The complete larval development of *Eurypanopeus canalensis* Abele and Kim, 1989 (Crustacea: Brachyura: Panopeidae) described from laboratory-reared material*

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SUMMARY: The estuarine panopeid crab *Eurypanopeus canalensis* Abele and Kim, 1989, is an eastern tropical Pacific species with a known distribution from the southeastern Gulf of California, Mexico, to Panama. Its complete larval development is fully described and illustrated from laboratory-reared material. The four zoeal stages and the megalopa are compared with two congeneric species from the West Atlantic, *E. abbreviatus* (Stimpson, 1860) and *E. depressus* (Smith, 1869). The main differences between larvae of *E. canalensis* and those of these two species include telson setation and the presence/absence of a stout hook-like spine in the megalopae cheliped ischium.

Keywords: Brachyura, *Eurypanopeus*, larvae, development.

RESUMEN: DESARROLLO LARVARIO COMPLETO DE *EURYPANOPEUS CANALENSIS* ABELE AND KIM, 1989 (CRUSTACEA: BRACHYURA: PANOPEIDAE) DESCRITO A PARTIR DE MATERIAL CULTIVADO EN EL LABORATORIO. – El cangrejo panopeido estuarino *Eurypanopeus canalensis* Abele and Kim, 1989 es una especie cuya distribución conocida va desde el Sureste del Golfo de California en México hasta Panamá. Su desarrollo larval completo ha sido descrito e ilustrado a partir de material producido en laboratorio. Los cuatro estadios zoea y la megalopa se han comparado con las larvas de dos especies congenéricas del Atlántico, *E. abbreviatus* (Stimpson, 1860) y *E. depressus* (Smith, 1869). Las principales diferencias entre *E. canalensis* y estas dos especies se encontraron en la setación del telson en las zoeas y en la presencia/ausencia de una espina con forma de gancho en el ísquio del quelípedo de las megalopas.

Palabras clave: Brachyura, *Eurypanopeus*, larvas, desarrollo.

INTRODUCTION

Mud crabs of the family Panopeidae Ortmann, 1893, are common in marine intertidal, shallow subtidal and estuarine habitats along the temperate and tropical coastline of the Americas. The eastern tropical Pacific, particularly rich in species of Brachyura (450 species to date; Hendrickx, 1995), includes the Gulf of California, Mexico, where 301 species of true crabs are found (Brusca *et al.*, 2001). The southeastern Gulf of California is characterised by extensive coastal lagoons and estuarine complexes, many of which are colonised by dense mangrove forests. According to Hendrickx (1996) and Salga-

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do-Barragán and Hendrickx (2002), 48 species of decapod crustaceans inhabit the lagoon-estuarine systems of the southeastern Gulf of California, including eight belonging to the family Panopeidae.

Panopeid crabs have long been included within the family Xanthidae MacLeay, 1838, but recent studies of the morphology of the adult and larvae of some species have indicated that many of the previously recognised subfamilies of xanthid crabs should be given family rank (see Guinot, 1978; Serène, 1984; Martin, 1984 and 1988; Martin *et al*., 1985; Martin and Davis, 2001). At present, 11 different families of Xanthoidea are recognised, including the Panopeidae, but the phylogenetic relationships within this group, as well as the generic composition of each family are still being debated (Schubart *et al*., 2000a; Martin and Davis, 2001),

The study of brachyuran larval morphology has been recognised as an important source of data to help elucidate relationships and resulting classifications of families, genera, and even species (Rice, 1980). In the case of panopeid crabs, much work has been done to describe their larval stages. For the American species of the Panopeidae, the complete zoeal development has been published for nine species of the genus *Panopeus*, one species of *Rhithropanopeus*, one species of *Eurytium*, one species of *Hexapanopeus,* and two species of *Eurypanopeus* (see Rodríguez and Spivak, 2001; Luppi *et al*., 2003, Vieira and Rieger, 2004). In addition, the larval development of two species of the recently proposed new genus *Acantholobulus* Felder and Martin, 2003, both previously included in *Panopeus*, have also been partly described (i.e. *A. schmitti* [Rathbun, 1930]; *A. bermudensis* [Benedict and Rathbun, 1891]). Some other partial descriptions exist, such as the first zoea of *P. purpureus* by Martin *et al*. (1998).

Eurypanopeus is widely distributed throughout the tropical and subtropical coastlines of the American and African continents. It is known in the West Atlantic from Massachusetts, USA, to southern Brazil (Santa Catharina), and in the East Pacific from the west coast of Mexico to Chile. There are 11 species recorded in America, one of them, *E. abbreviatus*, containing two subspecies. The current status of *E. a. abreviatus* and *E. a. alter* Rathbun, 1930, is still uncertain, but current molecular research may resolve this outstanding question (Darryl Felder, pers. comm.). Eight of the eleven species of *Eurypanopeus* are endemic to the east Pacific, and the other three are endemic to the West Atlantic (Hendrickx, 1995; Boschi, 2000). The genus itself would be endemic to the American continent were it not for the presence of one species, *E. blanchardi* (A. Milne Edwards, 1881), in the East Atlantic (from the Cape Verde islands and Mauritania southwards to Angola, including offshore islands (Manning and Holthuis, 1981).

The complete larval development has been described for two western Atlantic *Eurypanopeus* species: *E. depressus* (Smith, 1869) by Costlow and Bookhout (1961), and *E. abbreviatus* (Stimpson, 1860) by Negreiros-Fransozo (1986). In both species there are four zoeal stages and a megalopa. Recently, the first zoeal stage of *E. depressus* was re-described by Clark (unpublished data), who finds some differences in comparison to the previous description by Costlow and Bookhout (1961).

Eurypanopeus canalensis Abele and Kim, 1989 has been reported from Panama (the type locality) to the SE Gulf of California. It is known to inhabit coastal lagoons and estuarine environments along the tropical Pacific coast of Mexico, where it is frequently found living among mussel communities (*Mytella strigata* Hanley, 1843) attached to mangrove roots (Salgado Barragán and Hendrickx, 1997, 2002). Recently, ovigerous crabs were collected and the larvae were reared in the laboratory.

The purpose of this study is to describe in detail the larval development of *E. canalensis* and to compare the morphology of these eastern Pacific species with that of *E. depressus* and *E. abbreviatus*, from the western Atlantic.

MATERIALS AND METHODS

Three ovigerous *E. canalensis* crabs were collected from *Mytella strigata* communities attached to prop roots of *Rhizophora mangle* Linnaeus, 1753, in the Estero de Urias, Sinaloa, SE Gulf of California, in September of 2003. Specimens were maintained individually in seawater-filled aquaria with hollow bricks as a shelter. When hatching occurred, larvae (approx. 300 per female) were transferred to 12-litre conical tanks and kept at room temperature (25-28 ºC). Half of the water volume was changed every day and larvae were fed with recently-hatched *Artemia* nauplii throughout development. Moulting was recorded every day. Samples of 20 larvae of each stage were fixed in 4% formaldehyde and then preserved in 70% ethanol. The appendages were dissected in seawater and mounted in glycerine. All measurements were made with an ocular micrometer. Drawings were based on observations made on 10 larvae; measurements were taken on 20 larvae per stage. The drawings and measurements were made using a Wild MZ6 and a Zeiss Axioskop compound microscope equipped with a *camera lucida*. In zoeal stages, rostrodorsal 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 of carapace; and carapace width (CW) as the distance between the tips of the lateral protuberances. In the megalopa stage, carapace length (CL) was measured from the base of the rostrum to the posterior margin of the carapace; carapace width (CW) is the maximum width. The long natatory setae on the distal exopod segments of the first and second maxillipeds, as well as megalop pleopods, were drawn truncated. For megalopa figure, pereiopods were symmetrically arranged. Figures and descriptions are arranged according to the standard proposed by Clark *et al.* (1998). The spent female and complete larval series have been deposited in the crustacean reference collection (Colección de Referencia de Crustáceos) at UNAM, Mazatlán, Sinaloa, Mexico, under the voucher number EMU-6012.

