

Larval development of *Cyrtograpsus affinis* (Dana) (Decapoda, Brachyura, Varunidae) from Rio de la Plata estuary, reared in the laboratory*

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SUMMARY: The complete larval development of the crab *Cyrtograpsus affinis* (Brachyura, Varunidae) was obtained by culture in the laboratory. Five zoeal stages, the megalopa and the first crab are described and illustrated. Larval development from hatching to first crab took 29 days at 20° C and 35 PSU. The genus *Cyrtograpsus* only consists of three species. Larval development of *C. altimanus* and *C. angulatus* had been described previously. In the present study, morphological larval characters of the three species are compared. Generic larval features are also compared with those of other Varunidae genera.

Key words: *Cyrtograpsus affinis*, larval development, zoea, megalopa, Grapsoidea, Varunidae.

INTRODUCTION

The crab family Varunidae includes marine, brackish and freshwater species (Anger 1995). The genus *Cyrtograpsus* comprises three species that inhabit the temperate waters of the southwestern Atlantic: *C. angulatus* Dana, 1851, *C. altimanus* Rathbun, 1914 and *C. affinis* (Dana, 1851). The latter was included in *Hemigrapsus* by Rathbun (1918) but it was re-transferred to *Cyrtograpsus* by Boschi (1964).

Adults of *C. angulatus* and *C. altimanus* have wide geographical distributions and form dense and conspicuous littoral populations (Spivak, 1997).

They coexist in rocky intertidal habitats (Scelzo and Lichtschein de Bastida, 1979) and show different abilities for invading estuarine habitats (Spivak, in press). In addition to morphological differences, these *Cyrtograpsus* species markedly differ in size. *C. angulatus* adults are three times larger than *C. altimanus*: the maximum observed male body sizes are 58.8, and 19.0 mm carapace width respectively (Spivak, in press). *C. affinis*, a sublittoral species, is the smallest *Cyrtograpsus* and seems to be morphologically similar to juvenile *C. altimanus* (Boschi, 1964; Rathbun, 1918). Most of the scarce findings of *C. affinis* were made near the mouth of Rio de la Plata estuary: 94% of the 66 specimens examined by Rathbun (1918: 266) were collected "off Rio de la Plata"; Boschi (1964:39) reexamined part of this

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material and studied 4 new specimens that also correspond to that area.

A sample of males and females *Cyrtograpsus* sp. were collected in a subtidal muddy estuarine habitat in the Rio de la Plata, near the coasts of Montevideo, Uruguay, during a fishing cruise of the "BIP Dr. Eduardo Holmberg" (Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina). They were similar to *C. altimanus* but smaller (maximum observed male carapace width was 11.2 mm) and morphometrically different (males have larger chelipeds); they were assigned to *C. affinis*. (Spivak, unpublished).

The larval development of *C. altimanus* and *C. angulatus* was described from laboratory reared individuals (Scelzo and Lichtschein de Bastida 1979; Rieger and Vieira, 1997). The aim of this paper is to describe the larval development of *C. affinis* reared in the laboratory.

MATERIAL AND METHODS

Males and females of *Cyrtograpsus affinis* were collected in the Rio de la Plata estuary (35° 07' S, 56° 02' W) during a fishing cruise of the "BIP Dr. Eduardo Holmberg" (Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina) on November 19, 1997. The sample was taken with a bottom trawl, 1cm mesh size. The bottom (10 m deep) was muddy and had abundant empty bivalve shells. Water salinity and temperature at the bottom were 21.2 PSU and 18.1°C, respectively. One ovigerous crab, transported to the laboratory at Departamento de Biología, Universidad de Mar del Plata, was maintained in aquaria containing natural sea water until the eggs hatched (December 12, 1997). The larvae were transferred to beakers of 500 ml capacity for mass culture. Natural sea water was used at a temperature of 20°C and salinity of 35 PSU. Larvae were subjected to continual artificial light regime: 8/16 h (L/D). First zoeae were reared and fed with the algae *Chaetoceros calcitrans*. Zoea II were fed with a mixed diet of algae *C. calcitrans* and *Artemia* sp. nauplii. From zoea III to V, *Artemia* sp. nauplii was offered *ad libitum*.

Drawings and measurements were made using a Wild MZ6 and Olympus BH compound microscope, both equipped with a *camera lucida*. All measurements were made by an ocular micrometer. Drawings were based on 5 larvae, and measurements on 10 larvae per stage. In zoea larvae, 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; carapace width (CW) as the distance between the tips of the lateral spines. In the zoea I stage, dorsal and rostral spine length (DS and RS, respectively) were measured from the base to the tip of each one; carapace height (CH) was estimated as $RDL - (DS + RS)$. In the megalopa stage, carapace length (CL) was measured from the base of the rostrum to the posterior margin; anterior carapace width (CW1) as the distance between the tips of the anterolateral protuberances and posterior carapace width (CW2) as the maximum width. The long natatory setae on the distal exopod segments of the first and second maxillipeds are truncated in the Figures 7 and 8. Also, long aesthetascs of the antennules are truncated in the Figure 3.

Zoea I larvae of *Cyrtograpsus angulatus* and *C. altimanus* were obtained from ovigerous females collected from Mar Chiquita coastal lagoon (37°45' S; 57°26' W) and the rocky seashore of Santa Clara del Mar (37°50' S; 57°30' W), respectively. These larvae were also dissected, measured, and their morphology compared with the original descriptions of the larval development of these species by Rieger and Vieira (1997) and Scelzo and Lichtschein de Bastida (1979).

Quantitative relationships between morphometrical variables were described with least-square regressions (after *G* tests of homogeneity for normal distribution). Allometric growth of zoeae was studied using the potential model ($y = ax^b$). The null hypothesis of isometry ($b = 1$) was tested in *Cyrtograpsus affinis* by means of a *t* test (Zar, 1984: 271) after logarithmic transformation of the data.

Samples of larvae (zoea I to megalopa) and adult females of *C. affinis*, and zoea I of *C. altimanus* and *C. angulatus* were deposited at the United States National Museum of Natural History, Washington, under the catalog numbers USNM 260933, 260934, and 260935 respectively.

Description and figures are arranged according to the standard proposed by Clark *et al.* (1998).

RESULTS

The complete zoeal development of *Cyrtograpsus affinis* took place through five zoeal and one megalopa stages. Mean sizes, and first day of appearance of each zoeal stage are represented in the Table 1.

TABLE 1. – Mean (\pm SD) rostradorsal length (RDL), carapace width (CW), carapace length (CL) in mm, and first day of appearance of the larval stages of *Cyrtograpsus affinis* reared in the laboratory. Two measurements of megalopae and first crab carapace width were made between antero-lateral spines and between posterior protuberances (spines) (CW1 and CW2 respectively).

Stage	RDL	CW	CW1/ CW2	CL	1 st day to appear
Zoea I	0.89 \pm 0.04	0.52 \pm 0.02	-	0.41 \pm 0.01	0
Zoea II	1.32 \pm 0.08	0.62 \pm 0.02	-	0.50 \pm 0.02	4
Zoea III	1.60 \pm 0.07	0.73 \pm 0.05	-	0.65 \pm 0.04	8
Zoea IV	2.23 \pm 0.12	0.96 \pm 0.08	-	0.89 \pm 0.04	13
Zoea V	2.83 \pm 0.14	1.15 \pm 0.10	-	1.17 \pm 0.07	16
Megalopa	-	-	0.99 \pm 0.04/1.24 \pm 0.12	1.38 \pm 0.08	19
Crab 1	-	-	1.60 \pm 0.08/1.60 \pm 0.07	1.66 \pm 0.08	28

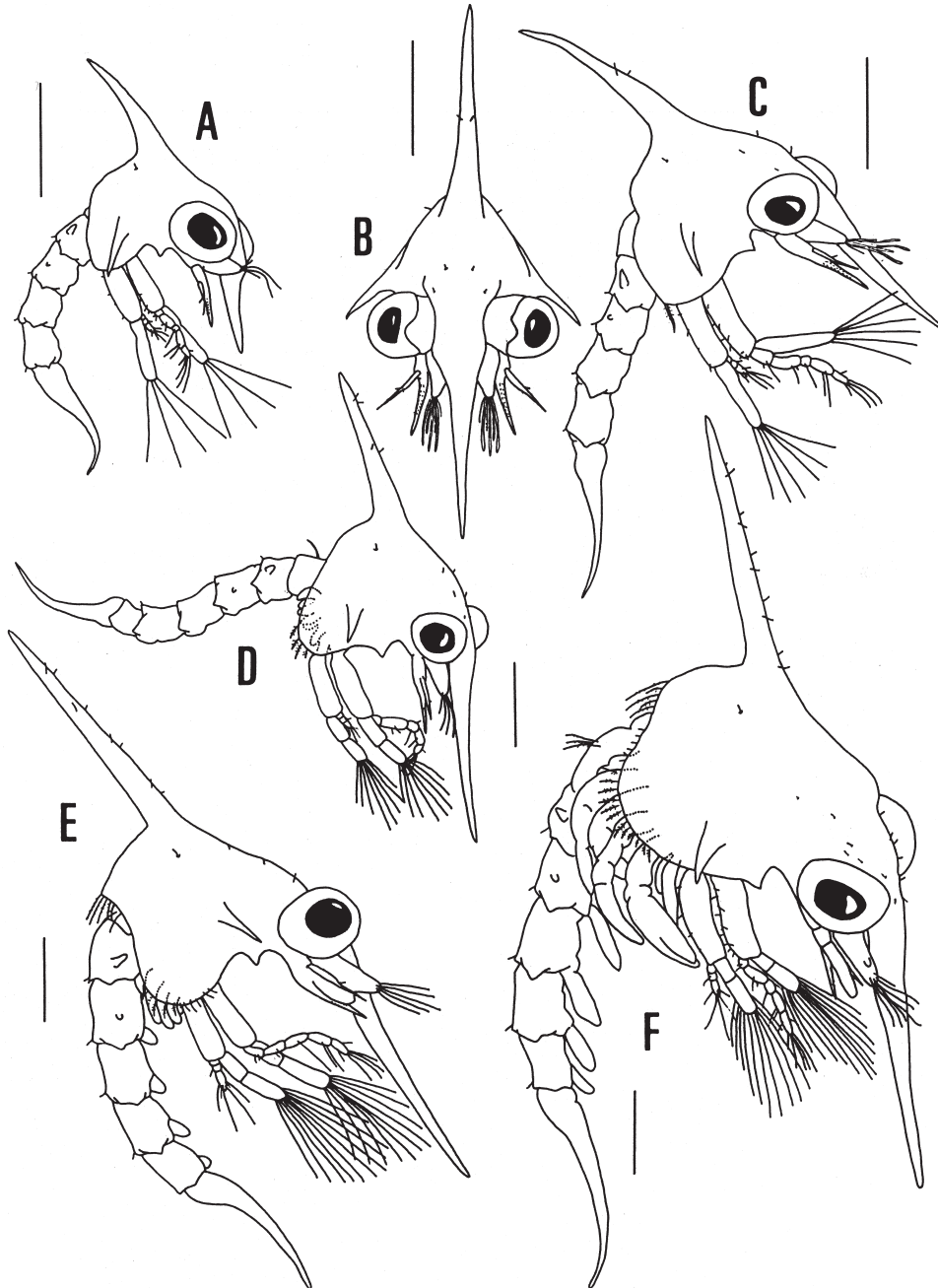


FIG. 1. – *Cyrtograpsus affinis* (Dana). Lateral view: A, zoea I; B, zoea II, frontal view; C, zoea II; D, zoea III; E, zoea IV; F, zoea V. Scale bars = 0.3 mm.

