

Pilumnus reticulatus* Stimpson, 1860 (Decapoda: Brachyura: Pilumnidae): a reappraisal of larval characters from laboratory reared material

EDUARDO D. SPIVAK¹ and ANTONIO RODRÍGUEZ^{2†}

¹Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Casilla de Correos 1216, 7600 Mar del Plata, Argentina. E-mail: espivak@mdp.edu.ar

²Instituto de Ciencias Marinas de Andalucía (C.S.I.C.). Polígono de Río San Pedro s/n, Apartado Oficial, 11510 Puerto Real, Cádiz, Spain. E-mail: antonio.rodriguez@icman.csic.es

SUMMARY: The pilumnid crab *Pilumnus reticulatus* Stimpson, 1860 is known to range from the Caribbean Sea to Argentina (Atlantic). It has also been recorded from the Pacific coast of Panama. Larvae of *Pilumnus reticulatus* from females collected in the mouth of the Rio de la Plata were reared in the laboratory from zoea I to megalopa. A reappraisal of larval characters is made by comparing the results of this present study with the previous descriptions of Montú *et al.* (1989) and with those from other *Pilumnus* species: *P. dasypodus*, *P. sayi*, *P. vespertilio*, *P. hirtellus*, *P. kempfi*, *P. scabriusculus* and *P. minutus*.

Key words: *Pilumnus reticulatus*, larval development, zoea, megalopa, Pilumnidae.

INTRODUCTION

Pilumnid crabs inhabit coastal waters worldwide and belong to the family Pilumnidae of the superfamily Xanthoidea (Guinot, 1977). Within *Pilumnus* Leach, 1815, complete zoeae development has been published for the following species: *P. dasypodus* Kingsley, 1879 by Sandifer, 1974 and Bookhout and Costlow, 1979; *P. sayi* Rathbun, 1897 by Bookhout and Costlow, 1979; *P. vespertilio* (Fabricius, 1793) by Lim and Tan, 1981; *P. hirtellus* (Linnaeus, 1761) by Salman, 1982 and Ingle, 1983, 1992; *P. reticulatus* Stimpson, 1860 by Montú *et al.*, 1989; *P. kempfi* Deb, 1987 by Siddiqui and Tirmizi, 1992; *P.*

scabriusculus Adams and White, 1849 by Terada, 1990; and *P. minutus* De Haan, 1835 by Terada, 1984 and Ko, 1994, 1997. Hale (1931) and Wear (1967) described abbreviated or direct development in *P. vestitus* Haswell, 1882, *P. novaezealandiae* Filhol, 1886 and *P. lumpinus* Bennet, 1964. Detailed descriptions and illustrations of some stages of different species of *Pilumnus*, obtained from northeastern Atlantic and Mediterranean plankton samples, have also been published (see Ingle, 1992, for a review).

Seven species of *Pilumnus* have been recorded from the coasts of the southwestern Atlantic (Melo, 1996). *Pilumnus reticulatus* is known from the Caribbean to the north of Argentina, and along the Pacific coast of Panama. It inhabits mainly the intertidal or shallow waters, but may reach 75 m in

† Corresponding author.

*Received January 16, 2001. Accepted July 2, 2001.

depth. It is the only species in the genus that crosses the Rio de la Plata biogeographical barrier (Rathbun, 1930; Boschi, 1964; Melo, 1996). Three other species have been synonymised under *P. reticulatus*, viz. *P. tessellatus* A. Milne Edwards, 1880, *P. meridionalis* Nobili, 1901, and *P. fragosus* A. Milne Edwards, 1880 (see Rathbun, 1930). Rathbun (1930), however, notes that there is considerable variation in *P. reticulatus*, and for convenience recognises two forms, “*forma fragosa*” and “*forma tessellata*”. The present South American specimens belong to Rathbun’s “*forma tessellata*” (Boschi, 1964).

Larvae of *Pilumnus reticulatus* from the Rio de la Plata differ in several characters from the previous description by Montú *et al.* (1989). However, this description was cited neither in later studies on other *Pilumnus* species (Terada, 1990; Siddiqui and Tirmizi, 1992; Ko, 1994, 1997) nor in regional treatises (Melo, 1996; Pohle *et al.*, 1999: 1335-1336). Therefore, the aim of this study is to describe and reappraise the morphology of *Pilumnus reticulatus* zoeas and megalopa by comparing the characters with those of Montú *et al.* (1989) and with those of the following *Pilumnus* species: *P. dasydodus*, *P. sayi*, *P. vespertilio*, *P. hirtellus*, *P. kempi*, *P. scabriusculus* and *P. minutus*.

MATERIAL AND METHODS

One male and four ovigerous females of *Pilumnus reticulatus* forma *tessellata* were collected in the Rio de la Plata Estuary (35°22’S, 55°36’W) during a fishing cruise of the “BIP Eduardo Holmberg” in November 1997 (Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina, Station 669). The sample was taken with a bottom trawl, 1cm mesh size. The bottom (12 m deep) was muddy, with abundant colonies of the tubicolous polychaete *Phyllochaetopterus socialis* (Claparède, 1868). *Pilumnus reticulatus* was found mainly in crevices

among the tubes. Water salinity and temperature at the bottom were 29.9 PSU and 17.3°C respectively.

Two ovigerous females were transported to the laboratory of the Departamento de Biología, Universidad de Mar del Plata, and maintained in an aquarium containing natural sea water until the eggs hatched (December 26, 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). From zoea I to megalopa, *Artemia* sp. nauplii were offered as food.

Drawings and measurements were made using a Wild MZ6 and a Zeiss Axioscop compound microscope, both equipped with a *camera lucida*. All measurements were made with an ocular micrometer. Drawings were based on five larvae, and measurements made on 20 larvae, per stage. For zoeae, rostro-dorsal length (RDL) was measured from the tip of the rostral to the tip of the dorsal spines; carapace length (CL) from the base of the rostrum to the posterior margin; and carapace width (CW) as the distance between the tips of the lateral spines. In the megalopa stage, carapace length (CL) was measured from the base of the rostrum to the posterior margin; carapace width (CW) as the maximum width. The long natatory setae on the distal exopod segments of the first and second maxillipeds of zoeae are drawn truncated in Figure 5. Also, long setae of the scaphognathite of the maxilla of zoea IV and the megalopa, and of pleopod 2-4 of megalopa, are drawn truncated (Figs. 4 and 7 respectively).

Samples of larvae and the two adult females of *Pilumnus reticulatus* are deposited in the United States National Museum of Natural History, Washington, under the catalog numbers USNM 291173 (females) and USNM 291174 (zoeae 1 to 4 and megalopa). Descriptions and figures are arranged according to the standard proposed by Clark *et al.* (1998).

TABLE 1. – Time to the first appearance of each larval stage and measurements of *Pilumnus reticulatus*.

Stage	Time elapsed after hatching (days)	Rostro-dorsal length (RDL) ± SD (mm)	Carapace width (CW) ± SD (mm)	Carapace length (CL) ± SD (mm)
Zoea I	0	1.02 ± 0.02	0.68 ± 0.02	0.58 ± 0.02
Zoea II	5	1.16 ± 0.03	0.68 ± 0.03	0.63 ± 0.02
Zoea III	9	1.44 ± 0.04	0.81 ± 0.03	0.79 ± 0.02
Zoea IV	13	1.48 ± 0.02	0.92 ± 0.02	0.92 ± 0.03
Megalopa	16	-	0.88 ± 0.01	1.05 ± 0.03

RESULTS

Larval development consisted of 4 zoeae and 1 megalopa stage and lasted 30 days, from hatching to the first crab. Body measurements are summarized in Table 1.

Larval description

Pilumnus reticulatus Stimpson, 1860
(Figs. 1-7)

Pilumnus reticulatus, previous description (Montú *et al.*, 1989: 165-190, Figs. 1-10)

