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# ABBREVIATED LARVAL DEVELOPMENT OF *Sesarma curacaoense* (RATHBUN, 1897) (DECAPODA: GRAPSIDAE) REARED IN THE LABORATORY

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## ABSTRACT

Larvae of a semiterrestrial grapsid crab that lives in mangrove swamps in Jamaica, *Sesarma curacaoense*, were reared in the laboratory from hatching through metamorphosis. The morphology of all larval stages and of the first juvenile crab instar is described in detail. It is compared with that in closely related coastal (*S. reticulatum*, *S. rectum*), freshwater (*S. bidentatum*), and terrestrial crab species (*Metopaulias depressus*, *Geosesarma perracae*). As in limnic and terrestrial relatives, the larval development of *S. curacaoense* is abbreviated, consisting of only two zoeal stages and a megalopa. The lack of a Zoea III stage as well as an exceptionally early appearance of advanced morphological features in the development of the maxilliped 3 and the pereiopods represent phylogenetically derived characters in *S. curacaoense*. However, in most of their morphological features (e.g. carapace spines, segmentation of the antennule, armature of the antennal exopod, and endopods of the maxillule and the maxilla), the larvae of *S. curacaoense* are similar to those of coastal rather than to freshwater and terrestrial species. In particular, they do not reveal significant reductions in spines or appendages. Most morphological differences between these species are striking in the zoeal stages, but disappear in the Megalopa or in the first juvenile crab stage. In conclusion, the larval development of *S. curacaoense* is intermediate between that of ancestral (coastal) and derived (terrestrial and freshwater) species. This corroborates the hypothesis that *S. curacaoense* is a close relative of the ancestral species, from which, in a process of adaptive radiation, a number of endemic Jamaican freshwater and terrestrial crabs have evolved.

**Keywords:** Crab larvae, abbreviated development, semiterrestrial, Grapsidae

## INTRODUCTION

The brachyuran crab family Grapsidae has been particularly successful in the transition from marine into freshwater and terrestrial environments. Within the subfamily Sesarminae, two conspicuous centres of adaptive radiation have been recognized, one in the indopacific region (Sèrene & Soh, 1970; Ng, 1988; Ng & Tan, 1995), the other on the Caribbean island of Jamaica (Hartnoll, 1964), where some species have become entirely independent from the sea. They

pass their entire life cycle in non-marine habitats and hence, have become true freshwater and land crabs (Burggren & McMahon, 1988; Hartnoll, 1988).

On Jamaica, endemic Sesarminae occur in mountain streams and rivers (*Sesarma bidentatum*, *S. windsor*), subterranean limestone caves (*S. verleyi*), in dry rubble and leaf litter of forest-covered hills (*S. jarvisi*, *S. cookei*), and on large bromeliad plants (*Metopaulias depressus*) (Rathbun, 1918; Hartnoll, 1964, 1971; Abele & Means, 1977; Türkay & Diesel 1994; Diesel & Horst, 1995). According to morphological and distributional patterns, all these endemic Jamaican freshwater and land crabs have evolved, in a process of adaptive radiation, from a common marine ancestor, which must have been very closely related to an extant semiterrestrial species, *S. curacaoense* (Hartnoll, 1964, 1965, 1971).

*S. curacaoense* lives in brackish coastal mangrove swamps on Jamaica and other Caribbean islands (Hartnoll, 1965; Chace & Hobbs, 1969; Abele, 1992). In recent studies of its larval ecology and physiology (Anger & Schultze, 1995; Anger, 1995a, b; Schuh & Diesel, 1995), an abbreviated development with only two zoeal stages and a megalopa was observed in *S. curacaoense*. The same reduction in the number of zoeal stages occurs, as far as this is known, also in fully limnic and terrestrial sesarminids: *M. depressus* and, probably, *S. bidentatum* (Hartnoll, 1964), *S. jarvisi* (Bäurle & Diesel, 1993; Diesel & Horst, 1995), *Geosesarma perracae* (Soh, 1969). This is in contrast to the larval development of coastal marine relatives, where normally at least three zoeal stages occur (Rabalais & Gore, 1985).

In the present paper, the larval morphology of *S. curacaoense* is described for the first time. It is compared with that in two endemic Jamaican species (*S. bidentatum*, *M. depressus*), other closely related neotropical *Sesarma* spp. (*S. reticulatum*, *S. rectum*), and in the only terrestrial sesarminid species from the indopacific region, for which a description of the larval stages is available, *Geosesarma perracae*.

## MATERIALS AND METHODS

Ovigerous *Sesarma curacaoense* females were collected in March 1993 in a coastal mangrove swamp near Mangrove Point (Trelawny, northern Jamaica) and transported to the Discovery Bay Marine Laboratory (DBML; St. Ann, Jamaica). The crabs were maintained at 25‰ salinity and constant 25°C, with a 12:12 h light:dark photoperiod.

Freshly hatched larvae were pipetted to glass bowls with 400 ml diluted seawater (25‰ S) and reared in groups of 40-50 individuals per bowl, at the same temperature and light conditions. Water and food (freshly hatched *Artemia* sp. nauplii; San Francisco Bay Brand[a]; ca. 10 nauplii/ml) were changed daily. Samples of intermoult larvae (10-20 individuals per stage) were preserved in 4% buffered seawater-formaldehyde. Later, they were examined under stereo and compound microscopes (Olympus), and drawings were made

with the aid of attached camera lucida. Additional material was obtained from rearing experiments at the Marine Biological Station Helgoland, Germany, at constant 24° C and 32‰ salinity, but otherwise identical conditions.

In the morphological description of appendages, we followed the terminology used by Ingle (1992). The classification of setae and spines is based on the system proposed by Watling (1989). The following abbreviations are used in the description: CL = carapace length from orbit to posterior carapace border; CW = carapace width measured at the widest part of the carapace (only in the megalopa and first juvenile); DS = dorsal spine; P = pereiopod; PL= pleopod; RS = rostal spine; S = setation, with characterization of setae: pl = plumose, pld = plumodenticulate, s = simple, se = serrate. Size measurements (from 10 individuals in each stage) are given as arithmetic mean ± standard deviation.

## RESULTS

The larval development of *Sesarma curacaoense* consists of two brief zoeal stages (ca. 1.5 to 3 days each at 24-25° C) and one megalopa (duration quite variable, ranging from 7-20 days). While some individual variability in body size and setation of appendages occurred (see below), no major morphological differences were observed between larvae originating from different females or reared at slightly different temperature or salinity conditions. No variability in the number of larval stages was observed.

### Zoea I

Carapace (Fig. 1A). CL 0.81±0.04 mm. Smooth, globose; lateral spines absent; DS and RS short, approximately equal in length to the antenna (less than 1/3 of CL); DS recurved; eyes unstalked.

Antennule (Fig. 2A). Exopod unsegmented, conical, with 3 aesthetascs (revealing subterminal pores) and 2 s setae of unequal size.

Antenna (Fig. 3A). Endopod bud prominent, length approximately 1/3 of protopod; long spinous process with acute tip and 2 rows of spines. Exopod extending into the distal half of the spinous process, terminating in 2 stout spines of unequal size.

Mandible (Fig. 4A). Symmetrical, molar and incisive parts well developed, variable number of teeth.

Maxillule (Fig. 5A). Endopod 2-segmented; S: 1 (smooth s), 5 (1 smooth s, 4 terminal pld). Basal endite with distal S: 3 pld, 2 pl setae, 3 small spines. Coxal endite with 6 pl setae.

Maxilla (Fig. 6A). Endopod bilobed, with 3, 2 terminal, sparsely pl setae; 80-100 minute s setae on external, ca. 10 s setae on internal margin. Basal endite bilobed, S: 4, 4-5 pld. Coxal endite S: 4, 4 pl setae, 1 small spine; ca.

10 minute s setae on margin. Scaphognathite with 4 (sometimes 3) pl setae with supracuticular socket.

Maxilliped 1 (Fig. 7A). Basis with 10 s setae; lower external margin with ca. 40 minute s setae. Exopod with 4 natatory pl setae. Endopod 5-segmented; S: 2 (1 s, 1 pl), 2 (1 s, 1 pl), 1 (pl), 2 (pl), 5 (2 pld, 3 pl); third segment with ca. 10 minute s setae.

Maxilliped 2 (Fig. 8A). Basis with 4 s setae. Exopod unsegmented, with 4 natatory pl setae. Endopod 3-segmented; S: 0, 1 (s), 5 (4 s, 1 se).

Maxilliped 3. Endopod indistinctly 3-segmented, with epipod and exopod buds.

Pereiopods (Fig. 10A). P1 (cheliped) 4-segmented, P2-P5 indistinctly 5-segmented; coxa and basis (in P1 also ischium) not differentiated.

Gills (Fig. 10 A). Two pairs of buds without lamellae.

Pleopods (Fig. 1A). Buds.

Abdomen (Fig. 12A). Five-segmented; first segment completely covered by carapace; all segments bear a pair of ventral, posteriorly-pointing spines; segments 2 and 3 bear a pair of dorso-lateral knobs; all bear a pair of minute, dorso-lateral s setae.

Telson (Figs. 1A, 12A). Three pairs of pl setae on posterior margins, length ca. 1/3 of furca; two rows of spinules on outer rami (1 dorsal, 1 on internal margin).

## Zoea II

Carapace (Fig. 1B). CL 0.92±0.07 mm. RS proportionally longer than in Zoea I (approximately twice the length of the antenna, more than 1/2 of CL); DS wider and longer than in Zoea I. Eyes stalked.

Antennule (Fig. 2B). As in Zoea I, but with 2 s setae and 6 aesthetascs.

Antenna (Fig. 3B). Two-segmented, endopod more developed; otherwise as in Zoea I.

Mandible (Fig. 4B). Larger than in Zoea I, with more, stronger teeth.

Maxillule (Fig. 5B). Endopod 2-segmented; S: 1 (pl), 5 (4 terminal pld, 1 subterminal pl). Basal endite with 9 setae (8 pld, 1 small smooth s seta) and 3 small spines. Coxal endite with 7 pld setae. Inner margin of protopod with 1 pl seta.

Maxilla (Fig. 6B). Endopod bilobed, S: 3, 2 (terminal pld); minute s setae as in Zoea I. Basal endite with 8-9 setae (4 pld, 3 smooth s, 1-2 pld); ca. 5 minute s setae on margin. Coxal endite bilobed; S: 4-5, 4 (pld); ca. 10 minute s setae on margin. Scaphognathite with 8 pl setae on distal margin and 3 pl setae on apical tip, all with supracuticular socket; ca. 80 minute s setae along lower margin.

Maxilliped 1 (Fig. 7B). Basis with 10 smooth s setae. Exopod with 6 natatory pl setae. Endopod 5-segmented; S: 2 (1 smooth s, 1 pl), 2 (1 smooth s, 1 pl), 1 (pl), 2 (pl), 5 (3 pl, 2 se).

Maxilliped 2 (Fig. 8B). Basis with 4 smooth s setae. Exopod with 6 natatory pl setae. Endopod S: 0, 1 (se), 6 (4 smooth s, 2 se).

