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LARVAL DEVELOPMENT OF THE GHOST SHRIMP *CALLICHIRUS ISLAGRANDE* (DECAPODA: THALASSINIDEA: CALLIANASSIDAE) UNDER LABORATORY CONDITIONS

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ABSTRACT

Descriptions of the zoeal and decapodid stages of the ghost shrimp *Callichirus islagrande* were based on laboratory cultures from a population inhabiting the coast of Louisiana. Whereas morphological studies were based upon animals from mass cultures, 40–120 larvae from each of 8 parental females were reared individually to obtain stage-duration data. Larvae passed through 4 or 5 zoeal stages before molting to the decapodid stage. The proportion of individuals that molted to a fifth zoeal stage varied widely (9–89%) between clutches of different parental females. The first juvenile stage was usually reached 16–20 days after hatching, and durations of larval stages were similar in larvae from different females. Morphological comparisons with congeneric species revealed larvae of *C. islagrande* to be more similar to larvae of *C. garthi,* a species from the coast of Chile, than to larvae of a Gulf of Mexico population of *Callichirus major.*

In a recent revision of the Callianassidae (Manning and Felder, 1991), the genus *Callianassa* was restricted from its former worldwide status to certain eastern Atlantic populations based on morphological characters. American species that were previously included in the genus *Callianassa* were placed in a number of genera, based on life history and morphology, as in the case of the genus *Callichirus*. As redefined by Manning and Felder (1986), the genus *Callichirus* now includes at minimum *C. major* (Say, 1818), *C. islagrande* (Schmitt, 1935), *C. seilacheri* (Bott, 1955), *C. garthi* (Retamal, 1975), and *C. adamas* (Kensley, 1974), and at least one undescribed species from the Atlantic coasts of Brazil and Colombia which has been often referred to as *C. major* (see Staton and Felder, 1995; D. L. Felder, personal observation). For a number of other callianassid species, generic status remains unresolved, and they will herein be referred to as *Callianassa* sensu lato (s.l.).

Detailed descriptions of larvae are available for relatively few species in the family Callianassidae, all of which currently fall into the subfamilies Callianassinae (*Callianassa* s.l. *kewalramanii* Sankolli, Sankolli, and Shenoy, 1975; *Neotrypaea uncinata* (H. Milne Edwards), Aste and Retamal, 1984; *C.* s.l. *petalura* Stimpson, Konishi *et al.*, 1990), and Callichirinae (*Callichirus* sp. (formerly *C. major*), Rodrigues, 1976; *C. garthi* (Retamal), Aste and Retamal, 1983; *Sergio mirim* (Rodrigues), Rodrigues, 1984; *Lepidophthalmus louisianensis* (Schmitt), *L. sinuensis* Lemaitre and Rodrigues, Nates *et al.*, 1997; *Callichirus major,* Strasser and Felder, 1999a). Larval development of *Callichirus islagrande* has not been described, even though this species is well studied (Felder and Griffis, 1994; Staton and Felder, 1995; Strasser and Felder, 1998, 1999b).

Callichirus islagrande is a Gulf of Mexico endemic found typically on barrier islands in low to high intertidal habitats. This species inhabits the northern and western Gulf of Mexico ranging from northwestern Florida to Paraiso, Tabasco, Mexico (Staton and Felder, 1995). A somewhat discontinuous distribution of *C. islagrande* occurs between southeastern Louisiana and the northeastern coast of Texas where shorelines tend to lack the cleaner quartzite sand and high energy beaches that *C. islagrande* prefers (Staton and Felder, 1995).

The present study describes the zoeal and decapodid stages, provides illustrations for identification, and reports the number and duration of larval stages of *Callichirus islagrande*. Comparisons of these characteristics in *C. islagrande* are made with other congeneric species and members of the family Callianassidae.