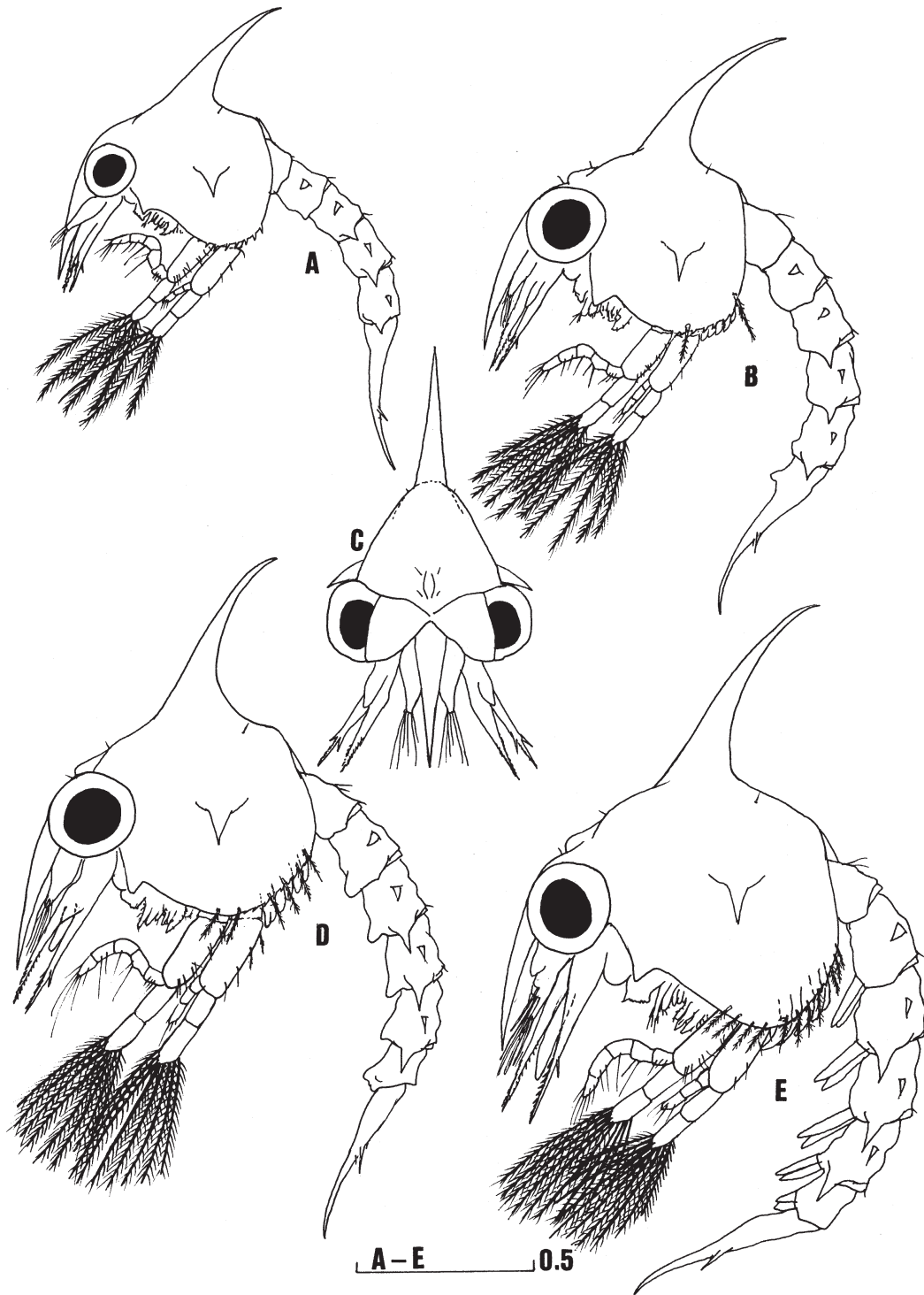


FIG. 1. – *Pilumnus reticulatus* (Stimpson). Lateral view: A, zoea I; B, zoea II; D, zoea III; E, zoea IV. Frontal view: C, zoea II. Scale bar in mm.

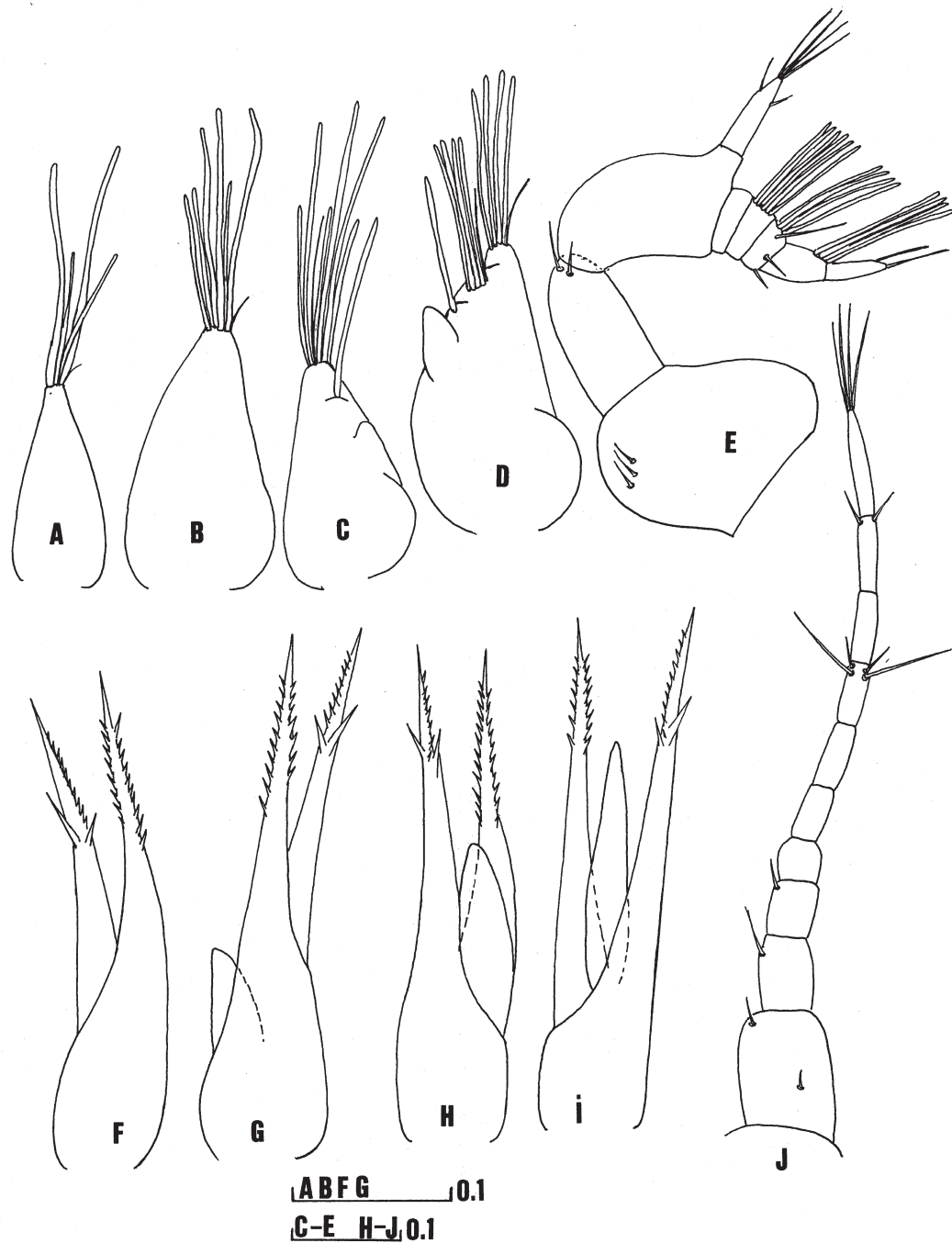


FIG. 2. – *Pilumnus reticulatus* (Stimpson). Antennule: A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa. Antenna: F, zoea I; G, zoea II; H, zoea III; I, zoea IV; J, megalopa. Scale bars in mm.

Zoea I

Carapace (Fig. 1A) globose, smooth and without tubercles, with dorsal and rostral spines (RDL/CL = 1.77 ± 0.04). Dorsal spine gently curved. Lateral spines short (CW/CL = 1.17 ± 0.02). One pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Ventral margin denticulate. Eyes sessile.

Antennule (Fig. 2A) uniramous. Endopod absent. Exopod unsegmented with 4 aesthetascs (2 long and 2 thin and short) and 1 seta.

Antenna (Fig. 2F), protopod well developed exceeding tip of rostral spine, bearing 2 rows of spines. Exopod elongated, as long as protopod, with 1 long and 1 smaller medial setae; distal half acute, with 1 row of even smaller spines.

Mandible (not figured), incisor and molar

processes differentiated. Endopod palp absent.

Maxillule (Fig. 3A), coxal endite with 7 sparsely plumose setae. Basial endite with 5 plumodenticulate and sparsely plumose setae. Endopod 2-segmented, with 1 sparsely plumose seta in proximal segment and 2 subterminal and 4 terminal sparsely plumose setae in distal segment. Exopod and epipod setae absent.

Maxilla (Fig. 4A), coxal endite slightly bilobed with 5+4 sparsely plumose setae. Basial endite

bilobed with 5+4 sparsely plumose setae. Endopod unsegmented, bilobed with 3 + 5 (2 subterminal and 3 terminal) sparsely plumose setae. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

First maxilliped (Fig. 5A), coxa without seta. Basis with 10 medial setae arranged 2, 2, 3, 3. Endopod 5-segmented with 3, 2, 1, 2, 5 (1 lateral + 3 terminal + 1 subterminal) setae. Exopod 2-segmented and 4 long terminal plumose natatory setae.