**Maxilliped 3**. Endopod indistinctly 4-segmented; exopod indistinctly 2-segmented; epipod as in Zoea I.

**Pereiopods** (Fig. 10B). More developed than in Zoea I; with clear segmentation, but not functional.

**Gills** (Fig. 10B). Two pairs of buds; more developed than in Zoea I, incipient formation of lamellae visible.

**Pleopods** (Fig. 1B). Buds longer, more developed.

**Abdomen** (Fig. 12B). Six-segmented, otherwise as in Zoea I.

**Telson** (Figs. 1B, 12B). As in Zoea I, but furca longer.

## Megalopa

**Carapace** (Figs. 1C, 1D). CL 1.04±0.07 mm; CW 0.65±0.04 mm. DS reduced (protuberance). Rostrum deflected downwards, approximately same length as antennule. Frontal region with small depressions between rostrum and DS. Lower and posterior margins fringed with numerous small s setae.

**Antennule** (Fig. 2C). Basis well developed, with 1 s seta. Peduncle 3-segmented (1st segment partly fused with basis), with 0, 1, 1 s setae. No endopod present. Exopod 3-segmented; S: 0, 3 (1 small s seta, 3 aesthetascs), 5 (2 s setae, 3 aesthetascs).

**Antenna** (Fig. 3C). Nine-segmented; S: 0, 1, 1, 0, 2, 1, 5, 0, 2 (s). Long spinous process and shorter exopod on basal segment, as in Zoea I and II.

**Mandible** (Fig. 4C). Symmetrical, semicircular, teeth reduced; palp 3-segmented; S: 0, 0, 4 (pl; 1 terminal, 3 slightly subterminal).

**Maxillule** (Fig. 5C). Endopod 2-segmented; S: 2 (pl), 4 (terminal pld). Basal endite with 11 terminal setae (6 pld, 5 se) and 2 subterminal s setae. Coxal endite with 9 setae (3 pl, 6 se). Protopod with 2 pl setae on margin.

**Maxilla** (Fig. 6C). Endopod bilobed; S: 6 (4 pld, 2 s), 7 (4 pld, 3 s). Basal endite bilobed; S: 6 (4 pld, 2 s), 7 (4 pld, 3 s). Coxal endite bilobed; S: 4 (pl), 7 (4 pl, 3 s). Scaphognathite with 22-24 marginal pl setae with supracuticular socket, 3 lateral s setae.

**Maxilliped 1** (Fig. 7C). Exopod 2-segmented; S: 2-3 (pl, with supracuticular socket), 5 (pl). Endopod 4-segmented; S: 2 (1 pl, 1 s), 1 (pl), 4 (3 pl, 1 s), 5 (4 pld, 1 s). Basal endite with 3- 4 s and 2-3 pld setae. Epipod with 4 sparsely pl setae.

**Maxilliped 2** (Fig. 8C). Exopod 2-segmented, with 0, 6 pl setae. Endopod 4-segmented; S: 1, 1, 4 (pld), 8 (3 pld, 2 se, 3 s). Basis with 4 s setae.

**Maxilliped 3** (Fig. 9A). Exopod 2-segmented, with 0, 5 pl setae. Endopod 5-segmented; S: 8 (6 pl, 2 s), 9 (5 pl, 4 s), 3 (1 pl, 2 s), 4 (3 pl, 1 s), 6 (pld). Protopod with 6 pl setae. Epipod with 14 setae (5 pappose, 9 sparsely pl).

**Pereiopods** (Fig. 10C). Spines on P1 (cheliped), from ischium to dactylus: 3-5, 3-5, 3-5, 8-13, 7-12; distal half of chela fingers with 2 pairs of teeth on incisive parts. Spines on P2: 4-6, 7-12, 4-6, 10-15, 10-15; P3: 3-5, 10-15, 5-10, 10-15, 10-15; P4: 3-5, 8-16, 6-8, 15-20, 10- 15; P5; 1-4, 5-10, 3-6, 5-7, 1-3; distal segment with 3 pl setae, their distal portion curved inward, serrated.

Gills. Four pairs with well-developed lamellae.

Pleopods (Figs. 1C, 11A,B,C,D,E). Five pairs on abdominal segments 2-6; exopod S: 12, 12, 12, 9, 6 (pl). Endopod of PL1-PL4 with 2 minute hooks; endopod of PL5 with 1 small pl seta.

Abdomen (Figs. 1C, 1D, 12C). Six-segmented; segments 1-4 with postero-lateral spines rounded, segment 5 with long postero-lateral spine; segments 2-6 with 2 pairs of minute setae on dorso-lateral knobs. Segments 1 and 6 with 3 pairs of short plumose setae on dorsal, somite 2 with 1 pair, segment 3 with 3 pairs, segments 4 and 5 with 4 pairs.

Telson (Figs. 1D, 12C). S on posterior margin: 3 inner pairs of pl (interior pair sparsely pl) setae; 7 small spines on dorsal surface.

## Crab I

Carapace (Fig. 1E). CL 1.15±0.04 mm; CW 0.96±0.04 mm. Quadrangular; surface and margins covered with numerous small spines. Rostrum quadrangular, with small depression in centre; bent downwards.

Antennules (Fig. 2D). Four-segmented; S: 1 (s), 1 (small s), 0, 5 (2 s, 3 aesthetascs). Basis enlarged with 4 pl setae.

Antenna (Fig. 3D). Ten-segmented; S: 2 (1 s, 1 pappose), 0, 1, 1, 0, 0, 2 (s), 1 (se), 5 (4 s, 1 long sparsely pl), 3 (s).

Mandible (Fig. 4D). Palp 2-segmented, with 0, 5 pl setae.

Maxillule (Fig. 5D). Endopod 2-segmented, with 2-3 s, 2-4 pl setae. Protopod with 0 or 1 s seta. Basal endite with 15 setae (4 pl, 5 s, 6 forked). Coxal endite with 10 setae (5 pld, 2 pl, 1 s, 1 forked, 1 se).

Maxilla (Fig. 6D). Endopod short and conical, with 1 subterminal pl, 0-1 terminal pl setae. Basal endite with 5 (4 s, 1 pl), 6-7 (3-4 s, 3 pld) setae. Coxal endite, S: 3 (pl), 7-8 (2 pld, 5-6 pl). Scaphognathite with 28-31 marginal pl setae (with supracuticular socket) and 5-7 lateral spines.

Maxilliped 1 (Fig. 7D). Exopod 2-segmented, with 2, 4 pl setae. Endopod unsegmented, with 3 s and 4 pl setae. Basal endite with 14-17 se and pld setae. Coxal endite with 8-9 pappose setae. Epipod with 5-6 long s setae.

Maxilliped 2 (Fig. 8D). Exopod 2-segmented, with 3-4, 4 pl setae. Endopod 4-segmented; S: 1, 1, 5-6 (pld), 8-9 (se). Basis with 3 pl setae.

Maxilliped 3 (Fig. 9B). Exopod 2-segmented, with 4-5, 5 pl setae. Endopod 4-segmented; S: 8- 11 (4 pl, 4-7 small s), 4 (3 s, 1 pl), 3-4 (pld), 5-6 (pld). Coxa and basis not differentiated, with 12-14 setae (7-8 s, 5-6 pl). Epipod with 12-14 long s setae. Protopod with 20-25 pl setae.

Pereiopods (Fig. 10D). S (s and pl spines), from ischium to dactylus: P1 (cheliped): 3-5, 14-17, 9-12, 11-14, 4-6; 7-8 irregular teeth on incisive parts of dactylus and propodus; segments 2 and 3 with small pl setae. P2: 4-5, 12-15, 9-12, 15-20, 9-12; all segments with small pl setae. P3: as in P2. P4: as in P2, but no pl setae. P5: 4-5, 9-12, 4-5, 8-12, 6-8; only segments 1, 2, and 3 with pl setae.

Gills. Four pairs, as in megalopa.

**Abdomen** (Fig. 12D). Bent under thorax, 6-segmented, with 5 pairs of reduced pleopods. Short spines on all segments: 8-10, 7-11, 7-11, 9-12, 3-5, 3-5.

## DISCUSSION

With its only two zoeal stages, *Sesarma curacaoense* clearly shows an abbreviated or, in Gore's (1985) terminology, an "advanced" development, compared with most other Grapsidae (Rabalais & Gore, 1985; Pereyra Lago, 1987). Since an abbreviation of the pelagic larval phase is in general considered a phylogenetically advanced type of development (Knowlton, 1974; Williamson, 1982; Rabalais & Gore, 1985), this status should be reflected also by a derived larval morphology. Rice (1980) listed a number of phylogenetically advanced morphological features, in particular reductions or losses: (1) of carapace spines, (2) in the number of abdominal somites carrying dorso-lateral knobs, (3) in the segmentation or setation of the antennule, (4) in the armature of the antennal exopod, (5) in the endopods of the maxillule and of the maxilla, and (6) in maxillipeds 1 and 2.

Most of those losses or reductions are conspicuous in the Zoea I of the terrestrial and limnic species *Geosesarma perracae*, *Metopaulias depressus*, and *Sesarma bidentatum* (Table 1). *S. curacaoense*, in contrast, is in all these characters rather conservative, closely resembling the semiterrestrial coastal congenors *S. rectum* and *S. reticulatum*. The zoea I bears rostral and dorsal carapace spines, has unstalked eyes, and does not show reductions in cephalic or thoracic appendages. The most striking differences between the zoeae of fully terrestrial or freshwater species and those of coastal species can be observed in morphological reduction or maintenance, respectively, of (1) the antennule, (2) the antenna, (3) the maxillule, (4) the endopod, and basal and coxal endites of the maxilla, (5) in the endopod and basis of maxillipeds 1 and 2. All these differences persist from hatching throughout zoeal development (Tables 1 and 2).

Thus, the advanced nature of the larval development of *S. curacaoense* is not reflected by reductions in carapace spines or appendages. Instead, it is visible in an exceptionally early development (from hatching) of morphological features that normally appear only in later developmental stages: maxilliped 3 and all pereiopods are almost fully developed, showing already an incipient segmentation, and pleopod buds are present. In all these advanced features, the two zoeal stages of *S. curacaoense* are similar to those of *G. perracae*, *M. depressus*, and *S. bidentatum*, resembling the final zoeal stage (zoea III) in *S. rectum* (Fransozo & Hebling, 1986) and *S. reticulatum* (Costlow & Bookhout, 1962). The latter two species are semiterrestrial, living in brackish water habitats. Compared with coastal marine Grapsidae, which normally have 4 or 5 zoeal stages (Rabalais & Gore, 1985), they also show an abbreviated (advanced) type of larval development. A further reduction of the larval phase

in *S. curacaoense* indicates that the phylogenetic position of this species is still closer to the limnic-terrestrial end of the scale.

While the zoeal stages of *S. curacaoense* are morphologically more advanced than those of *S. rectum* and *S. reticulatum*, these differences disappear in the megalopa stage. Hence, the abbreviation of larval development in *S. curacaoense* is restricted to the zoeal phase. The megalopa has in these semiterrestrial *Sesarma* species, as in all marine grapsids, fully developed pleopods, indicating that it retains its swimming capability and hence, its semibenthic (or semipelagic) nature. In the terrestrial species *G. perracae* and *M. depressus*, in contrast, some morphological reductions persist through the megalopa stage (Table 3), namely in the segmentation and setation of the pleopods. This shows that the megalopa is, in these species, an entirely benthic stage, with a similar behaviour as the juvenile. Pleopod reduction has been observed only exceptionally in brachyuran megalopae (Williamson, 1982; Felder et al., 1985; Martin, 1988). It represents a juvenile rather than a larval character and thus, may be considered another step towards complete reduction of the pelagic larval phase.

