

**THE LECITHOTROPHIC ZOEAE OF *CHIROSTYLUS ORTMANNI* MIYAKE & BABA, 1968
(CRUSTACEA: ANOMURA: GALATHEOIDEA: CHIROSTYLIDAE)
DESCRIBED FROM LABORATORY HATCHED MATERIAL**

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ABSTRACT. – The first stage zoea of the anomuran chirostylid crab *Chirostylus ortmanni* Miyake & Baba, 1968, is described and illustrated. Many characters, when compared with the typical zoeal development of Galatheoidea Samouelle, 1819, have appeared at a much earlier stage, including the antennule endopod; mandibular palp; well-developed pereopods and biramous third maxilliped, biramous pleopods and a sixth abdominal somite. The presence of all these characters suggests that the zoeal phase for this species is abbreviated prior to metamorphosis to megalop. In addition, the setal armature on the coxal, basal and endopodal segments of the maxillule, maxilla and first two maxillipeds is absent, indicating that the first stage zoea of *C. ortmanni* is lecithotrophic. The zoeal morphology of the mouthparts is compared with other known reports of lecithotropic brachyuran and anomuran larvae, and abbreviated zoeal development in association with yolk feeding is discussed.

KEY WORDS. – Crustacea, Anomura, Chirostylidae, single stage zoea, lecithotrophy, abbreviated development, systematics.

INTRODUCTION

Lecithotrophic decapod zoeae have previously been recognised for only one marine brachyuran, the dromiid *Cryptodromia pileifera* Alcock, 1899, by Tan et al. (1986) although it is more prevalent in freshwater sesarmids (see Soh, 1969; Hartnoll, 1964; Diesel & Schuh, 1993; Diesel & Horst, 1995). However, non-feeding zoeae have been recorded in a number of anomurans such as the Lithodidae Samouelle, 1819, e.g. *Lithodes maja* Linnaeus, 1758, by Anger, 1996; *L. aequispinus* Benedict, 1895, by Shirley & Zhou, 1997; *Lithodes santolla* Molina, 1782, by Anger et al., 2004; *Paralomis granulosa* (Jacquinot, in Hombron & Jacquinot, 1846) by Campodonico & Guzmán, 1981, McLaughlin et al., 2003 and Calcagno et al., 2004 and *P. hystrix* De Haan, 1844, by Konishi & Taishaku (1994); the Galatheidae Samouelle, 1819, e.g. *Munidopsis polymorpha* Koelbel, 1892, by Wilkens et al. (1990) and the Pylochelidae Bate, 1888, e.g. *Pomatocheles jeffreysii* by Konishi & Imafuku (2000).

The capture of an ovigerous chirostylid while SCUBA diving on shallow reefs off Sulawesi, Indonesia, presented the

opportunity to describe the first zoeal stage. In the laboratory the specimen was identified as *Chirostylus ortmanni* Miyake & Baba, 1968, and during examination the zoea it was realised that the mouth parts devoid of setae. Therefore, the purpose of this study is to fully illustrate the lecithotrophic morphology of the mouthparts and make a comparison with larvae possessing a similar feeding strategy.

MATERIALS EXAMINED

Ovigerous *Chirostylus ortmanni* Miyake & Baba, 1968, collected at Lembeh Straits, Sulawesi, Indonesia, coll. P. F. Clark & H. H. Tan, Jul.2003 by SCUBA, hatched in the Systematics and Ecology Laboratory, Department of Biological Sciences, National University of Singapore, 16 Aug.2003. A total of eight zoeae were obtained and all were preserved. Only four were dissected and examined. The remaining four zoeae and the spent female were deposited in the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, ZRC 2007.0701.

METHODS

The ovigerous adult was maintained in the laboratory aquarium for about a week after capture before the eggs hatched. The larvae were observed for several hours before they were preserved in 70% alcohol and later dissected on glass slides in polyvinyl lactophenol under a Leica MZ16. Appendages were allowed to clear for 24 h before examination. Cover slips were sealed with clear nail varnish. Appendages were drawn using an Olympus BH-2 microscope equipped with differential interference contrast (DIC) and a camera lucida. Setal ambiguities were resolved using a Leica DMR HC microscope with DIC. The sequence of the zoal appendage descriptions was based on the malacostracan somite plan and described from anterior to posterior. Setal armature of appendages was described from proximal to distal segments and in order of endopod to exopod (Clark et al., 1998). The long antennular aesthetascs and the long plumose natatory setae of the first and second maxillipeds were drawn truncated. The approximate measurement of the antennal endopod (for its ratio with the protopod) was taken from its base to the tip.