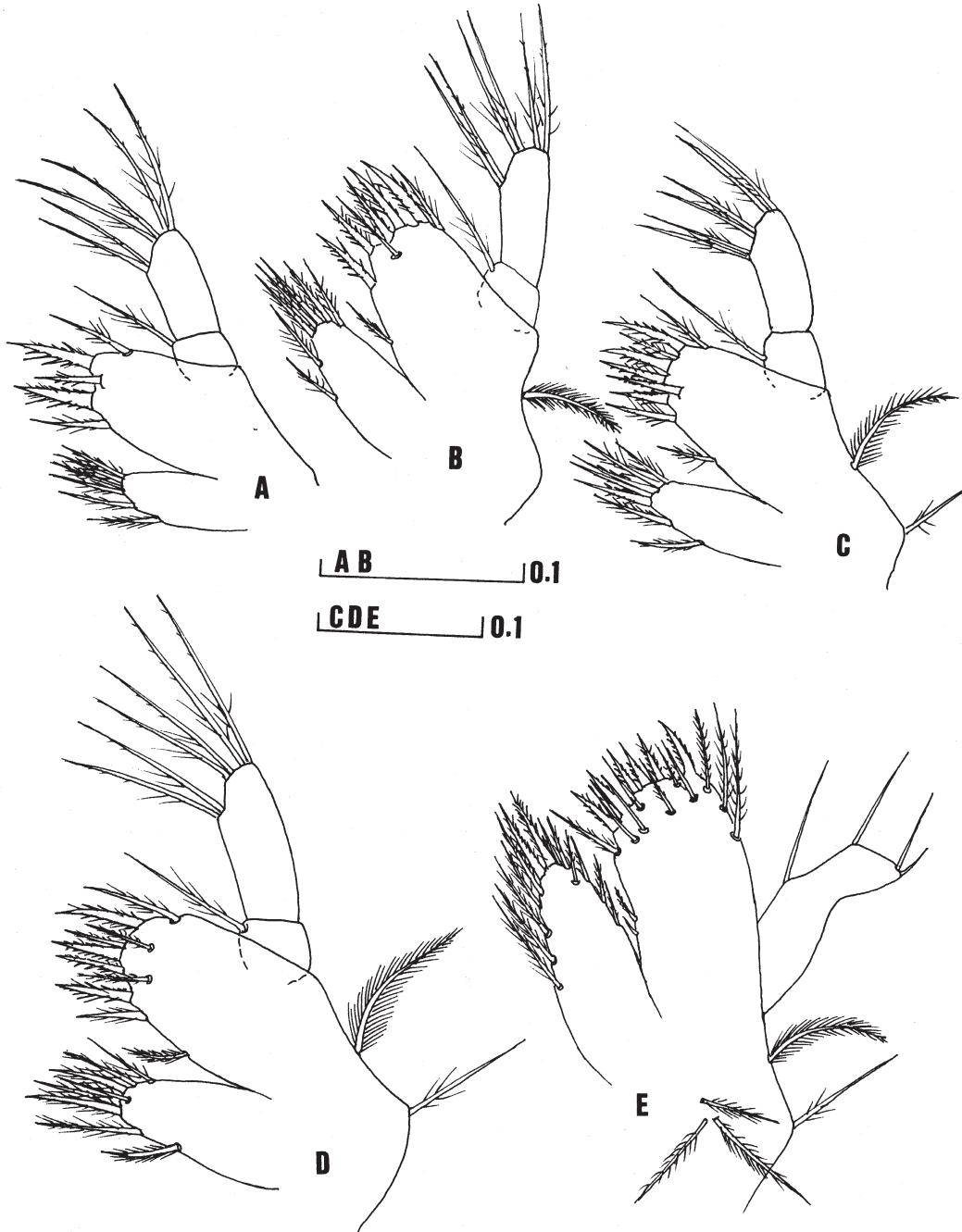


FIG. 3. — *Pilumnus reticulatus* (Stimpson). Maxillule: A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa. Scale bars in mm.

Second maxilliped (Fig. 5E), coxa without seta. Basis with 4 medial setae arranged 1, 1, 1, 1. Endopod 3-segmented with 1, 1, 6 (3 subterminal + 3 terminal) setae. Exopod with slight indication of segmentation and with 4 long terminal plumose natatory setae.

Third maxilliped present as small bud.

First pereopod bud present.

Abdomen (Fig. 6A) with five somites. Somites 2 and 3 with pair of dorsolateral processes; somites 4 and 5 with pair of mediolateral spines. Dorsolateral process on somite 2 stout, with tip directed anteriorly; on somite 3 short, sharp, with posteriorly pointed tip. Mediolateral spines on somites 4 and 5 directed posteriorly. Somites 3-5 with short posterolateral spines, each with posteriorly pointed tip. Somites 2-5 with pair of posterodorsal setae (Fig. 6A). Somites 2-5 with small denticles on posterodorsal margin. Pleopods absent.

Telson (Fig. 6A,a) bifurcated with 3 pairs of serrulate setae and medial cleft on posterior margin; 3 spines on proximal part of each furcal arm: 1 large lateral, 1 small lateral and 1 small dorsomedial. Furca and large lateral spine spinulated.

Zoea II

Carapace (Fig. 1B,C), RDL/CL = 1.84 ± 0.05 ; CW/CL = 1.08 ± 0.04 . 2 pairs of anterodorsal and 1 pair of posterodorsal setae. Each ventral margin denticulate with 2 sparsely plumose setae. Eyes stalked. Otherwise unchanged.

Antennule (Fig. 2B), exopod now with 6 aesthetascs + 1 seta. Otherwise unchanged.

Antenna (Fig. 2G), endopod present, approximately 1/4 the length of exopod. Otherwise unchanged.

Mandible unchanged.

Maxillule (Fig. 3B), coxal endite with 7 sparsely plumose setae. Basial endite with 8 plumodenticulate and sparsely plumose seta. Exopod present as long plumose marginal seta. Otherwise unchanged.

Maxilla (Fig. 4B), basal endite with 5+5 sparsely plumose setae. Scaphognathite with 9 plumose marginal setae and long posterior process reduced to size of other marginal setae. Otherwise unchanged.

First maxilliped (Fig. 5B), exopod with 6 long terminal plumose natatory setae. Otherwise unchanged.

Second maxilliped (Fig. 5F), exopod with 6 long terminal plumose natatory setae. Otherwise unchanged.

Third maxilliped, birameus rudiment, endopod and exopod present now.

Pereopods present as rudimentary buds, the first bilobed.

Abdomen (Fig. 6B,b), first somite with 1 mid-dorsal seta. Otherwise unchanged.

Telson (Fig. 6B) unchanged.

Zoea III

Carapace (Fig. 1D), RDL/CL = 1.83 ± 0.07 ; CW/CL = 1.03 ± 0.02 . Each ventral margin denticulate with 6 sparsely plumose setae. Otherwise unchanged.

Antennule (Fig. 2C), small endopod bud present. Exopod with 1 additional subterminal aesthetascs. Otherwise unchanged.

Antenna (Fig. 2H), endopod approximately 1/2 the length of exopod. Otherwise unchanged.

Mandible unchanged.

Maxillule (Fig. 3C), basial endite with 9 plumodenticulate and sparsely plumose setae and 1 long sparsely plumose epipodial seta. Otherwise unchanged.

Maxilla (Fig. 4C), basal endite with 6+6 plumodenticulate and sparsely plumose setae. Scaphognathite with 19-20 plumose marginal setae. Otherwise unchanged.

First maxilliped (Fig. 5C), endopod distal segment with 6 (2 subterminal + 4 terminal) setae. Exopod with 8 long terminal plumose natatory setae. Otherwise unchanged.

Second maxilliped (Fig. 5G), exopod with 8 long terminal plumose natatory setae. Otherwise unchanged.

Third maxilliped with 3 lobes, probably endopod, exopod and epipod.

Pereopods large, extending beneath carapace. Pereopod 1 bilobed and with slight indication of segmentation.

Abdomen (Fig. 6C) with 6 somites. First somite with 3 mid-dorsal setae. Somite 3 with process now smaller and directed posteriorly. Somite 6 without setae but with small denticles on posterior margin. Pleopod buds present on somites 2-6. Otherwise unchanged.

Telson (Fig. 6C) unchanged.

Zoea IV

Carapace (Fig. 1E), RDL/CL = 1.61 ± 0.05 ; CW/CL = 1.00 ± 0.03 . Each ventral margin with

