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On the Early Post-larval Stages of Some Leucosiid Crabs from Tosa Bay, Japan (Decapoda: Brachyura, Leucosiidae)¹⁾

By

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(With 18 Text-figures and 5 Tables)

Introduction

Zoeal and megalopal stages of leucosiid species are important components of the meroplankton of Tosa Bay (Shikoku), and their seasonal occurrence comprises about 9 months (Yatsuzuka and Quintana, 1985). Although their ecological and phylogenetic value is apparent, our knowledge of larval and post-larval forms of this group is still deficient. Despite *ca.* 79 species of the family Leucosiidae inhabiting the Japanese waters (*see* Miyake, 1983), there are few descriptions of megalopal and early crab stages, which should improve our knowledge in this group.

Early reports on larvae of this group include those given by Lebour (1928a, b) on North-European leucosiid crabs *Ebalia cranchii* Leach (1st-4th zoeas and the megalopa) and *E. tuberosa* (Pennant) (prezoea, 1st-4th zoeas, megalopa and the first crab), and those given by Aikawa on leucosiid larvae from Japanese waters, *Philyra pisum* de Haan (first zoea) and *Ebalia* sp. (first zoea) (Aikawa, 1929), *Ebalia longipedata* Ortmann (first zoea) (Aikawa, 1937) and eleven indeterminate leucosiid zoeas under the group name of "*Leucozoea*" (Aikawa, 1933). Other works dealing with zoeal stages in this group include those given by Sankolli (1961) on the first zoeal stages of *Philyra corallicola* Alcock and *Arcania*

1) This paper was presented during the Second International Symposium on Indo-Pacific Marine Biology held at Guam, Marianas Islands, U.S.A., 22 June-9 July, 1986.

septemspinosa, and Hashmi (1968) on the zoeal stages of *Leucosia pubescens* (Miers) and *L. sima* (Alcock). The first zoeal stage of *Ebalia nux* A. Milne Edwards has been described by Rice (1980), and recently, Salman (1982) has given detailed descriptions on larvae of leucosiids from North-Europe, *Ebalia tuberosa* (Pennant), *E. tumefacta* (Montagu) and *E. cranchii* Leach.

After the Aikawa's pioneer works, the most important papers are those given by Terada (1979, 1984) who has provided valuable information on larvae of several leucosiids (eight species) normally found at Enshunada, off Shizuoka Prefecture, but unfortunately these reports seem to be not well known abroad. Recently, Quintana (1984) incorporated to this list, observations on the larvae of *Leucosia craniolaris* L.

Although adults of the crabs studied here are distinguishable from each other, the post-larval stages cannot be identified at present due to the lack of adequate descriptions or illustrations.

This paper gives the first descriptions of the zoeal and megalopal stages of leucosiids occurring in the Japanese waters, and secondarily, provides information on the early crab stages due to they are frequently omitted in the current literature. On the other hand, since no keys are available for identifying young crabs, it is essential to rear early crabs up to a recognizable stage; several important characters do not appear but after three or four subsequent molts (depending on the species), being very difficult to assign specific level by observing young crabs.

Materials and Methods

As part of a routinary study on planktonic brachyuran larval stages in the Tosa Bay and adjacent waters (Yatsuzuka and Quintana, 1985), the author could collect advanced zoeas and megalopas during the period May to December, 1983 and further, rear them separately and individually under laboratory conditions (28.5-29.7 °C temperature and 33.0-33.4 ppt salinity). Similarly, during the larval season 1983, an appreciable number of zoeas and megalopas of leucosiid species were collected and preserved in a formalin solution in seawater for further observations and comparison with laboratory-reared material. Cultures were carried out in several occasions during the larval season 1983 in order to get an appropriate variety and number of young crabs of several leucosiids. During rearing, zoeas were fed *A. salina* nauplii; food for megalopas and crab instars consisting in minced clams (*Tapes japonica*) or small polychaetes was incorporated into culture-flasks every night and removed every morning at the moment of water change. Due to warm season, water change and fresh food were done twice a day. No aeration neither antibiotic treatment were supplied to cultures. Individual series from the last zoeal stage up to crabs stages were preserved in a solution formalin-ethylene glycol in seawater, so that both complete specimens and some exuviae (previously stained with methylene blue) were used for dissections and illustration of appendages. The identification was possible using advanced crabs

stages, following to Sakai (1976) and Miyake (1983) and also comparing with the available literature. Thus, the specific name was assigned to the respective larvae obtained from a single series of cultures. All figures were made to scale with aid of camera lucida. Some ethylene glycol-preserved specimens were selected for SEM observations; after distilled water-rinsed, these were dehydrated through a graded ethanol series, dried by critical point method, and finally, attached to metal stubs and sputter-coated with gold. Observations were made in a JEOL, JSM-T20 at gun potential of 20 kV. Setation is referred here from proximal to distal.

Results

The leucosiid zoeal and megalopal stages collected from Tosa Bay and reared individually in several occasions are summarized in Table 1. The corporal size of the studied species is given in Table 2 for different stages. Since illustrations are auto-explanatory, only relevant features will be noted here. Details of setation of appendages for zoeas, megalopas and first crab stages are indicated in Tables 3-5

Table 1. Rearing data for the present material. Cultures were carried out during the period June-Nov. 1983. Z, last zoeal stage; M, megalopa; C, crab stages.

Species	Series obtained	rearing period	duration (days)
<i>N. laminata</i>	M — *	Jul. 25 — ND	ND
	Z — M	Aug. 5 — 11	6
	M — 1st C	Sept. 5 — 13	8
	M — *	Sept. 5 — Oct. 5	ND
<i>A. undecimspinosa</i>	M — 4th C	Aug 5 — Sept 1	27
<i>M. coalita</i>	Z — 1st C	Jun. 30 — Jul. 8	8
	Z — 1st C	Aug. 23 — Sept. 14	22
	M — 2nd C	Oct. 5 — 15	10
	Z — 3rd C	Oct. 5 — Nov. 13	39
<i>P. platycheira</i>	Z — 6th C	Jun. 30 — **	ND

* died without molting to the 1st crab stage; **, not recorded when the fourth crab molted to the fifth instar; ND, no data.

Table 2. Mean size (mm) of some post-larval stages of leucosiid species observed in this study. C.L., carapace length; C.W., carapace width. Numbers in parenthesis indicate number of specimens measured.

Species	Megalopa		1st crab		2nd crab		3rd crab	
	C.L.	C.W.	C.L.	C.W.	C.L.	C.W.	C.L.	C.W.
<i>N. laminata</i>	1.30 (3)	1.30	1.54 (2)	1.82	ND		ND	
<i>A. undecimspinosa</i>	1.50 (6)	1.49	1.72 (4)	1.75*	1.85 (3)	1.89	2.01 (1)	2.03
<i>M. coalita</i>	2.15 (4)	1.73	3.51 (4)	2.88	4.16 (2)	3.51	4.92 (1)	4.08
<i>P. platycheira</i>	1.10 (10)	0.83	1.35 (8)	1.30	1.50 (5)	1.47	1.66 (3)	1.62
<i>L. craniolaris</i>	1.80 (4)	1.97	2.10 (3)	2.00	3.00 (2)	2.70	4.60 (2)	4.00

* maximum width, including the lateral spines; ND, no data.

respectively.

***Nucia laminata* (Dofflein, 1904)**

(Japanese name; Birohdo-kobushi)

(Figs. 1-4, 17)

Last zoeal stage

Minute larva (C.L. 1. 10 mm), carapace with rostral and dorsal spines similar in length (Fig. 1-A), well developed, measuring *ca* 4.8 mm from tip to tip of spines, and 2 shorter lateral spines.

Abdomen (Fig. 1, E-F): Typically leucosiid, with small lateral knobs on segments 2 and 3, and a broadly triangular *telson* with 6 medial setae on posterior margin and an acute minute spine on outermost angle (Fig. 1-e); first abdominal segment dorsally with 10 setae; pleopods on the segments 2-5 each one with rudimentary endopod. Rudiments of thoracic appendages visible laterally beneath carapace.

Antennule (Fig. 2-A): Conical, with aesthetascs not terminal but grouped in three tufts: the apical group bears 3 aesthetascs plus a fine seta; the mid one 3, and only one aesthetasc in the proximal group; a bud should correspond to the inner flagellum in the megalopal stage.

Antenna (Fig. 2-B): Very simple, unarmed and reduced in size.

Mandible (Fig. 2-E): Powerful, incisor process broad, with rounded teeth on cutting margin; molar process strong; no mandibular palp.

Maxillule (Fig. 2-H): With a single seta on marginal border of protopod.

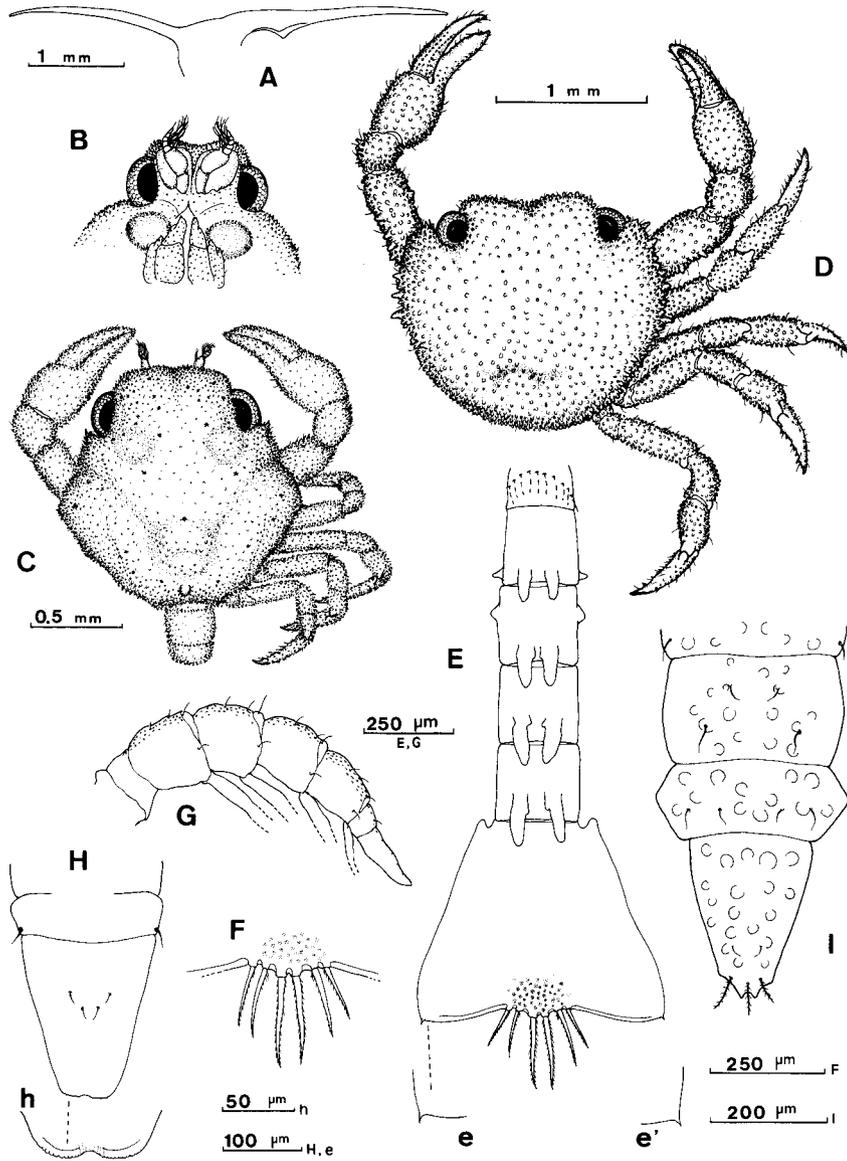


Fig. 1. *Nucia laminata* (Doflein). A, carapace (lateral view) of the last zoeal stage (lateral spines omitted); B, megalopa, epistome and frontal region, ventral view; C, megalopa, dorsal view; D, first crab, dorsal view; E, zoeal abdomen, ventral view; e, e', postero-lateral spine of telson; F, telsonal inner setae; G, abdomen of megalopa, lateral view (pleopods partially drawn); H, last abdominal segment and telson of megalopa, dorsal view; h, detail of posterior margin of telson; I, distal abdominal segments and telson of the first crab, dorsal view.

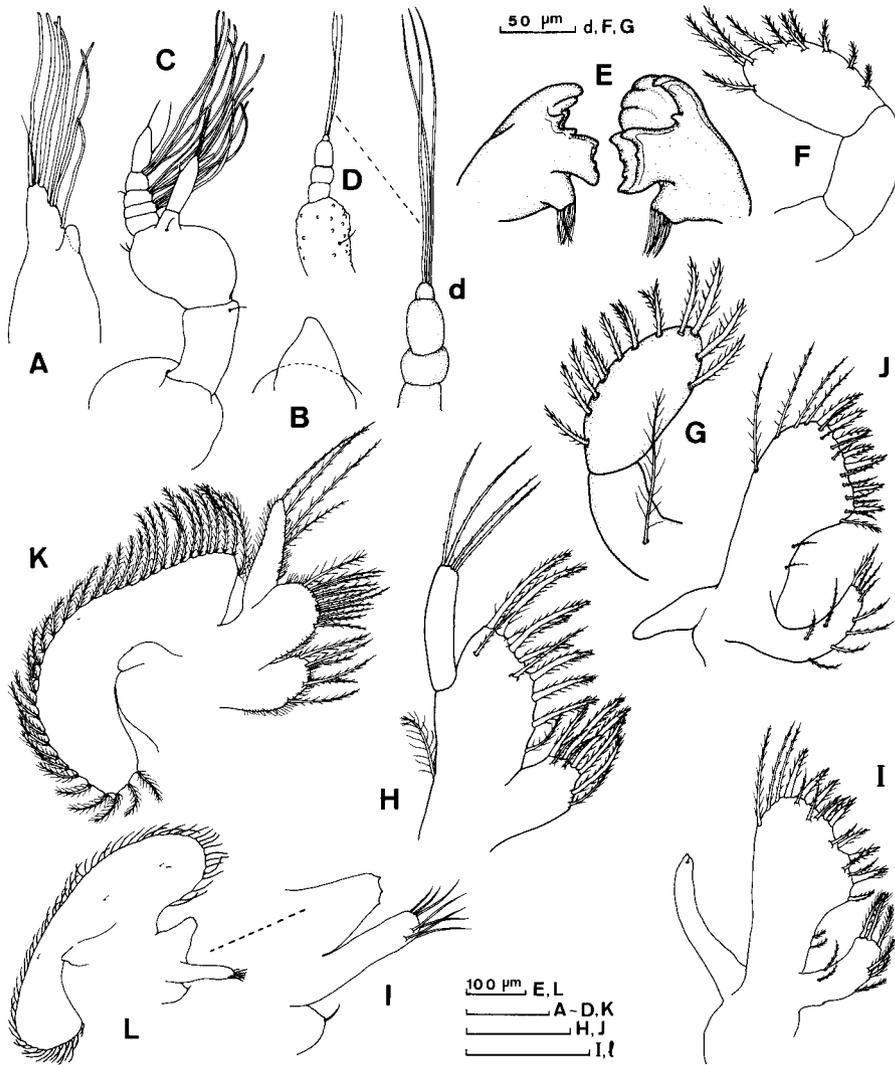


Fig. 2. *Nucia laminata* (Doflein). A, antennule of last zoeal stage; B, zoeal antenna; C, antennule of megalopa; D, antenna of megalopa; d, detail of peduncle and apical setae of antenna; E, mandibles of last zoeal stage; F, mandibular palp of megalopa; G, mandibular palp of first crab stage; H-J, maxillule of last zoea (H), megalopa (I) and first crab (J); K-L, maxilla of last zoea (K) and megalopa (L); 1, detail of inner endites. Scale bar = 100 μm, except for d, F, G.