Chirostylus ortmanni Miyake & Baba, 1968
(Figs. 1–7)

Description. – Zoea I: Carapace (Fig. 1a): multispinulate globose carapace, dorsal and lateral spines absent, rostral spine present and spinulate, ca. equal to antennal protopod; anterodorsal and posterodorsal setae absent; ventral margin without setae; eyes sessile.

Antennule (Fig. 1b): peduncle 3-segmented; endopod bud developed; exopod with 3 proximal subterminal, 3 distal subterminal and 5 terminal aesthetascs.

Antenna (Fig. 1c): endopod present, ca. 59% of protopod; protopod distally multispinulate.

Mandible: (Fig. 2a): palp present.

Maxillule (Fig. 2b): epipod seta absent; coxal endite without setae; basal endite without setae; endopod unsegmented, without setae; exopod seta absent.

Maxilla (Fig. 2c): coxal endite weakly bilobed, without setae; basal endite weakly bilobed, without setae; endopod not bilobed, without setae; exopod (scaphognathite) margin with 21 setae of equal length, distally naked.

First maxilliped (Fig. 3a): coxa without setae; basis without setae; endopod relatively short compared with that of second maxilliped, unsegmented, devoid of setae; exopod 2-segmented with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 3b): coxa without setae; basis without setae; endopod relatively long compared with that of first maxilliped, unsegmented, devoid of setae; exopod 2-segmented with 4 long terminal plumose natatory setae.

Third maxilliped (Fig. 3c): endopod 5-segmented, without setae; exopod 2-segmented, without setae.

Pereiopods (Fig. 4a–e): pereiopods 1–5 present with segmentation, coxa and basis not differentiated; pereiopods 1–4 with simple pair of gill buds; chela distinctly bilobed; pereiopod 5 markedly shorter than 1–4.

Abdomen (Figs. 5a–b; 6a–e): 6 somites; somite 1 unarmed;

somite 2 with 1 medial spine; somites 3–5 with 3 medial spines; somite 6 with 2 medial spines; somites 2–5 with biramous pleopods; somite 6 with markedly biramous uropod. Telson (Figs. 5a–b; 6f): posterior margin with 2 pairs of relatively small spines and 3 pairs of longer spines; each lateral margin with 4 long spines.

DISCUSSION

Anomuran hair (seta). – The anomuran hair (seta) has been recorded on the telson of many zoeas assigned to the Galatheaidea Samouelle, 1819. These include for example the Galatheaidea, *Galathea amoboinensis* De Man, 1888, by Fujita et al. (2003); *Agononida incerta* (Henderson, 1888) and *Munida striola* Macpherson & Baba, 1993, by Konishi & Saito (2000) and *Sadayoshia edwardsii* (Miers, 1884) by Fujita & Shokita (2005). Also the larval development of Porcellanidae Haworth, 1825, such as *Pachycheles serratus* Benedict, 1901, by Rodríguez et al. (2004); *Porcellana sayana* (Leach, 1820) by Hernández et al. (1998) and *Magalobranchium roseum* (Rathbun, 1900) by Hernández et al. (2002). However, the seta is not reported in the freshwater anomurans, the Aeglididae Dana, 1853. According to Bond-Buckup et al. (1996), *Aegla prado* Schmitt, 1942, undergoes direct development, hatching out as juveniles. The anomuran seta was not observed on the telson of *Chirostylus ortmanni*.

