

Larval development of a mangrove crab (*Perisesarma bidens* De Haan) (Crustacea: Brachyura: Sesarminae)

M. Sirajul Islam* and Shigemitsu Shokita

Department of Chemistry, Biology and Marine science,

University of the Ryukyus 1 Senbaru, Nishihara-Cho, Okinawa 903-0213, Japan

*Corresponding author

Abstract

Larval development of *Perisesarma bidens* (De Haan) was investigated in laboratory conditions. Morphology of all larval stages and 1st crab stage was described and illustrated in detail, and compared with other species of sesarmid crabs. The zoal morphological features of *P. bidens* are almost similar to other species of *Sesarma* in lacking a pair of lateral spines on carapace.

Key words: Mangrove crab, *Perisesarma bidens*, Morphology

Introduction

Sesarmid crabs are one of the brachyuran, which show various degrees of adaptation to semi-terrestrial existence, ranging from the sea-bound and intertidal preference terrestrial life. Many brachyuran crabs, particularly the members of Ocypodidae and Grapsidae (Sesarminae) have achieved the transition from life in the marine environment to terrestrial and freshwater habitats (Hartnoll 1988). While most of these species need to return to the sea in order to reproduce, others show abbreviated larval development as an adaptation to their life on land or in freshwater (Powers and Bliss 1983, Rabalais and Gore 1985, Zimmerman and Felder 1991).

The mangrove rearing sesarmid crab, *Perisesarma bidens* (De Haan), is widely distributed in the Indo-West Pacific region, the Bay of Bengal to the Andamans, Malay archipelago, Hong kong, Formosa, Korea and Japan (Sakai 1976, Aiyun and Siliang 1991). In Japan, this species mainly occurred from Tokyo Bay to Kyushu and the Ryukyu Islands (Miyake 1983). The present species generally live in burrow constructed in the edges or within the forests or in the reed marsh higher than ordinary high water mark. This crab commonly occurred in Okinawan mangal areas (Watanabe 1993).

Larval development of this crab is not well known. Watanabe (1993) described the population structure and feeding habits of it from Okinawa Island, but not investigated its larval development. The larval development of several sesarmid crabs have been described by many workers in the past (Terada 1976, Lago 1993, Mia and Shokita 1996 and 1997, Cuesta *et al.* 1999). But until now, the larval development of *P. bidens* have not been described. The objectives of the present study are to provide the detail

morphological descriptions of all the larval stages including megalopa and 1st crab of *P. bidens*, and to compare them with other species of sesarmid crabs.

Materials and methods

An ovigerous female of *Perisesarma bidens* (16.2 mm in carapace length and 19.3 mm in carapace width) was captured from the mouth of west bank of Nuha river in Manko estuary, Naha, Okinawa Island, Japan on 16 April'99, and placed it in a plastic holding tank. Then the crab was brought to the wet laboratory of the Department of Chemistry, Biology and Marine Science, and reared in a plastic trough containing seawater of $27\pm 1\%$ salinity with moderate aeration. During the experimental period, water temperature ranged from 21.3 to 23.5°C.

Hatching occurred on the morning of April 21. Among the hatched larvae, most photo positive zoeae were transferred to 10-liter capacity plastic bowls that were covered with black paper sheet outside and reared under the same conditions as mother. The water was also aerated and renewed 50% daily. The newly hatched nauplii of brine shrimps, *Artemia salina* were supplied to feed the larvae. The minced meat of clam with brine shrimps also supplemented to feed megalopa and 1st crab daily.

Everyday several numbers of larvae were preserved in 50% ethylene glycol solution for the identification of larval stages. The larvae were dissected under a binocular stereomicroscope. Drawings and measurements were performed with the aid of a profile projector and a dissecting microscope. At least 10 specimens of each stage were measured and dissected. Measurements were taken for the zoeal stages include the distance between the tips of dorsal and rostrum spines for total length (TL), from the base of rostral spine to the posterior margin of carapace for carapace length (CL) and maximum distance across the carapace for carapace width (CW). For the megalopa and 1st crab, distance between the tip of anterior margin to the posterior margin of carapace for CL and maximum distance across the carapace for CW. All measurements were taken following Konishi and Shikatani (1998). Specimens of all larval stages and 1st stage of *P. bidens* have been deposited in the Marine Science Laboratory of the University of the Ryukyus, Okinawa, Japan.

Results

The larvae of *P. bidens* hatched out of about 6.30 pm on 21 April'99 and reached to 1st crab stage after passing through 4 zoeal stages and one megalopa stage. Measurements of typical features are summarized in Table 1. Segmentation and setation of appendages of zoeae and megalopa are listed and compared with other species in Table 2 and 3, respectively. The major characteristics of each zoeal stages, megalopa stage and 1st crab stage are described in detail below.

Table 1. Measurements of morphological features of *Perisesarma bidens* larvae

Characters	Larval stages				Megalopa	1st crab
	ZI	ZII	ZIII	ZIV		
TL (mm)	0.78±0.05	0.95±0.02	1.08±0.11	1.39±0.13		
CL (mm)	0.45±0.07	0.51±0.02	0.62±0.05	0.64±0.01	0.95±0.01	1.85±0.04
CW (mm)	0.32±0.01	0.37±0.03	0.42±0.01	0.46±0.08	0.71±0.06	1.69±0.21
LD (day)	3.5±0.03	4.0±0.1	3.8±0.21	3.6±1.01	6.5±1.02	8.9±1.13

TL- total length, CL- carapace length, CW- carapace width, LD- larval duration.

