A Key to Genera of the Penaeid Larvae and Early Postlarvae of the Indo-west Pacific Region, with Descriptions of the Larval Development of *Atypopenaeus formosus* Dall and *Metapenaeopsis palmensis* Haswell (Decapoda: Penaeoidea: Penaeidae) Reared in the Laboratory

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ABSTRACT: The penaeid prawns *Atypopenaeus formosus* Dall and *Metapenaeopsis palmensis* Haswell were induced to spawn and their larvae and postlarvae were cultured in the laboratory. Three protozoea, three mysis, and early postlarval substages are described for each species. A key to genera of the penaeid larvae and early postlarvae of the Indo-west Pacific region was constructed from this information, from other unpublished data from our own larval reference collection, and from previously published larval descriptions. The key, based entirely on laboratory-reared larvae, identifies the genera *Atypopenaeus, Macropetasma, Metapenaeopsis, Metapenaeus, Parapenaeopsis, Parapenaeus, Penaeus,* and *Trachypenaeus*. A sternal spine formula, a previously undescribed taxonomic character, is used for identifying postlarvae.

Twelve genera of penaeid prawns are found in the Indo-west Pacific: *Atypopenaeus, Funchalia, Heteropenaeus, Macropetasma, Metapenaeopsis, Metapenaeus, Parapenaeopsis, Parapenaeus, Penaeopsis, Penaeus, Trachypenaeopsis*, and *Trachypenaeus*. Most of these genera are widespread and common; the exceptions are the monospecific genus *Macropetasma*, which occurs only near the southern coast of South Africa, and *Heteropenaeus* and *Trachypenaeopsis*, which are widespread but rare (Dall el al. in press).

In spite of the worldwide distribution, abundance, and commercial importance of penaeids, ecological studies of their larvae have been hampered by taxonomic problems (Rothlisberg et al. 1983a). Several keys to larval penaeid genera have been published; however, none of these are suitable for use in the Indo-west Pacific region. Cook's (1966a) key to the Gulf of Mexico penaeid genera was a milestone, and remains the most useful reference. However, many Indo-west Pacific genera do not occur in both regions (e.g., *Atypopenaeus* and *Metapenaeus*) and therefore could not be included. *Xiphopenaeus* is included but does not occur in the Indo-west Pacific. *Sicyonia* and *Solenocera*, which Cook included, are now regarded as separate families in the superfamily Penaeoidea (Bowman and Abele 1982).

The keys of Hassan (1974), Haq and Hassan (1975), and Muthu et al. (1978) dealt with three genera in the Indo-west Pacific—*Penaeus, Metapenaeus*, and *Parapenaeopsis*—while Paulinose (1982) covered all genera except *Heteropenaeus* and *Macropetasma*. He also included the nonpenaeids *Sicyonia, Aristaeomorpha*, and *Solenocera*. However, many of the identifications in Paulinose's work are based on doubtful reconstructions from the plankton and the key has several practical shortcomings (see Discussion).

Penaeus and *Metapenaeus* have worldwide commercial importance in fisheries and aquaculture, and the larvae of many species have been reared in the laboratory and described (for review see Dall et al. in press). There have been very few laboratory studies that describe the larval morphology of the remaining penaeid genera in the Indo-west Pacific region. *Parapenaeopsis stylifera* larvae were reared and described by Rao (1973) and Hassan (1984). Thomas et al. (1975) also reared the larvae in the laboratory but provided no figures or detailed descriptions. *Macropetasma africanum* was reared and described by Cockcroft (1985). Heldt (1938) described *Parapenaeus longirostris*, but all

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stages after protozoea I are based on exuviae of a single surviving specimen. *Trachypenaeus* larvae were described by Kirkegaard (1969), but only the protozoea I were reared in the laboratory; later stages were isolated from preserved plankton catches. The only other description of *Trachypenaeus* is by Pearson (1939), who also used a combination of plankton-caught and laboratory-reared larvae. The present study is the first description of larvae of any species of either *Atypopenaeus* or *Metapenaeopsis*, based on laboratory-reared specimens.

To date, our published studies of larval prawns in the Gulf of Carpentaria have dealt exclusively with the genus *Penaeus* (Rothlisberg et al. 1983a, 1985, 1987; Rothlisberg and Jackson 1987). The characteristics of this genus are well established and their larvae are quite distinct from those of other genera (Cook 1966a). In order to study other genera, we have reared larvae of all six penaeid genera which are found in the Gulf of Carpentaria: *Metapenaeus*, *Metapenaeopsis*, *Penaeus*, *Atypopenaeus*, *Trachypenaeus*, and *Parapenaeopsis*. For all but one genus we now have a reference collection of protozoea I through to postlarvae; for *Parapenaeopsis* we have only the nauplius and protozoeal stages (Rothlisberg et al. 1985).

In assembling this key to genera of Indo-west Pacific penaeid larvae, we have used both our own reference material and information from previously published descriptions and keys. We have relied completely on existing descriptions for *Macropetasma* (Cockcroft 1985) and *Parapenaeus* (Heldt 1938; Pearson 1939; Paulinose 1979), genera not represented in the Gulf of Carpentaria and hence absent from our reference collection. Several workers who have described larvae from plankton samples claim to be able to identify the genus or even the species of the larvae. In the absence of supporting evidence from laboratory-reared larvae we have not used these descriptions in constructing our key. No reliable information about *Funchalia*, *Heteropenaeus*, *Penaeopsis*, and *Trachypenaeopsis* is available as they have never been reared in the laboratory.

MATERIALS AND METHODS

Gravid female *Metapenaeopsis palmensis* selected from trawl catches near Groote Eylandt in the western Gulf of Carpentaria in November 1983 and from off Cairns, northeast Queensland, in April 1985 were brought to the Cleveland laboratory. Gravid female *Atypopenaeus formosus* were collected from commercial trawl grounds in Moreton Bay, adjacent to the Cleveland laboratory, in January 1985.

When female prawns arrived at the laboratory, one eyestalk was ablated and the prawns were placed in a 90 L fiberglass aquarium with 4 cm of clean sand substrate. Seawater in the aquarium was continually replaced at approximately 1 L per minute, and any eggs or larvae were retained by a 90 μm mesh screen on the overflow. Prawns were fed daily on a frozen mixture of prawn and squid. The aquarium water was inspected each morning for eggs. When eggs were detected they were examined microscopically and, if embryonic development was normal, the female prawns were removed and preserved. When the eggs hatched, the nauplii were siphoned off, their abundance was estimated, and they were transferred into culture vessels at a density of approximately 100 nauplii per liter.

The culture vessels used were round-bottomed, 100 mm diameter Pyrex[1] tubes of 3 L capacity, with aeration supplied through a nipple molded into the bottom of the tube. The tubes were placed in environmental cabinets that enabled control of temperature (27°C) and of photoperiod (12 h:12 h light:dark). On alternate days, approximately 2.5 L of water were drawn off from the larval cultures through a 140 μm screen, and replaced with 1 μm filtered seawater.

For larval food, the marine alga *Tetraselmis suecica* was produced by batch culture in 20 L glass carboys. During the log growth phase, 13 L of algal culture were removed and the algal cells concentrated using a modified cream separator. The aerated concentrate was stored at 4°C and used as stock for feeding the larvae. The stock was replaced every 3–4 days.

Twice daily, beginning at late nauplius stage and continuing through to postlarva, sufficient algal concentrate was added to the larval cultures to maintain an algal cell density of approximately 1.5×10^5 cells per mL. Cell density in the larval cultures was estimated by fluorometry based on the relationship between fluorescence and cell density (P. C. Rothlisberg[2]). After the larvae reached mysis I, freshly hatched, heat-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]Rothlisberg, P.C., Division of Fisheries, CSIRO Marine Laboratories P.O. Box 120, Cleveland, QLD 4163, Australia, unpubl. data.

killed *Artemia* nauplii were added daily, to a final concentration of 2–5 nauplii per mL.

Larval samples were removed from the cultures twice daily and preserved in 2% formaldehyde. At this sampling frequency, at least two samples were taken from any substage. For microscopic examination the preserved larvae were cleared in a polyvinyl alcohol solution to which Chlorazol Black had been added (Perkins 1956), and permanent slides both of whole animals and of dissections were made in this medium. For each larval substage described, at least five individuals were examined except where fewer larvae in good condition were available (Tables 1, 2). Where possible, the larvae examined came from different spawnings; otherwise, they came from the same spawning but were taken at different times.

Figures were drawn with the aid of a camera lucida used on a Wild M20 compound microscope. Measurements were made with a calibrated ocular micrometer. Body length was measured from the anterior border of the carapace (excluding the rostrum) to the posterior border of the telson, excluding any spines, and carapace length was measured to the posterior border of the carapace, along the midline.

RESULTS

General development

Atypopenaeus formosus and *Metapenaeopsis palmensis* followed the normal development pattern for penaeid larvae (Dall et al. in press): a number of nauplius substages, three protozoea substages, three mysis substages, and a series of postlarva substages gradually leading toward the juvenile form. While it may be possible to identify unknown penaeid nauplii into groups of one or more genera, preliminary studies confirmed the findings of Cook (1966a) that reliable generic identification of nauplii is not possible. To increase the numbers of cultured larvae available for sampling in later substages, the nauplius substages were not sampled and therefore are not described.

The protozoea I of both species was characterized by separate cephalothorax and abdomen, undeveloped eyes (which may be visible beneath the carapace), and a lack of uropods. Protozoea II had stalked eyes and a rostrum, while protozoea III had spines on a variable number of the abdominal segments and separate uropods. Mysis I lacked abdominal pleopods, mysis II had pleopods of a single segment, while the abdominal pleopods in mysis III had two segments. During the postlarval substages the pleopods became setose and the pereopod exopods became reduced. We have not attempted to describe specific instars or molt numbers of the postlarvae. Instead we have presented a single description which is representative of the first few instars; it is based on larvae sampled within two to three days of the first appearance of postlarvae. Earlier or later instars will, of course, differ in some respects. The most obvious changes with age are that the length of the 2nd antennal flagellum increases, the dorsal rostral spines increase in number, the telson becomes more pointed, the number of telson spines decreases, and the number of telson setae may increase.

Atypopenaeus formosus

The details of setation and segmentation for the various appendages are given in Figures 1 to 7 and in Table 1. Only general features, and those with some taxonomic significance, are described in the text below. For each major stage, the important features that do not vary between substages are presented first, followed by a brief description of the characteristics of each substage.

PROTOZOEA. Second antenna 0.7–1.0 times length of 1st in each substage. Setal formula of 2nd antennal protopod and endopod 1+2+2 [hereafter referred to as the 2nd antennal formula: the numbers of setae at the distal end of the protopod (Fig. $1d_1$), partway along the 1st endopod segment (Fig. $1d_2$), and at the distal end of the 1st endopod segment]. Second antennal exopod (Fig. $1d_3$) with 9 or 10 setae along inner margin, including those on distal segment. Telson with 7+7 setae in each protozoeal substage.

Protozoea I (Table 1, Fig. 1a) with pear-shaped carapace, less than half of total length, bearing a pair of frontal organs without overlying spines. Long labral spine present (Fig. 1b). Mandible asymmetry not yet pronounced, each mandible having a single, freestanding tooth between incisor and molar processes (Fig. 1e). First maxilla (Fig. 1f) protopod with 2 lobes, epipod (Fig. $1f_1$) with 4 long setae; 2nd maxilla protopod with 5 lobes (Fig. 1g). Segmentation of 1st and 2nd maxillipeds indistinct and variable (most common arrangement

TABLE 1.—Summary of larval characteristics of *Atypopenaeus formosus*. BL = body length (mm), number to left of colon indicates number of segments and numbers to right are setal counts for each served on different individuals. "*" indicates more than 10 setae too densely clustered to count appendage. Setal numbers are totals of all setal types on any segment. Reference to figures will

	Protozoea I (Fig. 1)	Protozoea II (Fig. 2)	Protozoea III (Fig. 3)	Mysis I (Fig. 4)
Number examined	8	8	10	8
BL mean (range)	0.7 (0.6–0.9)	0.9 (0.8–1.2)	1.6 (1.4–1.7)	2.0 (1.8–2.1)
CL mean (range)	0.3 (0.2–0.4)	0.4 (0.4–0.5)	0.6 (0.5–0.6)	0.6 (0.6–0.8)
First antenna				
Proximal part	3:1,2,5	3:1,6,5	4:0–2,1–3,3,5	3:6–7,4,3–5
Outer ramus	—	—	—	1:3
Inner ramus	—	—	—	1:1
Second antenna				
Protopod	2:0,1	2:0,1	2:0,1	2:0,0
Blade (seg: inner,outer)	9:9–10,2	9:9–10,2	10–12:9–10,2	1:8–11,1
Flagellum	2:4,4	2:4,4–5	2:4,4–5	1:4
Mandible				
Movable teeth (a:b)[1]	1:1	1:5	2:6	3:7
Palp	—	—	—	—
First maxilla				
Protopod	1:4–6/4	1:5–6/5–6	1:4–6/7–9	1:5–7/8–10
Endopod	3:2,1,4–5	3:2,1,4–5	3:2,1,5	3:1–2,0–1,4–5
Epipod	1:4	1:4	1:4	1:4
Second maxilla				
Protopod	1:6–7/1–2/3/ 3–5/2	1:8–10/2–3/2–4/ 4–7/2–3	1:9–10/3–4/4/ 4–5/2–3	1:12–14/4–6/5–10/ 7–8/3
Endopod	4:3,2,1–2,3	4:2,1–2,2,3	4:2–3,2,2,3	4:2,1–2,2–3,2–3
Epipod	1:4	1:5	1:5	1:7
First maxilliped				
Protopod	1–2:1–2,5–8	2:4–6,6–9	2:5–8,9–12	2:6–8,10–15
Endopod	4:3,1–2,2,5	5:3,2–3,2–3,2,4–5	4:3,2,1–2,5	4:2,2,1–2,3–4
Exopod	1:7	1:7	1:9	1:10
Second maxilliped				
Protopod	2:1,3	2:0–2,3	2:3,4–7	2:2–3,5–7
Endopod	4:1,1,1,5	4:1–2,1,1–2,5	4:2–3,1,2,4–6	4:4,3,1–2,3–4
Exopod	1:5–6	1:6	1:6–7	1:7
Third maxilliped				
Protopod	—	1:0	1:0	2:0,2–5
Endopod	—	1:0	1:3–4	5:1–2,2,1–2,3,4–5
Exopod	—	1:2–3	1:3–6	1:5–9
First percopod				
Protopod	—	—	—	2:0,0
Endopod	—	—	—	1:5–7
Exopod	—	—	—	1:11–15

[1]"a" side fewer teeth, "b" side more teeth. No attempt was made to match mandibles to either left or right sides.

CL = carapace length (mm). For each entry, unless otherwise indicated, segment from proximal to distal. "–" indicates range of setal numbers ob- reliably. Numbers separated by "/" are setal counts for separate lobes of an show distribution of setae along segments.