TABLE 1. – Time (in days) of the first appearance of each larval stage of *Eurypanopeus canalensis* and measurements (in mm) of larvae at different development stages. RDL, rostrodorsal length; CL, carapace length; CW, carapace width.

Stage	Time elapsed after hatching	RDL ± SD	CW ± SD	CL ± SD
Zoea I	0	1.11 ± 0.01	0.47 ± 0.01	0.38 ± 0.02
Zoea II	4	1.40 ± 0.03	0.64 ± 0.02	0.53 ± 0.03
Zoea III	7	1.66 ± 0.05	0.81 ± 0.04	0.67 ± 0.02
Zoea IV	11	2.22 ± 0.06	1.11 ± 0.04	0.86 ± 0.04
Megalopa	14	-	0.91 ± 0.06	1.00 ± 0.07

TABLE 2. – Morphological features and setation formulae of the zoeal stages of *Eurypanopeus canalensis*. Abbreviations: s, seta; a, aesthetasc; seg, segment; sp, spines; ls, lateral spines; ds, dorsal spines.

	Zoea I	Zoea II	Zoea III	Zoea IV	All zoeas
Carapace					
Anterodorsal s.	absent	2 pairs	3 pairs	3 pairs	
Posterodorsal s.					1 pair
Ventral margin s.	absent	1 pair	7 pairs	10 pairs	
Antennule					
Exopod	4 a + 1s	5 a	7 a	13 a	
Endopod	absent	absent	bud	present	
Antenna					
Endopod	absent	bud	present	present	
Maxillule					
Exopod s.	absent	present	present	present	
Coxal endite s.	7	7	8	10	
Basial endite s.	5	7	9	13	
Endopod					1, 6
Epipod	absent	absent	present	present	
Maxilla					
Coxal endite s.	4+4	4+4	4+4	5+5	
Basial endite s.	5+4	5+4	5+5	5+6	
Endopod s.					3+5
Scaphognathite	4 + process	13+ process	19	26-28	
First maxilliped					
Basis s.					2, 2, 3, 3
Endopod s.	3, 2, 1, 2, 5	3, 2, 1, 2, 5	3, 2, 1, 2, 6	3, 2, 1, 2, 6	
Exopod s.	4	6	8	10	
Second maxilliped					
Basis					1, 1, 1, 1
Endopod s.					1, 1, 5
Exopod	4	7	9	11	
Third maxilliped	absent	bud	bud	bilobed	
Pereiopods	absent	bud	1 bilobed	1 chelate	
Abdomen					
Somite 1 s.	0	1	3	3	
Somites 2-5 s.					1 pair
Somite 6 s.	-	-	absent	absent	
Pleopods	absent	absent	buds	bilobed	
Telson					
Furcal arm sp.					2 ls, 1 ds
Terminal s.	3 pairs	3 pairs	3 pairs	4 pairs	

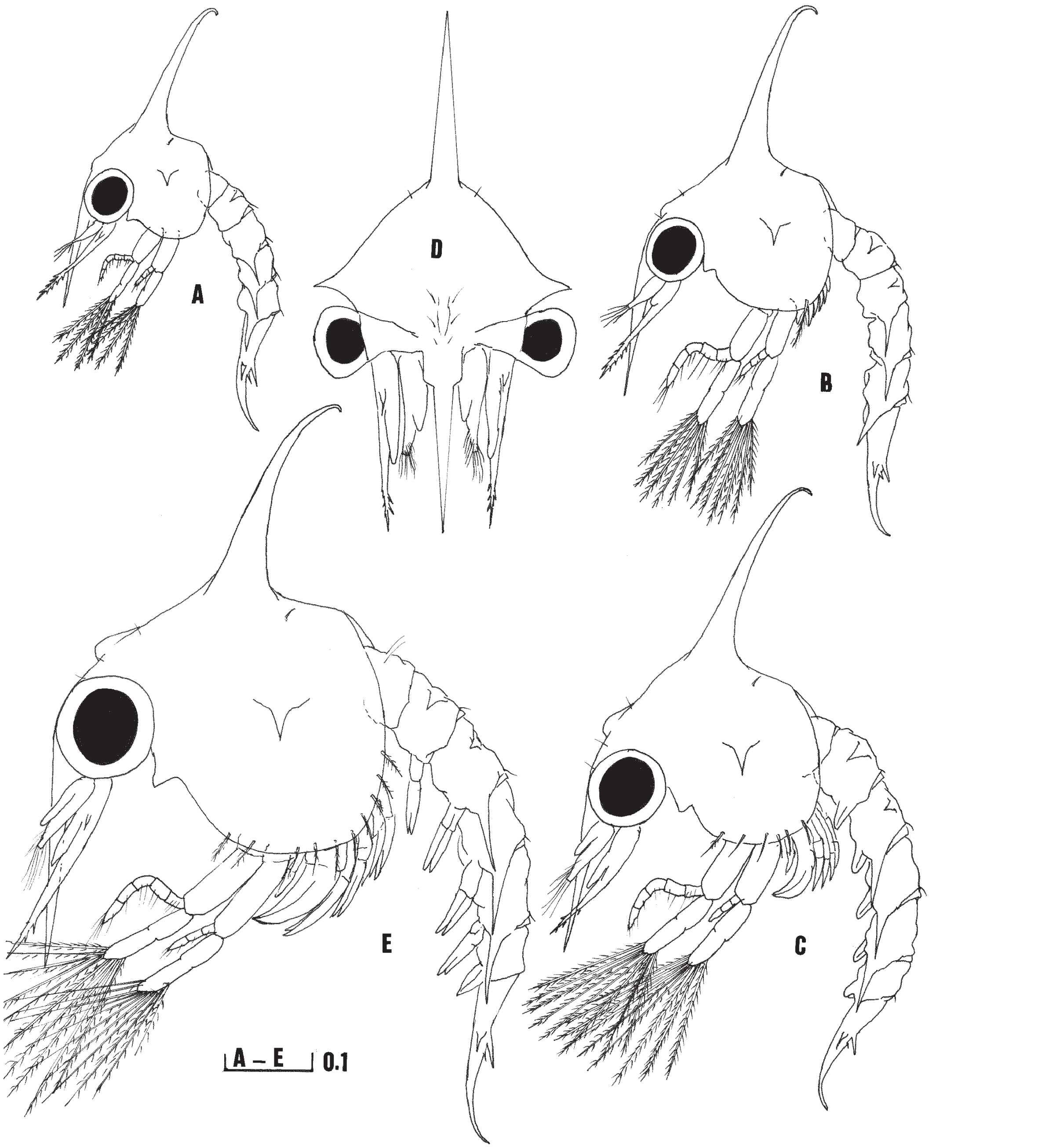

FIG. 1. – *Eurypanopeus canalensis*. A, zoea I; B, zoea II; C, D, zoea III; E, zoea IV. A, B, C, E, lateral view; D, frontal view. Scale bar in mm.

