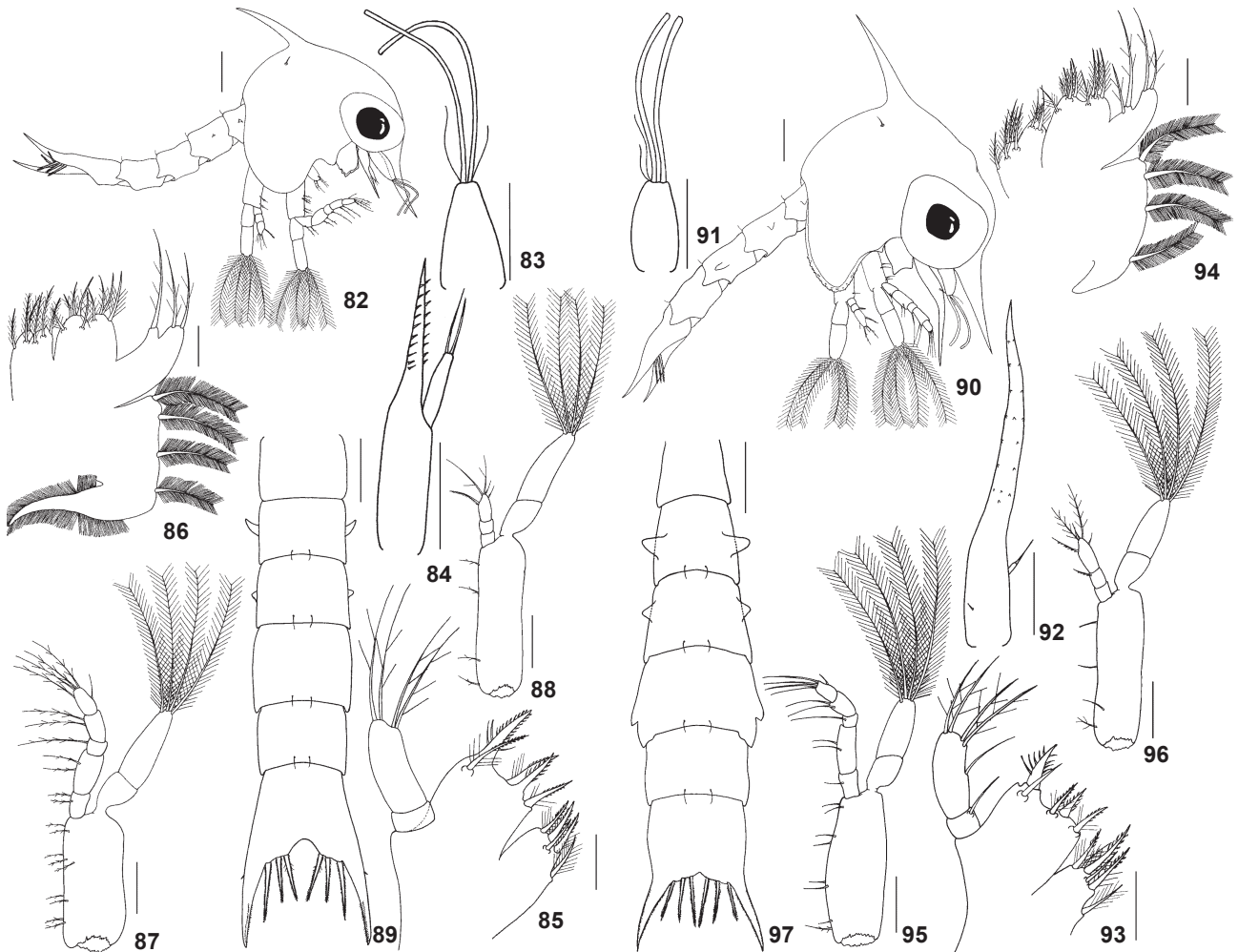
tending beyond antenna. Eyes sessile. **Antennule** (Fig. 83). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 2 simple setae.

