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LARVAL MORPHOLOGY AND SALINITY TOLERANCE OF A LAND CRAB FROM WEST AFRICA, *CARDISOMA ARMATUM* (BRACHYURA: GRAPSOIDEA: GECARCINIDAE)

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ABSTRACT

The complete larval development of a terrestrial crab from West Africa, *Cardisoma armatum* Herklots, 1851, was studied in laboratory rearing experiments carried out at various salinities ranging from 0.2‰ to 45‰. Six zoeal stages and one megalopa are described and illustrated. Our experimental results showed that zoeal stages of *C. armatum* are fairly euryhaline, zoea I to IV tolerating a salinity range of 15–45‰, and 15–35‰ during later development. However, salinity 15‰ tended to cause higher mortality and a significantly delayed development in most stages, while 25‰ allowed for maximum survival through metamorphosis. These observations suggest that *C. armatum* follows a limited export strategy, where the adults may live in brackish or even freshwater habitats, while a successful larval development is possible only in estuarine or coastal waters with higher salinities, presumably with an optimum in the lower parts of estuaries with 25‰. Before this study, only an incomplete description of the first zoeal stage of *C. armatum* was available, and complete larval development had been known only for *C. carnifex* and *C. guanhumi*. In the present paper, the larval morphologies of these three congeneric species are compared. Within the Gecarcinidae, the complete larval development has been described also for *Discoplax hirtipes* and *Gecarcinus lateralis*, while only data for the morphology of the first zoeal stage are available for the other two genera of this family, *Epigrapsus* and *Gecarcoidea*. Hence, there are at present no sufficient data, in particular on megalopal morphology, to allow for conclusive intergeneric comparison and identification of familial characters. Gecarcinid zoeal morphology, as far as this is known, is briefly discussed in relation to that in other grapsoid families.

The grapsoid family Gecarcinidae MacLeay, 1838, presently consists of 19 species that are distributed among six genera: *Cardisoma* Latreille, 1825; *Discoplax* A. Milne-Edwards, 1867; *Gecarcinus* Leach, 1814; *Gecarcoidea* H. Milne Edwards, 1837; *Johngarthia* Türkay, 1970; and *Epigrapsus* Heller, 1862. Crabs included in the Gecarcinidae are commonly referred to as "land crabs", based on the terrestrial habits shown by adults of most of the species, some being found several kilometers away from the coast (Gilchrist, 1988). Land crabs are defined by Burggren and McMahon (1988) as crabs that show significant behavioral, morphological, physiological, and/or biochemical adaptations permitting extended activities out of the water. However, no gecarcinid species is a truely terrestrial crab, as all of them must return to the sea for larval release (Cuesta *et al.*, 2002). The known zoeal stages of all gecarcinid species are marine planktonic, and complete larval development consists of five or six such stages followed by a megalopa.

In the present study, effects of salinity on larval survival and duration of development through successive stages were tested at seven salinities ranging from freshwater (at <0.2‰) to a hypersaline condition at 45‰. Larval tolerance of hypo- and hypersaline conditions would indicate a retention strategy allowing larval development to take place within the parental habitat of mangrove swamps with freshwater creeks and hypersaline ponds. In contrast, maximum survival and shortest development in seawater and/or slightly diluted media should indicate an export strategy, i.e., larval transport to lower estuarine or coastal marine waters.

Larval morphology data for the family Gecarcinidae are available for all six genera, but among these for only nine species. Within *Cardisoma*, complete larval development has been described for *C. carnifex* (Herbst, 1794) by Kannupandi *et al.* (1980) and Flores *et al.* (2003; redescription of zoea I), and *C. guanhumi* Latreille, 1825, by Costlow and Bookhout (1968). For *C. armatum* Herklots, 1851, only an incomplete description of the first zoea was provided by Cannon (1923). In the present study, the complete larval development of this West African crab species is described from laboratory-reared material, and larval morphology is compared among species of Gecarcinidae.

MATERIALS AND METHODS

Cardisoma armatum were purchased from an aquarium supply store in Munich, Germany, and kept in a private home aquarium with freshwater (F. Klostermann, pers. comm.). When one female layed eggs, it was transported to the Helgoland Marine Biological Laboratory (BAH) and subsequently maintained in brackish water (5‰) to imitate presumable habitat conditions in West African mangrove swamps where this species lives (Ameyaw-Akumfi, 1987, 1989; Oyenekan, 1995). Its identity was later confirmed by both morphological and molecular-genetic analysis (Schubart, unpubl. data).

Larvae hatched on 5 March, 2000. They were mass-reared in gently aerated 1-L beakers with about 100 larvae per beaker, kept at constant 24°C, 25‰ salinity, and an artificial 12:12 h L:D cycle. Water and food (*Artemia* sp., about 10 freshly hatched nauplii/mL) were changed daily, and the larvae were checked for moulting and mortality. About 50 specimens of each stage were removed from mass-cultures when moult occurred and fixed in 4% formaldehyde-seawater.

Salinity tolerance experiments were carried out in 30 mL glass vials with individual larvae, 50 larvae per treatment. Otherwise, rearing conditions were as for mass cultures. The tested salinity conditions comprised: tap water (<0.2‰), 1, 5, 15, 25, 35, and 45‰. All rearing salinities were obtained by dilution of filtered natural seawater from the North Sea (32‰) with deionized water, or by adding artificial sea salt (Tropic Marin®, Wartenberg, Germany), respectively. Salt concentrations were subsequently checked with a hand refractometer to the nearest 1‰ for conditions ≥15‰

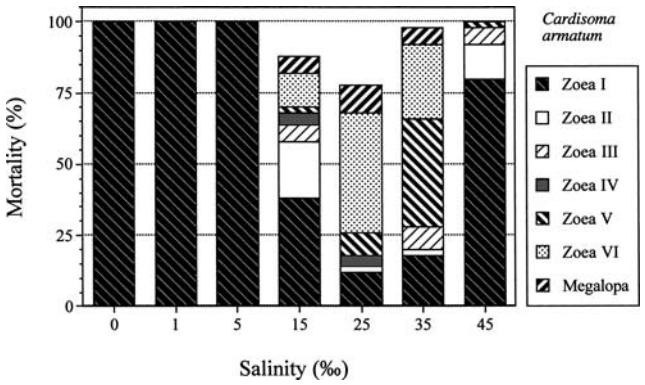

Fig. 1. *Cardisoma armatum* Herklots, 1851. Cumulative mortality rates in successive larval stages reared from hatching at different salinity conditions in the laboratory (initial $n = 50$ individuals per treatment).

or with a micro-osmometer Model 3MO (Advanced Instruments, Needham Heights, Ma., U.S.A.) for lower salinites. Mortalities and moults were recorded daily when water and food were changed.

Dissections were made under a Wild MZ6 stereo microscope, and drawings and measurements were made using a Zeiss Axioskop compound microscope equipped with a *camera lucida*. Semipermanent mounts on glycerol were made of whole larvae and dissected appendages. All measurements were made with a calibrated ocular micrometer. Drawings were based on 5 larvae, morphometrics on 10 larvae per stage. For zoeal stages, rostro-dorsal 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. For the megalopa, 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, exopod natatory setae of the first and second maxillipeds, and pleopods and uropod are drawn truncated. The description follows standards proposed by Clark *et al*. (1998).

Samples of all larval stages of *Cardisoma armatum* were deposited at the Smithosonian Institution, National Museum of Natural History, Washington D. C., under catalog number USNM 1074639.

Analysis of variance (ANOVA) and Student's t tests were used for multiple and subsequent pairwise statistical comparisons of mean values for development time through successive larval stages, respectively, after appropriate checks for normal distribution and equality of variance (Sokal and Rohlf, 1995). Contingency tables (mortality/survival data) were analyzed with Pearson's chi-square test.

Results

Salinity Tolerance

At salinities of less than 5‰, no larva was able to develop to the zoea II stage (Fig. 1). In freshwater and at 1‰, all larvae died within 24 hours compared to maximum survival of four days at 5‰. The highest salinity of 45‰ also caused very high mortality (80%) in zoea I, a few indivuals moulting through subsequent zoeal stages, as far as zoea V. At 15‰ the rate of survival through zoea I was significantly higher than at salinites of 0.2–5‰ (all $P < 0.001$), and at 25–35‰ it was significantly higher than at both 15‰ ($P < 0.01$) and 45‰ ($P < 0.001$). Only conditions of 15–35‰ allowed successful development through all larval stages, although generally at low overall survival (Fig. 1). Maximum survival through metamorphosis (20%) was observed at 25‰. While the observed difference in survival rates from hatching through metamorphosis at 15‰ and 25‰ was statistically insignificant ($P > 0.05$), that between 25‰ and 35‰ was highly significant ($P < 0.001$).

