

## THE LARVAL DEVELOPMENT OF *CARIDINA PSEUDODENTICULATA* (CRUSTACEA: DECAPODA: ATYIDAE) REARED IN THE LABORATORY, WITH A DISCUSSION OF LARVAL METAMORPHOSIS TYPES

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**ABSTRACT.** – The moult and metamorphosis types of *Caridina pseudodenticulata* were described and compared with the other atyid shrimps in this study. *C. pseudodenticulata* inhabits lakes or lentic waters of western Taiwan. The eggs of *C. pseudodenticulata* are larger and fewer than most of atyid shrimps. The newly hatched larvae were benthic and no planktonic behavior was observed. With water temperature of 21–28°C, larvae were metamorphosed into juvenile after five decapodid stages. Although larval metamorphosis type of this species belongs to complete suppression type, its larval morphology is between complete suppression type and abbreviate type. Therefore, in this study, the metamorphosis type of *C. pseudodenticulata* is suggested to be “complete suppression type B”, whereas the typical species as “complete suppression type A”.

**KEY WORDS.** – Larval development, *Caridina*, Atyidae, Freshwater shrimp.

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### INTRODUCTION

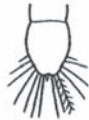
In Taiwan, small atyid shrimps typically inhabit clean freshwater areas, including rivers, streams, lakes, reservoirs, mountain creeks, pools, rice fields and irrigation canals. Atyid shrimps are omnivorous and primary consumers in an aquatic ecosystem. Most of the species feed on algae and organic matter that attached on surfaces of aquatic plants or rocks. The body lengths of most atyid shrimps are only about three centimeter. Although these shrimps are too small for edible use, they have been caught and even cultured as baits for carnivorous fishes.

There are 15 species in three genera (*Atyopsis*, *Caridina* and *Neocaridina*) of atyid shrimp in Taiwan (Hung et al., 1993; Shih & Cai, 2007). Most of these species produce relatively small-sized eggs; their larval metamorphoses are catadromous. On the other hand, there are a few species that produce relatively large eggs and lack planktonic stage in their life history. These large-egg atyid shrimps mostly live in land-locked fresh water areas for their whole life. Several authors have classified the egg size and larval development of freshwater shrimps. For example, Shokita (1981) classified the egg sizes of atyid shrimps into three types (large, medium, and small eggs) based on the diameters of the eggs. Sollaud (1923) divided larval metamorphoses of the palaemonid

prawns into common, abbreviated, and completely suppressed types. Shy et al. (1987) also used the same classification as Sollaud (1923) on larval metamorphoses of atyid shrimps based on both egg size and larval morphology (Table 1). The common type has 9–12 planktonic larval stages, and the pleopod of the first larval stage is not developed yet. The abbreviated type has fewer (4–7) planktonic stages, and the pleopods of the first larval stage are still only buds. In addition, complete suppression type has no planktonic larval stage, and the pleopod is well developed.

*Caridina pseudodenticulata* Hung et al., 1993 inhabits in the west of the Central Mountain in Taiwan and usually lives in quiescent or slow moving waters, such as the middle-streams of rivers, reservoirs, lakes and other water bodies. Hung et al. (1993) reported that the egg diameter of *C. pseudodenticulata* is about  $0.77 \times 0.50$  mm, which is in between those of abbreviated and completely suppressed types (Table 1; Shy et al., 1987). However, there is no documented information regarding the larval morphology and its metamorphosis pattern of *C. pseudodenticulata*. The present study describes the morphological characteristics of each larval stage of *C. pseudodenticulata* in detail, and discusses the pattern of metamorphosis of the species in comparison with other atyid species.

Table 1. Comparison of the egg sizes and the morphology of the first larval stage among three metamorphosis types of atyid shrimps.

| Characteristics                     | Common type                                                                       | Abbreviated type                                                                   | Complete suppression type                                                           |
|-------------------------------------|-----------------------------------------------------------------------------------|------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|
| Freshly-deposited egg diameter (mm) | $0.44 \times 0.26$                                                                | $0.64 \times 0.40$                                                                 | $1.20 \times 0.80$                                                                  |
| Pereiopods                          | Buds only in pereiopods I & II; not developed in pereiopods III–V                 | Developed                                                                          | Completely developed                                                                |
| Pleopods                            | Undeveloped                                                                       | Developed                                                                          | Completely developed                                                                |
| Telson                              |  |  |  |
| Stages                              | 9–12 planktonic stages                                                            | 4–7 planktonic stages                                                              | Benthic                                                                             |

## MATERIALS AND METHODS

Ovigerous females reared in this study were collected from Nei Hu District in Taipei City at 28 Jul.2004. The collected ovigerous females were brought back to the laboratory of National Penghu University (NPU). Ten ovigerous females were reared individually in one-litre beakers filled with 0.8 litre dechlorinated water. The water temperature was 21–28°C. Once larvae were hatched, mothers were removed from the tanks. The larvae were fed with artificial food (Gin Shar Miu, black granule power, Chuan Kuan Enterprise, Kaohsiung, Taiwan). Five individual larva were sampled and deposited in 95% alcohol every day for succeeding measurement and morphological examination. Measurement items included diameter of eyed egg, carapace length (postorbit length) and body length (from postorbit to posterior tip of the telson, exclusive of plumose setae). The larva of each stage was drawn with Nikon profile projector V-12 and Nikon digital counter CM-6S. All specimens were deposited in NPU.

