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Larval Development of *Pilumnopeus granulata* Balss, 1933 and *Pilumnus minutus* De Haan, 1835 (Crustacea: Brachyura: Pilumnidae), with a Key to the Known Pilumnid Zoeae

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The larval stages of *Pilumnopeus granulata* and the megalopal stage of *Pilumnus minutus* are described in detail. Comparisons are made with the known larvae of other species of the pilumnid genera, and the provisional key is provided for the pilumnid zoeae. The brachyuran genera *Heteropanope, Heteropilumnus, Actumnus, Pilumonopeus, Pilumnus, Parapilumnus,* and *Benthopanpe* are clearly classified on the basis of the zoeal characteristics, such as the lateral carapace spine, dorsal carapace spine, maxillule, and abdominal lateral knobs.

The family Pilumnidae consists of many taxonomically problematic genera. Balss (1933) considered the genera *Heteropanope* and *Pilumnopeus* as separate ones. Monod (1956) relegated *Pilumnopeus* to a subgenus of *Heteropanope* later. Davie (1989) reviewed these genera and established a new genus, *Benthopanope,* for a group of species previously classified in *Pilumnopeus*. Balss (1933) considered *Pilumnopeus granulata* as a subspecies of *Pilumnopeus serratifrons* (Kinahan) but later elevated it to a specific rank. However, Takeda and Miyake (1969) reported that the first pleopod of male of this species was morphologically very close to that of *P. serratifrons* and *B. indica*. Therefore, the availability of larval characteristics will aid in elucidating the generic placement of *P. granulata.*

The pilumnid crab *Pilumnopeus granulata* Balss, 1933, inhabits the interstices of rocks on beaches near the high watermark. In the Western Pacific, *P. granulata* has been recorded in Ryukyu Islands of Japan (Takeda and Miyake, 1969). The present record of this species is the first one for Korea. *Pilumnus minutus* De Haan, 1835, inhabits the crevices of rocks and roots of sea weeds from the littoral to the 50 m deep (Sakai, 1976).

The complete larval development of *Heteropanope glabra, Pilumnus dasypodus, P. hirtellus, P. vespertilio, Parapilumnus trispinosus, Benthopanope indica,* and *B. eucratoides* have been described (Bookhout and Costlow, 1979; Lim and Tan, 1981; Salman, 1982; Lim et al., 1984; Greenwood and Fielder 1984a; Lim et al., 1986; Ko, 1994a, 1995). For *Pilumnopeus makiana, P. serratifrons,* and *Pilumnus minutus,* only the zoeal stages have been described (Greenwood and Fielder, 1984b; Lee, 1993; Ko, 1994b). For *Heteropilumnus ciliatus* and *Actumnus setifer,* only the first zoeal stage was described (Aikawa, 1937; Takeda and Miyake, 1968). However, any larval stage of *Pilumnopeus granulata* and megalopal stage of *Pilumnus minutus* have not been described yet. In this paper the complete larval development of *Pilumnopeus granulata* and megalopal stage of *Pilumnus minutus* are described and compared with previous descriptions on larvae of the pilumnid crabs. The phylogenetic relationships in the pilumnid genera and the status of *Pilumnopeus granulata* are discussed, based on the larval morphology.

Materials and Methods

In June 1993, ovigerous females of *Pilumnopeus granulata* were collected from the crevices of a rocky beach on Cheju Island, and in June 1996, an ovigerous female of *Pilumnus minutus* was collected by scuba at 20 m in depth at Tadaepó, Pusan, Korea. In the laboratory, they were maintained in an aquarium containing sea water (salinity 33.3‰) at room temperature (20-25℃). When the embryos hatched, some larvae were immediately preserved in 10% neutral formalin for later examination. The remaining larvae were fed on *Brachionus* sp. and newly hatched nauplii of *Artemia* every day. The larvae were moved daily into new containers with fresh filtered sea water.

Specimens and exuviae of each developmental stage were preserved in 10% neutral formalin. Drawings were made using a camera lucida, and measurements were based on the mean of 10 specimens in each zoeal stage. The chromatophore patterns were determined by observation of living larvae.

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Results

Pilumnopeus granulata Balss, 1933

Four zoeal stages and one megalopal stage were recognized. A small number of megalopae molted into young crabs. Completion of larval stages required at least 20 days. The descriptions of the stages are presented as follows. The first zoea and the megalopa are described completely. For the second to the fourth zoeae only the main differences from the first zoea are detailed.

First Zoea (Fig. 1): Size. Carapace length 0.61 mm. Distance between tips of dorsal and rostral spines 0.89 mm.

Carapace (Fig. 1A). Dorsal spine not curved, with minute spinules, and longer than short rostral spine. Lateral spines present.

Antennule (Fig. 1B). With 3 aesthetascs and 3 simple setae (1 large and 2 small).

Antenna (Fig. 1C). Exopod equal in length to spinous process, with 2 medial spines.

Mandible (Fig. 1D). Asymmetrical: right and left molar processes with 4 and 2 teeth, respectively, confluent with incisor process. Right and left molar processes irregularly dentate.

Maxillule (Fig. 1E). Endopod 2-segmented: distal segment with 4 terminal and 2 subterminal plumodenticulate setae; proximal segment with 1 plumodenticulate seta. Basal and coxal endites each with 5 and 7 plumodenticulate setae, respectively.

Maxilla (Fig. 1F). Endopod 2-lobed, with 5 and 3 plumodenticulate setae. Basal and coxal endites each with 9 and 10 plumodenticulate setae, respectively. Scaphognathite bearing 4 marginal plumose setae and 1 terminal process.

First maxilliped (Fig. 1A and G). Basis with 2, 2, 3, 3 plumodenticulate setae. Endopod 5-segmented with 3, 2, 1, 2, and 1+4 plumodenticulate setae, segments increasing in length distally. Exopod with 4 plumose natatory setae.

Second maxilliped (Fig. 1A and H). Basis with 4 plumodenticulate setae. Endopod 3-segmented with 1, 1, and 6 plumodenticulate setae, segments increasing in length distally. Exopod with 4 plumose natatory setae.

Abdomen (Fig. 1A and I). With 5 somites; somite 1 naked, somites 2 and 3 with small lateral knobs, respectively, somites 2-5 each with pair of fine short setae on posterodorsal border.

Telson (Fig. 1A and I). With 3 setae (long lateral, short lateral and short dorsal) on each side at base of furca. Furcal surface covered with minute spinules. Inner posterior margin of telson with 3 pairs of denticulate setae.