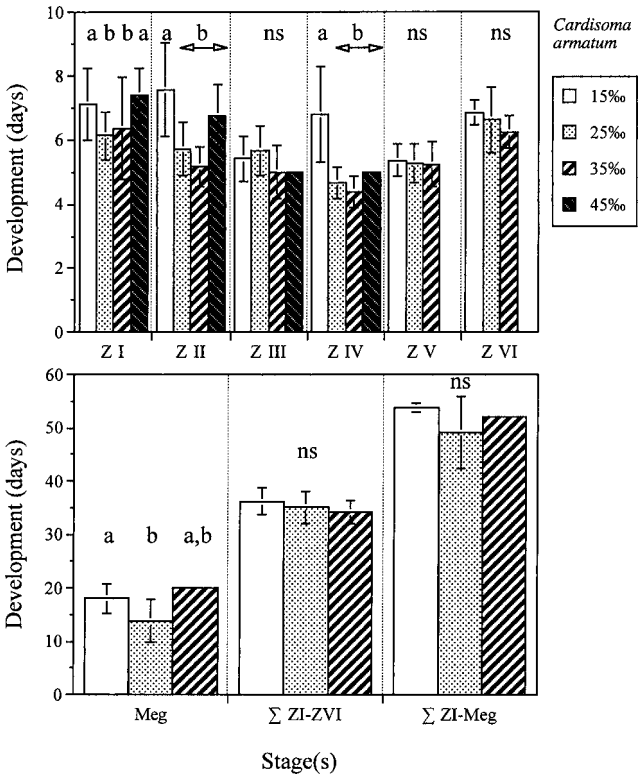

Fig. 2. *Cardisoma armatum* Herklots, 1851. Duration of development through successive larval stages (days; mean ± SD) reared at salinity conditions allowing for at least some survival (cf. Fig. 1); different letters near error bars indicate significant differences between stages at each salinity ($P < 0.05$); ns = statistically not significant.

The patterns of development duration through successive larval stages in relation to salinity (Fig. 2) were similar to those observed for mortality. Thus, within the tolerated salinity range there was a general tendency of delayed development at the lowest and highest salinities, i.e., at 15‰ and 45‰. However, generally poor survival in our experiments precluded the determination of consistent, statistically significant differences. As a consequence, data for cumulative developmental periods from hatching to the end of the zoeal phase or from hatching to metamorphosis (Fig. 2, lower graph) showed no significant effects of salinity. Significant developmental delays were found only at 15‰ vs. 25‰ in the zoea I, II, IV, and in the megalopa stage, as well as at 45‰ vs. 25‰ and 35‰ in the zoea I.

Larval Description

The first zoea and megalopa are described in detail, while for zoeae II to VI only differences from previous stages are described. Illustrations of appendages are made in detail only for zoea I, zoea VI, and the megalopa. For other stages only important morphological changes, but no mere changes in setal numbers, are illustrated.

Cardisoma armatum Herklots, 1851
Figs 3–11

Zoea I

Dimensions.—rdl: 0.85 ± 0.03 mm; cl:0.46 ± 0.02 mm.

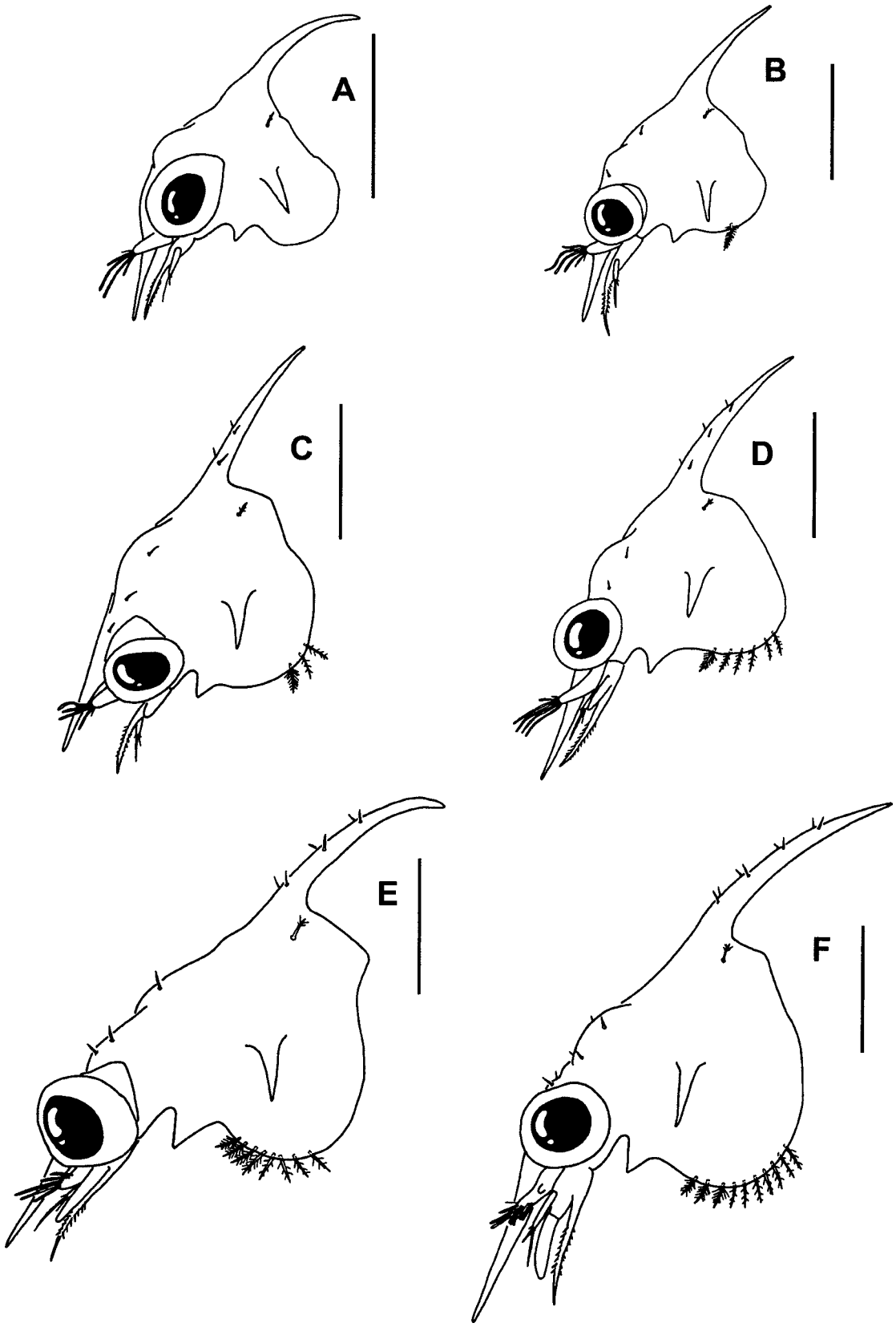

Fig. 3. *Cardisoma armatum* Herklots, 1851. Carapace, lateral view. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Zoea V; F, Zoea VI. Scale bars = 0.5 mm.

