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Larval development of the mud shrimp *Axianassa australis* (Decapoda: Thalassinidea) under laboratory conditions

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Abstract

Ovigerous females of *Axianassa australis* were obtained from intertidal mudflats in south Texas, and eggs were hatched in the laboratory. Zoeal stages (Z) and the first postlarval stage (decapodid) were obtained, though survival rates were low. A few larvae passed through eight zoeal stages before moulting to the decapodid. Duration ranged between 3 and 4 days for each stage between ZI and ZVII, and 4 and 5 days for ZVIII, which totalled about 1 month for the entire zoeal phase of development. Three specimens that reached the decapodid stage were preserved for morphological descriptions so duration of this stage is unknown. Morphology of the first three zoeal stages and decapodid stage is described and compared with that of related thalassinideans reported in literature. As possible, comparisons are also made with larvae reared from conspecific populations in east Florida and Brazil. Biogeographic implications of the larval life history are discussed.

Keywords: *Axianassa australis*, Decapoda, mud shrimp, larval development

Introduction

Larval life history of the genus *Axianassa* is poorly known compared to that of other thalassinideans. The adult habitat (mud flats associated with mangroves or other vegetation) and the apparently long planktonic larval history complicate collection of ovigerous females and rearing of a full larval series. Larvae from wild plankton samples taken in the Gulf of Mexico have been previously referred to the genus *Axianassa*, though the species identification has remained in question (Ngoc-Ho 1981). At the time those larvae were described, no member of the genus *Axianassa* was known to occur in the south-western Gulf of Mexico. However, the number of stages in plankton samples from the Gulf of Mexico suggested that they belonged to a species with a long water column life history and thus potential for broad dispersal. Subsequently, very similar zoeal stages were reported from waters off the coast of Louisiana (Truesdale and Andryszak 1983). While

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morphology of the ZI of *Axianassa australis* Rodriguez and Shimizu, 1992, was included with the species description of adult material from Brazil, apparent differences between the ZI of *A. australis* and the congeneric larvae described from the Gulf of Mexico suggested that these were not the same species (Table I).

In the present study, ovigerous females of *A. australis* were collected on the coasts of Texas and Florida. Larvae were subsequently hatched and reared in the laboratory.

Table I. Comparison of three larval descriptions for genus *Axianassa*.

	<i>A. australis</i> (Rodriguez and Shimizu 1992)	<i>Axianassa</i> sp. (Ngoc-Ho 1981)	<i>A. australis</i> (present study)
Rostrum	As long as antennae	As long as antennae	As long as antennae
Eyes	Round, sessile	Round, sessile	Round, sessile
Abdomen	Somite 6 fused with telson	Somite 6 fused with telson	Somite 6 fused with telson
	Somite 5 with lateral spines	Somite 5 with lateral spines	Somite 5 with lateral spines
Antennule	Unsegmented	Unsegmented	Unsegmented
Distal setae	3 aesthetascs+2 setae	3 aesthetascs+2 setae	6 aesthetascs
Subterminal plumose	Absent	Present	Present
Antenna			
Spine on peduncle	Absent	Present	Present
Exopod	Spine+10 setae	Spine+10 setae	Spine+8-10 setae
Endopod	3 apical setae	3 apical setae	3 apical setae
Mandibles	Asymmetrical	Asymmetrical	Asymmetrical
Maxillule			
Endopod	Unsegmented, 3 apical setae	Unsegmented, 3 apical setae	Unsegmented, 2-3 apical setae
Coxal endite	4 setae	4 setae	3-4 setae
Basal endite	4 setae	4 setae	2 setae, 2 spines
Maxilla			
Scaphognathite	5 setae	5 setae	3-5 setae
Endopod	Unsegmented, 2 setae	Unsegmented, 2 setae	Unsegmented, 2 setae
Coxal endite	4 setae	5 setae	3-5 setae
Basal endite	4 setae	8 setae	7-10 setae
Maxilliped 1			
Exopod	2-segmented, 4 apical setae	2-segmented, 4 apical setae	Unsegmented, 4 apical setae
Endopod	4-segmented, 1, 0, 1, 4 setae	4-segmented, 1, 1, 5 setae	4-segmented, 1, 1, 2, 4-5 setae
Basis	3 mesial, 2 lateral setae	1+2+1 setae	1+2+1 setae
Maxilliped 2			
Exopod	2-segmented, 4 apical, 3 lateral setae	2-segmented, 4 apical setae	Unsegmented, 4 apical setae
Endopod	4-segmented, 0, 0, 3, 5 setae	4-segmented, 0, 0, 2, 4 setae	4-segmented, 0-1, 0-1, 0-2, 4-5 setae
Basis	No setae	No setae	No setae
Maxilliped 3			
Exopod	2-segmented, no setae	2-segmented, no setae	2-segmented, no setae
Endopod	Absent	Absent	Absent
Pereopods	Absent	Pereopods 1 and 2 present as small buds	Bilobed bud of pereopod 1 present
Telson processes	7+7	7+7	7+7
Medial spine	Absent	Absent	Absent
Anomuran hair	Present	Present	Present

Morphology was examined for comparison to existing descriptions of both congeneric and other less closely related forms, as well as to recently obtained photographs of the ZI stage from conspecific Brazilian populations.

Materials and methods

Ovigerous females were collected from mud flats near Fort Pierce, Florida (Florida population) and Port Isabel, Texas (Texas population) with yabby pumps (as in Felder 1978). Adult females were maintained in 20-cm diameter finger bowls (at 27°C, salinity 35, psu scale) with daily water changes until eggs hatched. Larvae of the Texas population were reared in seawater taken offshore of Louisiana, filtered through steel wool, and aerated before use in cultures. Larvae of the Florida population were reared in water collected off Fort Desoto Park, Florida, otherwise treated as mentioned above.

To estimate stage durations, ZI larvae were moved to individual compartments of plastic trays upon hatching and maintained at 27°C, in filtered seawater (salinity 35, psu scale), on a 12 h light: 12 h dark cycle. Each day larvae were moved to clean trays with new seawater, fed freshly hatched nauplii of *Artemia* (Great Salt Lake), and examined to assess their stage of development. Observations were terminated when larvae expired or when the last few surviving decapodids were preserved. While most larvae died before reaching ZIV, two (out of 102) larvae from a single parental female of the Texas population were reared successfully through the decapodid stage. Larvae from other parental females of the Texas and Florida populations were also reared, but all died before the full course of zoeal development was completed.

Morphological studies were based on stages harvested from mass cultures and on moults from animals reared individually. Mass-cultured larvae were maintained in 20-cm diameter finger bowls (100–200 individuals per bowl) with daily water changes under conditions mentioned above. Animals were fixed in 70% ethanol, stained with chlorazol black, and transferred to glycerine prior to dissection. Unless otherwise noted, at least 10 animals were dissected for each described stage, and both right and left appendages were used for setal counts. Line illustrations were made on a Nikon inverted microscope fitted with a camera lucida. Measurements were made with a calibrated ocular micrometer. Carapace length (CL) was measured from the tip of the rostrum to the posterior midpoint of the carapace, and total length (TL) was measured from the rostral tip to the posterior midpoint of the telson. For each appendage, the arrangement of setae was listed sequentially from proximal to distal margins as in Nates et al. (1997) and Konishi (1989). Setal groups on successive segments were separated with a comma (,). Groups of setae on the same segment, or on different lobes of the same segment, article or endite, were separated with a plus (+). A question mark (?) was used to designate questionable distinctions between setae and aesthetascs. Roman numerals were used to describe the pattern of processes on the posterior margin of the telson.