Table 2. Distinguishing characters among the zoeae of *Perisesarma bidens*, *Sesarma guttatum**, *S. intermedia*** and *S. erythroductyla***

Stages and appendages	<i>P. bidens</i>	<i>S. guttatum</i>	<i>S. intermedia</i>	<i>S. erythroductyla</i>
Zoea I				
Maxillule: Setae on basal & coxal endites	6,5	5,6	5,5	5,5
Maxilla: Setae on basal and coxal endites	5+5, 3+5	5+3, 5+3	4+5, 3+5	4+5, 3+5
Zoea II				
Maxillule: Setae on basal & coxal endites	7,5	7,6	7,5	7,6
Maxilla: Setae on basal and coxal endites	5+5, 3+5	5+4, 5+3	4+5, 3+5	4+5, 3+5
Zoea III				
Maxillule: Setae on basal & coxal endites	7,7	7,6	7,5	7,6
Maxilla: Setae on basal and coxal endites	5+5, 3+5	5+5, 5+3	4+5, 3+5	5+5, 3+5
Setae on scaphognathite	12	11	11	12
Zoea IV				
Maxillule: Setae on basal & coxal endites	11,8	11,7	10,6	11,7
Maxilla: Setae on basal and coxal endites	5+6, 3+7	6+5, 7+4	5+5, 4+5	6+7, 4+5
Setae on scaphognathite	19	17	19	21

* Lago (1993), ** Terada (1976)

Table 3. Distinguishing characters (setal arrangement) among the megalopa of *Perisesarma bidens*, *Sesarma guttatum**, *S. intermedia*** and *S. erythroductyla***

Appendages	<i>P. bidens</i>	<i>S. guttatum</i>	<i>S. intermedia</i>	<i>S. erythroductyla</i>
Antenna				
Segments	8	8	9	8
Setae	10	13	13	7
Maxillule				
Endopod	7	6	6	6
Basal and coxal endites	15, 11	18, 11	18, 12	17, 12
Maxilla				
Endopod	0	3	0	5
Basal and coxal endites	12, 12	18, 15	12, 15	13, 12
Scaphognathite	32+2	36+2	35+2	29+2
1 st maxilliped				
Endopod	4	3	4	7
Exopod	3, 3	3, 3	3, 3	3, 4
Epipod	4	5	3	4
Basal and coxal endites	12, 9	11, 8	11, 7	9, 7
2 nd maxilliped				

Endopod	0, 1, 3, 6	0, 1, 4, 7	0, 1, 3, 7	0, 1, 5, 9
Exopod	1, 6	1, 7	1, 5	1, 7
3 rd maxilliped				
Endopod	9, 6, 3, 6, 9	8, 6, 2, 5, 7	9, 8, 4, 3, 7	8, 5, 3, 4, 6
Exopod	1, 3	1, 5	1, 5	1, 5
Epipod	9	24	15	12

* *Lago* (1993), ** *Terada* (1976)

Morphology of zoeal stages

Carapace (Fig. 1. A-D): Carapace smooth, inflated, no lateral spine, rostral spine relatively shorter than dorsal spine, which is all zoeal stages. Carapace increased in size in each moulting. Eyes sessile in zoea I but stalked or movable in zoeae II to IV.

Antennules (Fig. 2. A-D): Zoea I bear 3 equal size of broad flat terminal aesthetes. Zoeae II to III bear 4 broad flat terminal aesthetes and small seta. Zoeae IV has 4 broad flat terminal aesthetes and 3 small setae of which 2 were subterminal, small endopod bud appeared. Antennules also increased in size in each moulting.

Antennae (Fig. 2. E-H): Spinous process well developed, bearing 2 rows of denticles, exopod with 2 short setae in all zoeal stages. Endopod developed in zoea III, well developed and shorter than spinous process in zoea IV.

Mandibles (Fig. 2. I-L): Incisor and molar processes differentiated in zoea I, incisor processes with 4 teeth, molar process subcylindrical in zoea II, incisor processes with teeth on one side, unarmed on opposite, molar process denticulated in zoea III, incisor processes with 3 teeth on one side, masticatory surface of molar process gradually flattened, no palp in zoea IV.

Maxillules (Fig. 3. A-D): Endopod 2 segmented, distal segment with 4 terminal plus 1 subterminal hairy spine and 1 seta on inner of proximal segment which was constant in all zoeal stages. Basal and coxal endites of zoeae I to IV bear 6,5; 7,5; 7,7 and 11,8 hairy setae, respectively. One additional plumose seta was present at the base of endopod that was also constant in zoeae II to IV.

Maxillae (Fig. 3. E-H): Endopod unsegmented but bilobed with 3+2 hairy spines in all zoeal stages. Basal and coxal endites of zoeae I to IV also bilobed and bearing 5+5, 3+5; 5+5, 3+5; 5+5, 3+5 and 5+6, 3+7 hairy setae, respectively. Scaphognathite with 4 soft plumose setae on distal margin, apical process tapering with fine setae in distal half in zoea I, 5 soft plumose setae on distal margin, apical process flattened, distally rounded with 3 plumose setae in zoea II, 8 plumose setae on distal margin and 4 on apical process in zoea III, 19 long soft plumose setae in zoea IV.

1st maxillipeds (Fig. 4. A-D): Basis with 10 medial setae in all zoeal stages. Endopod 5 segmented with 2, 2, 1, 2, 5 setae in zoea I to II, 2, 2, 2, 2, 5 in zoea III and 2, 3, 2, 2, 5 in zoea IV from proximal to distal segments. Endopod 2 segmented, distal segment with 4, 6, 8 and 10 plumose natatory hairs in zoeae I to IV, respectively.