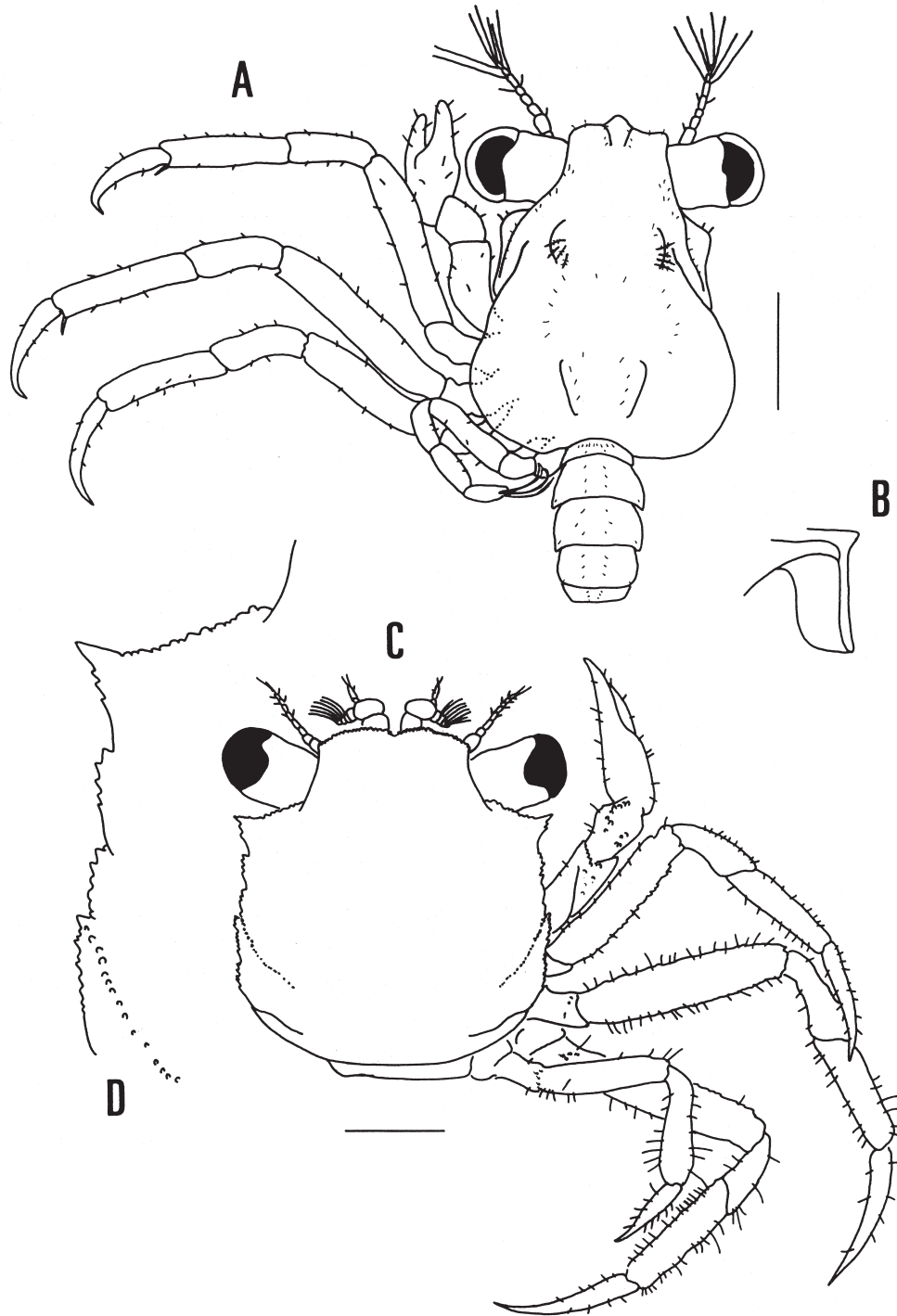


FIG. 2. — *Cyrtograpsus affinis* (Dana). A, megalopa, dorsal view; B, megalopa, lateral view of frontal region; C, first crab; D, first crab, antero-lateral denticulation. Scale bars = 0.5 mm.

Description

Zoea I

Carapace (Fig. 1A). Globose, smooth and without tubercles. Dorsal and rostral spines long and straight. Lateral spines well developed. A pair of

posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (Fig. 3A). Uniramous. Endopod absent. Exopod unsegmented with 3 aesthetascs (2 long a 1 thin and short) and 1 seta.

Antenna (Fig. 4A). Well developed protopod that did not reach at the middle of rostral spine and bear-

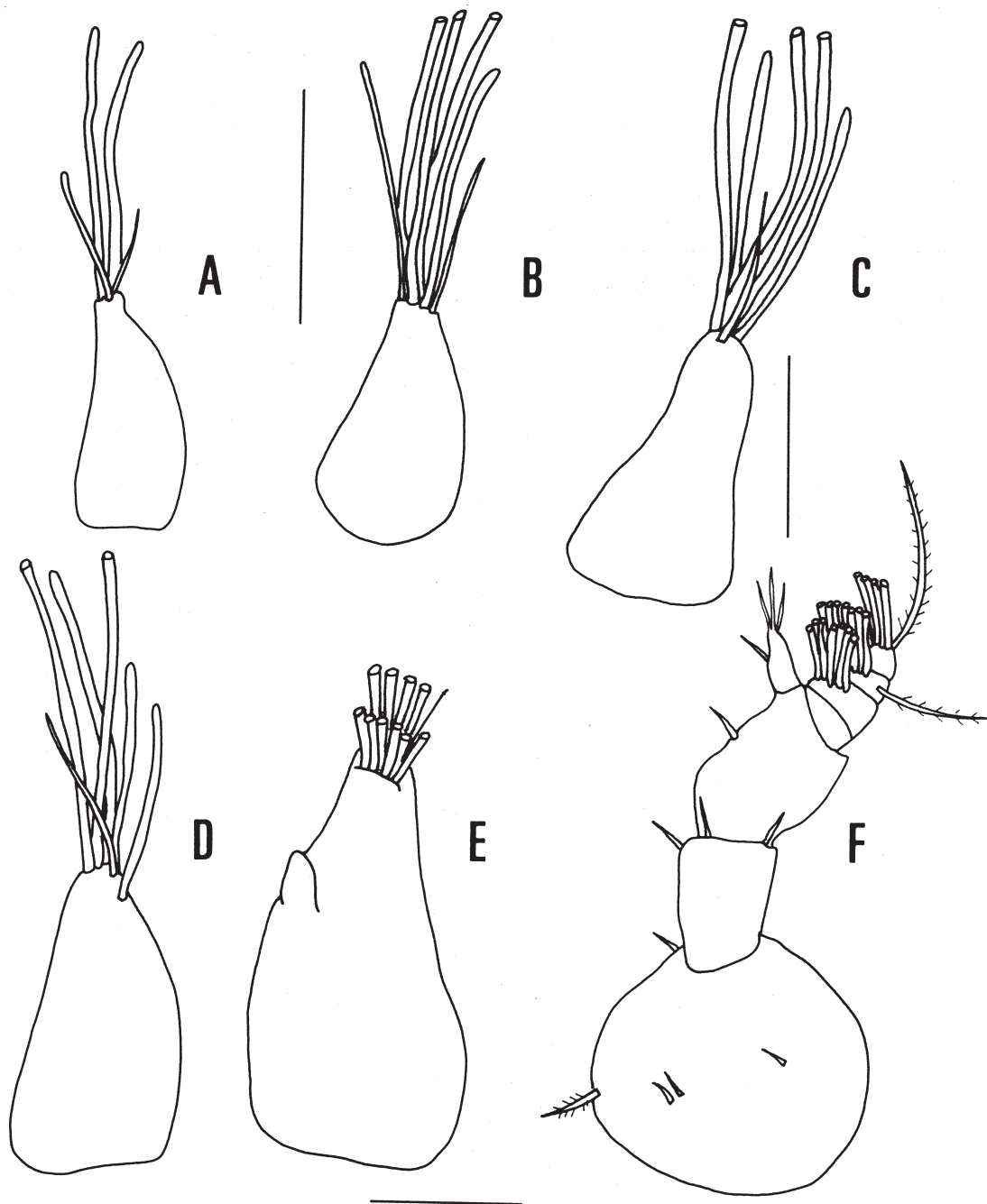


FIG. 3. — *Cyrtograpsus affinis* (Dana). Antennule. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalopa. Scale bars = 0.1 mm.

ing two rows of spines. The exopod is elongated, bears 2 lateral spines and is acute in its distal half.

Mandible. Endopod palp absent.

Maxillule (Fig. 5A). Coxal endite with 5 plumodenticulate setae. Basal endite with 5 setae (2 cuspidate and 3 plumodenticulate). Endopod 2-segmented with 1 plumodenticulate seta in the proximal segment and 1 subterminal and 3 terminal plumodenticulate setae in the distal segment. Exopod absent.