	Mysis II (Fig. 5)	Mysis III (Fig. 6)	Postlarva (Fig. 7)
Number examined	6	4	5
BL mean (range)	2.0 (1.8–2.1)	2.3 (2.2–2.4)	2.2 (1.9–2.7)
CL mean (range)	0.6 (0.6–0.7)	0.7 (0.6–0.8)	0.7 (0.6–0.8)
First antenna			
Proximal part	3:10–13,3–6,4–8	3:5–13,3,4–6	3:10–16,5–9,1
Outer ramus	1:4	2:0,4	3:0,0,3–5
Inner ramus	1:2–3	1:0	3·0,2–6,3–4
Second antenna			
Protopod	2:0,0	2:0,0	2:0,0
Blade (seg: inner,outer)	1:10–16,0	1:15–17,0	1:21–25,0
Flagellum	2:0,0–1	3:0,0,0	4:0,3,2,2
Mandible			
Movable teeth (a:b)[1]	2:7	3:6	0–1:1–5
Palp	—	1:0	2:2–5,5–15
First maxilla			
Protopod	1:6–7/8–14	1:6–7/10	1:7/10
Endopod	3:1–2,1–2,3–5	3:2,1,3–4	3:1,2,4
Epipod	0–1:4	—	—
Second maxilla			
Protopod	1:*/*/*/*	1:*/*/*/*	1:*/*/*/*
Endopod	4:2,1–2,2–3,2–3	4:2,1,0–1,3	1:*
Epipod	1:10–15	1:10–15	1:*
First maxilliped			
Protopod	2:6–8,8–12	2:5–8,13–15	1:*/*
Endopod	4:4,1–4,1–4,4	4:3,1–2,1–2,4–5	4:2,2,0,4
Exopod	1:6–7	1:5–7	1:5
Second maxilliped			
Protopod	2:2–3,5–7	2:3,4–5	2:4,*
Endopod	4–5:3,4,0–3, 3,4–5	5–6:3–4,3,0,2–3, 1–3,3–5	5:1,4–6,1,3,5
Exopod	1:3–5	1:4	1:5
Third maxilliped			
Protopod	2:0,2	2:0,1	2:1,3
Endopod	4:2,1,1,6	5:1,1–2,2–3,0,5	5:3,4,4,1,5–7
Exopod	1:3–6	1:4–7	1:6
First percopod			
Protopod	2:0,1	2:0,0	2:3,4
Endopod	2:2,3	4:0,1,2,4–7	4:1,3,5,3
Exopod	1:6–8	1:6–8	1:6

TABLE 2.—Summary of larval setation and segmentation of *Metapenaeopsis palmensis*. BL = body indicated, number to left of colon indicates number of segments and numbers to right are setal counts observed on different individuals. "*" indicates more than 10 setae too densely clustered to count appendage. "t" indicates terminal segment. Setal numbers are totals of all setal types on any seg-

	Protozoea I (Fig. 8)	Protozoea II (Fig. 9)	Protozoea III (Fig. 10)	Mysis I (Fig. 11)
Number examined	10	4	6	8
BL mean (range)	0.8 (0.7–0.8)	1.4 (1.4–1.5)	2.0 (1.9–2.1)	2.3 (2.1–2.7)
CL mean (range)	0.4 (0.3–0.4)	0.5 (0.5–0.6)	0.7 (0.6–0.7)	0.7 (0.6–0.8)
First antenna				
Proximal part	3:0–1,2,5	3:0–1,1–3,4–6	4:1,1,3,4–5	3:10–12,4,4–6
Outer ramus	—	—	—	1:4–5
Inner ramus	—	—	—	1:1–2
Second antenna				
Protopod	2:0,1	2:0,1	2:0,1	2:0,0
Blade (seg: inner,outer)	9:9–11,2	8–9:9–11,2	8–10:9–11,1	1:10–11,1
Flagellum	2:4,5	2:4,5	2:4,5	1:4
Mandible				
Movable teeth (a:b)[1]	1:2	1:4	2:6	3:7
Palp	—	—	—	—
First maxilla				
Protopod	1:5–7/3–5	1:6/6–7	1:4–8/8–10	1:6–8/8–12
Endopod	3:2–3,2–3,4–5	3:2,2,4–5	3:2,1–2,3–5	3:2,1–2,4
Exopod	1:4	1:4	1:4	1:4
Second maxilla				
Protopod	1:5–7/3/3/2–4/2	1:6–8/2/3–4/2/3–5	1:8–10/2–4/3–6/ 3–6/2–4	1:*/3–5/3–5/4–6
Endopod	4:1–2,1–2,2–3,3–4	3:1–2/1–2/2–3	4:2–3,2,2–3,2–3	4:2,1–3,1–3,3–4
Exopod	1:4	1:5	1:5	1:12
First maxilliped				
Protopod	1–2:12–17	2:5–9,8–9	2:5–11,8–10	2:8,11–13
Endopod	4:3–4,1–2,1,5–6	4:3,1–2,1–2,5	4:2–3,1–2,1–2,5	3–4:3,1–3,1,3–4
Exopod	1:7	1:7	1:8–10	1:10–11
Second maxilliped				
Protopod	1–2:5–7	2:4,3	2:3–4,5–7	2:4,7–8
Endopod	4:1–2,1–2,1–2,5	3–4:2,1,1,4–5	4:3,1–2,1–3,4–5	4:4,2,3–4,5
Exopod	1:6	1:6	1:8–9	1:5
Third maxilliped				
Protopod	—	1:0	2:0,0	2:0,4–5
Endopod	—	1:0	1:3	4–5:2,2–3,2–3,2, 4–5
Exopod	—	1:2–3	1:4–5	1:5
First pereopod				
Protopod	—	—	—	2:0,2
Endopod	—	—	—	3:2,2,7
Exopod	—	—	—	1:7

[1]"a" side had fewer teeth, "b" side had more teeth. No attempt was made to match mandibles to either left or right

length (mm), CL = carapace length (mm). For each entry, unless otherwise for each segment from proximal to distal. "–" indicates range of setal numbers reliably. Numbers separated by "/" are setal counts for separate lobes of an ment. Reference to figures will show distribution of setae along segments.

	Mysis II (Fig. 12)	Mysis III (Fig. 13)	Postlarva (Fig. 14)
Number examined	5	4	3
BL mean (range)	2.7 (2.5–2.8)	2.8 (2.7–2.9)	2.8 (2.6–3.0)
CL mean (range)	0.7 (0.7–0.8)	0.8 (0.7–0.8)	0.7 (0.7–0.8)
First antenna			
Proximal part	3:6–10,8–12,4–6	3:12–16,5,5	2:17–25,8–12
Outer ramus	1:4–6	1:5	2:0,4
Inner ramus	1:1–2	1:3	1:2
Second antenna			
Protopod	2:0,0	2:0,0	2:0,0
Blade (seg: inner,outer)	1:15–18,0	1:16–21,0	1:25–28,2
Flagellum	4–5:0,0,0,0,2	5–9:3t	15–25:(all 0–1),6t
Mandible			
Movable teeth (a:b)[1]	3:7	3:7	0–3:0–6
Palp	—	1:0	2:5–9,12–20
First maxilla			
Protopod	1:4–8/8–10	1:6–8/8–11	1:4–8/9–13
Endopod	3:2,2,3	3:2,1–2,3–5	1:0–7
Exopod	—	—	—
Second maxilla			
Protopod	1:*/5/6–8/2–4/ 1–2	1:*/2–4/5–7/4–5/2	1:3–5/3–5/4–8
Endopod	3:2–4,2–4,3	3–4:(all 1–3)	1:4
Exopod	1:11	1:10	1:25–35
First maxilliped			
Protopod	2:8–9,10–16	2:5–9,13–16	1:20–25/10–15
Endopod	4:3–4,2–3,1,4	3–4:3,2,1,5	3:2,0,1
Exopod	1:7–10	1:8–10	1:5
Second maxilliped			
Protopod	2:3–4,8–10	2:3–5,8–10	2:1,7
Endopod	5:4,2–3,2,1–2,6	5:4,3–5,2–3,2–3, 4–6	5:2–4,5,0,3,4–6
Exopod	1:6	1:5	1:0
Third maxilliped			
Protopod	2:0,2–3	2:0,1–2	2:1,0
Endopod	5:1–2,1–2,1–4,3,5	5:1–2,2–3,2–3,2,4	6:(all 3–6), 6t
Exopod	1:4	1:4–6	1:0
First pereopod			
Protopod	2:0,2	2:0,1–2	2:2,3
Endopod	4:1,1–2,2,3–4	4:0–1,1–2,2–3,4	4:2,0,2,6
Exopod	1:4	1:7–8	1:0

sides.

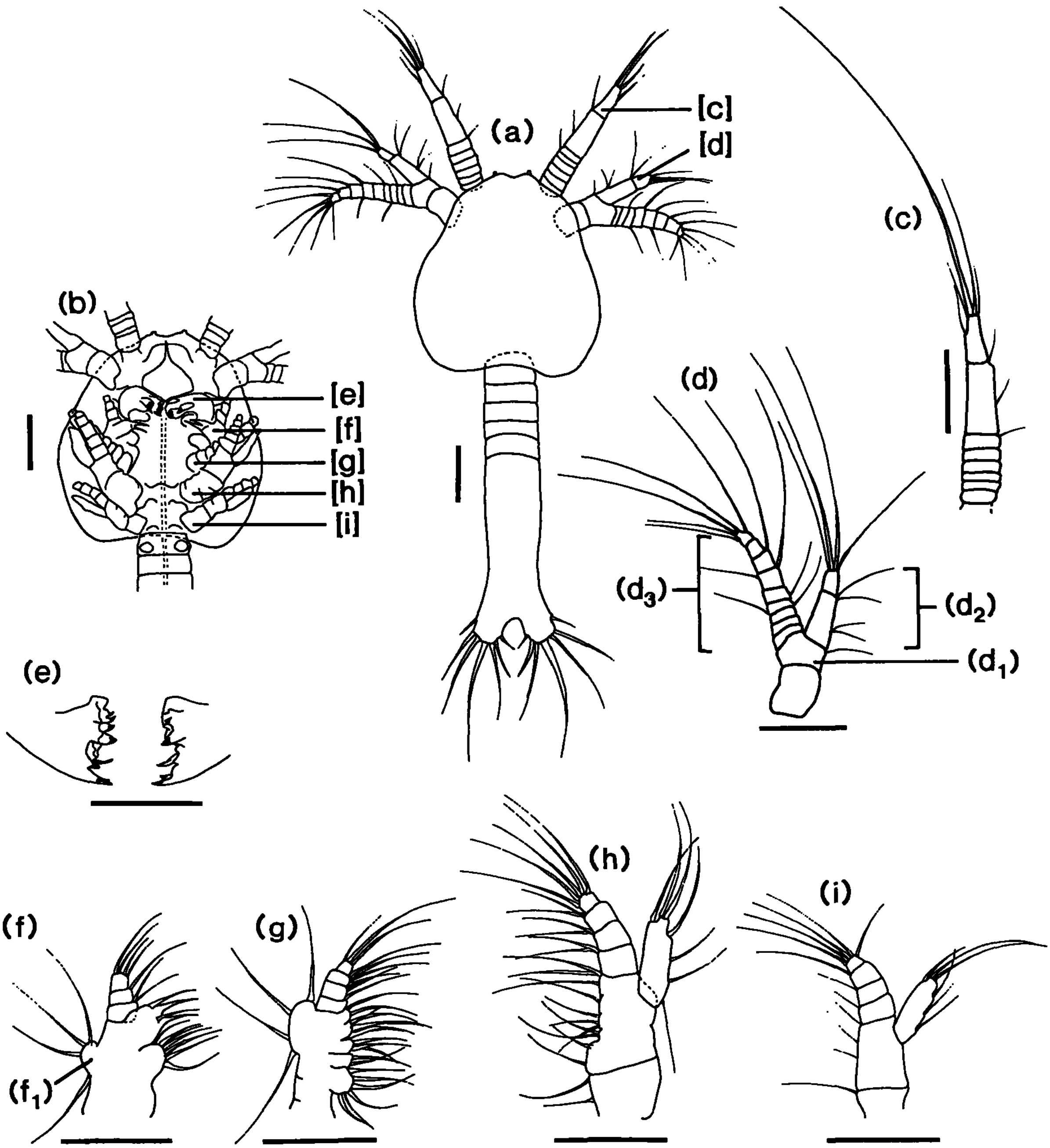

FIGURE 1.—*Atypopenaeus formosus* protozoea I. (a) whole animal, (b) ventral view of cephalothorax, (c) 1st antenna, (d) 2nd antenna, (d_1) protopod, (d_2) endopod, (d_3) exopod, (e) mandibles, (f) 1st maxilla, (f_1) epipod, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped. Letters in square brackets show origins of dissected appendages. Scale = 0.1 mm.

shown: Fig. 1h, i). Third maxilliped only a bud (Fig. 1b).

Protozoea II (Table 1, Fig. 2a) with long rostrum, extending beyond eye, and a single pair of supraorbital spines. Second antennal formula still 1+2+2 but first seta very small, sometimes difficult to see (Fig. 2c). Mandibles (Fig. 2d) now asymmetrical, one side with 5 serrate, free-standing teeth, other side only 1 (no attempt was made in any dissection to determine whether a particular mandible was originally from the left or the right side). First and 2nd maxillae (Fig. 2e, f), 1st and 2nd maxillipeds (Fig. 2g, h) similar to previous substage. Third maxilliped slightly more developed, biramous, however, still very small (Fig. 2i).

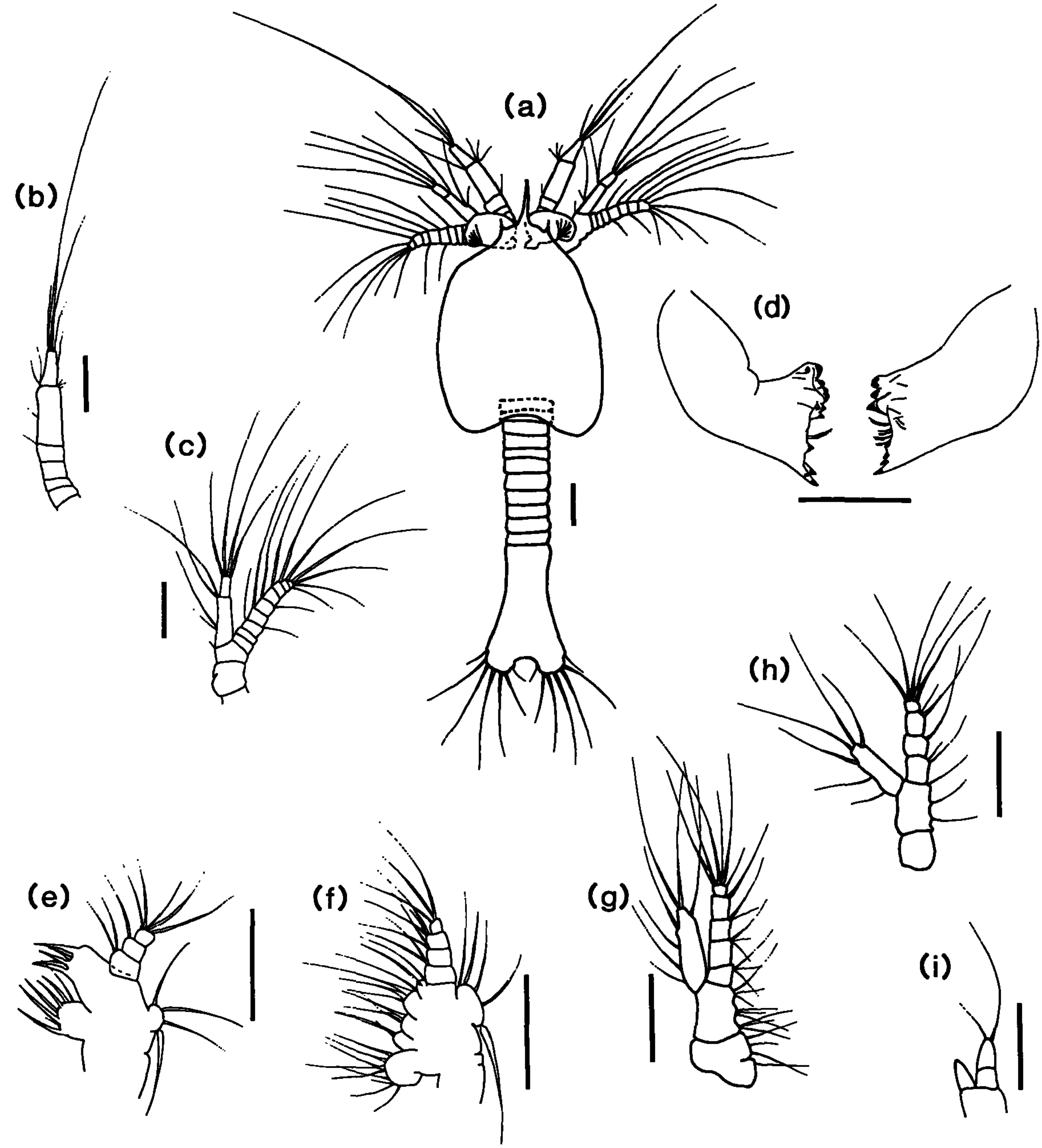

FIGURE 2.—*Atypopenaeus formosus* protozoea II. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

Protozoea III (Table 1, Fig. 3a) retaining long rostrum and supraorbital spines. Some setae in 2nd antennal formula of 1+2+2 are small but always present (Fig. 3c). Maxillae (Fig. 3e, f), maxillipeds (Fig. 3g, h, i) similar to previous substage, although generally more robust and more setose. Dorsal spines occasionally on 4th abdominal segment and always on 5th; lateral spines on 5th and 6th segments (Fig. 3a). Uropods present (Fig. 3a).