## RESULTS

Eyed-eggs of *C. pseudodenticulata* were oval-shaped and the average size was  $0.77 \pm 0.01$  mm  $\times$   $0.50 \pm 0.01$  mm ( $n = 5$ ). Hatched larvae were stayed on the bottom of the tanks. In this study, larvae were metamorphosed into juvenile after five decapodid stages. Descriptions of larvae characteristics are as follows.

**Stage 1: Hatching day (Fig. 1).** – Average carapace and body length were  $0.55 \pm 0.01$  mm and  $1.64 \pm 0.01$  mm, respectively.

Carapace (Fig. 1A, B): Rostrum without tooth, straight and reaching distal part of basal segment of antennular peduncle.

Eyes (Fig. 1A, B): stalked, movable.

Antennule (Fig. 1C): Antennule with 3 basal segments, inner border with one long plumose setae between segments.

Coxal segment with antennule spine, apex of spine with one plumose seta and 4 fine plumose setae on outer border. Inner and outer flagellum developed, inner flagellum 4 segmented, outer flagellum 2 segmented with five setae on apex.

Antenna (Fig. 1D): Antennal scale unsegmented, outer upper border with one immovable spine, inner border of scale with 15 plumose setae. Antennal flagellum with 23 segments.

Maxillule (Fig. 1E): Coxal, basal segments and palp developed. Coxal segment with 5 fine setae on apex. Basal segment with 7 spines on upper border. Palp unsegmented.

Maxilla (Fig. 1F): Scaphognathite, coxal and basal segments developed. Lower border of scaphognathite with 3 plumose spines, outer and upper borders with 15 plumose setae. Coxal segments with 6 plumose spines. Basal segment divided into dorsal and ventral lobes, with 4 plumose spines and 6 plumose spines, respectively.

Maxilliped I (Fig. 1G): Endopod small, slender. Apex of exopod with 2 pairs of plumose setae. Caridean lobe with fine setae.

Maxilliped II: (Fig. 1H) Endopod 3 segmented, 1 pair of plumose seta on the apex. Apex of exopod with 3 pairs of plumose setae.

Maxilliped III (Fig. 1I): Endopod 5 segmented, tip slender, pointed. Apex of exopod with 3 pairs of plumose setae.

Pereiopods I, II (Fig. 1J, K): 7 segmented, claws formed, with one distal fine seta except for propodus of pereiopod II.

Pereiopods III–V (Fig. 1L–N): Similar to each other. 7 segmented, inner borders of dactyli with one spine.

Abdominal somite (Fig. 1A, B): 6 segmented.

Pleopod I (Fig. 1O): Endopod bud like, without plumose seta; exopod long, wide, with plumose setae.

Pleopod II–V (Fig. 1P–S): Endo- and exopod with plumose setae.

