Journal of Plankton Research Vol.20 no.1 pp.61–84, 1998

First zoeal stages of four *Sesarma* species from Panama, with identification keys and remarks on the American Sesarminae (Crustacea: Brachyura: Grapsidae)

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Abstract. The first zoeal stage of the grapsid crabs *Sesarma aequatoriale* Ortmann, 1894, *S.rubinofforum* Abele, 1973, *S.rhizophorae* Rathbun, 1906, *S.curacaoense* de Man, 1892, *Armases ricordi* (H. Milne Edwards, 1853), *A.rubripes* (Rathbun, 1897) and *Cyclograpsus integer* H. Milne Edwards, 1837 was obtained from laboratory-hatched material in Panama. Zoeae I of the four *Sesarma* species are described and illustrated. Larvae of the other three species were used to complete or correct the chaetotaxy of the original descriptions. Larval features are compared among these species and with those of other American Sesarminae. In order to facilitate the study of plankton-collected material, two keys for identification of the known zoea I of sesarmine crabs from Panama are provided: one for Caribbean waters and the other for the Pacific coast. Remarks are given on the generic relationships within the American Sesarminae, the taxonomic position of the genera *Cyclograpsus* and *Chasmagnathus*, and the relevance of the reduction of larval stages.

Introduction

In his review of the American species of *Sesarma*, Abele (1992) recognized a total of 23 from 39 previously reported species as valid. Furthermore, he split the American representatives of this genus into two distinct genera, *Sesarma* and *Armases*, in accordance with their previous subgeneric division of *Sesarma* and *Holometopus* (= *Chiromantes*; see Holthuis, 1977) as redefined by von Hagen (1978). Recently, three new species of *Sesarma* have been described from Jamaica (Türkay and Diesel, 1994; Reimer *et al.*, in press; Schubart *et al.*, 1997) and another species was transferred from the genus *Metasesarma* to *Armases* (see Niem, 1993). Of the 27 currently recognized species of *Armases* and *Sesarma*, larval descriptions are only available for eight species: *Armases angustipes* (Dana, 1852) (see Kowalczuk, 1994), *A.cinereum* (Bosc, 1802) (see Hyman, 1924; Costlow and Bookhout, 1960), *A.ricordi* and *A.rubripes* (see Díaz and Ewald, 1968), *Sesarma bidentatum* Benedict, 1892 (see Hartnoll, 1964), *S.curacaoense* (see Anger *et al.*, 1995), *S.reticulatum* (Say, 1817) (see Hyman, 1924; Costlow and Bookhout, 1962) and *S.rectum* Randall, 1840 (see Fransozo and Hebling, 1986).

Rice (1980, 1983) emphasized the relevance of larval morphology for phylogenetic studies within the Brachyura. Since then, there has been an increasing number of comparative studies on larval morphology. Descriptions of new grapsid larvae are often accompanied by tables summarizing morphological characters of larvae from closely related species (e.g. Wilson, 1980; Pereyra Lago, 1993; Cuesta *et al.*, 1997). Information compiled in this way facilitates direct comparison and eventually helps to discern consistent morphological patterns, which in many cases reflect phylogenetic relationships. One of the more recent tables by Pereyra Lago (1993) summarizes information on larvae from the grapsid subfamilies Varuninae and Sesarminae. From this table, it becomes evident that larval morphology does not allow a clear separation of these two subfamilies as they are presently defined, since some characters which are consistent within the Varuninae are also shared by a few genera placed within the Sesarminae. In order to use larval morphology for phylogenetic studies of the Grapsidae, more larvae need to be reared, descriptions have to be standardized and older studies require revision, especially regarding the setation patterns.

The present description of zoea I from *S.curacaoense*, *S.aequatoriale*, *S.rubinofforum* and *S.rhizophorae* from Panama (the last three being new to science), and re-examination of zoea I from three other Sesarminae (*A.ricordi*, *A.rubripes* and *Cyclograpsus integer*), render important additional information on larval forms of crabs belonging to the family Grapsidae. Morphological characters of the known American Sesarminae larvae are summarized in a table updating previous overviews which considered larvae from this subfamily (Díaz and Ewald, 1968; Wilson, 1980; Pereyra Lago, 1993).

Method

Ovigerous crabs of four species of *Sesarma* were collected in March 1996 at several localities from the Pacific and Caribbean coast of Panama: one *S.aequatoriale* [carapace width (cw) 18.2 mm] under stones at the Miraflores Locks Spillway (ambient salinity 1‰), 3 March 1996; three *S.rubinofforum* (cw 5.8–9.8 mm) and one *S.rhizophorae* (cw 11.5 mm) from burrows in soft mangrove soil at Diablo Heights, 4 March 1996; one *S.curacaoense* (cw 13.5 mm) from burrows in soft mangrove soil adjacent to La Galeta (ambient salinity 8‰), 3 March 1996. Mean egg diameters from 10–20 individual eggs were 0.42×0.37 ($\pm 0.01 \times 0.01$) mm in *S.aequatoriale*, 0.46×0.4 ($\pm 0.02 \times 0.01$) mm in *S.rubinofforum*, 0.46×0.4 ($\pm 0.02 \times 0.01$) mm in *S.rhizophorae* and 0.69×0.61 ($\pm 0.02 \times 0.01$) mm in *S.curacaoense*.

At the Naos laboratories, ovigerous crabs were maintained in small compartments of a plastic dish, which was immersed in a large open-air water tank and thus exposed to ambient temperature and light regimes. Filtered seawater was used and further diluted with tap water. Larvae hatched in 8‰ (*S.rhizophorae*, 7 March 1996), 24‰ (*S.curacaoense*, 7 March 1996), 25‰ (*S.rubinofforum*, 7–8 March 1996) and 20‰ (*S.aequatoriale*, 9 March 1996). A few hours after the larvae hatched and active natatory behaviour was observed, samples of zoea I were fixed in 70% ethanol. The same conditions were used to collect zoea I of the Sesarminae species *A.ricordi*, *A.rubripes* and *C.integer* from the Caribbean coast of Panama. All larvae were dissected and their morphology compared with the original descriptions of these species by Díaz and Ewald (1968) and Gore and Scotto (1982), respectively.

The complete larval development was only obtained for *S.curacaoense*. In this species, development to the megalopa stage took 6–8 days and to the first crab stage 17–20 days under mass culture conditions, with an *Artemia* diet, and varying ambient temperatures. The high capability of resistance shown by *S.curacaoense* larvae is probably a consequence of their large size and the abbreviated development. Physiological capabilities of *S.curacaoense* larvae have been previously described by Schuh and Diesel (1995) and Anger (1995) from Jamaica. The description of the larval morphology by Anger *et al.* (1995) was still in press when the present descriptions were made. Later receipt of that study allowed a detailed comparison of the two descriptions of the zoea I and later developmental stages.

Drawings and measurements were based on 20 larvae for all species and were made using a Wild MZ6 and Zeiss compound microscope with Nomarski interference, both equipped with a camera lucida. All measurements were made by an ocular micrometer. Total length (tl) was measured from the tip of the rostral spine to the tip of the dorsal spine, carapace length (cl) from the base of the rostrum to the posterior margin, and carapace width (cw) as the greatest distance across the carapace. Semi-permanent mounts were made of whole larvae and dissected appendages were stained using CMC 10 and lignin pink. The long natatory setae on the distal exopod segments of the first and second maxilliped are truncated in Figures 3–6. The female crabs from which the larvae hatched and samples of zoea I of the four *Sesarma* species are deposited in the United States National Museum under the catalog number USNM: 284156–284159 (collection number 417871).

Description

Sesarma aequatoriale Ortmann, 1894

Zoea I

(Figures 1A; 3A–F; 7A and C)
Dimensions: tl = 0.93 ± 0.02 mm; cl = 0.49 ± 0.03 mm; cw = 0.41 ± 0.01 mm.

Carapace (Figure 1A). Globose, smooth and without tubercles. Dorsal spine approximately equal in length to rostral spine, recurved with conspicuous protuberances resulting in a serrated appearance. Rostral spine stout and almost equal in length with the antennal protopod. Lateral spines absent. A pair of dorso-lateral simple setae and two pairs of simple setae on the anterio-median region. Postero-lateral margin without setae. Eyes sessile.

Antennule (Figure 3A). Uniramous. Endopod absent. Exopod unsegmented with three aesthetascs and one seta.

Antenna (Figure 3B). Well-developed protopod as long as rostral spine and bearing two rows of spines. Endopod absent. Exopod of approximately two-thirds length of protopod, with two terminal simple setae.

