

## The larval development of the prawns *Macrobrachium equidens* and *Macrobrachium* sp. (Decapoda: Palaemonidae), reared in the laboratory

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(With 26 figures in the text)

The larval development of two species of *Macrobrachium* reared in sea water is described. In one of these species, *M. equidens* (Dana), the larvae metamorphosed successfully in normal sea water whilst in the other, *Macrobrachium* sp., the postlarvae were only obtained in water of slightly lower salinity. Descriptions of the larval stages of both species are given and compared with larvae of other species of *Macrobrachium*.

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### Introduction

All but one of the previous accounts of larval development in the genus *Macrobrachium* have dealt with species that require brackish or freshwater for their normal larval development. The exception is *Macrobrachium intermedium* (Stimpson) which has been reared in sea water and of which eight, out of a suggested total of ten, larval stages were obtained (Williamson, 1972).

The larvae of both of the species reported in this paper were obtained from females which had been collected in the sea, but, whereas the *M. equidens* was probably obtained relatively close inshore, the female of the as yet unidentified species was collected much further offshore. Nevertheless, the *equidens* larvae successfully metamorphosed in sea water of normal salinity, while it was necessary to reduce the salinity to obtain the post-larvae of the other species.

The identification of the two females presented some difficulties because both exhibited some immature features. It would seem that many species of *Macrobrachium* attain sexual maturity before reaching the definitive adult stage whereas taxonomic keys to the species of this genus use adult characters, especially those of adult males. The ovigerous *M. equidens* was identified provisionally by Prof. L. B. Holthuis of the Leiden Museum and

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later, when more material was obtained from the same area, this identification was confirmed.

It has not been possible to identify with certainty the other female *Macrobrachium* from which the larvae have been reared and described in this paper. This female, referred to here as *Macrobrachium* sp., has a body length of 56 mm and a rostral formula of  $\frac{10}{3}$ . In the rostral formula and size it is similar to *M. sintangense* (de Man) but differs from that species in having the rostral tip slightly curving upwards, in the comparative lengths of the carpus and merus of the second chelipeds, and by the shorter telson. In addition, *M. sintangense* is known only from freshwater (Holthuis, 1950) whilst the present specimen was taken from an offshore locality.

### Materials and methods

#### *Macrobrachium equidens*

The ovigerous female was obtained from offshore Phuket (Thailand) and maintained in a small aquarium at the Phuket Marine Center until the eggs hatched on 3 July, 1973. The larvae were reared in small glass vessels each containing approximately 60 ml of sea water, with 3 larvae per container during the first 3 stages and one larva per container from the 4th stage. Most of the larvae were placed in an aquarium room where the temperature varied between 26°–29.5°C, but some were kept in an air-conditioned room at 25°C ± 1°. The water, of salinity 32.9‰, had been stored in a cold room for more than 2 months and filtered before use.

#### *Macrobrachium* sp.

The ovigerous female was obtained from an area mentioned by fishermen as "very far from shore" and the eggs hatched on 29 September, 1973. From the first stage, the larvae were reared individually in small glass vessels each containing approximately 60 ml of sea water and were placed in an aquarium room where the temperature varied between 26°–29.2°C. From the day of hatching until 8 November, 1973, the water used for rearing was of 32.1–32.9‰ salinity and had been stored in a cold room for about a month and then filtered. On 8 November, 1973, 40 days after hatching, some larvae were retained in water of this salinity while others were transferred to 90‰ sea water (by volume) and a third group of larvae transferred to 85‰ sea water.

The larvae of both species were fed on newly hatched nauplii of *Artemia salina* (L.). In both rearings, the containers were examined for exuviae each day and the stage of the larvae recorded; at the same time, the larvae were transferred to fresh sea water and fed. The exuviae and specimens of each larval stage were preserved in 4% formalin. All the drawings were made, using a *camera lucida*, from whole larvae or dissected appendages mounted in a drop of water; 5 larvae or exuviae were usually compared with the drawings and variations in the number of setae and spines were noted.

The sizes of each stage given in the description are the carapace length (c.l.) measured from the tip of the rostrum to the posterior margin of the carapace and the total length (t.l.) measured from the tip of the rostrum to the tip of the telson, spines excluded.

In *M. equidens*, the distribution of chromatophores was not recorded until the 7th stage.

### Results

#### *Macrobrachium equidens*

The larvae of *M. equidens* moulted every two or three days and, for their complete development, passed through 15 to 19 moults; but after the 6th moult, development



became irregular and each moult did not produce a distinct larval stage. In all, 10 larval stages were recognized and these are described below.

Mortality was about 30% during the first three stages and was very low after the larvae had been separated individually in the containers. No deaths occurred between the last larval and the first post-larval stages, all living larvae successfully undergoing metamorphosis and giving rise to strong and active post-larvae.

The survival rates were similar for larvae kept at 26°–29.5°C and at 25°C, but development was slower at the lower temperature; at 26°–29.5°C, the larvae underwent metamorphosis 36–53 days after hatching, whilst at 25°C, the first post-larval stage was reached after 50–62 days.

### *Macrobrachium* sp.

As in *M. equidens*, the larvae of *Macrobrachium* sp. moulted every two or three days and passed through 14 to 17 moults before metamorphosis, but development became irregular after the 6th moult; in this case, 12 distinct stages are recognized.

During a period of 11 days, from 8 November to 19 November, 1973, 7 post-larvae were obtained from 90% sea water, two of them within 24 hours after being transferred to this salinity. No post-larvae were obtained from 85% sea water during the same time; nevertheless, the larvae remained alive at this salinity whilst most of those kept in normal sea water died.

Mortality was very low during the early stages and higher in the late stages. No deaths occurred between the last larval and the first post-larval stages in 90% sea water, but three out of the seven post-larvae obtained were less active than the remainder.

### Description of the larval stages of *Macrobrachium equidens* (Dana)

#### Stage I

c.l. 0.58–0.65 mm

t.l. 1.9–2.0 mm

*Carapace* (Fig. 1(a)) short with small rostral spine. Antero-lateral border (Fig. 1(b)) with 1 pterygostomian spine. Eyes large and sessile.

*Antennule* (Fig. 1(c)) exopod with 3 aesthetascs and 2 setae, the shorter one being plumose; peduncle unsegmented with 1 long plumose seta in position of the endopod.

*Antenna* (Fig. 1(d)) endopod unsegmented, terminating in a spine and a long plumose seta; exopod flattened, segmented distally, carrying 9 inner plumose and 1 outer nonplumose seta; peduncle unsegmented.

*Mandible* (Fig. 1(e)) without a palp, with 1 spine between molar and incisor processes.

*Maxillule* (Fig. 1(f)) endopod unsegmented, armed with 2 small spines, basal endite with 2 spines and 1 small seta, coxal endite with 4 spines.

*Maxilla* (Fig. 1(g)) endopod unsegmented with 1 plumose seta and 2 spines, scaphognathite with 4 distal plumose setae and 1 larger proximal one; basal and coxal endites, forming 3 inner lobes, armed with 4 spines and 4 setae.

*Maxilliped 1* (Fig. 1(h)) endopod small with 3 terminal setae, exopod unsegmented carrying 4 natatory setae, basis rounded with 1 seta.

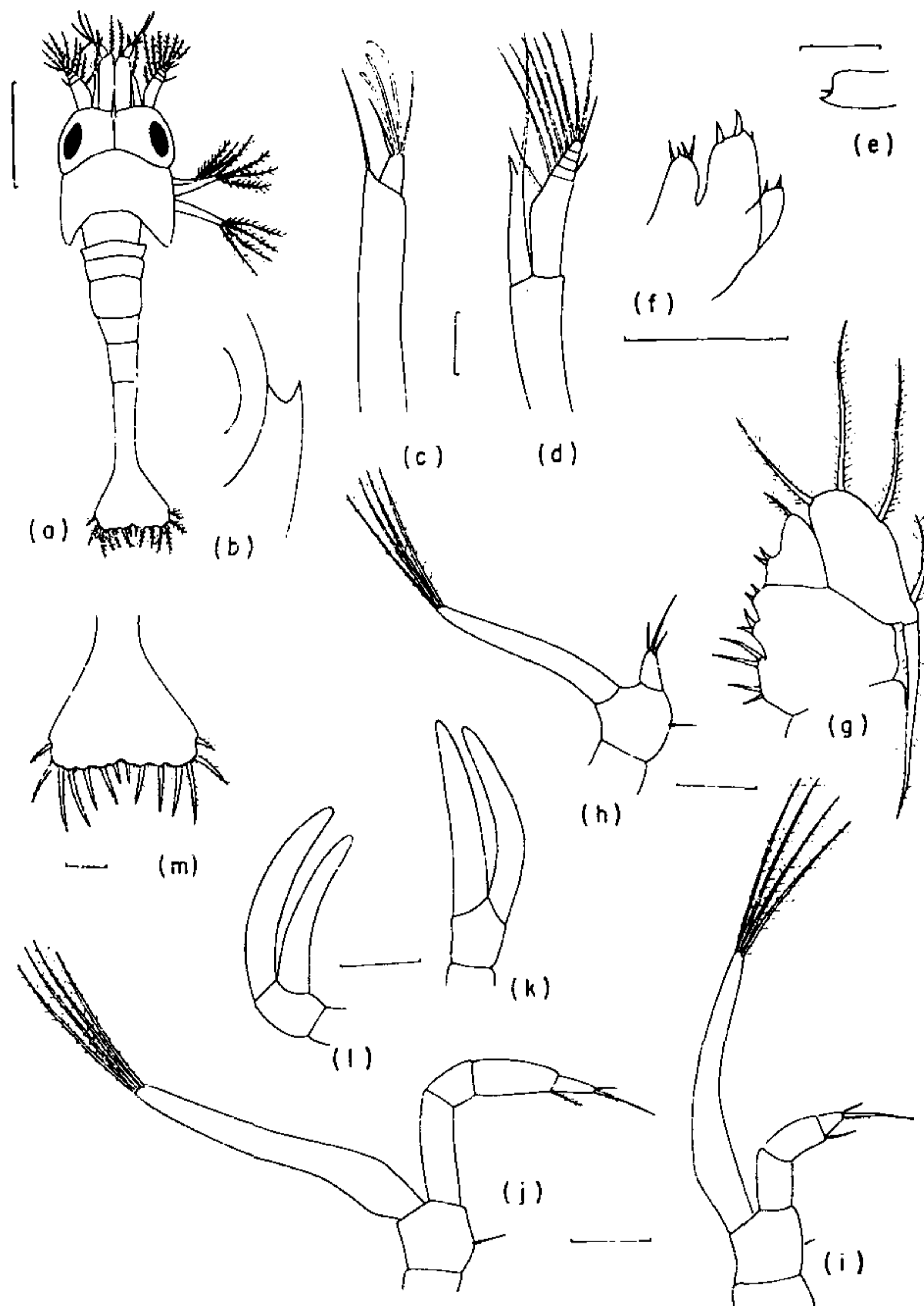


FIG. 1. *Macrobrachium equidens* (Dana). Zoeal stage I. (a) Dorsal view; (b) antero-lateral border of carapace; (c) antennule; (d) antenna; (e) mandible; (f) maxillule; (g) maxilla; (h)–(j) maxillipeds 1–3; (k), (l) pereiopods 1 and 2; (m) telson.

Scale=0.5 mm: (a); 0.1 mm: (c)–(m).

*Maxilliped 2* (Fig. 1(i)) endopod 3-segmented, last segment carrying 1 small seta and terminating in a long and serrate spine, penultimate segment with 1 seta; exopod unsegmented with 4 natatory setae; basis with 1 seta.

*Maxilliped 3* (Fig. 1(j)) endopod 4-segmented, last segment with 1 small seta and terminating in a serrate spine, penultimate segment with 1 seta; exopod unsegmented with 4 natatory setae; basis with 1 seta.

*Pereiopods 1 and 2* (Fig. 1(k), (l)) biramous, with 2-segmented protopods and unsegmented, unarmed exopods and endopods.

*Abdomen* (Fig. 1(a)) 5-segmented, 3rd segment the largest, 6th segment fused to telson; spines absent from all segments.

*Telson* (Fig. 1(m)) triangular, posterior border slightly concave, fringed with small spinules and carrying 7+7 plumose setae.

*Stage II*

c.l. 0.62-0.68 mm

t.l. 2.0-2.1 mm

*Carapace* (Fig. 2(a)) rostral spine now large, supra-orbital spines now present, antero-lateral border of carapace (Fig. 2(b)) still armed with 1 pterygostomian spine. Eyes stalked.

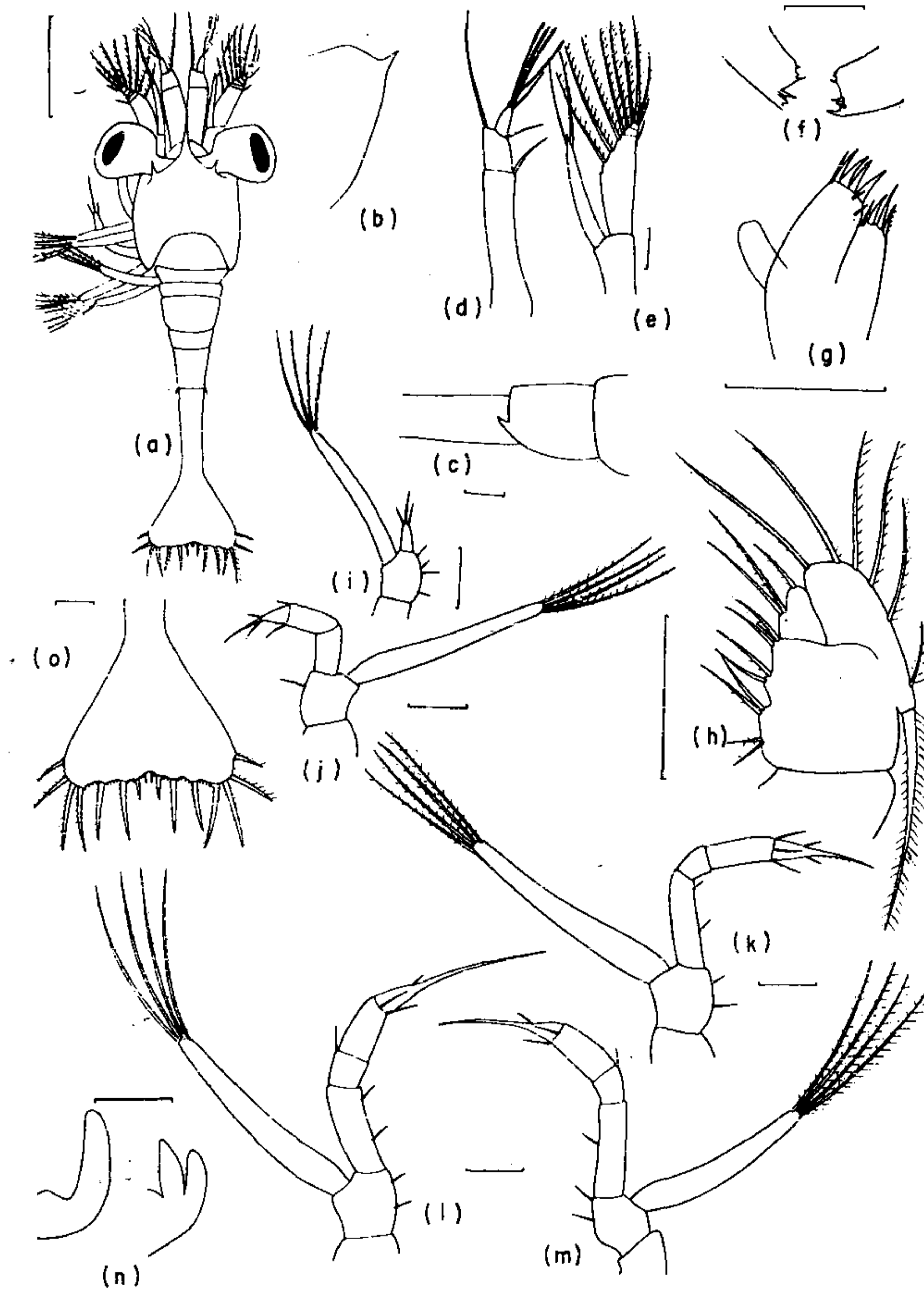


FIG. 2. *Macrobrachium equidens* (Dana). Zoeal stage II. (a) Dorsal view; (b) antero-lateral border of carapace; (c) abdominal somite 5 with part of 4 and 6 (lateral view); (d) antennule; (e) antenna; (f) mandible; (g) maxillule; (h) maxilla; (i)-(k) maxillipeds 1-3; (l), (m), (n), (o) pereiopods 1, 2, 3 and 5; (p) telson.

Scale=0.5 mm: (a); 0.1 mm: (d)-(p).



*Antennule* (Fig. 2(d)) exopod armed with 4 aesthetascs and 1 seta; peduncle now 2-segmented, each segment with 1 seta on distal border, last segment with 1 plumose seta in position of the endopod.

*Antenna* (Fig. 2(e)) endopod now has 2 setae at tip.

*Mandible* (Fig. 2(f)) small teeth now visible on incisor and molar processes; 2 spines between the processes.

*Maxillule* (Fig. 2(g)) endopod unsegmented, devoid of setae; basal and coxal endites large, basal endite with 4 spines and 3 setae, coxal endite with 3 spines and 1 seta.

*Maxilla* (Fig. 2(h)) endopod unsegmented with 3 setae, scaphognathite now with 7 setae, basal and coxal endites together with 9 setae.

*Maxilliped 1* (Fig. 2(i)) basis with 4 small setae.

*Maxilliped 2* (Fig. 2(j)) the penultimate and the last segments of the endopod have each 2 small setae.

*Maxilliped 3* (Fig. 2(k)) 1st segment of the endopod with 2 setae, penultimate segment with 3 setae and last segment with 2 setae; basis with 2 setae.

*Pereiopods 1 and 2* (Figs 2(l), (m)) similar in shape; endopods 4-segmented, each segment with 1 or 2 small setae and last segment with 1 terminal spine, terminal spine of pereiopod 1 longer than that of pereiopod 2; exopods unsegmented with 4 natatory setae; basis with 2 setae.

*Pereiopod 3* (Fig. 2(n)) a small biramous bud.

*Pereiopod 4* not developed.

*Pereiopod 5* (Fig. 2(o)) uniramous, unsegmented bud.

*Abdomen* (Fig. 2(a), (c)) a pair of lateral spines present on posterior border of abdominal segment 5.

*Telson* (Fig. 2(p)) an extra pair of small medial setae is added, giving a setal formula of 8+8.

### Stage III

c.l. 0.65–0.74 mm

t.l. 2.1–2.4 mm

*Carapace* (Fig. 3(a)) 1 epigastric spine present behind rostral spine, 1 small tubercle behind epigastric spine; antero-lateral border of carapace (Fig. 3(b)) now with another large spine, dorsal to pterygostomian.

*Antennule* (Fig. 3(c)) endopod small, not separated from peduncle, with 1 non-plumose seta; exopod conical, with 3 aesthetascs and 1 small seta; proximal peduncular segment now with small outer setae, distal segment with 2 plumose setae at the base of endopod and 3 small setae at the base of exopod.

*Antenna* (Fig. 3(d)) endopod now with a 2-segmented basal part and an unsegmented flagellum tipped with 4 small setae, exopod with 1 outer and 11 inner setae.

*Maxillule* (Fig. 3(e)) coxal endite with 3 spines and 2 setae.

*Maxilla* (Fig. 3(f)) scaphognathite with only 6 setae, endites now carrying 10 setae.

*Maxilliped 1* (Fig. 3(g)) endopod, basis and coxa with 4, 5 and 1 seta respectively.

