

## The complete larval development of the ghost shrimp, *Callianassa japonica* Ortmann, 1891 (Decapoda: Thalassinidea: Callianassidae), reared in the laboratory

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**Abstract.** — Larvae of the thalassinidean shrimp, *Callianassa japonica* Ortmann, 1891, were reared through their entire development in the laboratory, starting from zoea 1 released by females collected on an intertidal sandflat of Ariake Sound in western Kyushu, Japan, in the middle of June, 1997. The larval development consisted of five zoeal stages and a decapodid stage. Minimum durations of the zoeal stages 1–4 and the zoeal stage 5 were 3 days and 4 days, respectively, at water temperatures of 22.0–24.7°C and salinities of 33.2–33.8. Morphology of each stage was described in comparison with that of another Japanese callianassid, *C. petalura*. The two species can be distinguished at the zoeal stage 1 and the decapodid stage, based on the presence (*C. japonica*) or absence (*C. petalura*) of a coxal seta on maxilliped 2 (in zoea 1) and on the smaller number of segments of the antennal flagella in *C. japonica* (in decapodid: 20–21 vs. 24–25).

### Introduction

Thalassinidean shrimps are one of the most common mega-invertebrates in marine intertidal and subtidal sediments. The callianassids in particular, among a number of bioturbating thalassinideans, have been reported to generate both considerable disturbances to ambient sediments (e.g., Rowden & Jones, 1993) and consequent effects on benthic community structure (e.g., Wynberg & Branch, 1994). Recently, on an intertidal sandflat in western

Kyushu, Japan, a population explosion of *Callianassa japonica* Ortmann has occurred, causing a substantial change in composition of the benthic fauna due to the shrimp's bioturbating activities (e.g., Tamaki & Suzukawa, 1991; Tamaki, 1994). Tamaki *et al.* (1998) suspected that the population explosion of shrimp had resulted from a recent increase in the survival rate during its planktonic stage, but this hypothesis has yet to be proven.

In recent ecological studies on marine benthic populations and communities, increased attention has been paid to the possibility of repercussions on the variation in benthic populations caused by larval abundance fluctuations (supply-side ecology: e.g., Underwood & Fairweather, 1989). However, substantiation of this prediction has not progressed much to date (Ólafsson *et al.*, 1994). One apparent reason is the difficulty of identifying the relevant larval species from natural plankton samples, especially discriminating among multiple congeneric species. This is due to limited descriptions of complete larval development based on laboratory-reared materials. Of Japanese callianassids, morphology for the entire larval development has been described for only *Callianassa petalura* Stimpson on the basis of larvae obtained under laboratory conditions (Konishi *et al.*, 1990). Besides this, only limited records are available for *C. japonica* larvae (laboratory-hatched Z1—Miyazaki, 1937; plankton samples—Kurata, 1965). To proceed with our study on natural abundance patterns of *C.*

*japonica* larvae in the context of supply-side ecology, it is indispensable to describe its larval morphology.

Before going further, however, a taxonomic confusion must be resolved. In his revision of Japanese callianassids, Sakai (1969) concluded that several previously reported species of the genus *Callianassa* were assignable to two species, *C. petalura* Stimpson, 1860 and *C. japonica* Ortmann, 1891. Synonyms of *C. japonica* Ortmann included *C. harmandi* Bouvier, 1901, *C. californiensis* var. *japonica* Bouvier, 1901, and *C. californiensis* var. *bouvieri* Makarov, 1938. However, careful examination of specimens collected from a number of intertidal sandflats along the estuary-open sea gradient in western Kyushu, Japan [from Ariake Sound (estuary) to the East China Sea (open sea)] (see Fig. 1 in Tamaki & Ueno, 1998) has disclosed that the definition of *C. japonica* made by Sakai is misleading. The material examined above fits Sakai's definition of *C. japonica*, but, in fact, includes two species: one is the true *C. japonica* and the other can be referred to as '*Callianassa japonica*: de Man, 1928', which Sakai merged with the former species (Manning & Tamaki, in preparation; hereafter in the present paper, the latter species will be referred to as *Callianassa* sp.). The species previously misidentified as *C. japonica* Ortmann and investigated by the present last author (A. T.) and his co-workers (e.g., Tamaki & Suzukawa, 1991; Tamaki, 1994; Tamaki *et al.*, 1996, 1998) has proven to be *Callianassa* sp.

The present paper gives a description of the complete larval history of *C. japonica*, based on laboratory-reared material, and compares it with previous larval descriptions of *C. petalura* and *C. japonica*.

#### Materials and Methods

During low tide on June 17, 1997, six ovigerous females of *Callianassa japonica* which seemed to be imminently releasing

larvae were collected using a yabby pump on the Okoshiki sandflat in Ariake Sound, western Kyushu [130°32.2' E; 32°39.9' N; see Fig. 1 in Tamaki & Ueno (1998)]. Females were kept in an aquarium with filtered sea water until larvae were released. The larvae had hatched by the next morning. A number of these larvae from all females were transferred to a single polycarbonate tank containing 30 liters of filtered sea water. One third of the sea water was replaced by new sea water at intervals of 2 to 5 days during the first 9-day period, after which it was changed daily. The larvae were fed with both cultured rotifers, *Brachionus rotundiformis* (on the first day and daily from the fourth day), and newly-hatched *Artemia* spp. nauplii (daily from the third day). Following a daily examination of the progression of the larval stages, more than 100 larvae at the Z1 and decapodid stages and about 20 larvae at the Z2–Z5 stages were fixed and preserved in 5% buffered sea-water formalin; the specimens of presumed Z1 were fixed on June 19 and larvae at the presumed subsequent stages on June 21 and 22 (Z2), June 24 (Z3), June 27 and 28 (Z4), June 30 (Z5), and July 4 (decapodid). During the course of the culture, salinity and water temperature of the tank varied between 33.2 and 33.8 and between 22.0°C and 24.7°C, respectively. Salinity values were higher than those experienced by larvae under natural conditions [30.5 at 5-m deep water just offshore of the Okoshiki sandflat for a 10-year average (July data)], while temperature values were close to the natural range (24.5–25.0°C) (data given in Coastal Oceanography Research Committee, The Oceanographical Society of Japan, 1985).

Appendages of the fixed larvae were dissected with fine insect pins. To check any variations in characters of appendages, 5 examples of each appendage were removed and examined from at least 3 larvae of each stage. Drawings and measurements were made with a drawing tube attached

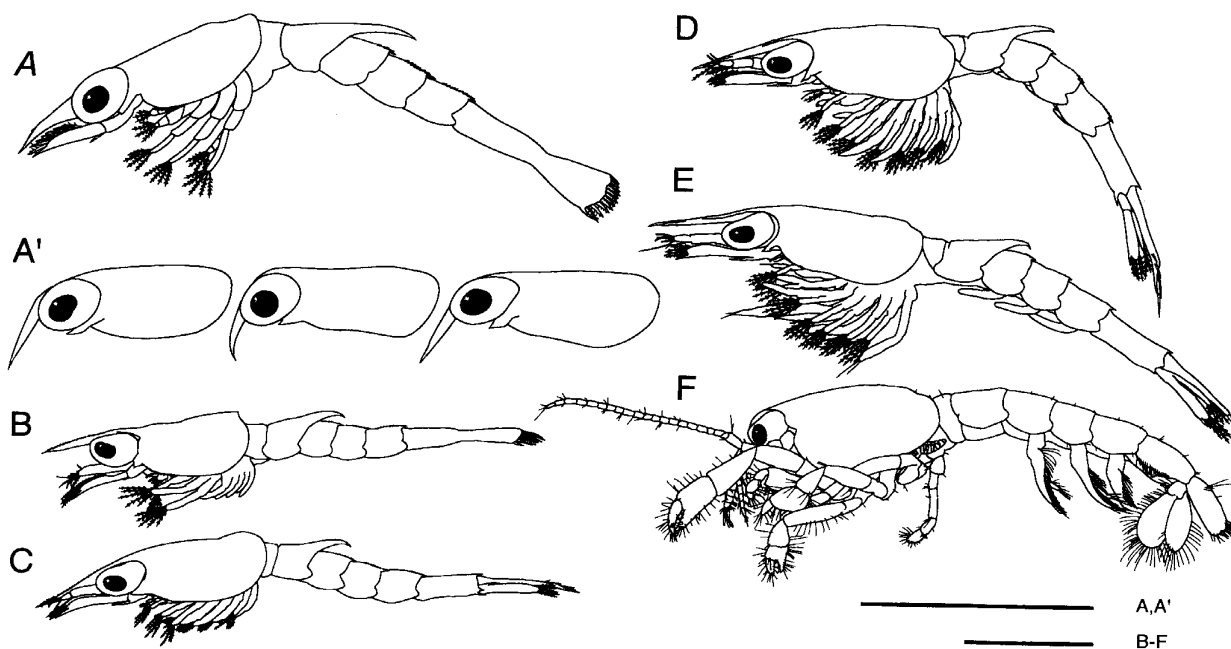


Fig. 1. *Callianassa japonica* Ortmann. A–F, lateral view of Z1–5 and decapodid; A', abnormal rostral spines of Z1 curving downwards. Scale = 1.0 mm.

to an Olympus BH-2 microscope or a Nikon Optiphot microscope. Terminology used in the present paper follows Konishi *et al.* (1990). The setal arrangement is described from proximal to distal. The segments are demarcated by 'commas'. Within a same segment, the respective setal groups are demarcated by 'plus' signs. 'T' and 'a' represent a dorso-lateral plumose seta and an aesthetasc, respectively. Carapace length (CL) was measured from tip of the rostral spine to the medial posterior margin of the carapace. For data on CL in the text, mean  $\pm$  SD [range;  $n$  = no. of larval specimens combined from the multiple (=6) clutches, each from a different female] values are given.

The specimens used in the present study have been deposited at the Zoological Institute, Faculty of Science, Hokkaido University under accession numbers, ZIHU1220–1226.

### Results

In the present rearing, we could not observe the prezoal stage. Complete larval

development consisted of five zoeal stages and a decapodid (= megalopa) stage. Minimum durations of Z1–Z4 and Z5 were 3 days and 4 days, respectively.

