J. Mar. Biol. Ass. U.K. (2005), **85**, 865–876
Printed in the United Kingdom

The complete larval development of *Pilumnus limosus* (Crustacea: Decapoda: Brachyura: Pilumnidae) described from laboratory reared material

Marcelo U. García-Guerrero*, Michel E. Hendrickx*‡, José A. Cuesta† and Antonio Rodríguez†

*Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, UNAM,
PO Box 811, Mazatlán, Sinaloa, 82000 Mexico. E-mail: marcelo@ola.icmyl.unam.mx
†Instituto de Ciencias Marinas de Andalucía (CSIC), Avenida República Saharaui, 2, 11510 Puerto Real, Cádiz, Spain.
E-mail: jose.cuesta@icman.csic.es; antonio.rodriguez@icman.csic.es
‡Corresponding author, e-mail: michel@ola.icmyl.unam.mx

The pilumnid crab *Pilumnus limosus* is known from Gonzaga Bay, Baja California, Mexico, to Zorritos, Paita, Peru. Larvae from a female collected in the intertidal rocky shore in Mazatlán, south-eastern Gulf of California, Mexico, were reared in the laboratory from Zoea I to megalopa. A complete description and illustration of larval features is provided and a comparison with closely related species showing known larval development is presented. As in most species of this genus, *P. limosus* larval development consists of four zoeae. All features observed in *P. limosus* are similar to those of *P. reticulatus* and *P. sayi*. All those larvae have lateral processes on abdominal somites 2–5 (2 or 3 in other species); posteromarginal denticles on abdominal somites 2–6 (absent in other species of the genus).

INTRODUCTION

The Family Pilumnidae Samouelle, 1819 (Xanthoidea MacLeay, 1838) contains small crabs inhabiting coastal waters worldwide, from the intertidal to continental shelf depths. In this family, the complete larval development (i.e. zoeae and megalopa) has been described for 13 species, whereas only the zoeal stages have been described for another seven species. Three other *Pilumnus* species feature direct development (hatching as megalopa) or an abbreviated development (hatching as a non-swimming zoea that transforms into a megalopa). A complete list of these larval descriptions is provided by Wear (1967), Spivak & Rodríguez (2002), Clark & Paula (2003) and Ko & Yang (2003). Among the 18 species with described zoeal development, eight belong to the genus *Pilumnus*, three to *Pilumnopeus*, two to *Heteropanope*, and one each to *Benthopanope*, *Heteropilumnus*, *Parapilumnus*, *Actumnus*, *Tanaocheles* and *Eurycarcinus*. In addition to this, some zoeal stages have been described for three species of *Pilumnus* (Martin, 1984; Ingle, 1992).

The genus *Pilumnus* is basically tropical and is the only genus of Pilumnidae recorded from the eastern tropical Pacific. Twelve species are currently recognized in this subregion, from the Gulf of California to northern Peru, one of which, *P. spinohirsutus* (Lockington, 1877), extends to California (Hendrickx, 1995). The genus *Pilumnoides*, represented by two species in the eastern tropical Pacific (Hendrickx, 1995), was excluded from the Pilumnidae based on the morphology of the sternum, abdomen, and gonopods. There has been no description of larvae of *Pilumnus* based on material collected in the East Pacific. One American species of *Pilumnus* described from specimens collected in St Thomas, West Indies (western Atlantic), *P. reticulatus* Stimpson, 1860, is so far considered amphiamerican. It was reported for the first time on the west coast of Panama and later in the southern Gulf of California, Mexico (Hendrickx, 1995). A more detailed analysis of Atlantic and Pacific populations, however, might reveal that these actually represent distinct species (or subspecies), in which case *P. reticulatus* would be restricted to the West Atlantic. Larval description for *P. reticulatus* was provided by Montú et al. (1989) and by Spivak & Rodríguez (2002) using adult female specimens collected in Brazil and Argentina, respectively.

Of the species of *Pilumnus* found in the rocky intertidal in the south-eastern Gulf of California, *P. limosus* Smith, 1869 has the widest distributional range, from Gonzaga Bay, in the northern Gulf of California, Mexico, to Zorritos (Paita), Peru (Hendrickx, 1995). Although it appears to be rare in the southern Gulf of California, an ovigerous female was captured and successfully transferred to laboratory facilities. The purpose of this study is to describe in detail the complete larval development of *P. limosus* from laboratory reared material, and to

Table 1. *Time of the first appearance and measurements of each larval stage of* Pilumnus limosus.

Stage	Days elapsed after hatching	Rostrodorsal length RDL ±SD (mm)	Carapace length CL ±SD (mm)	Carapace width CW ±SD (mm)
Zoea I	–	0.91 ±0.03	0.66 ±0.02	0.55 ±0.02
Zoea II	5	1.11 ±0.07	0.70 ±0.04	0.61 ±0.05
Zoea III	11	1.42 ±0.04	0.79 ±0.04	0.77 ±0.03
Zoea IV	15	1.46 ±0.08	0.91 ±0.05	0.90 ±0.05
Megalopa	18	–	0.83 ±0.03	1.01 ±0.04

Table 2. *Morphological features and setation formulae of the zoeal stages of* Pilumnus limosus.

	Zoea I	Zoea II	Zoea III	Zoea IV	All zoeas
Carapace					
anterodorsal s.	1 pair	2 pairs	2 pairs	3 pairs	
posterodorsal s.					1 pair
ventral margin s.	–	2 pairs	6 pairs	9 pairs	
Antennule					
exopod	4a, 1s	6a, 1s	8a, 1s	12a, 2s	
endopod	absent	absent	bud	present	
Antenna					
endopod	absent	bud	bud	present	
exopod					2s
Maxillule					
exopod s.	absent	present	present	present	
coxal endite s.	7	7	7	8	
basial endite s.	5	8	9	10	
endopod s.					1, 2+4
epipod	absent	absent	present	present	
Maxilla					
coxal endite s.	4+4	5+4	5+5	5+5	
basial endite s.	5+4	5+4	6+6	6+6	
endopod s.					3+5
scaphognathite s.	4+ process	6+3	19	21	
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.					1,1,1+5
exopod s.	4	6	8	10	
Third maxilliped	absent	bud	bud	bilobed	
Pereiopods	absent	absent	1 bilobed	1 chelate	
Abdomen					
somite 1 s.	0	1	3	4	
somites 2–5 s.					1 pair
Pleopods	absent	absent	bud	bilobed	
Telson					
furcal arm sp.					2l, 1d
terminal s.					3 pairs

s, seta; a, aesthetasc; seg, segment; sp, spines; ls, lateral spines; ds, dorsal spines.

compare its morphology with those of closely related congeneric species.

