THE LARVAL STAGES OF THE HARLEQUIN SHRIMP, *HYMENOCERA PICTA* (DANA)

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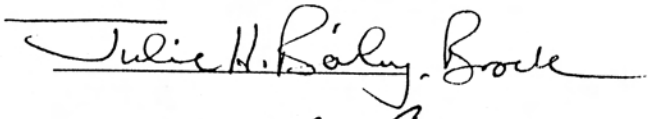

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Of course, the members of my committee deserve special "mahalos" for their patience and guidance, especially my committee chair, Ernie Reese.

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ABSTRACT

Larvae of Hawaiian *Hymenocera picta*, the harlequin shrimp, were successfully reared in the laboratory using mass culture techniques. At rearing temperatures in the 25° to 27° C range, larvae reached competence at approximately five weeks of age. Twelve zoeal stages and the first post larval stage were collected and described. Features illustrated include rostrum, maxillipeds, pereiopods, pleopods, and telson. A reasonably steady growth rate of carapace length was observed over all stages. Zoeal stages were observed in increasing, overlapping age ranges. *H. picta* larvae develop in a fashion similar to those previously described in the Palaemonidae, with the exception noted in the appearance of a developed periopod five. The stage one larvae bear a striking resemblance to first stage larvae of *H. picta* from the western Indo-Pacific and *Gnathophyllum americanum* both described by another author. Morphological evidence from the described larval *H. picta* provide supports for their recent inclusion in the Palaemonidae, but provides inconclusive evidence for the separation from the current subfamily Gnathophyllinae.

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CHAPTER 1
INTRODUCTION

Harlequin shrimp (*Hymenocera picta* Dana) are small (<5cm T.L.) decapods found throughout the tropical Indo-Pacific and the Red Sea (Debelius, 1986; Titgen, 1989). *H. picta* are classified as such: Superclass Crustacea, Order Decapoda, Suborder Natantia, Tribe Caridea, Family Palaemonidae. They have been recently placed in the Palaemonidae by Bruce (1986; 1988) based on their larval characteristics. Bruce therefore separated them from the family Gnathophyllidae, of which they were previously considered members (Holthuis, 1955; Shram, 1986).

These animals are easy to maintain and apparently exist solely on a diet of asteroid Echinoderms, including the well known "Crown of Thorns" starfish. Adult harlequin shrimp eat the viscera and ambulacra of their prey, often amputating an arm in the process. Harlequin shrimp have also been described as monogamous (Seibt & Wickler, 1979) and they are almost always found in pairs or singly in the field. They occur at depths of 1 to 30 meters. Their hardiness, bright colors, and apparent scarcity make them highly sought after by aquarists throughout the world.

Hymenocera picta molt every 18 to 26 days. Females produce a clutch of 100- 5000 eggs immediately after each molt, provided fertilization occurs (Seibt & Wickler, 1979; Kraul & Nelson, 1986). The eggs mature and hatch in approximately 17 to 24 days. *H. picta* larvae emerge as zoea and are released into the water column where they are planktotrophic. Previous rearing of larvae indicate that harlequin shrimp settle 5-7 weeks after hatching (Kraul & Nelson, 1986). The larvae may also orient to starfish (*Linckia multifora*) during settlement (Kraul & Nelson, 1986).

There are two color forms of *Hymenocera picta* that appear to have geographically distinct distributions. The red/maroon form is known from the Hawaiian Islands, while the blue/brown form is known from the Western Indo-Pacific and Red Sea. The color of shrimps from the Eastern Pacific (Panama & Costa Rica) is not mentioned in literature (from Glynn, 1981 & 1984). Debelius (1984) believes that these two are separate species and has termed the blue form as *Hymenocera elegans* Heller, and the red form as *H. picta*. There is no morphological basis for this separation, except for color, and further work needs to be performed to ascertain the relationship (Chace and Bruce, 1993). Comparison of the morphologies of larvae, as well as adults, could be used to address this question.

The first goal of this project is to successfully rear newly hatched *H. picta* to settlement and describe the larval stages. Previous rearing work did not thoroughly

document any individual stages (Kraul and Nelson, 1986), so this knowledge might prove valuable to future culture efforts. The second goal is to clarify the taxonomy of *Hymenocera picta* and related groups, based upon the larval stages. This could be of some systematic assistance in not only differentiating the two color forms, but the genus' overall taxonomic position. Although Bruce (1986) described the first larval stage of *H. picta* hatched from a female caught off the coast of Kenya, this is the blue color form, not examined in the current study. The added information of all the zoeal stages may further enhance what was previously assumed from only the first larval stage

CHAPTER 2
METHODS

Adult harlequin shrimp were obtained from the field using SCUBA and from local pet stores during 1990, 1991, and 1992. All animals were taken from waters surrounding the island of Oahu in Hawaii. Harlequin shrimp pairs and single individuals were maintained in 10 to 15 gallon glass aquaria with undergravel filtration systems. The adult shrimp were fed the sea star *Linckia multifora* such that food was available at all times. Water in the aquaria was changed upon a weekly or biweekly basis. Typically, the eggs of gravid shrimps were first examined on 18th day after a female's molting & mating event. If the color of the eggs was a light greyish brown, hatching was reliably predicted within a 24 hour period. As expected, hatching time varied with temperature. Ripe females were then carefully transported to a larval rearing tank, a 120 liter, slate-blue or black plastic trash can, in some efforts, and a 1200 liter tank in later trials. The female remained in lightly aerated sea water until the entire clutch was judged to have hatched. The female was then returned to her mate so additional breeding could occur. Clutches that were, inadvertently, not hatched in the rearing tanks were siphoned from aquaria using a turkey baster and flashlight.

All larval rearing was performed at the Hawaii Institute of Marine Biology, in Kaneohe on the island of Oahu. Larvae were maintained in the larval rearing tanks with filtered sea water for rearing purposes. Upon hatching, live foods were introduced into the tanks on a daily basis. Initial trials, in 1990, were conducted with the smaller larval rearing tanks, under various conditions varying both the rearing temperature and frequency of water changes. This was done to determine a suitable rearing method. More success was attained using the larger, 1200 liter rearing tanks indoors. Beginning in March 1991, nearly all trials (n=13) were conducted indoors at water temperatures between 26-30° C. Temperature was regulated via 100+ Watt submersible heaters. Light, steady aeration was provided at all times and sea water was changed as needed.

Several different feeding regimes were used during larval rearing. Previous work (Kraul & Nelson, 1986) suggested the use of rotifers and copepod nauplii in initial stages followed by newly-hatched *Artemia* nauplii until settlement. Newly hatched nauplii of *Artemia spp*. were the major component of the diet in nearly all rearing trials, and larvae were successfully reared with it alone. The other food items used in addition to *Artemia* nauplii did not appear to enhance the survival of *Hymenocer picta* larvae reared for this work. These other items include mass concentrations of phytoplankton (*Chaetoceros sp,*

Isochrysis sp. & Tetraselmis sp.), rotifers (*Brachionus plicatilis*) minced crab and bivalve, and <275-μm zooplankton collected from Kaneohe Bay via plankton net.

Larval morphology of live animals was initially examined using dissecting and light microscopes. Larvae were placed in a petri dish in 1 cm water depth or a on well slide and observed. Larvae were then preserved in 10% buffered formalin if a perceived change in morphology was noted. Preserved larvae were later examined with both types of microscopes. Since there were few later stage larvae, dead animals were frequently preserved to reduce the number of live animals sacrificed. A drawing tube on a Nikon compound microscope and a camera lucida mounted on a Wild dissecting scope were used to illustrate the larvae and their appendages at different developmental stages. Drawings of larval morphology are presented for animals of 13 stages. Illustrations for each stage were, for the most part, made from one specimen. Features illustrated were verified on other specimens from the same zoeal stage when possible. The carapace length of specimens was also recorded by measuring the shortest distance between the anterior tip of the rostrum, to the mid-dorsal, posterior margin of the carapace.

CHAPTER 3
RESULTS

General Information

Twelve larval stages and the postlarval settlement stage were collected. The mean carapace lengths of each are indicated in figure 1. The data for stage five was omitted, as the condition of the single specimen did not lend itself to proper measurement. The number of specimens measured is include on the figure. The growth of the carapace over the progression of larval stages is evident.

The ranges of age for each larval stage are presented in figure 2. Data for this graph were taken only from rearing trials that were performed in the most common temperature range employed, 25° to 27°C. Metamorphosis to the postlarval stage was first reached at 34 days of age under these conditions. It should be noted that under higher temperature regimes (28° and above) metamorphosis and settlement was observed in 28 day old larvae. However, none of the postlarvae in those efforts survived past one week. There is a high degree of overlapping ranges, especially in the later stages. The general trend for upper and lower range of age is upward, with each stage. The data for the postlarval stage does not take into account the termination of this stage by a molt, but rather the range of ages at which new postlarvae were observed in the rearing tank.

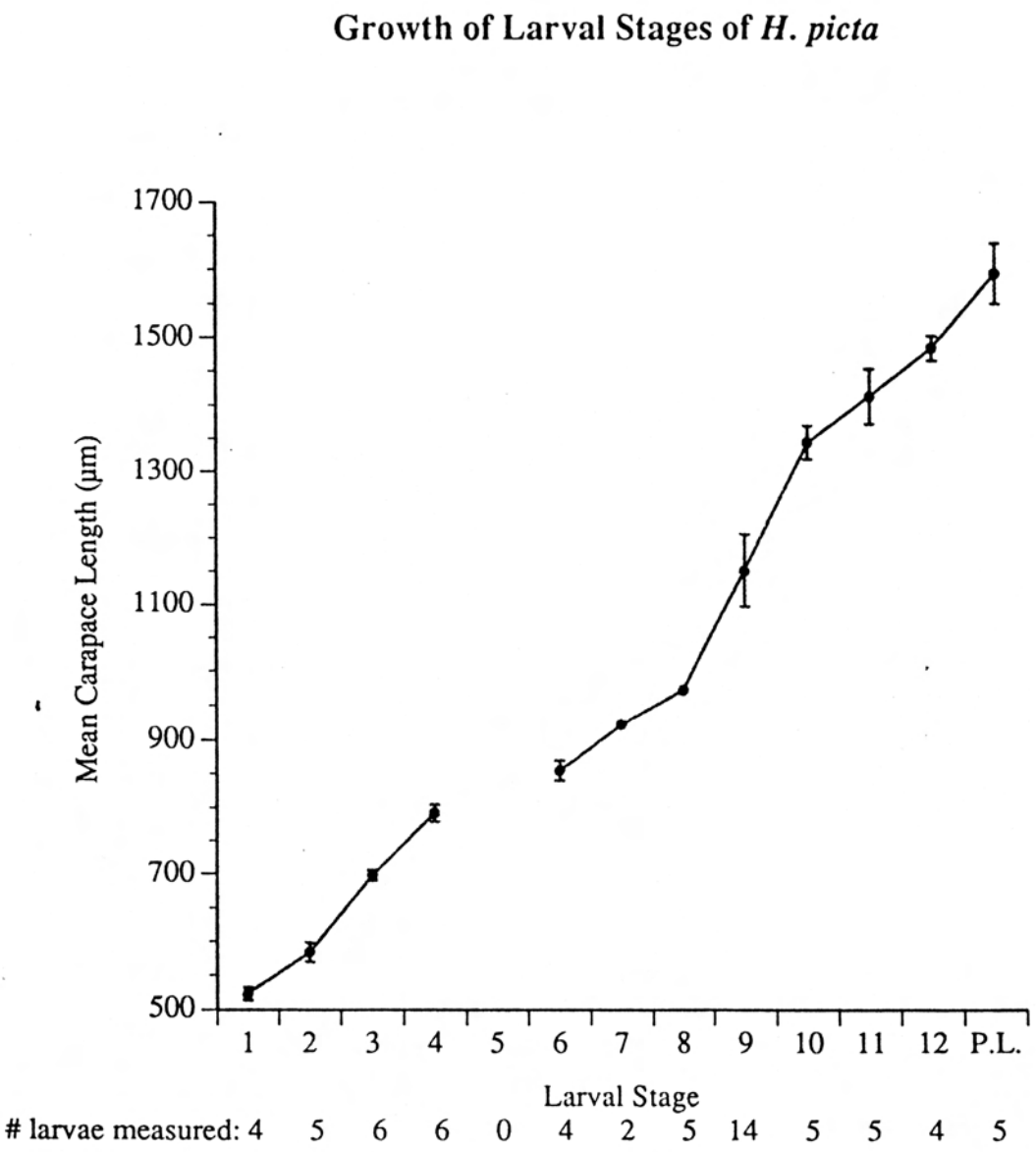

Figure 1. Mean size of each larval stage is plotted. Ranges given are plus/minus one standard deviation. Sample size is listed under the stage numbers on the x-axis.

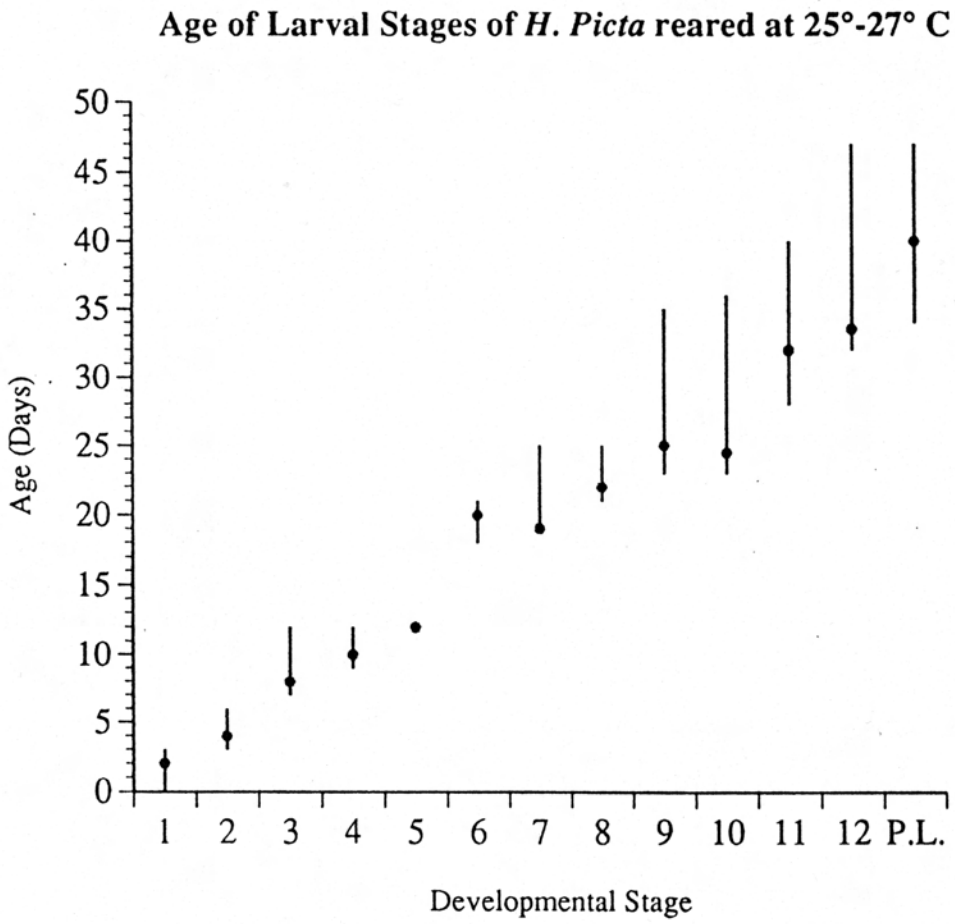

Figure 2. Age ranges of each larval stage for rearing performed between 25°-27°C. Points in the ranges are median age collected for the stage. Data for postlarvae only include age of first appearance.

Larval Descriptions

The illustrations for the following descriptions are grouped by stage in figures 3-16, with the exception of the tail illustrations (figure 16) which are presented together, so that the progression of development can be more easily seen.

Zoea 1 (Description refers to figures 3 & 31)

Carapace: No spines present. Simple rostrum that is nearly straight, only slightly down curved. Rostrum is without serrata or setae on either dorsal or ventral margin. Four globular structures, presumably oil droplets, are visible under the dorsal carapace.

Eyes: Sessile.

Antennule: Consists of an unsegmented peduncle, with two processes. The inner (medial) process is a simple plumose flagellum, with a medially curved termination. The outer (lateral) process is shorter (0.3 the length of inner flagellum) and more robust with five processes: 4 lateral asthetascs and 1 inner setose seta.

Antennae: Biramous appendage with broad, flattened exopodite and narrow inner endopodite. The endopodite is slightly shorter than the exopod, with a short spine and a nearly terminal plumose seta, 0.6 the length of the endopod. The exopod has at least 3 distal segments, one small lateral seta and 10 other plumose setae from the disto-lateral portion to the proximo-medial margin.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Biramous appendage; endopod a single tapering segment with two distal setae; exopod natatory, with four terminal plumose setae; protopod with 3 inner spines.

Figure 3. *Hymenocera picta*. first zoeal stage. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3, h: rudiments of pereiopod 1&2. Scale bars: a; c&d; e, f, &g=250μm. b=1mm.

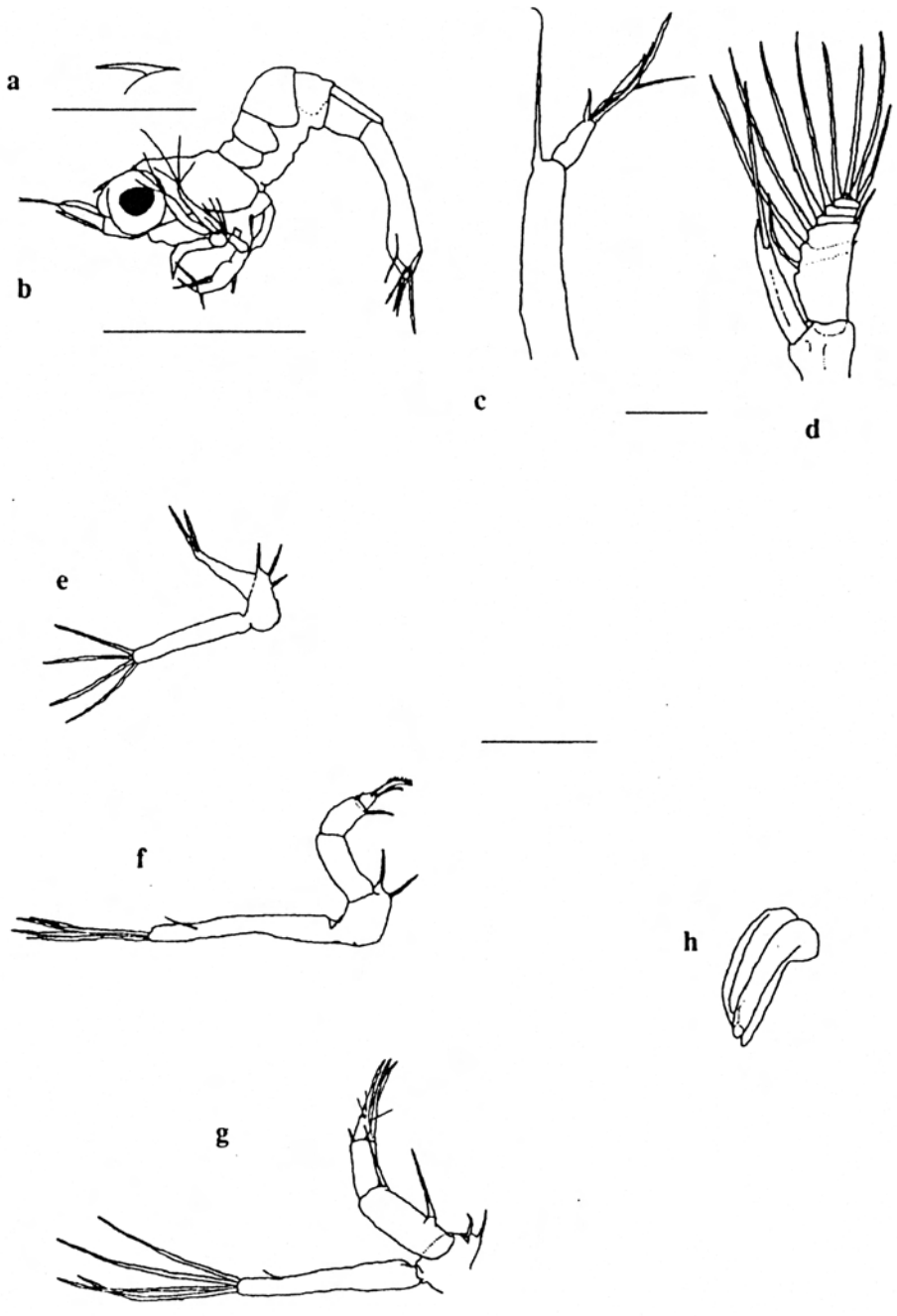

Figure 3. Stage 1.

Maxilliped 2: Biramous appendage; endopod with 3 segments, second segment with a short distal spine and one distal seta, terminal segment smallest, with one long, setose, distal spine, and two smaller spines; exopod like that of maxilliped 1, but larger and with a single seta near distal end; protopod with at least two spines.

Maxilliped 3: Biramous appendage; endopod with 3 segments, proximal segment with 2 strong medial spines, second segment with two large distal spines, distal segment with one large setulose spine and 3 smaller spines; exopod natatory, like previous example, but with one seta near the distal terminus; protopod with two spines.

Pereiopods 1&2: Both represented here as biramous buds only, with the other pereiopods (3, 4, & 5) absent.

Telson: (Figure 31a) Triangular & spatulate, with slightly concave distal margin. Possesses seven pairs of plumose setae. No exopods present.

Color: Translucent red-brown. Ingested food items, especially *Artemia spp*. can be seen in the digestive system. Essentially similar throughout all larval stages.

General behavior: Larvae at this stage swim head-down, with the telson oriented up and outward in the direction of motion, which is mostly in the ventral direction. This trend continues through to the postlarval stage. The maxilliped exopods appear to provide most of the propulsion, beating rapidly back and forth. Frequently, a flick, or quick horizontal movement is observed. This motion appears to be generated by the telson and may be an escape or feeding response. Another motion noted is spinning, horizontally, for a few seconds. Maxillipeds can be seen to flex and unflex, especially during prey capture where they grasp the food item while the animal masticates it with the smaller mouthparts. Larvae are strongly positively phototactic.

Zoea 2 (Description refers to figures 4 & 31)

Carapace: Small, single supraorbital spine present. Simple rostrum that is nearly straight, only slightly down curved. Rostrum is without serrata or setae on either dorsal or ventral margin, but a shallow protrusion noted on most proximal portion above the carapace.

