

LARVAL MORPHOLOGY OF THE SESARMID CRAB *ARMASES ANGUSTIPES* DANA, 1852 (DECAPODA, BRACHYURA, GRAPSOIDEA)

José A. Cuesta and Klaus Anger

(JAC, correspondence) Departamento de Ecología, Facultad de Biología, Apdo. 1095, 41080 Sevilla, Spain (mariscal@cica.es), present address: Department of Biology, Laboratory for Crustacean Research, University of Louisiana at Lafayette, P.O. Box 42451, Lafayette, Louisiana 70504-2451, U.S.A.; (KA) Biologische Anstalt Helgoland, Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung, 27498 Helgoland, Germany (kanger@awi-bremerhaven.de)

A B S T R A C T

Larvae of the sesarmid crab *Armases angustipes* Dana, 1852, captured from the coast of the state of São Paulo, Brazil, were reared in the laboratory from hatching to the megalopa stage. In this paper, the morphology of the four zoeal stages and the megalopa is described and illustrated. Morphological comparisons are made with all known descriptions for the larvae of *Armases* including an unpublished description of *A. angustipes* and of some closely related genera (*Aratus* and *Sesarma*). Several differences to the previous description of *A. angustipes* are shown, and additional characters such as the previously undescribed cephalothoracic setation of the larval stages are described and illustrated. Diagnostic characters are provided to differentiate the American genera *Sesarma* and *Armases*.

The Sesarmidae Say, 1817, are represented in the Americas by four genera (*Aratus* H. Milne Edwards, 1837; *Armases* Abele, 1992; *Metopaulias* Rathbun, 1896; *Sesarma* Say, 1817) with 29 species (for recent discussion of grapsoid taxonomy see Schubart *et al.*, 2000). The genus *Armases* was erected by Abele (1992) with 11 species formerly assigned to the genus *Sesarma*. Later, *Metasesarma rubripes* Rathbun, 1897, was transferred to *Armases* by Niem, 1996. Within this genus, larval morphology has been described for the following species: *A. cinereum* (Bosc, 1802) by Costlow and Bookhout (1960) and Schubart and Cuesta (1998); *A. ricordi* (H. Milne Edwards, 1853) and *A. rubripes* (Rathbun, 1897) by Díaz and Ewald (1968) and Schubart and Cuesta (1998); *A. angustipes* Dana, 1852, by Kowalczyk (1994); and *A. miersii* (Rathbun, 1897) by Cuesta *et al.* (1999). According to Niem (1996) and Schubart *et al.* (2000), the monotypic *Aratus pisonii* (H. Milne Edwards, 1837) is also closely related to *Armases* and therefore is included in our morphological comparison (see Warner, 1968; Fransozo *et al.*, 1998).

In adult morphology, *Armases angustipes* is very similar to *A. miersii*; the exact distribution and possible sympatry of these two species, e.g., in the Bahamas, remains unre-

solved (Abele, 1992; Cuesta *et al.*, 1999). However, clear differences are found when their larval morphology is compared. The main difference is the number of zoeal stages, with three in *A. miersii* (abbreviated development) and four in *A. angustipes*; further interspecific differences are found in their chaetotaxy. The larval development of *A. angustipes* was described from material originating from Farol Island, Brazil, in an unpublished Master of Science thesis by Kowalczyk (1994), but this did not meet fully with modern-day standards. In the present study, larval development of *A. angustipes* from the coast of the state of São Paulo (Brazil) is described and illustrated, intraspecific differences to the previous description are shown and discussed, and additional morphological characters are provided.

MATERIALS AND METHODS

An ovigerous crab *Armases angustipes* was collected in February, 1996, at the vicinity of São Sebastião Marine Biological Station of the University of São Paulo (USP, São Paulo, Brazil) and transferred live to the Helgoland Marine Biological Station (Germany). Larvae hatched on 12 March; they were mass-reared at constant 24°C and 25‰ using gently aerated beakers (1 l, about 100 larvae per beaker). Water and food (*Artemia* sp., about 10 freshly hatched nauplii/ml) were changed daily, and the larvae were checked for moulting and mortality. The rearing salinity was obtained by dilution of filtered natural sea water from the North Sea (32‰) with deion-

ized water; this condition was chosen because a previous experimental study had shown that a slightly reduced salinity was more favorable for the larval development of this species than full-strength sea water (Anger *et al.*, 1990). Samples of larvae and exuviae were fixed in 4% Formalin in sea water.

Drawings and measurements were made using a Wild MZ6 and an Olympus BH compound microscope, both equipped with a *camera lucida*. Semipermanent mounts were made of whole larvae; dissected appendages were stained using CMC 10 and lignin pink. All measurements were made with an ocular micrometer. Drawings were based on five larvae, size measurements on 10 larvae, per stage. In zoea larvae, rostrorod length (rdl) 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; carapace width (cw) as the greatest distance across the carapace. In the megalopa stage, carapace length (cl) was measured from the base of the rostrum to the posterior margin, and carapace width (cw) as the maximum width. Long aesthetascs of the antennules in Fig. 3, and the long natatory setae on the distal exopod segments of the first and second maxillipeds in Figs. 7 and 8 are drawn truncated. In Fig. 7, the basis of the zoea II–IV is not shown, because no differences in relation to that of zoea I were found; in Fig. 8, the second maxilliped of the zoea II and III are not shown, because they differed only in size. The long terminal natatory setae of the exopod of the second pleopod and uropod are truncated in Fig. 12. Description and figures are arranged according to the standard proposed by Clark *et al.* (1998).

Samples of larvae (zoea I to megalopa) of *Armases angustipes* were deposited at the Smithsonian Natural History Museum of Washington, under the catalog number USNM 266398.

RESULTS

The first zoeal stage of *Armases angustipes* is described completely. For the subsequent stages only the main differences from the first zoea are described in detail. Evolution of setation formulae and appendages through zoeal development is shown in Table 1.

Description

Armases angustipes Dana, 1852

(Figs. 1A, B; 2A, B; 3A–D; 4A–D; 5A–D; 6A–D; 7A–E; 8A–C; 9A–C; 10A–D; 11A–G; 12A–D)

Zoea I

Dimensions.—Rdl: 0.78 ± 0.04 mm; cl: 0.41 ± 0.02 mm; cw: 0.44 ± 0.02 mm.

Carapace (Fig. 1A).—Globose, smooth, without tubercles. Dorsal spine present, well developed, clearly recurved. Rostral spine present, straight, equal in length to antennary protopod. Lateral spines absent. Pair of setae on posterodorsal and anterodorsal regions. Posterior and ventral margin without setae. Eyes sessile.

Antennule (Fig. 3A).—Uniramous. Endopod absent. Exopod unsegmented, with 3 aesthetascs and 2 setae all terminal.

Antenna (Fig. 4A).—Well-developed protopod reaching tip of rostral spine and bearing 2 unequal rows of spines. Exopod elongated, with 4 terminal setae (1 long, 1 middle, and 2 minute).

Mandible.—Endopod palp absent.

Maxillule (Fig. 5A).—Coxal endite with 6 plumodenticulate setae. Basial endite with 5 setae (1 cuspidate, 4 plumodenticulate). Endopod 2-segmented, with 1 seta in proximal segment and 1 subterminal and 4 terminal plumodenticulate setae in distal segment. Exopod seta absent. Epipod seta absent.

Maxilla (Fig. 6A).—Coxal endite bilobed, with 5 + 3 plumodenticulate setae. Basial endite bilobed, with 5 + 4 plumodenticulate setae. Endopod unsegmented, bilobed, with 2 + 3 long plumodenticulate setae on inner and outer lobe respectively. Scaphognathite (exopod) with 4 plumose marginal setae and long, setose posterior process.

First Maxilliped (Fig. 7A).—Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented, with 2,2,1,2,5 (1 subterminal + 4 terminal) setae. Exopod 2-segmented, distal segment with 4 long, terminal, plumose natatory setae.

Second Maxilliped (Fig. 8A).—Coxa without setae. Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented, with 0,1,6 (3 subterminal + 3 terminal) setae. Exopod 2-segmented, distal segment with 4 long, terminal, plumose natatory setae.

Third Maxilliped.—Present as undifferentiated buds.

Pereiopods.—Present as undifferentiated bud.

Abdomen (Fig. 11A).—Five abdominal somites. Somites 2 and 3 with pair of dorso-lateral processes. Somites 2–5 with pair of posterodorsal setae. Pleopods absent.

Telson (Fig. 11A).—Telson bifurcated, with 3 pairs of serrulate setae on posterior margin. Two rows of teeth in inner distal part of each furcal branch.

Table 1. Evolution of setation formulae and appendages through zoeal development of *Armases angustipes*. Abbreviations: s, setation; a, aesthetasc; seg., segment; en, endopod; ep, epipod; ex, exopod. In carapace setation numbers indicate pairs of setae.