Mandible. Endopod palp absent.

Maxillule (Figure 3C). Coxal endite with five plumodenticulate setae. Basial endite with five plumodenticulate setae. Endopod 2-segmented; proximal segment with one simple seta, distal segment with five (one subterminal and four terminal) sparsely setose setae.

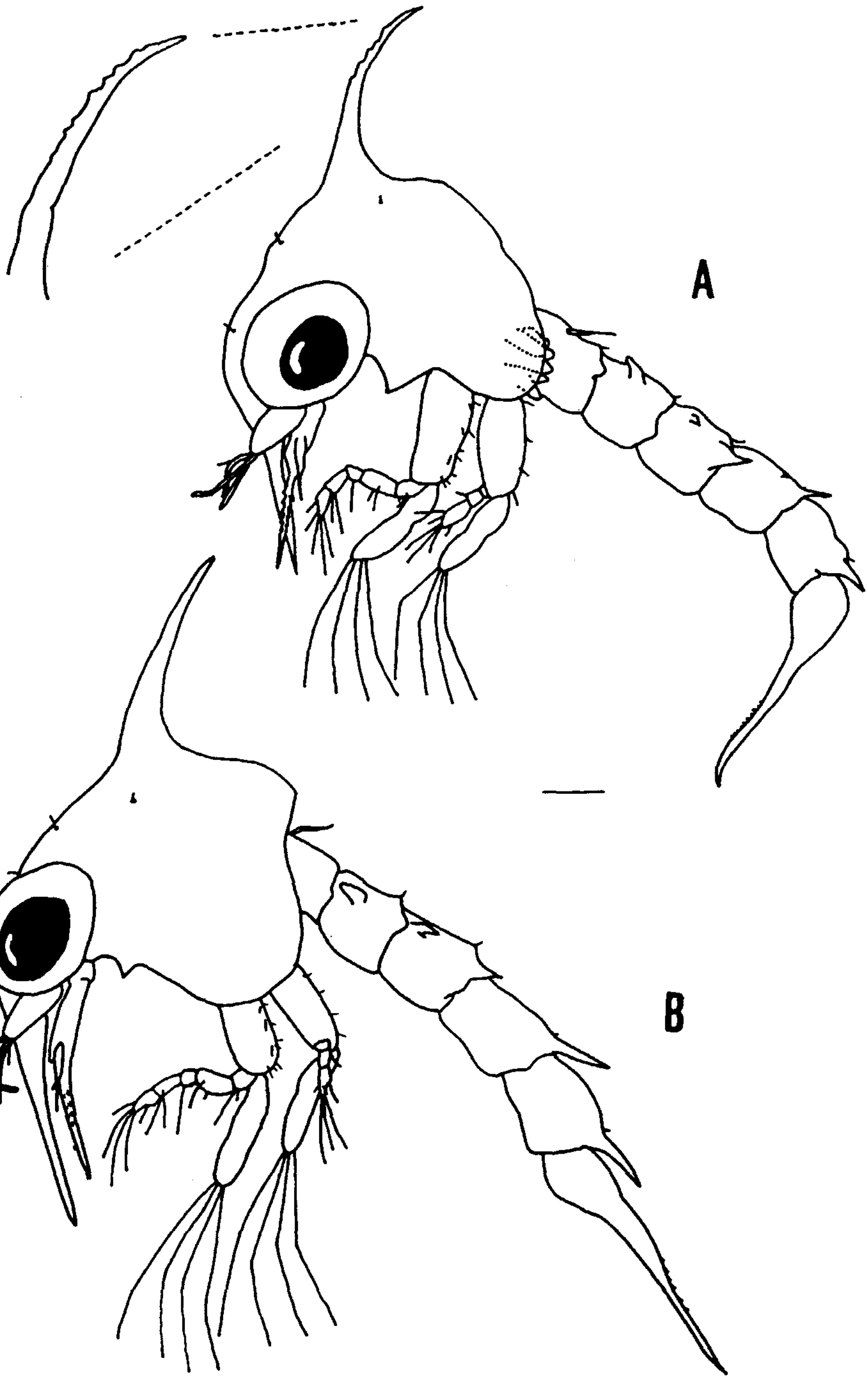

Fig. 1. Zoea I, lateral view. (**A**) *S.aequatoriale* Ortmann, 1894; (**B**) *S.rubinofforum* Abele, 1973. Scale bar = 0.1 mm.

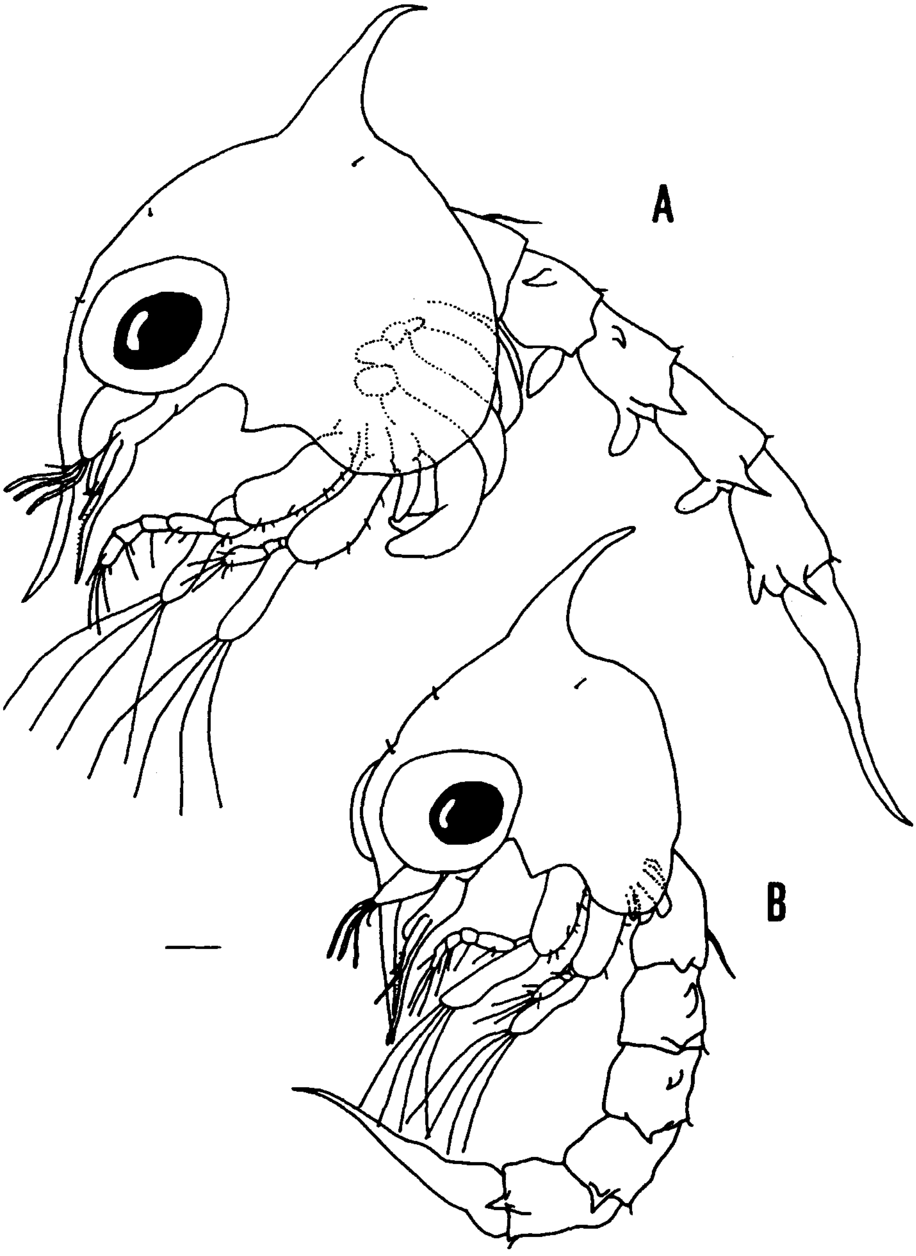

Fig. 2. Zoea I, lateral view. (**A**) *S.curacaoense* de Man, 1892; (**B**) *S.rhizophorae* Rathbun, 1906. Scale bar = 0.1 mm.

Maxilla (Figure 3D). Coxal endite bilobed with 4 + 4 setae. Basial endite bilobed with 5 + 4 setae. Endopod unsegmented, bilobed with two and three long sparsely setose setae on inner and outer lobe, respectively. Scaphognathite with four plumose marginal setae and a long stout posterior process.