MYSIS. Characteristics that are invariant in the mysis stage of *A. formosus* are rostrum extending beyond eye, lack of supraorbital and hepatic spines, presence of pterygostomial spine, 7+7 telson spines, 6th abdominal segment always

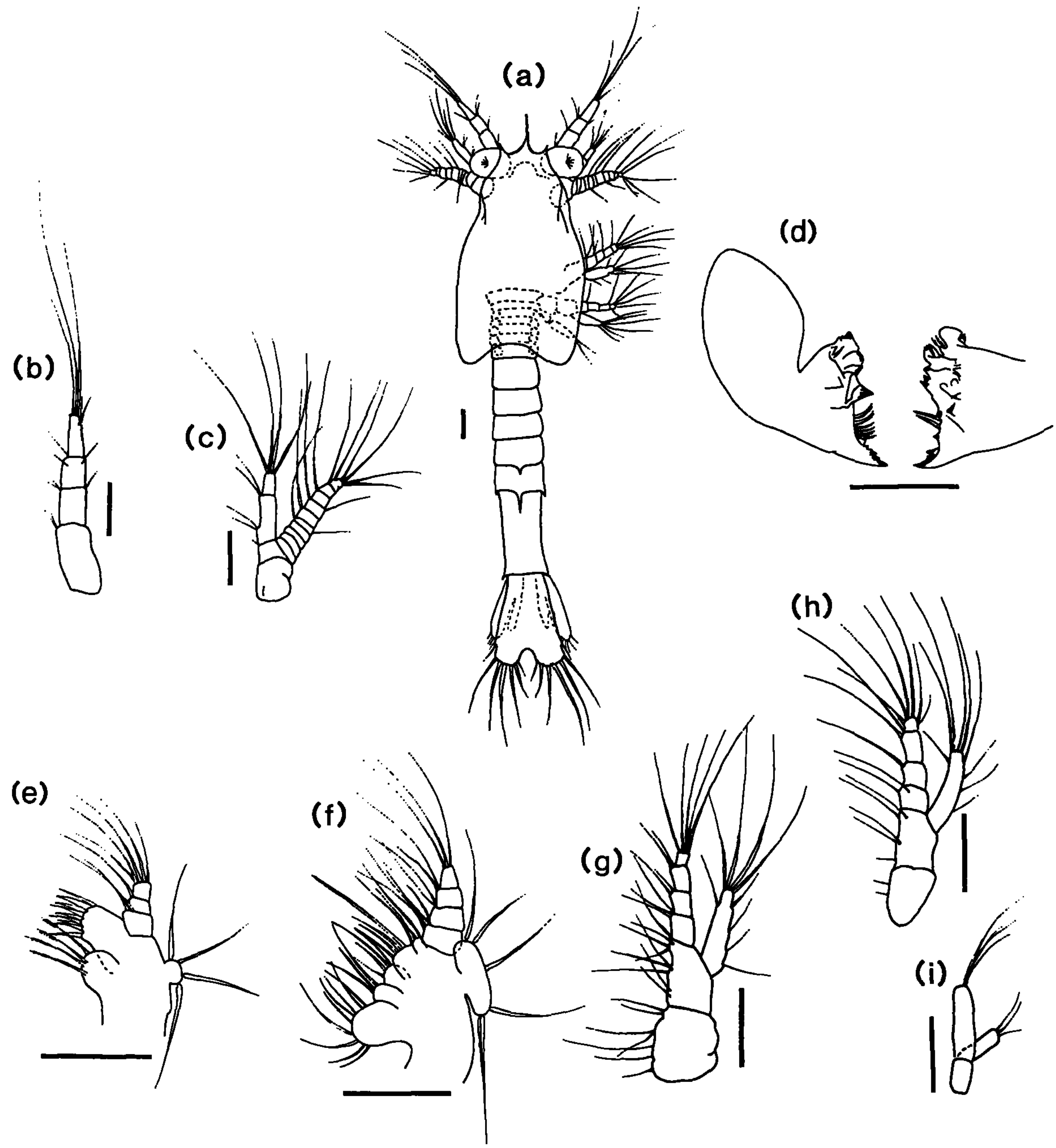

FIGURE 3.—*Atypopenaeus formosus* protozoea III. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

bearing a dorsal spine, lack of lateral abdominal spines.

Mysis I (Table 1, Fig. 4) without rostral teeth. First antenna biramous, bearing a strong ventral spine on first segment (Fig. 4c). Second antenna devoid of segmentation on both endopod and exopod (Fig. 4d). Mandibles similar to those of protozoea III, although stronger and with more teeth (Fig. 4e). Structure of 1st maxilla (Fig. 4f) similar, but epipod on 2nd maxilla, the formative scaphognathite, is beginning to increase in size (Fig. 4g). First 2 maxillipeds similar to previous substage but 3rd much more elongate (Fig. 4h, i, j). Rudiments of chelae appearing on 1st 3 pereopods (Fig. 4k). Usually a small dorsal spine on 5th abdominal segment,

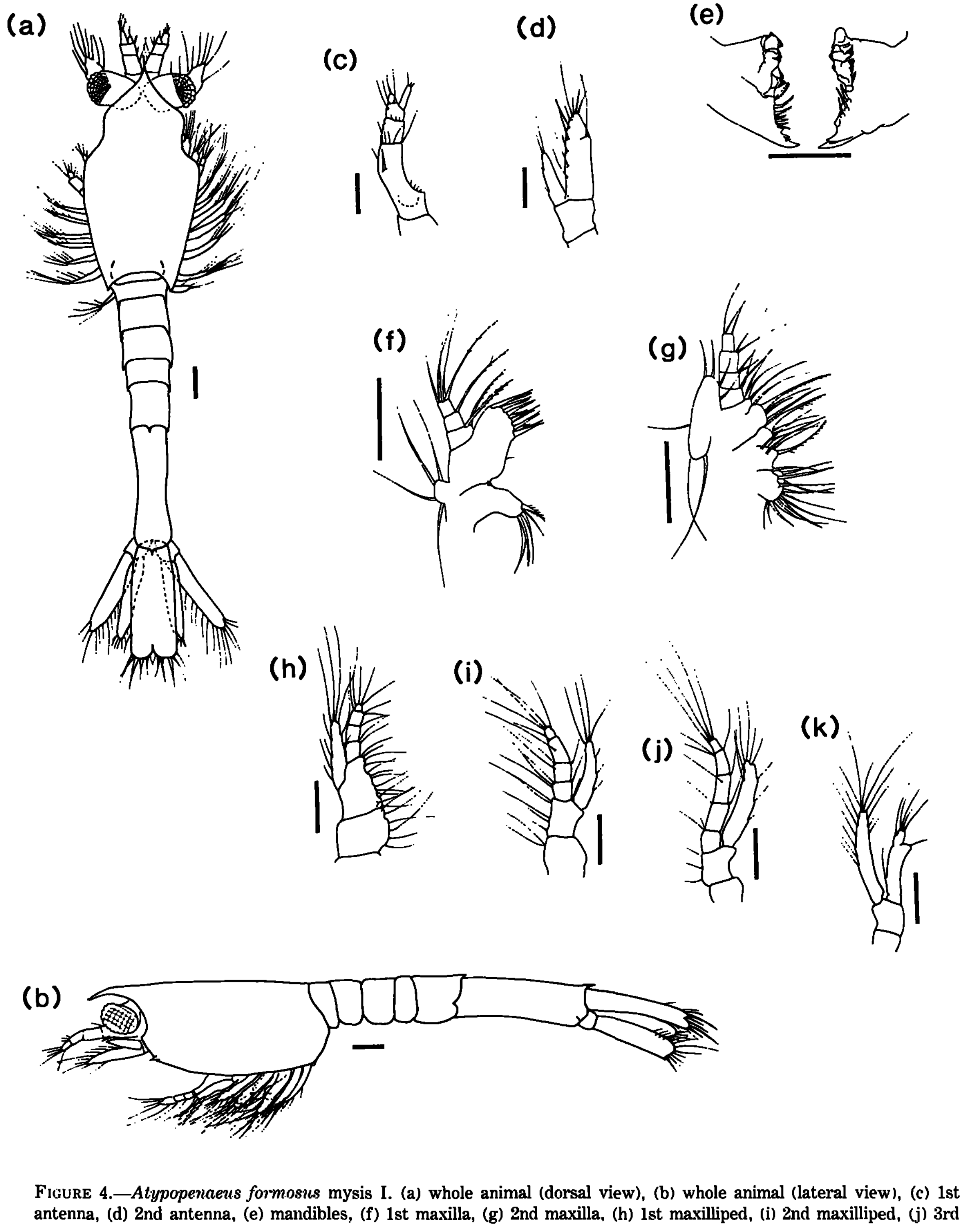

FIGURE 4.—*Atypopenaeus formosus* mysis I. (a) whole animal (dorsal view), (b) whole animal (lateral view), (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped, (j) 3rd maxilliped, (k) 1st pereopod. Scale = 0.1 mm

and a large one on the 6th. Telson retaining deep cleft with 7+7 spines (Fig. 4a).

Mysis II (Fig. 5) still with no rostral teeth. Dorsal spine on 5th abdominal segment either missing or very small; spine on 6th segment remains. Small statocyst sometimes present in 1st antenna (Fig. 5b). Second antenna with spine on blade, flagellum of 2 segments about half as long as blade (Fig. 5c). First maxilla now without epipod, although a small protuberance sometimes remains (Fig. 5e). Epipod of 2nd maxilla further enlarged, more setose (Fig. 5f). First maxilliped stouter than previous, exopod much reduced in size (Fig. 5g). Second and 3rd maxillipeds changing little (Fig. 5h, i); chelae on pereopods clearly defined (Fig. 5j).

Mysis III (Fig. 6) with 2 dorsal rostral teeth. Only 6th abdominal segment with dorsal spine.

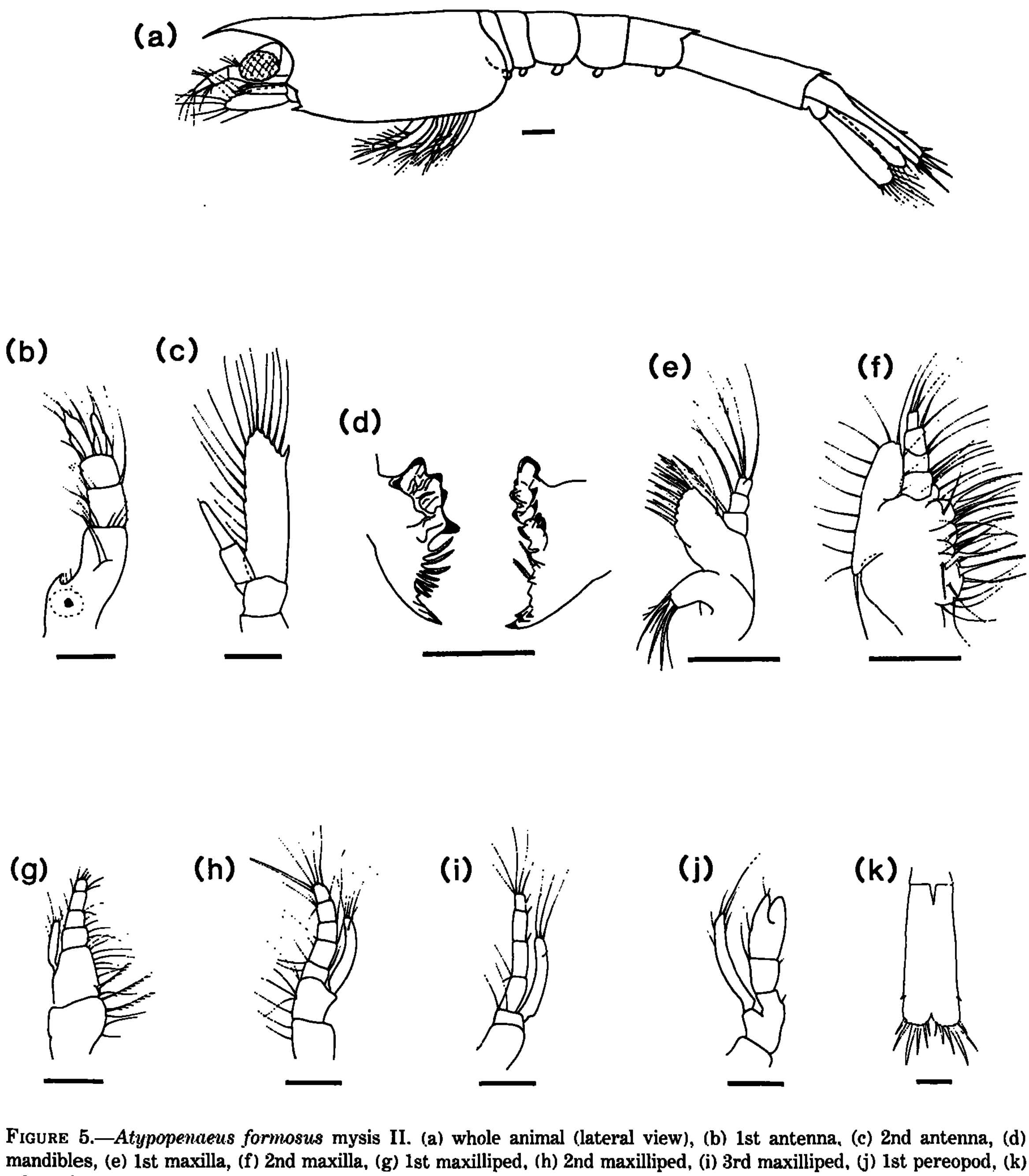

FIGURE 5.—*Atypopenaeus formosus* mysis II. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

Statocyst now normally present (Fig. 6b), antennal flagellum about the same length as in previous substage (Fig. 6c). Mandible with unsegmented palp (Fig. 6d). First maxilla similar to previous substage (Fig. 6e); epipod of 2nd maxilla continues to become larger and more setose (Fig. 6f). Three maxillipeds now bearing rudimentary gills (Fig. 6g, h, i), which vary in size in different individuals; pereopods now have functional chelae (Fig. 6j). Shallow telson cleft remains (Fig. 6k).