	Zoea I	Zoea II	Zoea III	Zoea IV
Carapace				
Anterodorsal s	1	3	3	4
Posterodorsal s	1	1	1	1
Posterior margin s	0	0	0	0
Ventral margin s	0	1	4	7
Antennule				
a + s	3 + 2	4 + 1	3 + 2	6 + 1
Antenna				
Endopod	absent	minute bud	elongated bud	2-segmented bud
Maxillule				
Exopodal setae	absent	present	present	present
Coxal endite s	6	6	6	7
Basial endite s	5	7	8	11
Maxilla				
Coxal endite s	3 + 5	3 + 5	3 + 5	4 + 6
Basial endite s	5 + 4	5 + 4	5 + 5	6 + 5
Scaphognathite	4	8	13	20
First maxilliped				
Endopod				
Proximal seg. s	2	2	2	2
2nd seg. s	2	2	3	3
3rd seg. s	1	1	2	2
4th seg. s	2	2	2	2
Distal seg. s	5	5	5	6
Exopod	4	6	8	10
Second maxilliped				
Endopod				
Proximal seg. s	0	0	0	0
2nd seg. s	1	1	1	1
Distal seg. s	6	6	6	6
Exopod	4	6	8	10
Third maxilliped				
	minute bud	small bud	exopod and endopod differentiated	now epipod also differentiated
			elongated buds	cheliped chelated
Pereiopods				
	minute buds	small buds	elongated buds	cheliped chelated
Abdomen				
Proximal somite s	0	0	1	3
2nd somite s	2	2	2	2
3rd somite s	2	2	2	2
4th somite s	2	2	2	2
5th somite s	2	2	2	2
6th somite s	absent	absent	slightly developed	developed

Zoea II

Dimensions.—Rdl: 0.97 ± 0.03 mm; cl: 0.53 ± 0.02 mm; cw: 0.68 ± 0.01 mm.

Carapace (Fig. 1B).—Three pairs of anterodorsal setae. Each ventral margin with 1 plumodenticulate seta. Eyes stalked. Otherwise unchanged.

Antennule (Fig. 3B).—Exopod with 1 additional shorter terminal aesthetasc and 1 seta. Otherwise unchanged.

Antenna (Fig. 4B).—Endopod bud present. Otherwise unchanged.

Mandible.—Unchanged.

Maxillule (Fig. 5B).—Basial endite with 7 setae. Exopod present as long, plumose marginal seta. Otherwise unchanged.

Maxilla (Fig. 6B).—Scaphognathite with 5 + 3 plumose marginal setae, long posterior process now reduced in size. Otherwise unchanged.

First Maxilliped (Fig. 7B).—Exopod distal segment with 6 long, terminal, plumose natatory setae. Otherwise unchanged.

Second Maxilliped.—Exopod distal segment

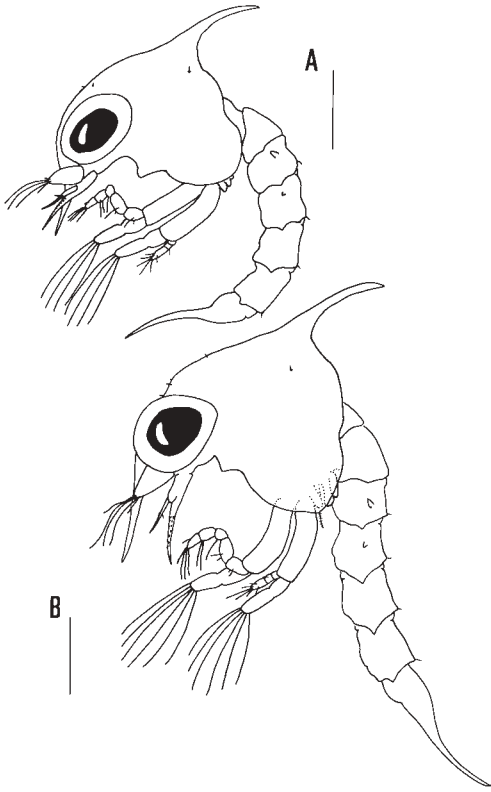


Fig. 1. *Armases angustipes* Dana, 1852. A, Zoea I; B, Zoea II. Scale bars = 0.2 mm.

with 6 long, terminal, plumose natatory setae. Otherwise unchanged.

Third Maxilliped.—More elongated bud.

Pereiopods.—More elongated buds.

Abdomen (Fig. 11B).—Unchanged.

Telson (Fig. 11B).—Unchanged.

Zoea III

Dimensions.—Rdl: 1.21 ± 0.03 mm; cl: 0.66 ± 0.03 mm; cw: 0.82 ± 0.02 mm.

Carapace (Fig. 2A).—Each ventral margin with 4 plumodenticulate setae. Otherwise unchanged.

Antennule (Fig. 3C).—Exopod unsegmented, with 3 aesthetascs and 2 setae. Otherwise unchanged.

Antenna (Fig. 4C).—Endopod bud elongated, as long as exopod. Otherwise unchanged.

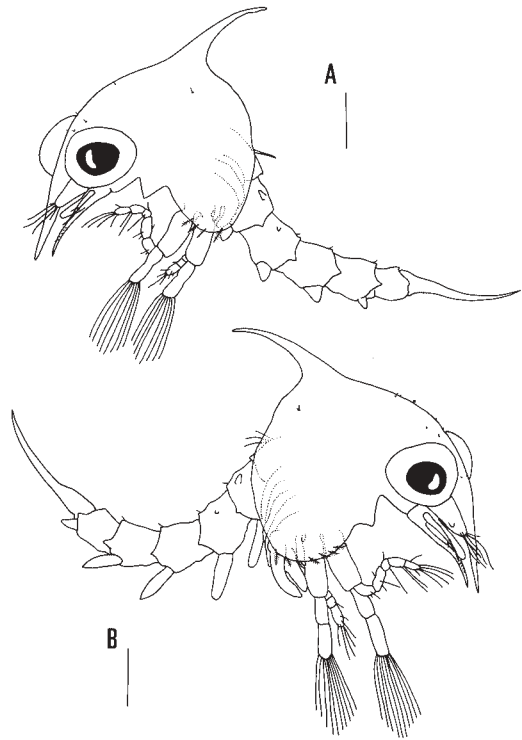


Fig. 2. *Armases angustipes* Dana, 1852. A, Zoea III; B, Zoea IV. Scale bars = 0.2 mm.

Mandible.—Unchanged.

Maxillule (Fig. 5C).—Basial endite with 8 setae. Epipod seta present. Otherwise unchanged.

Maxilla (Fig. 6C).—Basial endite bilobed, with 5 + 5 setae. Scaphognathite with 13 plumose marginal setae. Otherwise unchanged.

First Maxilliped (Fig. 7C).—Endopod segments 2 and 3 each with additional dorsal seta. Exopod distal segment with 8 long, terminal, plumose natatory setae. Otherwise unchanged.

Second Maxilliped.—Exopod distal segment with 8 long, terminal, plumose natatory setae. Otherwise unchanged.

Third Maxilliped (Fig. 9A).—Biramous, unsegmented.

Pereiopods (Fig. 10A).—Present, unsegmented. Chelipeds bilobed.

Abdomen (Fig. 11C).—First somite with 1 long mid-dorsal seta. Somite six now present,