Maxilla (Fig. 2-K): With basal and coxal endites broad, unilobed.

First maxilliped (Fig. 3-A): With endopod 5-segmented, longer exopod, with setal formula 2-2-1-2-4; protopod broad, with 8 marginal setae, arranged in 4 pairs.

Second maxilliped (Fig. 3-B): With endopod unsegmented, greatly reduced, with 3 setae.

Third maxilliped: Rudimentary, unsegmented (not drawn).

Megalopa

Body hard, globose, resembling a small crab in shape, hexagonal, as long as broad (Fig. 1-C). Carapace, chelipeds and pereopods uniformly covered with minute spinules and setae, except the abdomen which is almost glabrous (Fig. 1-G). Frontal area broad, subquadrate, inner orbital margins straight; branchial and cardiac regions moderately expanded; intestinal region with a small elevation. Eyes almost immerse and covered by carapace. In live specimens, two big, circular, greenish spots are close to orbits dorsally, and other two, ventrally, near the eyes, covered partially by exopod of third maxillipeds (Fig. 1-B). Chromatophores minute, star-shaped, yellowish-reddish, and abundant in frontal region and eye stalks. Ventrally, the sternum presents a deep abdominal groove in where the abdomen is folded beneath carapace, with some setae in anterior half, resembling this feature, the 1st crab condition. **Chelipeds** robust, moderate in size, shorter than carapace, similar in size and spinulation. All **pereopods** also similar, acute distally; propod-dactyl junction provided with a squamiform, rigid, smooth plate, partially imbricated (Fig. 3, H-K).

Antennule (Fig. 2-C): With 3-segmented peduncle; one and 3 setules on second and distal segments respectively. Inner flagellum unsegmented, with 3 apical, long setae and 2 subterminal, shorter setae. Outer flagellum apparently 5-segmented, with simple setae on third and apical segments; aesthetascs formula: 0-4-4-4-0.

Antenna (Fig. 2-D): With a hard peduncle, partially covered with minute spines, and provided with a medial plumodenticulate seta; flagellum with 4 short segments, glabrous, except the distal one, provided with 3 long, fine, simple setae, two times longer than flagellum.

Mandible: Now with a broadly triangular incisor plate (not drawn), margins unarmed; molar process almost absent; mandibular palp well-developed (Fig. 2-F), segmented, with 10 setae on outer margin of distal segment.

Maxillule (Fig. 2-I): Provided with a digitiform endopod, armed with a minute seta on tip.

Maxilla (Fig. 2-L): With endopod basally broad, unsegmented, and distal margin apparently irregular (Fig. 2-1); basal endite long, digitiform, with 7 fine setae distally; coxal endite reduced, with a minute setule; some minute setae on surface of scaphognathite.

First maxilliped (Fig. 3-E): With lanceolate endopod, fringed with 3 setae

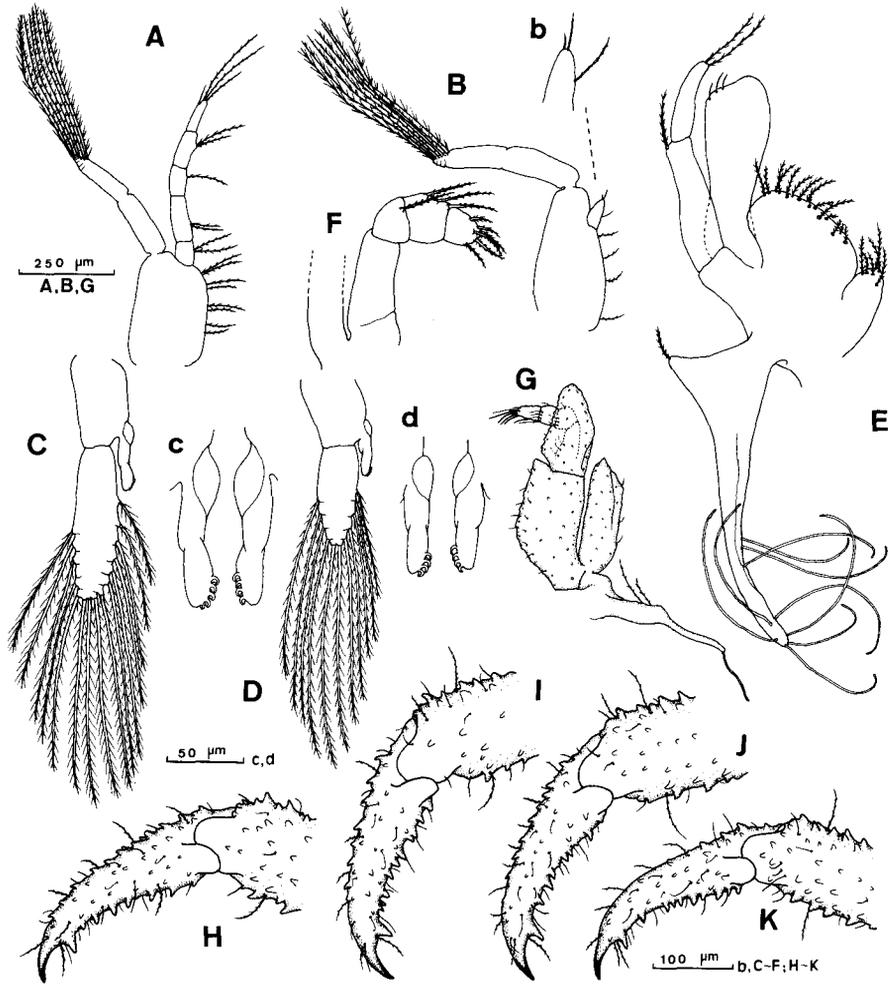


Fig. 3. *Nucia laminata* (Doflein). A-B, last zoeal stage, first (A) and second (B) maxillipeds; b, detail of endopod, second maxilliped; C-D, first (C) and last (D) pleopod of megalopa; c and d, endopod of first (c) and fourth (=last) (d) pair of megalopal pleopods; E-G, megalopa, first (E), second (F) and third maxilliped (G) of megalopa (exopod of second maxilliped not drawn); H-K, dactyli of pereopods 2-5 of megalopa, respectively.

on outer angle; exopod 2-segmented, longer than endopod, with one seta on proximal segment and 2 on distal segment; epipod well developed.

Second maxilliped (Fig. 3-F): With endopod 5-segmented, proximal segments fused, and setal formula 0-0-1-3-6; exopod 2-segmented, setose distally; no epipod.

Third maxilliped: Well calcified (Fig. 3-G), ischium and merus modified as rigid plates, sparsely covered with minute spinules; exopod is also a rigid plate, slightly longer than the broad ischium, and with 3 setae on outer margin; epipod slender, with 2 plumodenticulate setae on proximal portion and one simple seta distally.

Abdomen (Fig. 1-G): Subcylindrical, sparsely covered with minute spinules, setules on dorsal and lateral surfaces. In live specimens, the abdomen is folded in a deep ventral invagination in the sternum, and rarely is used for swimming as many other megalopas. Segments 2-5 with well-developed pleopods (Fig. 3, C-D); no uropods. Telsonal plate (Fig. 1-H) long, lateral margins unarmed, convergent, and posterior margin slightly concave (Fig. 1-h); 4 simple setae dorso-medially.

First crab

Carapace globose, semicircular in outline (Fig. 1-D), slightly broader than long. Carapace, chelipeds and pereiopods evenly covered with blunt spines and sparsely with short setae; tubercles are distributed randomly, and as revealed by

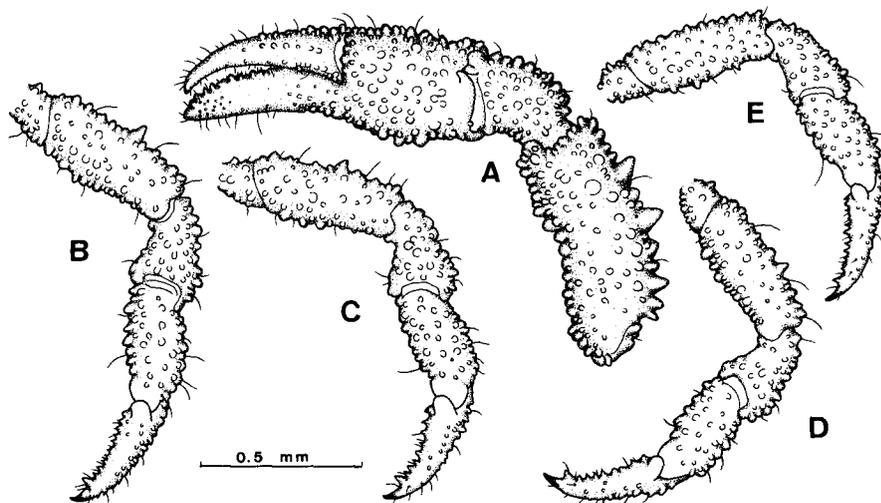


Fig. 4. *Nucia laminata* (Doflein), first crab. A, right cheliped; B-E, second to fifth pereiopods respectively.

SEM (Fig. 17, A-B), the bigger blunt spines are covered with smaller tubercles on the base, and minute granules on surface. Tubercles are bigger on the antero-lateral borders of carapace and outer surface of chelipedal merus; no big teeth along inner margin of fingers; immovable finger high, slightly longer than the movable finger; the latter with small tubercles, seemingly distributed in three longitudinal ridges.

Pereiopods: All similar, inner margin of each dactyl provided with sharp, stout spines; a subterminal acute spine is conspicuous (Fig. 4).

Abdomen (Fig. 1-I): Calcified, now dorso-ventrally flattened, sparsely covered with tubercles and setae; six abdominal segments, penultimate shorter than others, transverse.

Telson: Elongate, slightly triangular, posterior margin indented, with 3 plumodenticulate setae (Fig. 1-I); 2 setae dorsally on the distal one-third. Most of cephalic appendages have developed more setation, but basically, the morphological pattern does not differ markedly from the preceding megalopal stage.

Arcania undecimspinosa De Haan, 1841

(Japanese name: Jūichi-togekobushi)

(Figs. 5-7, 17)

Megalopa

Carapace slightly longer than broad (Fig. 5-A), narrowing anteriorly, globose, smooth, with a dorso-median elevation and another on cardiac region; rostrum broad, short, downwardly directed and produced medially; antero-lateral margins indistinctly serrated; gastro-hepatic regions slightly swollen. Surface of carapace covered with a very fine tomentum (not drawn in the megalopa) and very few setae, but some areas are smooth.

Chelipeds and **pereiopods** (Fig. 7, E-J): Covered with a fine tomentum and setae; **chelipeds** robust, similar in size, slightly longer than carapace length; merus with some blunt marginal teeth; fingers pointed terminally, as long as palm length, movable finger unarmed, rudimentary teeth are present on distal inner margin of immovable finger.

Pereiopods similar in shape and setation; dactyl acute distally, longer than merus, and with one minute spine on the distal portion with no tomentum.

Antennule (Fig. 6-A): With 3-segmented peduncle; proximal segment globose, finely tomentose, and covered with 7 long plumodenticulate setae; one minute seta distally on second segment, and 4 on distal segment, the outer longer. Inner flagellum unsegmented, distally with 4 simple setae and one short seta medially; outer flagellum 4-segmented, proximal segment unarmed, second, third and distal segments with 6, 6, and 4 aesthetascs respectively; penultimate segment with 2 outer setae, distal segment with 2 longer, plumodenticulate setae on distal portion.

