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Larvae of the Deep-Sea Squat Lobsters, *Agononida incerta* (Henderson, 1888) and *Munida striola* Macpherson and Baba, 1993 with Notes on Larval Morphology of the Family (Crustacea: Anomura: Galatheidae)

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ABSTRACT—There is little information on the larvae of squat lobsters of the family Galatheidae in spite of their abundance in mesopelagic and abyssal fauna. Larvae of two galatheid species, *Agononida incerta* (Henderson, 1888) and *Munida striola* Macpherson and Baba, 1993, are described and illustrated for the first time from the northwest Pacific region based on laboratory-hatched material. The zoeas of these two species are easily distinguished from each other by their size and the morphology of the antenna and maxillule. Previously-known zoeas of the family are compared and a provisional key for 6 galatheid genera is presented.

INTRODUCTION

Squat lobsters of the family Galatheidae are widely distributed in the ocean, and are conspicuous members of the fauna from the mesopelagic through abyssal habitats. According to Miyake (1982) more than 70 species ranging to 13 genera among the family are known from Japanese waters, and the number of recorded species is increasing (Baba *et al.*, 1986; Macpherson and Baba, 1993; Baba and de Saint Laurent, 1996). Indeed, the galatheid species represent more than 20 % in anomuran fauna of Japan (Table 1). We have, however, little information on larval development of the family, and no larval descriptions have been given in the northwest Pacific region, including Japan.

We had a chance to obtain newly-hatched zoeas of two squat lobsters during collections for mesopelagic crustaceans: *Agononida incerta* (Henderson, 1888) and *Munida striola* Macpherson and Baba, 1993. *A. incerta* is a common species of Japanese waters, which is recently transferred to *Agononida* Baba and de Saint Laurent, 1996 from *Munida* Leach, 1820 (Baba and de Saint Laurent, 1996). *M. striola* is recorded from Indonesia, Tosa Bay and north of Kyusyu, Japan in 215-300 m depth (Macpherson and Baba, 1993). These squat lobsters were collected together in large numbers from off Makurazaki, Kagoshima Prefecture, Japan.

This paper provides the first description of the larvae of squat lobsters of Japan. Diagnostic larval characteristics of the family are compared and a provisional key to the previously-known zoeas of galatheid genera.

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Table 1. Ranking of the number of species and the percentage of larval descriptions in the anomuran families of Japan.

Ranking	Family	Number of species*	(%)	Larval description	(%)
1	Galatheidae	60	20.8%	0	0.0%
2	Diogenidae	59	20.4%	9	15.3%
3	Paguridae	51	17.6%	11	21.6%
4	Porcellanidae	40	13.8%	14	35.0%
5	Chirostylidae	30	10.4%	1	3.3%
6	Lithodidae	23	8.0%	9	39.1%
7	Parapaguridae	9	3.1%	1	11.1%
8	Pomatochelidae	5	1.7%	0	0.0%
9	Coenobitidae	5	1.7%	5	100%
10	Albuneidae	4	1.4%	3	75.0%
11	Hippidae	3	1.0%	1	33.3%
	Total	289		54	

* after Miyake (1982)

MATERIAL AND METHODS

Ovigerous female squat lobsters were collected by a commercial shrimp trawler from a depth of 300 m off Makurazaki (130°E, 31°N), Kagoshima Prefecture, southern Japan, on 9 December 1995, 25 November and 4 December 1997. Animals were kept separately in cold water (11°C) and transported as fast as possible (within 10 hr) to the Port of Nagoya Public Aquarium (PNPA). First zoeas of *A. incerta* and *M. striola* were hatched on 8 January 1996 and 26 December 1997, respectively. Larvae were fixed and preserved in 5% formalin. The appendages were dissected with fine insect pins or sharpened tungsten needles under a Nikon SMZ-10 stereomicroscope and

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mounted on a silicon-coated glass slide. Drawings and measurements were made with a drawing tube attached to an Olympus BH-2 microscope. All illustrations were made with Illustrator™ 5.0J (Adobe Systems Inc.) on Macintosh™ OS (Apple Co. Ltd.). Setal terminology used in this paper follows mainly Ingle (1992). All setal arrangements are listed from proximal to distal. Roman numerals in setation denote dorso-lateral seta on segment of appendages. Carapace length (CL) was measured from the anterior margin of eye to medial posterior border of the carapace, and CL including rostral spine (CLR) was also given (see Fig.1). In the text, lengths are shown as the mean±SD and the range is given in parenthesis.

Specimens of larvae and the females from which zoeas were hatched are deposited at the Zoological Institute, Hokkaido University, Sapporo, under accession numbers of ZIHU 1324–1327 and PNPA, Nagoya.

DESCRIPTION OF ZOEAS

Agononida incerta (Henderson, 1888)

Size: CL=0.98±0.029 mm (range 0.90–1.05 mm); CLR =1.86±0.089 mm (range 1.68–2.07 mm); 36 specimens examined.

