

## Larval development of *Clastotoechus nodosus* (Streets, 1872) (Crustacea: Decapoda: Porcellanidae), under laboratory conditions\*

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**SUMMARY:** The larval development of *Clastotoechus nodosus* is described and illustrated from specimens obtained from four females collected in shallow waters from Cubagua island, Venezuela (southeastern Caribbean) and reared in the laboratory. *C. nodosus* hatches as a prezoa of less than 60 minutes' duration and then molts through two subsequent zoeal stages of 5-7 and 9-13 days' duration respectively, at 25°C and 37‰ salinity, before attaining the megalopa. There are major differences between the two zoeal stages and megalopa of *C. nodosus* and the only other congeneric species with known larval development [i.e. *C. vanderhorsti* (Schmitt, 1924); sin. *Madarateuchus vanderhorsti*]. Interspecific differences are striking in the setal formula of several appendages (e.g. antennulae, antennae, maxillulae, maxillae, and maxillipeds). The postorbital spines exhibited by the second zoeal stage of *C. nodosus* are a novelty for larvae of any porcellanid species described so far from the Americas.

**Key words:** zoea, megalopa, Caribbean.

**RESUMEN:** DESARROLLO LARVARIO DE *CLASTOTOECHUS NODOSUS* (STREETS, 1872) (CRUSTACEA: DECAPODA: PORCELLANIDAE), EN CONDICIONES DE LABORATORIO – El desarrollo larvario de *Clastotoechus nodosus* es descrito e ilustrado a partir de especímenes obtenidos de cuatro hembras colectadas en aguas someras de Isla Cubagua, Venezuela (Caribe sudoriental), y mantenidas en condiciones de laboratorio. *C. nodosus* presenta una prezoa cuya duración no excede los 60 minutos, y luego pasa por dos estadios consecutivos de zoea de 5-7 y 9-13 días, respectivamente, a 25°C y 37 ‰ de salinidad, antes de llegar a la megalopa. Los dos estadios de zoea y el de megalopa de *C. nodosus* presentan diferencias con los estadios equivalentes de la única especie congénica con desarrollo larvario documentado [i.e. *C. vanderhorsti* (Schmitt, 1924); sin. *Madarateuchus vanderhorsti*], principalmente en relación a las fórmulas de las setas de varios apéndices (e.g. anténula, antena, maxílula, maxila, y maxilípedos). Espinas postorbitales, tales como las presentes en el segundo estadio de zoea de *C. Nodosus*, no habían sido reportadas anteriormente en larvas de porcelánidos del continente americano.

**Palabras clave:** zoea, megalopa, Caribe.

### INTRODUCTION

The genus *Clastotoechus* was erected by Haig (1960) to receive those *Petrolisthes* species with lateral walls of carapace consisting of several pieces separated from each other by a membrane. It is

endemic to the Americas and comprises six species: *C. nodosus* (Streets, 1872), *C. vanderhorsti* (Schmitt, 1924), *C. diffractus* Haig, 1957, *C. gorgonensis* Werding and Haig, 1983, *C. hickmani* Harvey, 1999, and *C. lasios* Harvey, 1999. The two former species are restricted to the Western tropical Atlantic Ocean (see Haig, 1956; Gore and Abele, 1976; Werding, 1977, 1983; Scelzo, 1982; Harvey, 1999).

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Based on (a) the type of coverage of the carapace, chelipeds, walking legs and antennae, (b) the proximity degree of the teeth on the anterior margin of the carpus of chelipeds, (c) the presence and/or distribution of setae on propodus of chelipeds, and (d) the number of medial spines on propodus of walking legs, Harvey (1999) placed one of those species (i.e. *C. vanderhorsti*) in the junior genus *Madarateuchus*. The genus *Clastotoechus* has been recognised now and then, but the erection of the genus *Madarateuchus* has not been fully recognised yet, and has been only sparingly used.

The larval characters have been used for studying crustacean systematics and phylogeny (Martin and Davis, 2001). Thus, the detailed morphology of the zoeae and megalopa of *C. nodosus* provided herein is compared to those of *C. vanderhorsti*, which is the other congeneric species with available larval development (see Schoppe, 1994), assuming such comparison as a suitable starting point for the testing the adult-based relationships between *Clastotoechus* and *Madarateuchus*.

## MATERIAL AND METHODS

Larvae from hatchings of four females of *C. nodosus*, collected by hand in balanid conglomerates from Charagato Bay, Cubagua Island, Venezuela (10°51'N, 64°9'W) were incubated individually in 150 ml glass containers with filtered and UV-sterilised sea water at 25°C and 37‰ salinity; 60 to 80 larvae hatched in each batch. Larvae were fed daily with newly hatched *Artemia* nauplii. Water in the containers was changed daily. Survival and molting were recorded daily.

Samples of both dead and living zoeae and megalopa were preserved in a 1:1 mixture of glycerin and 70% isopropyl alcohol, and are currently deposited in the collection of the Laboratory of Crustaceans at the Universidad de Oriente. Drawings were made with the aid of an Olympus U-IT120 camera lucida using an Olympus BMAX-50 microscope. Measurements were made with a calibrated ocular. At least three specimens of each zoeal stage and megalopa from two or more females were measured, dissected, and analysed. The carapaces of zoeal stages and megalopa were measured in the standard way for Porcellanidae (Gore, 1968; Hernández *et al.*, 1998). These measurements are expressed as the arithmetic average of the number of measured specimens and their standard deviation. The following abbrevia-

tions are used: CL= carapace length; CW= carapace width; RL= rostral length; LPS= length of posterior spines of the carapace. The distribution of the chromatophores and coloration was determined on live specimens. The term seta is used as defined by Thomas (1960) and Gonor and Gonor (1973); the nomenclature for the different types of setae is based on the proposal by Stuck and Truesdale (1988) and has been used in previous publications by Hernández *et al.* (1998, 2000, 2002).