POSTLARVA. The postlarva of *A. formosus* (Fig. 7) has a rostrum with 3 dorsal teeth and an epigastric tooth. Pterygostomial spine present, but no supraorbital or hepatic spine. Proximal

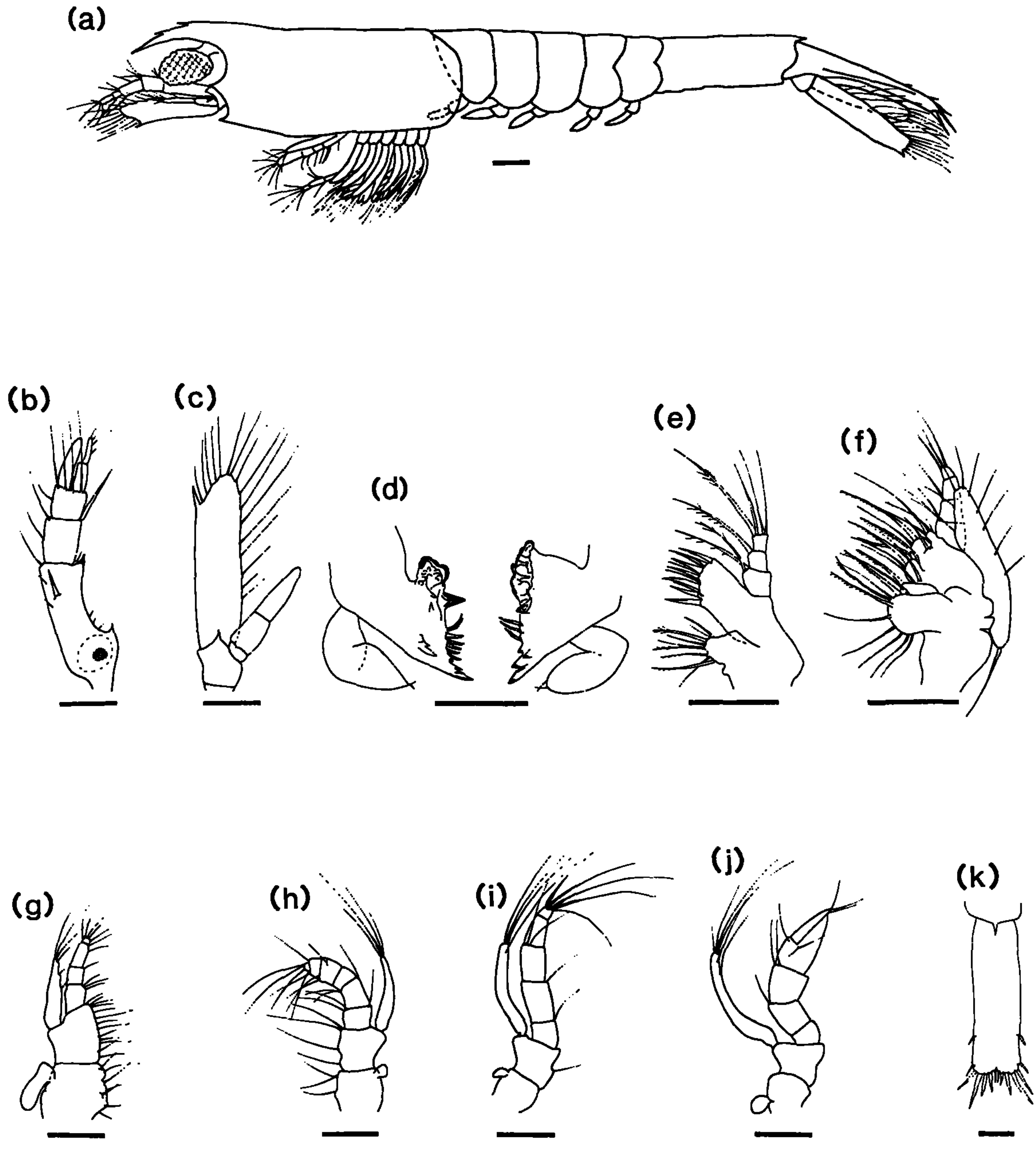

FIGURE 6.—*Atypopenaeus formosus* mysis III. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

segment of 1st antenna with 1 spine near statocyst, 1 distally; 2 rami now elongated (Fig. 7b). Antennal flagellum almost as long as blade (Fig. 7c). Most fine teeth and grinding teeth absent from mandible, now bearing 2-segmented, setose palp (Fig. 7d). First maxilla (Fig. 7e) unchanged; epipod of 2nd maxilla (Fig. 7f) extends from base to tip. Exopod and endopod of 1st maxilliped reduced in size (Fig. 7g). Second maxilliped little changed (Fig. 7h), endopod of 3rd maxilliped long and slender (Fig. 7i). Pereopods and chelae longer and stronger (Fig. 7j). One long median sternal spine on 4th thoracic segment, and 1 short median sternal spine on 5th (sternal spine formula 0+0+0+1+1) (see Figure 15e). Only 6th abdominal segment with dorsal spine (Fig. 7a). Posterior margin of telson rounded, without cleft. Telson spine formula remaining 7+7 with additional 2 long, feathery submedian setae (Fig. 7k).

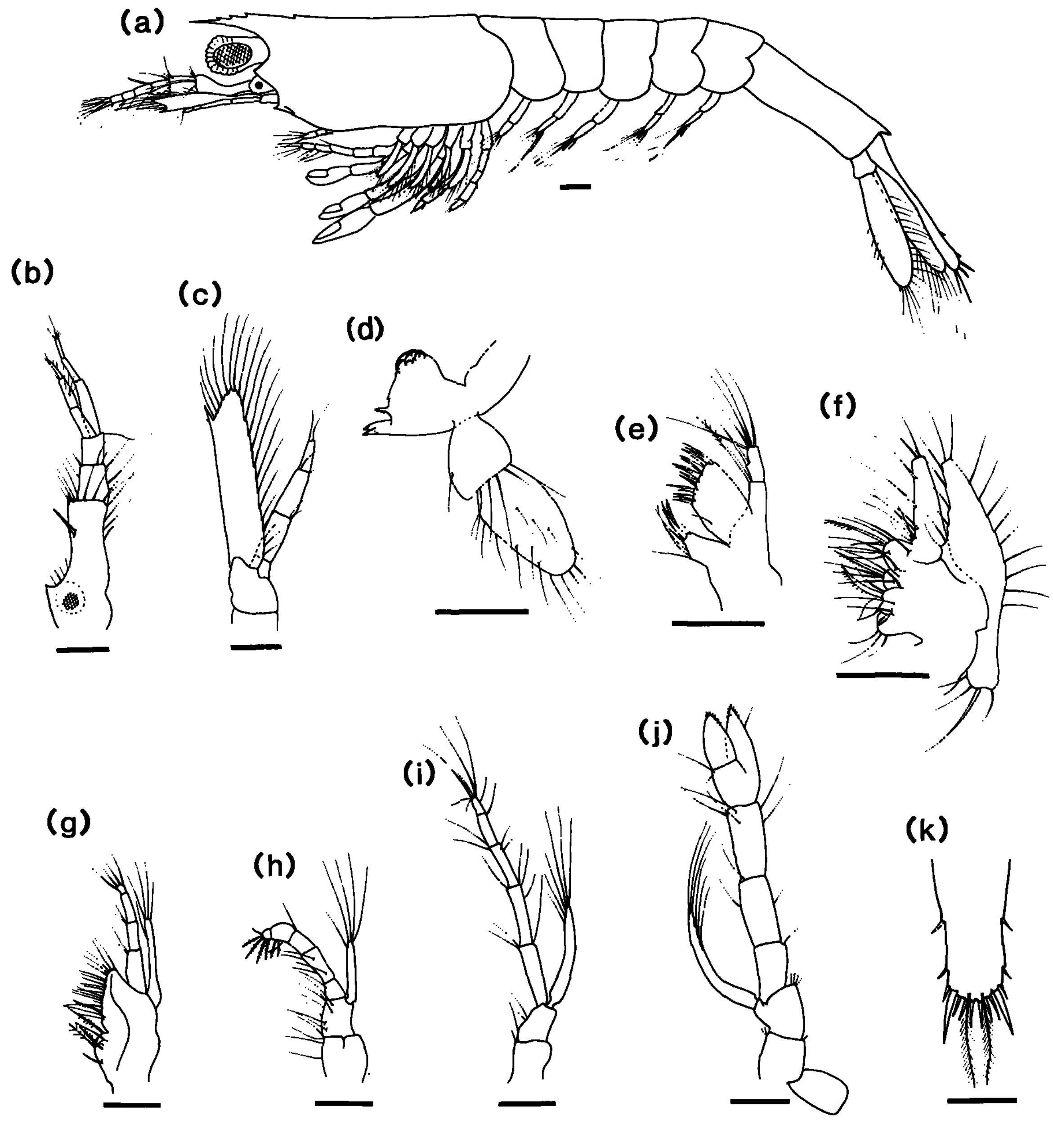

FIGURE 7.—*Atypopenaeus formosus* postlarva. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

Metapenaeopsis palmensis

The details of setation and segmentation for the various appendages are given in Figures 8 to 14 and in Table 2. The general development of *M. palmensis* parallels *A. formosus*, and only significant differences are given in the following text.

PROTOZOEA. Second antenna 0.7–1.0 times length of 1st antenna throughout protozoeal stage; 2nd antennal formula 1+2+2. Telson setal formula of 7+7 does not change until mysis II. Exopod of 2nd antenna bears 10 or 11 setae along its inner margin.

First substage (Table 2, Fig. 8a) with oval carapace bearing frontal organs and, above them, a prominent pair of pointed spines projecting forward between the 1st antennae. Length of these spines approximately equal to

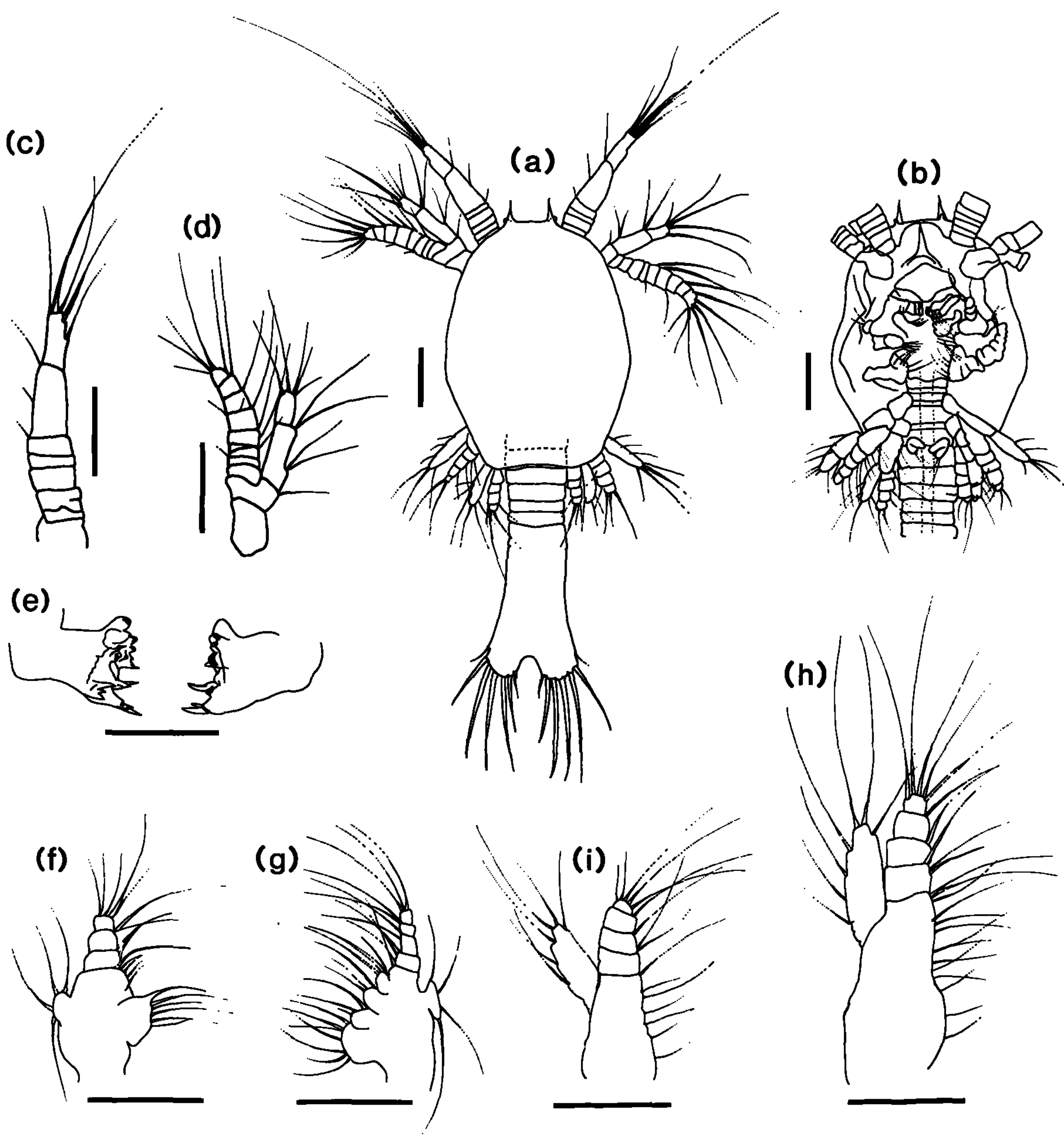

FIGURE 8.—*Metapenaeopsis palmensis* protozoea I. (a) whole animal, (b) ventral view of cephalothorax, (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped. Scale = 0.1 mm.

diameter of basal segment of 1st antenna. Carapace length about half total length. Long labral spine (Fig. 8b). As in *A. formosus*, segmentation of 1st and 2nd maxillipeds variable and often indistinct (Fig. 8h, i). Second substage (Fig. 9) with long, down-curved rostrum extending beyond tip of eye. Two pairs of supraorbital spines. Both 1st and 2nd antennae stouter than *A. formosus* (Fig. 9b, c). In 3rd substage (Fig. 10) the inner supraorbital spines have almost disappeared, leaving only a protrusion in the carapace border or sometimes 1 or 2 small denticles (Fig. $10a_1$). Outer supraorbital spines remain distinct. Dorsal spines present on first 5 abdominal segments; lateral spines on 5th and 6th segments (Fig. 10a).