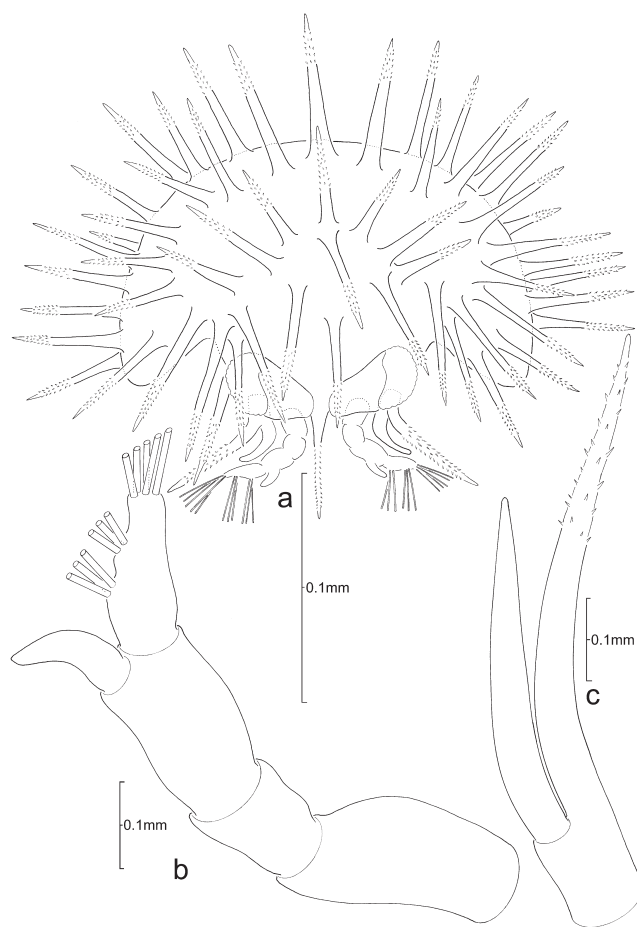


Fig. 1. *Chirostylus ortmanni* Miyake & Baba, 1968: a, anterior view of carapace; b, antennule; c, antenna.

The significance of this setal loss is not known. Konishi (1989) described the anomura hair as present in the first two zoeal stages of *Upogebia major* (de Haan, 1841), but in the third zoeal stage it had developed into a spine. A similar loss during anomuran development was recorded by Shenoy (1967) and Ngoc-Ho (1977, 1981). Perhaps an explanation could be that the zoea of *C. ortmanni* has hatched in such an advanced state that the seta has been completely lost (not expressed) from the telson during development.

Feeding. – The *Chirostylus ortmanni* zoea described in this study is unequivocally identified as the first stage because it hatched directly from the egg in the laboratory and the first two maxillipeds possess four long plumose natatory setae on the distal exopod segment. First stage *Chirostylus* zoeas have been described for *C. dolichopus* by Ogawa & Matsuzaki (1992) and although they considered this zoea to be incomplete, their description compares favourably with that of *C. ortmanni* described in this study. The main difference between the two descriptions are that Ogawa & Matsuzaki (1992) describe the distal exopod segment of the pleopods with what appears to be 5 to 6 short marginal setae compared with setal “buds” in the present study, Fig. 6a–e).

Although the exopod (scaphognathite) setae of the maxilla and those of the first two maxillipeds are present and appear to be fully functional, the former to create water currents to

oxygenate the branchial chamber and the latter natatory, in *C. ortmanni* the setae on the coxa, basis and endopod of the maxillule, maxilla, first maxilliped and the second maxilliped are absent (see Figs. 2b, c; 3a, b). In comparison, the coxa, basis and endopod of the maxillule, maxilla, first maxilliped and the second maxilliped of the anomuran *Galathea inflata* Potts, 1915 [Galatheidae] by Fujita et al. (2001) and the brachyuran *Pilumnus sluiteri* De Man, 1892 [Pilumnidae] by Clark & Ng (2004), for example, are prominently armed with setae. Furthermore, the strong muscles attached to the mandibles in typical anomuran and brachyuran zoeas are feeble in *C. ortmanni*. The distinct setal and musculature differences in cephalic appendages seem to suggest that the zoeas of *P. sluiteri* and *G. inflata* have a different feeding strategy than the zoea of *C. ortmanni*. Typical live anomuran and brachyuran zoeae, when reared in the laboratory actively feed on *Artemia* whereas those of *C. ortmanni* were inactive and swam sporadically. In fact, after hatching, instead of actively swimming towards a light (as is typical for most decapod zoeas), those of *C. ortmanni* remained on the bottom on the container. Further the zoeas of *C. ortmanni* were observed with a yellow yolk stored under the carapace. Therefore the evidence presented by this study suggests that the first zoeal stage of *C. ortmanni* is probably lecithotrophic, absorbing yolk stored in the body cavity.

