The larval development of the red mangrove crab *Sesarma meinerti* de Man (Brachyura: Grapsidae) reared in the laboratory

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The larval stages of the red mangrove crab *Sesarma meinerti* de Man were reared in the laboratory. Larval development consists of five zoeal stages and one megalopa. Zoeal development lasts an average of 25 days at 25°C. The external morphology of larvae is described in detail and their relationship with larvae of congeneric species is briefly discussed.

Die larwale stadia van die rooi krap *Sesarma meinerti* de Man is in die laboratorium ondersoek. Larwale ontwikkeling bestaan uit vyf zoea-stadiums en een megalopa. Ontwikkeling van zoea duur gemiddeld 25 dae teen 25°C. Die eksterne morfologie van larwes word in detail beskryf en hulle verhouding met larwes van gelykslagtige spesies word kortliks bespreek.

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The genus *Sesarma* Say (Brachyura: Grapsidae: Sesarminae) is the largest among southern African grapsid crabs and includes eight species (Barnard 1950; Kensley 1981). These are mostly euryhaline marine species and, together with some ocypodids (e.g. *Dotilla, Uca, Macrophthalmus,* and *Cleistostoma*), dominate the epibenthic fauna of subtropical and temperate estuaries on the south and east coasts of South Africa (Day 1981). Larvae of most of these crabs are present in the plankton of the mangrove estuaries of the Transkei coast (Figure 1). After copepods they are the most abundant invertebrate group during the late spring and summer months (unpubl. pers. obs.). Yet identification of these larvae beyond family level is almost always impossible, since there are no published reports on their morphology. Of all *Sesarma* species present in the area, only the larval stages of *Sesarma catenata* Ortmann have been previously described (Pereyra Lago 1987). In the present paper the larval stages of the red mangrove crab *Sesarma meinerti* de Man are described from laboratory-reared specimens, and comments are made on their morphological affinities with other larval grapsids.

Material and Methods

Ovigerous females of *Sesarma meinerti* were collected at the upper intertidal zone of the mangrove swamps fringing the Mntafufu River estuary (Figure 1). Females were kept separately in the laboratory in circulating sea water tanks (36‰ salinity) under a 12:12 L:D light cycle. Immediately after hatching larvae were transferred to 25 ml glass dishes filled with culture water (35‰ salinity, 25°C temperature, micropore-filtered and UV-irradiated sea water) in numbers of 10 larvae per dish. Lighting conditions were similar to those of adult females. Larvae were fed newly hatched (less than 6 h old) *Artemia* sp. nauplii. Every 24 h water was renewed in the cultures, fresh food added and larvae were examined under a binocular microscope to check for moulting and remove dead specimens.

Specimens used for illustration were anaesthetized with $MgCl_2$ and fixed in buffered 4% formalin. Larvae were dissected in 25% lactic acid and placed in excavated slides in a drop of the same solution for drawing. Illustrations were made with the aid of a camera lucida attached to a compound microscope. All features illustrated belonged to the same specimen. This specimen was selected from among five others examined from three different broods (two specimens each) and showed the characteristics most commonly encountered in the

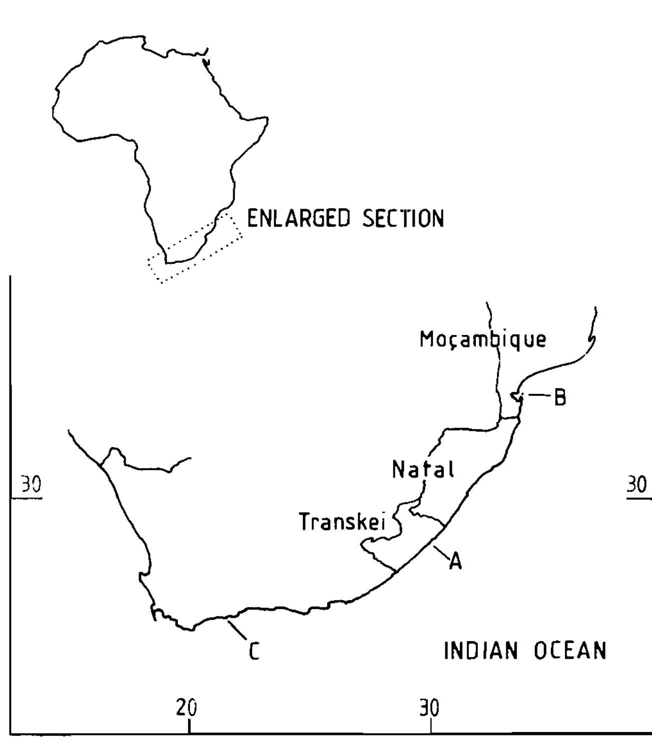

Figure 1 A = Mntafufu River: locality of collection of ovigerous females. B = Inhaca island. C = Breede River.

sample. Measurements were made with an ocular micrometer according to Webber & Wear (1981). Illustrations follow Rice's (1979) standards. All other methods, as well as construction of tables were similar to those used previously by the author (Pereyra Lago 1987, 1988).

Results

The larval development of *Sesarma meinerti* consists of five zoeae and one megalopa stages. Larval life span and survival in the cultures are shown in Figure 2. Measurements of zoeal morphological features are summarized in Table 1. Segmentation and setation of appendages of zoea and megalopa stages are listed in Tables 2 and 3 respectively.

First zoea (Figure 3A, 4A–H)

Carapace subtriangular, smooth, extended postero-laterally. Dorsal spine short, tapering evenly to a point and extending posteriorly; its outline rather straight with downbent distal section. Rostral spine straight, directed downwards and slightly forward. Lateral spines absent.

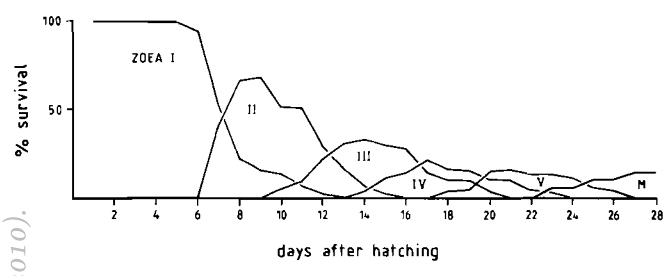

Figure 2 Survival of *Sesarma meinerti* larvae reared in the laboratory at 25°C and 35‰ salinity. Initial n = 100.