Results

Prior to hatching, eggs changed gradually in colour from bright orange-red to a translucent brown. Late-stage embryos that were dropped by the female before hatching and larvae that hatched as prezoaeas were not viable, even with aeration. Prezoaeal stages did not appear to be fully developed and could not swim. Although small in size, zoeal stages fed readily on nauplii of *Artemia*.

Larvae of *Axianassa australis* passed through eight zoeal stages in laboratory cultures before moulting to the decapodid (Figure 1), but these data are based on only three animals that survived the full course of larval development. Duration of each stage from ZI to ZVIII ranged from 3 to 5 days each, and larvae thus required approximately 1 month to reach the decapodid stage. While the sample size is small (only five animals survived past ZIII and only three reached the decapodid stage), this estimate suggests a lengthy period for potential planktonic dispersal.

The zoeal stages were found to have distinctive chromatophore patterns (Figure 1). Two large red chromatophores were present consistently on the telson and posterior margin of the last abdominal segment. One to three small, red chromatophores were present on the lateral margins of the carapace. Although not always easily observed at ZI, chromatophores on the carapace were typically well developed by stage ZIII. Although only two decapodids were available for dissection (one died prior to preservation), specimens did not vary in any marked way. Although setal numbers on various appendages may have varied, the ranges (between left and right sides) overlapped.

Because of high mortality in the moult to ZIV, the need to keep the survivors alive for studies of stage durations and the need to get at least some individuals through complete larval development, few materials were available for descriptions of the later zoeal stages. Thus illustrations and descriptions were limited to the first three zoeal stages (which most comparative materials are also limited to) and decapodid. Stages ZIV–ZVIII were, however, found to vary considerably in morphology from the few specimens observed.

Setal patterns are given from proximal to distal segments for each appendage. Where setation varies, illustrations represent the most common morphology observed. Carapace length (CL) and total length (TL) are given as the mean \pm standard deviation (in mm), followed by the range of measurements from 10 specimens unless otherwise noted (as in stage D where only two specimens were available).

Zoea I (Figures 1, 2a–k)

Size. CL = 0.77 ± 0.015 mm, range 0.748–0.794 mm; TL = 1.56 ± 0.02 mm, range 1.53–1.60 mm.

Carapace (Figure 1). About same length as abdomen; rostrum elongate, rounded in cross-section, smooth; eyes fused to carapace.

Abdomen (Figure 1). Somite 5 with posterolateral projections about half length of somite; lacking dorsal spines.

Antennule (Figure 2a). Elongate, exopodal and endopodal lobes not distinct; six terminal aesthetascs; one long plumose seta on future endopodal lobe.

Antenna (Figure 2b). Protopod with one distal spine between rami, one specimen with small distal spine near base of endopod; endopod with three long, plumose setae; scaphocerite (exopod) armed with one strong distolateral spine, 8–10 plumose setae on inner margin.

Mandible (Figure 2c, d). Mandibles asymmetrical; right mandible with two prominent teeth at base, lower plate with numerous small teeth, distal end pointed but not as strongly

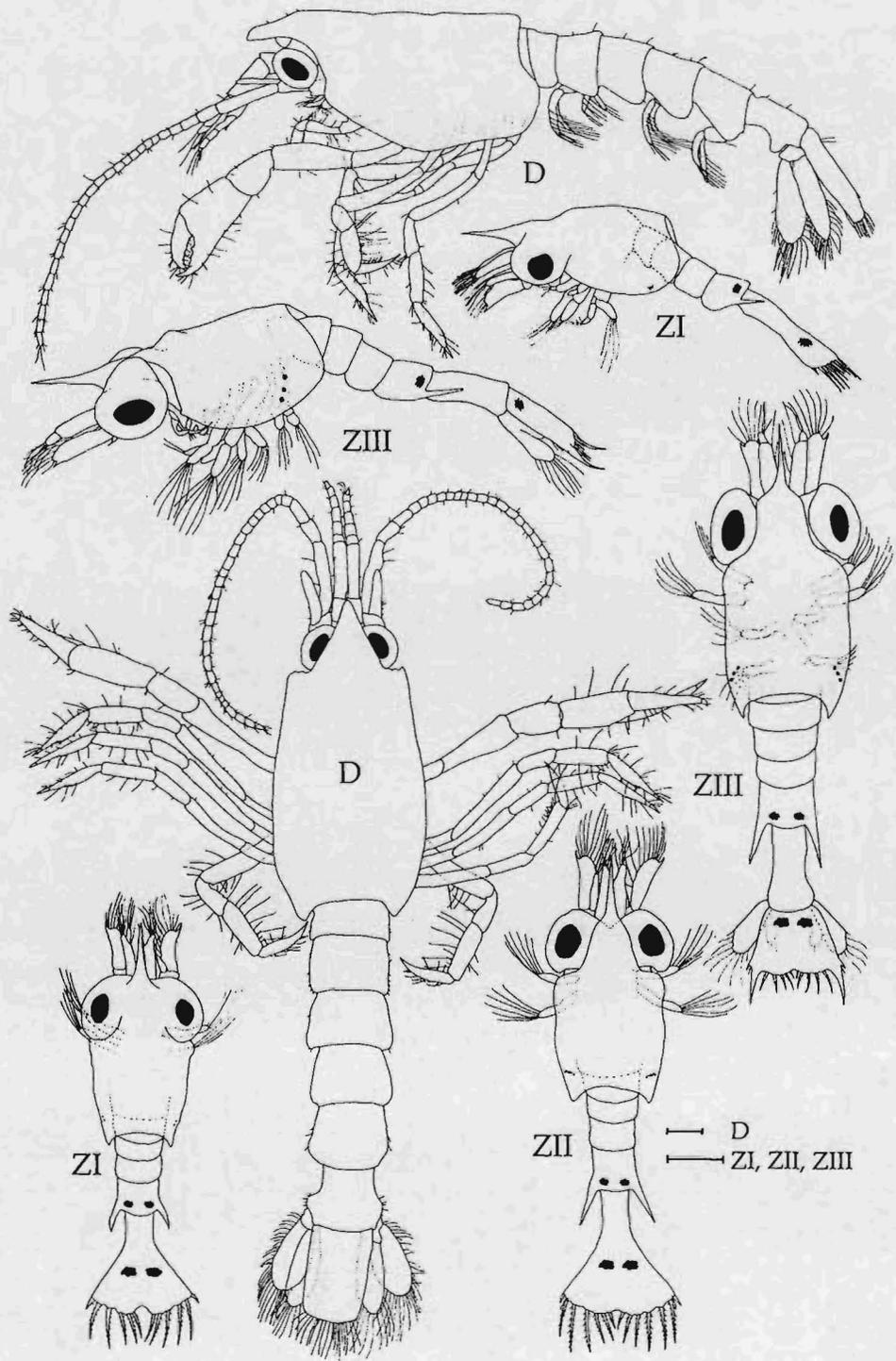


Figure 1. *Axianassa australis*, dorsal view of ZI, ZII, ZIII, and decapodid; lateral view of ZI, ZIII, and decapodid. Dark shading represents positions of chromatophores in live specimens. Scale bars: 0.2 mm.