Carapace (Fig. 1A): Rostral spine well developed, extending to level of tip of antenna. Carapace produced into acute spine posteriorly, and posterolateral and dorsomedial margins fringed with numerous denticules. Eyes large, diameter almost half of CL and sessile.

Antennule (Fig. 2A): Uniramous, rod-like process with

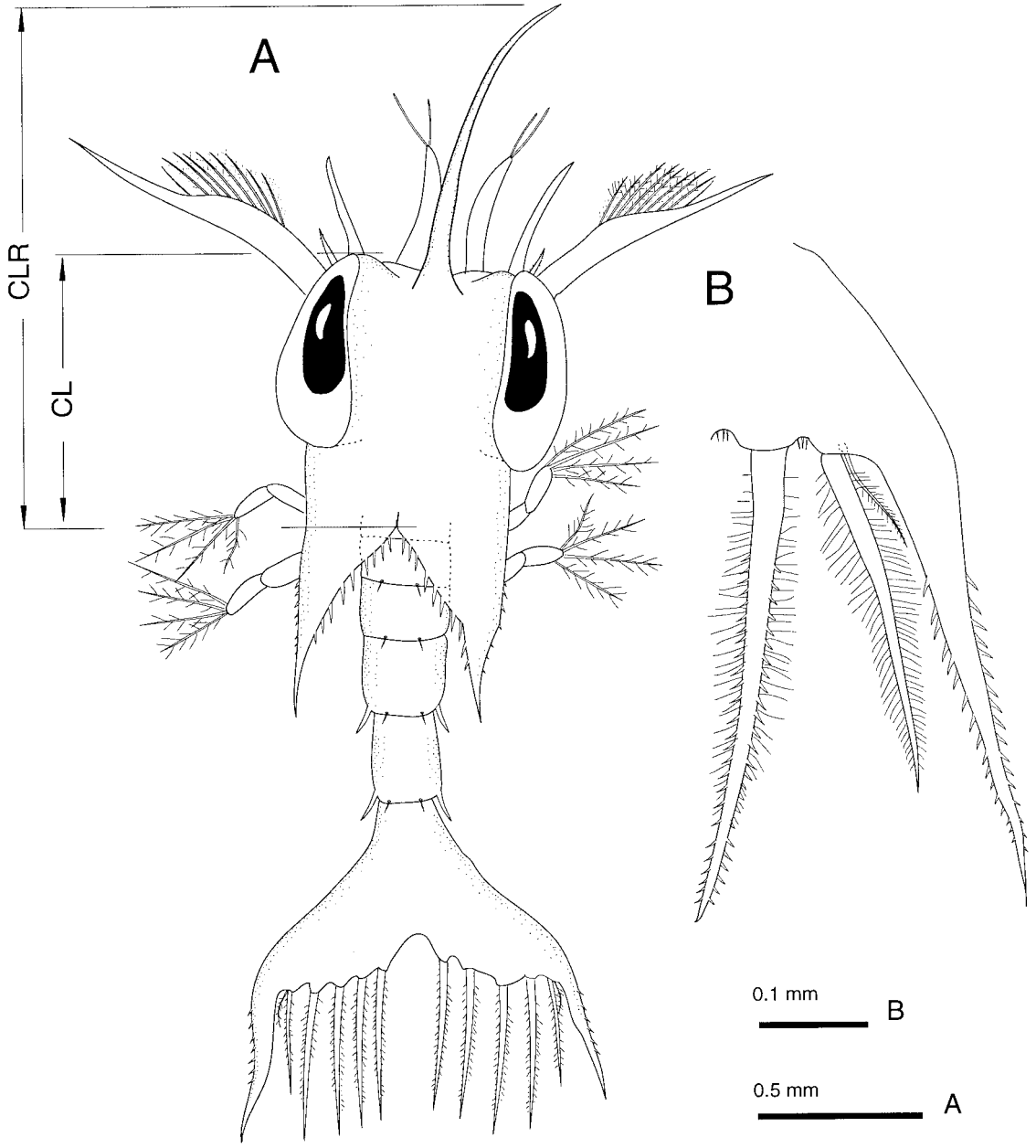


Fig. 1. *Agononida incerta* (Henderson, 1888), zoea 1. A, whole animal in dorsal view; B, telson.

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3 long aesthetascs plus 3 simple setae distally, and 1 long plumose seta subterminally.

Antenna (Fig. 2B): Endopod almost 1/3 of exopod length, rod-shaped without setae, but rarely with 1 thin terminal simple seta (Fig. 2B'). Exopod (= scaphocerite) with 8 plumose plus an uppermost simple seta on its inner margin, and