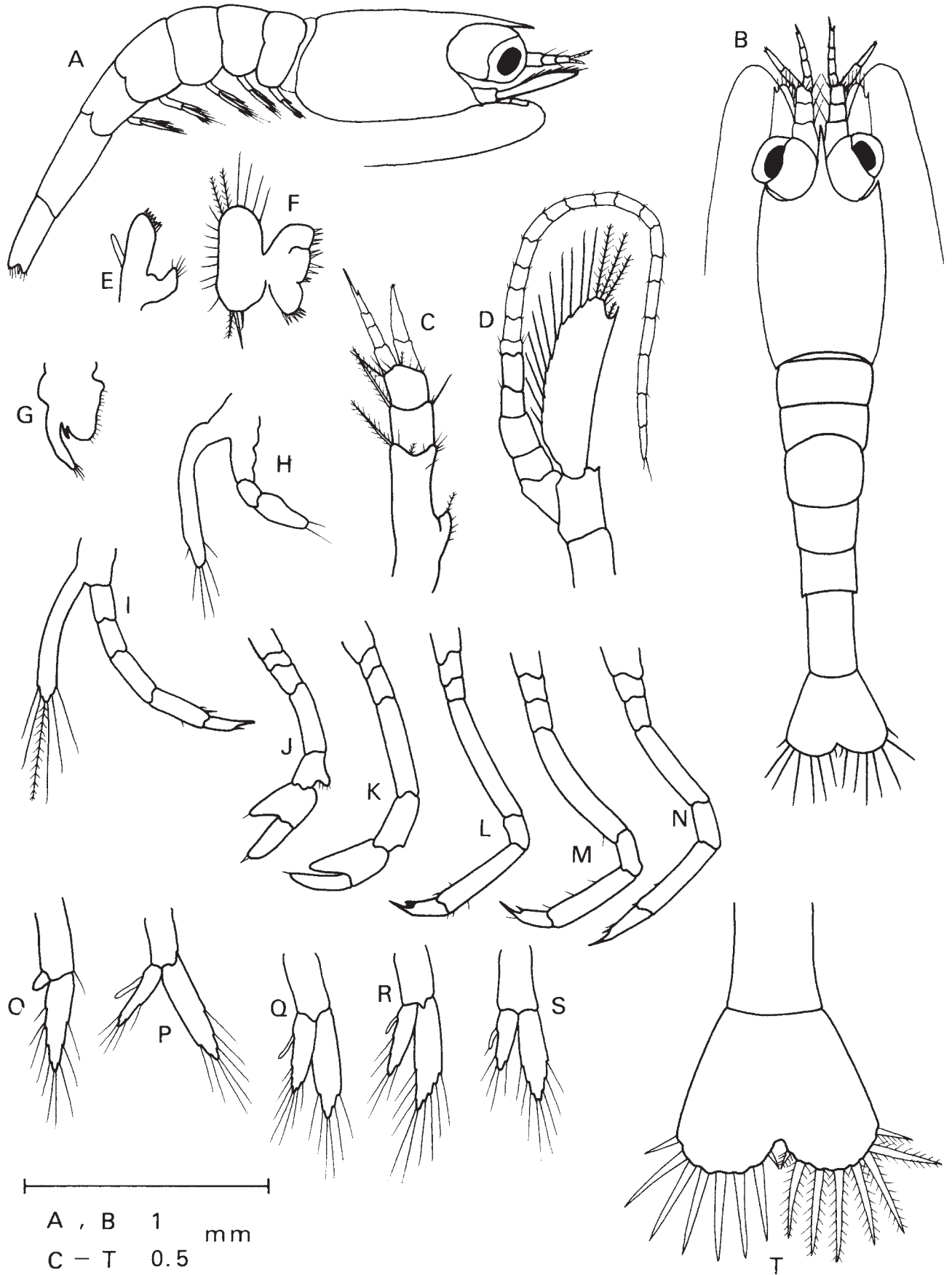


Fig. 1. *Caridina pseudodenticulata* 1st larval stage: A, lateral view; B, dorsal view; C, antennule; D, antenna; E, maxillule; F, maxilla; G-I, maxillipeds I-III; J-N, pereopods I-V; O-S, pleopods I-V; T, telson.

Rhipidura (Fig. 1T): Telson developed, lower border with 8 pairs of spines, outer most spine with setae only on inner border. Uropod undeveloped.

**Stage 2 (Fig. 2).** – The larvae moulted into stage 2 at the second day after hatching. Average carapace and body lengths were  $0.58 \pm 0.01$  mm and  $1.67 \pm 0.02$  mm, respectively.

Carapace (Fig. 2A, B): Rostrum tooth undeveloped. Antennule (Fig. 2D): Outer flagellum with one seta on apex. Inner flagellum 4 segmented, apex blunt, with 3 fine setae.

Antenna (Fig. 2C): Inner border of scale with 17 plumose setae. Antennal flagellum with 28 segments.

Maxillule (Fig. 2E): Upper border of basal segments with 9 spines. Apex of coxal segment with 3 fine spines.

Maxilla (Fig. 2F): Scaphognathite with 16 plumose setae. Dorsal and ventral lobes of basal segment with 5 and 12 plumose spines, respectively. Coxal segment with 13 plumose spines.

Maxilliped I (Fig. 2G): Similar to previous stage.

Maxilliped II (Fig. 2H): Endopod with 4 segments. Dactylus with plumose spines, similar to those of adult.

Maxilliped III (Fig. 2I): Endopod 4 segmented, with small spines on propodus and dactylus. Apex of exopod with 4 plumose setae.

Pereiopods I–V (Fig. 2J–N): Similar to previous stage.

Pleopod I (Fig. 2O): Endopod with plumose seta.

Pleopod II–V (Fig. 2P–S): Similar to previous stage.

Rhipidura (Fig. 2T): Uropod developed, with endo- and exopod. Apex of endopod with 2 fine setae. Distal border of exopod with 10 plumose setae, Disto-outer border with one movable spine. Distal border of telson with 7 pairs of plumose spine and 1 naked outer most spine.

**Stage 3 (Fig. 3).** – The larvae moulted into stage 3 during the fourth to fifth day after hatching. Average carapace and body lengths were  $0.62 \pm 0.01$  mm and  $1.84 \pm 0.02$  mm, respectively.

Carapace (Fig. 3A, B): Upper border of rostrum with 2–4 teeth.

Antennule (Fig. 3C): Inner flagellum with 3 segments, apex of terminal segment with 3 fine setae, second segment with 3 aesthetes. Outer flagellum with 6 segments.

Antenna (Fig. 3D): Inner border of scale with 20 plumose setae. Antennal flagellum with 31 segments.

Maxillule (Fig. 3F): Basal and coxal segments with 12 and 10 spines, respectively. Palp segmented.

Maxilla (Fig. 3G): Scaphognathite with 2 plumose spines on posterior end.

Maxillipeds I–III, Pereiopods I–V, Pleopods I–V (Fig. 3H–T): Similar to previous stage.

Rhipidura (Fig. 3U): Inner to distal borders of endopod and exopod with 10 and 14 plumose setae, respectively, disto-outer part with one movable and one unmovable spines. Telson with one pair of lateral spine, distal border with 7 pairs of plumose spines.

**Stage 4 (Fig. 4).** – The larvae moulted into stage 4 during the ninth to tenth day after hatching. Average carapace and body lengths were  $0.76$  mm  $\pm$   $0.01$  and  $1.99 \pm 0.02$  mm, respectively.

Carapace (Fig. 4A, B): Upper border of rostrum with 3–4 teeth.

Antennule (Fig. 4C): Inner flagellum with 2 aesthetes. Outer flagellum with 7 segments.

Antenna (Fig. 4D): Inner border of scale with 21 plumose setae. Antennal flagellum with 34 segments.