Materials and Methods

Ovigerous females were collected in March, May, and July, 1996, from the bayward side of a barrier island (Isles Dernieres, Louisiana) with yabby pumps (as in Felder, 1978). Adult females were maintained in 20-cm diameter finger bowls (at 27°C, 25 ppt salinity) with daily water changes until eggs hatched. Sea water was taken from well offshore Louisiana, filtered through a 30-μm screen, aerated, and diluted to 25 ppt salinity with deionized water before use in the culture of animals. To determine stage durations, 40–120 larvae from each of 8 parental females were reared individually through the first juvenile stage (J1). ZI (first zoeal stage) larvae were moved to individual compartments upon hatching and maintained at 27°C, in filtered sea water, on a 12:12 light : dark cycle. Each day larvae were moved to containers with new sea water, fed freshly hatched nauplii of *Artemia* (Great Salt Lake), and examined to assess their stage of development. Observations were terminated when animals reached the first juvenile stage (J1).

Animals used for morphological comparisons were obtained from mass cultures. 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 chlorozol black, and transferred to glycerine prior to dissection. At least 10 animals were dissected for each 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 Konishi (1989) and Nates *et al.* (1997). 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

Although there was no attempt to quantify the duration of embryonic development, ovigerous females were held for up to 28 days before the eggs hatched (usually at night). Prior to hatching, eggs changed gradually in color from bright orange-red to a translucent-brown. Late-stage embryos that were dropped by the female before hatching and larvae that hatched as prezoeae were not viable, even with aeration. Prezoeae did not appear to be developed fully and could not swim. All zoeal stages fed readily on nauplii of *Artemia* as well as on each other. The decapodid stage (D) appeared to consume much less than did the preceding zoeal stage. Strong positive phototaxis was exhibited by the first three zoeal (ZI to ZIII) stages. The fourth zoeal stage (ZIV) in general appeared to be attracted to light, although some larvae reacted indifferently. Decapodids did not exhibit obvious phototaxis.

Larvae of *Callichirus islagrande* passed through four or five zoeal stages before molting to D (Fig. 1); these were usually completed 11–14 days after hatching. Mean durations of each stage were relatively consistent between larvae from different females (Table 1). However, duration of ZIV was approximately a day shorter when animals molted from ZIV to ZV than when animals molted directly to D (Table 2). Among the eight cultures observed in this study, the percentage of animals molting to ZV ranged from 9–89% of the larvae that survived past ZIV.

Description of Zoeal and Decapodid Stages

Near the mandibles, the larval stages and decapodid had two red chromatophores which usually appeared fused when expanded. Sev-

Table 1. Mean duration in days (±95% CI) of the first to fifth zoeal stages (ZI to ZV), and the decapodid stage (D) in larval cultures from 8 ovigerous females of *Callichirus islagrande*. Each culture consists of larvae from a different parental female. Only animals that reached J1 (N) were used to calculate mean durations; N_0 is the starting number of ZI larvae.

Culture	N	N_0	ZI	ZII	ZIII	ZIV	ZV	D
1	100	120	2.26 (±0.09)	2.04 (±0.05)	2.22 (±0.09)	3.88 (±0.09)	3.89 (±0.12)	5.70 (±0.22)
2	14	60	2.07 (±0.16)	2.00 (±0.00)	2.50 (±0.31)	3.36 (±0.60)	4.30 (±0.28)	6.64 (±1.17)
3	34	55	2.06 (±0.08)	2.06 (±0.08)	2.44 (±0.17)	4.21 (±0.24)	4.20 (±0.16)	5.68 (±0.39)
4	102	120	2.05 (±0.04)	2.02 (±0.05)	2.32 (±0.10)	3.59 (±0.10)	3.20 (±0.09)	5.18 (±0.28)
5	31	40	2.05 (±0.11)	2.00 (±0.00)	2.26 (±0.16)	3.23 (±0.28)	4.00 (±0.37)	4.94 (±0.23)
6	49	60	2.06 (±0.07)	2.04 (±0.08)	2.43 (±0.14)	3.39 (±0.20)	3.64 (±0.18)	5.47 (±0.46)
7	36	54	2.17 (±0.13)	2.11 (±0.11)	2.14 (±0.12)	2.94 (±0.21)	3.27 (±0.15)	4.39 (±0.19)
8	44	60	2.16 (±0.13)	2.25 (±0.15)	2.36 (±0.17)	3.16 (±0.26)	3.42 (±0.17)	4.30 (±0.30)