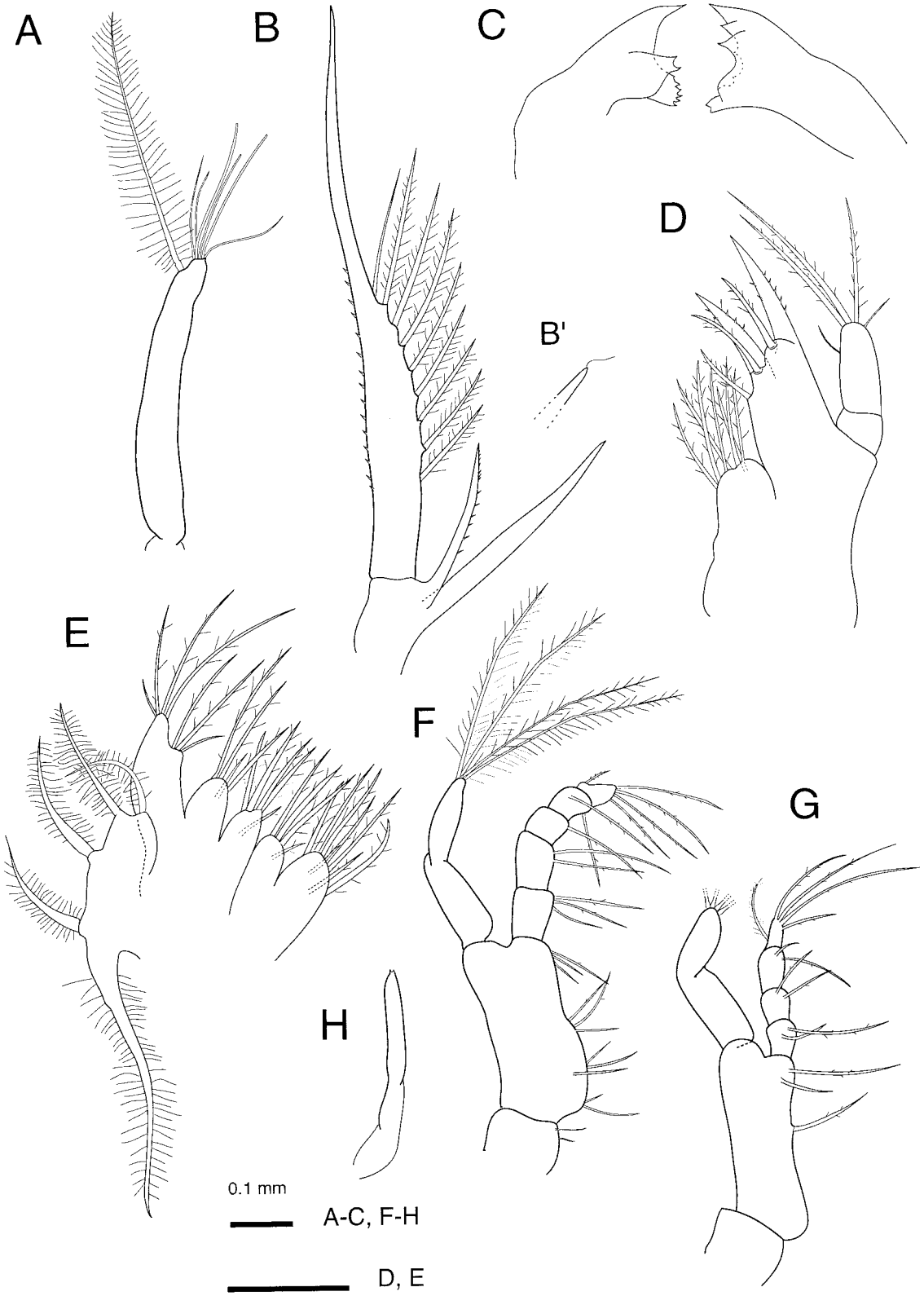


Fig. 2. *Agononida incerta* (Henderson, 1888), zoea 1. A, antennule; B, antenna; B', tip of endopod with a thin seta; C, mandibles; D, maxillule; E, maxilla; F, maxilliped 1; G, maxilliped 2; H, maxilliped 3.

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numerous spinules on its surface. Serrated protopodal spine, 1/4 of exopod length, at base of endopodal junction.

Mandibles (Fig. 2C): Incisor and molar processes distinguished; asymmetrical in dentation.

Maxillule (Fig. 2D): Coxal endite with 7 plumodenticulate setae. Basial endite with 2 stout cuspidate spines and 3 plumodenticulate setae. Endopod two-segmented, without setae on the proximal segment, and distal segment with 3 plumodenticulate setae plus 2 subterminal simple setae.

Maxilla (Fig. 2E): Coxal and basial endite bilobed, with 8(7)+4 and 5+4 plumodenticulate setae, respectively. Endopod unsegmented bilobed, with 3+4 plumodenticulate setae. Scaphognathite with 4 marginal plumose setae and a long plumose posterior process.

Maxilliped 1 (Fig. 2F): Coxa with 2 short simple setae. Basis with 2+3+3+3 setae on inner side. Endopod five-segmented with 3,2,1,2,4+I setae (I = subterminal dorsal seta), respectively. Exopod with 4 natatory plumose setae.