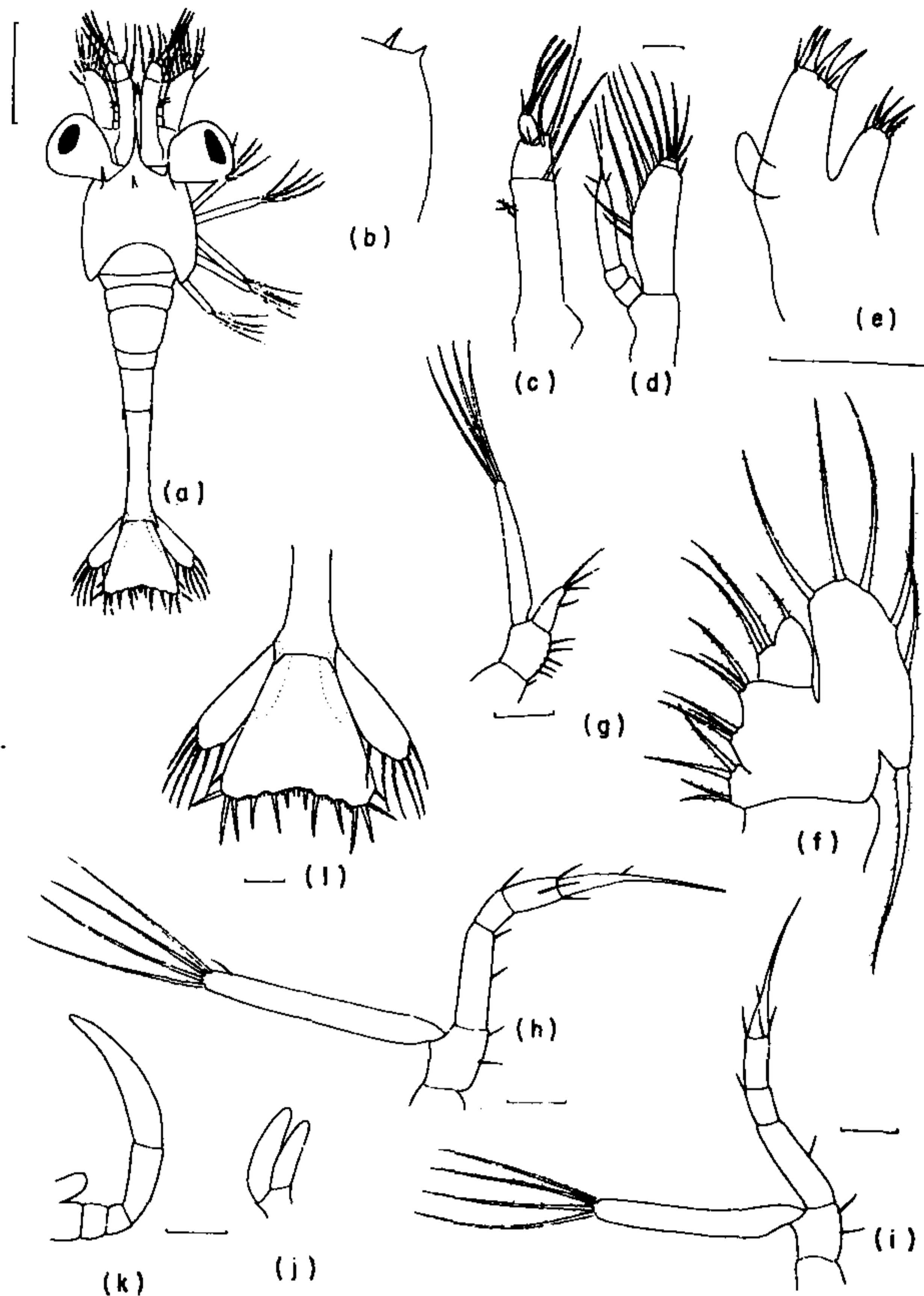


FIG. 3. *Macrobrachium equidens* (Dana). Zoeal stage III. (a) Dorsal view; (b) antero-lateral border of carapace; (c) antennule; (d) antenna; (e) maxillule; (f) maxilla; (g) maxilliped 1; (h), (i) (j) pereiopods 1, 2 and 3; (k) pereiopods 4 and 5; (l) telson and uropods.

Scale=0.5 mm: (a); 0.1 mm: (c)-(l).

*Pereiopods 1 and 2* (Fig. 3(h), (i)) endopods with one more seta at the base of last segments.

*Pereiopod 3* (Fig. 3(j)) now provided with a small protopod.

*Pereiopod 4* (Fig. 3(k)) a small rounded bud.

*Pereiopod 5* (Fig. 3(k)) large, uniramous; endopod 3-segmented, non setose.

*Abdomen* (Fig. 3(a)) 6th abdominal segment now separated from telson, terminating posteriorly in 2 lateral spines.

*Telson* (Fig. 3(l)) telson shape and setal formula unchanged.

*Uropods* (Fig. 3(l)) unsegmented; endopod small, devoid of setae; exopod with 6 plumose setae.

*Stage IV*

c.l. 0.71–0.79 mm

t.l. 2.2–2.5 mm

*Carapace* (Fig. 4(a)) second epigastric spine behind the first, a small tubercle behind second spine; small ventral serrations present on epigastric and sub-orbital spines; antero-lateral border of carapace (Fig. 4(b)) with both spines large.

*Antennule* (Fig. 4(c)) endopod now separated from peduncle; peduncle with 3 inner

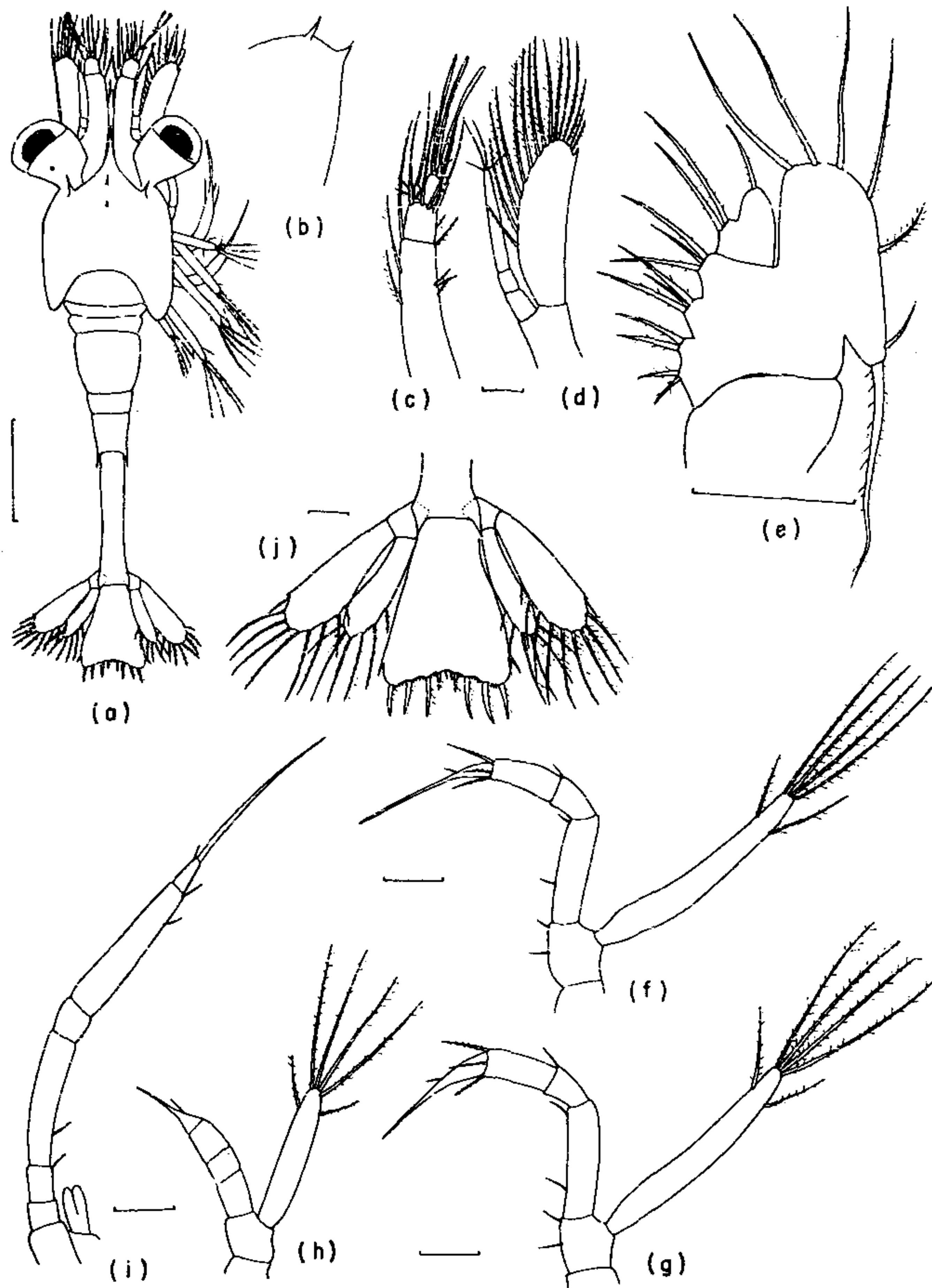


FIG. 4. *Macrobrachium equidens* (Dana). Zoeal stage IV. (a) Dorsal view; (b) antero-lateral border of carapace; (c) antennule; (d) antenna; (e) maxilla; (f), (g), (h) pereiopods 1, 2 and 3; (i) pereiopods 4 and 5; (j) telson and uropods.

Scale=0.5 mm: (a); 0.1 mm: (c)–(j).



plumose setae on 1st segment, 4 setae on distal border of 2nd segment and 3 small setae on a tubercle at the base of endopod.

*Antenna* (Fig. 4(d)) exopod now armed with 14–15 setae and 1 lateral spine.

*Maxilla* (Fig. 4(e)) scaphognathite with 7 setae.

*Maxilliped 3*, exopod with 6 natatory setae.

*Pereiopods 1 and 2* (Fig. 4(f), (g)) exopods with 6 natatory setae.

*Pereiopod 3* (Fig. 4(h)) endopod 4-segmented, last segment with 1 seta and ending in a spine; exopod unsegmented with 6 natatory setae.

*Pereiopod 4* (Fig. 4(i)) a small biramous bud.

*Pereiopod 5* (Fig. 4(i)) endopod 5-segmented with a few small setae on the segments, exopod absent.

*Telson* (Fig. 4(j)) narrower than in previous stage, telson formula now reduced to 6+6 setae.

*Uropods* (Fig. 4(j)) endopod with 5–6 setae, exopod with 1 lateral spine and 9–10 setae, protopod well developed.

#### *Stage V*

c.l. 0.79–0.86 mm

t.l. 2.6–2.9 mm

*Antennule* (Fig. 5(b)) endopod now large; peduncle now basally expanded with small outer setae, proximal segment with 4 inner setae.

*Antenna* (Fig. 5(c)) exopod with 16–17 setae.

*Mandible* (Fig. 5(d)) with 3 spines between incisor and molar processes.

*Maxillule* (Fig. 5(e)) coxal endites with 1 subterminal seta.

*Maxilliped 1* (Fig. 5(f)) with a rudiment of epipod on coxa.

*Maxilliped 2*, exopod with 6 natatory setae.

*Pereiopods 1, 2 and 5* (Fig. 5(g), (h), (k)) unchanged.

*Pereiopod 3* (Fig. 5(i)) with more setae on endopod, and first and penultimate segments relatively longer than in previous stage.

*Pereiopod 4* (Fig. 5(j)) now with a separated protopod; exopod and endopod large but unsegmented and unarmed.

*Pleopods* (Fig. 5(l)) small rounded buds on abdominal segments 1–5.

*Telson* (Fig. 5(m)) narrower, telson formula now 8+8, setae 2, 3 and 8 being very small.

*Uropods* (Fig. 5(m)) endopod with 8–9 setae, exopod with 11–13 setae.

#### *Stage VI*

c.l. 0.86–1.05 mm

t.l. 2.9–3.4 mm

*Carapace* with 1 or 2 small setae near the base of the anterior epigastric spine.

*Antennule* (Fig. 6(b)) endopod with 2 or 3 setae; exopod carrying 4 aesthetascs and

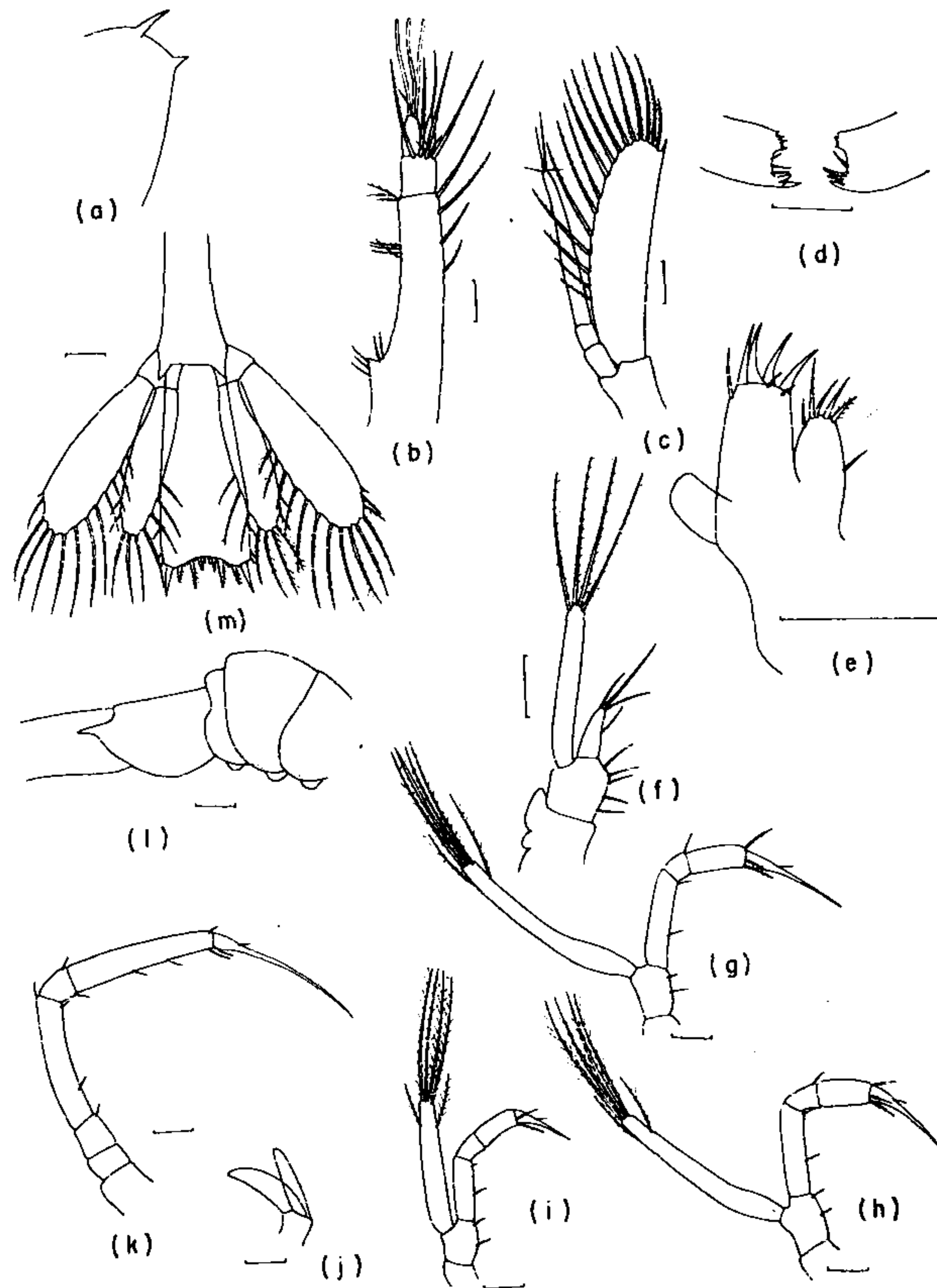


FIG. 5. *Macrobrachium equidens* (Dana). Zoeal stage V. (a) Antero-lateral border of carapace; (b) antennule; (c) antenna; (d) mandible; (e) maxillule; (f) maxilliped 1; (g)–(k) pereopods 1–5; (l) part of abdomen and pleopods; (m) telson and uropods.

Scale=0.1 mm.

terminating in a small bud tipped with 1 or 2 setae; peduncle now with 1 ventral spine, 7–8 inner plumose setae and a row of small setae on proximal segment and 5 setae distally.

*Antenna* (Fig. 6(c)) flagellum of endopod now 2-segmented distally, exopod with 18–20 setae.

*Maxilla* (Fig. 6(d)) scaphognathite with 10–11 setae.

*Maxilliped 1* (Fig. 6(e)) endopod with 5 setae, exopod with 0–1 seta on caridean lobe, basis with 6 setae.

*Pereopods 1 and 2* (Fig. 6(f), (g)) with developing chelae and more setae on endopods.

*Pereiopods 3 and 5* (Fig. 6(h), (j)) with more setae on endopods.

*Pereiopod 4* (Fig. 6(i)) now functional; endopod 4-segmented, with a few small setae on each segment, last segment ending in a spine; exopod unsegmented with 6 natatory setae; basis with 2 setae.

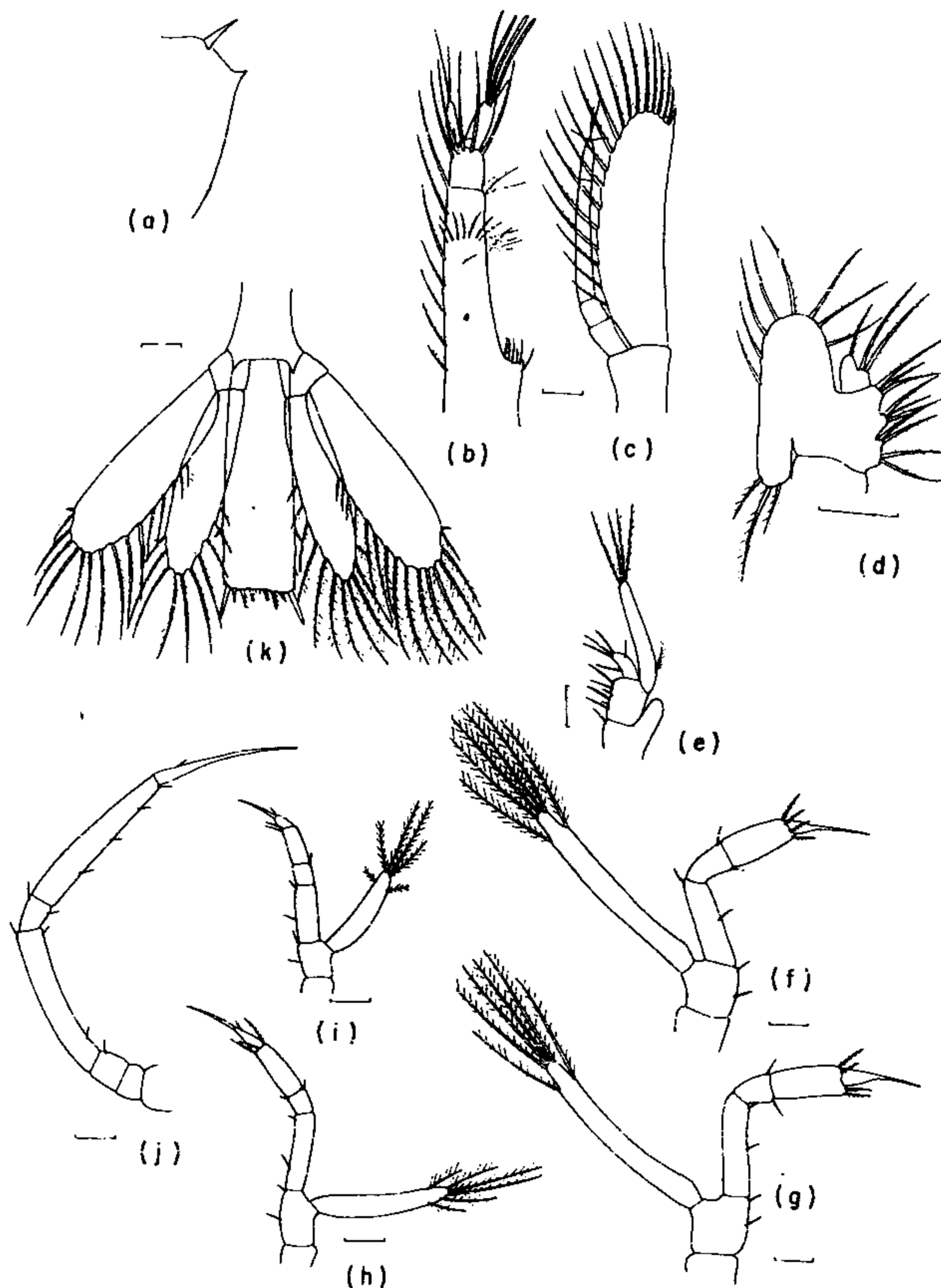


FIG. 6. *Macrobrachium equidens* (Dana). Zoeal stage VI. (a) Antero-lateral border of carapace; (b) antennule; (c) antenna; (d) maxilla; (e) maxilliped 1; (f)-(j) pereopods 1-5; (k) telson and uropods. Scale=0.1 mm.