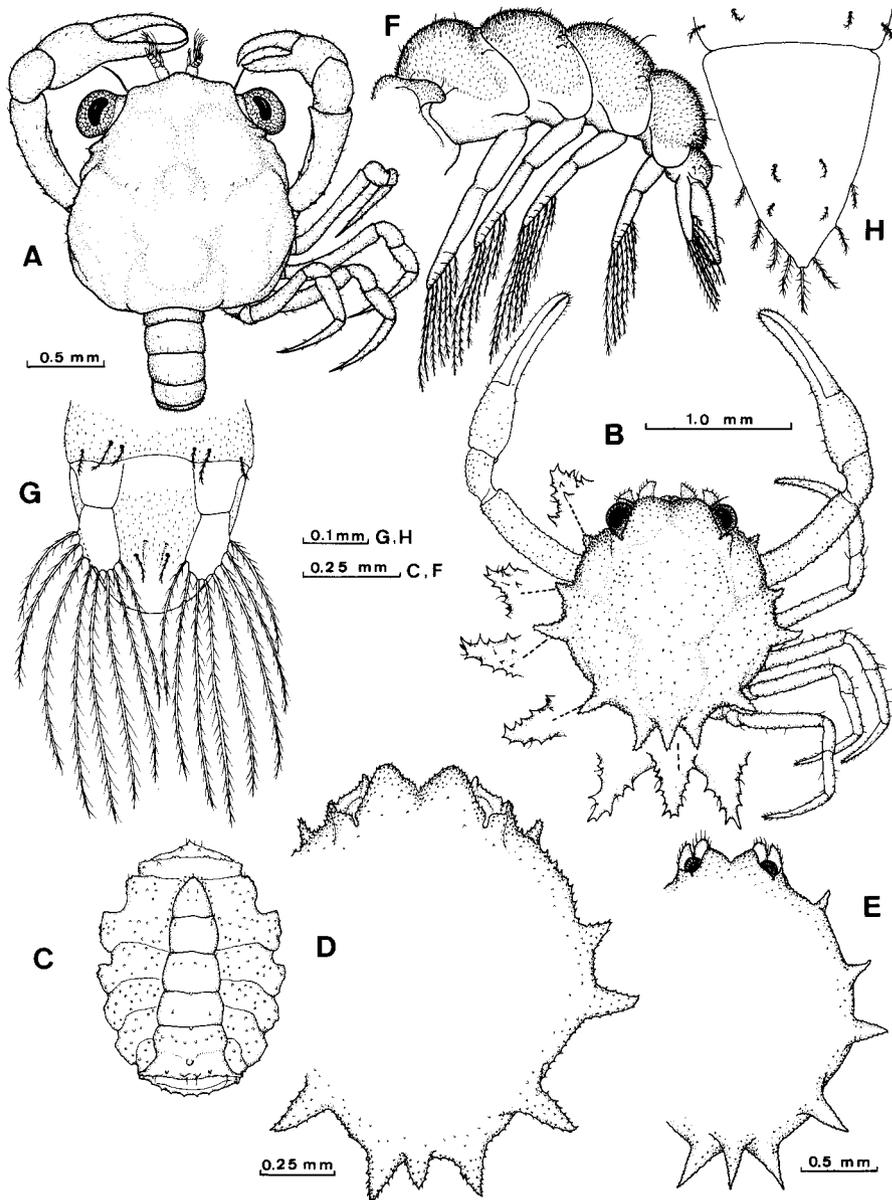


Fig. 5. *Arcania undecimspinosa* (De Haan). A, megalopa, dorsal view; B, first crab, dorsal view, with a detail of each marginal spinous process (left side); C, sternum and abdomen of first crab; D, outline of carapace of second crab; E, outline of carapace of fourth crab; F, abdomen of megalopa (complete), lateral view; G, uropods and telson of first crab; H, telson of the megalopa.

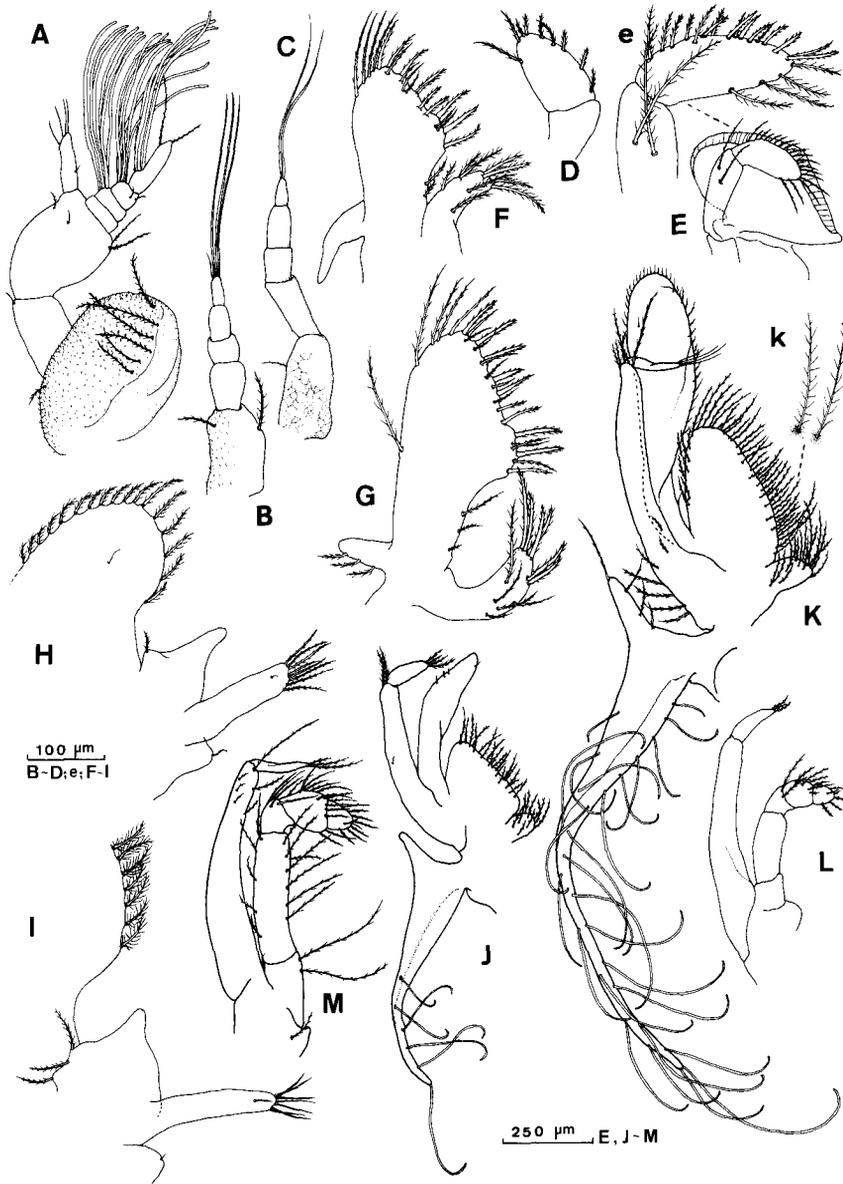


Fig. 6. *Arcania undecimspinosa* (De Haan). A, antennule of megalopa; B-C, antenna of megalopa (B) and of first crab (C); D, mandibular palp of megalopa; E, mandible of first crab; e, detail of mandibular palp, first crab; F-G, maxillule of megalopa (F) and of first crab (G); H-I, maxilla of megalopa (H) and first crab (I), scaphognathite partially drawn; J-K, first maxilliped of megalopa (J) and of first crab (K); k, detail of endites setation; L-M, second maxilliped of megalopa (L) and of first crab (M).

Antenna: 5-segmented (Fig. 6-B), proximal segment sparsely tomentose, with 2 distal setae; intermediate segments glabrous, distal segment with 3 very long and one short terminal setae.

Mandible (Fig. 6-D): With rigid triangular incisor plate, unarmed on margins (not drawn), palp apparently 2-segmented, well-developed, proximal segment unarmed, distal fringed with 9 setae.

Maxillule (Fig. 6-F): With unsegmented and unarmed endopod; coxal endite digitiform, downwardly curved.

Maxilla (Fig. 6-H): With endopod broad, with a single seta proximally; basal endite long, with 8 plumodenticulate setae on its truncate distal margin and one short subterminal seta; coxal endite reduced, with a single seta distally; scaphognathite setae longer on rounded distal margin.

First maxilliped (Fig. 6-J): With an oval endopod, fringed subapically with 3 short setae on outer margin and one on inner margin; basal and coxal endites with setation as indicated in Table 4; exopod long, 2-segmented, proximal segment with 2 moderately long setae on outer distal border, and one short seta medially; distal segment with 4 plumodenticulate setae; epipod long, triangular on base and curved on distal half.

Second maxilliped (Fig. 6-L): With a 5-segmented endopod, slightly shorter than basal segment of exopod, curved and setose on distal half as indicated in Table 4; distal segment of exopod with 3 terminal setae; no epipod.

Third maxilliped (Fig. 7-A): Well calcified, finely tomentose in some areas of external surface, except ischium; basis indistinctly demarcated from coxa; coxal segment tomentose, with 11 long plumodenticulate setae fringing the lower margin and 3 medially, on inner border; merus with outer margin expanded, fringed with 3 short setae, and one subterminal seta on the subacute tip; palp is connected internally to the median portion of merus; exopod is a rigid plate, pointed distally, longer than ischium, with plumodenticulate setae and small tubercles along outer margin; epipod slender, with 4 setae proximally and 2 long, simple setae distally.

Abdomen: Subcylindrical, dorsal and laterally tomentose (Fig. 5-F), with additional setae on surface; segments 2-5 armed ventrally with well-developed, paired pleopods, each with endopod invested with hooked short setae on inner distal border (Fig. 7, C-D); sixth segment shorter, with 3 setae near the base of uropods (Fig. 5-G), the latter with long, plumose setae, only in the distal segment.

Telson: Slightly long, oval, unarmed on margin, but with 2 setae, dorsal and ventrally on the tomentose median area.

First crab

Carapace globose, rounded in outline, slightly broader than long, covered dorsally with spinules, more abundant on frontal margin and outer hepatic regions. Margins of carapace armed with 11 spines (Fig. 5-B), nearly equal in size, the anterior two anterolateral spines slightly shorter; the median posterior

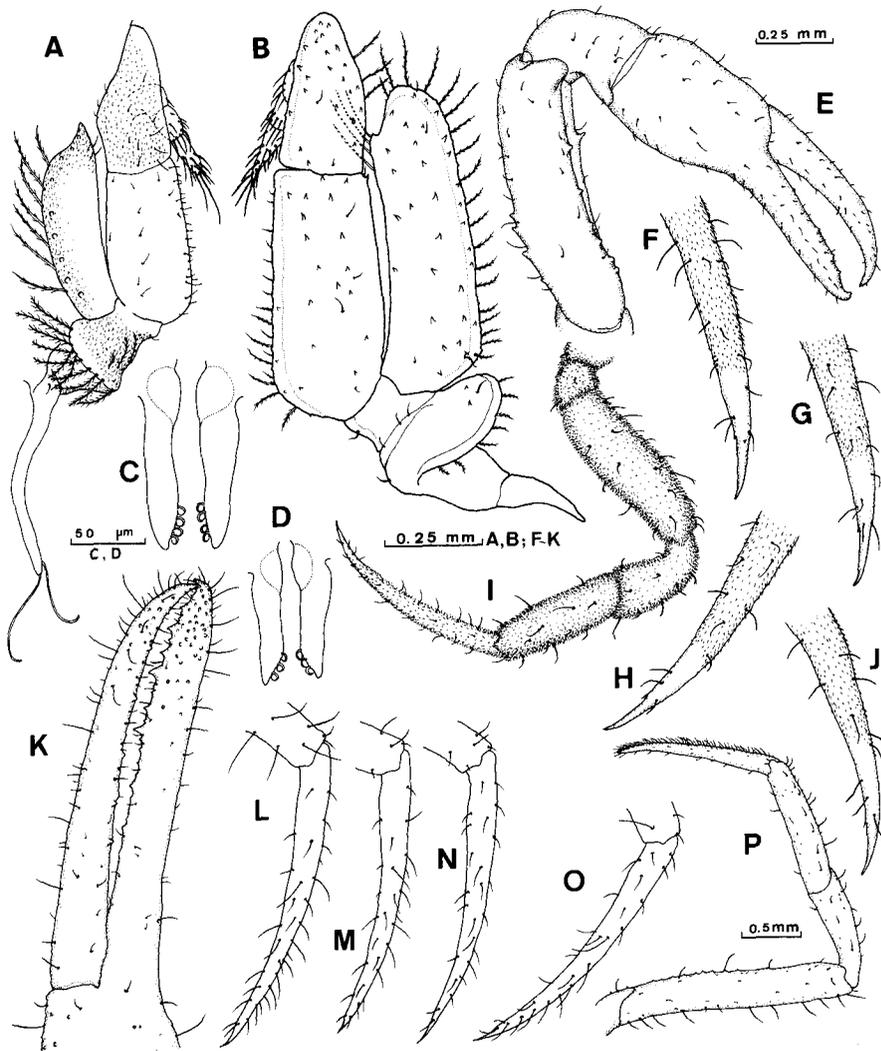


Fig. 7. *Arcania undecimspinosa* (De Haan). A-B, third maxilliped of megalopa (A) and of first crab (B); C-D, endopods of the first (C) and fourth (D) pair of megalopal pleopods; E-J, right cheliped (E) and dactyli (distal half) of pereopods 2 to 5 (F-H, J) of megalopa; I, fifth pereopod of megalopa, complete; K-O, left chela (K) (inner view) and dactyli of pereopods 2-5 (L-O) of the first crab; P, fifth pereopod (left) of the fourth crab.

spine emerges dorsally from the intestinal region; each of the eleven spines is irregularly pointed and covered with minute sharp spinules and sparse short setae. Frontal lobes broad, not produced beyond the orbits; external maxillipeds can be observed dorsally beyond the front.

Chelipeds (Fig. 7-K): Long, covered with spinules; merus as long as fingers; the latter slender, longer than palm, more setose distally; movable finger with few short teeth; inner margin of immovable finger dentate, with stout big and shorter teeth; some small granules distally, tip up-curved. *Pereiopods* 2-5 slender, sparsely spinulose (Fig. 7, L-O); dactyl acute distally, with setation as shown in figure.

Antennule (not drawn): Very similar, as in the megalopal stage, but aesthetascs have increased in number.

Antenna (Fig. 6-C) with distal article reduced to 2 long simple, terminal setae; setation of basal segment also reduced to one seta.

Mandible: Similar to previous stage in shape, but now with more numerous setae on distal segment of palp (Fig. 6-E); proximal segment armed subdistally with 2 long plumodenticulate setae, similar in length to the distal segment.

Maxillule (Fig. 6-G): Now with the unsegmented endopod shorter and fringed with 3 setae on inner margin.

Maxilla (Fig. 6-I): With 3 setae on outer proximal margin; although basal and coxal endites are similar in setation as in previous stage, the number of setae fringing the scaphognathite has increased markedly.

First maxilliped (Fig. 6-K): With endopod broadly oval, rounded anteriorly, fringed marginally with numerous short setae; basal and coxal endites now profusely setose; protopod with 7 setae on outer margin; proximal segment of exopod now with 3 moderately long and 2 long setae distally; epipod with 4 plumodenticulate setae on proximal margin; inward-curved portion now with about 26-27 long simple setae.