The megalopa of *S. curacaoense* differs morphologically, in the presence of a dorsal spine, from that of all the other species compared here (Table 3). However, the general significance of this character for the evaluation of taxonomic relationships, or that of the status of a species (primitive vs. advanced) remains doubtfull, at least until more detailed descriptions have become available (Martin, 1988).

The morphology of the larval stages of *S. curacaoense* is intermediate between that of fully terrestrial or limnic and coastal marine Sesarminae. This corroborates Hartnoll's (1964, 1971) conclusion from adult morphological characters, in particular of male pleopod structure, that *S. curacaoense* is closely related to the ancestral *Sesarma* species, from which, through adaptive radiation, endemic terrestrial and freshwater crabs have evolved in Jamaica .

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## REFERENCES

ABELE, L.G., 1992. A review of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae:) in America, with the description of a new genus. Smithsonian Contr. Zool., 527: 1-60

ABELE, L.G. & D.B. MEANS, 1977. *Sesarma jarvisi* and *Sesarma cookei*: montane, terrestrial grapsid crabs in Jamaica (Decapoda). Crustaceana 32: 91-93

ANGER, K. 1995a. Starvation resistance in larvae of a semiterrestrial crab, *Sesarma curacaoense* (Decapoda: Grapsidae). J. exp. mar. Biol. Ecol. 187: 161-174

ANGER, K. 1995b. The conquest of freshwater and land by marine crabs: adaptations in life-history patterns and larval bioenergetics. J.exp.mar. Biol.Ecol. 193:119-145

ANGER, K. & K. SCHULTZE, 1995. Elemental composition (CHN), growth, and exuvial loss in the larval stages of two semiterrestrial crabs, *Sesarma curacaoense* and *Armases miersii* (Decapoda: Grapsidae). Comp. Biochem. Physiol. 111A: 615-623

BÄURLE, G. & R. DIESEL, 1993. Breeding in a snail shell: behavioral and developmental adaptations in the Jamaican terrestrial crab *Sesarma jarvisi* (Decapoda, Grapsidae). Intern. Senckenberg Symp. Crustacea Decapoda, Frankfurt a.M., 18.-22. Okt. 1993, Abstract Volume, p. 84.

BURGGREN, W.W. & B.R. McMAHON (eds.) 1988. Biology of the land crabs. Cambridge University Press, New York, 479 pp.

CHACE, F.A. & H.H. HOBBS, 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. Bull.Nat.Mus.U.S., Wash. 292: 1-298

COSTLOW, J.D. & C.G. BOOKHOUT, 1962. The larval development of *Sesarma reticulatum* Say reared in the laboratory. Crustaceana 4: 281-294

DIESEL, R. & D. HORST, 1995. Breeding in a snail shell: ecology and biology of the Jamaican montane crab *Sesarma jarvisi* (Decapoda:Grapsidae). J.Crust.Biol. 15: 179-195

FELDER, D.L., J.W. MARTIN & J.W. GOY, 1985. Patterns in early postlarval development of Decapods. In: Wenner, A.M. (ed.), Larval Growth, A.A. Balkema, Rotterdam, pp. 163- 225

FRANSOZO, A. & N.J. HEBLING, 1986. Desenvolvimento larval de *Sesarma* (*Holometopus*) *rectum* Randall, 1840 (Decapoda, Grapsidae), em laboratório. Rev. Brasil. Biol. 46: 353-364

GORE, R.H. 1985. Molting and growth in Decapod larvae. In: Wenner, A.M. (ed.), Larval Growth, A.A. Balkema/Rotterdam/Boston, pp. 1-65

HARTNOLL, R.G. 1964. The freshwater grapsid crabs of Jamaica. Proc. Linn. Soc. Lond. 175: 145-169

HARTNOLL, R.G. 1965. Notes on the marine grapsid crabs of Jamaica. Proc. Linn. Soc. Lond. 176: 113-147

HARTNOLL, R.G., 1971. *Sesarma cookei* n.sp., a grapsid crab from Jamaica. Crustaceana, 20: 257-262

HARTNOLL, R.G. 1988. Evolution, systematics, and geographical distribution. In: Burggren, W.W. & McMahon, B.R. (eds.) 1988. Biology of the land crabs. Cambridge University Press, New York, pp. 6-54

INGLE, R. 1992. Larval stages of northeastern Atlantic crabs. An illustrated key. British Museum (Natural History) Publications, Chapman & Hall, London, England, pp. 1-363

KNOWLTON, R.E. 1974. Larval developmental processes and controlling factors in decapod Crustacea, with emphasis on Caridea. Thalassia Jugoslavica 10: 139-158

MARTIN, J.W. 1988. Phylogenetic significance of the brachyuran megalopa: evidence from the Xanthidae. In: Fincham, A.A. & Rainbow, P.S., Aspects of Decapod Crustacean Biology, Symposia of the Zoological Society of London 59, Clarendon Press, Oxford, 365 pp., pp. 69-102

NG, P.K.L. 1988. The freshwater crabs of Peninsular Malaysia and Singapore. Department of Zoology, National University of Singapore: pp. i-viii, 1-156

NG, P.K.L. & C.G.S. TAN. 1995. *Geosesarma notophorum* sp. nov. (Decapoda, Brachyura, Grapsidae, Sesarminae), a terrestrial crab from Sumatra, with novel brooding behaviour. Crustaceana 68: 390-395

PEREYRA LAGO, R. 1987. Larval development of *Sesarma catenata* Ortmann (Brachyura, Grapsidae, Sesarminae) reared in the laboratory. S. Afr. Tydrskr. Dierk. 22: 200-212

RABALAIS, N.N. & R.H. GORE, 1985. Abbreviated development in Decapods. In: Wenner, A.M. (ed.), Larval Growth, A.A. Balkema, Rotterdam, Boston, pp. 67-126

RATHBUN, M.J. 1918. The grapsoid crabs of America. Bull.Smiths.Inst.U.S.Nat.Mus. 97: 447 pp.

RICE, A.L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. Trans. zool. Soc. Lond. 35: 271-42

SCHUH, M. & R. DIESEL, 1995. Effects of salinity and starvation on the larval development of *Sesarma curacaoense* de Man, 1892, a mangrove crab with abbreviated development (Decapoda: Grapsidae). J.Crust.Biol. 15: 645-654

SÈRENE, R. & C.L. SOH, 1970. New Indo-Pacific genera allied to *Sesarma* Say 1817 (Brachyura, Decapoda, Crustacea). Treubia, 27: 387-416

SOH, C.L. 1969. Abbreviated development of non-marine crab, *Sesarma* (*Geosesarma*) *perracae* (Brachyura; Grapsidae), from Singapore. J. Zool., Lond. 158: 357-370

TÜRKAY, M. & R. DIESEL. 1994. Description of a new species of *Sesarma* from Jamaica with notes on its occurrence and biology (Crustacea: Decapoda: Brachyura). Senckenb. Biol. 74:157-161

WATLING, L. 1989. A classification system for crustacean setae based on the homology concept. In: Felgenhauer, B.E., Watling, L. & Thistle, A.B. (eds.), Functional morphology of feeding and grooming in Crustacea. Crustacean Issues 6, A.A. Balkema, Rotterdam/Brookfield, pp. 15-26

WILLIAMSON, D.I. 1982. Larval morphology and diversity. In: Abele, L.G. (ed.), Embryology, Morphology and Genetics, The Biology of Crustacea. Vol. 2. Academic Press New York, pp. 43-110

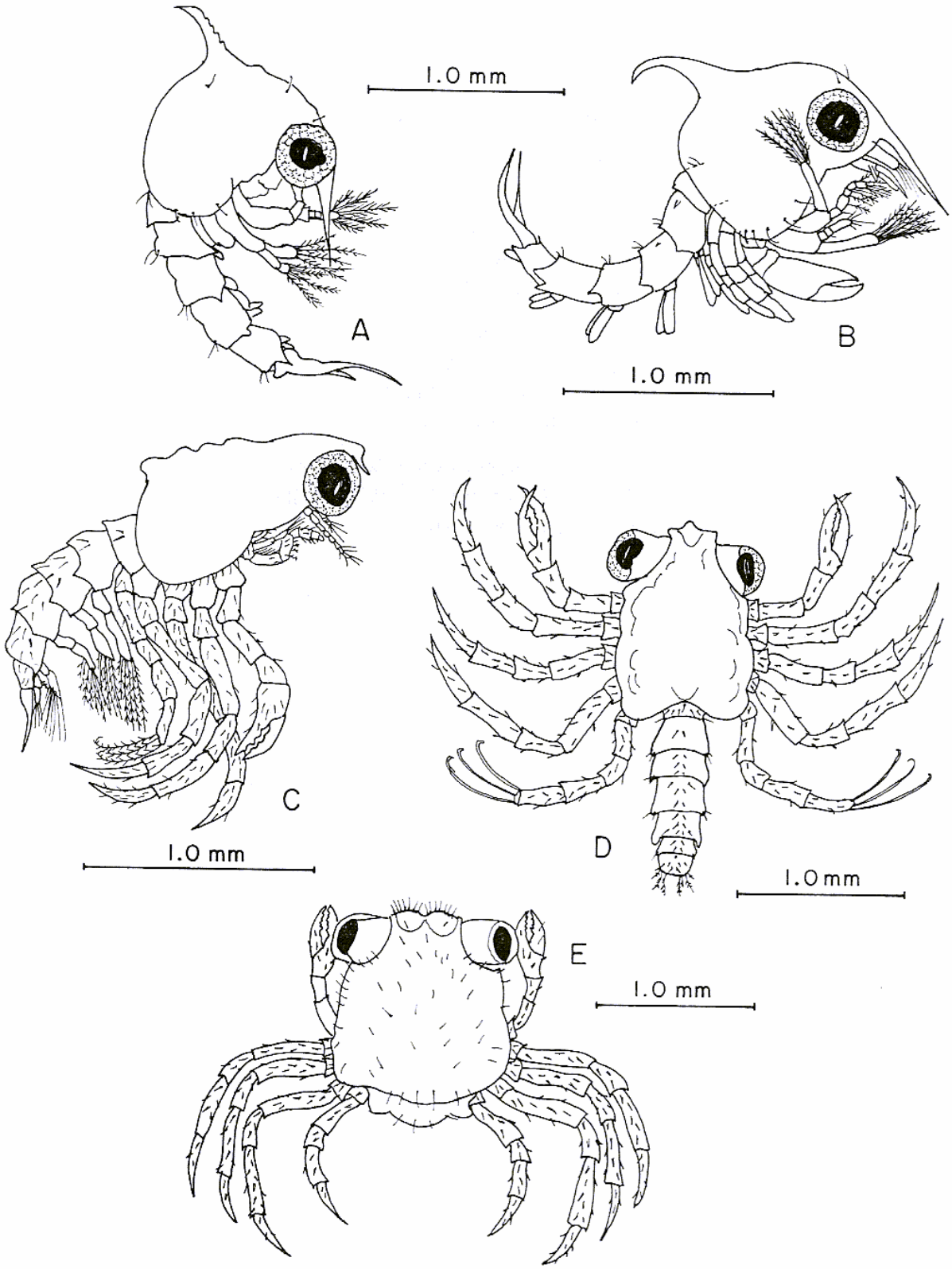


Fig. 1. *Sesarma curacaoense*. Lateral and dorsal view of the different developmental stages. A: Zoea I; B: Zoea II; C and D: Megalopa; E: Crab I.