2nd maxillipeds (Fig. 4. E-H): Basis with 4 medial setae in all zoeal stages. Endopod 3 segmented with 0, 1, 6 setae in all zoea stages. Endopod 2 segmented, distal segment with 4, 6, 8 and 10 plumose natatory hairs in zoeae I to IV, respectively. Small but segmented 3rd maxilliped (Fig. 5.I) bud appeared in zoeae IV.

Pereiopods (Fig. 1. C-E): Present as small bud in zoea III, elongated and segmented in zoeae IV.

Abdomens and telsons (Fig. 5. A-D): Five somites plus telson in zoeae I and II, while 6 somites plus telson in zoeae III and IV. Somites 2 and 3 with a pair of spines on dorsolateral margins, former directed anteriorly and the latter posteriorly, posterolateral margin on somites 2 to 5 produced moderately in all zoeal stages. One pair of lateral spines presents on 2 to 5 somites in each stage. Telson bifurcated, each fork moderately widened, slightly longer than basal portion, bearing minute hairs on inner margins, posterior margin with 3 pairs of setae. Somites 2 and 5 with posterolateral pleopod buds in zoea III, pleopods well developed but unsegmented in zoea IV, Somites 6 with buds of uropods in zoeae III and IV. Structure of telson unchanged in all zoeal stages.

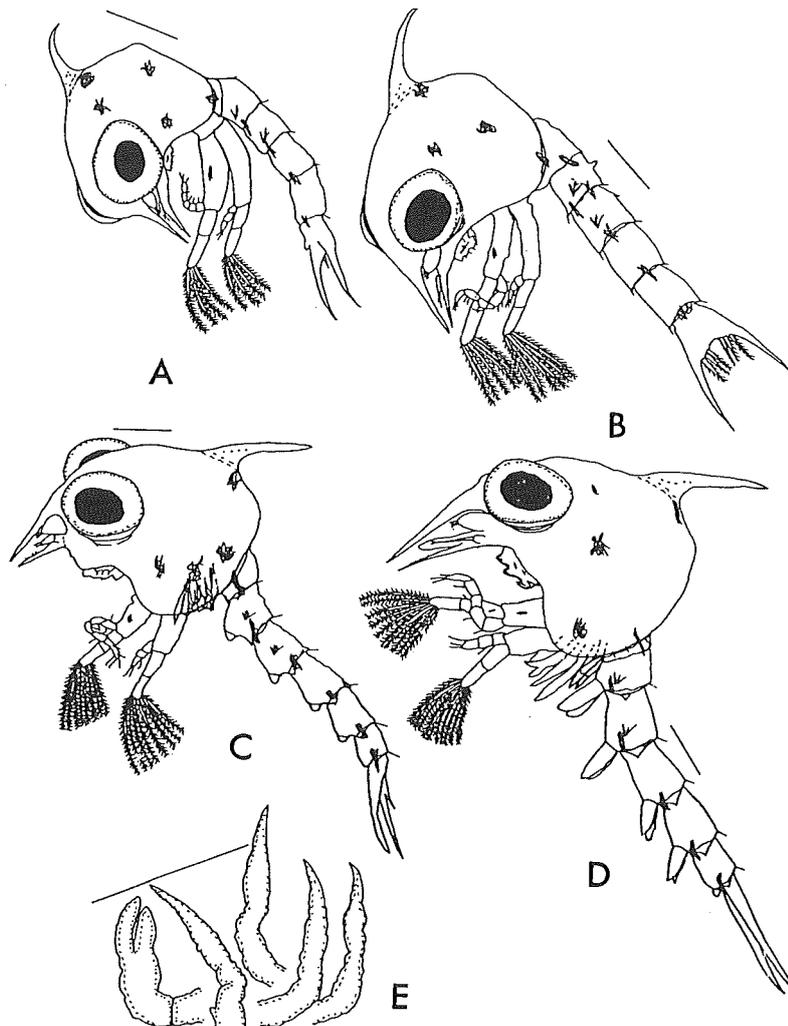


Fig. 1. *Perisesarma bidens* (De Haan). Zoeal stages: A- zoea I; B- zoea II; C- zoea III; D- zoea IV; E- pereiopods rudiment of zoea IV (scale bars= 0.2 mm).

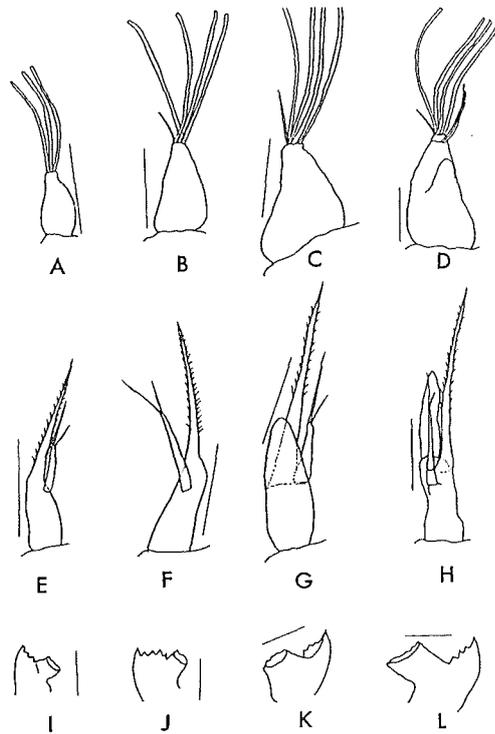


Fig. 2. *Perisesarma bidens* (De Haan). Antennules: A-D, zoea I-IV; Antennae: E-H: zoeae I-IV; Mandibles: I-L, zoeae I-IV (scale bar= 0.1 mm).