Antenna (Fig. 84). Protopod well-developed, bearing 2 rows of small spines equal-sized. Exopod with 2 simple setae of similar size. **Mandible**. Symmetric, palp absent, incisor process with a prominent tooth associated with three small teeth of unequal size and two teeth arranged separately on the inner margin. Molar process with a large tooth in base and circular regions provided of small and irregular teeth. **Maxillule** (Fig. 85). Coxal endite with 4 (3 plumodenticulate + 1 simple subterminal) setae and 1 plumodenticulate subterminal lateral seta. Basial endite with 2 cuspidate and 3 plumodenticulate (1 subterminal) setae. Endopod 2-segmented with proximal segment lacking setae and 4 sparsely plumose terminal setae in distal segment. **Maxilla** (Fig. 86). Coxal endite bilobed with 3 (1 subterminal) + 4 (2 subterminal, 1 similar to hamate) plumose setae. Basial endite bilobed with 5 (2 subterminal) + 4 (1 subterminal) sparsely plumose setae. Endopod bilobed with 1+2 sparsely plumose setae. Scaphognathite with 4 marginal plumose setae and a long distal process with microtrichias. **First maxilliped** (Fig. 87). Basis with 2+2+3+2 sparsely plumose setae in the inner margin. Endopod 5-segmented with 2,2,1,2,5 (1 simple lateral) sparsely plumose setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Second maxilliped** (Fig. 88). Basis with 1+1+1+1 sparsely plumose setae in the inner margin. Endopod 3-segmented with 0,0,5 (1 denticulate + 2 sparsely plumose + 2 simple) setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Abdomen** (Fig. 89). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Somites 2-5 with short posterolateral spines and a pair of small simple posterodorsal setae. Telson bifurcated with a minute lateral spine. Inner margin with 6(3+3) plumodenticulate setae separated by a medial arch. Distal inner margin with a serrated furca.

Grapsidae

Pachygrapsus gracilis (Saussure, 1858)

Carapace (Fig. 90). Globose, smooth with 1 pair of posterodorsal simple seta. Anterior region showing a small protuberance. Dorsal spine present and only slightly sloped. Lateral spines absent. Posteroventral margin with small irregular tubercles. Rostral spine slightly sloped, almost equal to the antennal length. **Antennule** (Fig. 91). Uniramous, conical-shaped and unsegmented with 2 aesthetascs and 2 unequal simple setae. **Antenna** (Fig. 92). Protopod well-developed with 1 small seta in the base, provided with minute spines irregularly arranged medially to distally on the shaft. Exopod much reduced, with 1 simple terminal seta. **Mandible**. Symmetric, palp absent, incisor process with two prominent teeth separated by two small and two teeth arranged separately on the inner margin. Molar process with a large tooth in the base and



Figures 82-97. (82-89) *Ucidetes cordatus*: lateral view (82); antennule (83); antenna (84); maxillule (85); maxilla (86); first maxilliped (87); second maxilliped (88); abdomen and telson (89); (90-97) *Pachygrapsus gracilis*: lateral view (90); antennule (91); antenna (92); maxillule (93); maxilla (94); first maxilliped (95); second maxilliped (96); abdomen and telson (97). Scale bars: 82 = 0.13 mm; 83, 95, 96 = 0.06 mm; 84, 91, 92 = 0.05 mm; 85, 86, 94 = 0.03 mm; 95 = 0.025 mm; 87, 88, 90, 97 = 0.08 mm; 89 = 0.1 mm.

circular regions provided of small and irregular teeth. **Maxillule** (Fig. 93). Coxal endite with 5 (3 plumodenticulate + 1 sparsely plumose + 1 simple) setae and 1 plumose subterminal lateral seta. Basial endite with 2 cuspidate, 2 plumodenticulate and 1 simple subterminal setae. Endopod 2-segmented with 1 simple seta in proximal segment, while the distal segment showing 1 simple medial and 4 sparsely plumose terminal setae. **Maxilla** (Fig. 94). Coxal endite bilobed with 5 (2subterminal) + 3 (2 subterminal) plumose setae. Basial endite bilobed, with 5 (subterminal) + 4 (1 subterminal) plumose setae. Endopod bilobed with 2+2 sparsely plumose setae. Scaphognathite with 4 plumose marginal setae with a distal process little developed. **First maxilliped** (Fig. 95) Basis with 2 (1 sparsely plumose)+ 2+2+2, simple setae in the inner margin. Endopod 5-segmented with