Figure 4. *Hymenocera picta*. second zoeal stage. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3, h: pereiopod 1, i: pereiopod 2, j: pereiopod 3 bud. Scale bars: b=1mm. a=250μm. c-g=250μm for remaining bar.

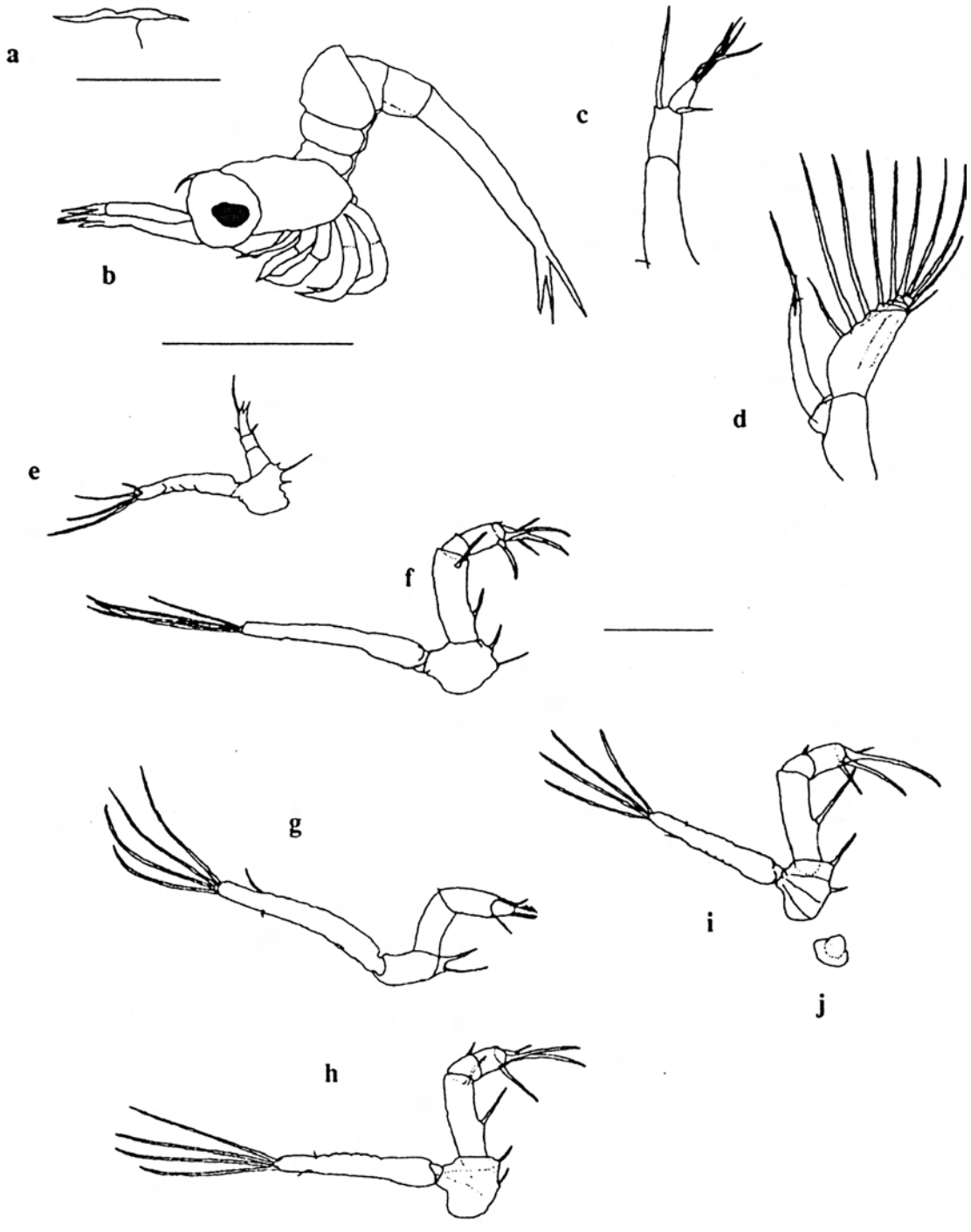

Figure 4. Stage 2.

Eyes: Stalked.

Antennule: Consists of singly segmented peduncle, with three processes on the second, most distal segment. The inner process is a simple plumose flagellum. The large outer process is shorter and more robust with four processes, 4 lateral asthetascs. The third process originates at the base of the second process and is somewhat plumose.

Antennae: Biramous appendage with broad, flattened exopodite (scaphocerite) and narrow inner endopodite (antennal flagellum). The endopodite has two segments, the distal with two processes: one a short spine with two plumose flagella, the other a long spine half the length of the segment. The exopod has at least 3 distal segments and 10 other plumose setae from the disto-lateral portion to the proximo-medial margin.

Mandible: Not shown.

Maxillula: Less symmetry than previous stage and very complex.

Maxilla: Not shown.

Maxilliped 1: Biramous appendage; endopod three tapering segments, with three distal setae and two basal setae on the terminal segment; exopod natatory, with four terminal plumose setae; protopod with 3 medial spines. All natatory exopods in this stage possess two small setose spines near the terminus of the appendage, but it isn't shown in all illustrations.

Maxilliped 2: Essentially identical to that in stage 1.

Maxilliped 3: Very similar to previous stage, with the addition of one segment to the endopod. Biramous appendage. Endopod with 4 segments: proximal segment with 2 strong medial spines, second segment small and unadorned, third segment with two large distal spines, distal segment with one small basal and one large setulose spine adorned with two spines located about half the distance of the segment. Exopod natatory, like previous example. Protopod with two medial spines.

Pereiopod 1: Biramous appendage. Endopod with 4 segments: proximal segment with 2 strong medial spines; second segment small with one small lateral spine; third segment with two large distal spines; distal segment with one large setulose spine adorned with one spine near proximal portion. Exopod natatory, as before. Protopod adorned with 2 medial spines.

Pereiopod 2: Similar to Pereiopod 1. Exceptions are that the proximal endopod segment appears to have only one, very large medial spine.

Pereiopod 3: Represented here as a small, nearly biramous bud, barely evident.

Pereiopod 4 & 5: Not visible or present at this stage.

Telson: (Figure 31b) Same as in stage one. Rudiments of future uropod exopods often seen in some specimens.

General behavior: Essentially the same as in previous stage, except that the newly appeared 1st pereiopod contributes to feeding and locomotion, as the maxillipeds do.

Zoea 3 (Description refers to figures 5 & 31)

Carapace: No significant change from stage 2.

Eyes: No significant change from stage 2.

Antennule: Consists of peduncle of 3 segments, with three processes on the third, most distal segment. The inner process is, again, a simple plumose flagellum. The large outer process is shorter and more robust with four processes, 4 lateral asthetascs. The third process is the antennular lobe, dorso-lateral to the inner plumose flagellum. There are five feathered setae originating at the antennular lobe. There are several other plumose setae found on this appendage at this stage. Four large plumose setae are seen on the medial and distal margins and several smaller ones, mostly on the distal margins fringing the segment junctions. The proximo-lateral base of this appendage bears the beginnings of the stylocerite, as well as a single plumose seta.

Figure 5. *Hymenocera picta*. third zoeal stage. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3, h: pereiopod 1, i: pereiopod 2, j: rudiments of pereiopods 3-5. Scale bars: b=1mm; a, c&d=250μm; e-j=250μm for scale bar adjacent to i.

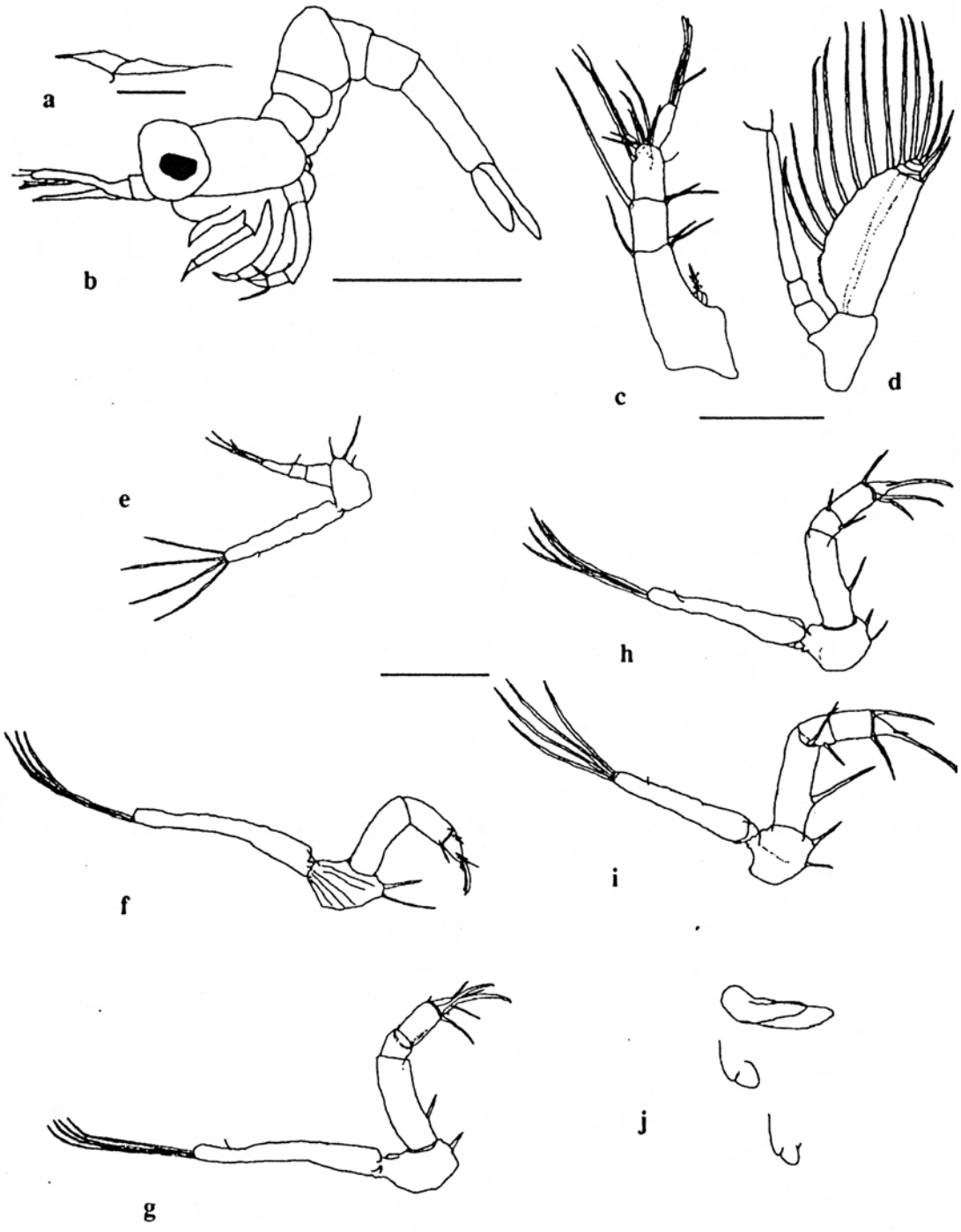

Figure 5. Stage 3

Antennae: In this stage, the anntennal flagellum has 3 clear segments, terminating in two very small flagella on the long distal segment. The scaphocerite bears 13 plumose setae from the disto-lateral portion to the proximo-medial margin. The scaphocerite still displays at least 3 distal segments.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Endopod similar to previous stage, except that the terminal segment possesses three distinct distal setae and two basal setae; second segment with a single small disto medial seta. Natatory exopod essentially same as in previous stage.

Maxilliped 2: Essentially identical to that in stage 2, except for the appearance of at least three additional spines on the terminal spine (segment).

Maxilliped 3: Identical to the previous stage, except for the appearance of two additional small spines on the terminal segment. Some features were occluded in this specimen.

Pereiopod 1: Similar to that in stage 2. Endopod segments show the addition of 2 spines. The first, a third large spine on the distal margin on the third segment. The second is a an additional spine on the distal margin of the second segment. Natatory exopod identical to previous stage.

Pereiopod 2: Similar to that in previous stage, with addition of three spines on the endopod. As in pereiopod 1, a single large spine is added to the third segment and a smaller spine on the distal margin of segment two. The third additional spine is found on the proximal margin of the second segment. Similar to Pereiopod 1. Exceptions are that the proximal endopod segment appears to have only one, very large medial spine.

Pereiopod 3: Represented here as a larger, biramous bud, compared to that found in the previous stage.

Pereiopod 4 & 5: Barely visible as small, perhaps biramous buds at this stage.

Telson & uropods: (Figure 31c) Telson still heart-shaped, but with 5 pairs of large plumose setae, and one pair of very small seta. Biramous uropods evident. Endopod unadorned, mostly occluded by the telson. Exopod if nearly twice the length of endopod with 6 plumose setae.

General behavior: Similar to the previous stage, with the addition of the 2nd periopod.

Zoea 4 (Description refers to figures 6, 7, & 31)
Carapace: No significant change from stage 3, except that rudiment of first rostral spine is evident.

Eyes: Appear less ovoid than in previous stage, almost bi-partate. Compound lens section somewhat separate from medial portion of eye.

Antennule: Very similar to that in stage 3. The inner process of the terminal segment is much larger, nearly the same length as the lateral process. One additional large plumose seta on the medial margin of the second segment evident. Smaller plumose setae are more prominent along junctions of segments 1&2 and 2&3. Stylocerite, increases in prominence in this stage.

Antennae: In this stage, the anntennal flagellum has 4 clear segments, terminating in four very small flagella on the long distal segment. The scaphocerite bears 17 plumose setae from the disto-lateral portion to the proximo-medial margin and a short spinous process at the disto-lateral extremity. The scaphocerite has no obvious segmentation.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Identical, with the exception of a single additional spine on the proximal portion of the third segment of the endopod.

Figure 6. *Hymenocera picta*. fourth zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c-g=250μm for scale bar above.

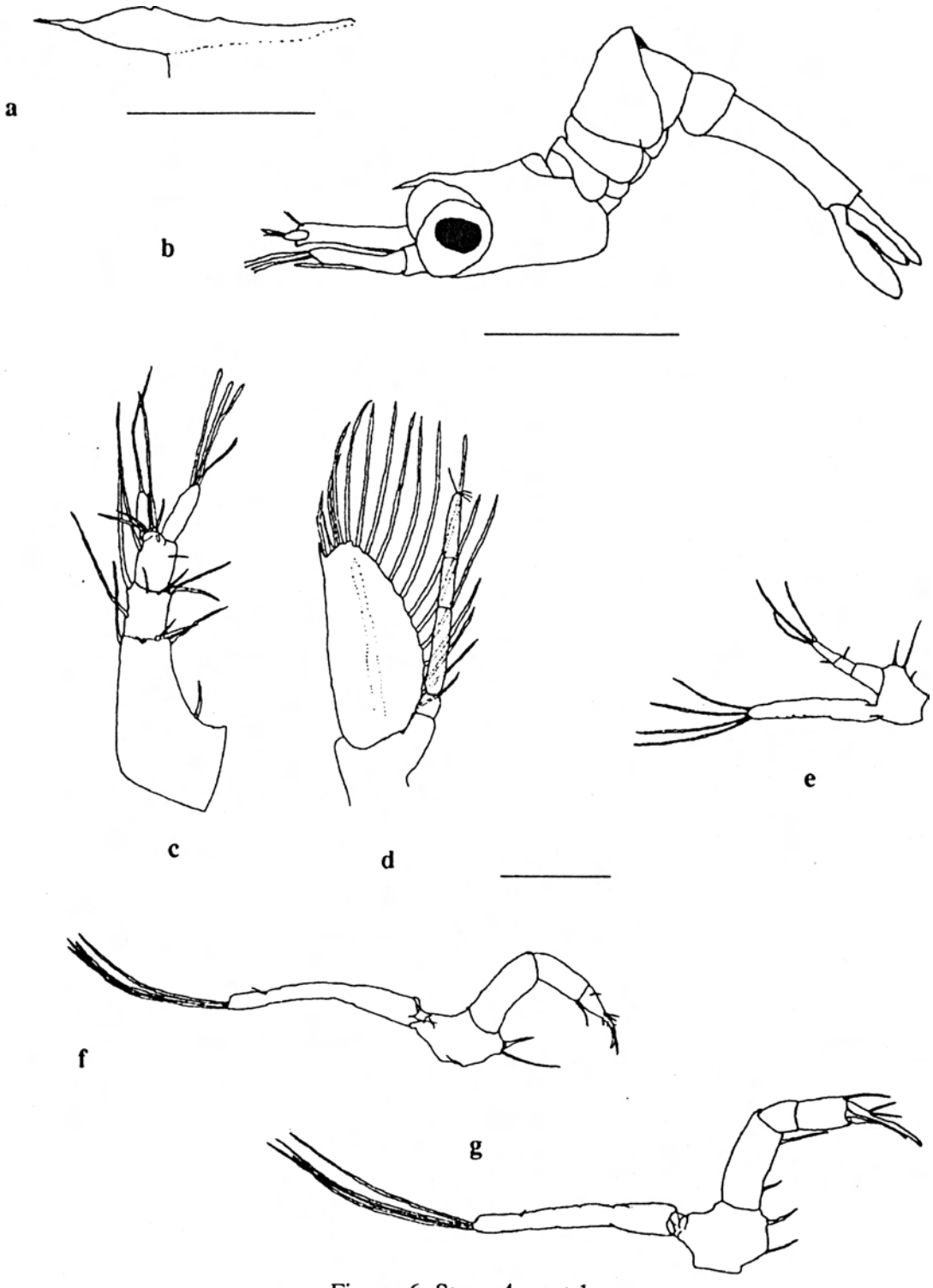

Figure 6. Stage 4, part 1

Figure 7. *Hymenocera picta* zoeal stage 4, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3, d: rudiments of pereiopods 4&5. Scale bar: a-d=250μm.

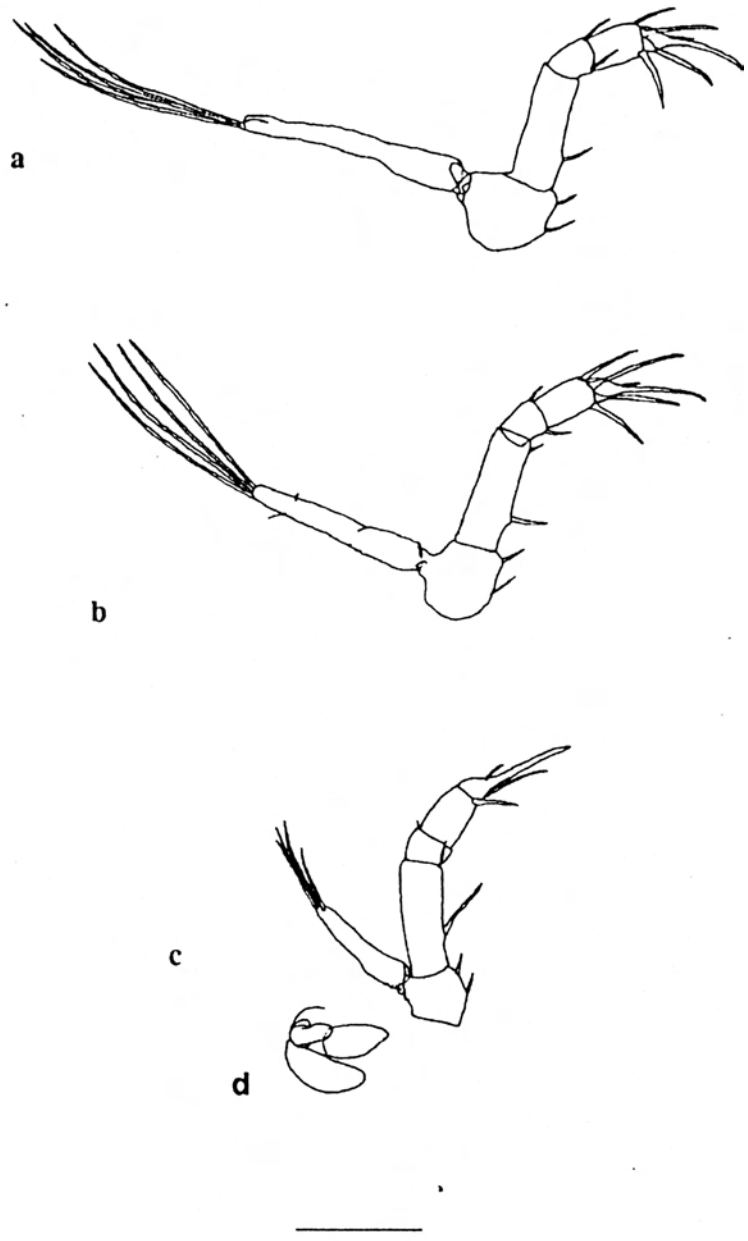

Figure 7. Stage 4, part 2

Maxilliped 2: Essentially identical to that in stage 3.

Maxilliped 3: Essentially identical to that in previous stage, except for the addition of a single large spine on the distal portion of the first segment of the endopod. Some features were occluded in this specimen.

Pereiopod 1: Similar to that in stage 3, except for the addition of a fourth large spine on the distal margin on the third segment.

Pereiopod 2: Similar to that in stage 3, except for the addition of a fourth large spine on the distal margin on the third segment and a small spine on the distal portion of the first segment.

Pereiopod 3: A developed, biramous appendage in this stage. Endopod with four segments; one small and one large medial spine on the distal-medial and proximo-medial portions (respectively) of first segment; one small spine on the disto-lateral margin of the second segment; two large on the distal margin of third segment; fourth segment a large, strong spine, with one small accessory spine. Exopod is reduced, but natatory as in other appendages.

Pereiopod 4: A large, biramous bud.

Pereiopod 5: A large, uniramous bud, closely associated with pereiopod 4.

Telson & uropods: (Figure 31d) Both distinctly more developed than in previous stage. Telson is now more elongate with very little tapering of width from the concave distal to the proximal margin; distal margin with 3 pairs large and 1 pair small plumose setae; length of setae much reduced, relative to telson length. Uropod protopod distinct; endopod approximately 2/3 length of exopod, with 8 plumose setae distributed from lateral to medial margins; exopod extends just beyond telson margin, with 11-12 large and 1 small plumose seta; both exopod and endopod display several very small plumose setae anchored on dorsal and ventral surfaces.

General behavior: Similar to that seen in the first stage, except for the added contribution of the 3rd pereiopod. Uropod occasionally seen to flex and unflex.

Zoea 5 (Description refers to figures 8, 9, & 31)
Carapace: Similar to stage 4, except that rostrum with more depth and now has one small spine.

Eyes: Similar to previous stage.