### Description of larval stages

#### First Zoea

**Carapace** (Figs. 1A and 2A): CL =  $1.09 \pm 0.05$  mm (0.99–1.20 mm;  $n = 61$ ). Longer than broad, rostral spine pointed with denticles laterally (Fig. 2A'), but occasionally curved downwards like a beak (Fig. 1A'); antero-lateral margin denticulated, with 9 denticles. Eyes sessile.

**Antennule** (Fig. 3A): Unsegmented rod-like process with 3 long aesthetascs and 3 thin simple setae terminally; 1 long plumose subterminal seta.

**Antenna** (Fig. 4A): Protopod with 1 stout serrated spine. Endopod with 1 long apical plumose seta distally. Exopod (= scaphocerite) forming a terminal spine, with 8 inner plumose setae and 1 outer minute simple seta.

**Mandibles** (Fig. 5A): Symmetrical, but

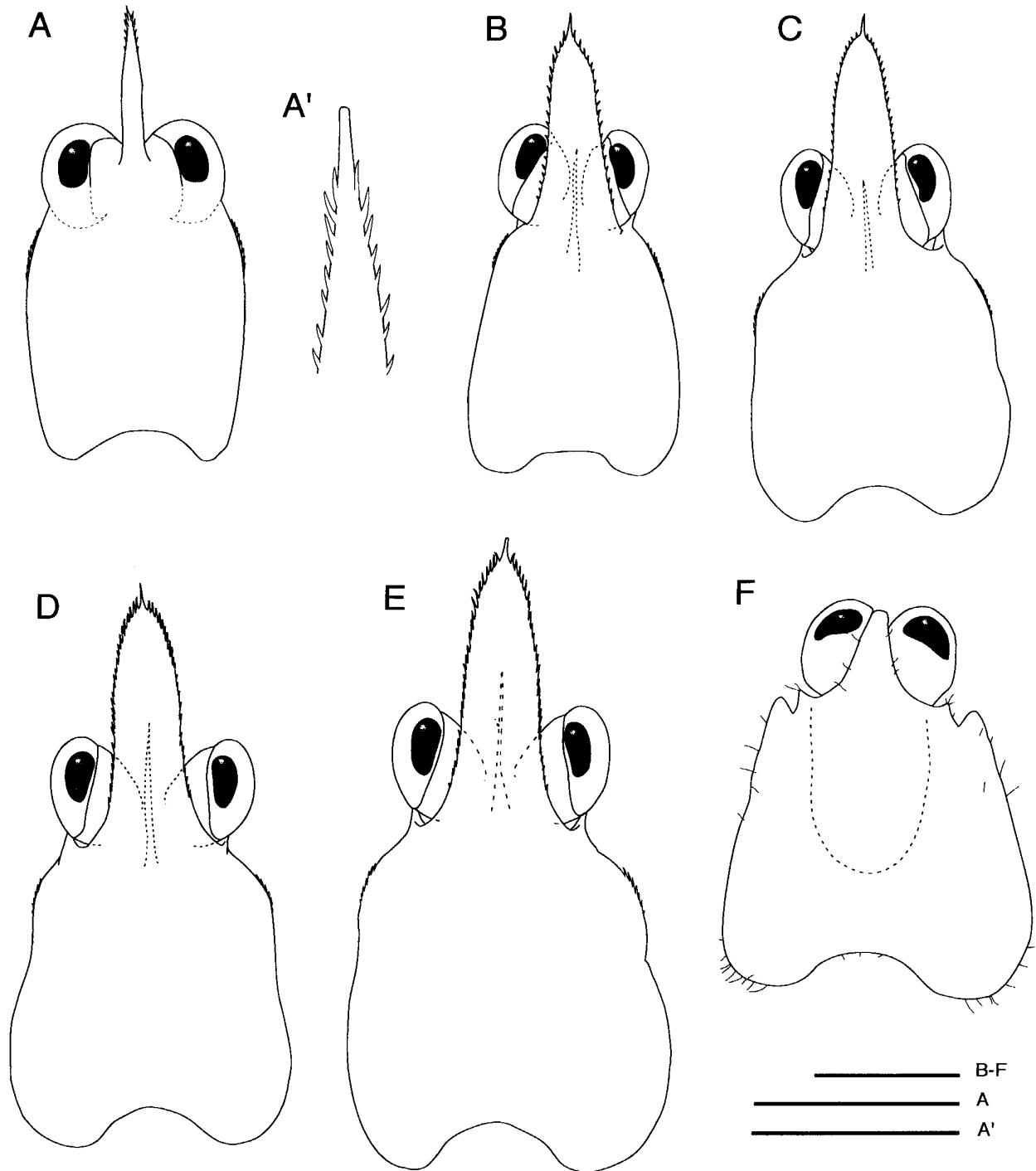


Fig. 2. *Callianassa japonica* Ortmann. A–F, dorsal view of carapace of Z1–5 and decapodid; A', tip of rostral spine of Z1. Scale = 0.5 mm for A–F, and 0.1 mm for A'.

slightly different in dentition on each side. Incisor and molar processes not clearly defined; no palp.

**Maxillule** (Fig. 6A): Coxal endite with 7 setae; basal endite with 2 stout serrated spines and 3 setae. Endopod 3-segmented,

with 3, 2, 2+2 setae.

**Maxilla** (Fig. 7A): Both coxal and basal endites bilobed, with 11+4 and (7–8)+6 setae, respectively. Endopod 2-segmented, with 4+2+2, 2+3 setae. Scaphognathite with 4 marginal soft plumose setae and 1

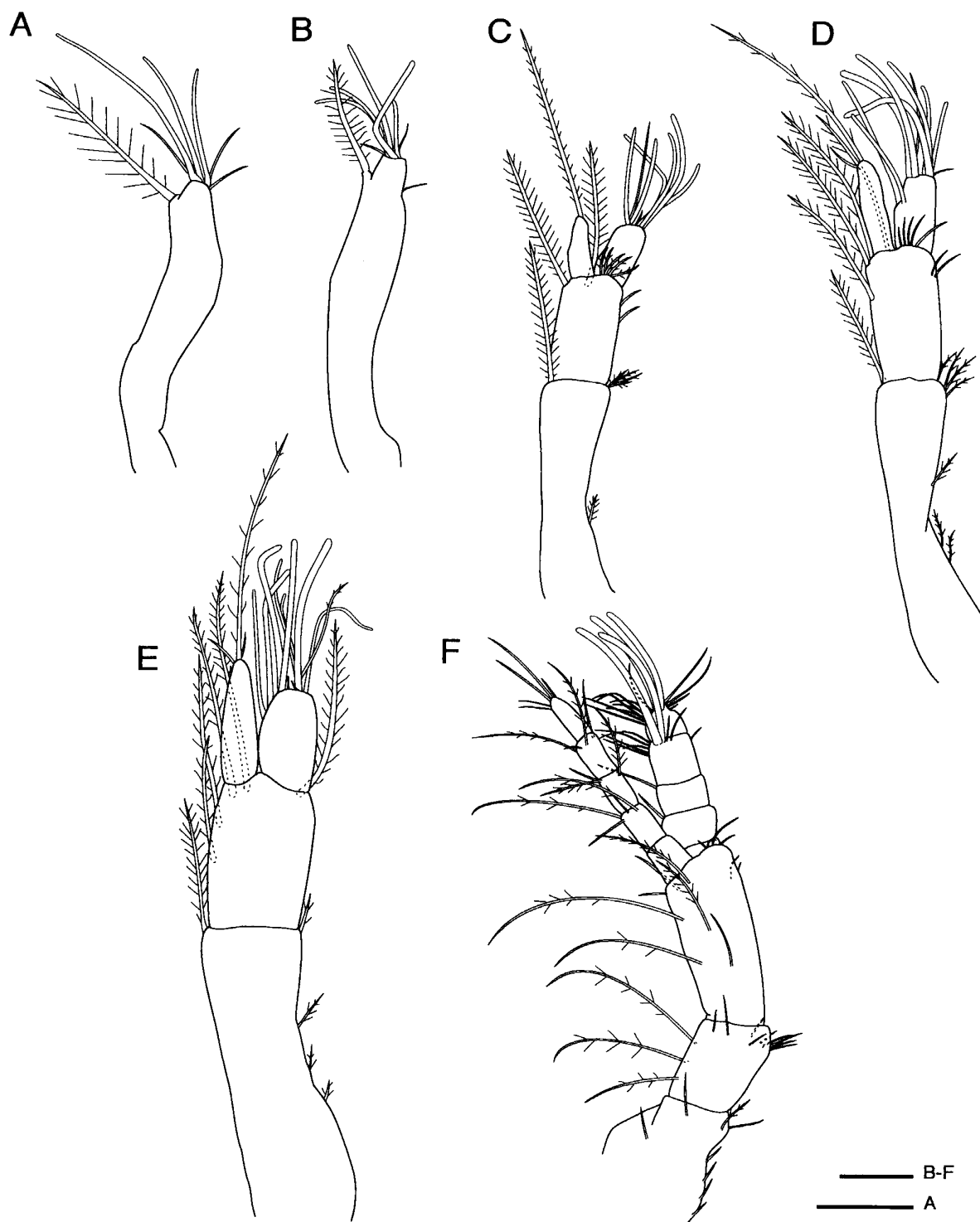


Fig. 3. *Callianassa japonica* Ortmann. A-F, antennule of Z1-5 and decapodid. Scale = 0.1 mm.

long posterior plumose seta.

**Maxilliped 1** (Fig. 8A): Coxa with 3+2+2 setae. Basis with 3+3+3+3 setae. Endopod 4-segmented, with 3, 2, 2, 3+I setae. Exopod with 4 long natatory setae

terminally.

**Maxilliped 2** (Fig. 9A): Coxa with 1 seta. Basis with 1+1+1+2 setae. Endopod 4-segmented, with 2, 2, 2, 4+I setae. Exopod as in maxilliped 1.