MATERIALS AND METHODS

One late ovigerous crab of *Pilumnus limosus* was collected from the rocky intertidal habitat at Cerritos beach, Mazatlán, Mexico. The crab was transported to a controlled-temperature aquarium at the Mazatlán marine station facilities. When hatching occurred, larvae were transferred to a 4-l jar with marine (36 psu) filtered water and kept at ambient temperature (26°C) with permanent aeration. The first zoeal stage was fed with rotifers and further stages with recently hatched *Artemia* nauplii. Culture conditions were checked daily. When a new stage was observed, ten larvae were fixed with 10% neutral formaldehyde and later preserved in 70% ethanol. Specimens were dissected using an Olympus SZ40 stereomicroscope. Appendages were mounted in polyvinyl lactophenol, coverslips were sealed with clear nail varnish and were examined under a Wild MZ6 and Zeiss Axioskop compound microscope equipped with a *camera lucida*, which was utilized for the drawings. In zoeal stages, rostrum dorsal length (zoea) (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; carapace width (CW) as the distance between the tips of the lateral spines. In the megalopa stage, CL was measured from the base of the rostrum to the posterior margin of the carapace; CW is the maximum width. Setal counts and measurements were based on approximately ten specimens for each stage. The criteria and sequence of the descriptions are based all on the proposal by Clark et al. (1998). All stages were observed and illustrated in detail. The long, plumose natatory setae of the first and second

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

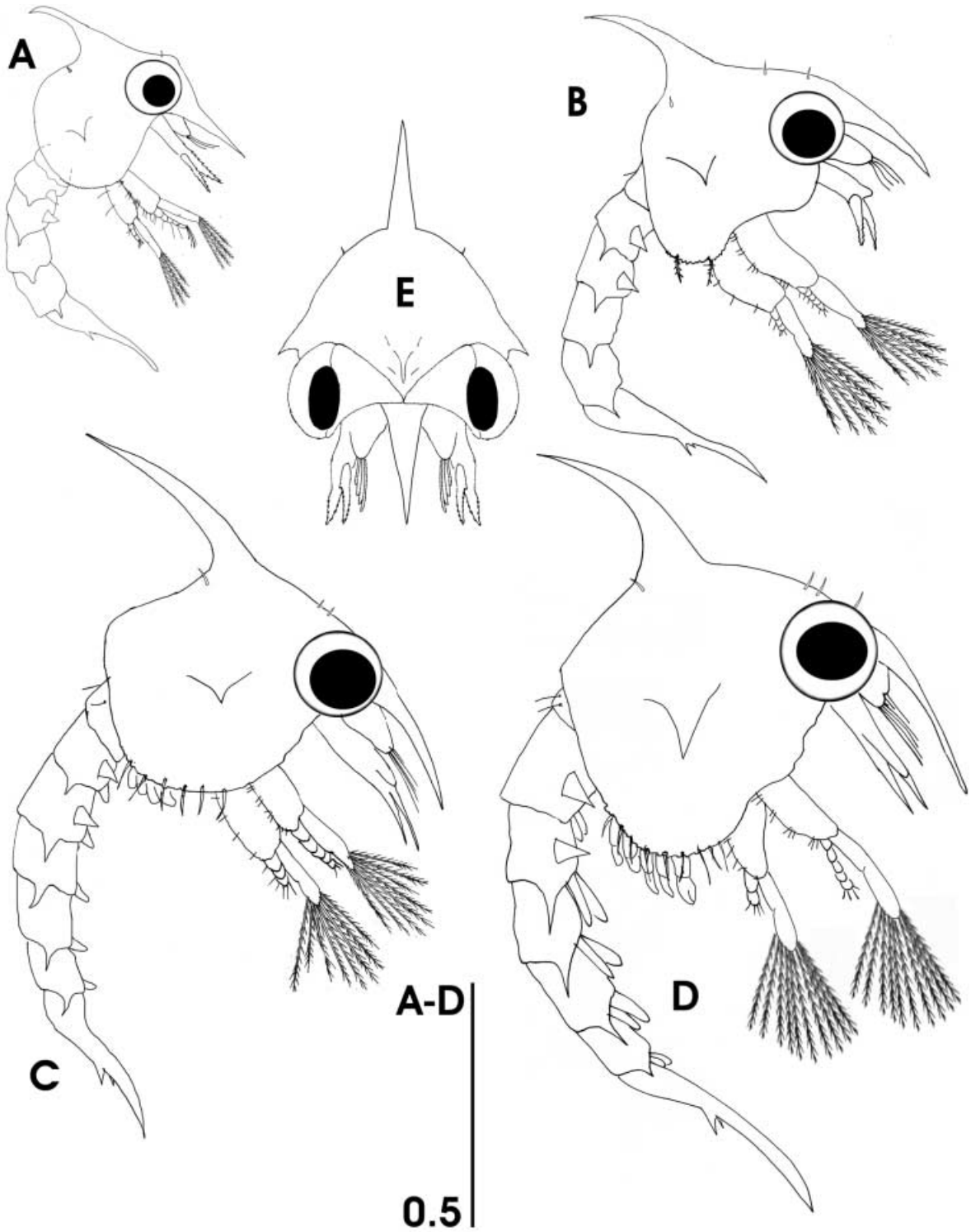

Figure 1. *Pilumnus limosus* Smith, 1869 zoeal stages. Lateral view (A–D) and frontal view (E). (A) Zoea I; (B) Zoea II; (C) Zoea III; (D) Zoea IV; (E) Zoea II. Scale bar in mm.

maxillipeds were drawn truncated. 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 no. EMU-6481.

RESULTS

The complete development from hatching to megalopa takes 18 days at 26°C. Four zoeal and one megalopa stages were obtained. Body measurements are summarized in Table 1, and morphological features and setation formulae of the zoeal development are listed in Table 2. Zoea I and megalopa are fully described. For Zoea II–IV, only differences from the previous stage are mentioned.

Pilumnus limosus (Smith, 1869)
Figures 1–7

Zoea I

Carapace (Figure 1A). Globose, smooth. Dorsal spine present, long, curved distally. Rostral spine present, as long