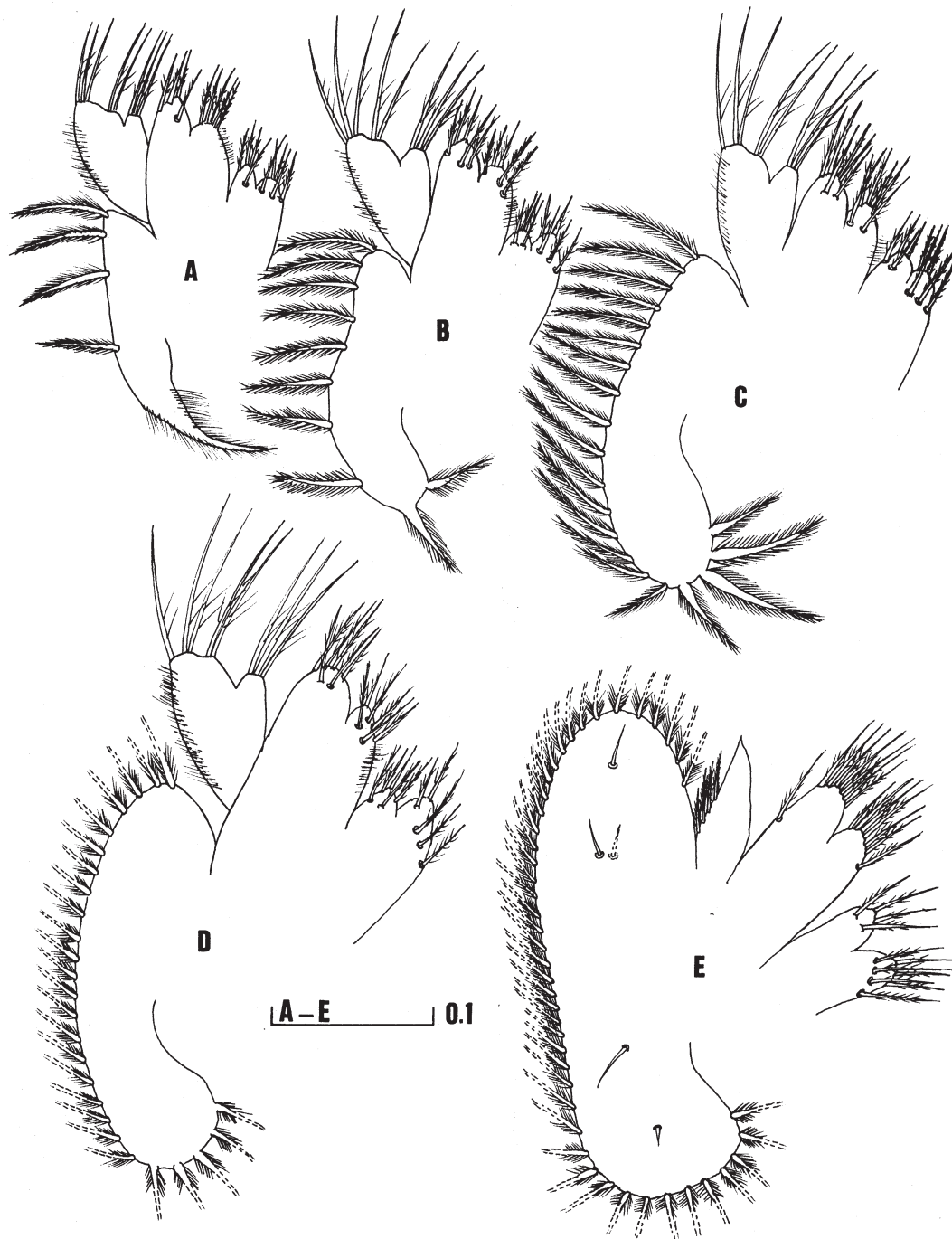


FIG. 4. – *Pilumnus reticulatus* (Stimpson). Maxilla: A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa. Scale bar in mm.

smaller denticles and 11 sparsely plumose setae. Otherwise unchanged.

Antennule (Fig. 2D) biramous. Endopod longer. Exopod with 5 (1+4) subterminal and 4 terminal aesthetascs, and 1 subterminal simple seta.

Antenna (Fig. 2I), endopod approximately 3/4 length of exopod, reaching proximal spines of exopod. Otherwise unchanged.

Mandible, palp bud present.

Maxillule (Fig. 3D), coxal endite with 8 plumodenticulate and sparsely plumose setae. Basal endite with 10 plumodenticulate and sparsely plumose setae. Otherwise unchanged.

Maxilla (Fig. 4D) scaphognathite with 25-27 plumose marginal setae. Otherwise unchanged.

First maxilliped (Fig. 5D), exopod with 10 long plumose natatory setae on distal segment. Otherwise unchanged.

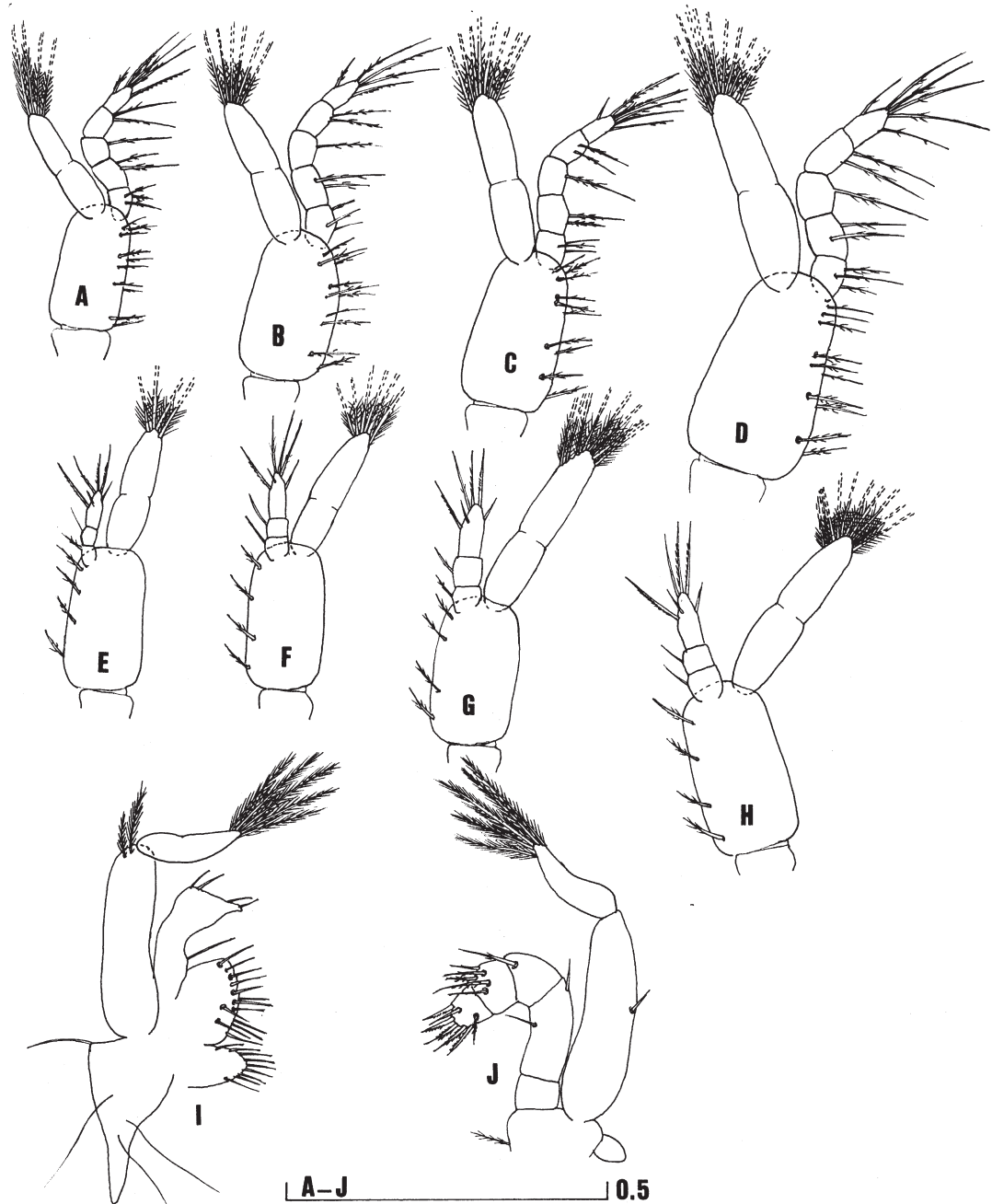


FIG. 5. — *Pilumnus reticulatus* (Stimpson). First maxilliped: A, zoea I; B, zoea II; C, zoea III; D, zoea IV; I, megalopa. Second maxilliped: E, zoea I; F, zoea II; G, zoea III; H, zoea IV; J, megalopa. Scale bar in mm.

Second maxilliped (Fig. 5H), exopod with 10 long plumose natatory setae on distal segment. Otherwise unchanged.

Third maxilliped three-lobed, showing signs of segmentation.

Pereiopods segmented.

Abdomen (Fig. 6D), first somite with 4 mid-dorsal setae. Pleopods uniramous. Otherwise unchanged.

Telson (Fig. 6D) with 2 small dorsal setae. Otherwise unchanged.

Megalopa

Carapace (Fig. 7A) longer than broad ($CW/CL = 0.84 \pm 0.02$). Rostrum directed obliquely downward. Setal arrangement as figured.

Antennule (Fig. 2E), peduncle 3-segmented with 3, 2, 0 setae respectively. Endopod unsegmented with 2 subterminal and 4 terminal setae. Exopod 4-segmented with 0, 6, 4, 4 aesthetascs and 0, 0, 3, 2 setae.