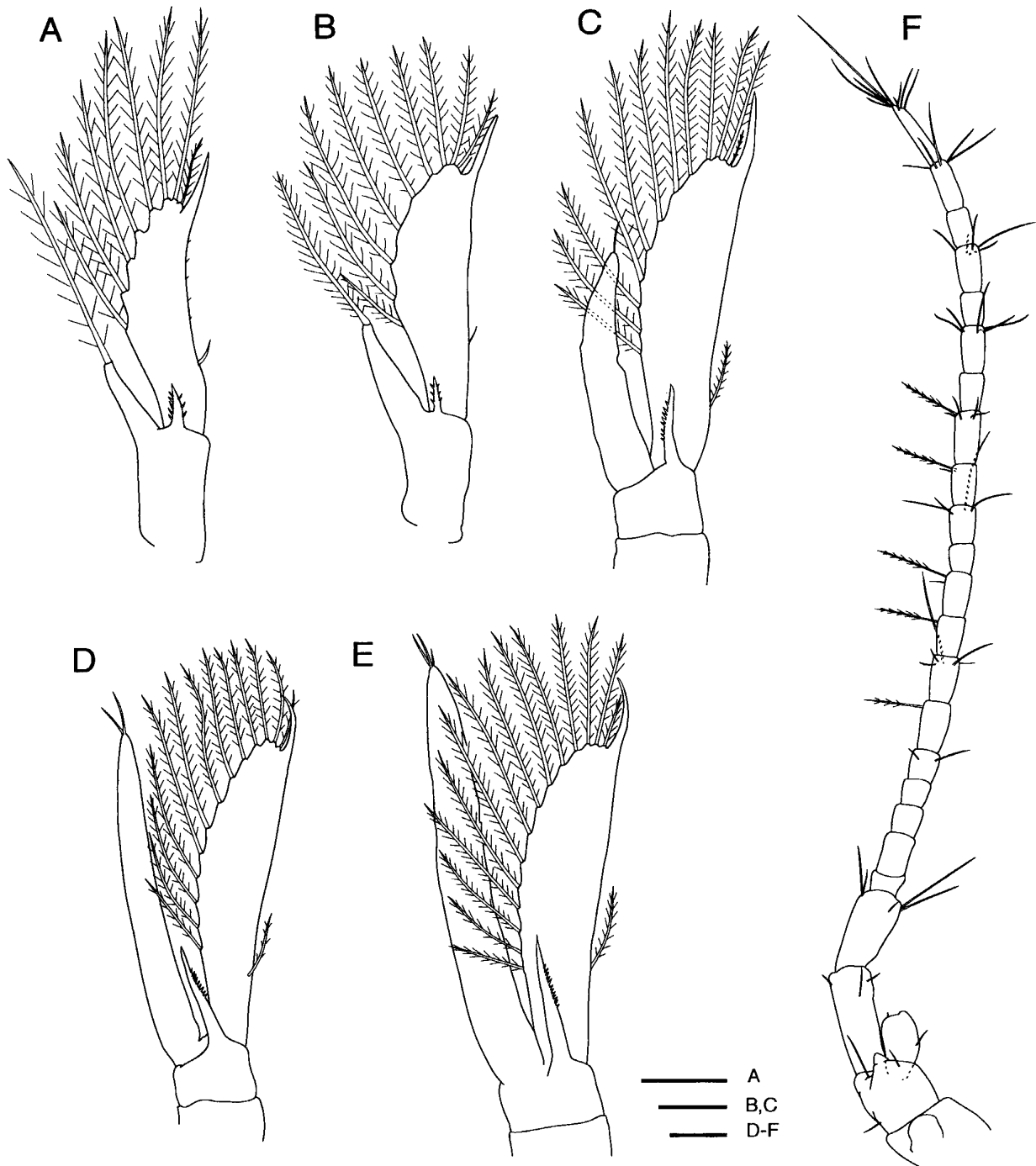


Fig. 4. *Callianassa japonica* Ortmann. A-F, antenna of Z1-5 and decapodid. Scale = 0.1 mm.

**Maxilliped 3** (Fig. 10A): Coxa without setae. Basis with 2 distal setae. Endopod 3-segmented, with 0, 2, 3+I setae. Exopod with 5 natatory plumose setae distally.

**Pereopods** : Not developed.

**Abdomen** (Figs. 1A and 14A): Five somites and 1 triangular telson. Somite 2 with 1 prominent dorso-posterior spine;

somite 3-5, with 1 minute dorso-posterior spine and minute denticles on the dorso-median surface. Telson with 1 prominent median and a pair of outermost unarticulated stout denticulate processes, and 5 articulated plumose processes on either side of the median process; 1 thin plumose seta, so-called an anomuran hair, located

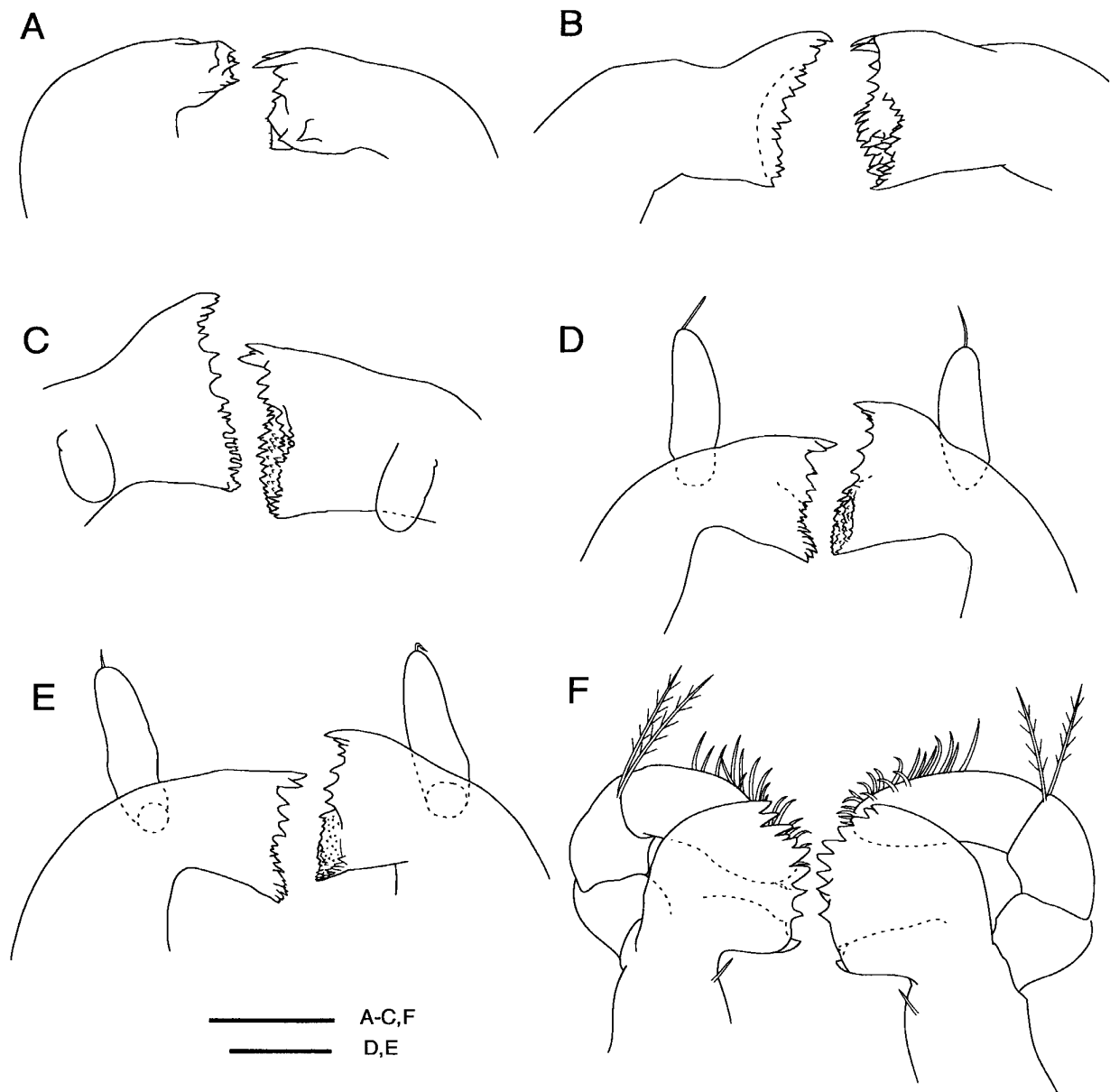


Fig. 5. *Callianassa japonica* Ortmann. A-F, mandibles of Z1-5 and decapodid. Scale = 0.1mm.

between the outermost process ('process 1') and the second process ('process 2') (Fig. 14A'); anal spine absent. Two pairs of minute setae on the dorsal surface.

*Pleopods* : Not developed.

*Uropod* : Not developed.

#### Second Zoea

*Carapace* (Figs. 1B and 2B): CL =  $1.41 \pm 0.12$  mm (1.21-1.60 mm;  $n = 10$ ). Rostral spine flattened, denticulated lat-

erally; antero-lateral margin denticulated, with 8 denticles; 1 longitudinal medial carina evident. Eyes stalked.

*Antennule* (Fig. 3B): With 5 aesthetascs and 2 thin setae terminally; 1 long subterminal plumose seta also present; 1 short subterminal seta.

*Antenna* (Fig. 4B): Exopod with 10 inner plumose setae, of which distal seta simple and much smaller than the other plumose ones; no other changes.