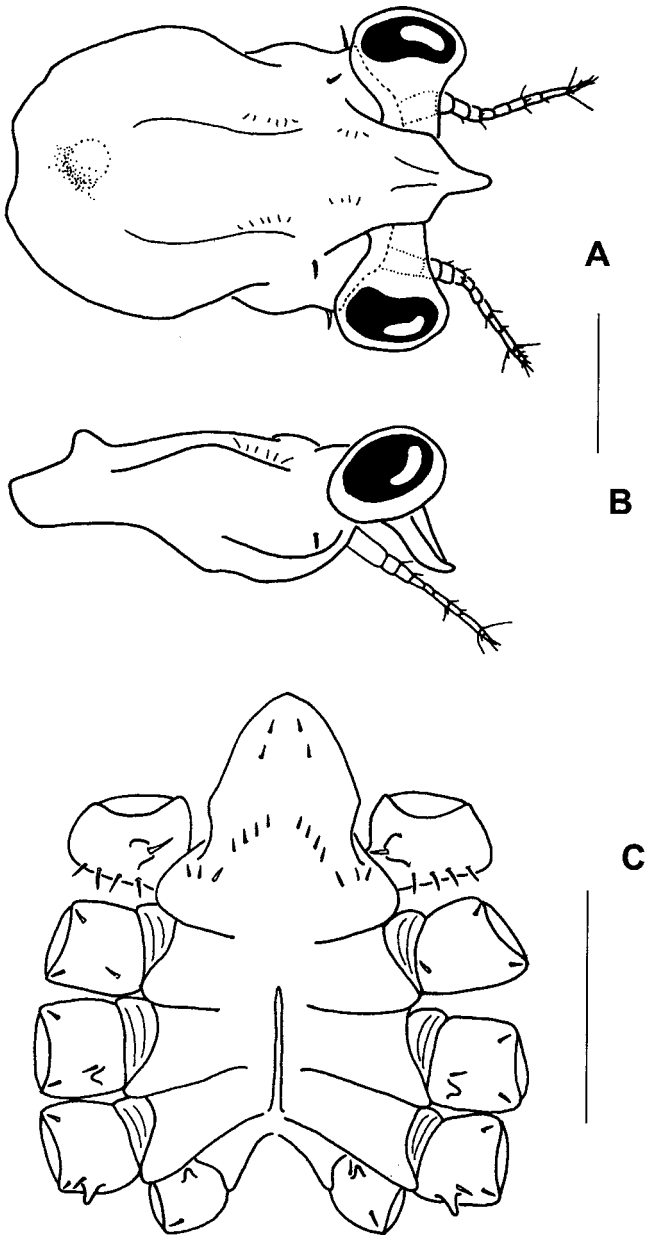

Fig. 4. *Cardisoma armatum* Herklots, 1851. Megalopa. A, carapace, dorsal view; B, lateral view; C, sternal plate and coxa of pereiopods. Scale bars = 0.5 mm.

Carapace (Fig. 3A).—Globose, smooth, bearing anterodorsal protuberance. Dorsal spine long, recurved. Rostral spine straight, as long as antennary protopod. Lateral spines well developed, directed down-forward. Pair of posterodorsal setae. Posterior and ventral margin without setae. Eyes sessile.

Antennule (Fig. 5A).—Uniramous. Endopod absent. Exopod unsegmented, with 4 aesthetascs (2 long, 2 thin and shorter) and 1 seta, all terminal.

Antenna (Fig. 5E).—Well-developed protopod reaching tip of rostral spine and bearing 2 unequal rows of spines. Exopod elongated, with 4 terminal setae (1 long, 1 shorter, and 2 minute).

Mandible.—Endopod palp absent.

Maxillule (Fig. 6C).—Coxal endite with 5 plumose setae. Basial endite with 5 setae (3 cuspidate and 2 plumodenticulate). Endopod 2-segmented, with 1 simple seta on proximal segment and 1 subterminal and 4 terminal plumodenticulate setae in distal segment. Exopod seta absent. Epipod seta absent.

Maxilla (Fig. 7A).—Coxal endite bilobed, with 5+3 plumodenticulate setae. Basial endite bilobed, with 5+4 plumodenticulate setae. Endopod unsegmented, bilobed, with 2 (1 long, 1 short) + 3 (2 long, 1 short) plumodenticulate setae on inner and outer lobe respectively. Scaphognathite (exopod) with 4 plumose marginal setae and long setose posterior process.

First Maxilliped (Fig. 8A).—Coxa with 1 seta. Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented, with 2,2,1,2,5 (1 subterminal simple + 4 terminal) plumodenticulate setae. Exopod 2-segmented, distal segment with 4 long, terminal, plumose natatory setae.

Second Maxilliped (Fig. 9A).—Coxa without setae. Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented, with 1,1,6 (3 subterminal + 3 terminal) setae. Exopod 2-segmented, distal segment with 4 long, terminal, plumose natatory setae.

Third Maxilliped.—Absent.

Pereiopods.—Absent.

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

Telson (Fig. 11A, B).—Telson bifurcated, with 3 pairs of serrulate setae on posterior margin. Each furcal arm with 2 minute lateral spines and 2 rows of teeth in inner distal part.

Zoea II

Dimensions.—rdl: 1.21 ± 0.04 mm; cl: 0.54 ± 0.02 mm.

Carapace (Fig. 3B).—Two pairs of anterodorsal setae. Ventral margin with 1 plumose seta. Eyes stalked.

Antennule.—Exopod with 1 additional shorter terminal aesthetasc.

Antenna.—Unchanged.

Mandible.—Unchanged.

Maxillule (Fig. 6D).—Coxal endite with 6 setae. Basial endite with 7 setae. Exopod present as long plumose marginal seta.

Maxilla.—Coxal endite with 5+4 setae. Scaphognathite with 8 plumose marginal setae.

First Maxilliped.—Exopod distal segment with 6 long, terminal, plumose natatory setae.

Second Maxilliped.—Exopod distal segment with 6 long, terminal, plumose natatory setae.

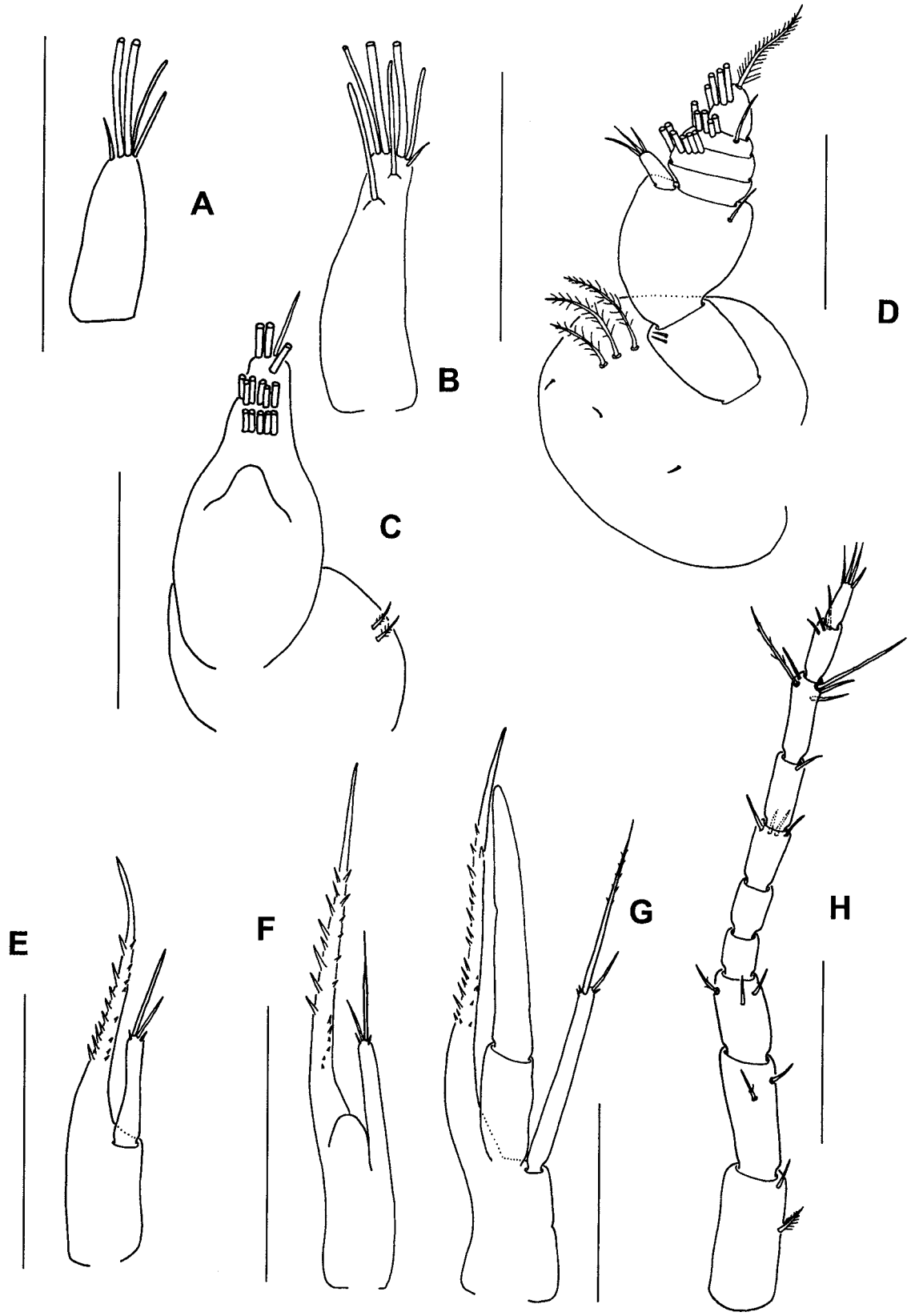

Fig. 5. *Cardisoma armatum* Herklots, 1851. Antennule. A, Zoea I; B, Zoea IV; C, Zoea VI; D, Megalopa. Antenna. E, Zoea I; F, Zoea III; G, Zoea VI; H, Megalopa. Scale bars, A–C, E–G = 0.25 mm, D, H = 0.2 mm.