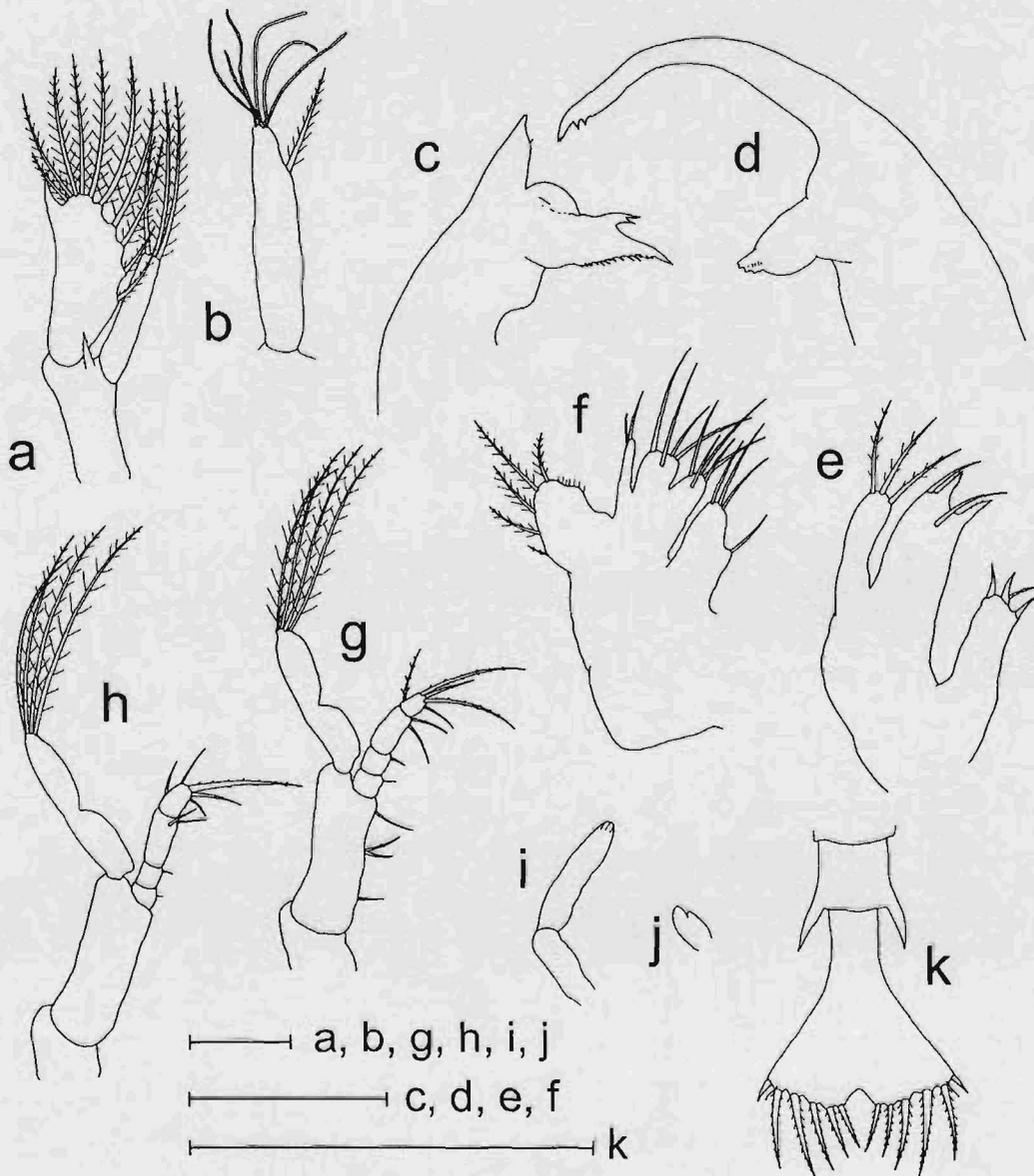


Figure 2. *Axianassa australis*, ZI. (a) Antenna; (b) antennule; (c) right mandible; (d) left mandible; (e) maxillule; (f) maxilla; (g) maxilliped 1; (h) maxilliped 2; (i) maxilliped 3; (j) pereopod 1; (k) telson. Scale bars: 0.2 mm.

produced as on left mandible, sometimes with small denticles; left mandible sickle-shaped, distal end pointed with several teeth, inner surface of base with three to five teeth.

Maxillule (Figure 2e). Coxal endite with three to four marginal setae; basal endite with two setae and two large dentate spines; endopodal lobe not distinct from protopod, with two to three setae on distal margin; protopod without setae.

Maxilla (Figure 2f). Coxal endite bilobed, zero or one setae on proximal lobe, and three to four setae on distal lobe; basal endite bilobed with four to five setae on proximal lobe, three to five setae on distal lobe; endopod with one long and one short terminal setae; scaphognathite with three to five plumose setae.

Maxilliped 1 (Figure 2g). Coxa without setae; basis with 1+2+0-1 setae; endopod four-segmented, with 1, 1, 2, (4-5) setae; exopod unsegmented, four plumose setae on distal margin.

Maxilliped 2 (Figure 2h). Coxa and basis without setae; endopod four-segmented, (0-one), (0-one), (0-two), (4-5) setae; exopod unsegmented, four plumose setae on distal margin.

Maxilliped 3 (Figure 2i). Two segments present, both without setae.

Pereopods (Figure 2j). Pereopod 1 developed as small bilobed bud.

Pleopods. Not developed.

Telson (Figure 2k). Narrow anterior not differentiated from abdominal segment 6, triangular posterior with medial cleft, anal spine absent; (7)+(7) processes on posterior margin arranged as (I, II, III, III, II, I), where I is outermost naked seta, II is very thin "anomuran hair", III is five plumodenticulate setae.

Zoea II (Figures 1, 3a-k)

Size. CL=0.759 ± 0.053 mm, range 0.656-0.824 mm; TL=1.56 ± 0.08 mm, range 1.41-1.69 mm.

Carapace (Figure 1). About same length as abdomen; rostrum elongate, rounded in cross-section, smooth; eyes separate from carapace.

Abdomen (Figure 1). No change from ZI.

Antennule (Figure 3a). Elongate, exopodal and endopodal lobes not distinct; six to seven terminal aesthetascs, one to two thin subterminal aesthetascs; one long plumose seta on future endopodal lobe.