*Mandibles* (Fig. 5B): Larger, but gen-

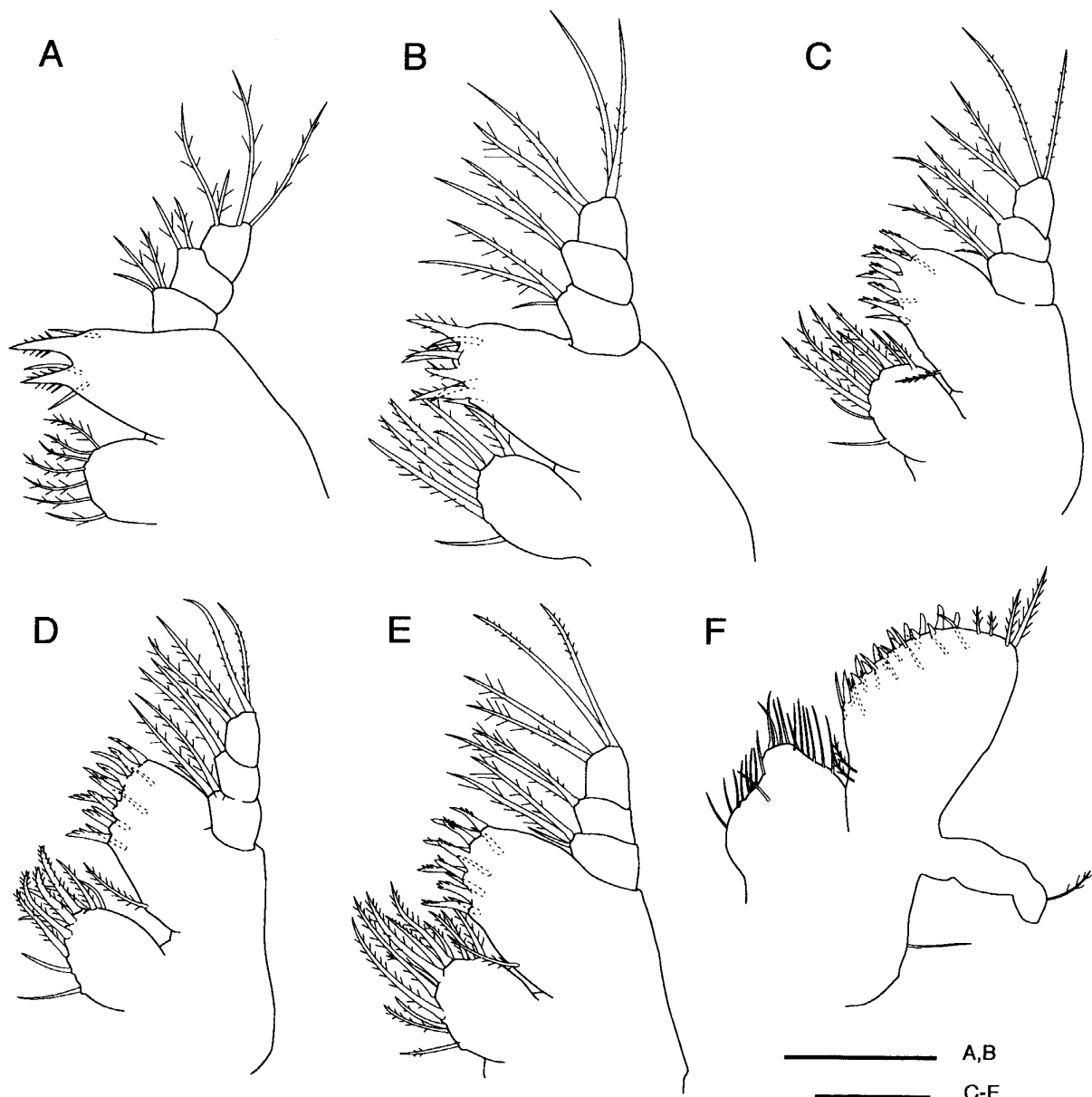


Fig. 6. *Callianassa japonica* Ortmann. A-F, maxillule of Z1-5 and decapodid. Scale = 0.1 mm.

erally as in Z1.

**Maxillule** (Fig. 6B): Basal endite with 5 stout serrated spines and 3 setae; no other changes.

**Maxilla** (Fig. 7B): Coxal endite bilobed, with 10+4 setae; basal endite bilobed, with 9+7 setae; endopod 2-segmented, with 4+2+2, 4-5 setae; scaphognathite with 7 marginal plumose setae and 1 long posterior plumose seta.

**Maxilliped 1** (Fig. 8B): Setal groups in coxa and basis not clearly demarcated

unlike the previous stage; coxa with 6 setae; basis with 14 setae; endopod with 3+I, 2, 2, 3+I setae; exopod with 5 long natatory plumose setae terminally.

**Maxilliped 2** (Fig. 9B): Endopod with 2+I, 2, 2+I, 4+I setae. Exopod with 5 long natatory plumose setae terminally; no other changes.

**Maxilliped 3** (Fig. 10B): Endopod with 0, 2+I, 3+I setae; no other changes.

**Pereopods 1-4** (Figs. 11A, F and 12A, F): Biramous buds.



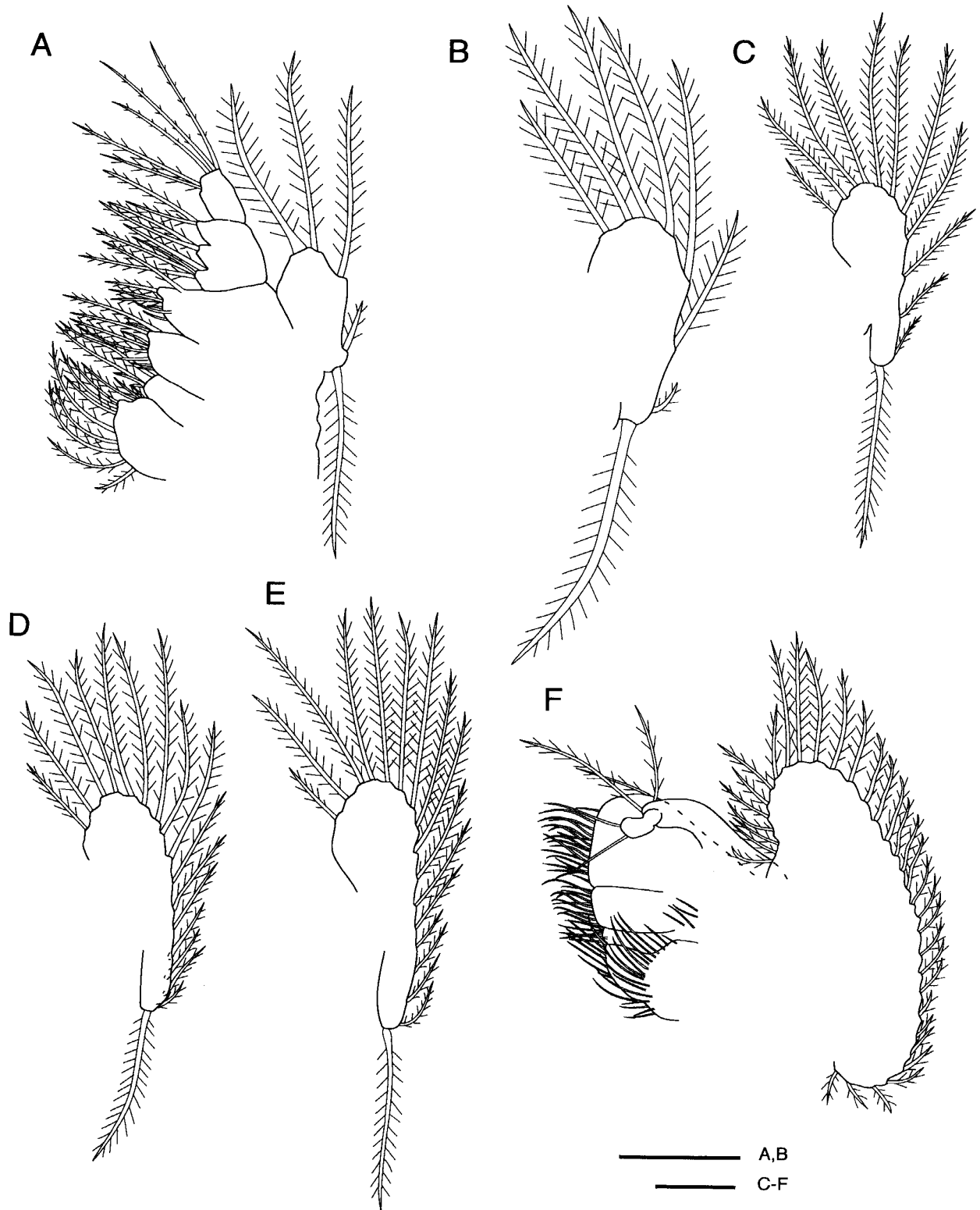


Fig. 7. *Callianassa japonica* Ortmann. A-F, maxilla of Z1-5 and decapodid. Endopod and endites are omitted in B-E. Scale = 0.1 mm.

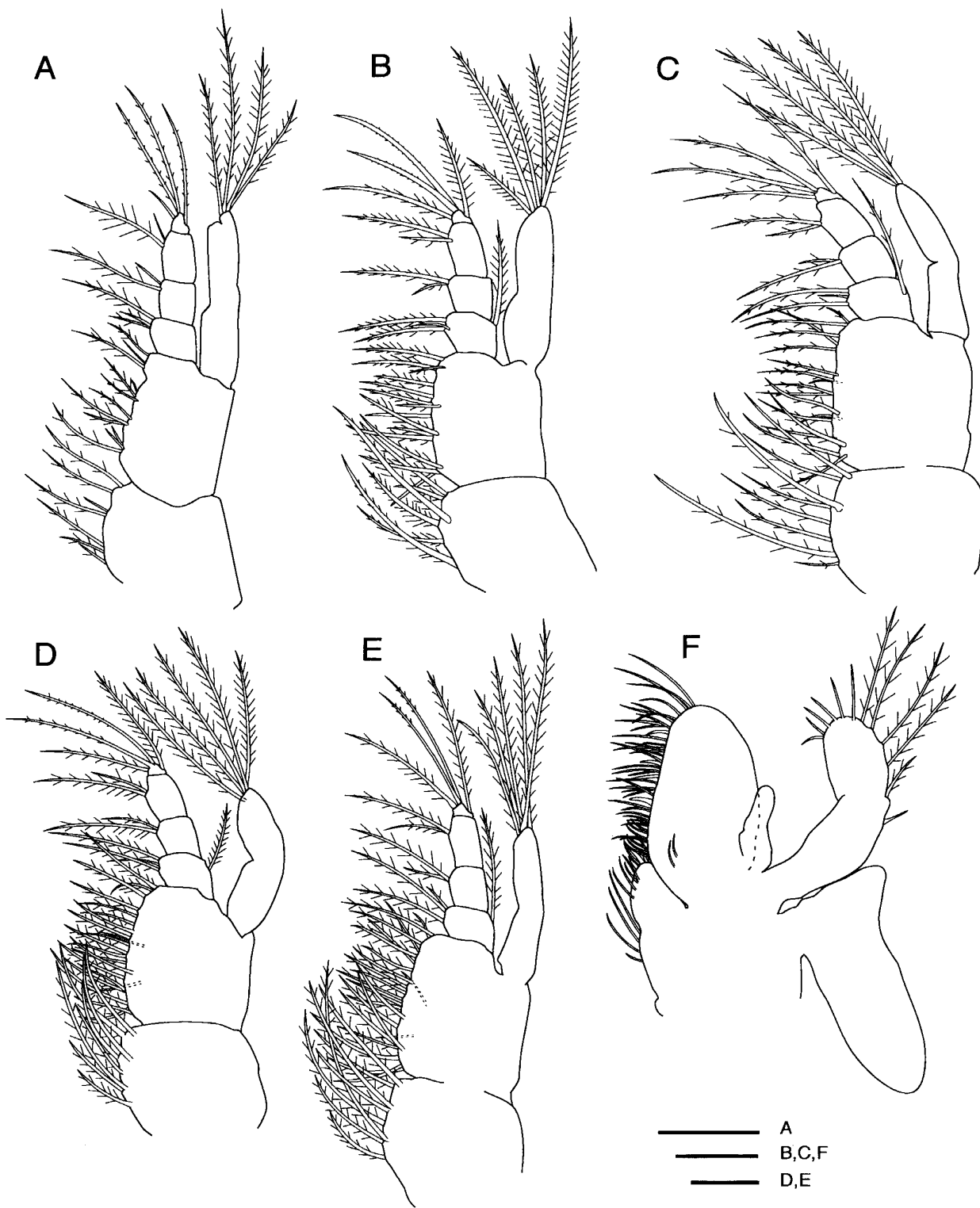


Fig. 8. *Callianassa japonica* Ortmann. A-F, maxilliped 1 of Z1-5 and decapodid. Scale = 0.1 mm.