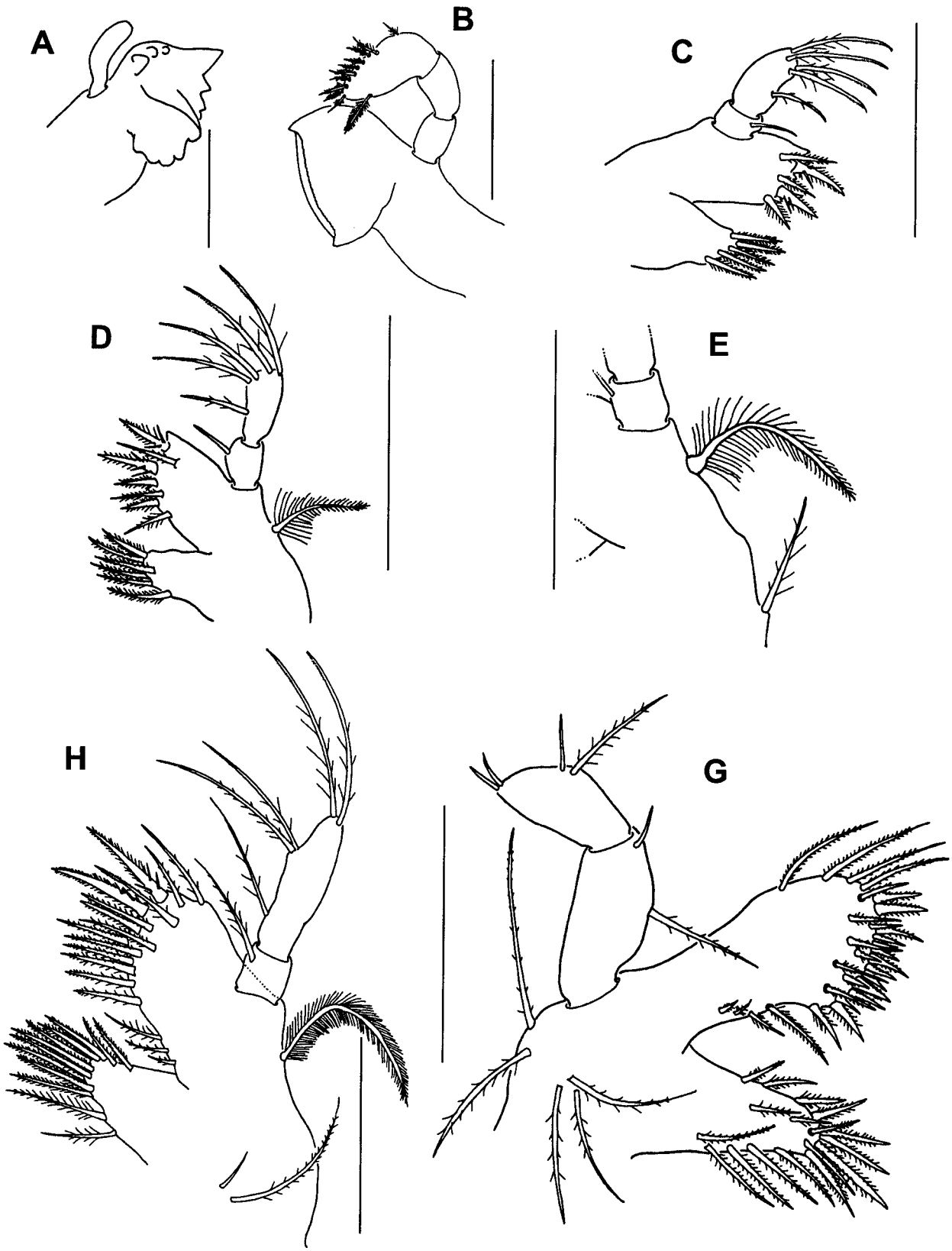

Fig. 6. *Cardisoma armatum* Herklots, 1851. Mandible. A, Zoea VI; B, Megalopa. Maxillule. C, Zoea I; D, Zoea II; E, Zoea IV; F, Zoea VI; G, Megalopa. Scale bars = 0.2 mm.

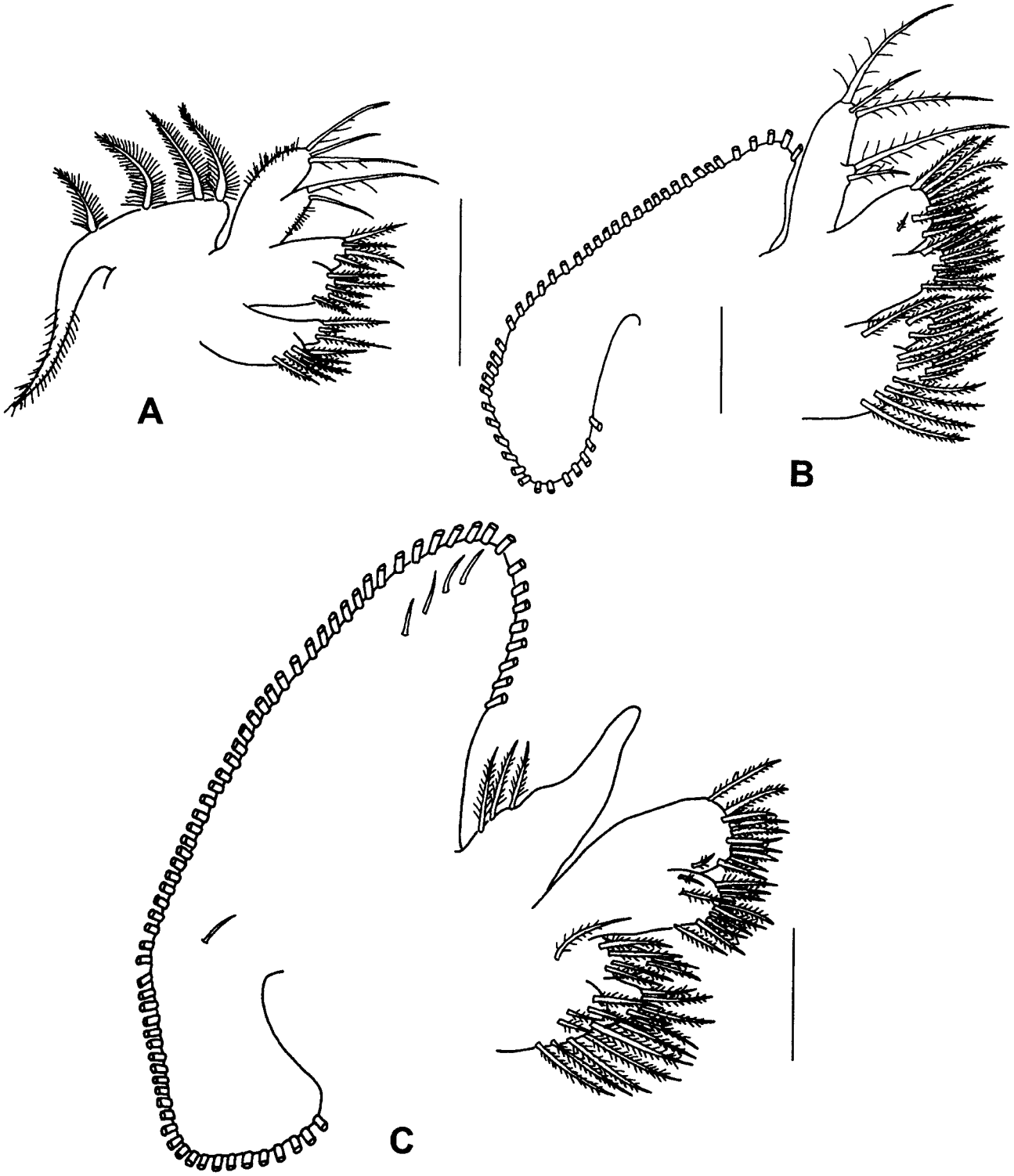

Fig. 7. *Cardisoma armatum* Herklots, 1851. Maxilla. A, Zoea I; B, Zoea VI; C, Megalopa. Scale bars = 0.1 mm.

Third Maxilliped.—Unchanged.

Pereiopods.—Unchanged.

Abdomen.—First somite with 1 long mid-dorsal seta.

Telson.—Minute outer spines reduced in size and present only in few specimens.

Zoea III

Dimensions.—rdl: 1.61 ± 0.03 mm; cl: 0.60 ± 0.02 mm.