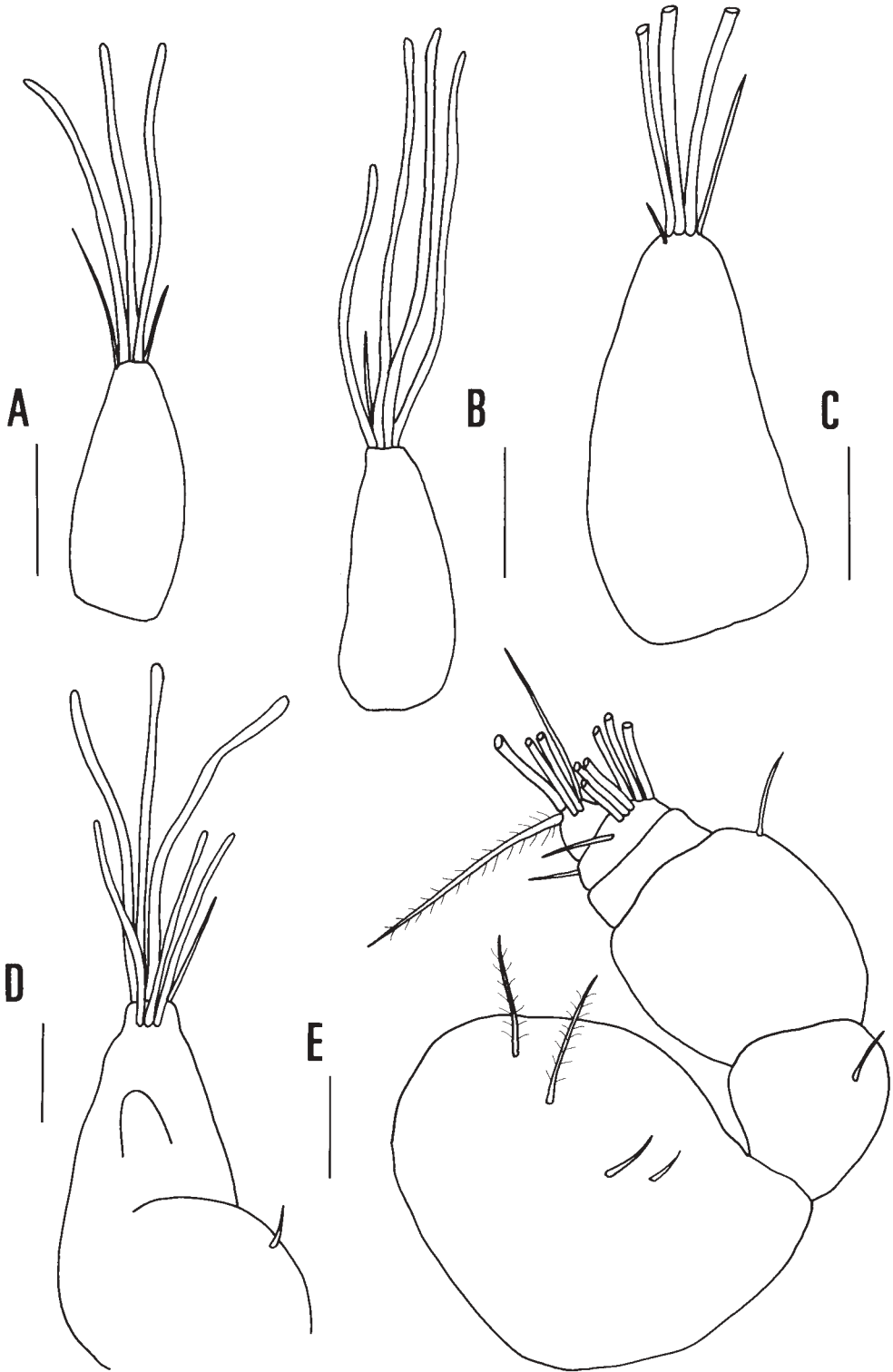


Fig. 3. *Armases angustipes* Dana, 1852, antennule. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa. Scale bars = 0.05 mm.

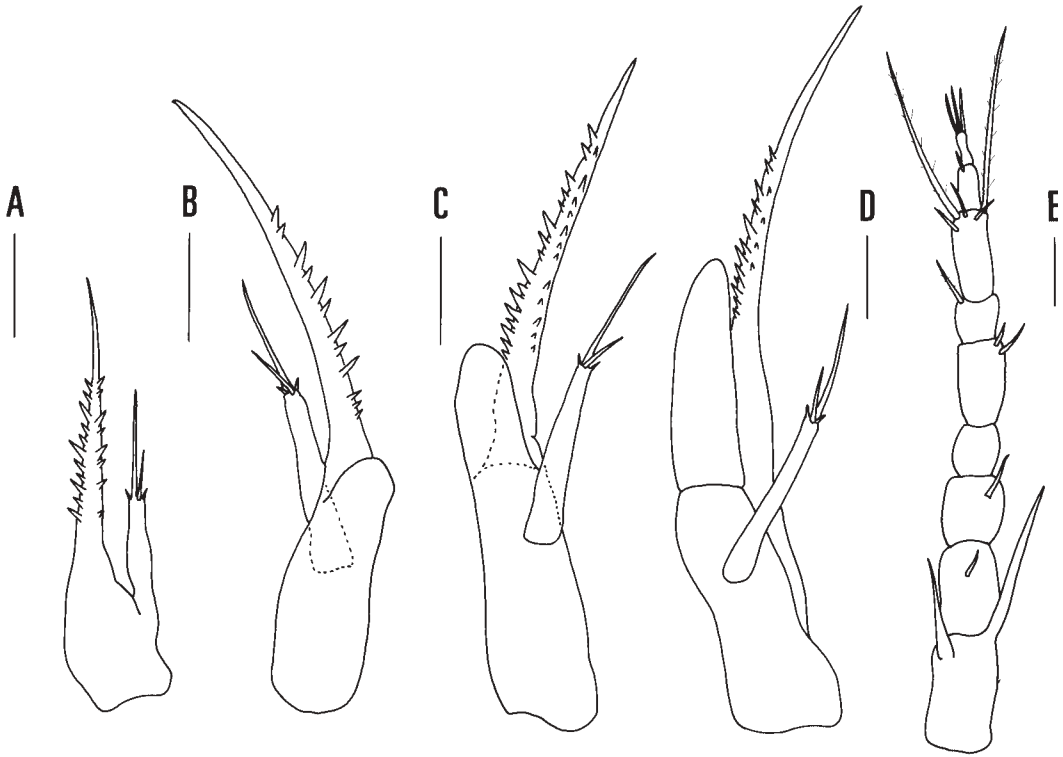


Fig. 4. *Armases angustipes* Dana, 1852, antenna. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa. Scale bars = 0.05 mm.

without setae. Pleopod buds present on somites 2–5, endopods absent. Otherwise unchanged.

Telson (Fig. 11C).—Unchanged.

Zoea IV

Dimensions.—Rdl: 1.30 ± 0.04 mm; cl: 0.71 ± 0.02 mm; cw: 0.89 ± 0.03 mm.

Carapace (Fig. 2B).—Four pairs of anterodorsal setae. Each ventral margin with 7 plumodenticulate setae. Otherwise unchanged.

Antennule (Fig. 3D).—Now biramous. Endopod bud present. Exopod unsegmented, with 1 basal seta, 6 aesthetascs (3 subterminal, 3 terminal), and 1 terminal seta.

Antenna (Fig. 4D).—Endopod 2-segmented, longer reaching middle of protopod length. Otherwise unchanged.

Mandible.—Palp bud present.

Maxillule (Fig. 5D).—Coxal endite with 7

plumodenticulate setae. Basial endite with 11 setae. Otherwise unchanged.

Maxilla (Fig. 6D).—Coxal endite bilobed, with 6 + 4 setae. Basial endite bilobed with 6 + 5 setae. Scaphognathite with 20 or 21 plumose marginal setae. Otherwise unchanged.

First Maxilliped (Fig. 7D).—Fifth segment of endopod with additional subterminal seta. Exopod distal segment with 10 long, plumose, natatory setae on distal segment. Otherwise unchanged.

Second Maxilliped (Fig. 8B).—Exopod distal segment with 10 long, plumose, natatory setae on distal segment. Otherwise unchanged.

Third Maxilliped (Fig. 9B).—Epipod rudiment now present.

Pereiopods (Fig. 10B).—Cheliped and pereiopods 2–5 slightly segmented.

Abdomen (Fig. 11D).—First somite with 3 long mid-dorsal setae. Pleopod buds elon-