Antenna (Figure 3b). Protopod with one well-developed distal spine between rami and one small distolateral spine near base of endopod; endopod with two to three long, plumose setae; scaphocerite (exopod) armed with one strong distolateral spine, 10-12 plumose setae on inner margin, one specimen with seta on scaphocerite split into two branches at distal end.

Mandible (Figure 3c, d). No change from ZI.

Maxillule (Figure 3e). Coxal endite with three to four marginal setae; basal endite with two to three setae and two to four large dentate spines on distal margin, a single specimen with one seta on lateral margin; endopodal lobe not distinct from protopod, three setae on distal margin; protopod without setae.

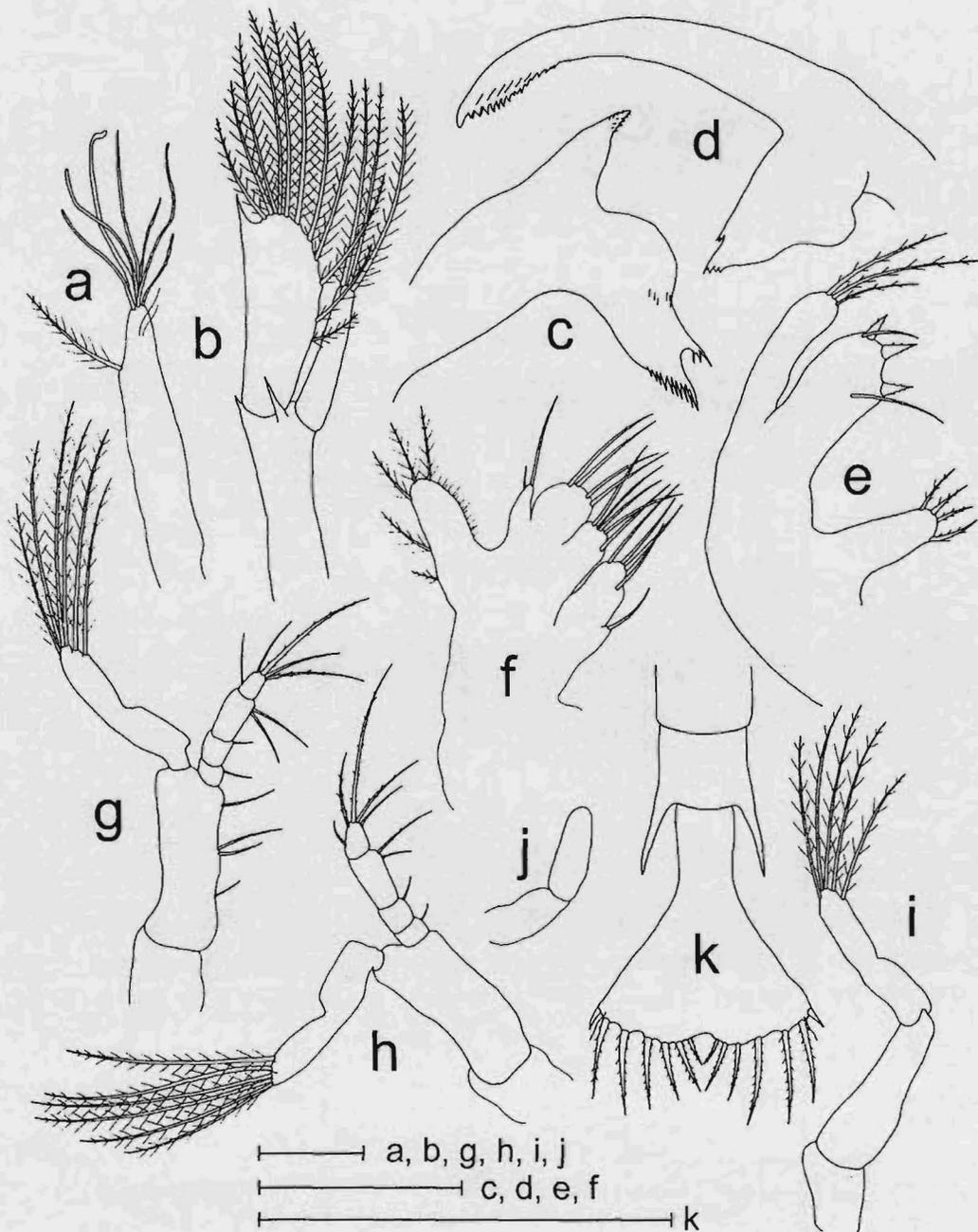


Figure 3. *Axianassa australis*, ZII. (a) Antennule; (b) antenna; (c) right mandible; (d) left mandible; (e) maxillule; (f) maxilla; (g) maxilliped 1; (h) maxilliped 2; (i) maxilliped 3; (j) pereopod 1; (k) telson. Scale bars: 0.2 mm.

Maxilla (Figure 3f). Coxal endite bilobed, one seta on proximal lobe, four setae on distal lobe; basal endite bilobed, four to five setae on proximal lobe, three to four setae on distal lobe; endopod with one long and zero or one short terminal setae; scaphognathite with three to seven plumose setae, row of setal hairs on mesial margin.

Maxilliped 1 (Figure 3g). Coxa without setae; basis with (0-1)+2+1 setae; endopod four-segmented, with 1, 1, 2, (4-5) setae; exopod unsegmented, six plumose setae on distal margin.

Maxilliped 2 (Figure 3h). Coxa and basis without setae; endopod four-segmented, (0-1), (0-1), (1-2), (4-5) setae; exopod unsegmented, six plumose setae on distal margin.

Maxilliped 3 (Figure 3i). Two segments present, distal segment with five plumose setae.

Pereopods (Figure 3j). Pereopod 1 with two segments, no setae present on either segment.

Pleopods. Not developed.

Telson (Figure 3k). Narrow anterior not differentiated from abdominal segment 6, triangular posterior with reduced medial cleft, anal spine absent; (8)+(8) processes on posterior margin arranged as (I, II, III, III, II, I), (I), where I is outermost naked seta, II is very thin "anomuran hair", III is six plumodenticulate setae.

Zoea III (Figures 1, 4a-m)

Size. CL=0.928 ± 0.037 mm, range 0.855-0.992 mm; TL=1.97 ± 0.066 mm, range 1.84-2.06 mm.

Carapace (Figure 1). No change from ZII.

Abdomen (Figure 1). No change from ZII.

Antennule (Figure 4a). Elongate, exopod distinct with six to seven terminal aesthetascs, two to four thin subterminal aesthetascs; endopod not distinct with two long plumose setae on future endopodal lobe; two long plumose setae, two to four small aesthetascs on protopod.

Antenna (Figure 4b). Protopod with one well-developed distal spine and one small distolateral spine near base of scaphocerite (exopod); endopod with one to three long, plumose setae; scaphocerite armed with one strong distolateral spine, 10-13 plumose setae on inner margin, one specimen with seta on scaphocerite split into two branches at distal end.

Mandible (Figure 4c, d). No change from ZII.

Maxillule (Figure 4e). Coxal endite with three to four marginal setae; basal endite with three setae and three to five large dentate spines on distal margin, a single specimen with one seta on lateral margin; endopodal lobe not distinct from protopod, three setae on distal margin; protopod without setae.