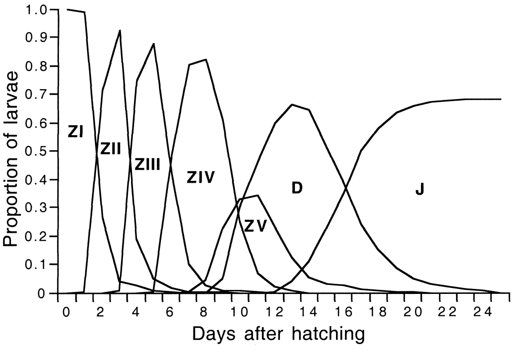

Fig. 1. Mean proportion of larvae at each stage during development of *Callichirus islagrande*. Mean proportions are derived from the individual rearings of 8 parental females. The first through fifth zoeal stages (ZI to ZV), the decapodid stage (D), and all first-stage juveniles that passed D (J) are labeled under the peak of each line.

eral other red chromatophores were present on the lateral edges of the carapace forming a red line when expanded.

Morphological descriptions of *Callichirus islagrande* are as detailed below for stages ZI to ZIV, and D. ZV resembled ZIV in appearance. However, appendages were like those of ZIV, D, or some gradation between the two. Setal patterns are given from proximal to distal segments for each appendage. Carapace length (CL) and total length (TL) are given as the mean ± 95% CI in mm, followed by the range of measurements from 10 specimens.

Zoea I
Figs. 2a, 3a–j

Size.—CL = 1.23 ± 0.06 mm, range 1.10–1.41 mm; TL = 3.26 ± 0.07 mm, range 3.11–3.36 mm.

Carapace (Fig. 2a).—Shorter than abdomen; rostrum elongate, rounded in cross section, and smooth; eyes fused to carapace.

Abdomen (Fig. 2a).—Somites 2–5 with posterolateral projections and posterodorsal spines; dorsal spine elongate on somite 2, sometimes extending beyond posterior margin of somite 3; short dorsal spines on somites 3–5.

Antennule (Fig. 3a).—Elongate, exopodal and endopodal lobes not distinct; 4–6 terminal aesthetascs; 1 long plumose seta on future endopodal lobe.

Antenna (Fig. 3b).—Protopod with 1 distal spine between rami; endopod with 2 long, plumose setae; scaphocerite (exopod) armed with 1 strong distolateral spine, 8 plumose setae on inner margin, and 1 plumose seta on outer margin.

Mandible (Fig. 3c, d).—Incisor process with 6 or 7 teeth on right mandible, 5–7 teeth on left mandible; molar process denticulate on both mandibles.

Maxillule (Fig. 3e).—Coxal endite with 8–10 marginal setae; basal endite with 3 plumose setae, 3 or 4 large dentate spines, and 4 or 5 smaller dentate spines, inner margin with 0 or 1 plumose seta; endopod 3-segmented, distinction between segments sometimes obscure, 2, 2, (3 or 4) setae; protopod without setae.

Maxilla (Fig. 3f).—Coxal endite bilobed, 11 or 12 setae on proximal lobe, and 4 or 5 se-

Table 2. Percentage of larval *Callichirus islangrande* that molted from the fourth zoeal stage (ZIV) to the fifth zoeal stage (ZV), or directly to the decapodid stage (D) in larval cultures from 8 ovigerous females (Culture numbers 1–8). Each batch consisted of larvae from a different parental female. N_0 = number surviving beyond ZIV; N_1 = number molting ZIV to ZV; N_{1J} = percentage of N_1 surviving to J1; N_2 = number molting ZIV to D; N_{2J} = percentage of N_2 surviving to J1. The mean duration in days (±95% CI) is given for animals that molted from ZIV to ZV, and from ZIV to D.