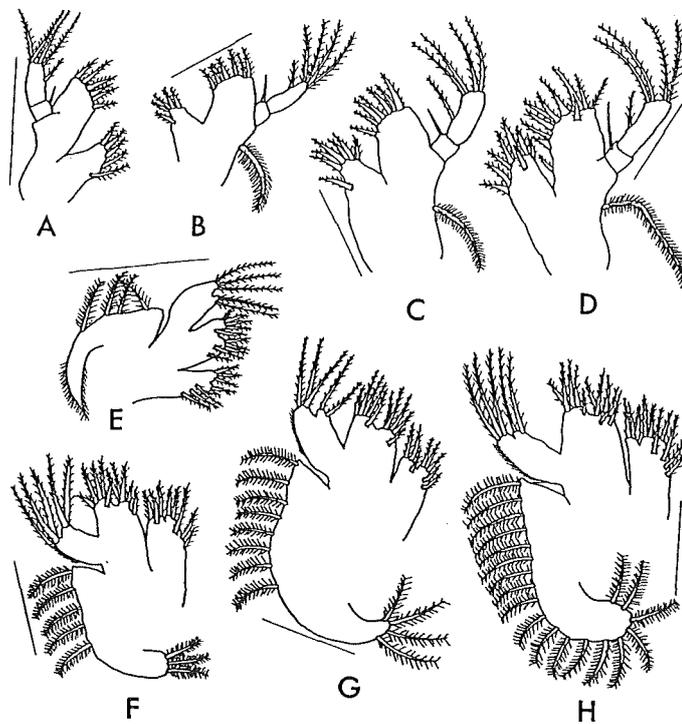


Fig. 3. *Perisesarma bidens* (De Haan). Maxillules: A-D, zoeae I-IV; Maxillae: E-H, zoeae I-IV (scale bar= 0.1 mm).

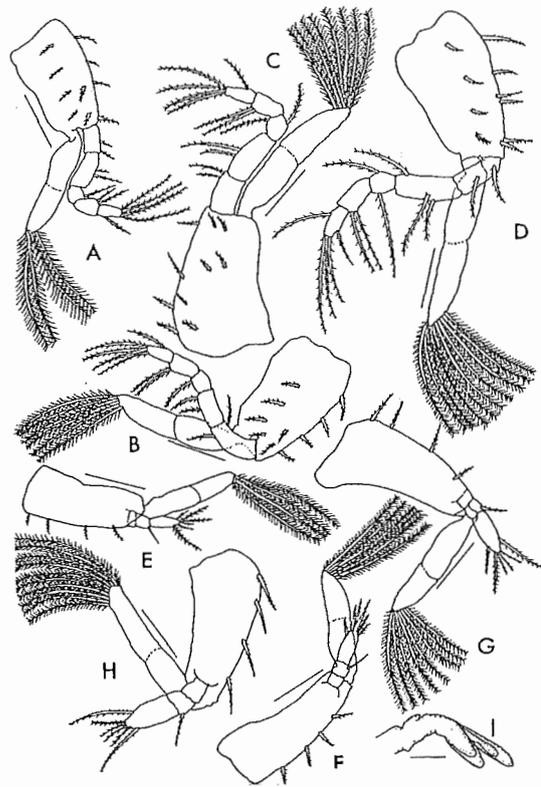


Fig. 4. *Perisesarma bidens* (De Haan). 1st maxillipeds: A-D, zoeae I-IV; 2nd maxillipeds: E-H, zoeae I-IV; 3rd maxilliped bud: I, zoea IV (scale bar = 0.1 mm).

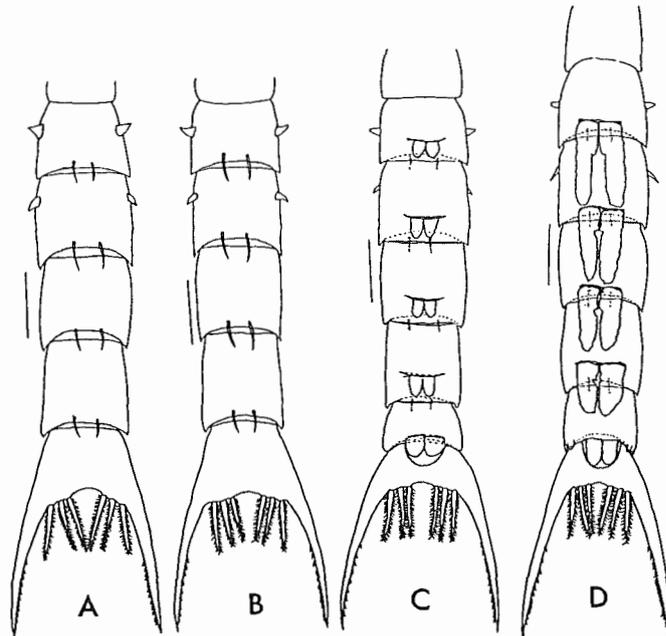


Fig. 5. *Perisesarma bidens* (De Haan). Abdomens: A-B, dorsal view of zoeae I-II; C-D, ventral view of zoeae III-IV (scale bar = 0.1 mm).

Morphology of megalopa

Carapace (Fig. 6.A): Dorsal surfaces smooth, longer than broad, eyes large and stalked.

Antennule (Fig. 6.B): Enlarged base with out seta. Peduncle 2 segmented inner flagellum absent, outer flagellum with 8 aesthetascs and 3 short setae.

Antenna (Fig. 6.C): Peduncle 3 segmented with 0, 1, 1, 5, 2 setae.

Mandible (Fig. 6.D): Cutting edge rounded, palp 2 segmented distal segment with 5 short setae.