## RESULTS

*Clastotoechus nodosus* hatches as a prezoaea of less than 60 minutes' duration, and then passes through two subsequent zoeal stages which last 5-7 and 9-13 days respectively before the megalopa is reached. The duration of the megalopa was not recorded.

### First zoea

Size: CL =  $1.50 \pm 0.06$  mm, range = 1.40-1.60 mm; RL =  $4.51 \pm 0.29$  mm, range = 4.25-5.33 mm; LPS =  $2.00 \pm 0.05$  mm, range = 1.88-2.08 mm. Specimens measured = 10. Specimens examined = 10.

Carapace (Fig. 1A) - Typically porcellanid, with 2 pairs of setulose setae dorsally; ventrolateral margin unarmed. Rostral spine 3 times the length of carapace proper, with numerous acute spinules (Figs. 1B,C), tip unarmed. Posterior spines about 1.3 times the length of carapace proper, with acute spinules ventrally (Fig. 1D). Eyes sessile.

Antennule (Fig. 2A) - With 3 unequal aesthetascs, and 3 setae (2 setulose, 1 simple).

Antenna (Fig. 2D) - Exopodite and endopodite with acute tip. Exopodite 1.5 times longer than endopodite, with 2 setulose setae on distal third plus a minute spine subterminally. Endopodite with 1 setulose seta subterminally.

Mandibles (Fig. 3A) - Asymmetrically dentate processes; incisor process with acute teeth, molar process roughened. Palp absent.

Maxillule (Fig. 3D) - Coxal endite with 8 setae (3 setulose, 5 setulodenticulate). Basial endite with 9 setae (3 setulose, 6 serrate). Endopodite with 1 small spine subterminally plus 1+3 setulose setae terminally; microtrichia on outer margin. Exopodite absent.

Maxilla (Fig. 3H) - Coxal endite with 7 and 4 setae on proximal and distal lobe respectively.

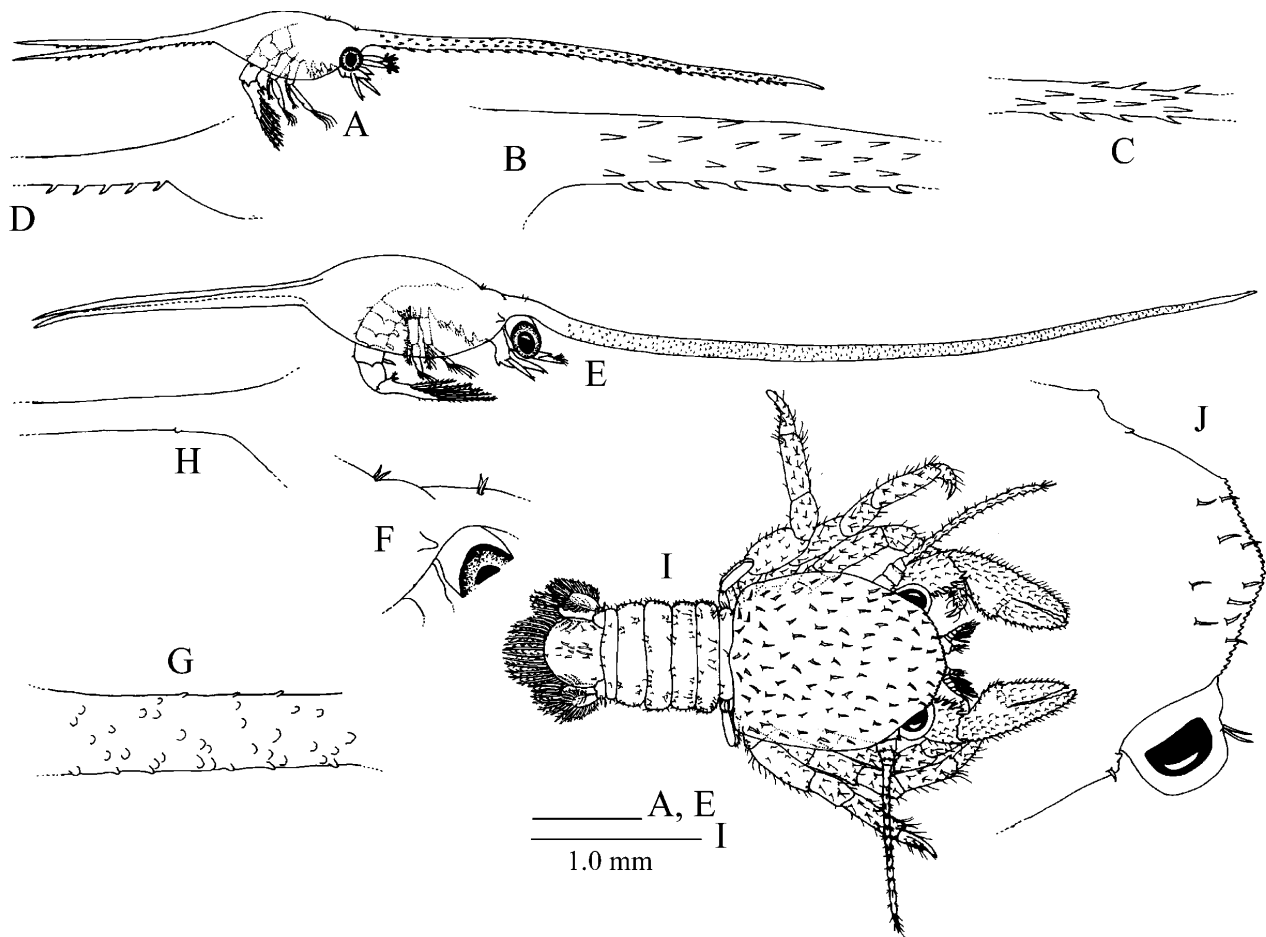


FIG. 1. – *Clastotoechus nodosus*. Lateral view of zoea I (A) and zoea II (E); proximal (B), and medial (C) portions of rostrum of zoea I; details of postorbital spine of zoea II (F); proximal portion of posterior spines of zoea I (D) and zoea II (H); medial portion of rostrum of zoea II (G); dorsal view of megalopa (I) and details of its front (J).