*Telson* (Fig. 6(k)) lateral borders nearly parallel, posterior border straight or slightly convex, telson formula unchanged but setae 1, 2 and 3 now more separated from one another than in previous stage.

*Uropods* (Fig. 6(k)) endopod with 10-12 setae, exopod with 14-17 setae.



*Stage VII*

c.l. 1.08-1.17 mm

t.l. 3.3-3.7 mm

*Carapace*, anterior epigastric spine provided with 3 small setae.

*Antennule* (Fig. 7(a)) endopod long with 3 setae; exopod with 3 setae at tip and with aesthetascs divided into 2 groups, distal group of 4 and proximal group of 1 or 2.

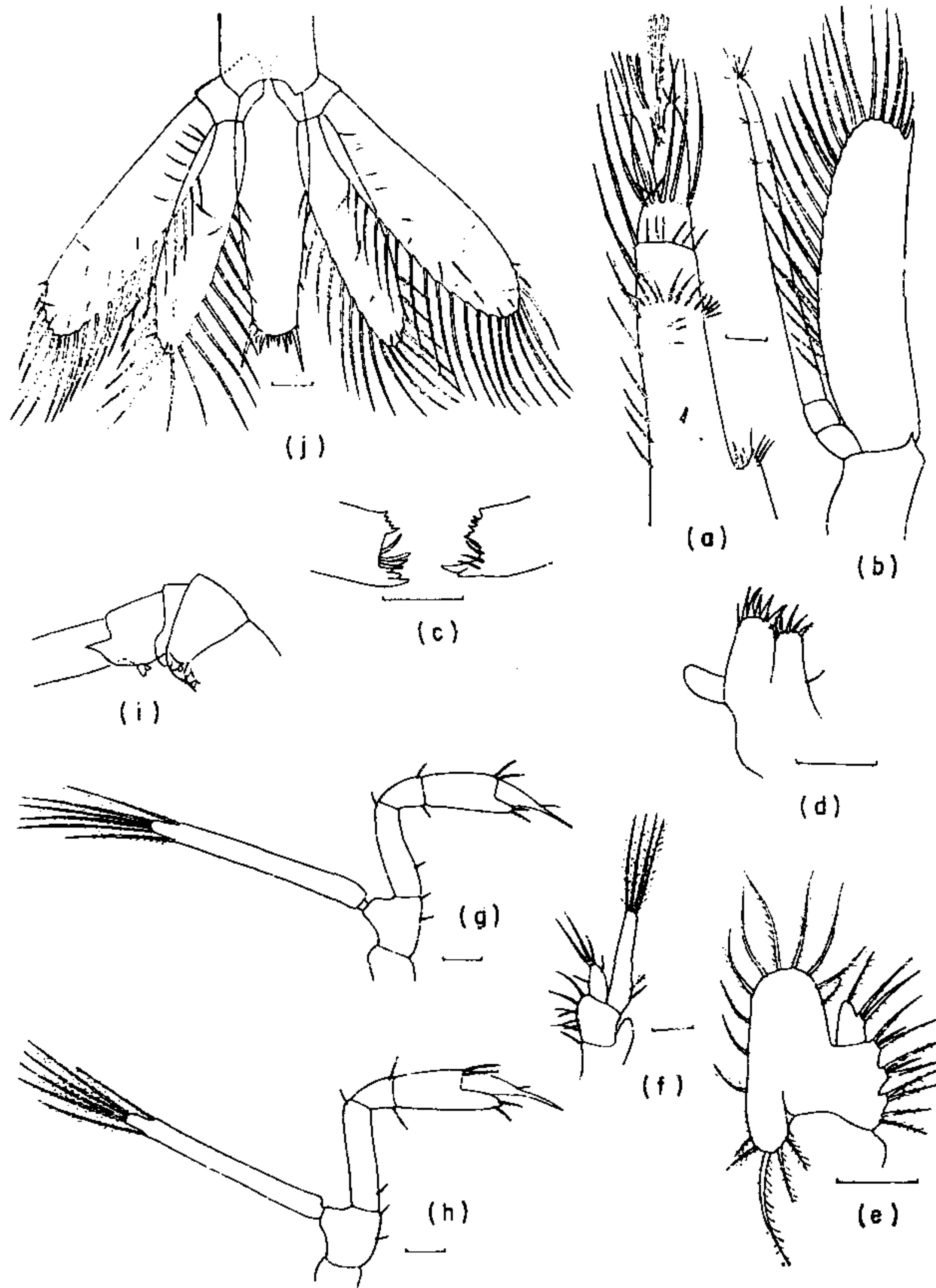


FIG. 7. *Macrobrachium equidens* (Dana). Zoeal stage VII. (a) Antennule; (b) antenna; (c) mandible; (d) maxillule; (e) maxilla; (f) maxilliped 1; (g), (h) pereiopods 1 and 2; (i) part of abdomen and pleopods; (j) telson and uropods. Scale=0.1 mm.

*Antenna* (Fig. 7(b)) flagellum of endopod 3-segmented distally, tipped with 5-6 setae; exopod with 22-23 setae; peduncle with 1 spine on distal border.

*Mandible* (Fig. 7(c)) with 4 spines between incisor and molar processes.

*Maxillule* (Fig. 7(d)) basal endite now with 5 spines and 3 setae.

*Maxilla* (Fig. 7(e)) scaphognathite with 14–16 setae.

*Maxilliped 1* (Fig. 7(f)) exopod with 2 or 3 setae on caridean lobe, basis with 6–7 setae, epipod large.

*Pereiopods 1 and 2* (Fig. 7(g), (h)) chelae well developed, fixed fingers with 2 setae at tip.

*Pleopods* (Fig. 7(i)) large, biramous buds.

*Telson* (Fig. 7(j)) distal part now narrower than proximal, posterior border convex, spine formula unchanged.

*Uropods* (Fig. 7(j)) endopod with 14–17 setae, exopod with 19–20 setae.

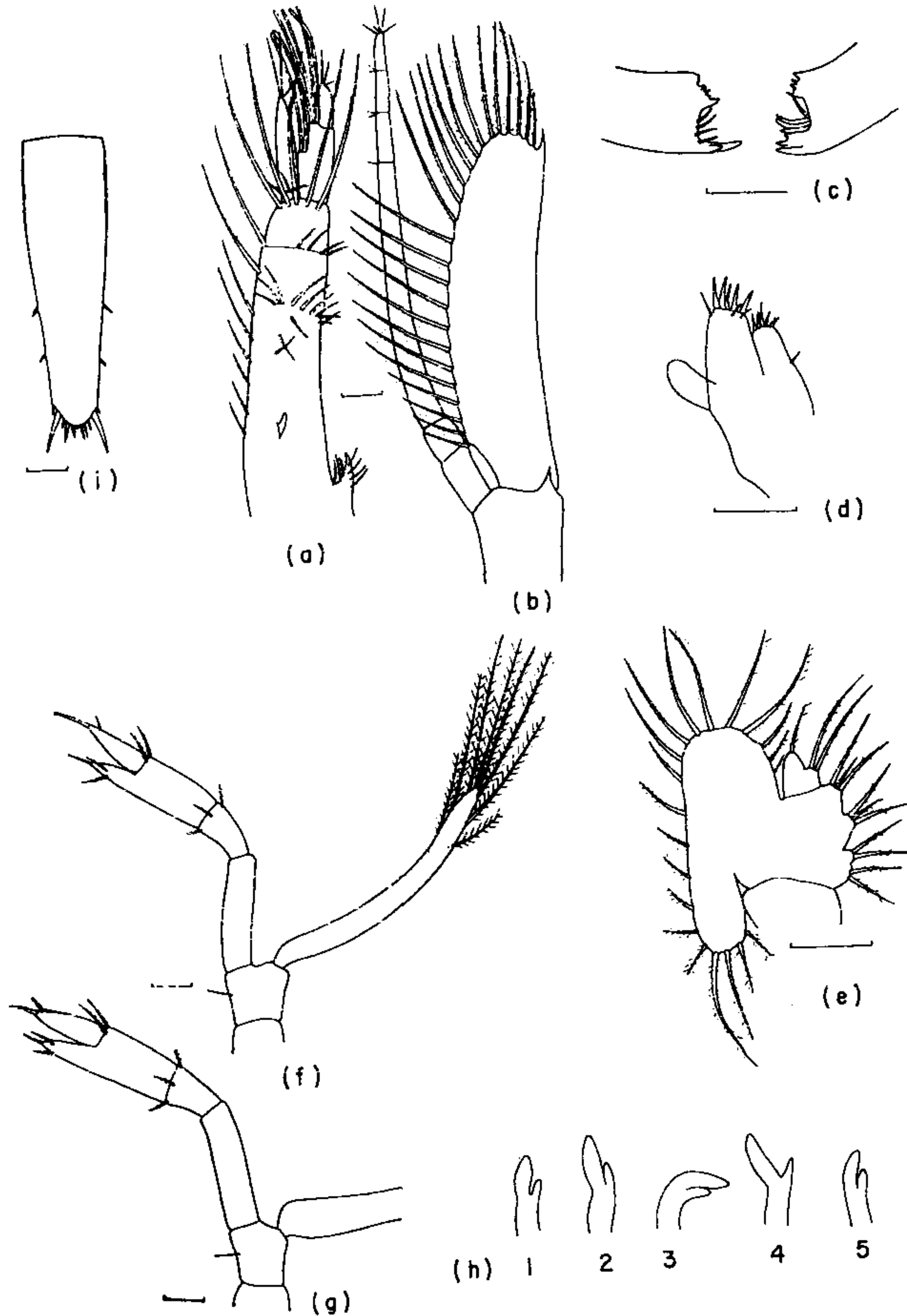


FIG. 8. *Macrobrachium equidens* (Dana). Zoeal stage VIII. (a) Antennule; (b) antenna; (c) mandible; (d) maxillule; (e) maxilla; (f), (g) pereiopods 1 and 2; (h) 1–5, pleopods 1–5; (i) telson.  
Scale=0.1 mm.

*Distribution of chromatophores*

Small red chromatophores on basis of antennule and antenna.

Small red chromatophores on eye-stalks.

Red chromatophores on the sides of carapace.

Red and dark chromatophores with dendrites on 3rd abdominal segment.

One red chromatophore on 6th abdominal segment near telson.

Red chromatophores with dendrites on endopods of all maxillipeds and pereopods.

*Stage VIII*

c.l. 1.17–1.30 mm

t.l. 3.8–4.2 mm

*Antennule* (Fig. 8(a)) incipient inner ramus of exopod with 2 groups of 4 and 2 aesthetascs, outer ramus fairly large, tipped with 2 small setae and articulated with the main body of the exopod.

*Antenna* (Fig. 8(b)) flagellum of endopod 4-segmented, exopod with 23–24 setae.

*Mandible* (Fig. 8(c)), *maxillule* (Fig. 8(d)) unchanged.

*Maxilla* (Fig. 8(e)) scaphognathite with 19–21 setae.

*Pereopods 1 and 2* (Fig. 8(f), (g)) large, both dactylus and fixed finger of endopods ending in short spines; exopods with 8 natatory setae.

*Pleopods* (Fig. 8(h)) large, biramous but unsegmented.

*Telson* (Fig. 8(i)) distal part narrower than proximal part still, posterior border more convex.

*Uropods*, endopod with 17–18 setae, exopod with 20–21 setae.

*Stage IX*

c.l. 1.24–1.39 mm

t.l. 4.2–4.4 mm

*Antennule* (Fig. 9(a)) endopod with 4 small setae; exopod bifid, outer ramus 2-segmented tipped with 4 setae, inner ramus with 4 terminal and 2 subterminal aesthetascs; proximal segment of peduncle now with 10 inner setae.

*Antenna* (Fig. 9(b)) flagellum of endopod 5-segmented, each segment with a few small setae; exopod with 24–26 setae.

*Maxillule* (Fig. 9(d)) unchanged.

*Maxilla* (Fig. 9(c)) scaphognathite with 23–25 setae.

*Maxilliped 1* (Fig. 9(e)) exopod with 4 setae on caridean lobe, epipod large.

*Pereopods 1 and 2* (Fig. 9(f), (g)) large, and pereopod 2 distinctly larger than pereopod 1.

*Pleopods* (Fig. 9(h)) large, biramous buds, still unsegmented.

*Telson* (Fig. 9(i)) distal part now about half as large as proximal, posterior border now devoid of the 2 small medial setae, telson formula reduced to 7+7.

*Uropods*, endopod with 19–21 setae, exopod with 22–23 setae.



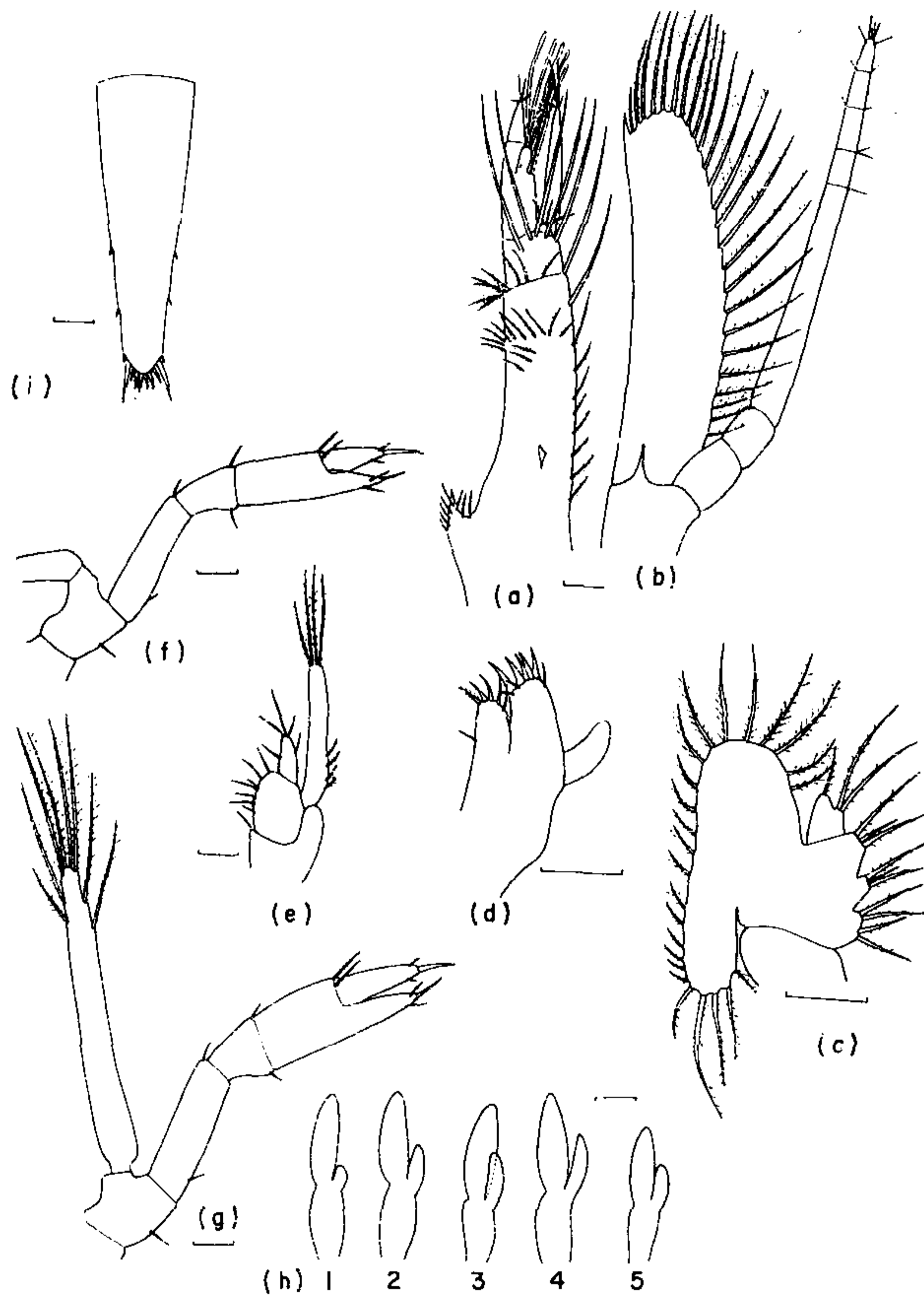


FIG. 9. *Macrobrachium equidens* (Dana). Zoal stage IX. (a) Antennule; (b) antenna; (c) maxilla; (d) maxillule; (e) maxilliped 1; (f), (g) pereopods 1 and 2; (h) 1-5, pleopods 1-5; (i) telson. Scale=0.1 mm.

*Stage X*

c.l. 1.35-1.55 mm

t.l. 4.3-4.9 mm

*Carapace*, anterior epigastric spine now has 4 setae near its base; rostrum remains smooth (Fig. 10(l)).

*Antennule* (Fig. 10(c)) endopod 3-segmented; outer ramus of exopod now 4-segmented, inner ramus unchanged.

*Antenna* (Fig. 10(b)) flagellum of endopod long and 8-segmented, exopod with 28-29 setae.

*Mandible* (Fig. 10(d)) with 5 spines between incisor and molar processes.

*Maxillule* (Fig. 10(e)) unchanged.

*Maxilla* (Fig. 10(f)) scaphognathite with 28–32 setae.

*Maxilliped 1* (Fig. 10(g)) exopod with well developed caridean lobe armed with 6 setae, basis with 8 setae.

*Maxillipeds 2 and 3* (Fig. 10(h), (i)) with more setae on endopods.

*Pereiopods 1 and 2* (Fig. 10(k)) large but terminal spines of both dactylus and fixed fingers smaller than in previous stage.

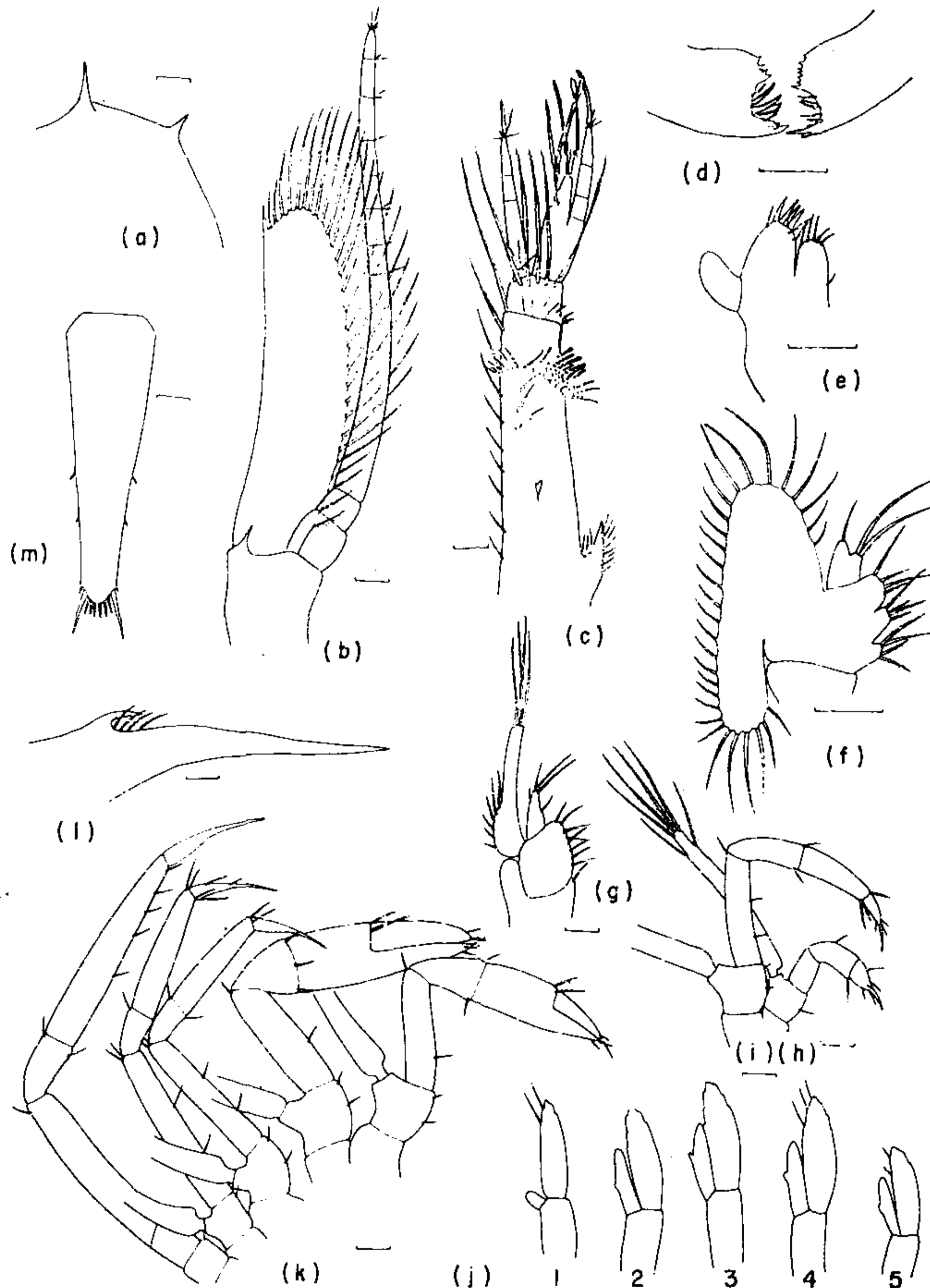


FIG. 10. *Macrobrachium equidens* (Dana). Zoeal stage X. (a) Antero-lateral border of carapace; (b) antenna; (c) antennule; (d) mandible; (e) maxillule; (f) maxilla; (g)–(i) maxillipeds 1–3; (j) 1–5, pleopods 1–5; (k) pereopods; (l) rostrum in lateral view; (m) telson.