Antennule: Similar to previous stage with the addition of several setae and a well-developed stylocerite. Lateral process of distal segment with 4 asthetascs and 1 small seta. Several additional plumose setae on the medial margin of the first, second, & third segments evident. Stylocerite, increases in prominence in this stage, with at least 7 small plumose setae, medially & laterally.

Antennae: This is nearly identical to that in the previous stage, except that the anntennal flagellum now has 6 clear segments.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Essentially identical to that in previous stage. Spines missing or broken on lone damaged specimen.

Maxilliped 2: Essentially identical to that in stage 3.

Maxilliped 3: Similar to that in stage 4, except for the addition of a small spine on the distal margin of the second segment of the endopod.

Pereiopod 1: Similar to that in stage 4, except for the addition of a large spine on the distal margin of the first segment of the endopod.

Pereiopod 2: Essentially identical to that in stage 4.

Figure 8. *Hymenocera picta*. fifth zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c-g=250μm for scale bar above.

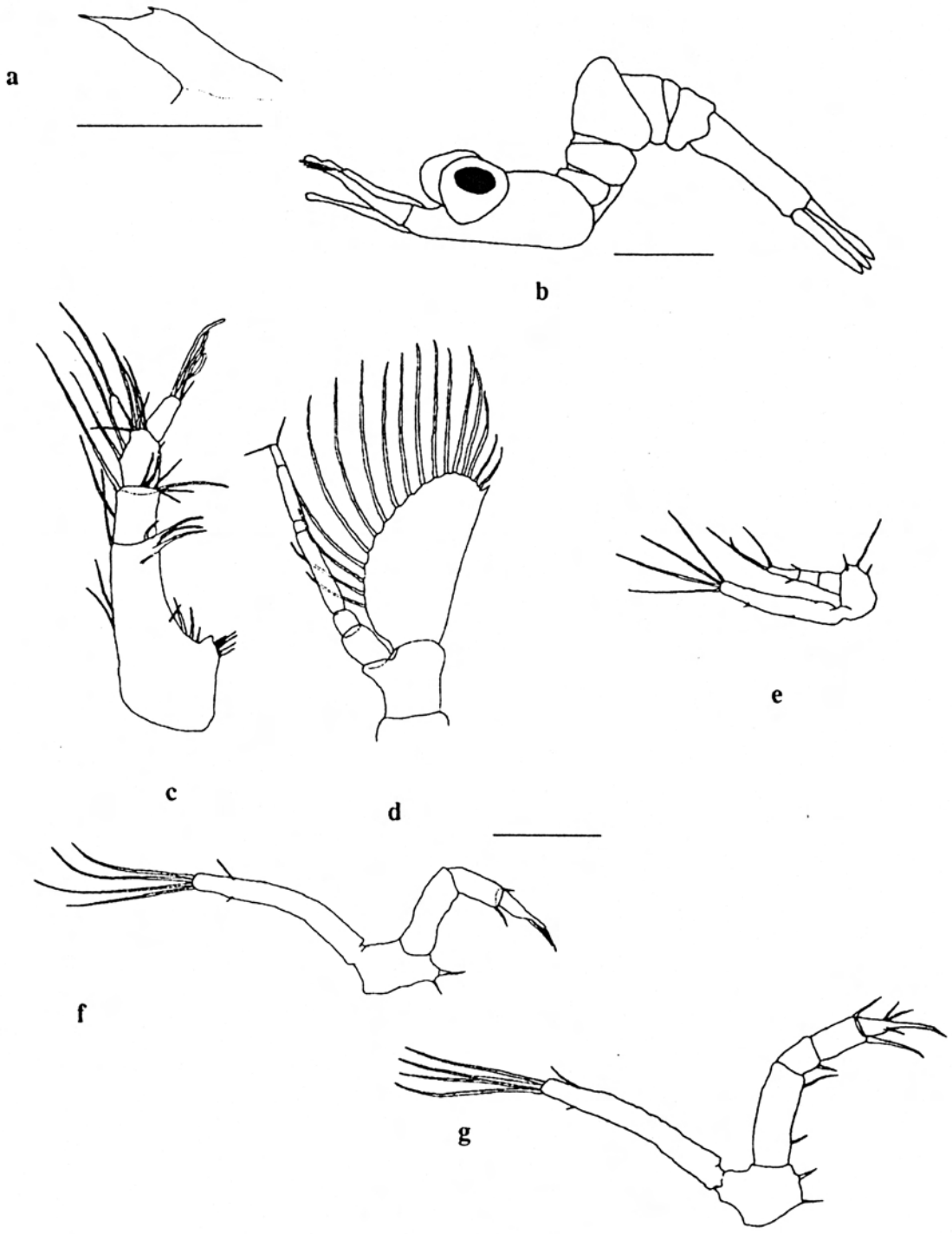

Figure 8. Stage 5, pt 1

Figure 9. *Hymenocera picta* zoeal stage 5, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3, d: pereiopod 4, e: left and right pereiopod 5. Scale bar: a-e=250μm.

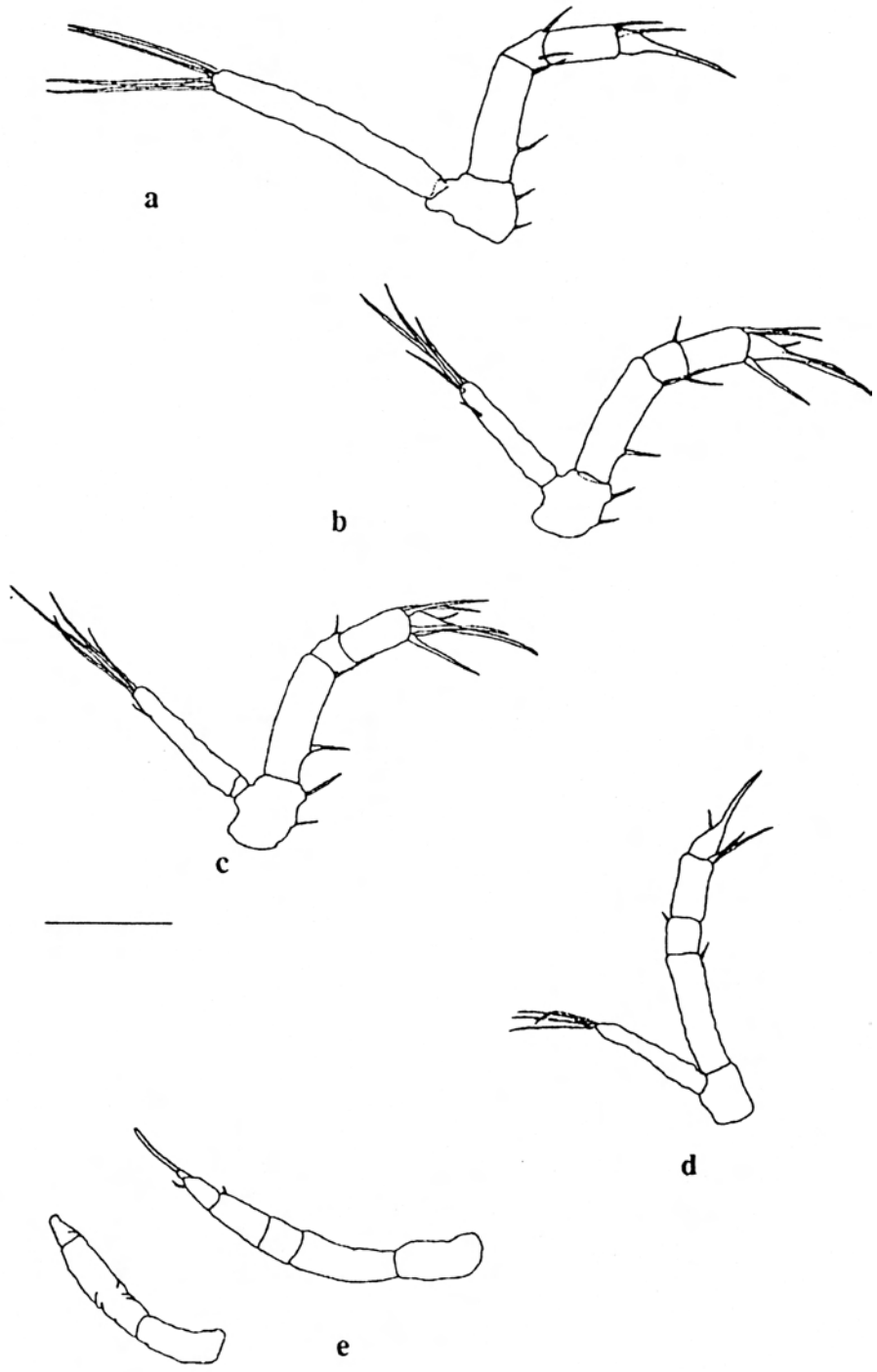

Figure 9. Stage 5, part 2.

Pereiopod 3: Very similar to that in the previous stage, except for the addition of a third spine on the distal margin of the third segment of endopod.

Pereiopod 4: A developed, biramous appendage. Endopod with four segments; one small spine on the distal-medial portion of first segment; one small spine on the disto-lateral margin of the second segment; two large on the distal margin of third segment; fourth segment a large, strong spine, with one small accessory spine. Exopod is reduced, but natatory as in other appendages.

Pereiopod 5: Single specimen shows two morphologies of this appendage. Left appendage with four segments, excluding protopod; third segment adorned with one small distal spine; fourth segment a strong spine adorned with a single small spine; protopod unadorned. Right appendage appears to be a large unadorned, three segmented bud; no protopod shown here.

Telson & uropods: (Figure 31e) Similar to that in stage 4, except that endopod & exopod of uropod are longer, compared to the telson; endopod extends, distally, out to the same distance as the exopod.

General behavior: Same as in previous stage, except for contribution of the last two pereipods.

Zoea 6 (Description refers to figures 10, 11, & 31)
Carapace: Similar to stage 5. Rostral spine appears more pronounced.

Eyes: Essentially identical to previous stage.

Antennule: Very similar to that of previous stage. Lateral process of distal segment with 3-4 asthetascs and 2 small setae.

Antennae: Scaphocerite is more elongate than in previous stage, tapering distally; scaphocerite with one additional plumose seta, bringing the total to 18. Antennal flagellum appears similar, but with some small accessory setae at segment junctions.

Mandible: Not shown.

Figure 10. *Hymenocera picta*. sixth zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c-g=250μm for scale bar above f.

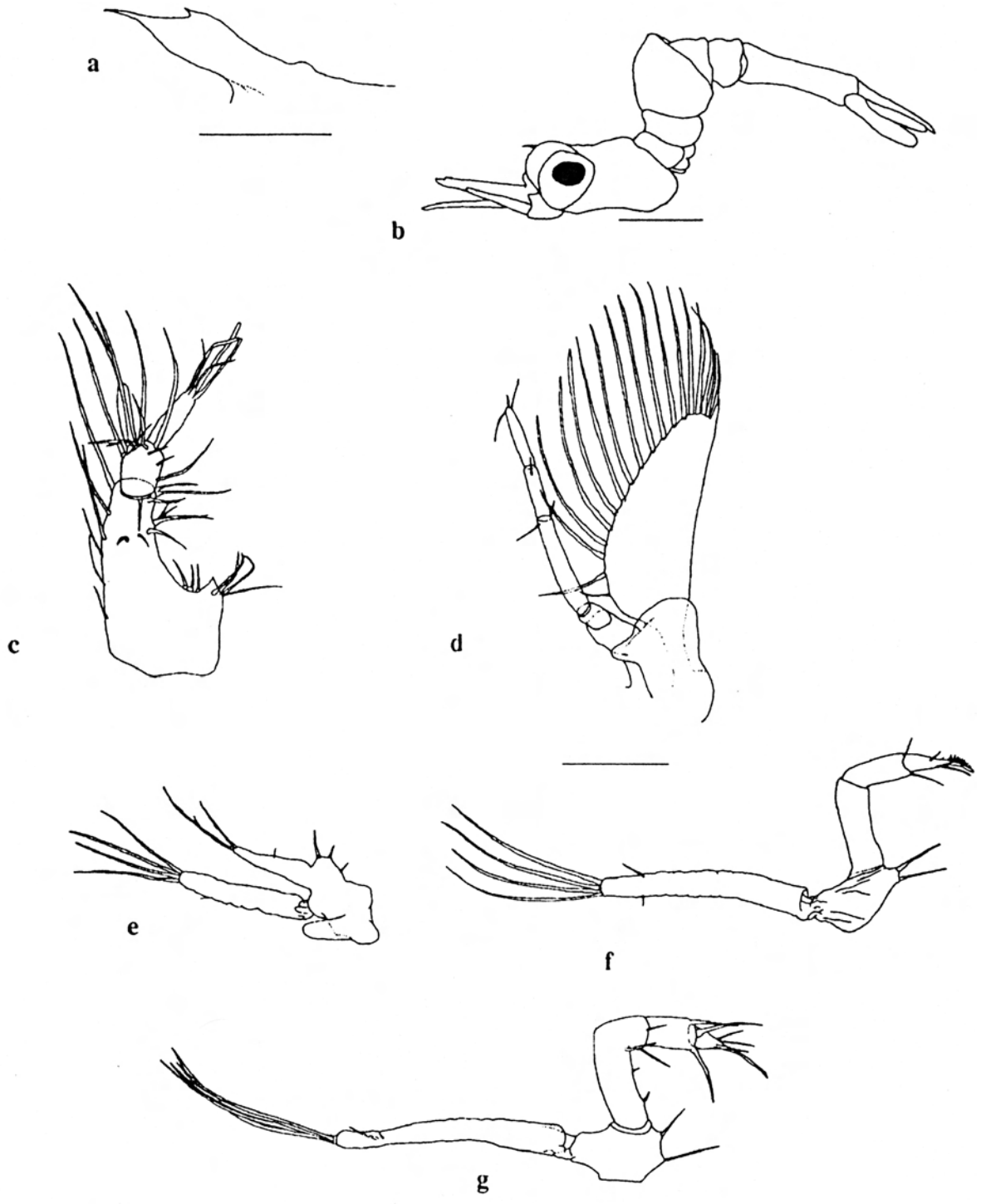

Figure 10, stage 6, part 1

Figure 11. *Hymenocera picta* zoeal stage 6, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3, d: pereiopod 4, e: pereiopod 5. Scale bar: a-e=250μm.

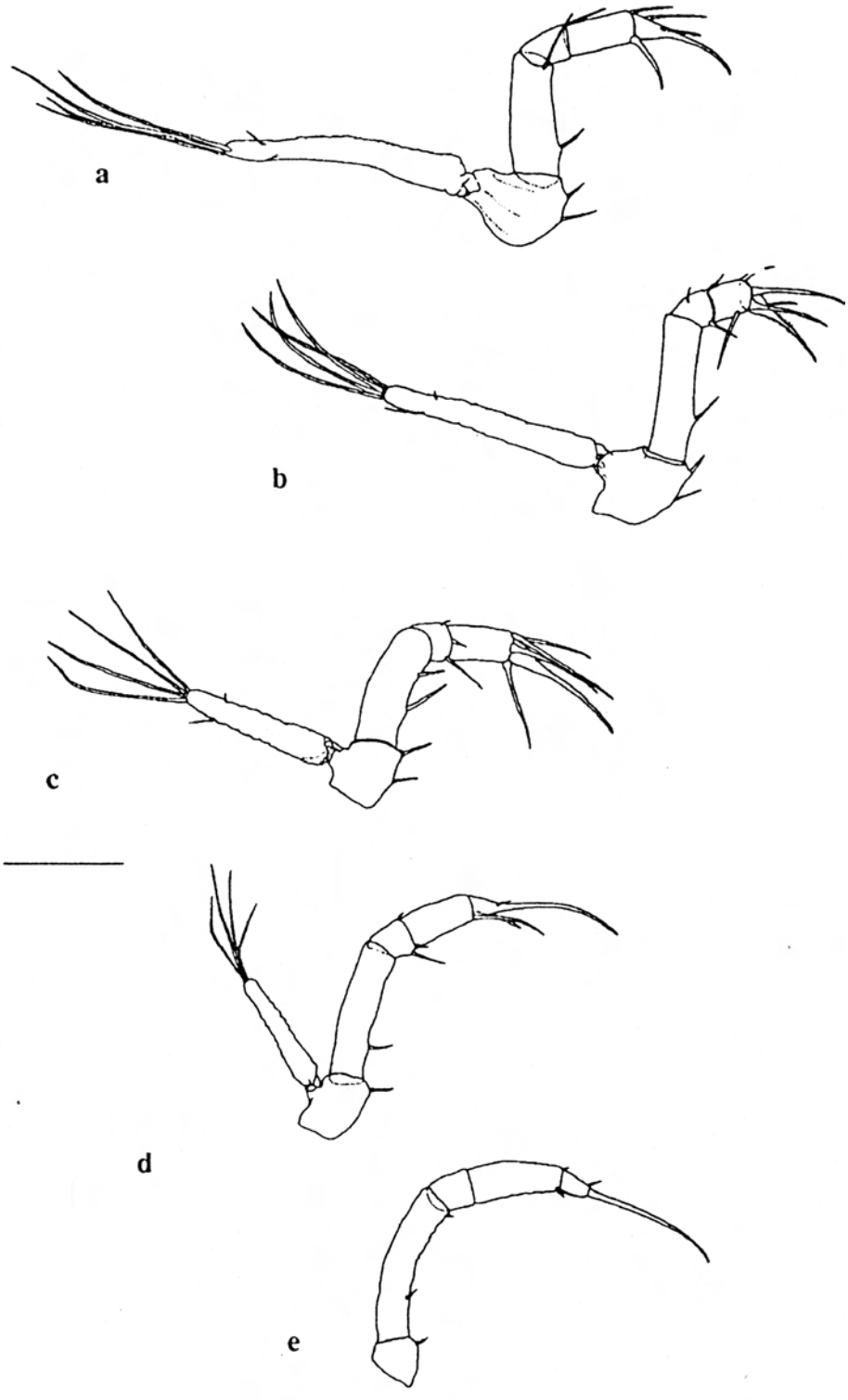

Figure 11. Stage 6, part 2.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Similar to that in previous stage. Segmentation of endopod is less apparent.

Maxilliped 2: Essentially identical to that in stage 5.

Maxilliped 3: Similar to that in stage 5, except for the addition of a small spine on the medial margin of the first segment of the endopod.

Pereiopod 1: Essentially identical to that in stage 5.

Pereiopod 2: Similar to that in stage 5, except that the exopod is longer in this stage.

Pereiopod 3: Similar to that in stage 5, with the addition of a single small spine on the medial margin of the first segment, distal of the large spine.

Pereiopod 4: Similar to that in stage 5, showing more development. Two small spines appear on the protopod. Endopod displays additional spines, as well. One spine is found on the first segment; the second segment is proximally tapered with two stout spines on the disto-medial margin.

Pereiopod 5: Similar to the developed appendage in previous stage, with no exopod. One small spine appears on the disto-medial protopod; first segment with two small spines on the medial margin. Other spines are as displayed in previous stage.

Telson & uropods: (Figure 31f) Similar to that in stage 5, except for the following exceptions. Second pair of spines on distal margin of telson reduced. Overall telson shape begins to taper, slightly, towards distal margin. Exopodite and endopodite of uropod begin to taper, slightly, towards proximal direction.

General behavior: Same as in previous stage, essentially. Basket of thoracic appendages very effective at capturing and holding live foods.

Zoea 7 (Description refers to figures 12, 13, & 31)
Carapace: Similar to stage 6. Rostral spine appears more pronounced.

Eyes: Similar to previous stage, except for a small crease appearing on the dorsal surface of the medial portion of the eye.

Antennule: Very similar to that of previous stage. Inner process of distal segment now with two flagella.

Antennae: Very similar to that in previous stage, with exception of a single additional plumose seta on the scaphocerite, bringing the total to 19.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Essentially identical to that in previous stage.

Maxilliped 2: Essentially identical to that in stage 6.

Maxilliped 3: Essentially identical to that in stage 6. Appendage drawn is less flexed than in previous stage.

Pereiopod 1: Essentially identical to that in stage 6.

Pereiopod 2: Essentially identical to that in stage 6.

Pereiopod 3: Essentially identical to that in stage 6.

Pereiopod 4: Essentially identical to that in stage 6.

Pereiopod 5: Essentially identical to that in stage 6.

Figure 12. *Hymenocera picta*. seventh zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c-g=250μm for scale bar between c&d.

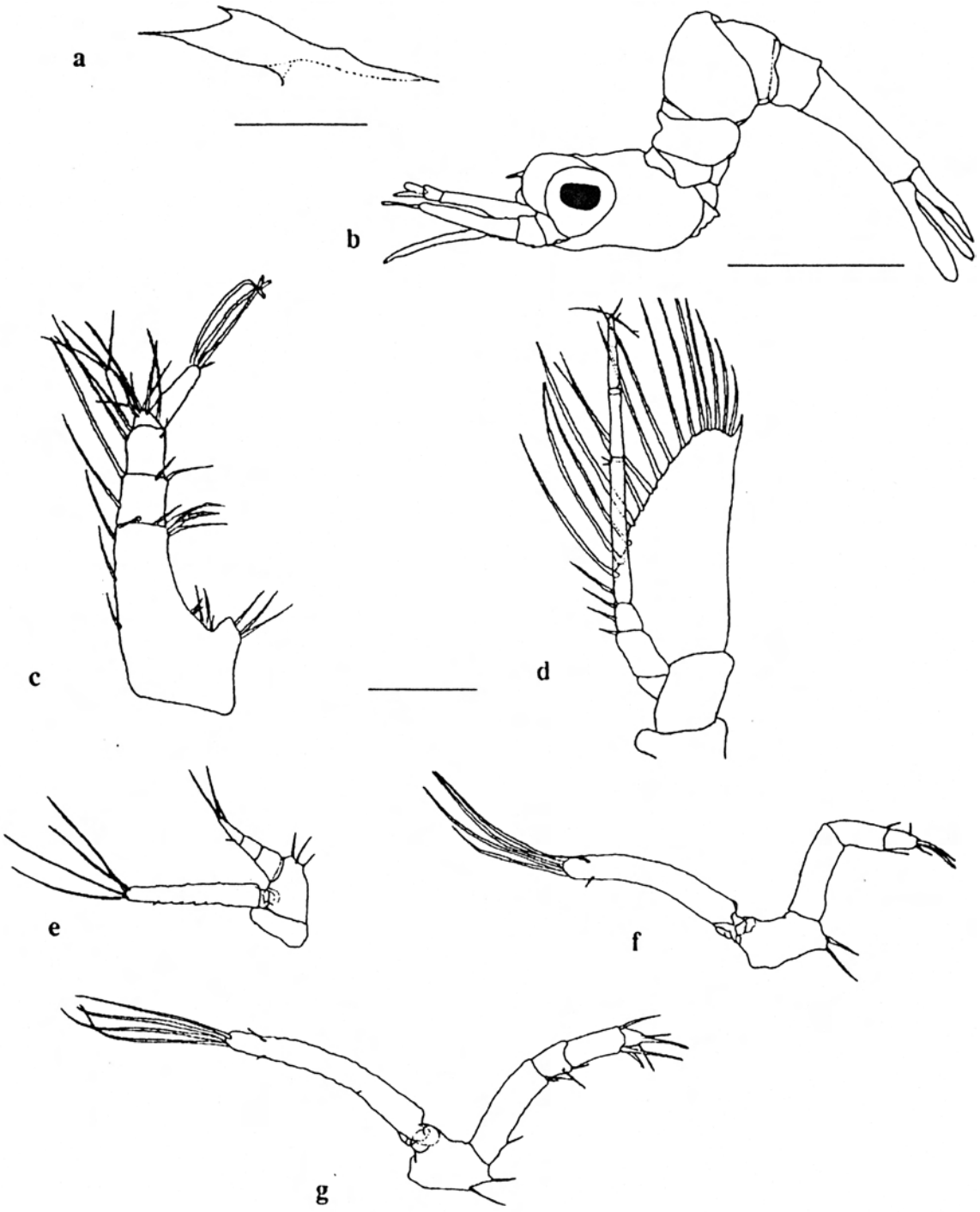

Figure 12, stage 7, part 1

Figure 13. *Hymenocera picta* zoeal seventh zoeal stage, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3, d: pereiopod 4, e: pereiopod 5, f: pleopod buds 2&3. Scale bar: a-e=250μm(bar left of d); f=250μm..