Carapace (Fig. 3C).—Two pairs of setae on dorsal spine. Three pairs of anterodorsal setae. Each ventral margin with 3 setae (1 plumose, 2 plumodenticulate).

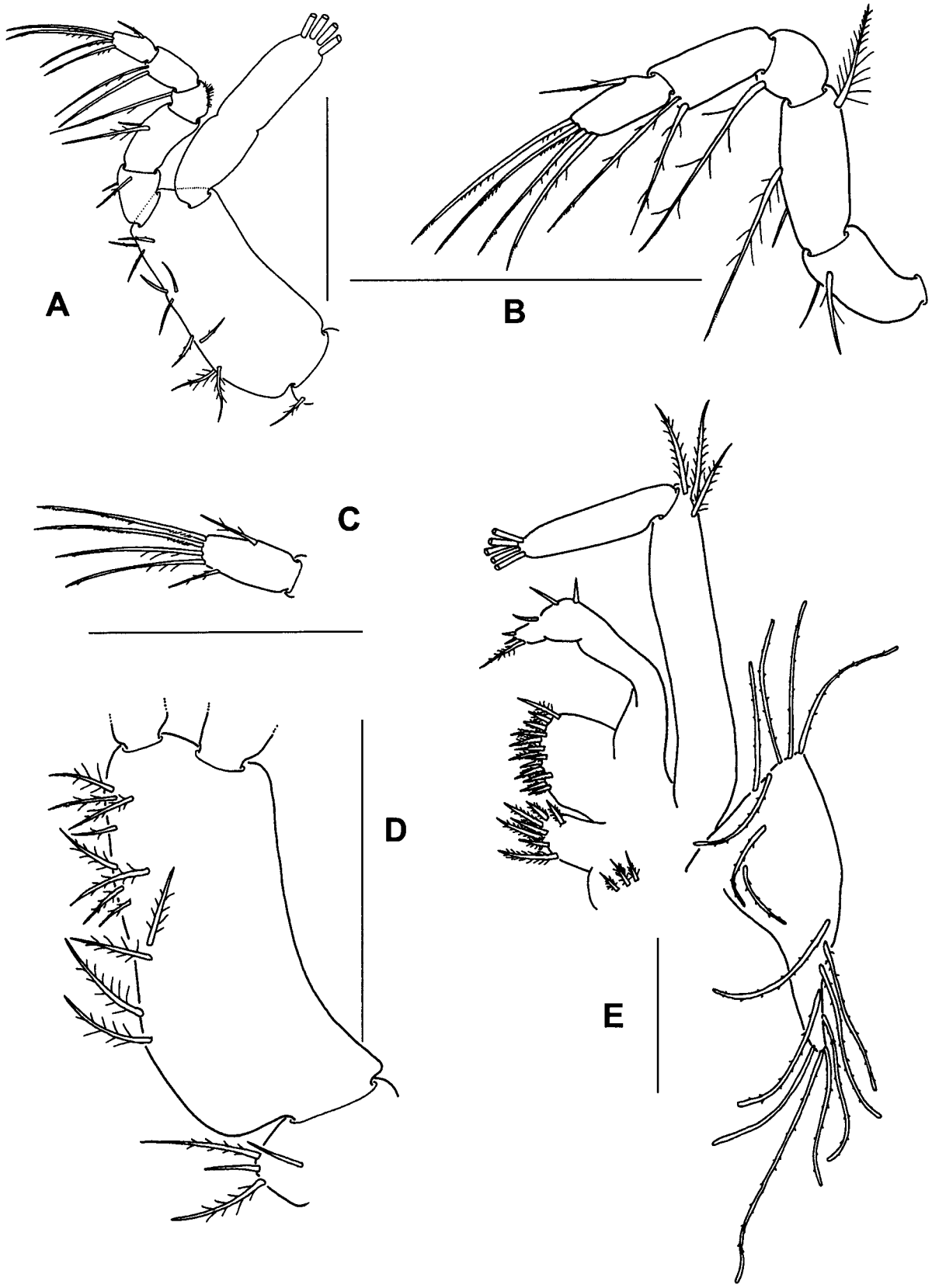

Fig. 8. *Cardisoma armatum* Herklots, 1851. First maxilliped. A, Zoea I; B, Zoea III, endopod; C, Zoea IV, fifth segment of endopod; D, Zoea VI, coxa and basis; E, Megalopa. Scale bars, A–D = 0.25 mm, E = 0.2 mm.

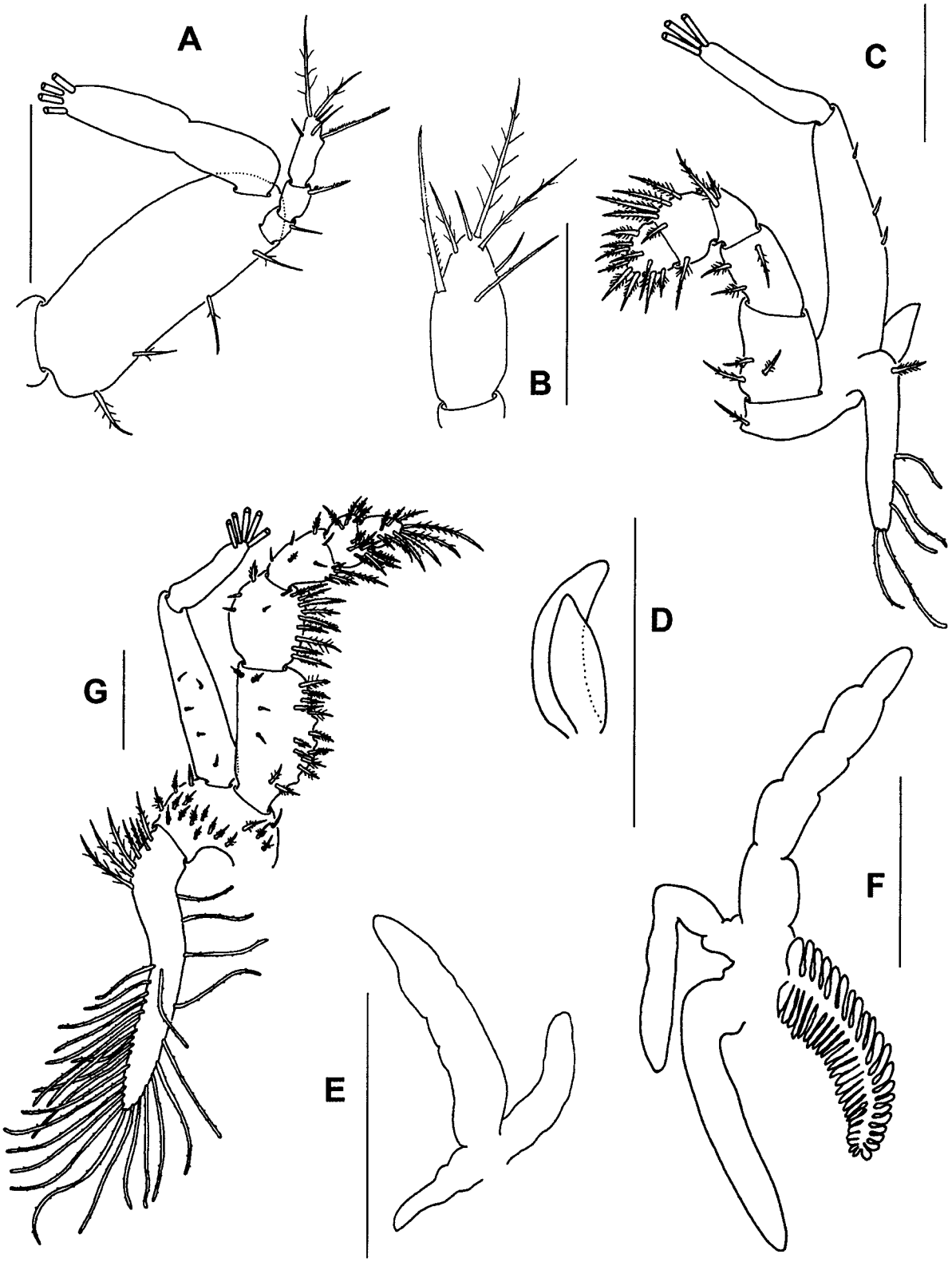

Fig. 9. *Cardisoma armatum* Herklots, 1851. Second maxilliped. A; Zoea I; B, Zoea VI, terminal segment of the endopod; C, Megalopa. Third maxilliped. D, Zoea III; E, Zoea V; F, Zoea VI; G, Megalopa. Scale bars = 0.2 mm.