Chromatophores (Fig. 1A) predominantly brown, but ranging from dark brown or almost black to pale brown and yellow with variable red pigment. These occurring on bases of antennule, antenna, labrum and mandible, behind and between eyes, on abdominal somites 1-4 and telson, on marginal expansion of carapace, and on bases of first and second maxillipeds.

Second Zoea (Fig. 2): Size. Carapace length 0.70 mm. Distance between tips of dorsal and rostral spines 1.07 mm.

Antennule (Fig. 2B). With 3 aesthetascs and 3 simple setae.

Antenna (Fig. 2C). With endopod bud.

Maxillule (Fig. 2E). Basal endite with 8 plumodenticulate setae; coxal endite unchanged. Distolateral margin with plumose seta.

Maxilla (Fig. 2F). Basal endite with 10 plumodenticulate setae; coxal endite unchanged. Scaphognathite with 11 plumose setae.

First and second maxillipeds (Fig. 2A). Setation of basis and endopod unchanged. Exopod with 6 plumose natatory setae.

Abdomen (Fig. 2G). First somite with 2 dorsal setae; otherwise unchanged.

Third Zoea (Fig. 3): Size. Carapace length 0.87 mm. Distance between tips of dorsal and rostral spines 1.30 mm.

Carapace (Fig. 3A). With 4 plumose setae on posterolateral carapace border. Dorsal spine slightly curved. Buds of thoracic appendages visible through carapace.

Antenna (Fig. 3C). Endopod bud more developed than that of previous stage.

Mandible (Fig. 3D). Left molar process with 3 teeth, confluent with incisor process.

Maxillule (Fig. 3E). Basal endite with 9 plumodenticulate setae; coxal endite unchanged. Seta now present on proximolateral margin.

Maxilla (Fig. 3F). Basal and coxal endites unchanged. Scaphognathite with 20 plumose setae.

First maxilliped (Fig. 3A and G). Endopod with 3, 2, 1, 2, and 1+5 plumodenticulate setae. Exopod with 8 plumose natatory setae.

Second maxilliped (Fig. 3A). Setation of basis and endopod unchanged. Exopod with 8 plumose natatory setae.

Abdomen and telson (Fig. 3H). Abdomen composed of 6 somites: first somite with 4 dorsal setae, somites 2-6 with pleopod buds. Inner posterior margin of telson with 4 pairs of denticulate setae.

Fourth Zoea (Fig. 4): Size. Carapace length 1.08 mm. Distance between tips of dorsal and rostral spines 1.49 mm.

Carapace (Fig. 4A). With 10 plumose setae on posterolateral border. Dorsal spine slightly curved.

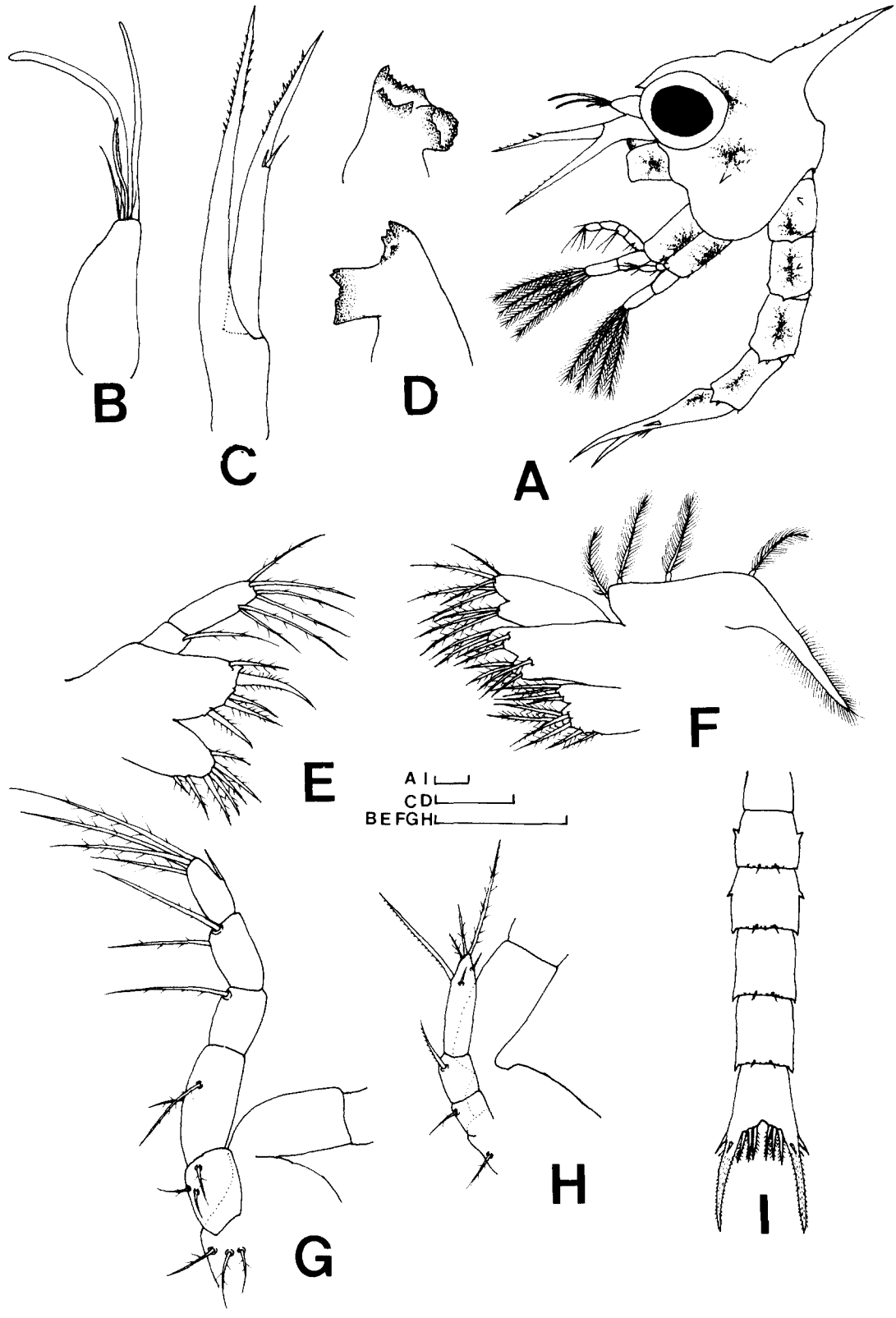

Fig. 1. *Pilumnopeus granulata* Balss, first zoeal stage. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, dorsal view of abdomen and telson. Scale bars=0.1 mm.