Maxillule (Fig. 6.E): Endopod unsegmented, bearing 3 terminal, 3 marginal and 1 lateral setae. Basal and coxal endites with 16 and 11 setae, respectively. Basis with 1 long simple seta.

Maxilla (Fig. 6.F): Endopod simple with out seta. Basal and coxal endites bilobed with 5+7 and 5+10, respectively. Scaphognathite with 30 plumose setae on marginal and 2 simple setae on blade surface.

1st maxilliped (Fig. 7.A): Endopod with 3 terminal and 1 subterminal setae, exopod 2 segmented with 3, 3 plumose setae, epipod with 4 long simple setae of moderate length. Basal and coxal endites with 12 and 9 setae, respectively.

2nd maxilliped (Fig. 7.B): Endopod 4 segmented with 0,1,3,6 setae, exopod 2 segmented with 1, 6 plumose setae, short epipod with 4 marginal setae.

3rd maxilliped (Fig. 7.C): Endopod 5 segmented with 9,6,3,6,9 setae, exopod 2 segmented with 1, 3 setae. Basis and coxa fused, bearing 4 hairy setae. Epipod elongated with 9 long plumose setae.

Pereiopods (Fig. 8.F-J): Cheliped of 1st pereiopod was subequal in shape and size, tooth with irregular cutting edge. Second to 4th pereiopods were similar in structure, dactylus tapering and slightly curved inwards with several setae on both surfaces. Dactyls of the 5th pereiopod with 2 long setae.

Abdomen and telson (Fig. 7.C): Six somites, posterolateral margins of each somite rounded, somites 2 to 6 with several setae on posterolateral posterodorsal margins. Functional pleopods (Fig. 8A-D) present on somites 2 to 4, endopod with 3 minute hooks, unsegmented exopod of pleopods 1 to 4 bearing 13,13,13 and 11 plumose natatory setae, respectively. Uropods (Fig. 8E) segmented, bearing 6 natatory plumose setae on distal and 1 on proximal segment.

Morphology of 1st crab

Carapace (Fig. 9A): Carapace as long as broad, dorsal surface unsmooth, narrowing anteriorly, eyes large and movable, antenna situated out side of orbit.

Antennule (Fig. 9B): Enlarged basal segment with 9 marginal and 10 lateral setae. peduncle 2 segmented, basal segment 2 setae, inner flagellum absent, outer flagellum with 3 aesthetascs and 1 seta.

Antenna (Fig. 9C): Peduncle 3 segmented with 1, 4, 3 setae, flagellum 5 segmented with 2, 2, 3, 6, 2 setae.

Mandible (Fig. 9D): Cutting edge sharp and almost straight, palp 3 segmented with 3, 4, 15 setae.

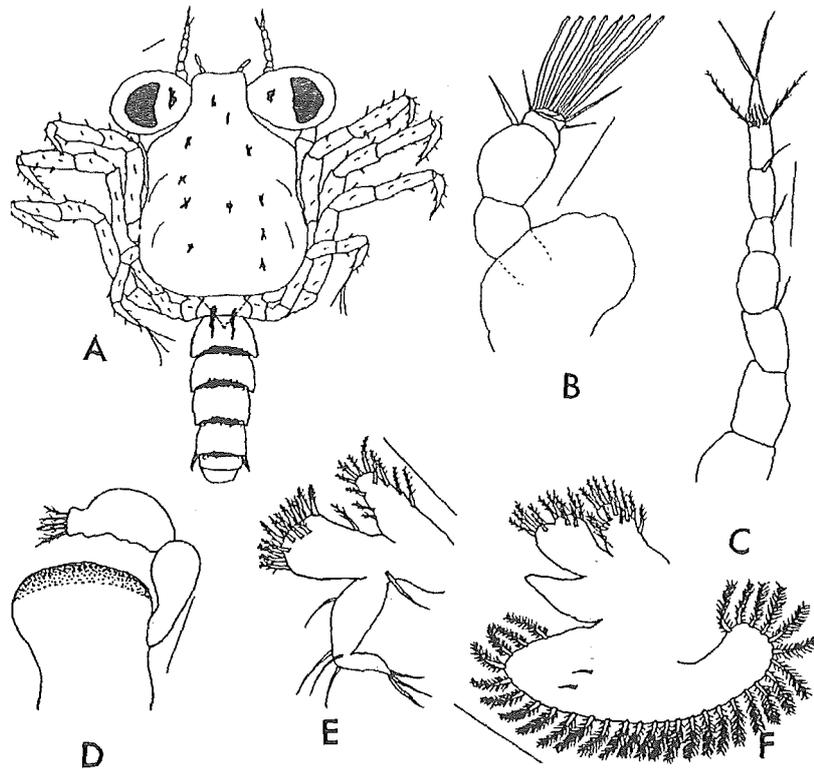


Fig. 6. *Perisesarma bidens* (De Haan). Megalopa: A- dorsal view; B- antennule; C- antenna; D- mandible; E- maxillule; F- maxilla (scale bar= 0.1 mm).