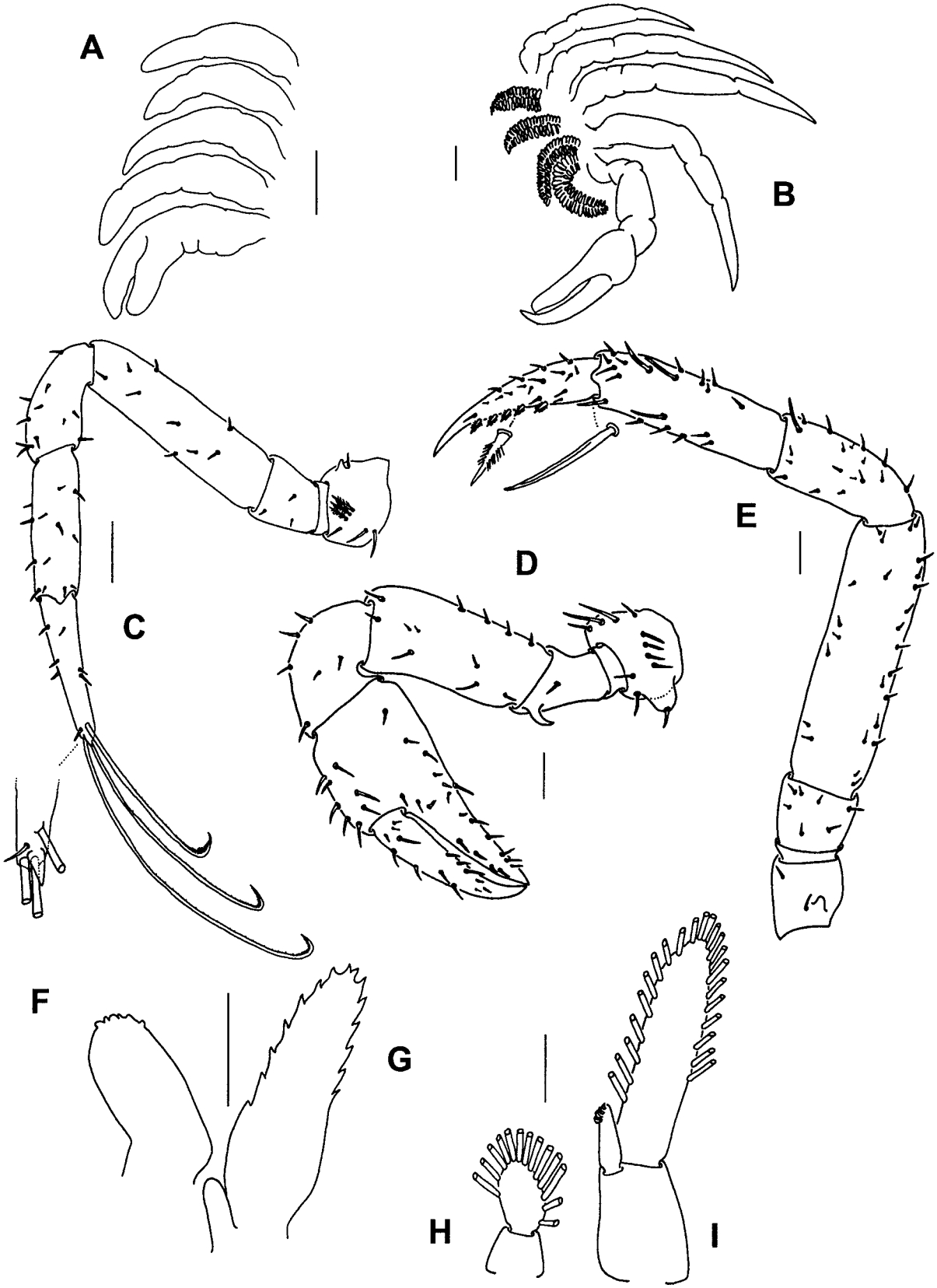

Fig. 10. *Cardisoma armatum* Herklots, 1851. Pereiopods. A, Zoea IV; B, Zoea VI; C, Megalopa, fifth pereiopod; D, Megalopa, cheliped; E, Megalopa, second pereiopod. Pleopod, first pair. G, Zoea VI; I, Megalopa. Uropod. F, Zoea VI; H, Megalopa. Scale bars = 0.1 mm.

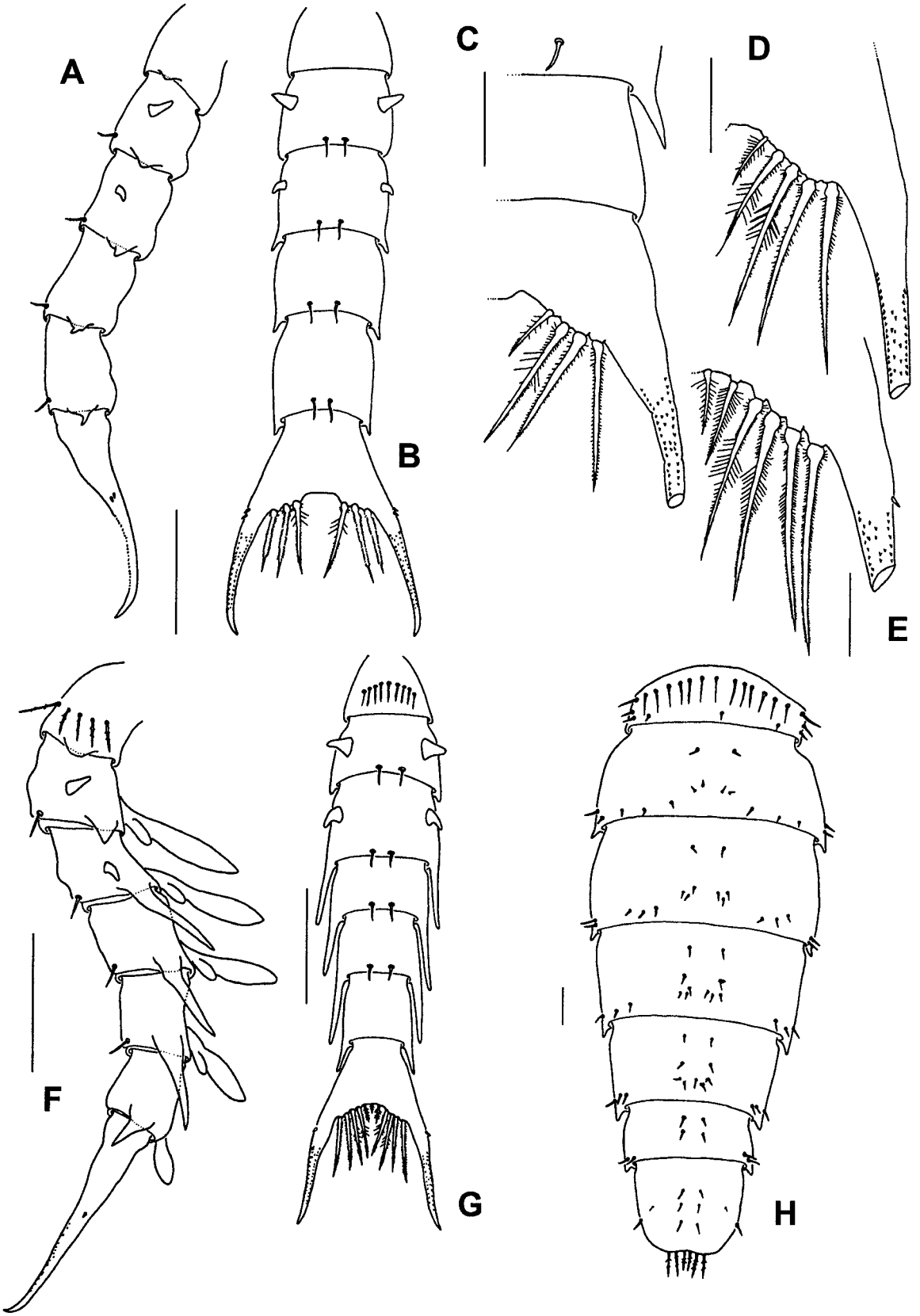

Fig. 11. *Cardisoma armatum* Herklots, 1851. Abdomen, and telson magnification. A, Zoea I, lateral view; B, Zoea I, dorsal view; C, Zoea III; D, Zoea IV; E, Zoea VI, telson showing small lateral spine; F, Zoea VI, lateral view; G, Zoea VI, dorsal view; H, Megalopa, dorsal view. Scale bars = 0.1 mm.