*Pereopod 5* (Fig. 12K): Uniramous bud.

*Abdomen* (Figs. 1B and 14B): Telson with a pair of additional posterior articulated processes beside the median process.

*Pleopods* : Not developed.

*Uropod* : Not developed.

Third Zoea

*Carapace* (Figs. 1C and 2C): CL =

1.74 ± 0.04 mm (1.70–1.82 mm;  $n = 10$ ). Antero-lateral margin denticulated, with 7–9 denticles; no other changes.

*Antennule* (Fig. 3C): Biramous; coxa with 1+4 setae and 1 long distal plumose seta; basis with 1+1+5 setae and 2 long plumose setae; endopod with 1 long terminal plumose seta; exopod with 6 aesthetascs and 2 thin setae terminally.

*Antenna* (Fig. 4C): Coxa and basis separated; endopod elongated, with 1 short distal simple seta or none; exopod with 11 inner plumose setae, 1 shorter distal seta and 1 outer seta.

*Mandibles* (Fig. 5C): Palps emerged as rudimentary buds.

*Maxillule* (Fig. 6C): Coxal endite with 9–10 setae; basal endite with 7 serrated stout spines and 4 setae; no other changes.

*Maxilla* (Fig. 7C): Coxal endite bilobed, with 14+(4–5) setae; basal endite bilobed, with 9+9 setae; endopod with 4+2+2, 5 setae. Scaphognathite with 11–12 marginal plumose setae and 1 long posterior plumose seta.

*Maxilliped 1* (Fig. 8C): Coxa with 8 setae; basis with 17–18 setae; exopod with 4–5 natatory setae; no other changes.

*Maxilliped 2* (Fig. 9C): Basis with 1+1+2 setae; endopod 5-segmented, with 2+I, 2, I, 2, 4+I setae; no other changes.

*Maxilliped 3* (Fig. 10C): Endopod 4-segmented, with 2+I, 1+I, 2, (4–5) +I setae; no other changes.

*Pereopod 1* (Fig. 11B): Coxa without setae; basis with 2 distal setae; endopod subchelate and 4-segmented, with 0, 1+I, 2, 2+I setae; exopod with 5 setae.

*Pereopod 2* (Fig. 11G): Generally as in pereopod 1.

*Pereopod 3* (Fig. 12B): Coxa and basis with no setae; endopod 3-segmented, with I, 2, 2+I setae; exopod with 5 setae.

*Pereopod 4* (Fig. 12G): Coxa and basis with no setae; endopod 3-segmented, with 0, 1, 2 setae; exopod with 5 setae.

*Pereopod 5* (Fig. 12L): Penultimate segment with 2 distal setae; ultimate seg-

ment with 2 terminal setae.

*Abdomen* (Figs. 1C and 14C): Somite 6 separated from telson, bearing uropods, with 1 posterior dorsal spine. Telson elongated trapezoid form, with 1 median and 8 pairs of posterior processes as in Z2 stage, but processes 1, 2, and 3 spinulose; 2 pairs of dorsal minute setae added.

*Pleopods*: Buds occasionally emerged on somite 3–5 (in 3 of 10 specimens examined).

*Uropod* (Fig. 14C): Biramous; endopod without setae; exopod with 9 marginal plumose setae.

#### Fourth Zoea

*Carapace* (Figs. 1D and 2D): CL = 1.90 ± 0.12 mm (1.73–2.17 mm;  $n = 10$ ). Antero-lateral margin denticulated, with 6–8 denticles; no other changes.

*Antennule* (Fig. 3D): Coxa with 2+1+4 setae and 1 long distal plumose seta; basis with 2+5 short setae, and 4 long distal plumose setae; endopod with 1 long distal plumose seta and 1 thin seta; exopod with 6 terminal aesthetascs, 2 subterminal aesthetascs, and 2 thin setae terminally.

*Antenna* (Fig. 4D): Endopod more elongated with 2 terminal small setae; exopod with 13 inner and 1 outer setae.

*Mandibles* (Fig. 5D): Palp bud elongated, with 1 simple terminal seta.

*Maxillule* (Fig. 6D): Coxal endite with 11 setae; basal endite with 9–10 serrated stout spines and 5 setae; no other changes.

*Maxilla* (Fig. 7D): Coxal endite bilobed, with 16+6 setae; basal endite bilobed, with 10+11 setae; endopod with 4+2+2, 5 setae; scaphognathite with 15–16 marginal plumose setae and 1 long posterior plumose seta.

*Maxilliped 1* (Fig. 8D): Coxa with 7–8 setae; basis with 21 setae; exopod with 5 natatory setae; no other changes..

*Maxilliped 2* (Fig. 9D): Basis with 1+1+2+2 setae; endopod with 2+I, 2+I, I, 2+I, 5+I setae; no other changes.

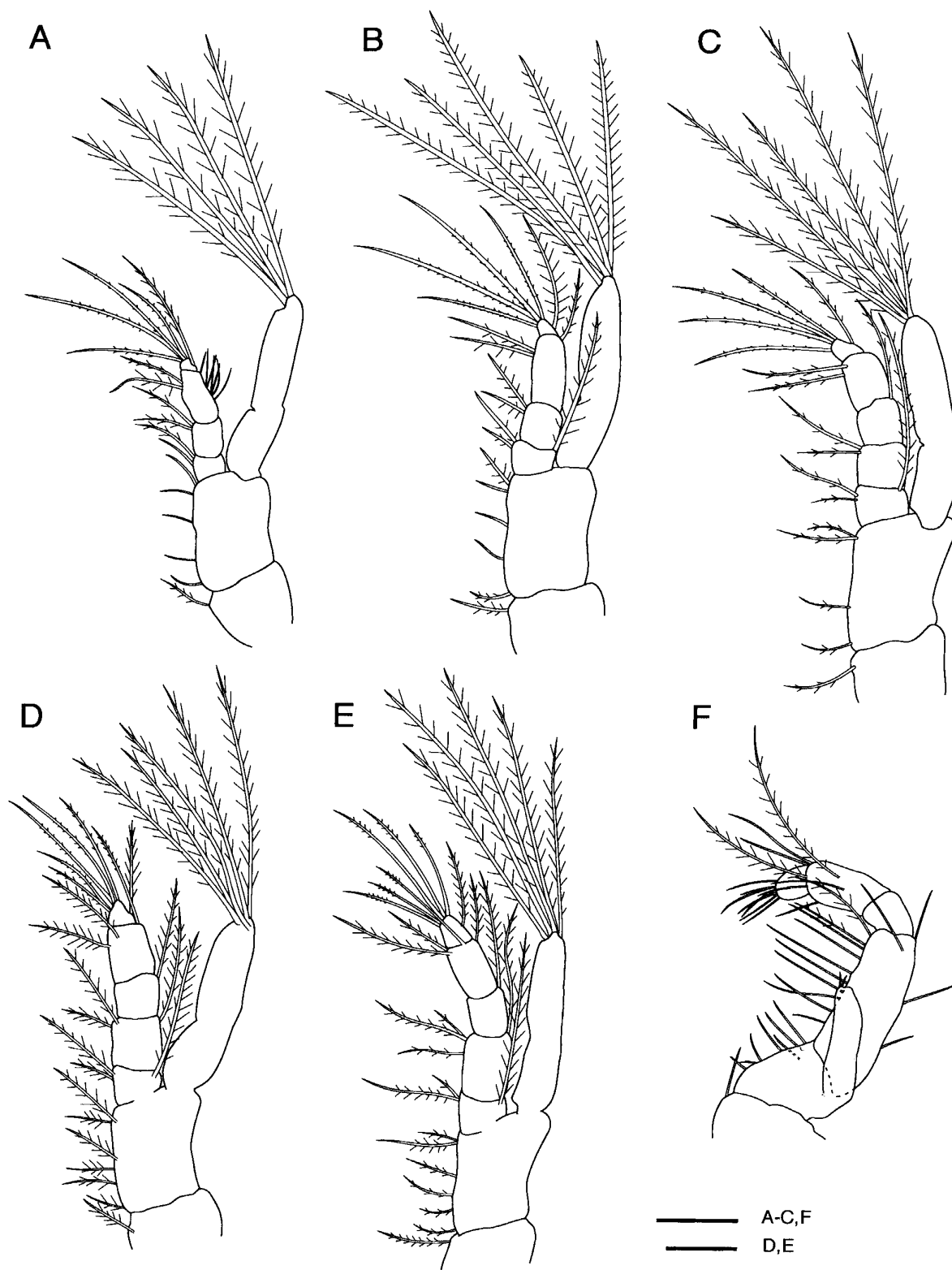


Fig. 9. *Callianassa japonica* Ortmann. A-F, maxilliped 2 of Z1-5 and decapodid. Scale = 0.1 mm.