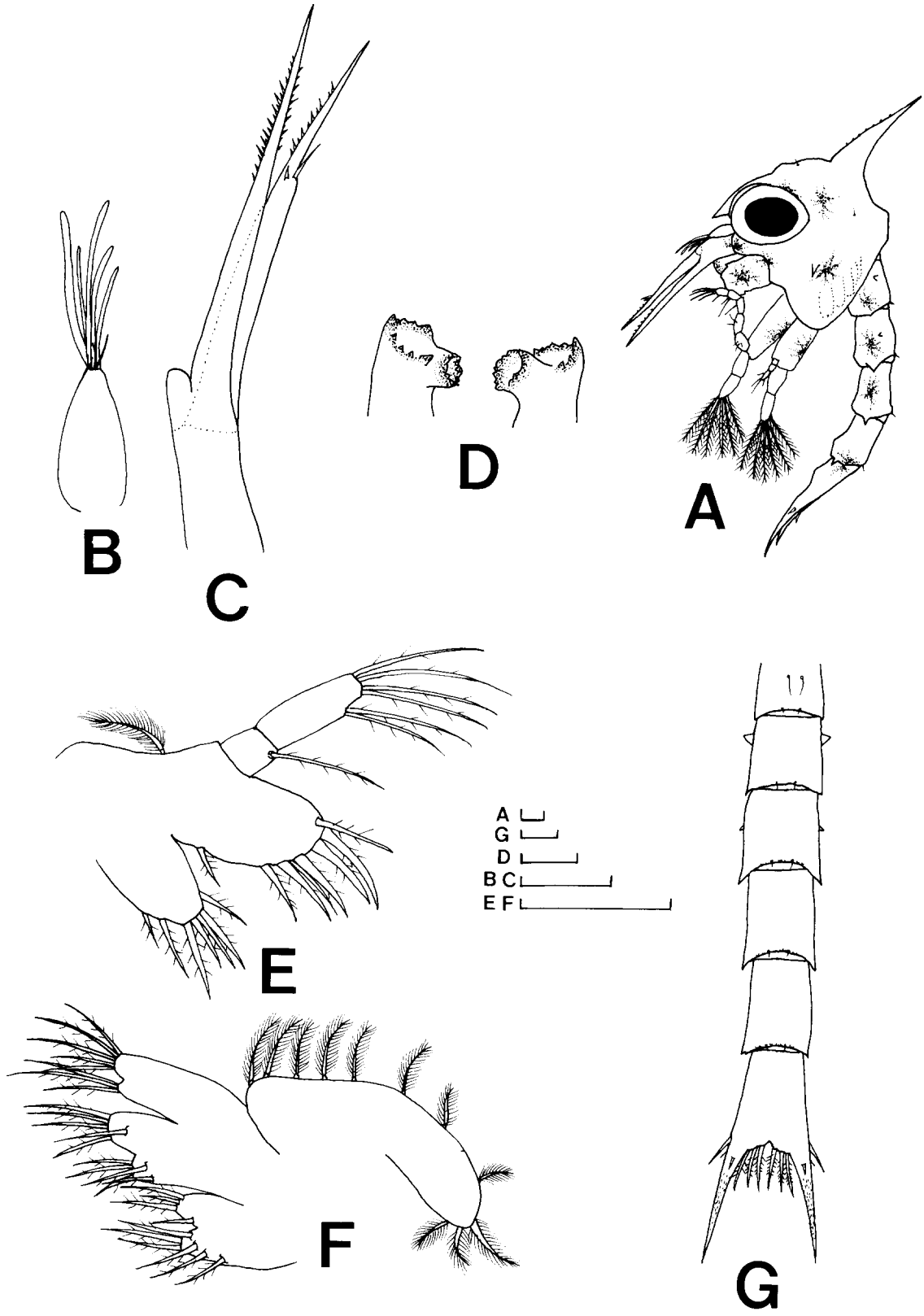

Fig. 2. *Pilumnopeus granulata* Balss, second zoeal stage. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, dorsal view of abdomen and telson. Scale bars=0.1 mm.