Second maxilliped (Fig. 6-M): Similar to that in previous stage, but now all segments setose, specially the basis and ischium of endopod.

Third maxilliped (Fig. 7-B): Now covered with short, stout spines and setae on surface; all segments fringed with numerous setae, specially the outer margin of exopod, now with *ca.* 20 setae; basis-coxa junction well demarcated now; epipod reduced to a short projection, unarmed, pointed distally.

Abdomen: Now dorso-ventrally flattened, with small tubercles and setae dorsally on each of the 6 segments (Fig. 5-C); proximal segment with lateral borders projected laterally; segments 2-5 with lateral borders convex; distal segment (Fig. 5-H) with lateral borders convergent, fringed with 8 setae, 4 shorter setae dorsally as indicated in figure; pleopods rudimentary (not drawn).

Second crab (Fig. 5D)

Subcircular in outline, with the same 11 external spines, each covered with spinules. Front progressively narrower, and lobes produced anteriorly.

Third crab (not drawn)

Not different in external features as in previous crab stages, but setation of appendages progressively more setose, and frontal notch deeper.

Fourth crab (Fig. 5E)

Similar to previous crab stages, front deeply grooved in the median line, extending anteriorly beyond the eyes. External maxillipeds are visible in dorsal view of carapace. Pereiopods 2-5 slender, sparsely setose in general, but more setose along outer margin of each dactyl; merus and ischium of fifth pereopod (Fig. 7-P) cristate on inner margin as shown in figure; this was already exhibited in the first crab stage.

Remarks: As observed by SEM (Fig. 17, C-D), the spinules covering the carapace are acutely pointed and curved distally.

Myra coalita Hilgendorf, 1978

(Japanese name: Hime-tenagakobushi)

(Figs. 8-11, 17, 18)

Last Zoeal stage

Carapace (C.L. 1.05 mm) with well-developed spines, rostral, dorsal and the two lateral spines long, similar in length (Fig. 8-A). Abdomen subcylindrical (Fig. 8, E-F), 5-segmented, with proximal segment setose dorsally, and segments 2-3 with lateral knobs; segments 2-5 ventrally with rudimentary, unsegmented pleopods. **Telson** broadly triangular, with outermost apices provided with a fine, acute seta; posterior border slightly concave, with 6 setae medially, the innermost longer (Fig. 8-G, g); very minute, fine dots are visible to high magnification in front of setae. Chelipeds and pereiopods rudimentary.

Antennule (Fig. 9-A): Conical, flagellum apparently 3-segmented, with 5 aesthetascs on penultimate and distal segments respectively; rudiment of endopod emerges near the base of proximal segment.

Antenna (Fig. 9-B): Simple, reduced, unarmed.

Mandible massive, powerful (Fig. 9-F), with incisor and molar processes armed with rounded teeth on margins; no rudiment of mandibular palp.

Maxillule (Fig. 9-I): With setation as indicated in Table 3, with the addition of a single plumodenticulate seta in the outer margin of protopod.

Maxilla (Fig. 9-L): With a very fine, short setule on margins of endopod and endites; setation as indicated in Table 3.

First maxilliped (Fig. 10-A): With a broad protopod, fringed with 8 denticulate setae on inner margin; setation of the 5-segmented endopod and the 2-segmented exopod as indicated in the figure.

Second maxilliped (Fig. 10-B): With 4 setae on inner margin of protopod;

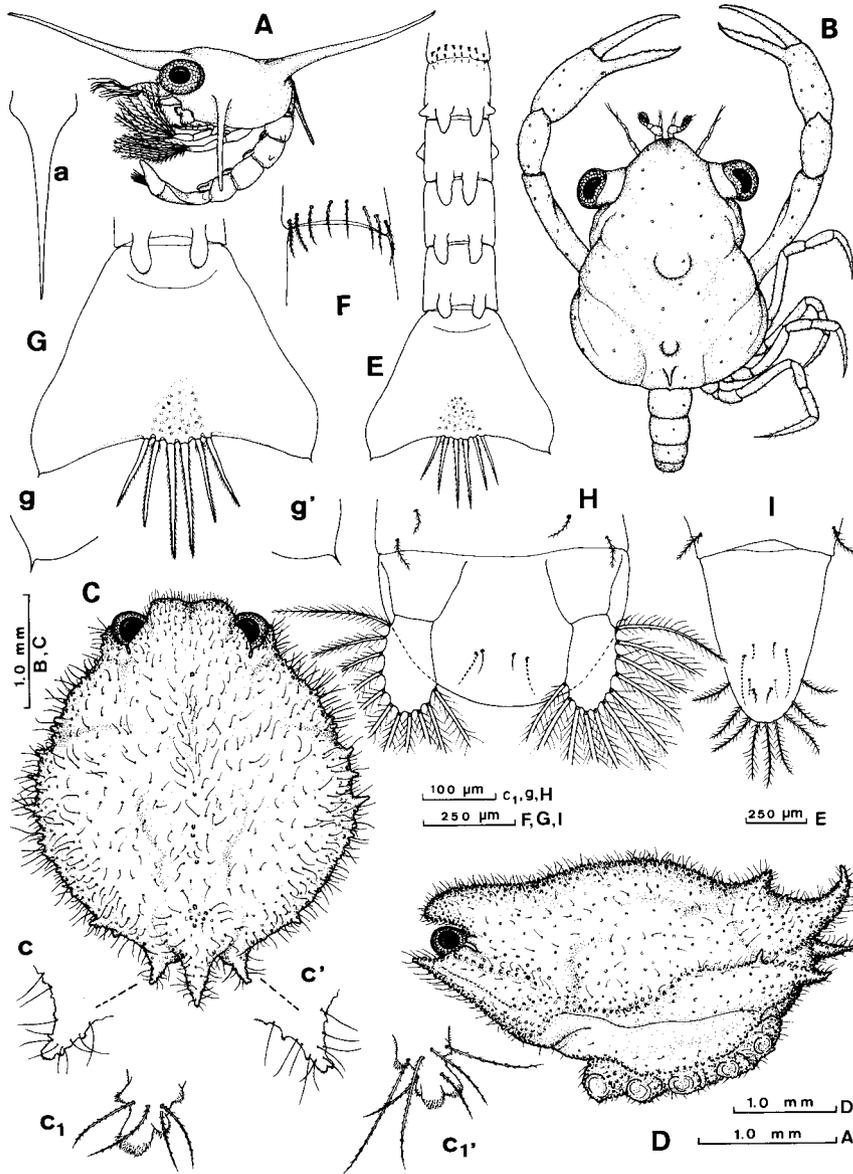


Fig. 8. *Myra coalita* Hilgendorf. A, last zoea, complete, lateral view; a, zoal rostral spine; B, megalopa, dorsal view; C, carapace of the first crab, dorsal view, and detail (c, c₁) of tips of posterior spines of carapace; D, second crab, lateral view; E, abdomen of last zoeal stage, ventral view; F, setation of the first abdominal somite, dorsal view; G, zoal telson and detail (g) of postero-lateral borders; H, uropods and telson of megalopa; I, telson of the first crab.

endopod very short, unsegmented, with 2 (occasionally 3) short terminal setae and one long subterminal seta, equal in length to the endopod; exopod apparently 2-segmented.

Third maxilliped rudimentary, unsegmented (not illustrated).

Megalopa

Carapace (Fig. 8-B) oval, posterior margin rounded, lateral margins convergent anteriorly; front broad, produced anteriorly beyond ocular stalks, frontal margin indistinctly notched medially; outer borders of both hepatic regions laterally expanded; dorsal elevations on gastric and cardiac regions; a posterior spine, backwardly directed emerges from intestinal region. Sternum with short protuberances and additional setae on sternites 2-4. In live specimens, the chelipedal carpus can be observed in dorsal view extending beyond the frontal margin, and also the last pereopods folded over the carapace, along a shallow groove on branchial regions, probably for grooming.

Chelipeds: Long, extended longitudinally are longer than carapace (Fig. 8-B); fingers longer than palm, downwardly curved, with rudimentary dentition on inner margin of immovable finger (Fig. 11-A), both fingers normally are crossed at tips when closed. **Pereopods 2-5** (Fig. 11, B-E) similar in shape and setation; dactyli acutely pointed.

Antennule (Fig. 9-C): With basal segment globose, with 7 setae on surface; outer flagellum 4-segmented, segments 2-4 with aesthetascs arranged in groups of 8, 6, and 3 respectively; distal segment with a short, apical, simple seta and a long subterminal seta, 3 simple setae on penultimate segment; inner flagellum unsegmented, with 6 setae in total.

Antenna (Fig. 9-D) with 7 articles, the basal with 2 setae subapically, none on segments 2-5, three on penultimate, and 4 terminal setae on distal segment, the longer equal to length of segments 2-4.

Mandible now with incisor process broadly triangular (Fig. 9-G), cutting edge sharp, unarmed; molar process greatly reduced, rudimentary; palp 2-segmented, curved, with setae only on distal segment.

Maxillule (Fig. 9-J): With coxal endite broad, with 23 setae, but occasionally 21 setae; a single seta on outer margin, in front of basal endite. Apparently no endopod was observed in this appendage, but after observation of subsequent stages, an endopod is more likely to be present.

Maxilla (Fig. 9-M): With one seta on base of broad endopod, and apically on reduced coxal endite; setation of basal endite and expanded scaphognathite as indicated in Table 4.

First maxilliped (Fig. 10-C): With endopod expanded anteriorly, with 6 setae on rounded apical margin; setation of endites as indicated in Table 4; exopod 2-segmented, with 2 setae on the long proximal segment, and 2 terminal setae on distal segment; epipod slender distally, triangular base armed with a single seta.

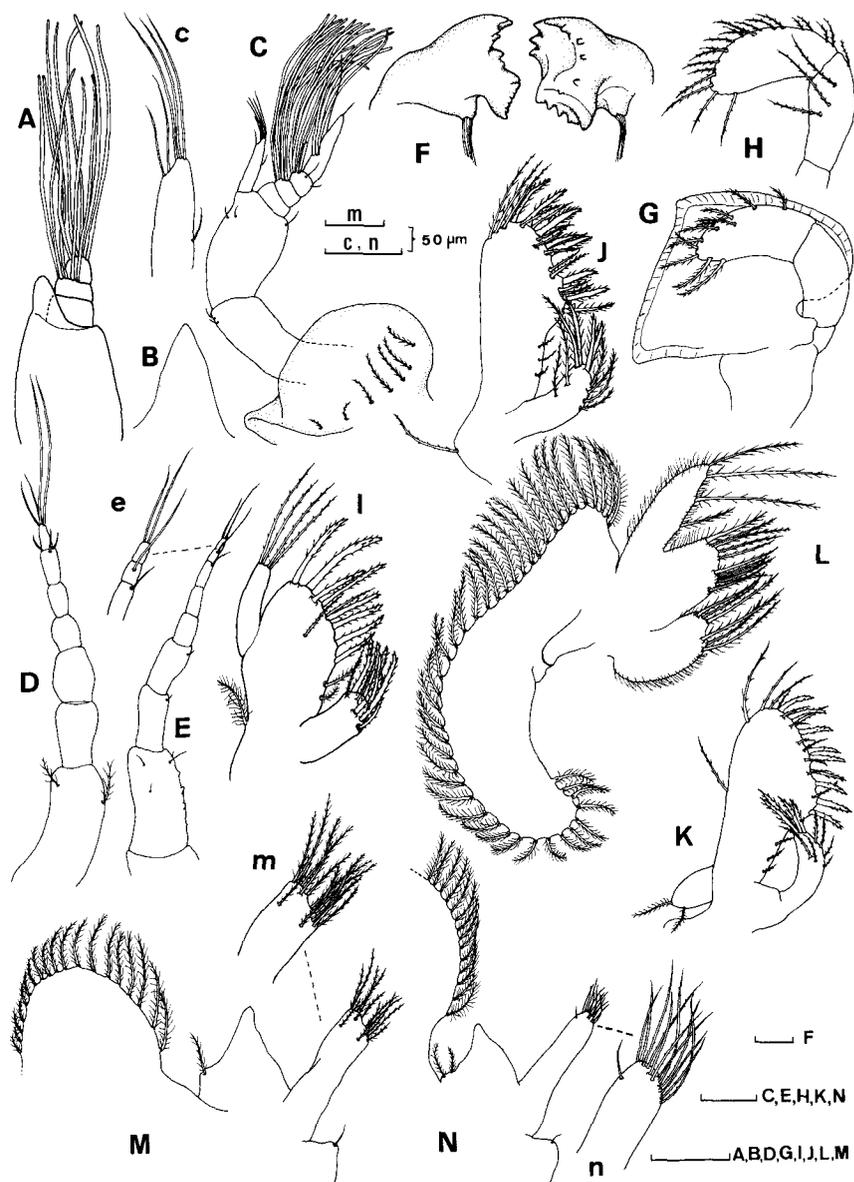


Fig. 9. *Myra coalita* Hilgendorf. A, antennule and antenna (B) of last zoeal stage; C, antennule of megalopa; c, detail of antennular inner flagellum; D-E, antenna of megalopa (D) and of first crab (E); e, apical detail of E; F, mandibles of last zoeal stage; G, mandible of megalopa; H, mandibular palp of first crab; I-K, maxillule of last zoeal stage (I), megalopa (J) and first crab (K); L-N, maxilla of last zoeal stage (L) (complete), megalopa (M) and first crab stage (N), scaphognathite partially drawn; m, n, detail of basal endite of respective maxilla. Scale bar = 100 μ m, except for c, m, n.