1,2,1,2,5 (4 terminal +1 lateral subterminal) simple setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Second maxilliped** (Fig. 96). Basis with 1 (sparsely plumose)+1+1+1 simple setae on the inner margin. Endopod 3-segmented with 0,1 (denticulate), 5 (1 denticulate + 2 sparsely plumose) setae from proximal to distal segment. Exopod 2-segmented with 4 terminal long plumose natatory setae. **Abdomen** (Fig. 97). With 5 somites and telson. Somites 2 and 3 with a pair of dorsolateral spines. Posterior margin of the 4th somite laterally extended with 1 spine. Somites 2-5 with a pair of small posterolateral spines and a pair of small simple posterodorsal setae. Telson bifurcated with the inner margin provided of 6(3+3) plumodenticulate setae separated by a small arch, margins of the furca serrated.

Key to identification of Zoea I of the described species

- 1a. Carapace with lateral spines (Figs 1, 9, 50, 58) 2
- 1b. Carapace lacking lateral spines (Figs 17, 26, 34, 42, 66, 74, 82, 90) 5
- 2a. Antenna with elongate protopod, distally armed with strong spines in more than 2 rows (Figs 3, 11) 3
- 2b. Antenna with protopod not particularly elongate, and with 2 rows of spines only (Figs 19, 28, 36, 44, 52, 60, 68, 76 and 84) 4
- 3a. Antennule distally with 2 aesthetascs and 2 simple setae (Figs 9 and 10) *Eurytium limosum*
- 3b. Antennule distally with 2 aesthetascs and 3 simple setae (Figs 1 and 2) *Panopeus americanus*
- 4a. Fourth abdominal somite with posterior margin expanded laterally (Figs 50 and 57) *Ocypode quadrata*
- 4b. Abdominal somites similar, without lateral expansion (Figs 58 and 65) *Uca maracoani*
- 5a. Abdomen lacking Pleopods (Figs 26, 34, 66, 74, 82, 90) . 6
- 5b. Abdomen with pleopods (Fig. 17) *Sesarma curacaoense*
- 6a. Fourth abdominal somite with posterior margin laterally expanded, bearing 1 robust spine (Figs 90 and 97)
..... *Pachygrapsus gracilis*
- 6b. Abdominal somites similar, without lateral expansion and spine (Figs 33, 41, 49, 89) 7
- 7a. Antennal protopod with 2 rows of unequal-sized spines arranged sparsely and relatively widely apart (Figs 28, 36, 44) 8
- 7b. Antennal protopod with 2 rows of minute equal-size spines, arranged relatively close to each other (Figs 76, 68, 84) 10
- 8a. Antennal endopod present (Figs 26 and 28)
..... *Sesarma rectum*
- 8b. Antennal endopod absent (Figs 35, 43, 68, 76, 84) 9
- 9a. Carapace with 2 pairs of simple anterodorsal simple setae between eyes; antennal exopod with 2 minute terminal spines (Figs 42 and 44) *Aratus pisonii*
- 9b. Carapace with 1 pair of simple anterodorsal setae between eyes; antennal exopod lacking spines (Figs 34 and 36)
..... *Armases rubripes* (Fig. 34)
- 10a. Abdominal somites 3-5 with short posterolateral spines; telson inner margin of distal region with furcal ramous distinctly serrate (Figs 82 and 89) *Ucides cordatus*
- 10b. Abdominal somites 3-5 with rounded posterolateral knobs, furcal ramous not distinctly serrate using light microscopy (Figs 73 and 81) 11
- 11a. Carapace with dorsal spine posteriorly strongly curved, furcal ramous with 1 minute proximal lateral spine arranged (Figs 66 and 73) *Uca rapax*
- 11b. Carapace with dorsal spine posteriorly not strongly curved, bearing minute spines randomly arranged on the anterior surface; furcal ramous lacking proximal lateral spines (Fig. 74) *Uca thayeri*

DISCUSSION

The morphological characteristics of brachyuran larvae, especially in the early stages, are essential to systematic and phylogenetic studies (CLARK *et al.* 1998), because they help to establish character states as primitive or derived (RICE 1983).

According to RICE (1983), the evolutionary trends of Eubrachyuran larvae (zoea) indicate that more derived taxa show a reduction in spines, setae and segmentation, compared with the more primitive taxa. However, such trends, which are presumably associated with a more efficient exploration of the pelagic environment, may evolve independently. Characters of the larval stages, as well as characters of the adults, are liable to convergence (RIEGER 1998).