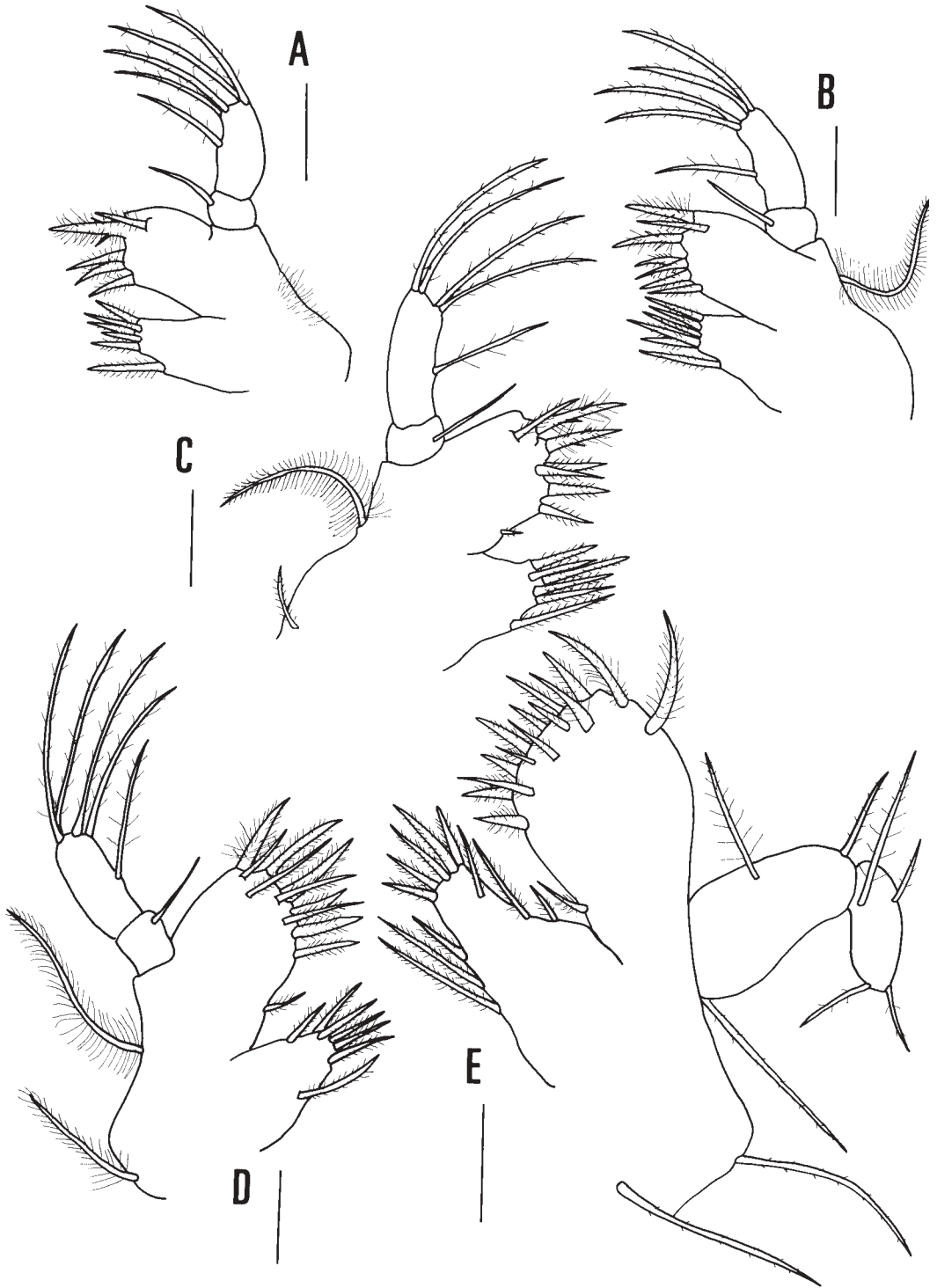


Fig. 5. *Armases angustipes* Dana, 1852, maxillule. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa. Scale bars = 0.05 mm.

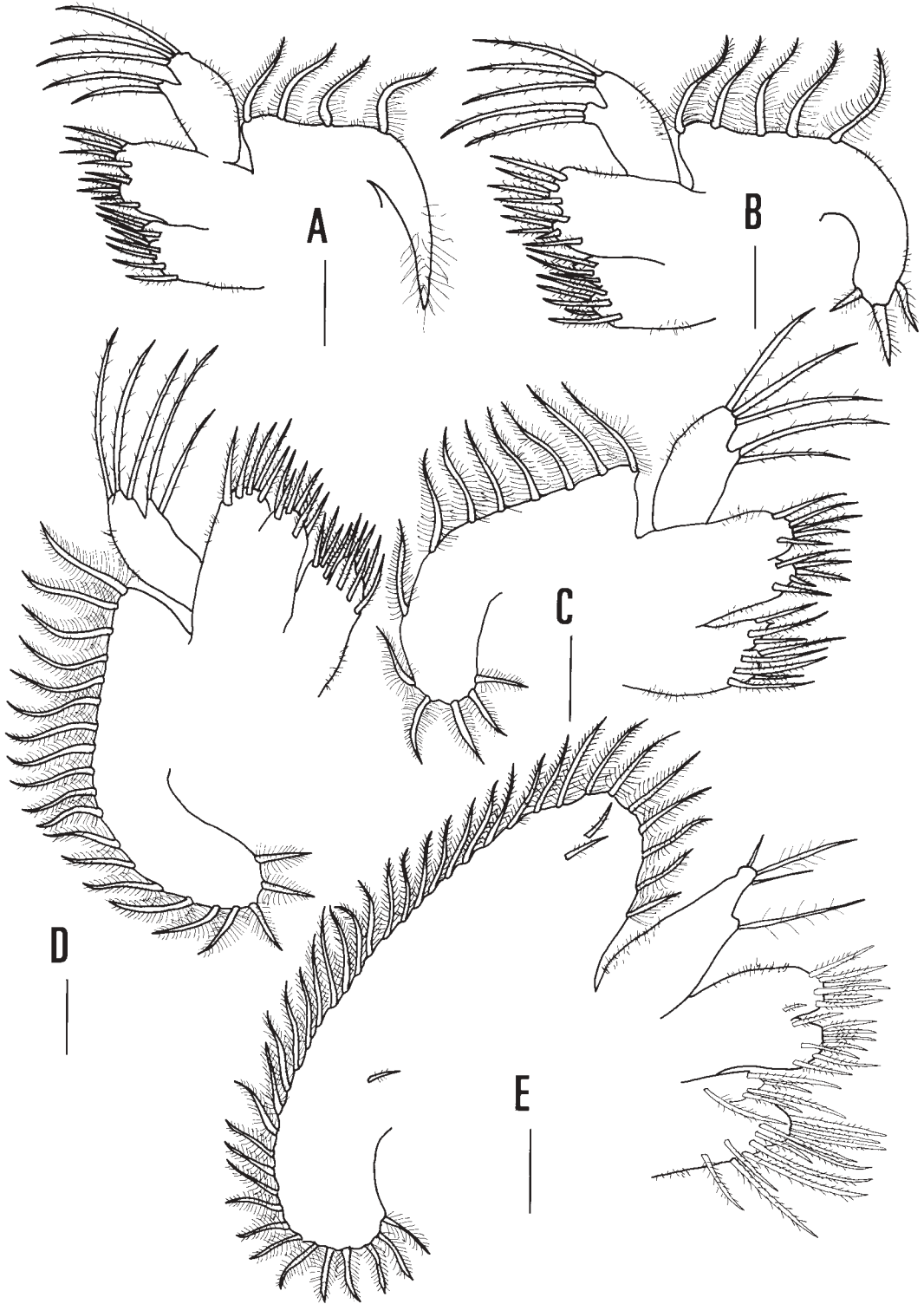


Fig. 6. *Armases angustipes* Dana, 1852, maxilla. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa. Scale bars = 0.05 mm.