Maxilla (Fig. 6A). Coxal endite slightly bilobed with 3+3 plumodenticulate setae. Basal endite bilobed with 5+4 plumodenticulate setae. Endopod unsegmented, bilobed with 2 long plumodenticulate setae on each lobe. Scaphognathite with 4 plumose marginal setae and a 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 lateral + 4 terminal) setae. Exopod unseg-

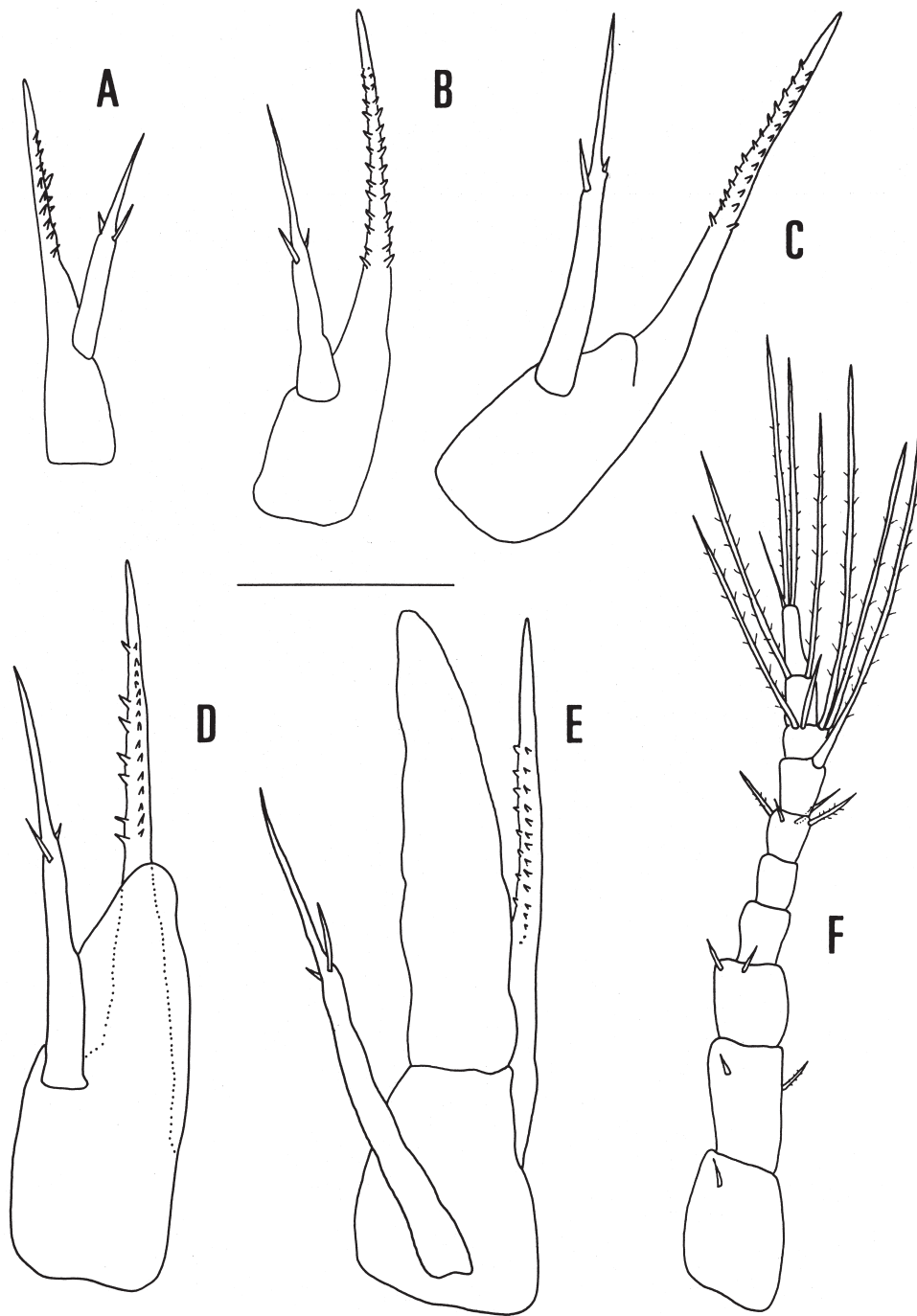


FIG. 4. — *Cyrtograpsus affinis* (Dana). Antenna. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalopa. Scale bar A-E = 0.1 mm, F = 0.2 mm.

mented, with 4 long terminal plumose natatory setae.

Second Maxilliped (Fig. 8A). Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (3 subterminal + 3 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Third Maxilliped. Absent.

Pereiopods. Absent.

Abdomen (Fig. 11A). Five abdominal somites. Somites 2 and 3 with pair of dorsolateral processes. Somites 2-4 with a pair of posterodorsal setae. Pleopods absent.

Telson (Fig. 11A). Telson bifurcated with 3 pairs of serrulate setae on posterior margin. In the inner distal part of each furcal arm a row of teeth, 4 terminal longer than the rest.

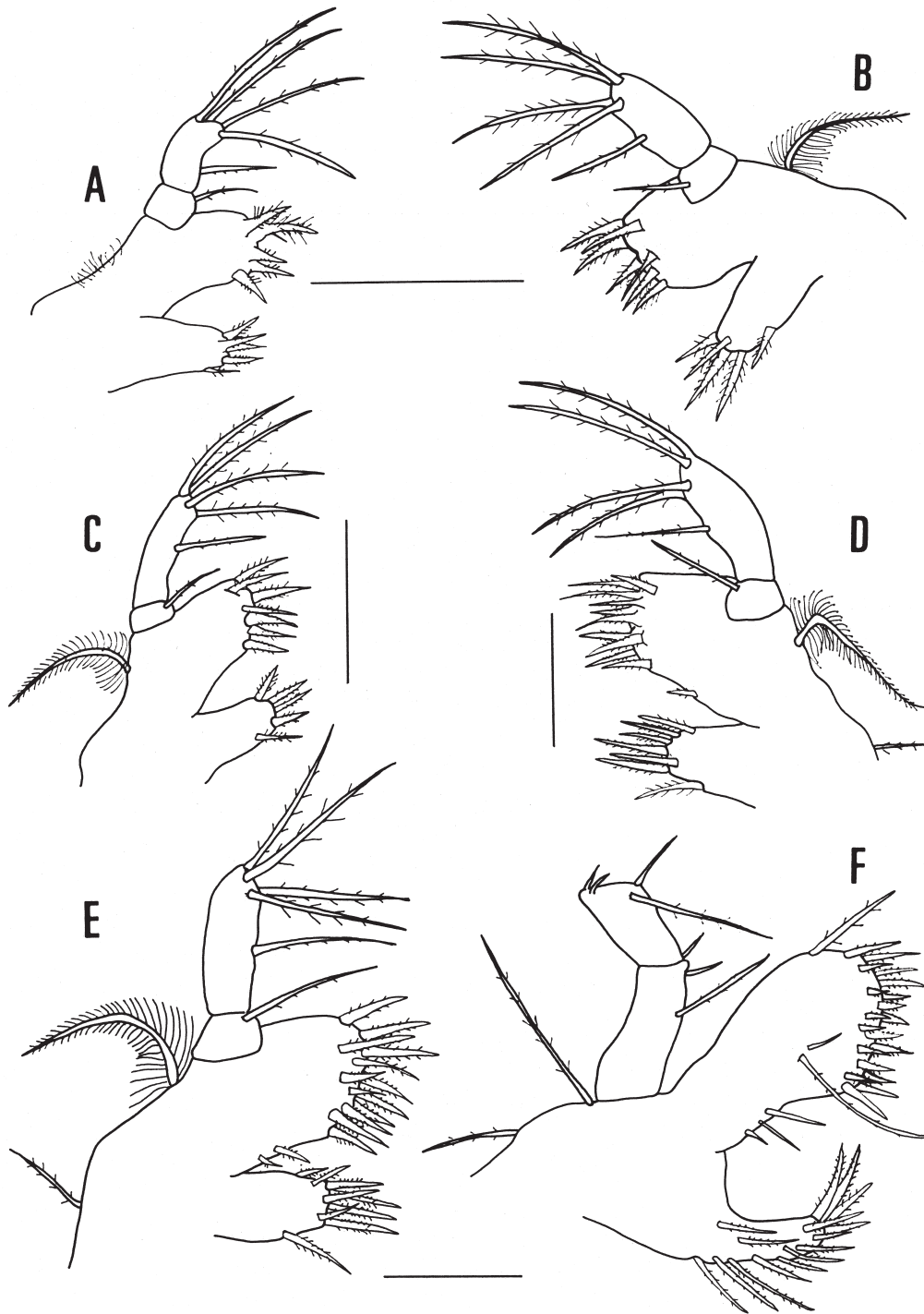


FIG. 5. – *Cyrtograpsus affinis* (Dana). Maxillule. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalopa. Scale bars = 0.1 mm.

Zoea II

Carapace (Fig. 1B,C). One pair of simple seta on the middle part of dorsal spine. Two pairs of anterodorsal setae. Each ventral margin with 1 plumodenticulated setae. Eyes stalked. Otherwise unchanged.

Antennule (Fig. 3B). Exopod with 2 additional aesthetascs. Otherwise unchanged.

Antenna (Fig. 4B). Unchanged.

Mandible. Unchanged.