**Maxilliped 3** (Fig. 10D): Coxa with 1 seta; endopod with 2+2+2+I, 1+I, 1+3+I, 5 setae; no other changes.

**Pereopod 1** (Fig. 11C): Coxa with 1 short seta; basis with 2 distal setae; endopod chelate shape, larger than exopod,

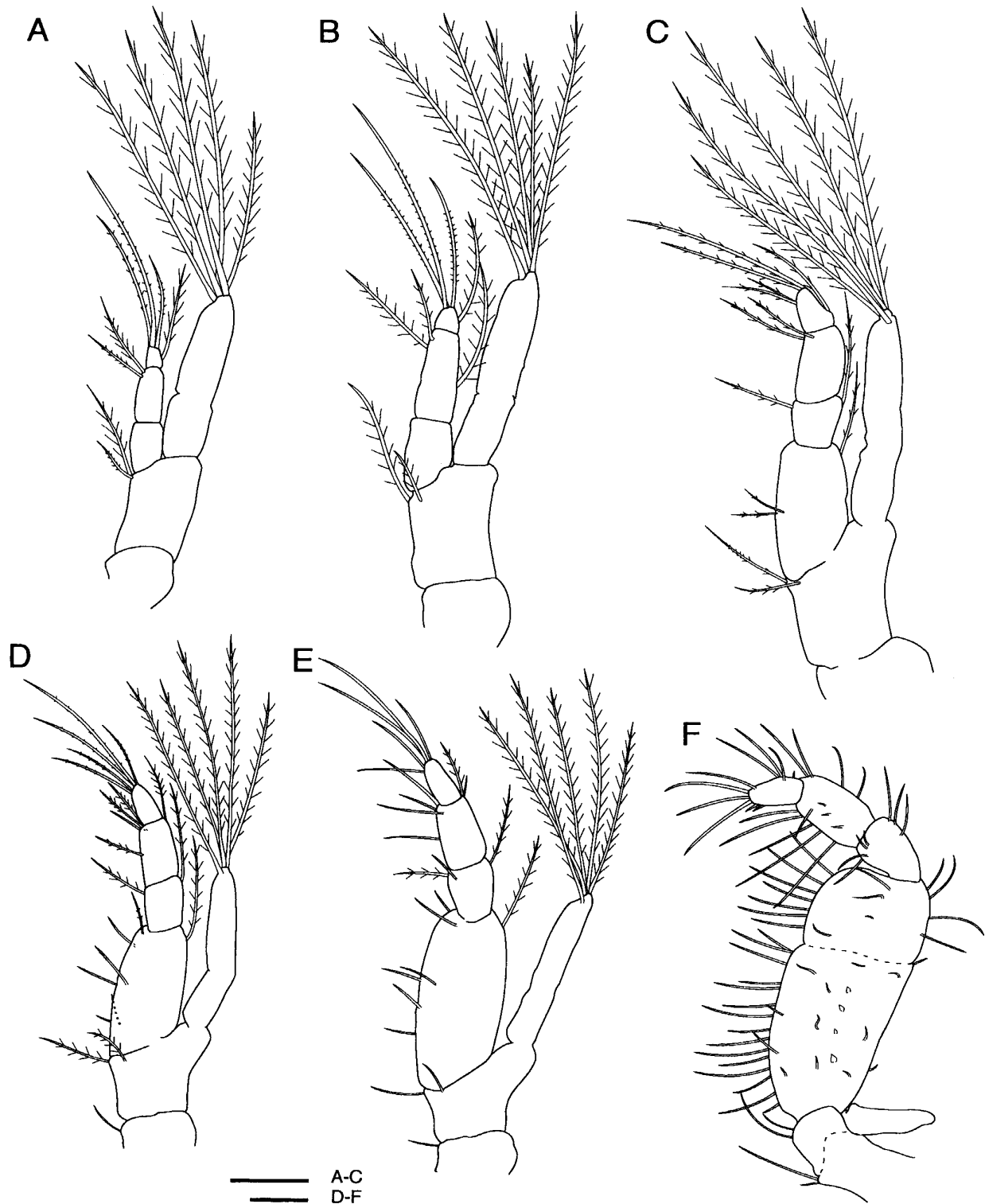


Fig. 10. *Callianassa japonica* Ortmann. A-F, maxilliped 3 of Z1-5 and decapodid. Scale=0.1 mm.

with 2+I, 1+I, 5, 2 setae; exopod with 5 natatory setae distally.

*Pereopod 2* (Fig. 11H): Coxa with 1 short seta; basis with 2 distal setae;

endopod chelate shape, with 2+I, 1+I, 5, 2 setae; exopod with 5 natatory setae distally.

*Pereopod 3* (Fig. 12C): Coxa with 1 short seta; basis with 1 distal seta; endopod

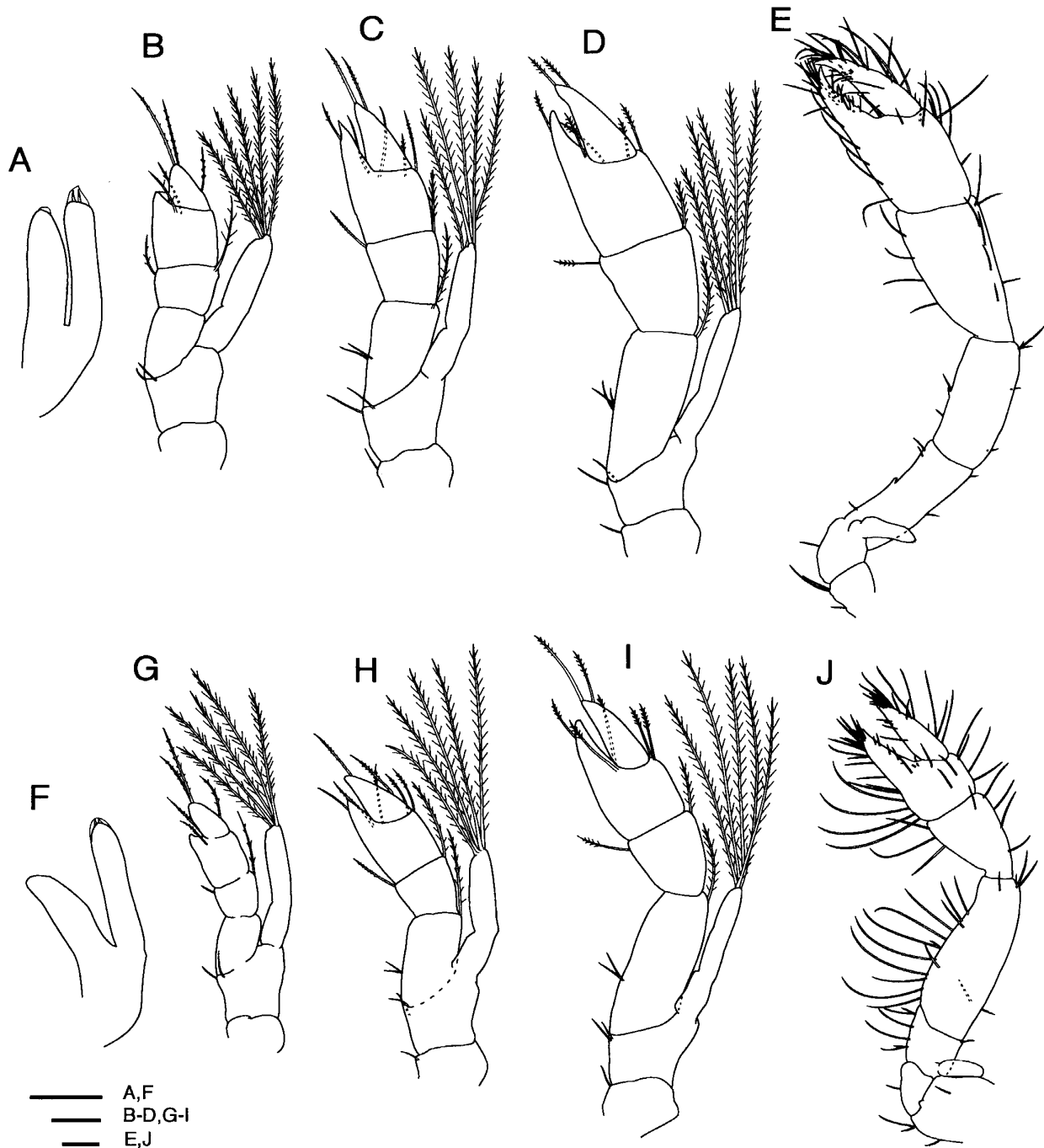


Fig. 11. *Callianassa japonica* Ortmann. A-E, pereopod 1 of Z2-5 and decapodid; F-J, pereopod 2 of Z2-5 and decapodid. Scale = 0.1 mm.

with I, 1+I, 4, 2 setae; exopod with 5 natatory setae distally.

**Pereopod 4** (Fig. 12H): Endopod with I, 1+I, 4, 2 setae; exopod with 5 natatory setae distally; no other changes.

**Pereopod 5** (Fig. 12M): Penultimate

segment with 4 setae; ultimate with 2 terminal setae.