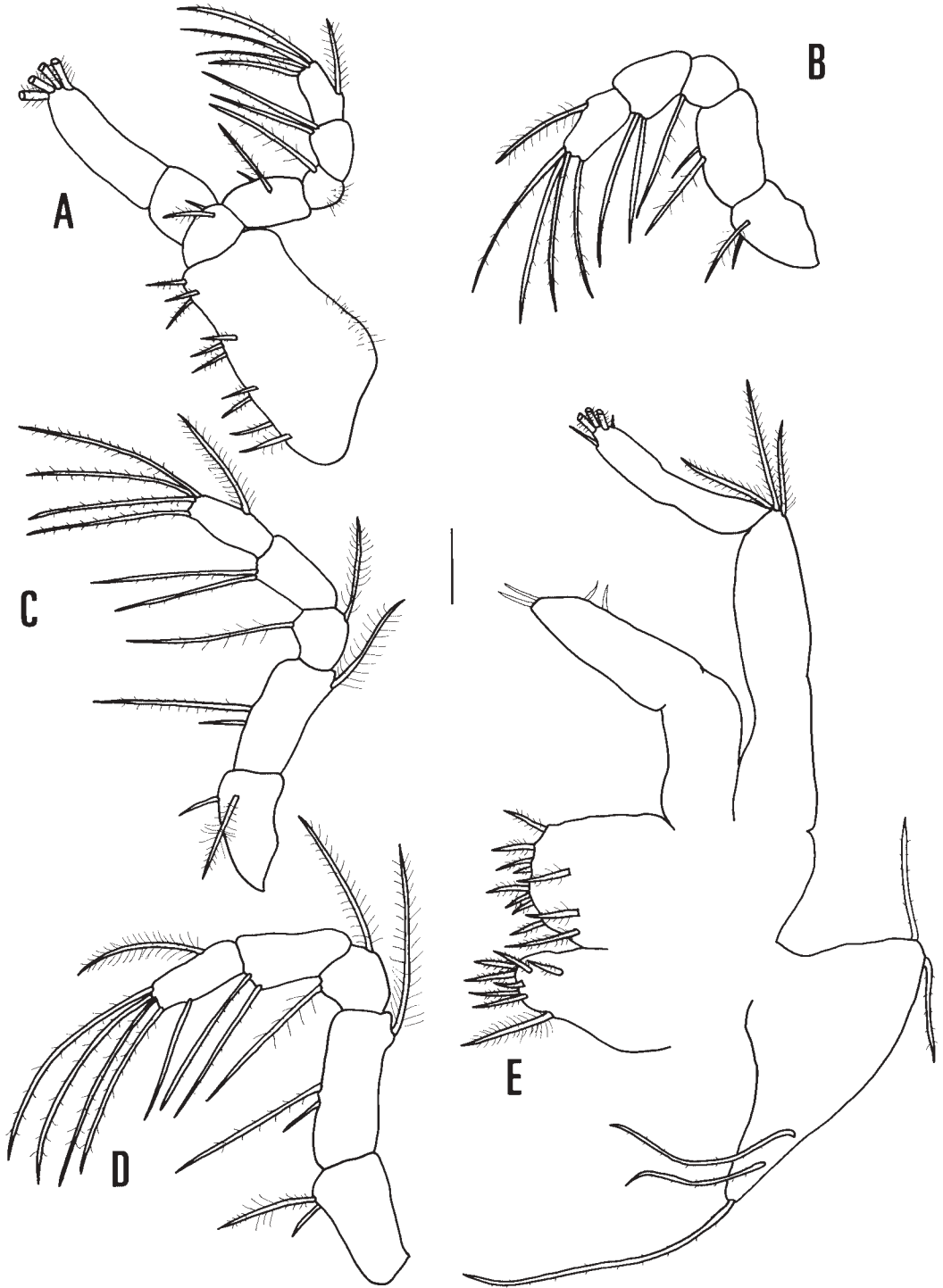


Fig. 7. *Armases angustipes* Dana, 1852, first maxilliped. A, Zoea I; B, Zoea II, endopod; C, Zoea III, endopod; D, Zoea IV, endopod; E, Megalopa. Scale bars = 0.05 mm.

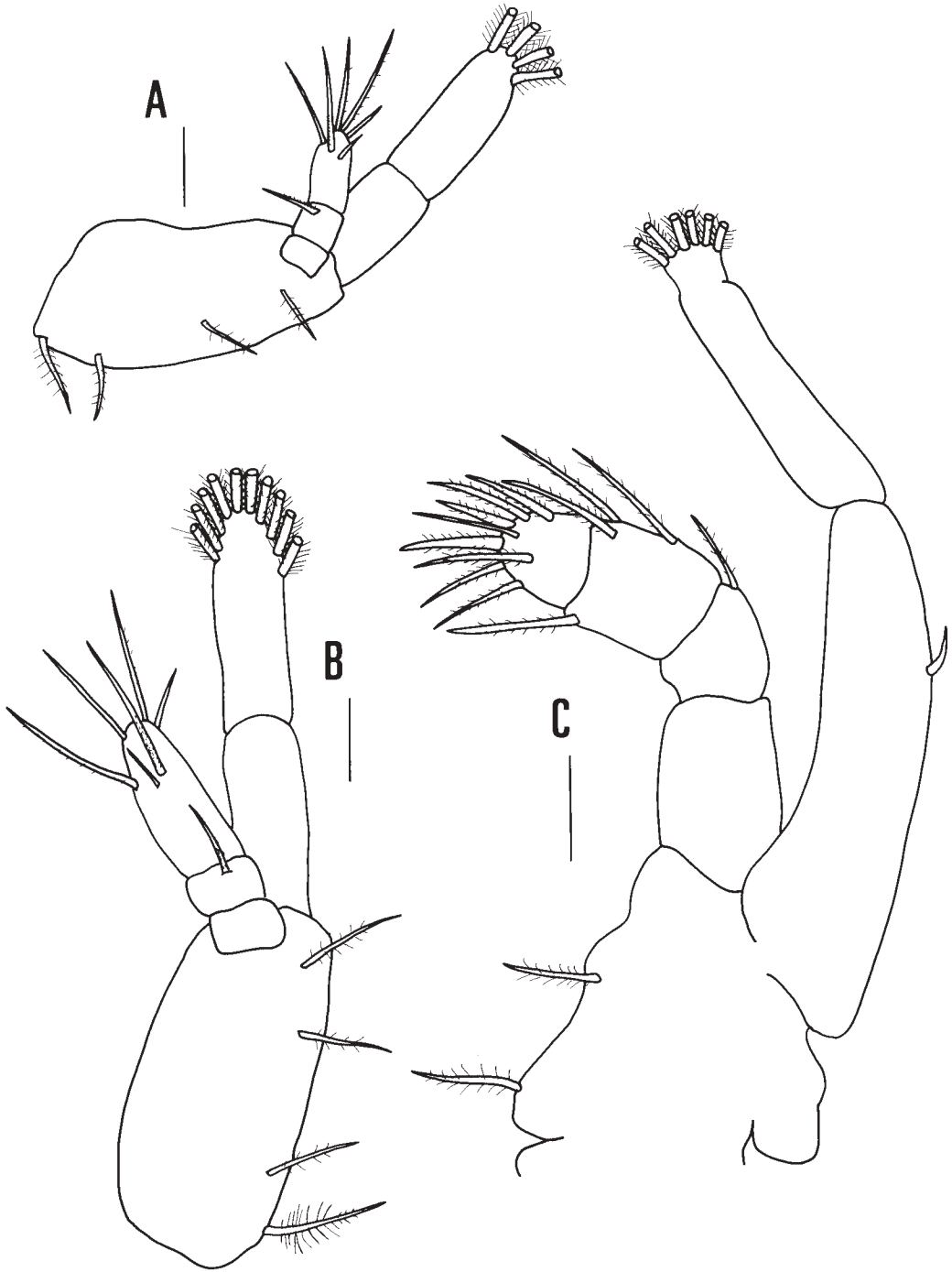


Fig. 8. *Armases angustipes* Dana, 1852, second maxilliped. A, Zoea I; B, Zoea IV; C, Megalopa. Scale bars = 0.05 mm.

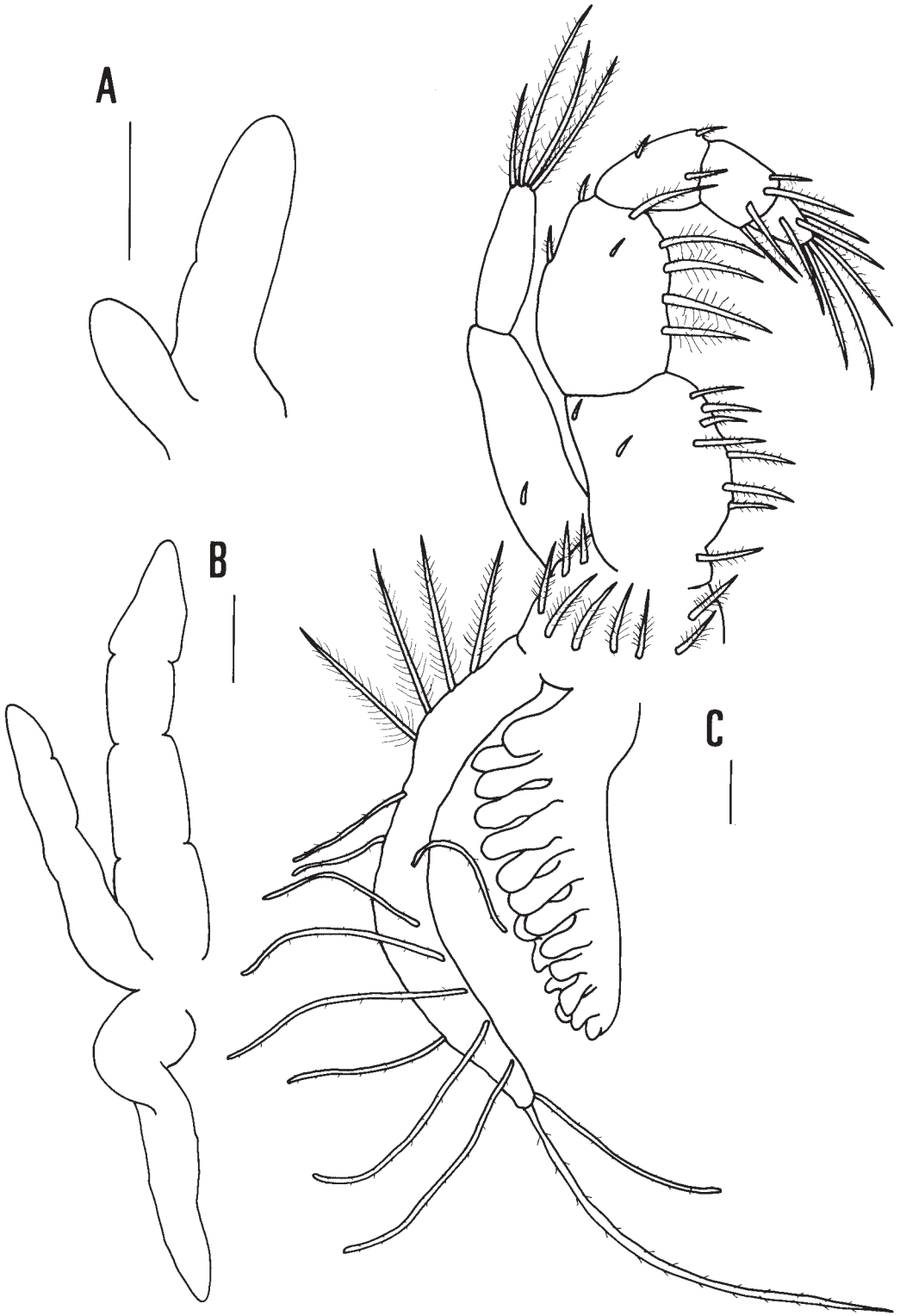


Fig. 9. *Armases angustipes* Dana, 1852, third maxilliped. A, Zoea III; B, Zoea IV; C, Megalopa. Scale bars = 0.05 mm.