Maxillule (Fig. 4F): Basal and coxal segments with 12 and 11 spines, respectively. Palp 2 segmented, terminal segment with 2 fine setae on apex.

Maxilla (Fig. 4G): Scaphognathite border with 18 plumose spines. Dorsal and ventral lobes of basal segment with 6 and 21 plumose spines, respectively. Coxal segment with 17 plumose spines.

Maxillipeds I–III, Pereiopods I–V, Pleopods I–V (Fig. 4H–Q): Similar to previous stage.

Rhipidura (Fig. 4R): Inner to distal border of endopod and exopod with 13 and 17 plumose setae, respectively; sutural with 2 movable spines. Telson with 3 pairs of lateral spines, distal border with 5 pairs of plumose spines.

**Stage 5 (Fig. 5).** – The larvae moulted into stage 5 during the fifteenth to seventeenth days after hatching. Average carapace and body lengths were  $0.85 \pm 0.01$  mm and  $2.32 \pm 0.03$  mm, respectively.

Carapace (Fig. 5A): Upper and lower borders of rostrum with 6–7 and 1 teeth, respectively.

Antennule (Fig. 5B): Antennule spine elongated. Inner flagellum 5 segmented.

Antenna (Fig. 5C): Inner border of scale with 25 plumose setae. Antennal flagellum with 38 segments.

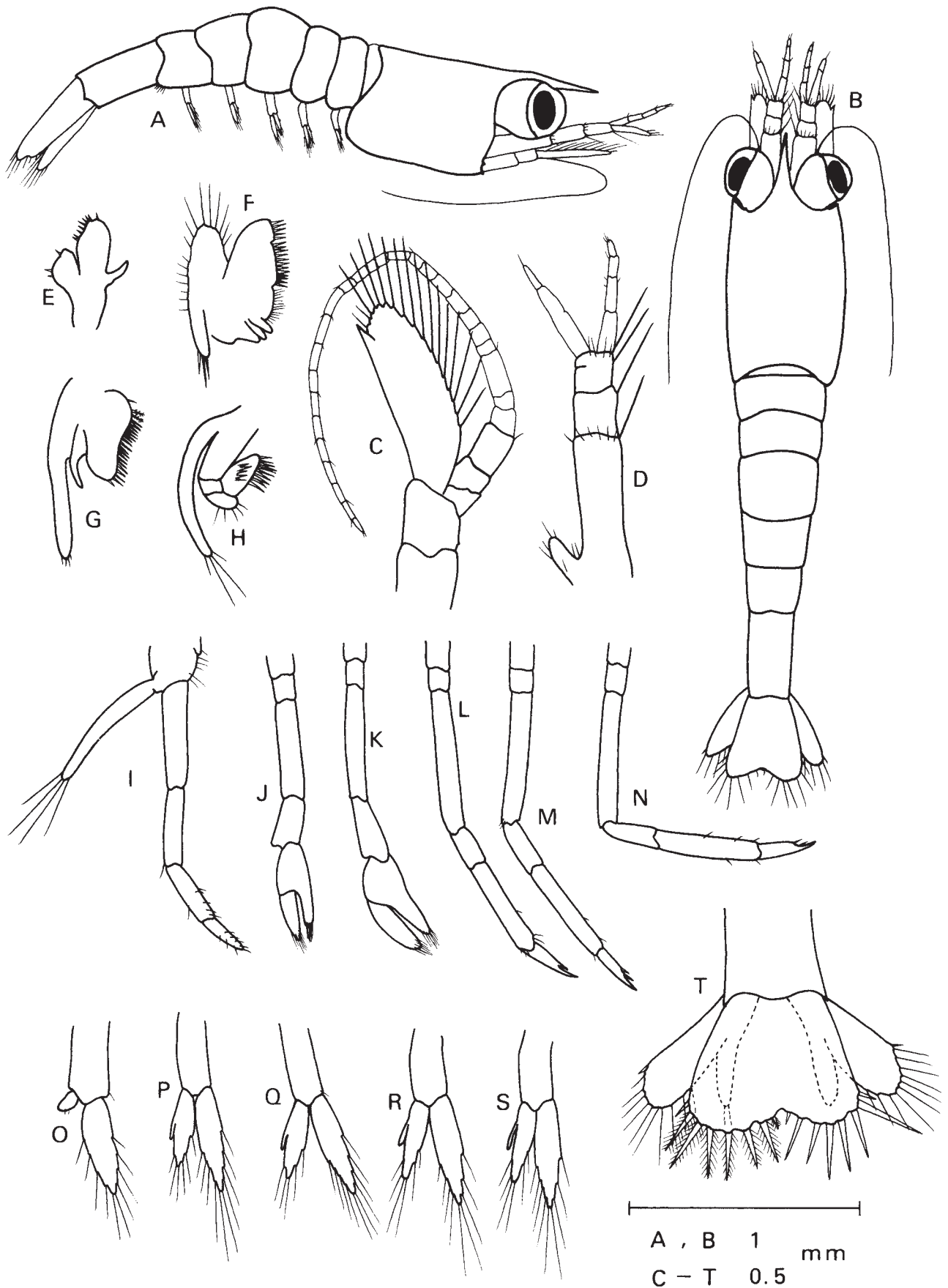


Fig. 2. *Caridina pseudodenticulata* 2nd larval stage: A, lateral view; B, dorsal view; C, antennule; D, antenna; E, maxillule; F, maxilla; G-I, maxillipeds I-III; J-N, pereiopods I-V; O-S, pleopods I-V; T, rhytidula.