	From ZIV	To ZV			To D		
Culture	N_0	N_1	Survived to J1 N_{1J}	Duration of ZIV	N_2	Survived to J1 N_{2J}	Duration of ZIV
1	105	11	82	3.0 (±0.30)	94	97	4.0 (±0.08)
2	47	42	24	3.2 (±0.23)	5	80	4.4 (±1.11)
3	45	8	62	3.0 (±0.0)	37	78	4.4 (±0.18)
4	109	10	50	3.1 (±0.78)	99	98	3.6 (±0.10)
5	38	19	79	2.8 (±0.26)	19	84	3.7 (±0.27)
6	58	35	80	3.1 (±0.17)	23	91	3.9 (±0.30)
7	48	30	73	2.6 (±0.23)	18	78	3.4 (±0.25)
8	51	29	83	2.6 (±0.19)	22	91	3.8 (±0.19)

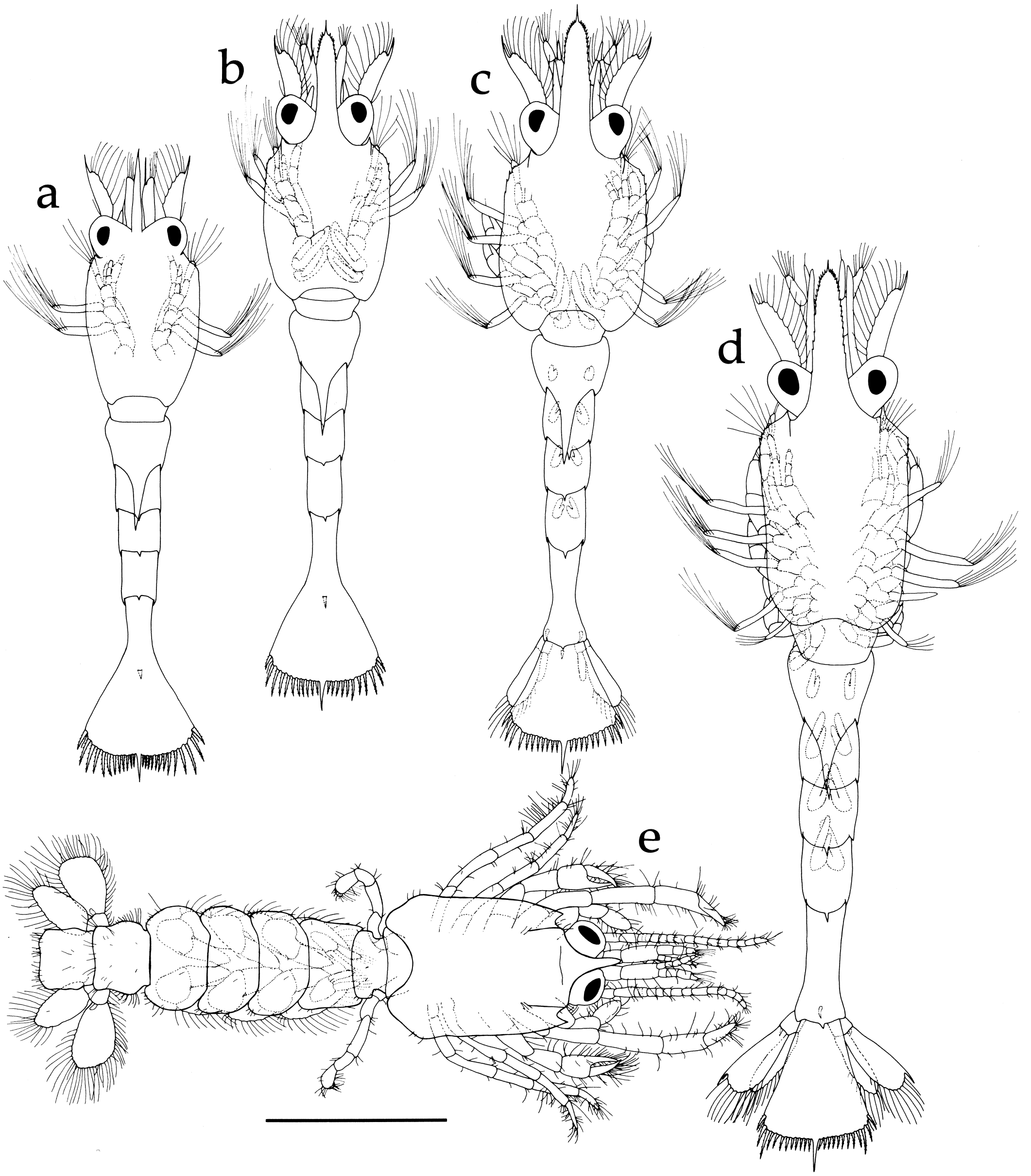

Fig. 2. *Callichirus islagrande,* dorsal view of larvae and decapodid: a, ZI stage; b, ZII stage; c, ZIII stage; d, ZIV stage; e, decapodid stage. Scale = 1 mm.

tae on distal lobe; basal edite bilobed with 6–9 setae on each lobe; endopod with 5 lobes, 3+2+2+2+(2 or 3) setae; scaphognathite with 16–19 setae; all setae plumose.

Maxilliped 1 (Fig. 3g).—Coxa with 4–8 setae; basis with 12–17 setae; endopod 4-segmented, (3 or 4), (1 or 2), (1–3), (3 or 4) setae; exopod 2-segmented, proximal segment without setae, distal segment with 5 or 6 setae on distal margin; bilobed epipod without setae; all setae plumose.

Maxilliped 2 (Fig. 3h).—Coxa with 1 or 2 setae; basis with 3–6 setae; endopod 4-segmented, (4 or 5), (0 or 1), (1 or 2), (3–6) setae; exopod unsegmented, 6–8 setae on distal margin; all setae plumose.