Table 1 Measurements of morphological features of *Sesarma meinerti* zoeal stages. CL = carapace length. DL = length of dorsal spine. RL = length of rostral spine. DRL = distance from tip of dorsal spine to tip of rostral spine. LTC = length of left telson cornua. AP = length of antennal protopodite. AEn = length of antennal endopodite. AEx = length of antennal exopodite. All measurements are means (n = 6) and are expressed in mm

	Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V
CL	0,41	0,51	0,57	0,70	0,78
DL	0,19	0,28	0,34	0,40	0,43
RL	0,13	0,21	0,25	0,37	0,41
DRL	0,67	0,84	1,08	1,36	1,42
LTC	0,19	0,21	0,25	0,30	0,33
AP	0,12	0,15	0,16	0,21	0,25
AEn	—	—	bud	0,05	0,12
AEx	0,03	0,07	0,08	0,10	0,12
DL/CL	0,46	0,54	0,59	0,57	0,55
RL/CL	0,31	0,41	0,43	0,52	0,52
AEn/AP	—	—	—	0,23	0,48
AEx/AP	0,25	0,46	0,50	0,47	0,47

One small seta present dorsally at base on either side of dorsal spine and two setae present frontally above the eyes. Eyes sessile. Antennal protopodite extending over the same length as rostral spine. Abdomen with five somites plus telson. Somites 2–3 as broad as long; somites 4–5 longer than broad. Postero-lateral margins of somites 1–5 with sharp-pointed, broad-based projections. One pair of dorso-lateral knobs present on somites 2 and 3. One pair of small setae present dorsally on posterior margin of somites 2–5. Telson with two strong, straight cornua slightly bent dorsally on distal section (Figure 4H). Postero-medial margin with median notch and three pairs of spines fringed laterally with spinules. Dorsal surface of cornua with two rows of small teeth. Setation of appendages as in Figure 4 and Table 2.

Second zoea (Figure 3B, 5A–I)

Carapace subtriangular and smooth. One pair of setae now present mid-frontally about half way between the eyes and dorsal spine. One sparsely plumose seta present on each postero-lateral margin. Eyes slightly stalked. Abdomen as in previous stage except for: (a) one seta present medially on dorsal surface of somite 1, and (b) middle and distal sections of telson cornua covered ventrally with minute spinules (Figure 5I). Setation of appendages as in Figure 5 and Table 2.

Third zoea (Figure 3C, 6A–G)

Carapace subtriangular. One pair of sparsely plumose setae present on each postero-lateral margin. Eyes fully stalked. Antennal protopodite not reaching the tip of rostral spine. Buds of third maxilliped and pereiopods 1–5 present underneath carapace. Abdomen with six somites plus telson. Sixth somite shorter than broad with smooth postero-lateral margins. Small pleopod buds present on somites 2–4. Telson morphology as in second zoea. Setation of other appendages as in Figure 6 and Table 2.

Fourth zoea (Figures 3D, 7A–G)

Carapace subcircular and smooth. Five pairs of small setae present on dorsal and frontal sections as illustrated in Figure 3D. Five sparsely plumose setae present on either postero-lateral margins. Third maxilliped and pereiopods 1–5 further developed, protruding from underneath the carapace. Epipodite buds of pereiopods 1–3 appearing beneath the carapace. Abdomen with six somites plus telson. Pleopod buds on somites 2–5 further developed and partially segmented laterally. Pleopod buds on somite 6 present. Somite 6 with small, blunt postero-lateral projections. Telson morphology unchanged from previous zoeae. Setation of other appendages as in Figure 7 and Table 2.

Fifth zoea (Figure 3E, 8A–G)

Carapace subcircular. Several pairs of small setae present on frontal and dorsal surfaces as illustrated (Figure 3E). Dorsal spine now more evenly curved than in previous zoeae, its distal section is not noticeably bent downwards. Pereiopods 1–5 well developed but not yet

Table 2 Segmentation and setation of appendages of *Sesarma meinerti* zoeal stages. A = aesthetasc, S = simple, D = denticulate, PD = plumodenticulate, P = plumose, SP = sparsely plumose, HP = highly plumose, pdt = PD terminal, dt = D terminal. All symbols except 'A' refer to setae

	Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V
Antennule					
Terminal	3A,1S	3A,1S	4A,1S	3A,1S	3A,1S
Subterminal	0	1A	0	1S	1S
Antenna					
Protopodite	2 rows teeth	idem	idem	idem	idem
Exopodite	2S + 2 teeth	idem	idem	idem	idem
Endopodite	absent	absent	bud	= ⅓ prot.	= ½ prot.
Maxillule					
Coxopodite	0	1HP	1HP	1HP	1HP
Basal end.	2D,3PD	4D,3PD	2D,5PD	7D,3PD,1S	7D,3PD,1S
Coxal end.	5PD	1D,4PD	1D,4PD	6PD	3D,4PD
Endopodite prox.seg.	1S	1S	1S	1S	1SP
dist.seg.	4SP,1S	4SP,1S	3SP,2SPpdt	3SP,2SPpdt	3SP,2SPpdt
Maxilla					
Basal endite prox.	4PD + 1S	4PD	5PD	5PD	7PD
dist.	4PD	4PD	4PD	5PD	6PD
Coxal endite prox.	5PD	5PD	5PD	5PD	7PD
dist.	3PD	3PD	3PD	3PD	3PD
Endopodite prox.	1S,1SP	1SP,1SPpdt	2SP	2SP	1SP,1SPpdt
dist.	2SP,1S	3SP	2SPpdt,1SP	2SP,1SPpdt	2SP,1SPpdt
Scaphognathite	4HP	8HP	10HP	11HP	21HP
First maxilliped					
Basipodite	8S,2SPpdt	8S,1SP,1SPpdt	9SP,1S	8SP,2S	8SP,2S
Endopodite prox.seg.	2S	2S	1S,1SP	1SP,1S	2SP
2 seg.	1S,1SP	1S,1SP	1S,1SP	1S,1SP	2SP
3 seg.	1P	1SPpdt	1SP	1SP,1P	1SP,1S
4 seg.	1SP,1SPpdt	2SP	1SP,1S	1SP,1S	1SP,1Pdt
5 seg.	4SPpdt,1SP	4SP,1SPpdt	5SP	1P,2SP,3SPpdt	3SP,2SPpdt
Exopodite	4P	6P	8P	10P	11P
Second maxilliped					
Basipodite	2SPpdt,2S	2S,1SPpdt,1PD	4SP	3SP,1S	1SP,3SPpdt
Endopodite prox.seg.	0	0	0	0	0
2 seg.	1PD	1PD	1SP	1PD	IPD
3 seg.	5S,1PD	5S,1PD	5S,1PD	5S,1PD	4S,2PD
Exopodite	4P	6P	8p	10P	11P

segmented. Third maxilliped (not illustrated in Figure 8) appearing as an unsegmented, three-lobed structure. Abdomen with six somites plus telson. Sixth somite longer than broad, with sharp postero-lateral projections and two small pleopod buds. Pleopods on somites 2–5 well developed, showing endopodite bud. One long medial and two shorter lateral sparsely plumose setae now present dorsally on somite 1. Telson morphology unchanged. Setation of other appendages as in Figure 8 and Table 2.