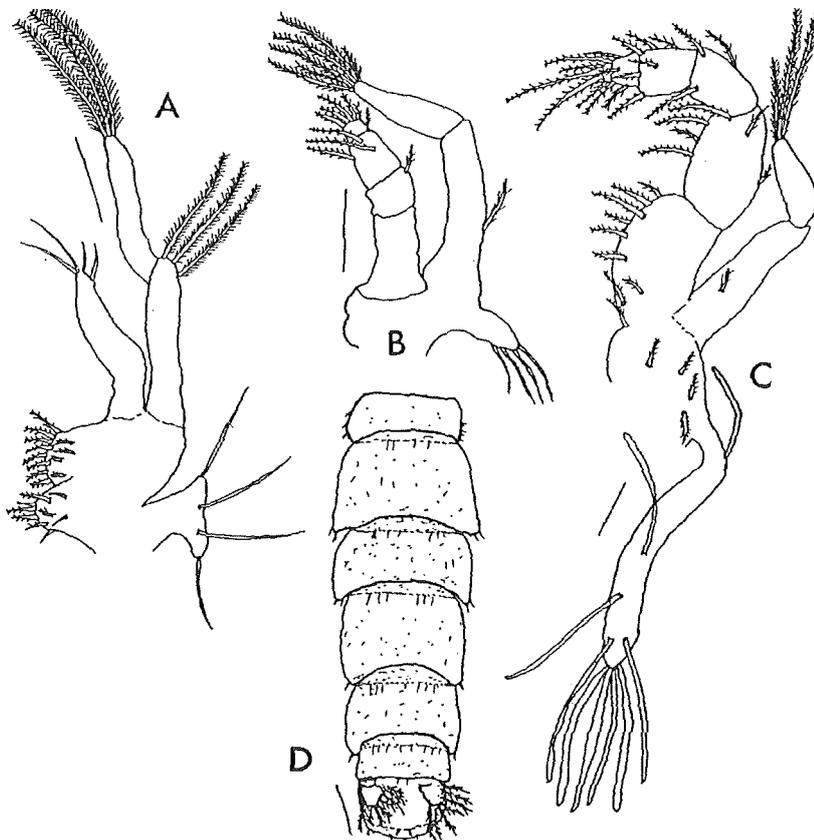


Fig. 7. *Perisesarma bidens* (De Haan). Megalopa: A- 1st maxilliped; B- 2nd maxilliped; C- 3rd maxilliped; D- abdomen (dorsal view) (scale bar= 0.1 mm).

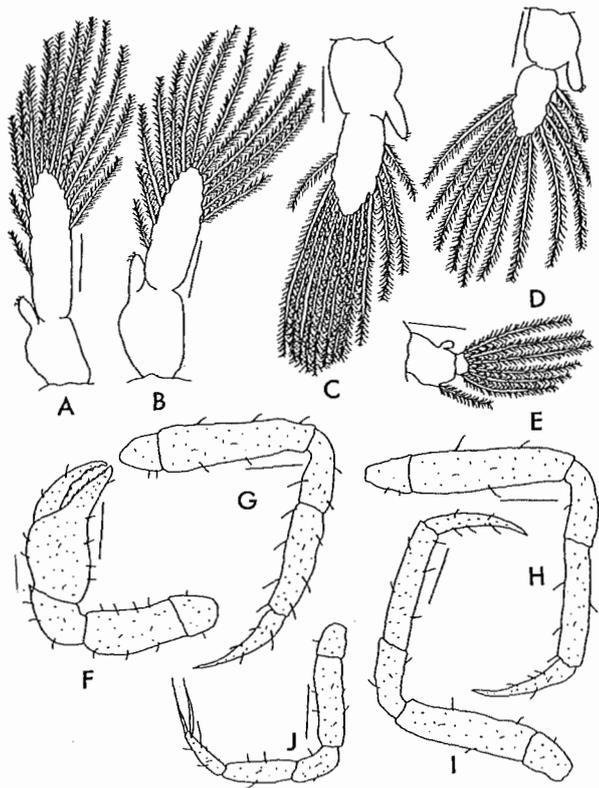


Fig. 8. *Perisesarma bidens* (De Haan). Megalopa: A-D: 1st-4th pleopods; E- uropod; F-J: 1st-5th pereopods (scale bar= 0.1 mm).

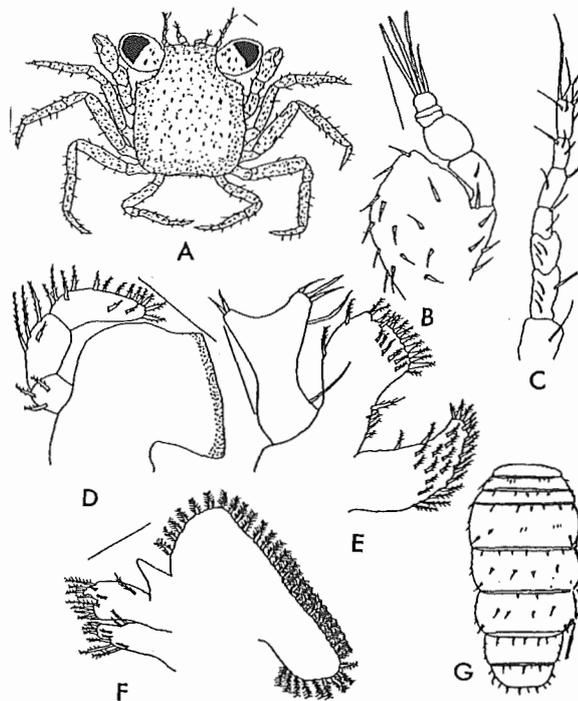


Fig. 9. *Perisesarma bidens* (De Haan). 1st crab: A- dorsal view; B- antennule; C- antenna; D- mandible; E- maxillule; F- maxilla; G- dorsal view of abdomen (scale bar= 0.2 mm).