First maxilliped (Figure 3E). Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (one subterminal + four terminal) setae. A tuft of fine setae on the back of segment 3. Exopod unsegmented, with four long terminal plumose natatory setae.

Second maxilliped (Figure 3F). Basis with four medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (three subterminal + three terminal) setae. Exopod unsegmented, with four long terminal plumose natatory setae.

Third maxilliped. Undifferentiated bud.

Pereiopods. Undifferentiated buds.

Abdomen (Figures 1A and 7C). Five abdominal somites, first somite with a long mid-dorsal seta, somites 2 and 3 with pair of dorso-lateral processes and somites 3–5 with postero-lateral projections of nearly triangular shape. Pleopods absent.

Telson (Figure 7A). Telson bifurcated, each fork with lateral and dorsal spines absent and with three pairs of spinuous processes on posterior margin. Two short rows of minute spines on each furca.

Sesarma rubinofforum Abele, 1973

Zoea I

(Figures 1B; 4A–F; 7B and D)
Dimensions: tl = 1.14 ± 0.02 mm; cl = 0.51 ± 0.01 mm; cw = 0.32 ± 0.02 mm.

Carapace (Figure 1B). Globose, smooth and without tubercles. Dorsal spine shorter than rostral spine, slightly recurved. Rostral spine stout. Lateral spines absent. A pair of dorso-lateral simple setae and two pairs of simple setae on the anterio-median region. Postero-lateral margin without setae. Eyes sessile.

Antennule (Figure 4A). Uniramous. Endopod absent. Exopod unsegmented with three aesthetascs and one seta.

Antenna (Figure 4B). Well-developed protopod, shorter than rostral spine and bearing two rows of spines. Endopod absent. Exopod reaches half of the length of protopod, with two terminal simple setae.

Mandible. Endopod palp absent.

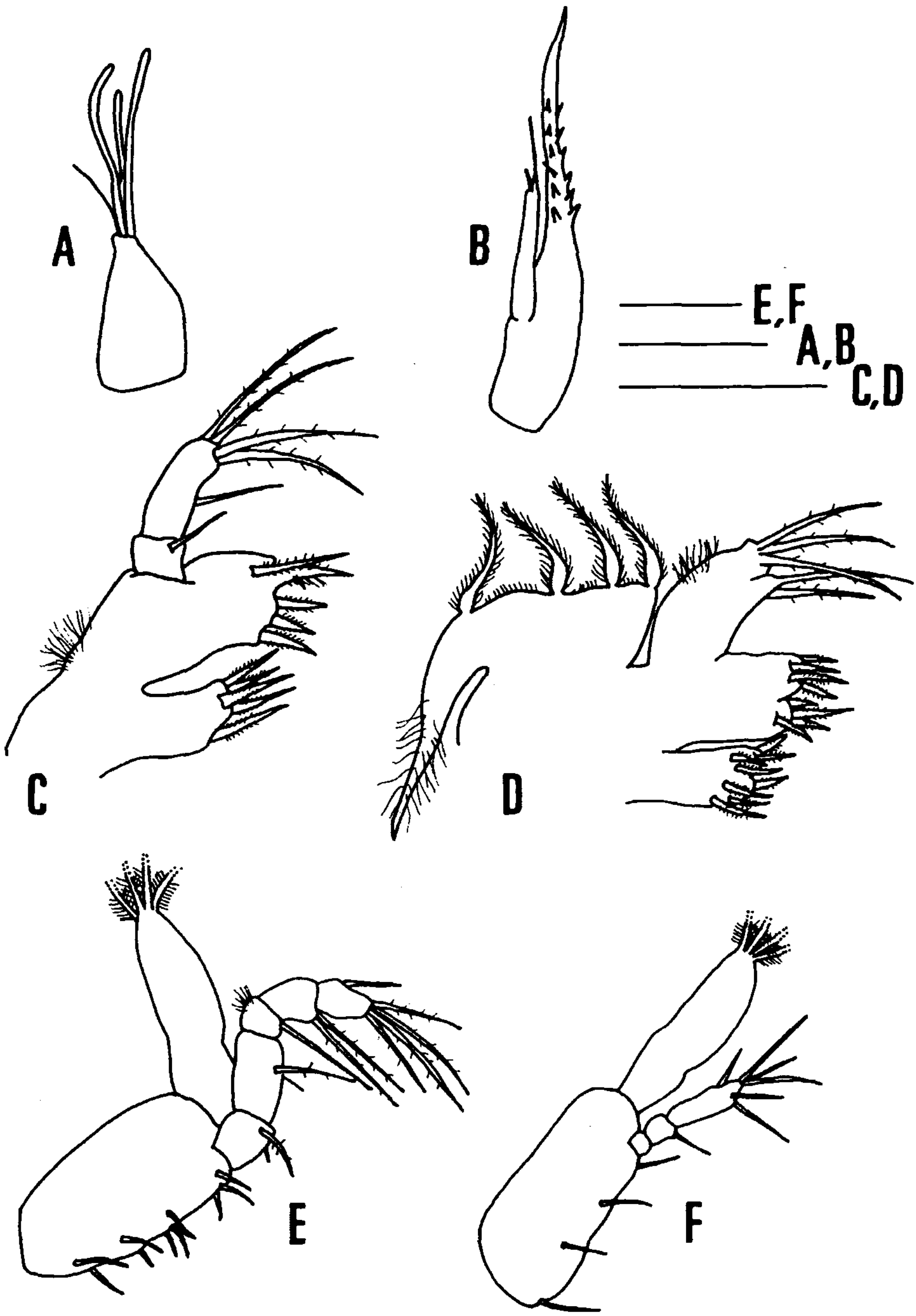

Fig. 3. First zoea of *S.aequatoriale* (Ortmann, 1899). (**A**) Antennule; (**B**) antenna; (**C**) maxillule; (**D**) maxilla; (**E**) first maxilliped; (**F**) second maxilliped. Scale bars = 0.1 mm.