Maxilliped 2 (Fig. 2G): Coxa without setae. Basis with 1+2 inner setae. Endopod four-segmented with 2,2,2,4+I

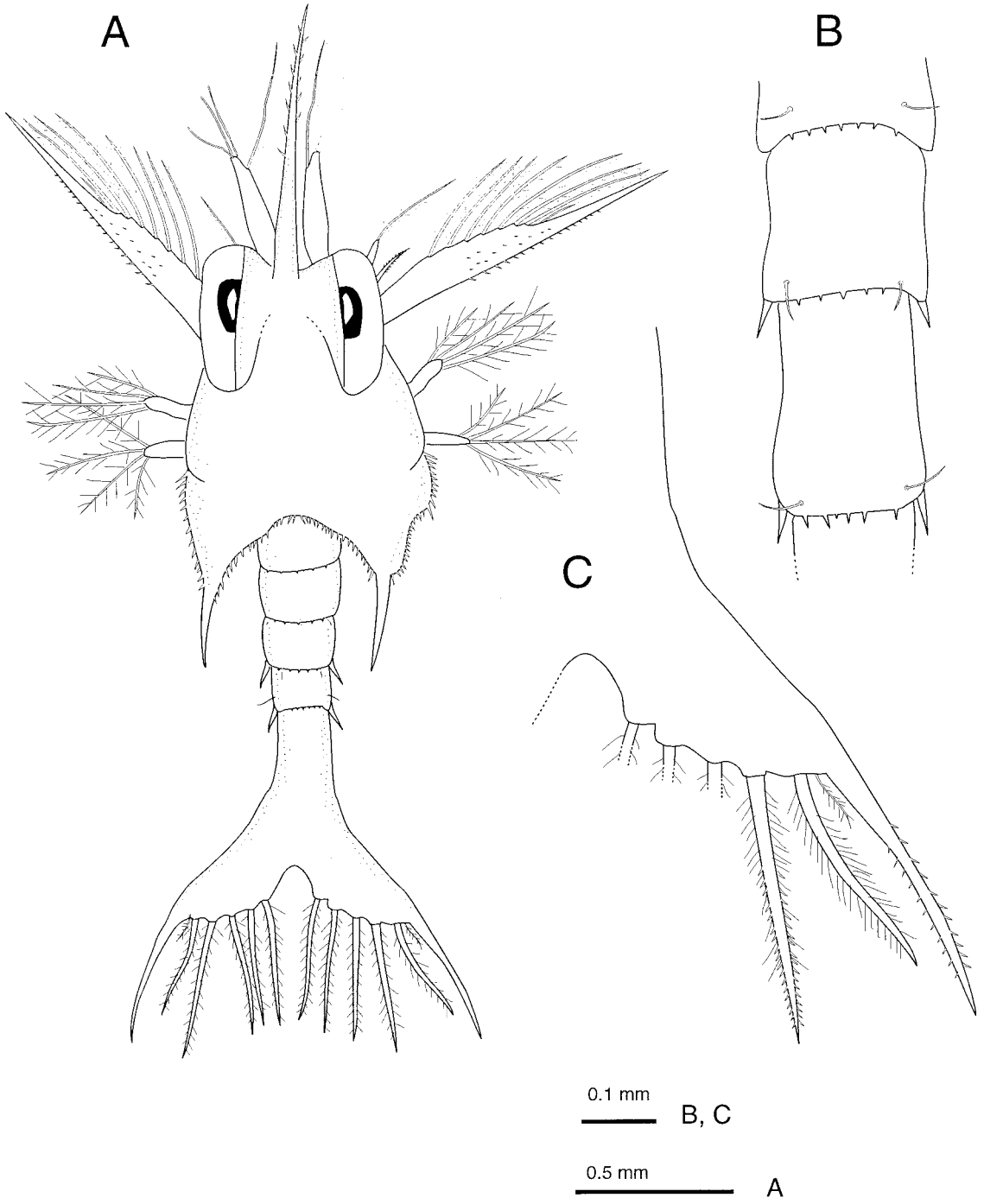


Fig. 3. *Munida striola* Macpherson and Baba, 1993, zoea 1. A, whole animal in dorsal view; B, abdominal somites; C, telson.

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setae, respectively. Exopod as in maxilliped 1.

Maxilliped 3 (Fig. 2H): Rudimentary rod-like bud.

Pereiopods: Uniramous, small buds.

Abdomen (Fig. 1A): Five somites plus forked telson. Postero-dorsal margin of abdominal somite with 5 -8 spinules. Somite 4 and 5 with a pair of posterolateral spines, respec-