RESULTS

The larval development consisted of four zoeae and one megalopa stage and lasted 14 days, from hatching to the megalopa. No prezoeae were observed. Body measurements are summarised in Table 1, and morphological features and setation formulae of the zoeal development are listed in Table 2. The first zoeal stage is completely described, while only differences are described for subsequent stages.

Description

Eurypanopeus canalensis Abele and Kim, 1989 (Figs. 1-6)

Zoea I

Carapace (Fig. 1A). Globose, smooth. Dorsal spine present, long, curved distally. Rostral spine present, as long as protopod of antenna. Small lateral spines present. Anterodorsal protuberance pre-

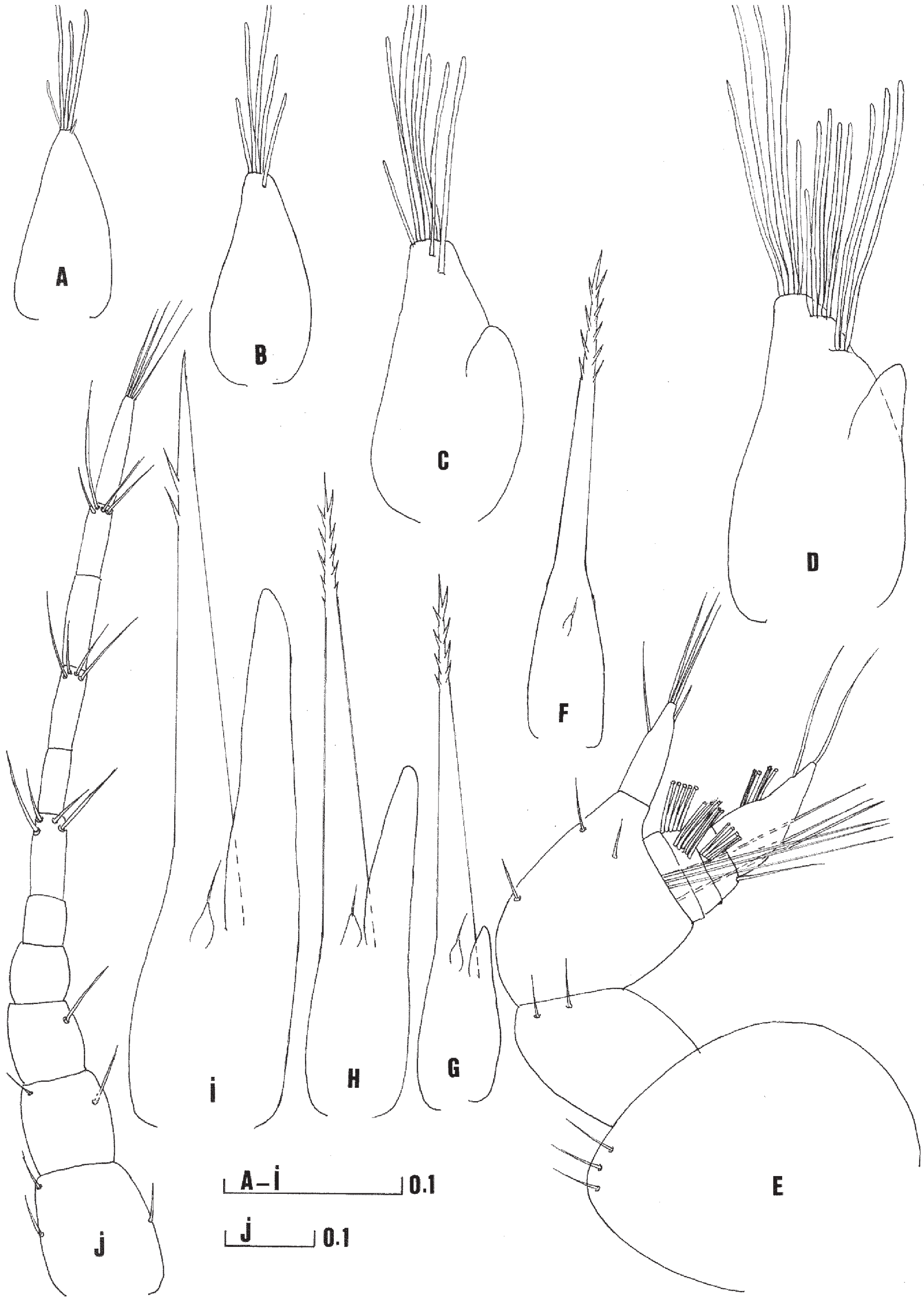

FIG. 2. – *Eurypanopeus canalensis*. Antennule. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa. Antenna. F, zoea I; G, zoea II; H, zoea III; I, zoea IV; J, megalopa. Scale bars in mm.

sent. A pair of dorsolateral setae. Ventral margin without setae. Eyes sessile.

Antennule (Fig. 2A). Uniramous. Endopod absent. Exopod unsegmented, with 4 aesthetascs of unequal length plus a short seta.

Antenna (Fig. 2F). Protopod well developed, as long as rostral spine, bearing multispinulate on distal part. Endopod absent, exopod minute, with single terminal seta.

Mandible. Palp absent. Incisor and molar processes well developed.

Maxillule (Fig. 3A). Coxal endite with 7 plumose setae. Basial endite with 5 plumodenticulate setae. Endopod 2-segmented, proximal segment with one sparsely plumose seta, distal segment with 2 subterminal and 4 terminal plumodenticulate setae. Exopod and epipod seta absent.

Maxilla (Fig. 4A). Coxal endite bilobed with 4 + 4 sparsely plumodenticulate setae. Basial endite bilobed with 5 + 4 sparsely plumose setae. Endopod unsegmented, bilobed with 3 + 5 (2 subterminal + 3 terminal) plumodenticulate setae in each lobe