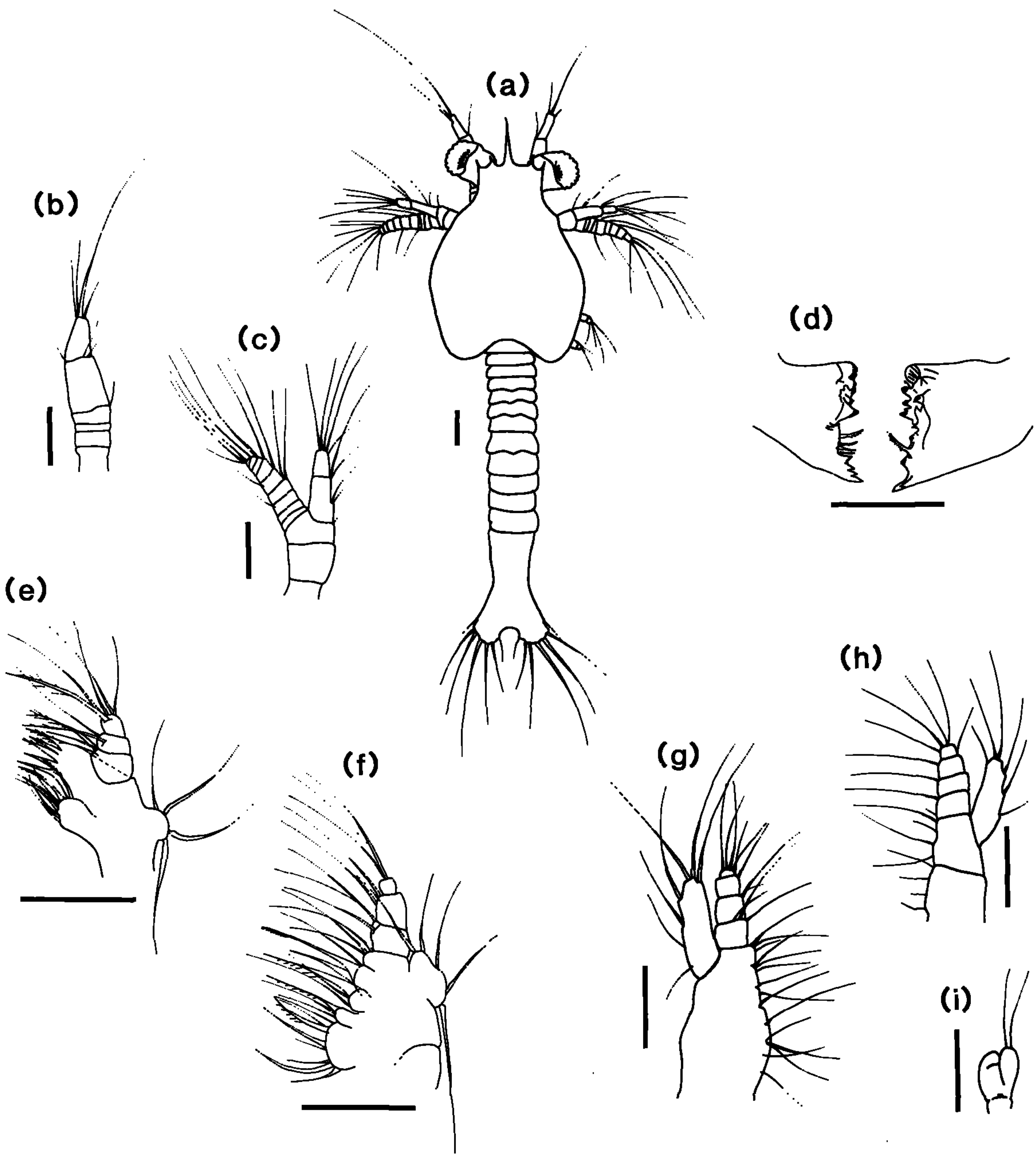

FIGURE 9.—*Metapenaeopsis palmensis* protozoea II. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

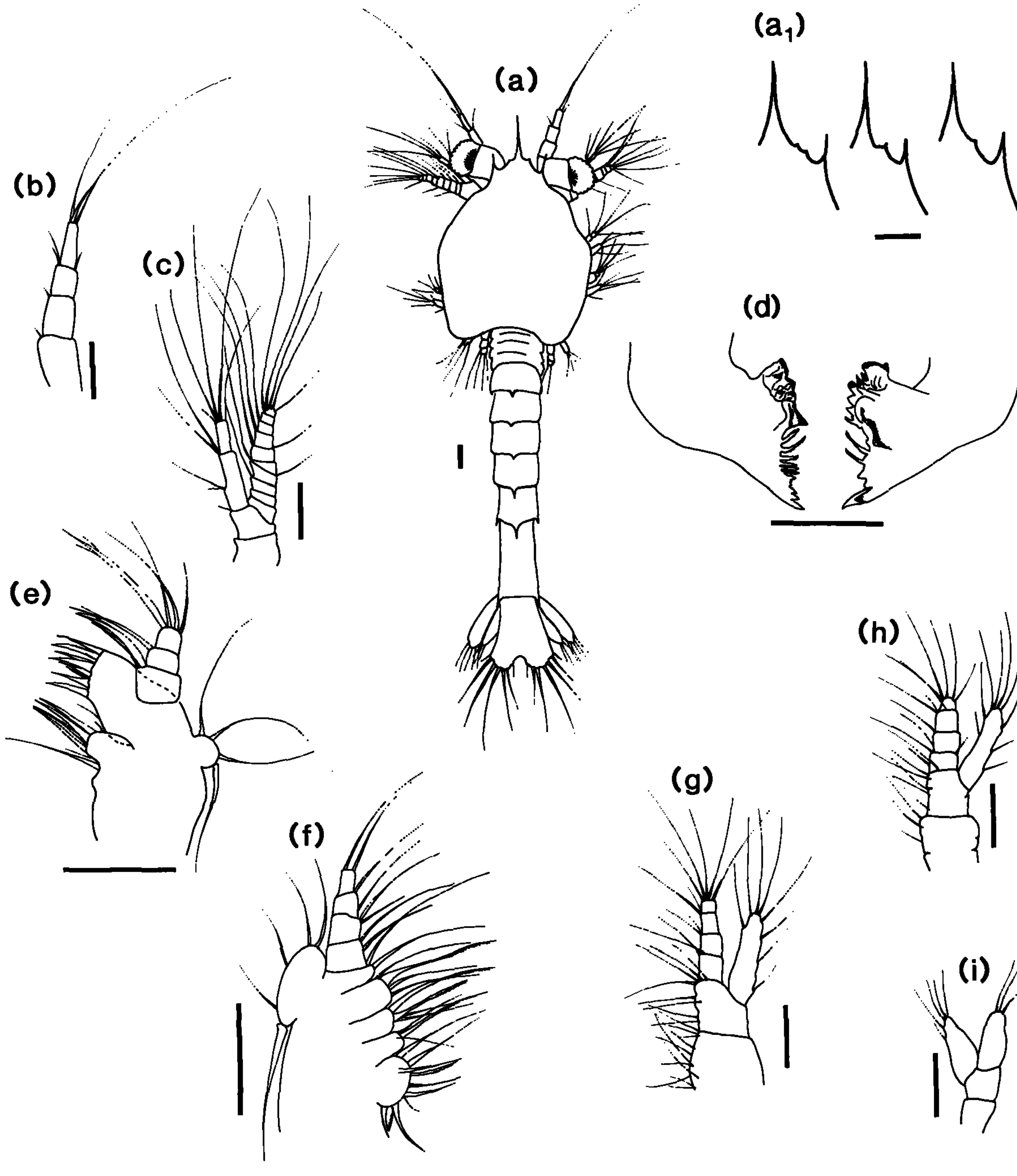

FIGURE 10.—*Metapenaeopsis palmensis* protozoea III. (a) whole animal, (a_1) detail – variation in form of inner supra-orbital spine rudiment, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

MYSIS. In each substage, the carapace bears a distinctive series of spines or serrations along its anteroventral border (Fig. $11b_1$). The rostrum, down-curved, extends beyond eye. All mysis substages have supraorbital and pterygostomial spines. Small hepatic spine may be absent in 1st substage but always present afterwards. Dorsal spines sometimes on 4th abdominal segment, always on 5th and 6th, and lateral spines on 5th and 6th segments.

Mysis I of *M. palmensis* (Table 2, Fig. 11) retains 1 pair of supraorbital spines; rostrum has

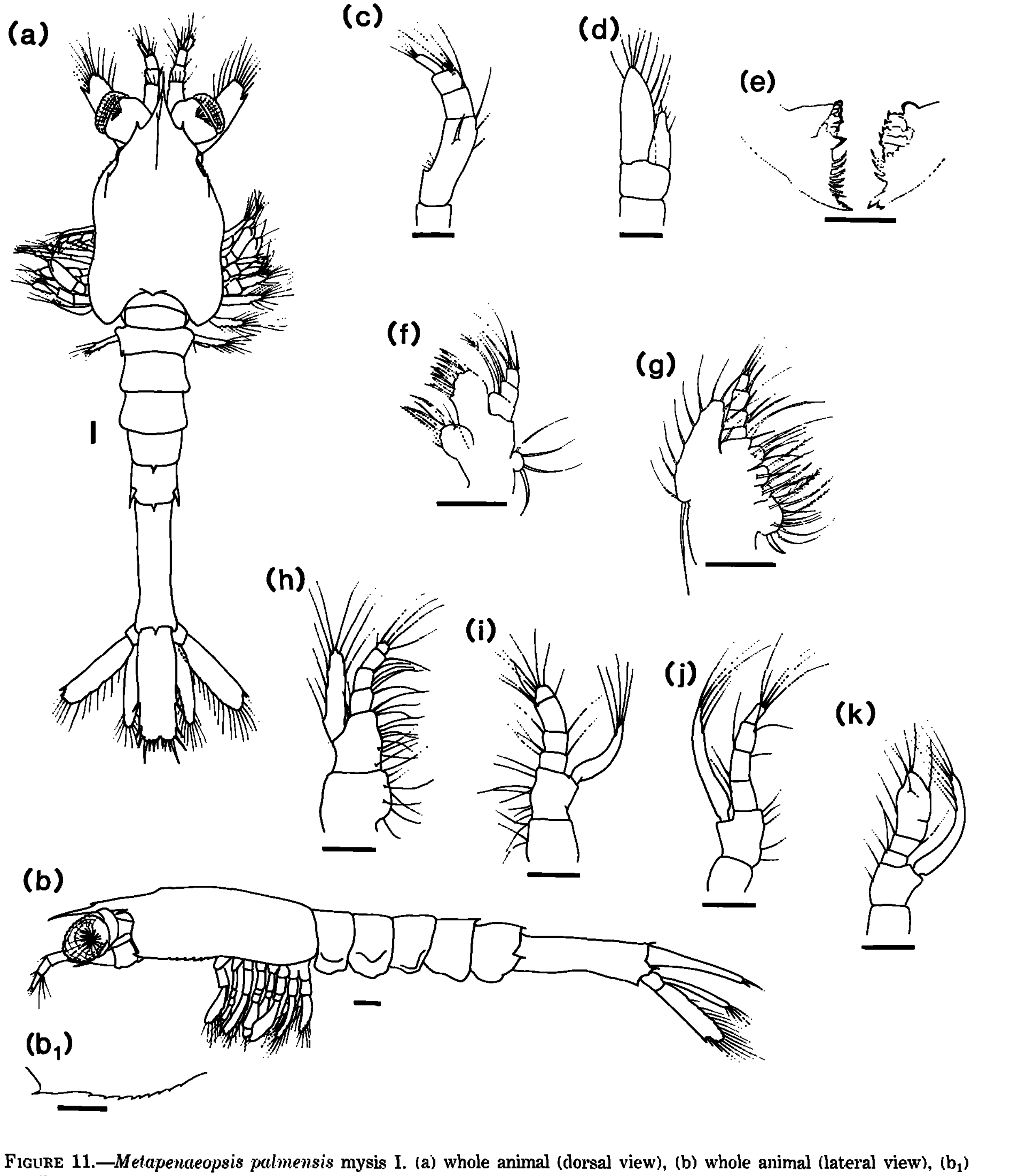

FIGURE 11.—*Metapenaeopsis palmensis* mysis I. (a) whole animal (dorsal view), (b) whole animal (lateral view), (b_1) detail-serrated anteroventral carapace margin, (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped, (j) 3rd maxilliped, (k) 1st pereopod. Scale = 0.1 mm.

at most 1 dorsal tooth; small hepatic spine sometimes present (Fig. 11a, b). Epipod of 2nd maxilla (Fig. 11g) more enlarged than that of *A. formosus* at same substage. Mysis II (Fig. 12) with 2 dorsal rostral teeth, hepatic spine always present (Fig. 12a). In contrast to *A. formosus*, still no statocyst in 1st antenna (Fig. 12b), but 2nd antennal flagellum already as long as blade (Fig. 12c). Posterior border of telson with only slight cleft, and small median spine (telson formula now 7+1+7) (Fig. 12k). Mysis III (Fig. 13) with 2 or 3 dorsal rostral teeth and an epigastric tooth. First antenna now usually with a small statocyst (Fig. 13b); 2nd antennal flagellum longer than blade (Fig. 13c). Mandibles with unsegmented palp (Fig. 13d). Telson notch absent, posterior margin slightly rounded. Median spine still very short (Fig. 13k).