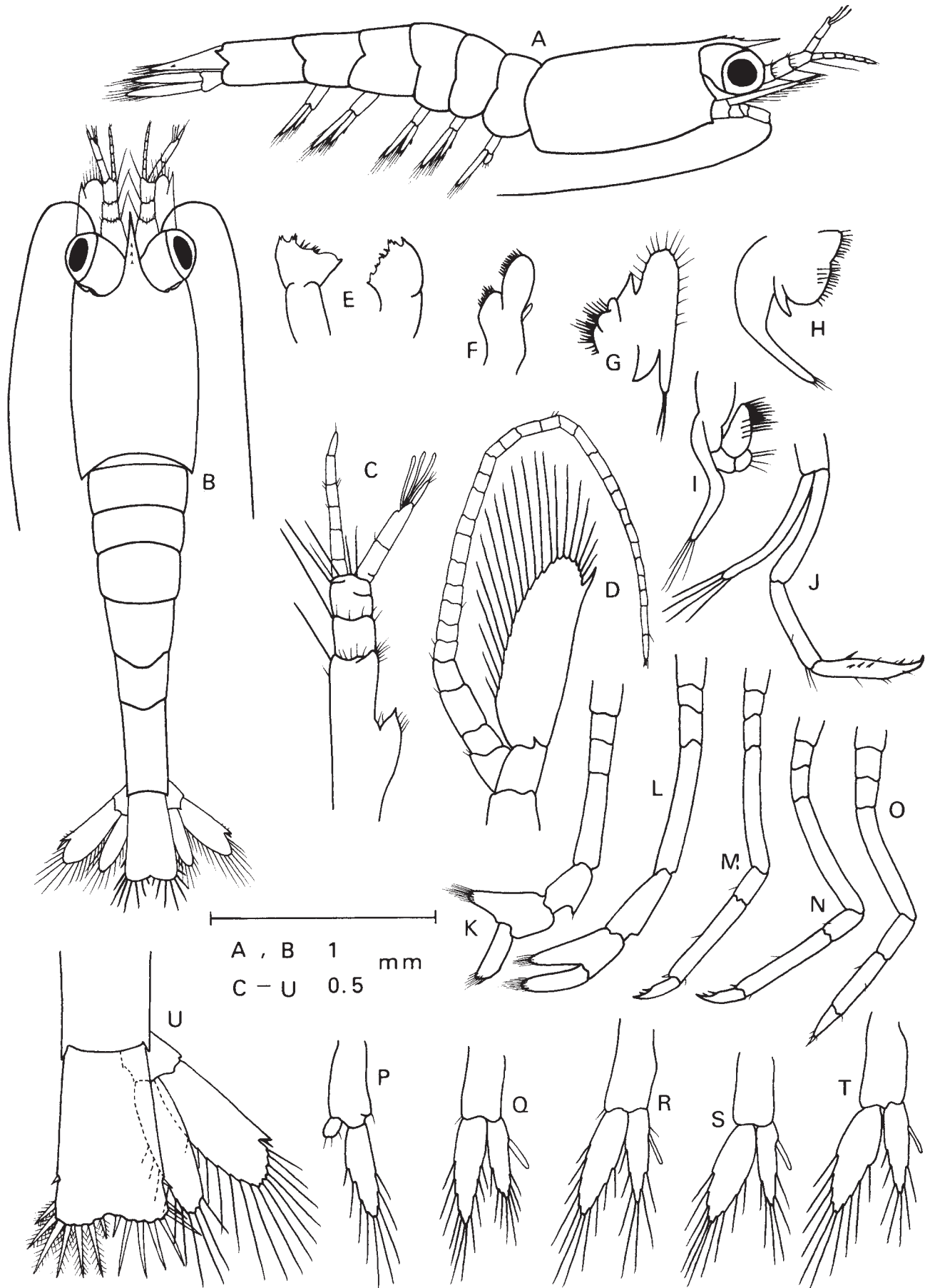


Fig. 3. *Caridina pseudodenticulata* 3rd larval stage: A, lateral view; B, dorsal view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H-J, maxillipeds I-III; K-O, pereopods I-V; P-T, pleopods I-V; U, rhyphidula.