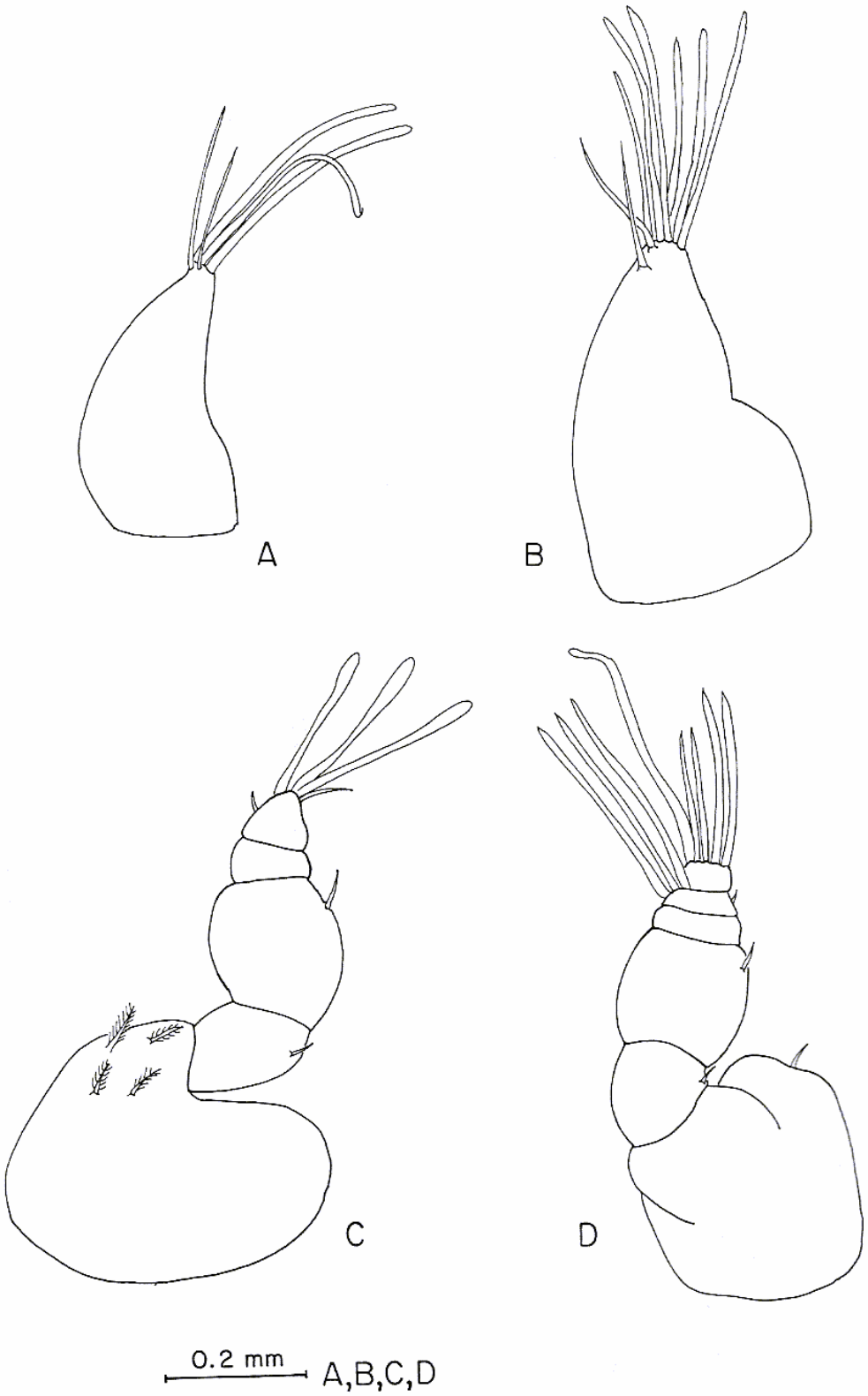


Fig. 2. *Sesarma curacaoense*. Antennule. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

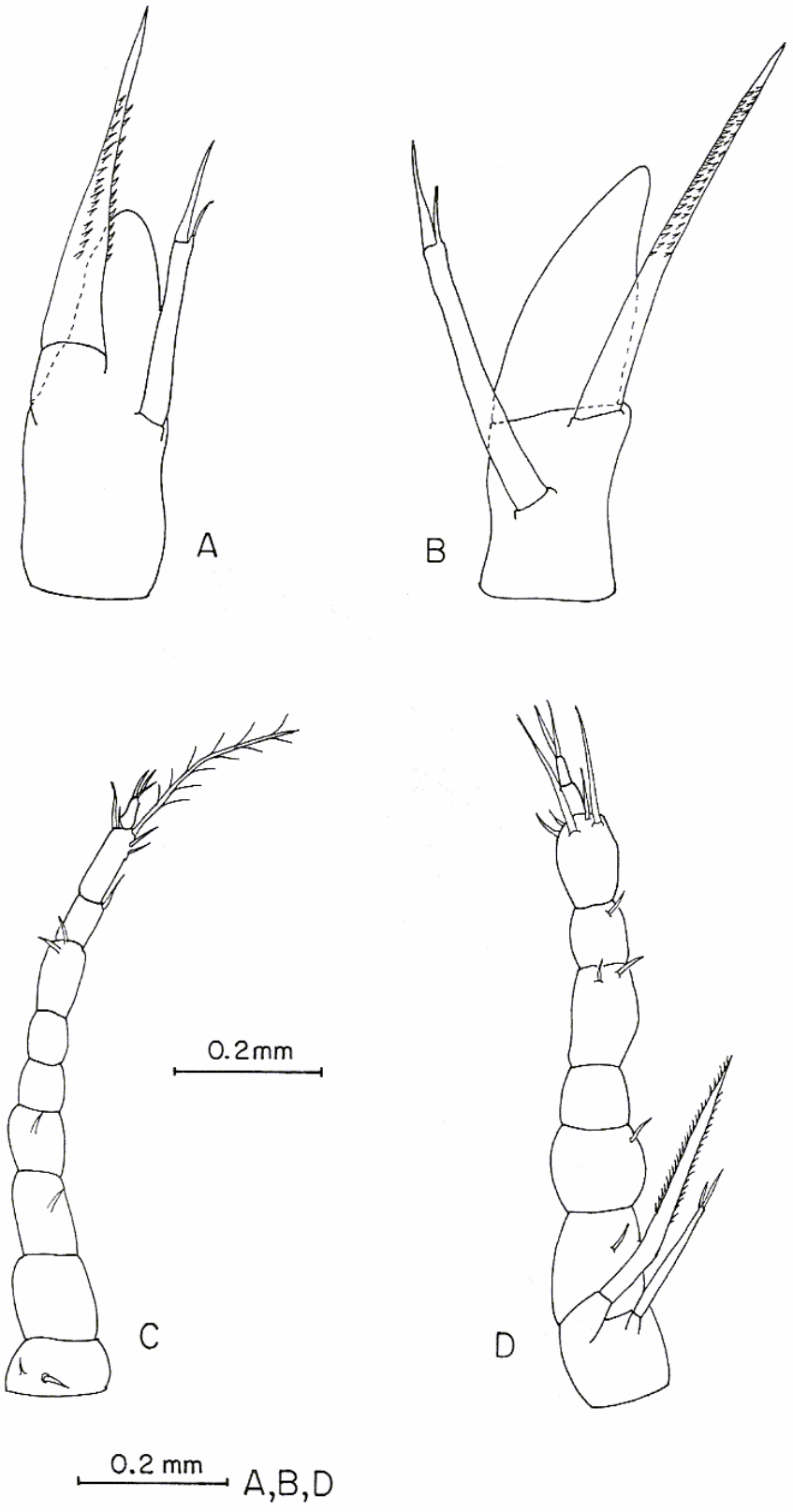


Fig. 3. *Sesarma curacaoense*. Antenna. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

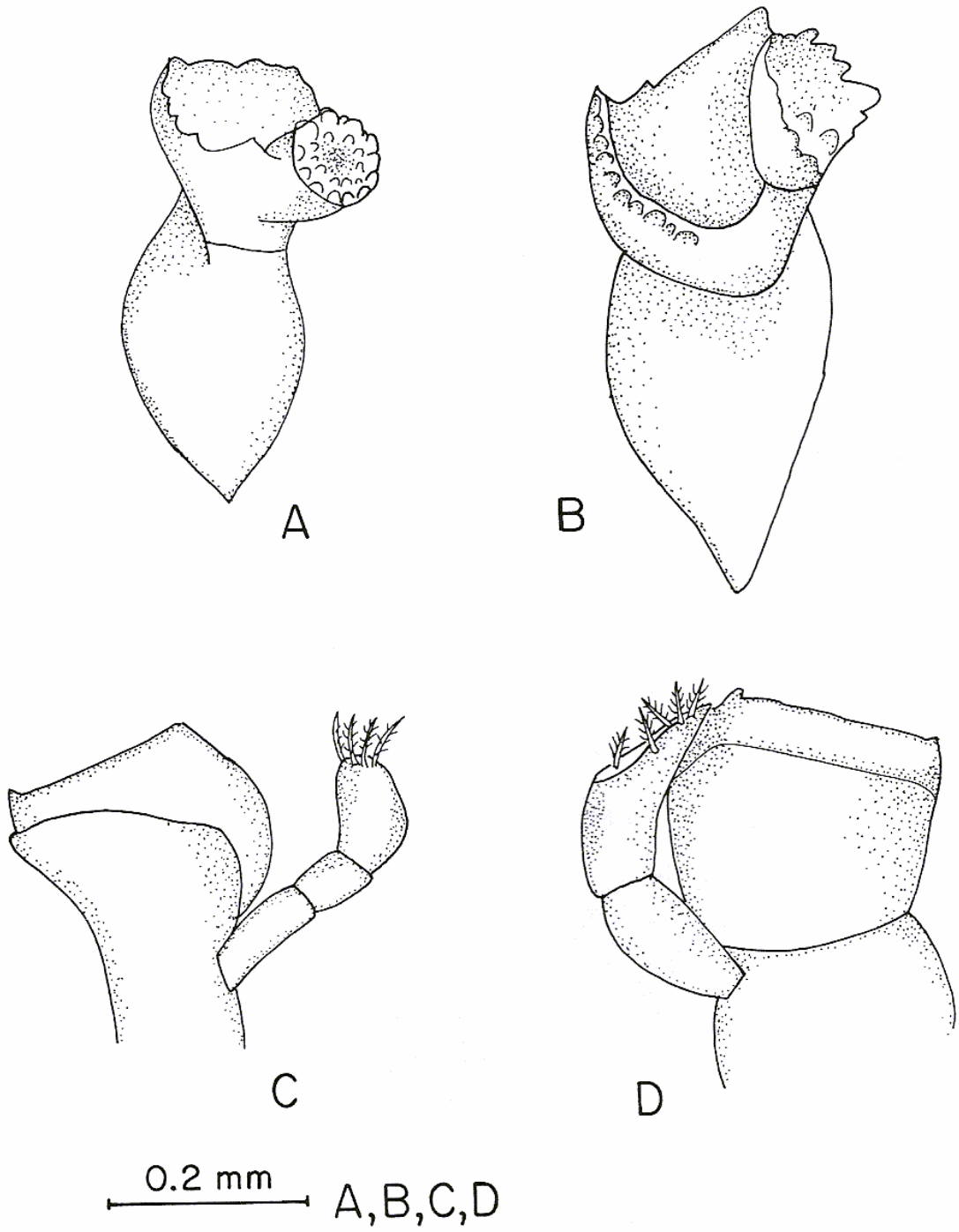


Fig. 4. *Sesarma curacaoense*. Mandible. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