**Abdomen** (Figs. 1D and 14D): One anal spine emerged at somite 6; the anomuran hairs of telson stout form.

**Pleopods** (Fig. 1D): Buds emerged on

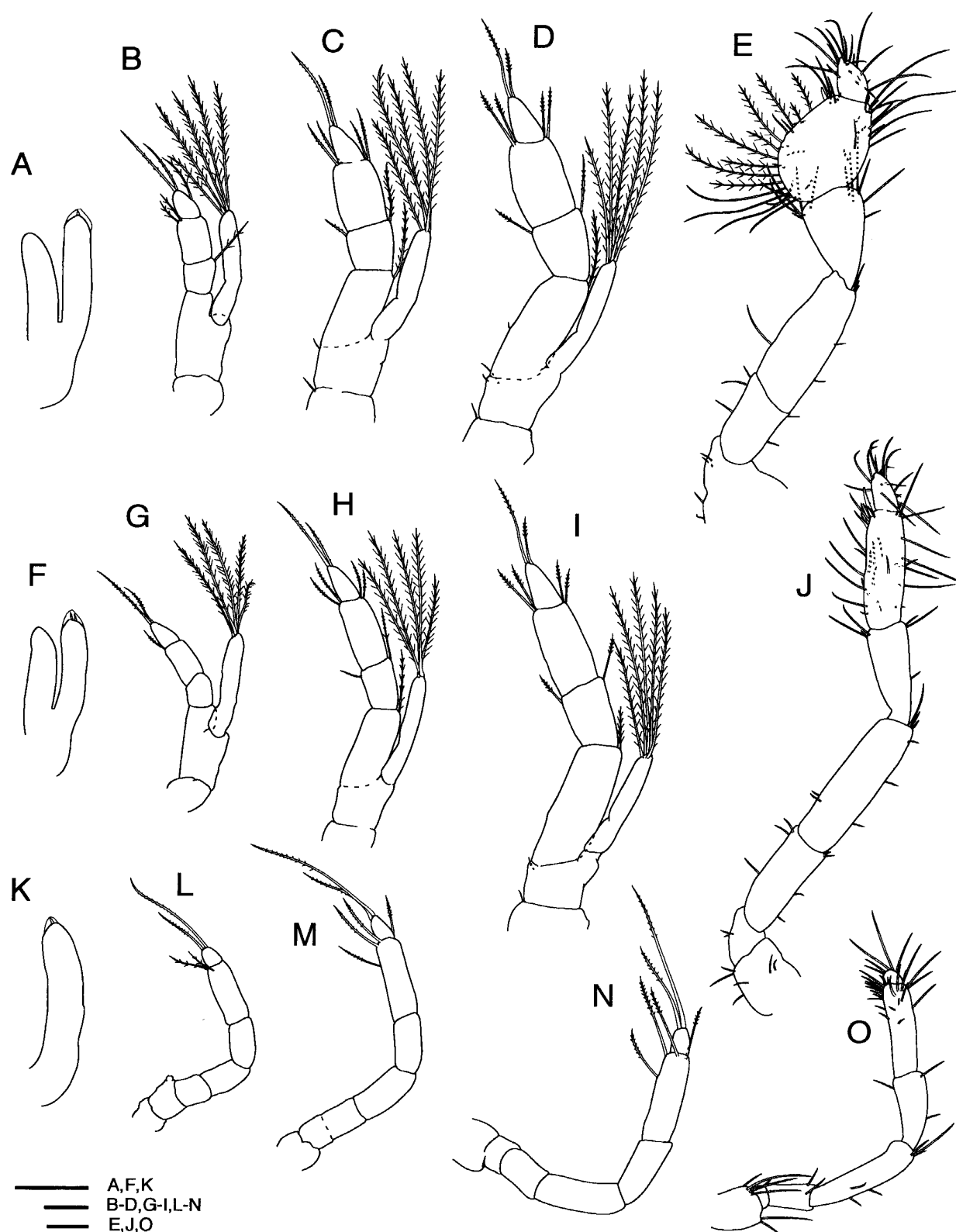


Fig. 12. *Callianassa japonica* Ortmann. Pereopods of Z2 (A, F, K), Z3 (B, G, L), Z4 (C, H, M), Z5 (D, I, N) and decapodid (E, J, O). A–E, pereopod 3; F–J, pereopod 4; K–O, pereopod 5. Scale = 0.1 mm.

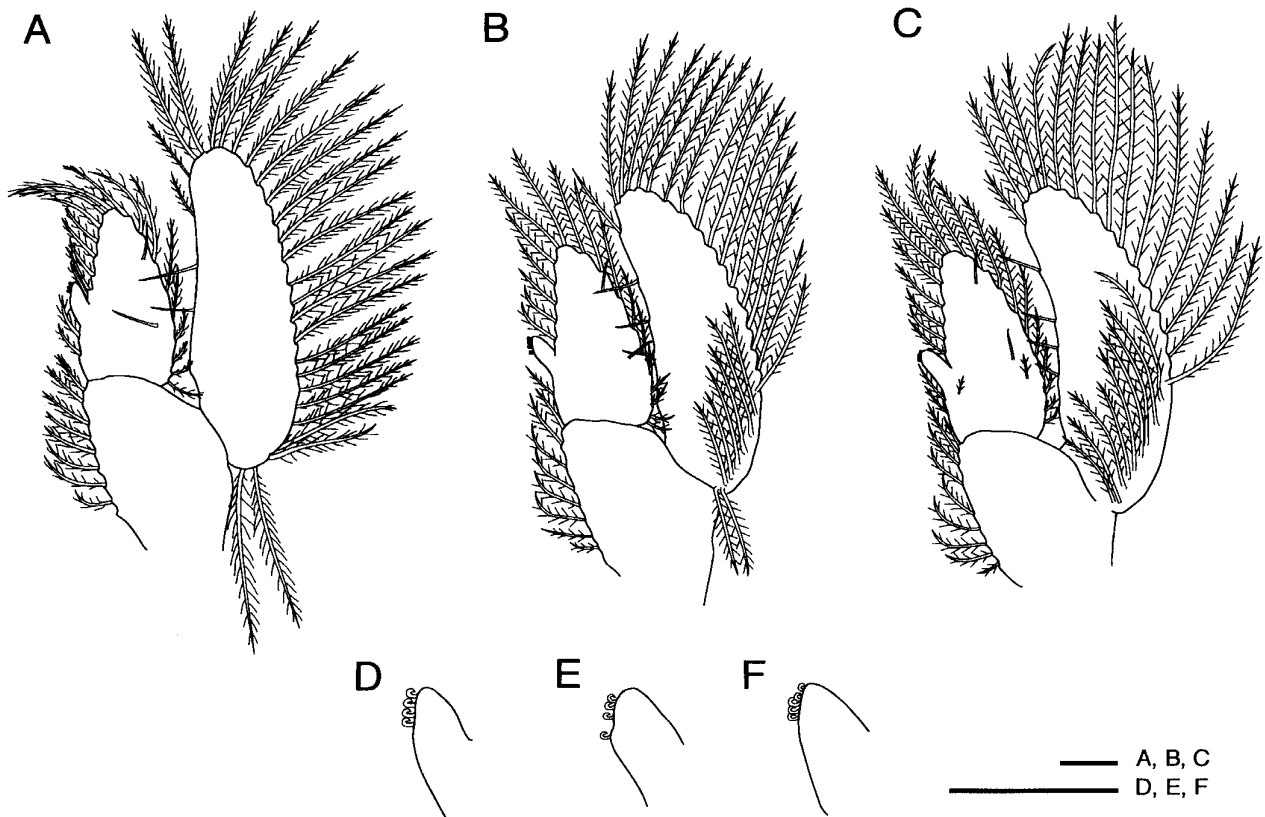


Fig. 13. *Callianassa japonica* Ortmann. A–C, pleopod on abdominal somite 3–5 of decapodid; D–F, tip of *appendix interna*, enlarged. Scale = 0.1 mm.

somite 3–5 in all (= 10) specimens.

**Uropod** (Fig. 14D): Endopod and exopod with 8 and 12 marginal setae, respectively; exopod with 1 distal spine, not present in the Z3 stage.

#### Fifth Zoea

**Carapace** (Figs. 1E and 2E): CL =  $2.03 \pm 0.11$  mm (1.90–2.22 mm;  $n = 10$ ). Antero-lateral margin denticulated, with 7–9 denticles; no other changes.

**Antennule** (Fig. 3E): Coxa with 4–7 short setae and 1 long distal plumose seta; basis with 4–8 long plumose setae; endopod with 1 long distal plumose seta and 2 thin setae; exopod with 6 terminal aesthetascs, 2 subterminal aesthetascs, and 3 thin setae terminally.

**Antenna** (Fig. 4E): Endopod more elongated with 2–4 terminal thin setae; exopod with 14 inner and 1 outer setae.

**Mandibles** (Fig. 5E): No change.

**Maxillule** (Fig. 6E): Coxal endite with 13 setae; basal endite with 9 serrated stout spines and 5 setae; no other changes.

**Maxilla** (Fig. 7E): Coxal endite bilobed, with (16–17)+6 setae; basal endite bilobed, with 12+11 setae; endopod with 3+2+2, 5 setae; scaphognathite with 16 marginal plumose setae and 1 long posterior plumose seta.

**Maxilliped 1** (Fig. 8E): Coxa with 8 setae; basis with 21–24 setae; no other changes.

**Maxilliped 2** (Fig. 9E): Coxa with 1–2 setae; basis with 1+1+2+2 setae; exopod unchanged; endopod with 2+I, 3+I, I, 3+I, 5+I setae.