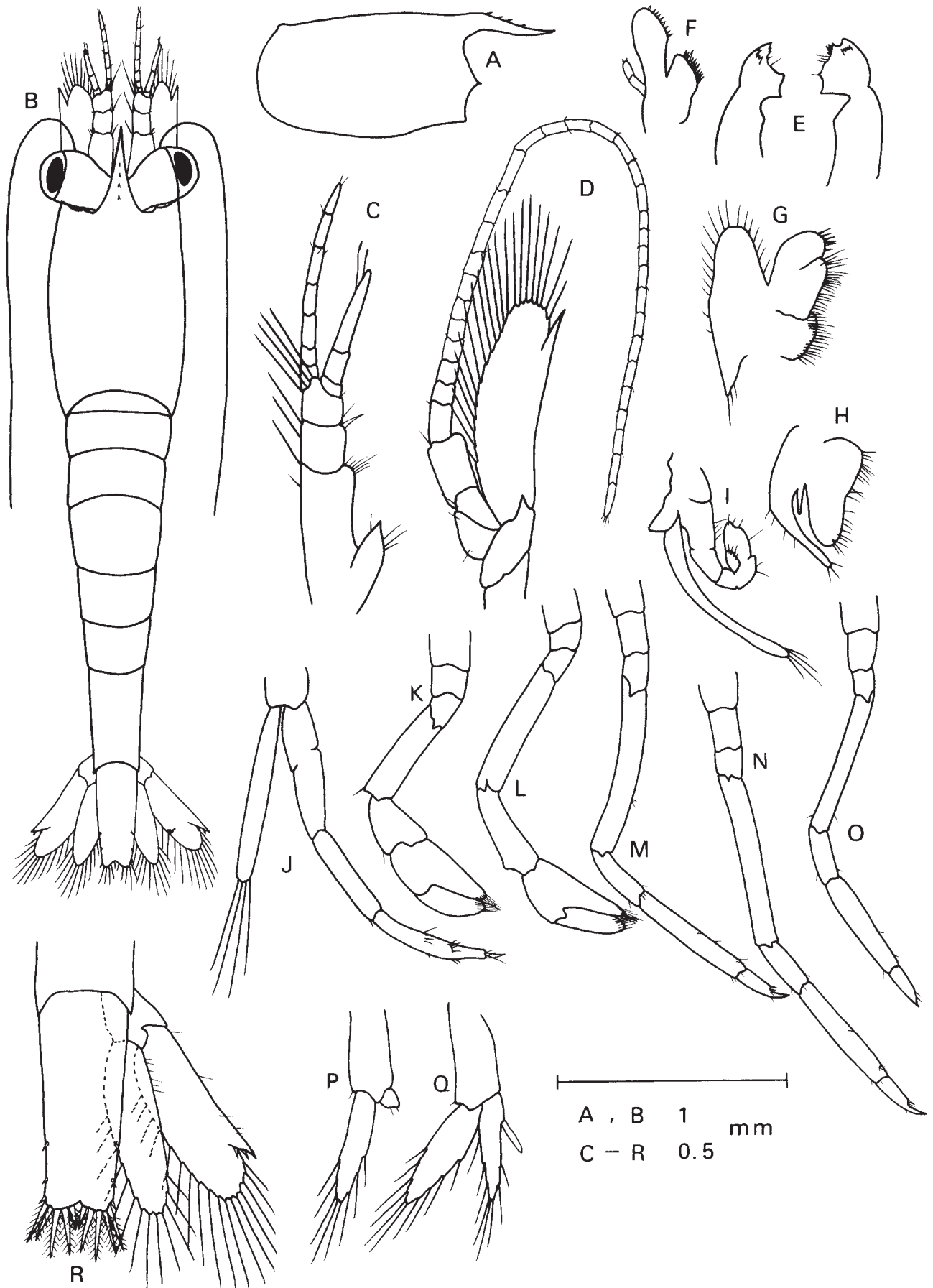


Fig. 4. *Caridina pseudodenticulata* 4th larval stage: A, lateral view of carapace; B, dorsal view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H-J, maxillipeds I-III; K-O, pereopods I-V; P, pleopod I; Q, pleopod II; R, rhytidula.