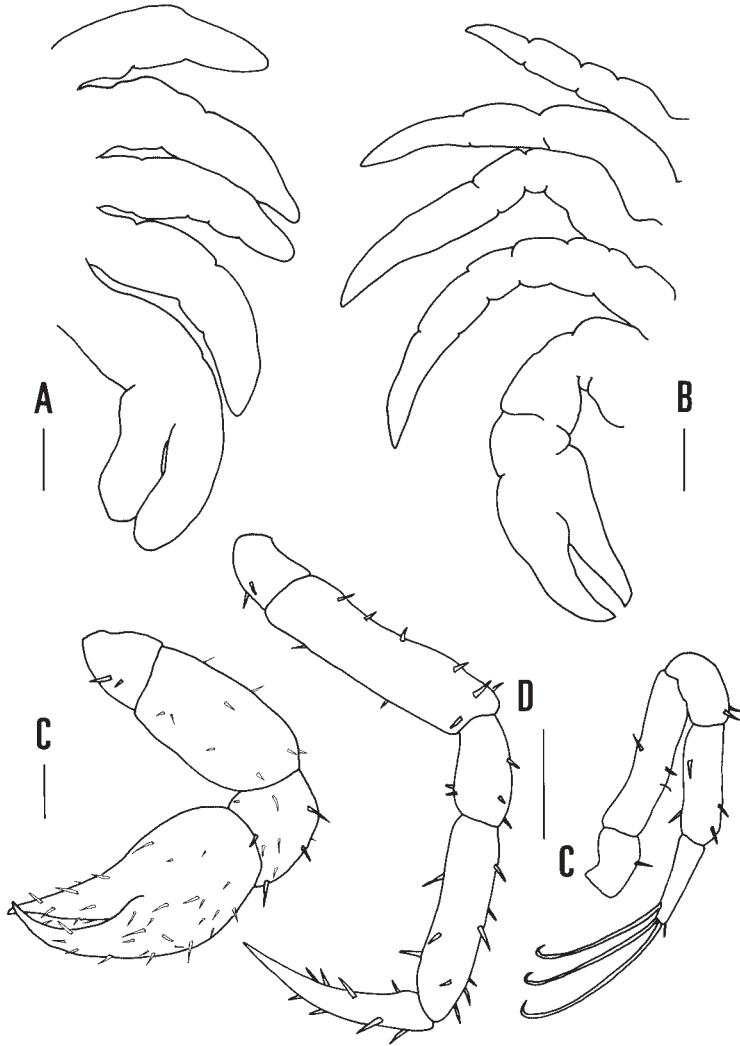


Fig. 10. *Armases angustipes* Dana, 1852, pereopods. A, Zoea III; B, Zoea IV; C, Megalopa, cheliped; D, Megalopa, third pereopod; E, Megalopa, fifth pereopod. Scale bars = 0.05 mm.

gated, endopod buds present. Otherwise unchanged.

Telson (Fig. 11D).—Unchanged.

Megalopa

Dimensions.—Cl: 0.66 ± 0.05 mm; cw: 0.48 ± 0.03 mm.

Carapace (Fig. 12A).—Longer than broad. Rostrum ventrally deflected (approximately 90°), with median cleft. Setal arrangement as figured.

Antennule (Fig. 3E).—Peduncle 3-segmented, with 4,1,1 setae respectively. Endopod absent.

Exopod 3-segmented, with 0, 6, and 3 aesthetascs respectively and 0,2,2 (1 terminal long, plumose seta) setae.

Antenna (Fig. 5E).—Peduncle 3-segmented, with 0,1,1 setae respectively. First segment retaining the exopod and modified protopod. Flagellum 6-segmented, with 0,2,1,5,1,3 setae respectively.

Mandible (Fig. 12B).—Palp 2-segmented, with 4 (1 subterminal, 3 terminal) setae on distal segment.

Maxillule (Fig. 5E).—Coxal endite with 11 setae. Basial endite with 15 setae. Endopod

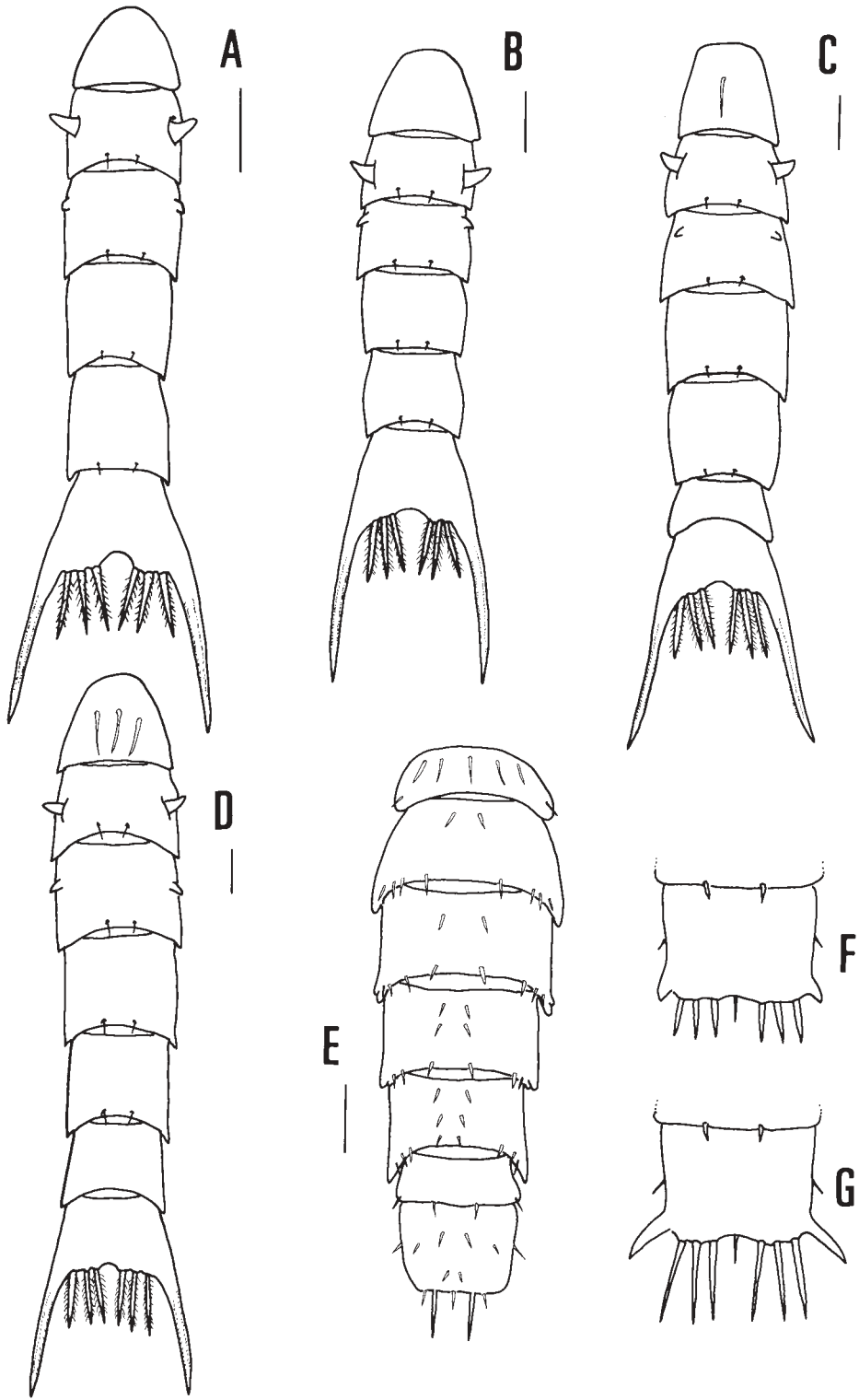


Fig. 11. *Armases angustipes* Dana, 1852, abdomen. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, modified telson; G, modified telson. Scale bars = 0.1 mm.