**Maxilliped 3** (Fig. 10E): Endopod with 1+1+2+2+I, 2+I, 6, 5 setae; no other changes.

**Pereopod 1** (Fig. 11D): Endopod larger than exopod, with 3+I, 1+I, 5, 2 setae; no other changes.



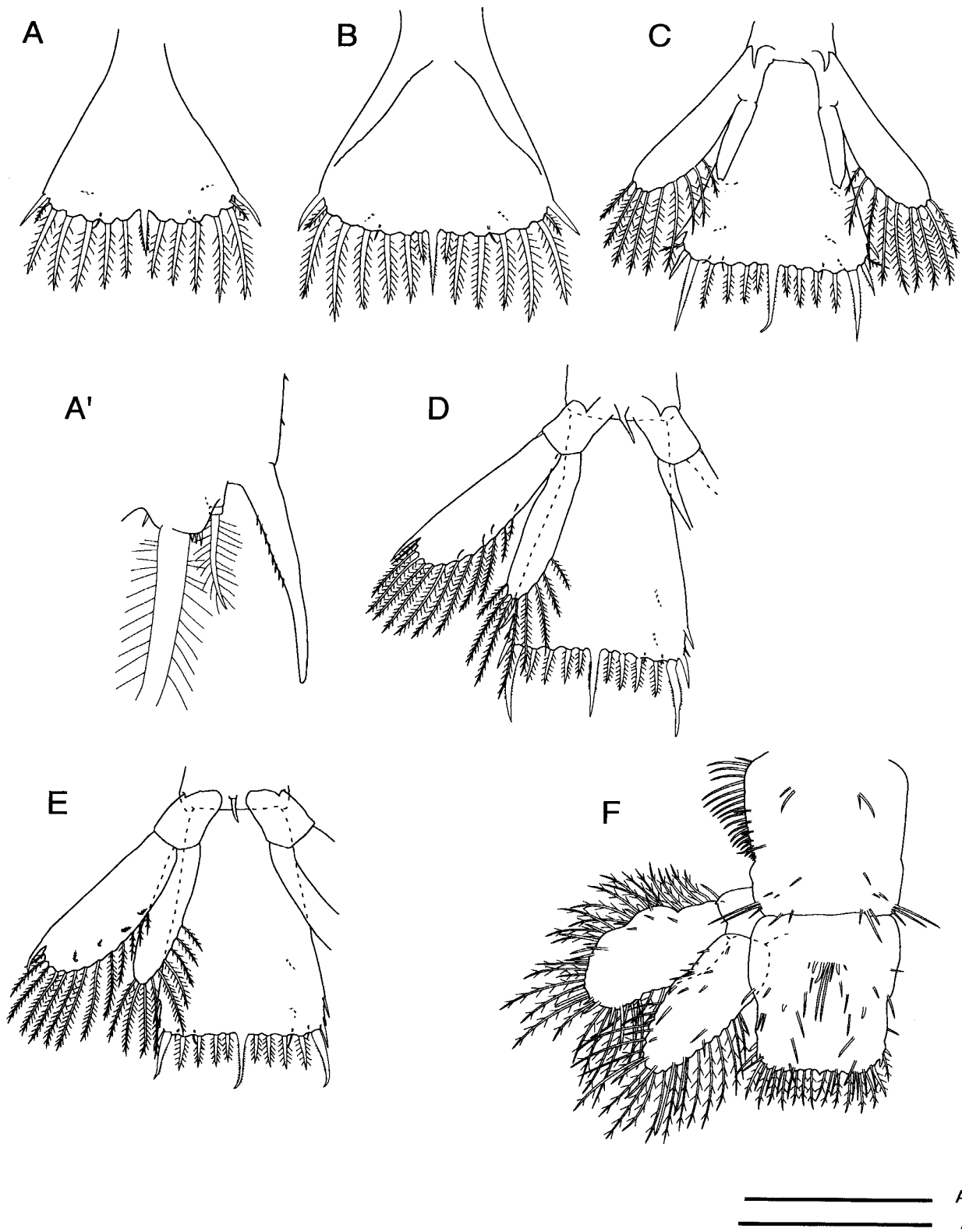


Fig. 14. *Callianassa japonica* Ortmann. A-F, telson of Z1-5 (ventral view) and decapodid (dorsal view); A', distal part of telsonal fork of Z1, enlarged. Scale = 0.5 mm for A-F and 0.1 mm for A'.

*Pereopod 2* (Fig. 11I): Endopod larger than exopod, with 2+I, 1+I, 5, 2 setae; no other changes.

*Pereopod 3* (Fig. 12D): Basis with 2 distal short setae; endopod with 1+I, 2, 4, 2 setae; no other changes.

*Pereopod 4* (Fig. 12I): Both coxa and basis with 1 short seta; endopod larger than exopod; no other changes.

*Pereopod 5* (Fig. 12N): Penultimate segment with 4 setae; no other changes.

*Abdomen* (Figs. 1E and 14E): No change.

*Pleopods* (Fig. 1E): Buds more elongated.

*Uropod* (Fig. 14E): Endopod and exopod with 9–11 and 13 marginal setae, respectively.

#### Decapodid (Megalopa)

*Carapace* (Figs. 1F and 2F): CL =  $1.28 \pm 0.05$  mm (1.23–1.35 mm;  $n = 10$ ). Rostral spine reduced, curved downwards, with a setose blunt end. Cervical groove recognizable but *linea thalassinica* not recognizable.

*Antennule* (Fig. 3F): Peduncle 3-segmented, with proximal segment with 4–9 setae, penultimate segment with 12 setae, and distal segment with 13 terminal setae; inner flagellum (= endopod) slender, 5-segmented, with 0, 4, 2+I, 3+I, 5 setae; outer flagellum (= exopod) 5-segmented, with 0, 1, 1, 2a+8, 2a+ (10–12) setae.

*Antenna* (Fig. 4F): Peduncle 3-segmented; rudimentary exopod present on the proximal segment; distal segment with 6–9 terminal setae; flagellum composed of 20 (occasionally 21) segments.

*Mandibles* (Fig. 5F): Incisor and molar processes distinct; basal part with 1 proximal seta; palp 3-segmented, with 2 long setae on penultimate segment and with 20 setae or minute spines on distal segment.

*Maxillule* (Fig. 6F): Coxal and basal endites spatulated, with numerous setae or spines; endopod unilobed, with 1 subterminal seta; outer side of proximal

portion with 1 seta.

*Maxilla* (Fig. 7F): Endites flattened, with numerous setae or spines; endopod reduced, 2-segmented, with 2 distal setae on each segment; scaphognathite with 32–35 soft plumose marginal setae.

*Maxilliped 1* (Fig. 8F): Coxal and basal endites with 7–11 and numerous setae, respectively; endopod unsegmented, without setae; exopod with 12 setae on outer side; epipod emerged, roughly triangular in shape.

*Maxilliped 2* (Fig. 9F): Coxa with 1–3 setae; basis with 7–8 setae; endopod 4-segmented, with numerous setae on proximal, 2 long setae on penultimate, and numerous setae on distal segment; exopod unsegmented, with 2 terminal setae.

*Maxilliped 3* (Fig. 10F): Coxa with 2–3 setae and basis with 2 setae, with segmentation between coxa and basis inconspicuous; 5-segmented endopod with numerous long setae, with segmentation between merus and ischium inconspicuous; endopod unsegmented, without setae.

*Pereopod 1* (Fig. 11E): Chelate and setose as in adult form; exopod reduced, without setae.

*Pereopod 2* (Fig. 11J): Similar to pereopod 1.

*Pereopod 3* (Fig. 12E): Uniramous; endopod 5-segmented, with numerous setae and with penultimate segment with 1 short stout spine distally.

*Pereopod 4* (Fig. 12J): Uniramous; endopod 5-segmented, with numerous setae and with penultimate segment with 1 subterminal stout spine.

*Pereopod 5* (Fig. 12O): Each segment with numerous setae.

*Abdomen* (Figs. 1F and 14F): Six somites and 1 quadrate telson; somite 3–5 with well-developed pleopods; margin of telson with 20 posterior processes and many short setae on dorsal surface.

*Pleopods 1 and 2*: Absent.

*Pleopod 3* (Figs. 13A and 13D): Bi-

ramous; inner margin of protopod, endopod, and exopod with 8 plumose, 18–20 simple or plumose, and 28–30 simple or plumose setae, respectively; *appendix interna* (= stylamblys) of endopod with 4–6 distal hooks.

*Pleopod 4* (Fig. 13B and 13E): Biramous; inner margin of protopod, endopod, and exopod with 7–9 plumose, 16–20 simple or plumose, and 28 simple or plumose setae, respectively; *appendix interna* of endopod with 4 distal hooks.

*Pleopod 5* (Fig. 13C and 13F): Biramous; inner margin of protopod, endopod, and exopod with 9 plumose, 18–22 simple or plumose, and 29 simple or plumose setae, respectively; *appendix interna* of endopod with 5–6 distal hooks.

*Uropod* (Fig. 14F): Endopod with 7 simple and 18–19 plumose setae marginally; exopod with 17–21 simple and 30–40 plumose setae on its margin.

### Discussion

In the limited number of studies done so far on the larval development of callianassids, the number of zoeal stages has been recorded as either 2 (abbreviated development) or 5–6 [see reviews in Konishi *et al.* (1990), Tamaki *et al.* (1996), and Nates *et al.* (1997)]. In the present study, *C. japonica* had 5 zoeal stages. For *C. petalura*, 6 zoeal stages were recorded from laboratory-reared material (Konishi *et al.*, 1990). Since their Z4 and Z5 did not possess clear differences in both carapace length and morphology of appendages, their Z6 could be regarded as the 'true' Z5. Five zoeal stages might be a standard instar number for species of *Callianassa* except for those with abbreviated development. Of those species with 5–6 zoeal stages, the larval period of *C. japonica* (16 days: from hatching to decapodid) is the shortest, just identical to that of *C. petalura* (see Table 6 in Tamaki *et al.*, 1996). As discussed in Tamaki *et al.*

(1996), larval periods will vary not only in a species-specific way but also depending on environmental variables such as temperature, salinity, and food supply, and these effects on larval physiology should be examined in the future.

The zoeal morphology of *C. japonica* was generally the same as that of previously reported species of *Callianassa*, excluding species with abbreviated development. In particular, those of *C. japonica* and *C. petalura* were quite similar (cf., Konishi *et al.*, 1990). However, the two species can be distinguished at the Z1 and decapodid stages, based on presence (*C. japonica*) or absence (*C. petalura*) of a coxal seta on maxilliped 2 (in Z1) [Fig. 9A in the present paper and Fig. 9A in Konishi *et al.* (1990)] and on the smaller number of segments of the antennal flagella in *C. japonica* (in decapodid: 20–21 vs. 24–25) [Fig. 4F in the present paper and Fig. 4G in Konishi *et al.* (1990)]. In addition, in larvae of only *C. japonica*, rudimentary buds of pleopods were acquired as early as Z3 and a seta was recognized at the tip of the mandibular palp in Z4 and Z5 [Figs. 5D, E in the present paper and Fig. 5D in Konishi *et al.* (1990)].

The zoeal stage 1 described by Miyazaki (1937) does not seem to be Z1 of *C. petalura* because his specimens had a coxal seta on maxilliped 2. Although Miyazaki (1937) gave no detailed account of the morphological character of adult specimens, two lines of evidence suggest that his species would be *C. japonica* (Tamaki & Ueno, 1998): 1) the reproductive season was from mid-March to around the end of August at his study site in the middle of Tokyo Bay, and 2) the burrow cast (his Fig. 1) consisted of alternating shafts and chambers, with a single surface opening. Kurata (1965) described zoeal stages 1–4 for *Callianassa (Trypaea) subterranea japonica* Ortmann, using plankton samples collected in the Sea of

Japan off Hokkaido. However, it is difficult to identify the species due to his insufficient description as judged by recent standards for larval morphological study. In particular, his Z1 has 2 long plumose setae at the tips of the endopods of the antennae (his Fig. 4), suggesting that his material was different from both *C. petalura* and *C. japonica*.

In order to elucidate the distribution and dynamics of larvae of the three species of *Callianassa* occurring in the waters from Ariake Sound to the East China Sea [see Fig. 1 in Tamaki & Ueno (1998)], the description of larval morphology of the other one species, *Callianassa* sp., will be a next prerequisite step.

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## [Addendum]

After submission of the present paper, the taxonomic status of *Callianassa japonica* Ortmann, *Callianassa* sp., and *C. petalura* Stimpson has been revised [see Manning, R. B., & Tamaki, A., 1998. *Proceedings of the Biological Society of Washington*, 111 (4): 889–892].