Maxilla (Figure 4f). Coxal endite bilobed, zero or one setae on proximal lobe, three to four setae on distal lobe; basal endite bilobed, four to six setae on proximal lobe, three to five setae on distal lobe; endopod with one long and one short terminal setae; scaphognathite with five to nine plumose setae, sometimes with row of setal hairs on mesial margin.

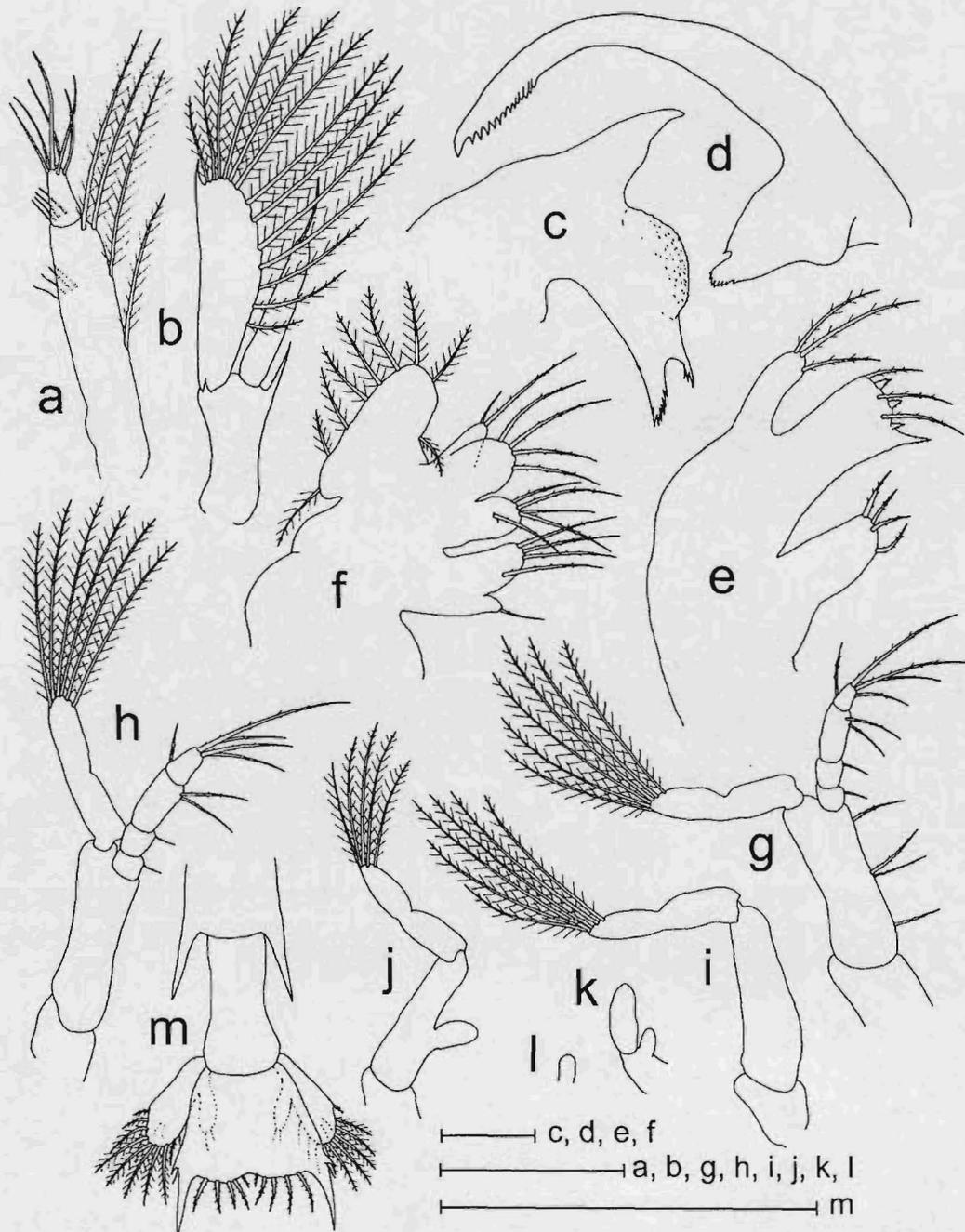


Figure 4. *Axianassa australis*, ZIII. (a) Antennule; (b) antenna; (c) right mandible; (d) left mandible; (e) maxillule; (f) maxilla (plumose condition not shown); (g) maxilliped 1; (h) maxilliped 2; (i) maxilliped 3; (j) pereopod 1; (k) pereopod 2; (l) pereopod 3; (m) telson and uropods. Scale bars: 0.2 mm.

Maxilliped 1 (Figure 4g). No change from ZII.

Maxilliped 2 (Figure 4h). No change from ZII.

Maxilliped 3 (Figure 4i). Two segments present, distal segment with six plumose setae.

Pereopod 1 (Figure 4j). Endopod produced as small lobe without setae, exopod differentiated from basis, with four to six plumose setae.

Pereopod 2 (Figure 4k). Endopod produced as small lobe without setae, exopod differentiated from basis, without setae in most specimens; one specimen with developed appendage bearing four to five setae on exopod.

Pereopod 3 (Figure 4l). Produced as small bud in most specimens, as bilobed structure in one specimen.

Pleopods. Not developed.

Telson and uropods (Figure 4m). Telson subquadrate, anterior differentiated from abdominal segment 6, anal spine absent; (7-9)+(5-9) processes on posterior margin arranged as (I, II, III, IV, IV, III, II, I), where I is outermost unarticulated spine, II is very thin "anomuran hair", III is elongate unarticulated spine, IV is two to six plumodenticulate setae; one specimen with additional small spine located between processes II and III. Uropods biramous, endopod produced as a large lobe not fully separated from exopod, bearing two small setae, exopod with 8-10 marginal plumose setae, zero to two submarginal setae.

Decapodid (first postlarva) (Figures 1, 5a-k, 6a-m)

Size. CL=1.63mm, range 1.62-1.64 mm; TL=4.02 mm, range 4.01-4.03 mm.

Carapace (Figure 1). Shorter than abdomen, no anterolateral serrations, with pterygostomial projections; rostrum reduced, without serrations, slightly deflected between eyes.

Abdomen (Figure 1). Somites rectangular in dorsal outline, posterior projections rounded, bearing zero to five setae.

Antennule (Figure 5a). Peduncle three-segmented, proximal segment with 9-12+1 setae, 9-12 of these associated with statocyst; intermediate segment with 5-6+1 setae; distal segment of peduncle with eight setae, three of these clumped at distal end; endopod with two or three segments, with 0, 1, 3 setae; exopod five-segmented, (0), (2 setae+1 asthetasc), (2-3 setae+2 asthetascs), (2-3 setae+2 asthetascs), (4-5 setae).

Antenna (Figure 5b). Peduncle four-segmented (proximal segment not shown) with 0-1 setae, 2-3 setae and small spine on inner margin, 5-6 setae, 4 setae; flagellum ranging from 23-29 segments with zero to nine setae per article; exopod reduced to lobe with two to four setae.