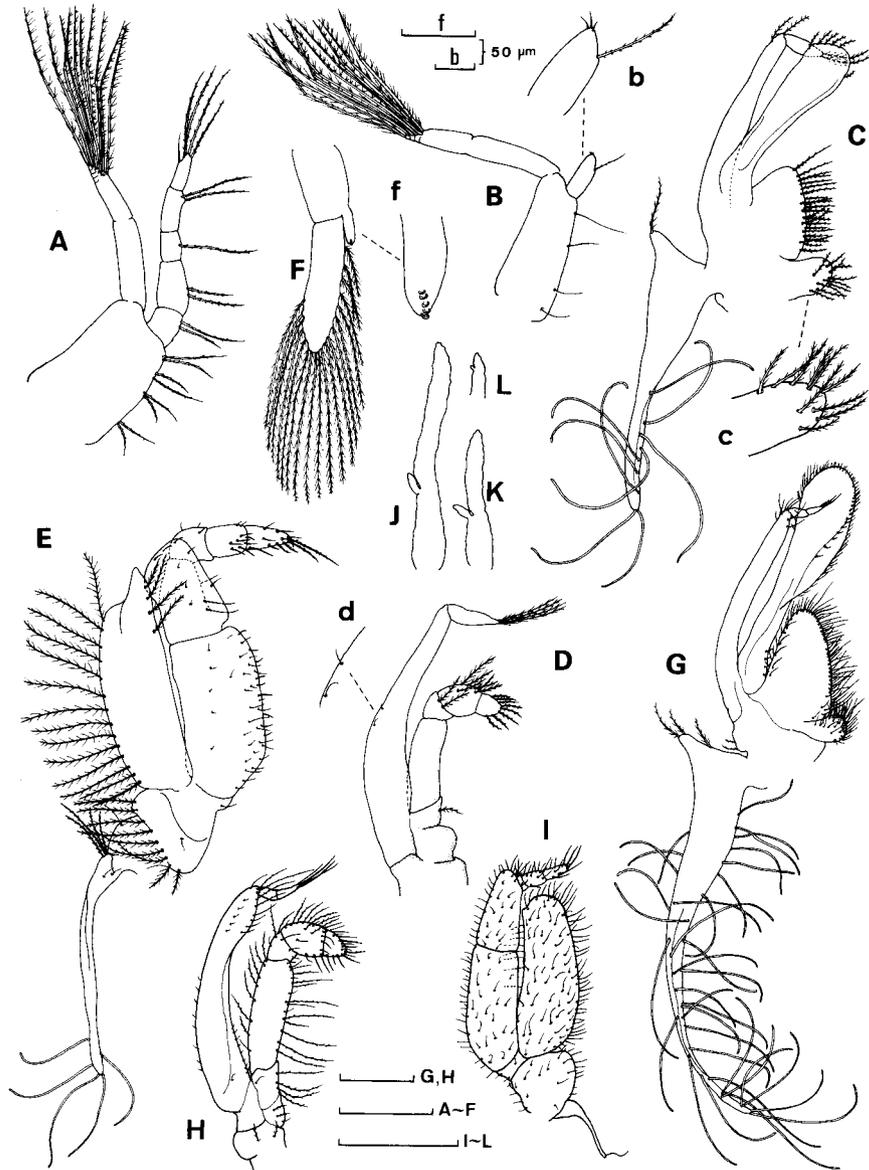


Fig. 10. *Myra coalita* Hilgendorf. A-B, last zoeal stage, first (A) and second (B) maxillipeds; b, detail of endopod; C-E, megalopa, first (C), second (D) and third (E) maxillipeds; c, detail of basal endite; d, detail of outer setae on exopod; F, fourth pleopod of megalopa, and detail (f) of endopod; G-I, first crab, first (G), second (H) and third (I) maxillipeds; J-L, first crab, first (J), penultimate (K) and last (L) pleopods. Scale bar = 250 μ m, except for f and b.

Second maxilliped (Fig. 10-D): With basis-coxa junction of endopod not defined, 5-segmented, invested with 1-0-2-6-8 setae respectively. Exopod with basal segment longer than endopod, armed with 2 short setae medially; distal segment with 4 terminal setae.

Third maxilliped (Fig. 10-E): With ischium and merus rigid, broad, and covered with numerous short setae; basis with a single seta, coxa with 9 long plumodenticulate setae on proximal margin, and a short setae submarginal. Exopod also rigid, expanded, pointed distally, reaching in length up to distal one-fourth of merus; 14 long plumodenticulate setae fringe the outer margin and 4 setae, similar in length, the distal inner margin. Epipod slender, broader basally, with one seta, a group of 4 longer and 2 short setae proximally; 5 long, fine setae on distal part.

Abdomen: Subcylindrical, 6-segmented plus the telson, with pleopods ventrally to segments 2-5, each with numerous long plumose setae (Fig. 10-F), always more than 16 on distal segment of exopod, proximal segment glabrous; endopod short, with hooked setae distally. A pair of well-developed uropods ventrally to ultimate abdominal somite, with distal segment extending beyond the telson (Fig. 8-H).

Telson: Short, with margins almost perfectly circular; no setae on borders, but 2 short and 2 long setae medially on dorsal and ventral surfaces.

First crab

Carapace globose dorsally, subcircular in outline, slightly longer than broad, covered uniformly with setae and sparsely with small tubercles (Fig. 8-C). Three large spines are conspicuous on posterior margin of carapace; one shorter posterolateral and several spines of diverse size along the anterolateral border can be differentiated on each side. Small tubercles on marginal borders and in the metagastric region; a group of several tubercles in the cardiac region. Each of posterior large spines with irregular borders and covered with long setae and small tubercles; in addition, every small tubercle is covered with many fine setules on distal margin (seen at high magnification). Front extending moderately beyond the orbits.

Chelipeds: Longer than carapace, movable finger longer than palm; chelipeds entirely covered with long setae (Fig. 11-F), small tubercles (specially on palm and merus) and very small, fine setules on surface; fingers setose, distally inward-curved, with inner margins invested with numerous teeth of several sizes.

Pereiopods: Slender (Fig. 11, G, H; g-j), all similar, setose, dactyl acutely pointed, with length equal to propodus-carpus length; setation of each dactyl as indicated in figures.

Antenna: Flagellum 8-segmented (Fig. 9-E); basal segment covered with sparse minute tubercles and 4 setae on surface, a short seta on segments 2 and 3, no setae on segments 4-5, a long seta on segments 6 and 7, distal segment with 2 setae.

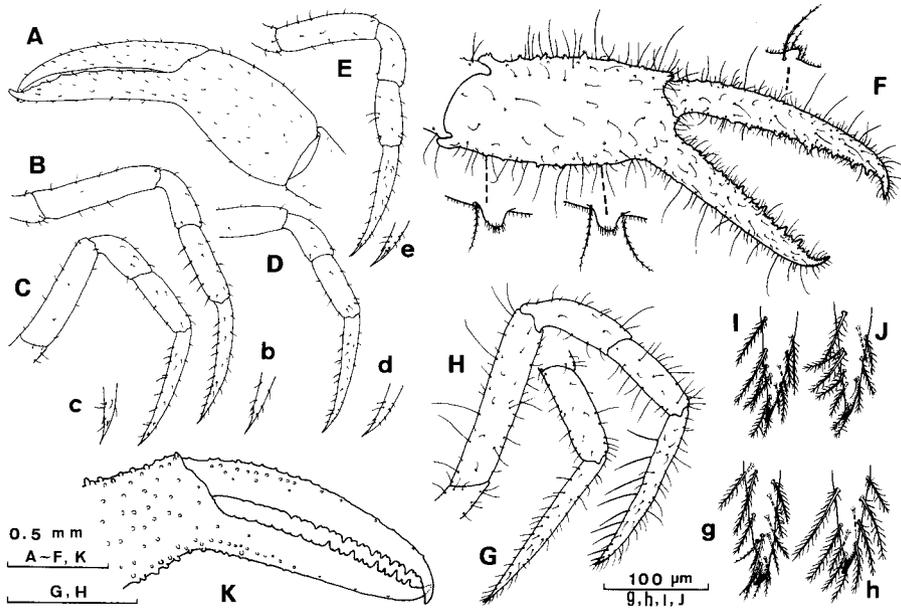


Fig. 11. *Myra coalita* Hilgendorf. A-E, megalopa, right cheliped (A) and pereopods 2-5 (B-E), each with a detail of tip of dactyl; F-H, first crab, right chela (F), fourth (G) and fifth (H) pereopod; g-j, detail of tips of dactyli 2-5 of the first crab; K, outline of right chela of the second crab (setation has been omitted for showing the inner borders of fingers).

Mandibular palp (Fig. 9-H) now with setation on proximal and distal segments.

Maxillule (Fig. 9-K): Provided with a short endopod, fringed with 2 plumodenticulate setae; basal and coxal endites slightly increased in setation.

Maxilla (Fig. 9-N): Setation almost invariable, as in previous stage, except the number of marginal setae of scaphognathite, which has increased to 124 setae.

First maxilliped (Fig. 10-G): Profusely setose in all segments.

Second maxilliped (Fig. 10-H): Also setose, specially in the segments without setae in the previous stage (see Fig. 10-D); endopod and exopod nearly equal in length, exopod with numerous setae on surface.

Third maxilliped (Fig. 10-I): Profusely setose on surface of all segments; epipod greatly reduced, slender, distally with a single seta.

Abdomen: Dorsoventrally flattened, 6-segmented, with bud of biramous pleopods, progressively small in size; last abdominal segment oblong, narrowing distally (Fig. 8-I), with setae on posterior rounded margin and 8 setae medially.

Second crab

Carapace subcircular in outline, globose; height of body (in lateral view) contained about 1.5 times in the longitudinal length of carapace (Fig. 8-D). Carapace and pereopods evenly covered with small granules and setae dorsally and laterally; a very fine tomentum covering the whole surface can be observed at high magnification. Front slightly extended beyond the orbits; the posterior portion of carapace with a major large, obliquely upwardly directed acuminate spine, emerging from intestinal region; a small not acuminate protuberance emerges dorsally from cardiac area; a short spine on each lateroposterior border; 2 larger backwardly directed spines; each of these spines covered with setae, small tubercles and a very fine tomentum. Chelipeds evenly covered with setae and small tubercles, sparse on fingers; fingers setose and profusely toothed along inner borders (Fig. 11-K).

Remarks. In the successive crab stages, as observed by SEM (Figs. 17-F, 18, A-B), the tomentose structure of surface covers also every tubercle.

Philyra platycheira De Haan, 1841

(Japanese name : Hirate-kobushi)

(Figs. 12-15, 18)

Last Zoeal stage

Small larva (C.L., 0.60 mm, measured laterally from anterior margin of eyes to posterior edge of carapace). Body globose (Fig. 12-A), abdomen strongly flexed beneath carapace; no dorsal nor lateral spines on carapace, rostral spine reduced to a short rostrum, downwardly curved. **Abdomen** subcylindrical (Fig. 12-G), 5-segmented, with rudimentary pleopods on segments 2-5; first abdominal somite with setae dorsally, and somites 2 and 3 with lateral knobs; segments 2-5 each with 4 minute setules dorsally. **Telson** broad, triangular, slightly concave ventrally, invested with 3 minute spines (the innermost longer) on each posterolateral rounded margin, and a median group of 6 broad setae on posterior border, the innermost longer (Fig. 12-g); minute dots near the base of median setae.

Antennule: Conical (Fig. 13-A), unsegmented, with a bud of endopod, and a terminal tuft of 4 aesthetascs and 3 fine setules.

Antenna (Fig. 13-D) rudimentary, conical, unarmed, unsegmented.

Mandible (Fig. 13-I) powerful, massive, with incisor plate broad, with several rounded teeth on cutting edge; molar process directed inward, with molar surface irregular.

Maxillule (Fig. 13-L): With setation as indicated in Table 3, with the addition of one plumose seta on outer margin, in front of basal endite.

Maxilla (Fig. 13-Q): With very fine setules on margins of endopod and endites; setation as indicated in Table 3.

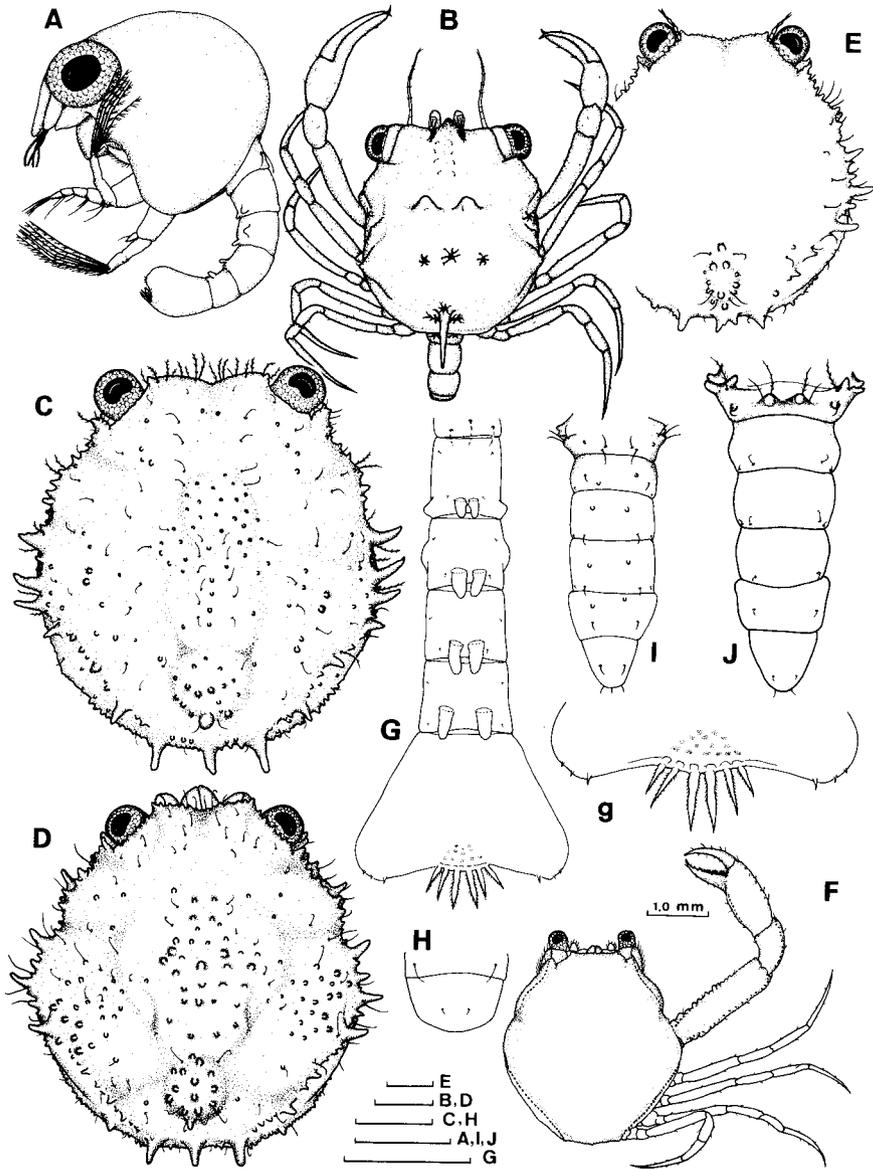


Fig. 12. *Philyra platycheira* De Haan. A, last zoeal stage, complete, lateral view; B, megalopa, dorsal view; C, carapace of the first crab; D, carapace of the second crab; E, outline of carapace of the third crab; F, sixth crab, dorsal view; G, abdomen of last zoeal stage, ventral view; g, detail of posterior margin of zoeal telson; H, telson of megalopa; I-J, abdomen of the first (I) and second (J) crabs. Scale bar = 250 μ m, except for F.