Megalopa (Figure 9, 10)

Carapace subrectangular and smooth. Anterior region broad with convex or wide-angled frontal edge, ending in a small rostrum bent downwards (Figure 9A). Orbicular edge wide and smooth with two rounded postero-lateral angles. Posterior edge with a number of small setae (25–39). Eyes stalked. Abdomen with six somites plus telson. Somites 3–5 with posterior sharp-pointed ventro-lateral projections; in somite 5 reaching ⅔ the length of somite 6 (Figure 9B). Sixth somite with smooth and rounded posterior margins. Pleopods well developed. Endopodite about ⅕ length of exopodite, with two hook-like setae disto-laterally. Exopodite bearing 14, 13, 13, 11 plumose setae on pleopods 1, 2, 3, 4 respectively (Figure 9I). Telson oval-shaped with smooth edges. Two small notches present on each side of posterior margin (Figure 9C). One highly plumose seta present medially on posterior margin. Uropods bisegmented. One short lateral plumose seta present externally on proximal segment. Six plumose setae on terminal segment (Figure 9C). Setation of other appendages as in Figure 9 and 10, and Table 3.

Table 3 Segmentation and setation of appendages of *Sesarma meinerti* megalopa larvae. All symbols as in Table 2

Antennule	Peduncle	2SP+1S,1S,1S
	Terminal flagellum prox. seg.	0
	2 seg.	6A + 1S
	3 seg.	5A + 1S
Antenna	prox. seg.	0
	2 seg.	1S
	3 seg.	1S
	4 seg.	0
	5 seg.	2S
	6 seg.	1S
	7 seg.	2S,2D
	8 seg.	1S
	9 seg.	3S
Maxillule	Basal endite	18PD
	Coxal endite	13PD
	Endopodite	3SP,3S
	Basipodite	3SP
Maxilla	Basal endite prox.	6PD
	dist.	5PD + 1S
	Coxal endite	13PD
	Endopodite	0
	Scaphognathite	33HP + 3S
First maxilliped	Basal endite	11PD
	Coxal endite	6PD,1S
	Endopodite	1S
	Exopodite prox. seg.	2HP
	dist. seg.	3P
	Epipodite	5SP
Second maxilliped	Endopodite prox. seg.	0
	2 seg.	1P
	3 seg.	3PDdt
	4 seg.	3PDdt,1PD,2S
	Exopodite prox. seg.	1S
	2 seg.	5P
Third maxilliped	Endopodite prox. seg.	6PD,1S
	2 seg.	5PDdt,3S
	3 seg.	3S,1PDdt
	4 seg.	3PDdt,1S
	5 seg.	7PDdt
	Exopodite prox. seg.	0
	2 seg.	4P
	Epipodite prox.	3SP
	dist.	9SP
	Basipodite	8PD

Discussion

Wear (1970) distinguished four groups of grapsid zoea larvae using as diagnostic characters: presence of lateral carapace spines, shape and length of the dorsal spine, and relative length of the antennal protopodite and exopodite. Two of these groups were homogeneous and included all the then known larvae of subfamilies Plagusinae and Grapsinae. The other two groups are more heterogeneous and share taxa from subfamilies Sesarminae and Varuninae.

The validity of this grouping has been questioned ever since two grapsids, *Pachygrapsus crassipes* (Grapsinae) (Schlotterbeck 1976) and *Cyclograpsus cinereus* (Sesarminae) (Costlow & Fagetti 1967) were reported to acquire lateral carapace spines from the second zoea onwards, and a third species, *Helice leachi* (Sesarminae), possibly on the fourth and fifth zoea (Baba, Fukuda & Nakasone 1984). However, analysing zoeal features not dealt with by Wear (1970), Rice (1980) comfirmed this basic division as useful and meaningful.

Rice (1980) grouped the genus *Sesarma* together with *Metasesarma* and *Chiromantes*. These taxa all possess 3 + 2 setae on the endopodite of the maxilla, almost always 3 pairs of posterior telson spines throughout zoeal development, and lack lateral carapace spines. Comparison of the setation pattern of larval appendages (first zoea and megalopa) of *Metasesarma* (2 spp.), *Chiromantes* (1 sp.) and *Sesarma sensu lato* (9 spp.) (including genera *Bresedium* and *Sesarmops)* (Pereyra Lago 1987) revealed a very similar larval morphology. Common features among most larvae studied were: 7–8,9 setae on the endites of the maxilla of the first zoea, and the setal formula 0, 1, 3, 6 in the endopodite of the second maxilliped of the megalopa in all but two species of *Sesarma* and *Metasesarma* (Pereyra Lago 1987, Tables 5 & 6). This analysis, although taking into account a large number of larval features, did not suggest, however, generic differences in larval morphology.

The setation pattern of cephalothoraxic appendages of *Sesarma meinerti* larvae closely resembles that of other *Sesarma*, *Metasesarma* and *Chiromantes* species. As pointed out by Rice (1980), appendage setation in brachyuran larvae is an evolutionary conservative character, revealing close links within and among families which differ considerably in general appearance. On the other hand, more conspicuous and easily observable characters (e.g. carapace spines and spine complement of the telson), although useful to distinguish larvae at generic and specific level, are usually too variable for identifying higher taxa.

Eight species of *Sesarma* inhabit southern African waters (Kensley 1981). They all have an Indo-Pacific or Indian Ocean distribution range, the only exception being *S. catenata,* which is endemic to southern Africa. Of these 8 species, only the larval stages of *S. catenata* have previously been described (Pereyra Lago 1987). *S. catenata* inhabits estuarine saltmarshes and mangrove swamps from the Breede River to Inhaca Island (Mozambique) (Day 1974). *S. meinerti* lives in association with mangroves and, together with the trees, does not extend further south and westward than the Transkei coast (Figure 1) (Ward & Steinke 1982). The distribution of these two crab species therefore overlaps along the Transkei and Natal coasts for approximately 900 km (Figure 1) and their larvae are most likely to be found together in estuarine and coastal plankton samples from this area.

Zoeae of *Sesarma meinerti* can be easily distinguished from those of *Sesarma catenata* by the presence in the former of spinous postero-lateral projections on the abdominal somites 1–5 (Figure 3A–E) and two rows of