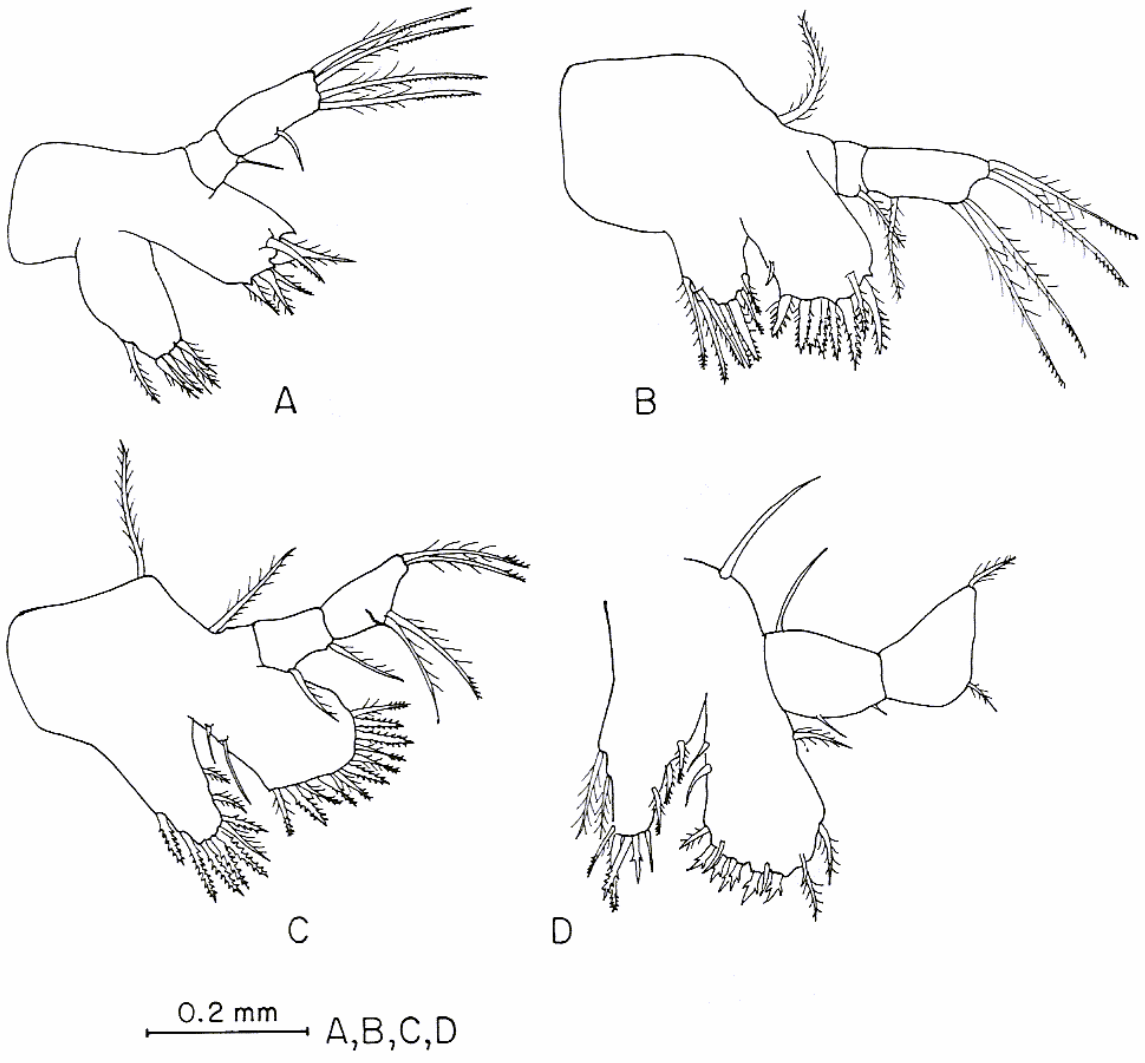


Fig. 5. *Sesarma curacaoense*. Maxillule. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

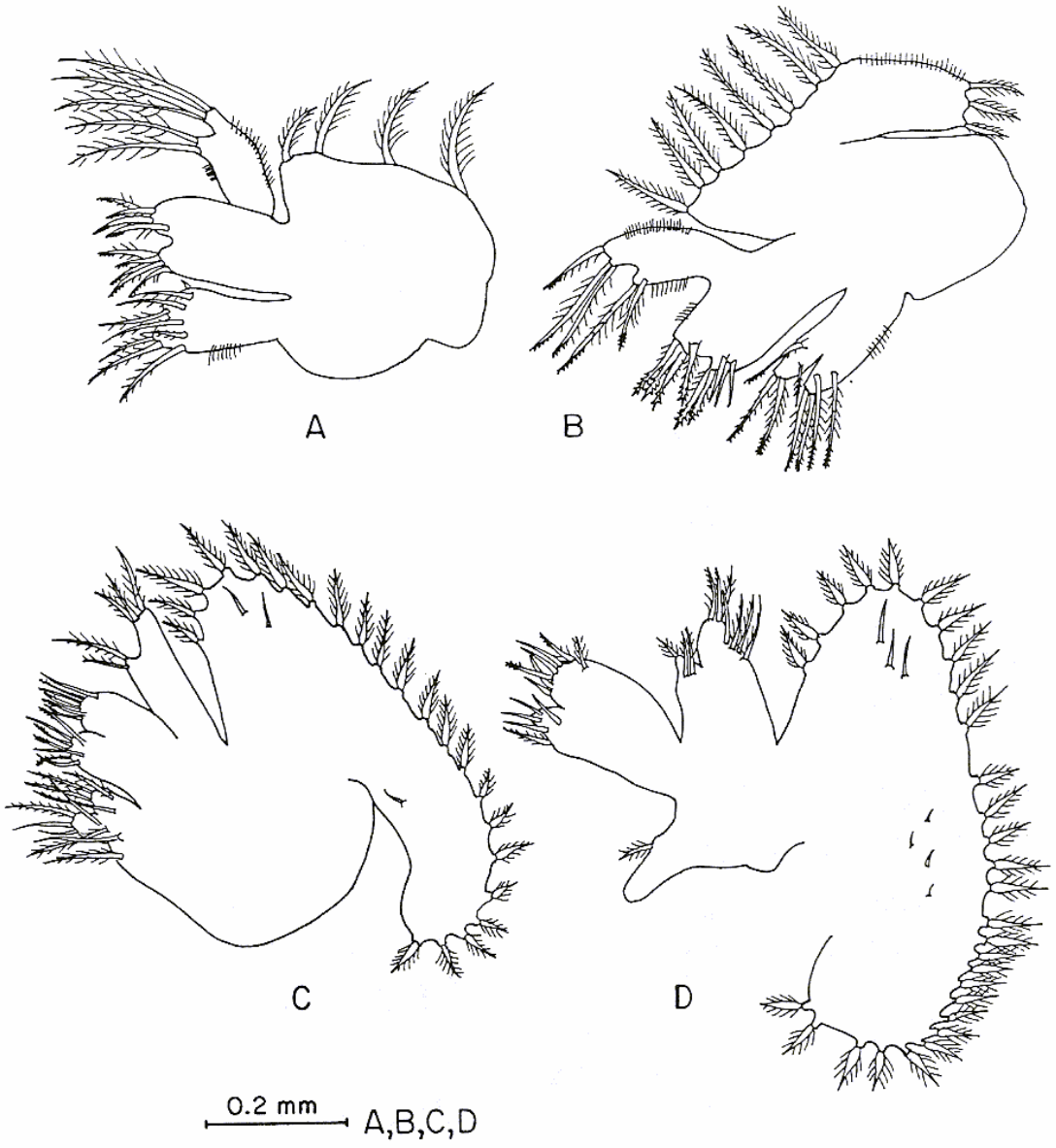


Fig. 6. *Sesarma curacaoense*. Maxilla. A: Zoea I; B:Zoea II; C: Megalopa; D: Crab I.

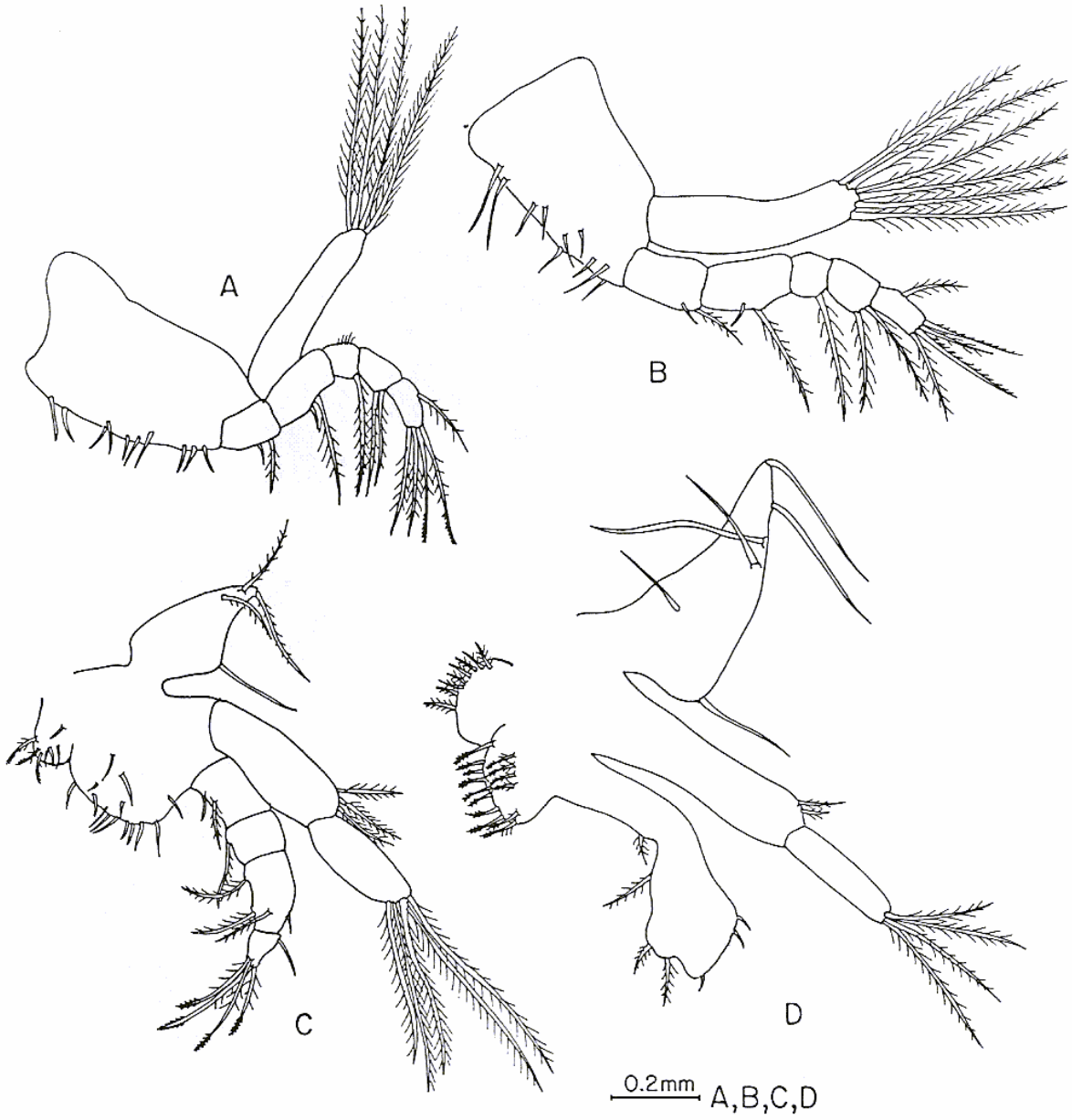


Fig. 7. *Sesarma curacaoense*. Maxilliped 1. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