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

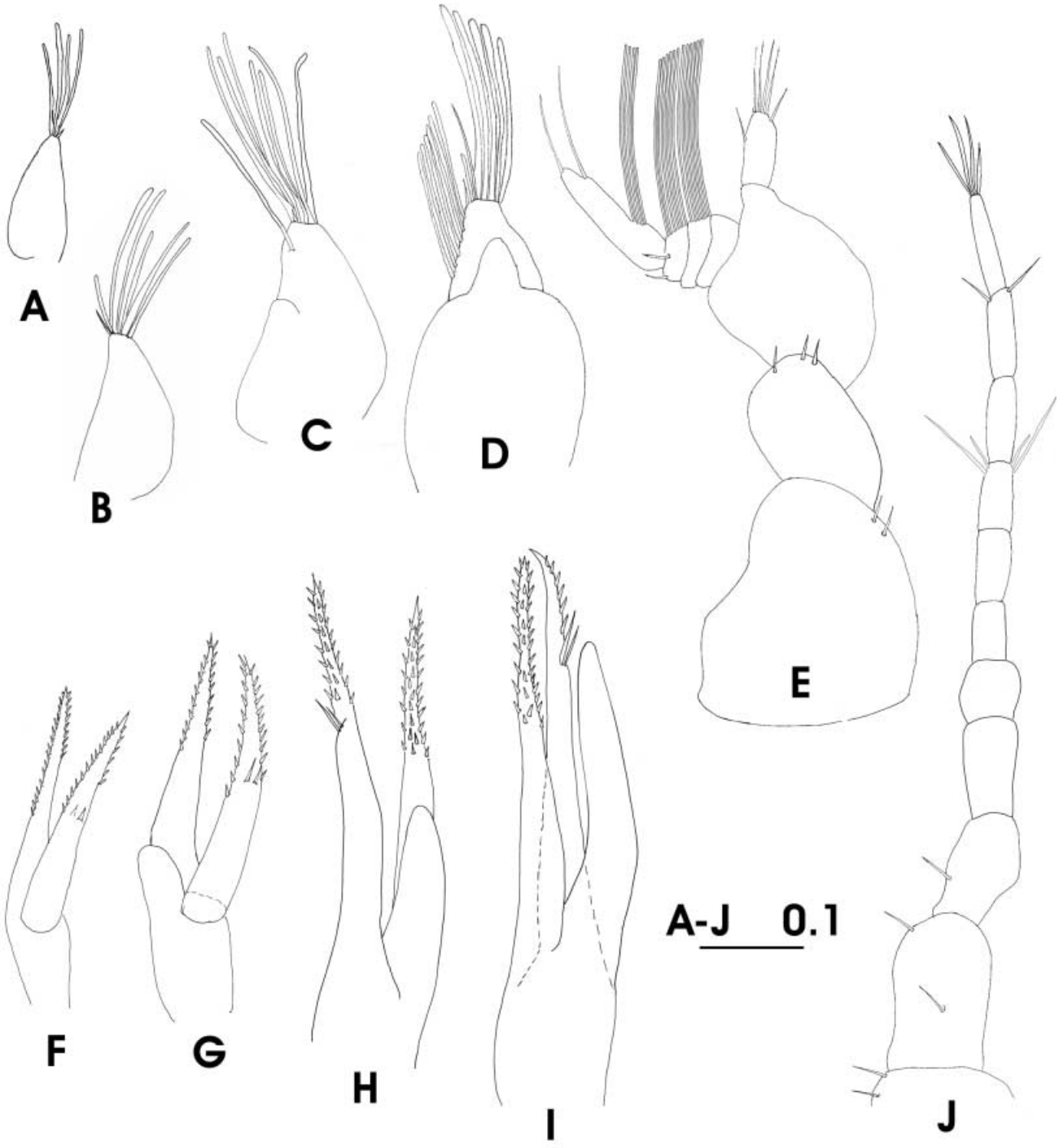

Figure 2. *Pilumnus limosus* Smith, 1869. Antennule. (A) Zoea I; (B) Zoea II; (C) Zoea III; (D) Zoea IV; (E) megalopa. Antenna. (F) Zoea I; (G) Zoea II; (H) Zoea III; (I) Zoea IV; (J), megalopa. Scale bar in mm.

as protopod of antenna. One small lateral spine at each side. One pair of dorsolateral setae. One pair of anterodorsal setae. Ventral margin slightly serrated and without setae. Eye sessile.

Antennule (Figure 2A). Uniramous. Endopod absent. Exopod unsegmented, with four aesthetascs and a minute seta.

Antenna (Figure 2F). Protopod well developed, exceeding tip of rostral spine, bearing two rows of spines. Endopod absent. Exopod elongated, almost as long as protopod, with two medial setae. Distal half with two rows of minute spines.

Mandible. Palp absent. Incisor and molar processes differentiated.

Maxillule (Figure 3A). Coxal endite with seven plumose setae. Basial endite with five plumodenticulate setae. Endopod 2—segmented, proximal segment with one sparsely plumose seta, distal segment with two subterminal

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

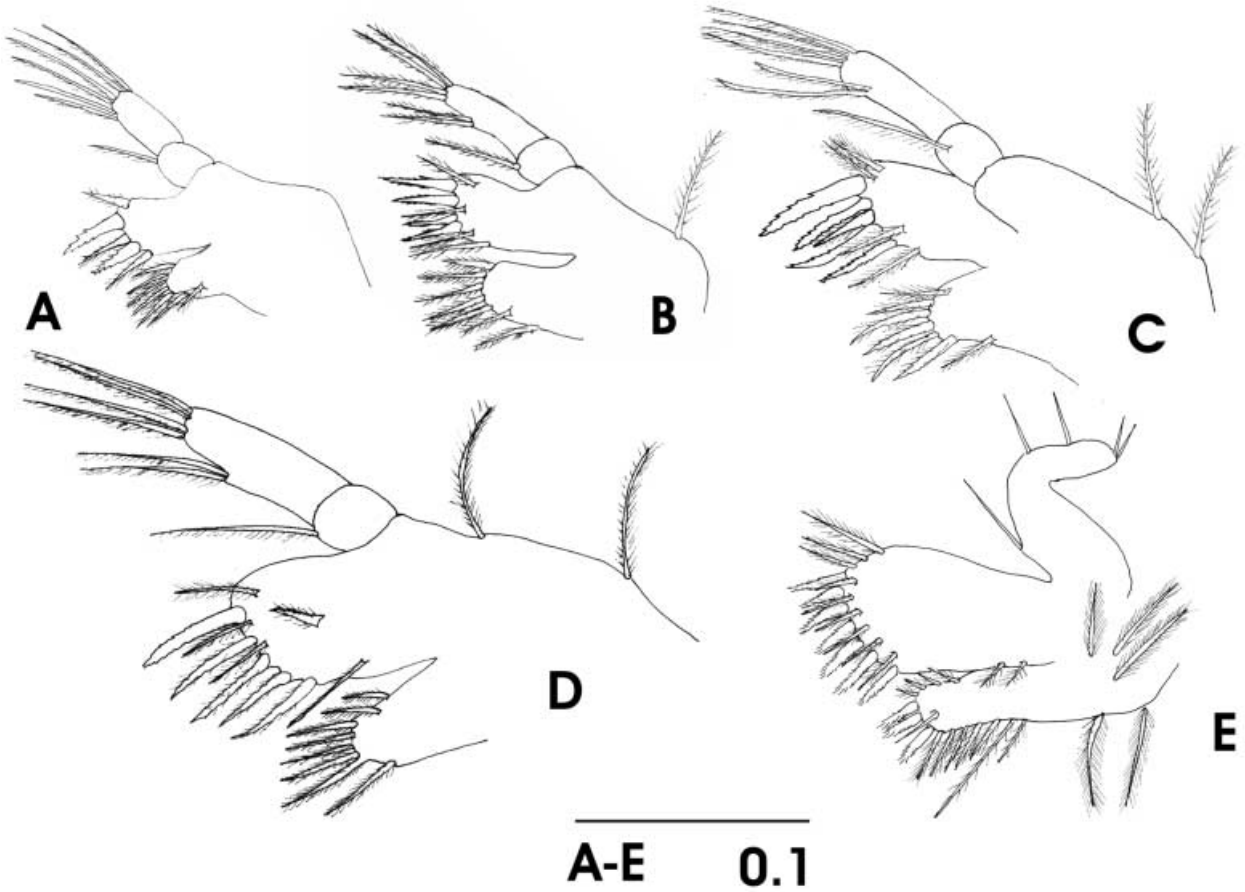

Figure 3. *Pilumnus limosus* Smith, 1869 maxillule. (A) Zoea I; (B) Zoea II; (C) Zoea III; (D) Zoea IV; (E) megalopa. Scale bar in mm.

and four terminal plumodenticulate setae. Exopod and epipod setae absent.

Maxilla (Figure 4A). Coxal endite bilobed with 5+4 sparsely plumodenticulate setae. Basial endite bilobed with 5+4 sparsely plumose setae. Endopod unsegmented, bilobed with 3+5 plumodenticulate setae in each lobe respectively. Microtrichia as figured. Scaphognathite with four plumose, marginal setae and a long setose posterior process.