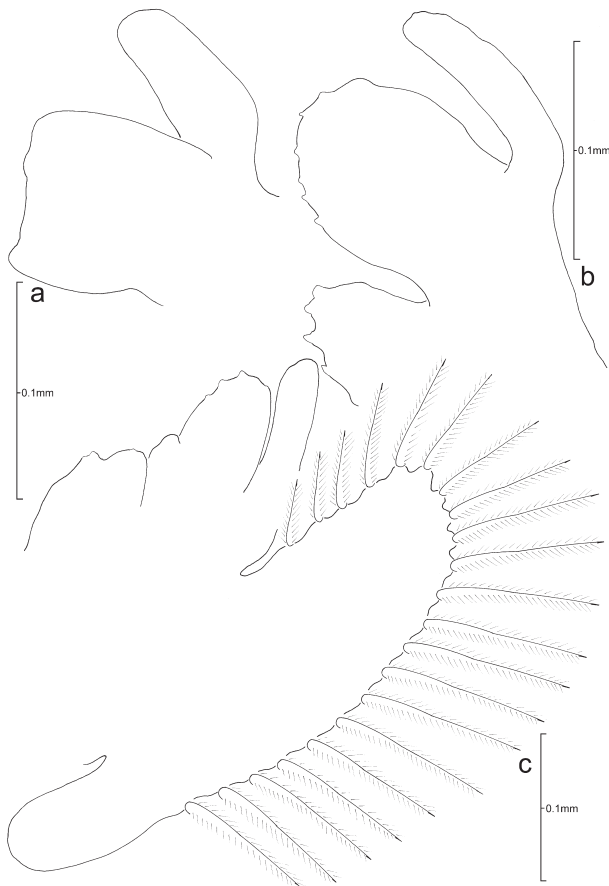


Fig. 2. *Chirostylus ortmanni* Miyake & Baba, 1968: a, mandible; b maxillule; c, maxilla.

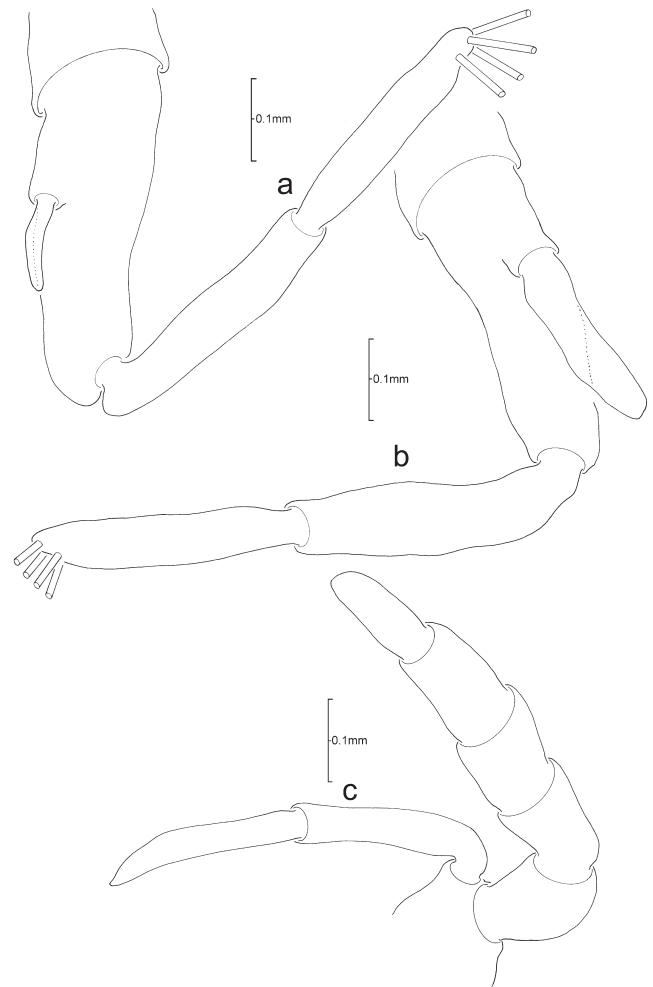


Fig. 3. *Chirostylus ortmanni* Miyake & Baba, 1968: a, first maxilliped; b, second maxilliped; c, third maxilliped.

The larvae of two other chirostyloid genera are known. Pike & Wear (1969) described the first stage zoeas of *Gastroptychus novaezelandiae* Baba, 1974 [as *Gastroptychus* n. sp.] and *Uroptychus tomentosus* Baba, 1974 [as *Uroptychus* cf. *politus* Henderson, 1885]. Their study, however, does not meet with modern standards, as they did not describe fully the maxillule and the maxilla. A redescription of these appendages may provide evidence of yolk feeding zoeas for these species as well.

Lecithotrophic decapod zoeas have previously been recognised by a number of authors for marine brachyuran including Issel (1910) who described the larval mouthparts of *Paguristes oculatus*, now *P. emerita* (Linnaeus, 1767), as lacking setae. Although Fage and Monod (1936) reported on the abbreviated development of *Munidopsis polymorpha* Koelbel, 1892, it was Wilkens et al. (1990) that recorded the first and second zoeas of this species possessed a large supply of yolk, did not feed and were almost unable to undergo locomotion. Samuelsen (1972) noted that the yolk in the three zoeal stages of *M. tridentata* (Esmark, 1857) appeared to be the only source of food, their mouthparts were reduced and they did not feed. Harvey (1992) stated that the two zoeal stages of *Coenobita variabilis* McCulloch, 1909, had fully developed setosed mouthparts, but were non-feeding and Saito & Konishi (2002) described the first zoea of *Pylocheles mortenseni* (Boas, 1926) as advanced, planktonic and

lecithotrophic. However, there are two further decapod larval descriptions for which the authors did not appreciate the strategy of lecithotrophic feeding. These include the brachyuran cymonid *Cymonomus bathamae* Dell, 1971, by Wear & Batham (1975) and chirostyloid *Chirostylus dolichopus* Ortmann, 1892, by Ogawa & Matsuzaki (1992).