Scale=0.1 mm.

*Pereiopods 3-5* (Fig. 10(k)) large.

*Pleopods* (Fig. 10(j)) now segmented, pleopod 5 the smallest; endopod of pleopod 1 small, endopods of pleopods 2-5 larger with a small inner bud; exopods large with a few setae.

*Telson* (Fig. 10(m)) very elongated, distal part less than half as broad as proximal, posterior border increasingly convex; setal formula still 7+7, but seta 4 now very large compared to the remainder.

*Uropods*, endopod with 23-24 setae, exopod with 24-26 setae.

*First postlarval stage*

c.l. 1.58-1.68 mm

t.l. 4.9-5.2 mm

*Carapace* (Fig. 11(a), (b)) longer than broad; rostrum (Fig. 11(c)) with 9 teeth and a few small setae dorsally, 1 or 2 teeth ventrally; antero-lateral border of carapace now showing 1 antennal spine whilst pterygostomian spine has moved slightly backwards.

*Antennule* (Fig. 11(f)) endopod slender, 10-segmented with a few small setae; exopod bifid, outer ramus 9-segmented with a few small setae, inner ramus 3-segmented with 3 groups of 2, 2 and 3 aesthetascs; peduncle 4-segmented, 1st segment broad with 1 outer spine and small setae, 2nd and 3rd segments with 10 inner setae and small setae on distal borders, distal border of 2nd segment also provided with 1 outer spine, 4th segment with 3 small setae on a tubercle at the base of endopod.

*Antenna* (Fig. 11(e)) endopod with a 2-segmented basal part and a long multisegmented flagellum; exopod with a lateral spine and a number of inner setae; peduncle unsegmented and unarmed.

*Mandible* (Fig. 11(d)) without a palp, with a long molar process and small teeth on incisor process.

*Maxillule* (Fig. 11(g)) endopod unsegmented and unarmed; basal and coxal endites large, fringed with numerous setae and spines.

*Maxilla* (Fig. 11(h)) endopod unsegmented and unarmed; scaphognathite large with 34-35 setae, basal and coxal endites with 5 and 6 setae respectively.

*Maxilliped 1* (Fig. 12(a)) endopod unsegmented with 1 subterminal plumose seta, exopod unsegmented with 6 natatory setae distally and 8 setae on caridean lobe, basal and coxal endites with a number of setae and spines, epipod well developed.

*Maxilliped 2* (Fig. 12(b)) endopod 5-segmented with many setae on the last and penultimate segments; exopod slender, unsegmented with 6 natatory setae; basis and coxa with a few setae; epipod fairly large.

*Maxilliped 3* (Fig. 12(c)) endopod large, 5-segmented, inner border of all segments, especially the penultimate one, fringed with setae; exopod unsegmented with 8 natatory setae; basis and coxa with a few setae; epipod small.

*Pereiopods 1 and 2* (Fig. 12(d<sub>1</sub>), (d<sub>2</sub>)) well developed chelipeds, cheliped 2 larger than cheliped 1; endopods 5-segmented with numerous small setae on dactylus and fixed fingers.

*Pereiopods 3-5* (Fig. 12(d<sub>3</sub>)-(d<sub>5</sub>)) similar in size and form, endopods 5-segmented with small setae on each segment.



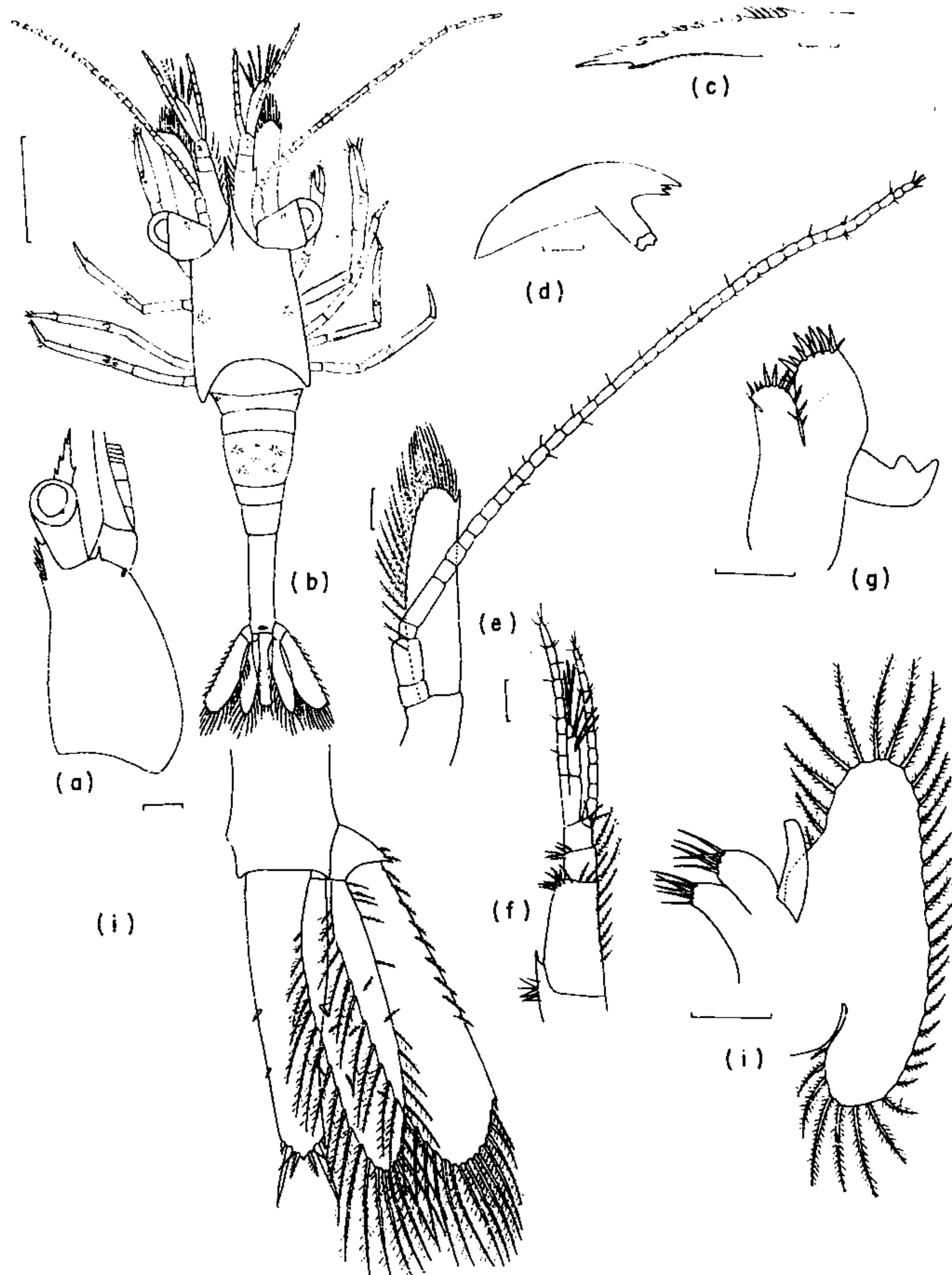


FIG. 11. *Macrobrachium equidens* (Dana). First postlarval stage. (a), (c) carapace and rostrum in lateral view; (b) postlarva in dorsal view; (d) mandible; (e) antenna; (f) antennule; (g) maxillule; (h) maxilla; (i) telson and uropods.

Scale=1 mm: (b); 0.2 mm: (c)-(e); 0.1 mm: (f)-(i).

*Pleopods* (Fig. 12(e)) endopod of pleopod 1 the smallest with 1 or 2 setae, endopods of pleopods 2-5 with 5-6 plumose setae and 1 *appendix interna*; exopods large, flattened with 10-11 plumose setae; protopods unarmed.

*Telson* (Fig. 11(i)) telson formula now 6+6, setae 1 and 2 now dorsal, seta 4 the largest, seta 5 very fine, only seta 6 is plumose, a small pointed medial prominence present between setae 6.

*Uropods* (Fig. 11(i)) endopod and exopod well developed, fringed with many setae, 1 lateral spine present on exopod.

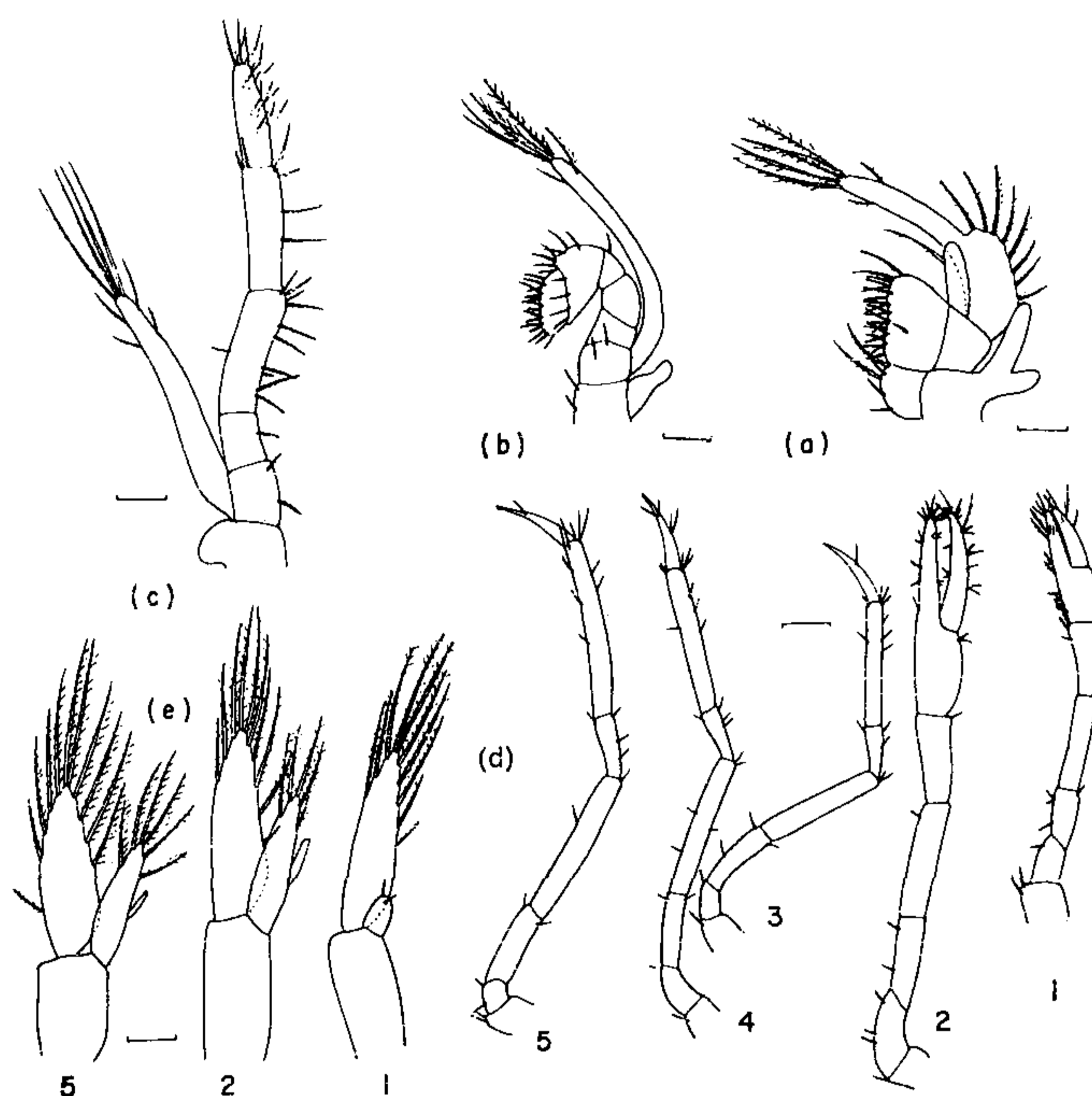


FIG. 12. *Macrobrachium equidens* (Dana). First postlarval stage. (a)-(c) Maxillipeds 1-3; (d) 1-5, pereiopods 1-5; (e) 1, 2, 5, pleopods 1, 2 and 5.  
Scale=0.1 mm: (a), (b), (c), (e); 0.2 mm: (d).

#### *Distribution of chromatophores*

- Red chromatophores with dendrites on peduncles of antennule and antenna.
- Red chromatophores with dendrites on eye-stalks and on the sides of carapace.
- Small red chromatophores with dendrites on all legs.
- Large red chromatophores with dendrites on 1st and 3rd abdominal segments.
- A small red chromatophore on 6th abdominal segment near telson.

#### **Description of the larval stages of *Macrobrachium* sp.**

##### *Stage I*

c.l. 0.62-0.71 mm

t.l. 1.9-2.0 mm

*Carapace* (Fig. 13(a), (b)) short with small rostral spine. Antero-lateral border with 1 pterygostomian spine. Eyes large and sessile.

*Antennule* (Fig. 13(c)) exopod with 3 aesthetascs and 2 setae, one of which is plumose; peduncle unsegmented with 1 long plumose seta in position of the endopod.

*Antenna* (Fig. 13(d)) endopod unsegmented, terminating in a spine and a long plumose

seta; exopod flattened, segmented distally, carrying 9 inner plumose setae and 1 outer non-plumose seta; peduncle unsegmented with 1 spine at the base of endopod.

*Mandible* (Fig. 13(e)) without a palp, with 1 spine between molar and incisor processes.

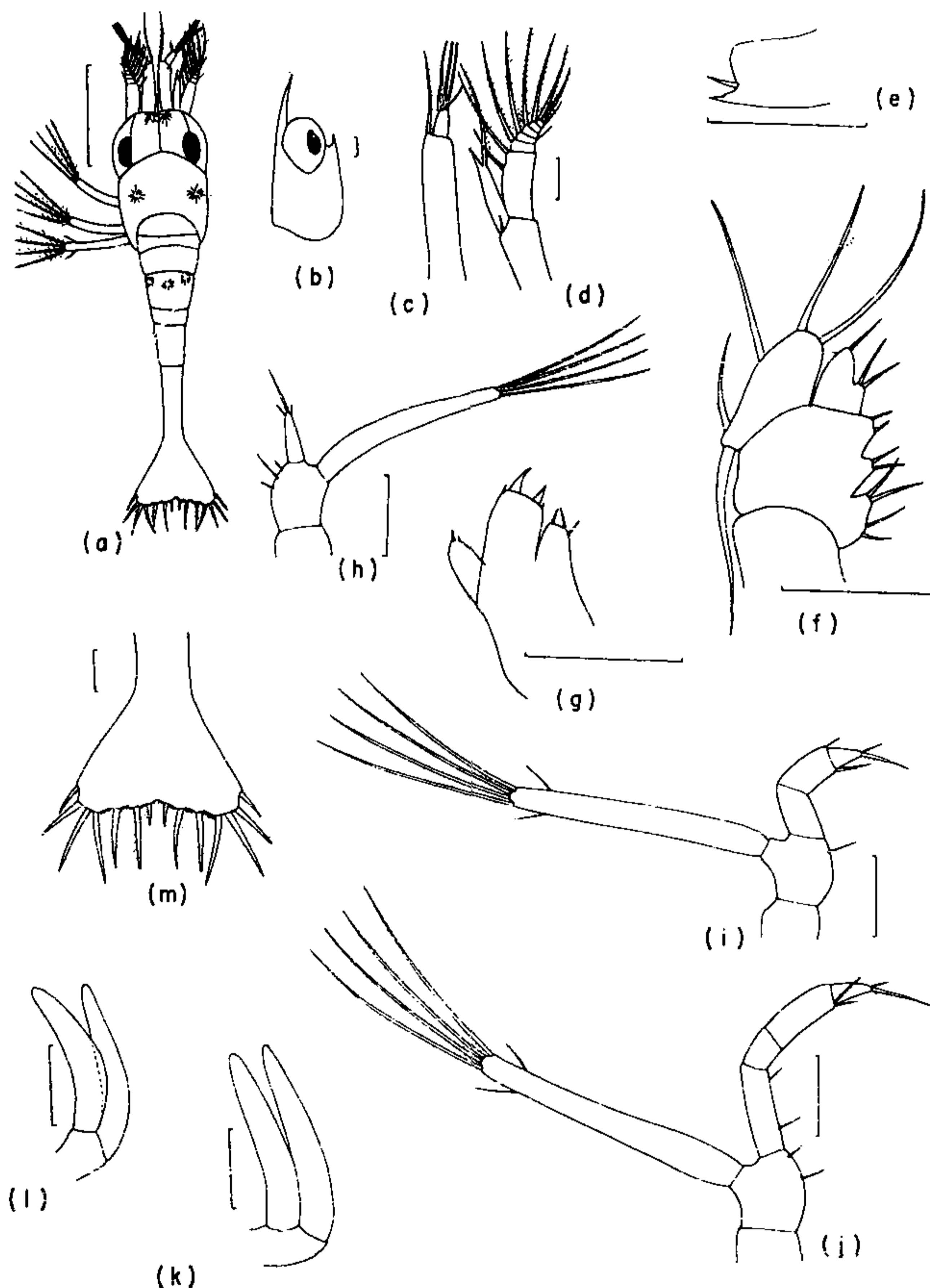


FIG. 13. *Macrobrachium* sp. Zoeal stage I. (a) Dorsal view; (b) carapace in lateral view; (c) antennule; (d) antenna; (e) mandible; (f) maxilla; (g) maxillule; (h)–(j) maxillipeds 1–3; (k), (l) pereopods 1 and 2; (m) telson. Scale=0.5 mm: (a); 0.2 mm: (b); 0.1 mm: (c)–(m).

*Maxillule* (Fig. 13(g)) endopod unsegmented, armed with 2 spines; basal endite with 2 spines and 2 small setae, coxal endite with 3 spines.

*Maxilla* (Fig. 13(f)) endopod unsegmented with 3 setae, scaphognathite with 4 distal plumose setae and 1 larger proximal one; basal and coxal endites, forming 3 inner lobes, armed with 8 setae.



*Maxilliped 1* (Fig. 13(h)) endopod small and unsegmented with 3 terminal setae; exopod unsegmented carrying 4 natatory setae, basis rounded with 3 setae.

*Maxilliped 2* (Fig. 13(i)) endopod 3-segmented, penultimate segment with 2 setae, last segment with 1 small seta and terminating in a long and serrate spine; exopod unsegmented with 6 natatory setae; basis with 1 seta.

*Maxilliped 3* (Fig. 13(j)) endopod 4-segmented, proximal and penultimate segments each with 2 setae, last segment with 1 seta and terminating in a long and serrate spine; exopod unsegmented with 6 natatory setae; basis with 2 setae.

*Pereiopods 1 and 2* (Fig. 13(k), (l)) biramous, with well separated protopods and unsegmented, unarmed exopods and endopods.