Maxillule (Fig. 5B). Basal endite with 7 setae (2 plumodenticulate cuspidate and 5 plumodenticulate). Exopod present as a long plumose marginal

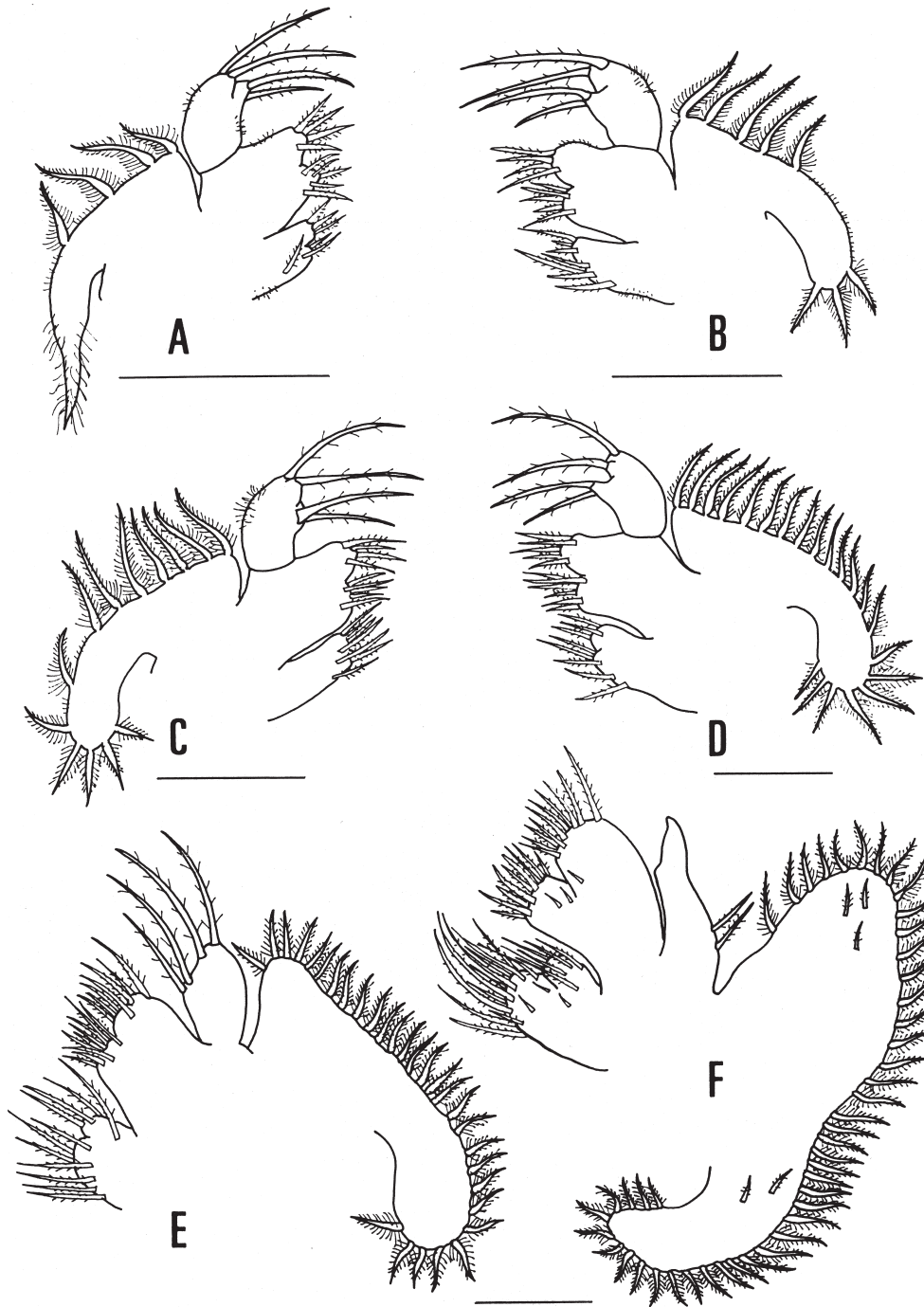


FIG. 6. – *Cyrtograpsus affinis* (Dana). Maxilla. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalopa. Scale bars = 0.1 mm.

seta. Otherwise unchanged.

Maxilla (Fig. 6B). Coxal endite bilobed with 3+4 plumodenticulated setae. Scaphognathite with 5+3 plumose marginal setae. Otherwise unchanged.

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

Second Maxilliped. Exopod unsegmented, with 6

long terminal plumose natatory setae. Otherwise unchanged.

Third Maxilliped. Absent.

Pereiopods. Absent.

Abdomen (Fig. 11B). Unchanged.

Telson (Fig. 11B). Inner distal part of each furcal arm with a row of 7-8 teeth increasing in size distally. Otherwise unchanged.

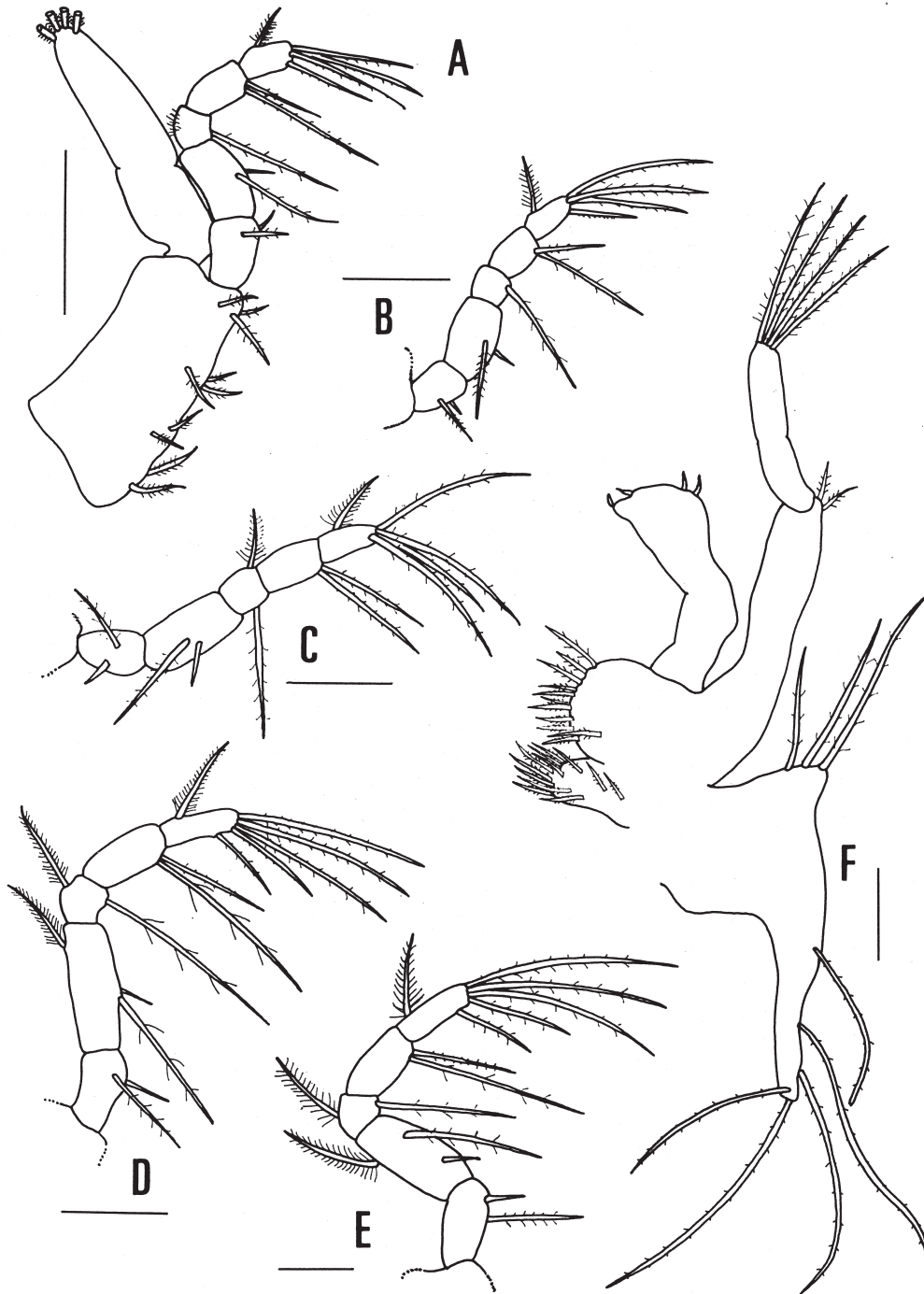


FIG. 7. — *Cyrtograpsus affinis* (Dana). First maxilliped. A, zoea I; B, zoea II, endopod; C, zoea III, endopod; D, zoea IV, endopod; E, zoea V, endopod; F, megalopa. Scale bars = 0.1 mm.

Zoea III

Carapace (Fig. 1D). Dorsal spine with 2 pairs of simple setae. Each ventral margin with 4 plumodenticulated setae. Otherwise unchanged.

Antennule (Fig. 3C). Unchanged.

Antenna (Fig. 4C). Endopod bud present. Otherwise unchanged.

Mandible. Unchanged.

Maxillule (Fig. 5C). Unchanged.

Maxilla (Fig. 6C). Scaphognathite with 13 plumose marginal setae. Otherwise unchanged.

First Maxilliped (Fig. 7C). Endopod 3rd segment with one additional dorsal plumose setae. Exopod unsegmented, with 8 long terminal plumose natatory setae. Otherwise unchanged.