In common with *Chirostylus ortmanni*, all zoeal stages of *Geosesarma perracae*, *Cryptodromia pileifera*, *Cymonomus bathamae*, and *Chirostylus dolichopus* have either poorly defined (reduced) mouthparts or are devoid of setae on the coxa, basis and endopod of the maxillule, maxilla and first two maxillipeds (see Figs. 2b, c; 3a, b). All these appendages suggest a non-feeding strategy.

Wilkens et al. (1990) studied the population biology and larvae of the anchialine anomuran *Munidopsis polymorpha* [Galatheidae] from Lanzarote, Canary Islands. According to them the two zoeal stages did not swim or feed; instead, for the latter, the larvae possessed a huge supply of yolk. Unfortunately, the mouthparts of the zoeas were not independently figured so the setal formula of the coxa, basis and endopod for these appendages remains unknown. A modern description of *Munidopsis polymorpha* larval stages including setation of mouthparts would be desirable.

Of further interest is the larval sequence of the brachyuran majid *Achaeus fissifrons* (Haswell, 1879) described by Wear & Fielder (1985) from laboratory hatched eggs, with its supposedly one zoeal stage and a megalop. However, Wear

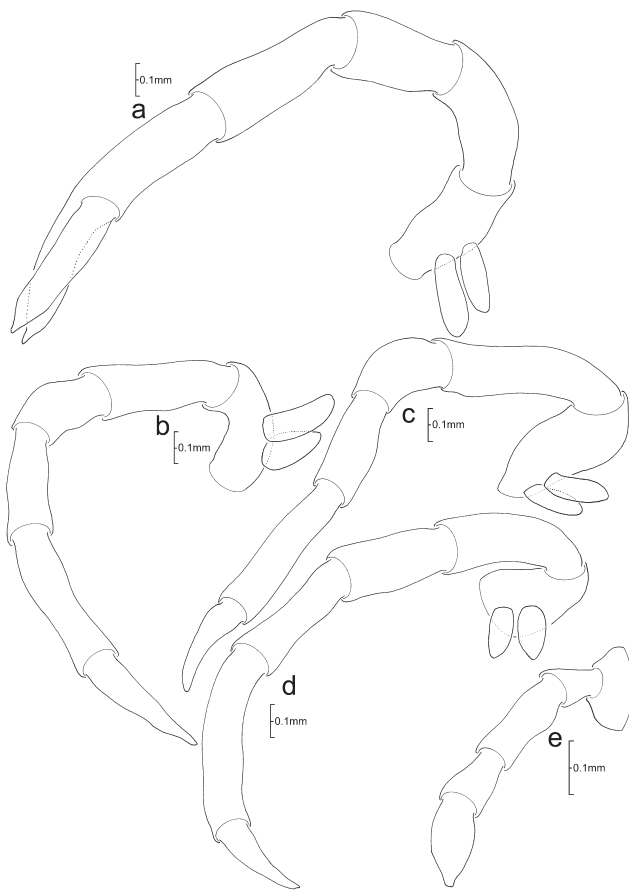


Fig. 4. *Chirostylus ortmanni* Miyake & Baba, 1968: a, first (chela) pereopod; b, second pereopod; c, third pereopod; d, fourth pereopod; e, fifth pereopod.

