Description of the first zoea of *Paromola macrochira* Sakai (Brachyura: Homolidae) with notes on larval characters of archaeobrachyuran families

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Abstract. — The first zoea of a deep-water crab, *Paromola macrochira* Sakai, is described based on laboratory-reared material. Larval characters of described zoeas of the family Homolidae are compared and discussed together with those of the other archaeobrachyuran families. Within the genus *Paromola*, the zoea of *P. macrochira* much resembles that of *P. cuvieri* (Risso), but differs from that of *P. japonica* Parisi mainly in maxilla and carapace ornamentation. Homolid and dromiid zoeas have many anomuran features in common, and two types are recognized among them. The zoeas of the Raninidae show a number of larval characters of the higher brachyurans. The zoeas of the Latreillidae also closely resemble those of the Homolidae, but can be distinguished by the setation of the endopod of maxilliped 2. It is suggested that homolid and latreillid zoeas seem to show an intermediate level of evolutionary processes between morphologically advanced raninids and more primitive dromiids.

Introduction

The deep-water crabs of the family Homolidae are included in a subsection Archaeobrachyura *sensu* Guinot (1978) based on the gonopore position in the adult stage. The systematic position of the primitive archaeobrachyuran crabs has been discussed by many carcinologists, but larval knowledge of this group, which will be helpful for any phylogenetic study, to date remains poor and fragmen-

tary. Most previous larval studies of this family have been concerned with specimens obtained from the planktons or have dealt with the first larval stage (Pike & Williamson, 1960; Rice, 1964, 1970, 1971; Rice & Von Levetzov, 1970; Williamson, 1965). Complete larval development has been described only for *Homola barbata* (Fabricius) (Rice & Provenzano, 1970). In Japan, the family Homolidae includes 8 genera and 13 species (Miyake, 1983; Guinot & Richer de Forges, 1995); the larval stages are known for two species: *Paromola japonica* Parisi and *H. orientalis* Henderson (Aikawa, 1937; Terada, 1987).

This paper describes the zoeal morphology of the homolid crab, *Paromola macrochira* Sakai, and compares the larval characters of archaeobrachyuran families.

Material and Methods

Adult crabs were collected from off Enshunada, Pacific coast of Japan, at a depth of 200–300 m in March 1993. The crabs were kept in an aquarium at 10 °C and laid eggs in the following year. First zoeas hatched on 5 February 1995. The zoeas were fed with newly-hatched *Artemia* nauplii. Most of first zoeas died without molting by the 30th day after the hatching, and 12 larvae molted to the second zoea. However, we could not examine the specimens of the second zoea because of bad condition in preservation. The larvae and exuviae were fixed in 5% formalin and preserved in 70% ethanol. Tech-

Fig. 1. First stage zoea of *Paromola macrochira* Sakai, 1961: A, lateral view; B, dorsal view of carapace; C, abdomen; C', posterior process of telson; enlarged. Scale bars = 0.1 mm.

niques for dissection, and drawings were almost the same as in previous works (Konishi & Taishaku, 1994; McLaughlin & Konishi, 1994).

Total carapace length (TCL) was mea-

sured between the tip of rostral spine and the mid-posterior margin of carapace. Setal counts are from proximal to distal. Voucher specimens have been deposited in the Natural History Museum and Insti-

Table 1. Comparison of the main larval characters of first zoeas of Homolidae.