Antennule.—Exopod unsegmented, with 4 aesthetascs and 1 seta.

Antenna (Fig. 5F).—Endopod bud present.

Mandible.—Unchanged.

Maxillule.—Unchanged.

Maxilla.—Basial endite bilobed, with 5+5 setae. Scaphognathite with 15 plumose marginal setae.

First Maxilliped (Fig. 8B).—Second segment of endopod with additional dorsal plumose setae. Exopod distal segment with 8 long, terminal, plumose natatory setae.

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

Third Maxilliped (Fig. 9D).—Present as biramous, unsegmented bud.

Pereiopods.—Present as unsegmented buds.

Abdomen (Fig. 11C).—First somite with 3 long mid-dorsal setae. Somite 6 now present, without setae.

Telson (Fig. 11C).—Additional pair of shorter plumodenticulate setae on posterior margin.

Zoea IV

Dimensions.—rdl: 1.90 ± 0.05 mm; cl: 0.73 ± 0.03 mm.

Carapace (Fig. 3D).—Three pairs of setae on dorsal spine. Ventral margin with 6 setae (2 plumose, 4 plumodenticulate).

Antennule (Fig. 5B).—Exopod unsegmented, with 6 aesthetascs (2 subterminal, 4 terminal) and 1 terminal seta.

Antenna.—Endopod longer, reaching middle of protopod length.

Mandible.—Unchanged.

Maxillule (Fig. 6E).—Basial endite with 10 setae. Epipod seta present.

Maxilla.—Coxal endite bilobed with 6+5 setae. Basial endite bilobed with 6+5 setae. Scaphognathite with 21 plumose marginal setae.

First Maxilliped (Fig. 8C).—Coxa with 2 setae. Fifth segment of endopod with additional subterminal plumodenticulate seta. Exopod distal segment with 10 long, plumose natatory setae on distal segment.

Second Maxilliped.—Exopod distal segment with 10 long, plumose natatory setae on distal segment.

Third Maxilliped (Fig. 9E).—Epipod present as elongated rudiment.

Pereiopods (Fig. 10A).—Cheliped bud bilobed. Pereiopod 2–5 buds elongated.

Abdomen.—First somite with 5 long mid-dorsal setae. Pleopod buds present on somites 2–5, endopods absent.

Telson (Fig. 11D).—Additional fifth pair of shorter plumodenticulate setae on posterior margin.

Zoea V

Dimensions.—rdl: 2.11 ± 0.03 mm; cl: 0.86 ± 0.02 mm.

Carapace (Fig. 3E).—Each ventral margin with 8 setae (2 plumose, 6 plumodenticulate).

Antennule.—Now biramous. Endopod bud present. Exopod unsegmented, with 2 basal setae, 8 aesthetascs (4 subterminal, 4 terminal) and 1 terminal seta.

Antenna.—Endopod 2-segmented, longer, two-thirds of protopod length.

Mandible.—Small palp bud present.

Maxillule.—Coxal endite with 9 setae. Basial endite with 14 setae.

Maxilla.—Basial endite bilobed, with 6+6 setae. Scaphognathite with 28–30 plumose marginal setae.

First Maxilliped.—Coxa with 3 setae. Fifth segment of endopod with additional subterminal seta. Exopod distal segment with 12 long, plumose natatory setae on distal segment.

Second Maxilliped.—Coxa with 1 seta. Exopod distal segment with 12 long, plumose natatory setae on distal segment.

Third Maxilliped.—Unchanged.

Pereiopods.—Cheliped and pereiopods 2–5 slightly segmented.

Abdomen.—First somite with 7 long mid-dorsal setae. Pleopod buds elongated, endopod buds present.

Telson.—Unchanged.

Zoea VI

Dimensions.—rdl: 2.41 ± 0.04 mm; cl: 1.10 ± 0.03 mm.

Carapace (Fig. 3F).—Four pairs of setae on dorsal spine. Each ventral margin with 10 setae (3 plumose, 7 plumodenticulate).

Antennule (Fig. 5C).—Peduncle 2-segmented, proximal segment with 2 simple setae. Endopod bud elongated. Exopod unsegmented, with 14 aesthetascs (arranged 5, 6, and 3 terminal) and 1 terminal seta.

Antenna (Fig. 5G).—Endopod 2-segmented, elongating to near protopod tip.

Mandible (Fig. 6A).—Palp bud elongated.

Maxillule (Fig. 6F).—Coxal endite with 11 plumodenticulate setae. Basial endite with 17 setae. An additional seta close to epipodal one.

Maxilla (Fig. 7B).—Coxal endite bilobed, with 9+5 setae. Basial endite bilobed, with 9+10 setae. Scaphognathite with 42–44 plumose marginal setae.

First Maxilliped (Fig. 8D).—Coxa with 4 setae. Basis with 12 medial setae arranged 2,2,4,4. Exopod distal segment with 14 long, plumose natatory setae.

Second Maxilliped (Fig. 9B).—Distal segment of endopod with 7 setae. Exopod distal segment with 14 long, plumose natatory setae.

Third Maxilliped (Fig. 9F).—Endopod slighly segmented. Gill present.

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

Abdomen (Fig. 11F,G).—First somite with 9 long mid-dorsal setae. Pleopods buds elongated, endopod buds present (Fig. 10F).

Telson (Fig. 11E).—Single small, medial seta on posterior margin. Some specimens present minute lateral spine on outer margin of each furcal arm.

Megalopa

Dimensions.—cl: 1.54 ± 0.05 mm; cw: 1.17 ± 0.04 mm.

Carapace (Fig. 4A, B).—Longer than broad. Rostrum ventrally deflected (about 45°) with medial cleft. Two long lateral ridges, and mid-posterior protuberance. Setal arrangement as figured.

Antennule (Fig. 5D).—Peduncle 3-segmented, with 6 (3 long plumodenticulate, 3 short simple), 2, 1 setae respectively. Endopod unsegmented, with 3 terminal simple setae. Exopod 4-segmented with 0, 6, 5, and 4 aesthetascs respectively and 0, 0, 1, 1 (terminal long plumose) setae.

Antenna (Fig. 5H).—Peduncle 3-segmented, with 2, 2, 3 setae respectively. Flagellum 7-segmented with 0, 0, 4, 1, 5 (2 longer reaching basal part of terminal segment), 3, 4 plumodenticulate setae respectively.

Mandible (Fig. 6B).—Palp 3-segmented, with 11 plumodenticulate setae on distal segment.

Maxillule (Fig. 6G).—Coxal endite with 17 setae. Basial endite with 30 setae. Endopod 2-segmented, proximal segment with 2 setae, distal segment with 4 setae (2 subterminal, 2 terminal).

Maxilla (Fig. 7C).—Coxal endite bilobed, with 15+7 setae. Basial endite bilobed, with 11+11 setae. Endopod unsegmented, with 3 long basal setae. Scaphognathite with 67–70 plumose marginal setae and 4 anterior and 1 posterior lateral seta.

First Maxilliped (Fig. 8E).—Three protopodal plumodenticulate setae. Coxal endite with 7 plumodenticulate setae. Basial endite with 13 plumodenticulate setae. Endopod unsegmented, with 4 subterminal and 2 terminal setae. Exopod 2-segmented, proximal segment with 3 distal long plumodenticulate setae, distal segment with 5 long, terminal plumose setae. Epipod with 15 long plumodenticulate setae.

Second Maxilliped (Fig. 9C).—Coxa and basis not differentiated, with 1 seta. Endopod 5-segmented, with 3, 3, 2, 6 and 10 setae respectively. Exopod 2-segmented, proximal with 3 medial setae and distal segment with 3 long, terminal plumose setae. Epipod with 6 setae.

Third Maxilliped (Fig. 9G).—Coxa and basis not differentiated, with 17 plumodenticulate setae. Endopod 5-segmented, ischium, merus, carpus, propodus, and dactylus with 17, 14, 10, 12, and 10 setae respectively. Exopod 2-segmented, proximal segment with 5 simple setae and distal segment with 5 long, terminal plumose setae. Epipod elongated, with 7 plumodenticulate setae on proximal part, and 27 long plumodenticulate setae on distal part.

Sternal Plate (Fig. 4C).—Setation as figured.

Pereiopods (Fig. 10C–E, 4C).—All segments well differentiated and with setae as figured. Tubercles, with different degree of development, present on coxa of chelipeds and pereiopods 3–5. Chelipeds with well-developed hooked ischial spine. Dactylus of fifth pereiopod with 3 long terminal setae and 1 short terminal spine.