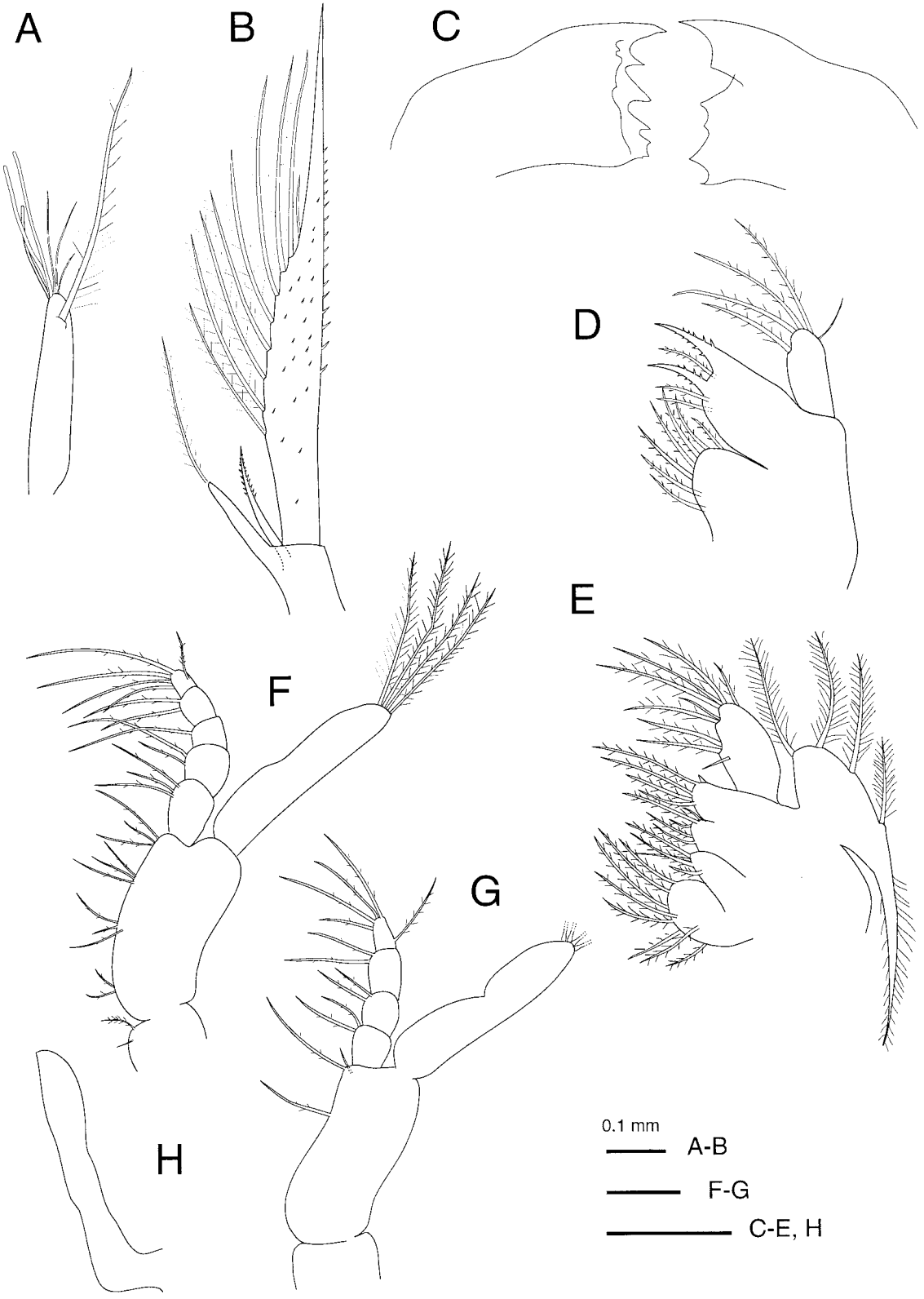


Fig. 4. *Munida striola* Macpherson and Baba, 1993, zoea 1. A, antennule; B, antenna; C, mandibles; D, maxillule; E, maxilla; F, maxilliped 1; G, maxilliped 2; H, maxilliped 3.

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tively.

Telson (Fig. 1B): Posterior margin with median cleft and 7+7 posterior processes, outermost a fused spine, second 1 small pappose seta (= anomuran hair), third plumose, fourth to seventh large plumodenticulate setae. Anal spine not found.

Munida striola Macpherson and Baba, 1993

Size: CL=0.84±0.049 mm (range 0.73–0.91 mm); CLR =1.59±0.075 mm (range 1.43–1.73 mm); 32 specimens examined.

Carapace (Fig. 3A): Rostral spine well developed, with spinules on its surface. Posterior acute spines and posterolateral and dorsomedial margins with numerous denticules as in A. incerta. Eyes sessile, diameter about 1/3 of CL.

Antennule (Fig. 4A): Rod-like process with 3 long aesthetascs and 3 simple setae distally; a long plumose seta subterminally.

Antenna (Fig. 4B): Endopod about 1/4 of exopod length, rod-shaped with a long terminal plumose seta. Exopod (scaphocerite) bearing many spinules on its surface with 8 plumose and 1 simple setae on its inner margin.

Mandibles (Fig. 4C): Incisor and molar processes distinguished. Asymmetrical in dentation.

Maxillule (Fig. 4D): Coxal endite with 7 plumodenticulate setae. Basial endite with 2 stout cuspidate spines and 3 plumodenticulate setae. Endopod unsegmented, with 3 plumodenticulate and 1 simple setae, and 1 subterminal plumose seta.

Maxilla (Fig. 4E): Coxal and basial endite bilobed, with 8+4 and 4(5)+4 setae, respectively. Endopod unsegmented with 3+2+4 setae. Scaphognathite with 4 soft plumose setae and 1 long plumose posterior process.