Basal endite with 7 setae on each lobe. Endopodite with 3+6 setulose setae. Scaphognathite with 6 setulose setae plus 1 seta apically. Microtrichia on both rami and on endites.

Maxilliped 1 (Fig. 4A) - Coxopodite without setae but with spinelike process dorsally. Basipodite with 2+2+2+2 setulose setae. Endopodite 4-segmented, with 3, 3, 2+3, 8+I setulose setae; microtrichia on dorsal margin of articles 2-3. Exopodite incompletely 2-segmented, with 4 setulose setae distally.

Maxilliped 2 (Fig. 4D) - Coxopodite unarmed. Basipodite with 1+2 setulose setae. Endopodite 4-segmented, with 2,2,1+2,5+I setulose setae; microtrichia on dorsal margin of articles 2-3. Exopodite incompletely 2-segmented, with 4 setulose setae distally.

Maxilliped 3 (Fig. 4G) - Biramous, undifferentiated buds, without segmentation and setae.

Pereiopods (Fig. 5A) - Rudimentary buds, without signs of segmentation or chelation.

Abdomen (Fig. 6A) - Constituted by 5 somites; with lateral spines increasing in size posteriorly, on somites 3-5, plus one pair of setae dorsolaterally on somites 4 and 5. Pleopods absent.

Telson (Fig. 6D) - Slightly wider than long. Anal spine present. Three pairs of setae dorsally. Seven pairs of processes on posterior margin: first pair represented by 1 spinulose spine (Fig. 6E), second a small setulose seta, third to seventh long setuloserate setae (Figs. 6F-J); fifth pair of long setae on central prominence; microtrichia on central prominence.

Color - Rostrum with three orange bands transversely. Posterolateral spines with one orange band distally. Red chromatophores on carapace dorsolaterally. Rest of body translucent.

## Second zoea

Size: CL =  $2.45 \pm 0.08$  mm, range = 2.30-2.55 mm; RL =  $7.39 \pm 0.24$  mm, range = 7.08-7.83 mm;