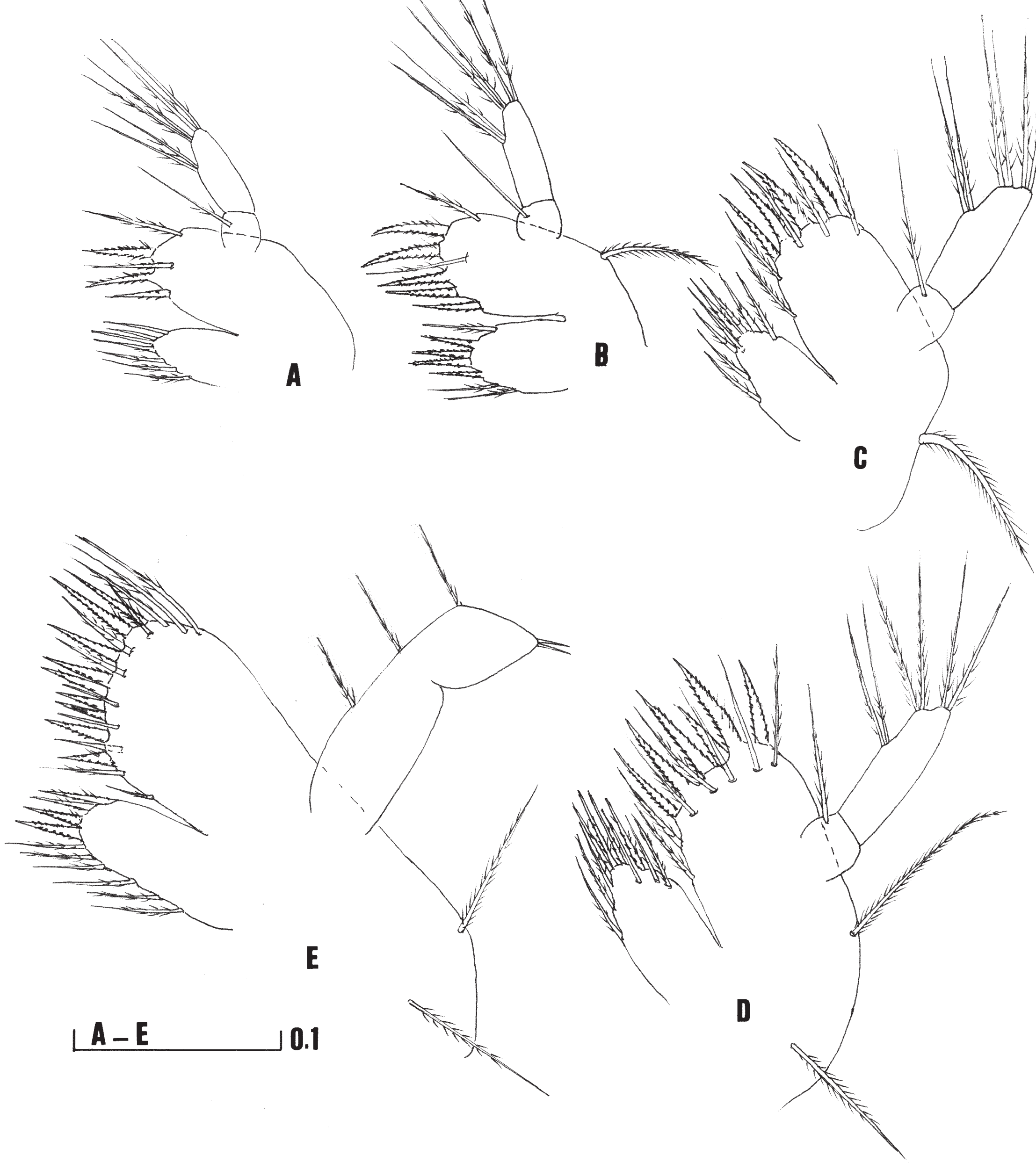

FIG. 3. – *Eurypanopeus canalensis*. Maxillule. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa. Scale bar in mm.

respectively. Scaphognathite exopod with 4 plumose marginal setae and one long distal stout process.

First maxilliped (Fig. 5A). Coxa with a single seta. Basis with 10 medial setae arranged 2, 2, 3, 3. Endopod 5-segmented with 3, 2, 1, 2, 5 setae. Exopod 2-segmented, distal segment with 4 plumose natatory setae.

Second maxilliped (Fig. 5E). Coxa without setae. Basis with 4 medial setae arranged 1, 1, 1, 1. Endopod 3-segmented with 1, 1, 5 setae (2 subterminal + 3 terminal). Exopod 2-segmented with 4 long plumose natatory setae.

Third maxilliped. Absent

Pereiopods. Absent

Abdomen (Fig. 6A). Five somites; somites 2 and 3 with a pair of dorsolateral processes; somites 3-5 with long posterolateral processes of triangular shape; somites 2-5 with a pair of posterodorsal setae each. Pleopods absent.

Telson (Fig. 6A). Bifurcated; posterior margin with 3 pairs of serrulate setae, inner pair with 4 long setulae each. One long lateral spine, one smaller lateral setae, and one dorsal medial spine on each furcal arm.

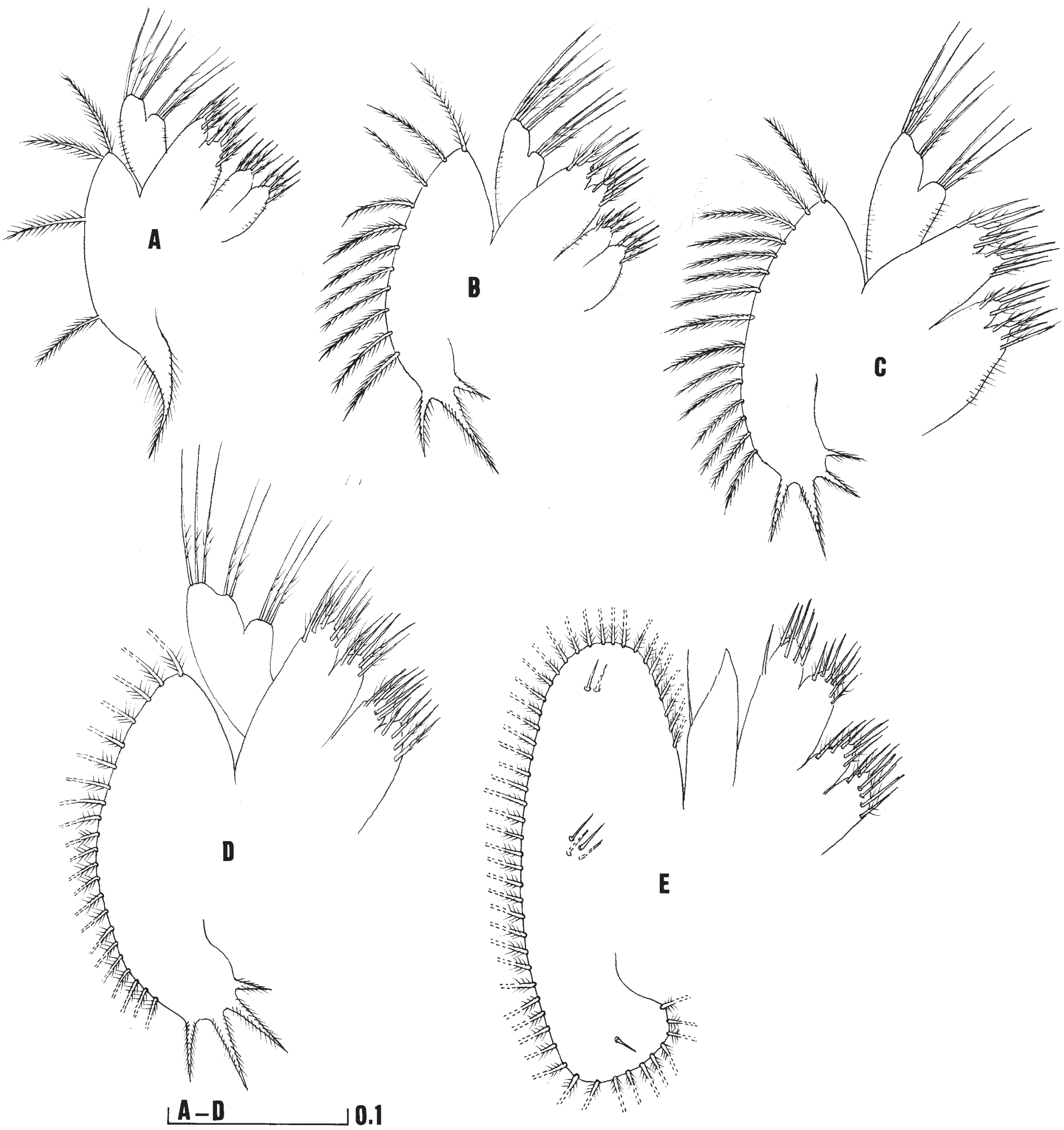

FIG. 4. – *Eurypanopeus canalensis*. Maxilla. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa. Scale bar in mm.