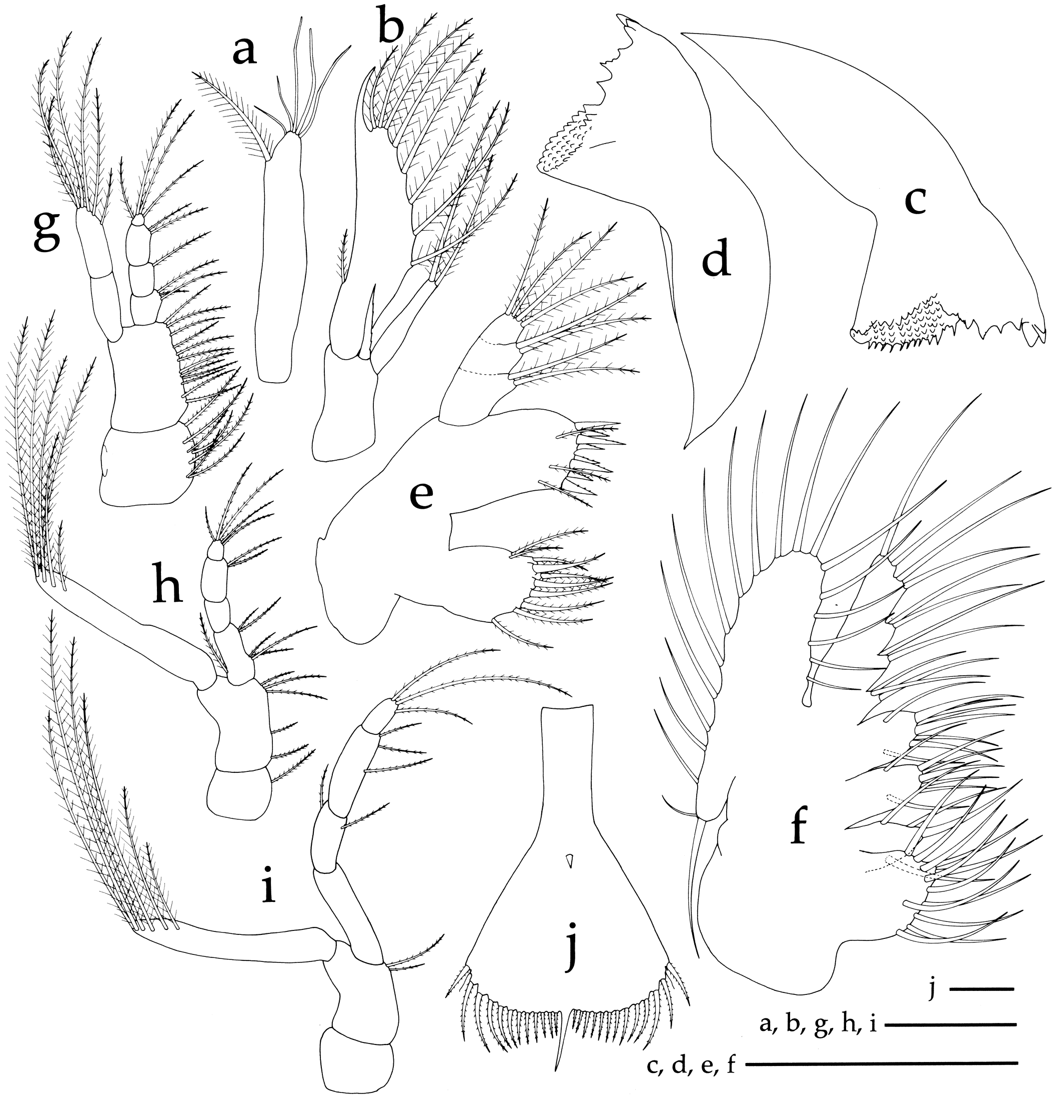

Fig. 3. *Callichirus islagrande,* ZI stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2; i, maxilliped 3; j, telson. Scales = 0.2 mm.

Maxilliped 3 (Fig. 3i).—Coxa with 0 or 1 seta; basis with 1 or 2 setae; endopod 4-segmented, (0 or 1), (0–2), (2 or 3), (3–5) setae; exopod unsegmented, 6–8 setae on distal margin; all setae plumose.

Pereiopods.—Not developed.

Pleopods.—Not developed.

Telson (Fig. 3j).—Narrow anterior not differentiated from abdominal segment 6, triangular posterior, anal spine present; with (12–14)+1+(13 or 14) processes on posterior margin arranged as (I, II, III, IV, III, II, I), (I) outermost process a plumodenticulate seta, (II) second process "anomuran hair," (III) 10–12 plumodenticulate setae, and (IV) center process a naked spine, longer than other processes.

Zoea II

Figs. 2b, 4a–l

Size.—CL = 1.44 ± 0.03 mm, range 1.38–1.53 mm; TL = 3.64 ± 0.06 mm, range 3.55–3.80 mm.

Carapace (Fig. 2b).—With antennal spines, anterolateral margins serrated; rostrum broad and dorsoventrally flattened, with thin distal projection and distolateral serrations; eyes separated from carapace.

Abdomen (Fig. 2b).—No marked change from stage ZI.

Antennule (Fig. 4a).—Elongate, weakly bilobed; peduncle weakly 2-segmented, 0–3 short setae on distal margin of proximal segment, 2 long plumose setae and 0–3 short setae on distal end of distal segment; endopod with 1 terminal plumose seta; exopodite with 6–8 terminal aesthetascs.

Antenna (Fig. 4b).—Protopod with 2 distal spines, 1 on outer margin and 1 between rami; endopod without setae; scaphocerite armed with 1 strong distolateral spine, 10 or 11 plumose setae on inner margin, and 1 plumose seta on outer margin.

Mandible (Fig. 4c, d).—No marked change from ZI.

Maxillule (Fig. 4e).—Coxal endite with 8–10 marginal plumose setae; basal endite with 3 plumose setae, 4 or 5 large dentate spines, and 4 or 5 smaller dentate spines, inner margin with 0 or 1 plumose seta; endopod 3-segmented, distinction between segments sometimes obscure, 2, 2, (4 or 5) setae; protopod without setae.