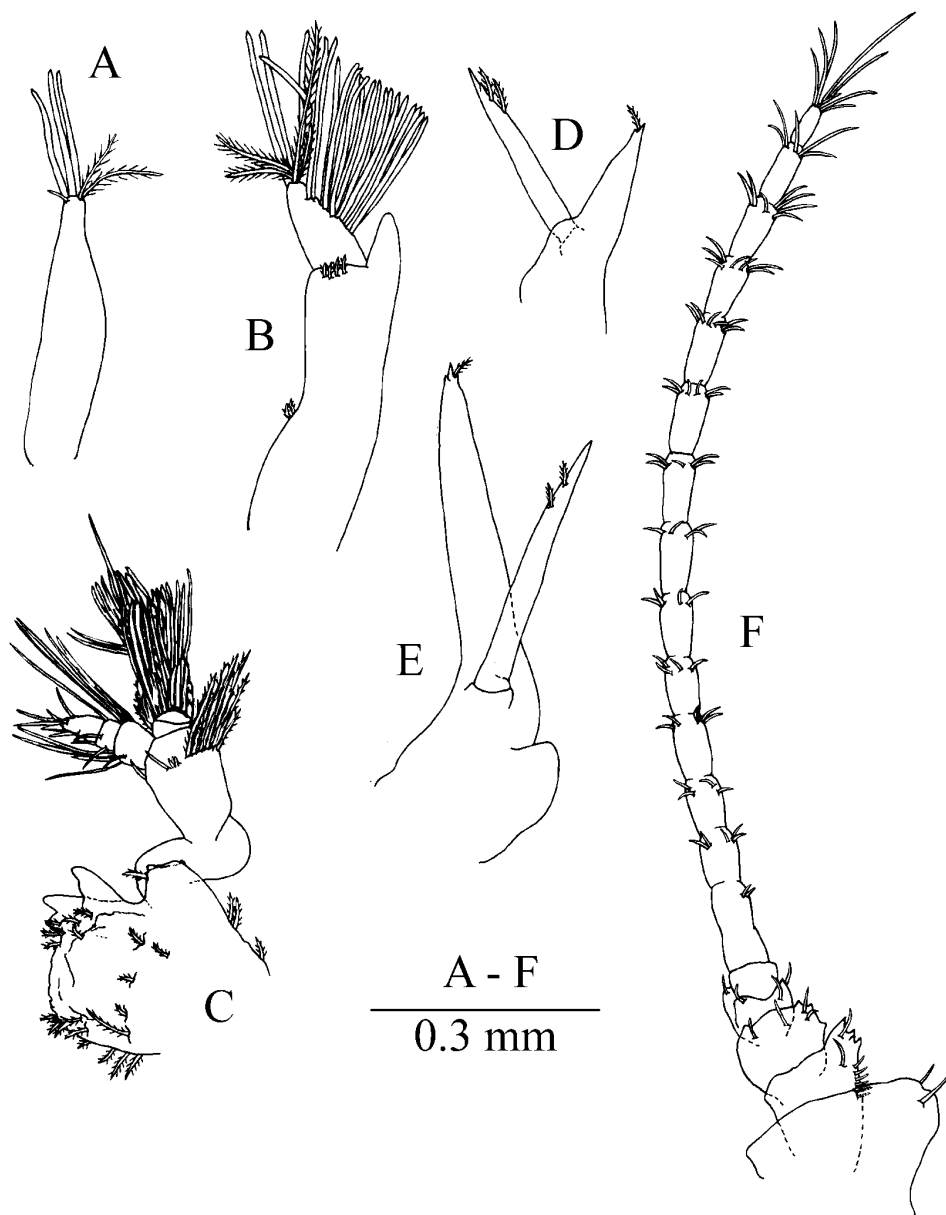


FIG. 2. – *Clastotoechus nodosus*. Antennule of zoea I (A), zoea II (B) and megalopa (C); antenna of zoea I (D), zoea II (E) and megalopa (F).

LPS =  $2.77 \pm 0.19$  mm, range = 2.40-3.00 mm. Specimens measured = 10. Specimens examined = 8.

Carapace (Fig. 1E) - Dorsal setation unchanged; postorbital spine present (Fig. 1F). Rostral spine 2.5 times the length of carapace proper, with low rounded granules (Fig. 1G), tip unarmed. Posterior spines almost unarmed (Fig. 1H), about 1.1 times the length of carapace proper. Eyes pedunculate.

Antennule (Fig. 2B) - Biramous. Protopodite with 2 setulose setae basally plus 4 on junction of exopodite. Endopodite unarmed. Exopodite with aesthetascs progressing distally as 5+5,3+3,2,4; plus 4 setulose setae terminally.

Antenna (Fig. 2E) - Setae on endopodite and

exopodite retained; the latter lacking the short spine. Exopodite about 0.7 as long as endopodite; one specimen with 3 setae instead 2.

Mandibles (Fig. 3B) - Similar to zoea I, but larger and with palp.

Maxillule (Fig. 3E) - Coxal endite with 10 setae (8 setulodenticulate, 2 setulose). Basal endite with 10 setae (7 serrate, 3 setulose). Endopodite unchanged. Exopodite absent.

Maxilla (Fig. 3I) - Coxal and basal endites with 11,6 and 10,9-10 setulose setae on proximal and distal lobe respectively. Endopodite unchanged. Scaphognathite margin with 22 setulose setae and sparse microtrichia.