*Abdomen* (Fig. 13(a)) 5-segmented, 3rd segment the largest, 6th segment fused to telson; spines absent from all segments.

*Telson* (Fig. 13(m)) triangular, posterior border slightly concave, fringed with small spinules and carrying 7+7 plumose setae.

#### *Distribution of chromatophores*

Small red chromatophores on antennular peduncles.

Red chromatophores with dendrites at the base of rostrum.

Red chromatophores on the sides of carapace and on 3rd abdominal segment.

#### *Stage II*

c.l. 0.71–0.80 mm

t.l. 2.0–2.2 mm

*Carapace* (Fig. 14(a), (b)) rostral spine now large, supra-orbital spines present. Eyes stalked.

*Antennule* (Fig. 14(d)) exopod now with 4 aesthetascs and 1 seta; peduncle now 2-segmented, each segment with a few small setae on distal border, last segment with 1 plumose seta in position of the endopod.

*Antenna* (Fig. 14(c)) endopod now has 2 setae at tip.

*Mandible* (Fig. 14(e)) incisor and molar processes provided with teeth; 2 spines between the processes.

*Maxillule* (Fig. 14(f)) endopod unsegmented with 1 spine; basal endite with 4 spines and 3 setae, coxal endite with 4 spines and 1 seta.

*Maxilla* (Fig. 14(g)) endopod unsegmented with 3 setae, scaphognathite now with 6 or 7 setae, basal and coxal endites together with 9 setae.

*Maxilliped 1* (Fig. 14(h)) endopod with 4 setae, basis and coxa with 6 and 1 setae respectively.

*Maxillipeds 2 and 3* (Fig. 14(i), (j)) unchanged.

*Pereiopods 1 and 2* (Fig. 14(k), (l)) similar in shape; endopods 4-segmented, each segment with 1 or 2 setae and last segment with 1 terminal spine, terminal spine of pereiopod 1 slightly longer than that of pereiopod 2; exopods unsegmented with 6 natatory setae, basis with 2 setae.

*Pereiopod 3* (Fig. 14(m)) a small biramous bud.

*Pereiopod 4* not developed.

*Pereiopod 5* (Fig. 14(n)) uniramous, unsegmented bud.

*Abdomen* (Fig. 14(a)) a pair of lateral spines present on posterior border of abdominal segment 5.

*Telson* (Fig. 14(o)) an extra pair of small medial setae is added, giving a setal formula of 8+8.

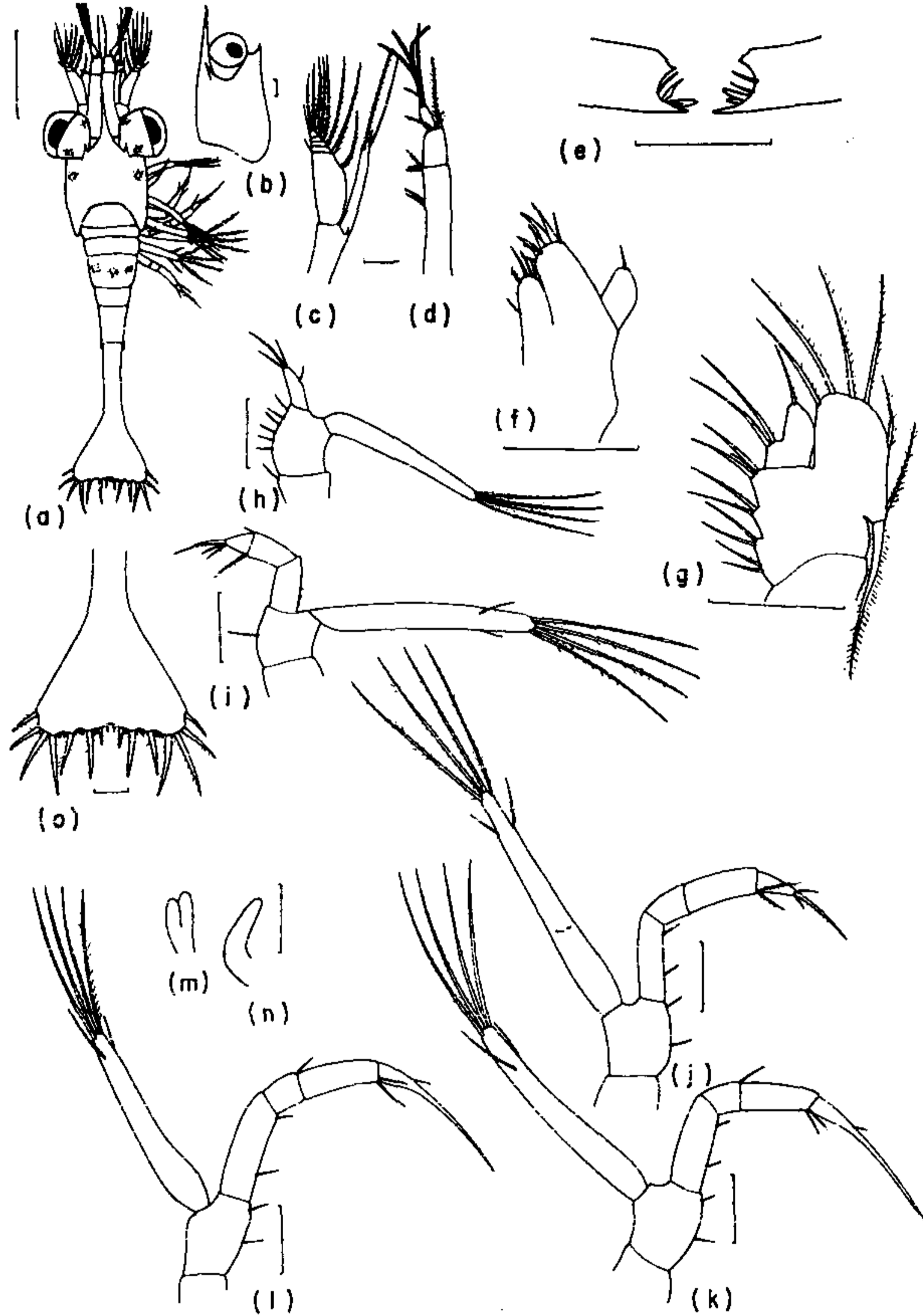


FIG. 14. *Macrobrachium* sp. Zoeal stage II. (a) Dorsal view; (b) carapace in lateral view; (c) antenna; (d) antennule; (e) mandible; (f) maxillule; (g) maxilla; (h)–(j) maxillipeds 1–3; (k), (l), (m), (n) pereopods 1, 2, 3 and 5; (o) telson. Scale=0.5 mm: (a); 0.2 mm: (b); 0.1 mm: (c)–(o).

#### *Distribution of chromatophores*

In addition to those present in the previous stage, there are: two pairs of red chromatophores on eye-stalks, small red chromatophores on endopods of pereopods.

*Stage III*

c.l. 0.71–0.83 mm

t.l. 2.3–2.4 mm

*Carapace* (Fig. 15(a), (b)) an epigastric spine present behind rostral spine and followed by a small tubercle; antero-lateral border of carapace now with another large spine, dorsal to pterygostomian.

*Antennule* (Fig. 15(d)) endopod small with 1 non-plumose seta, exopod conical with 3 aesthetascs and 1 seta; proximal peduncular segment now with small outer and 2 inner plumose setae, distal segment with 2 plumose setae and 3 smaller ones at the base of endopod.

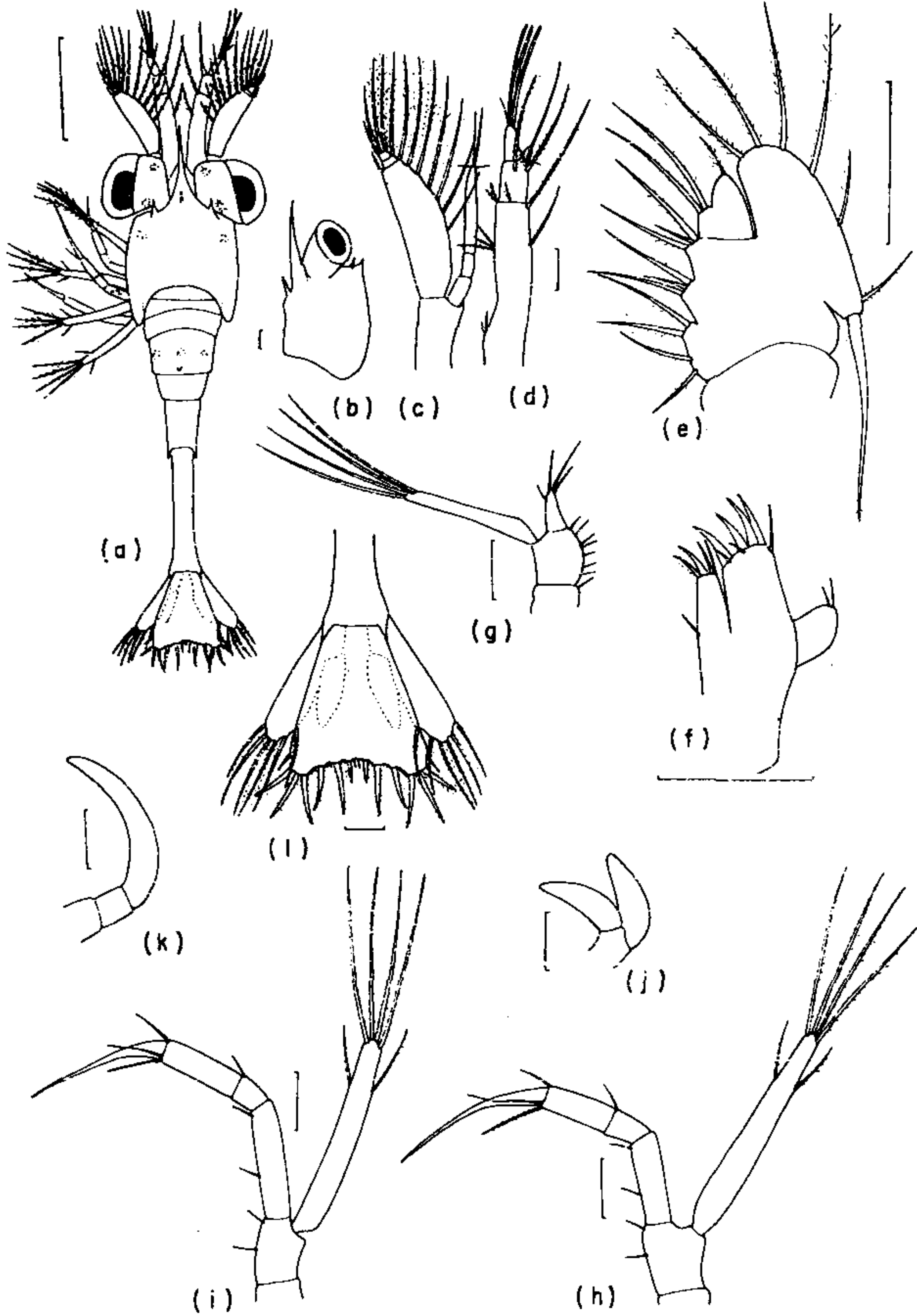


FIG. 15. *Macrobrachium* sp. Zoeal stage III. (a) Dorsal view; (b) carapace in lateral view; (c) antenna; (d) antennule; (e) maxilla; (f) maxillule; (g) maxilliped 1; (h), (i), (j), (k) pereiopods 1, 2, 3 and 5; (l) telson and uropods. Scale=0.5 mm: (a); 0.2 mm: (b); 0.1 mm: (c)–(l).



*Antenna* (Fig. 15(c)) endopod with a 2-segmented basal part and an unsegmented flagellum tipped with 4 setae, exopod with 1 outer and 12 inner setae.

*Maxillule* (Fig. 15(f)) endopod with 2 spines.

*Maxilla* (Fig. 15(e)) scaphognathite with 7 setae, endites carrying 10 setae.

*Maxilliped 1* (Fig. 15(g)) basis now with 7 setae.

*Pereiopods 1 and 2* (Fig. 15(h), (i)) unchanged.

*Pereiopod 3* (Fig. 15(j)) now provided with a small protopod.

*Pereiopod 4* not developed.

*Pereiopod 5* (Fig. 15(k)) uniramous, with a 2-segmented protopod and an unsegmented and unarmed endopod.

*Abdomen* (Fig. 15(a)) 6th abdominal segment now separated from telson and terminating posteriorly in 2 lateral spines.

*Telson* (Fig. 15(l)) telson shape and setal formula unchanged.

*Uropods* (Fig. 15(l)) unsegmented; endopod small, devoid of setae; exopod with 6 plumose setae.

#### *Stage IV*

c.l. 0.77–0.89 mm

t.l. 2.4–2.9 mm

*Carapace* (Fig. 16(a), (b)) second epigastric spine behind the first and followed by a small tubercle; small ventral serrations present on epigastric and sub-orbital spines; antero-lateral border of carapace with both spines large.

*Antennule* (Fig. 16(d)) peduncle now basally expanded with 1 ventral spine, 5–6 inner plumose setae and smaller setae forming a row on proximal segment and 4 plumose setae on distal border of 2nd segment.

*Antenna* (Fig. 16(c)) exopod now armed with 1 lateral spine and 16–17 inner plumose setae, peduncle now unarmed.

*Maxillule* (Fig. 16(f)) coxal endite with 1 seta and 5 spines.

*Maxilla* (Fig. 16(e)) scaphognathite with 9 setae.

*Maxilliped 1* (Fig. 16(g)) endopod and exopod each with 5 setae, basis with 6 setae, a rudiment of epipod present on coxa.

*Pereiopods 1 and 2* (Fig. 16(h), (i)) unchanged.

*Pereiopod 3* (Fig. 16(j)) endopod 4-segmented, each segment with 1 or 2 setae and last segment with 1 terminal spine; exopod unsegmented with 6 natatory setae; basis with 1 seta.

*Pereiopod 4* (Fig. 16(k)) a small biramous bud.

*Pereiopod 5* (Fig. 16(k)) endopod 5-segmented with a few small setae and last segment with a terminal spine; exopod absent

*Telson* (Fig. 16(l)) narrower than in previous stage, telson formula reduced to 6+6 setae.

*Uropods* (Fig. 16(l)) endopod with 7 setae, exopod with 1 lateral spine and 10–11 setae, protopod well developed.

*Distribution of chromatophores*—a small red chromatophore is added on 6th abdominal segment near telson.

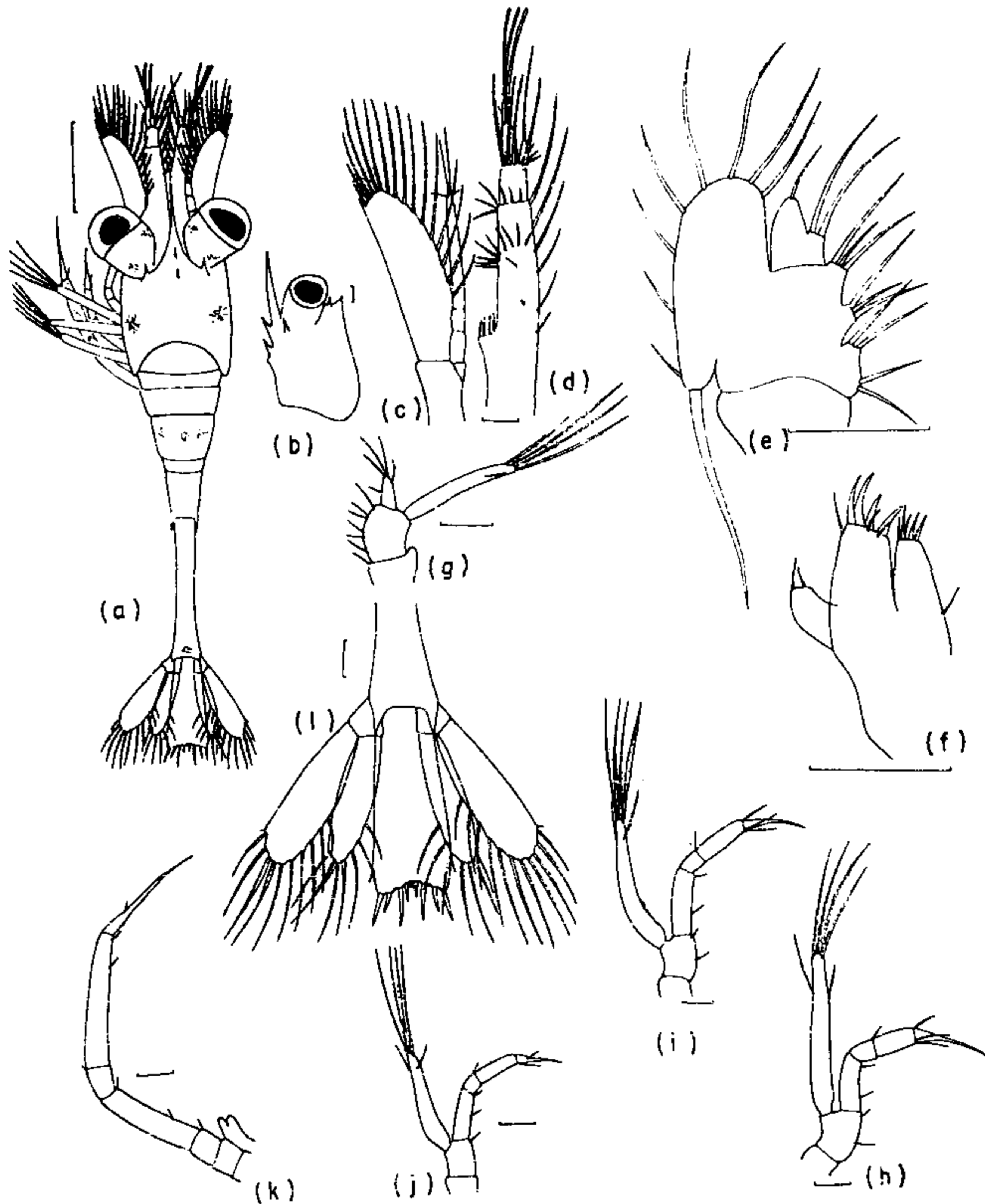


FIG. 16. *Macrobrachium* sp. Zoeal stage IV. (a) Dorsal view; (b) carapace in lateral view; (c) antenna; (d) antennule; (e) maxilla; (f) maxillule; (g) maxilliped 1; (h)–(j) pereiopods 1–3; (k) pereiopods 4 and 5; (l) telson and uropods.

Scale=0.5 mm: (a); 0.2 mm: (b); 0.1 mm: (c)–(l).

*Stage V*

c.l. 0.86–0.96 mm

t.l. 2.9–3.2 mm

*Antennule* (Fig. 17(b)) exopod with 3 aesthetascs and 2 small setae, proximal peduncular segment with 7 inner plumose setae.

*Antenna* (Fig. 17(c)) exopod with 18–19 setae.

*Maxilla* (Fig. 17(d)) scaphognathite with 10–12 setae.

*Maxilliped 1* (Fig. 17(e)) exopod with 1 seta on caridean lobe.

*Pereiopods 1 and 2* (Fig. 17(f), (g)) unchanged.

*Pereiopods 3 and 5* (Fig. 17(h), (j)) with more setae on penultimate segments.