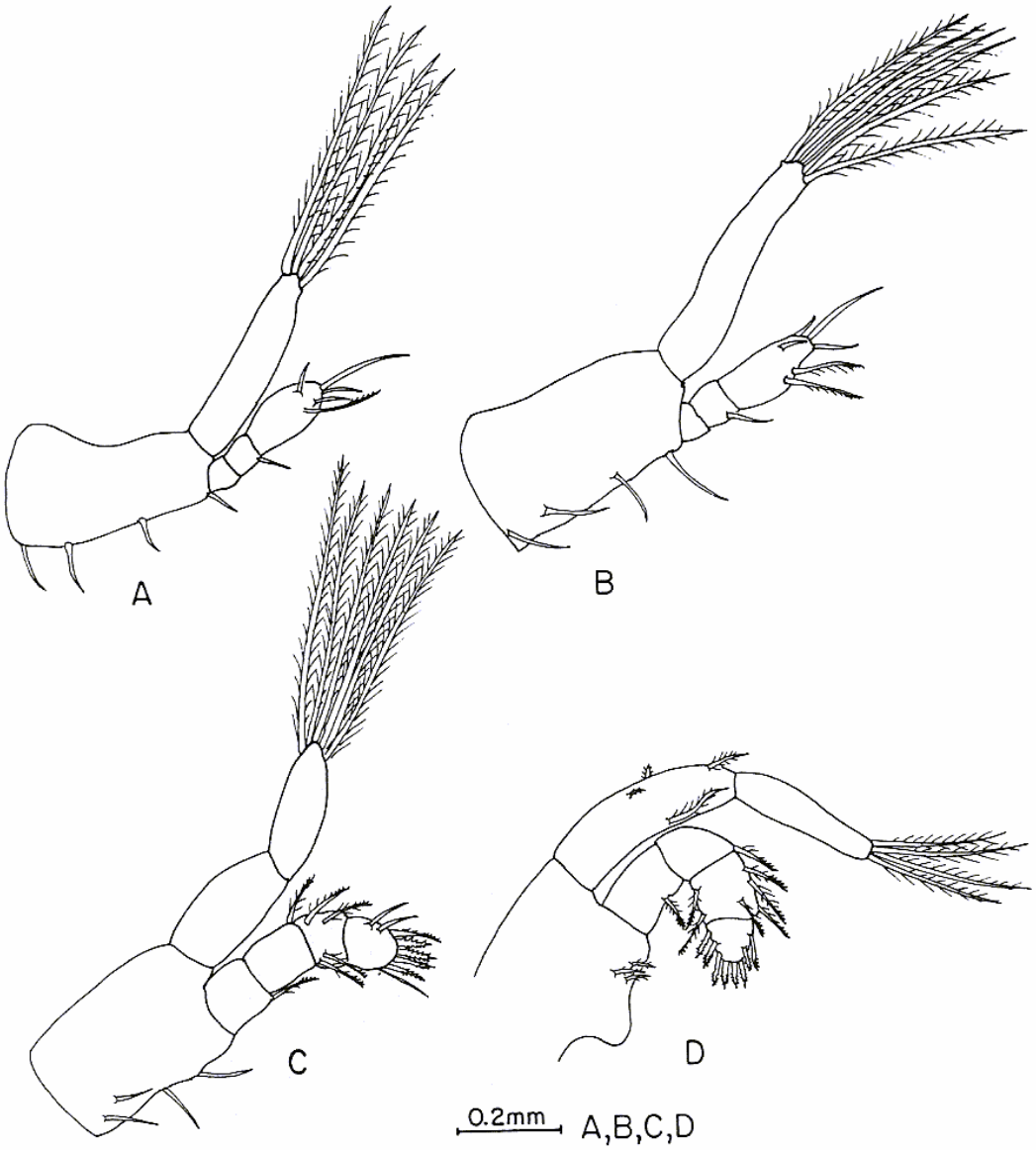


Fig. 8. *Sesarma curacaoense*. Maxilliped 2. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

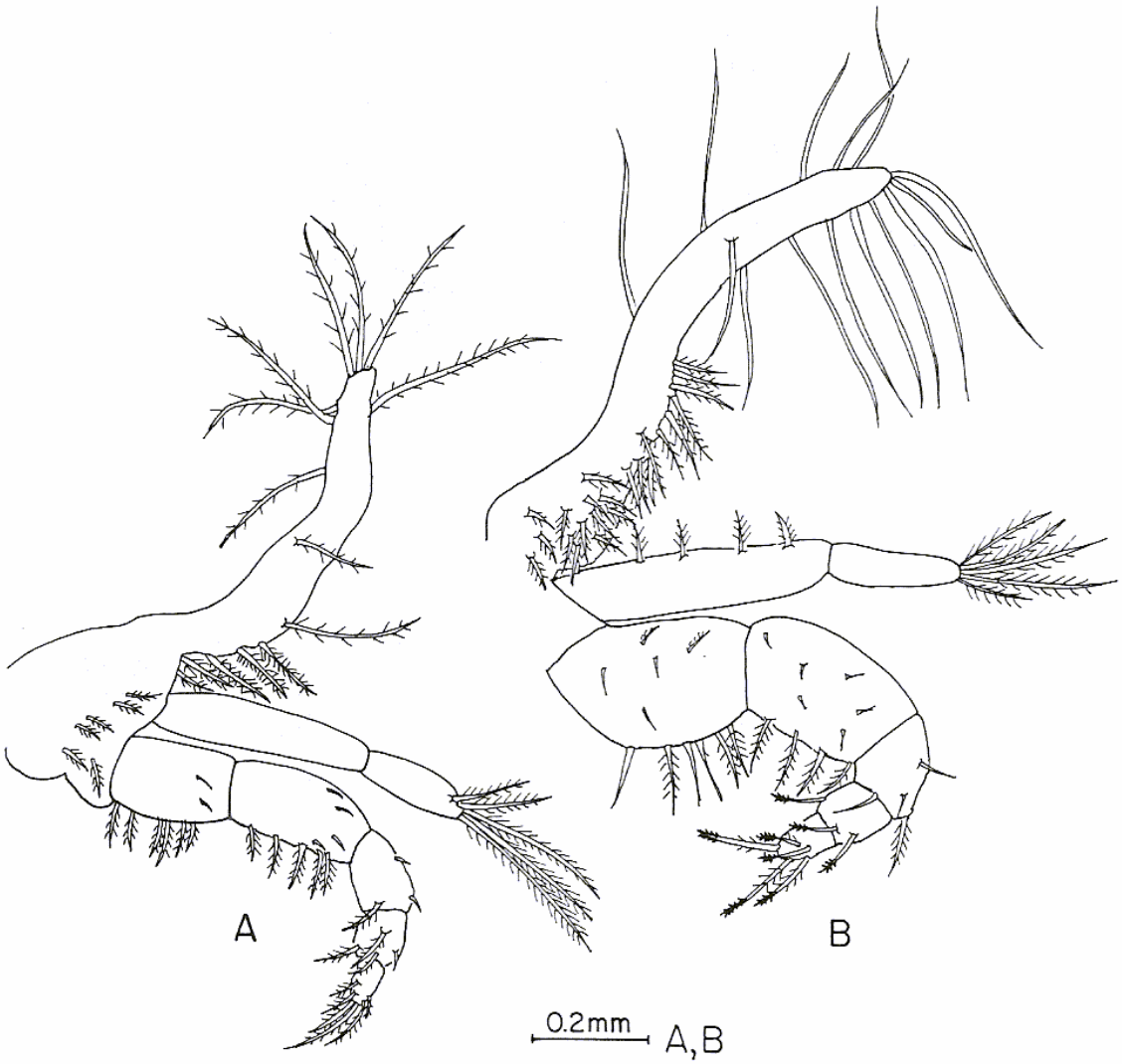


Fig. 9. *Sesarma curacaoense*. Maxilliped 3. A: Megalopa; B: Crab I.

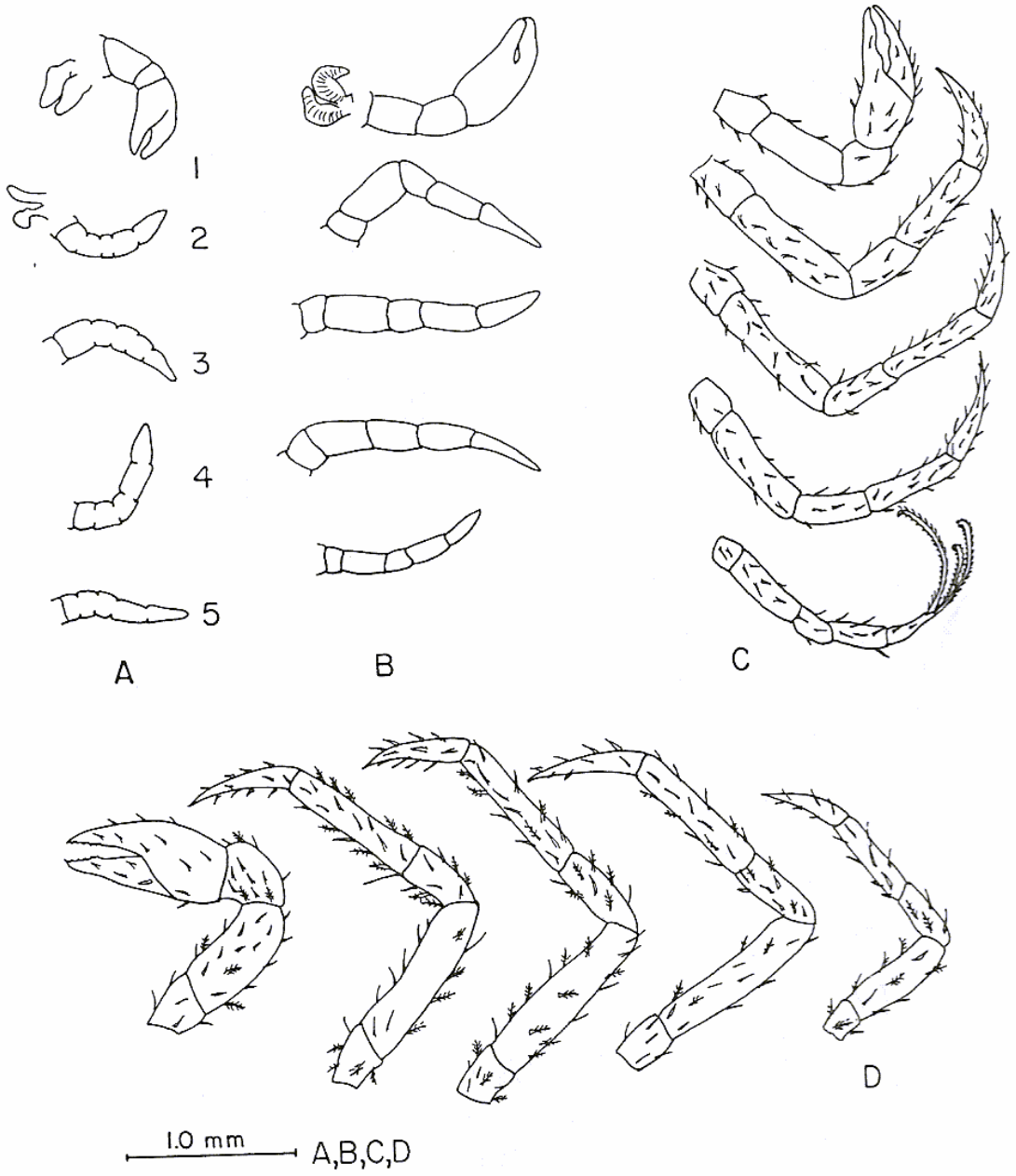


Fig. 10. *Sesarma curacaoense*. Pereiopods (1-5) in A, B, C, D; gills in A, B. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