Nevertheless, the use of larval characteristics in systematics has been widely accepted and applied by taxonomists (CUESTA & ANGER 2001). Furthermore, as more larvae are being described, morphological comparisons become more feasible (RIEGER 1998).

However, it is important to emphasize that it is difficult to differentiate among the larvae of some species, especially congeners, since their distinctions are based only on minor morphological differences. In such cases, the reliability of specific descriptions may be feasible only when the specimens described are born in the laboratory. Descriptions of larvae collected in the field are often generic due to the difficulty in identifying larvae at the level of species (KORNIENKO & KORN 2009). One example of this problem are *Hemigrapsus sanguineus*, *H. penicillatus* and *H. longitarsis*, described by HWANG *et al.* (1993), HWANG & KIM (1995) and PARK & KO (2001), respectively. These species have almost identical initial stages, and can only be distinguished when they develop into more advanced stages.

The close similarity observed among species of *Hemigrapsus* was also noted in the present study for species in the Panopeidae, *P. americanus* and *E. limosum*. Even though our description of *P. americanus* agrees with that by NEGREIROS-FRANZOZO (1986), it differs from it in various aspects. NEGREIROS-FRANZOZO (1986) described some different features, such as a pair of posterodorsal simple setae on the carapace, a small protuberance on the anterior and posterior carapace regions, and an additional small spine on each side of the telson furca; there is also a difference in the aesthetasc, and seta numbers on the antennules compared to those described by NEGREIROS-FRANZOZO (1986) (Table III). There are also discrepancies in number of setae of the coxal endite of the maxillule, and the basal and coxal endites of the maxilla. Other differences found in the description of *P. americanus* refer to the types of setae originally described. NEGREIROS-FRANZOZO (1986) reported the presence of feathery, i.e. plumose setae on most appendages for which we described plumodenticulate or sparsely plumose setae. This was also observed for other species described in this paper.

When describing *Eurytium limosum*, KURATA *et al.* (1981) did not consider morphological and meristic features of several appendages, including the number of aesthetascs and setae on

Table III. Morphological comparison between the present study and previous descriptions of *Panopeus americanus*., *Eurytium limosum* and *Sesarma curacaoense*.

Structure	<i>Panopeus americanus</i>		<i>Eurytium limosum</i>		<i>Sesarma curacaoense</i>		
	NEGREIROS-FRANZOZO (1986)	Present study	KURATA <i>et al.</i> (1981)	Present study	ANGER <i>et al.</i> (1995)	SCHUBART & CUESTA (1998)	Present study
Carapace	s nd	1pair s	s nd	1pair	2+1pair# s	2+1pair s	2+1pair s
Antennule	3aes, 1s	2aes, 3s	?	2aes, 2s	3aes, 2s	3aes, 1s	3aes, 1s
Antennal exopod	1s, 0sp	1s, 0sp	?	1s, 0sp	0s, 2sp	2s, 0sp	2s, 0sp
Maxillule							
CE	5pls	6pls+1s	?	3pds+1pls+1s	6pls	6pds	2pls+4pds
BE	6pls	2cps+3pds	?	2cps+3pds	3pds+2pls+3sps	5pds	2cps+3pds
Maxilla							
CE	5pls	8pls	?	7pls+1hs	8pls+1sp	9##	8pls+ 1hs
BE	6pls	8pls+1pds	?	6pls+3pds	9-10pds	9##	4pls+3pds+1ds
Telson							
Furca	2sp	3sp	2sp	3sp	2 rows of spines	2 rows of spines	2 rows of spines
	(1dorsal+1lateral)	(1dorsal+2lateral)	(1dorsal+1lateral)	(1dorsal+2lateral)			

(CE) coxal endite, (BE) basal endite, (s) simple seta, (pls) plumose seta, (pds) plumodenticulate seta, (cps) cuspidate seta, (aes) aesthetascs, (sp) spine, (sps) sparsely plumose seta, (hs) seta similar to the hamate, (nd) not described, (?) not defined, (#) only illustrated by the author, (##) type of seta not specified.

the antennules, the type and quantity of setae on the maxillule, maxilla, as well as maxillipeds, among other characteristics (Table III). While CLARK *et al.* (1998) argue that taxonomists should be discouraged to establish relationships based on incomplete descriptions, the description of KURATA *et al.* (1981) has much in common with the present one, for instance in the abdomen, antenna, telson, and carapace spines. However, *E. limosum* is very similar to other species of Panopeidae, and larvae can only be distinguished from the second stage of the zoea on, which has the antenna without any spinous process.