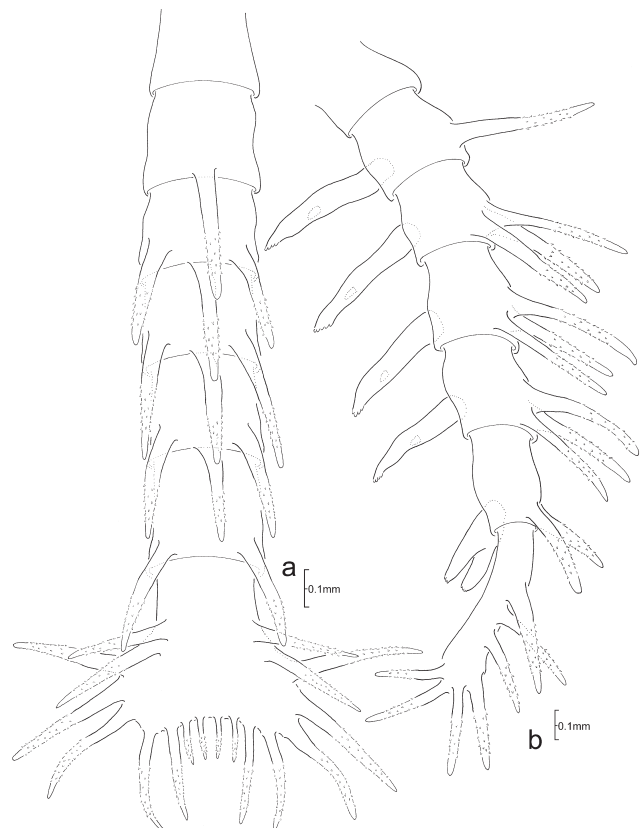


Fig. 5. *Chirostylus ortmanni* Miyake & Baba, 1968: a, dorsal view of abdomen; b, lateral view of abdomen.

& Fielder (1985: Figs. 74, 75) do not fully describe the maxillule, maxilla and, first and second maxilliped. Their whole zoeal figure (Wear & Fielder, 1985: Fig. 74) in lateral view seems to depict the first and second maxilliped devoid of endopod. Whether this is in error or a tantalising hint of a majid zoea adapted for lecithotrophic feeding remains an uncertainty until this larval stage can be re-examined.

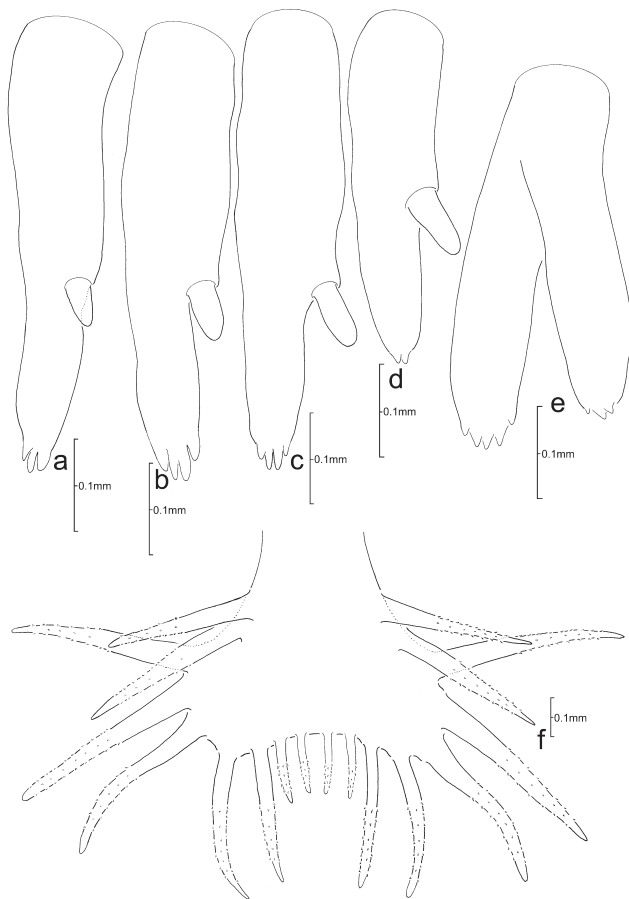


Fig. 6. *Chirostylus ortmanni* Miyake & Baba, 1968: a, second pleopod; b, third pleopod; c, fourth pleopod; d, fifth pleopod; e, uropod; f, dorsal view of telson.

Abbreviated zoeal development. – Lecithotrophic feeding larvae seem to be associated with abbreviated zoeal development. For example, if the first stage zoea of *Chirostylus ortmanni* is compared to the description of *Galathea inflata* by Fujita et al. (2001), its development appears to be equivalent to the fourth or fifth stage zoea of this galatheid. Developmental characters common to these *Chirostylus* and *Galathea* zoeas are the antennular and antennal endopods; a distinct mandibular palp; well-developed pereopods and biramous third maxilliped, biramous pleopods, and the sixth abdominal somite is differentiated. A comparison of the *C. ortmanni* first stage zoea with the second stage zoea of the brachyuran *Pilumnus sluiteri*, for which Clark & Ng (2004) described two zoeal stages prior to the metamorphosis to megalop is interesting. The zoeal phase of *P. sluiteri* was described in detail by Clark & Ng (2004) and it has all of the advanced or abbreviated characters exhibited in the *C. ortmanni* first stage zoea; i.e. antennule and antennal endopods; mandibular palp; well-developed pereopods and biramous third maxilliped, biramous pleopods and the presence of the sixth abdominal somite. For the larvae of two other chirostylid genera *Gastroptychus novaezelandiae* and *Uroptychus tomentosus*, Pike & Wear (1969: 194) stated that the zoeas of both species hatched in an advanced condition equivalent to a normal fourth or fifth stage galatheid larva.