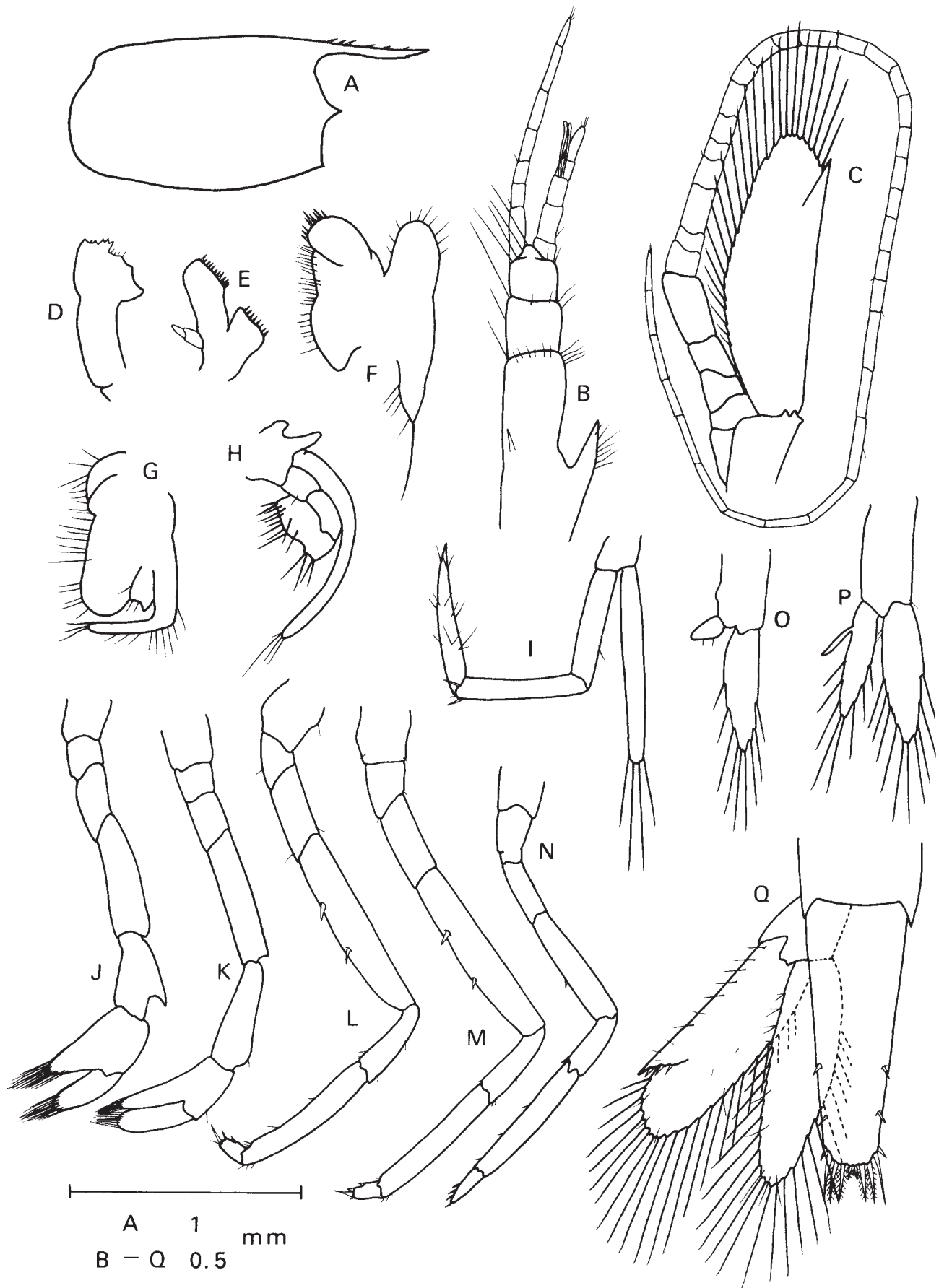


Fig. 5. *Caridina pseudodenticulata* 5th larval stage: A, lateral view of carapace; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G-I, maxillipeds I-III; J-N, pereopods I-V; O, pleopod I; P, pleopod II; Q, rhytidula.



Table 2. Larval characteristics of *Caridina pseudodenticulata* reared under the laboratory condition of water temperature 21–28°C. ACL, average carapace length; ABL, average body length.

| Larval stage | Days  | A.C.L. (mm) | A.B.L. (mm) | Characteristics                                                                                                                                                |
|--------------|-------|-------------|-------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1            | 1     | 0.55 ± 0.01 | 1.64 ± 0.01 | Stalked eyes;<br>Abdomen 7-segmented;<br>Telson: 8 pairs of plumose setae;<br>Uropod undeveloped                                                               |
| 2            | 2     | 0.58 ± 0.01 | 1.67 ± 0.02 | 1st & 2nd pereopods fingers with setae;<br>Uropod developed;<br>Rostrum without teeth.                                                                         |
| 3            | 4–5   | 0.62 ± 0.01 | 1.84 ± 0.02 | Upper margin of rostral teeth developed;<br>Coxopodite of uropod developed;<br>Telson: 1 pair of lateral spines;<br>Telson: 7 pairs of plumose setae.          |
| 4            | 9–10  | 0.76 ± 0.01 | 1.99 ± 0.02 | Sutural of uropod exopod developed;<br>Telson with 3 pairs of lateral spines;<br>Telson: 5 pairs of plumose setae.<br>Lower margin of rostral teeth developed; |
| 5            | 15–17 | 0.85 ± 0.01 | 2.32 ± 0.03 | Telson: <br>Telson: 4 pairs of plumose setae.                               |

Maxillule (Fig. 5E): Similar to previous stage.

Maxilla (Fig. 5F): Number of plumose setae of scaphognathite, coxal segment and ventral lobe of basal segment decreased, plumose spine increased to 9 on dorsal lobe.

Maxillipeds I–III, Pereiopods I–V, Pleopods I–V (Fig. 5G–P): Similar to previous stage.

Rhipidura (Fig. 5Q): Outer border of exopod of uropod with a line of fine plumose setae, and distal to inner border with 22 plumose setae, sutural with 3 movable spines. Inner to outer borders of endopod with 23 plumose setae. Telson with 3 pairs of plumose spine on distal border and 1 naked outer most spine.

The major morphological characters for each stage described above are shown in Table 2.

## DISCUSSION

**Comparison of first larval stage.** – Morphology of the first larval stage of *Caridina pseudodenticulata* was compared with those of *C. nilotica aurensis* (Roux, 1911) (abbreviated metamorphosis type, reported by Glaister, 1976) and *N. denticulata* (De Haan, 1844) (completely suppressed types, reported by Shy et. al., 1992) (Table 3).

**Antennule:** The inner and outer flagella of the antennule of the abbreviated type larva (*C. nilotica aurensis*) are not segmented. On the other hand, those of completely suppressed types (*N. denticulata*) are similar to those of adult stage. The length and the number of segments of inner and outer flagellum of *C. pseudodenticulata* are less developed than

those of the *N. denticulata*. The outer flagellum of the first antennule of the completely suppressed type has setae, while *C. pseudodenticulata* does not possess it.

**Antenna:** The flagellum of the *C. nilotica aurensis* larva is not segmented and the antennal scale has many segments, while the antenna of *N. denticulata* and *C. pseudodenticulata* possess similar appearances with the adult stage. *C. pseudodenticulata* has shorter flagellum with fewer segments.

**Maxilla:** Although the maxilla of *C. nilotica aurensis* is not like an adult form yet, the maxilla of *N. denticulata* already shows an adult-like appearance. Compared with *N. denticulata*, a posterior extension of the scaphognathite of *C. pseudodenticulata* has not been developed.