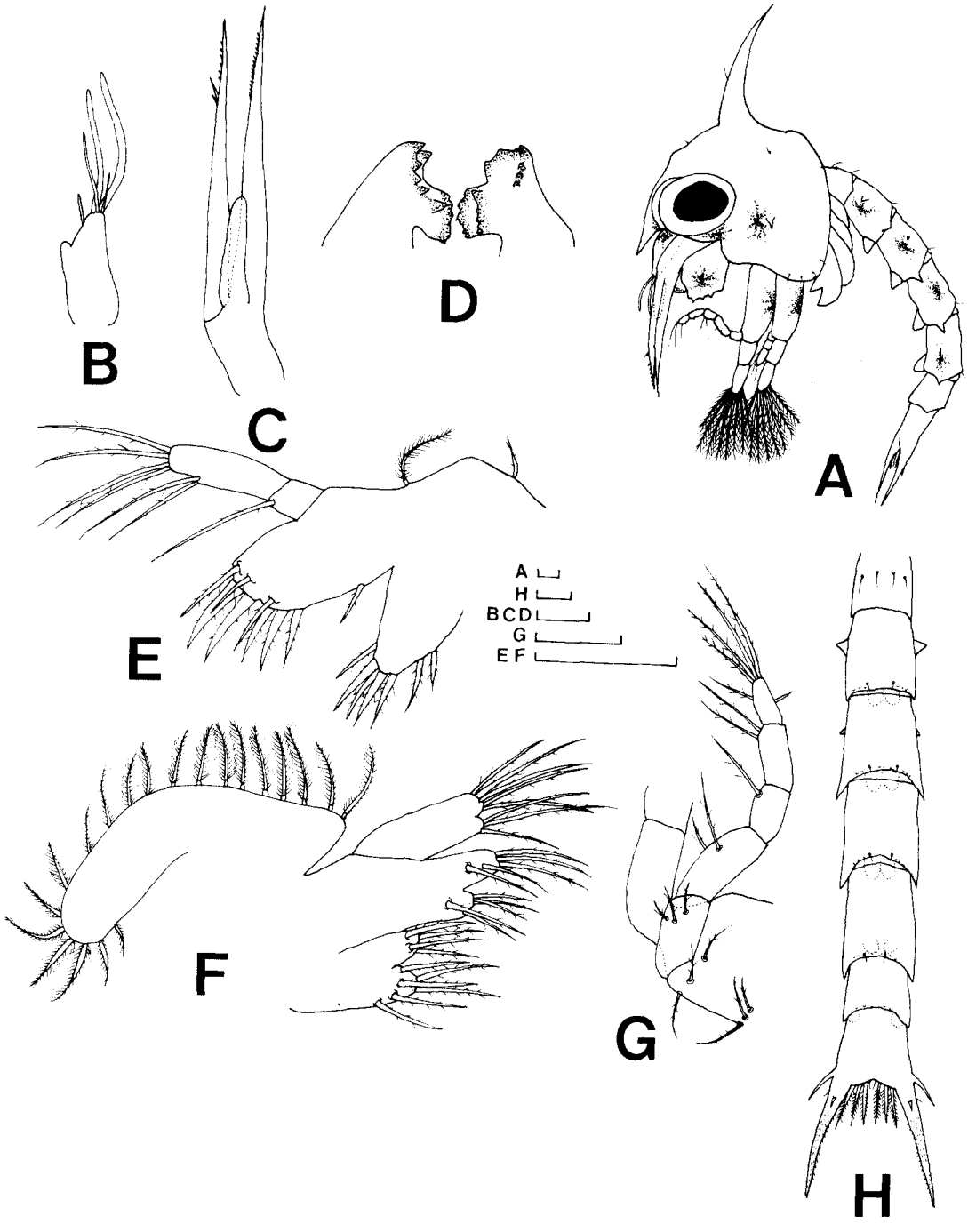

Fig. 3. *Pilumnopeus granulata* Balss, third zoeal stage. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, dorsal view of abdomen and telson. Scale bars=0.1 mm.

Thoracic appendages more developed than in previous stage.

Antennule (Fig. 4B). With 9 aesthetascs and terminal seta. Endopod bud present.

Maxillule (Fig. 4E). Basal and coxal endites each with 10 and 9 plumodenticulate setae, respectively.

Maxilla (Fig. 4F). Basal endite with 12 plumodenticulate setae; coxal endite unchanged. Scaphognathite with 27 plumose setae.

First and second maxillipeds (Fig. 4A). Endopod setation unchanged. Exopod with 10 plumose natatory setae.

Abdomen and telson (Fig. 4A and G). Pleopod buds 1 larger than in previous stage. Telson with 2 small dorsal setae.

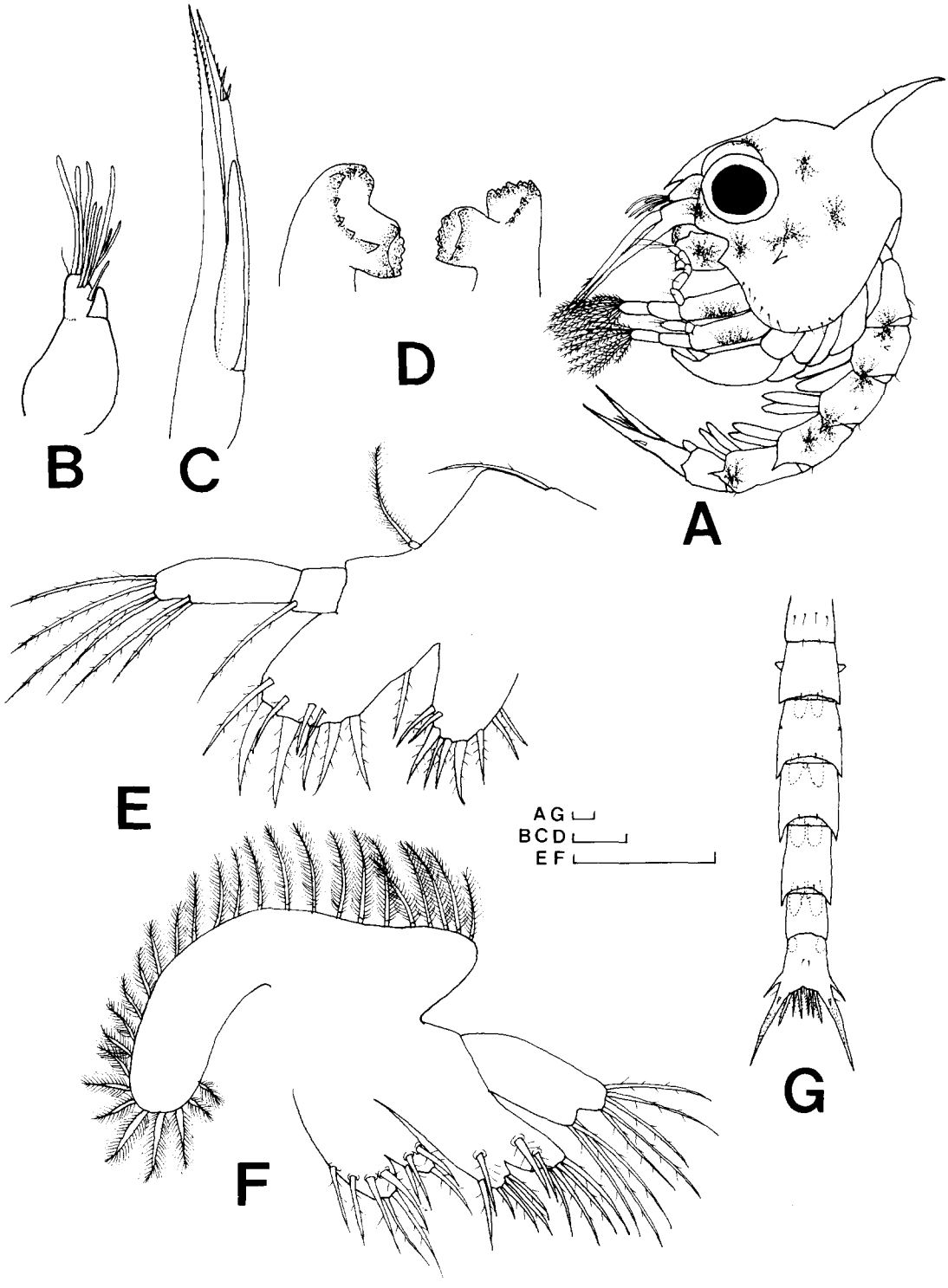

Fig. 4. *Pilumnopeus granulata* Balss, fourth zoeal stage. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, dorsal view of abdomen and telson. Scale bars=0.1 mm.

Megalopa (Fig. 5): Size. Carapace length 1.26 mm. Carapace width 0.99 mm.