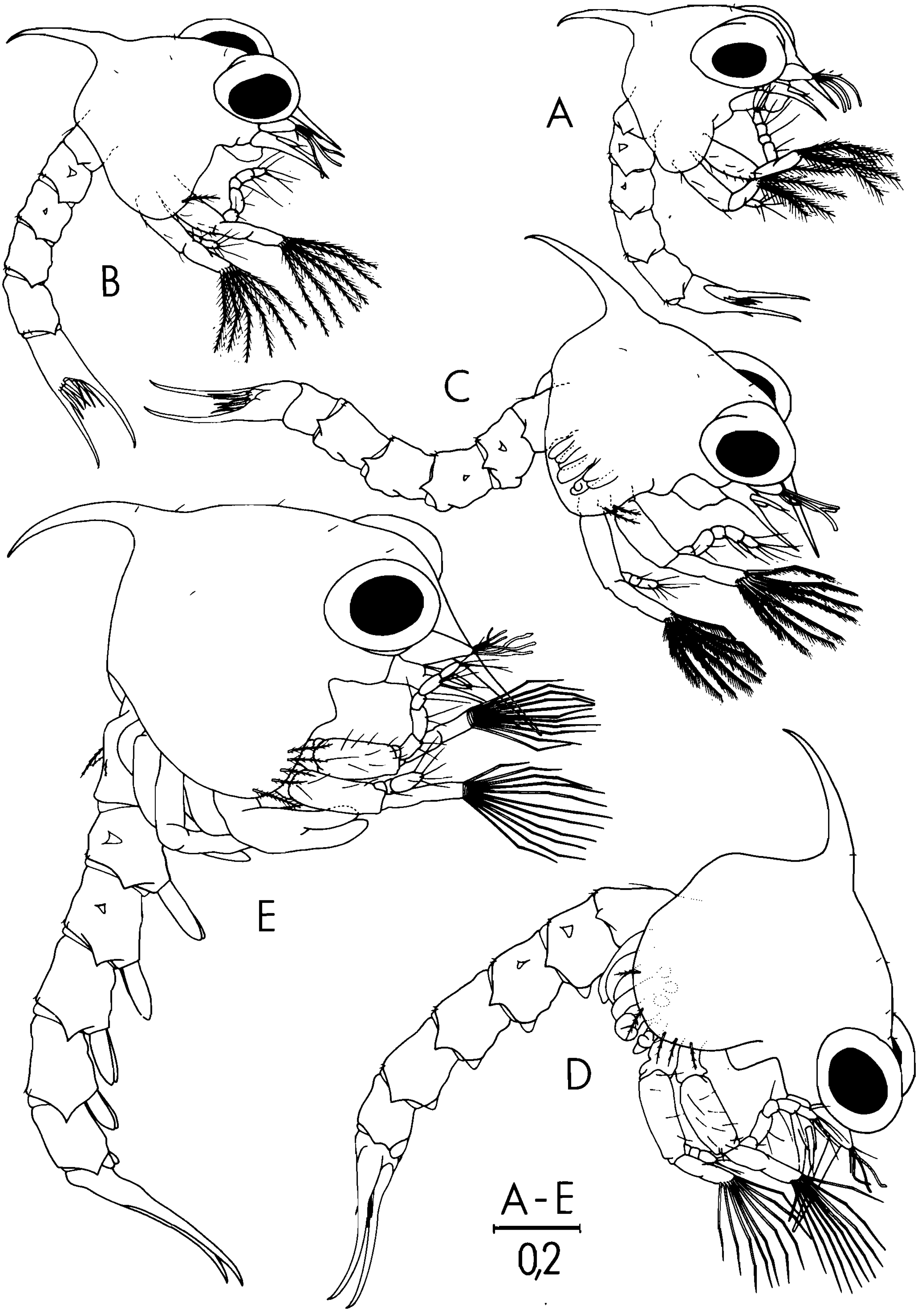

Figure 3 *Sesarma meinerti* zoeal stages. A = first zoea. B = second zoea. C = third zoea. D = fourth zoea. E = fifth zoea. Scale bars in Figures 3–10 are in mm.

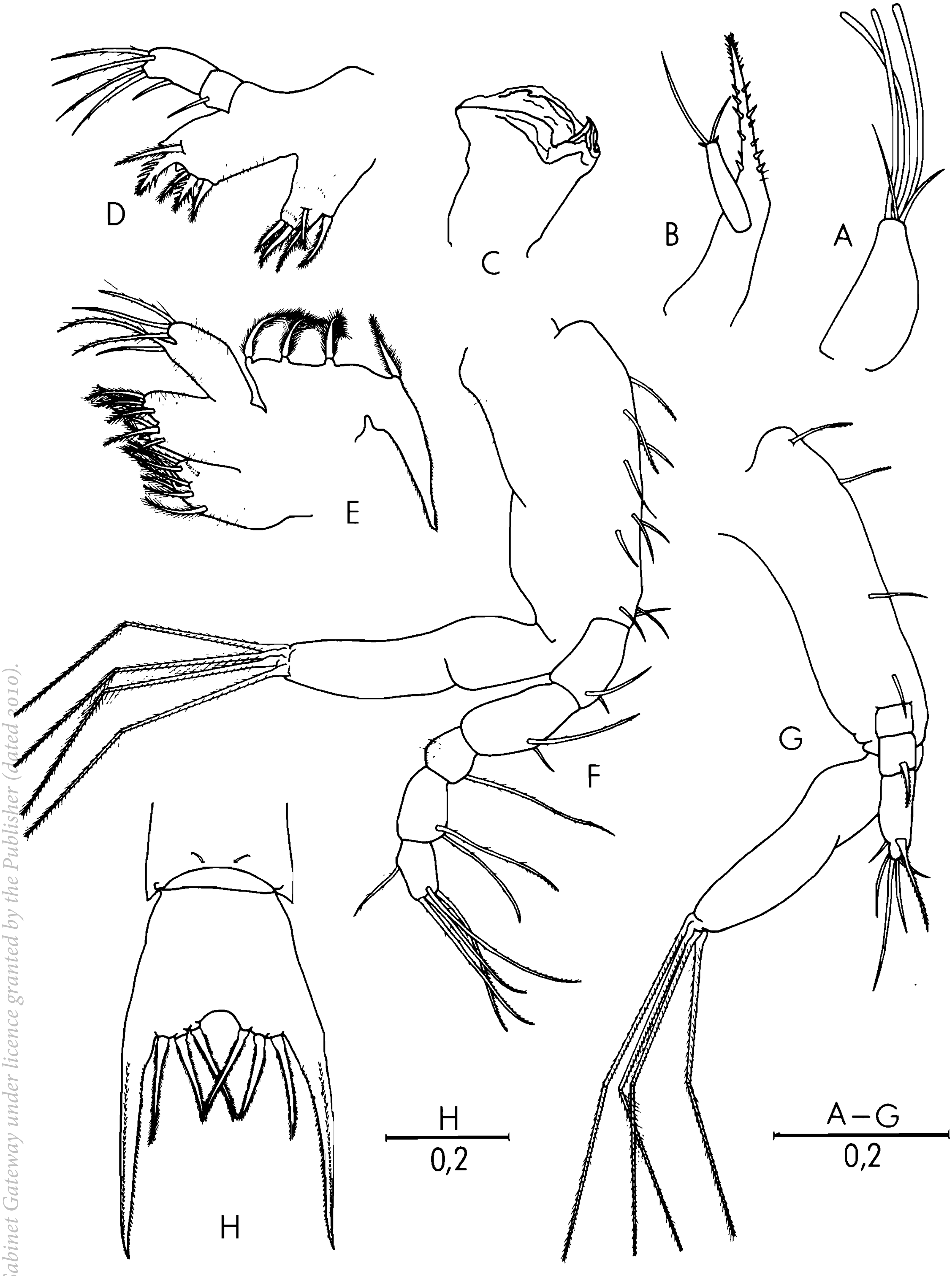

Figure 4 *Sesarma meinerti* first zoea. Cephalothoraxic appendages. A = antennule. B = antenna. C = mandible. D = maxillule. E = maxilla. F = fist maxilliped. G = second maxilliped. H = telson, dorsal view.