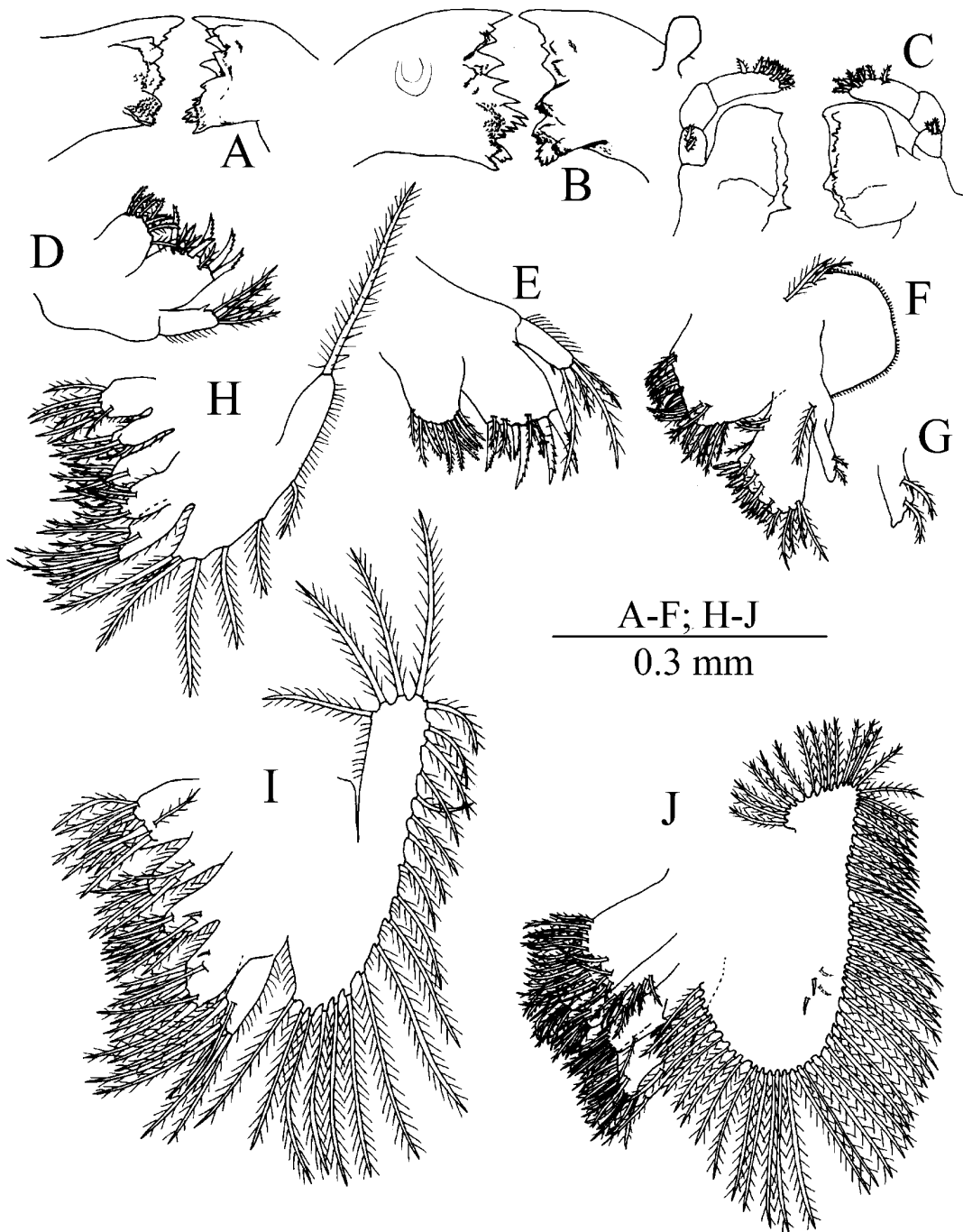


FIG. 3. – *Clastotoechus nodosus*. Mandibles of zoea I (A), zoea II (B) and megalopa (C); maxillule of zoea I (D), zoea II (E) and megalopa (F); detail of endopodite of megalopal maxillule (G); maxilla of zoea I (H), zoea II (I) and megalopa (J);

Maxilliped 1 (Fig. 4B) - Coxopodite without spinelike process. Basipodite unchanged. Endopodite now with 1 additional setulose seta dorsally on articles 1-3. Exopodite partially 2-segmented, with 12 setulose setae distally.

Maxilliped 2 (Fig. 4E) - Coxopodite and basipodite unchanged. Endopodite with 1 additional setulose setae dorsally on articles 1-3. Exopodite partially 2-segmented, with 12 setulose distally.

Maxilliped 3 (Fig. 4H) - Endopodite with traces of segmentation. Exopodite shorter than endopodite.

Pereiopods (Fig. 5B) - Increasing in size and assuming segmentation as stage progresses.

Abdomen (Fig. 6B) - With 1 pair of biramous pleopods on each somites 2-5.

Telson (Fig. 6K) - Additionally with both 1 setulose seta on central prominence and 1 pair of setae dorsally.

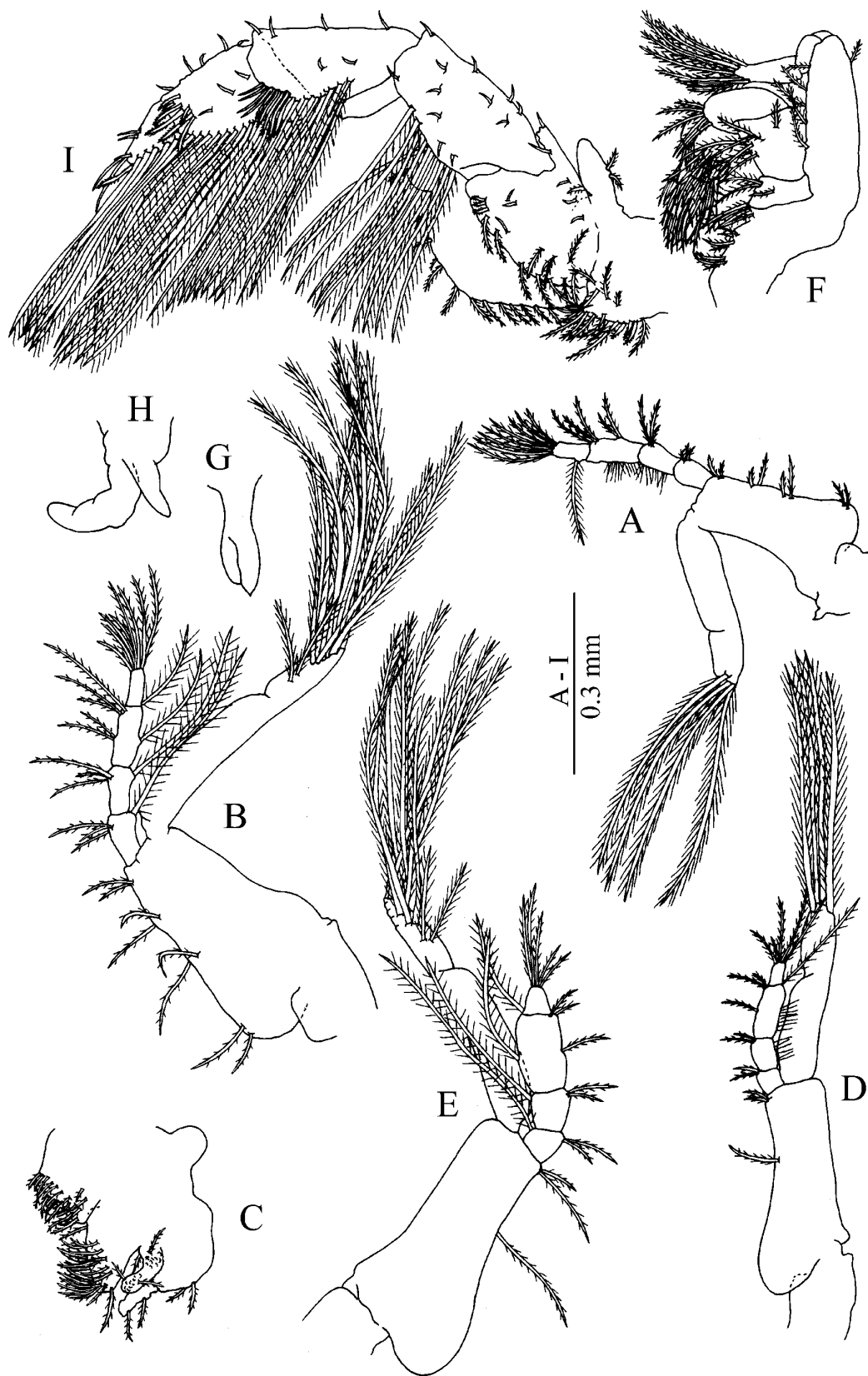


FIG. 4. – *Clastotoechus nodosus*. Maxilliped 1 of zoea I (A), zoea II (B) and megalopa (C); maxilliped 2 of zoea I (D), zoea II (E) and megalopa (F); maxilliped 3 of zoea I (H), zoea II (G) and megalopa (I).