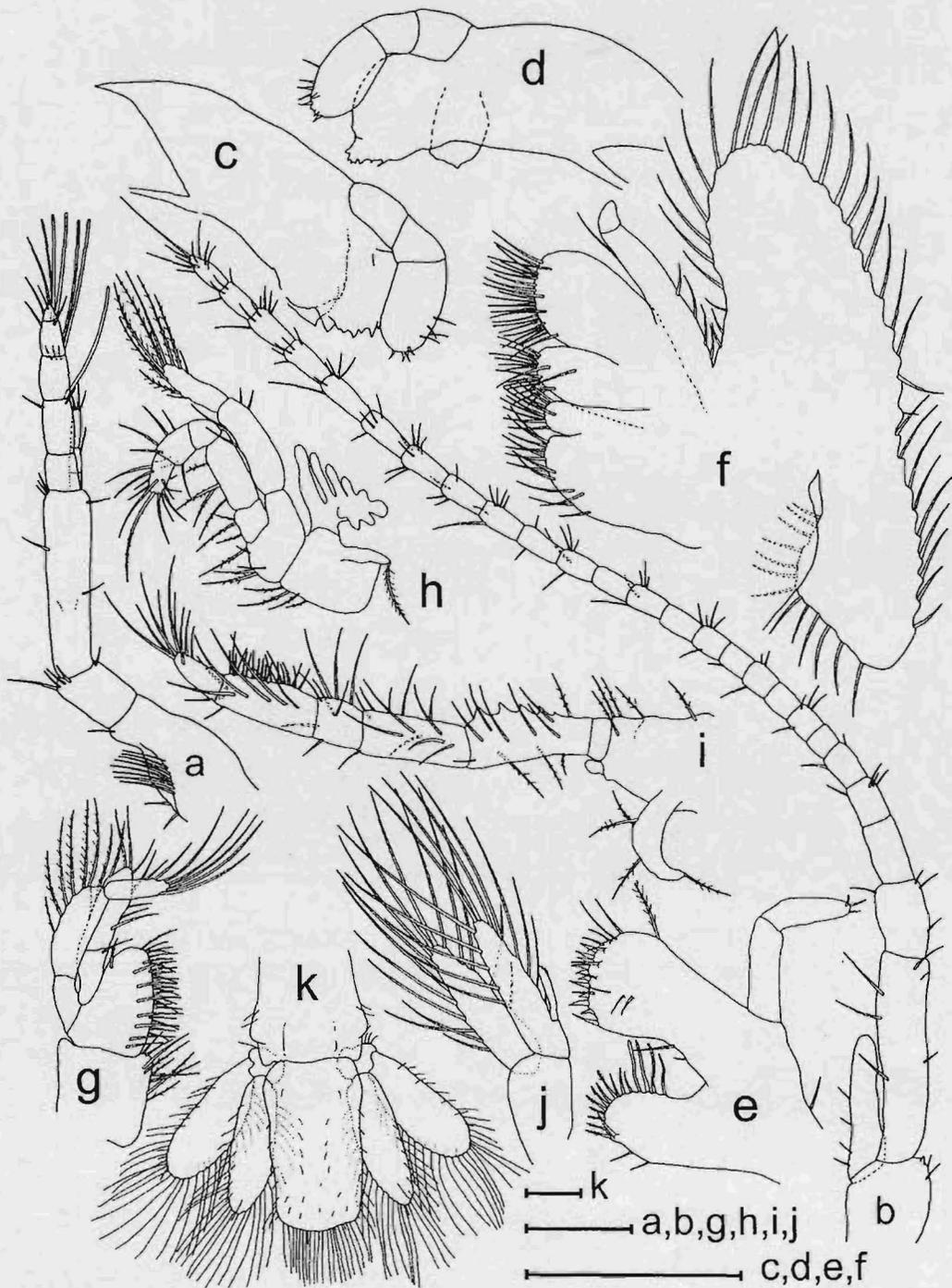


Figure 5. *Axianassa australis*, decapodid. (a) Antennule; (b) antenna; (c) right mandible; (d) left mandible; (e) maxillule; (f) maxilla (plumose condition not shown); (g) maxilliped 1; (h) maxilliped 2; (i) maxilliped 3; (j) pleopod (plumose condition not shown); (k) telson and uropods (plumose condition not shown). Scale bars: 0.2 mm.

Mandible (Figure 5c, d). Right and left mandibles similar, incisor process with five to six teeth, molar process with small ridges; palp three-segmented, 0, 0, (8–11) setae.

Maxillule (Figure 5e). Coxal endite with 16–18 setae; basal endite with two lateral plumose setae, eight to nine submarginal setae, 11–12 dentate spines, one plumose seta on inner margin; endopod two-segmented with 0, 3 setae.

Maxilla (Figure 5f). Coxal endite bilobed, (13–16)+(7–8) setae; basal endite bilobed, 16–18 setae on proximal lobe, 22–29 setae on distal lobe; endopod reduced with 3–4+1 setae; scaphognathite with 37–48 setae.

Maxilliped 1 (Figure 5g). Coxa with 9–12 setae; basis highly setose with 29–34+1 setae; endopod two-segmented, with 1, 10–12 setae; exopod three-segmented with 0, 6–7, 7 setae.

Maxilliped 2 (Figure 5h). Coxa with four to five setae; basis with four to five setae; endopod five-segmented, with 2–3, 4–5, 0, 6–7, 9–12 setae; exopod two-segmented, proximal segment with one or two setae on inner margin, two to three setae on distal outer margin, distal segment with seven to nine setae; epipod with zero or one setae.

Maxilliped 3 (Figure 5i). Coxa partially fused to basis, with zero to two setae; basis with zero to two setae; endopod five-segmented, 5 spines+(9–11) setae, 12, 8, (22–28), (8–11) setae; exopod small lobe without setae, epipod present with four to five setae.

Pereopod 1 (Figure 6a). Chelate, seven-segmented; coxa with 1–2+3–5 setae; basis with one to four setae; ischium with six to eight setae; merus with seven to nine setae; carpus with three to six setae; propodus with 27–30 setae and five to six spines on inner margin of immovable finger; dactylus with 20–24 setae; exopod absent.

Pereopod 2 (Figure 6b). Seven-segmented; coxa with two to six setae; basis with zero to two setae; ischium with four to six setae; merus with 16–18 setae; carpus with six to eight setae; propodus with 19–22 setae; dactylus with 15–17 setae and few small spines on inner margin; exopod reduced with zero to four setae, or absent.

Pereopod 3 (Figure 6c). Seven-segmented; coxa with zero to three setae; basis with zero to three setae; ischium with four to six setae; merus with 9–11 setae; carpus with five to six setae; propodus with 13–16 setae; dactylus with 12–14 setae and six spines on inner margin, and one small spine on outer margin; exopod absent.

Pereopod 4 (Figure 6d). Seven-segmented; coxa (not shown) without setae; basis with zero to two setae; ischium with five to six setae; merus with 8–10 setae; carpus with four to five setae; propodus 9–11 setae; dactylus with 12–13 setae, seven unarticulated spines on inner margin, two articulated spines on outer margin; exopod reduced with four setae, or absent.