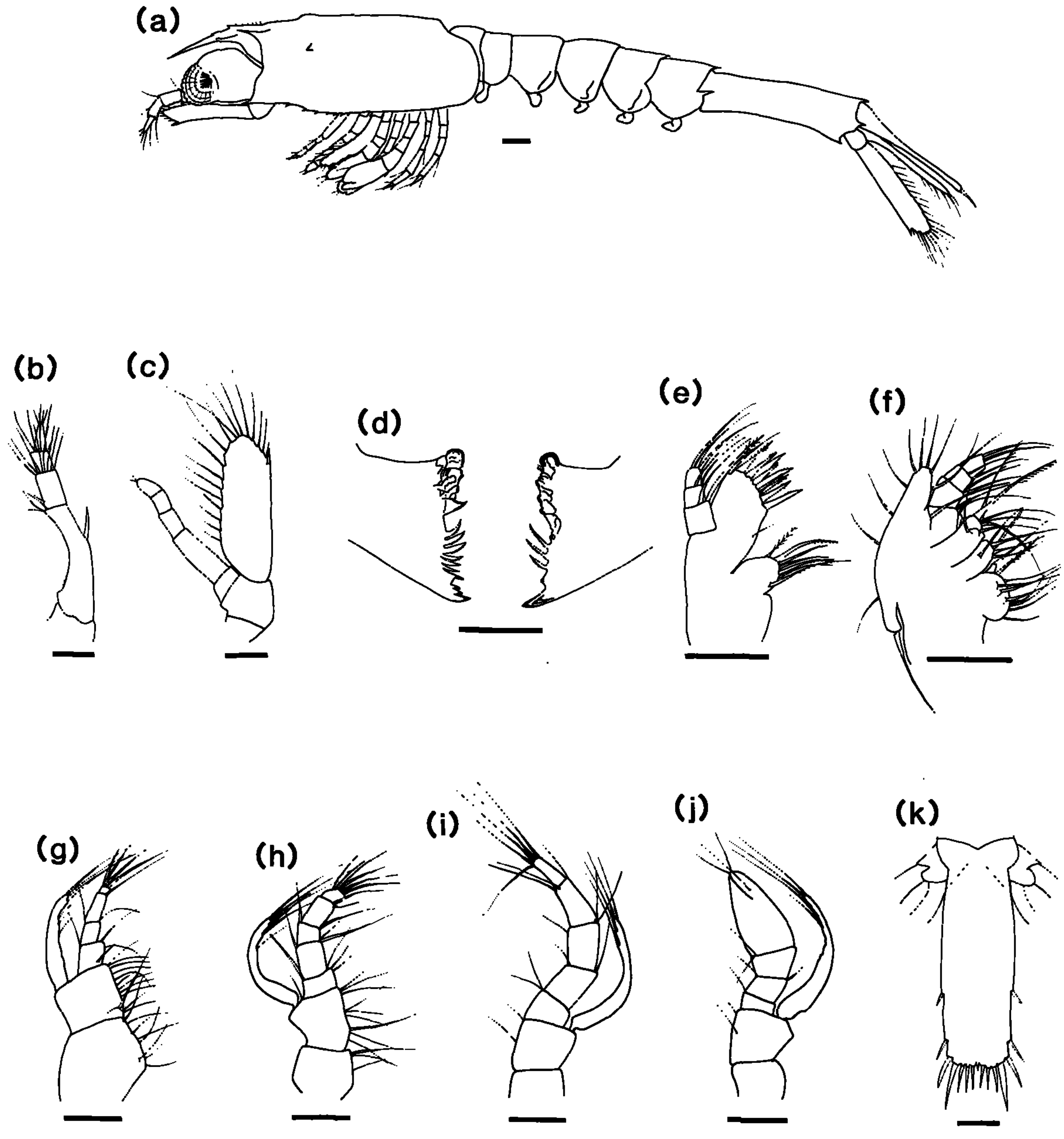

FIGURE 12.—*Metapenaeopsis palmensis* mysis II. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

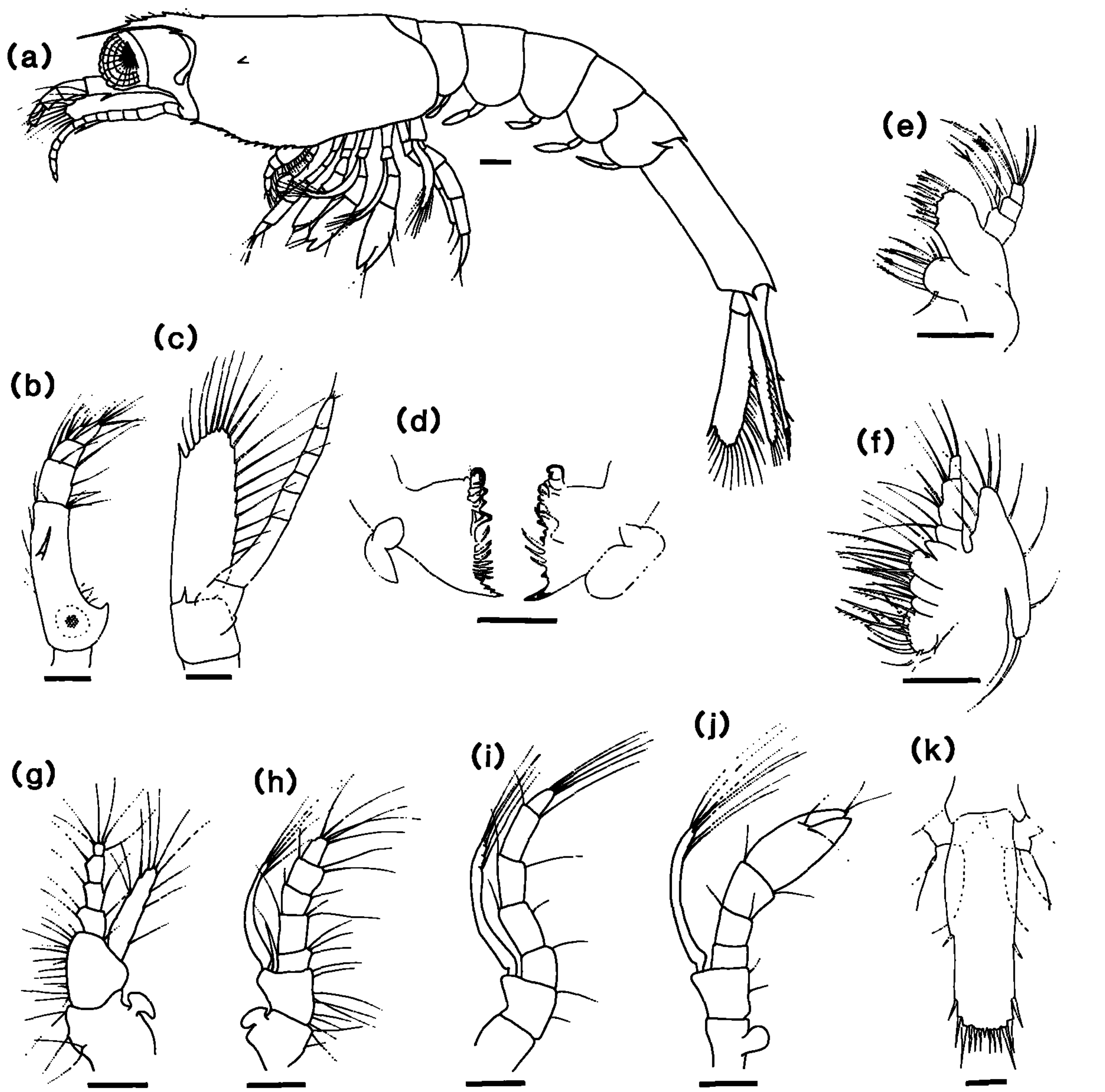

FIGURE 13.—*Metapenaeopsis palmensis* mysis III. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

POSTLARVA. The postlarva of *M. palmensis* (Table 2, Fig. 14) lacks the supraorbital spines and carapace serrations of the mysis substages. Pterygostomial spine and hepatic spine remain, now also a small antennal spine (Fig. 14a). Rostrum slightly shorter than eye, with 3 or 4 dorsal teeth and an epigastric tooth (Fig. 14a). First antenna lacking distal spine which *A. formosus* bears on proximal segment. Two small sternal spines on 1st thoracic segment, 2 long spines on 2nd thoracic segment (thoracic sternal spine formula 2+2+0+0+0) (Fig. 15d). Abdominal spination reduced, only 1 dorsal spine on 6th segment. Posterior margin of telson more V-shaped, spine formula remaining 7+1+7 (Fig. 14k). Median spine now large. Telson also bearing 3 or 4 small setae on each side of its posterior margin.

Generic Characteristics of Penaeid Larvae

The distribution of setae on the protopod and

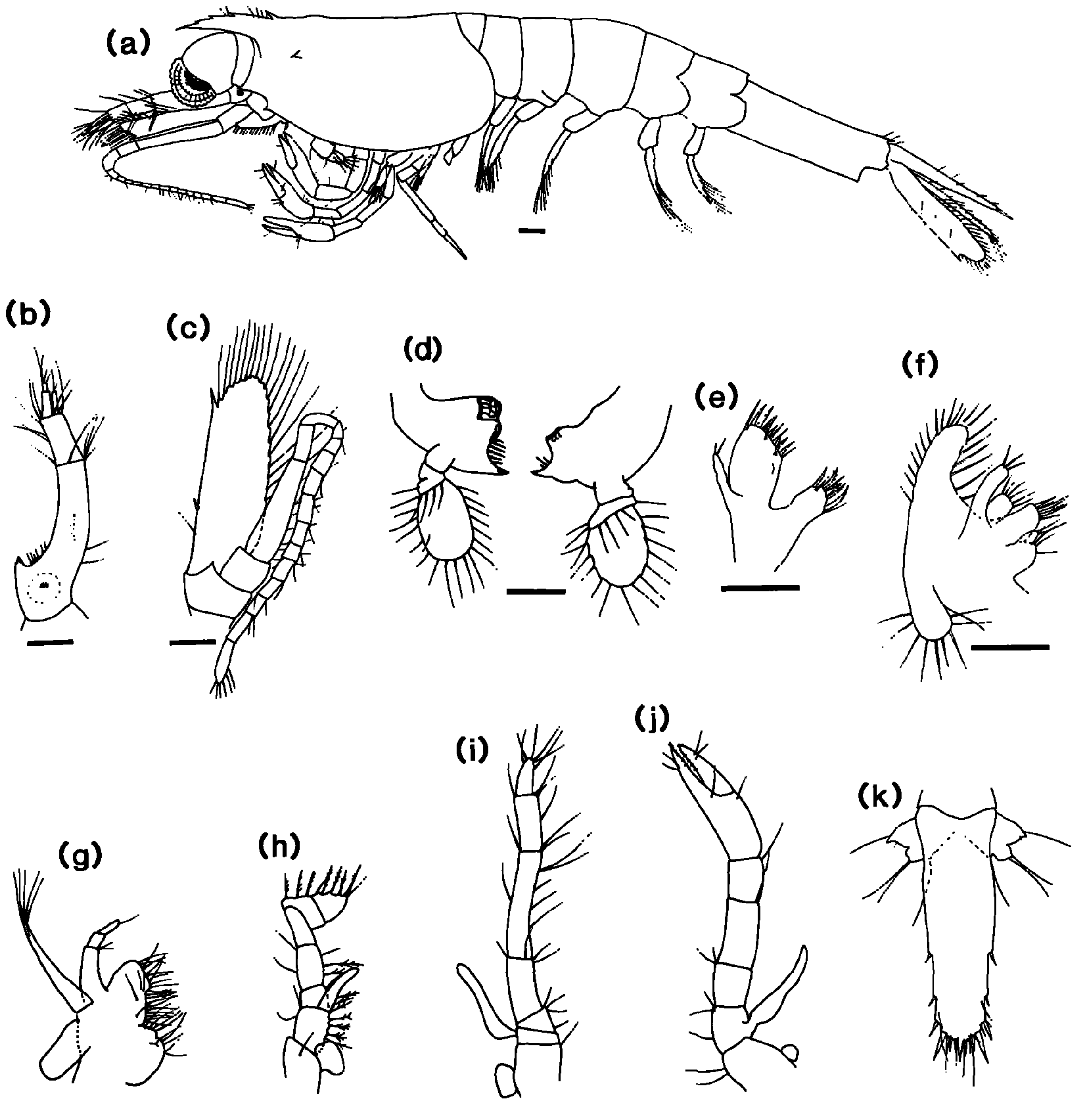

FIGURE 14.—*Metapenaeopsis palmensis* postlarva. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

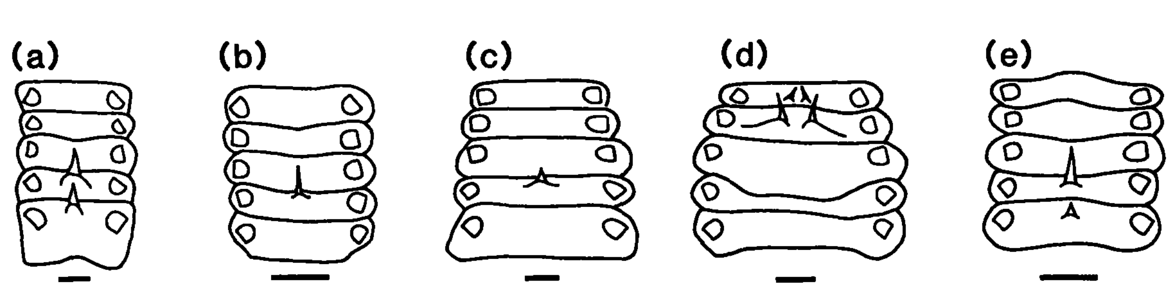

FIGURE 15.—Thoracic sternal spine distribution of postlarvae. (a) *Penaeus* (except for subgenus *Litopenaeus*; see text), (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*. Scale = 0.1 mm.

endopod of the 2nd antenna has been used for generic identification of protozoea (Cook 1966a; Hassan 1974; Haq and Hassan 1975). While this character is often referred to as the setal formula of the 2nd antennal endopod, this is not correct as the first seta referenced arises from the protopod.

We compared the 2nd antennal formulae of protozoeae in our reference collection with published formulae. All *Penaeus* larvae in our collection have the formula 1+1+2, in agreement with other published descriptions. The three species of *Trachypenaeus* in our collection (*T. anchoralis*, *T. fulvus*, and *T. granulosus*) have the formula 0+2+2, which is in agreement with the only existing published descriptions by Kirkegaard (1969) and Pearson (1939). *Parapenaeopsis* is represented in our reference collection by the protozoeae of *P. cornuta*, which also have the formula 0+2+2. This confirms the formula found by Hassan (1984) for *P. stylifera*. Rao (1973) also described larvae of *P. stylifera*, and his figures seem to indicate the same formula of 0+2+2, although no detailed drawings of appendages are provided.

However, the 2nd antennal formula is not consistent in all genera. There are five species of *Metapenaeus* in our reference collection: *M. bennettae*, *M. eborocensis*, *M. endeavouri*, *M. ensis*, and *M. insolitus*. These larvae normally have the formula 1+2+3, but on some occasions the formula is 1+2+2. This difference occurs at random (although rarely) among most species. Menon (1951), Morris and Bennett (1951), Raje and Ranade (1972), Kurata and Vanitchkul (1974), Courties (1976), and Hassan (1980) agreed that *Metapenaeus* have 1+2+2, while Vanitchkul (1970), Hassan (1974), and Haq and Hassan (1975) found both 1+2+2 and 1+2+3. In our larvae, the third seta in the most distal group was often small and hard to distinguish when present, and could easily have been overlooked. Similarly, the 2 species of *Metapenaeopsis* we have reared are not consistent. *Metapenaeopsis palmensis* is always 1+2+2, but *M. novaeguinae*, although normally exhibiting the same formula, occasionally has 1+2+3.

In the mysis stage, the presence of a serrate anteroventral carapace margin (Fig. $11b_1$) is a character that has not previously been described for laboratory-reared penaeid larvae. At present the only genus in which it is definitely present is *Metapenaeopsis*—both *M. palmensis* and *M. novaeguinae* from our reference collection.

The number and placement of thoracic sternal spines have not been mentioned in previous studies. In cleared and stained specimens it is an easy character to assess and makes postlarval identification straightforward, and it is an important generic character in our key for postlarvae. Unfortunately these spines have not been described by other workers and so we have no information about the sternal spine formulae for genera that are not represented in our reference collection. Partly owing to this we have used other characters to help identify some genera; however, when both the size and position of the sternal spines are taken into account, they are sufficient to identify five genera: *Atypopenaeus*, *Metapenaeopsis*, *Metapenaeus*, *Penaeus*, and *Trachypenaeus* (Fig. 15). Within the genus *Penaeus*, the sternal spine formula has taxonomic value at the subgenus level. We have examined postlarvae from 3 species within the subgenus *Litopenaeus* (*P. setiferus*, *P. stylirostris*, and *P. vannamei*), all of which have only a single, small sternal spine on the 4th segment (formula 0+0+0+1+0). All other *Penaeus* examined have a large spine on the 4th segment and a small spine on the 5th (formula 0+0+0+1+1): *P. aztecus* from the subgenus *Farfantepenaeus*; *P. indicus* and *P. merguiensis* from the subgenus *Fenneropenaeus*; *P. japonicus* from the subgenus *Marsupenaeus*; *P. latisulcatus*, *P. longistylus*, and *P. plebejus* from the subgenus *Melicertus*; and *P. esculentus*, *P. monodon*, and *P. semisulcatus* from the subgenus *Penaeus*. Species of *Litopenaeus* do not occur in the Indo-west Pacific region and so will not be wrongly identified by our key.