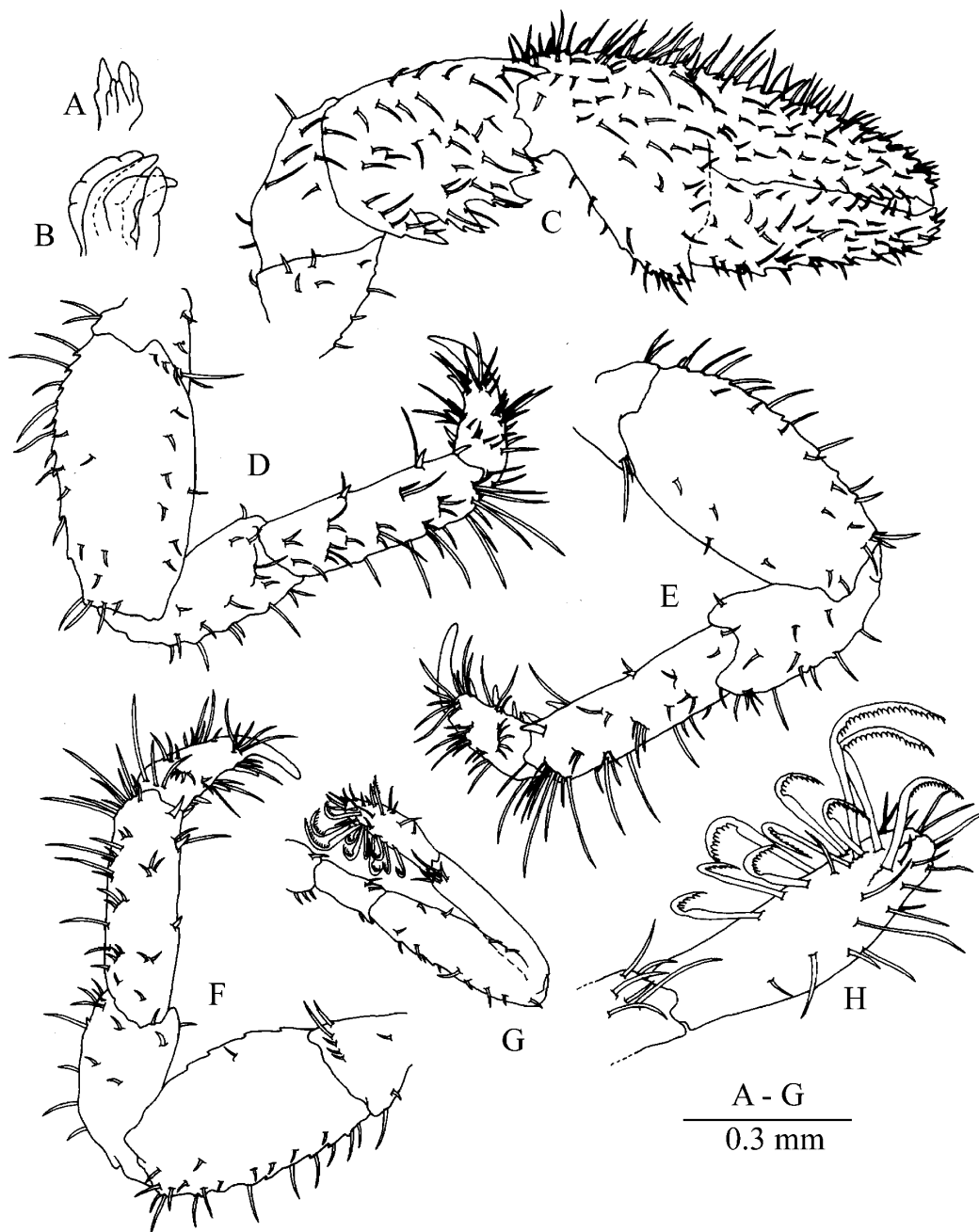


FIG. 5. – *Clastotoechus nodosus*. Pereiopods of zoea I (A), zoea II (B) and megalopa (C-G); details of chela of pereiopod 5 (H).

Color - Same as in zoea I, but with additional red chromatophores on pereiopods and abdomen.

### Megalopa

Size: CL =  $1.42 \pm 0.09$  mm, range = 1.28-1.60 mm; CW =  $1.24 \pm 0.11$  mm, range = 1.05-1.48 mm. Specimens measured = 10. Specimens examined = 8.

Carapace (Fig. 1I) - Convex both longitudinally and transversely, slightly longer than wide, subovate, with sparse short setae. Front produced; anterior

margin irregular (Fig. 1J). Ocular peduncle with 2 short setae.