Antenna (Fig. 2J), peduncle 3-segmented with 2, 1, 1 setae respectively. Flagellum 7-segmented with

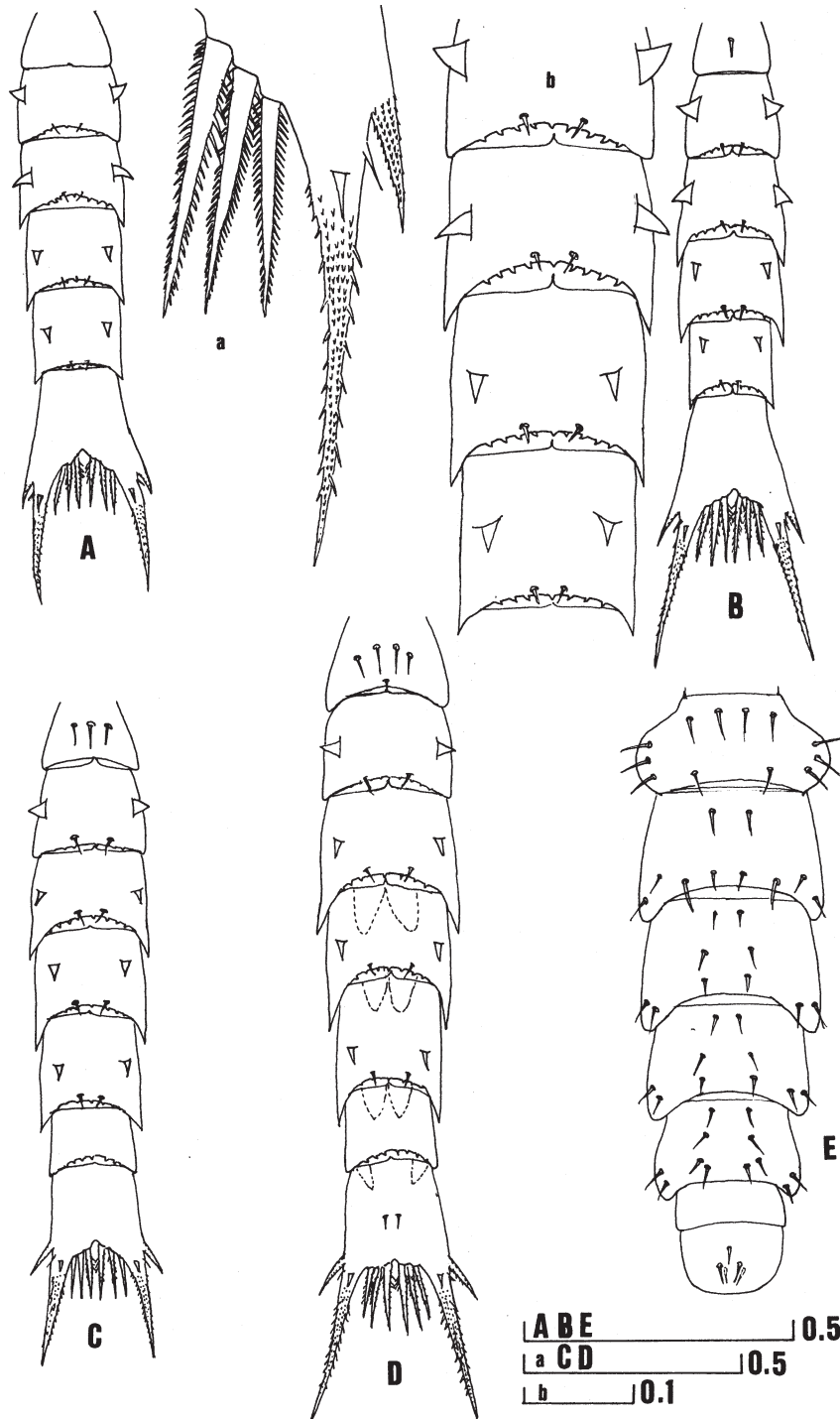


FIG. 6. — *Pilumnus reticulatus* (Stimpson). Abdomen, dorsal view: A, zoea I; B, zoea II; C, zoea III; D, zoea IV; E, megalopa; a, telson of zoea I enlarged and b, abdomen of zoea II enlarged. Scale bars in mm.

0, 0, 0, 4, 0, 3, 4 (terminal) setae.

Mandible (Fig. 7B), palp 3-segmented with 8-9 setae on distal segment.

Maxillule (Fig. 3E), coxal endite with 13 plumodenticulate and sparsely plumose setae. Basial endite with 17 sparsely plumose and plumodenticu-

late distal setae and 2 inner sparsely plumose setae. Endopod unsegmented, with 4 (1 basal, 1 subterminal and 2 shorter terminal) setae. Three proximal plumose setae. Otherwise unchanged.

Maxilla (Fig. 4E), coxal endite bilobed with 8 + 4 plumodenticulate and sparsely plumose setae.

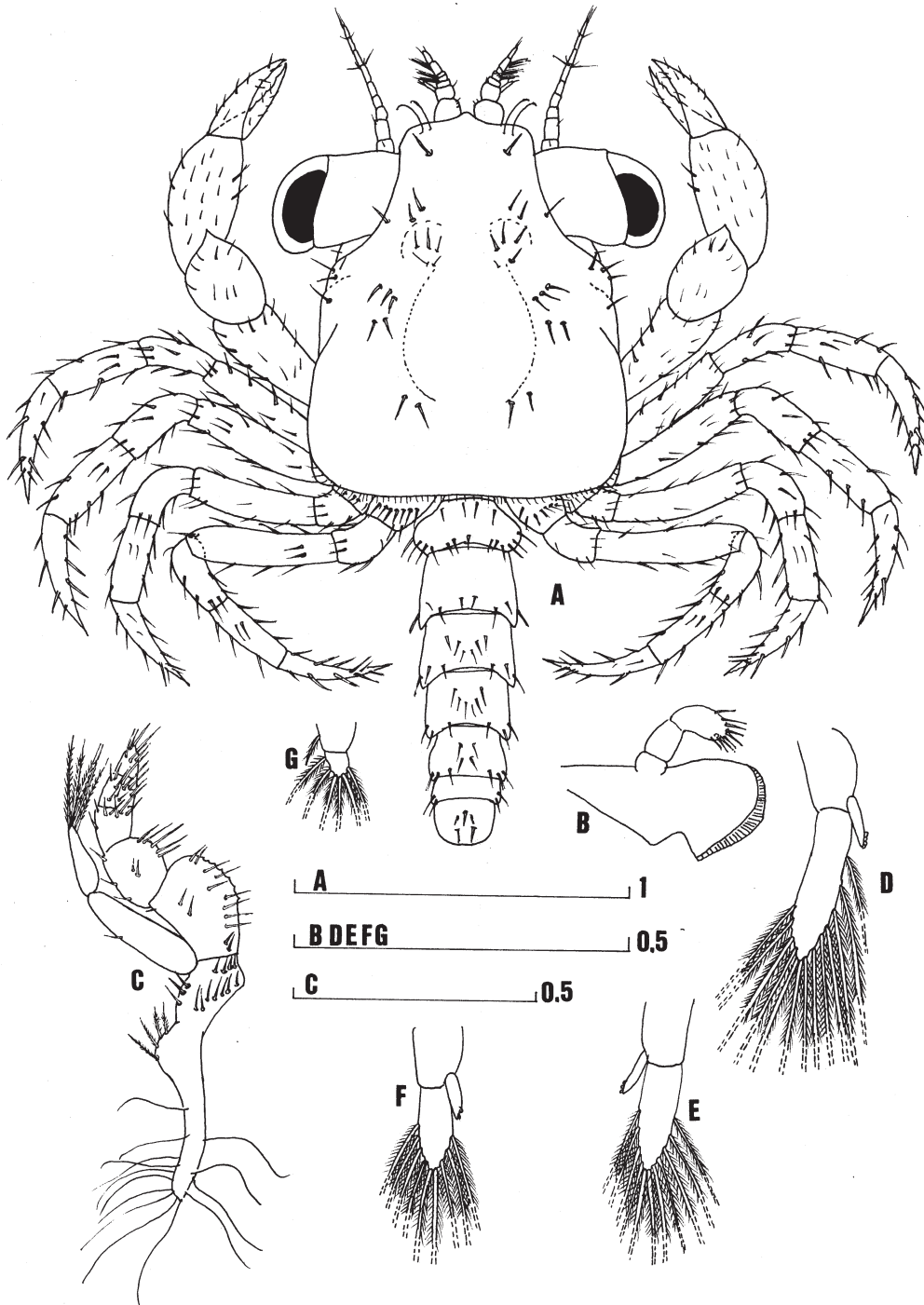


FIG. 7. *Pilumnus reticulatus* (Stimpson). Megalopa: A, dorsal view; B, mandible; C, third maxilliped; D, first pleopod; E, third pleopod; F, fourth pleopod; G, uropod. Scale bars in mm.

Basal endite bilobed with 6 + 8 sparsely plumose setae. Endopod unsegmented with 3-4 marginal setae. Scaphognathite with 40-45 plumose marginal setae and 5 inner setae (4 dorsal + 1 ventral).

First maxilliped (Fig. 5I), coxal endite with 9 setae. Epipod with 6 long setae. Basal endite with 13 setae. Endopod unsegmented with 1 proximal, 2 subterminal and 2 terminal simple setae. Exopod 2-

segmented, proximal segment with 2 distal sparsely plumose setae, distal segment with 5 long terminal plumose setae.

Second maxilliped (Fig. 5J), coxa and basis not differentiated and armed with 1 seta. Epipod rudimentary. Endopod 5-segmented, ischium unarmed, merus, carpus, propodus and dactylus with 2, 1, 5 and 7 sparsely plumose and plumodenticulate setae

respectively. Exopod 2-segmented, proximal segment with 1 medial seta and distal segment with 5 long terminal plumose setae.

Third maxilliped (Fig. 7C), coxa and basis not differentiated with 14 sparsely plumose setae. Coxa-epipod joint indistinct. Epipod elongated with 2 pairs of sparsely plumose proximal setae and about 14 long (gill-grooming) distal setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 14, 10, 7, 10 and 6 sparsely plumose setae, respectively. Exopod 2-segmented, proximal segment with 1 medial simple seta and distal segment with 5 long terminal plumose setae.