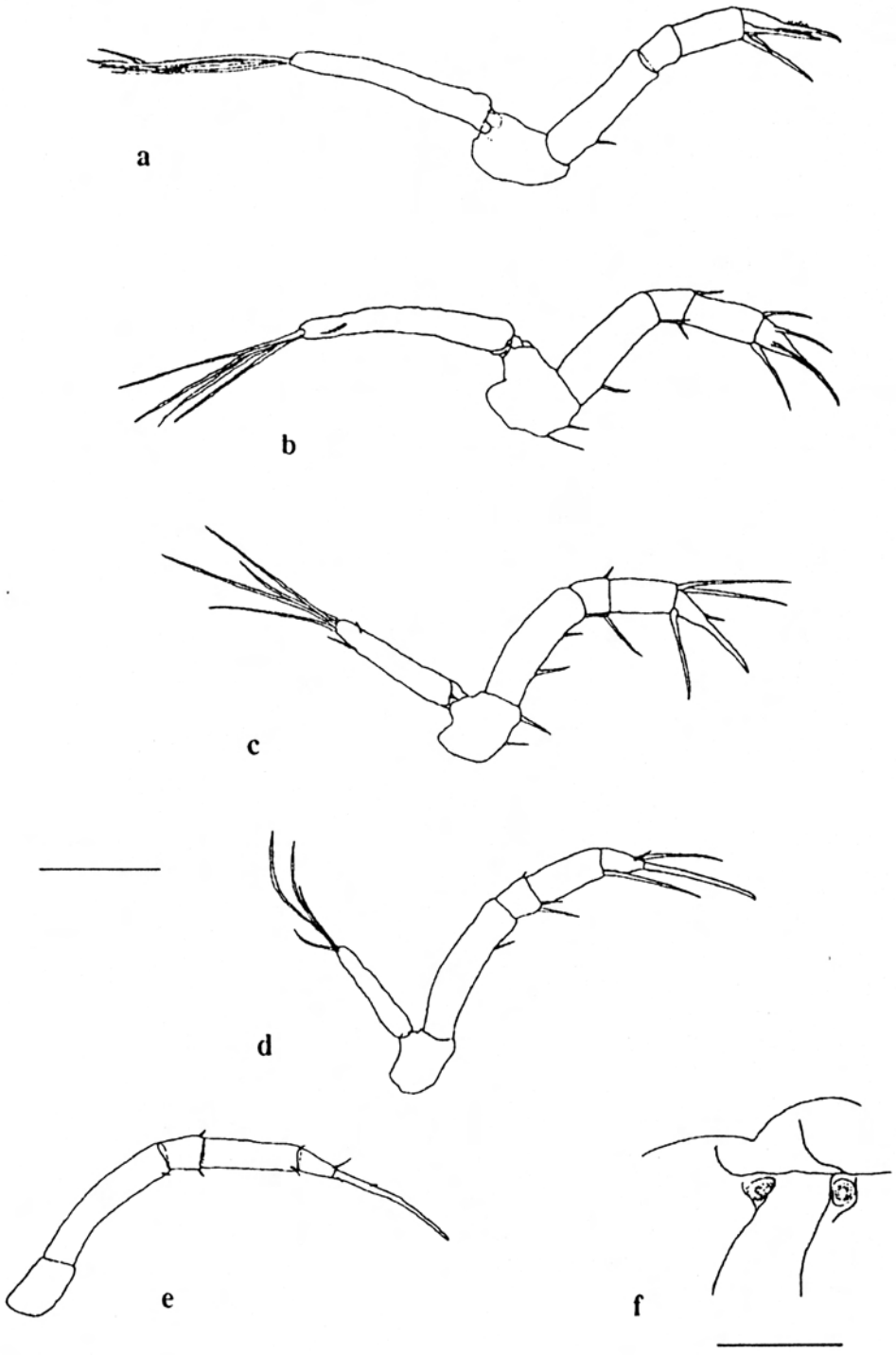

Figure 13. Stage 7, part 2.

Pleopods: Two very small buds appear on 2nd & 3rd segments of abdomen in some specimens.

Telson & uropods: (Figure 31g) Telson tapered more than in previous stage, with distal margin much thinner than proximal margin and no longer convex. Second pair of distal spines on distal telson margin nearly absent in this stage, with the center spines nearly equal in length to the outer spines. Exopodite and endopodite of uropod now extend beyond distal margin of telson, with 15-16 and 10-11 plumose setae, respectively.

General behavior: Same as in previous stage.

Zoea 8 (Description refers to figures 14, 15, & 32)
Carapace: Carapace shape more elongate. Rudiment of second rostral spine appears.

Eyes: Similar to previous stage.

Antennule: Base of proximal segment broadened, with several additional plumose setae adjacent to stylocerite. Inner process of terminal segment uniformly slender, with 3 terminal flagella. Lateral process of terminal segment with a disto-lateral lobe.

Antennae: Very similar to that in previous stage, with exception of additional plumose setae on the scaphocerite, bringing the total to 23.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Protopod now with 5 medial spines. Appendage similar to previous stage otherwise.

Maxilliped 2: Similar to that in stage 7, with the addition of some small spines on the terminal segment of endopod.

Figure 14. *Hymenocera picta*. eighth zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c&d=250μm (bar between c&d); e-g=250μm (bar above g).

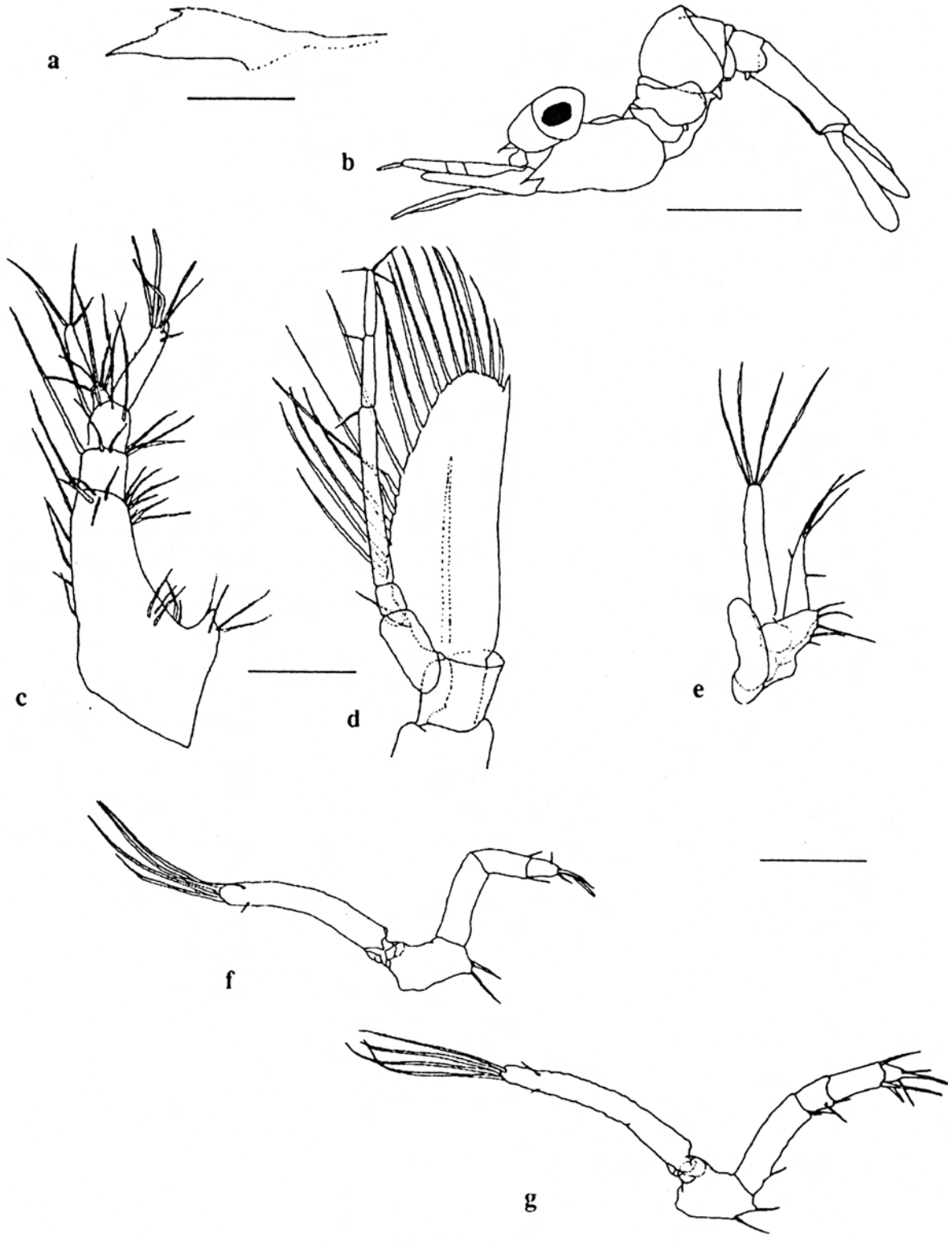

Figure 14, stage 8, part 1

Figure 15. *Hymenocera picta* zoeal eighth zoeal stage, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3, d: pereiopod 4, e: pereiopod 5, f: pleopod buds 1-5. Scale bar: a-f=250μm.

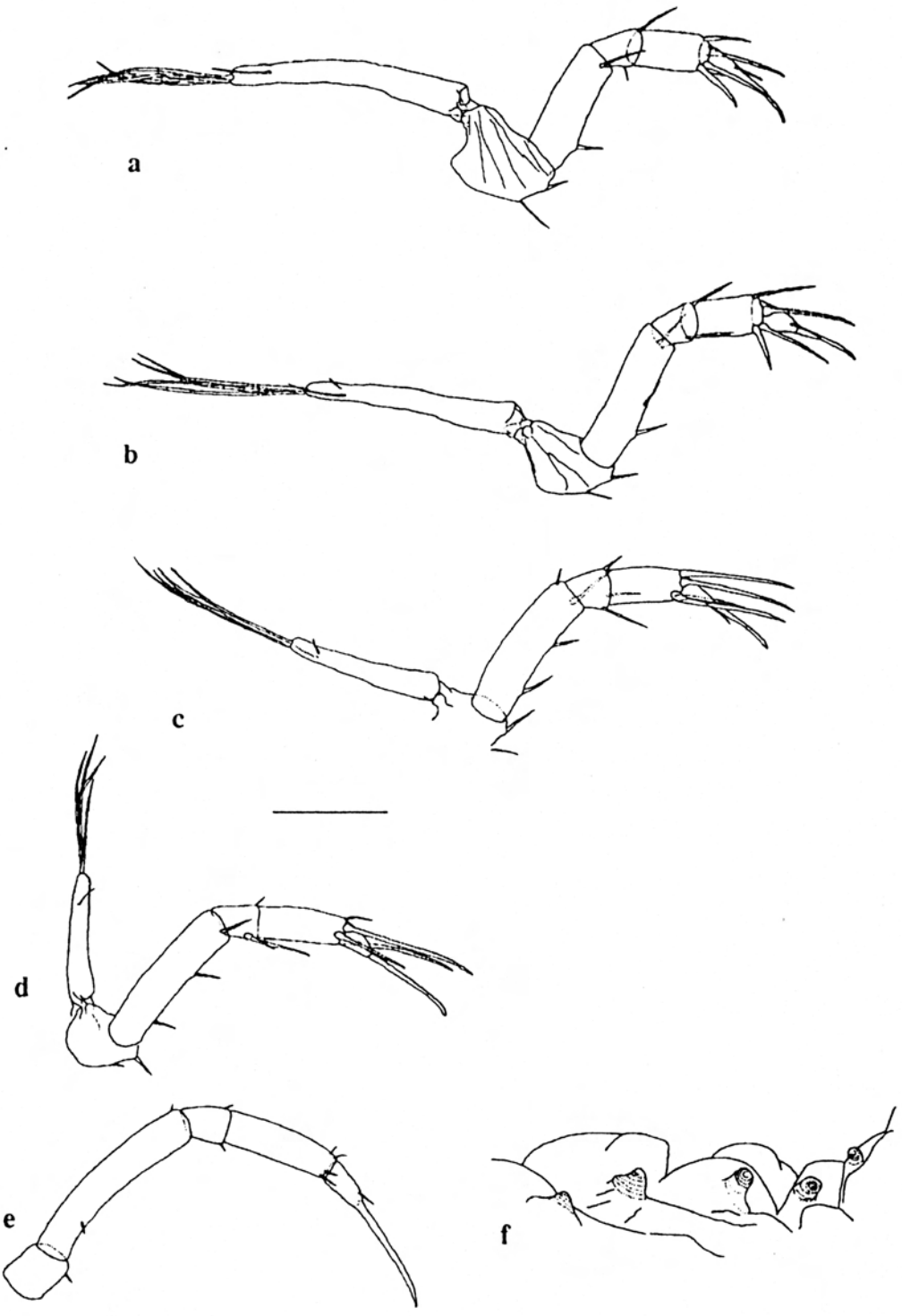

Figure 15. Stage 8, part 2.

Maxilliped 3: Similar to that in stage 7, with the following exceptions. Entire appendage appears larger and more robust than in previous stage. Endopod with more spines; second segment now with a third spine on the distal margin; terminal spine segment with additional small spine. Subterminal accessory plumose seta now extends beyond exopod terminus.

Pereiopod 1: Very similar to that in stage 7.

Pereiopod 2: Essentially identical to that in stage 7.

Pereiopod 3: Similar to that in stage 7, except for the addition of a third spine on the distal margin of second endopod segment.

Pereiopod 4: Similar to that in stage 7, with the following exceptions on the exopod. Proximal segment with two additional spines; one on the medial margin, bringing the total to two; the second additional spine on the distal margin. The spines on the second segment nearly twice as long. Distal margin of third segment now with two large spines, extending nearly to the end of the terminal spine, and two smaller spines

Pereiopod 5: Very similar to that in stage 7, except for several additional small spines on distal margin of 3rd segment.

Pleopods: Small uniramous buds evident on abdominal segments 1-5.

Telson & uropods: (Figure 32a) Telson tapered more than in previous stage. Second pair of distal spines on distal telson margin nearly absent in this stage, with the center spines nearly equal in length to the outer spines. Exopodite of uropod with 19 plumose setae Endopodite of uropod with 13 plumose setae.

General behavior: Same as in previous stage.

Zoea 9 (Description refers to figures 16, 17, 18, & 32)

Carapace: Carapace similar to previous stage, but larger. Second (inner) rostral spine much more prominent. A single small seta is present between the two spines and three minuscule setae are seen on the posterior of the rostrum.

Figure 16. *Hymenocera picta*. ninth zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c&d=250μm (bar between c&d); e-g=250μm (bar above f).

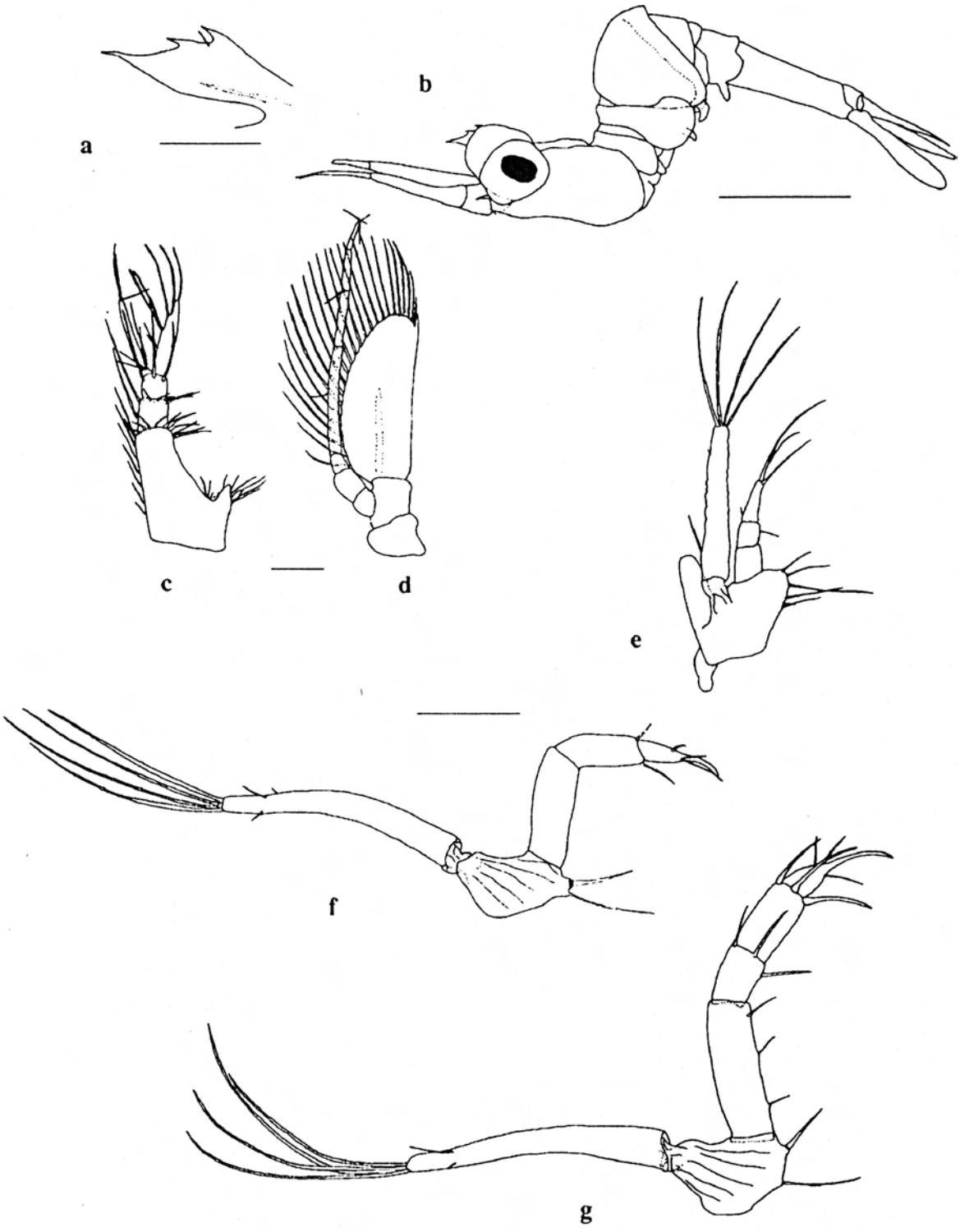

Figure 16, stage 9, part 1

Figure 17. *Hymenocera picta* zoeal ninth zoeal stage, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3. Scale bar: a-c=250μm.

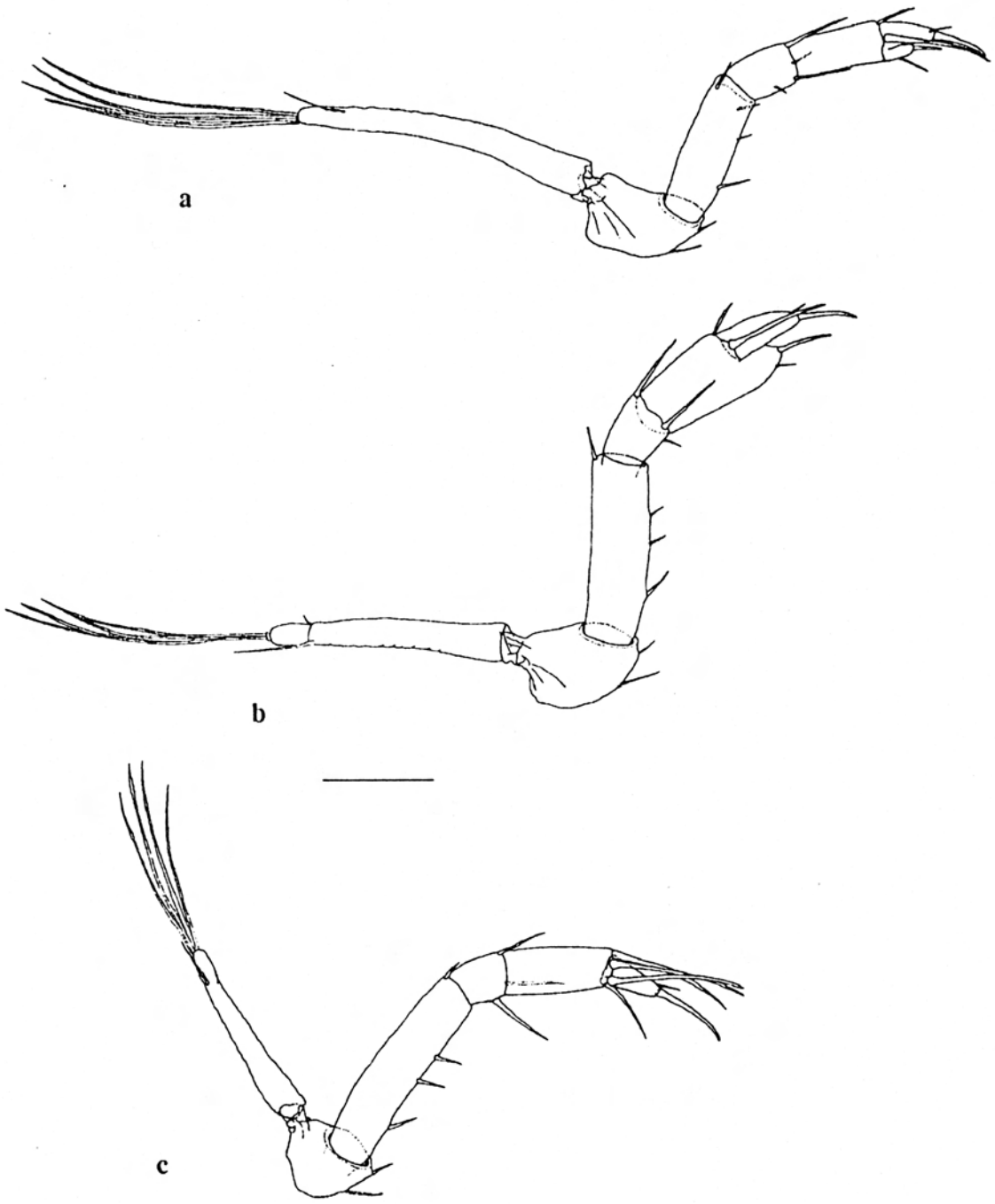

Figure 17. Stage 9, part 2.