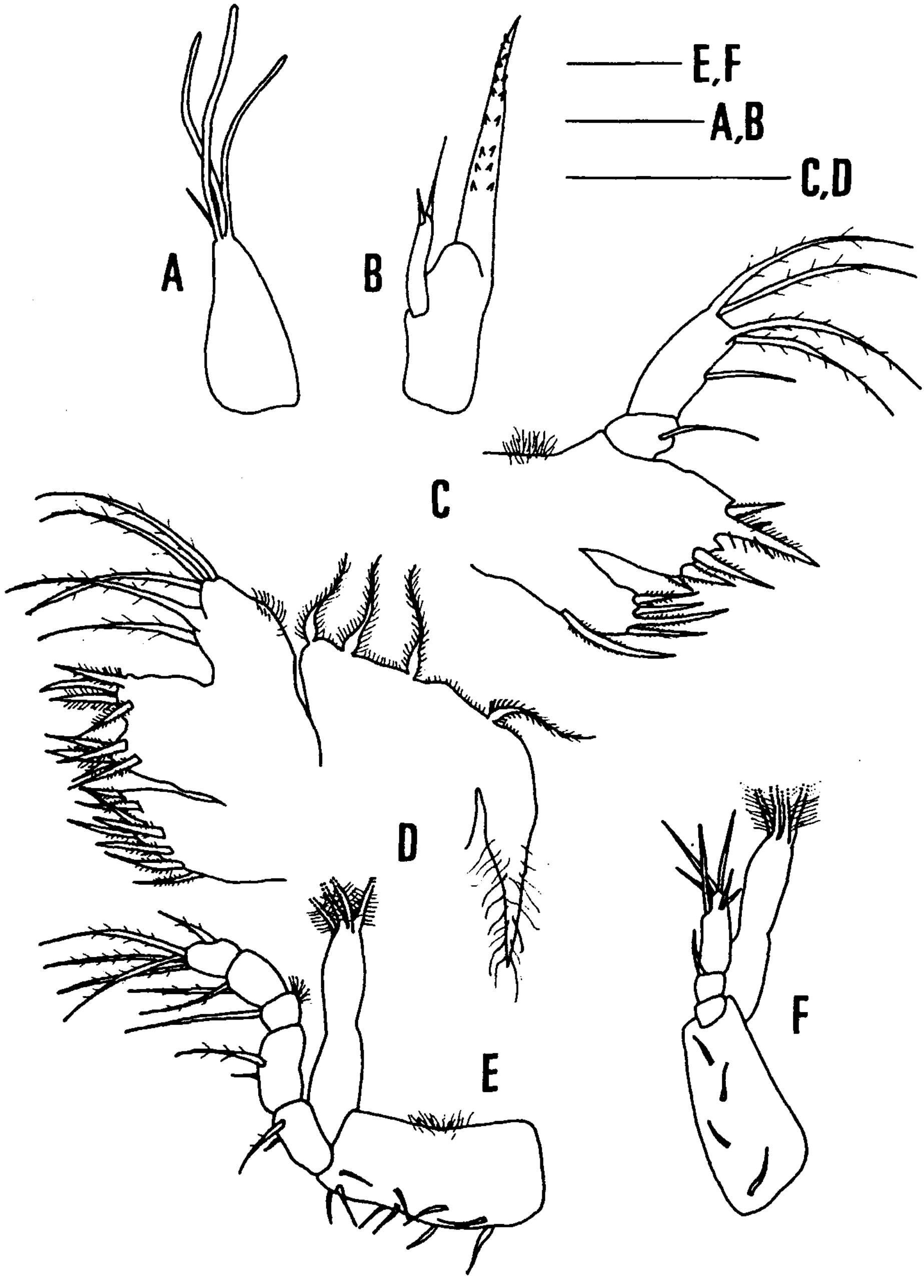

Fig. 4. First zoea of *S.rubinofforum*. (**A**) Antennule; (**B**) antenna; (**C**) maxillule; (**D**) maxilla; (**E**) first maxilliped; (**F**) second maxilliped. Scale bars = 0.1 mm.

Maxillule (Figure 4C). Coxal endite with five plumodenticulate setae. Basial endite with five plumodenticulate setae. Endopod 2-segmented; proximal segment with one simple seta, distal segment with five (one subterminal and four terminal) sparsely setose setae.

Maxilla (Figure 4D). Coxal endite bilobed with 4 + 4 setae. Basial endite bilobed with 5 + 4 setae. Endopod unsegmented, bilobed with two and three long sparsely setose setae on inner and outer lobe respectively. Scaphognathite with four plumose marginal setae and a long stout posterior process.

First maxilliped (Figure 4E). Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (one subterminal + four terminal) setae. A tuft of fine setae on the back of segment 3 and on basis. Exopod unsegmented, with four long terminal plumose natatory setae.

Second maxilliped (Figure 4F). Basis with four medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (three subterminal + three terminal) setae. Exopod unsegmented, with four long terminal plumose natatory setae.

Third maxilliped. Absent.

Pereiopods. Absent.

Abdomen (Figures 1B and 7D). Five abdominal somites, first somite with a long mid-dorsal seta, somites 2 and 3 with pair of dorso-lateral processes, and somites 2–5 with postero-lateral projections which progressively increase in size towards caudal, being almost as long as base of subsequent somite (or telson) in somites 3–5. Pleopods absent.

Telson (Figure 7B). Telson bifurcated, each fork with lateral and dorsal spines absent and with three pairs of spinuous processes on posterior margin. Two rows of well-developed spines on each furca.

Sesarma curacaoense de Man, 1892

Zoea I

(Figures 2A; 5A–I; 8A and C)
Sesarma curacaoense. Anger *et al.*, 1995: 129–130 (Figures 1A, 2A, 3A, 4A, 5A, 6A, 7A, 8A, 10A and 12A).
Dimensions: tl = 1.23 ± 0.03 mm; cl = 0.74 ± 0.02 mm; cw = 0.51 ± 0.02 mm.

Carapace (Figure 2A). Subcircular, smooth and without tubercles. Dorsal spine clearly shorter than rostral spine, recurved. Rostral spine slightly recurved in distal part. Lateral spines absent. A pair of dorso-lateral simple setae and two pairs of simple setae on the anterio-median region. Postero-lateral margin without setae. Eyes sessile.

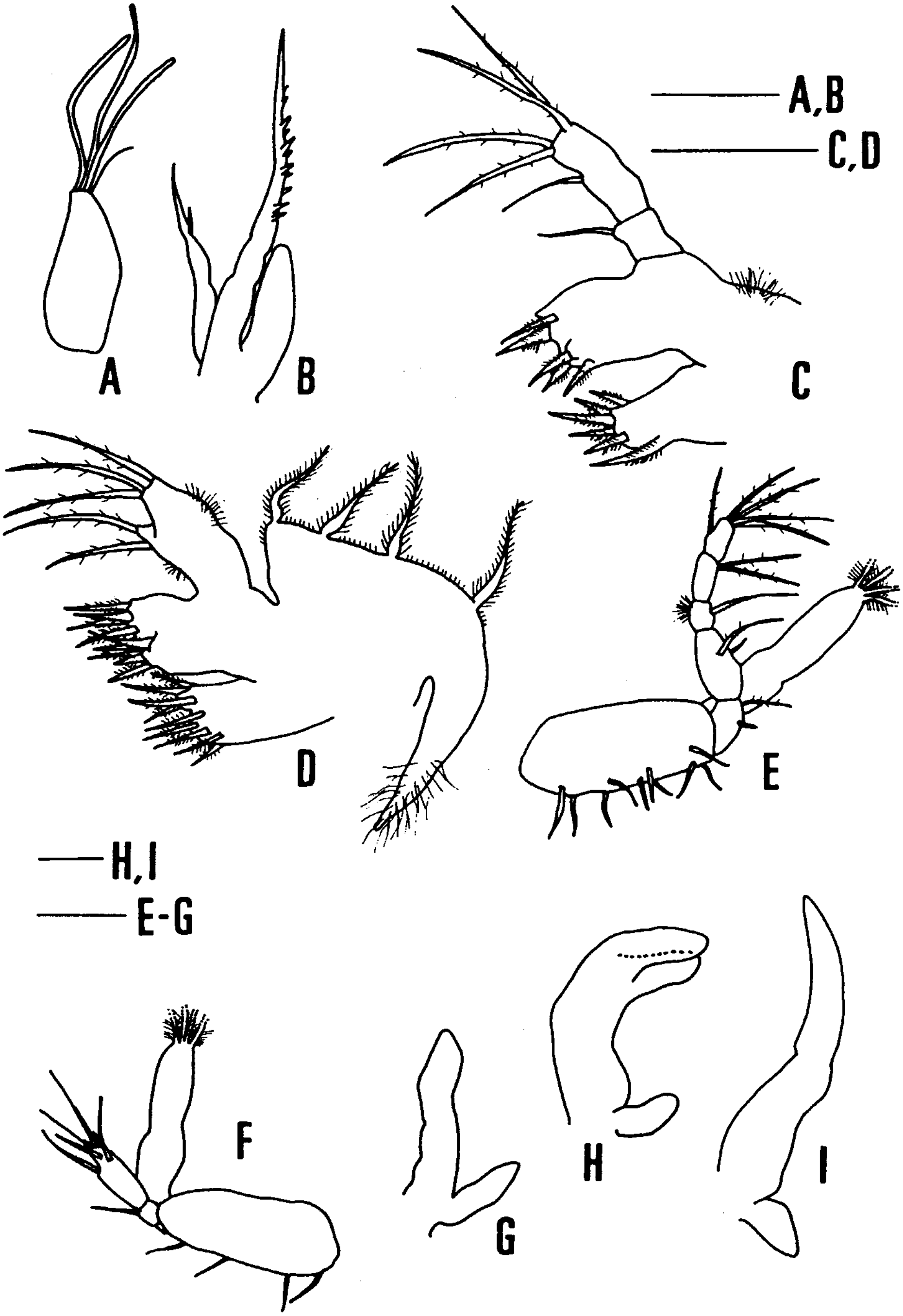

Fig. 5. First zoea of *S.curacaoense* (de Man, 1892). (**A**) Antennule; (**B**) antenna; (**C**) maxillule; (**D**) maxilla; (**E**) first maxilliped; (**F**) second maxilliped; (**G**) third maxilliped; (**H**) first pereiopod; (**I**) third pereiopod. Scale bars = 0.1 mm.

Antennule (Figure 5A). Uniramous. Endopod absent. Exopod unsegmented with three aesthetascs and one seta.

Antenna (Figure 5B). Well-developed protopod shorter than rostral spine and bearing two rows of strong spines. Endopod elongated, reaching half the length of exopod. Exopod reaching half the length of protopod, with two terminal simple setae.

Mandible. Endopod palp absent.