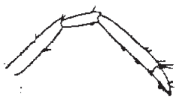
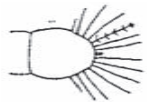
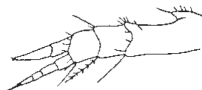
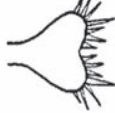
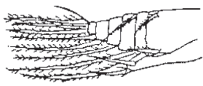
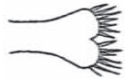
**First maxilliped:** The caridean lobe of the first maxilliped of *C. nilotica aurensis* is undeveloped, while it is developed well in that of *N. denticulata*.

**Second maxilliped:** The endopod of the second maxilliped of *C. nilotica aurensis* is similar to that of common type as it has 5 segments. However, *N. denticulata* already shows an adult form. The endopod of *C. pseudodenticulata* has the dactylus and propodus being not developed like its adult.

**Third maxilliped:** The endopod of *C. nilotica aurensis* has 5 segments as observed in the second maxilliped. On the other hand, *N. denticulata* shows adult-like form. *C. pseudodenticulata* has five segments in the endopod, which is more than that of *N. denticulata*, but *C. pseudodenticulata* has fewer fine setae.

**Pereiopods:** The pereiopods of *C. nilotica aurensis* are bud-like processes, while those of *N. denticulata* and *C.*

Table 3. Morphological comparison of first larval stages of completely suppressed type [*Neocaridina denticulata* (Shy, et. al., 1992)], complete suppression type-B [*Caridina pseudodenticulata* (present study)] and abbreviated type [*C. nilotica aurensis* (Glaister, 1976)].

| Characters                   | Fresh-laid egg diameter (mm) | Antennule                                                                            | Antenna                                                                              | Maxilla                                                                               | Maxilliped I                                                                          | Maxilliped II                                                                         | Maxilliped III                                                                      | Pereiopod I, II                                                                     | Pereiopod V                                                                         | Pleopod I                                                                           | Telson                                                                              |
|------------------------------|------------------------------|--------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|
| Completely suppressed type A | 1.10 × 0.71                  |   |   |    |    |    |    |    |    |    |    |
| Completely suppressed type B | 0.77 × 0.50                  |   |   |    |    |    |    |    |    |    |    |
| Abbreviated type             | 0.64 × 0.40                  |  |  |  |  |  |  |  |  |  |  |

*pseudodenticulata* are adult-like. The tips of movable and immovable fingers of the first and second pereopods of *C. pseudodenticulata* only have one small spine, whereas those of *N. denticulata* have several fine setae.

First pleopod: As seen in the pereopods, the pleopod of *C. n. aurensis* is bud-like, while the pleopods of *N. denticulata* are well-developed. The endopod of *C. pseudodenticulata* has not been fringed with fine setae yet.

Telson: The telson of *C. nilotica aurensis* is fused to sixth abdominal somite, and posterior end is bilobate. The telson of *N. denticulata*, however, is fan-like, not bilobate. The telson of *C. pseudodenticulata* shows intermediate form of former two species: the telson is segmented from the sixth abdominal somite and the posterior margin of the telson is bilobate.

**Larval metamorphoses patterns.** – In general, the first stage larvae of *C. pseudodenticulata* is less developed than the species with completely suppressed larval stage, such as *C. formosae* (reported by Shy et al., 1987 as *Neocaridina brevirostris*); *N. denticulata* (reported by Mizue & Iwamoto, 1961; Shy et al., 1992), *N. ishigakiensis* (reported by Shokita, 1976), *N. cf. iriomotensis* (reported by Shokita, 1973, see Naruse et al., 2006 and Cai et al., 2006 for its taxonomy) and *C. singhalensis* (reported by Benzie & Sliva, 1983). For example, the first larval stage of *C. pseudodenticulata* still has bud-like endopod of the first pleopod, while the endopod of *N. denticulata* already forms adult-like shape. On the other hand, the first stage larva of *C. pseudodenticulata* is more developed than the other species of abbreviated type, such as *C. nilotica aurensis* (Glaister, 1976). For example, the pleopod of the first larval stage of *C. pseudodenticulata* is at least segmented into basal segment, endo- and exopods, whereas *C. nilotica aurensis* only possesses rudimentary buds. Moreover, hatched larva of *C. pseudodenticulata* is benthic, which is closer behavior to complete suppression type, such as *N. denticulata* (see Shy et al., 1987). Therefore, it is suggested that the metamorphosis pattern of *C. pseudodenticulata* should be placed in between the completely suppressed type and the abbreviated type. The hatched larvae of both *N. denticulata* and *C. pseudodenticulata* stay on the bottom; this benthic behaviour suggests that the development pattern of *C. pseudodenticulata* is closer to that of *N. denticulata*. It seems to be best to differentiate the metamorphosis pattern of *C. pseudodenticulata* from both completely suppressed and the abbreviated types and place it in between them. In conclusion, besides common type and abbreviated type in larval development of the atyid shrimps, the complete suppression type is suggested to be further divided into complete compression type A (e.g. *N. denticulata*; also called typical complete suppression type), and complete suppression type B (e.g. *C. pseudodenticulata*, Table 3). The presence of this suppression type B gives an insight into the evolutionally transitional process of the post-embryonic life histories of freshwater shrimps toward adaptations to the freshwater environment.

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