Zoea II

Carapace (Fig. 1B). Two pairs of anterodorsal setae. Each ventral margin with 1 sparsely plumose seta. Eyes stalked.

Antennule (Fig. 2B). Exopod with 1 additional subterminal aesthetasc.

Antenna (Fig. 2G). Endopod bud present.

Maxillule (Fig. 3B). Basial endite with 7 plumodenticulate setae. Exopod present as long plumose marginal seta.

Maxilla (Fig. 4B). Scaphognathite with 13 plumose marginal setae plus setose posterior process.

First maxilliped (Fig. 5B). Exopod distal segment with 6 terminal natatory setae.

Second maxilliped (Fig. 5F). Exopod distal segment with 7 natatory setae.

Third maxilliped. Present as small bud.

Pereiopods. Present as small buds.

Abdomen (Fig. 6B). First somite with one long, mid-dorsal plumose seta. Posterolateral processes on somites 3-5 elongated.

Zoea III

Carapace (Fig. 1C,D). Now with 3 pair of anterodorsal setae. Six sparsely plumose setae on ventral margins.

Antennule (Fig. 2C). Now biramous, endopod present as bud. Exopod with 1 additional terminal

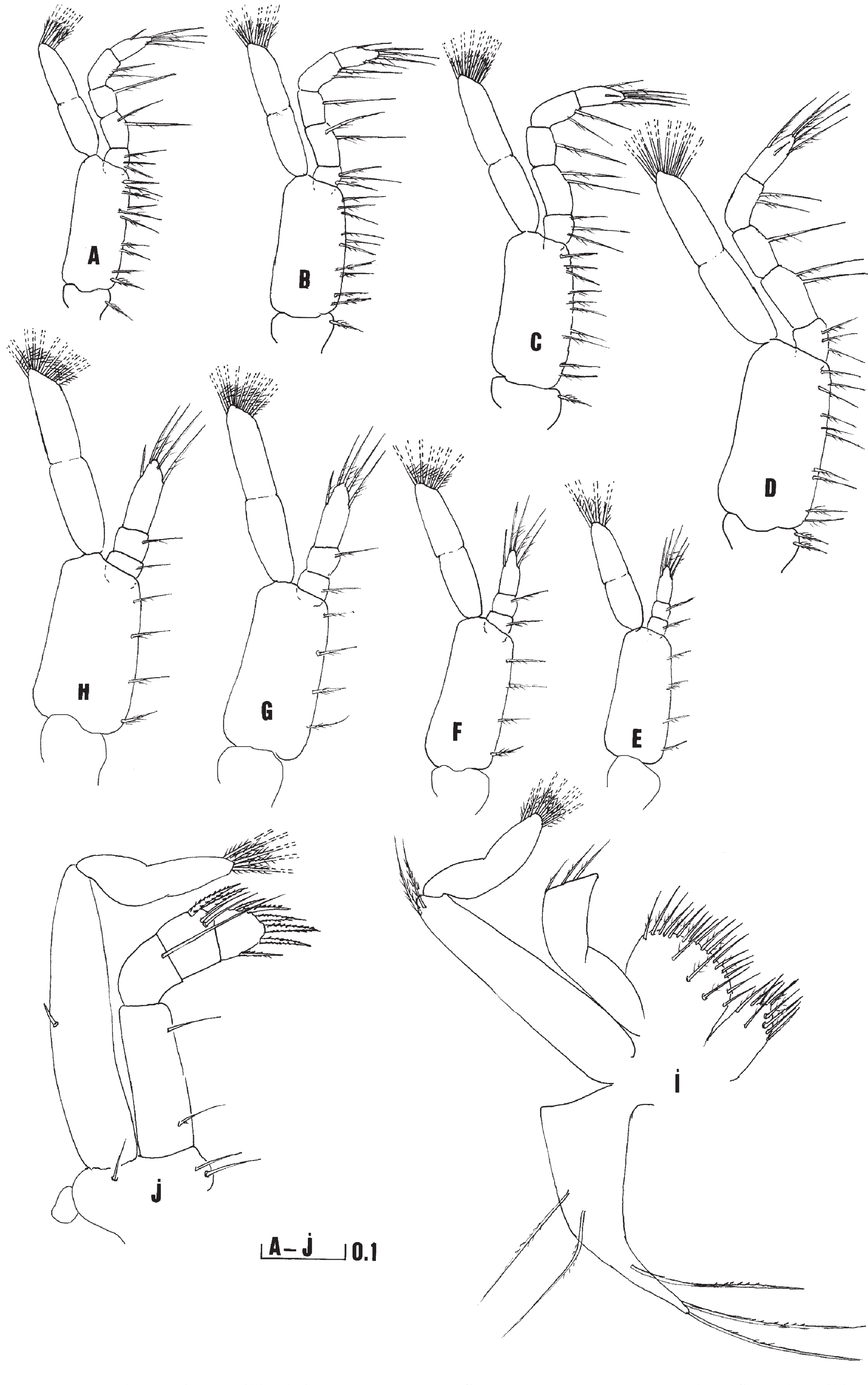

FIG. 5. – *Eurypanopeus canalensis*. First maxilliped. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; I, megalopa. Second maxilliped. E, zoea I; F, zoea II; G, zoea III; H, zoea IV; J, megalopa. Scale bar in mm.