Maxillule (Figure 5C). Coxal endite with six plumodenticulate setae. Basial endite with five plumodenticulate setae. Endopod 2-segmented; proximal segment with one simple seta, distal segment with five (one subterminal and four terminal) sparsely setose setae.

Maxilla (Figure 5D). Coxal endites bilobed with 5 + 4 setae. Basial endite bilobed with 5 + 4 setae. Endopod unsegmented, bilobed with two and three long sparsely setose setae on inner and outer lobe, respectively. Scaphognathite with four plumose marginal setae and a long stout posterior process.

First maxilliped (Figure 5E). Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (one subterminal + four terminal) setae. A tuft of fine setae on back of segment 3. Exopod unsegmented, with four long terminal plumose natatory setae.

Second maxilliped (Figure 5F). Basis with four medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (three subterminal + three terminal) setae. Exopod unsegmented, with four long terminal plumose natatory setae.

Third maxilliped (Figure 5G). Rudimentary, biramous, unsegmented and unarmed bud, with differentiated endopod and exopod.

Pereiopods (Figure 5H and I). Unarmed, unsegmented buds, first pair bilobed (cheliform). All pereiopods with pleurobranch gills.

Abdomen (Figures 2A and 8C). Five abdominal somites, first somite with one or, more often, two long mid-dorsal setae, somites 2 and 3 with pair of dorso-lateral processes and somites 3–5 with posterior-lateral projections of nearly triangular shape. Pleopod buds present.

Telson (Figure 8A). Telson bifurcated, each fork with lateral and dorsal spines absent and with three pairs of spinuous processes on posterior margin. Two long rows of minute spines on each furca.

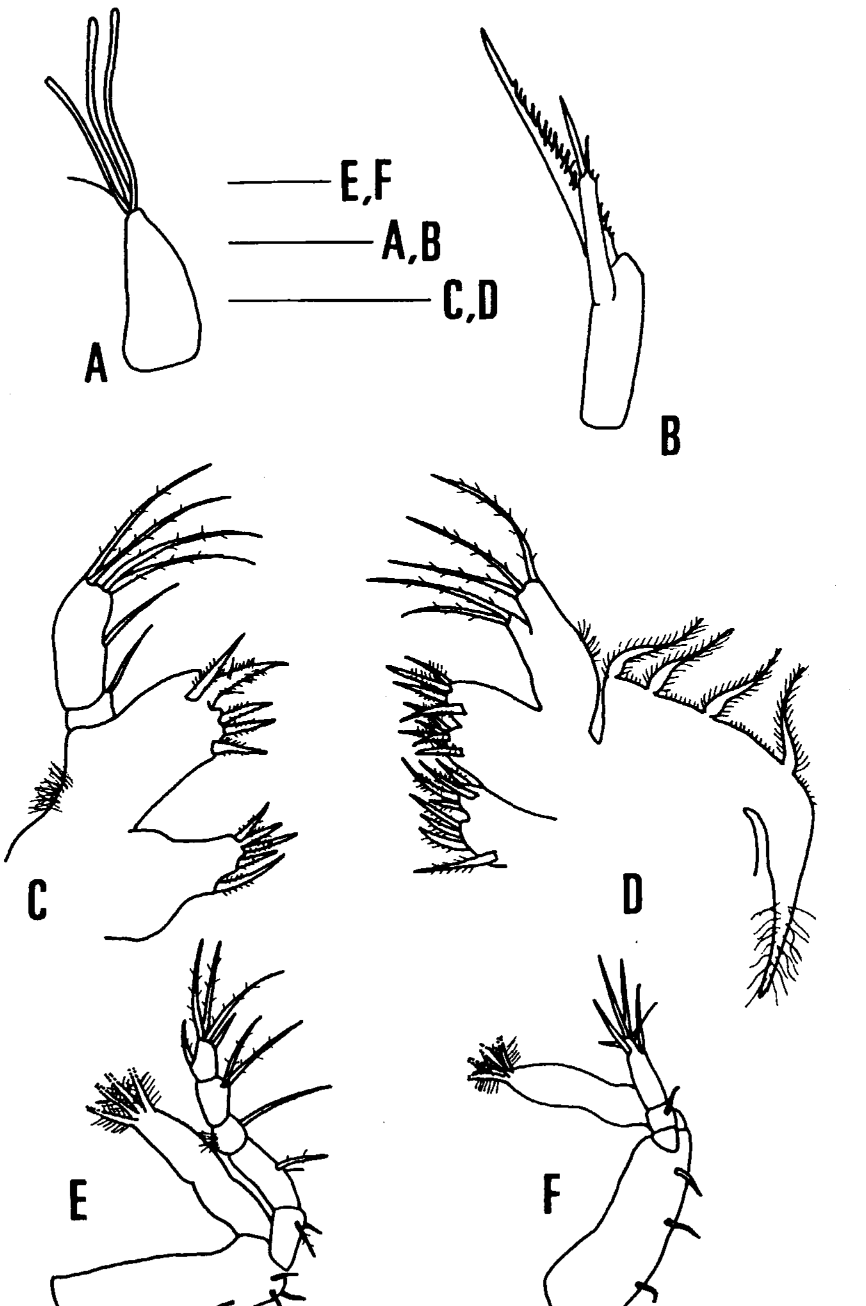

Fig. 6. First zoea of *S.rhizophorae* (Rathbun, 1906). (**A**) Antennule; (**B**) antenna; (**C**) maxillule; (**D**) maxilla; (**E**) first maxilliped; (**F**) second maxilliped. Scale bars = 0.1 mm.

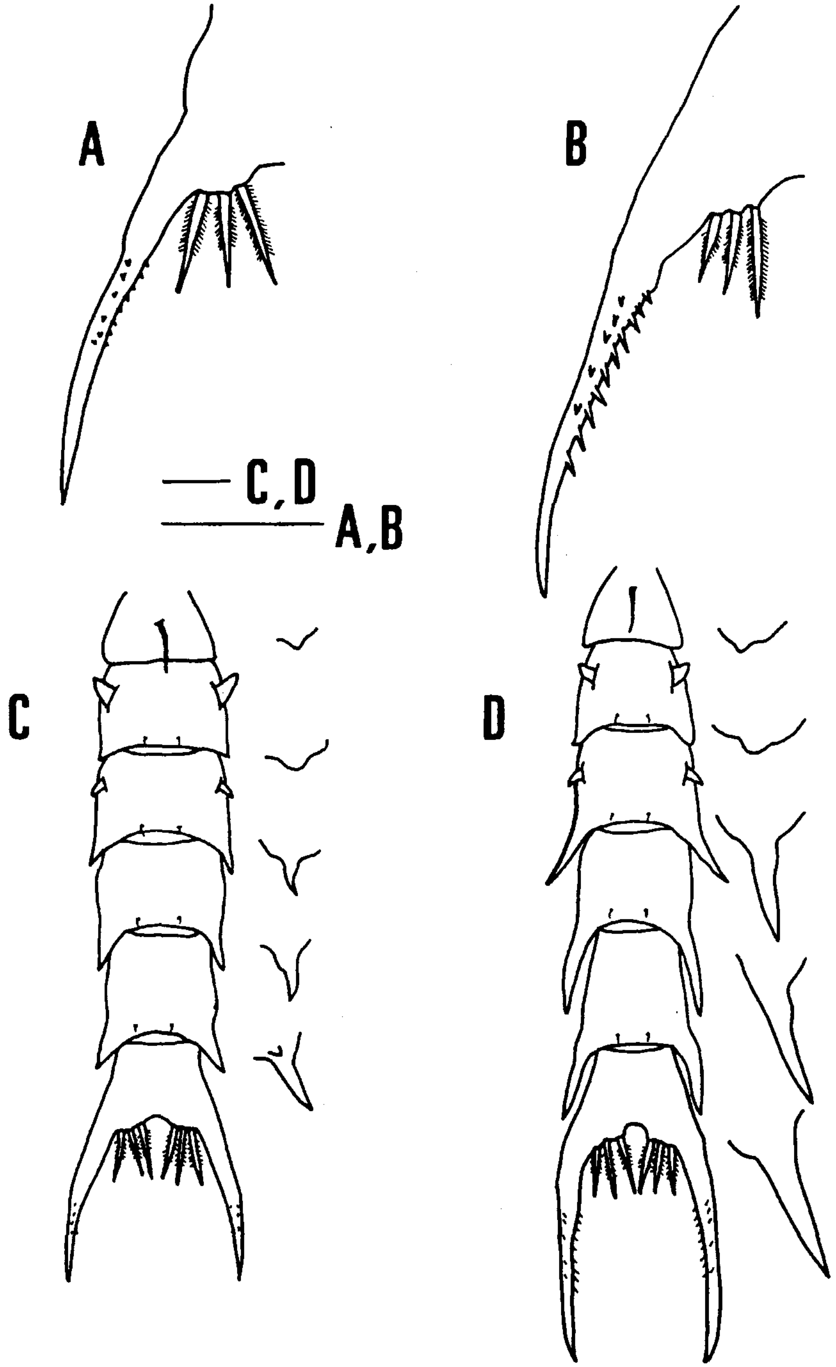

Fig. 7. Zoea I, dorsal view of abdomen (with magnification of postero-lateral margins of abdominal somites) and telson. (**A, C**) *S.aequatoriale* (Ortmann, 1894); (**B, D**) *S.rubinofforum* (Abele, 1973). Scale bars = 0.1 mm.