Figure 18. *Hymenocera picta* zoeal ninth zoeal stage, part 3. a: pereiopod 4, b: pereiopod 5, c: rudimentary pleopods 1-5. Scale bar: a-c=250μm.

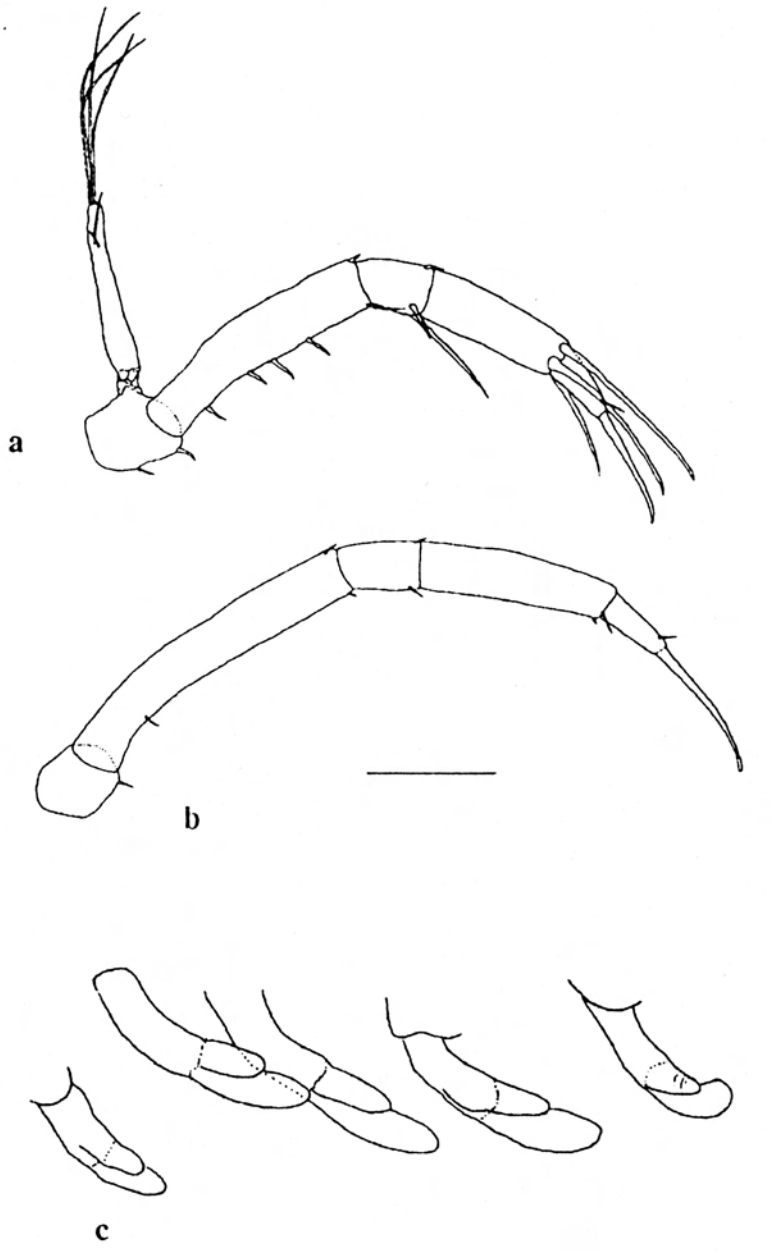

Figure 18. Stage 9, part 3.

Eyes: Similar to previous stage.

Antennule: Larger, overall, than that in previous stage. Lateral process of terminal segment now broad with three serrata with 3, 2, &1 asthetascs respectively.

Antennae: Scaphocerite now with 24 plumose setae. Antennal flagellum now extends beyond the reach of the most distal scaphocerite setae. Appendage larger overall in this stage.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Similar to that in previous stage, with the addition of a plumose seta near the proximal base of the natatory exopod.

Maxilliped 2: Very similar to that in stage 8, with the addition of a small plumose seta subterminally to the natatory exopod.

Maxilliped 3: Appendage larger than in previous stage, with some morphological alterations. Terminal three segments broader and flattened in the plane the appendage is illustrated in (anterior/posterior plane).

Pereiopod 1: Appendage much broader and morphologically altered, becoming chelate. Two additional spines appear on the proximal segment of the endopod. Second segment with one additional spine on the distal margin. Third and fourth segments now form the rudiment of a chelate appendage, with the terminal lobe of the third segment extending distally and similar diameter of terminal spine of fourth segment. Terminal lobe of third segment with rounded terminus and a small setulose spine. Terminal spine of fourth segment now with a broad base, and a single setulose spine. There are now only two spines on the distal margin of the third segment, adjacent to the fourth segment.

Pereiopod 2: Endopod of this appendage much like that of pereiopod 1, but with a more advanced chelate condition. First segment now with four spines, three on the medial margin and one on the disto-lateral margin. Second segment now with one small (medial) and two large setulose spines. Third segment similar to that in pereiopod 1, but with a strong terminal setulose spine on the terminus of the medial chelate lobe.

Pereiopod 3: Morphologically similar to that in previous stage, but larger.

Pereiopod 4: Similar to that in stage 8, but larger and first segment of endopod now with 4 spines along the medial margin.

Pereiopod 5: Very similar to that in stage 8, but larger.

Pleopods: All five are unequally biramous buds with no other ornamentation.

Telson & uropods: (Figure 32b) Both larger than in previous stage. Telson tapered more than in previous stage. Exopodite of uropod with 24-25 plumose setae Endopodite of uropod with 19 plumose setae.

Zoea 10 (Description refers to figures 19, 20, 21, & 32)
Carapace: Lobe of carapace under suborbital spine more prominent. A third small rostral spine appears anterior to second spine.

Eyes: Similar to previous stage, becoming more elongate in the medial/lateral plane.

Antennule: Slightly broader, than in previous stage. Lateral process of terminal segment with 4 serrata with 2, 4, 2&2 asthetascs respectively, from the distal to the proximal serratum.

Antennae: Scaphocerite now with at least 27 plumose setae. Antennal flagellum now extends well beyond the reach of the most distal scaphocerite seta, with at least 8 segments.

Mandible: Not shown.

Maxillula: Not shown.

Figure 19. *Hymenocera picta*. tenth zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c&d=250μm (bar between c&d); e-g=250μm (bar above g).

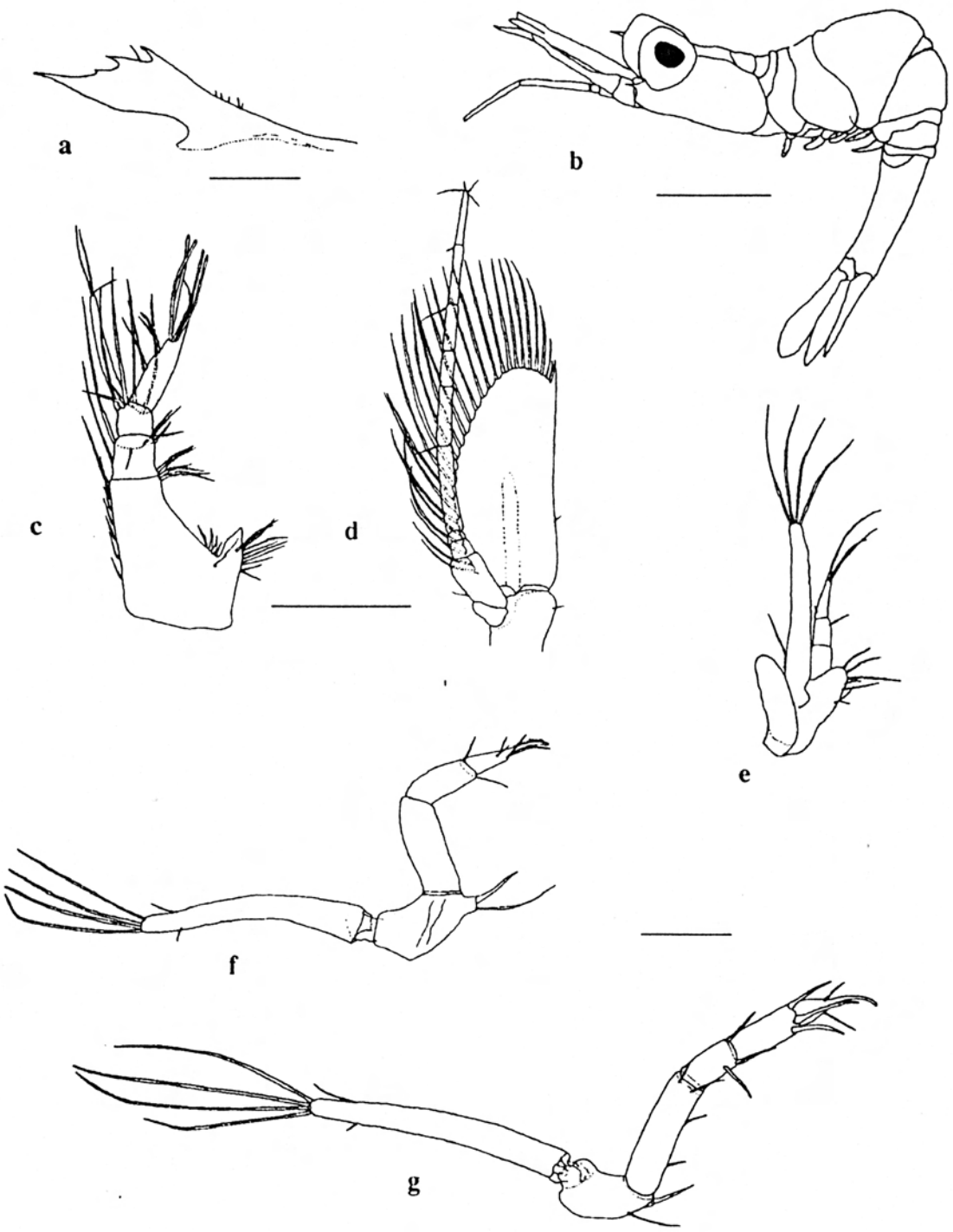

Figure 19. stage 10, part 1.

Figure 20. *Hymenocera picta* zoeal tenth zoeal stage, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3. Scale bar: a-c=250μm.

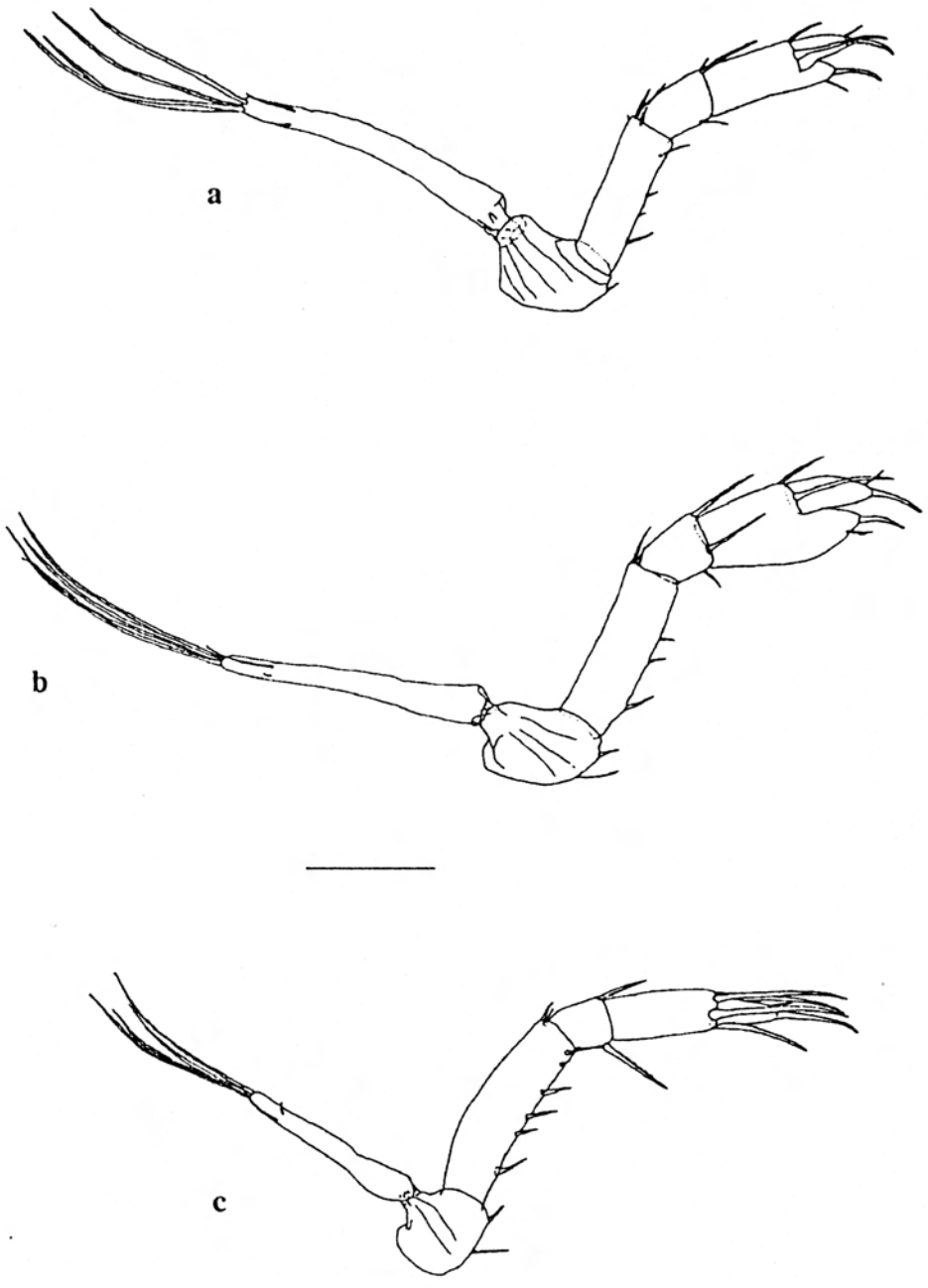

Figure 20. Stage 10, part 2.

Figure 21. *Hymenocera picta* zoeal tenth zoeal stage, part 3. a: pereiopod 4, b: pereiopod 5, c: pleopods 1-5. Scale bar: a-c=250μm.

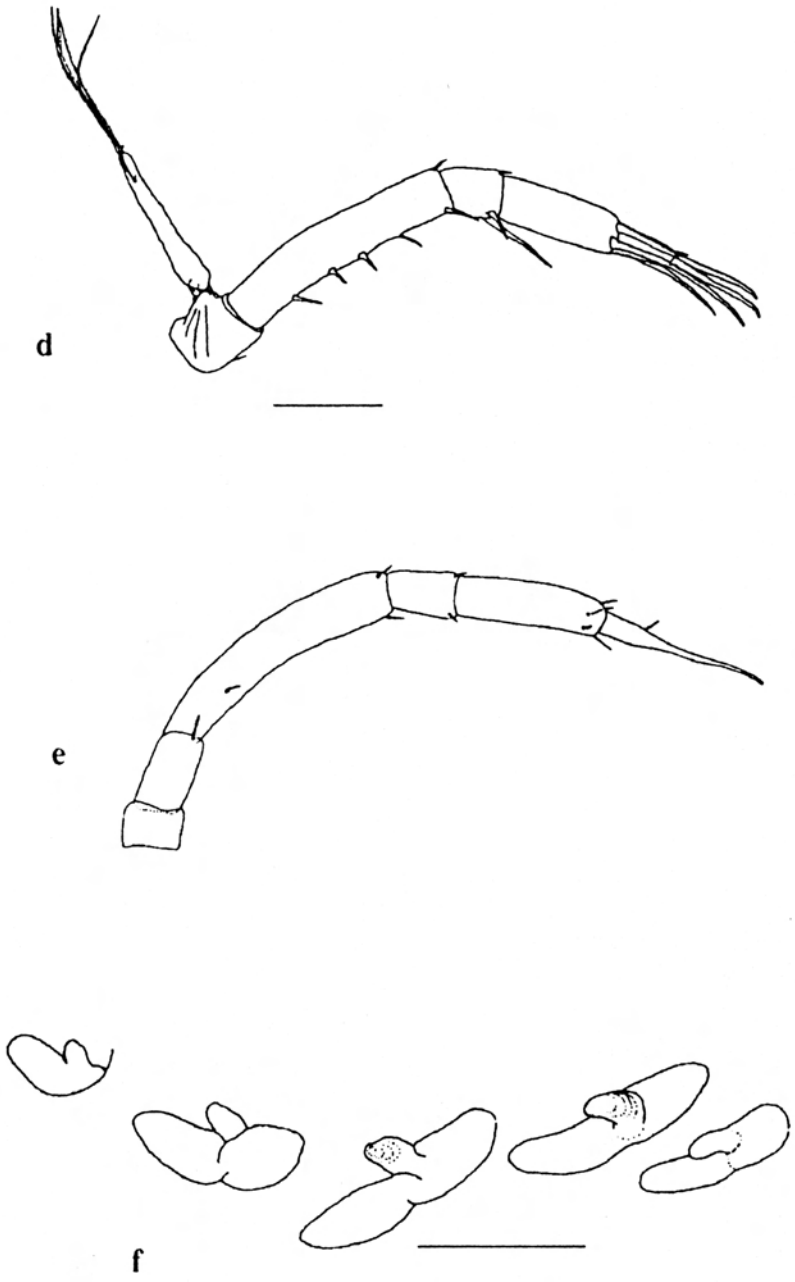

Figure 21. Stage 10, part 3.

Maxilla: Not shown.

Maxilliped 1: Very similar to that in previous stage. Plumose setae near the proximal base of the natatory exopod more prominent.

Maxilliped 2: Very similar to that in previous stage, but much more robust, overall.

Maxilliped 3: Similar to that in stage 9, but more robust. Subterminal plumose seta on exopod now extends beyond terminus of exopod.

Pereiopod 1: Appendage more robust. Distal lobe of 3rd endopod segment now with strong terminal spine, curved medially. This lobe also extends further, distally.

Pereiopod 2: Similar to that of previous stage, but increasingly more robust. Third segment much broader, and appearing more chelate.

Pereiopod 3: Morphologically similar to that in stage 9, but more robust. First proximal segment of endopod with four medial & two distal spines.

Pereiopod 4: Similar to that in stage 9, but larger, overall.

Pereiopod 5: Essentially identical to that in stage 9.

Pleopods: Larger, in this stage, with distinct separation between exopod and endopod. Segmentation evident between propodus and exo/endopods.

Telson & uropods: (Figure 32c) Similar to that in previous stage. Exopodite of uropod with 24-25 plumose setae Endopodite of uropod with 20 plumose setae.

General behavior: Same as in previous stage, except that rudimentary pleopods sometimes seen to move slightly.

Zoea 11 (Description refers to figures 22, 23, 24, & 32)

Carapace: Lobe of carapace under suborbital spine now blunt and rectangular. Third rostral spine more prominent. Rostrum now with two (one small, one larger) setae between 1st & 2nd spine, and one seta between second and third spine. Four sets of small setae can be seen just posterior to first rostral spine.

Eyes: Similar to that in previous stage.

Antennule: Slightly broader, than in previous stage. Lateral process of terminal segment with, still, 4 serrata with 2, 4, 2&2 asthetascs respectively , from the distal to the proximal serratum. Inner process now with four terminal flagella. Stylocerite now adorned (dorsally) with many additional plumose setae.

Antennae: Scaphocerite now with at least 31 plumose setae. Antennal flagellum now extends well beyond the reach of the most distal scaphocerite seta, with at least 9 segments.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Very similar to that in previous stage.

Maxilliped 2: Essentially identical to that in previous stage.

Maxilliped 3: Proximal segment of endopod now with four medial spines. Second segment now tapers strongly in the proximal direction, with a significant change in shape. Third and fourth segments now more fusiform, and flattened.

Pereiopod 1: Second segment now almost triangular, tapering proximally. Third segment broad proximally; distal lobe (propodus), extending nearly equally to the distal extent of the terminal segment, or dactylus.

Pereiopod 2: Endopod similar to that of previous stage, with changes in adornment. First segment now with four medial spines. Third segment broader, extending further, as in pereiopod 1; strong distal spine now absent; several small setae appear on margins of this propodus. Dactylus (last segment) of chela also displays additional small setae.

Figure 22. *Hymenocera picta*. eleventh zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c&d=250μm (bar between c&d); e-g=250μm (bar above g).