A great similarity among larvae of species in the same genus has also been demonstrated for Sesarmidae (GUERAO *et al.* 2004, CUESTA *et al.* 2006b, GUERAO *et al.* 2007). Although the morphology of species of *Aratus*, *Armas* and *Sesarma* is quite similar in the first zoea, these species can be distinguished, in most cases, by minor differences in the pattern of their setae (SCHUBART & CUESTA 1998). Some species, such as *S. curacaoense* (ANGER *et al.* 1995, SCHUBART & CUESTA 1998), are more clearly differentiated, mainly by the presence of pleopods on the abdominal somites and partially differentiated pereopods (observed but not described in this paper) that are not present in other species. These characteristics, together with the number and pattern of setae, maxillule and maxilla (SCHUBART & CUESTA 1998) (Table III) characterize *S. curacaoense* morphologically as more derived compared to other species of the genus, such as *S. reticulatum* and *S. rectum* (ANGER *et al.* 1995). Both ANGER *et al.* (1995) and SCHUBART & CUESTA (1998) described a very conservative pattern of appendages and setae for *S. curacaoense*, which is consistent with the results of the present study. However, they differentiated the setae only as simple, plumose and plumodenticulate.

Unlike the description of *S. curacaoense*, our description of *S. rectum* differs in several respects from the one previously

given by FRANZOZO & HEBLING (1986). The latter did not report the presence of a pair of posterodorsal setae, and two pairs of simple setae on the anterodorsal portion of the carapace, as well as the following features: two rows of unequal spines on the antennal protopod, cuspidate and plumodenticulate setae on the basal endite, and plumodenticulate and simple setae on the coxal endite of the maxillule. Further differences are present in various structures, particularly in the maxilla, where the type or the number of setae arranged on the basal and coxal endites vary (Table IV). Discrepancies in the description of those characters, according SCHUBART & CUESTA (1998), are generally due to subject interpretations of various taxonomists, regional, or intraspecific variation. However, caution is needed when making observations on those variations, because descriptions are often based on features commonly regarded as highly conservative, as the pattern of setae on the appendages (FLORES *et al.* 2003).

According to CLARK *et al.* 1998, many recent studies have failed to provide detailed descriptions of some features, mainly involving the pattern of setae of the appendages. This is more common in older contributions, including the description of *A. rubripes* by DÍAZ & EWALD (1968). The morphological differences between that description and the present study are likely due to DÍAZ & EWALD's failure to observe the two unequal rows of spines on the antennal protopod, an additional seta on the antennule and coxal endites of the maxillule and maxilla, among other features (Table IV). Possibly the lack of criteria for publishing a description has resulted in such discrepancies.

Descriptions of *A. pisonii* larvae were published by HARTNOLL (1965), WARNER (1968), FRANZOZO *et al.* (1998) and CUESTA *et al.* (2006a). When evaluated against modern standards for larval descriptions, the information provided by HARTNOLL (1965) and WARNER (1968) can be considered limited (see CLARK *et al.* 1998).

Although the descriptions by FRANSOZO *et al.* (1998) and CUESTA *et al.* (2006a) are relatively recent, both differ in several aspects from the present description (Table IV), particularly when it comes to setal types. This may be the reason why CUESTA *et al.* (2006a) have not considered it.

CUESTA *et al.* (2006b) re-examined the samples described by FRANSOZO *et al.* (1998), and found several differences between the two descriptions. These data, together with those presented in this study, point to the existence of interspecific variability (CUESTA *et al.* 2006b). Thus, morphological consistency among populations of *A. pisonii* may be questioned, and highlights the need for studies that address phylogenetic aspects to assist the resolution of disagreements regarding the morphology of this species.

Although not using current descriptive standards, DIAZ & COSTLOW (1972) described in detail the morphological features of *O. quadrata* larvae. Their description did not differ significantly from the present one, but lacked some information, such as the presence of a pair of posterodorsal simple setae on the carapace, an additional simple seta on the coxal endite of the maxillule and two minute spines on the antennal exopod (Table V). These differences may have to do with methodological limitations in the preparation of the larvae for microscopy, or result from optical limitations, possibly impairing the description of the appendages. However, other plausible reasons such as population and interspecific variation cannot be ruled out.