Abdomen (Fig. 11H).—Six somites, somite 1 with 3 pairs of lateral setae, 13 mid-dorsal simple setae, and 3 simple setae. Setation on somites 2 to 6 as figured. Somites 2–5 with 1 pair of biramous pleopods.

Pleopods (Fig. 10I).—Endopod unsegmented, with 3 cincinuli. Exopod unsegmented, with 22, 22, 20, 18 long, marginal, plumose natatory setae on pleopods 1–4 respectively.

Uropods (Fig. 11H).—Two-segmented on somite 6, proximal segment without setae, distal segment with 13 long, marginal, plumose natatory setae.

Telson (Fig. 11C).—Semisquared, with 1 pair of lateral setae, 4 pairs of medial setae, and 6 long setae on posterior margin.

Discussion

Although most terrestrial crabs of the family Gecarcinidae, including *Cardisoma armatum*, tolerate brackish water and even freshwater, their larvae require, as far as known, at least 15‰ salinity for successful development to metamorphosis (cf. Costlow and Bookhout, 1968). The osmotic sensitivity of the larval stages forces ovigerous females to migrate to the sea to release the larvae in waters with higher salinities (Adiyodi, 1988). The results of the salinity experiments in our present study also show that the larvae of *C. armatum* tolerate reduced salinities to about 15‰, but not oligohaline or freshwater conditions of habitats where adults of this species live and produce eggs (cf. Ameyaw-Akumfi, 1987, 1989; Oyenekan, 1995). Interestingly, the larvae appear to prefer moderately brackish conditions of about 25‰ rather than full-strength seawater (Figs. 1, 2), which suggests adaptation to some larval retention within the lower estuarine parts of coastal mangrove swamps adjacent to the habitats of the adults.

The larval morphology of the Gecarcinidae, in general, is poorly documented. The complete larval development was only described for four species, one of the genus *Gecarcinus*, two of *Cardisoma*, and one of *Discoplax*. For

Table 1. Morphological differences between zoeal stages of *Cardisoma armatum*, *C. carnifex*, and *C. guanhumi*. Abbreviations: a, aesthetascs; s, setae; cs, coxal endite setation; bs, basial endite setation; tp, terminal processes; e, endopod; es, endopod setation; scs, scaphognathite setation.

Zoeal stage and feature	*C. armatum* (present study)	*C. carnifex* (Kannupandi *et al.* 1980)	*C. carnifex* (Flores *et al.* 2003)	*C. guanhumi* (Costlow and Bookhout, 1968)
Zoea I				
Antennule (a,s)	4, 1	3, 1	3, 1	2, 2
Maxillule (cs,bs)	6, 5	6, 5	6, 5	5, 5
Maxilla (es)	2, 3	7	2, 3	2, 3
Maxilliped 1 (es)	2, 2, 1, 2, 5	2, 2, 2, 2, 5	2, 2, 1, 2, 5	2, 2, 1, 2, 5
Maxilliped 2 (es)	1, 1, 6	1, 3, 3	1, 1, 6	1, 1, 6
Zoea II				
Maxillule (bs)	7	8	–	6
Telson (tp)	3	3	–	3
Zoea III				
Antenna (e)	present	absent	–	absent
Maxillule (bs)	7	9	–	7
Zoea IV				
Antennule (a,s)	6, 1	7, 0	–	5, 2
Maxillule (bs)	9	12	–	10
Zoea V				
Antennule (a,s)	8, 1	10, 0	–	10, 1
Maxillule (cs, bs)	7, 13	10, 14	–	9, 16
Maxilla (cs, bs, scs)	12, 12, 32	14, 15, 37	–	12, 14, 34
Zoea VI	present	absent	–	absent

species of *Epigrapsus*, *Gecarcoidea*, and *Johngarthia*, only the first zoeal stage has been described.

Apparently zoeae of Gecarcinidae display a unique combination of characters differing from the rest of the grapsoid families. Cuesta *et al.* (2002) observed a typical combination of antennal and telson morphology, together with a distinct setation on the endopod of the second maxilliped (1, 1, 6), not found in zoeae of any other species within the Grapsoidea. Among the genera of Gecarcinidae, the only important differences observed were in the setation of the maxillar endopod, the number of abdominal somites with remarkable dorsolateral processes, and in the degree of development of the lateral spines of the telson.

Cuesta *et al.* (2002) distinguished two major groups within the Gecarcinidae, as follows: (1) *Epigrapsus*, *Gecarcinus*, and *Gecarcoidea* are characterized by a 2, 2 maxillar endopod setation and two pairs of well-developed lateral spines on the telson of the first zoea. (2) The genera *Cardisoma* and *Discoplax* present a 2, 3 maxillar endopod setation and minute lateral spines on the telson of the first zoeal stage. The latter character was shown for the first time for the first zoeal stages of *Cardisoma armatum*, *C. carnifex*, *C. guanhumi*, and *Discoplax hirtipes* in Cuesta *et al.* (2002). In a redescription of the first zoea of *C. carnifex* (Flores *et al.*, 2003), these minute spines were illustrated for the first time, but with only one pair, while Cuesta *et al.* (2002) observed two pairs in the same species. In *C. armatum*, we observed now that two pairs of such minute spines were invariably present in the zoea I stage, but they tended to disappear in subsequent zoeal stages. Two pairs of spines occurred occasionally also in the zoea II stage. In zoeal stages III–V, no minute spines at all were observed on the telson. In the zoea VI stage, however, a few individuals showed again a pair of such spines, suggesting that this character may occasionally occur also in the later stages, although probably very rarely. A re-examination of the zoeal stages II–V of *Cardisoma carnifex*, *C. guanhumi*, *Discoplax hirtipes*, and *Gercarcinus lateralis* is thus required to know if the presence of minute lateral spines on the telson furcae of the first zoeal stage, followed by a disappearance of this character in later zoeal stages, is perhaps generic or even a familial character.

Minor differences in setation occur between the larval stages of the four species of *Cardisoma* with complete larval development described. Some of the main differences of *C. carnifex* are probably due to inaccuracies in the description and illustration of the larvae of this species. Some of these errors were corrected by Cuesta *et al.* (2002: 1682) and in the redescription of the zoea I by Flores *et al.* (2003; see Table 1). The main difference in the larval development of *C. armatum*, *C. carnifex*, and *C. guanhumi* is in the number of zoeal stages, with six in *C. armatum* and five in two other species. This could be an explanation for diffences in the setation (normally with a smaller number of setae for the same appendage) between equivalent zoeal stages of *C. armatus* and the other species (Table 1).

The zoea VI of *C. armatum* cannot be considered an "extra" stage, because no zoea V larvae moulted directly to a megalopa. As in other species with an extended mode of larval development, however, this stage presents an unusual setation pattern that breaks the expected rule: On the basis of the first maxilliped, the setation 2,2,4,4 differs clearly from the expected 2,2,3,3, which consistently has been found in the zoeal development of all other gecarcinids studied so far (Fig. 8D). In the second maxilliped, the endopod setation is 1,1,7 (Fig. 9B) instead of the typical gecarcinid pattern of 1,1,6.

Based on zoeal morphology, the group represented by the genera *Epigrapsus*, *Gecarcinus*, and *Gecarcoidea* shows clear affinities to the family Varunidae. The genera *Cardisoma* and *Discoplax*, by contrast, share antennal and abdominal morphology, as well as the setation pattern of the maxillar endopod (2, 3), with the Sesarmidae. The presence of lateral spines on the carapace and telson, as well as the setation of the endopod of the second maxilliped (1,1,6), on the other hand, are clearly distinguishing characters.

The scarce available data on megalopal morphology do not allow for intergeneric comparisons. However, there may be a distinct character common to species of *Cardisoma*: the chelipeds of the megalopae of *C. carnifex*, *C. guanhumi*, and *C. armatum* consistently present a hooked ischial spine. This character has not been described or illustrated for *Discoplax hirtipes* and *Gecarcinus lateralis*. A re-examination of the megalopae of these species may show whether this feature has been overlooked, so that it could be typical of *Cardisoma* or, more generally, the family Gecarcinidae. Because no other grapsoid megalopae are known to show this character, it could possibly distinguish *Cardisoma* or gercacinid megalopae from those of other grapsoids.

The presence of tubercles on the coxae of chelipeds and pereiopods 3–5 may be another common feature which has

not previously been described for gercarcinid megalopae. In *Cardisoma armatum*, this character is more developed on the chelipeds and on the fourth pereiopods than on other walking legs (Figs. 4C, 10C–E). Perhaps, this feature has been overlooked in previous descriptions of gecarcinid megalopae, requiring another re-examination of the available materials in order to evaluate its potential taxonomic and phylogenetic value.

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