First maxilliped (Figure 5A). Coxa without setae. Basis with ten medial setae arranged 2, 2, 3, 3. Endopod 5—segmented with 3, 2, 1, 2, 4+1 setae. Exopod 2—segmented, distal segment with four plumose natatory setae.

Second maxilliped (Figure 5F). Coxa without setae. Basis with four medial setae arranged 1, 1, 1, 1. Endopod 3—segmented with 1, 1, 6 setae (2 subterminal+4 terminal). Exopod 2—segmented with four long plumose natatory setae.

Third maxilliped. Absent.

Pereiopods. Absent.

Abdomen (Figures 1A & 6A). Five somites; somites 2 and 3 with a pair of dorsolateral processes; somites 3–5 with long posterolateral processes; somites 2–5 with a pair of posterodorsal setae each. Somites 2–5 with small denticles on posterodorsal margin and a pair of setae in posterodorsal margin of somites 2–5.

Telson (Figure 6A). Bifurcated, with three pairs of serrulate setae on posterior margin. Three spines on proximal part of each furcal arm, one large lateral and spinulated, one small lateral and one large dorsomedial. Furcae large and slightly covered by spines.

Zoea II

Carapace (Figure 1B,E). Two pairs of anterodorsal setae. Each ventral margin with 2 sparsely plumose setae. Eyes stalked.

Antennule (Figure 2B). Exopod now with six aesthetascs of unequal length.

Antenna (Figure 2G). Endopod bud present.

Maxillule (Figure 3B). Coxal endite with seven sparsely plumose setae. Basial endite with four stout denticulate and four subterminal plumodenticulate setae. Exopodal seta present.

Maxilla (Figure 4B). Coxal endite bilobed with 5+4 sparsely plumose setae. Basial endite with 5+4 sparsely plumose setae. Microtrichia as figured. Scaphognathite with nine (6+3 terminal) plumose marginal setae.

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

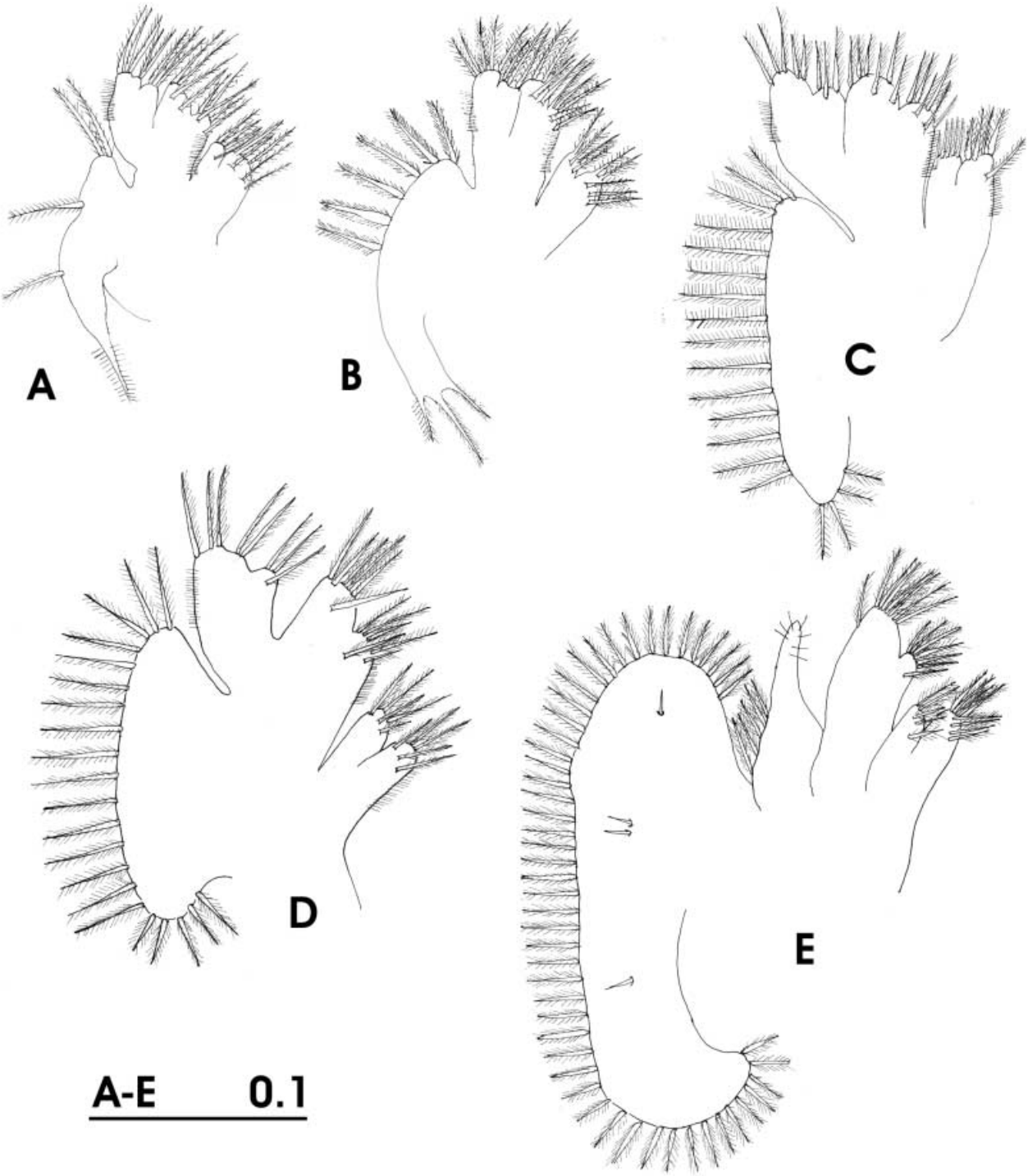

Figure 4. *Pilumnus limosus* Smith, 1869 maxilla. (A) Zoea I; (B) Zoea II; (C) Zoea III; (D) Zoea IV; (E) megalopa. Scale bar in mm.

First maxilliped (Figure 5B). Exopod with six terminal natatory setae.

Second maxilliped. Exopod distal segment with six terminal plumose natatory setae.

Third maxilliped. Present as small bud.

Pereiopods. Present as small buds.

Abdomen (Figures 1B & 6B). First somite with one long mid-dorsal plumose seta.

Telson (Figure 6B). Furca elongated and spinulated.

Zoea III

Carapace (Figure 1C). Each ventral margin with six sparsely plumose setae.

Antennule (Figure 2C). Endopod present as bud. Exopod with one additional aesthetasc terminal and another one subterminal.

Antenna (Figure 2H). Endopod bud elongated, almost reaching the middle of protopod.