Table IV. Morphological comparison between the present study and previous descriptions of *Sesarma rectum*, *Armases rubripes* and *Aratus pisonii*.

Structure	<i>Sesarma rectum</i>		<i>Armases rubripes</i>		<i>Aratus pisonii</i>		
	FRANSOZO & HEBLING (1986)	Present study	DIAZ & EWALD (1968)	Present study	FRANSOZO <i>et al.</i> (1998)	CUESTA <i>et al.</i> (2006a)	Present study
Carapace	s nd	2+1 pair s	s nd	1+1 pair s	2+1 pair s	2+1 pair s	2+1 pair s
Antennule	3aes, 2s	3aes, 2s	3aes, seta?	3aes, 2s	3aes, 2s	4aes	3aes, 2s
Antennal exopod	2s, 0sp	2s, 0sp	2 ?, 0sp	2s, 0sp	3s, 0sp	2s, 2sp	2s, 2sp
Maxillule							
CE	5pls	3pds+1ps+2s	5 ser sp	3pds+1pls+2s	5pds	5pds	3pds+1pls+2s
BE	5pls	2cps+3pds	5 ser sp	2cps+3pds	5pds	1cps+4pds	2cps+3pds
Maxilla							
CE	8pls	8cpl+1hs	8 sp	8pls+1hs	8pds	8pds	8pls+11hs
BE	8pls	3pds+5pls+1s	9 sp	8pls+1s	8pds	9pds	1pds+7pls+1s
Telson							
Furca	nd	2 rows of spines	nd	2 rows of spines	nd	2 lateral sp+2 rows sp	2 lateral sp+2 rows sp

(CE) coxal endite, (BE) basal endite, (s) simple seta, (pls) plumose seta, (pds) plumodenticulate seta, (cps) cuspidate seta, (aes) aesthetascs, (sp) spine, (spd) plumodenticulate seta, (ser sp) serrated spine, (sps) sparsely plumose seta, (hs) seta similar to the hamate, (nd) not described, (?) not defined.

Table V. Morphological comparison between the present study and previous descriptions of *Ocypode quadrata*, *Uca maracoani* and *Uca rapax*.

Structure	<i>Ocypode quadrata</i>		<i>Uca maracoani</i>		<i>Uca rapax</i>	
	DIAZ & COSTLOW (1972)	Present study	NEGREIROS-FRANSOZO <i>et al.</i> (2009)	Present study	SERBINO (2008)	Present study
Carapace	s nd	1 pair s	s nd	1 pair s	s nd	1 pair s
Antennule	2aes, 2s	2aes, 2s	3aes, 1s	2aes, 2s	3aes, 1s	2aes, 2s
Antennal exopod	2s, 0sp	2s, 2sp	2s, 0sp	3s, 0sp	2s, 1sp	2s, 0sp
Maxillule						
CE	5sers+2pro	4pds+1s	3? + 2s	3pds+1pls+1s	5pds	2pds+2pls+1s
BE	5sers	2cps+3pds	3cps+4s	2cps+3pds	2pds-cps+3pds	2cps+3pds
Maxilla						
CE	6pls	6pls+1 hs	6s	6pls+1hs	6pds	6pds+1hs
BE	9pls	9pls	7-10s+2sers	9pls	9pds	9pls
Telson						
Furca	–	–	2 lateral sp + nd	2 lateral sp + 2 rows sp	nd	1lateral sp

(CE) coxal endite, (BE) basal endite, (s) simple seta, (pls) plumose seta, (pds) plumodenticulate seta, (cps) cuspidate seta, (aes) aesthetascs, (sp) spine, (spd) plumodenticulate seta, sers (serrate seta), (ser sp) serrated spine, (sps) sparsely plumose seta, (hs) seta similar to the hamate, (pro) protuberance, (nd) not described, (?) not defined.

The recent description of *U. maracoani* by NEGREIROS-FRANZOZO *et al.* (2009) differs from ours in a number of ways, often related to the omission or classification of setal types, such as coxal and basal endites of the maxillule and maxilla, carapace and abdominal somites (Table V). Such inconsistencies have raised questions about the stability of the morphological pattern of this species, establishing the need to investigate possible population variations.