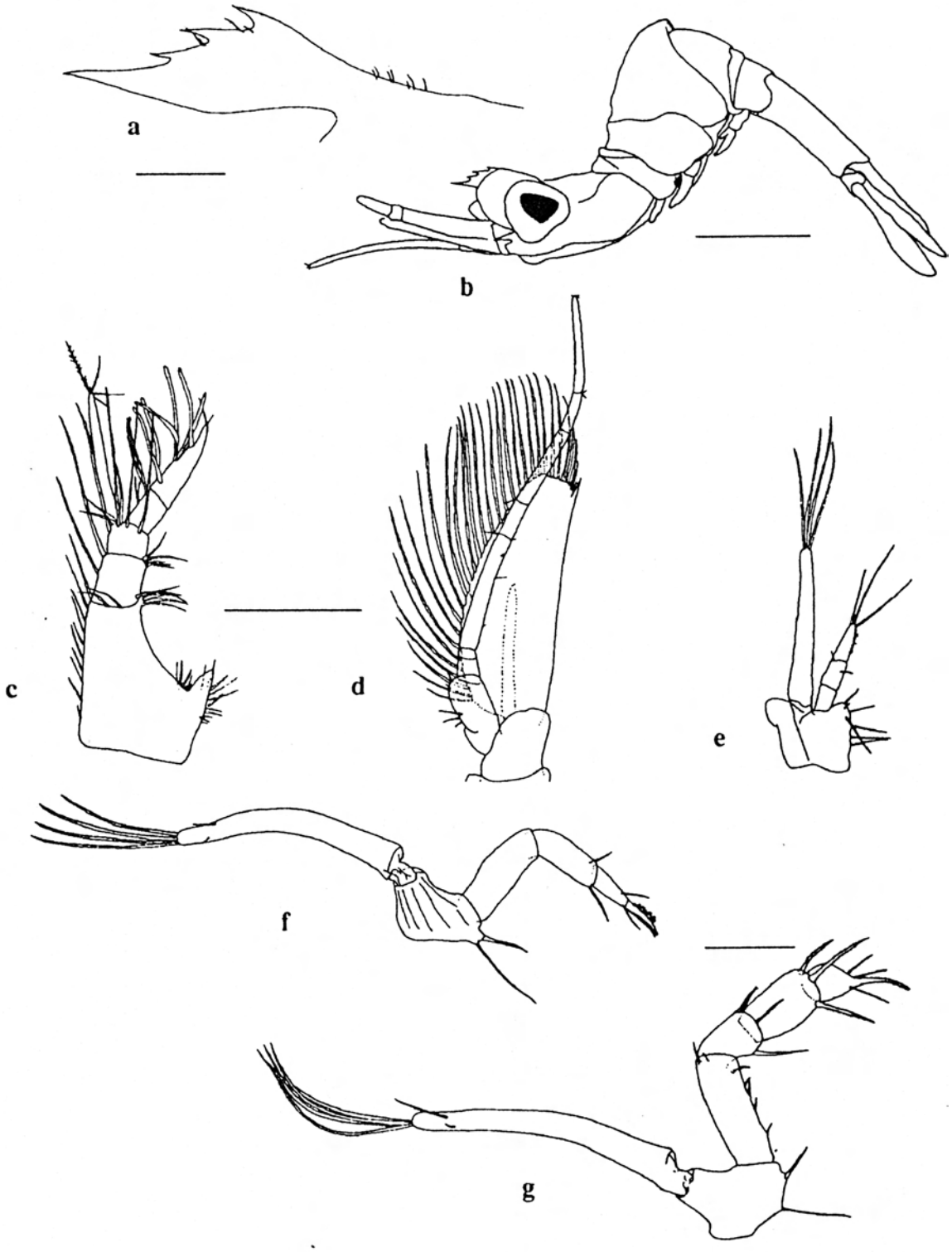

Figure 22. Stage11, part 1

Figure 23. *Hymenocera picta* zoeal eleventh zoeal stage, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3. Scale bar: a-c=250μm.

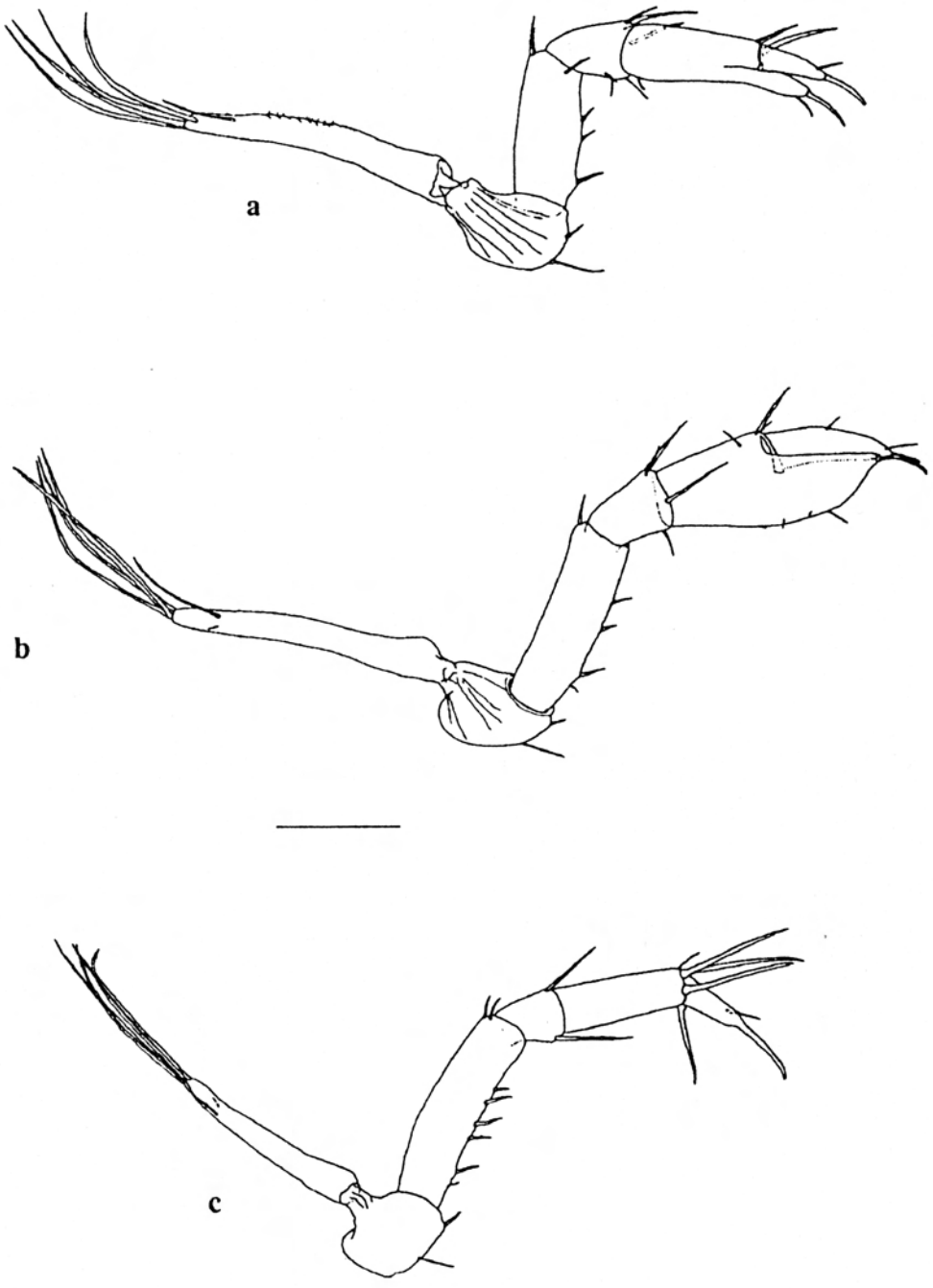

Figure 23. Stage 11, part 2.

Figure 24. *Hymenocera picta* zoeal eleventh zoeal stage, part 3. a: pereiopod 4, b: pereiopod 5, c: pleopods 1-5. Scale bar: a&b, c=250μm.

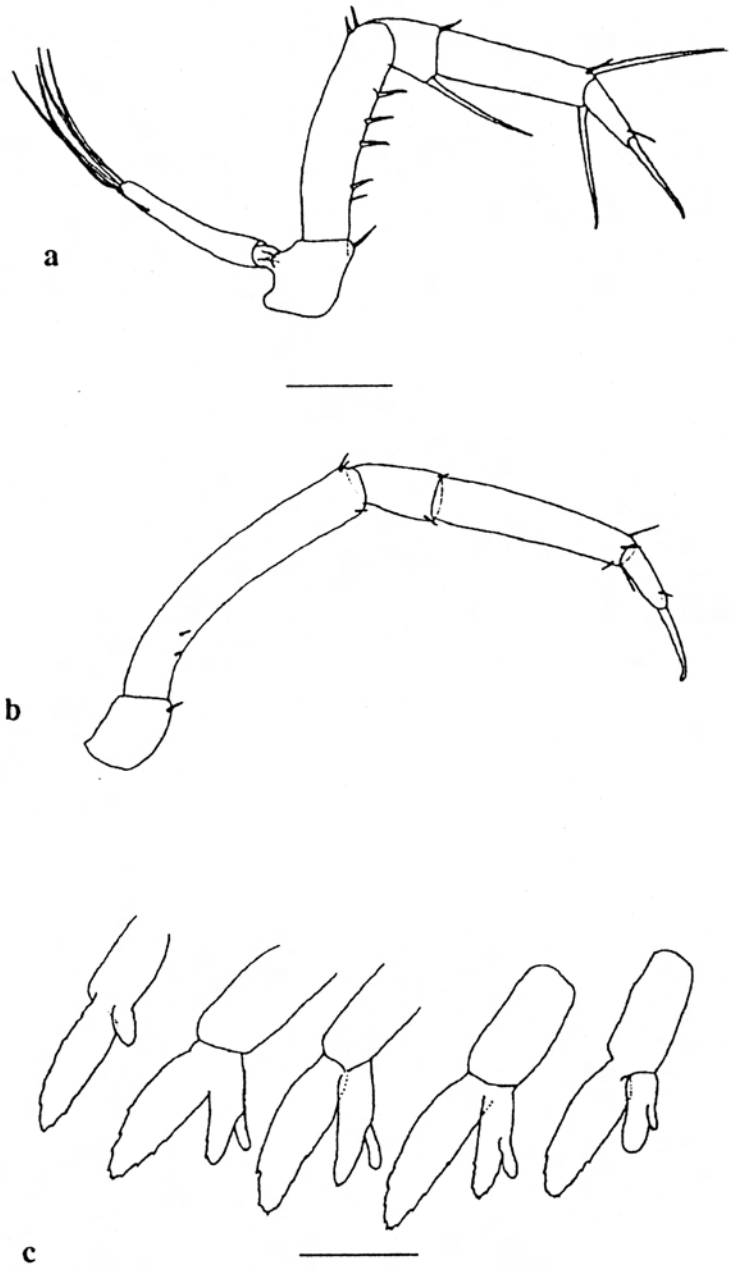

Figure 24. Stage 11, part 3.

Pereiopod 3: Similar to that in previous stage with the following exceptions. First segment of endopod now with 6 medial spines; second segment more triangular in shape. Appendage larger, overall.

Pereiopod 4: Very similar to that in stage 10, but larger, overall. First segment of endopod with one additional medial spine, now bringing the total to 5.

Pereiopod 5: Essentially identical to that in stage 10, with some increase in size.

Pleopods: Larger, in this stage, with distinct separation between exopod and endopod. Appendix internae (smaller buds) appear on the endopodites of pleopods 2-5. Serrata also appear on all exopods and some endopods, but no setae.

Telson & uropods: (Figure 32d) Similar to that in previous stage with the following exceptions. Telson tapers more drastically in the distal fifth of the appendage; distal margin is now not as wide as the four terminal spines. Exopodite of uropod now with at least 32 plumose setae Endopodite of uropod now with 24-25 plumose setae.

General behavior: Same as in previous stage.

Zoea 12 (Description refers to figures 25, 26, 27, & 32)
Carapace: Rostrum now with four spines and one small seta between spine 3 and 4.

Eyes: Similar to that in previous stage.

Antennule: Stylocerite very pronounced, extending to nearly 1/2 the length of the first segment. Slightly broader, than in previous stage. Lateral process of terminal segment with, still, 6 serrata with 2, 3, 2, 4, 3, 3, & 1 asthetascs respectively , from the distal to the proximal serratum. Inner process now with four terminal flagella and three segments with lateral setae. Stylocerite now adorned (dorsally) with many additional plumose setae.

Antennae: Scaphocerite now with 32-33 plumose setae. Antennal flagellum with at least 10 segments.

Figure 25. *Hymenocera picta*. twelfth zoeal stage, part 1. a: rostrum, b: profile, c: antennule, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c&d=250μm (bar between c&d); e-g=250μm (bar right of f).

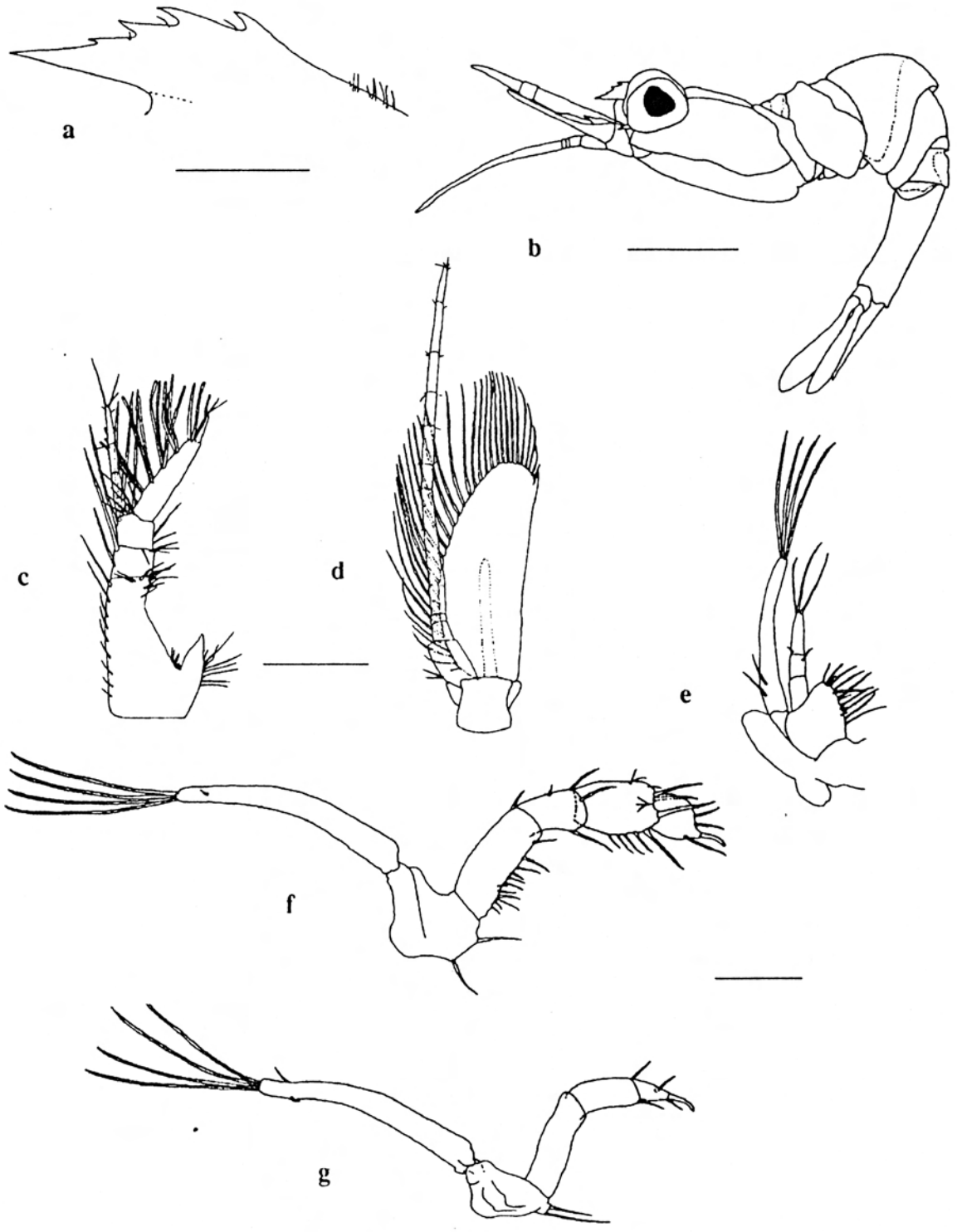

Figure 25. Stage12, part 1

Figure 26. *Hymenocera picta* zoeal twelfth zoeal stage, part 2. a: pereiopod 1, b: broad view of pereiopod 2, c: pereiopod 2 with exopod (from side), d: pereiopod 3. Scale bar: a,b, d (bar below a) & c=250μm.

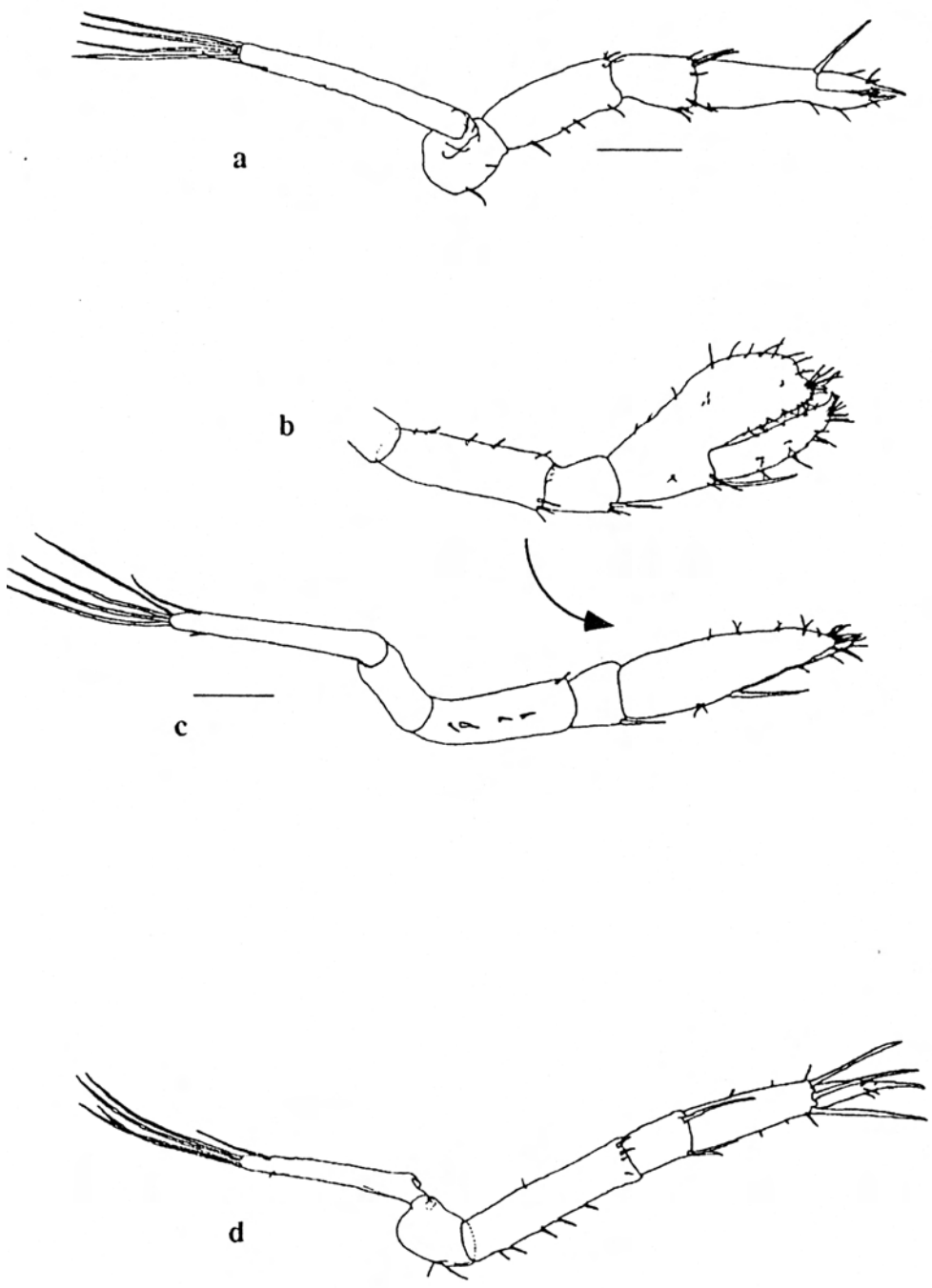

Figure 26. Stage 12, part 2.

Figure 27. *Hymenocera picta* twelfth zoeal stage, part 3. a: pereiopod 4, b: pereiopod 5, c: pleopods 1-5. Scale bar: a&b=250μm, c=250μm.

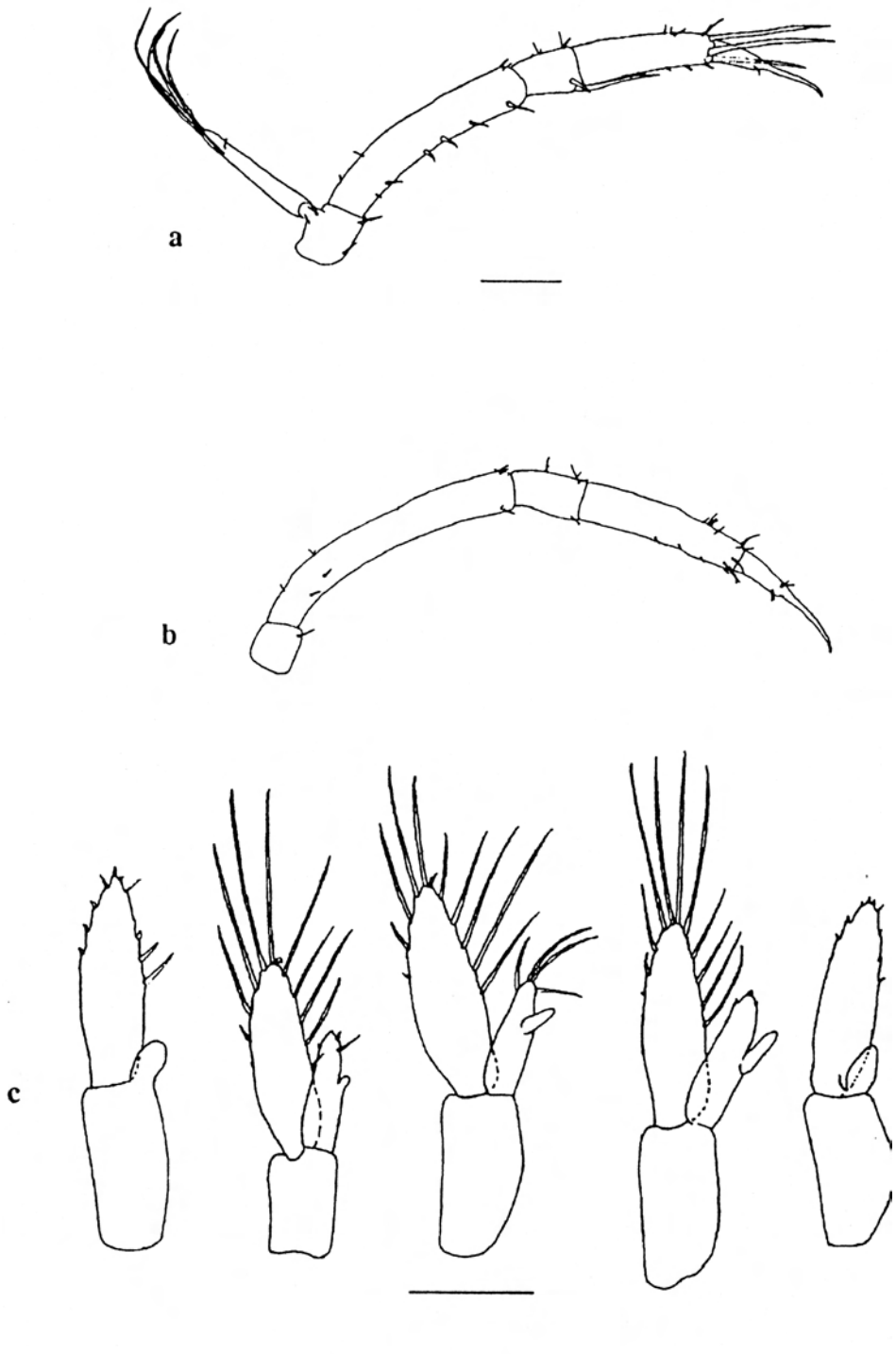

Figure 27. Stage 12, part 3.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Maxilliped 1: Protopod now adorned with 14 medial spines. Exopod now with two proximal plumose setae.