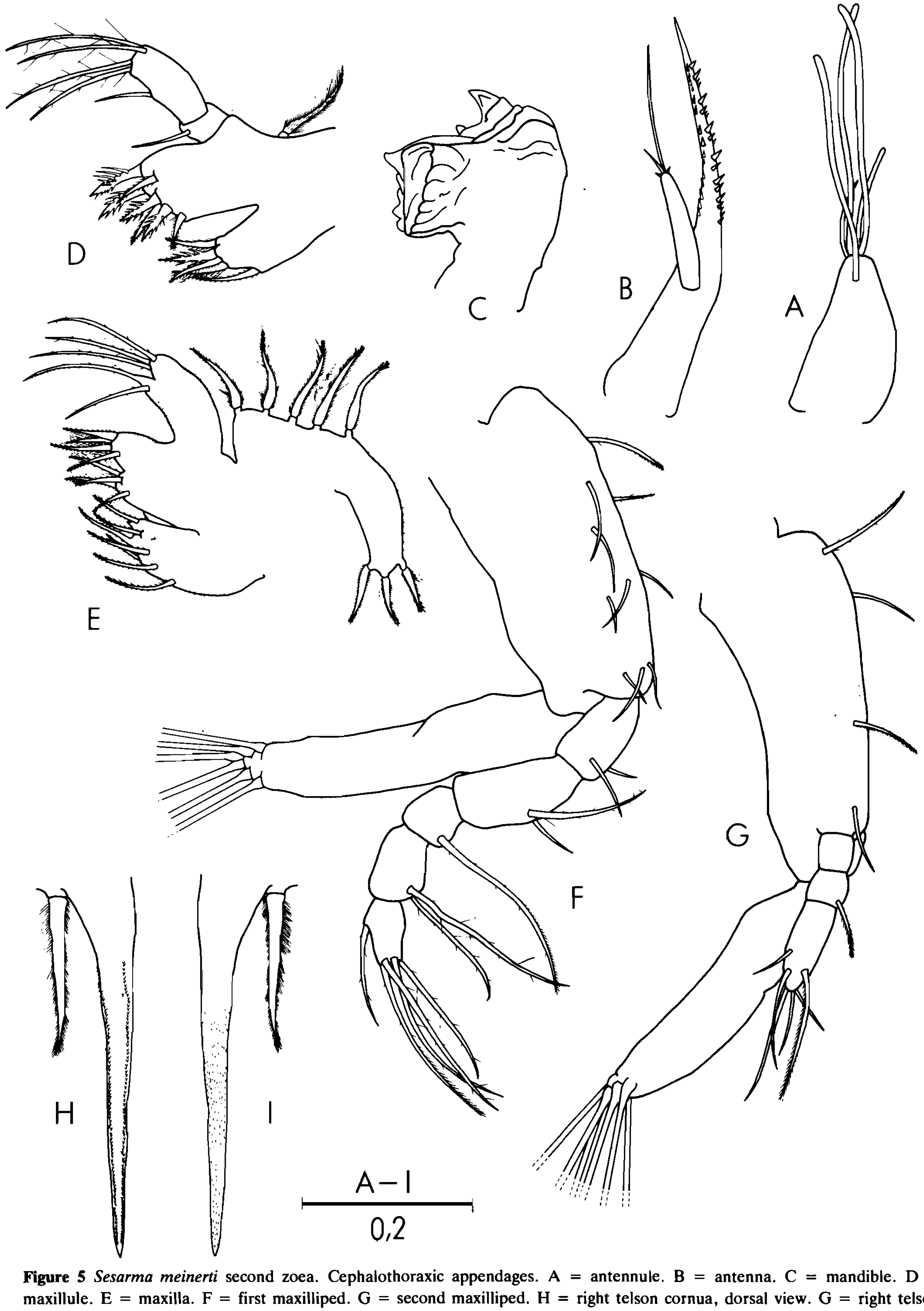

Figure 5 *Sesarma meinerti* second zoea. Cephalothoraxic appendages. A = antennule. B = antenna. C = mandible. D = maxillule. E = maxilla. F = first maxilliped. G = second maxilliped. H = right telson cornua, dorsal view. G = right telson cornua, ventral view.