Carapace (Fig. 5A). Subquadrate, with 2 antero-gastric lateral, 2 posterogastric lateral, and 1 median tubercles.

Abdomen (Fig. 5A). With 6 somites.

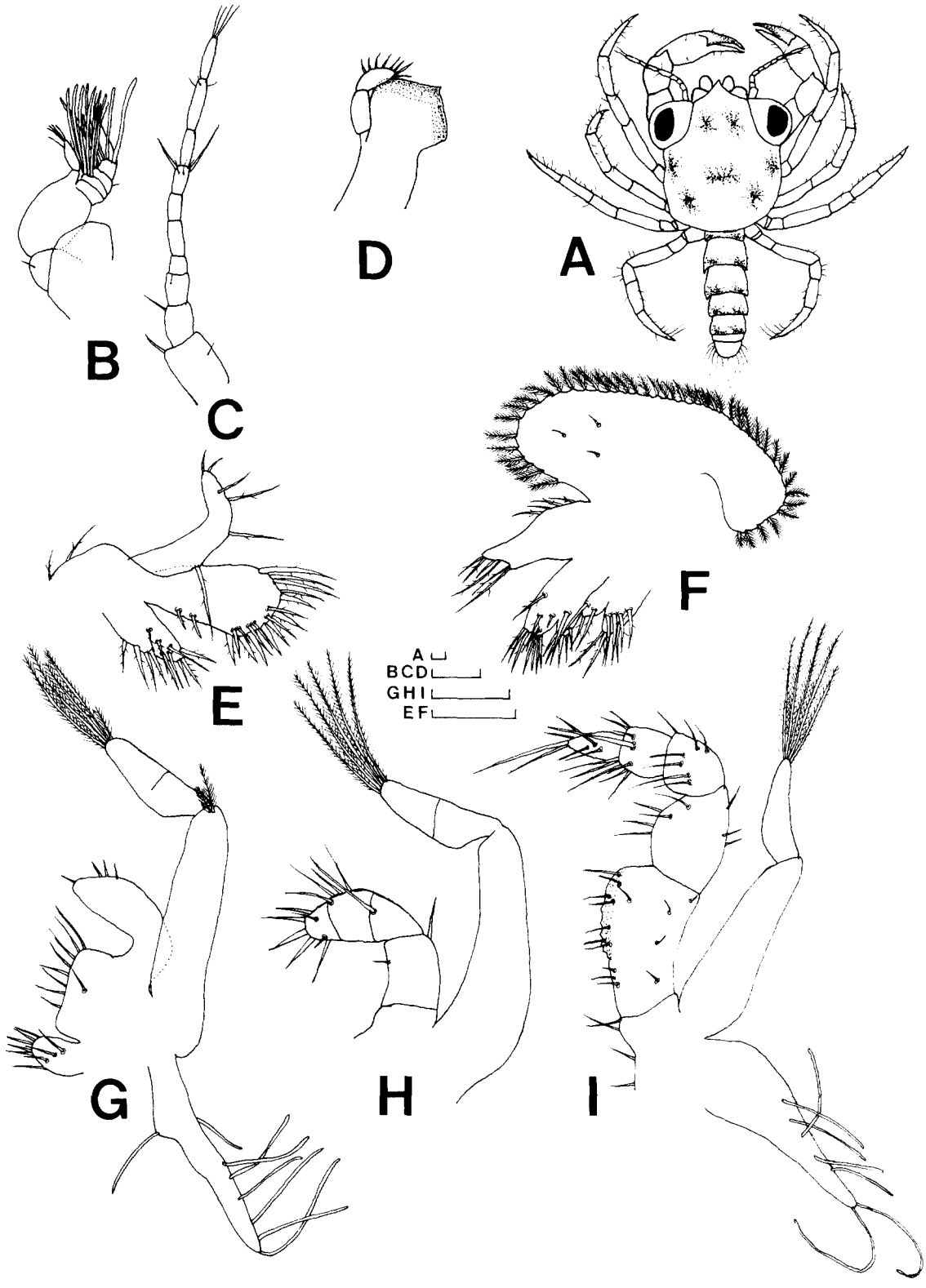

Fig. 5. *Pilumnopeus granulata* Balss, megalopal stage. A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped. Scale bars=0.1 mm.