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

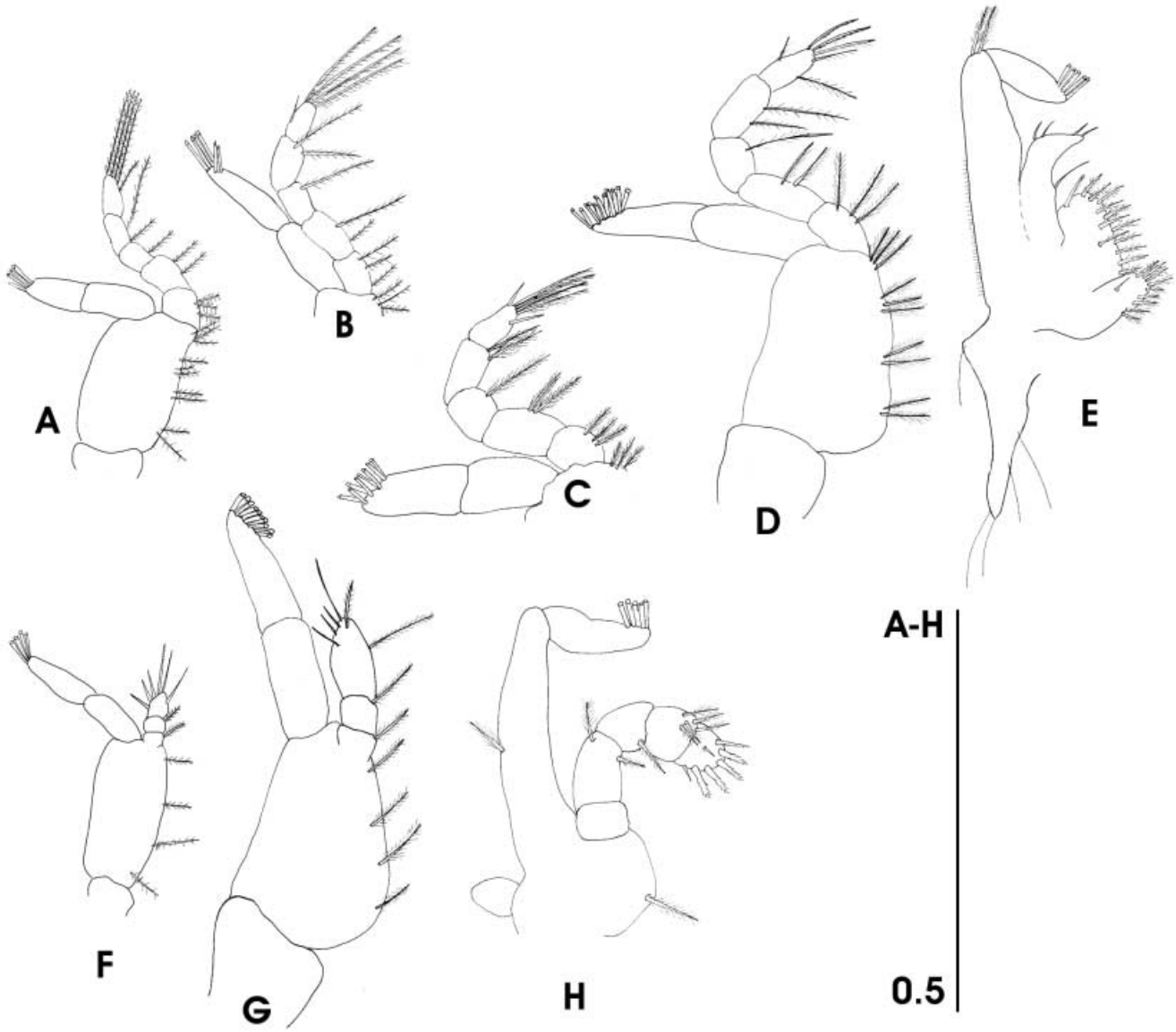

Figure 5. *Pilumnus limosus* Smith, 1869. First maxilliped. (A) Zoea I; (B) Zoea II; (C) Zoea III; (D) Zoea IV; (E) megalopa. Second maxilliped. (F) Zoea I; (G) Zoea IV; (H) megalopa. Scale bar in mm.

Maxillule (Figure 3C). Basial endite with five stout terminal plus four plumodenticulate subterminal setae. Epipod seta present.

Maxilla (Figure 4C). Coxal endite with 5+5 plumodenticulate setae and microtrichia in anterior margin. Basial endite with 6+6 plumodenticulate setae. Microtrichia as figured. Scaphognathite with 19 plumose marginal setae.

First maxilliped (Figure 5C). Distal endopod segment with an additional subterminal seta. Exopod distal segment with eight terminal natatory setae.

Second maxilliped. Exopod distal segment with eight terminal natatory setae.

Third maxilliped. Biramous, elongated bud.

Pereiopods. Chelipeds bilobulated and pereiopods slightly segmented.

Abdomen (Figures 1C & 6C). First somite with three long mid-dorsal plumose setae. Sixth somite present. Pleopod buds on somites 2–6.

Telson (Figure 6C). Furcae elongated.

Zoea IV

Carapace (Figure 1D). Nine sparsely plumose setae on each ventral margin. An additional pair of anterodorsal setae.

Antennule (Figure 2D). Biramous, endopod elongated. Exopod with six subterminal and six terminal aestetaschs plus two simple setae.

Antenna (Figure 2I). Endopod almost of exopod length, reaching its proximal spines.

Mandible. Endopod palp present as small bud.

Maxillule (Figure 3D). Coxal endite with eight plumodenticulate setae. Basial endite with five terminal stout and five subterminal plumodenticulate setae.