Sesarma rhizophorae Rathbun, 1906

Zoea I

(Figures 2B; 6A–F; 8B and D)
Dimensions: tl = 0.94 ± 0.03 mm; cl = 0.55 ± 0.02 mm; cw = 0.36 ± 0.02 mm.

Carapace (Figure 2B). Globose, smooth and without tubercles. Dorsal spine shorter than rostral spine, recurved. Rostral spine stout. Lateral spines absent. A pair of dorso-lateral simple setae and two pairs of simple setae on the anterio-median region. Postero-lateral margin without setae. Eyes sessile.

Antennule (Figure 6A). Uniramous. Endopod absent. Exopod unsegmented with three aesthetascs and one seta.
Antenna (Figure 6B). Well-developed protopod as long as rostral spine and bearing two rows of well-developed spines. Endopod absent. Exopod approximately two-thirds length of protopod, with four terminal simple setae (one long, one short and two minute).

Mandible. Endopod palp absent.

Maxillule (Figure 6C). Coxal endite with five plumodenticulate setae. Basial endite with five plumodenticulate setae. Endopod 2-segmented; proximal segment with one simple seta, distal segment with five (one subterminal and four terminal) sparsely setose setae.

Maxilla (Figure 6D). Coxal endite bilobed with 4 + 4 setae. Basial endite with 5 + 4 setae. Endopod unsegmented, bilobed with two and three long sparsely setose setae on inner and outer lobe, respectively. Scaphognathite with four plumose marginal setae and a long stout posterior process.

First maxilliped (Figure 6E). Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (one subterminal + four terminal) setae. A tuft of fine setae on the back of segment 3. Exopod unsegmented, with four long terminal plumose natatory setae.

Second maxilliped (Figure 6F). Basis with four medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (one subterminal + four terminal) setae. Exopod unsegmented, with four long terminal plumose natatory setae.
Third maxilliped. Undifferentiated bud.

Pereiopods. Undifferentiated buds.

Abdomen (Figures 2B and 8D). Five abdominal somites, first somite with a long mid-dorsal seta, somites 2 and 3 with pair of dorso-lateral processes and somites 3–5 with postero-lateral projections of almost triangular shape. Pleopods absent.
Telson (Figure 8B). Telson bifurcated, each fork with lateral and dorsal spines

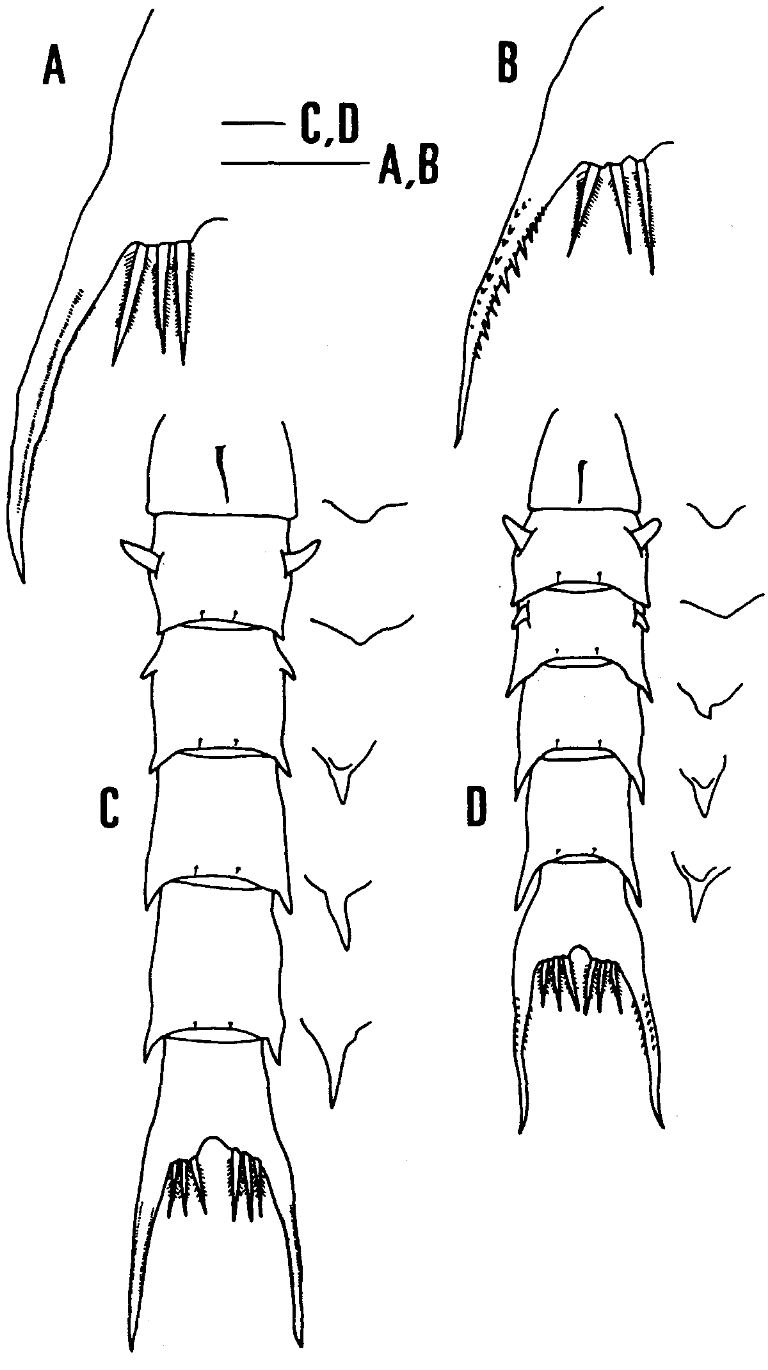

Fig. 8. Zoea I, dorsal view of abdomen (with magnification of postero-lateral margins of abdominal somites) and telson. (**A, C**) *S.curacaoense* (de Man, 1892); (**B, D**) *S.rhizophorae* (Rathbun, 1906). Scale bars = 0.1 mm.

Table I. Morphological features of the known zoeae I of American Sesarminae. Data were obtained from previous descriptions, illustrations and the present study

Species	Antennule	Antenna Exopod Setae		Mouthparts setation									No. of zoeal stages	References
				Maxillule		Maxilla			First maxilliped		Second maxilliped			
			Size[a]	C.e.	B.e.	C.e.	B.e.	Endopod	Basis	Endopod	Basis	Endopod		
Chasmagnathus granulata	3a, 1s	2	2/3	5	6	6	10	2,2	2,2,2,2[b]	1,2,1,2,5	1,1,1,1	0,1,5	4(5)[c]	Boschi *et al.*, 1967
Cyclograpsus cinereus	2a, 2s	2	2/3	5	5	6	9	2,2	1,2,3,3	2,1,1,2,5	1,1,1,1	0,1,5	5	Costlow and Fagetti, 1967
Cyclograpsus punctatus	2a, 2s	3	2/3	5	5	6	9	2,2	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	5	Fagetti and Campodonico, 1971
Cyclograpsus integer	3a, 1s	2	1/1	5	5	7	9	2,2	2,2,2,2	2,2,1,2,5	1,1,1,1	0,1,6	5(6)	Gore and Scotto, 1982; present study
Aratus pisonii	3a, 2s[b]	3[b]	4/5[b]	5	5	8[b]	8	2,3	2,2,3,3[b]	2,2,1,2,5[b]	1,1,1,1[b]	0,1,6[b]	4[d]	Warner, 1968
Armases cinereum	3a, 2s	2	1/3	5	5	7	9	2,3	?	1,1,1,2,4[e]	?	0,1,5	4	Costlow and Bookhout, 1960
Armases ricordi	3a, 2s	4	1/3	5	5	8	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	4	Díaz and Ewald, 1968; present study
Armases rubripes	3a, 1s	3	3/4	5	5	8	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	4(5)[f]	Díaz and Ewald, 1968; present study
Armases angustipes	3a, 2s	3	2/3	6	5	8	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	4	Kowalczuk, 1994
Sesarma aequatoriale	3a, 1s	2	2/3	5	5	8	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	?	Present study
Sesarma rectum	3a, 2s	2	1/3	5	5	8	8	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,5	3	Fransozo and Hebling, 1986
Sesarma reticulatum	4a, 1s	2	1/3	5	5	7	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,5	3	Costlow and Bookhout, 1962