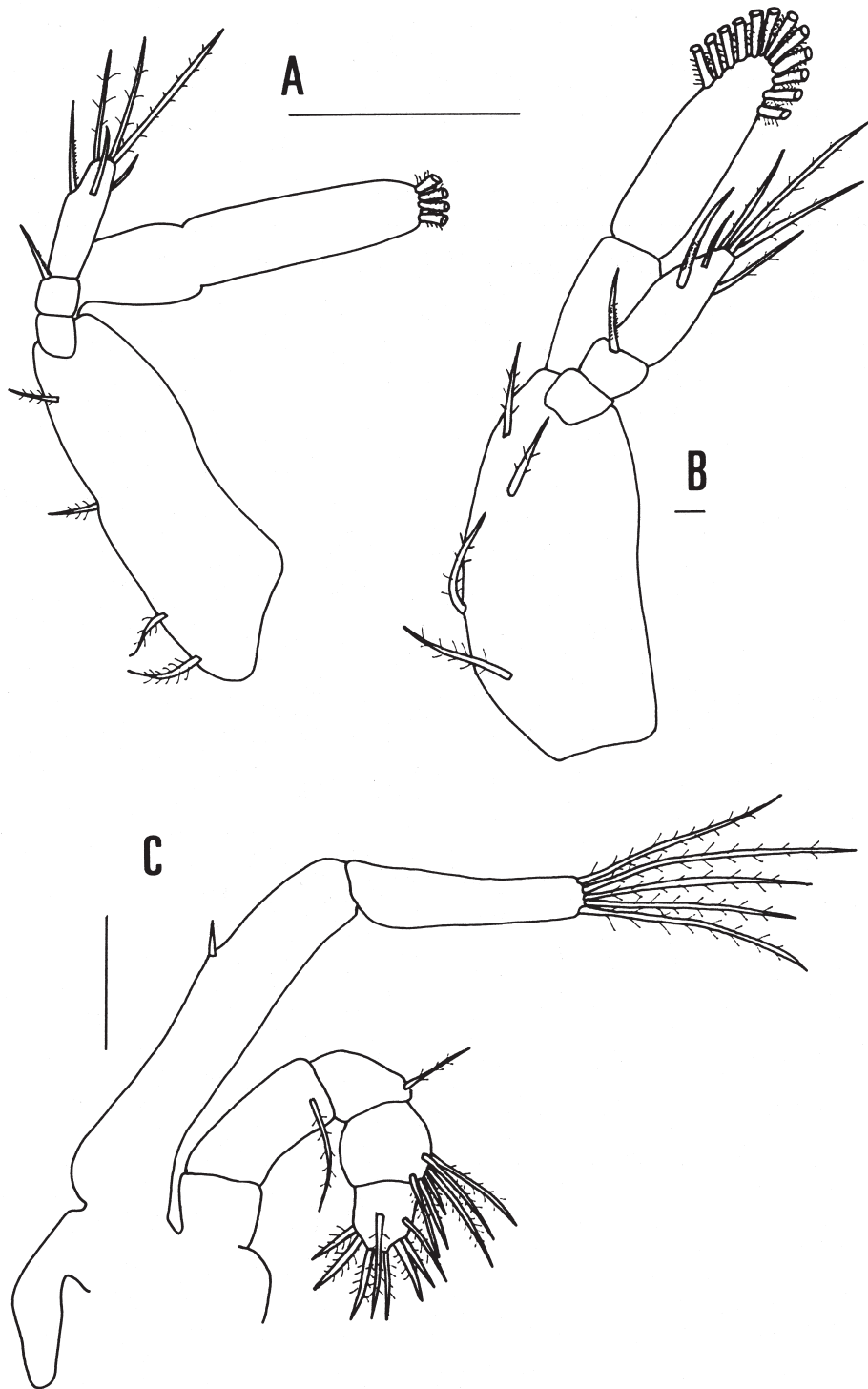


FIG. 8. — *Cyrtograpsus affinis* (Dana). Second maxilliped. A, zoea I; B, zoea V; C, megalopa. Scale bars = 0.1 mm.

Second Maxilliped. Exopod unsegmented, with 8 long terminal plumose natatory setae. Otherwise unchanged.

Third Maxilliped. Present as undifferentiated bud.

Pereiopods. Present as rudimentary buds.

Abdomen (Fig. 11C). First somite with 1 long mid-dorsal setae. Somite sixth now present, without setae. Otherwise unchanged.

Telson (Fig. 11C). Posterior margin with 4 pairs of serrulate setae. One row with 9-10 teeth in the inner distal part of each furcal arm. Otherwise unchanged.

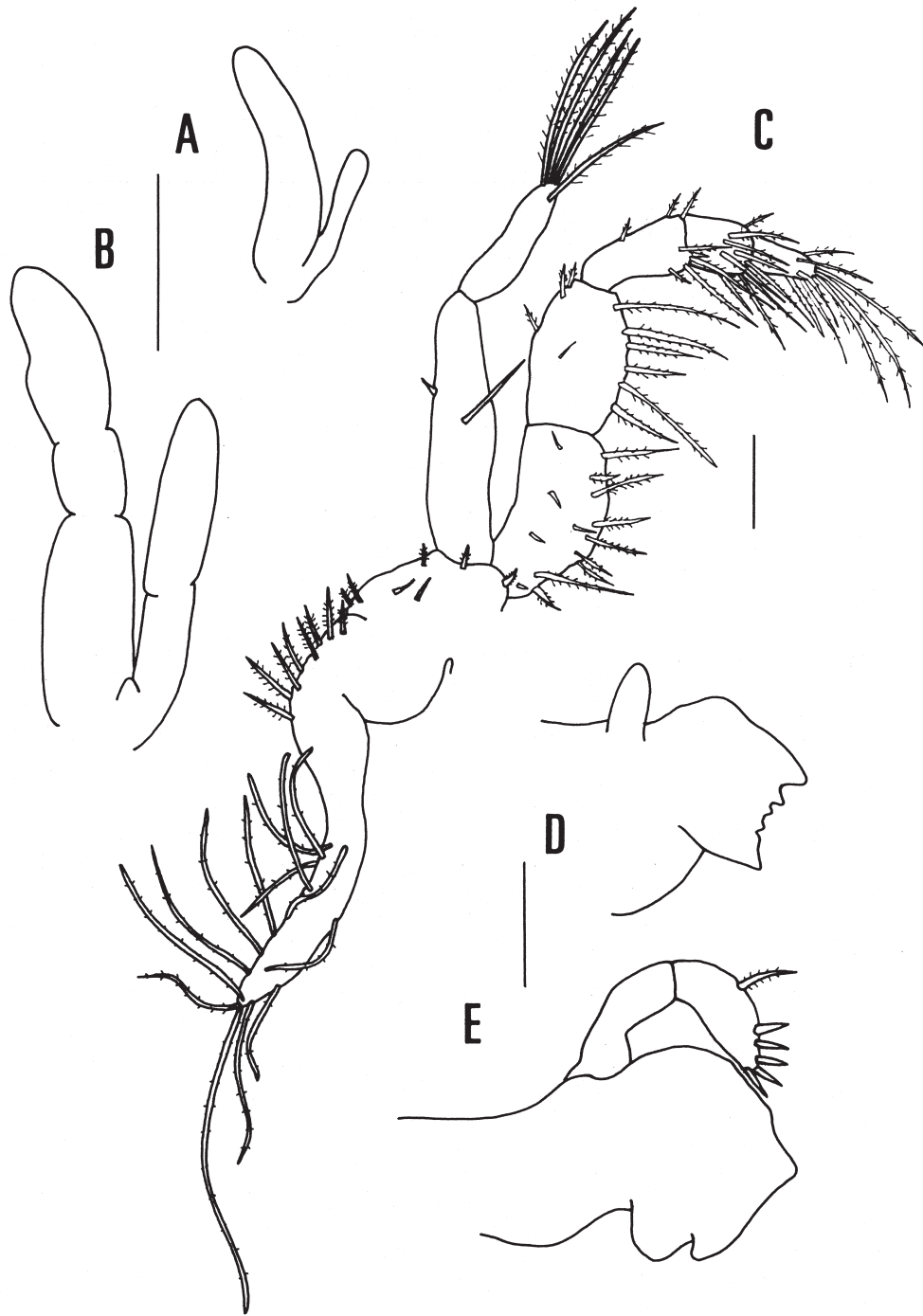


FIG. 9. — *Cyrtograpsus affinis* (Dana). Third maxilliped: A, zoea IV; B, zoea V; C, megalopa. Mandible: D, zoea V; E, megalopa. Scale bars = 0.1 mm.

Zoea IV

Carapace (Fig. 1E). Dorsal spine with 4 pairs of simple setae. Posterior margin with 4 long plumodenticulated setae. Each ventral margin with 10 plumodenticulated setae. Otherwise unchanged.

Antennule (Fig. 3D). Unchanged.

Antenna (Fig. 4D). Endopod longer, almost 1/2 of protopod length. Otherwise unchanged.

Mandible. Unchanged.

Maxillule (Fig. 5D). Coxal endite with 7 plumodenticulated setae. Basial endite with 11 setae (2 plumodenticulate cuspidate and 9 plumodenticulate). Epipodal seta present. Otherwise unchanged.

Maxilla (Fig. 6D). Coxal endite bilobed with 3+5 plumodenticulated setae. Basial endite bilobed with 6+5 plumodenticulate setae. Scaphognathite with 21 plumose marginal setae. Otherwise unchanged.

First Maxilliped (Fig. 7D). Endopod 2nd segment with one additional dorsal seta; distal segment with 6 (2 subterminal + 4 terminal) setae. Exopod 2-segmented, with 10 long plumose natatory setae on the distal segment. Otherwise unchanged.

Second Maxilliped. Exopod 2-segmented, with 10 long plumose natatory setae on the distal segment. Otherwise unchanged.

Third Maxilliped (Fig. 9A). Biramous and unsegmented.

Pereiopods (Fig. 10A). Present, undifferentiated. Chelipeds bilobed.

Abdomen (Fig. 11D). First somite with 3 long mid-dorsal setae. Pleopods buds present on somites 2-5. Otherwise unchanged.

Telson (Fig. 11D). One row with 11-12 teeth in the inner distal part of each furcal arm. Otherwise unchanged.

Zoea V

Carapace (Fig. 1F). Dorsal spine with 5 pairs of setae. Seven pairs of anterodorsal setae. Posterior margin with 5 long plumodenticulated setae. Each ventral margin with 13 plumodenticulated setae. Otherwise unchanged.

Antennule (Fig. 3E). Biramous. Endopod bud present. Exopod with 6 subterminal and 4 terminal aesthetascs and 1 terminal simple seta.

Antenna (Fig. 4E). Endopod 2-segmented, longer than protopod. Otherwise unchanged.

Mandible (Fig. 9D). Unsegmented palp present.

Maxillule (Fig. 5E). Coxal endite with 9 plumodenticulated setae. Basial endite with 15 setae (2 plumodenticulate cuspidate and 13 plumodenticulate). Otherwise unchanged.

Maxilla (Fig. 6E). Coxal endite bilobed with 4+7 plumodenticulated setae. Basial endite bilobed with 9+7 plumodenticulate setae. Scaphognathite with 29 plumose marginal setae. Otherwise unchanged.

First Maxilliped (Fig. 7E). Exopod 2-segmented, with 12 long plumose natatory setae on the distal segment. Otherwise unchanged.

Second Maxilliped (Fig. 8B). Exopod 2-segmented, with 12 long plumose natatory setae on the distal segment. Otherwise unchanged.

Third Maxilliped (Fig. 9B). Endopod and exopod slightly segmented.

Pereiopods (Fig. 10B). Chelipeds and pereiopods slightly segmented.

Abdomen (Fig. 11E). First somite with 5 long mid-dorsal setae. Pleopods elongated. Otherwise unchanged.