Species	<i>P. macrochira</i>	<i>P. japonica</i>	<i>P. cuvieri</i>	<i>H. barbata</i>	<i>H. orientalis</i>
References	This study	Aikawa, 1937	Samuelsen, 1976	Rice <i>et al.</i> , 1970	Terada, 1987
CARAPACE:					
length (mm) ¹⁾	1.15–1.27	1.3	1.6–1.9	0.67–0.76	0.6
rostral spine	+	+	+	+	+
dorsal spine	r	–	r	–	–
lateral spine	+	–	+	+ ²⁾	–
fringe	S	D	S	D	D
ANTENNULE:					
aesthetascs	3	?	3	3	2
setae	3	?	3	3	2
ANTENNA:					
endopod	2	2	2	2	2
exopod	7+1	7+1	6+1	9	9
MAXILLULE:					
coxae endite	7	?	7	?	7–8
basal endite	5	?	5	?	5
endopod	1, 5	1, 5	1+5	?	1, 5
MAXILLA:					
coxae endite	5+4	?	8+4	?	6+4
basal endite	5+4	?	6+5	?	5+4
endopod	3+6	2+6	3+6	3+5	3+4
scaphognathite	4+a	3+a	4+a	4+a	4+a
MAXILLIPED 1:					
coxa	1	?	?	?	?
basis	2+2+2+3	?	2+2+2+3	2+2+2+3	2+2+2+3
endopod	1, 1, 1, 2, 4+I	?	1, 1, 1, 2, 4+I	1, 1, 1, 2, 4+I	1, 1, 1, 2, 4+I
MAXILLIPED 2:					
basis	1+1+1+2	?	1+1+1+1	1+1+1+1	1+1+1+2
endopod	1, 1, 1, 4+I	1, 1, 2, 4+I	1, 1, 1, 4+I	0, 0, 2, 4+I	1, 1, 2, 4+I
ABDOMEN:					
DS on somite 1	6	?	8	4	4
DS on somite 2	2	?	4	?	2
TELSON:					
posterior spines	6+6	6+6	6+6	6+6	6+6
outer spines	–	–	–	5+5	–

1) total carapace length; 2) measured from figure; +, present, –, absent; a, apical plumose process; r, reduced or vestigial form; D, double, DS, dorsal spine, I, dorsal seta, S, single

Fig. 2. First stage zoea of *Paromola macrochira* Sakai, 1961: A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped 1; G, maxilliped 2; H, telson. Scale bars = 0.1 mm.

tute, Chiba under accession numbers CBM-ZC-1952, 1953 and 1954.

Description of first zoea

TCL: 1.15–1.27 mm (mean 1.20 mm, SD = 0.028, 35 specimens).

Carapace (Fig. 1A, 1B): Rostral spine directed forward, dorsal spine very short, and pair of short lateral spines. Posterior part of carapace fringed with denticles.

Antennule (Fig. 2A): Conical, slightly 2-segmented with 3 aesthetascs and 3 short simple setae.

Antenna (Fig. 2B): Protopodal process long with spines, endopod with 2 distal plumose setae, exopod flattened, with inner 7 plumose setae and 1 outer plumose seta.

Mandibles (Fig. 2C): Stout incisor process, molar processes developed.

Maxillule (Fig. 2D): Coxal endite with 6 plumodenticulate setae and 1 simple seta. Basal endite with 2 stout setae, 2 plumodenticulate setae, and a thin serrated seta. Two-segmented endopod, with 1+5 setae on distal segment.

Maxilla (Fig. 2E): Coxal and basal endites bilobed, with 5+4 and 5+4 plumodenticulate setae, respectively. Unsegmented endopod with 3+6 setae. Scaphognathite with 4 marginal setulate plumose setae and 1 long plumose projection.

Maxilliped 1 (Fig. 2F): Coxa with 1 short seta. Basis with 2+2+2+3 simple setae. Endopod five-segmented with 1, 1, 1, 2, 4+I setae (Roman numeral denotes dorsal seta). Exopod unsegmented with 4 long plumose natatory setae distally.

Maxilliped 2 (Fig. 2G): No coxal seta. Basis with 1+1+1+2 setae. Four-segmented endopod with 1, 1, 1, 4+I setae. Exopod as in maxilliped 1.

Maxilliped 3 (Fig. 2H): Rudimentary, biramous bud.

Pereiopods: Rudimentary, uniramous bud.

Abdomen (Fig. 1C): Five somites plus wide triangular telson, with a pronounced

medio-posterior sinus. Abdominal somite 2-5 with pair of dorsoposterior setules, and somite 2 and 3 with lateral knobs. No pleopods on abdominal somites. Telson with 6+6 posterior plumose spines: outermost spine short and naked.