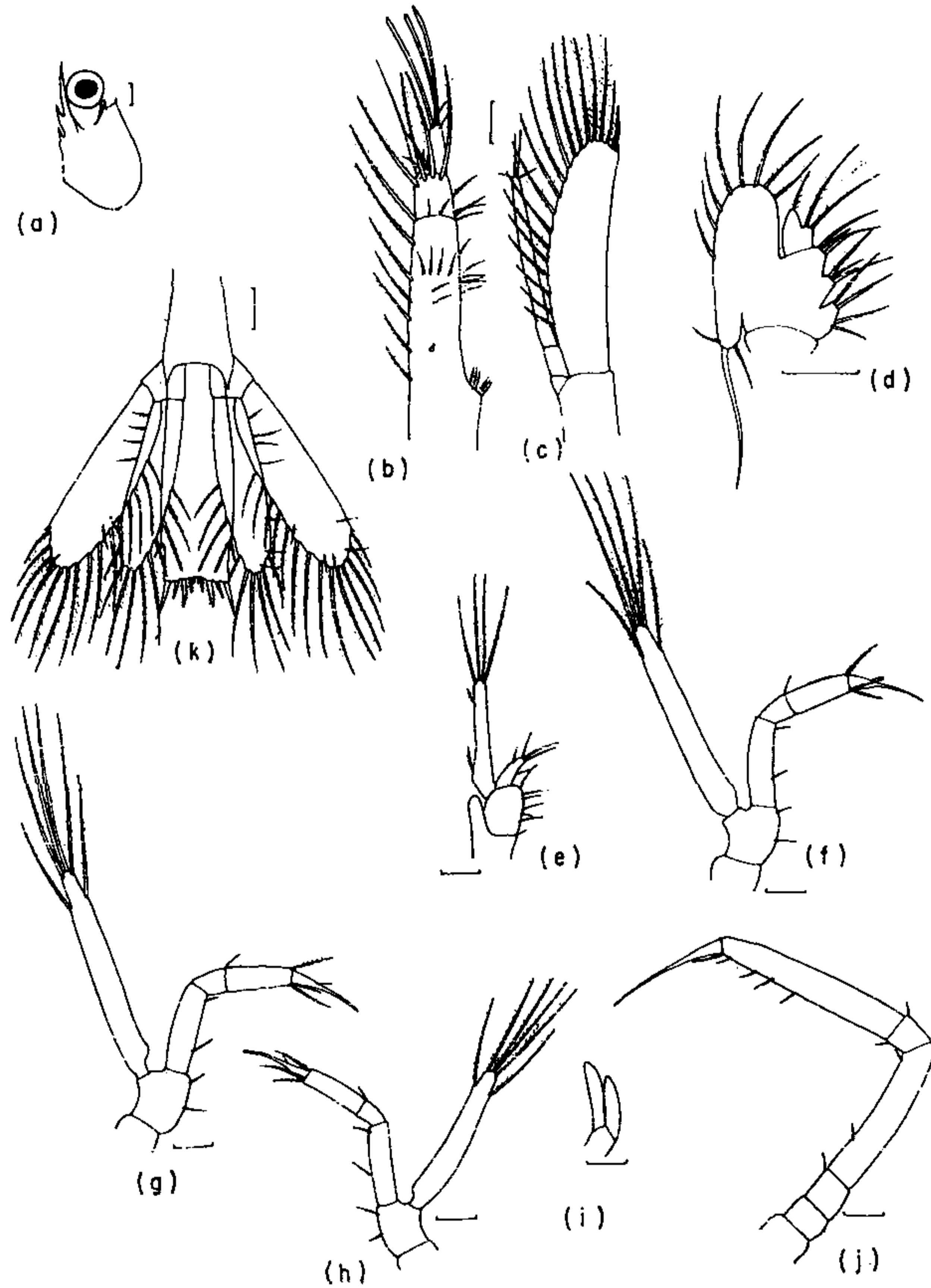


FIG. 17. *Macrobrachium* sp. Zoeal stage V. (a) Carapace in lateral view; (b) antennule; (c) antenna; (d) maxilla; (e) maxilliped 1; (f)–(j) pereiopods 1–5; (k) telson and uropods.

Scale=0.2 mm: (a); 0.1 mm: (b)–(k).

*Pereiopod 4* (Fig. 17(i)) now with a separated protopod; endopod and exopod large but unsegmented and unarmed.

*Telson* (Fig. 17(k)) narrower than in previous stage, setal formula unchanged.

*Uropods* (Fig. 17(k)) endopod with 10 setae, exopod with 14–15 setae.



*Stage VI*

c.l. 0.93–1.08 mm

t.l. 3.2–3.6 mm

*Carapace* (Fig. 18(a)) a small seta present near the base of the anterior epigastric spine.

*Antennule* (Fig. 18(c)) endopod with 2 setae, exopod carrying 4 aesthetascs and terminating in a small bud tipped with 1 small seta, peduncle now has 8–9 inner plumose setae on proximal segment and 5 setae distally.

*Antenna* (Fig. 18(b)) exopod with 20–21 setae.

*Mandible* (Fig. 18(d)) with 3 spines between incisor and molar processes.

*Maxilla* (Fig. 18(e)) scaphognathite with 12–14 setae.

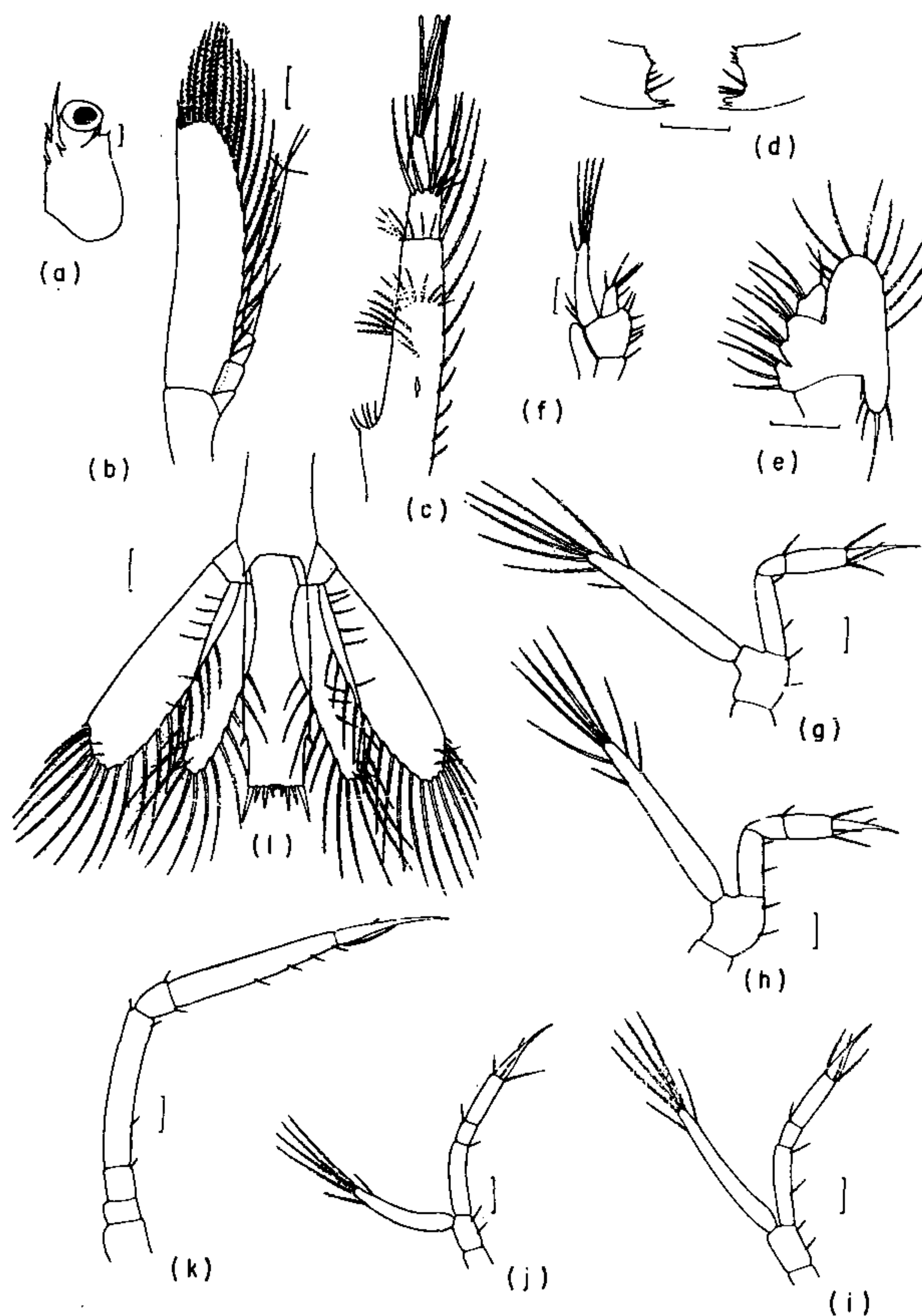


FIG. 18. *Macrobrachium* sp. Zoeal stage VI. (a) Carapace in lateral view; (b) antenna; (c) antennule; (d) mandible; (e) maxilla; (f) maxilliped 1; (g)–(k) pereiopods 1–5; (l) telson and uropods.

Scale=0.2 mm: (a); 0.1 mm: (b)–(l).

*Maxilliped 1* (Fig. 18(f)) exopod with 2 setae on caridean lobe.

*Pereiopods 1 and 2* (Fig. 18(g), (h)) with 8 natatory setae on exopods.

*Pereiopods 3 and 5* (Fig. 18(i), (k)) unchanged.

*Pereiopod 4* (Fig. 18(j)) now functional; endopod 4-segmented, each segment with a few setae and last segment ending in a spine; exopod unsegmented with 6 natatory setae; basis with 2 small setae.

*Telson* (Fig. 18(l)) lateral borders nearly parallel, posterior border straight, telson formula unchanged.

*Uropods* (Fig. 18(l)) endopod with 13-14 setae, exopod with 17-18 setae.

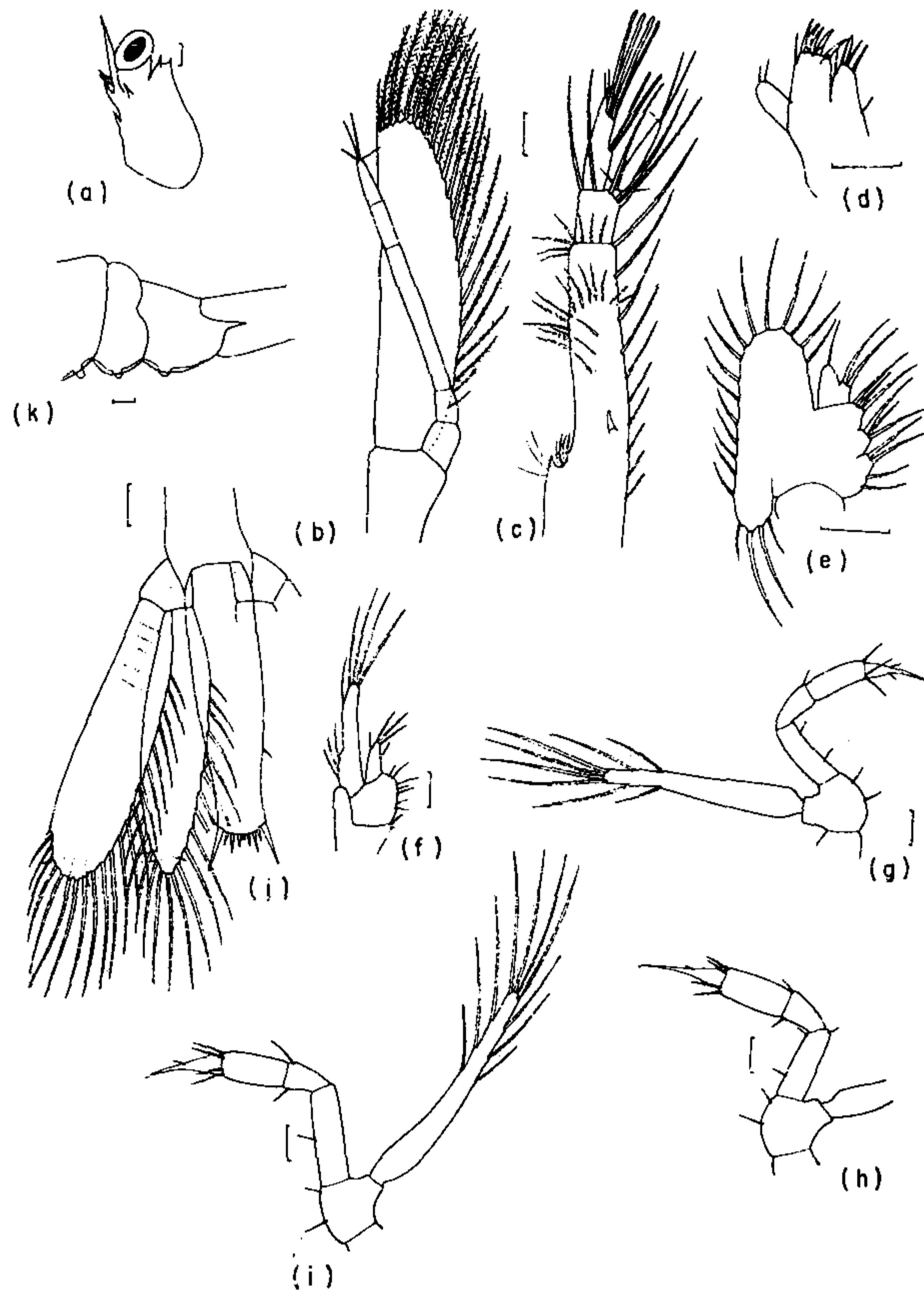


FIG. 19. *Macrobrachium* sp. Zoeal stage VII. (a) Carapace in lateral view; (b) antenna; (c) antennule; (d) maxillule; (e) maxilla; (f), (g) maxillipeds 1 and 3; (h), (i) pereiopods 1 and 2; (j) telson and uropods; (k) part of abdomen and pleopods.

Scale = 0.2 mm: (a); 0.1 mm: (b)-(k).

*Stage VII*

c.l. 1.02–1.30 mm

t.l. 3.6–4.3 mm

*Carapace* (Fig. 19(a)) anterior epigastric spine provided with 2 setae.

*Antennule* (Fig. 19(c)) endopod long with 3 setae; exopod with 2 setae at tip and with aesthetascs divided into 2 groups, a proximal group of 2 and a distal group of 4; proximal peduncular segment with 9–10 inner plumose setae.

*Antenna* (Fig. 19(b)) flagellum of endopod 2 or 3-segmented distally, tipped with 4–5 small setae; exopod with 22–23 setae.

*Maxillule* (Fig. 19(d)) basal endite now with 5 spines and 3 setae.

*Maxilla* (Fig. 19(e)) scaphognathite with 16–20 setae.

*Maxilliped 1* (Fig. 19(f)) exopod with 3 setae on caridean lobe, basis with 7 setae, coxa with 2 setae.

*Maxilliped 3* (Fig. 19(g)) exopod with 8 natatory setae.

*Pereiopods 1 and 2* (Figs 19(h), (i)) with 4 setae on penultimate segments, exopods with 10 natatory setae.

*Pereiopods 3 and 4* exopods with 6–8 natatory setae.

*Pleopods* (Fig. 19(k)) small rounded buds on abdominal segments 1–5.

*Telson* (Fig. 19(j)) distal part narrowing, posterior border straight or slightly convex.

*Uropods* (Fig. 19(j)) endopod with 17–19 setae, exopod with 19–22 setae.

*Stage VIII*

c.l. 1.20–1.45 mm

t.l. 4.0–4.6 mm

*Carapace* (Fig. 20(a)) anterior epigastric spine with 3 setae.

*Antennule* (Fig. 20(c)) incipient inner ramus of exopod with 2 groups of 4 and 2 aesthetascs; outer ramus large, tipped with 2 small setae.

*Antennae* (Fig. 20(b)) exopod with 24–25 setae.

*Mandible* (Fig. 20(d)) now with 4 spines between incisor and molar processes.

*Maxillule* (Fig. 20(e)) unchanged.

*Maxilla* (Fig. 20(f)) scaphognathite with 24–28 setae.

*Maxilliped 1* (Fig. 20(g)) exopod with 4–5 setae on caridean lobe, basis with 8–9 setae.

*Pereiopods 1 and 2* (Figs 20(h), (i)) with developing chelae, fixed fingers with 2 setae at tip.

*Pereiopods 3 and 4*, exopods with 8 natatory setae.

*Pleopods* (Fig. 20(k)) small biramous buds.

*Telson* (Fig. 20(j)) distal part narrower than proximal, posterior border convex; the pair of small medial setae is lost, telson formula now reduced to 5+5 setae.

*Uropods* endopod with 20–22 setae, exopod with 23–25 setae.



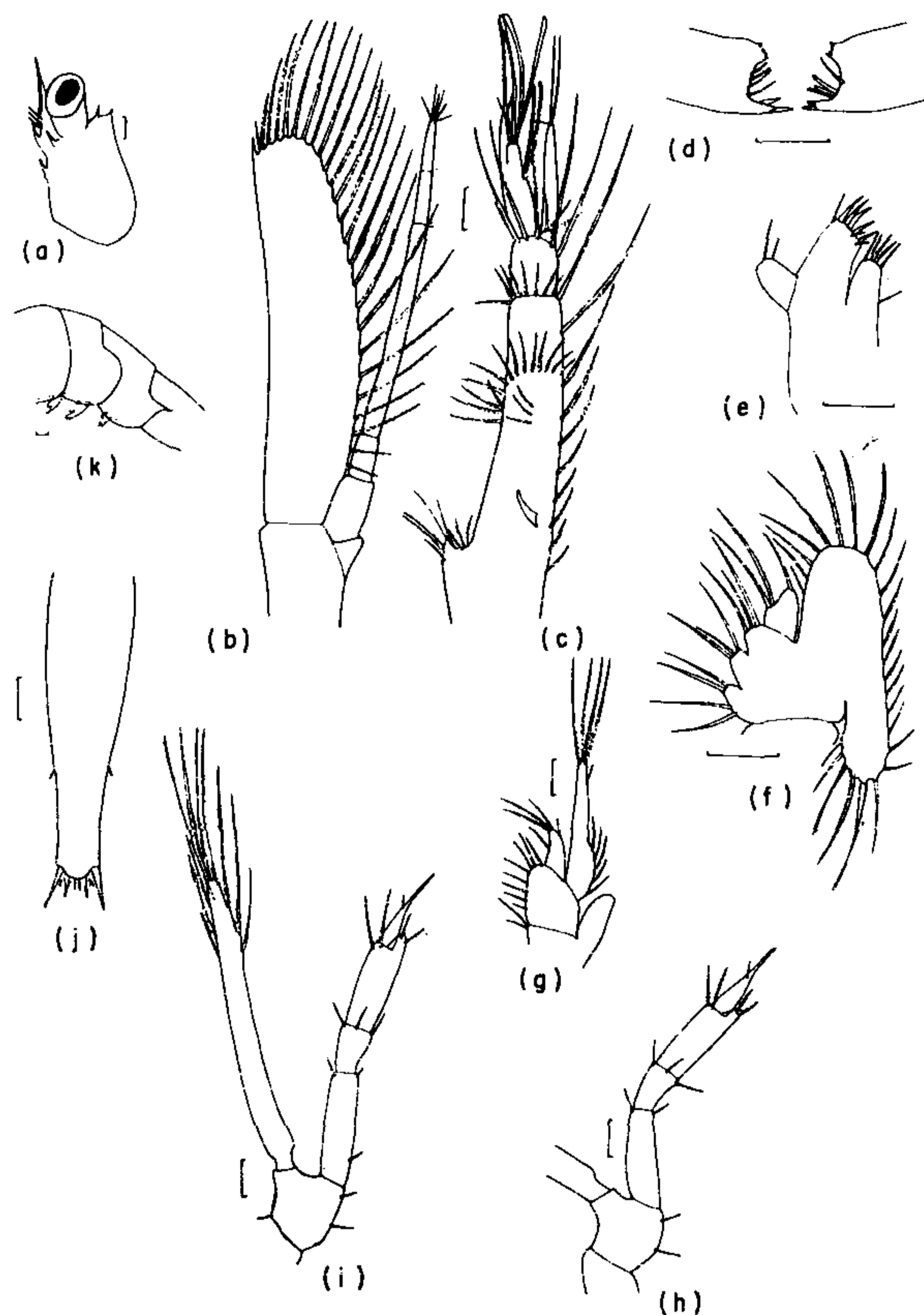


FIG. 20. *Macrobrachium* sp. Zoeal stage VIII. (a) Carapace in lateral view; (b) antenna; (c) antennule; (d) mandible; (e) maxillule; (f) maxilla; (g) maxilliped 1; (h), (i) pereopods 1 and 2; (j) telson; (k) part of abdomen and pleopods.

Scale=0.2 mm: (a); 0.1 mm: (b)-(k).

#### *Distribution of chromatophores*

Two red chromatophores are added on lateral sides of carapace.

One red chromatophore added on lateral sides of abdominal segments 1 and 2.

#### *Stage IX*

c.l. 1.39-1.64 mm

t.l. 4.4-5.1 mm

*Carapace* (Fig. 21(a)) anterior epigastric spine with 4 setae.

*Antennule* (Fig. 21(c)) inner ramus of exopod with 3 groups of 4, 3 and 2 aesthetascs, outer ramus 2-segmented.