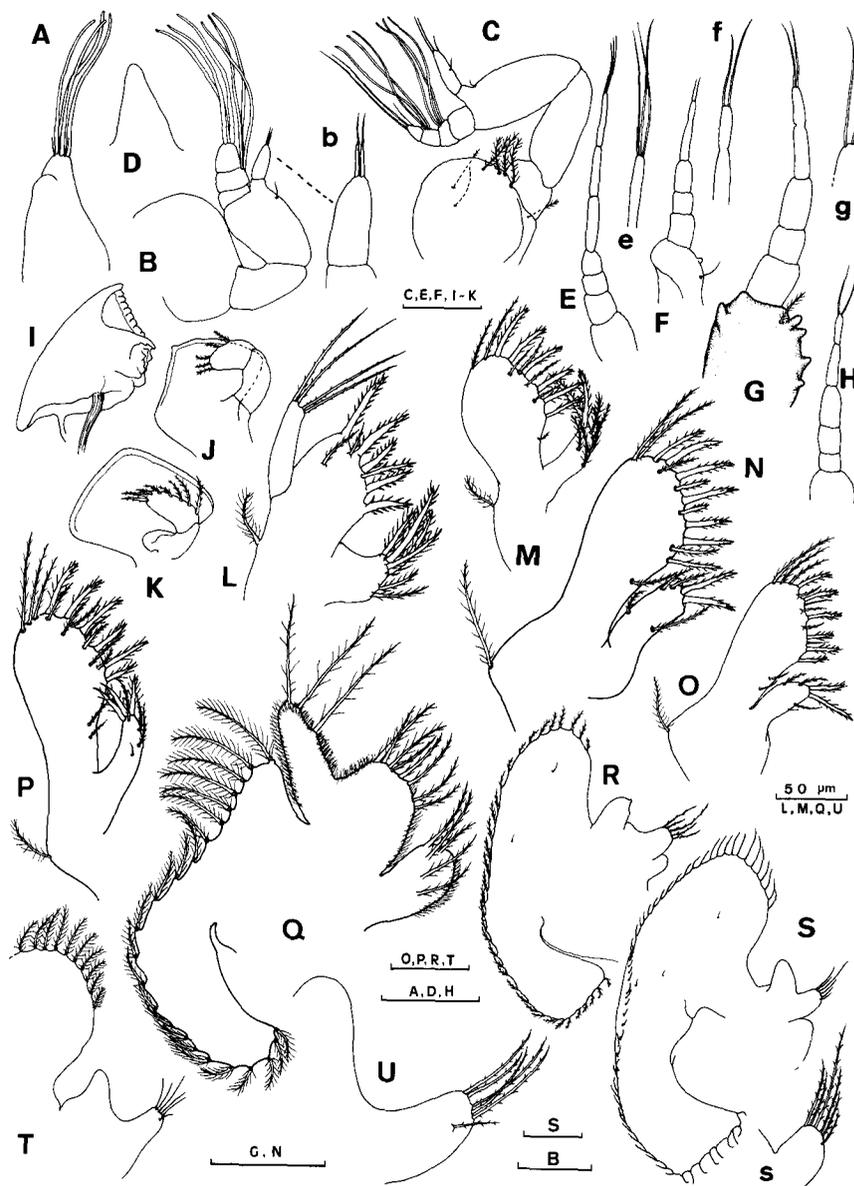


Fig. 13. *Philyra platycheira* De Haan. A-C, antennule of last zoeal stage (A), megalopa (B) and first crab (C); D-H, antenna of last zoeal stage (D), megalopa (E), first crab (F), second (G) and third (H) crabs; e-g, apical detail of respective antenna; I-K, mandibles of last zoea (I), megalopa (J) and first crab (K); L-P, maxillule of last zoea (L), megalopa (M), first crab (N), second (O) and third (P) crabs; Q-U, maxilla of last zoea (Q), megalopa (R), first crab (S, s), second crab (T), scaphognathite partially drawn, and third crab (U), scaphognathite omitted. Scale bar = 100 μ m, except for L, M, Q, U.

First maxilliped (Fig. 14-A): With a broad protopod, fringed with 8 setae on inner margin; endopod 5-segmented, shorter than exopod, with 2 setae on proximal segment, 2-1-2-4 setae respectively; exopod 2-segmented, with apical long plumose setae.

Second maxilliped (Fig. 14-B): With 4 setae on inner margin of protopod; endopod rudimentary, unsegmented, armed with 2 short, terminal and one longer, subterminal setae; exopod well-developed, 2-segmented, with long plumose setae apically.

Third maxilliped (Fig. 14-C) rudimentary, unarmed, unsegmented, curved inward.

Megalopa

Body small, only 1.10 mm (C.L); carapace longer than broad, almost smooth, with a pointed rostrum, curved downward and a conspicuous dorso-posterior spine, obliquely directed backward (Fig. 12-B); 2 dorsal protuberances emerge from mesogastric region; hepatic and mesobranchial regions swollen, each with a seta, two longitudinal tiers of setae on frontal region and 2 setae on base of mesogastric protuberances. Chromatophores as indicated in figure. The sternum presents ventrally 4 pairs of cornua, directed forward, in front of coxae 2-5, decreasing gradually in size, 2 rigid setae, one, and one shorter setae on inner margin of cornua 1-3 respectively.

Chelipeds: Longer than carapace, armed with few, minute setae on surface; fingers curved downward, crossed on tip when closed, longer than palm; inner margin of immovable finger with 2 acute elevations near tip.

Pereiopods (Fig. 15, D-G): Slender, almost glabrous, with sharply pointed dactyli, each longer than propodus-carpus length.

Antennule (Fig. 13-B): With proximal segment of peduncle globose, unarmed, a single seta on distal segment of peduncle; inner flagellum unsegmented, with 2 apical setae; outer flagellum 3-segmented, with 3 aesthetascs on second and distal segments respectively, those of distal segment are apical in position.

Antenna (Fig. 13-E): 7-segmented, the four proximal are short, but the remaining three apical segments are long, slender, setose only the distal one, with 3 fine setae apically.

Mandible (Fig. 13-J): With broadly triangular incisor plate, slightly concave; palp bisegmented, with setae only on the distal segment.

Maxillule (Fig. 13-M): With setation of endites as indicated in Table 3, with an additional seta, proximally, in front of coxal endite.

Maxilla (Fig. 13-R): With endopod digitiform, acuminate distally, unarmed; coxal endite also unarmed; scaphognathite with numerous marginal setae.

First maxilliped (Fig. 14-D): With endopod oval, expanded distally, longer than exopod, with 3 setae on anterior outer border; exopod with 4 distal plumose setae; epipod curved distally, with few simple setae.

Second maxilliped (Fig. 14-E): With endopod apparently 5-segmented

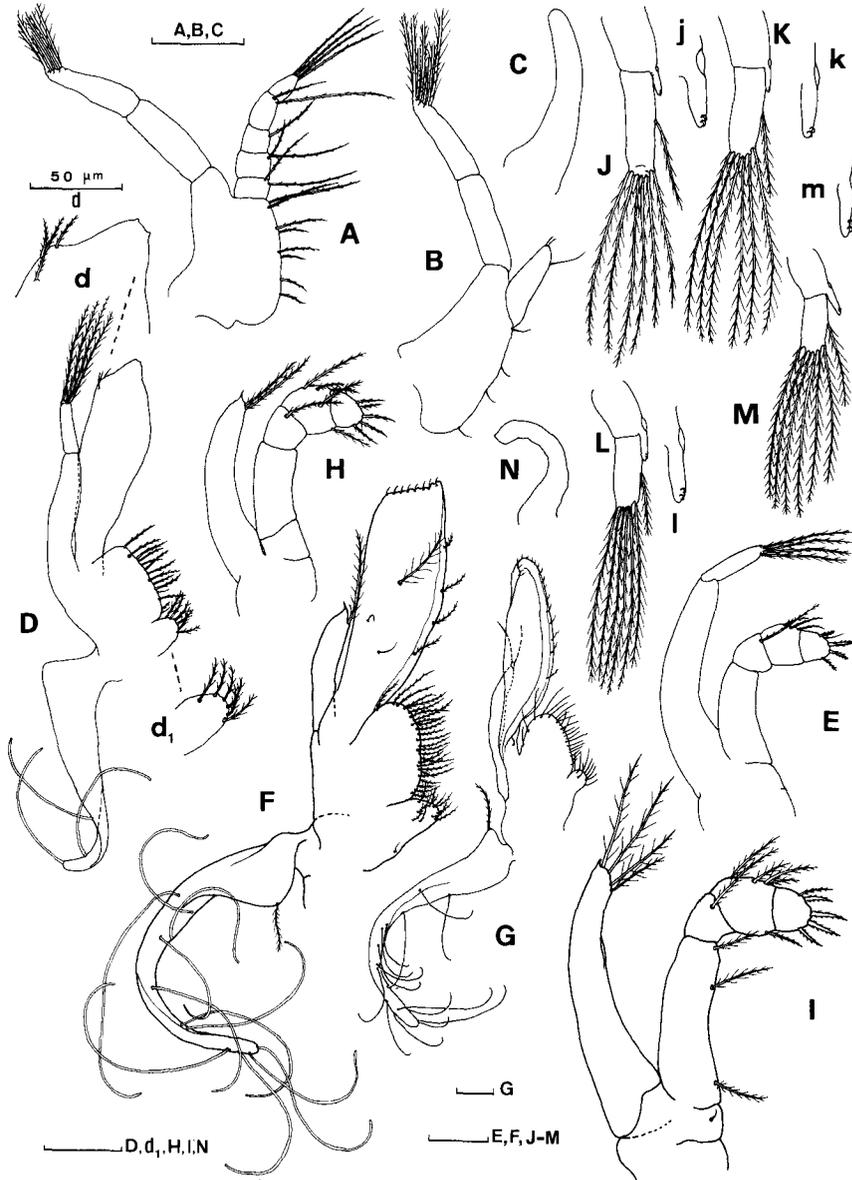


Fig. 14. *Philyra platycheira* De Haan. A-C, last zoeal stage, first (A), second (B) and third (C) maxillipeds; D-E, megalopa, first (D) and second (E) maxillipeds; d, detail of outer apical margin of endopod; d₁, detail of basal endite; F-G, first maxilliped of the first (F) and second (G) crabs; H-I, second maxilliped of the first (H) and second (I) crabs; J-M, pleopods of megalopa (first to fourth); j-m, endopods of their respective pleopods; N, first pleopod of the first crab. Scale bar = 100 μm, except for d.

(proximal segments indistinctly demarcated), curved inward, with setae on segments 3-5; exopod long, bisegmented, with 4 setae distally.

Third maxilliped (Fig. 15-A): With broad ischium and merus; basis-coxa indistinct; coxa with 4 marginal setae; exopod broad, narrowing distally, extending beyond the ischium.

Abdomen: Subcylindrical, pleopods 2-5 (Fig. 14, J-M) each with 2 hooked setae on endopod; no uropods.

Telson (Fig. 12-H): Short, broader than long, rounded posterior margin, 2 short setae medially.

First crab

Carapace small, subcircular in outline (Fig. 12-C), slightly longer than broad; cardiac and intestinal regions swollen; front truncate, produced disto-laterally into short rounded processes; frontal margin setose, medially invaginated, not extending beyond orbits. Several blunt spines, tubercles and sparse setae on margins of carapace, being conspicuous those of outer borders of both branchial regions and those of posterior margin of carapace; several small tubercles and setae are distributed dorsally on carapace, the longer arranged on the intestinal elevation.

Chelipeds: Longer than carapace, with rounded spines, tubercles and setae in all segments; fingers nearly equal to palm in length (Fig. 15-H), with inner margins sharp, indented.

Pereiopods 2-5 (Fig. 15, I-J): Similar in size and setation, each with dactyl slender, acutely pointed.

Antennule (Fig. 13-C): With proximal segment of peduncle globose, covered with several plumodenticulate setae; outer flagellum 4-segmented, with tufts of 3 aesthetascs on segments 2 and 3 respectively, distal segment with 2 very long, apical, fine setae and one shorter, subterminally.

Antenna (Fig. 13-F): Short, apparently 6-segmented, distal segments indistinctly demarcated, with 2 apical setae; one single seta and one tubercle on proximal article.

Mandible (Fig. 13-K): With palp reduced, in contrast with the broad incisor plate; setation only in the distal segment of palp.

Maxillule (Fig. 13-N): Very similar to that in previous stages; a single marginal seta in front of coxal endite.

Maxilla (Fig. 13-S): Almost unchanged in setation of endites; endopod unilobed; scaphognathite now with numerous marginal setae and 3 minute setae on surface.