Antennule (Fig. 2C) - Basal segment as long as wide, anterior margin with about 3 spines; numerous simple or setulose setae as illustrated. Peduncle 3-segmented; with 0, 0, 5+14 setulose setae. Lower ramus 3-segmented, with 11, 5, 8 simple setae. Upper ramus 6-segmented; first article unarmed; second with 5+7 aesthetascs, third with 7 aesthetascs plus 2 simple setae, fourth with 3+3 aesthetascs plus 2 simple setae; fifth with 3 aes-

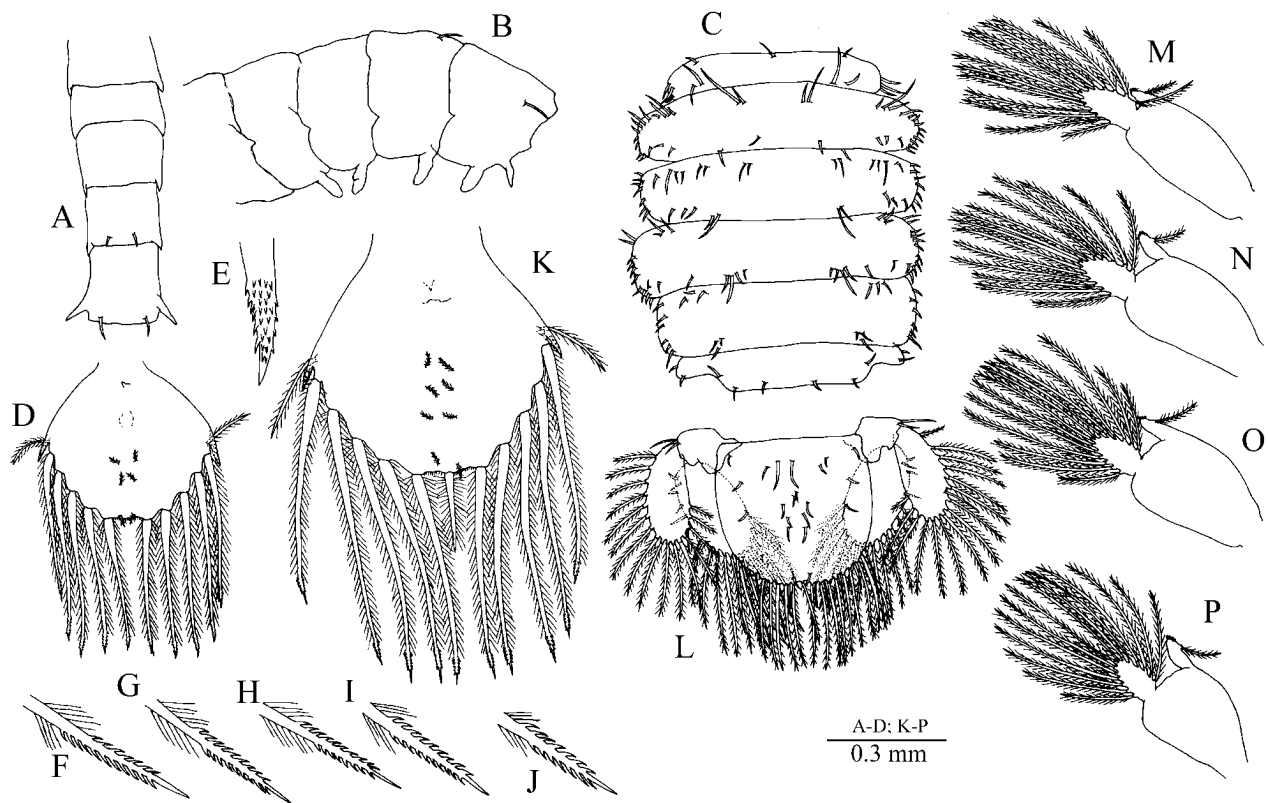


FIG. 6. – *Clastotoechus nodosus*. Dorsal view of the abdomen of zoea I (A), and megalopa (C); lateral view of abdomen of zoea II (B); dorsal view of telson of zoea I (D) and zoea II (K); dorsal view of tail fan of megalopa (L); details of telsonal lateral spine of zoea I (E); tip of major setae on telson of zoea I (F-J); pleopods 1-4 of megalopa (M-P).

thetascus plus 2 simple setae; sixth with 5 simple setae.

Antenna (Fig. 2F) - Basal segment with 2 setae on short lateral rounded projection. Peduncle 3-segmented, with 6+2, 4, 4 simple setae. Flagellum with 16 articles; articles 1 to 3 without apparent articulation, articles 1 and 2 unarmed, articles 3 with 2 setae, articles 4-15 with 4-7 simple setae, last article with 8 simple setae.

Mandibles (Fig. 3C) - Asymmetrically scoop-shaped processes with thin blades; each with 3-segmented palp; first article of palp with 2 setulose setae, second unarmed, third with 10 setulodenticulate setae.

Maxillule (Fig. 3F) - Coxal endite with about 34 setae, and 2 long setulose setae near base and elongated basal lobe fringed with microtrichia. Basial endite with about 29 setae (17 denticulate, rest setulose). Endopodite indistinctly 2-segmented, with 1+2 setulose setae, and irregular tip (Fig. 3G). Exopodite absent.

Maxilla (Fig. 3J) - Coxal endite with about 44 and 22 setulose setae on proximal and distal lobe respectively. Basial endite with about 25 and 32

setulose setae on proximal and distal lobe respectively. Endopodite with 4 setulose setae. Scaphognathite with about 60-62 setulose setae around outer margin, flattened surface with 4 simple setae (2 dorsally, 2 ventrally).

Maxilliped 1 (Fig. 4C) - Coxopodite with 24 setulose setae. Basipodite with 38-40 setulose setae. Endopodite appears uncalcified, with 4 setulose setae. Exopodite 2-segmented with 2,2 setulose setae.