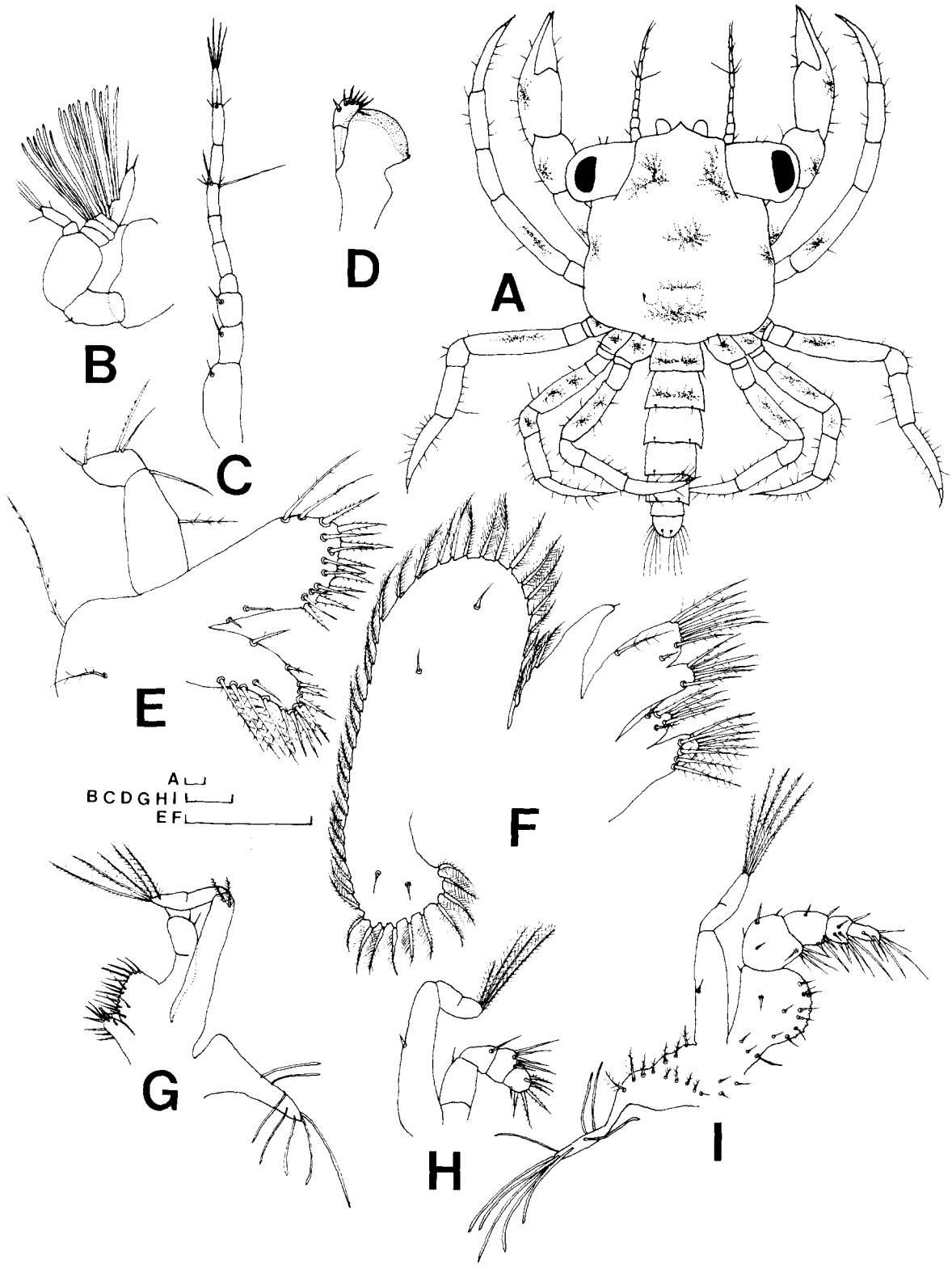

Fig. 6. *Pilumnus minutus* De Haan, megalopal stage. A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped. Scale bars=0.1 mm.

Antennule (Fig. 5B). Exopod 4-segmented with total of 12 aesthetascs and 4 setae. Endopod with 4 terminal and 2 subterminal setae.

Antenna (Fig. 5C). Ten-segmented, with 2, 1, 1, 0, 0, 0, 5, 0, 3, and 4 setae, respectively.

Mandible (Fig. 5D). Palp 2-segmented with 8 setae on distal segment.

Maxillule (Fig. 5E). Endopod bearing 6 plumodenticulate setae. Basal and coxal endites each with 19 and 12 plumodenticulate setae, respectively. 2 setae present on proximolateral margin.

Maxilla (Fig. 5F). Endopod with 10 plumodenticulate setae. Basal and coxal endites each with 17 and 11 plumodenticulate setae, respectively. Scaphognathite bearing 43 marginal plumose setae and 3 plumodenticulate surface setae.

First maxilliped (Fig. 5G). Endopod with 4 terminal setae. Basal and coxal endites both with 9 plumodenticulate setae. Exopod incompletely 3-segmented, proximal segment with 2 plumose setae and distal segment with 5 plumose setae. Epipod with 8 long curved simple setae.

Second maxilliped (Fig. 5H). Endopod 4-segmented with 2, 1, 4, and 7 plumodenticulate setae, increasing in length distally. Exopod incompletely 3-segmented, with 5 plumose setae on terminal segment.

Third maxilliped (Fig. 5I). Endopod 5-segmented with 15, 8, 7, 10, and 6 plumodenticulate setae, segments increasing in length distally. Exopod 2-segmented with 5 plumose setae on distal segment. Epipod with 7 long curved simple setae.

Pilumnus minutus De Haan, 1835

Megalopa (Fig. 6): Size. Carapace length 1.11 mm. Carapace width 0.91 mm.

Carapace (Fig. 6A). Subquadrate, with 2 anterogastric lateral, 2 posterogastric lateral, and 1 median tubercles.

Abdomen (Fig. 6A). With 6 somites.

Antennule (Fig. 6B). Exopod 4-segmented with total of 17 aesthetascs and 3 setae. Endopod with 4 terminal and 2 subterminal setae.

Antenna (Fig. 6C). Ten-segmented, with 1, 1, 1, 0, 0, 0, 5, 0, 3, and 4 setae, respectively.

Mandible (Fig. 6D). Palp 2-segmented with 8 setae on distal segment.

Maxillule (Fig. 6E). Endopod bearing 2 plumodenticulate setae on proximal and 4 plumodenticulate setae on distal segments. Basal and coxal endites each with 19 and 15 plumodenticulate setae, respectively. Two setae present on proximolateral margin.

Maxilla (Fig. 6F). Endopod with 3 plumose setae on proximal and small terminal seta. Basal and coxal endites each with 15 and 14 plumodenticulate setae, respectively. Scaphognathite bearing 41 marginal plumose setae and 4 plumodenticulate surface setae.

First maxilliped (Fig. 6G). Endopod with 3 terminal setae. Basal and coxal endites each with 16 and 9 plumodenticulate setae. Exopod incompletely 3-segmented, proximal segment with 2 plumose setae and distal segment with 5 plumose setae. Epipod with 7 long curved simple setae.

Second maxilliped (Fig. 6H). Endopod 4-segmented with 1, 1, 5, and 7 plumodenticulate setae, increasing in length distally. Exopod incompletely 3-segmented, with simple medial seta on proximal segment and 4 plumose setae on distal segment.

Third maxilliped (Fig. 6I). Endopod 5-segmented with 14, 9, 5, 9, and 7 plumodenticulate setae, segments increasing in length distally. Exopod incompletely 3-segmented with simple medial seta on proximal segment and 5 plumose setae on distal segment. Epipod with 9 long curved simple setae.