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

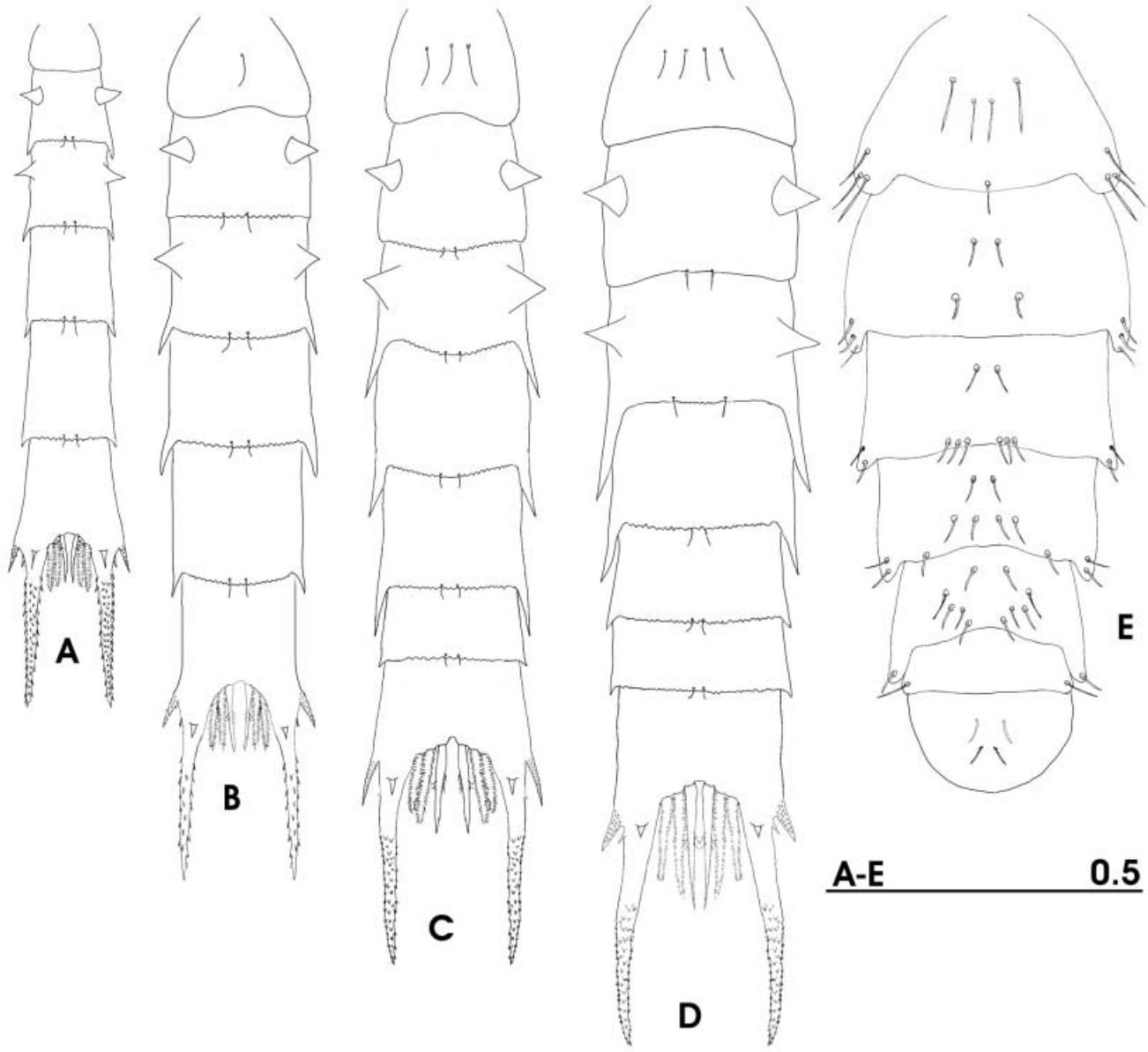

Figure 6. *Pilumnus limosus* Smith, 1869 abdomen in dorsal view. (A) Zoea I; (B) Zoea II; (C) Zoea III; (D) Zoea IV; (E) megalopa. Scale bar in mm.

Maxilla (Figure 4D). Scaphognathite with 20–22 plumose marginal setae.

First maxilliped (Figure 5D). Exopod distal segment with ten terminal natatory setae.

Second maxilliped (Figure 5G). Exopod distal segment with ten terminal natatory setae.

Third maxilliped. Epipodite bud present.

Pereiopods. Chelipeds and pereiopods larger and segmented.

Abdomen (Figures 1D & 6D). First somite with four long, mid-dorsal plumose setae. Pleopod buds more developed and biramous in somites 2–6.

Telson (Figure 6D). With small setules in the upper pair of lateral spines.

Megalopa

Carapace (Figure 7A). Longer than broad, with a slight hump in middle. Rostrum directed obliquely downward, seta arrangement as figured.

Antennule (Figure 2E). Peduncle 3—segmented with 2, 3, 0 setae. Endopod unsegmented with two subterminal and four terminal setae. Exopod 4—segmented with 0, 6, 6, 4 aesthetascs, and 0, 0, 2, 2 setae.

Antenna (Figure 2J). Peduncle 3—segmented with 2, 2, 1, setae. Flagellum 7—segmented with 0, 0, 0, 4, 0, 2, 4 setae.

Mandible (Figure 7F). Incisive process with semi-triangular shape. Palp 3—segmented with 0, 0, 9 plumodenticulate setae.

Maxillule (Figure 3E). Coxal endite with 15 plumodenticulate and scattered setae. Basial endite with seven stout

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

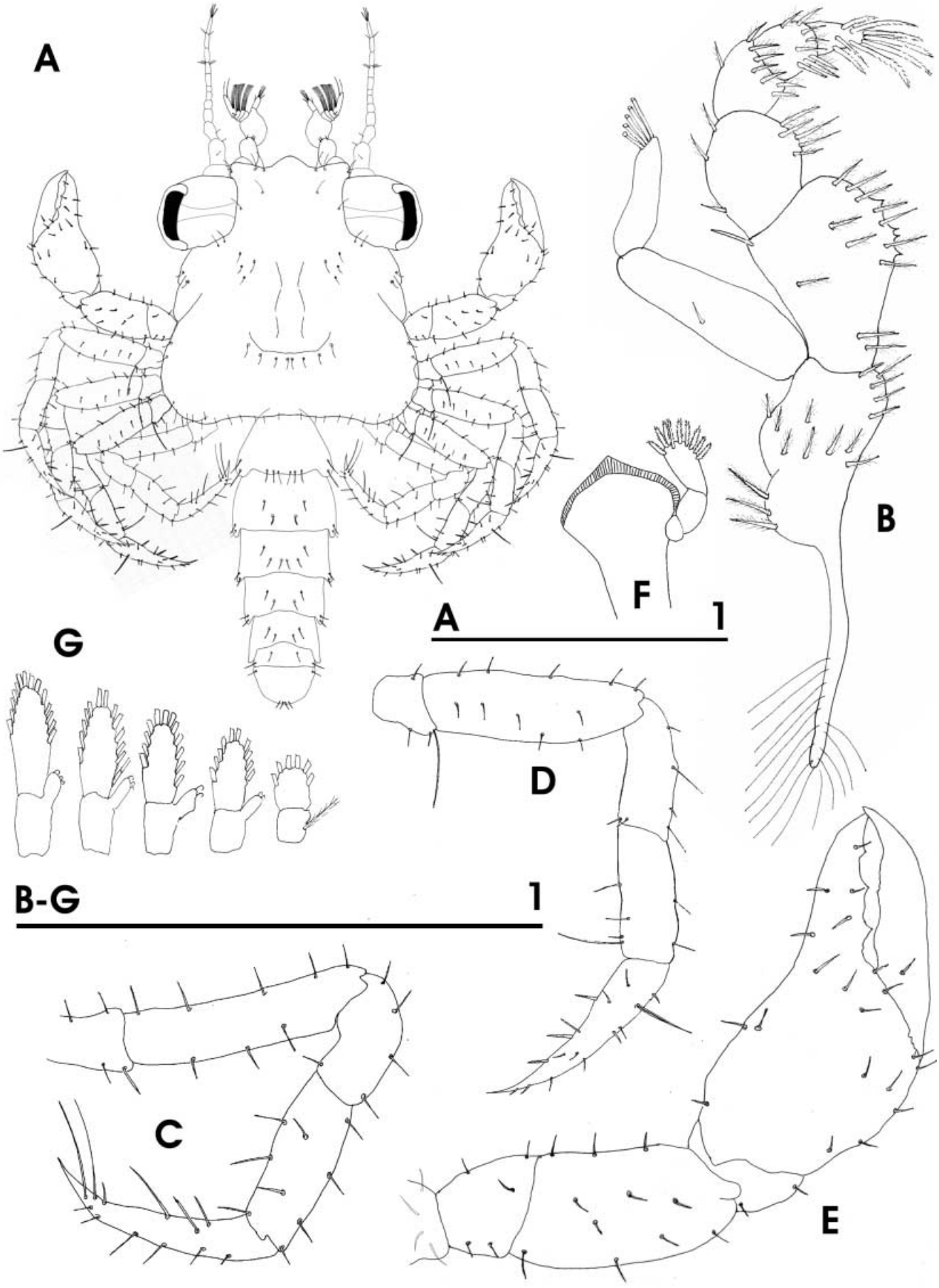

Figure 7. *Pilumnus limosus* Smith, 1869 megalopa. (A) Dorsal view; (B) third maxilliped; (C) 5th pereiopod; (D) 3rd pereiopod; (E) right cheliped; (F) mandible; (G) pleopods, from left to right, 1, 2, 3, 4 and uropod. Scale bars in mm.

https://doi.org/10.1017/S0025315405011823 Published online by Cambridge University Press

marginal, nine submarginal plumodenticulate and two inner plumose setae. Endopod unsegmented, with one basal, two medial and two terminal setae. Protopod with three large plumose setae as figured.