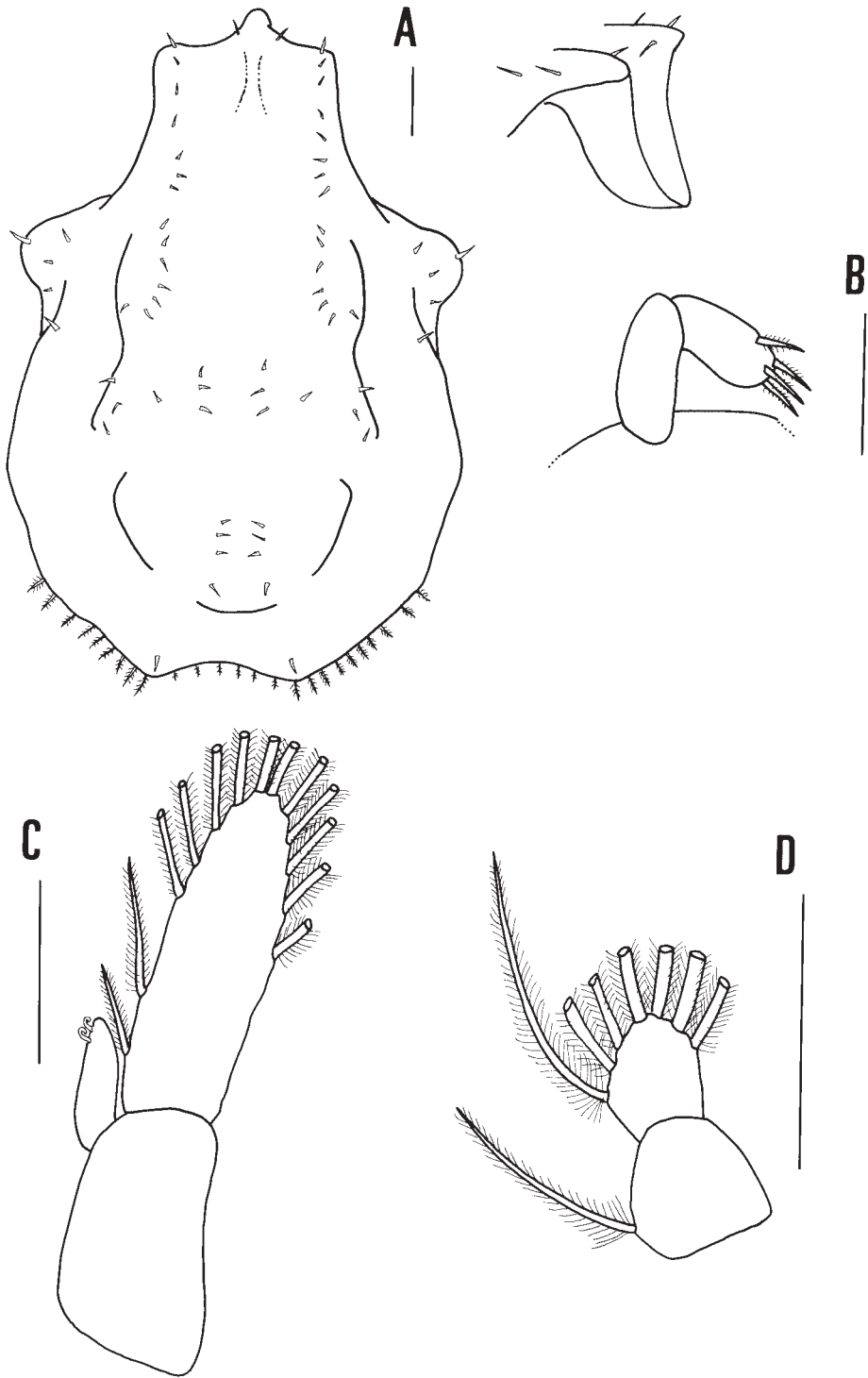


Fig. 12. *Armases angustipes* Dana, 1852, Megalopa. A, dorsal view of the cephalothorax and detail of lateral view of the rostrum; B, palp of the mandible; C, first pleopod; D, uropod. Scale bars = 0.1 mm.

2-segmented, proximal segment with 2 setae, distal segment with 4 setae (2 basal, 2 terminal).

Maxilla (Fig. 6E).—Coxal endite bilobed, with 11 (5 inner) + 5 (1 inner) plumodenticulate setae. Basial endite bilobed, with 8 (3 inner) + 7 (1 inner) plumodenticulate setae. Endopod unsegmented, with 1 long subterminal seta and 3 terminal setae. Scaphognathite with 39 plumose marginal setae and 2 anterior and 1 posterior lateral setae.

First Maxilliped (Fig. 7E).—Epipod with 5 long setae. Coxal endite with 8 plumodenticulate setae (3 inner). Basial endite with 11 plumodenticulate setae (3 inner). Endopod slightly 2-segmented, with 4 simple terminal setae. Exopod 2-segmented, proximal segment with 3 distal, long plumodenticulate setae, distal segment with 4 long, terminal, plumose feeding setae.

Second Maxilliped (Fig. 8C).—Epipod rudimentary. Coxa and basis not differentiated, with 2 setae. Endopod 4-segmented with 0,1,4,8 plumodenticulate setae respectively. Exopod 2-segmented, proximal segment with 1 medial seta, distal segment with 6 long, terminal, plumose feeding setae.

Third Maxilliped (Fig. 9C).—Epipod elongated with 15 long setae. Gill present. Coxa and basis not differentiated with 9 plumodenticulate setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 10, 8, 3, 4 and 6 (3 subterminal, 3 terminal) plumodenticulate setae respectively. Exopod 2-segmented, proximal segment with 1 simple basal seta and distal segment with 4 long terminal plumose raptatory setae.

Pereiopods (Fig. 10C–E).—All segments well differentiated and with setae as figured. Dactylus of fifth pereiopod with three long terminal setae and 1 short terminal spine (Fig. 10E).

Abdomen (Figs. 11E, 12C, D).—Six somites present. Somite 1 with 1 pair of lateral setae and 5 mid-dorsal simple setae. Setation on somites 2 to 6 as figured. Somites 2–5 each with pair of biramous pleopods, endopod unsegmented, with 3 terminal hooks, exopod unsegmented; pleopods 1–4 with 13,16,17,15 long marginal plumose natatory setae respectively. Uropods 2-segmented on somite 6, proximal segment with 1 and distal seg-

ment with 7 long, marginal, plumose natatory setae respectively.

Telson (Fig. 11E–G).—Shape square, with pair of lateral setae, 3 pairs of middle setae, and 2 long and 3 short setae on posterior margin. In several cases, telson with 3 pairs of long setae and 1 middle seta on posterior margin; furcal branches present in 2 different degrees of development (Fig. 11F, G).

DISCUSSION

Cuesta *et al.* (1999) compared larval characters and setation patterns of *Aratus* with those of *Armases* and showed differences between *A. angustipes* and *A. miersii*. However, these species also share some characters that distinguish them from the rest of the *Armases* species for which larval descriptions have become available: (a) the setation pattern of the endopod of the first maxilliped; (b) both species have six setae on the coxal endite of the maxillule, whereas the others have only five; (c) the antennal exopod has in both species four terminal simple setae, but there are two or three in the other *Armases* species.

A comparison of the previous description of the larval development of *A. angustipes* (Kowalczyk, 1994) and the present results is given in Table 2. The setation of the carapace was not described by Kowalczyk (1994) and therefore this character cannot be compared here; a detailed description is given above (see text and figures). Hence, this character is not included in Table 2. An important difference was found in the setation of the antennal exopod, which has two or three terminal setae in Kowalczyk's material but four in the present material. Within the genus *Armases*, this character is shared only with *A. miersii*. Another important difference was observed on the inner surface of the scaphognathite of the megalopal maxilla. In the present study, two setae were observed on the anterior and one seta on the posterior area; the latter was not described by Kowalczyk (1994). This is significant insofar as the setation (2 + 1) is a typical character which allows one to distinguish sesarmid megalopae from all other grapsoid megalopae (Cuesta, 1999). Further differences show intraspecific variation in the setation of various appendages.

Most of the megalopa characters described in the present study for *A. angustipes* showed

Table 2. Morphological differences between larval-development descriptions of *Armases angustipes* given by Kowalczyk (1994) and in the present study. Abbreviations: s, setation; a, aesthetasc; seg., segment; dlp, dorsolateral processes; en, endopod; ep, epipod; ex, exopod.