Maxilliped 2 (Fig. 4F) - Protopodite with 11 setulose setae. Endopodite 5-segmented; first article with 3 setulose setae, second with 8 setulose setae, third with 6 setulose setae, fourth with 25-29 setae (2 serrate, rest setulose), fifth with 30-35 (2 serrate, rest setulose). Exopodite 2-segmented, with 6,9-10 setulose setae respectively.

Maxilliped 3 (Fig. 4I) - Protopodite with 16 setae (4 serrate, rest setulose). Endopodite 5-segmented; ischium with 19 setae (2 spike-like setae, rest setulose); merus with 10 pairs of long setulose setae plus several smaller ones; carpus with 33 setae (7 serrate, rest setulose); propodus with about 39 setae (7 serrate, rest setulose); dactylus with 20-21 setae (1 serrate, rest setulose). Exopodite with 3 setulose setae.



Pereiopods (Figs. 5C-H) - Chelipeds subequal, with numerous scattered setae and spines as illustrated; carpus with 3 spines on flexor and 1 spine on extensor margin distally; propodus with numerous spines interspersed with setae on outer and inner margins; dactylus with about 11 spines on dorsal margin (Fig. 5C). Walking legs setose; propodus with 1+1+2 robust setae distally on flexor margin; dactylus with 1+1+1+1 robust setae on flexor margin (Figs. 5D-F). Pereiopod 5 chelate, gape dentate, with 10 serrate setae on chela (Figs. 5G,H).

Abdomen (Fig. 6C) - Now consisting of 6 somites, with numerous setae dorsally. Four pairs of biramous pleopods on somites 2 to 5, all of them with 14, setulose setae on exopodite, and 4 retinacula plus 1 setulose seta on endopodite distally (Figs. 6M-P). Uropodal endopodite with 18 setulose setae, exopodite with 16 setulose setae (Fig. 6L).

Telson (Fig. 6L) - With 18 setulose setae on posterior margin; dorsal surface with 20 setae appearing to be simple.

Colour - Not recorded.

## DISCUSSION

*Clastotoechus nodosus* and *C. vanderhorsti* have been reported from the Caribbean, frequently sharing several local areas (Scelzo, 1982; Werding, 1977; Harvey, 1999). Although the former species prefers rocky intertidal shores (especially on balanid conglomerates) and the latter lives as a commensal on echinoids of the genus *Echinometra*, the zoeae and/or megalopae of both species could occur eventually in samples of plankton or benthos respectively from many Caribbean areas.

Zoeal stages of *C. nodosus* can be easily differentiated from those of *C. vanderhorsti* by some setal or spinal formulas of carapaces, several appendages, and telson (Table 1). The presence/absence of (a) spinules on the telsonal lateral spine (both zoeal stages), (b) the spinelike projection on coxopodite of maxilliped 1 (zoea I), and (c) the postorbital spine (zoea II), seem to support the disaggregation of *C. nodosus* and *C. vanderhorsti* into the two different genera *Clastotoechus* and *Madarateuchus*. Never-

TABLE 1. – Main morphological differences in the zoeal stages of two *Clastotoechus* species.

	<i>C. nodosus</i> (Present study)	<i>C. vanderhorsti</i> (fide Schoppe, 1994)
First zoea		
ANTENNULE	3 aesthetascs, 2+1 setae	3 aesthetascs, 2+0 setae
ANTENNA		
Endopodite	1 seta	2 setae
MAXILLULE		
Endopodite	Spine present	Spine absent
MAXILLA		
Coxal endite	7,4 setae	6,4 setae
Basal endite	7,7 setae	6,7 setae
Endopodite	3+6 setae	8 setae
MAXILLIPED 1		
Coxopodite	Spinelike process present, setae absent	Spinelike process absent, setae present
Basipodite	2+2+2+2 setae	2+2+2+3 setae
ABDOMEN	Spines and setae on somites 3-5	Spines on somites 2-5; setae not reported
TELSON	Lateral spines spinulate	Lateral spines entire
Second zoea		
CARAPACE	Postorbital spine present	Postorbital spine absent
ANTENNULE	5+5,3+3,2,4 aesthetascs, 4 setae	10 aesthetascs, 3 setae
ANTENNA	Endopodite with 1 seta	Endopodite with 2 setae
MAXILLULE		
Basal endite	10 setae	8 setae
Endopodite	Small spine present subterminally	Small spine absent subterminally
MAXILLA		
Coxal endite	11,6 setae	9,6 setae
Basal endite	10,9-10 setae	9,9 setae
Scaphognathite	22 setae	21 setae
MAXILLIPED 1		
Basipodite	2+2+2+2 setae	2+2+2+3 setae
Exopodite	12 setae	11 setae
MAXILLIPED 2		
Exopodite	12 setae	11 setae
TELSON	Lateral spines spinulate	Lateral spines entire

theless, according to Werding *et al.* (2001), the *C. nodosus*/*C. vanderhorsti* clade is 100% supported on the basis of molecular characters. Both the knowledge of the larval morphology of the remaining *Clastocheus* species and subsequent DNA sequencing analysis of all the species involved are essential to obtain a valid conclusion.

Neither of these genera is unique in having such larval morphological features. The spinulation on the telsonal lateral spines has been reported for *Porcellana sayana*, *P. sigsbeiana*, and *Ancylocheles gravelei* (see Hernández *et al.*, 1998); a similar spinelike projection on coxopodite of maxilliped 1 for both zoeal stages has been observed in several *Petrolisthes* species (i.e. *P. tridentatus*, *P. tonsorius*, *P. violaceus*, and *P. magdalenensis*); and a similar postorbital spine has not been hitherto reported for the American porcellanids, but it has been described for the larvae of the Indopacific species *Petrocheles spinosus* and *P. australiensis* (see Gurney, 1924; Wear, 1965).

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