Pereopod 5 (Figure 6e). Seven-segmented; coxa with zero or one setae; basis with zero to two setae; ischium with four to five setae; merus with five setae; carpus with three setae; propodus with 19–22 setae and two small unarticulated spines; dactylus with seven to nine setae and row of small unarticulated spines; exopod absent.

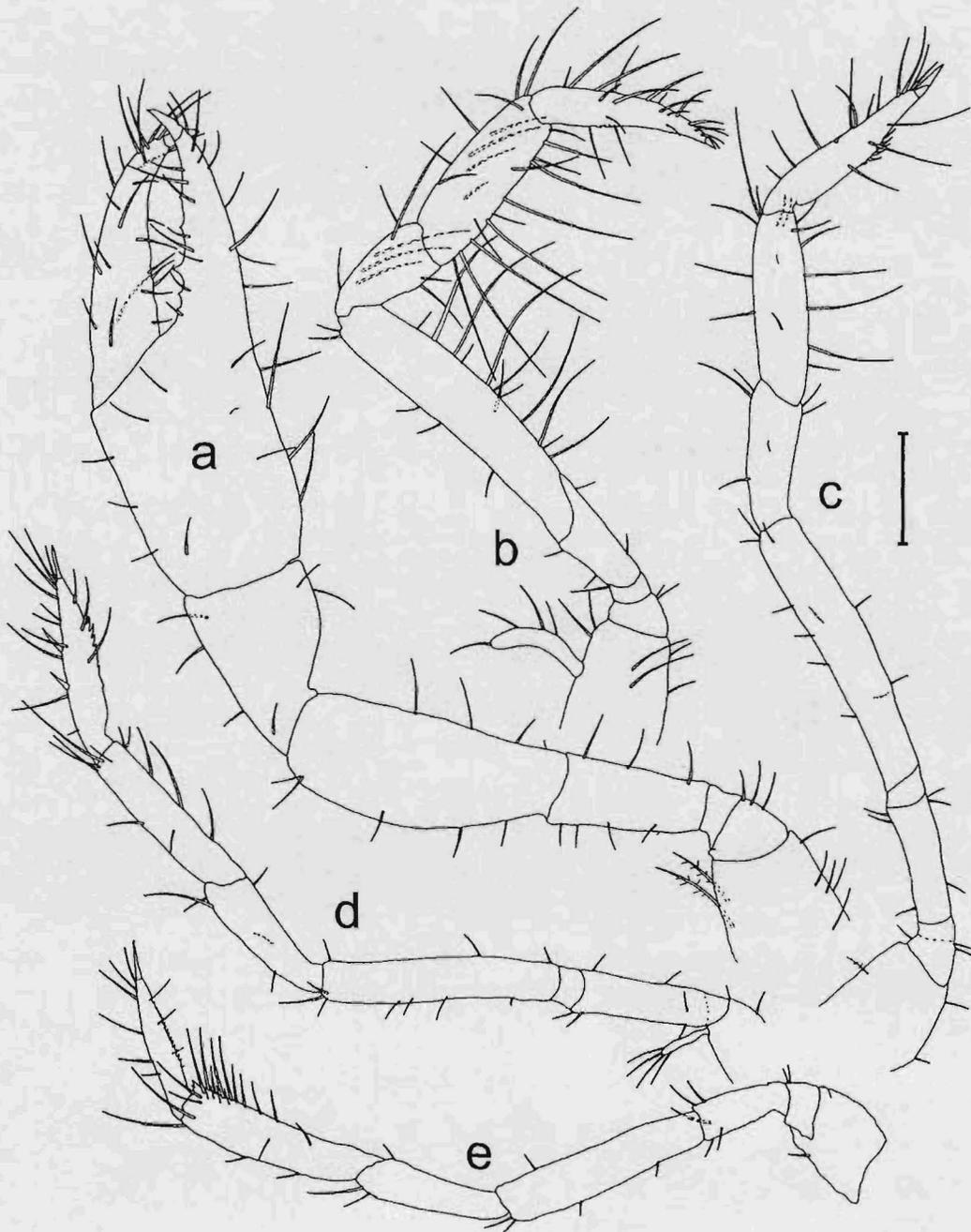


Figure 6. *Axianassa australis*, decapodid. (a) Pereopod 1; (b) pereopod 2; (c) pereopod 3; (d) pereopod 4; (e) pereopod 5. Scale bar: 0.2 mm.

Pleopods (Figure 5j). Biramous, coxa fused to basis, without setae; basis without setae; endopod with four to five hooked setae on appendix interna, 11–13 marginal plumose setae; exopod with 13–15 marginal, plumose setae.

Telson and uropods (Figure 5k). With 34–38 marginal processes, numerous small setae on dorsal surface; uropods biramous, endopod with 24–25 marginal plumose setae, six to seven submarginal setae, exopod with 28–33 marginal plumose setae, nine submarginal setae, protopod with one to three setae.

Discussion

Although there appear to be some differences between wild-caught larvae of *Axianassa* from the southwestern Gulf of Mexico (Ngoc-Ho 1981), larvae of *A. australis* described from Brazil (Rodriguez and Shimizu 1992) and the presently reported larvae of *A. australis* from the northern Gulf of Mexico and Atlantic coast of Florida, numerous similarities (Table I) suggest that these larvae represent the same or very closely related species. This is supported by preliminary comparisons of gene sequences of adult populations from these four areas (Felder 2001; R. Robles and D. Felder, personal communication). It was previously reported that ZI larvae of *A. australis* from Brazil had a single orange chromatophore on the mid-anterior section of the carapace (Rodriguez and Shimizu 1992). This would differ strikingly from the chromatophore patterns we observed in Texas and Florida populations of *A. australis*, which include large, red, paired chromatophores on the telson and fifth abdominal somite, as well as smaller, paired chromatophores on the lateral-proximal ends of the carapace (Figure 2). However, recently obtained photographs of larvae hatched from a Brazilian female specimen identified as *A. australis* (F. Mantelatto, personal communication) indicate that these zoeal stages also have the distinctive paired chromatophores characteristic of the larvae we reared from the northern Gulf of Mexico and Florida. There thus appears to be little or no difference in carapacial chromatophore patterns.

The long dispersal phase of *A. australis* (likely to be at least 1 month) could certainly account in part for its extended distribution in the western Atlantic. The larvae of *A. australis* appear to be very close to those reported by Gurney (1938) as “Laomediid D.I.”, which might be interpreted to suggest an even broader distribution. Among materials that Gurney assigned to this form were specimens from Samoa, the Great Barrier Reef and the western Atlantic, the latter from off the north-east coast of Brazil and apparently the materials he illustrated. Rodriguez and Shimizu (1992) noted that the ZI they described for

Table II. Important similarities and differences of *Axianassa australis* with members of the family Ubogebiidae.