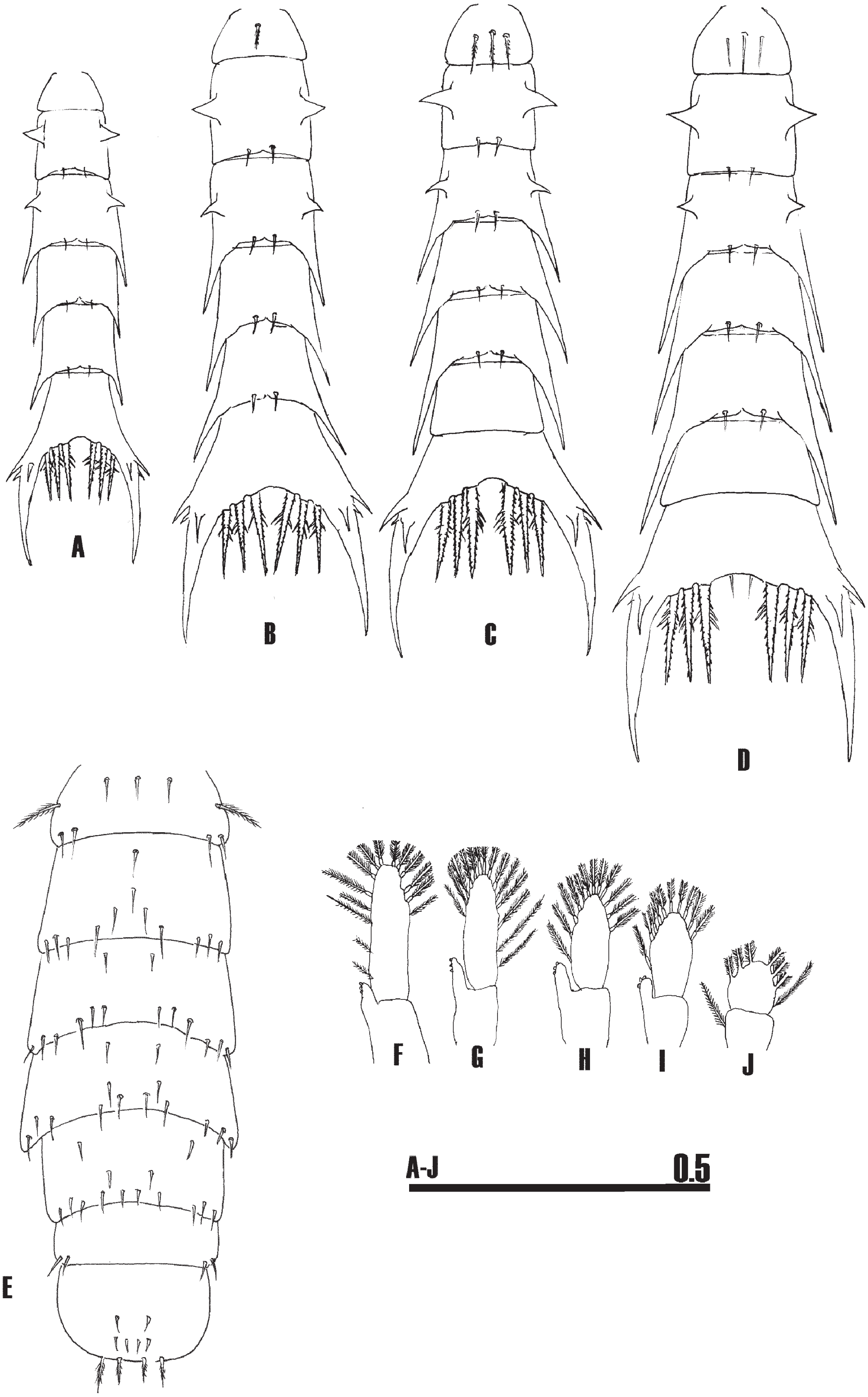

FIG. 6. – *Eurypanopeus canalensis*. Abdomen in dorsal view. A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa; F-J, pleopods 1 to 5 (from left to right). Scale bar in mm.

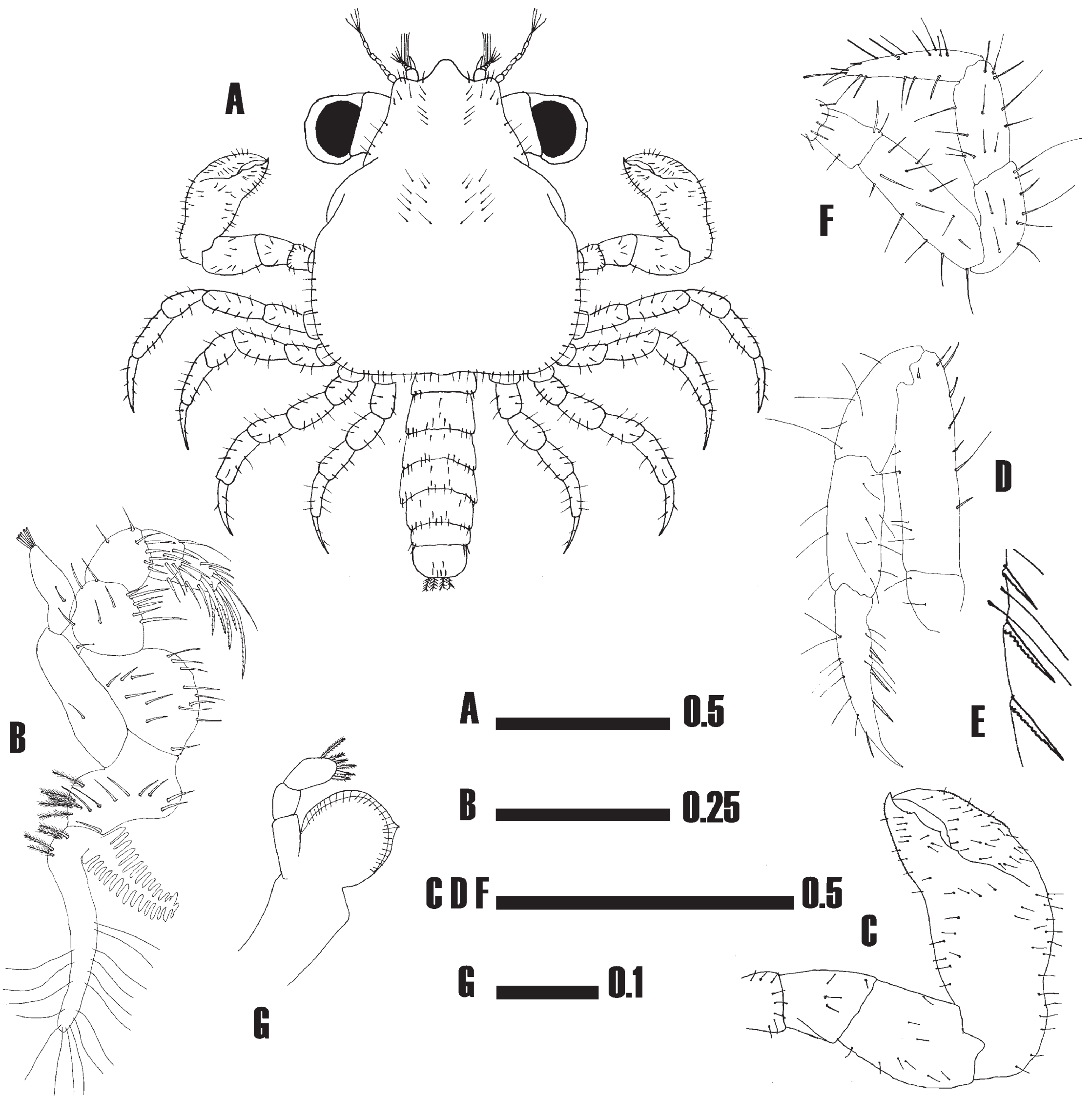

FIG. 7. – *Eurypanopeus canalensis*. Megalopa. A, dorsal view; B, third maxilliped; C, right cheliped; D, 3rd pereiopod; E, amplification of pereiopod 3 dactylus; F, 5th pereiopod; G, mandible. Scale bars in mm.

and another one subterminal aesthetascs.

Antenna (Fig. 2H). Endopod bud elongated, almost reaching middle of protopod length.

Maxillule (Fig. 3C). Coxal endite with 8 plumose setae. Basial endite with 6 terminal plus 3 subterminal plumodenticulate setae.

Maxilla (Fig. 4C). Basial endite with 5 + 5 plumose and plumodenticulate setae. Scaphognathite with 19 plumose marginal setae.

First maxilliped (Fig. 5C). Distal segment of endopod now with 6 seta (2 subterminal + 4 terminal), exopod distal segment with 8 terminal natatory setae.

Second maxilliped (Fig. 5G). Exopod distal segment with 9 terminal natatory setae.

Third maxilliped. Biramous, elongated bud.

Pereiopods. Chelipeds bilobated; pereiopods slightly segmented.

Abdomen (Fig. 6C). Sixth somite present. Somite 1 with 3 mid-dorsal plumose setae. Pleopod buds on somites 2-6.

Zoea IV

Carapace (Fig. 1C, D). Anterodorsal prominence strongly marked. Ten sparsely plumose setae on ventral margins.

Antennule (Fig. 2 D). Endopod bud elongated. Exopod with 13 aesthetascs arranged 3 (subterminal), 5 (subterminal) and 5 (terminal).