Maxilliped 2: Very similar to that in previous stage.

Maxilliped 3: Endopod continues trend of becoming flattened in this stage; first segment with slight medial invagination and 10 small medial spines of non-uniform size; third segment creased on distal margin with 4 small medial spines, 3 small disto-lateral setae, and 4 distal spines; fourth segment very rounded, with reduced terminal spine.

Pereiopod 1: Propodus of chela more elongate with several small setae and one additional stout spine near the distal terminus. Dactylus also adorned with several small setae along the terminal and medial margin. Second segment of endopod adorned with several small setae. Exopod flexed parallel to length of endopod, instead of perpendicular.

Pereiopod 2: Chela (propodus & dactylus) now much larger, and densely adorned with small setae from the medial to lateral margins; propodus with blunt terminus and two, stout spines added; dactylus now with two (similar) stout, overlapping spines, without the slender terminal spine previously present. First two proximal segments of the endopod are articulated such that endopod is strongly flexed.

Pereiopod 3: Similar to that in previous stage, but larger overall.

Pereiopod 4: Very similar to that in stage 11 but larger, overall and with several small additional setae and spines on all endopod segments.

Pereiopod 5: Very similar to that in stage 11 but larger, overall and with several small additional setae and spines on all endopod segments.

Pleopods: All pleopods richly adorned with plumose setae.

Telson & uropods: (Figure 32e) Similar to that in previous stage with the following exceptions. Exopodite of uropod now with at least 32 plumose setae Endopodite of uropod now with 27-28 plumose setae.

General behavior: Same as in previous stage, except for possible contribution of pleopod motion to locomotion. Larvae appear to remain lower in the water column and near margins.

Postlarval Stage (Description refers to figures 28, 29, 30, & 32)
Carapace: Dorsal/ventral depth posterior cephalothorax apears deeper than in previous stage. Rostrum still with four spines, but extended anteriorly, such that most proximal spined is beyond base of rostrum/carapace junction.

Eyes: More elongate, laterally (not shown)..

Antennule: Statocyst apparent, medial of stylocerite. Lateral margin of first segment broad and flattened, with a stout terminal process extending beyond proximal margin of 2nd segment. Lateral process of terminal segment now broad, and nearly paddle-shaped with 3 clear segments; ventral surface with 5 series of asthetascs 1, 3, 3, 3, &3 asthetascs respectively , from the distal to the proximal margin of the segment. Inner process now with four segments. Stylocerite now adorned (dorsally) with many additional plumose setae.

Antennae: Scaphocerite still with 32-33 plumose setae, but oriented more laterally. Antennal flagellum with at least 10 segments; more than twice the length of the scaphocerite.

Mandible: Not shown.

Maxillula: Not shown.

Maxilla: Not shown.

Figure 28. *Hymenocera picta*. first postlarval stage, part 1. a: rostrum, b: profile, c: antennule with ventral face of flat, inner process, d: antenna, e: maxilliped 1, f: maxilliped 2, g: maxilliped 3. Scale bars: b=1mm; a=250μm; c&d=250μm (bar between c&d); e-g=250μm (bar below e).

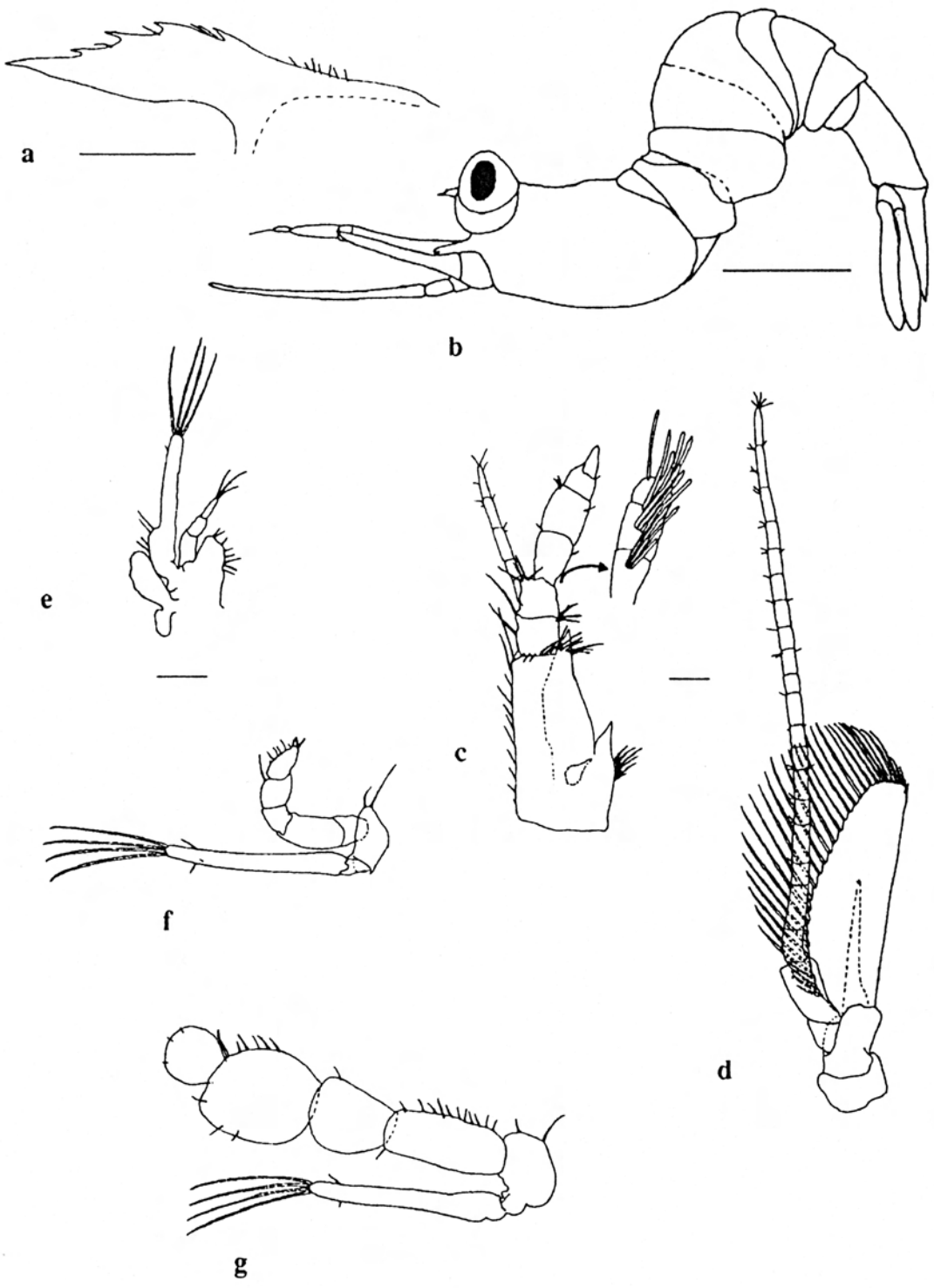

Figure 28. 1st Postlarva, part 1.

Figure 29. *Hymenocera picta* zoeal first postlarval stage, part 2. a: pereiopod 1, b: pereiopod 2, c: pereiopod 3. Scale bar: a-c=250μm.

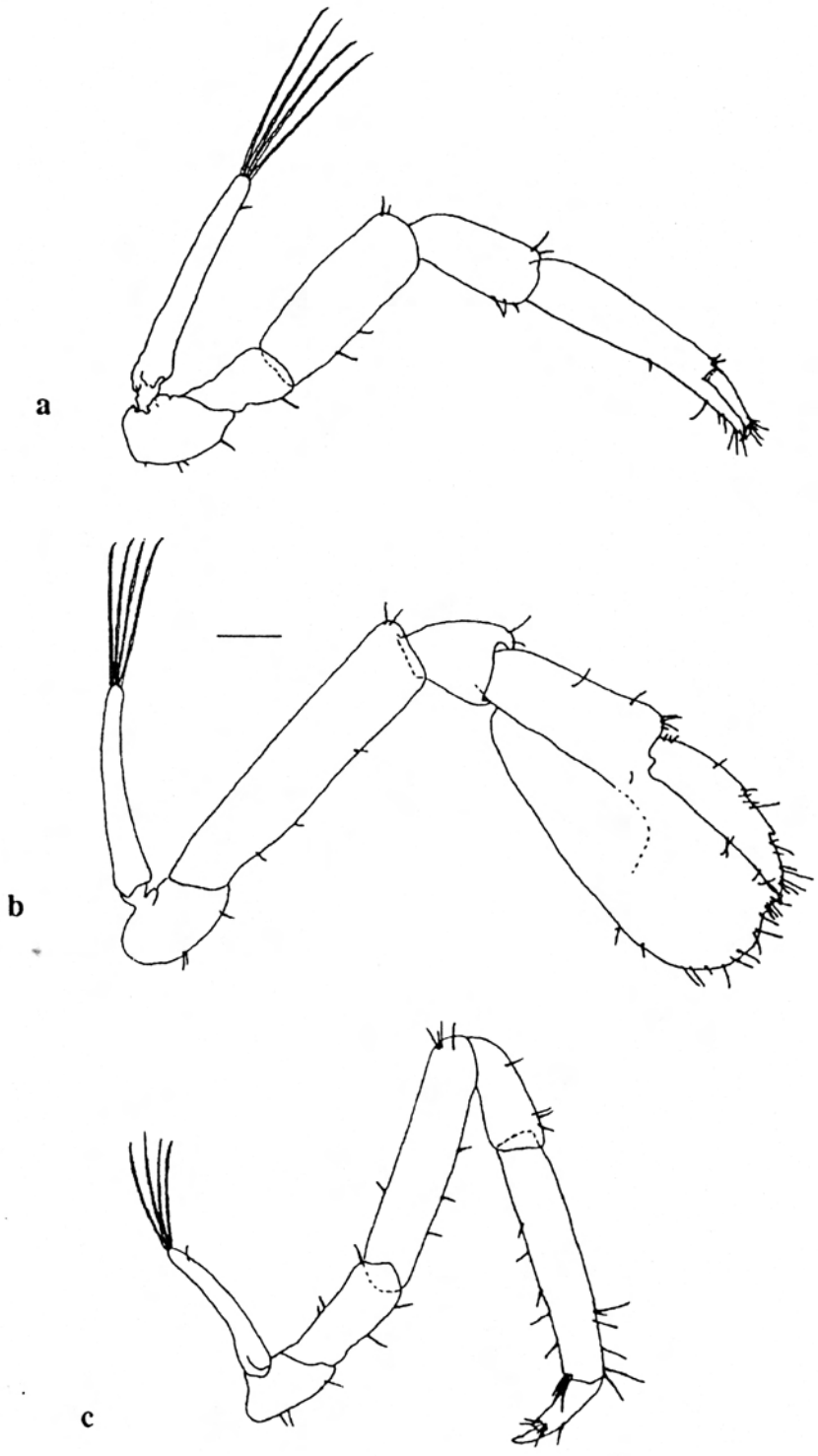

Figure 29. 1st postlarva, part 2.

Figure 30. *Hymenocera picta* first postlarval stage, part 3. a: pereiopod 4, b: pereiopod 5, c: pleopods 1-5. Scale bar: a-c=250μm.

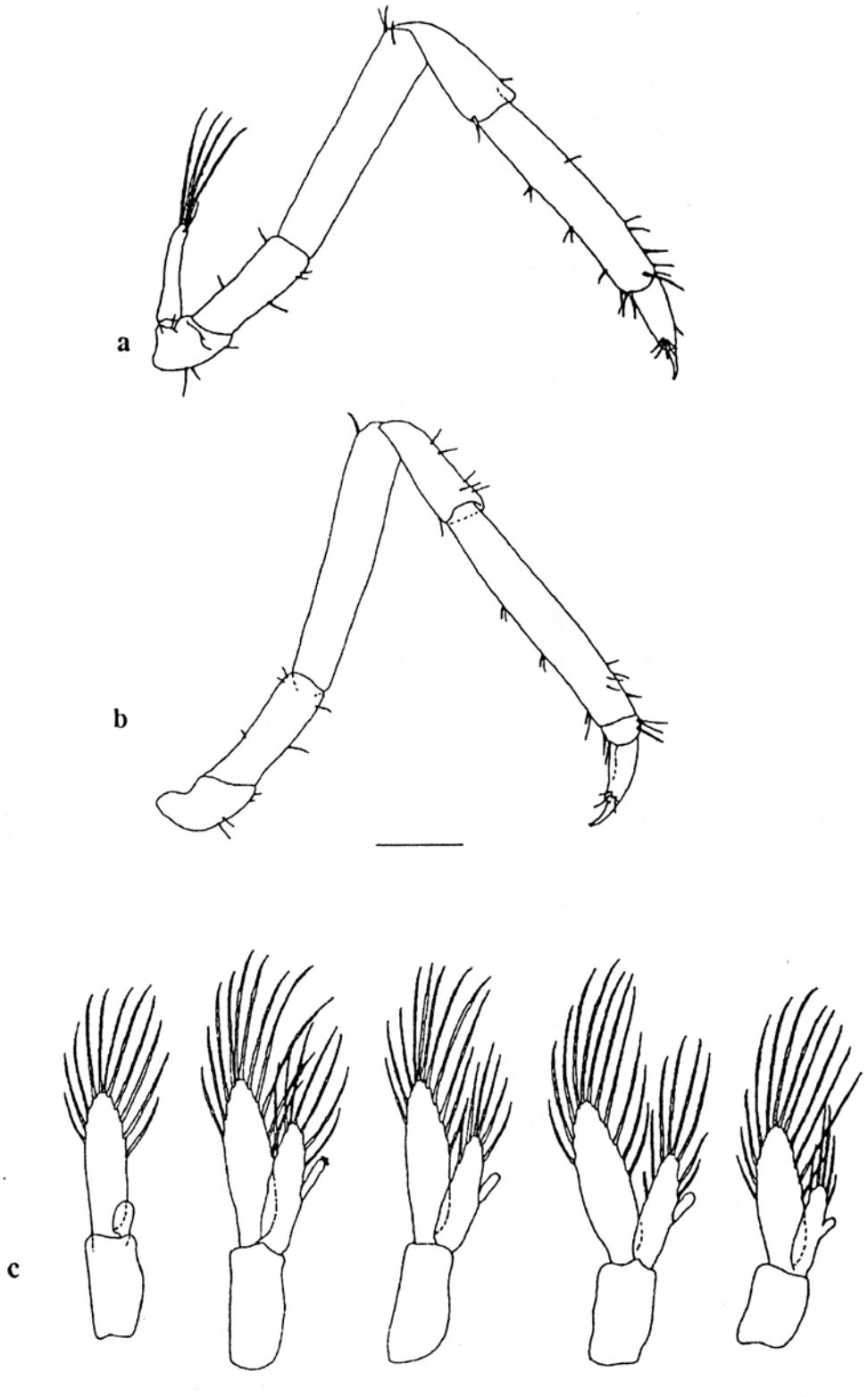

Figure 30. 1st postlarva, part 3.

Maxilliped 1: Exopod now with 4 proximal plumose setae originating on a lateral lobe Endopod segments rounded and appendage is curved medially.

Maxilliped 2: General appearance much different. Endopod segments round and curved 90° medially; there are now 5 segments; terminal segment with extremely reduced terminal spine and 6 small lateral setae. Terminal plumose setae of exopod appear reduced in length.

Maxilliped 3: Exopod reduced to nearly the lenth of and oriented parallell to the endopod. Endopod segments progress along same axis, making appendage appear unflexed. General shape of exopod becomes more foliaceous, like in adult; first segment rounded & elongate with 11 small medial spines; second segment rounded, but still tapering proximally and with one small medial seta; third segment nearly circular with 1 small proximo-medial spine, 5 small medial and 4 small lateral setae; terminal segment now nearly a third the size of the adjacent segment and nearly circular, adorned only with 3 very small setae.

Pereiopod 1: Exopod reduced, as in periopod 1. Endopod with one additional, proximal tapering segment; strong spines reduced or absent from previous stage; chela elongate with propodus lobe and dactylus tapering in a parallel fashion.

Pereiopod 2: Natatory exopod much reduced and nearly vestigal. Endopod appears very similar to adult stage, having lost or reduced all of the strong spines found on segments in the previous stage; medial lobe of propodus very broad and flattened, becoming foliate, extending distally beyond dactylus; dactylus with two lateral serrata; articulation of dactylus & propodus appears as a socket.

Pereiopod 3: Exopod very reduced, almost vestigial. Endopod now appears as an ambulatory appendage; strong spines on all segments absent or reduced; articulation between the 2nd and 3rd segments (merus & carpus) strongly flexed, laterally; terminal segment stout, compared to that in previous stage with notch along medial margin.

Pereiopod 4: Very similar to pereiopod 3..

Pereiopod 5: Very similar to pereiopods 3 & 4, but without exopod.

Pleopods: All pleopods richly adorned with plumose setae; 1-4 possess appendix internae.

Figure 31. *Hymenocera picta* telson & uropods, part 1. a: zoeal stage one, b: stage two, c: stage three, d: stage four, e: stage five, f: stage six, g: stage seven. Scale bar: a-c=250μm (bar under a), d-e=250μm (bar in center).

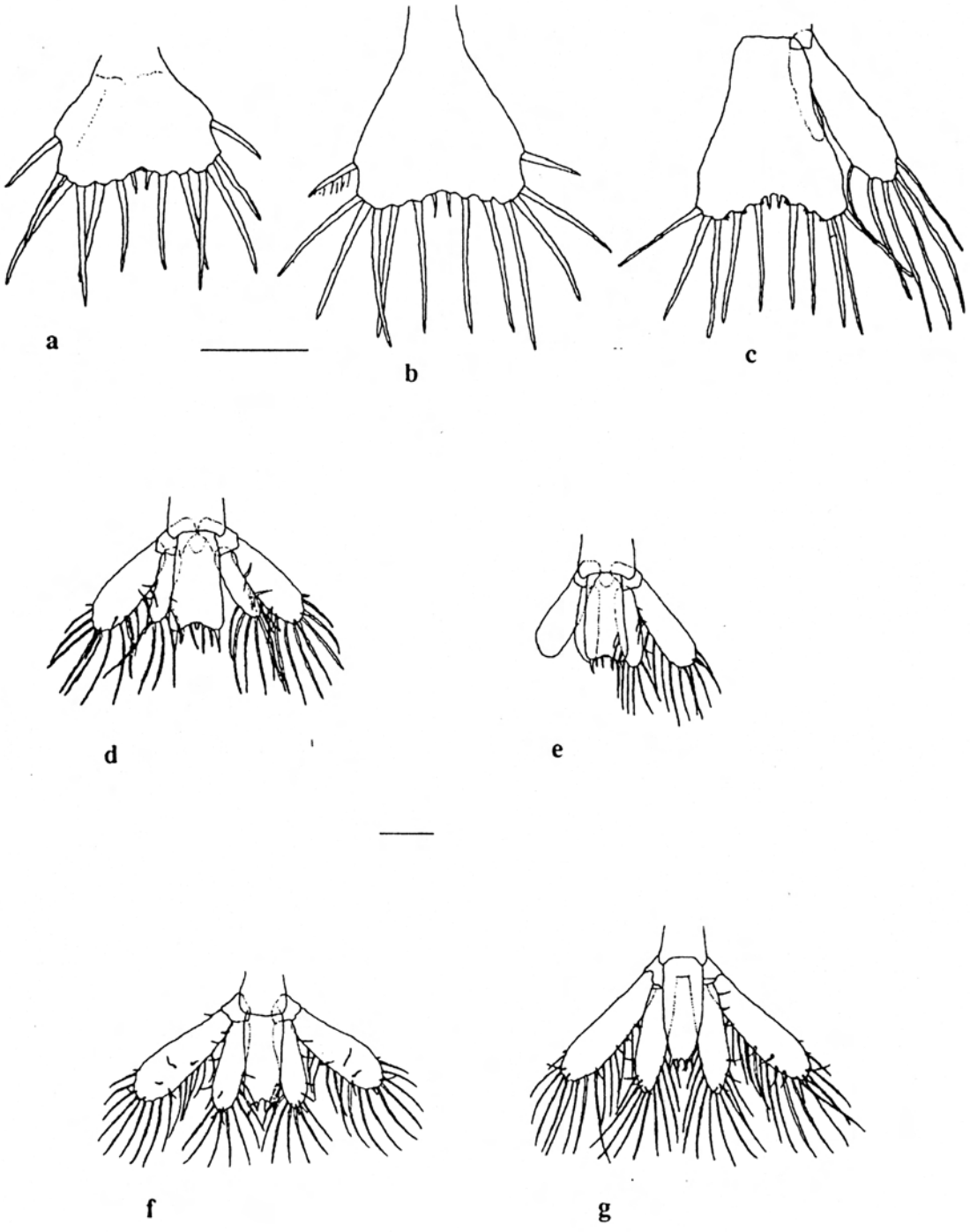

Figure 31. Telsons & uropods of larval stages, part 1.

Figure 32. *Hymenocera picta* telson & uropods, part 2. a: zoeal stage eight, b: stage nine, c: stage ten, d: stage eleven, e: stage twelve, & f: first postlarval stage. Scale bar: a-f=250μm.