Discussion

Table 1 lists the larval characters of known zoeas of the Homolidae. The larval morphology of the present species closely resembles that of *Paromola cuvieri* Risso. Another congeneric species, *P. japonica* described by Aikawa (1937) is superficially similar to that of the genus *Homola* rather than the genus *Paromola*. In his description, however, an unusual feature is found in the maxillar scaphognathite, which is provided with 3 setulate marginal setae; it is unlikely that the zoeas of the same genus differ in this character. Thus re-examination of the larval morphology of *P. japonica* should be undertaken in the future. Williamson (1965) divided the homolid larvae into two groups mainly based on the ornamentation of the carapace and abdomen. His Homolidae, however, included the Latreillidae which is recognized as separate family at present classification.

Significant larval characters in the main brachyuran groups based on Guinot's (1978) system are summarized in Table 2. Guinot's section Podotremata consisted of 7 families divided into 2 subsections: the Dromiacea and Archaeobrachyura. In the subsection Dromiacea, no larval descriptions have been reported for the Homolodromiidae or the Dynomenidae. The dromiids, the most primitive brachyurans, have many anomuran features in their zoeal stages as follows: anteriorly-directed rostral spine, anomuran hair in telson, flattened antennal exopod, etc. Among the subsection Archaeobrachyura, consisting of Homolidae, Latreillidae, Raninidae, and Tymolidae, the raninid zoeas share a number of characters with those of

Fig. 3. A key to Japanese homolid zoeas showing diagnostic features by numerals: 1, anteriorly directed rostral spine; 2, serrated margin; 3, flattened exopod; 4, no anomuran hair; 5, wide triangular telson; 6, proximal endopod segment without seta; 7, proximal endopod segment with seta; 8, simple posterior margin; 9, folded posterior margin. * Based on Terada's (1987) figures.

Table 2. Comparison of the main larval characters in major brachyuran groups.

Section	PODOTREMATA				"EUBRACHYURA" ⁽¹⁾ (many families)
Subsection	Archaeobrachyura			Raninidae	
Family	Dromiacea	Homolidae	Latreillidae		
CARAPACE:					
direction of rostral spine	Dromiidae	anterior	anterior	ventral	ventral
ANTENNA:					
endopod	developed	developed	developed	reduced	absent
exopod	flattened	flattened	flattened	flattened	rod
MAXILLIPED 2:					
coxal seta	+	-	-	-	-
endopod	4 segments	4 segments	4 segments	3 segments	1-3 segments
MAXILLIPED 3:					
endopod	+	+	+	+	-
TELSON:					
shape	triangular	wide triangular	wide triangular	forked	forked
anomuran hair	+	-	-	-	-

1) Eubrachyura *sensu* De Saint-Laurent (1980) = Heterotremata + Thoracotremata; +, present; -, absent

Eubrachyura sensu De Saint-Laurent (1980), consisting of so-called "higher brachyurans" which contains the sections *Heterotremata* and *Thracotremata sensu* Guinot. These zoeas have a ventrally-directed rostral spine and a rod-shaped antenna without an exopod. In this point, raninid zoeas with this type of rostral spine, differ from those of other archaeobrachyurans. The homolid zoeas, on the other hand, are very similar to dromiids in rostral spine direction and antenna as have been commented on by several previous authors of the larval studies (e.g. Rice, 1980). Zoeas of the Latreillidae also closely resemble homolid zoeas, but can be distinguished by the setation of the endopod of maxilliped 2. In addition, the known larvae of the Tymolidae show strong abbreviated features (Wear & Batham, 1975), which are inappropriate for comparison of larval affinities. Thus the larval features of the homolid and latreillid zoeas are intermediate between more advanced raninids and the most primitive dromiid larvae.

Rice (1980, 1981) discussed on the relationship between lower and higher brachyurans based on zoeal evidence. He stated that the homolids became separated from the primitive brachyuran line at an earlier stage than the raninids. Recent comparative spermatology has been also shown that the homolids differ markedly from the *Heterotremata-Thracotremata* assemblage while agreeing with dromiids in morphology (Jamieson *et al.*, 1994; Guinot *et al.*, 1994).

An illustrated key to the Japanese homolid zoeas is given in Fig. 3. Each diagnostic item is indicated by a numeral. In this key, the data of *P. japonica* zoea is not included because it contains some uncertain features as noted above.

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