Maxilla (Fig. 4f).—Coxal endite bilobed, 12–15 setae on proximal lobe, 4 or 5 setae on distal lobe; basal endite bilobed with 6–8 setae on proximal lobe, 5–9 setae on distal lobe; endopod with 5 lobes, (2 or 3)+2+2+2+3 setae; scaphognathite with 19–24 setae; all setae plumose.

Maxilliped 1 (Fig. 4g).—Coxa with 4–8 setae; basis with 13–17 marginal setae; endopod 4-segmented, (3 or 4), (2 or 3), (1 or 2), 4 setae; exopod 2-segmented, proximal segment without setae, distal segment with 6 or 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

Maxilliped 2 (Fig. 4h).—Coxa with 0–2 setae; basis with 4–6 setae; endopod 4-segmented, (4–7), 1, (2 or 3), (4–6) setae; exopod unsegmented, 7 or 8 setae on distal margin; all setae plumose.

Maxilliped 3 (Fig. 4i).—Coxa without setae; basis with 0–2 setae; endopod 4-segmented, (l or 2), (1–3), (2–4), (3–6) setae; exopod unsegmented, 6–8 setae on distal margin; all setae plumose.

Pereiopods (Fig. 4j, k).—First and second pereiopod present, both without setae.

Pleopods.—Not developed.

Telson (Fig. 4l).—No change from ZI.

Zoea III

Figs. 2c, 5a–h, 6a–h

Size.—CL = 1.65 ± 0.03 mm, range 1.60–1.72 mm; TL = 4.13 ± 0.09 mm, range 3.99–4.36 mm.

Carapace (Fig. 2c).—No marked change from ZII.

Abdomen (Fig. 2c).—Somites 2–5 with posterolateral projections; dorsal spine elongate on somite 2, sometimes extending beyond posterior margin of somite 3; short dorsal spines on somites 3–6.

Antennule (Fig. 5a).—Biramous, peduncle 2-segmented; proximal segment with (0 or 1)+(2 or 3) short setae on outer margin and 1 long plumose seta on inner margin; distal segment with 2 or 3 setae on inner margin, 1 seta between rami, and 0–3 short seta on outer margin; endopod with 0 or 1 terminal plumose seta; exopod with 6 or 7 terminal, and 0–2 subterminal aesthetascs.

Antenna (Fig. 5b).—Protopod with 1 spine at outer distal margin; endopod with 0 or 1 short seta; scaphocerite armed with 1 strong distolateral spine, 11–13 plumose setae on inner margin, and 1 plumose seta on outer margin.

Mandible (Fig. 5c, d).—Incisor process with 7 or 8 teeth on right mandible, 6–8 teeth on left mandible; molar process denticulate on both mandibles; buds of palps present.

Maxillule (Fig. 5e).—Coxal endite with 10–12 marginal plumose setae; basal endite with 3 plumose setae, 4 or 5 large dentate spines, and 4 or 5 smaller dentate spines, inner margin with 1 plumose seta; endopod 3-segmented, distinction between segments sometimes obscure, 2, 2, 4 setae; protopod without setation.

Maxilla (Fig. 5f).—Coxal endite bilobed, 14–17 setae on proximal lobe, 4–6 setae on distal lobe; basal endite bilobed with 7–10 se-