Pereiopods (Fig. 7A) all segments well differentiated and with setae as figured. Ischium of cheliped unarmed. Dactylus of pereiopod 2-5 with 3 pairs of short spines.

Abdomen (Fig. 6E) with six somites adorned with plumose setae as shown (Table 4). Somites 2-5 with 1 pair of biramous pleopods (Fig. 7 D-F). Exopods of pleopods 1-4 with 13, 13, 11, 9 long marginal plumose natatory setae respectively, on distal segments. Endopods of pleopods 1-4 with 3 or 4, 3, 3 and 2 coupling hooks on inner margin respectively.

Uropods (Fig. 7G) without endopods, with 1 seta on the proximal segment and 6 natatory setae on distal segment.

Telson (Fig. 6E), posterior margin rounded, with 3 dorsal and 2 ventral setae.

Interspecific comparisons

Zoae development in *Pilumnus* comprises four stages except in *P. vespertilio* (three stages; Lim and Tan, 1981) and *P. kempfi* (two stages; Siddiqui and Tirmizi, 1992). The size and shape of zoeae varies among *Pilumnus* species. When the distance between the tips of dorsal and rostral carapace spines (RDL) in zoea I is considered, their sizes increase in the following sequence: *Pilumnus minutus*, *P. scabriusculus*, *P. reticulatus*, *P. dasypodus*, *P. sayi*, *P. hirtellus*, *P. vespertilio* and *P. kempfi* (Table 3). However, the carapace length (CL) of *P. reticulatus* was similar to that of the larger *P. hirtellus* and its carapace width (CW) was the largest among all the species (Table 3). When the RDL/CL ratio was considered, all the species could be divided into two groups: *P. scabriusculus*, *P. minutus* and *P. reticulatus* had ratios of < 1.8 and *P. dasypodus*, *P. sayi*, *P. hirtellus* and *P. vespertilio* had ratios of >2.7. There was a statistically significant difference in the medi-

TABLE 2. – Comparison of morphological features and setation formulae of the larval development of *Pilumnus reticulatus*, between Montú *et al.* (1989) and this study. Abbreviations: s, setation; a, aesthetascs; seg., segment; so: somites; nd: not described.

	this study	Montú <i>et al.</i> 1989
Zoea		
Carapace		
Anterodorsal s (from zoea II)	2 pairs	nd
Posterodorsal s (all zoea)	1 pair	nd
Ventral margin s (zoea I-last zoea)	0-2-6-11 pairs	6-10-5/6-9 pairs
Posterolateral margin denticles	all stages	only in zoea IV
RDL (zoea I-last zoea, mm)	1.02 to 1.48	0.93 to 1.30
CL (zoea I-last zoea, mm)	0.58 to 0.92	0.49-0.81
CW (zoea I-last zoea, mm)	0.68 to 0.92	nd
RDL/CL (all zoea + SD)	1.76±0.10	1.62±0.2
Antennule		
a, s (zoea I-last zoea)	4-6-7-9, 1-1-1-1	3-4-3/4-6, 2-2-2-1
Mandibule		
Palp (stage of appearance)	zoea IV	nd
Maxillule		
Coxal endite s (zoea I-last zoea)	7-7-7-8	6-7-7-8
Maxilla		
Basial endite s (zoea I)	5+4	4+4
Endopod (last zoea)	3+5	4+5
Endopodial fringe of microtrichia	present	nd
Scaphognathite s (zoea II-last zoea)	10-20-25/27	11-18-25
First maxilliped		
Basis s. (zoea I)	10	4
Endopod (proximal seg.) s (zoea I)	3	1
Endopod (distal seg.) (zoea I)	5	4
Second maxilliped		
Basis s. (zoea I)	4	3
Endopod s (zoea I)	1+1+6	1+1+5
Abdomen		
Proximal so s (zoea I-last zoea)	0-1-3-4	0-0-2-2
Telson		
s (only last zoea)	1 pair	nd
Megalopa		
Carapace		
CW-CL (mm)	0.88-1.05	0.81-0.99
CL/CW	0.84	0.82
Antennule		
Peduncle s	3,2,0	nd,2,0
Endopod s	6	0,5
Exopod a	0,6,4,4	0,6,6,4
Exopod s	0,0,3,2	0,0,2,3
Mandibule		
Palp s	0,0,8/9	0,0,6
Maxillule		
Coxal endite s	13	15
Endopod s	4	2,4
Proximal segment s	4	2
Epipod	present	nd
Maxilla		
Coxal endite s	12 (8+4)	10
Basial endite s	14(6+8)	13
Endopod	3/4	nd
Scaphognathite (marginal,internal) s	40/45,5	41,nd
First maxilliped		
Coxa s	9	6
Epipod s	6	8
Basis s	13	12
Second maxilliped		
Coxa + Basis s	1	2
Exopod (proximal, distal) s	1,5	0,5
Third maxilliped		
Coxa + Basis s	14	10
Epipod (basal,long distal) s	4,14	4,10
Endopod (is.me.ca.pr.da) s	14,10,7,10,6	13/14,9/10,6,8
Exopod (proximal, distal) s	1,5	0,2,4
Abdomen		
first somite s (a,m,p,l)	4,0,2,3+3	nd
second somite s	2,0,4,2+2	nd
third somite s	2,2,2,2+2	nd
fourth somite s	2,2,2,2+2	nd
fifth somite s	2,2,4,2+2	nd
Pleopod		
fourth, exopod nat s	9	10
first to fourth, endopod hooks	4-3-3-2	3-2-2-2
Telson		
dorsal, ventral s	3,2	2, nd

an values among species (Kruskal-Wallis one way ANOVA on Ranks, $p = 0.00361$), but the group or groups that differ from the others could not be isolated. However, when the length of both carapace spines was compared, the rostral spine was short in *P. minutus*, *P. kempfi*, *P. scabriusculus* and *P. vespertilio*, intermediate in *P. hirtellus*, *P. dasypodus* and *P. sayi* and longest in *P. reticulatus*.

DISCUSSION

The characteristics of the larvae of family Pilumnidae were summarised by Ko (1997), who stated that the larval development of 13 species had been described up to that moment, based on laboratory rearing. The descriptions of the larval development of *Pilumnus kempfi* (Siddiqui and Tirmizi, 1992), *P. scabriusculus* (Terada, 1990) and *P. sayi* (Bookhout and Costlow, 1979) were not mentioned by Ko (1997). In fact, *P. sayi* and *P. dasypodus* larval development were very similar, although Bookhout and Costlow (1979) showed few, but clear, differences. Including *P. reticulatus* larvae, the postembryonic development of eight *Pilumnus* species can be compared.

Rice (1980) and Martin (1984) suggested classifications of xanthoid larvae including 4 and 6 groups respectively. In both classifications *Pilumnus* correspond to group II, characterised by “antennal exopod acutely tipped”, about equal in length to a protopod, armed with small spines distally and with prominent outer setae about halfway along their length; antennal protopod longer than rostrum. Group II xanthoids have 4 zoeae stages.

Pilumnus is a uniform group within the Pilumnidae (Ko, 1997), but the zoeae characterisation made by this author needs some modifications. All *Pilumnus* zoeae are characterised by a hook-like or slightly curved dorsal spine and the presence of lateral spines, or dorso-lateral processes, on abdominal somites 2 and 3. The process of the second abdominal somite was often described as a knob (Lim and Tan, 1981; Salman, 1982; Ko, 1994) or as a projection that is “stout with horn-like tip directed anteriorly” (Bookhout and Costlow, 1979); that of the third somite is described as a spine (Bookhout and Costlow, 1979), a hook (Salman, 1982) or a knob (Lim and Tan, 1981; Ko, 1994), and is usually posteriorly curved.

Sandifer (1974) stated that the armature of the abdomen (presence of mediolateral processes on somites 4 and 5, and posterolateral spines on somite

2) may be important as an aid in the identification of *Pilumnus* zoeae. Other characters that are present throughout the development are: RDL/CL ratio, carapace setae, a fringe of microtrichia on the maxillar endopod, the number of setae on the distal segment of the endopod of the first maxilliped, postero-marginal denticles on abdominal somites 2 to 6, and the number of spines on the furca. The following characters varied among the 8 species studied: *P. reticulatus*, *P. sayi* and *P. minutus* have mediolateral spines on abdominal somites 4 and 5; there are posterolateral spines on abdominal somites 3 to 5, except in *P. vespertilio* and *P. kempfi* (2 to 5); *P. reticulatus*, *P. kempfi* and *P. hirtellus* have denticles on the posterior margin of abdominal somites 2 to 5, and 6 when it was distinguished from the telson; the telson carries 3 pairs of spines on the distal border of all species except *P. minutus*, which had an additional internal pair from Z2; there were 3 spines in the base of each furcae (large and small lateral, small dorsal) except in *P. vespertilio* (2 spines). Interestingly, the basis of the first maxilliped has 10 setae (2, 2, 3, 3) in all species.