We have not used the distribution of abdominal spines in protozoea III or mysis substages (e.g., Cook 1966a; Muthu et al. 1978), since their presence can be variable, at least for *M. palmensis*. Paulinose (1977) suggested that the dentition and asymmetry of the mandibles might be useful for both generic and specific identification of penaeid larvae. We have not investigated this possibility since the operational use of this character would not be practical due to the time-consuming dissections necessary.

Key to Penaeid Genera

Our key was constructed from both our own reference collection and published descriptions. Many species were referred to in characterizing the genera *Penaeus*, *Metapenaeus*, and *Trachypenaeus*. However, there is much less reference material available for other genera. Although

Metapenaeopsis has more species than any other penaeid genus found in the Indo-west Pacific region (Dall et al. in press), our key is based on just 2 species, both from our own reference collection. Characteristics of the genera *Atypopenaeus, Parapenaeopsis*, and *Parapenaeus* have been based on a single species. For this reason, and because the genera *Heteropenaeus, Trachypenaeopsis*, and *Penaeopsis* have been omitted, the key must be regarded as provisional, and subject to revision as more descriptions are published.

The protozoeae of *Metapenaeus, Atypopenaeus*, and *Metapenaeopsis*, and *Parapenaeus* are very similar. For protozoea II and III, distinction between these genera relies on the shape of the telson, rostrum, and supraorbital spines. These characters should be assessed with reference to Figures 17 and 18 and, if there is any doubt, the suite of characteristics in Table 3. In most cases the characters used in the key should be sufficient to identify mysis larvae and postlarvae without difficulty. However, as an additional check, the general shape of the antennal blades is a useful generic character, and should be compared with those shown (Fig. 16).

The family Penaeidae no longer includes members of the Aristaeidae, Solenoceridae, Sergestidae, or Sicyoniidae; these are now separate families within the superfamily Penaeoidea (Bowman and Abele 1982). We have restricted our key to the family Penaeidae. However, lar-

TABLE 3.—Characteristics of protozoeal stages of the genera *Atypopenaeus, Metapenaeopsis, Metapenaeus*, and *Parapenaeus*. Sources of information: *Atypopenaeus, Metapenaeopsis, Metapenaeus*—present study and reference collection of larvae held by the authors; additional sources for *Metapenaeus* species—see Dall et al. (in press) for review; specific sources referenced in table—*Parapenaeus stylifera* – [1]Heldt 1938, [2]Pearson 1939; *Metapenaeus monoceros* – [3]Courties 1976, [4]Raje and Ranade 1972.

	Atypopenaeus	*Metapenaeopsis*	*Metapenaeus*	*Parapenaeus*
Protozoea I				
Number of setae on 2nd antenna exopod inner margin	9-10	9-11	10	11
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	0+2+2[1] or 1+2+2[2]
Anterior carapace	no spines	long spines	short spines except none for *M. ensis, M. monoceros*[3,4]	long spines
Protozoea II				
Number of setae on 2nd antenna exopod inner margin	9-10	9-11	10	11
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	1+2+2[1] or 1+2+3[2]
Rostrum	longer than eye	longer then eye, curved	about eye length	longer than eye
Supraorbital spines	one	two similar size	one except for *M. ensis, M. monoceros*[3,4] (inner much smaller than outer)	two similar size
Protozoea III				
Number of setae on 2nd antenna exopod inner margin	9-10	10-11	10	11[2] or 12[1]
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	0+2+2[1] or 1+2+3[2]
Rostrum	longer than eye	longer than eye, curved	about eye length	longer than eye
Supraorbital spines	one	one plus rudiment of second (Fig. $10a_1$)	one	two (inner smaller than outer)
Telson spines	7+7	7+7	7+7	8+8

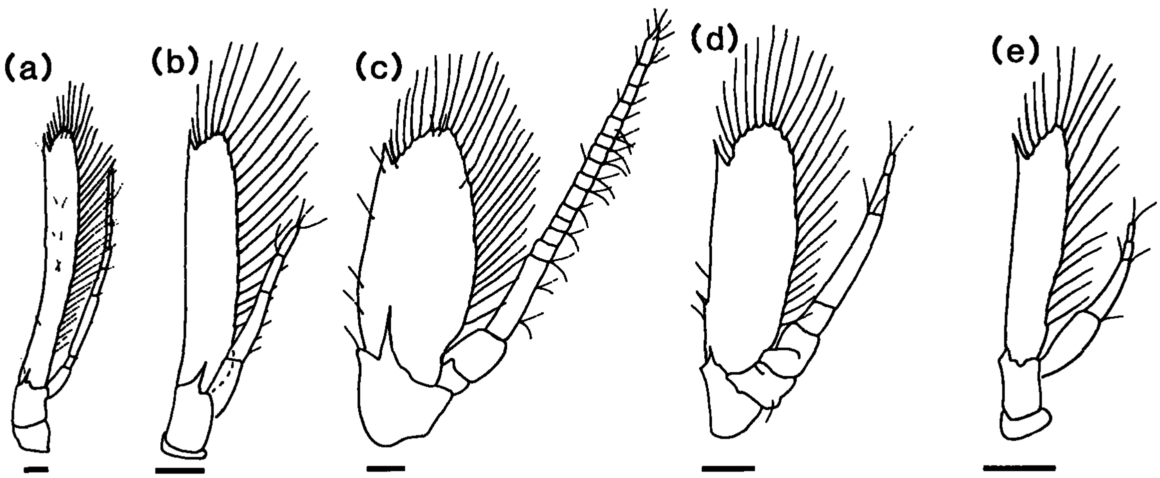

FIGURE 16.—Second antenna of postlarvae. (a) *Penaeus*, (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*. Scale = 0.1 mm.

vae from other families within the superfamily Penaeoidea might occur with penaeids. Characteristics that can identify larvae of related families are described by Cook (1966a) and Dall et al. (in press).

The key is not useful for later postlarval stages. It is difficult to define the cutoff point for older postlarvae, but the following characteristics may indicate that the postlarva is too old for accurate identification: there are more than 4 rostral spines; the antennal flagellum is longer than half the body length; the telson has a pronounced V-shape; and there are many setae on the telson.

Key

Protozoea

1 Setal formula on 2nd antennal protopod and endopod 1+1+2 . . . . *Penaeus*
2nd antennal formula 0+1+2 . . . . *Macropetasma*
2nd antennal formula not 1+1+2 or 0+1+2 2

2(1) 2nd antennal formula 0+2+2 3
2nd antennal formula 1+2+2 or 1+2+3 5

3(2) 2nd antennal exopod with 11 setae on inner margin . . . . *Parapenaeus*
2nd antennal exopod with 10 setae on inner margin 4

4(3) Dorsal surface of carapace with small hump; telson notch moderately wide (Fig. 17c, i). . . . . *Trachypenaeus*
Dorsal surface of carapace smooth; telson notch very wide (Fig. 17f, l). . . . . *Parapenaeopsis*

5(2) Eyes immobile (protozoea I) 6
Eyes mobile (protozoea II or III) 9

Protozoea I

6(5) Strong spines above frontal organs, length at least 0.7 of 1st antenna diameter (Fig. 8a) . . . . *Metapenaeopsis*
Spines above frontal organs small or missing. 7

7(6) 2nd antennal exopod with 11 setae on inner margin . . . . *Parapenaeus*
2nd antennal exopod with 10 setae on inner margin 8

8(7) Carapace about 0.5 of total length; usually small spines above frontal organs. . . . . *Metapenaeus*
Carapace about 0.4 of total length; no spines above frontal organs . . . . *Atypopenaeus*

9(5) Uropods absent (protozoea II). 10

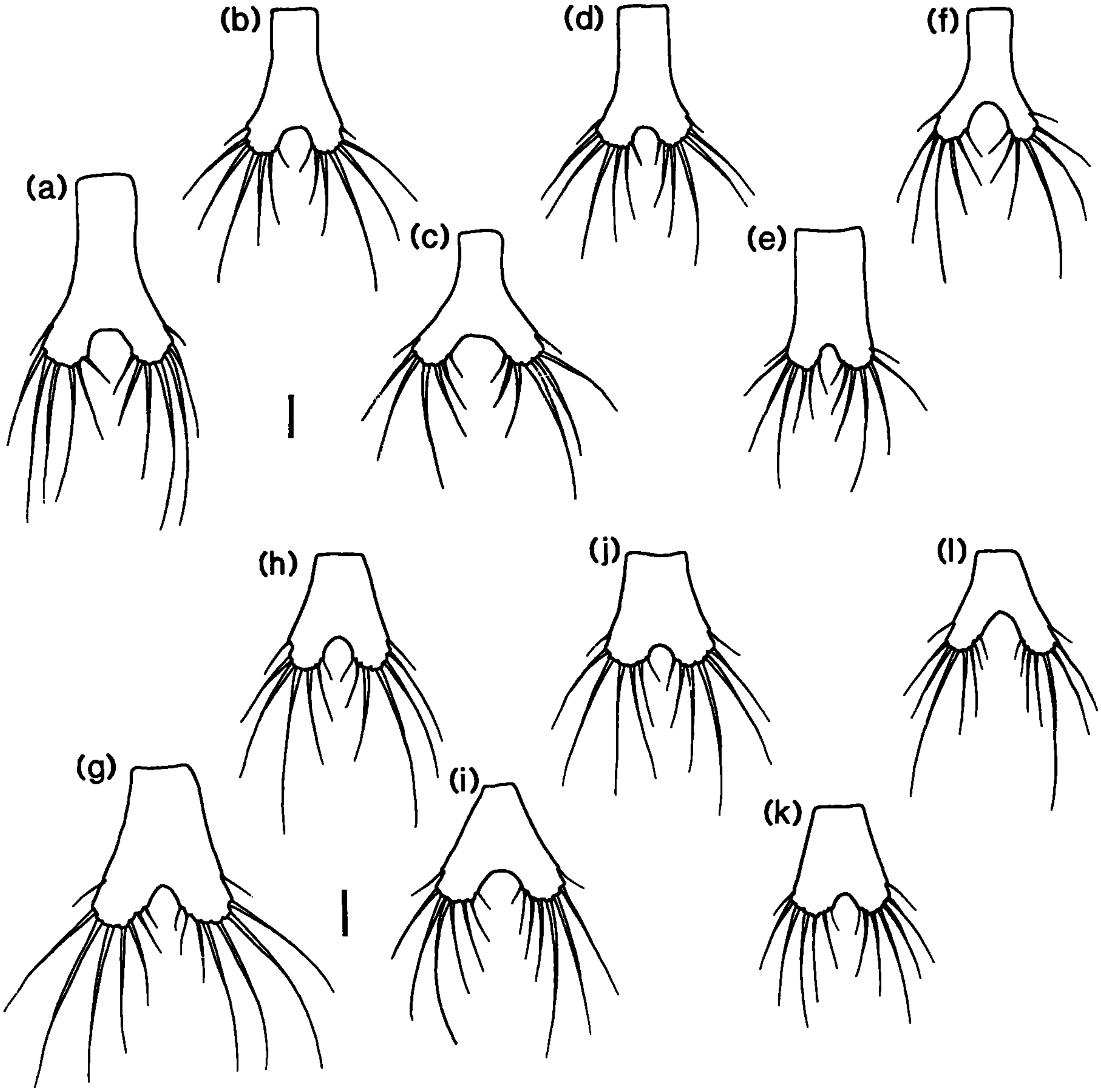

FIGURE 17.—Telson shapes of protozoeae. Protozoea II – (a) *Penaeus*, (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*, (f) *Parapenaeopsis*. Protozoea III – (g) *Penaeus*, (h) *Metapenaeus*, (i) *Trachypenaeus*, (j) *Metapenaeopsis*, (k) *Atypopenaeus*, (l) *Parapenaeopsis*. Scale = 0.1 mm.

Uropods present (protozoea III) 14

Protozoea II

10(9) A single pair of supraorbital spines (Fig. 2a) 11
Two pairs of supraorbital spines (Fig. 9a) 12

11(10) Telson wedge-shaped, with no distinct angle in lateral border (Fig. 17e) . . . . *Atypopenaeus*
Telson with a distinct angle in lateral border (Fig. 17b) . . . . *Metapenaeus*

12(10) Inner pair of supraorbital spines filamentous and less than half as long as outer pair (Fig. 18) . . . . *Metapenaeus*[3]
Inner pair of supraorbital spines robust, similar in size to outer pair (Fig. 9a) 13

13(12) Body length greater than 1.6 mm . . . . *Parapenaeus*
Body length less than 1.6 mm . . . . *Metapenaeopsis*

[3]*M. ensis* or *M. monoceros*.

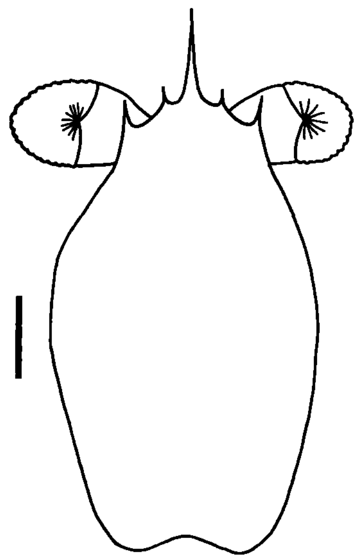

FIGURE 18.—Carapace of *Metapenaeus ensis* protozoea II. Scale = 0.1 mm.