Telson (Fig. 11E). One pair of dorsomedial simple seta on the telson plate. One row with 17-18 teeth in the inner distal part of each furcal arm. Otherwise unchanged.

Megalopa

Carapace (Fig. 2A,B). Rostrum ventrally deflected (approximately 90°) with a medium cleft. Setal arrangement as figured.

Antennule (Fig. 3F). Peduncle 3-segmented with 5, 3, 1 setae respectively. Endopod unsegmented with 1 subterminal and 3 terminal setae. Exopod 4-segmented with 0, 7, 7 and 4 aesthetascs respectively and 0, 0, 1, 1 long plumose setae respectively.

Antenna (Fig. 4F). Peduncle 3-segmented with 1, 2, 2 setae respectively. Flagellum 7-segmented with 0, 0, 4, 1, 4, 2, 3 (terminal) setae respectively.

Mandible (Fig. 9E). Palp 2-segmented with 5 (1 subterminal, 4 terminal) setae on distal segment.

Maxillule (Fig. 5F). Coxal endite bilobed with 13 marginal and 2 inner plumodenticulated setae. Basial endite with 24 marginal and 2 inner (1 longer) plumodenticulated setae. Endopod 2-segmented, proximal segment with 2 setae, distal segment with 5 (1 basal, 2 subterminal and 2 shorter terminal). Exopodal and epipodal setae present.

Maxilla (Fig. 6F). Coxal endite bilobed with 6 (4 inner) + 15 (3 inner) plumodenticulated setae. Basial endite bilobed with 11 (2 inner) + 11 (1 inner) plumodenticulate setae. Endopod unsegmented with two setae on low external margin. Scaphognathite with 46 plumose marginal setae and 5 inner setae.

First Maxilliped (Fig. 7F). Epipod with 8 long setae. Coxal endite with 12 plumodenticulated setae (6 inner). Basial endite with 11 plumodenticulated setae (1 inner). Endopod unsegmented with 4 simple setae. Exopod 2-segmented, proximal segment with two distal plumodenticulated setae, distal segment with 4 long terminal plumose feeding setae.

Second Maxilliped (Fig. 8C). Epipod rudimentary. Coxa and basis not differentiated and unarmed. Endopod 5-segmented, isquium unarmed, merus, carpus, propodus and dactylus with 1, 1, 6 and 8 plumodenticulate setae respectively. Exopod 2-segmented, proximal with one medial setae and distal segment with 5 long terminal plumose feeding setae.

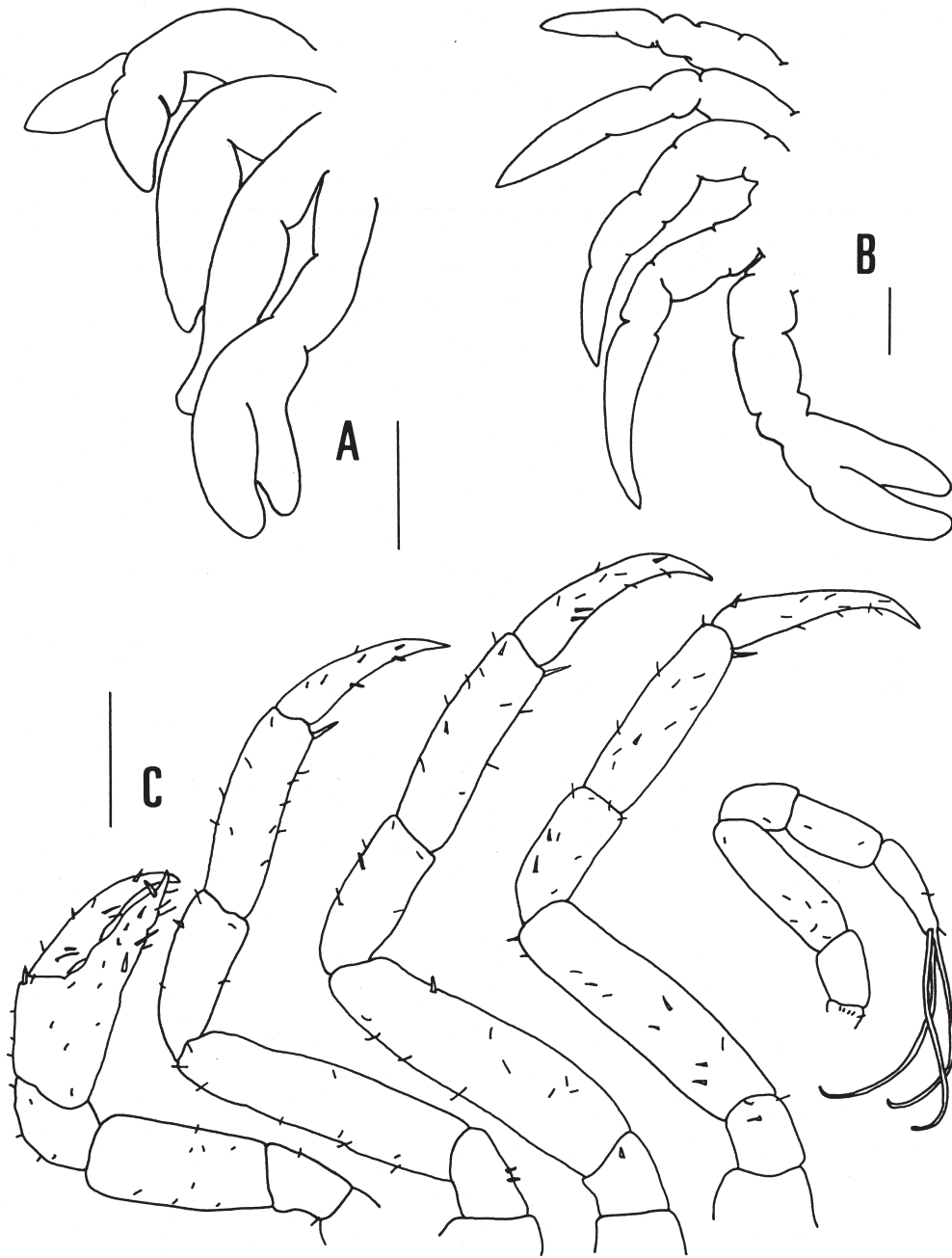


FIG. 10. – *Cyrtograpsus affinis* (Dana). Pereiopods. A, zoea IV; B, zoea V; C, megalopa. Scale bars = 0.3 mm.

Third Maxilliped (Fig. 9C). Epipod elongated with 14 long setae. Coxa and basis not differentiated with 17 plumodenticulated setae. Endopod 5-segmented, isquium, merus, carpus, propodus and dactylus with 14, 10, 8, 9 and 9 plumodenticulate setae respectively. Exopod 2-segmented, proximal segment with 2 medial setae (1 simple, 1 plumodenticulated) and distal segment with 1 long subterminal and 4 long terminal plumose raptatory setae.

Pereiopods (Fig. 10C). All segments well differentiated and with setae as figured. Propodus of pereiopods 2-4 with a long terminal inner spine. Dactylus of fifth pereiopod with three long subterminal setae.

Sternal plate (Fig. 12A). Setation as figured.

Abdomen (Fig. 11F,G). Six somites present. Somite 1 with 3 pairs of lateral setae and 9 mid-dorsal simple setae. Somite 2 with 4 pairs of lateral

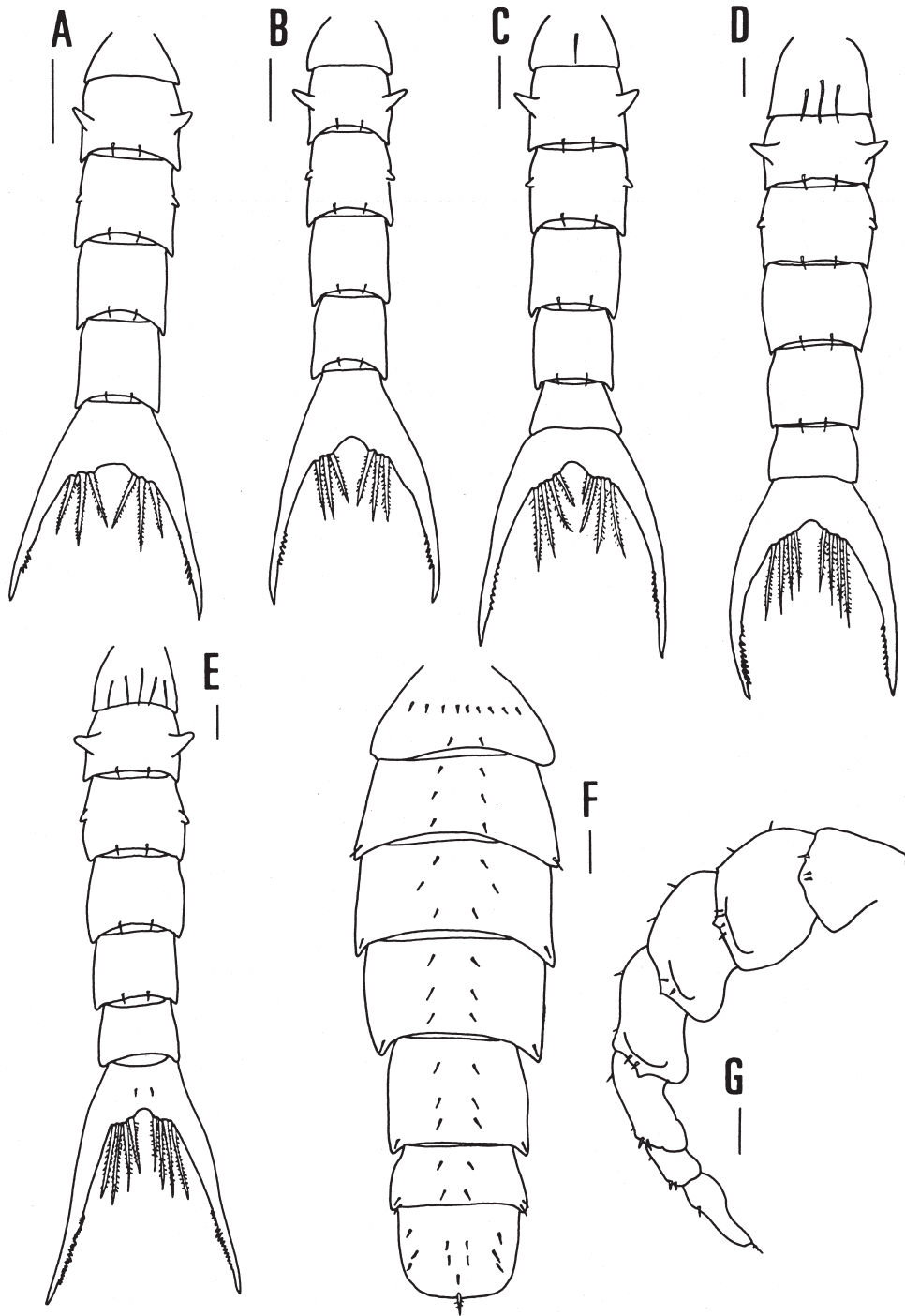


FIG. 11. – *Cyrtograpsus affinis* (Dana). Abdomen, dorsal view. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, zoea V; F, megalopa, G, megalopa, lateral view. Scale bars = 0.1 mm.