Maxilliped 1 (Fig. 4F): Coxa with 1 short simple plus 1 short pappose setae. Basis with 2+3+3+3 setae on inner side. Endopod five-segmented with 3,2,1,2,4+I setae, respectively. Exopod unsegmented with 4 long natatory plumose setae.

Maxilliped 2 (Fig. 4G): Coxa without setae. Basis with 1+2 inner setae. Endopod four-segmented with 2,2,2,4+I setae, respectively. Exopod as in maxilliped 1.

Maxilliped 3 (Fig. 4H): Rudimentary rod-like bud.

Pereiopods: Rudimentary small buds.

Abdomen (Fig. 3A, B): Five somites plus a forked telson. Each abdominal somite with a pair of posterodorsal setae and 3–7 spinules on posterodorsal border. Somite 4 and 5 with a pair of posterolateral spines.

Telson (Fig. 3C): Each telsonal fork with numerous spinules. Posterior margin with median cleft and 7+7 posterior processes, outermost a fused spine, second a small anomuran hair, third large plumose seta, and fourth to seventh large plumodenticulate seta. Anal spine not found.

DISCUSSION

The general morphological features of the zoeas in the present study are of typical galateids, having a pair of posterolateral spines with a serration, according with the diagnostic larval features reported by Gurney (1942). In addition to his criteria, galatheid zoeas possess a long posterior plumose process on the maxillar scaphognathite, except for the larvae showing abbreviated development. The present zoeas are easily distinguished by three diagnostic characteristics as follows: (1) body size of *A. incerta* is clearly larger than *M. striola* as shown in Fig. 5, (2) the antennal endopod of *M. striola* has an apical plumose seta, while none in *A. incerta*, and (3) the maxillular endopod of *A. incerta* is two-segmented, while unsegmented in *M. striola*. Furthermore, the eyes of *Agononida* are considerably larger in proportion to the body size: i.e., maximum diameter of the eye is about 1/2 of CL. These comparative larval characteristics of the morphology clearly show a difference at a generic or higher taxonomic level. Thus evidence from larvae of the present study supports the taxonomic revision of the adult squat lobsters by Baba and de Saint Laurent (1996): transfer of *M. incerta* from *Munida* to *Agononida*.

Larval studies of the Galatheidae have been made for 5 genera: *Galathea* (Sars, 1889; Lebour, 1930, 1931; Gurney, 1938; Bourdillon-Casanova, 1960; Pike and Williamson, 1972; Christiansen and Anger, 1990), *Munida* (Sars, 1889; Stephensen, 1912; Lebour, 1930; Huus, 1934; Roberts, 1973; Vera and Bacardit, 1986), *Cervimunida* (Fagetti, 1960), *Munidopsis* (Sars, 1889; Samuelsen, 1972; Wilkens *et al*., 1990), and *Pleuroncodes* (Boyd, 1960; Fagetti and Campodonico, 1971; Gore, 1979). These previous studies dealt with the Atlantic and eastern Pacific species. Among the galatheid genera, *Munidopsis* shows an abbreviated development.

Gore (1979) gave a synopsis of the galatheid larvae in 5 genera: *Cervimunida*, *Galathea*, *Munida*, *Munidopsis* and *Pleuroncodes*. The present study requires some modification and adds new larval data of *Agononida* to his synopsis. Table 2 shows the main larval characteristics of the previously-known species of the family Galatheidae. Comparison of larval characteristics is based on the works by the laboratory-rearing method. The descriptions from several early larval studies,

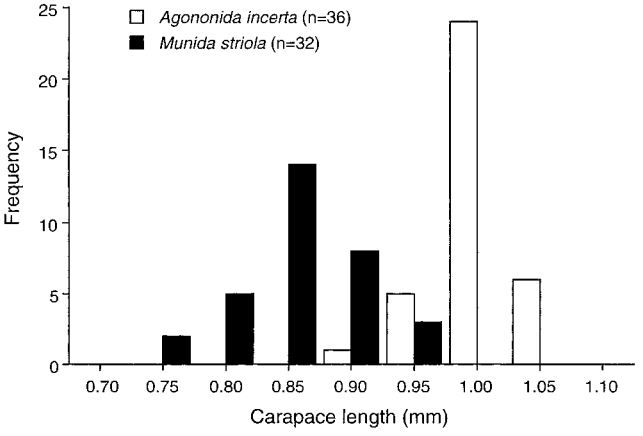


Fig. 5. Carapace lengths in zoea 1 of *Agononida incerta* (Henderson, 1888) and of *Munida striola* Macpherson and Baba, 1993.

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Table 2. Comparison of the larval characters in zoea 1 of 10 galatheid species from 6 genera.