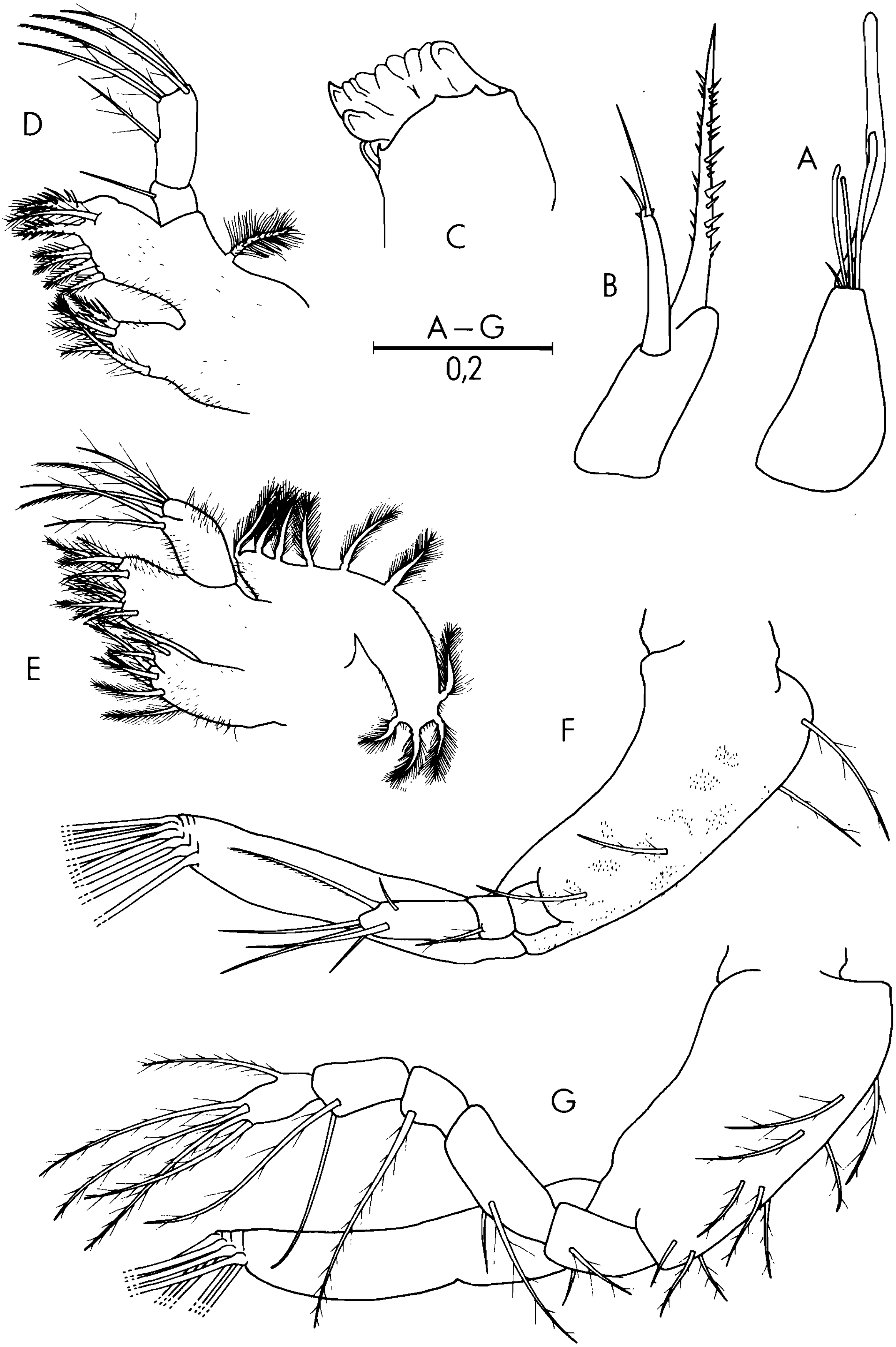

Figure 6 *Sesarma meinerti* third zoea. Cephalothoraxic appendages. A = antennule. B = antenna. C = mandible. D = maxillule. E = maxilla. F = second maxilliped. G = first maxilliped.

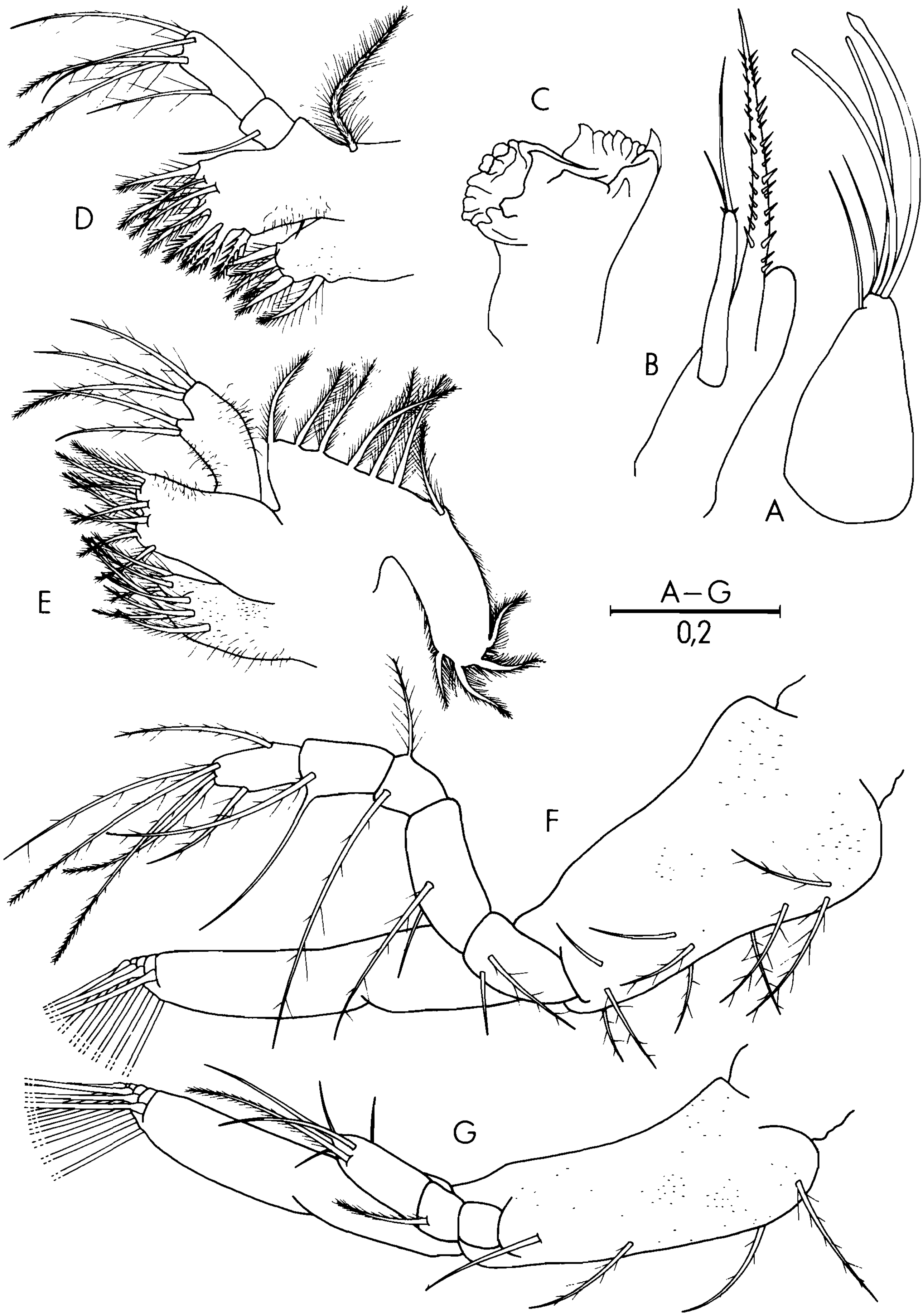

Figure 7 *Sesarma meinerti* fourth zoea. Cephalothoraxic appendages. A = antennule. B = antenna. C = mandible. D = maxillule. E = maxilla. F = first maxilliped. G = second maxilliped.