Protozoea III

14(8) A single supraorbital spine, with straight carapace border between supraorbital spine and rostrum (Fig. 3a) 15
2 supraorbital spines, or 1 supraorbital spine with 1 or 2 small denticles, or a protrusion in carapace border between supraorbital spine and rostrum (Fig. $10a_1$) 16

15(14) Rostrum about same length as eye ... . *Metapenaeus*
Rostrum about 1.5 times eye length .. .. *Atypopenaeus*

16(14) Two well-defined supraorbital spines . ... *Parapenaeus*
One supraorbital spine with 1 or 2 small denticles, or a protrusion in carapace border between supraorbital spine and rostrum (Fig. 10b)......... .... *Metapenaeopsis*

Mysis

1 Anteroventral margin of carapace serrated (Fig. $11b_1$) .... *Metapenaeopsis*
Anteroventral margin of carapace smooth 2

2(1) 3rd abdominal segment with large dorsal spine; abdomen permanently flexed at 3rd abdominal segment (Fig. 19c) .. .. *Parapenaeus*
3rd abdominal segment with no spine or a small spine; no permanent flexion of abdomen 3

3(2) 5th abdominal segment with a large dorsal spine, equal in length to diameter of segment (Fig. 19a) .... *Macropetasma*
5th abdominal segment with no spine or with a spine of length less than half diameter of segment 4

4(3) Telson spine formula 8+8............. 5
Telson spine formula 7+7............. 7

5(4) Hepatic spine present .... *Penaeus*
Hepatic spine absent................. 6

6(5) Rostrum very short, less than half eye length .... *Trachypenaeus*
Rostrum longer than half eye length.. .... *Parapenaeopsis*

7(4) Rostrum down-curved, longer than eye .... *Atypopenaeus*
Rostrum straight, shorter than eye... .... *Metapenaeus*

Postlarva

1 3rd abdominal segment with large dorsal spine; abdomen permanently flexed at 3rd abdominal segment (Fig. 19d)..................... *Parapenaeus*
3rd abdominal segment with no spine or a small spine; no permanent flexion of abdomen 2

2(1) Rostrum with more than one dorsal tooth.............................. 3
Rostrum with zero or one dorsal teeth .... *Macropetasma*

3(2) Telson with a median spine............ 4
Telson without a median spine......... 5

4(3) Telson with 8+1+8 spines........... .... *Parapenaeopsis*
Telson with 7+1+7 spines; thoracic sternal spine formula 2+2+0+0+0 (Fig. 15d) .... *Metapenaeopsis*

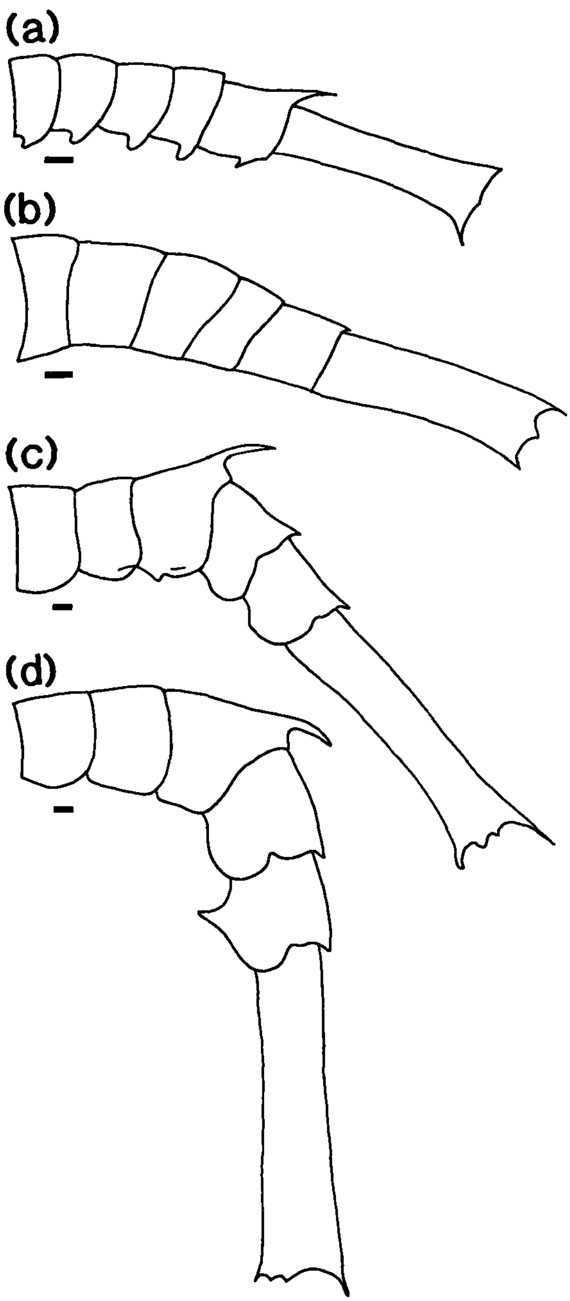

FIGURE 19.—Abdomen of *Macropetasma* (a) mysis II, (b) postlarva (redrawn from Cockcroft 1985) and *Parapenaeus* (c) mysis II, (d) postlarva (redrawn from Heldt 1938). Scale = 0.1 mm.

5(3) Telson with 8+8 spines............... 6
Telson with 7+7 spines............... 7

6(5) Thoracic sternal spine formula 0+0+0+1+1 (Fig. 15a) .... *Penaeus*
Thoracic sternal spine formula 0+0+0+1+0 (Fig. 15c) .... *Trachypenaeus*

7(5) Thoracic sternal spine formula 0+0+0+1+0 (Fig. 15b) .... *Metapenaeus*
Thoracic sternal spine formula 0+0+0+1+1 (Fig. 15e) .... *Atypopenaeus*

DISCUSSION

Previous Descriptions of Penaeid Larvae

The only way to describe the morphology and to be certain of the identity of penaeid larvae is to rear them in the laboratory, beginning with eggs from adults of known identity. Techniques for inducing penaeids to spawn and for culturing the larvae have been known for many years (Hudinaga 1942). For the genera *Penaeus* and *Metapenaeus* there are over 30 descriptions of larvae whose identity is certain (Dall et al. in press). Laboratory-reared larvae of other penaeid genera, also commercially important, are less well described. There are only a few useful descriptions of any species of *Parapenaeopsis* (Hassan 1984; Rao 1973), *Parapenaeus* (Heldt 1938; Pearson 1939) or *Trachypenaeus* (Pearson 1939; Kirkegaard 1969, protozoea I only), and this study is the first description of any species of *Metapenaeopsis* or *Atypopenaeus* based on laboratory-reared material.

Many workers have attempted to describe particular species or genera of penaeid larvae, based solely on planktonic material (see Dall et al. in press, for review). However the morphology of penaeid larvae undergoes major changes between each stage: egg to nauplius, nauplius to protozoea, and protozoea to mysis. Even between the protozoeal substages, changes are so great as to defy any attempt to link one substage with the next. A full larval life history cannot, we believe, be accurately reconstructed from larvae caught from the plankton unless at least some substages are subsequently reared (as in Pearson 1939).

The presence of commercial fisheries for a certain species is also a poor guide to the identity of larvae found in the same area. There may be significant populations of penaeid genera present that are not, for various reasons (small size, untrawlable habitat), represented in commercial catches. Larvae also have considerable potential for advection up to 150 km (Rothlisberg 1982; Rothlisberg et al. 1983b).

In several older studies, workers based their identification of larvae from the plankton on the temporal or spatial distribution of the adult prawns, and were later found to be in error. For example, Heegard (1953) identified larvae from plankton collections as *Penaeus setiferus*. However, the protozoea I figured has a 2nd antennal setal formula of 0+2+2 and a wide telson notch, characters not seen in *Penaeus* but consistent with either *Trachypenaeus* or *Parapenaeopsis*. The protozoea II figured has the same 2nd antennal setal formula as the protozoea I, and the form of the rostrum and supraorbitals are not characteristic of *Penaeus*. However, this substage has supraorbital spines, which *Trachypenaeus* and *Parapenaeopsis* larvae do not. Heegard's protozoea III is consistent with *Penaeus* in some respects, such as the long rostrum, but its 2nd antennal setal formula is now 1+2+2, whereas the *Penaeus* formula is 1+1+2. It is likely that the protozeae described are from several genera, although the figures do not show sufficient detail for an accurate identification. On the other hand, Heegard's mysis figures are generally consistent with *Penaeus*, although the specific identification is in doubt since *P. aztecus*, *P. duorarum*, and *P. setiferus* all exist in the collection area. Similarly Dakin (1938) identified plankton-caught larvae as *P. plebejus*, but they were probably a combination of *Trachypenaeus* (based on the relative lengths of the 1st and 2nd antennae of protozoea III) and *Metapenaeus* (a 2nd antennal setal formula of 1+2+3 and telson with 7+7 spines in protozoea III). As a final example, Subramanyam (1965) reported a high density of penaeid eggs in the plankton off the Madras coast, and identified them as *P. indicus* after culturing several nauplius substages. However, the large egg diameter (0.45 mm) and large perivitelline space indicate that the eggs were probably *Trachypenaeus*, since *Penaeus* eggs have a diameter between 0.23 mm and 0.31 mm and a narrow perivitelline space (Dall et al. in press).

Descriptions of the lesser known penaeid genera from plankton samples may also be based on mistaken identifications. The only published description of larvae of the genus *Penaeopsis* is of *P. rectacuta* (Paulinose 1973), but the author gave no support for his choice of genus. The larvae were collected from areas of the Indian Ocean where species of other previously undescribed genera are common, including *Atypopenaeus stenodactylus*, *Metapenaeopsis andamensis*, *M. barbata*, *M. hilarula*, *M. mogiensis*, *M. philippii*, and *M. stridulans*, all of which are sufficiently abundant to support some commercial fishing (Dall et al. in press). The present description of *Metapenaeopsis palmensis* has much in common with several of the substages described by Paulinose (1973). The 2nd antennal formula of 1+2+2, a reduced second supraorbital spine in protozoea III, the rostrum length, the shape and spination of the mysis, and the serrate anteroventral carapace margin of the mysis substages are all consistent with *M. palmensis* described in the present study. Protozoea II is probably from a different genus, since it has no supraorbital spines [in all penaeids described except *Macropetasma africanum* (Cockcroft 1985) the presence or absence of supraorbital spines is the same for both protozoea II and III]. However, the figure of this substage shows the 2nd antennal exopod (on the whole animal) as symmetrical, with about 9 setae along both the interior and the exterior borders, whereas the drawing of the dissected appendage shows the more typical penaeid form of 10 setae along the inner border and 2 on the outer border. More subtle characters may also have been represented incorrectly, so confident identification is difficult; however, the characteristics shown (lack of supraorbital spines, a deep and wide telson notch and a relatively short rostrum) are consistent with both *Trachypenaeus* and *Parapenaeopsis*.

Paulinose (1986) described mysis I and II and an early postlarva (which, because of lack of setae on the pleopods, we call mysis III) from the Indian Ocean. He tentatively identified it as *Atypopenaeus stenodactylus*. However, these larvae resemble our *Metapenaeopsis palmensis* and differ from our *A. formosus* in the following important characters: rostrum length and shape (long and curved); the presence of a serrated anteroventral carapace margin; telson spine formula (7+7 for mysis I, 7+1+7 for mysis II and III) and abdomen spination (dorsal spines on the fourth, fifth, and sixth segments and lateral spines on the fifth and sixth segments). Although there are some differences between *M. palmensis* and the larvae described by Paulinose (1986), we feel that these larvae are not *Atypopenaeus* but most likely an unidentified species of *Metapenaeopsis*.

Most recently, Paulinose (1988) described mysis and postlarval stages of *Metapenaeopsis mogiensis*, *M. andamanensis*, and *M. barbata* from widely spread locations in the Indian Ocean. Unfortunately, genus and species were again assigned by comparison with known distributions of adult prawn species, and by linking substages based on similarity of appearance.

While the larvae have many similarities, there were two important characters missing from the *M. palmensis* described here, which Paulinose claims to be diagnostic for the genus: a dentate postero-inferior carapace margin, and serrated abdominal pleura. Given the large number of *Metapenaeopsis* species, these characters may vary within the genus.

Morphological Variation

The larval descriptions given in this study were based on a number of individuals sampled, where possible, from a number of spawnings. However, previous studies have shown that with the degree of intraspecific variation in morphology, hundreds of larvae from many spawnings should be examined, and each substage should be sampled several times to account for intramolt growth (Rothlisberg et al. 1983a; Jackson 1986). In this study, there was insufficient material for such exhaustive examination, and so the full range of variations may not be described.

Some morphological variation can be induced by environmental factors such as salinity and temperature (Jackson 1986), and the special environment of the laboratory may do the same. In an unsuitable laboratory environment, obvious deformities can occur (Rao and Kathirval 1973), and less extreme environmental conditions may result in more subtle morphological effects. Therefore, while in this study much emphasis has been placed on laboratory rearing as a means of ensuring correct larval identification, more work is needed to discover to what degree laboratory-reared larvae differ from those in the natural environment. Differences between field-caught and laboratory-reared larvae have been found for the carid shrimp *Pandalus jordani* (Rothlisberg 1980), both in morphology and in the number of substages.

While many workers have searched for taxonomic characters to separate species of penaeid larvae within genera, they have generally been unsuccessful (Cook 1966b; Cook and Murphy 1971; Courties 1976). The only reliable way of distinguishing species of larval penaeids is to make a discriminant analysis of a number of morphological characters (Rothlisberg et al. 1983a; Jackson 1986). Discriminant analysis is less successful for postlarvae, and a technique based on electrophoresis is being developed (Lavery and Staples in press). The descriptions presented in this study are therefore of limited value in species identification.

Keys to the Genera of Larval Penaeids

The genera *Penaeus, Metapenaeus, Parapenaeopsis, Parapenaeus, Trachypenaeus, Metapenaeopsis, Atypopenaeus, Penaeopsis, Funchalia, Trachypenaeopsis, Sicyonica, Aristaeomorpha*, and *Solenocera* are included in Paulinose's (1982) key to penaeid larvae. Reconstructions of larval series from plankton collections were used as reference material for most of the genera. The protozoea key uses the length of the rostrum, the distribution of dorsal abdominal spines and the number of telson setae without qualifying these characters according to the substage. Most protozoeae would not be identified correctly because protozoea I does not have a rostrum; only protozoeae III have dorsal abdominal spines; and telson spines in *Penaeus, Trachypenaeus, Parapenaeopsis, Macropetasma*, and *Parapenaeus* vary in number between protozoea II and protozoea III. In the mysis key, *Atypopenaeus* are identified by a telson setal formula of 7+1+7, although the present study shows *A. formosus* has 7+7. *Metapenaeopsis* mysis larvae are said to have the pleura of the first five abdominal segments serrated ventrally, a characteristic not found in *M. palmensis* in the present study.

This is the first generic key for the Indo-west Pacific penaeid larvae that relies on descriptions of laboratory-reared larvae. Relying on laboratory rearings restricted the number of descriptions and species available for reference, but we feel this was justified by the improved precision obtained. In the present study, it was not possible to include *Funchalia, Heteropenaeus, Penaeopsis*, or *Trachypenaeopsis*, as no laboratory-reared larvae of these genera have been described. Owing to their rarity, the omission of three of these will have little effect on the practical application of the key. The fact that *Penaeopsis* is not included is more unfortunate since this genus is relatively abundant (Dall et al. in press). The key will be enhanced when larvae from the above genera are reared, as well as more species of *Atypopenaeus, Metapenaeopsis, Parapenaeopsis, Parapenaeus*, and *Trachypenaeus*. We have reared several species of *Trachypenaeus* and are preparing descriptions of *T. fulvus* larvae to compare with other *Trachypenaeus* species in our reference collection.

ACKNOWLEDGMENTS

Studying marine larval ecology and physiology is difficult: laboratory studies, requiring larval culture, are only now becoming routine, and field studies are fraught with taxonomic and sampling problems. Combined laboratory and field studies that provide real insight into the factors that affect larval distribution, abundance, and survival are that much more difficult and rare. Dr. Reuben Lasker and his group were pioneers and pre-eminent in this integrated approach. Taxonomic studies such as the present work are the basis for such research, which is only now beginning on tropical penaeids. We dedicate this paper to Reuben's inspiring example.

Many people assisted in larval rearing, including A. Chamberlain, R. Coles, P. Crocos, S. Frusher, D. Gwyther, G. Mawhinney, A. Ness, J. Salini, I. Somers, C. Tanakani, T. Wassenberg, and I. Zagorskis. Larval specimens were provided by M. Autrand, N. Hicks, H. Kurata, A. Lawrence, H. Motoh, J. Racovolis, L. Smith, and K. Yasuda. We also thank W. Dall, F. R. Harden Jones, V. Mawson, and D. Staples who provided helpful criticism of the manuscript.

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