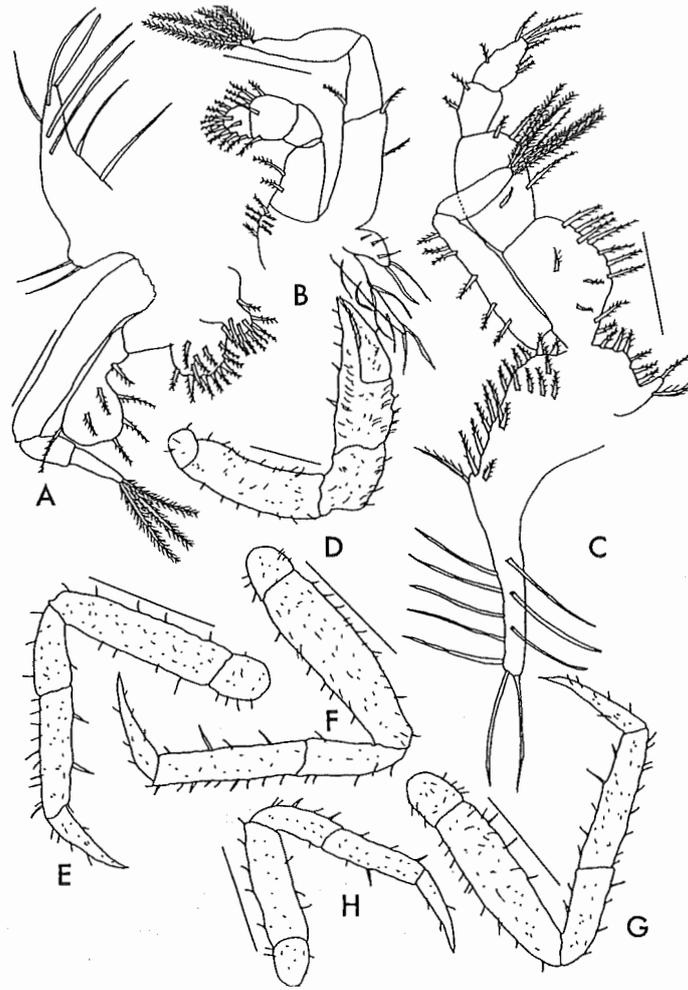


Fig. 10. *Perisesarma bidens* (De Haan). 1st crab: A- 1st maxilliped; B- 2nd maxilliped; C- 3rd maxilliped; D-H: 1st–5th pereopods (scale bar= 0.2 mm).

Maxillule (Fig. 9E): Endopod unsegmented, Y shaped, bearing 3 plumose and 4 simple setae no margin. Basal and coxal endites with 27 and 28 setae.

Maxilla (Fig. 9F): Endopod simple without seta. Basal and coxal endites bilobed with 5+6 and 8+4, respectively. Scaphognathite with 38 hairy setae on margin.

1st maxillipeda (Fig. 10A): Endopod triangular in shape with 5 marginal and 2 lateral setae, exopod 3 segmented, distal segment with long plumose setae, epipod elongated with 9 long plumose setae of moderate length. Basal and coxal endites bilobed with 13 and 9 setae, respectively.

2nd maxilliped (Fig. 10B): Endopod 4 segmented with 2,0,5,10 setae, exopod 3 segmented with 2,1,4 plumose setae, epipod bilobed with 5+7 naked setae. Basis and coxa fused with 7 setae.

3rd maxilliped (Fig. 10C): Endopod wider than in megalopa. Exopod and epipod similar to those of megalopa, but setation of exopod and epipod more complex than in megalopa.

Pereopods (Fig. 10D-H): Chelipeds equal in size with numerous setae, 2nd to 4th pereopods similar in structure, pointed, nearly equal to propodus in length, 3rd pereopod largest, 5th one smallest.

Abdomen and telson (Fig. 9G): Six somites, each somite with several setae on dorsal on surface and lateral margin of telson round with numerous setae. Pleopods and uropods degenerated.

Discussion

The characteristics which are useful for the identifying *Perisesarma bidens* larvae include: the absence of lateral spine on the carapace, the setation patterns of the antennule and the basal and coxal endites of the maxillule and maxilla, the segmentation and setation on the exopods of maxillipeds and the presence of dorsomedian setae on the abdominal segments (Table 2). The following characters that were constant through all the zoeal stages of *P. bidens*, found during the experimental period: a) absent of lateral spine on the carapace, b) the patterns of setae on the endopod of maxillule were 1,5; the protopod of 1st maxilliped were 2, 2,3,3; the same of 2nd maxilliped were 1,1,1,5; the endopod of 2nd maxilliped were 0,1,6; c) the telson belong to A₀ type (Aikawa 1937).

The characters which undergo changes in the development progresses, the following were common to all the specimens examined: a) in the zoea stage I, antenna has rudiment endopod, b) in zoea stage II, a plumose setae appears on the basis of the maxillule to persist through subsequent stages, c) the endopod, basal and coxal endites on the maxilla were bilobed in all zoeal stages, d) the 1st maxillule has setae as 2-2-1-2-5 on the endopod in first two stages, e) natatory setae on the endopod of the 1st and 2nd maxillipeds increase in their number after a formula of 2X (S+1+, where S is the ordinal number of zoeal stages, f) the endopod rudiment of antenna becomes distinct in the final stage, g) plumose seta on the scaphognathite of maxilla increase with the stages.

In order to identify brachyuran zoeae, Aikawa (1929, 1937) proposed the following characters: a) grouping of chromatophores, b) character of the telson, including its armature, c) character of the 2nd antenna, d) presence or absence of spines on the carapace. According to these criteria, the character of the zoeae of *P. bidens* may be summarized as follows: a) chromatophores of dark brown color present on 2nd to 6th abdominal segments, the protopodite of 1st maxilliped, carapace and mandible; d) telson was A₀ type; e) second antenna was B₂ type and d) rostral and dorsal spines present on the carapace but absent in lateral spine.