Antenna (Fig. 2H). Protopod with 2 subterminal spines. Endopod almost 3/4 of protopod length.

Mandible. Palp present as small bud.

Maxillule (Fig. 3D). Coxal endite with 10 plumose setae. Basial endite with 8 terminal and 5 subterminal plumose or plumodenticulate setae, as figured. Epipodal seta present.

Maxilla (Fig. 4D). Coxal endite with 5 + 5 setae. Basial endite with 5 + 6 setae. Scaphognathite with 26-28 plumose marginal setae.

First maxilliped (Fig. 5D). Coxa with two setae. Exopod distal segment with 10 terminal natatory setae.

Second maxilliped (Fig. 5H). Exopod distal segment with 11 terminal natatory setae.

Third maxilliped. Epipod bud present.

Pereiopods. Chelipeds and pereiopods more developed and segmented than in previous stage.

Abdomen (Fig. 6D). Pleopod buds more developed and biramous in somites 2-6.

Telson (Fig. 6D). An additional pair of short terminal setae on mid-posterior margin.

Megalopa

Carapace (Fig. 7A). Rostrum ventrally deflected. Setal arrangement as figured.

Antennule (Fig. 2E). Peduncle 3-segmented with 3, 2, 3 + 6 long setae. Endopod unsegmented with 2 subterminal and 3 terminal setae. Exopod 4-segmented with 0, 10, 4, 4 aesthetascs, and 0, 0, 1, 2 setae.

Antenna (Fig. 2J). Peduncle 3-segmented with 3, 2, 1, setae. Flagellum 8-segmented with 0, 0, 4, 0, 4 0, 4, 4 setae.

Mandible (Fig. 7G). Palp 3-segmented with 0, 0, 6-7 setae.

Maxillule (Fig. 3E). Basial endite with 13 marginal, 7 submarginal and plumose or plumodenticulate setae, as figured. Endopod unsegmented, with 1 long plumose seta proximally and 4 setae distally (1 basal, 1 subterminal and 2 terminal).

Maxilla (Fig. 4E). Coxal endite with 7 + 6 plumose setae. Basial endite with 7 + 6 plumose setae. Endopod no longer bilobed, tapering, with 1 long seta on inner margin. Scaphognathite with 50 plumose marginal setae and 7 lateral setae, as figured.

First maxilliped (Fig. 5I). Epipod with 5 long setae. Coxal endite with 9 sparsely plumose setae. Basial endite with 20 plumose setae (4 inner). Endopod unsegmented with 3 sparsely plumose setae. Exopod 2-segmented, proximal segment with 2 terminal setae, distal segment with 7 long terminal plumodenticulate feeding setae.

Second maxilliped (Fig. 5J). Epipod with 1 seta plus gill bud. Coxa and basis not differentiated, with 3 setae. Endopod 4-segmented with 2, 1, 4, 6 plumose-plumodenticulate setae respectively. Exopod 2-segmented, proximal segment with 1 short medial seta, distal segment with 5 long terminal, plumodenticulate feeding setae.

Third maxilliped (Fig. 7B). Epipod elongated with 16 setae. Coxa and basis not differentiated, with 14 sparsely plumose setae. Endopod 5-segmented, with 15, 11, 8, 7, 10 sparsely plumose setae. Exopod 2-segmented, proximal segment with 1 medial simple setae, distal segment with 1 medial simple seta plus 5 long terminal plumodenticulate raptorial setae. Gill developed.

Pereiopods (Figs. 7 C-E). All segments well differentiated and with setae as figured. Cheliped (7C) without ischial spine. Pereiopods 2-4 (as in Fig. 7E) with 3 serrulate spines (7G) on inner margin of dactylus. Pereiopod 5 (7D) without ischial spine.

Abdomen (Figs. 6E, F-J). 6-segmented, setation as figured. Pleopods (Figs. 6F-J) decreasing in size from 1st to 4th; endopod unsegmented, with 3 distal cincinuli on outer margin, and exopod with 14, 13, 12 and 10 marginal plumose natatory setae respectively. Uropods 2-segmented, proximal segment with 1 long marginal plumose natatory setae, distal segment with 7 marginal, plumose natatory setae.

Telson (Fig. 6E). Sub-rectangular, with 3 pairs of mid-dorsal setae and 4 long plumose setae on posterior margin.

DISCUSSION

Based mainly on recommendations of Takeda (1976) and Guinot (1977, 1978), the former Xanthidae are now treated as a superfamily containing 11 families. Xanthids originally contained a wide variety of disparate forms and was the largest single family of Decapoda, with an estimated 130 genera and over 1,000 species (Martin and Davis, 2001). The taxonomic history of this group is confusing, and superficial similarities in morphology of the adults often make species identification very difficult. Still today, there are many genera that are inadequately defined or that cannot be assigned with confidence to one of the eleven currently recognised families, and some species that have been with-drawn from their original genera assignment have not been assigned to a new genus. In addition to standard morphological characters, Martin and Davis (2001), on the basis of some previously published results, suggested that molecular evidence warranted separate family status for some of the former Xanthidae subfamilies. There is little doubt that future research in that direction will allow the (partial or complete) reorganisation of the 32 family and subfamilies that have been proposed for the Xanthidae s.l. (Manning and Holthuis, 1981). In the meantime, Xanthoidea phylogenetic relationships are still uncertain.

Within the Panopeidae, the most complex family of Xanthoidea currently recognised, recent examination of adult and larval morphology of a limited number of species indicates that some genera are not monophyletic units (see Felder and Martin, 2003), and molecular evidence is supporting this (Schubart *et al*., 2000a, 2000b).

Earlier studies of larvae of American panopeids have revealed unique characters in zoeal morphology (Martin, 1984; Martin *et al*., 1985; Felder and Martin, 2003). As in the case of the morphology of male first pleopods (i.e. ornemantation of tip and shaft), the study of larval characters of zoeae and megalopae is considered an important tool for classifying species and genera correctly. One example of this is the new genus *Acantholobulus* Felder and Martin, 2003, recently proposed to include some species formerly considered to be members of *Hexapanopeus* and *Panopeus*. Several authors working with xanthoid crabs have suggested significant changes in the classification and phylogenetic relationships of this group based primarily on strong larval evidence (Van Dover *et al*., 1986; Ng and Clark, 1999; 2000). However, detailed descriptions are available only for a small number of xanthoid species, and some of the previous descriptions are—at least to some extent—inaccurate.

When we compare the larval morphological of the three *Eurypanopeus* species for which complete larval development is known (i.e. *E. depressus*, *E. abbreviatus* and *E. canalensis*), the monophyly of this genus becomes uncertain. Among the morphological and meristic characters described for these three species (Tables 3, 4), two differences are noted that cannot be attributed to intrageneric variability. In *E. depressus* Costlow and Bookhout (1961), a single dorsal spine is observed on the furcal arms of the telson of all zoeal stages, while a dorsal and two laterals spines occur in both *E. abbreviatus* and *E. canalensis*. However, the recent re-examination of the first zoeal stage of this species by Clark (unpublished data) demonstrates that actually a second pair of minute spines in the furca exists in this stage. It is possible that this additional pair is also present in further zoeal stages and was overlooked by Costlow and Bookhout (1961). Another possibility is that spines may not really be present in further stages.