Maxilla (Figure 4E). Coxal endite with 7+5 plumose setae. Basial endite with 6+8 plumose setae. Endopod no longer bilobed, with several scattered setules on the tip and five marginal setae. Scaphognathite with 50–52 plumose marginal setae plus four (1+2+1) lateral setae, as figured.

First maxilliped (Figure 5E). Coxal endite with nine sparsely plumose setae. Basial endite with 13 plumose setae (4 inner). Endopod unsegmented with one proximal, two medial and two terminal sparsely plumose setae. Exopod 2— segmented, proximal segment with two distal sparsely plumose setae, distal segment with five long terminal plumodenticulate feeding setae. Epipod with five long setae.

Second maxilliped (Figure 5H). Coxa and basis not differentiated, with one seta. Endopod 5—segmented, ischium unarmed, merus, carpus, protopodus and dactylus with 2, 1, 5, 7 plumodenticulate setae, respectively. Exopod 2—segmented, proximal segment with one medial seta, distal segment with five long terminal, plumodenticulate feeding setae. Epipod rudimentary.

Third maxilliped (Figure 7B). Coxa and basis not differentiated, with 12–13 sparsely plumose setae. Endopod 5—segmented, ischium, merus, carpus, protopodus and dactylus with 13, 8, 8, 8 sparsely plumose and eight plumodenticulate setae respectively. Exopod 2—segmented, proximal segment with one medial simple seta, distal segment with five long terminal plumose raptorial setae. Epipod elongated with three setae and approximately 14 long distal gill setae.

Pereiopods (Figure 7C–E). All segments well differentiated and with setae as figured.

Abdomen (Figure 6E). Six-segmented, setation as figured. Pleopods (Figure 7G) decreasing in size from 1st to 4th, endopod unsegmented, with three distal cincinuli on outer margin, and exopod with 14, 13, 12 and 10 marginal plumose natatory setae respectively. Uropods (Figure 7G) 2—segmented, proximal segment with one long marginal plumose natatory seta, distal segment with six marginal, plumose natatory setae.

Telson (Figure 6E). Posterior margin rounded, with three pairs of dorsal setae, two on posterior margin.

DISCUSSION

While reviewing larval features of xanthid crabs (*sensu* Balss, 1957), Wear (1970), following Hyman (1925), concluded that the relative length of the antennal exopodite and protopodite could be used as a major character to separate zoeae in two groups. One of these groups features an exopodite and protopodite of similar length; it contains all species of *Pilumnus* (all Pilumninae *sensu* Balss, 1957) with described larvae, and includes *P. limosus* described in this paper. In their classification of xanthoid larvae, Rice (1980) and Martin (1984) separate *Pilumnus* based on the same character. In both cases *Pilumnus* species correspond to Group II. Exopodite and protopodite of similar length were reported by Spivak & Rodriguez (2002) for larvae of *P. reticulatus* Stimpson, 1860, and of seven other species of *Pilumnus* for which the complete larval development (zoeae plus megalopa) is known, i.e. *P. vespertilio* (Fabricius, 1793) and *P. sayi* Rathbun, 1897 by Lim & Tan (1981); *P. hirtellus* (Linnaeus, 1761) by Salman (1982); *P. minutus* De Haan, 1835 by Terada (1984); *P. scabriusculus* Adams & White, 1849 by Terada (1990); *P. kempi* Deb, 1987 by Sidiqui & Tirmizi (1992); and *P. dasypodus* Kingsley, 1879 by Sandifer (1974). Among the most relevant similarities between *Pilumnus* zoeae is the fact that the antennal exopod is always acutely tipped and is armed with minute spines distally (also see Martin's classification, 1984), and a curved dorsal spine and lateral spines are present on the carapace (Spivak & Rodriguez, 2002); they all belong to Group II of xanthoid larvae (as defined by Martin, 1984) in which the 'antennal exopod [is] acutely tipped, about equal in length to or slightly longer than [the] protopod, [is] armed with small spinules distally and with prominent outer setae about halfway along its length'.

Pilumnus limosus presents a zoeal phase with four stages, as usual in this genus (Martin, 1984; Ko, 1997; Spivak & Rodriguez, 2002), although there are some exceptions, i.e. *P. vespertilio* has only three (Lim & Tan, 1981) and *P. kempi* only two (Sidiqi & Tirmizi, 1992). Extreme cases in reduction of larval stages in *Pilumnus* are presented by *P. vestitus* Haswell, 1882 and *P. novaezealandiae* Fihol, 1886, both hatching as megalopa, and in *P. lumpinus* Bennet, 1964, that hatches as an advanced, non-swimming, zoea that rapidly moults to megalopa (see Wear, 1967; Martin, 1984). Reasons for these abbreviated developments are unclear despite speculations proposed by some authors (see Rice, 1980; Martin, 1984; Ko & Yang, 2003) and there seems to be no phylogenetic pattern for this phenomenon (Wear, 1967).

The genus *Pilumnus* has long been used as a convenient group for hosting small, somewhat hairy species of xanthid (*sensu lato*) crabs which did not fit properly into other genera. Consequenly, several species originally included in *Pilumnus* have since been transferred to other genera, sometimes to other families (e.g. *Globopilumnus* Balss, 1933; *Parapilumnus* Kossmann, 1877; *Pilumnoides* Milne-Edwards & Lucas, 1843) and others might be transferred in the future. There is therefore still a great deal of confusion within this genus. Nevertheless, a comparison of the 12 species of *Pilumnus* for which the complete larval development is known indicates that larvae have many common features. These 12 species include the eight species considered by Spivak & Rodriguez (2002: Table 3), *P. limosus* described in the present paper, plus the three species (*P. vestitus*; *P. novaezealandiae*; *P. lumpinus*) with an abbreviated or direct development. When the zoeal stage characters of *P. limosus* are compared with the information provided by Spivak & Rodriguez (2002), in addition to the obvious variation in mean size and in proportion of carapace structures, outstanding differences are also observed in the setation of carapace and abdomen, and in the number and distribution of aesthetascs of the

antennule, while less noticeable differences are observed in mouthparts and maxilliped setation. As shown by Spivak & Rodriguez (2002), these variations are common among zoeae of *Pilumnus*. Considering these features, *P. limosus* is close to *P. reticulatus* and *P. sayi*. These three species are, indeed, distinguished by a set of characters that include: lateral processes on abdominal somites 2–5 (also in *P. minutus*) (2 or 3 in other species); posteromarginal denticles on abdominal somites 2–6 (also in *P. vespertilio*) (absent in other species). In turn, they differ most from *P. minutus* and *P. vespertilio* (e.g. setation on carapace, antennula endopod and maxilla; stage of appearance of antenna endopod, mandible palp, third maxillipeds, pereiopods buds, sixth somite and pleopods). Additional differences or similarities are found regarding the stage of appearance of some structures; in this respect, *P. limosus* shows exactly the same pattern as in *P. reticulatus* when the following characters are considered: antenna endopod, third maxilliped and pereiopods buds appear at Stage II; antennular endopod, sixth abdominal somite and pleopods buds appear at Stage III; mandibular palp appears at Stage IV. Spivak & Rodriguez (2002) attempted to divide the species they reviewed in two groups taking into account the RDL/CL ratio of first zoea, but their results were not supported by the analysis of other characters. As it is the case with other species of *Pilumnus* for which zoeae are known, the last zoea of *P. limosus* differs greatly from the advanced zoea that hatches from eggs of *P. lumpinus* which, among other features, lacks dorsal, rostral and lateral spines on the carapace (as in other non-xanthid zoeas), and in which natatory setae on exopods of first and second maxillipeds are rudimentary and not adapted to swimming.