Discussion

With this work the number of pilumnid species of which larvae are described, based on laboratory rearing, increases to 13. These 13 species belong to seven genera and the larval descriptions of the four genera *Heteropanope, Heteropilmunus, Actumnus,* and *Parapilumnus* have been done with only a single species each. Therefore, the larval data of pilumnid crabs are relatively sparse. Despite of this sparseness, the morphological characteristics of the family Pilumnidae can be summarized as follows: number of zoeal stage is usually four, rarely three in *Pilumnus vespertilio* and *Benthopanope eucrates;* length of rostral carapace spines varies from 0.2 A to 6.8 A (A=Ratio to length of an antennular conical rod); lateral carapace spines are usually present, rarely absent in genera *Parapilumnus* and *Benthopanope;* length and shape of dorsal carapace spines range from 2.2 A to 9.6 A and are curved or straight, respectively; exopod of antenna is nearly equal or slightly exceeded to spinous process and has two medial setae; setation of endopod of maxillule is always 1, 6; coxal endite of maxillule almost has seven setae, rarely five and six setae, in *Pilumnopeus makiana* and *P. serratifrons,* respectively; endopod of maxilla mostly has eight setae, rarely seven in *Pilumnopeus makiana;* setation of endopod of first maxilliped is 3, 2, 1, 2, 5, rarely 2, 2, 1, 2, 5 in *Pilumnus vespertilio* and 3, 2, 1, 2, 6 in *Benthopanope eucratoides;* setation of endopod of second maxilliped is usually 1, 1, 6, but 1, 1, 5 in *Heteropilumnus ciliatus, Pilumnopeus makiana,* and *Actumnus setifer;* abdominal lateral knobs are usually on somites 2 and 3, rarely on somites 2, 3, 4, and 5 in *Pilumnus minutus* and genus *Parapilumnus,* or on somite 2 in genus *Benthopanope;* telson usually has three outer setae, rarely two setae in *Heteropilumnus ciliatus* and *Pilumnus vespetilio.*

Readily observable morphological features are use-

ful in distinguishing the zoeae of the pilumnid crabs in the plankton. As indicated in Table 1, the author uses the ratio of length of an antennular conical rod in the expression of the length of carapace spines because the length and shape of the antennular conical rod is nearly constant in all the pilumnid species. Wear (1968) gave attention to the reduced or vestigial rostral carapace spine and considered it to be a generic character of the family Piumnidae. Also Rice (1980) reported that the vestigial rostral carapace spine was simply an extreme form of a tendency to reduce this spine in many pilumnids. However, the length of the rostral carapace spine seems not to be very significant, because, for example, it varies from 0.5 A to 2.0 A within the genus *Pilumnus*. The family Pilumnidae can be divided into two groups: straight and curved, based on the shape of the dorsal spine. Also, the length of dorsal carapace spine appears to be somewhat constant within a genus (*Pilumnus* or *Benthopanope*) or species. Therefore, it seems that the dorsal carapace spine is more important as a structure than the lateral and rostral carapace spines in comparison of larval morphology.

The pilumnid genera, *Heteropanope, Heteropilumnus, Pilumnopeus, Pilumnus, Parapilumnus, Actumnus,* and *Benthopanope* are clearly classified on the basis of the characteristics of the carapace spines and the abdominal lateral knobs. Of these, *Heteropanope, Heteropilumnus,* and *Pilumnopeus* are distinguished from the remaining genera by having long and straight dorsal carapace spines. The lengths of the dorsal carapace spines of *Heteropanope, Heteropilumnus,* and *Pilumnopeus* are 9.6 A, 5.2 A, and more than 4.0 A, respectively. Within the genus *Pilumnopeus,* it is interesting that *P. makiana* has a 4.0 A dorsal spine in the first zoeal stage, but in the later stage the dorsal spine is more than 7.0 A, which is somewhat coincided with that of the *P. serratifrons.* Also, the present material, *Pilumnopeus granulata,* exhibits 4.0 A dorsal carapace spine length and a straight dorsal carapace spine in the first zoeal stage. The length of a dorsal carapace spine becomes gradually shortened during larval development, and it comes to 2.5 A in the fourth zoeal stage. And the shape of a dorsal carapace spine unusually changes to be of a curved form from the second through the fourth zoeal stages. Moreover, this species has seven setae on the coxal endite of the maxillule whereas *Pilumnopeus makiana* and *P. serratifrons* have five and six setae, respectively. Most of the larval characteristics of this species seem to be typical of the genus *Pilumnus.* Therefore, It seems that *Pilumnopeus granulata* resembles more closely to the *Pilumnus* species than the *Pilumnopeus* species and that this species should be separated from the genus *Pilumnopeus.*

The genera *Pilumnus, Actumnus, Parapilumnus,* and *Benthopanope* have short and curved dorsal carapace spines. The *Pilumnus* has 2.2 A-3.3 A dorsal carapace spine in length and lateral carapace spines. The *Actumnus* has 3.8 A dorsal carapace spine in length, lateral carapace spines, and 1.3 A rostral carapace spine in length. The *Parapilumnus* has about 2.4 A dorsal carapace spine in length, no lateral carapace spines, and lateral knobs on the abdominal somites 2, 3, 4, and 5. The *Benthopanope* has 2.2 A or 2.3 A dorsal carapace spine length, no lateral carapace spines, and lateral knobs on the abdominal somite two. Ko (1994b) reported

Table 1. Morphological characteristics of the first zoeae of 13 species of the pilumnid crabs

Species	Carapace spine			Abdomen	Maxillule	Maxilla	Maxilliped 1, 2	Sources
	Rostral	Lateral	Dorsal	Lateral knobs	Endopod setation	Endopod seta	Endopod setation	
Heteropanope								
H. grabra	6.8A	+	S, 9.6A	2, 3	1, 6	8	32125, 116	Greenwood and Fielder, 1984a
Heteropilumnus								
H. ciliatus	4.8A	+	S, 5.2A	2, 3	1, 6	8	32125, 115	Takeda and Miyake, 1968
Pilumnopeus								
P. makiana	2.4A	+	S, 4.0A	2, 3	1, 6	7	32125, 115	Lee, 1993
P. serratifrons	0.4A	+	S, 7.2A	2, 3	1, 6	8	32125, 116	Greenwood and Fielder, 1984b
P. granulata	0.2A	+	S, 4.0A	2, 3	1, 6	8	32125, 116	Present study
Pilumnus								
P. dasypodus	1.2A	+	C, 2.4A	2, 3	1, 6	8	32125, 116	Bookhout and Costlow, 1979
P. hirtellus	2.0A	+	C, 2.3A	2, 3	1, 6	8	32125, 116	Salman, 1982
P. vespertilio	0.5A	+	C, 2.2A	2, 3	1, 6	8	22125, 116	Lim and Tan, 1981
P. minutus	0.9A	+	C, 3.3A	2, 3, 4, 5	1, 6	8	32125, 116	Ko, 1994b
Actumnus								
A. setifer	1.3A	+	C, 3.8A	2, 3	1, 6	8	no data, 115	Aikawa, 1937
Parapilumnus								
P. trispinosus	0.6A		C, 2.4A	2, 3, 4, 5	1, 6	8	32125, 116	Ko, 1994a
Benthopanope								
B. indica	0.3A		C, 2.2A	2	1, 6	8	32125, 116	Ko, 1995
B. eucratoides	1.9A		C, 2.3A	2	1, 6	8	32126, 116	Lim et al., 1986

* A, ratio to length of an antennular conical rod; + or -, present or absent; S or C, straight or curved.