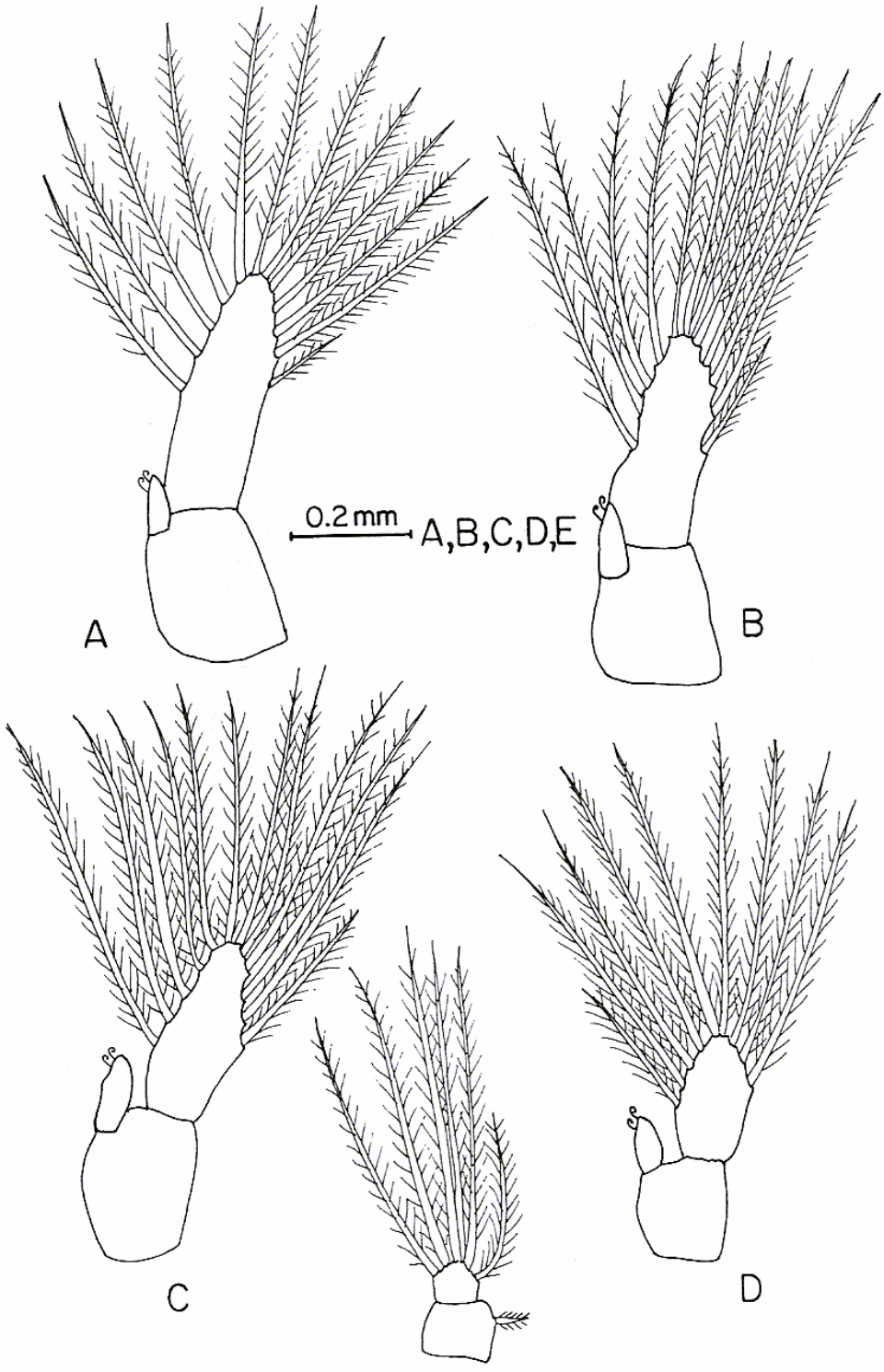


Fig. 11. *Sesarma curacaoense*. Pleopods of Megalopa. A: P1; B: P2; C: P3; D: P4; E: P5.

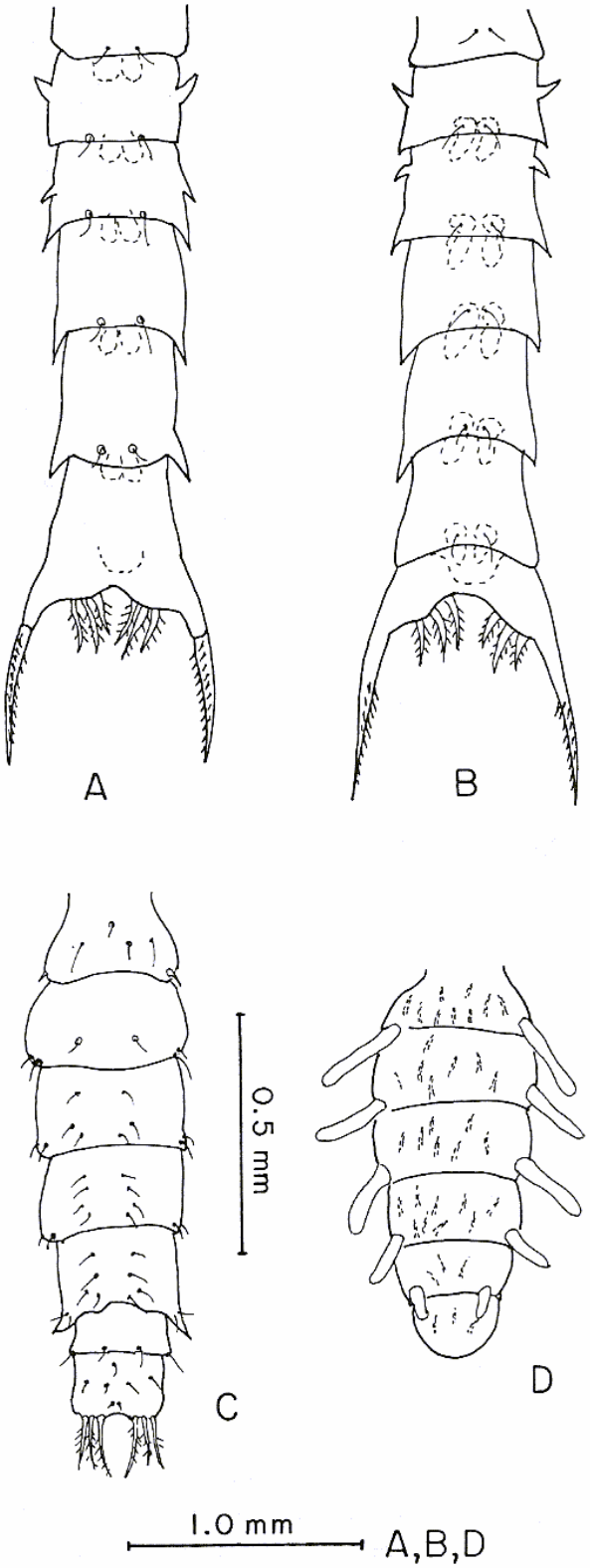


Fig. 12. *Sesarma curacaoense*. Abdomen and telson, dorsal view in A, B, C; ventral view in D. A: Zoea I; B: Zoea II; C: Megalopa; D: Crab I.

Table 1. Morphological differences between the Zoea I of *Geosesarma perracae* (Nobili) (Soh, 1969), *Metopaulias depressus* Rathbun (Hartnoll, 1964), *Sesarma bidentatum* Benedict (Hartnoll, 1964), *S. curacaoense* de Man (present study), *S. rectum* Randall (Fransozo & Hebling, 1986), and *S. reticulatum* Say (Costlow & Bookhout, 1962). Abbreviations: a=aesthetascs; CL=carapace length; S=setation; s=number of setae; seg.=segments; (?)=not clear from original description; (*)=indistinct segmentation.

| Zoea I | *Geosesarma perracae* | *Metopaulias depressus* | *Sesarma bidentatum* | *Sesarma curacaoense* | *Sesarma rectum* | *Sesarma reticulatum* |
|---|---|---|---|---|---|---|
| **Carapace:** | | | | | | |
| CL (mm) | 2.0 | 1.7 | 1.8 | 0.8 | 0.7 | 0.5 |
| dorsal spine | absent | absent | absent | present | present | present |
| eyes | stalked | stalked | stalked | sessile | sessile | sessile |
| **Antennule:** S | 2s | 2s | 2s | 2s, 3a | 2s, 3a | 2s, 3a |
| **Antenna:** protopod, exopod | absent | reduced | reduced | present | present | present |
| **Maxillule** | | | | | | |
| endopod: seg. | 1 | 1 | 1 | 2 | 2 | 2 |
| endopod: S | 3 (?) | 0 | 0 | 6 | 6 | 6 |
| basal, coxal endite: S | 2, 4 (?) | 0, 0 | 0, 0 | 8, 6 | 5, 5 | 5, 5 |
| **Maxilla** | | | | | | |
| endopod: S | 0 | 0 | 0 | 5 | 5 | 5 |
| basal, coxal endite: S | 0, 0 | 0, 0 | 0, 2 | 8-9, 8 | 8, 8 | 9, 7 |
| scaphognathite : S | 29 | 7 | 26 | 3-4 | 5 | 5 |
| **Maxilliped 1** | | | | | | |
| exopod: seg. | 1 | 1 | 2 | 1 | 2 | 2 |
| exopod: S | 4 | 4 | 4 | 4 | 4 | 4 |
| endopod: seg. | 1 | 3 | (3*) | 5 | 5 | 5 |
| endopod: S | 0 | 0, 0, 2 | 0, 0, 2 | 2, 2, 1, 2, 5 | 2, 2, 1, 2, 5 | 2, 2, 1, 2, 5 |
| basis: S | 0 | 0 | 0 | 10 | 10 | 10 |
| epipod | absent | present | present | absent | absent | absent |
| **Maxilliped 2** | | | | | | |
| exopod: seg. | 1 | 1 | 2 | 1 | 2 | 1 |
| exopod: S | 4 | 4 | 4 | 4 | 4 | 4 |
| endopod: seg. | 1 | 1 | 1 | 3 | 3 | 3 |
| endopod: S | 0 | 0 | 0 | 0, 1, 5 | 0, 1, 5 | 0, 1, 5 |
| basis: S | 0 | 0 | 0 | 4 | 5 | 3 |
| **Maxilliped 3** | buds | buds | buds | buds | absent | absent |
| endopod: seg. | 1 | (3)* | (4)* | (3)* | 0 | 0 |
| **Pereiopods** | segmented | segmented (*) | segmented (*) | segmented (*) | buds (?) | buds (?) |
| **Pleopods** | buds | buds | buds | buds | absent | absent |
| **Abdomen:** seg. | 6 | 6 | 6 | 5 | 5 | 5 |