For crabs in the family Sesarmidae, Soh (1969) described two zoeal stages for the Malaysian wholly freshwater *Geosesarma peraccae* that metamorphosed to megalop within 55 to 60 hours; as has also been documented for several species of *Sesarma* and *Metopaulias* in Jamaica (see Hartnoll, 1964; Diesel & Schuh, 1993; Diesel & Horst, 1995). For marine crabs, Tan et al. (1986) reported only one zoeal stage for *Cryptodromia pileifera*. However, the actual number of zoeal stages described by Wear & Batham (1975) remains unclear. They described and figured the first stage zoea of *Cymonomus bathamae*, but according to their study (Wear & Batham, 1975: 116), the second author observed a stage two zoea about six hours after hatching as stage one (= first stage zoea). This second stage zoea was observed live and sketched by him but according to the authors, the larva was unfortunately later mislaid, and the figures of the second stage

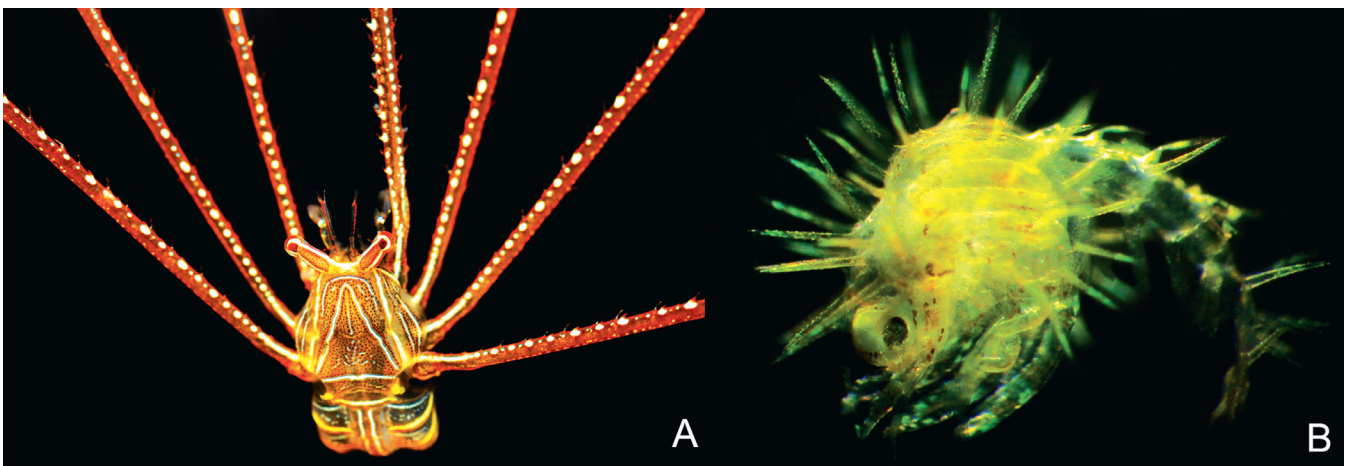


Fig. 7. *Chirostylus ortmanni* Miyake & Baba, 1968: A, gravid female (ZRC 2007.0701); B, whole view of first stage zoea (ZRC 2007.0701).

zoea are not included in the paper. Consequently, the authors (Wear & Batham, 1975: 116) were uncertain if *C. bathamae* had two zoeal stages with a first stage zoea of short duration before moulting to second stage zoea or one single zoeal stage that moulted directly to megalop. Ogawa & Matsuzaki (1992) also seem unaware that the zoeal characters they describe for *C. dolichopus* suggest that the next moult will be the metamorphosis to megalop.

For *Munidopsis polymorpha*, Wilkens et al. (1990) described its larval development with two zoeal stages, the second of which “moults into a small crab, morphologically identical to the adult” thereby suggesting that the megalop phase is lost. This interpretation of the larval development may be incorrect, as there have been no records in the literature of zoea metamorphosing directly into first crab stage. Their Fig. 1 definitely illustrates two different zoeal stages as shown by the four and six natatory setae on the distal exopod segment of the first two maxillipeds, however, the first crab stage was probably the megalop.