Table 2. Comparison of morphologically important megalopal characteristics in the pilumnid crabs

Species	Mandibular Palp Setae	Antenna Setation of the last 3 segments	Maxillipeds 1, 2, and 3 Exopods Setae
Heteropanope			
H. glabra	5	0, 3, 4	5, 5, 6
Pilumnopeus			
P. granulata	8	0, 3, 5	5, 5, 5
Pilumnus			
P. dasypodus	7	0, 4, 4	6, 6, 6
P. hirtellus	9	0, 3, 4	5, 5, 5
P. vespertilio	4 or 5	0, 3, 3	5, 4, 6
P. minutus	8	0, 3, 4	5, 4, 5
Parapilumnus			
P. trispinosus	8	0, 3, 4	5, 5, 5
Benthopanope			
B. indica	6	0, 3, 4	8, 8, 5
B. eucratoides	6	0, 3, 4	4, 5, 6

that the *Pilumnus minutus* has lateral knobs on the abdominal somites 2, 3, 4, and 5. These characteristics were found in the *Parapilumnus trispinosus*, although *Pilumnus minutus* has lateral carapace spines which were absent in *Parapilumnus trispinosus*. It seems that the *Pilumnus minutus* has some affinity to the *Parapilumnus trispinosus*.

As in Table 2, three appendages (mandible, antenna, and exopods of 3 maxillipeds) are morphologically important because of no individual variation in megalopae. The megalopae of *Pilumnopeus granulata, Pilumnus minutus,* and *Pilumnus hirtellus* are coincided with that of *Parapilumnus trispinosus* at least on the respects of two characters. In the case of the *Benthopanope* megalopae, *B. indica* and *B. eucratoides* have the same characteristics on the mandible and antenna, therefore, it can be considered that the morphology of the mandible and antenna are more significant in larval comparisons than the exopods of maxillipeds. The megalopae of *Pilumnus minutus* and *Parapilumnus trispinosus* have eight setae on the mandibular palp and 0, 3, 4 setation of the last segment of the antenna. Hence, the *Pilumnus minutus* resembles more with *Parapilumnus trispinosus* than *Pilumnopeus granulata* on the respects of the megalopal morphology.

Consequently, the larvae of *Pilumnopeus granulata, Pilumnus minutus,* and *Parapilumnus trispinosus* closely resemble with each other. The *Pilumnus minutus* resembles more with *Parapilumnus trispinosus* than *Pilumnopeus granulata* on the basis of the larval characteristics. It is desirable to re-examine the taxonomical status of these crabs.

Lebour (1928) determined the primitive or advanced status of brachyuran larvae based on the antennal development and the number of zoeal stages. Using Lebour's criteria, Scott (1979) provided a detailed discussion of the importance of larval characters in determining phylogenetic relationships in the genus *Menippe* (Oziidae). But these characters are useless in the case of the pilumnid larvae, because the antenna of all known pilumnid larvae is uniform and the number of zoeal stage of all known pilumnids is usually four. Aikawa (1937) gave phylogenetic significances to the characters of antenna, telson, carapace spines, and mouthpart setation. He suggested additionally that the characteristics of the abdominal lateral knobs might be of some value. It is possibly a primitive feature to have them on many somites. Based on the larval characteristics of the carapace spines and abdominal lateral knobs, larvae of the family Pilumnidae may be divided into five groups: 1) the genus *Heteropanope,* 2) the genara *Heteropilumnus* and *Pilumnopeus,* 3) the genera *Pilumnus* and *Actumnus,* 4) the genus *Parapilumnus,* and 5) the genus *Benthopanope.* Assuming that the well-developed carapace spines and the abdominal lateral knobs are good indications of the degree of the relative primitiveness among the pilumnid species, it can be concluded that the primitive state is seen in the genus *Heteropanope*, while the advanced state in the genus *Benthopanope.* The *Pilumnopeus* and *Pilumnus* occupy somewhat the intermediate state.

The following provisional key is provided for identification of the pilumnid zoeae.

Key to zoeal stages of the family Pilumnidae

1. Carapace with lateral spines 2
   Carapace without lateral spines 11
2. Carapace with straight dorsal spine 3
   Carapace with curved dorsal spine 7
3. Endopod of maxilla with 7 setae
   ..... *Pilumnopeus makiana*
   Endopod of maxilla with 8 setae 4
4. Carapace with developed rostral spine 5
   Carapace with vestigial rostral spine 6
5. Dorsal carapace spine about 9.6 times of antennular conical rod length; endopod of 2nd maxilliped with 1, 1, 6 setation
   ..... *Heteropanope glabra*
   Dorsal carapace spine about 5.2 times of antennular conical rod length; endopod of 2nd maxilliped with 1, 1, 5 setation
   ..... *Heteropilumnus ciliatus*
6. Dorsal carapace spine about 7.2 times of antennular conical rod length
   ..... *Pilumnopeus serratifrons*
   Dorsal carapace spine about 4.0 times of antennular conical rod length
   ..... *Pilumnopeus granulata* (zoea 1)
7. Lateral Knobs on somites 2, 3, 4 and 5
   ..... *Pilumnus minutus*
   Lateral Knobs on somites 2 and 3 8
8. Carapace with vestigial rostral spine; endopod of 1st maxilliped with 2, 2, 1, 2, 5 setation
   ..... *Pilumnus vespertilio*

Carapace with vestigial rostral spine; endopod of 1st maxilliped with 3, 2, 1, 2, 5 setation ..... *Pilumnopeus granulata* (zoea 2, 3 and 4)

9. Carapace with short rostral spine, which is 2.0 times of antennular conical rod length ..... *Pilumnus hirtellus*
   Carapace with short rostral spine, which is 1.2-1.3 times of antennular conical rod length 10
10. Dorsal carapace spine 2.4 times of antennular conical rod length; endopod of 2nd maxilliped with 1, 1, 6 setation ..... *Pilumnus dasypodus*
    Dorsal carapace spine 3.8 times of antennular conical rod length; endopod of 2nd maxilliped with 1, 1, 5 setation ..... *Actumnus setifer*
11. Lateral knobs on somites 2, 3, 4 and 5 ..... *Parapilumnus trispinosus*
    Lateral knobs on somite 2 12
12. Rostral carapace spine vestigial ..... *Benthopanope indica*
    Rostral carapace spine short and 1.9 times of antennular conical rod length ..... *Benthopanope eucratoides*

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