Differences from upogebiids (Ngoc-Ho 1981) (in part)
• Higher number of larval stages
• Unsegmented endopod of maxillule and general shape of maxillule and maxilla
• Asymmetrical mandibles (left being sickle-shaped)
• Rudimentary endopod of maxilliped 3
• Presence of appendix interna on pleopod of postlarva
• Absence of anal spine
Important similarities to ubogebiids (not found in other Laomediids): (<i>U. edulis</i> Shy and Chen 1993; <i>U. guddusiae</i> Siddiqui and Tirmizi 1995; <i>U. affinis</i> and <i>Upogebia</i> sp. Ngoc-Ho 1981)
• Presence of lateral spines on abdominal somite 5
• Laterodistal spine on scale of antenna
• Rostrum straight or curved downward
• Telson with first process as articulated spine, second as anomuran hair, 3-i as plumose/plumodenticulate setae in ZI
• Medial cleft present but not extremely pronounced

A. australis was similar to Gurney's description except for their lacking a spine on the antennal protopod and rudimentary pereopod 1 that occur in the ZI of "Laomediid D.I." Both of these characters are present in the ZI of *A. australis* from Texas and Florida, as well as in larvae of *Axianassa* sp. described by Ngoc-Ho (1981), although a rudimentary pereopod 2 was also noted in the latter description. However, neither our specimens nor those of Ngoc-Ho have pleural spines on somites 2-4 at any zoeal stage, and these are conspicuously evident in the illustrated materials of "Laomediid D.I." It is likely that these pleural spines are present in the ZI of "Laomediid D.I.", as no mention was made to the contrary, but they do not appear in the ZI of *A. australis* illustrated by Rodriguez and Shimizu (1992).

Gurney (1938) specifically referred to the pleural spines on somites 2-4 of "Laomediid D.I." as one of few features distinguishing it from otherwise very similar materials reported by Menon (1933) from Madras. Thus, it is doubtful that Gurney's materials are conspecific

Table III. Comparison of first zoeal stage in *Axianassa australis*, *Laomedea astacina* (Fukuda 1982) and *Naushonia crangonoides* (Goy and Provenzano 1978), and *Jaxea novaezealandiae* (Gurney 1924; Wear and Yaldwyn 1966).

Comparison of ZI characters	<i>L. astacina</i> (Fukuda 1982), Kumamoto, Japan	<i>N. crangonoides</i> (Goy and Provenzano 1978), Virginia, USA	<i>J. novaezealandiae</i> (Gurney 1924; Wear and Yaldwyn 1966), New Zealand	<i>A. australis</i> (present study), Florida and Texas, USA
Important similarities				
Antennal scale unsegmented, endopod with 3 plumose setae	Yes	Yes	? ^a	Yes
Mandibles asymmetrical, left mandible sickle-shaped	Yes	Yes	Yes	Yes
Anal spine absent	Yes	Yes	Yes (likely)	Yes
Major differences				
Comparison of general body shape	Long and narrow, CL about one-third of TL	Long and narrow, CL about one-third of TL	Long and narrow, CL < one-third of TL ^b	Stout, CL about one-half of TL
Procurved pleural spines on abdominal segments 1-5	Present	Present	Present	Absent
Lateral spines on abdominal segment 5	Absent	Absent	Absent	Present
Laterodistal spine on scale of antenna	Absent	Absent	Likely absent ^c	Present
Rostrum	Distally trifid	Curves upward at tip	Curves downward, ending in point	Straight, ending in point
Telson: shape	Deep medial cleft	Deep medial cleft	Deep medial cleft	Medial cleft present but not as pronounced
Telson: article 1	Unarticulated spine	Unarticulated spine	Unarticulated spine	Articulated spine
Maxilliped 1: endopod	With 2, 1, 2, 5 setae	With 2, 1, 2, 5 setae	?	With 1, 1, 2, 4-5 setae

^aDescriptions of the first zoeal stage of *Jaxea novaezealandiae* (Wear and Yaldwyn 1966) and *Jaxea* sp. (Gurney 1924) were not complete. ^bCarapace length estimated from illustration (Figure 3A) by Wear and Yaldwyn (1966).

^cDistal spine is likely absent on scaphocerite of antenna in ZI as it is not mentioned by Gurney (1924) and appears to be absent at ZIII (Wear and Yaldwyn 1966).

Table IV. Important differences between the decapodid stage of *Axianassa australis*, *Jaxea novaezealandiae* (Wear and Yaldwyn 1966), and *Naushonia crangonoides* (Goy and Provenzano 1978).

Comparison of decapodid characters	<i>N. crangonoides</i> (Goy and Provenzano 1978)	<i>J. novaezealandiae</i> (Wear and Yaldwyn 1966)	<i>A. australis</i> (present study)
Carapace	With supra-antennal spines		Without supra-antennal spines
Antennule: peduncle	4-segmented	?	3-segmented
Telson	Posterior margin very rounded, with small lateral spines	Rectangular in dorsal outline, lateral margins toothed	Rectangular in dorsal outline, with posterior margin slightly rounded, without small lateral spines
Pereopod 1	Subchelate	Chelate	Chelate
Uropods	Serrate transverse sutures on endopods and exopods	Serrate transverse sutures on endopods and exopods	Transverse sutures not present
Pleopods: appendix interna	Absent	?	Present

with *A. australis*, and there is no reason to conclude from his reports that the latter species ranges into Pacific Ocean waters. While *A. australis*, in the absence of pleural spines on somites 2–4 and several other features, does resemble the larvae from Madras that Menon (1933) tentatively placed with the upogebiids, it differs in a number of other characters (summarized by Ngoc-Ho 1981, p 251) from those Indian Ocean materials. Nonetheless, the occurrence of such similar larvae in Pacific and Indian Ocean waters suggests a broad distribution for close relatives of *A. australis*, which has yet to be established on the basis of adult materials.

The genus *Axianassa* has at times been placed in the monotypic family Axianassidae or alternatively grouped with several other genera in the Laomediidae (see Kensley and Heard 1990 for review). Ngoc-Ho (1981) placed her larval specimens of *Axianassa* sp. into a group separated from other genera of laomediids (*Naushonia*, *Jaxea*, and *Laomedia*) on the basis of their distinct morphology. Major defining characters include the presence of lateral spines on abdominal somite 5, an appendix interna on the pleopods of the decapodid (presumed by Ngoc-Ho, demonstrated in present study), and an apical spine on the antennal scale in *Axianassa*, all of which can serve to distinguish this genus and thus separate the Axianassidae from the Laomediidae s.s. The separation is also apparently supported by lack of transverse uropodal sutures in the postlarvae of *Axianassa*, a feature present in all known postlarvae of the true laomediids s.s.

It would appear that larval development of *Axianassa* has almost as many similarities with species of the family Upogebiidae (Table II) as it does with those of the family Laomediidae s.s. (Tables III, IV), which accounts for why Menon (1933) placed larvae of this form in the former group. Recent molecular genetic studies also argue for phylogenetic placement of *Axianassa* in an intermediate position between these families, and thus for resurrection of the family Axianassidae (Tudge and Cunningham 2002). As now known, larval morphology clearly supports this conclusion.

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