Furthermore, according to the description of Costlow and Bookhout (1961) there is a large and obvious hook-like spine on the ischium of the megalopal cheliped of *E. depressus*, and this spine is absent in both *E. abbreviatus* and *E. canalensis*. These differences are beyond the limits of variation among species within a genus, thus suggesting that *E. depressus* probably belongs to a different genus. The presence of a hook-like spine on the cheliped of the megalopa of *E. depressus,* as described by Costlow and Bookhout (1961), also modifies the key to Panopeidae megalopae of the warm-temperate southwestern Atlantic proposed by Rodríguez and Spivak (2001), since this feature (absence of ischial hook in the cheliped) distinguishes the megalopa of *E. depressus* from those of all other species included in this key.

Some unexpected differences in setation patterns were also noted among the three species (see Tables 3, 4); these might be due to a lack of accuracy when the zoeae of *E. depressus* and *E. abbreviatus* were illustrated. This suggestion could be support for *E. depressus* by the differences in the recent description provided by P. Clark (unpublished data). For instance, the setation pattern of the endopod of the second maxilliped of *E. abbreviatus* should be 1, 1 ,5 (instead of 1, 1, 4; see Negreiros-Fransozo, 1986: Fig. 4), as in the other two species since this feature seems to be invariable among species of the same genera. The minute fifth seta was probably overlooked. Another example is the setation of the basis of the first maxilliped. This was not considered to be an important character in the description of *E. depressus* by Costlow and Bookhout, (1961) (Figs. 8, 16), where the setation pattern is represented only in the first and second zoea (8 setae on the basis). However, this setation was checked for zoea I by P. Clark (unpublished data). In the case of *E. abbreviatus*, the information is available in the text only for zoea IV (10 setae arranged 2, 2, 3, 3) and illustrated for the zoeae I-IV (number varies from 8 to 10) (see Negreiros-Fransozo, 1986: Fig. 4). Consider-

TABLE 3. – Morphological and meristic differences between the zoeal stages of the species *E. depressus* (Costlow and Bookhout, 1961), *E. abbreviatus* (Negreiros-Fransozo, 1986), and *E. canalensis* (present work) (*from Clark, unpublished data) Abbreviations as in Table 2.

	E. depressus	*E. abbreviatus*	*E. canalensis*
ZOEA I			
Antennule	*4 a, 1 s	2 a, 1 s	4 a + 1s
Maxilla			
Coxal endite s.	*4+4	3+4	4+4
Endopod s.	*3+5	3+5	3+5
Scaphognathite s.	*4	4	4
First maxilliped			
Basis s.	*10 (2, 2, 3, 3)	9 (3, 2, 2, 2)	10 (2, 2, 3, 3)
Second maxilliped			
Endopod	*1, 1, 5	1, 1, 4	1, 1, 5
Telson			
Furcal arms sp.	*2 ls, 1 ds	2 ls, 1 ds	2 ls , 1 ds
ZOEA II			
Antenna			
Endopod	absent	absent	bud
Maxillule			
Basial endite s.	7-8?	5	7
Maxilla			
Endopod	3+5	2+5	3+5
Scaphognathite s.	10	10	14
First maxilliped			
Basis s.	8 (1, 1, 3, 3)	9 (3, 2, 2, 2)	10 (2 ,2, 3, 3)
Second maxilliped			
Endopod	1, 1, 5	1, 1, 4	1, 1, 5
Telson			
Furcal arm sp.	1 ds	2 ls, 1 ds	2 ls, 1ds
ZOEA III			
Antennule	4 a, 1 s	4 a, 1 s	7 a
Maxillule			
Basial endite s.	8	5	9
Maxilla			
Coxal endite s.	3+5	3+5	4+4
Basial endite s.	5+5	5+4	5+5
Endopod s.	3+5	2+5	3+5
Scaphognathite s.	17	15	19
Second maxilliped			
Endopod	1, 1, 5	1, 1, 4	1, 1, 5
Exopod	9	8	9
Telson			
Furcal arm sp.	1 ds	2 ls, 1 ds	2 ls, 1ds
Terminal s.	4 pairs	4 pairs	3 pairs
ZOEA IV			
Antennule			
Exopod	12 a, 1 s	6 a, 1 s	13 a
Endopod	bud	bud	elongated bud
Maxillule			
Coxal endite s.	8	8	10
Basial endite s.	10	10	13
Maxilla			
Coxal endite s.	5+4	4+5	5+5
Basial endite s.	6+6	5+5	5+6
Endopod s.	3+5	3+4	3+5
Scaphognathite s.	25	25	26-28
First maxilliped			
Exopod s.	9	9	10
Second maxilliped			
Endopod	1, 1, 5	1, 1, 4	1, 1, 5
Telson			
Terminal s.	4 pairs + 1	4 pairs +1	4 pairs

TABLE 4. – Morphological and meristic differences between the megalopae of the species *E. depressus* (Costlow and Bookhout, 1961), *E. abbreviatus* (Negreiros-Fransozo, 1986), and *E. canalensis* (present work). Abbreviations as in Table 2.

	E. depressus	*E. abbreviatus*	*E. canalensis*
Carapace horns	no	yes	no
Hook on cheliped ischium	yes	no	no
Antennule			
Peduncle s.	1, 1, 6	0, 2, 2+6	3, 2, 3+6
Endopod s.	1+3	0+4	2+3
Exopod (a,) (s.)	(6,6,3) (0,0,1)	(4,4,3,3)(0,0,0,1)	(0,10,4,4)(0,0,1,2)
Antenna			
Peduncle s.	3,4,1	1,1,1	3,2,1
Flagellum s.	1,0,0,3,4,0,3,4	0,0,3,0,4,0,4,4	0,0,4,0,4,0,4,4
Mandible			
Palp s.	7	6-7	6
Maxillule			
Basial endite s.	10+5	6+6	13+7
Endopod s.	3+5		1+4
Maxilla			
Coxal endite s.	6+4	7+5	7+6
Basial endite s.	6+9	6+6	7+6
Scaphognathite s.	70-71	38	50+7
First maxilliped			
Epipod s	6	no data	5
Coxal endite s.	9	12	9
Basial endite s.	15	18	20
Endopod s.	5	5	3
Exopod s.	2,5	0,5??	2, 7
Second maxilliped			
Endopod s.	3,1,5,11	4,1,3,11	2,1,4,6
Exopod s.	0, 7	0, 5	1, 5
Third maxilliped			
Epipod s.	12	12	16
Coxa and basis s.	10	11	14
Endopod s.	17,11,7,6,8	15,8,3,5,7	15,11,8,7,10
Abdomen			
Pleopods s.	13,12,11,9,5	15,15,13,12	14,13,12,10
Uropod s.	no data	no data	1,7

ing that this setation pattern is constant during the entire development (see *E. canalensis*), it is likely that some errors were introduced either in the text or in the figures. Unfortunately, carapace setation cannot be compared since this information was not provided for *E. depressus* and *E. abbreviatus*.

The comparative study of three species of *Eurypanopeus* reinforces the hypothesis of paraphyly within this genus previously suggested by Schubart *et al.* (2000a,b). The type species of the genus is *E. crenatus* (Milne Edwards and Lucas, 1834), known from Ecuador to Chile (Rathbun, 1930; Hendrickx, 1995), for which a larval description is not available. A comparative review of the morphology of the type species and of (at least) the three species of *Eurypanopeus* included in this study, combined with a description of the larvae of *E. crenatus* and molecular analysis of all species, is therefore needed in order to decide on the final generic assignment of these species.

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