*Antenna* (Fig. 21(b)) flagellum of endopod now 4-segmented distally, exopod fringed with 26–29 setae.

*Maxillule* (Fig. 21(d)) basal endite with 6 spines and 3 setae, coxal endite with 6 spines and 1 seta.

*Maxilla* (Fig. 21(e)) scaphognathite with 29–32 setae.

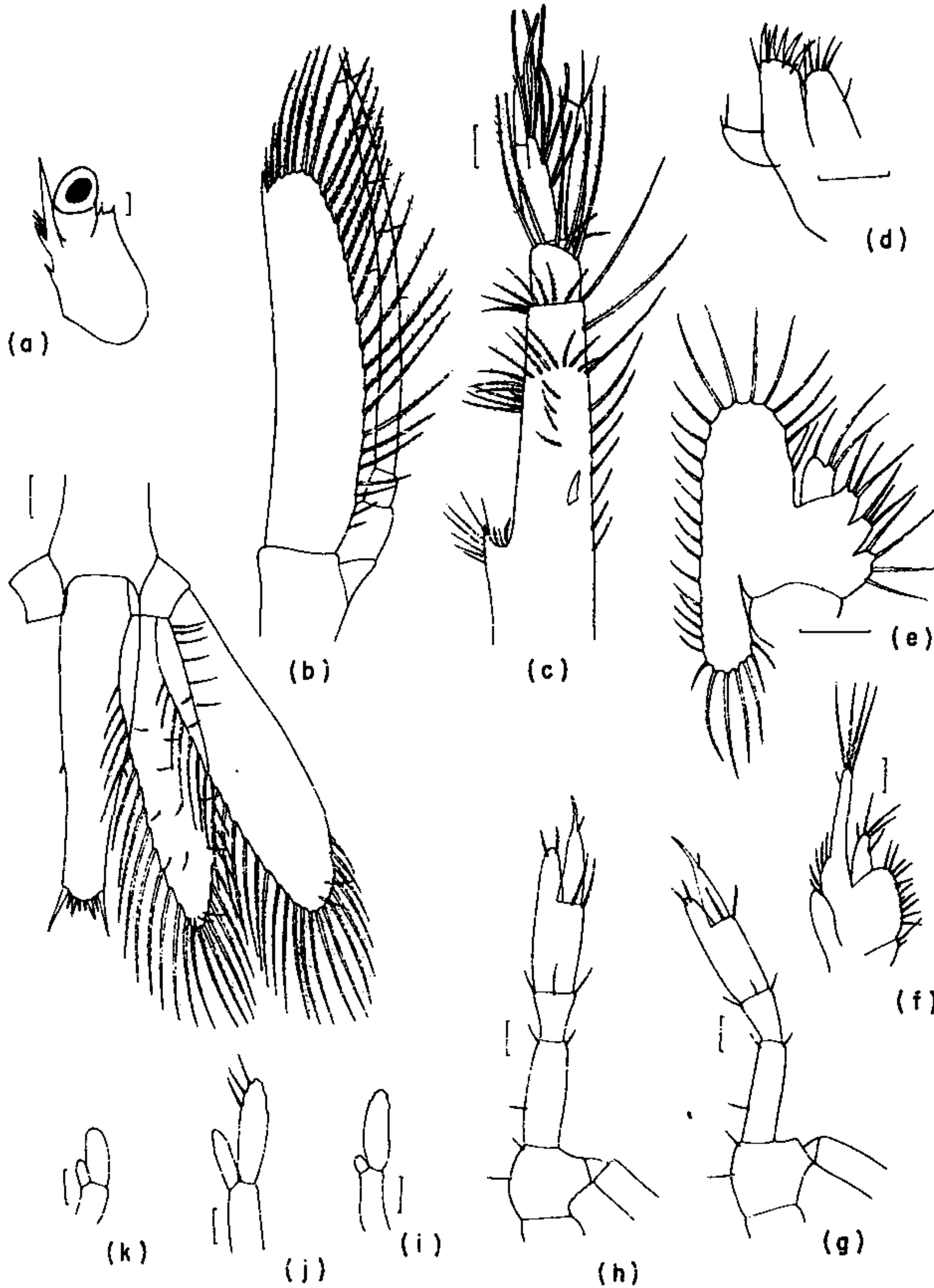


FIG. 21. *Macrobrachium* sp. Zoeal stage IX. (a) Carapace in lateral view; (b) antenna; (c) antennule; (d) maxillule; (e) maxilla; (f) maxilliped 1; (g), (h) pereopods 1 and 2; (i), (j), (k) pleopods 1, 2 and 5; (l) telson and uropods. Scale=0.2 mm: (a); 0.1 mm: (b)–(l).

*Maxilliped 1* (Fig. 21(f)) exopod with 5 setae on caridean lobe, basis with 10–12 setae.

*Pereopods 1 and 2* (Figs 21(g), (h)) with well developed chelae.

*Pleopods* (Figs 21(i), (j), (k)) now with well developed protopods; endopod of pleopod 1 small and rounded, endopods of pleopods 2–5 larger and unarmed; exopods large and flattened, exopods of pleopods 2 and 3 with a few setae, exopods of pleopods 1, 4 and 5 unarmed.

*Telson* (Fig. 21(l)) longer and posterior border narrower than in previous stage, setal formula unchanged.

*Uropods* (Fig. 21(l)) endopod with 23–25 setae, exopod with 26–27 setae.

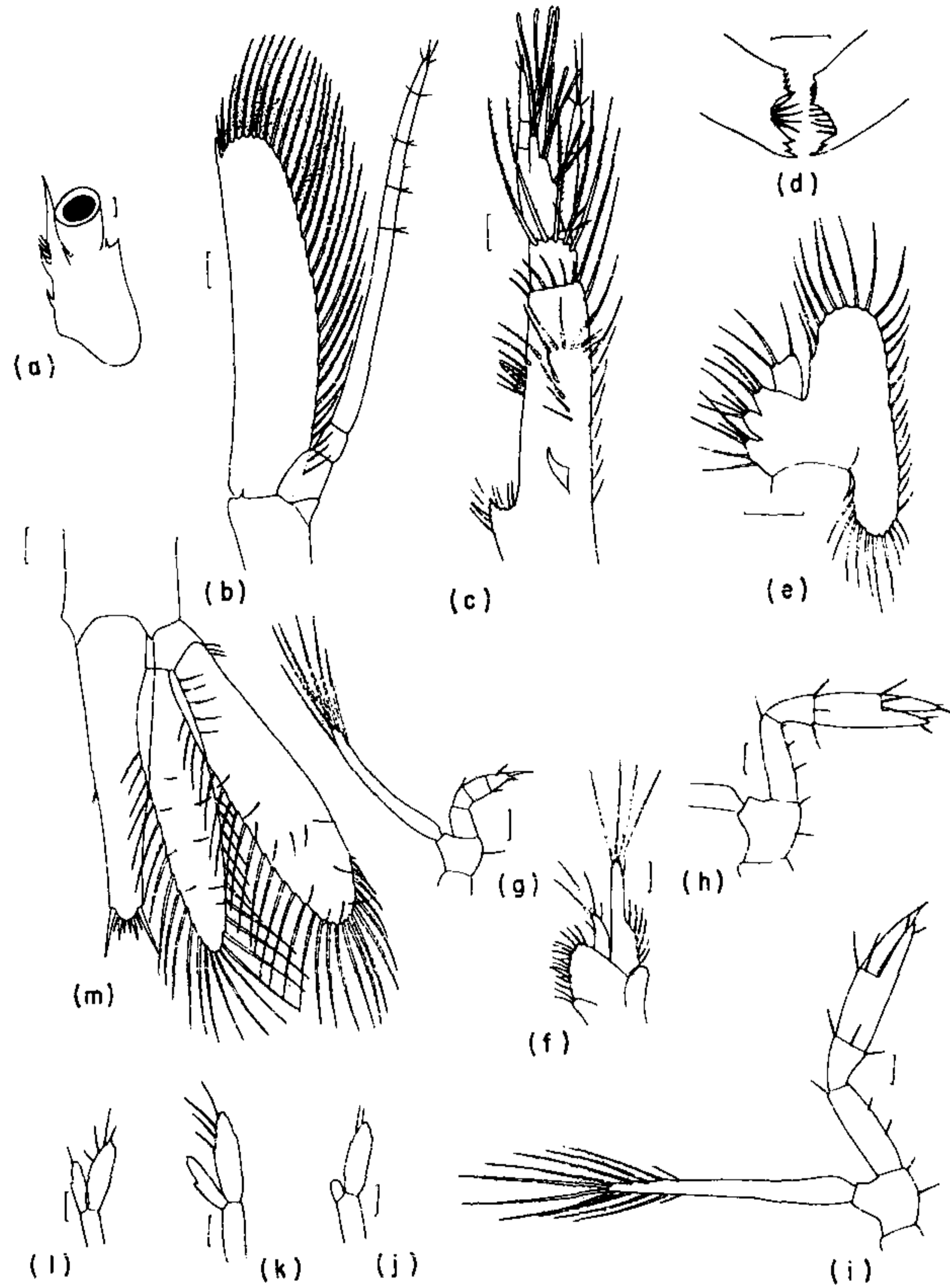


FIG. 22. *Macrobrachium* sp. Zoeal stage X. (a) Carapace in lateral view; (b) antenna; (c) antennule; (d) mandible; (e) maxilla; (f), (g) maxillipeds 1 and 2; (h), (i) pereopods 1 and 2; (j), (k), (l) pleopods 1, 2 and 5; (m) telson and uropods.

Scale=0.2 mm: (a); 0.1 mm: (b)–(m).

#### Stage X

c.l. 1.48–1.79 mm

t.l. 4.7–5.8 mm

*Carapace* (Fig. 22(a)) anterior epigastric spine provided with 4 or 5 setae.

*Antennule* (Fig. 22(c)) endopod now 2-segmented, outer ramus of exopod 3-segmented, proximal peduncular segment with 11 inner setae.



*Antenna* (Fig. 22(b)) flagellum of endopod 5-segmented distally, exopod with 30–32 setae, peduncle now provided with a small spine.

*Mandible* (Fig. 22(d)) with 5 spines between incisor and molar processes.

*Maxilla* (Fig. 22(e)) scaphognathite now carrying 34–36 setae, endites with 12 setae.

*Maxilliped 1* (Fig. 22(f)) exopod with 6–7 setae on caridean lobe, basis with 14–15 setae.

*Maxilliped 2* (Fig. 22(g)) endopod now 4-segmented.

*Maxilliped 3* exopod with 10 setae.

*Pereiopods 1 and 2* (Fig. 22(h), (i)) now large and pereiopod 2 distinctly larger than pereiopod 1, exopods of both legs with 12 natatory setae.

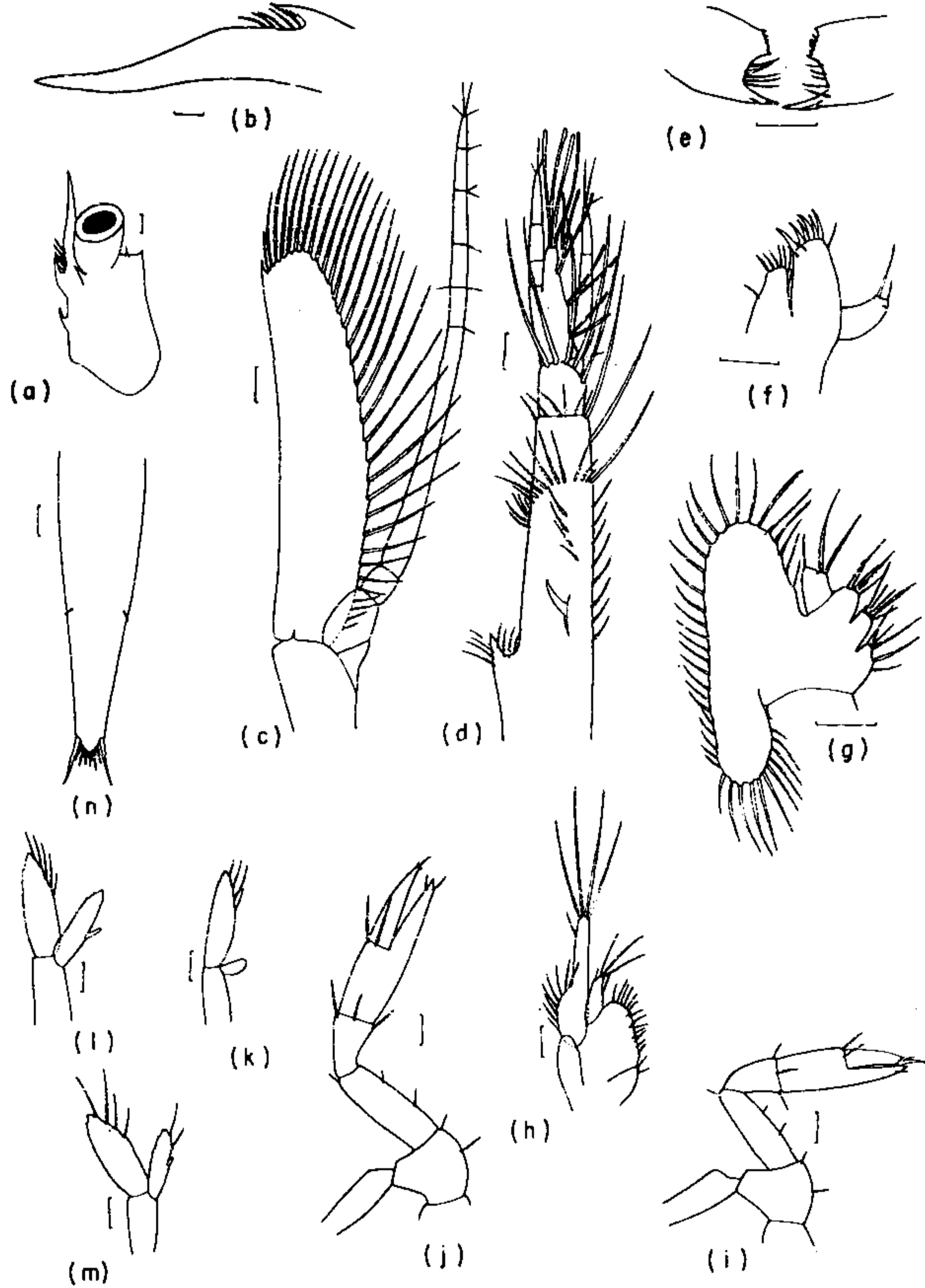


FIG. 23. *Macrobrachium* sp. Zoeal stage XI. (a), (b) Carapace and rostrum in lateral view; (c) antenna; (d) antennule; (e) mandible; (f) maxillule; (g) maxilla; (h) maxilliped 1; (i), (j) pereiopods 1 and 2; (k), (l), (m) pleopods 1, 2 and 5; (n) telson.

Scale=0.2 mm: (a); 0.1 mm: (b)–(n).

*Pereiopods 3 and 4* exopods with 10 natatory setae.

*Pleopods* (Fig. 22(j), (k), (l)) endopods of pleopods 2–5 now with a small inner bud and endopod of pleopod 5 with 1 or 2 setae; exopods of all pleopods large, each with a few setae.

*Telson* (Fig. 22(m)) longer than in previous stage and distal part narrower still compared to proximal; setal formula unchanged but seta 2 now much larger than the remainder.

*Uropods* (Fig. 22(m)) endopod with 25–28 setae, exopod with 27–30 setae.

#### Stage XI

c.l. 1.70–1.92 mm

t.l. 5.3–6.3 mm

*Carapace* (Fig. 23(a), (b)) rostral spine still smooth, anterior epigastric spine with 5 setae.

*Antennule* (Fig. 23(d)) endopod 3-segmented; inner ramus of exopod now carrying 4 groups of 4, 3, 2 and 2 aesthetascs, outer ramus 4-segmented.

*Antenna* (Fig. 23(c)) flagellum of endopod 6-segmented, exopod with 33–35 setae.

*Maxillule* (Fig. 23(f)) coxal endite now with 1 seta and 7 spines.

*Maxilla* (Fig. 23(g)) scaphognathite with 38–42 setae, endites with 14–15 setae.

*Maxilliped 1* (Fig. 23(h)) exopod with 7–8 setae on caridean lobe, basis with 15–16 setae.

*Pereiopods 1 and 2* (Fig. 23(i), (j)) have increased in size.

*Pereiopod 3* exopod with 12 setae.

*Pleopods* (Fig. 23(k), (l), (m)) inner buds on endopods of pleopods 2–5 now large.

*Telson* (Fig. 23(n)) distal part now less than half as large as proximal, posterior border increasingly convex, setal formula unchanged but seta 1 now small and dorsal.

*Uropods* endopod with 27–30 setae, exopod with 29–31 setae.

#### Stage XII

c.l. 1.79–2.05 mm

t.l. 5.4–6.6 mm

*Carapace* (Fig. 24(a), (b)) rostral spine now provided with minute teeth and a few small setae.

*Antennule* (Fig. 24(d)) endopod 4-segmented, outer ramus of exopod 4 or 5-segmented.

*Antenna* (Fig. 24(c)) flagellum of endopod long and 9 or 10-segmented, exopod carrying 35–36 setae.

*Mandible* (Fig. 24(e)) with 6 spines between incisor and molar processes.

*Maxillule* (Fig. 24(f)) coxal endite with 1 seta and 7 or 8 spines.

*Maxilla* (Fig. 24(g)) scaphognathite with 43–46 setae.

*Maxilliped 1* (Fig. 24(h)) exopod with 9–10 setae on caridean lobe, basis with 18–19 setae.

*Maxillipeds 2 and 3* (Fig. 24(i), (j)) unchanged.

*Pereiopods* (Fig. 24(n)) large; pereiopods 1 and 2 with well developed chelae, dactylus and fixed fingers terminating in short spines; exopods of pereiopods 1 and 2 with 12 or 14 setae, exopods of pereiopods 3 and 4 with 12 and 10 setae respectively.

*Pleopods* (Fig. 24(k), (l), (m)) with more setae on endopods and exopods.

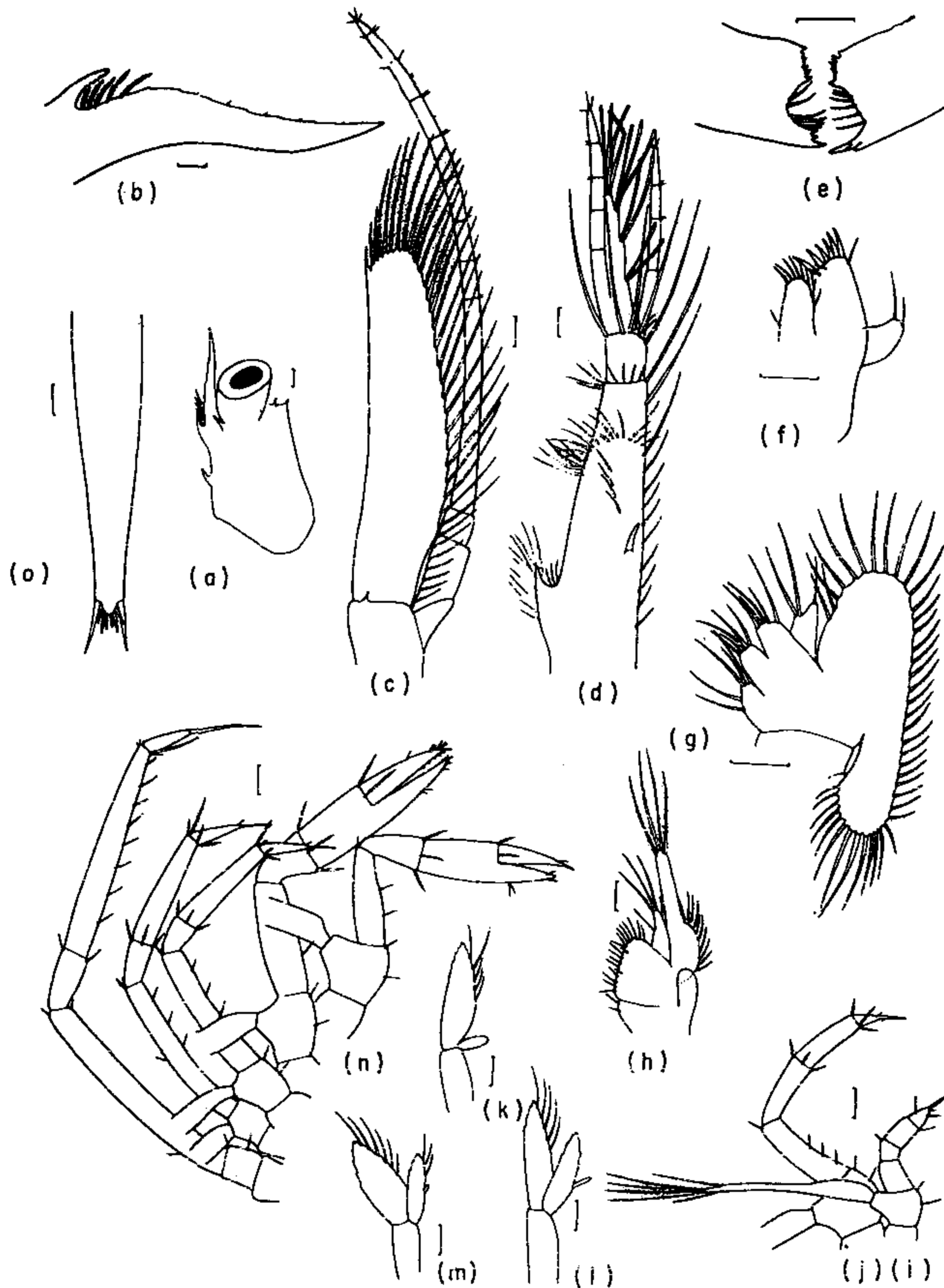


FIG. 24. *Macrobrachium* sp. Zoeal stage XII. (a), (b) Carapace and rostrum in lateral view; (c) antenna; (d) antennule; (e) mandible; (f) maxillule; (g) maxilla; (h)–(j) maxillipeds 1–3; (k)–(m) pleopods 1, 2 and 5; (n) pereopods; (o) telson.