Table I. continued

Species	Antennule	Antenna Exopod Setae	Mouthparts setation									No. of zoeal stages	References
				Maxillule		Maxilla			First maxilliped		Second maxilliped			
			Size[a]	C.e.	B.e.	C.e.	B.e.	Endopod	Basis	Endopod	Basis	Endopod		
Sesarma rhizophorae	3a, 1s	4	2/3	5	5	8	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	?	Present study
Sesarma rubinofforum	3a, 1s	2	1/2	5	5	8	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	?	Present study
Sesarma curacaoense	3a, 1s	2	1/3	6	5	9	9	2,3	2,2,3,3	2,2,1,2,5	1,1,1,1	0,1,6	2	Anger *et al.*, 1995; present study
Sesarma bidentatum	2s[g]	[g]	[g]	0	0	0	0	1,1	0	2[g]	0	2[g]	?	Hartnoll, 1964
Metopaulias depressus	2s[g]	[g]	[g]	0	0	0	0	0,0	0	0,0,2[g]	0	0	2	Hartnoll, 1964

C.e., coxal endite; B.e., basal endite; a, aesthetascs; s, setae.
(?) No data available.
[a]Size relative to antennal protopod.
[b]After Fransozo *et al.* (1997).
[c]Additional zoea V stage described by Pestana and Ostrensky (1995).
[d]Variable, 2, 3 or 4 stages according to Díaz and Bevilacqua (1987).
[e]Probably erroneous observation, the zoea II already having 2,2,1,2,5.
[f]Additional zoea V stage described by Montú *et al.* (1990).
[g]Highly modified appendages.

absent and with three pairs of spinuous processes on posterior margin. Two rows of well-developed spines on each furca.

Results

In addition to the complete descriptions of the four *Sesarma* species, first-stage zoeae of *Cyclograpsus integer*, *Armases ricordi* and *A.rubripes* from Panama were studied and their setation pattern established and included in Table I for comparison with the original descriptions of these species and with other zoea I of American Sesarminae. Dimensions of 20 first-stage zoeae of these species are tl = 0.72 ± 0.02 mm, cl = 0.48 ± 0.01 mm, cw = 0.33 ± 0.01 mm for *A.ricordi*; tl = 0.63 ± 0.03 mm, cl = 0.37 ± 0.02 mm, cw = 0.3 ± 0.01 mm for *A.rubripes*; tl = 0.64 ± 0.02 mm, cl = 0.43 ± 0.01 mm, cw = 0.3 ± 0.02 mm for *C.integer*.

Discussion

Eleven crab species of the subfamily Sesarminae have so far been reported from Panama (Abele, 1976, 1977; Abele and Kim, 1989). In addition, *Armases rubripes* was collected for the present study in a dry area of a mangrove swamp adjacent to La Galeta, Caribbean coast of Panama. From these 12 Sesarminae, information on larval development was available for five species, only including one species of *Sesarma* [*S.curacaoense*, described from Jamaican material by Anger *et al.* (1995)]. In the present study, the first zoeal stage of three species of *Sesarma* is described for the first time, together with the zoea I of *S.curacaoense* from Panama, thereby increasing the number of described sesarmine zoeae occurring in Panamanian waters to eight. In order to facilitate the identification of plankton-collected Sesarminae larvae, two keys are provided for the known zoea I from Panama: one for Caribbean waters and the other for Pacific waters.

Key for the known first zoea of Sesarminae from the Caribbean coast of Panama

1 A. Dorsal carapace spine short and stout. Antennal exopod as long as protopod. Maxillar endopod with 2 + 2 setae. Abdominal somite 4 laterally expanded and with a pair of minute dorso-lateral knobs .... *Cyclograpsus integer*

1 B. Dorsal carapace spine short and recurved. Antennal exopod shorter than protopod. Maxillar endopod with 2 + 3 setae. Abdominal somite 4 not laterally expanded and without dorso-lateral knobs 2

2 A. Pereiopod buds well developed, first pair chelated (Figures 2A, 5H and I) .... *Sesarma curacaoense*

2 B. Without pereiopod buds...3

3 A. Antennal exopod clearly smaller than protopod (1/3) and terminating in four unevenly sized setae. Tuft of fine setae on segment 3 of the endopod from the first maxilliped.. *Armases ricordi*

3 B. Antennal exopod almost as long as protopod (3/4 to 4/5) and terminating in

three unevenly sized setae. No tuft of fine setae on segment 3 of the endopod from the first maxilliped 4

4 A. Antennule with three aesthetascs and one seta. Abdominal lateral processes of somites 3 and 4 rounded and smooth. Carapace with one pair of dorso-lateral setae and one pair of mid-anterior dorsal setae .... *Armases rubripes*

4 B. Antennule with three aesthetascs and two setae. Abdominal lateral processes of somites 3 and 4 nearly rounded and with bilobed termination. Carapace with a pair of dorso-lateral setae and two pairs of mid-anterior dorsal setae .... *Aratus pisonii*

Key for the known first zoea of Sesarminae from the Pacific coast of Panama

1 A. Lateral processes of abdominal somites rounded and bilobed. Antennule with three aesthetascs and two setae. Antennal exopod almost as long as the protopod .... *Aratus pisonii*

1 B. Lateral processes of abdominal somites pointed and subtriangular. Antennule with three aesthetascs and one seta. Antennal exopod not longer than 2/3 of protopod length 2

2 A. Lateral processes of abdominal somites 3, 4 and 5 elongated, almost as long as base of subsequent somite (or telson) (Figure 7D) .... *Sesarma rubinofforum*

2 B. Lateral processes of abdominal somites 3, 4 and 5 moderately developed, never as long as base of subsequent somite (or telson) 3

3 A. Dorsal spine distally serrated. Two rows of minute spines on each furca (Figures 1A and 7A) .... *Sesarma aequatoriale*

3 B. Dorsal spine distally smooth. Two rows of well-developed spines on each furca (Figures 2B and 8B) .... *Sesarma rhizophorae*

When compared with known first-stage zoeae of Panamanian Sesarminae, *C.integer* possesses a number of distinct characters. These include differences in setation pattern, the shape of the dorsal spine and the antenna. The other three genera (*Aratus*, *Armases* and *Sesarma*) show a remarkably similar morphology for first-stage zoea. In most cases, they can only be distinguished by minor differences in setation (antennules, antennae, maxillae and endopod of second maxilliped) or armature of the telson. Separation of the four species of *Sesarma* described in the present study is possible when regarding the following characters. Zoeae I of *S.curacaoense* can be distinguished due to their well-developed pereiopod buds from which the first pair is chelated (Figure 5H and I). *Sesarma rubinofforum* is distinct by having the most strongly developed postero-lateral processes at the abdominal somites recorded within the American Sesarminae (Figure 7D). The dorsal spine of *S.aequatoriale* is distally serrated (Figure 1A) and the spines on the furca are clearly reduced in size (Figure 7A). The antennal exopod of *S.rhizophorae* is armed with four setae (Figure 6B). For the identification keys, those characters were emphasized that can be recognized without dissection of the larvae. Differences in setation are summarized in Table I.

The larvae of *S.curacaoense* require further comment, because this species shows abbreviated development consisting of two zoeal stages and one megalopa stage as noted by Schuh and Diesel (1995) and Anger (1995), and described by Anger *et al.* (1995). Morphological characters of the zoea I suggesting an abbreviated development are the overall increased size (Figure 2A), the well-developed pereiopod buds (Figure 5H and I) and an advanced setation pattern of the maxillule and the maxilla (Figure 5C and D; Table I). The other species were not cultured beyond the first zoeal stage, but the presence of pereiopod buds in the zoea I of *S.aequatoriale* and *S.rhizophorae* suggests a development through three zoeal stages similar to the other American *Sesarma* (with the exception of *S.curacaoense* and the Jamaican endemic species). The first zoeal stage of *S.rubinofforum* does not have pereiopod buds, possibly indicating that this species has four zoeal stages similar to *Armases*, *Aratus* and most *Sesarma* of Africa and Asia (Pereyra Lago, 1993; Table I). The tendency towards an abbreviated development (2–3 zoeae) is thus once more confirmed for the American representatives of the genus *Sesarma* and can be regarded (with the possible exception of *S.rubinofforum*) as characteristic for this group.