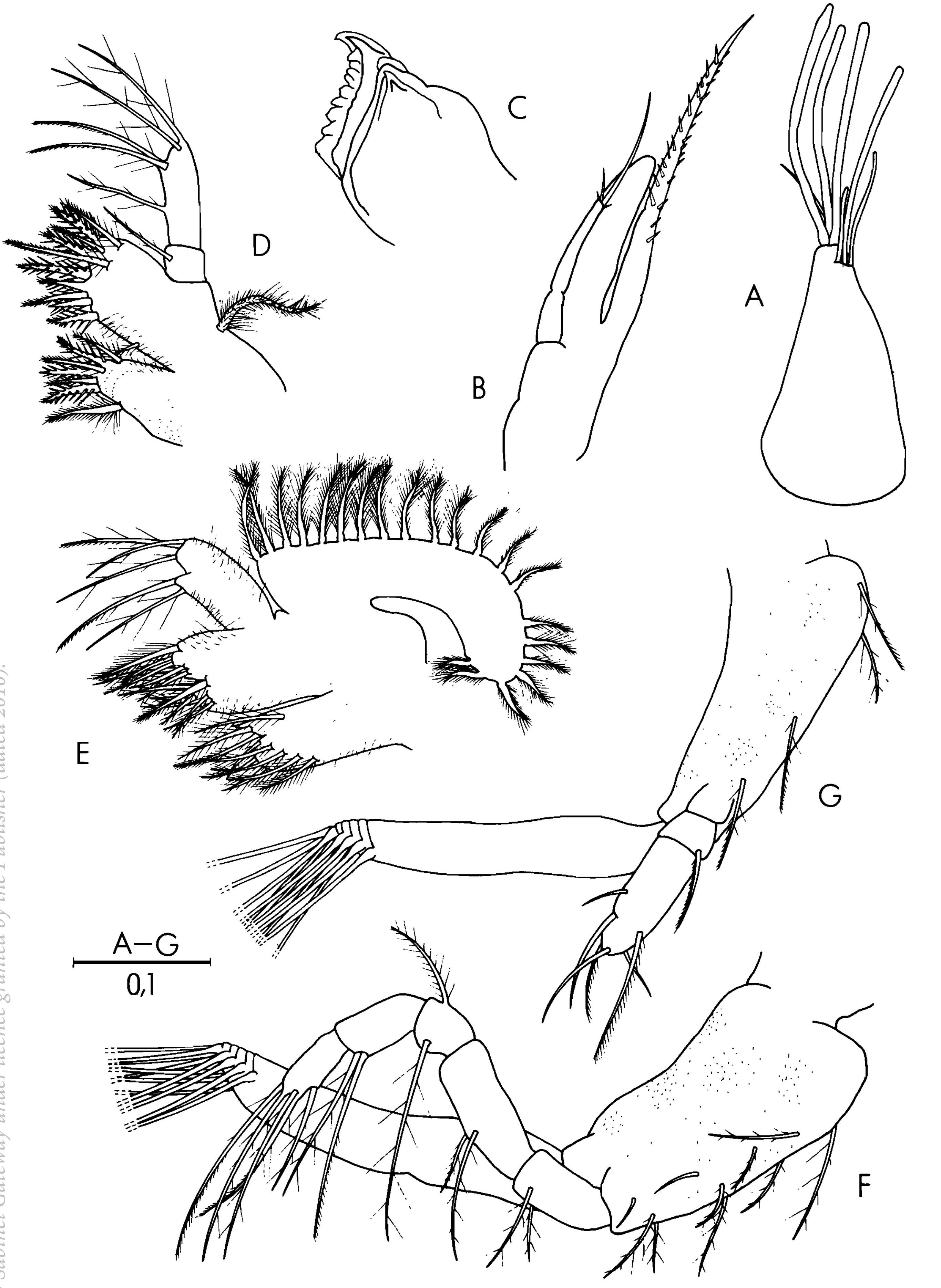

Figure 8 *Sesarma meinerti* fifth zoea. Cephalothoracic appendages. A = antennule. B = antenna. C = mandible. D = maxillule. E = maxilla. F = first maxilliped. G = second maxilliped.

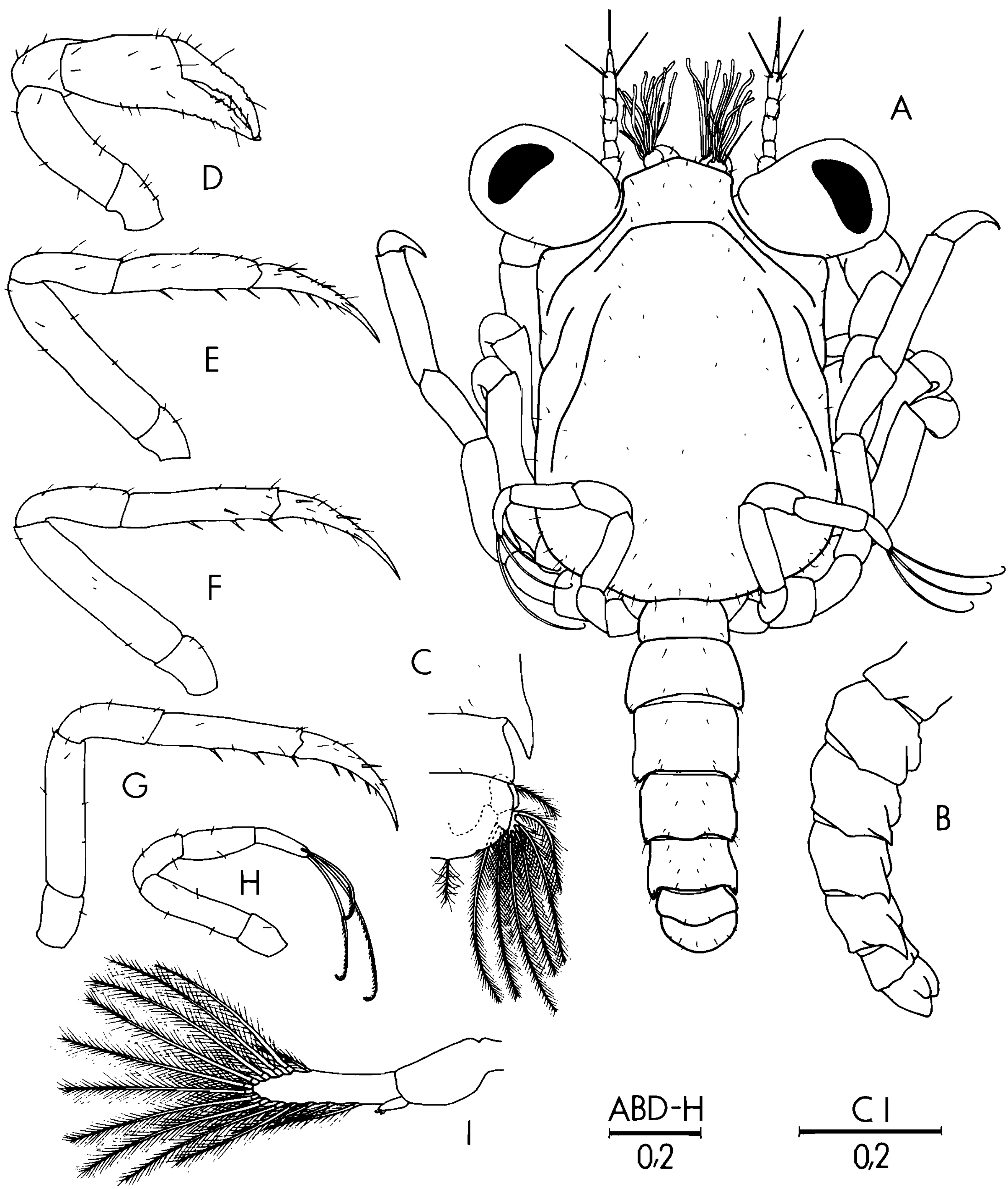

Figure 9 *Sesarma meinerti* megalopa. A = dorsal view. B = abdomen, lateral view. C = telson, dorsal view. D = first pereiopod. E = second pereiopod. F = third pereiopod. G = fourth perpeiopod. H = fifth pereiopod. I = first pleopod.