setae and 2 pairs of mid-dorsal setae. Somite 3-6 with 2 pairs of lateral setae. Somite 3-5 with 2 pairs of mid-dorsal setae. Somite 6 with 1 pair of mid-dorsal setae. Somites 2-5 with one pair of biramous pleopods, endopod unsegmented with 3 terminal hooks, exopod unsegmented, pleopods 1-4 with 14, 16, 17, 15 long marginal plumose natatory setae

respectively. Uropods 2-segmented on somite 6, proximal segment with 1 long marginal plumose natatory seta and distal segment with 8 long marginal plumose natatory setae.

Telson (Fig. 11F,G). Squared in shape, with 5 mid-dorsal setae, 3 pairs of dorsolateral setae and 1 posterior margin seta.

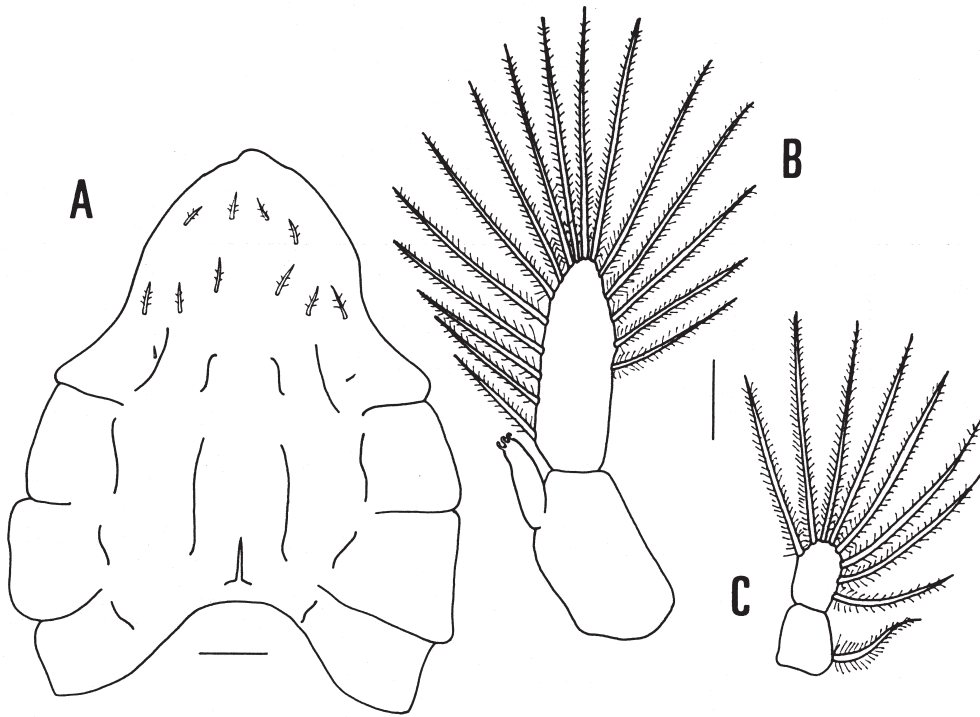


FIG. 12. – *Cyrtograpsus affinis* (Dana). Megalopa. A, sternum; B, second pleopod, C, uropod. Scale bars = 0.1 mm.

First crab

General morphology (Fig. 2B). Carapace slightly longer than broad with 3 denticulated teeth on the anterolateral margin. Frontal margin rounded, strongly denticulated and with a medial dip. Posterior margin of ocular orbit denticulated. Cheliped equal in size. Cheliped and pereopods setation as figured.

Morphometry and growth

The proportions between some morphological traits changed through zoeal growth in *Cyrtograpsus affinis*. A potential relationship exists between RDL and CL and between CW and CL (Fig. 13a). The slope of these lines is 1.07 for RDL and 0.75 for CW indicating slightly positive ($P < 0.01$) and negative ($P < 0.001$) allometric growth, respectively. On the other hand, RDL, CL and CW increase exponentially throughout the zoeal development (Fig. 14a). Within stage growth (zoea $n+1$ /zoea n), total growth (zoea 5/zoea 1), and mean growth (average size increase within stage) are shown in Table 2 and differ among RDL, CL and CW.

Some morphometrical information of *Cyrtograpsus altimanus* and *C. angulatus* zoeae was obtained from data of Scelzo and Lichtschein de Bastida

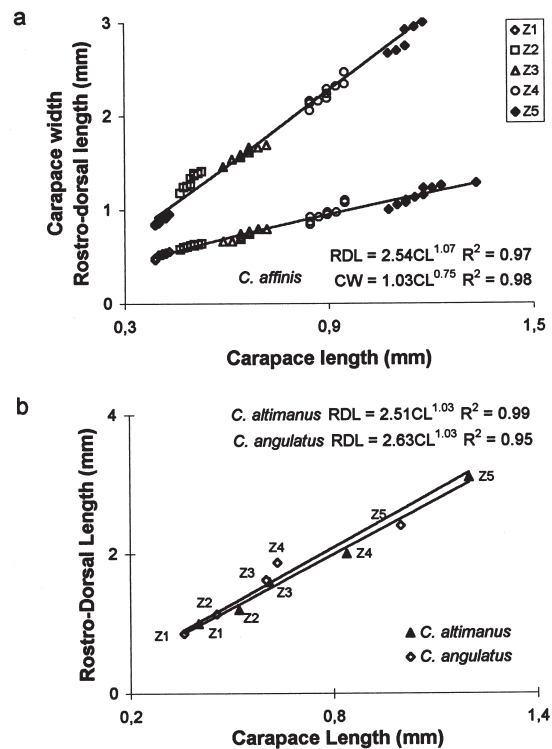


FIG. 13. – *Cyrtograpsus* spp. Relative growth during zoeal development. a) *C. affinis* (Dana): 10 specimens were measured per zoeal stage, except RDL of zoea 5 ($n = 6$). b) *C. altimanus* Rathbun (closed triangles) and *C. angulatus* Dana (open diamonds). One value per zoeal stage was calculated from data of Scelzo and Lichtschein de Bastida (1979) and from drawings of Rieger and Vieira (1997, p. 607), respectively ($n = 5$). RDL: rostro-dorsal length; CL: carapace length; CW: carapace width.

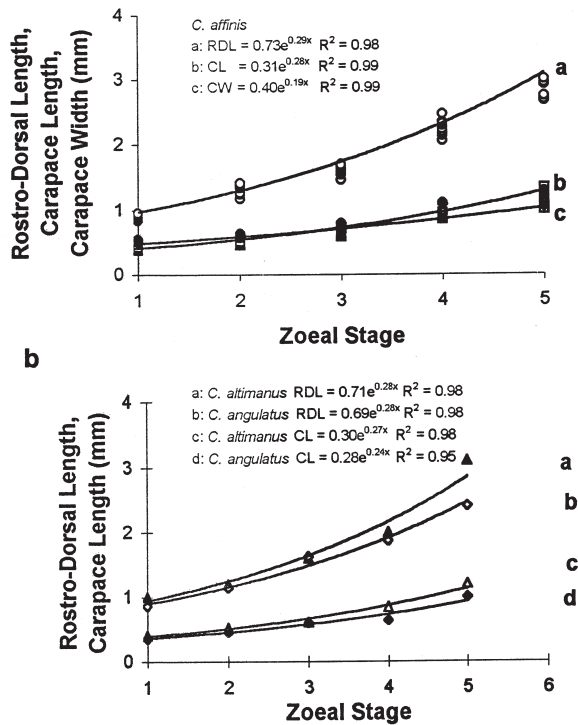


FIG. 14. – *Cyrtograpsus* spp. Absolute growth during zoeal development. a) *C. affinis* (Dana), open circles: RDL, closed circles: CW, open squares: CL. Ten specimens were measured per zoeal stage (n = 50). b) *C. altimanus* Rathbun (triangles, closed: RDL, open CL) and *C. angulatus* Dana (diamonds, open: RDL, closed CL). One value per zoeal stage was calculated from data of Scelzo and Lichtschein de Bastida (1979) and from drawings of Rieger and Vieira (1997, p. 607), respectively (n = 5). RDL: rostro-dorsal length; CL: carapace length; CW: carapace width.

(1979) and from drawings of Rieger and Vieira (1997, p. 607), respectively. There is a potential relationship between RDL and CL; its slope is 1.03 in both species (Fig. 13b). RDL and CL increase exponentially during development (Fig. 14b). Within stage growth, total growth, and mean growth calculated from RDL and CL values, are shown in Table 2.

Size differences among zoeae I of *Cyrtograpsus* species are detected in all examined morphological traits (Fig. 15). RDL, CW, DS and RS are larger, and

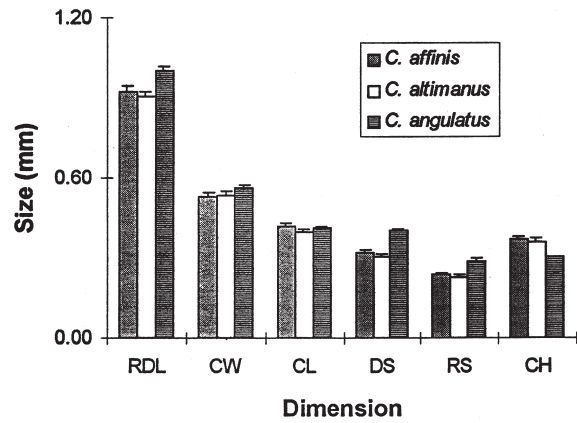


FIG. 15. – *Cyrtograpsus* spp. Comparison of morphological traits among zoeae I: rostro-dorsal length (RDL); carapace length (CL); carapace width (CW); dorsal and rostral spine length (DS and RS, respectively) and carapace height (CH). Ten specimens of each species were measured. Values are means + SD.