Genus	*Agononida*		*Munida*		*Galathea*		*Cervimunida*	*Pleuroncodes*		*Munidopsis*
Species	*incerta*	*striola*	*tenuimana*	*subrugosa*	*intermedia*	*rostrata*	*johni*	*planipes*	*monodon*	*tridentatus*
Reference	this study	this study	*1	*2	*3	*4	*5	*6	*7	*8
Carapace:										
rostral spine	+	+	+	+	+	+	+	+	+	–
anterolateral spine	–	–	–	–	–	–	–	–	–	+
posterior spine	+	+	+	+	+	+	+	+	+	–
Antennule:	3a+3+l	3a+3+l	3a+1+l	3a+2+l	3a+3+l	3a+3+l	3a+3+l	3a+3+l	(6a)+l	8a+1+l
Antenna:										
protopod	1	1	1	1	1	1	1	1	2	2
endopod (en)	–	1	–	–	1	1	–	–	–	2
exopod (ex)	9	9	8	8	9	9	8	8	8	14–17
pp/ex length	en<ex	en<ex	en<<ex	en<ex	en<ex	en<ex	en=ex	en=ex	en=ex	en<ex
Mandible (*palp*):	–	–	–	–	–	–	–	–	–	+
Maxillule:										
coxal endite	7	7	5	6	6–7	6–7	7	6	7	r
basial endite	5	5	6	5	5	5	5	5	5	r
endopod	0,5	5	5	5	0,5	0,4	6	5	5	1
Maxilla:										
coxal endite	8+4	8+4	5+3	6+3	7+3	7+3	6+4	6+4	5+4	r
basial endite	5+4	5+4	3+4	4+4	4+4	8+4	4+4	4+4	4+4	r
endopod	3+4	3+6	3+4	3+4	3+6	3+4	3+4	3+4	3+4	1
scaphognathite	4+a	4+a	4+a	4+a	4+a	4+a	4+a	4+a	4+a	32-34
Maxilliped 1:										
coxa	2	2	2	2	2	2	?	1	1	?
basis	2+3+3+3	2+3+3+3	2+3+3+3	2+3+3+3	2+3+3+3	2+3+3+3	2+3+3+3	2+3+3+2	2+3+3+2	–
endopod	3,2,1,2,4+l	3,2,1,2,4+l	3,2,1,2,4+l	3,2,1,2,4+l	3,2,1,2,4+l	3,2,1,2,4+l	2,2,1,2,4+l	2,2,1,2,4+l	2,2,1,2,4+l	0,1,1,3+l
Maxilliped 2:										
basis	1+2	1+2	1+2	1+2	1+2	1+2	1+2	1+2	1+2	1
endopod	2,2,2,4+l	2,2,2,4+l	2,2,2,4+l	2,2,2,4+l	2,2,2,4+l	2,2,2,4+l	2,2,2,4+l	2,2,2,4+l	2,2,2,4+l	0,0,1,2
Telson:										
process	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	7+7	13+13
Abdomen (*PLS*):										
somite 4	+	+	+	+	–	+	+	+	+	–
somite 5	+	+	+	+	+	+	+	+	+	+

*1, Huus (1934); *2, Roberts (1973); *3, Christiansen & Anger (1990); *4, Gore (1979); *5, Fagetti (1960); *6, Boyd (1960); *7, Fagetti & Campodonico (1971); *8, Sars (1889) & Samuelsen (1972). PLS, posterolateral spine; r, reduced; +, present; –, absent; ?, no data.

however, show less definitively the morphological characteristics and we can not compare the data with those by recent standards for larval description (cf. Clark *et al*. 1998). Among the 6 galatheid zoeas, *Munidopsis* is noticeably different from the others by the possession of the prominent anterolateral spines and the lack of elongate posterior spines on the carapace. In addition, *Munidopsis* zoeas show some unique characteristics which are usually found in decapod larvae with an abbreviated development: e.g., large body size and rudimentary mouthparts.

The zoeas of the other 5 galatheid genera are distinguished from each other by the morphology of the following appendages: antenna, maxillule, and maxilliped 1. Antenna of *Cervimunida* bears 2 protopodal process, spinulose dorsal and unarmed ventral, unlike typical galatheid first zoeas. The coxae of the maxilliped 1 in *Cervimunida* and *Pleuroncodes* have one seta and those of the remaining genera have 2 setae. The endopods of the maxillule in *Agononida* and *Galathea* is two-segmented, while unsengmented in the remaining genera. The endopods of the antenna in *Munida striola* and *Galathea* bears apical long plumose seta. This and the marginal plumose setae on antennal exopod the zoeas of *M. striola* are similar to those of *Galathea*. General zoeal features of *M. striola* are different from the congeners, and rather resemble those of *Galathea*. In recent years, reappraisal of the adult taxonomy of squat lobsters has been in progress, e.g., Baba (1988), Baba and de Saint Laurent (1996), and Macpherson (1998). The true taxonomic position of these *Munida* species will possibly be clear in the near future.

We herewith give a provisonal key to six genera of the previously-known galatheid zoeas based on laboratory-reared material.