Description of megalopa for *Pilumnus* is available for the eight species reviewed by Spivak & Rodriguez (2002) and for the three species with direct (*P. vestitus* and *P. novaezealandiae*) or almost direct (*P. lumpinus*) development. For the eight species they reviewed, Spivak & Rodriguez (2002) concluded that, within the genus, morphology of megalopa presents many variations (both interspecific and intraspecific) but that no clear pattern is to be found when comparing setation or presence of aesthetascs. We have reviewed the megalopa descriptions for *P. vestitus*, *P. novaezealandiae* and *P. lumpinus* and found variation in the general setation distribution pattern on most appendages similar to what was observed by Spivak & Rodriguez (2002). The major differences consist of a very irregular setal pattern on the carapace and abdomen of the megalopa (in *P. lumpinus* and to a lesser degree in *P. novaezealandiae*) and the presence of 6+6 long plumose setae on the frontal margin of the carapace vs none in *P. limosus* and in the eight species reviewed by Spivak & Rodriguez (2002), except in *P. reticulatus* which features 2+2 such setae. What Wear (1967: figure 43) calls the megalopa of *P. novaezealandiae* is actually very similar to the first crab stage he describes in the same contribution.

M. García-Guerrero is indebted to Consejo Superior de Investigaciones Científicas (CSIC, Spain), Consejo Técnico de la Investigación Científica (UNAM, México) and Dr A. Gracia Gasca for their financial aid. José A. Cuesta's participation was funded by a research contract 'Ramon y Cajal' from 'Ministerio de Educación y Ciencia' (Spain). We are also indebted to the two anonymous referees for their suggestions during the revision procedure. The authors also wish to thank Nino González from ICMAN, Clara Ramírez, José Salgado and Germán Ramírez from ICML, UNAM and Gabriela Velasco from CIAD for their assistance.

REFERENCES

Balss, H., 1957. Decapoda. In *Dr. H. G. Bronns Klassen und Ordnungën des Tierreichs. Fünfter Band, I. Abteilung, 7. Bunch*, **12**, Lief, 1505–1672, figs 1131–1199.

Clark, P.F., Calazans, D.K. & Pohle, G.W., 1998. Accuracy and standardization of brachyuran larval descriptions. *Invertebrate Reproduction and Development*, **33**, 27–144.

Clark, P.F. & Paula, J., 2003. Descriptions of ten xanthoidean (Crustacea: Decapoda: Brachyura) first stage zoeas from Inhaca island, Mozambique. *The Raffles Bulletin of Zoology*, **51**, 323–378.

Hendrickx, M.E., 1995. Checklist of brachyuran crabs (Crustacea: Decapoda) from the Eastern Tropical Pacific. *Bulletin de l'Institut Royal des Sciences Naturelle de Belgiques*, **65**, 125–150.

Hyman, O.W., 1925. Studies on the larvae of crabs of the family Xanthidae. *Proceedings of the United States National Museum*, **67**, 1–22.

Ingle, R.W., 1992. *Larval stages of Northeastern Atlantic crabs. An illustrated key*. London: Natural History Museum Publications and Chapman & Hall, pp. xxi+1–363, figs 1–2, 40.

Ko., H.S., 1997. Larval development of *Pilumnopeus granulata* Balss, 1933 and *Pilumnus minutus* De Hann, 1835 (Crustacea, Brachyura, Pilumnidae) with a key to the known Pilumnid larvae. *Korean Journal of Biological Sciences*, **1**, 31–42.

Ko, H.S. & Yang, J., 2003. Zoeal development of *Heteropilumnus ciliatus* (Decapoda: Pilumnidae), with a key to the known pilumnid zoeas in Korea and adjacent waters. *Journal of Crustacean Biology*, **23**, 341–351.

Lim, S.S. & Tan, Y., 1981. Larval development of the hairy crab *Pilumnus vespertilio* (Fabricius) (Brachyura: Xanthidae) in the laboratory and comparisons with the larvae of *Pilumnus dasyposus* Kingsley and *Pilumnus sayi* Rathbun. *Crustaceana*, **41**, 71–88.

Martin, J., 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. *Bulletin of Marine Science*, **34**, 220–239.

Montú, M., Bakker, C. & Loureiro Fernandes, L., 1989. Desarrollo larval de *Pilumnus reticulatus* Stimpson, 1860 (Decapoda, Brachyura, Xanthidae) criada en el laboratorio. *Nerítica*, **4**, 165–190.

Rice, A.L., 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society, London*, **35**, 271–424.

Salman, S., 1982. Larval development of the crab *Pilumnus hirtellus* (L.) reared in the laboratory (Decapoda, Brachyura, Xanthidae). *Crustaceana*, **42**, 113–126.

Sandifer, P., 1974. Larval stages of *Pilumnus dasypodus* Kingsley (Crustacea, Brachyura, Xanthidae), obtained in the laboratory. *Bulletin of Marine Science*, **24**, 378–391.

Siddiqui, F. & Tirmizi, N., 1992. The complete larval development, including the first crab stage of *Pilumnus kempi* Deb, 1987 (Crustacea, Decapoda, Brachyura, Pilumnidae) reared in the laboratory. *Raffles Bulletin of Zoology*, **40**, 229–244.

Spivak, E. & Rodriguez, A., 2002. *Pilumnus reticulatus* Stimpson, 1860 (Decapoda: Brachyura: Pilumnidae): a reappraisal of larval characters from laboratory reared material. *Scientia Marina*, **66**, 5–19.

Terada, M., 1984. Zoeal development of two pilumnid crabs (Crustacea: Decapoda). *Proceedings of the Japanese Society of Systematic Zoology*, **28**, 29–39.

Terada, M., 1990. Zoeal development of five species of xanthid crabs reared in the laboratory. *Researches in Crustacea*, **18**, 23–47.

Wear, R.G., 1967. Life history studies on New Zealand Brachyura 1. Embryonic and postembryonic development of *Pilumnus novaezelandiae* Filhol, 1886 and *P. lumpinus* Bennet, 1964 (Xanthidae, Pilumninae). *New Zealand Journal of Marine and Freshwater Research*, **1**, 482–535.

Wear, R.G., 1970. Notes and bibliography on the larvae of xanthid crabs. *Pacific Science*, **24**, 84–89.

Submitted 30 March 2005. Accepted 17 May 2005.