Table 2. Morphological differences between the Zoea II of *Geosesarma perracae* (Nobili) (Soh, 1969), *Metopaulias depressus* Rathbun (Hartnoll, 1964), *Sesarma curacaoense* de Man (present study), *S. rectum* Randall (Fransozo & Hebling, 1986), *and S. reticulatum* Say (Costlow & Bookhout, 1962). References and abbreviations as in Table 1.

| **Zoea II** | *Geosesama perracae* | *Metopaulias depressus* | *Sesama curacaoense* | *Sesama rectum* | *Sesama reticulatum* |
|---|---|---|---|---|---|
| **Carapace**: CL (mm) | ? | 1.8 | 0.9 | 0.8 | 0.6 |
| dorsal spine | absent | absent | present | present | present |
| **Antennule**: S | 3s | 2s | 2s, 6a | 1s, 4a | 2s, 4a |
| **Antenna**: prodopod, exopod | absent | reduced | present | present | present |
| **Maxillule** | | | | | |
| endopod: seg. | 1 | 1 | 2 | 2 | 2 |
| endopod: S | 0 | 0 | 6 | 6 | 6 |
| basal, coxal endite: S | ? | 0, 0 | 9, 7 | 7, 5 | 7, 5 |
| protopod S | 5, 2 | 0 | 1 | 1 | 1 |
| **Maxilla** | | | | | |
| endopod: S | 0 | 0 | 5 | 5 | 5 |
| basal, coxal endite: S | 0, 0 | 0, 0 | 8-9, 8-9 | 9, 8 | 9, 8 |
| Scaphognathite: S | 53 | 14 | 11 | 8 | 8 |
| **Maxilliped 1** | | | | | |
| exopod: seg. | 1 | 1 | 1 | 2 | 1 |
| exopod: S | 10 | 13-14 | 6 | 0, 6 | 6 |
| endopod: seg. | 1 | 3 | 5 | 5 | 5 |
| endopod: S | 0 | 0, 0, 0 | 2, 2, 1, 2, 5 | 2, 2, 1, 2, 5 | 2, 2, 1, 2, 5 |
| basis: S | 0 | 0 | 10 | 10 | 11 |
| epipod | absent | present | absent | absent | absent |
| **Maxilliped 2** | | | | | |
| exopod: seg. | 1 | 1 | 1 | 2 | 1 |
| exopod: S | 10-11 | 12-13 | 6 | 6 | 6 |
| endopod: seg. | 1 | 1 | 3 | 3 | 3 |
| endopod: S | 0 | 0 | 0, 1, 6 | 0, 1, 6 | 0, 1, 6 |
| basis: S | 0 | 0 | 4 | 4 | 3 |
| **Maxilliped 3** | | | | | |
| exopod: seg. | 2 | 1 | (2*) | buds (?) | buds (?) |
| endopod: seg. | 3 | 4 | (4*) | buds (?) | buds (?) |
| **Pereiopods** | segmented | segmented | segmented | buds (?) | buds (?) |
| **Pleopods** | differentiated | differentiated | differentiated | small buds | small buds |

Table 3. Morphological differences between the Megalopa of *Geosesama perracae* (Nobili) (Soh, 1969), *Metopaulias depressus* Rathbun (Hartnoll, 1964), *Sesarma curacaoense* de Man (present study), *S. rectum* Randall (Fransozo & Hebling, 1986), and *S. reticulatum* Say (Costlow & Bookhout, 1962). References and abbreviations as in Table 1 + CW=carapace width.

| **Megalopa** | *Geosesama perracae* | *Metopaulias depressus* | *Sesarma curacaoense* | *Sesarma rectum* | *Sesarma reticulatum* |
|---|---|---|---|---|---|
| **Carapace** | | | | | |
| CL (mm) | 2.1 | 1.9 | 1.0 | 1.0 | 1.0 |
| CW (mm) | 1.9 | 1.9 | 0.6 | 0.8 | 0.6 |
| dorsal spine | absent | absent | present | absent | absent |
| **Antennule** | | | | | |
| segments | 3 | 3 | 6 | 4 | 4 |
| protopod +exopod S: | 0, 0, 4 | 0, 0, 0 | 0, 1, 1, 0, 4, 5 | 1, 1, 5, 7 | 0, 1, 5, 5 |
| basis: S | 1 (?) | 0 | 1 | 3 | 3 |
| **Antenna** | | | | | |
| segments | 8 | 5 | 9 | 9 | 7 |
| S | 0,3,1,0,0,0,1,0 | 0,0,0,0,0 | 0,1,1,0,2,1,5,0,2 | 0,1,1,0,2,0,4,0,4 | 1,1,1,0,1,4,4 (?) |
| **Maxillule** | | | | | |
| endopod: seg. | 1 | 1 | 2 | 2 | 2 |
| endopod: S | 11 | 2 (?) | 2, 4 | 1, 5 | 1, 5 |
| basal, coxal endite: S | 13, 2 | 10, 5 (?) | 13, 9 | 13-15, 7 | 15, 10 |
| protopod: S | ? | ? | 2 | 2 | 2 (?) |
| **Maxilla** | | | | | |
| endopod: S | 1 | 0 | 5 | 0 | 4 |
| basal, coxal endite: S | 12, 10 | 10, 5 (?) | 13, 11 | 12, 12 | 15, 12 |
| scaphognathite: S | 53 (?) | 44 (?) | 22-24 | 33-36 | 32 (?) |
| **Maxilliped 1** | | | | | |
| exopod: seg. | 2 | 1 | 2 | 2 | 2 |
| exopod: S | 0, 2 | 0 | 2-3, 5 | 2, 4 | 1, 8 |
| endopod: seg. | 1 | 1 | 4 | 1 | 4 |
| endopod: S | 3 | 4 (?) | 2, 1, 4, 5 | 2 | 3, 2, 2, 5 |
| basal, coxal endite: S | 7, 6 | 6, 6 (?) | 13-14, 5-7 | 10, 6 | 14, 5 |
| epipod: S | 4 | 9 (?) | 4 | 5 | 4 |

Table 3. Continued.

| Megalopa | *Geosesarma perracae* | *Metopaulias depressus* | *Sesarma curacaoense* | *Sesarma rectum* | *Sesarma reticulatum* |
|---|---|---|---|---|---|
| **Maxilliped 2** | | | | | |
| exopod: seg. | 2 | 2 | 2 | 2 | 1 |
| exopod: S | 2, ? | 0 | 0, 6 | 2, 4 | 7 |
| endopod: seg. | 5 | 4 | 4 | 4 | 4 |
| endopod: S | 0, 0, 0, 4, 7 | 0, 0, 2, 7 (?) | 1, 1, 4, 8 | 0, 1, 3, 6 | 1, 1, 3, 9 |
| basis: S | ? | ? | 4 | 2 | 4 |
| **Maxilliped 3** | | | | | |
| exopod: seg. | 2 | 1 | 2 | 2 | 2 |
| exopod: s | 4, 4 | 4 (?) | 0, 5 | 0, 5 | 0, 5 |
| endopod: seg. | 5 | 4 | 5 | 5 | 5 |
| endopod: S | 14, 8, 4, 2, 4 (?) | 14, 3, 3, 5 (?) | 8, 9, 3, 4, 6 | 8-9, 6, 3, 4, 5-6 | 8, 6, 2, 4, 6 |
| protopod: S | 21 (?) | 5 (?) | 6 | 7 | 5 |
| epipod: S | 20 (?) | 15 (?) | 14 | 15 | 10 |
| **Pleopods** | reduced | reduced | developed | developed | developed |
| exopod: S | 0 | 0 | 12, 12, 12, 9, 6 | 13, 13, 13, 11, 6 | 14, 13, 12, 11, 6 |

Table 4. Morphological differences between the Crab I of *Geosesarma perracae* (Nobili) (Soh, 1969), *Metopaulias depressus* Rathbun (Hartnoll, 1964), and *Sesarma curacaeoense* de Man (present study). References and abbreviations as in Table 3.

| **Crab I** | *Geosesarma perracae* | *Metopaulias depressus* | *Sesarma curacaoense* |
|---|---|---|---|
| **Carapace:** CL (mm) | 2.2 | 2.3 | 1.2 |
| CW (mm) | 2.0 | 2.0 | 1.0 |
| **Antennule**: seg | 3 | 2 | 4 |
| S | 1, 1, 2 | 3 (?) | 1, 1, 0, 5 |
| basis: S | 12 (?) | 0 | 4 |
| **Antenna**: seg. | 8 | 5 | 10 |
| S | 0, 2, 3, 0, 0, 0, 2, 1 | 0, 0, 0, 0, 4 (?) | 2, 0, 1, 1, 0, 0, 2, 1, 5, 3 |
| **Mandible**: palp: S | 0, 1, 9 | 0, 5 | 0, 5 |
| **Maxillule** | | | |
| endopod: seg. | 1 | 1 | 2 |
| endopod: S | 3 | 1 | 2-3, 2-4 |
| basal, coxal endite: S | 13, 3 (?) | 13, 9 (?) | 15, 10 |
| protopod: S | ? | ? | 0-1 |
| **Maxilla:** endopod: S | 0 | 0 | 1 |
| basal, coxal endite: S | 12, 6 | 10, 10 (?) | 11-12, 10-11 |
| scaphognathite: S | 64 | 60 (?) | 28-31 |
| **Maxilliped 1** | | | |
| exopod: seg. | 2 | 2 | 2 |
| exopod: S | 2, 3 | 0, 4 (?) | 2, 4 |
| endopod: seg. | 2 | 1 | 1 |
| endopod: S | 0, 9 | 5 (?) | 7 |
| basal, coxal endite: S | 16, 11 (?) | 8, 8 (?) | 14-17, 8-9 |
| epipod: S | 9 (?) | 16 (?) | 5-6 |
| **Maxilliped 2** | | | |
| exopod: seg. | 2 | 2 | 2 |
| exopod: S | 11, 3 | 5, 3 (?) | 3-4, 4-5 |
| endopod: seg. | 5 | 4 | 4 |
| endopod: S | 0, 1, 1, 7, 9 (?) | 2, 1, 4, 8 (?) | 1, 1, 5-6, 8-9 |
| basis: S | ? | ? | 3 |
| **Maxilliped 3** | | | |
| exopod: seg. | 2 | 2 | 2 |
| exopod: S | 11, 3 | 4, 4 (?) | 4-5, 5 |
| endopod: seg | 5 | 5 | 4 |
| endopod: S | 32, 18, 8, 6, 5 (?) | 8, 3, 5, 1, 6 (?) | 8-11, 4, 3-4, 5-6, 12-14 |
| protopod: S | 37 (?) | 13 (?) | 20-25 |
| epipod: S | 19 (?) | 18 (?) | 12-14 |