In order to clarify the specific difference of the larvae of *P. bidens*, some comparisons have been made among the species of some sesarmid crabs, and the information related to the larval development on the basis of the previous studies and the present research are compiled in Table 2. The number of zoeal stages comprised in entire course of development differs according to species, this being 4 in *P. bidens*, and 5 in other three species when compared (Table 2). There were 10 setae on the basal endites of zoea I of *P. bidens*, while 8 in *S. guttatum* (Lago 1993), 9 in *S. intermedia* and *S. erythroductyla* (Terada 1976). Differences also observed in the patterns of plumose setae on the scaphognathite of maxilla of zoeae III and IV stages (Table 2).

Generic differences in the characters of megalopa of *P. bidens* are compared with other species (Table 3). No remarkable differences were noted among the other three

species of sesarmid crabs, little variation was found in the setation of some appendages: endopod of maxillule bear 7 setae in *P. bidens* while 6 in other three species (Table 3). In maxilla, basal and coxal endites bears 12+12 setae *P. bidens*, 18+15 in *S. guttatum*, 12+15 in *S. intermedia* and 13+12 in *S. erythroductyla*, respectively. Differences also observed among these four species when compared in the setal arrangement on the basal and coxal endites of 1st maxillipeds, the endopods of 2nd maxillipeds, and the epipod of 3rd maxilliped (Table 3).

There is no available information related to the development through 1st crab of *S. guttatum*, *S. intermedia* and *S. erythroductyl*. The carapace length of 1st crab of *P. bidens* always larger than the other species of sesarmid crabs including *Helice formosensis* (Mia and Shokita 1997), *Helice leachi* (Mia and Shokita 1996) and *Helice Japonica* (Baba and Moriyama 1972) when compared.

References

- Aikawa, H, 1929. On larval forms of some brachyura. Records of Oceanographic Works of Japan, 2; 17- 55.
- Aikawa, H, 1937. Further notes on brachyuran larva. Records of Oceanographic Works of Japan, 9; 87- 162.
- Aiyun, D and Y. Siliang, 1991. Crabs of the China seas. China Ocean press, Beijing, China. 682 pp.
- Baba, K. and Y. Fukuda, 1972. Larval development of *Chasmagnathus convexus* De Haan (Crustacea, Brachyura) reared in the laboratory. Memory of the Faculty of Education, Kumamoto University, Japan, 21: 90-96.
- Baba, K. and K. Miyata, 1971. Larval development of *Sesarma (Holometopus) dehaani* H. milne Edwards (Crustacea, Brachyura) reared in the laboratory. Memory of the Faculty of Education, Kumamoto University, Japan, 19: 54-64.
- Baba, K. and M. Moriyama, 1972. Larval development of *Helice tridens wuana* Rathbun and *Helice tridens tridens* de Haan (Crustacea, Brachyura) reared in the laboratory. Memory of the Faculty of Education, Kumamoto University, Japan, 20(1): 49-68.
- Cuesta, J.A., M. Schuh, R. Diesel and C.D. Schubart, 1999. Abbreviated development of *Armass miersii* (Grapsidae: Sesarminae), a crab that breeds in supralittoral rock pools. *J. Crustacen Biol.*, 19(1): 26-41.
- Hartnoll, R.G. 1988. Evolution, systematics, and geographical distribution. In: Biology of the land crabs (eds. W.W Burggren and B.R. McMahon). Cambridge University Press. 654 pp.
- Konishi, K. and N. Shikatani, 1998. Identification manual for larvae of commercially important crabs in Japan. I. Practical techniques for observation in identification of larvae. Bulletin of National Research Institute of Aquaculture, 27: 13- 26.
- Lago, R.P. 1993. Larval development of *Sesarma guttatum* A, Milne Edwards (Decapoda: Brachyura: Grapsidae) reared in the laboratory, with comments on larval generic and familial characters. *J. Crustacen Biol.*, 13 (4): 745-762.
- Mia, M.Y. and S. Shokita, 1996. Description of larval and juvenile stages of the grapsid crab *Helice leachi* Haan (Brachyura: Grapsidae) reared under laboratory conditions. *Crustacean Research*, 25: 104-120.

- Mia, M.Y. and S. Shokita, 1997. Larval development of a grapsid crab *Helice formosensis* Rathbun (Crustacea: Brachyura) reared in the laboratory. *Species Diversity*, 2 (1): 7-23.
- Miyake, S. 1983. Japanese Crustacean Decapods and Stomatopods in Color. Hoikusha Publishing. 182-183.
- Powers, L.W. and D.E. Bliss, 1983. Terrestrial adaptations. *In: The Biology of Crustacea*, 8 Environmental adaptations (eds. F.J. Verberg and W.B. Vernberg). Academic Press, Inc. Orlando, 271-333.
- Rabalais, N.N. and R.H. Gore, 1985. Abbreviated Development in Decapods. *In: Larval Growth* (ed. A. M. Wenner). A. A. Balkema, Rotterdam, Crustacean Issues, 2: 67-126.
- Sakai, T., 1976. Crabs of Japan and Adjacent Seas. Kodansha Ltd., Tokyo, Japan. 773pp.
- Terada, M., 1976. Comparison of the larval developments of nine crabs belonging to the subfamily Sesarminae. *Research on Crustacean*, 7: 138-169.
- Watanabe, S., 1993. Population dynamics and feeding habits of the sesarmid crab, *Perisesarma bidens* (De Haan) in Okinawa island. Master thesis in Marine Science, University of the Ryukyus, Japan. 30 pp.
- Zimmerman, T.L. and D.L. Felder, 1991. Reproductive ecology of an intertidal brachyuran crab, *Sesarma* sp. (nr. *Reticulatum*), from the Gulf of Mexico. *Biological Bulletin*, 181: 387-401.

(Manuscript received 16 September 1999)