However, reduction of larval stages is common within many brachyuran families (e.g. Goodbody, 1960; Rabalais and Cameron, 1983) and must be assumed to be a convergent phenomenon (Rabalais and Gore, 1985). Anger *et al.* (1995) described the abbreviated larval development of *S.curacaoense* (not Rathbun, 1897 as cited in the title, but de Man, 1892) from Jamaica and compared it with the larval development of the endemic Jamaican freshwater species *S.bidentatum* and *Metopaulias depressus* Rathbun, 1896. In these two species, the larval development passes through two lecithotrophic zoeal stages. On the other hand, the zoeal morphology of *S.curacaoense* and the Jamaican endemics is strikingly different, in that the latter have a clearly reduced overall setation, lack carapace spines, and appendages are modified or missing (Hartnoll, 1964; Anger *et al.*, 1995; Table I). The larvae of *S.bidentatum* and *M.depressus* may be considered derived in consequence of their adaptation to freshwater habitats. With their modified morphology, they resemble more the zoeal larvae of the East Asian *Geosesarma peraccae* (Nobili, 1903), which is also a freshwater-restricted sesarmine crab species (Soh, 1969), than any of the other American Sesarminae. The conclusion that *S.curacaoense* is 'a close relative of the ancestral species' (Anger *et al.*, 1995) or 'the closest relative of an ancestral *Sesarma* species, from which adaptive radiation of endemic Jamaican freshwater and terrestrial crabs began' (Anger, 1995) is therefore only based on ontogenetic similarities, but not on larval morphology.

The comparison of first zoeal morphology of *S.curacaoense* from this description and the one by Anger *et al.* (1995) based on Jamaican material revealed differences in the shape of the dorsal spine, the setation and the overall size. The dorsal carapace spine in Anger *et al.* (1995, Figure 1A) is of a serrated appearance, resembling the dorsal carapace spine of *S.aequatoriale* (Figure 1A), but not the smooth dorsal carapace spine of *S.curacaoense* from Panama (Figure 2A). Anger *et al.* (1995) counted three aesthetascs and two setae on the antennule (versus 3,1 of the present study) and 0,1,5 setae on the endopod of the second maxilliped (versus 0,1,6 of the present study). One or two long mid-dorsal setae on the first abdominal somite and a long stout posterior process of the scaphognathite of the maxilla, as described in the present study, are not mentioned or drawn by Anger *et al.* (1995). The only measurement given by Anger *et al.* (1995) for the zoea I is cl: 0.81 ± 0.04 mm (figured specimen cl = 0.95 mm; tl = 1.54 mm; estimated from scale bar). This is considerably larger than the zoea I described in the present study (cl = 0.74 ± 0.02 mm; tl = 1.23 ± 0.03 mm). Also in the zoea II larvae (tl = 1.63 mm; estimated from scale bar) and the megalopa (cl = 1.04 mm; cw = 0.65) Anger *et al.*'s Jamaican material is larger than the Panamanian zoea II (tl = 1.3–1.33 mm) and megalopa (cl = 0.92–0.94 mm; cw = 0.61–0.66 mm). Again in the zoea II, Anger *et al.* (1995) do not describe the long mid-dorsal setae on the first abdominal somite (3 in the Panamanian zoea II). Instead they describe three pairs of long setae on the posterior margin of the telson of the megalopa, which are absent in the Panamanian megalopa. The question arose whether the differences found between these descriptions are due to the different observers, regional variation, or intraspecific variation in general. The abbreviated development of *S.curacaoense*, resulting in a reduced dispersal potential, could favour a genetic regional variation. Additional first-stage zoeae of *S.curacaoense* from Jamaica raised by CDS and different from the material of Anger *et al.* (1995) were therefore studied. The setation pattern for antennule and second maxilliped, the smooth appearance of the dorsal carapace spine, the presence of mid-dorsal setae on the first abdominal somite and a long stout posterior process of the scaphognathite as described from Panamanian material were thereby confirmed. Furthermore, these Jamaican zoea I larvae had a similar size (tl = 1.25–1.28 mm) to those from Panama. The differences found by Anger *et al.* (1995) for the first-stage zoea can thus not be attributed to regional variation.

The larval development of *A.ricordi* and *A.rubripes* was described by Díaz and Ewald (1968). Comparison of all larval stages led the authors to the conclusion that there are no reliable differences between the larvae of these species. The setation pattern given by Díaz and Ewald (1968) mostly agrees with what has been found for other *Armases*, *Aratus* and *Sesarma* species (Table I). Their count of 10 setae on the basis of the first maxilliped did not specify the arrangement. The present re-examination of first-stage zoeae of these species yielded the expected 2,2,3,3 arrangement. Furthermore, three and four unevenly sized setae (not two) were found on the antennal exopod of *A.rubripes* and *A.ricordi*, respectively. Three setae on the antennal exopod are also found in *A.pisonii* and can be used to distinguish this species and *A.rubripes* from *A.ricordi*. Also, the size of the antennal endopod compared to the protopod differed in *A.rubripes*: 3/4 instead of 1/3. Panamanian specimens of *A.rubripes* showed two rows of teeth on the antennal protopod, the same as *A.ricordi*. Consequently, this character cannot be used for possible separation of these species, as proposed by Díaz and Ewald (1968), who only recognized one row in *A.rubripes*. What these authors did not mention or draw are two pairs of setae on the zoeal carapace, which were found in the present material of both species. A newly recognized tuft of fine setae on segment 3 of the endopod from the first maxilliped of *A.ricordi* (similar to that found in the four described *Sesarma* species) can be used as an additional character to separate *A.ricordi* from *A.rubripes*.

As noted above, *C.integer* zoeae are morphologically the most distinct of the Panamanian Sesarminae. Gore and Scotto (1982) described the setation pattern of the basis of the first maxilliped as an unusual 2,2,3,2. This study of Panamanian material from this species revealed a 2,2,2,2 arrangement, which is also characteristic for the genus *Chasmagnathus* (Table I). The comparison with other American members of the genus *Cyclograpsus*, for which larval development is known, showed a high variability of characters between species. Next to differences in setation (Table I), the development of lateral carapace spines is also variable, being present in the zoea I of *C.punctatus* H. Milne Edwards, 1837, but not appearing before the zoea II in *C.integer* and *C.cinereus* Dana, 1852 (see also Cuesta and Rodríguez, 1994). Lateral carapace spines are otherwise always absent in the zoea of the American Sesarminae, the other exception being *Chasmagnathus granulata* Dana, 1851. *Cyclograpsus* and *Chasmagnathus* also share the setation arrangement 2,2 on the endopod of the maxilla, while the other American Sesarminae (except the derived Jamaican endemics) all have 2,3. In the table of Pereyra Lago (1993), the 2,2 arrangement is constantly present within the subfamily Varuninae. Terada (1982) also noted that the genera *Helice*, *Cyclograpsus* and *Chasmagnathus* differ markedly in zoeal morphology from the genera formerly included in *Sesarma* [*sensu lato*]. All these findings support results from 16S mitochondrial DNA sequence of various American grapsid crabs, which suggest that *Cyclograpsus integer* and *Chasmagnathus granulata* should not remain within the Sesarminae, being much closer to species currently included in the subfamily Varuninae than to *Aratus*, *Armases* and *Sesarma* (C.D.Schubart *et al.*, unpublished data).

Acknowledgements

Material for this study was obtained during a visit to the Smithsonian Tropical Research Institute at Naos, where we found kind support by John Christy and the local staff. Permits were granted by IN.RE.NA.RE. Recursos Marinos. J.A.C. was financially supported by the 'Junta de Andalucía' and C.D.S. by the 'Deutsche Forschungsgemeinschaft' (grant Di 479-2/1 to Rudolf Diesel). Klaus Anger provided a copy of their (at that time) unpublished description of *S.curacaoense*. Special thanks are due to Paul Clark from the Natural History Museum, London, for valuable comments on two versions of the manuscript.

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Received on April 15, 1997; accepted on September 2, 1997