CH smaller, in *C. angulatus* larvae than in *C. altimanus* and *C. affinis* larvae. On the other hand, clear differences among the three species are found in RDL, DS and RS, *C. altimanus* larvae being the smallest. Since larvae are from only one hatch, data are not independent and cannot be used for statistical analysis.

DISCUSSION

Larval morphology

Based on DNA and larval evidences re-definition of the former grapsid subfamily Varuninae H. Milne Edwards, 1853 seemed necessary (Cuesta and Schubart, 1997; Schubart and Cuesta, 1998; Schubart *et al.*, in press). Next to the exclusion of three genera (*Euchirograpsus* H. Milne Edwards, 1853, *Glyptograpsus* Smith, 1870 and *Platychirograpsus* de Man, 1896), several genera, anteriorly placed in Sesarinae Dana, 1851 (e.g. *Cyclograp-*

TABLE 2. – Growth factors during zoeal development of *Cyrtograpsus* spp. *C. affinis*: each date represents the mean value of 10 specimens measured per zoeal stage; *C. altimanus* and *C. angulatus*: data calculated from Scelzo and Lichtschein de Bastida (1979) and Rieger and Vieira (1997), respectively.

growth factor	<i>C. affinis</i>			<i>C. altimanus</i>		<i>C. angulatus</i>	
	RDL	CL	CW	RDL	CL	RDL	CL
Zoea2/zoea1	1.48	1.22	1.18	1.20	1.30	1.32	1.27
Zoea3/zoea2	1.21	1.32	1.19	1.33	1.17	1.42	1.32
Zoea4/zoea3	1.39	1.36	1.31	1.25	1.38	1.15	1.06
Zoea5/zoea4	1.27	1.31	1.20	1.55	1.43	1.29	1.58
mean	1.34	1.30	1.22	1.33	1.32	1.30	1.31
Zoea5/zoea1	3.18	2.88	2.20	3.10	3.00	2.80	2.79

TABLE 3. – Morphological differences in the zoeal stages of *Cyrtograpsus affinis*, *C. angulatus* and *C. altimanus*. Abbreviations: S, setation; a, aesthetascs; s, setae. Exponent numbers ¹ to ³ mean: ¹, 3a,1s and ², absent, in the zoeae I of *C. altimanus* examined in the present study; ³, 3+3 in the zoeae I of *C. angulatus* examined in the present study.

	<i>C. affinis</i> (present study)	<i>C. angulatus</i> (Rieger and Vieira, 1997)	<i>C. altimanus</i> (Scelzo and Lichtschein de Bastida, 1979)
Zoea I			
Antennule	3a, 1s	3a, 1s	2a, 2s ¹
Maxillule			
Exopodal Seta	Absent	Absent	Present ²
Maxilla			
Coxal Endite S	3 + 3	3 + 2 ³	3 + 3
Zoea II			
Antennule	5a, 1s	5a, 1s	4a, 2s
Maxilla			
Coxal Endite S	3 + 4	3 + 3	3 + 4
Zoea III			
Antennule	5a, 1s	5a, 1s	3a, 3s
Maxilliped			
Endopod S	2, 2, 2, 2, 5	2, 2, 2, 2, 6	2, 2, 2, 2, 5
Zoea IV			
Antennule	5a, 1s	4a, 1s	3a, 1s
Maxillule			
Coxal Endite S	7	5	6
Basial Endite S	11	8	11
Maxilla			
Basial Endite	6 + 5	5 + 5	6 + 5
Scaphognatite	21	22	19
Maxilliped			
Endopod S	2, 3, 2, 2, 6	2, 2, 2, 2, 6	2, 3, 2, 2, 6
Zoea V			
Antennule	10a, 1s	9a	9a, 1s
Maxillule			
Coxal endite S	9	8	9
Basial endite S	15	14	14
Maxilla			
Coxal endite S	4 + 7	3 + 8	5 + 5
Basial endite S	9 + 7	8 + 7	8 + 6
Scaphognatite	29	26	27
Maxilliped			
Endopod S	2, 3, 2, 2, 6	2, 2, 2, 2, 6	2, 3, 2, 2, 6

sus H. Milne Edwards, 1837 and *Chasmagnathus* de Haan, 1835) are now included in the family Varunidae (Schubart *et al.*, in press). *Cyrtograpsus* is the second polyspecific genus of Varunidae for which larval development has been described for all species.

Larval development of *Cyrtograpsus affinis* corresponds in its general morphology to those of *C. altimanus* and *C. angulatus*. The few differences found in zoeal morphology are listed in Table 3. The megalopae stages of *C. altimanus*, *C. angulatus* and *C. affinis* have practically the same setation in antenna, mouthparts, pleopods and uropods. The main observed differences among the megalopae are in the morphology of antennule and the mandible: the setation of basal segment of antennular peduncle (3 setae in *C. angulatus*, 2 in *C. altimanus* and 5 in *C. affinis*), the number of aesthetascs on the three

terminal segment of antennular flagellum (5,7,6 in *C. angulatus*, 7,6,4 in *C. altimanus* and 7,7,4 in *C. affinis*), and the number of setae on mandibular palp (0,8 in *C. angulatus*, 0,6 in *C. altimanus* and 0,5 in *C. affinis*).

In the present study, newly hatched zoea I of *C. altimanus* and *C. angulatus* have been examined. Opposed to previous descriptions of Scelzo and Lichtschein de Bastida (1979) and Rieger and Vieira (1997), we have not found intrageneric differences in the setation of antennule and coxal endite of the maxilla. Also, we have not observed the presence of exopodal setae on maxillule of the zoea I of *C. altimanus* (see Table 3). Therefore, the rest of differences in setation of other stages, shown in Table 3, must be considered with care. Obvious differences between *Cyrtograpsus* zoeae can be observed only in morphometry as explained below.

Based on larval morphology, the genus *Cyrtograpsus* is closely related to *Brachynotus* de Haan, 1853. These genera can be separated from the rest of grapsoid genera on the basis of the development of the zoeal telson: *Cyrtograpsus* and *Brachynotus* acquire only one pair of serrulate setae in the posterior margin of the telson, as *Gaetice depressus* (de Haan, 1833) and *Helice leachii* Hess, 1865. However, *Cyrtograpsus* and *Brachynotus* can be easily differentiated from the latter species due to the presence of lateral carapace spines. Also *Metaplex distincta* H. Milne Edwards, 1852 presents 4 pairs of serrulate setae in the posterior margin of the telson in the last zoeal stage, but differs from *Cyrtograpsus* and *Brachynotus* zoeae in the setation of the second maxilliped endopod: 1 seta on the proximal segment in *Metaplex distincta* versus unarmed in *Cyrtograpsus* and *Brachynotus*. The zoeae of the remaining species of Varunidae, with known larval development, acquire more than one pair of serrulate setae through development.

There are no diagnostic morphological differences between *Cyrtograpsus* and *Brachynotus* larvae, but both genera have a very distinct distribution and it would be unlikely to find larvae of these genera in the same plankton samples. *Brachynotus* is restricted to the Mediterranean Sea and eastern Atlantic coast in vicinity of Mediterranean Sea while *Cyrtograpsus* is present only in South-Western Atlantic and South-Eastern Pacific.

Morphometry and growth

Hartnoll (1982: 163) stated that in Crustacea “there is an almost total lack of comprehensive biometric data on larval stages, in contrast to the extensive morphological descriptions”. In spite of the time passed since Hartnoll’s review, this lack of information seems to continue. The proportions between some morphometrical traits change through zoeal growth in *Cyrtograpsus affinis*: the distance between the tips of the lateral spines (CW) grows slower, and the distance from the tip of the rostral spine to the tip of the dorsal spine (RDL) a little faster, than the distance from the base of the rostrum to the posterior margin (CL). The slope of the potential relationship between RDL and CL is similar in the other *Cyrtograpsus* species (Fig. 13). Size, measured as RDL, CL and CW, increase exponentially throughout the zoeal development of *Cyrtograpsus* spp. (Fig. 14). An exponential size increase in the larval stages of some decapod crustacean species

(“Brook’s law”, Kurata, 1962) was shown by Rice (1968), but other species reveal a linear rather than an exponential pattern (Anger, 1998). The growth within the zoeal stages in Decapoda was examined by Gore (1985), who calculated a series of growth factors using morphometrical data compiled from literature descriptions (not from illustrations, even if available). The total (lat zoea/zoea 1) and mean growth factors of the Grapsidae (18 species) averaged 2.59 and 1.28, respectively. These values are in agreement with those calculated in *Cyrtograpsus affinis*, *C. altimanus* and *C. angulatus* although it is important to note that growth factors differed according to the trait measured (Table 2).

Measurements of morphological traits have been used to distinguish similar larvae of two *Carcinus* species (Rice and Ingle, 1975) and two *Paralithodes* species (Jensen *et al.*, 1992); to differentiate among several co-occurring majid species (Pohle, 1991); and to characterize intraspecific variability in *Cancer magister* (Shirley *et al.* 1987) and *Pachygrapsus transversus* (Cuesta and Schubart, 1998). Morphometry may also be used for discriminating among *Cyrtograpsus* zoeae: at least, *C. angulatus* differs from the other two species in all examined morphological traits (Fig. 15). Most of the measurements included the carapacial spines lengths (RDL, RS, DS, CH, CW). However, the use of spines to distinguish zoeae from related species may be acceptable only within geographical regions, since their length vary with temperature and latitude (Shirley *et al.* 1987). Morphometrical information on the *Cyrtograpsus* species presented here came from populations collected in geographically proximate areas (from 32 to 38° S) with similar environmental temperatures. However, *C. altimanus*, and mainly *C. angulatus*, have extensive distributions and, consequently, more detailed studies on zoeal morphometry of these species will be needed.

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