Several other differences among *Pilumnus* zoeae were observed regarding the setation formulae (Table 3): the number of setae of carapace, antennular exopod (including the aesthetascs), maxillular and maxillar coxal and basal endite, scaphognathite, distal segment of the endopod of first maxilliped, abdominal proximal somite and telson, and the presence of fringes of microtrichia in the maxilla. Additional differences concerning the timing of appearance of some structures in the larval sequence are summarised in Table 3: the bud of antennular and antennal endopod, the epipod of maxilla, the mandibular palp, the buds of third maxilliped, pereopods and pleopods and the sixth abdominal somite. The abbreviated development can account for the observed early appearance of these structures in *P. vespertilio* and *P. kempfi* (Lim and Tan, 1981, Siddiqui and Tirmizi, 1992). The zoeae examined during this study were larger (see Table 2) than those previously described by Montú *et al.* (1989), and also differed in setation.

On the other hand, megalopae of different *Pilumnus* species are similar in general morphological features and there is considerable variation in the setation formula among them (Table 4). Lim and Tan (1981) stated that “the megalops of *P. vespertilio* and *P. dasypodus* appear almost identical in general and gross features”. Setation formula varies among species but also within them, and there are remarkable differences

TABLE 3. – Comparison of morphological features and setation formulae of the zoeae development of *Pilumnus* species (*P. dasypodus*, Sandifer, 1974; Bookhout and Costlow, 1979; *P. sayi*, Bookhout and Costlow, 1979; *P. vespertilio*, Lim and Tan, 1981; *P. hirtellus*, Salman, 1982; *P. minutus*, Terada, 1984; Ko, 1994; *P. scabriusculus*, Terada, 1990; *P. kempi*, Siddiqui and Tirmizi, 1992; *P. reticulatus*, this study). Abbreviations: s, setation; a, aesthetacs; seg., segment; so: somites; nd: not described.

	<i>P. reticulatus</i>	<i>P. dasypodus</i>	<i>P. sayi</i>	<i>P. hirtellus</i>	<i>P. minutus</i>	<i>P. vespertilio</i>	<i>P. kempi</i>	<i>P. scabriusculus</i>
Number of stages	4	4	4	4	4	3	2	4
Carapace								
Rostral spine length (*)	long	intermediate	intermediate	very short	very short	short	short	
Dorsal spine s (from zoea III)	absent	absent	present	absent	absent	-	nd	
Anterodorsal s (from zoea II)	2 pairs	absent	2 pair	absent	absent	absent	nd	
Posterodorsal s (all zoea)	1 pair	absent	1 pair	absent	absent	absent	nd	
Ventral margin s (zoea I-last zoea)	0 to 11 pairs	few-several	few	absent	absent	absent	nd	
Posterolateral margin denticles	present	present	absent	present (*)	present (*)	absent	nd	
RDL (zoea I-last zoea, mm)	1.02 to 1.48	1.20 to 2.09	1.31 to 2.44	1.56 to 2.72	0.71 to 1.18	1.78 to 2.53	2.5 to 2.25	0.77 to 1.18
CL (zoea I-last zoea, mm)	0.58 to 0.92	0.44 to 0.77	0.47 to 0.86	0.59 to 0.97	0.45 to 0.77	0.71 to 0.89	1.1 to 1(*)	0.53 to 0.94
CW (zoea I-last zoea, mm)	0.68 to 0.92	0.40 to 0.61	0.36 to 0.74	nd	0.37 to 0.73	0.54 to 0.76	nd	nd
RDL/CL 1.76±0.10 (average from all zoea + SD)	2.72±0.04	2.82±0.03	2.71±0.07	1.62±0.06	2.78±0.25	2.26±0.01	1.27±0.16	
Antennule								
Endopod (stage of bud appearance)	zoea III	zoea IV	zoea III	zoea IV	zoea III	zoea II	zoea IV	
a, s (zoea I-last zoea)	4 to 9, 1 to 1	4 to 12, 2 to 2	4 to 13, 2 to 0	2 to 6, 1 to 1	3 to 8, 2 to 1	7 to 17, 1 to 0	3 to 6, 1 to 1	
Antenna								
Endopod (stage of bud appearance)	zoea II	zoea II	zoea II	zoea II	zoea I	zoea I	zoea II	
Mandibule								
Palp (stage of appearance)	zoea IV	zoea IV	nd	nd	zoea III	zoea II	nd	
Maxillule								
Coxal endite s (zoea I-last zoea)	7 to 8	7 to 10	7 to 8	7 to 9	7 to 7	7 to 8	7 to 8	
Basial endite s (zoea I-last zoea)	5 to 10	5 to 10	5 to 12	5 to 11	5 to 10	5 to 9	5 to 10-11	
Maxilla								
Coxal endite s (zoea I-last zoea)	5+4 to 5+5	5+3 to 6+4	5+4 to 5+4	6+4 to 6+4	6+3 to 6+4	5+4 to 6+4	6+4 to 6+4	
Basial endite s (zoea I-last zoea)	5+4 to 6+6	5+4 to 7+6	5+6 to 4+6	4+6 to 5+6	4+4 to 6+5	4+4 to 6+5	5+4 to 5-6+5-6	
Endopodial fringe of hairs	present	absent	present	absent	present	present	nd	
Scaphognathite s (zoea II-last zoea)	10 to 27	12 to 2	8 to 25	10 to 25	14 to 24	22	11 to 23/26	
First maxilliped								
Endopod s	3+2+1+2+(5-6)	3+2+1+2+(5-6)	3+2+1+2+(5-6)	3+2+1+2+(5-6)	3+2+1+2+5	3+2+1+2+5	3+2+1+2+5	
Third maxilliped and pereopods (stage of bud appearance)	zoea II	zoea I	zoea II	nd	zoea I	zoea I	zoea I	
Abdomen								
Lateral processes	2 nd - 5 th so	2 nd - 3 rd so	2 nd - 5 th so	2 nd - 3 rd so	2 nd - 5 th so	2 nd - 3 rd so	2 nd - 3 rd so	2 nd - 3 rd so
Posterolateral spines	3 rd - 5 th so	3 rd - 5 th so	3 rd - 5 th so	3 rd - 5 th so	2 nd - 5 th so	2 nd - 5 th so	3 rd - 5 th so	
Posteromarginal denticles (so 2 to 6)	present	absent	present	absent	absent	present(*)	nd	
Proximal so s (zoea I-last zoea)	0 to 4	0 to 4	0 to 5	0 to 4	2 to 4	nd	nd	
sixth so (stage of appearance)	zoea III	zoea III	zoea III	zoea III	zoea II	zoea II	zoea III	
Pleopods (stage of bud appearance)	zoea III	zoea III	zoea III	zoea III	zoea II	zoea II	zoea III	
Telson								
Proximal spines on furcae s (only last zoea)	3 1 pair	3 1 pair	3 nd	3 1 pair	2 absent	3 absent	3 absent	nd

(*) data obtained from figures in the literature

even between the two descriptions of *P. dasypodus* megalopae (Sandifer, 1974; Bookhout and Costlow, 1979). Consequently, it is not possible to use setation for detailed interspecific comparisons. Regarding size and shape, the megalopa of *P. reticulatus*, *P. vespertilio* and *P. dasypodus* were shorter than those of *P. sayi*, *P. minutus* and *P. kempi* but the former had a wider carapace relative to its length.

The megalopae examined during this study are slightly larger than those described by Montú *et al.* (1989) and differed in the setation of the mandibular palp, maxillule (coxa endite, endopod, proximal segment), maxilla (coxa and basial endite, endopod), first maxilliped (coxa, epipod, basis), second maxilliped (coxa, basis, exopod proximal), third

maxilliped (coxa, basis, epipod distal, endopod, exopod), pleopod (exopod, endopod) (see Table 2). The setae of scaphognathite (internal), abdominal somites 1-5 and telson were not described by Montú *et al.* (1989).

Some of the differences between our observations and those of Montú *et al.* (1989) are normally found between zoeae stages or megalopae of congeneric species (e.g. size, setation of carapace, antennula, mandibular palp, pleopods), showing the need to deepen the study of South American crab morphology and taxonomy, including both larvae and adults. However, other differences (e.g. maxilliped setation patterns, that are normally consistent at higher taxonomic levels like genus, subfamily, or

TABLE 4. – Comparison of morphological features and setation formulae of the megalopa development of *Pilumnus* species. Abbreviations: s, setation; a, aesthetascs; nat.s.: natatory setae; is: isquium; me: merus; ca: carpus; pr: propodus; da: dactylus; a: anterior; m: middle; p: posterior; l: lateral; nd: not described; ii: incomplete information (see p. 13, Bookhout and Costlow, 1979). *: data from Fig. 6A (Ko, 1997), ** data from Fig. 4a (Siddiqui and Tirmizi, 1992). When there was variation or discrepancies between authors in the number of setae, the maximum value was chosen. Other references: see Table 3.