Scale=0.2 mm: (a); 0.1 mm: (b)–(o).

*Telson* (Fig. 24(o)) very elongated, distal part very narrow and posterior border increasingly convex; the pair of small mid-lateral spines is lost, telson formula reduced to 4+4 setae.

*Uropods* endopod with 31–33 setae, exopod with 32–34 setae.



*First postlarval stage*

c.l. 1.86–2.48 mm

t.l. 5.5–7.0 mm

*Carapace* (Fig. 25(a), (b)) longer than broad; rostrum (Fig. 25(e)) with 9 teeth and a few small setae dorsally and 3 teeth ventrally; anterior border of carapace now showing 1 antennal spine whilst pterygostomian spine has moved slightly backwards.

*Antennule* (Fig. 25(c)) endopod slender with 9–12 segments and a few small setae; exopod bifid, outer ramus 11-segmented with a few small setae, inner ramus 3-segmented with 4 groups of 3, 3, 2 and 2 aesthetascs. Peduncle 4-segmented; 1st segment with 1 outer spine and a few small setae; 2nd and 3rd segments with 13–14 inner setae and small setae

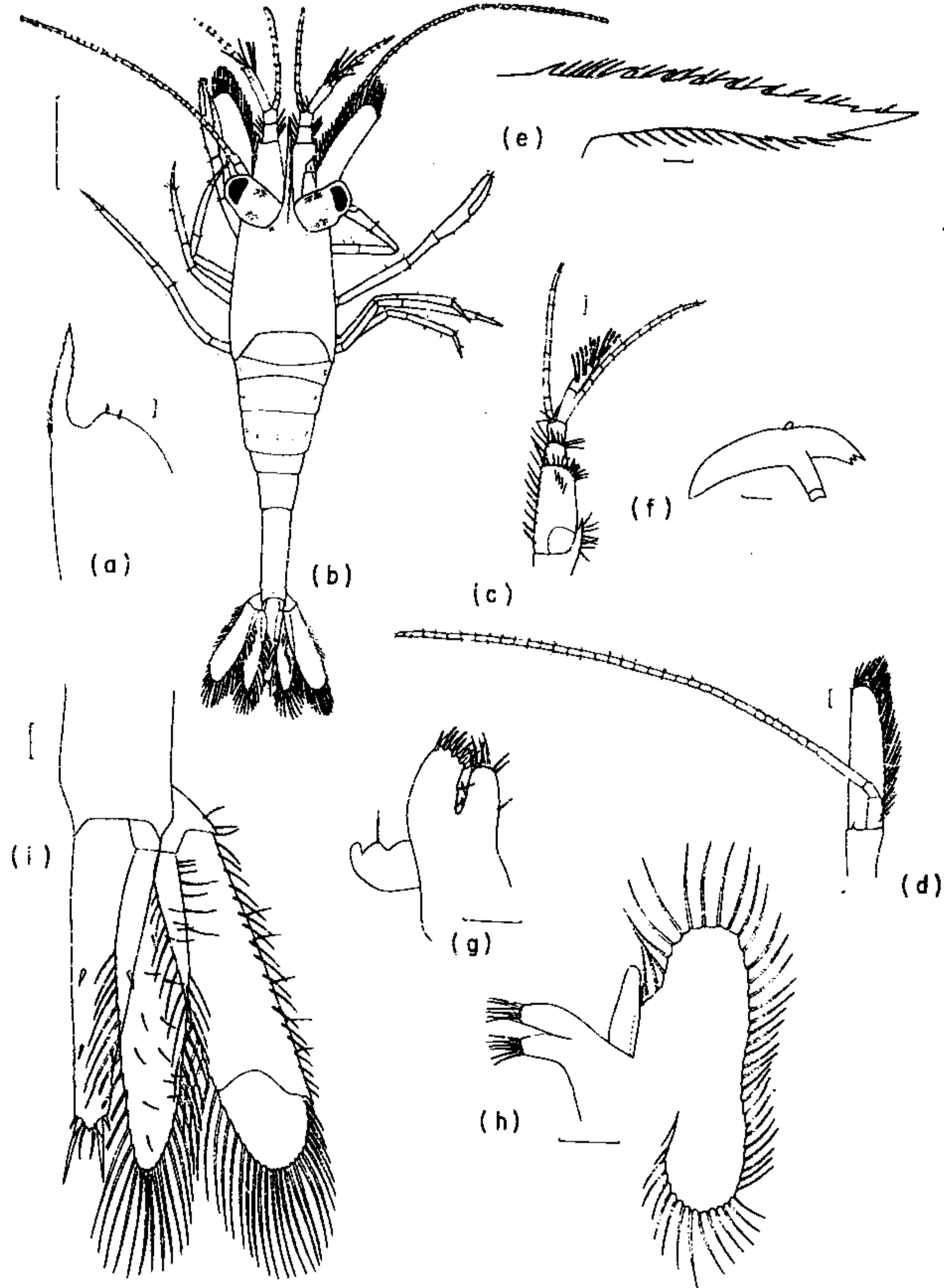


FIG. 25. *Macrobrachium* sp. First postlarval stage. (a), (e) Anterior part of carapace and rostrum in lateral view; (b) postlarva in dorsal view; (c) antennule; (d) antenna; (f) mandible; (g) maxillule; (h) maxilla; (i) telson and uropods.

Scale=1 mm: (b); 0.2 mm: (a), (c), (d); 0.1 mm: (e)–(i).

on distal borders, distal border of 2nd segment also provided with a small spine; 4th segment with 3 setae on a tubercle at the base of endopod.

*Antenna* (Fig. 25(d)) endopod with a 2-segmented basal part and a long multisegmented flagellum, exopod with 1 lateral spine and a number of inner setae, peduncle unsegmented with 1 distal spine.

*Mandible* (Fig. 25(f)) with a long molar process, 3 teeth on incisor process and a small rounded bud in position of the palp.

*Maxillule* (Fig. 25(g)) endopod unsegmented with 1 seta; basal and coxal endites large, fringed with numerous setae and spines.

*Maxilla* (Fig. 25(h)) endopod unsegmented and unarmed, scaphognathite large with 45–48 setae, basal and coxal endites each with 6 setae.

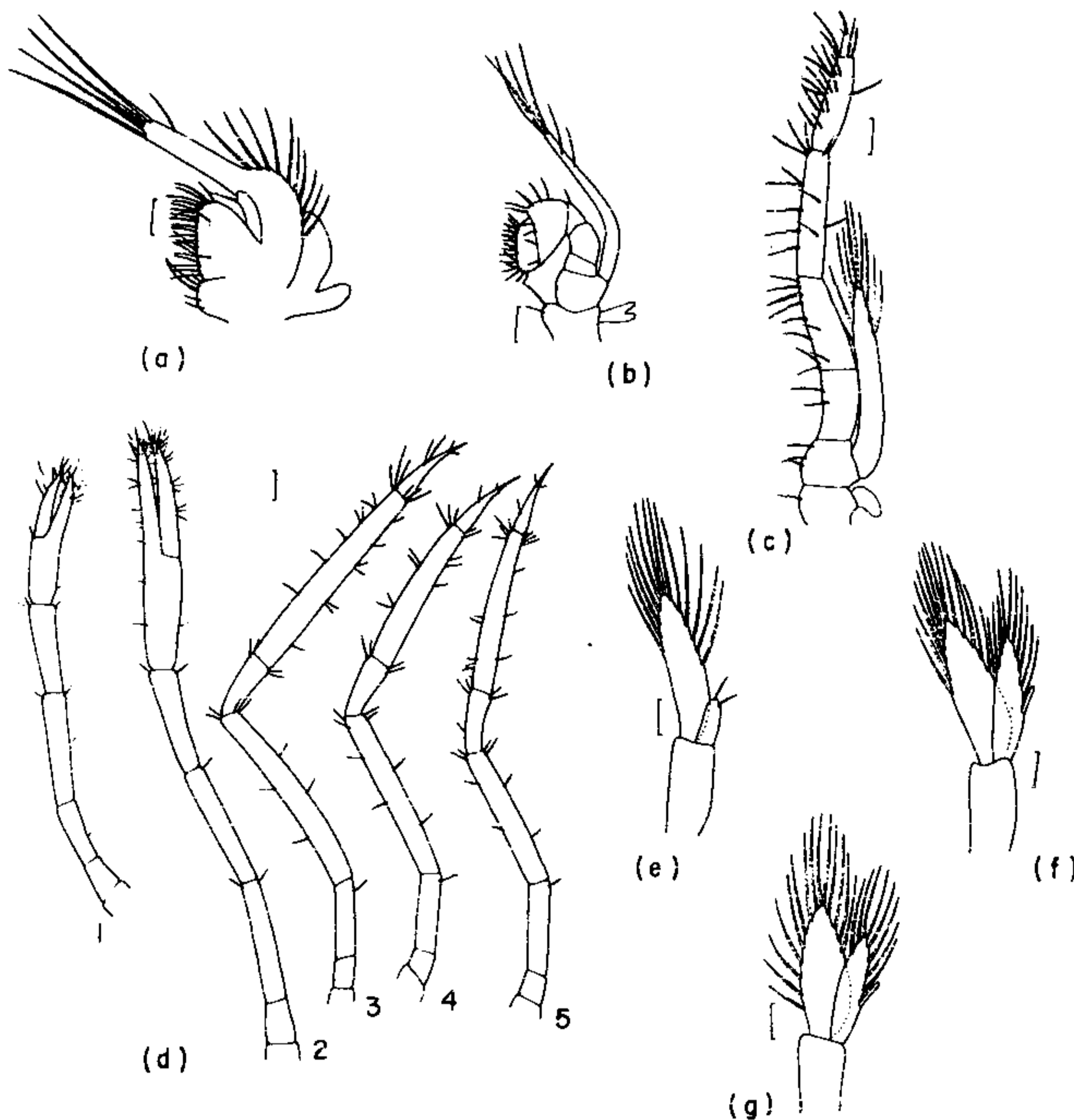


FIG. 26. *Macrobrachium* sp. First postlarval stage. (a)–(c) Maxillipeds 1–3; (d) 1–5, pereiopods 1–5; (e)–(g) pleopods 1, 2 and 5.

Scale=0.1 mm.

*Maxilliped 1* (Fig. 26(a)) endopod unsegmented with 1 subterminal plumose seta, exopod unsegmented with 5 setae distally and 10–11 setae on caridean lobe, basal and coxal endites fringed with numerous setae, epipod well developed.

*Maxilliped 2* (Fig. 26(b)) endopod 5-segmented with numerous setae on the last and

penultimate segments; exopod slender, unsegmented with 6–8 natatory setae; coxa and basis with a few setae; epipod smaller than that of maxilliped 1.

*Maxilliped 3* (Fig. 26(c)) endopod large, 5-segmented, inner border fringed with many setae; exopod unsegmented with 10–12 natatory setae; basis and coxa with a few setae; epipod small.

*Pereiopods 1 and 2* (Fig. 26(d<sub>1</sub>), (d<sub>2</sub>)) well developed chelipeds, cheliped 2 larger than cheliped 1; endopods 5-segmented with numerous small setae on dactylus and fixed fingers.

*Pereiopods 3–5* (Fig. 26 (d<sub>3</sub>)-(d<sub>5</sub>)) similar in size and form; endopods 5-segmented with small setae on each segment.

*Pleopods* (Fig. 26(e), (f), (g)) endopod of pleopod 1 the smallest with 1 or 2 setae, endopods of pleopods 2–5 larger with 8–12 setae and an *appendix interna*; exopods large, flattened, fringed with 12–14 setae; protopods unsegmented and unarmed.

*Telson* (Fig. 25(i)) telson formula now 6+6; setae 1 and 2 dorsal, seta 4 the largest, seta 5 very fine, only seta 6 plumose; a pointed medial prominence present between setae 6.

*Uropods* (Fig. 25(i)) endopod and exopod well developed, fringed with many setae; exopod with 1 suture and 1 lateral spine.

#### *Distribution of chromatophores*

Small red chromatophores on basis of antennule and antenna.

Large red chromatophores with dendrites on eye-stalks.

Small red chromatophores on lateral sides of carapace and on basis of all pereiopods.

Red chromatophores on lateral sides of abdominal segments 1, 2, 3 and on dorsal side of abdominal segment 3.

One red chromatophore on 6th abdominal segment near telson.

#### **Discussion**

Johnson (1973) stated that *M. equidens* is predominantly an inhabitant of high-salinity brackish water but is also found in sea water where it can probably breed. This last observation is confirmed by the present successful rearing of this species entirely in sea water.

The ovigerous female of the *Macrobrachium* sp. probably lived also in a marine habitat, but it seems certain that the later larval stages require water of less than normal salinity to metamorphose successfully to the post-larval stage. This is because after the 12th–13th moult, whilst in sea water, many were found dead on the upper walls of the culture vessels, presumably in an attempt to come to the surface layers, and none moulted to post-larvae. By contrast, larvae transferred to 90% sea water moulted to post-larvae, two of them within 24 hours. It is possible that post-larvae can live in both sea and brackish water and only require this reduced salinity to metamorphose successfully into that stage. It is interesting to note that this unidentified species breeds from September to November when heavy rains are frequent. These rains temporarily lower the surface salinity of the sea, and the larvae then probably come to the surface layers seeking waters of suitable salinity in which to metamorphose.

The occurrence of variation in form among larvae of the same moulting history and of



larval moults without morphological changes have been described for *Palaemonetes pugio* Holthuis, *P. vulgaris* (Say), *P. kadiakensis* Rathbun, *Macrobrachium rosenbergii* (de Man), *M. acanthurus* (Wiegmann), *M. carcinus* (L.) (Broad, 1957a, b; Broad & Hubschman, 1963; Uno & Kwon, 1969; Choudhury, 1970, 1971). Similarly from the 6th stage in *M. equidens* and *Macrobrachium* sp., larvae of the same intermolt showed variation in their form and this became more evident in the later stages. Some larvae with rapid development reached the last larval stage after the 13th or 14th moult, whilst others had moulted 16 to 18 times before reaching the same anatomical stage. This variation does not seem to be related to diet and culture conditions which were here mainly uniform.

Moulting giving rise to larvae morphologically indistinguishable from the previous stage also occurred in the development of *M. equidens* and *Macrobrachium* sp. after the 6th moult; in particular, in *M. equidens*, some larvae were observed to repeat the last larval form through two or more intermoult before metamorphosis, resembling in this respect *Palaemonetes pugio*, *P. vulgaris*, *P. kadiakensis* (Broad, 1957a, b; Broad & Hubschman, 1963). But in *Palaemonetes*, while some larvae repeat the last larval form, others may skip it and pass directly from the penultimate stage to the post-larvae. In *M. equidens* metamorphosis only occurred after the last stage in which the larvae had the antennular endopod and exopod segmented, the antennal flagellum long and segmented, the pereopods very large and the pleopods setose; none of the post-larvae obtained has been observed to omit that stage. In *Macrobrachium* sp. the last larval stage is very characteristic, having a rostrum provided with minute teeth and a telson devoid of the two mid-lateral spines; in the present culture none of the post-larvae obtained had repeated this stage before metamorphosis, but none had omitted it either.

Several *Macrobrachium* larvae with non-abbreviated development have been described with sufficient detail to permit comparison with those of *M. equidens* and *Macrobrachium* sp. These species are as follows: *M. rude* (Heller) (Menon, 1938); *M. carcinus* (L.) (Lewis & Ward, 1965; Choudhury, 1971); *M. rosenbergii* (de Man) (Ling, 1969; Uno & Kwon, 1969); *M. acanthurus* (Wiegmann) (Choudhury, 1970); *M. intermedium* (Stimpson), *M. niloticum* (P. Roux) (Williamson, 1972).

With the exception of *M. niloticum*, the larvae of *M. equidens* and *Macrobrachium* sp. resemble these previously described *Macrobrachium* larvae in the absence of legs 3–5 in stage I, in having two epigastric spines on the carapace, and in having a pair of lateral spines on the 5th abdominal somite. They resemble the larvae of *M. acanthurus*, *M. carcinus* and *M. rosenbergii* in having all the pereopods present and functional only from stage VI, and therefore are less advanced than those of *M. intermedium* and *M. niloticum* in which all legs are functional from stage V. It is interesting to note that whereas in other brackish and freshwater *Macrobrachium* larvae the rostrum is always distinctly toothed in the late larval stages, the larvae of *M. equidens*, which spend their whole larval life in marine water, have their rostrum devoid of all teeth before the post-larval stage is reached; and in *Macrobrachium* sp. only the last larval stage, which possibly in nature lives in water of slightly reduced salinity, has a rostrum provided with very small teeth. Nevertheless, more material of marine larvae of *Macrobrachium* is required before it is possible to know whether the presence or absence of teeth on the rostrum of these larvae are specific characters or if they are related to their habitat. From stage V onwards, the larvae of *Macrobrachium* sp. are readily distinguished from those of all other *Macrobrachium* species previously described in having a particular setal telson formula.

Both *M. equidens* and *Macrobrachium* sp. larvae have the same mode of development of the antero-lateral carapace spines, and in this respect they resemble those of *M. rosenbergii* (c.f. Uno & Kwon, 1969) and *M. niloticum* (c.f. Williamson, 1972) and differ from those of other *Macrobrachium* species. In these four species the more ventral of the two spines near the antero-lateral margin of the carapace develops first, occupies the pterygostomian position throughout the zoeal stages and moves slightly toward the hepatic position in the post-larval stage; the eventual antennal spine does not appear until stage III and occupies a branchiostegal position during the remaining zoeal stages. In this case, the antennal spine does not derive from the pterygostomian. This mode of formation of these antero-lateral carapace spines was described by Gurney & Lebour (1941) as particular to the larvae of the subfamily Pontoniinae. Williamson (1972) thought that his larvae of *M. niloticum* were the first of the subfamily Palaemoninae in which this order of development of these carapace spines had been noted. In fact, the same situation had already been reported in *M. rosenbergii* (Uno & Kwon, 1969) and it has now also been observed in *M. equidens* and *Macrobrachium* sp.

From stage I to stage IV, the larvae of *M. equidens* and *Macrobrachium* sp. are apparently very similar but can be distinguished by the setation of the maxillule, of the maxillipeds, and particularly by the presence of a spine on the antennal peduncle of the latter. From stage V, as mentioned above, the larvae of *Macrobrachium* sp. are easily distinguished from those of *M. equidens* and of other *Macrobrachium* larvae previously described by having a particular telson formula. The first post-larvae of the two species differ from one another by the setation of the appendages, the number of rostral spines and a slightly larger size in *Macrobrachium* sp.

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