In describing the first larval stage of *U. rapax*, SERBINO (2008) mentioned more details than NEGREIROS-FRANZOZO *et al.* (2009) in their description of *U. maracoani*, and description of *U. thayeri* by ANGER *et al.* (1990). However, her description is somewhat different from that in the present study, particularly regarding the number of setae and aesthetascs on the antennule, the types of setae on the basal endite of the maxilla, the coxal and basal endites of the maxillule (Table V), and the type of setae on the basis and endite of the first and second maxilliped.

According to ANGER *et al.* (1990), there is great need for further laboratory investigations on the larval stages of species of *Uca*. Such investigations would contribute to the clarification of the taxonomic relationships of the group, and allow the identification of larvae in ecological studies. SERBINO (2008) noted that many species of this genus have unique characteristics, while others species have variable characters, and some do not have any features that can be used to distinguish them.

We also found several differences with respect to the description of *Uca thayeri* by ANGER *et al.* (1990). However, these were not as pronounced as for *U. maracoani*. The disagreements involve mainly the terminology used for setae of the maxillule and maxilla, and the number of setae on the antennules, coxal endite of the maxillule and coxal and basal endites of the maxilla (Table VI).

The description of *U. cordatus* by RODRIGUES & HEBLING (1989) does not differ much from that in the present study. The former did not report the presence of a single seta on the antennule and a small lateral spine on each furca, which also have serrated margins (Table VI). Although few, these differences may interfere with the identification of specimens collected in the plankton, which may hinder or even jeopardize comparative morphological or ecological studies of zooplankton.

Among all the larval descriptions analysed in the present study, we found that the one of *P. gracilis* by BROSSI-GARCIA & RODRIGUES (1993) differed the most (Table VI). This relates not only to inadequate descriptions of some appendages, but also to discrepancies in the patterns of setae.

According to CLARK *et al.* (1998), the format of descriptions of brachyuran larvae may vary considerably among authors. But in some cases this variation is clear, establishing a morphological pattern, which is not very satisfactory for comparative studies. Therefore, in addition to more detailed studies on the larval morphology relating to variability, we also need the help of molecular analyses to clarify certain taxonomic relationships.

Despite these shortcomings, the present study provides additional information on the morphology of brachyuran larvae to assist in the identification of plankton samples from different regions, and to update knowledge on comparative morphology of larvae among the groups investigated here.

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Table VI. Morphological comparison between the present study and previous descriptions of *Uca thayeri*, *Ucides cordatus* and *Pachygrapsus gracilis*.

Structure	<i>Uca thayeri</i>		<i>Ucides cordatus</i>		<i>Pachygrapsus gracilis</i>	
	ANGER <i>et al.</i> (1990)	Present study	RODRIGUES & HEBLING (1989)	Present study	BROSSI-GARCIA & RODRIGUES (1993)	Present study
Carapace	s nd	1 pair s	s nd	1 pair s	s nd	1 pair s
Antennule	2aes, 1s	2aes, 2s	2aes, 1s	2aes, 2s	2aes, 1s	2aes2s
Antennal exopod	3s, 0sp	2s, 2sp	2s, 0sp	2s, 0sp	?	1s
Maxillule						
CE	4ser sp	3pds+1pls+1s	4 ?	4pds+1s	5pls	3pds+2pls+1s
BE	4 pl sp+1pls	2cps+3pds	5 ?	2cps+3pds	5-6cps+2-3s	2cps+2pds+1s
Maxilla						
CE	6 pl sp	6pls+1hs	6pls	6pls+1hs	7pls	8pls
BE	8 pl sp	9pls	9pls	9pls	8pls	9pls
Telson						
Furca	-	-	nd	1lateral sp+serrate margin	nd	serrate margin

(CE) coxal endite, (BE) basal endite, (s) simple seta, (pls) plumose seta, (pds) plumodenticulate seta, (cps) cuspidate seta, (aes) aesthetascs, pl sp (plumose spine), (sp) spine, (spd) plumodenticulate seta, (sers) serrate seta, (ser sp) serrated spine, (sps) sparsely plumose seta, (hs) seta similar to the hamate, (nd) not described, (?) not defined.

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