teeth on the telson cornua (Figures 4H & 5H), features which are lacking in the latter. Also the dorsal spine of *S. meinerti* zoeae (Figure 3A–E) is proportionally shorter than in *S. catenata* and less curved posteriorly, and the carapace is twice as large (Table 4) (Pereyra Lago 1987, Figure 3A–D). Finally, *S. meinerti* possesses five zoeal stages while *S. catenata* has only four. Megalopa larvae of both species can be distinguished by the long and spinous ventrolateral projections on the abdominal somites 3–5 and the posterior single plumose seta on the

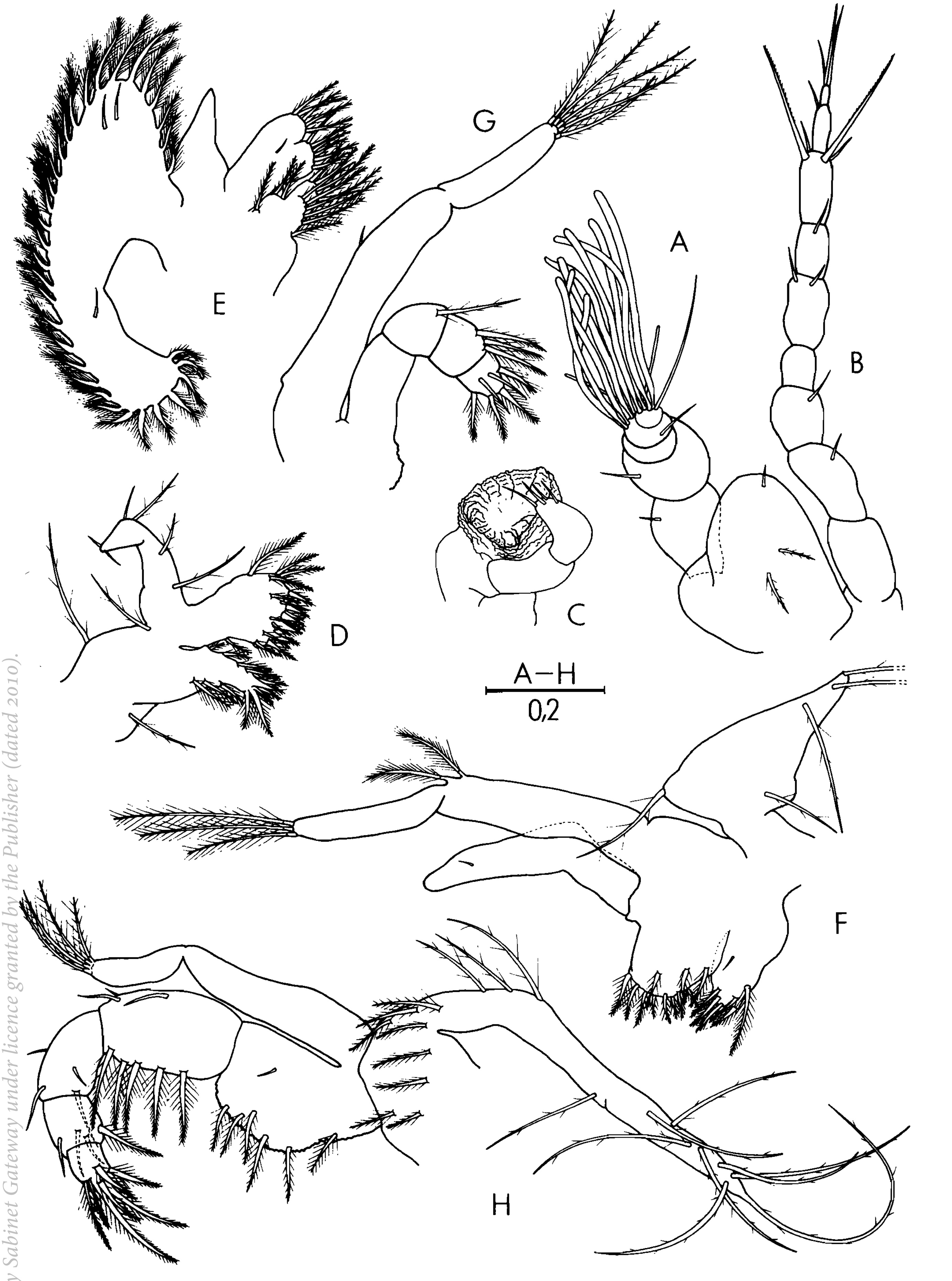

Figure 10 *Sesarma meinerti* megalopa. Cephalothoraxic appendages. A = antennule. B = antenna. C = mandible. D = maxillule. E = maxilla. F = first maxilliped. G = second maxilliped. H = third maxilliped.

Table 4 Morphological differences between zoeal stages of (A) *Sesarma catenata* and (B) *Sesarma meinerti*. MXL I = First maxilliped. All other symbols as in Table 1. All measurements are in mm

	Zoea I		Zoea II		Zoea III		Zoea IV / V		
	A	B	A	B	A	B	A	B	B
CL	0,23	0,41	0,26	0,51	0,28	0,57	0,41	0,70	0,78
DL	0,16	0,19	0,18	0,28	0,20	0,34	0,28	0,40	0,43
DRL	0,44	0,67	0,98	0,84	1,09	1,08	1,50	1,36	1,42
LTC	0,26	0,19	0,26	0,21	0,31	0,25	0,33	0,30	0,33
MXL I									
Endopodite setae	4	4	6	6	8	8	9	10	11
Carapace postero-lateral setae	0	0	2	1	4	2	8	5	5
Pereiopod buds	abs.	abs.	pres.	abs.	pres.	pres.	pres.	pres.	pres.

telson of *S. meinerti*, which are lacking in *S. catenata*. Also, the setation of the terminal flagellum of the antennule is 1S, 4A+1S, 2A+2S in *S. catenata* (Pereyra Lago 1987, Table 3) and 0, 6A+1S, 5A+1S in *S. meinerti* (Table 3).

Observation of these features does not require dissection of appendages, and can thus be used to identify large numbers of animals in plankton samples. Although appropriate to discriminate between larvae of *S. meinerti* and *S. catenata*, these characters will probably be insufficient when larvae of more of the remaining six *Sesarma* species are present in the same sample. Larval descriptions of all the coexisting *Sesarma* species is therefore urgently required before larval dynamics can be studied in detail.

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