	<i>P. reticulatus</i>	<i>P. dasypodus</i>	<i>P. sayi</i>	<i>P. hirtellus</i>	<i>P. minutus</i>	<i>P. vesperilio</i>	<i>P. kempfi</i>
Carapace							
Width (CW) (mm)	0.88	0.71	0.87	nd	0.91	0.79	0.97**
Length (CL) (mm)	1.05	1.03	1.12	1.30	1.11	0.94	1.14**
CL/CW	0.84	0.69	0.78	-	0.82	0.84	1.18**
Antennule							
Peduncle s	3,2,0		0,1,1	4,1,0	0,1,0	0,1,0	0,0,0
Endopod s	2+4		2+4	2+3	2+4	1+4	2+3
Exopod a	0,6,4,4		0,8,6,4	0,6,7,4	18	0,3,3,3	9,3
Exopod s	0,0,3,2		0,0,3,3	0,0,3,2	3	0,0,0,2	1,2
Antenna							
Peduncle s	2,1,1		2,1,1	2,1,1	1,1,1	1,1,1	1,11
Flagellum (last 4 segments) s	4,0,3,4		5,0,3,4	5,0,3,4	5,0,3,3	5,0,3,3	5,0,3,2
Mandibule							
Palp s	0,0,8-9		0,0,8	0,0,9	0,0,8	0,0,5	0,0,6
Maxillule							
Coxal endite s	13		14	14	15	9	9
Basial endite s	19		18	18	19	16	15
Endopod s	4		1,6	2,3	2,4	1,6	1,3
Proximal segment s	3		nd	nd	1	nd	1
Epipod	present		present	present	present	present	present
Maxilla							
Coxal endite s	12		13	11	14	11	10
Basial endite s	14		19	15	15	13	9
Endopod	3-4		11	3	4+1	2	0
Scaphognatite							
marginal s	40-45		39	36	41	34	33
internal s	5 few		few	4	few	nd	
First maxilliped							
Coxa s	9		11	9	9	7	7
Epipod s	6		7	8	7	4	7
Basis s	13		16	12	16	13	10
Endopod s	5		6+few	3	3	5	0
Exopod (proximal, distal) s	2,5		2,7	2,5	2,5	0,5	1,4
Second Maxilliped							
Coxa + Basis s	1		3	0	nd	0	0
Epipod	rudiment		rudiment	rudiment	nd	rudiment	rudiment
Endopod (me,ca,pr,da) s	2,1,5,7		3,1,6,10	2,1,5,7	1,1,5,7	1,1,5,7	1,1,5, 5+1
Exopod (proximal, distal) s	1,5		small, 6	1,5	1,4	0,4	1,5
Third maxilliped							
Coxa + Basis s	14		18	11	nd	12	Nd
Epipod (basal, long distal) s	4,14		3,9	3,9	9	0,10	7
Endopod (is,me,ca,pr,da) s	14,10,7,10,6		15,10,6,11,7	15,9,5,6,6	14,9,5,9,7	9,8,6,7,4	few, 6,3,6,5
Exopod (proximal, distal) s	1,5		1,6	1,5	1,5	0,3	1,5
Abdomen							
first somite s (a,m,p,l)	4,0,2,3+3		nd	3,0,1,3+3	2 p *	nd	nd
second somite s	2,0,4,2+2		nd	2,2,2,2+2	2 p *	nd	nd
third somite s	2,2,2,2+2		nd	2,4,2,2+2	2 p *	nd	nd
fourth somite s	2,2,2,2+2		nd	2,4,2,2+2	2 p *	nd	nd
fifth somite s	2,2,4,2+2		nd	2,6,0,3+3	2 p *	nd	nd
Pleopod exopod nat s	13-13-11-9	13-14-12-10	ii	14+14+13+11	nd	14-14-14-11	nd
Pleopod endopod hooks	4-3-3-2	2-2-2-2	3-3-3-3	nd	3-3-3-3	nd	nd
Uropod s, nat s	1,6	1,6	1,6	1,7	nd	1,7	nd
Telson							
dorsal, ventral s	3,2	several	2	2,2	2*	2	2

indeed family) are probably mistakes in the previous description.

ACKNOWLEDGEMENTS

This paper was written as part of Spanish-Argentine cooperative programme between the Instituto de

Ciencias Marinas de Andalucía (CSIC) (Spain) and the Universidad de Mar del Plata (Argentina). It was funded by the Ministerio de Educación y Cultura and the Dirección General del Instituto de Cooperación Iberoamericana de la Agencia Española de Cooperación Internacional grant to AR and the Universidad de Mar del Plata grant 15/E082 to EDS. We

are grateful to the authorities and colleagues from the Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina, for the invitation to EDS to take part in the fishing cruise. We wish to thank José A. Cuesta for his suggestions and comments on an early version of the manuscript.

REFERENCES

- Bookhout, C.G. and J.D. Costlow Jr. – 1979. Larval development of *Pilumnus dasypodus* and *Pilumnus sayi* reared in the laboratory (Decapoda Brachyura, Xanthidae). *Crustaceana*, Suppl. 5: 1-16.
- Boschi, E.E. – 1964. Los crustáceos decápodos Brachyura del litoral bonaerense (R. Argentina). *Bol. Inst. Biol. Mar.*, Mar del Plata, 6: 1-96.
- Clark, P.F., D.K. Calazans and G.W. Pohle. – 1998. Accuracy and standardization of brachyuran larval descriptions. *Inv. Rep. Dev.*, 33: 127-144.
- Guinot, D. – 1977. Principes d'une classification évolutive des Crustacés Décapodes Brachyours. *Bull. Biol. Fr. Belg.*, 112: 211-292.
- Hale, H.H. – 1931. The post-embryonic development of an Australian xanthid crab (*Pilumnus vestitus* Haswell), *Rec. S. Aust. Mus.*, 4: 321-331.
- Ingle, R.W. – 1983. A comparative study of the larval development of *Monodaeus couchi* (Couch), *Xantho incisus* (Leach) and *Pilumnus hirtellus* (Linnaeus) (Crustacea: Brachyura: Xanthidae), *J. Nat. Hist.*, 17: 951-978.
- Ingle, R.W. – 1992. *Larval stages of Northeastern Atlantic crabs. An illustrated key*. Natural History Museum Publications and Chapman and Hall, London, pp. xii + 1-363, figs. 1-2, 40 (Publication date 28th November 1991).
- Ko, H.S. – 1994. The zoeal stages of *Pilumnus minutus* de Haan, 1835 (Decapoda: Brachyura: Pilumnidae) in the laboratory. *Korean J. Syst. Zool.* 10: 145-155.
- Ko, H.S. – 1997. Larval development of *Pilumnopeus granulata* Balss, 1933 and *Pilumnus minutus* De Haan, 1835 (Crustacea: Brachyura: Pilumnidae), with a key to the known pilumnid larvae. *Korean J. Biol. Sci.* 1: 31-42.
- Lim, S.S.L. and L.W.H. Tan. – 1981. Larval development of the hairy crab, *Pilumnus vespertilio* (Fabricius) (Brachyura, Xanthidae) in the laboratory and comparisons with larvae of *Pilumnus dasypodus* Kingsley and *Pilumnus sayi* Rathbun. *Crustaceana* 41: 71-88.
- Martin J.W. – 1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeas of the western Atlantic and Gulf of Mexico. *Bull. Mar. Sci.* 34: 220-239.
- Melo, G.A.S. – 1996. *Manual de Identificação dos Brachyura (Caranguejos e siris) do litoral brasileiro*. Editora Plêiade/FAPESP, São Paulo, pp. 1-604.
- Montú, M., C. Bakker and L.L. Fernádes. – 1989. Desarrollo larval de *Pilumnus reticulatus* Stimpson, 1860 (Decapoda, Brachyura, Xanthidae) criada en laboratorio. *Nerítica*, Pontal do Sul, 4: 165-190.
- Pohle, G., F.L.M. Mantelatto, M.L. Negreiros-Fransozo and A. Fransozo. – 1999. Larval Decapoda (Brachyura). In: D. Boltovskoy (ed.), *South Atlantic Zooplankton*, pp. 1281-1351. Backhuys Publishers. Leiden, The Netherlands.
- Rathbun, M.J. – 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae, *Bull. U.S. Natn. Mus.*, 152: 1-609.
- Rice, A.L. – 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Trans. Zool. Soc. London*, 35: 271-424.
- Salman, S.D. – 1982. Larval development of the crab *Pilumnus hirtellus* (L.) reared in the laboratory (Decapoda Brachyura, Xanthidae), *Crustaceana*, 42: 113-126.
- Sandifer, P.A. – 1974. Larval stages of the crab, *Pilumnus dasypodus* Kingsley (Crustacea, Brachyura, Xanthidae), obtained in the laboratory, *Bull. Mar. Sci.*, 24: 379-391.
- Siddiqui, F. and N.M. Tirmizi. – 1992. The complete larval development, including, the first crab stage of *Pilumnus kempi* Deb, 1987 (Crustacea: Brachyura: Pilumnidae) reared in the laboratory. *Raff. Bull. Zool.*, 40: 229-244.
- Terada, M. – 1984. Zoeal development of two pilumnid crabs (Crustacea, Decapoda). *Proc. Jap. Soc. Syst. Zool.*, 28: 29-39.
- Terada, M. – 1990. Zoeal development of five species of xanthid crabs, reared in the laboratory. *Res. Crustacea*, 18: 23-47.
- Wear, R.G. – 1967. Life-history studies on New Zealand Brachyura. 1. Embryonic and postembryonic development of *Pilumnus novaezealandiae* Filhol, 1886, and of *P. lumpinus* Bennet, 1964 (Xanthidae, Pilumninae). *New Zeal. J. Mar. Fresh. Res.*, 1: 482-535.

Scient. ed.: K. Anger