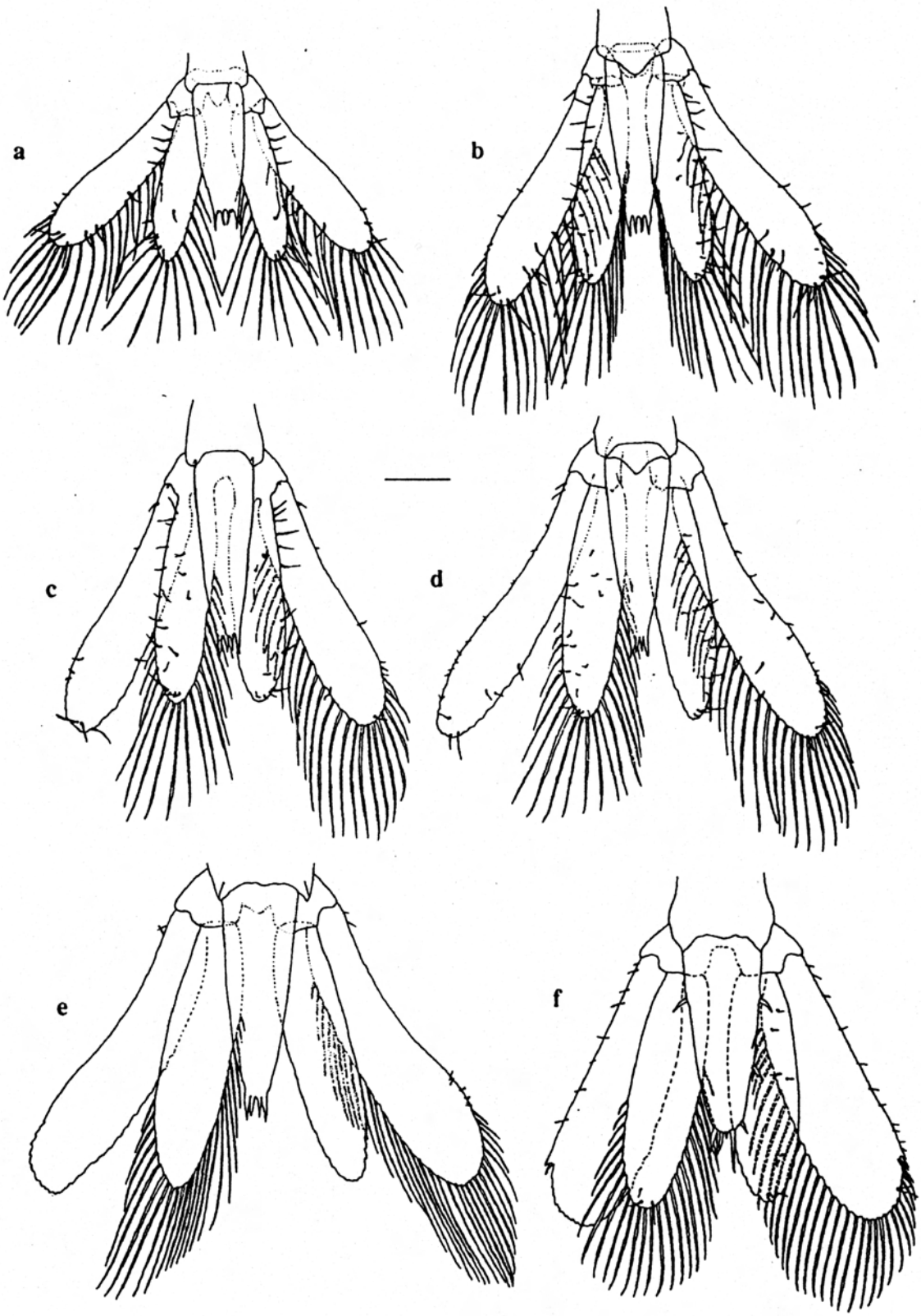

Figure 32. Telsons & uropods of larval stages, part 2.

Telson & uropods: (Figure 32f) Telson armored with 3 pairs of stout lateral spines and 2 pairs of terminal spines. Exopodite of uropod now with a stout spine at the disto-lateral margin; and at least 32 plumose setae Endopodite of uropod now with at least 25 plumose setae.

Color: First postlarvae are translucent pink, with darker pink an white spots. Later postlarval stages show a progressive increase in solid white color base, with darkening red spots.

General behavior: Much different than previous stages. No feeding is observed in this stage. Individuals are seen most frequently sitting, via pereiopods 3-5, on walls or bottom of rearing tank, much like adults. Infrequently, first postlarvae launch themselves from substrate, swimming mostly upright with rapidly beating pleopods and large chela of 2nd pereiopods noticeably extended in the ventral direction, angled somewhat posteriorly. The contribution of the now reduced swimming exopods of pereiopods is not known. Some stereotypical behaviors seen in adults are noted here as well. These include circular motion of the 2nd chelae, lateral rotation of entire abdomen, and simultaneous raising of 2nd chelae. Feeding is observed (on starfish) at 5 days after metamorphosis, but it is not known which postlarval stage.

Descriptive Summary

The 12 zoeal stages and postlarvae can be easily distinguished by the recognition characters in table 1.

Table 1. Diagnostic characteristics for larval stages of *Hymenocera picta*.

Stage:	Characteristics:
Z1	Sessile eyes
Z2	Stalked eyes; pereiopods 1&2 present only
Z3	Telson & uropod separate; uropod endopodite unadorned.
Z4	Uropod endopodite adorned; pereiopods 1-3 present.
Z5	One rostral tooth/spine; pereiopods 4&5 are no longer rudimentary
Z6	18 plumose setae on scaphocerite;anterior & posterior margins of telson equal width.
Z7	Telson tapers posteriorly; uropods now extend well posterior of telson. Pleopod buds appear.
Z8	Two rostral teeth/spines; 5 uniramous pleopod buds present
Z9	Pereiopods 1&2 appear nearly chelate; pleopod buds biramous
Z10	Three rostral teeth/spines
Z11	Dactylus & propodus of pereiopod 1, 2 now subequal; pleopods 1-4 with appendix internae.
Z12	Four rostral spines/teeth; pleopods adorned with plumose setae; chelipeds adorned with many small setae.
PL	General appearance and form that of a translucent adult; most natatory strongly reduced.

CHAPTER 4
DISCUSSION

Viability of Described Stages

Since the larvae described were collected from several efforts of mass culture, there is a danger that some zoeal stages could be overlooked. It appears, however, that nearly all the larval stages were observed and described in this effort. There are two lines of evidence supporting this. The first is the gradual development of the larvae themselves. There don't appear to be any major "holes" in the development of any of the appendages described. A regular progression of the appearance of features can be seen throughout stages 1 through 12. Arthropods cannot change or develop without an ecdysis, or molting event. If a definitive molt or stage was missed, this would have been apparent. There are major morphological differences, however, between the 12th and the first postlarval stages, but this is to be expected. This change is a true "metamorphosis", both morphologically and behaviorally.

The second piece of supporting evidence can be found in figure 1. The general pattern of growth for the larval stages is, for the most part, regular and progressive. At stage 9, however, a drastic change in the slope of growth is noted. This observation becomes more worrisome since the standard deviation of the mean carapace length for stage 9 is rather high (figure 1). In fact the carapace length data for stage 9 appears to be bimodal (not shown).

Several explanations are possible. The first is that there are actually two zoeal stages being observed at stage 9. This could be possible, even though the morphological characteristics appear to be consistent throughout stage 9 specimens. Substages and mark-time molting, where growth with little morphological development occurs, have been described in some decapod crustaceans (Gore, 1985). Crustacean growth is thought to be discontinuous, punctuated by ecdysis and there is little evidence of growth actually occurring during the intermolt period (Gore, 1985). Since larvae in the present effort were obtained from mass culture, it is difficult, at best to ascertain whether any of these phenomena actually occurred.

Another possibility is that the variable measured is not particularly suitable for this situation. During measurement of carapace length, it was often difficult to determine the posterior limit of the carapace under the microscope. Dead larvae that were preserved and collected often displayed various degrees of decay. Perhaps carapace flexion was affected by the amount of time between specimen death and fixation. Although care was taken to

record data from specimens in good condition, carapace dimensions may have been altered by the fixation method. In addition, it was casually observed that lateral growth may have been more significant than anterior/posterior growth at certain zoeal stages. Although Gore (1985) demonstrated that most any fixed larval dimension for length is suitable for generating predictable growth curves in palaemonids, a width based measure might be more appropriate for *H. pcita* larvae.

Perhaps the variance in size for stage 9 is not so unusual or unexpected. All the later stages possess a fairly high variability in not only size, but in age (figure 2). This, coupled with the larger sample size measured, may explain the high standard deviation. Another possibility is that the increased size of later stages allows more accurate measurement of carapace length, which in turn makes any inherent variability more obvious.

The issue of the age of the larval stages is a bit vexing as well. Rearing conditions were such that the temperature of larval rearing tanks was often difficult to control. Though the data for age ranges graphed in figure 2 are from rearing efforts that maintained a temperatures between 25° and 27° C, this two degree range could account for a large degree of variation. During one rearing effort, where temperatures were 28° C or more, larvae reached competence in only 28 days, nearly a week less than all other known efforts. However, one might expect even larger age ranges for later stages if one considers individual differences. Individual larvae begin life in a fairly narrow size range at stage one. Over time, individuals would likely vary in their physiological progress. The differences might become even larger. Since growth and development in arthropods is not a continuous process, but meristic, punctuated by ecdysis, the individuals further along in physiological state might be at different stages. Since the length of a stage may be several days, individual developmental differences could appear to be magnified.

The questions on the number of stages and their variation, as well as age range, could be answered by use of a technique employed by Reese & Kinzie (1968) and Diaz & Kasahara (1987). In those efforts, larvae were isolated individually, in small containers. Water was changed regularly and the containers examined for the presence of an exuviate, or molt. It was possible with this method to determined exactly when and how molting occurred. Descriptions could also be made directly from the molts, as well. The power of this rearing technique was made quite obvious by Diaz & Kasahara (1987), as they discovered six additional zoeal stages in *Macrobrachium rosenbergii*. For 20 years prior to their work, this important aquaculture animal was thought to have fewer larval stages, based upon mass-culture techniques. They also noted, but presented no data, that

the size of all the stages was dependent upon variables such as rearing temperature, salinity, and broodstock origin.

This technique was considered for the present effort, but not employed. This should not, however diminish or negate the systematic value of the current descriptions. In support of this, Diaz & Kasahara (1987, p.47) state, "We consider that earlier descriptions are very complete from the taxonomic point of view...".

Comparison with other work on *H. picta* larvae

Comparison of Hawaiian specimens with the stage one larval description by Bruce (1986) shows that the present description is very similar. The differences seen are noted in the most anterior appendages. First, the antennule described here (figure 3) has two thin setae or flagella, in addition to the two larger asthetascs on the lateral process. Bruce's description lacks the two thin processes. Further, the scaphocerite of the antenna (figure 3) in both descriptions shows 10 strong plumose setae, but the two most lateral setae depicted by Bruce are much more reduced. The last difference is in the third maxilliped. In the present description, the endopod has no apparent segmentation, and no adornment other than the two distal setae or spines. Bruce's depiction of the maxilliped 1 endopod illustrates clear segmentation, with three distal setae, and two small subterminal setae.

Descriptions of this maxilliped for the other stages show a morphology similar to Bruce's, sometimes with and without obvious segmentation and subterminal setae. Therefore, it is likely that the stage one maxilliped in this effort may not have been intact, or was difficult to illustrate. It should be noted that even upon excising maxilliped 1, segmentation was not always obvious. The difference in the number of terminal (distal) setae may have been a result of microscope resolution, or the lack thereof. The shorter, more medial of the setae (figure 3) might actually be two smaller setae that overlap.

The discrepancies in the first maxilliped, the antennule, and antenna might be due to differences in the condition of specimens or microscope resolution. Bruce's specimens were quite old (1986), collected in 1973, compared to the larvae in this effort.

The possibility of individual or population differences cannot be ruled out, however. As mentioned in the introduction, there are two color forms of *H. picta*. Larvae described here are the red eastern Pacific form from Hawaiian waters. Bruce's specimens were hatched from an ovigerous female collected at Mombasa Island, Kenya. This was, apparently, the blue brown form found the western Pacific, Indian Ocean, and Red sea. It is not known whether the two forms are actually different species, isolated populations, or pigmentation variations based upon diet. A comparative study might be in order here.

Systematic considerations

Gurney (1942, p. 15) states, "The two genera *Campylonotus* and *Gnathophyllum* will never be securely placed until their larvae are identified." He goes on to say that this is so, as the adult morphology has not provided sufficient clues. Bruce (1986) makes note of Gurney's observations in his 1986 proposal to alter the position and composition of the family, Gnathophyllidae. He goes on to provide some evidence from the first stage larvae of *Gnathophyllum americanum*, the common bumblebee shrimp, in comparison with other caridean shrimp. Before explaining his rationale and how larval data from the present effort fits in, one must understand how the classification of the genus *Hymenocera* and *Gnathophyllum* has vacillated. Calman (1909) published a phylogeny as follows:

Family Palaemonidae
- Subfamily Palaemoninae
- Subfamily Pontoniinae
- Subfamily Hymenocerinae

Family Gnathophyllidae

No reason was given for the separation of the genera *Hymenocera* and *Gnathophyllum*.

More recently, Holthuis (1955) placed the Gnathophyllidae & Palaemonidae within the superfamily Palaemonoida, and, apparently, included *H. picta* within the former family, based in part upon the broad "foliate" third maxilliped found in adults. The other characteristic he used to unite the Palaemonidae was the *presence* of an incisor process on the mandible. Balss (1957), further muddied the picture by placing the Gnathophyllidae within the Crangoidea. Since then, authors seemed to have favored Holthuis version in their keys and taxonomic lists of caridean genera (Burnkowski, 1982; Bowman & Abele, 1982; Glaessner, 1969). It is worthwhile to review the uniting characteristics of the Palaemonoida, Palaemonidae, and Gnathophyllidae to better understand Holthuis' reasoning. This list of characters that follows is somewhat paraphrased from Holthuis' key to Carideans (1955):

Superfamily Palaemonoida:

a. 1st pereiopods chelate or simple

b. Cutting edges of dactylus of all chelae *not* all pectinate (comb-like)

c. Carpus of 2nd pereiopods entire, 1st pereiopod always with developed chelae.

d. Last 2 joints of maxilliped 2, *not* placed side by side at the end of the penultimate joint. Dactylus not extremely long.

e. Chelae of 1st pereiopod with only 1 movable dactylus (finger)

f. First pereiopods usually more slender than and rarely subequal to 2nd pereiopods.

g. Pereiopods lacking exopods & chelae without terminal brushes with hairs.

Palaemonidae	Gnathophyllidae
Upper antennular flagellum bifid	Same...
Pereiopods lacking arthrobranchs or epipods.	Same...
Mandible with incisor process, *if not* then .	Mandible without incisor process.
3rd maxilliped *not* expanded or leaf-like	Third maxilliped leaf-like.

Note that the last two characters for the Palaemonidae are actually a catchall, representing one option on Holthuis' dichotomous key. It is these two characteristics that Bruce (1986) employed to modify the families.

Bruce proposed to resurrect the separation of the genus *Hymenocera* and the family Gnathophyllidae (1986) by placing them into separate subfamilies *within* the Palaemonidae, as follows:

Family Palaemonidae

Subfamily Hymenocerinae

Hymenocera picta

Phyllognatha spp.

Subfamily Euryrhynchinae

Subfamily Palaemoninae

Subfamily Typhlocaridinae

Subfamily Desmocaridinae

Subfamily Gnathophyllinae

Gnathophyllum spp.

Levicaris sp.

Pycnocaris sp.

and the former Pontoniine shrimp

Subfamily Anchistidioidinae

Note that the superfamily Palaemonoida was kept intact. His reasons for separating the two are based upon the *adult* morphology of the third maxilliped (Bruce, 1986). This appendage is fully articulated in the Hymenocerinae, while Gnathophyllinae, the first two segments (ischium & merus) are fused, or inarticulate. He even went so far as to amalgamate the Pontoniinae subfamily with the Gnathophyllinae. Further evidence of this may come from adult behavior of both groups, as they are known to consist of primarily commensal or parasitic shrimp.

The are two reasons for including both phyletic groups within the Palaemonidae. The first is the uniformity of the first *larval* stage with that of described palaemonids, especially that of Gnathophyllum and several pontoniine genera (Bruce, 1986; Bruce 1988). The second reason was the presence and absence of mandibular incisor processes and widened third maxillipeds in both gnathophyllids and pontoniines There is one gnathophyllid genera (*Pycnocaris*) with at least a rudimentary incisor process and some Pontoniinae have a greatly reduced or lack incisor processes on the mandible (Bruce, 1986). Plus, a recent description of a gnathophyllid in Hawaii, *Gnathophyllum precipium* illustrates a small incisor process on the mandible (Titgen, 1989). Bruce also made mention of some Pontoniinae with a very broad proximal segment (ischiomerus) of the third maxilliped. These two pieces of information led Bruce to conclude that the gnathophyllids (excluding the genera *Hymenocera* and *Phyllognatha*) should be joined somehow.

Since he was in possession of only the first larval stages of *Gnathophyllum* and *Hymenocera picta*, his comparisons could benefit from the complete larval descriptions of either species. The descriptions presented here should bolster his contention to include the genus *Hymenocera* within the palaemonid family.

The general development of *H. picta* seems to be very typical of many palaemonids. In discerning the different zoeal stages of *Hymenocera picta*, the larval stages of *Macrobrachium spp*. were initially used as a guide. Most of the changes in the initial stages seem to coincide with that of many described palaemonids, excepting those with abbreviated development. The only significant departure appears to be the order of pereiopod development.

Development of pereiopods is consistent with *Macrobrachium rosenbergii*, *M. nipponense*, *Palaemon pacificus,* and *Palaemon serratus* up to stage 3 (Uno & Kwon, 1969; Shy, et al., 1987; Shy & Yu, 1988; & Fincham, 1983). *H. picta* is adorned with only 3 developed pleopods and two buds in stage 4. The aforementioned palaemonids have 4: pereiopods 1, 2, 3, & *5*, with 4 as a biramous bud in stage 4. The development of

pereiopod 5 occurs before that of 4 in these species. In stage 5, the 4th and 5th pereiopods first appear as developed appendages in *H. picta*. The early development of pereiopod 5 is characteristic of many palaemonids according to Gurney (1942) and Schram (1986), although there is no mention of whether this is universal throughout that family. It is also worth noting that the 5th pereiopod is *uniramous* in *H. picta* and the aforementioned palaemonids. Since there was only one specimen of stage 5 available in this effort, and the timing of its appearance coincides with a critical period (mass mortality) in larval survival (unpublished data) the possibility of a missing stage comes to mind.

The order and scope of telson, uropod, antennule, antennae, and rostral development are very similar to that of *M. rosenbergii*, *M. nipponense*, *Palaemon pacificus,* and *Palaemon serratus* (Diaz & Kasahara, 1987; Uno & Kwon, 1969; Shy, et al., 1987; Shy & Yu, 1988; & Fincham, 1983). The first stage alone was enough for an experienced *Macrobrachium* aquaculture expert to quip, upon viewing *H. picta* larvae under a microscope, that he was the victim of a prank as he was of the opinion that the larvae was identical to that of the giant prawn (de Parseval, pers. comm.).

The evidence previously presented supports the inclusion of the genus *Hymenocera* within the Palaemonidae, or at least an alliance of the taxa somehow. The issue of whether *H. picta* should be separate from the Gnathophyllinae may be another matter. Although mention was made of the 3rd maxilliped morphology, nothing was discussed about the nature of the incisor process of the mandible of the newly erected *Hymenocerinae*. One of the available references shows the mandible of *Hymenocera picta* as simple with *no* incisor process (Edmondson, 1923). The other described adult characteristics fit the profile of the Palaemonidae, with exception of the contentious 3rd maxilliped. If we set aside the issue of adult maxilliped morphology, the first stage larvae of *H. picta* presented here appears no more different to that of *Gnathophyllum americanum* than it does to any of the other established palaemonids discussed previously. The question of gnathophyllid phylogeny may never be better understood until the larvae of *Gnathophyllum*, *Phyllognatha*, and many pontoniine shrimp are described completely. Although these might be arduous tasks, the value of being able to definitively understand the phylogeny of these genera with particularly strong symbiotic and predatory links with other invertebrates may be very significant. Frederick Schram, in his 1986 book, *Crustacea*, bemoans the lack of a thorough body of comparative larval studies for caridean taxa and states that many systematic issues are still not properly understood at both higher and lower taxonomic levels. That this has been the case since Gurney's time is somewhat disturbing.

There are still some detailed morphological studies that have yet to be thoroughly applied to these groups. Felgenhauer and Abele (1982) detailed the microscopic anatomy of the foreguts of several decapods with electron microscopy. For the groups in question here, they found some interesting trends, with a limited species pool. Although the focus of their application was on higher classification, they did examine one gnathophyllid, an unidentified species of *Gnathophyllum*, and four palaemonids from the genera *Palaemonetes*, *Palaemon*, *Macrobrachium*, and *Pontonia*.. They reported that the gastric mill is greatly reduced to absent in the four palaemonids, and completely absent in the lone gnathophyllid. This digestive structure is thought to aid in the grinding of food. Crustaceans without the mill are thought to ingest small grains of sand somehow, to augment grinding (Schram, 1984). They provided no details, however, on the gastric mill possessed by the pontoniine examined. Without those details, and the same sort of study on other gnathophyllids and the hymenocerine shrimp, it is difficult to pass further judgment. However, this does illustrate that the value of such techniques should not be underestimated. The combination of the life history characteristics along with accurate phylogeny, be it determined morphologically, molecularly, or via larval development, could be a particularly powerful tool in understanding evolutionary patterns.

In the author's opinion, the revision of the Palaemonidae and Gnathophyllidae by Bruce (1986) is provisionally valid. The basis of his key is sound, considering the incomplete knowledge that we have. It does not completely invalidate or repudiate Holthuis' 1955 groupings, but generates a likely alternative, based upon current information. In any case, it provides a template for future studies. If we can take into consideration the close predatory and symbiotic associations of members of the Gnathophyllinae (and the included Pontoniinae), and the Hymenocerinae with other invertebrates, the possibility of some further systematic link is not out of the question in the author's view. A thorough comparison of life histories may provide the information to resolve these questionable relationships.

Conclusions:

1. There are 12 distinct zoeal stages of *Hymenocera picta* reared in the laboratory.

2. The stage one larvae of the Hawaiian *Hymenocera* are very similar to the stage one larvae from a population of *Hymenocera* in the Western Indo-Pacific.

3. Characteristics of *H. picta* larval stages indicate that they should be included in the Palaemonidae.

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