	<i>Armases angustipes</i> (Kowalczyk, 1994)	<i>Armases angustipes</i> (present study)
ZOE A I		
Antenna		
Exopod s	2–3	4
Third maxilliped	No data	Small buds
Pereiopods	No data	Small buds
Abdomen dlp	Somite 2	Somites 2 and 3
ZOE A II		
Antennule a + s	3 + 2	4 + 1
Antenna		
Exopod s	2–3	4
Maxilla		
Scaphognathite s	5 + 2	5 + 3
Third maxilliped	No data	Elongated buds
Pereiopods	No data	Elongated buds
Abdomen		
Somite 1°	1 long mid-dorsal seta	mid-dorsal seta not present
ZOE A III		
Antennule a + s	3 + 1	3 + 2
Antenna		
Exopod s	2–3	4
Maxilla		
Basial endite s	5 + 4	5 + 5
Scaphognathite s	11–15	13
Third maxilliped	No data	Elongated buds
Pereiopods	No data	Elongated buds
ZOE A IV		
Antennule a + s	6 + 1	6 + 2
Antenna		
Exopod s	2–3	4
Maxilla		
Basial endite s	5–6 + 4–6	6 + 5
Scaphognathite s	19–23	20–21
First maxilliped		
Exopod s	9	10
MEGALOPA		
Antennule		
peduncle s	5, 1, 1	4, 1, 1
Antenna		
peduncle s	0, 1, 1	0 (exopod + protopod), 1, 1
flagellum s	0, 3, 1, 5, 1, 2	0, 2, 1, 5, 1, 3
Maxillule		
Coxal endite s	13	11
Basial endite s	18	15
Maxilla		
Basial endite s	8 + 6	8 + 7
Endopod s	unarmed	1, 3
Scaphognathite margin s	34–37	39
Scaphognathite inner s	2	2 + 1
First maxilliped		
Endopod s	unarmed	2, 2
Exopod s	3, 3	3, 4
Epipod s	7	5
Second maxilliped		
Endopod s	0, 1, 3, 6	0, 1, 4, 8
Exopod s	1, 5	1, 6
Third maxilliped		
Protopod s	10	9
Endopod s	9, 8, 4, 4, 5	10, 8, 3, 4, 6
Exopod s	1, 5	1, 4
Epipod s	16	15

morphological peculiarities that differ clearly from those described by Kowalczyk (1994). The characters all represent remnants of zoeal morphology: (1) the first segment of the antennular peduncle has a rudimentary exopod and protopod; (2) the endopod of the maxilla is bilobed and with similar setation as in the zoeas (but with setation 1,3 instead of 2,3); (3) the telson shows a rudimentary furca and three pairs of serrulate setae on the posterior margin. The other morphological and meristic characters showed no important differences to Kowalczyk's description.

Similar traits were found also in the megalopae of two other American sesarmid species. The megalopae of *Aratus pisonii* (as described by Warner, 1968) and *Sesarma reticulatum* (see Costlow and Bookhout, 1962) showed the same remaining zoeal characters. In the case of *Aratus pisonii* the first segment of the antennular peduncle retained only the protopod, and the megalopa showed a small dorsal spine on the cephalothorax. The megalopa of *S. reticulatum* had an exopod on the first segment of the antennular peduncle, and it retained a long and straight rostral spine on the cephalothorax instead of the normally short and ventrally deflected rostrum. In both species, the megalopae have on the endopod of the maxillule the same morphology and setation as in the zoeal stages (2-segmented, setation: 1,1 + 2 + 2).

The retainment of zoeal characters in the megalopa is difficult to explain, if this is a species-specific trait. Because retarded development of morphology of decapod larvae has been shown to occur especially under conditions of stress, the incidence of such characters in *A. angustipes* and some related species might indicate some unfavorable factors in the respective cultures or, in our material, maybe stress exerted during the long transport of egg-bearing females from Brazil to Europe. This question remains unresolved until not only more inter-, but also more intraspecific morphological comparisons between hatches, populations, and treatments become available.

Comparing the larval morphology of American Sesarmidae, we found clear differences between *Sesarma*, *Aratus*, and *Armases*. Not included in this comparison was *Metopaulias* because it presents an abbreviated development with strongly modified larval morphology (see recent comparison in Anger et

al., 1995, and Schubart and Cuesta, 1998). In the first zoeal stage of *Armases* and *Aratus*, the ratio FL/BT (FL: furcal length, BT: base of telson length) is < 1.9 , but > 2.0 in *Sesarma* species. First zoeas of *Sesarma* have longer furcal branches than in *Armases* and *Aratus*. In the megalopa stage of *Armases* and *Aratus*, a uropod setation of 1,7 was found, whereas *Sesarma* has 1,6. The similarity in these characters support the presumably close relationship between the genera *Armases* and *Aratus*. At present, the larval development remains unknown for 15 American *Armases* and *Sesarma* species; it is thus possible that this apparently typical suite of characters must later be re-evaluated when more descriptions become available.

ACKNOWLEDGEMENTS

The second author thanks Prof. Dr. G. S. Moreira and the staff of the Centro de Biologia Marinha at São Sebastião (CEBIMar) for an invitation, kind hospitality, and support as a visiting scientist, as well as the German Academic Exchange Service, DAAD (Bonn), and the Coordenadoria de Aperfeiçoamento de Pessoal do Ensino Superior, CAPES (Brasília), for financial support. Dr. D. Ismael helped to search for and eventually discovered the ovigerous *A. angustipes* that rendered this study possible. Kim Riesebeck provided technical assistance in the rearing experiments on Helgoland. We are grateful to Paul Clark and two anonymous referees for their comments and criticism that clearly improved the manuscript.

LITERATURE CITED

- 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 Contributions to Zoology 527: 1–60.
- Anger, K., J. Harms, M. Montú, and C. de Bakker. 1990. Effects of salinity on the larval development of a semi-terrestrial tropical crab, *Sesarma angustipes* (Decapoda: Grapsidae).—Marine Ecology Progress Series 62: 89–94.
- , D. Schreiber, and M. Montú. 1995. Abbreviated larval development of *Sesarma curacaoense* (Rathbun, 1897) (Decapoda: Grapsidae) reared in the laboratory.—Nauplius 3: 127–154.
- Clark, P. F., D. K. Calazans, and G. W. Pohle. 1998. Accuracy and standardization of brachyuran larval descriptions.—Invertebrate Reproduction and Development 33: 127–144.
- Costlow, J. D., Jr., and C. G. Bookhout. 1960. The complete larval development of *Sesarma cinereum* (Bosc) reared in the laboratory.—Biological Bulletin 118: 203–214.
- , and ———. 1962. The larval development of *Sesarma reticulatum* Say reared in the laboratory.—Crustaceana 4: 281–294.
- Cuesta, J. A. 1999. Morfología larval de la familia Grapsidae (Crustacea, Decapoda, Brachyura).—Ph.D. thesis. University of Seville. 291 pp.

- , M. Schuh, R. Diesel, and C. D. Schubart. 1999. Abbreviated development of *Armases miersii* (Grapsidae: Sesarminae), a crab that breeds in supralittoral rock pools.—*Journal of Crustacean Biology* 19: 26–41.
- Dana, J. D. 1852. Crustacea, Part 1. *In*: United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. Philadelphia, v. 13. 685 pp.
- Díaz, H., and J. J. Ewald. 1968. A comparison of the larval development of *Metasesarma rubripes* (Rathbun) and *Sesarma ricordi* H. Milne Edwards (Brachyura, Grapsidae) reared under similar laboratory conditions.—*Crustaceana Supplement* 2: 225–248.
- Fransozo, A., J. A. Cuesta, and M. L. Negreiros-Fransozo. 1998. First zoeal stage of two species of Grapsidae (Decapoda, Grapsidae) and a key to such larvae from the Brazilian coast.—*Crustaceana* 71: 331–343.
- Kowalczyk, V. G. L. 1994. Estrutura populacional de *Armases angustipes* (Dana, 1852) (Decapoda: Brachyura: Grapsidae) da Ilha do Farol, Caiobá, PR e seu desenvolvimento pos-embriônico sob condições de laboratório.—M.Sc. Dissertation, Universidade Federal do Parana, Curitiba, PR, Brazil.
- Niem, V. H. 1996. Phylogenetic relationships among American species of *Sesarma* (subgenus *Armases*) (Brachyura, Grapsidae).—*Crustaceana* 69: 248–330.
- Schubart, C. D., and J. A. Cuesta. 1998. The first zoeal stages of four *Sesarma* species from Panama, with identification keys and remarks on the American Sesarminae (Crustacea: Brachyura: Grapsidae).—*Journal of Plankton Research* 20: 61–84.
- , ——, R. Diesel, and D. L. Felder. 2000. Molecular phylogeny, taxonomy, and evolution of non-marine lineages within the American grapsoid crabs (Crustacea: Brachyura).—*Molecular Phylogenetics and Evolution* 15: 179–190.
- Warner, G. F. 1968. The larval development of the mangrove tree crab *Aratus pisonii* (H. Milne-Edwards) reared in the laboratory (Brachyura, Grapsidae).—*Crustaceana Supplement* 2: 249–258.

RECEIVED: 29 February 2000.

ACCEPTED: 29 January 2001.