The first larva of the paguroidean pomatochelid hermit crab *Pomatocheles jeffreysii* Miers, 1879 (supposedly a prezoa-like stage) was described by Konishi & Imafuku (2000). This hatching was premature, and only one of five eggs survived to reach this point, and the one that “hatched” had to be dissected out of the cuticle. But the importance of the Konishi & Imafuku (2000) report was that it provided the first glimpse of pylochelid larval development. In the discussion on the first larval stage of *Pylocheles mortensenii*, Saito & Konishi (2002) indicated that the development of this species was advanced in the same characters as the present authors have found in *C. ortmanni*. Also like *C. ortmanni*, *P. mortensenii* zoeas had four natatory setae on the exopods of the first and second maxillipeds as in other planktonic zoeas. Saito & Konishi (2002) when comparing *P. mortensenii* to *Pomatocheles jeffreysii*, concluded that the latter species hatched at a more advanced stage of development.

To conclude this section, abbreviated development and reports of “inactive” zoeas appear to suggest that the dispersal of decapod species with a lecithotrophic phase is localised and not over a wide area.

Chirostylid systematics. – Chirostylids are currently assigned to the Galatheoidea (Martin & Davis, 2001; Ng, 1998), together with the marine families Galatheidae and Porcellanidae. The only other taxon assigned to this superfamily is the Aeglidae, whose members are wholly freshwater with their larvae developing directly into juvenile crabs (Bond-Buckup & Buckup, 1994). The classification of the family in Galatheoidea has never been challenged (e.g., see Baba, 2005), although McLaughlin et al. (2007) recently argued that the aeglids should be placed in their own superfamily.

Apart from the brachyuran-like shape of the chirostylid zoea, there are additional characters that differ from the generally more caridean-like larvae (i.e., elongate and laterally compressed) of the galatheids as exemplified by *Galathea*

inflata described by Fujita et al. (2001). *Chirostylus ortmanni* also does not possess posterolateral spines on the carapace. A segmented antennular peduncle is in marked contrast to the antennule described by Fujita et al. (2001: Figs. 2A, 4A, 6A, 8A, 10A) for *G. inflata*. The antenna of *C. ortmanni* (Fig. 1) is brachyuran-like, minus the exopod (e.g., see *P. sluiteri*, Clark & Ng, 2004: Figs. 5a, b) and without the typical anomuran scaphocerite armed with marginal plumose setae (Fujita et al., 2001: Figs. 2b, 4B, 6B, 8B, 10B). The uropod of *C. ortmanni* (Fig. 5e), although biramous, is relatively small and not well developed with plumose marginal setae on the endopod and exopod when compared with *G. inflata* (see Fujita et al. 2001: Figs. 5C, 7C, 9C).

The larvae of two other chirostylid genera are known. Pike & Wear (1969) described the first stage zoeas of *Gastroptychus novaezelandiae* and *Uroptychus tomentosus*, and some comparisons with *Chirostylus ortmanni* and *C. dolichopus* are appropriate. The setae on the coxa, basis and endopod of the first and second maxillipeds for *U. tomentosus* (Pike & Wear, 1969: Fig. 5) and *G. novaezelandiae* (Pike & Wear, 1969: Fig. 12) are reduced, the abdomen is six segmented (Pike & Wear, 1969: Figs. 1-2, 8-9 respectively) and a biramous uropod (Pike & Wear, 1969: 193, Fig. 14 respectively) is prominent. For both species, the carapace of the zoea appears to be brachyuran-like and without posterolateral spines. Further the peduncle of the antennule appears to be segmented. These characters are common to the *Chirostylus* as described by Ogawa & Matsuzaki (1992) and in the present study.

The differences documented here are intriguing. Are the many differences in general zoeal shape, carapace characters, and antennular, antennal and uropod morphology observed all merely a consequence of their abbreviated development; or indicative of more significant phylogenetic differences between chirostylids and galatheids? How closely related are the three families now placed in the Galatheoidea Samouelle, 1819, should perhaps be re-examined. Interestingly, McLaughlin et al. (2007) noted that within the Galatheoidea, the porcellanids and galatheids were more closely related, with the chirostylids coming out as a separate clade. In light of the substantial larval differences observed, the affinities of the chirostylids with other galatheids will need to be re-examined. There is some precedence – substantial larval differences observed in the zoea of some brachyuran genera have later been supported by revised morphological and/or molecular data sets that demonstrated that the old classification was flawed [e.g., *Tanaocheles* in Pilumnidae and not Xanthidae (Ng & Clark, 2000); and *Xenograpsus* in its own family and not Varunidae (Jeng et al., 2004; Ng et al., 2007)].

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