First maxilliped (Fig. 14-F): Endopod greatly expanded, with 8 short setae on truncate distal margin, 4 on outer margin and 3 on surface; basal endite profusely setose, with 26 plumodenticulate setae; coxal endite invested with 12 setae; exopod short, half of endopod length, pointed distally, with a single plumodenticulate seta subterminally; epipod well-developed, proximally triangu-

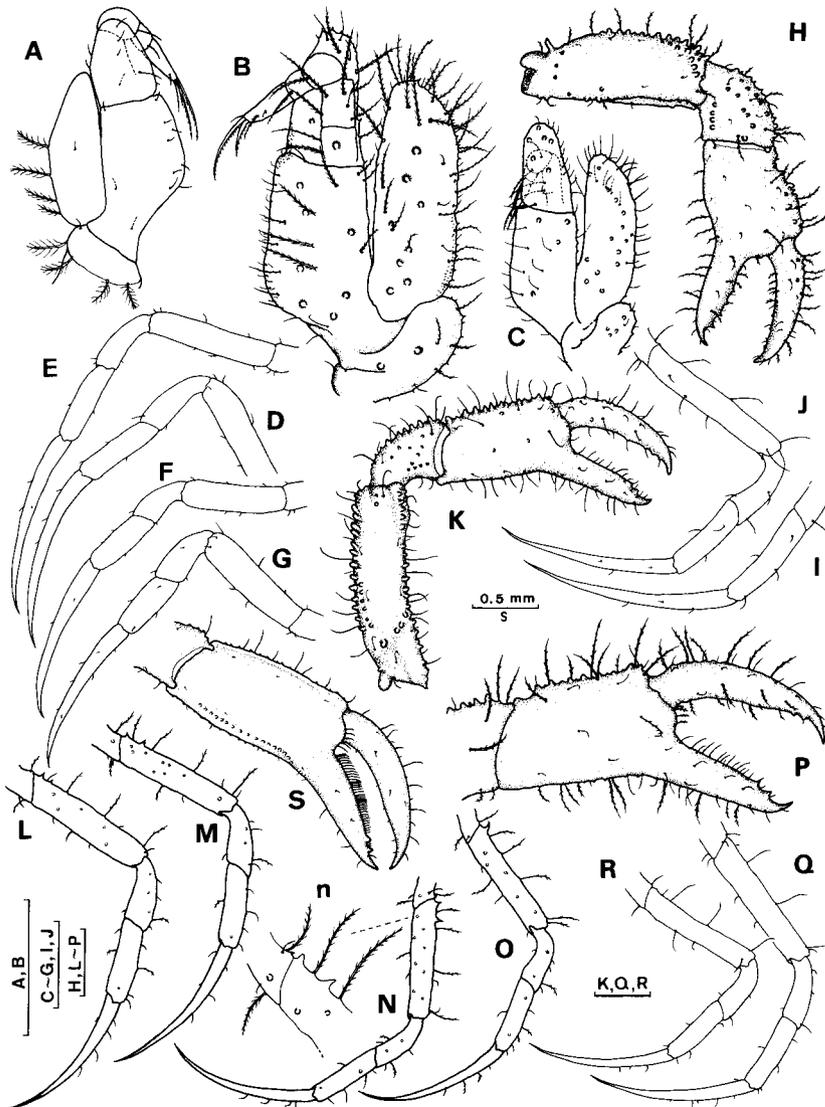


Fig. 15. *Philyra platycheira* De Haan. A-C, third maxilliped of megalopa (A), first (B) and second (C) crabs; D-G, megalopa, second of fifth pereopods; H-J, first crab, cheliped (H), second (I) and fifth (J) pereopods; K-O, second crab, right cheliped (K) and pereopods 2-5 (L-O); n, detail of ischium-merus junction of the fourth pereopod; P-R, third crab, left chela (P), second (Q) and fifth (R) pereopods; S, right chela of the sixth crab. Scale bar = 250 μ m, except for S.

lar, slender distally, with a single proximal seta and 10-11 long, simple setae.

Second maxilliped (Fig. 14-H): With endopod 5-segmented, with 0-0-1-5-5 setae; exopod now reduced, shorter than endopod, unsegmented, pointed distally, with 2 subterminal setae; basis-coxa indistinctly demarcated.

Third maxilliped (Fig. 15-B): Similar in shape and proportion of segments, but now profusely setose on surface and margins, with the addition of tubercles on surface; outer margin of coxa, merus and exopod finely cristate.

Abdomen 6-segmented (Fig. 12-I): Dorsoventrally flattened, first segment expanded laterally, setose; segments 1-5 with short setae dorsally and 2 small tubercles; penultimate segment slightly broader; sixth segment as long as broad, narrowing distally, invested dorsally with 2 and 3 setae on the rounded posterior margin; pleopods present, but rudimentary (Fig. 14-N).

Second crab

Carapace subcircular (Fig. 12-D), similar to previous stage; front narrower, margin irregular, depressed medially, with a blunt spine latero-distally; branchial and metacardiac regions moderately swollen; margin of carapace with more irregular blunt spines, and dorsal tubercles more prominent, specially those from cardiac region.

Chelipeds: Longer than carapace, unchanged in shape, but with more tubercles and blunt spines, specially on merus, carpus and upper borders of palm and movable finger (Fig. 15-K); inner margin of fingers with acute teeth on the distal one-third.

Pereiopods (Fig. 15, L-O): Similar in size and setation, now with sparse small tubercles on each merus, and more sparsely on carpus; upper proximal portion of each merus armed with blunt spines; each dactyl fine, acute distally and slightly curved.

Antenna (Fig. 13-G): Simple, with a well calcified peduncle, with tubercles on margins and a distal seta; flagellum with 3 unarmed, proximal segments, the distal article slender, constricted medially, apparently unsegmented, with 2 apical setae.

Maxillule (Fig. 13-O): With 15-17 setae on basal endite, 6 on coxal endite, and a simple proximal seta emerging in front of coxal endite (this feature has been invariable from megalopal stage).

Maxilla (Fig. 13-T): With endopod rounded distally, basal endite digitiform, short, with 5-6 terminal setae; coxal endite apparently absent; scaphognathite fringed with 70-72 setae.

First maxilliped (Fig. 14-G): Now profusely setose; endopod oval, distal margin rounded; epipod now with 14-15 long setae.

Second maxilliped (Fig. 14-I): Endopod with 1-3-1-5-5 setae respectively; exopod with 4 plumodenticulate setae distally.

Third maxilliped (Fig. 15-C): More rigid, hard, and similar as in previous crab stage.

Abdomen (Fig. 12-J): 6-segmented, narrow, dorso-ventrally flattened; first segment expanded laterally, with tubercles and setae; penultimate segment broader than segments 2-4; last segment rounded posteriorly, with 2 setae marginally, and 2 short setae dorso-medially.

Third crab

Carapace (Fig. 12-E) similar in outline and sculpture, but antero-lateral borders slightly convergent anteriorly.

Chelipeds: Basically similar to those from previous stage, but now more setose on inner margin of fingers, specially in the immovable finger (Fig. 15-P); a group of 3-4 setae emerge distally in the palm, between both fingers.

Pereiopods (Fig. 15, Q-R): Not markedly different from previous stages.

Antenna (Fig. 13-H): Unchanged, as in previous stage.

Maxillule (Fig. 13-P) similar to previous stage, with setation of 18 and 7 setae on basal and coxal endites respectively; the proximal single seta remains.

Maxilla (Fig. 13-U): With endopod unilobed, unarmed: basal endite also lobed, with 6 terminal and one subterminal setae; scaphognathite with numerous marginal setae.

Remarks: In the successive crab stages, the carapace progressively becomes hexagonal in outline, and dorsal surface seems to be smooth (observed at low magnification) by reduction of tubercles and marginal blunt spines. In addition, the setation of inner margin of immovable finger is also progressively apparent. As revealed by SEM, the carapacial dorsal sculpture in the 5th crab stage is composed by depressed tubercles evenly distributed, but the bigger tubercles on

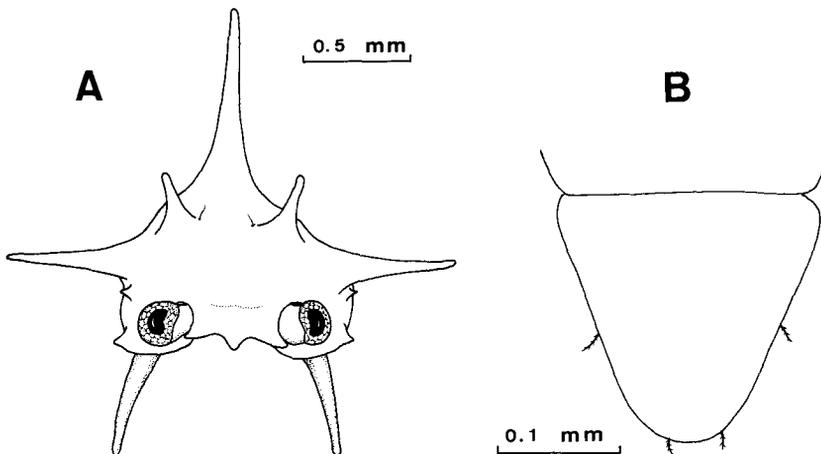


Fig. 16. *Leucosia craniolaris* (L.). A, frontal view of megalopa (ventral processes correspond to sternal cornua); B, telson of the first crab stage, dorsal view.

chelipedal merus are verrucose; the inner setae of immovable finger are numerous and plumodenticulate on the distal half (Fig. 18, C-E).

Sixth crab

Carapace length, 3.14 mm. Carapace hexagonal in outline (Fig. 12-F); hepatic borders slightly expanded. Minute tubercles along carapacial borders; front truncate, as broad as the transverse posterior margin of carapace. Chelipeds long, about 1.5 times longer than carapace; 2 inner sharp teeth, subterminally on the immovable finger, a tier of numerous setae, equal in length is arranged along inner margin (Figs. 15-S); movable finger sparsely setose, edented, acuminate distally.

Table 3. Main differences on zoal characters for the leucosiid species observed in this study. Invariable setation of some appendages has been omitted when present in the four species.

Characters	<i>N. lam.</i>	<i>M. coal.</i>	<i>P. plat.</i>	<i>L. cran.</i> *
Carapacial spines :	present	present	absent	present
Antennule :				
aesthetascs	7	10	4	3
Maxillule :				
basipod	11	11-12	8	8
coxopod	8	7-8	6	6
Maxilla :				
endopod	4	4	3	3
basipod	11	11	8	8
coxopod	6	6	5	5
scaphognathite	35	43-44	23	28
1st, 2nd Maxilpds. :				
exopod	8	10	6	6
Abdomen : (dorsally)				
1st somite	10	8	3	5
Telson :				
distolateral spinules	1	1	3	4

N. lam., *Nucia laminata*; *M. coal.*, *Myra coalita*; *P. plat.*, *Philyra platycheira*; *L. cran.*, *Leucosia craniolaris*. * after Quintana (1984: 8).

***Leucosia craniolaris* (L., 1758)**

(Japanese name: Tatejima-kobushi)

(Figs. 16, 18)

Although the early post-larval stages were described previously (Quintana, 1984), new information and SEM observations (Fig. 18-F) are included in this paper for comparison with other allied species. The telson of the first crab is broadly triangular, slightly broader than long, armed with 2 setae on posterior margin, and one on each lateral margin (Fig. 16-B).

Discussion and Conclusions

Larval phases of brachyuran, including those of leucosiids have been considered highly significant in a phylogenetic sense by Rice (1980, 1981) and Van Dover (1982). Descriptions of megalopal and subsequent post-larval stages are rather scarce in the current literature. In early reports, the megalopa of *Ebalia cranchii* and *E. tuberosa*, and the first and second crabs of the latter species were described by Lebour (1928 a, b), but subsequent papers mentioned only zoeal stages for a number of leucosiid species. Salman (1982) redescribed the complete larval development of *E. tuberosa*, including four zoeal stages and one megalopa. The report given by Terada (1984) includes descriptions of megalopas of the following species: *Arcania undecimspinosa elongata* Yokoya, *Myra fugax* (Fabricius), *Philyra pisum* de Haan, *P. syndactyla* Ortmann, *Leucosia anatum* (Herbst) and *L. obtusifrons* de Haan. A recent review of megalopal characters within a number of leucosiids have been presented by Quintana (1986).

The present material of leucosiid species is compared in the next Tables (3, 4 and 5), taking into account important differences.

1) ZOEAL STAGES

The number of zoeal stages before reaching the megalopal stage is variable in the leucosiid species: four in *Ebalia* species (Salman, 1982), five in *Arcania* and *Myra* species, and three in *Philyra* and *Leucosia* species (Terada, 1979; Quintana, 1984). This evidence, together with additional characters of morphology and setation of zoeal appendages in these species supported the assumption that the material presented here as "last zoeal stage" should probably correspond to the 5th zoeal stage in case of *Myra coalita*, and to the 3rd zoeal stage in *Philyra platycheira*. Because the complete larval development for *Nucia* species have not yet been recorded in the literature, the "last zoeal stage" referred here to *Nucia laminata* will remain doubtful up to know in detail the number of zoeal stages in this genus. No zoeal stages were obtained for *Arcania undecimspinosa*, but as mentioned previously, this species probably should also present five zoeal stages.

On the other hand, the lack of zoeal carapacial spines seems to be significant

Table 4. Main differences on megalopal characters for the leucosiid species observed in this study. Invariable characters have been omitted. Species names as in Table 3, except for *Arcania undecimspinosa* (*A. und.*).

Characters	<i>N. lam.</i>	<i>A. und.</i>	<i>M. coal.</i>	<i>P. plat.</i>	<i>L. cran.</i>
Rostrum :	absent	rudimentary	short, broad	pointed	pointed
Carap. spines :	absent	absent	1	1	9
Antennule :					
aesthetascs	12	16	17	6	5
Mandible : (palp)					
distal segment	10	9	11	5	6
Maxillule :					
basipod	20	22	23	13	13
coxopod	8	9	10	7	7
Maxilla :					
basipod	7	9	12	5	5
scaphognathite	67	76	76	35-36	44
1st Maxilliped :					
basipod	15	20	23	14	14
coxopod	6	9	10	6	6
epipod	9	6	8-9	3-4	8
2nd Maxilliped :					
endopod					
prox. segmt.	0	0	1	0	0
2nd	0	0	0	0	0
3rd	1	2	2	1	1
4th	3	7	6	3	3
distal segmt.	6	6	8	5	5
3rd Maxilliped : (exopod)					
(outer margin)	3	7	14	4	3
Pleopods 2-5 :					
exopod*					
1st pair	14-15	17	17-18	7	8
2nd	15	17	18	7	8
3rd	14	16	16-17	7	7-8
4th	11-12	14	19	7	7-8
endopod**					
1st pair	4	4	4	2	2
2nd	4	4	3	2	2
3rd	4	4	3	2	2
4th	4	3	5	2	2
Uropods :	absent	8	11	absent	absent

* plumose setae ; ** distal hooked setae.

Table 5. Main differences on 1st crab characters for the leucosiid species observed in this study. Species names as indicated in Tables 3 and 4.