A1. Carapace with rostral spine and elongate posterior spines ..... B
A2. Carapace with anterolateral spines and no posterior spines ..... *Munidopsis*
B1. Endopod of maxillule with 4 or 5 setae distally C
B2. Endopod of maxillule with 6 setae distally ..... *Cervimunida*
C1. Coxa and first endopodal segment with 2 and 3 setae, respectively ..... D
C2. Coxa and first endopodal segment with 1 and 2 setae, respectively ..... *Pleuroncodes*
D1. Endopod of maxillule 2-segmented ..... E

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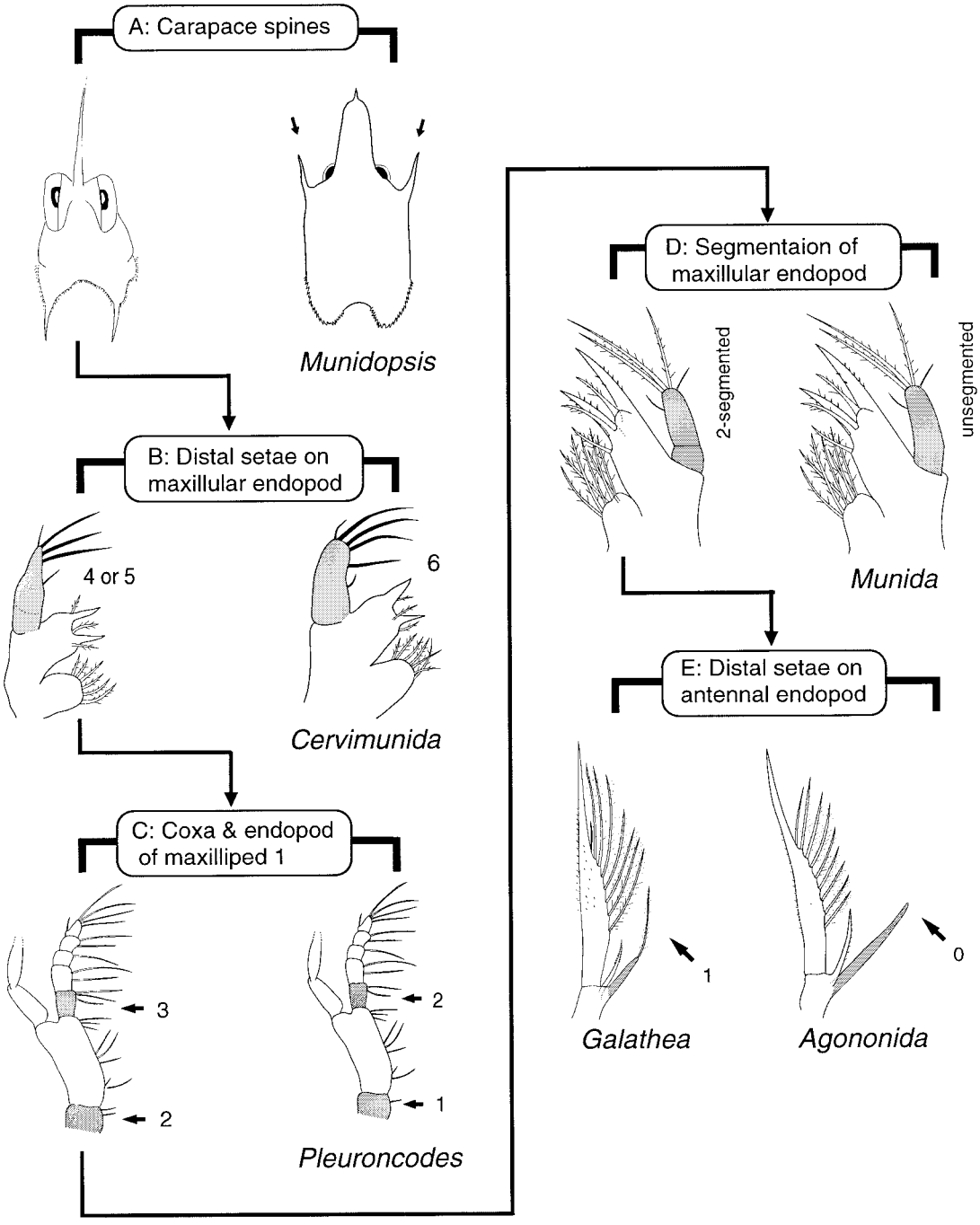


Fig. 6. Diagrammatic key to the previously-known zoeas of the 6 genera in the family Galatheidae. Arrows and dotted portions indicate the main characteristics.

D2. Endopod of maxillule unsegmented ..... *Munida*
E1. Tip of antennal endopod with a long plumose seta .... *Galathea*
E2. Tip of antennal endopod with a vestigial thin seta or no seta ..... *Agononida*

A diagrammatic key is also presented in Fig. 6.

Our knowledge on the larvae of Galatheidae remains poor especially in the Indo-Pacific region. More descriptive works and reappraisals of larval characteristics are still required. The reason for the shortage of information on larvae of galatheid anomurans may be due to the difficulty in obtaining ovigerous females from the deep-sea and larval rearing in optimal conditions as well as lacking of commercial species. Recent advances in collection methods and rearing techniques should allow this to be.

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