Characters	<i>N. lam.</i>	<i>A. und.</i>	<i>M. coal.</i>	<i>P. plat.</i>	<i>L. cran.</i> ¹⁾
Antenna :					
segments	4	4	8	6	5
Mandib. palp :					
prox. segmt.	1	2	4	0	0
dist. segmt.	4	20	19	8	11
Maxillae :					
basipod	22-23	28	25	14	16
coxopod	10	11	10	6	7
Maxilla :					
basipod	*	8	13	6	5
scaphognat.	*	115-117	124	58	85
1st Maxilliped. :					
epipod	**	26-27	33-35	10-11	32

* not dissected ; ** not observed ; ¹⁾, after Quintana (1984).

since they are absent in *P. platycheira*, but are well-developed in *N. laminata* and *M. coalita*.

2) MEGALOPAL STAGE

As shown in figures and descriptions, clear external, morphological differences can be observed in the present leucosiid megalopas, e.g. carapace spines (or projections), ventral cornua on the sternum, rostrum and proportion of chelipeds, but an analysis of the megalopal antennule (segmentation and position of the aesthetascs) showed a high correspondence (Quintana, 1986) with the traditional taxonomical arrangement in this group. Thus, the subfamily Ebaliinae (*Nucia*) shows an outer flagellum 5-segmented, no aesthetascs on distal segment, and a relatively high total number of aesthetascs. In the Philyrinae, there are clearly two groups: the genera *Arcania* and *Myra* have invariably a 4-segmented flagellum, and the tuft of aesthetascs is medial in position on the distal segment. The another group, with 3-segmented outer flagellum and terminal or subterminal aesthetascs is composed of the genera *Philyra* (subfamily Philyrinae) and *Leucosia* (Subfamily Leucosiinae). For this reason, it seems to be relatively easy to separate into three groups the present material by using the segmentation of outer flagellum. On the other hand, another correspondence can be observed for the group *Arcania-Myra* in the setation of outer margin of the exopod of the third maxilliped in the megalopal stage. These two genera exhibit the highest number of lateral setae, 7 (*Arcania*) and 14 (*Myra*). All the remaining species show only

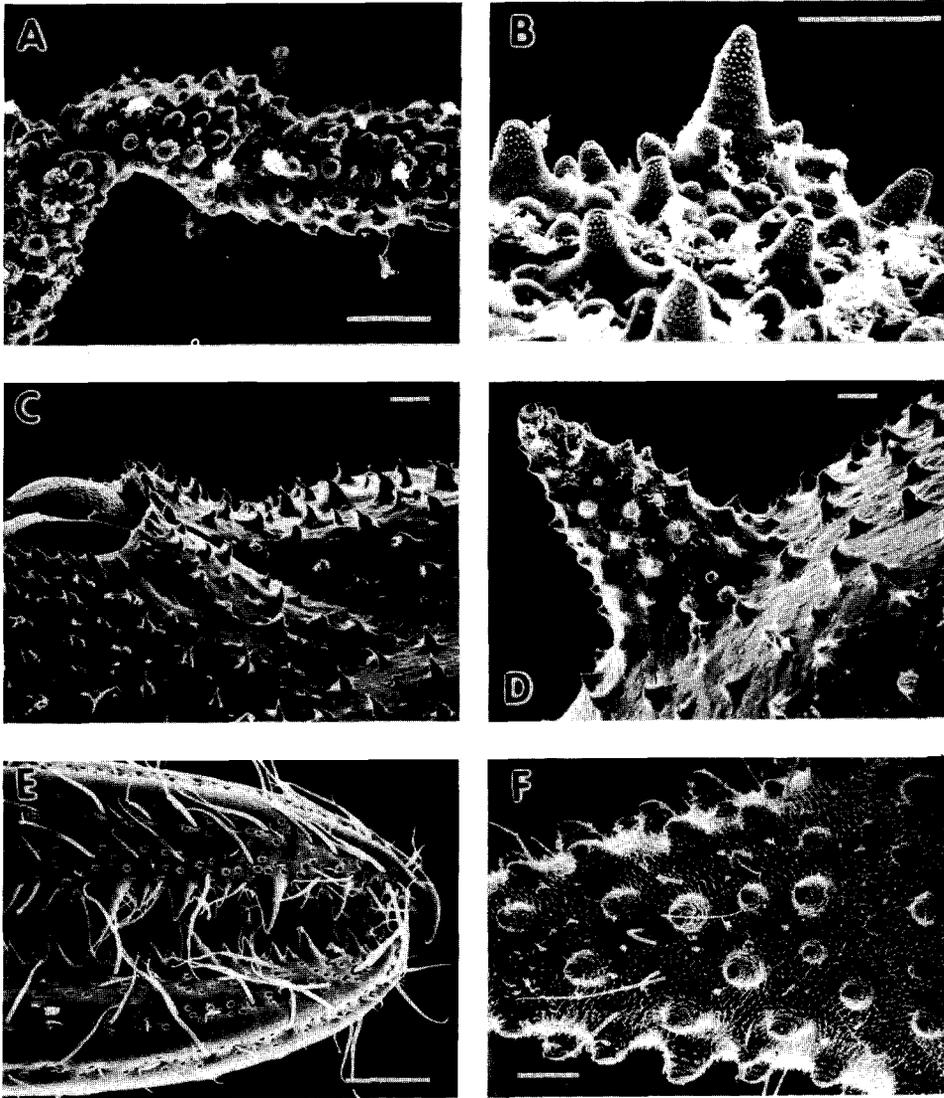


Fig. 17. A, B, *Nucia laminata* (Doflein), first crab. A, fifth pereopod (left margin corresponds to merus; right margin, proximal portion of dactyl); B, mid-lateral portion (right side) of carapace; C-E, *Arcania undecimspinosa* (De Haan). C, third crab, right antero-lateral region of carapace; D, third crab, postero-lateral spine (left side) of carapace; E, fourth crab, anterior third of chela, outer view; F, *Myra coalita* Hilgendorf, third crab; detail of surface of the mid-posterior spine of carapace. Scale bar = 100 μm .

3 marginal setae, with the exception of 4 setae in *P. Platycheira*.

3) CRAB INSTARS

With regard to the early crab stages, and the use of morphological features for a reliable identification, the author is aware that using the traditional taxonomical keys for adult forms, it is very difficult (if no impossible) to assign specific level since many of the diagnostical characters are not expressed or well-defined in early crab stages. In the present material of *Nucia laminata*, and according to Sakai (1976) and Miyake (1983), the genus *Nucia* comprises three species in the Japanese waters, and although similar to *N. perlata* Sakai, 1963 the sculpture of carapace (soft fur, tiny granules and vesicular tubercles), and the intestinal region isolated by a shallow groove, in contrast to big pearly granules on the carapace, and grooves in frontal, hepatic and intestinal regions of *N. perlata*, were clear to identify the present material as *Nucia laminata*.

In case of *Arcania undecimspinosa* (six species of this genus in Japanese waters, according to these authors), this species and *A. undecimspinosa elongata* Yokoya, 1933 are closely related, but the latter exhibits as diagnostical character the two anterolateral spines (of the eleven marginal spines) greatly reduced in size. In the present material, in all the stages obtained, these spines are well-developed. In addition to the differences observed in the megalopal stages listed in Table 4, the telson of *A. undecimspinosa* is clearly oval, narrowing posteriorly, whereas in the megalopa of *A. undecimspinosa elongata* is subquadrate, 1.3 times broader than long, and weakly rounded on posterior margin. The exopod of the third maxilliped in the former species is acuminate distally, and clearly rounded in the latter species. On the other hand, *A. undecimspinosa* is also similar to *A. erinaceus* (Fabricius, 1798), both present the marginal spines covered with secondary spinelets, but are different because the fingers of chelipeds are apparently shorter than the palm (in adult forms of *A. erinaceus*). Although no more advanced crabs than the 4th instar was possible to rear, the fingers in the present material are 1.65 times longer than the palm. For this reason, the present series megalopa-fourth crab instar are likely to be a *A. undecimspinosa* De Haan, 1841.

The present material of *Myra coalita* did not present difficulties for identification because only two species of the genus are present in Japanese waters. Both from the differences between both species pointed out by Sakai (1976: 102), and from the differences of megalopal characters (Table 4), it seems evident that the series fifth zoea-third crab obtained belongs to *Myra coalita* Hilgendorf, 1878.

In case of *Philyra platycheira*, the diagnostical character of "... cutting edge of immovable finger fringed with hairs ..." (Sakai, 1976: 108), appears in this species from the fourth crab instar. In spite of this unique feature and the progressive disappearance of spines and granules on dorsal surface of carapace in adult form, the chelipeds are slender and more than twice the length of carapace. In the present material, this proportion was 1.26 times in the first crab stage, 1.52 in the second; this proportion was always less than twice, at least up to the sixth

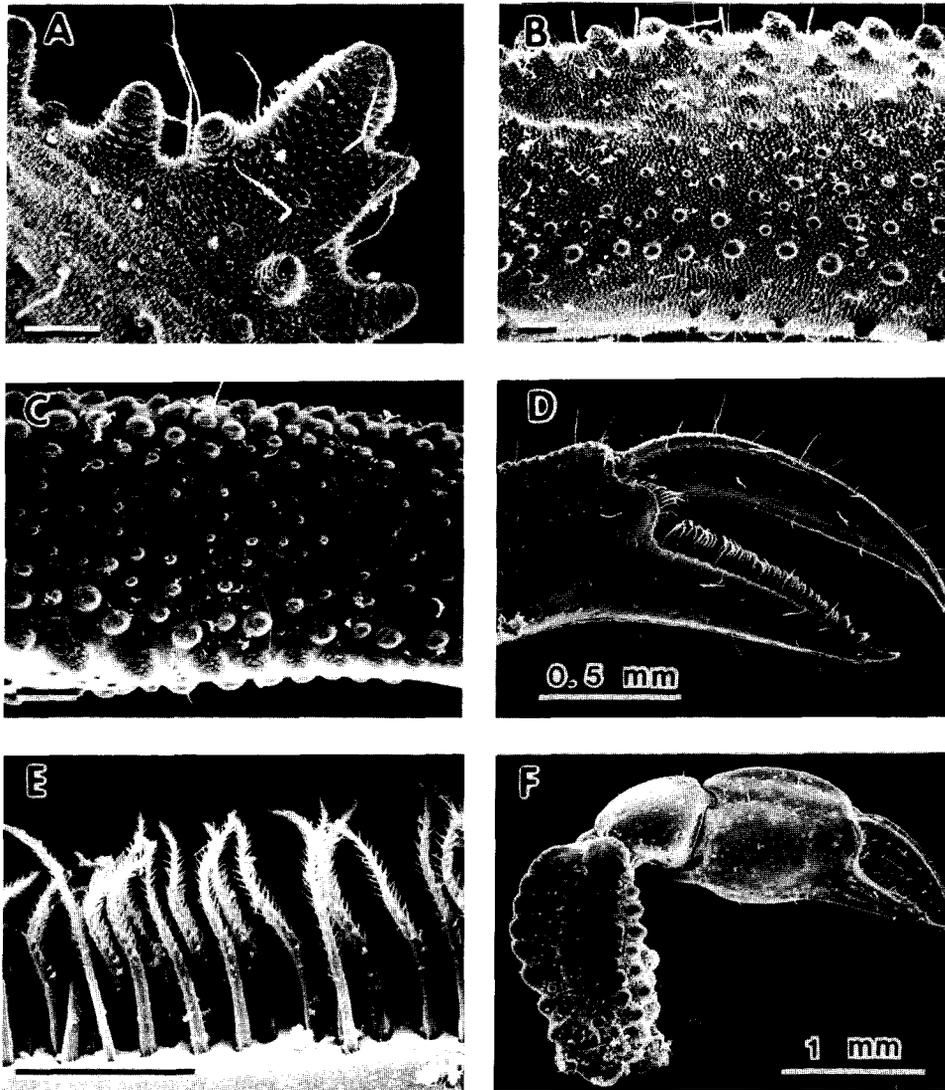


Fig. 18. A, B, *Myra coalita* Hilgendorf, third crab. A, detail of postero-lateral spinous processes (right side) of carapace; B, distal half of merus of left cheliped; C-E, *Philyra platycheira* De Haan, fifth crab. C, portion of merus of left cheliped; D, left chela; E, inner setae of immovable finger, right chela; F, *Leucosia craniolaris* (L.), cheliped of the third crab. Scale bar = 100 μ m, except for D and F.

crab obtained. Probably this feature should appear in the successive juvenile crabs. For the early post-larval stages of *Leucosia craniolaris*, this was already discussed by Quintana (1984) in a series third zoeal stage-third crab instar.

From an analysis of a number of characters and setation (Tables 3-5), it is apparent than *P. platycheira* and *L. craniolaris* are closely related each other than other species in this study. This strengthens the traditional taxonomical arrangement (*cf.* Sakai, 1976) done in the species belonging to the subfamilies Philyrinae and Leucosiinae.

Since the assumption of Rice (1980) and Salman (1982) with regard to scarce reports on larvae of leucosiid species, a gradual advance seems to arise in this group, as indicated by recent literature, but our knowledge of early post-larval stages is still deficient. As suggested recently by Martin *et al.* (1985) for their well documented study on xanthid zoeal characters, a better knowledge between larval phases and adults should be recommended if more descriptions of zoeas, megalopas and juveniles should be available.

Similarly, for the research carried out using plankton-caught material, it is necessary to rear the larvae beyond the fourth or fifth crab instars because characters are not well-defined before these stages. Otherwise, the efforts made in giving detailed descriptions and illustrations should be of limited value for the current research.

Summary

Later zoeal stages and megalopas of leucosiid crabs obtained alive from Tosa Bay, Southern Japan were reared in the laboratory up to advanced young crab stages, at 28.5-29.7°C and 33.0-33.4 ppt salinity. The knowledge of larval characters on Leucosiidae species is supplemented here with descriptions and detailed illustrations of zoeas, megalopas and early post-larval stages of the Ebaliinae *Nucia laminata* (Doflein, 1904), and the Philyrinae *Arcania undecimspinosa* De Haan, 1841, *Myra coalita* Hilgendorf, 1878 and *Philyra platycheira* De Haan, 1841, with the addition of new observations on the Leucosiinae *Leucosia craniolaris* L.

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