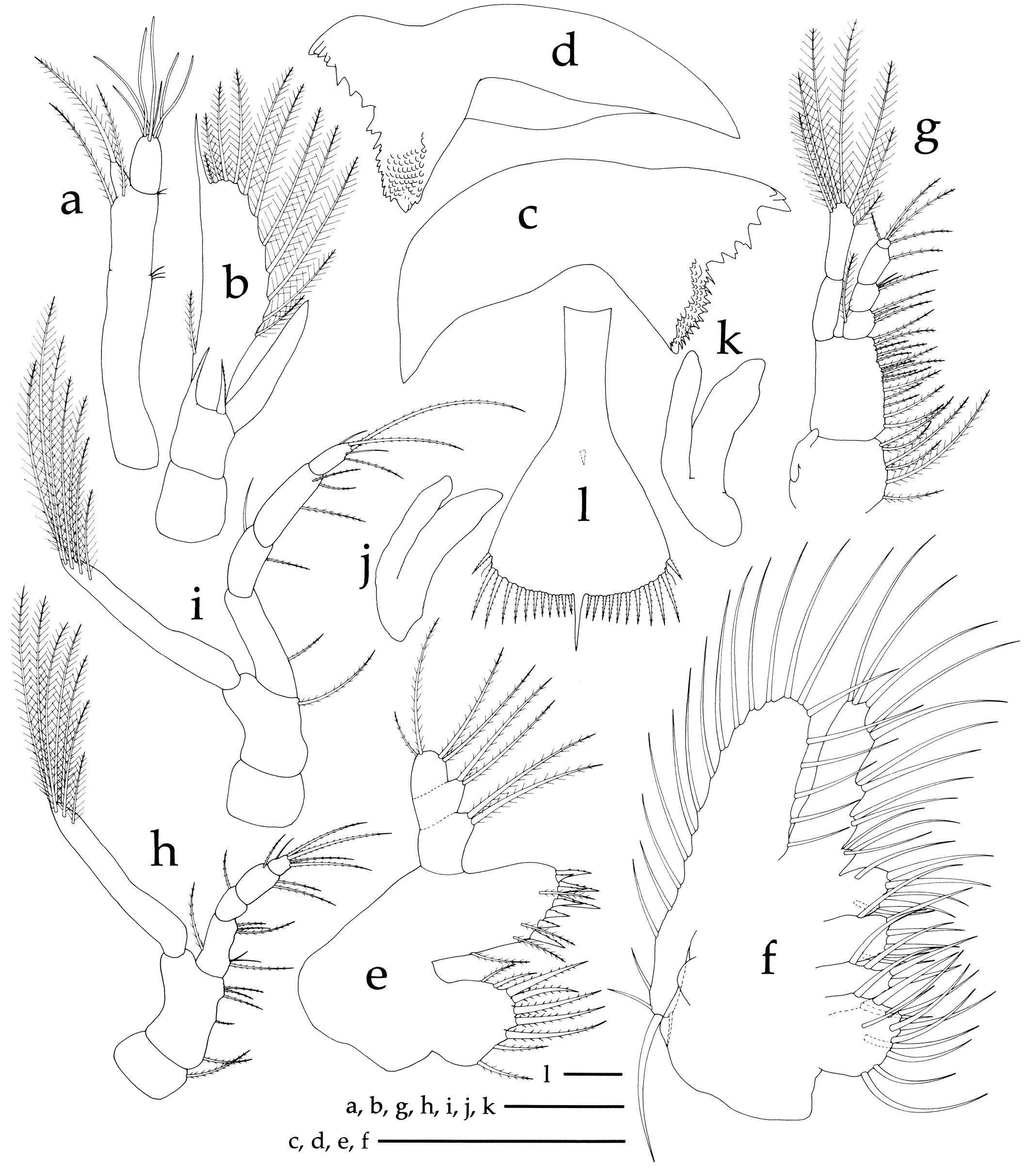

Fig. 4. *Callichirus islagrande,* ZII stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2; i, maxilliped 3; j, pereiopod 1; k, pereiopod 2; 1, telson. Scales = 0.2 mm.

tae on proximal lobe, 6–9 setae on distal lobe; endopod with 5 lobes, 3+2+2+2+(2 or 3) setae; scaphognathite with 21–26 setae; all setae plumose.

Maxilliped 1 (Fig. 5g).—Coxa with 4–9 setae; basis with 14–18 marginal setae; endopod 4-segmented, (3 or 4), 2, 2, (3 or 4) setae; exopod 2-segmented, proximal segment without setae, distal segment with 5–7 setae on distal margin; bilobed epipod without setae; all setae plumose.

Maxilliped 2 (Fig. 5h).—Coxa with 0–2 setae; basis with 5 or 6 setae; endopod 4-segmented, (4–6), 1, 3, (4–6) setae; exopod unsegmented, 7 or 8 setae on distal margin; all setae plumose.

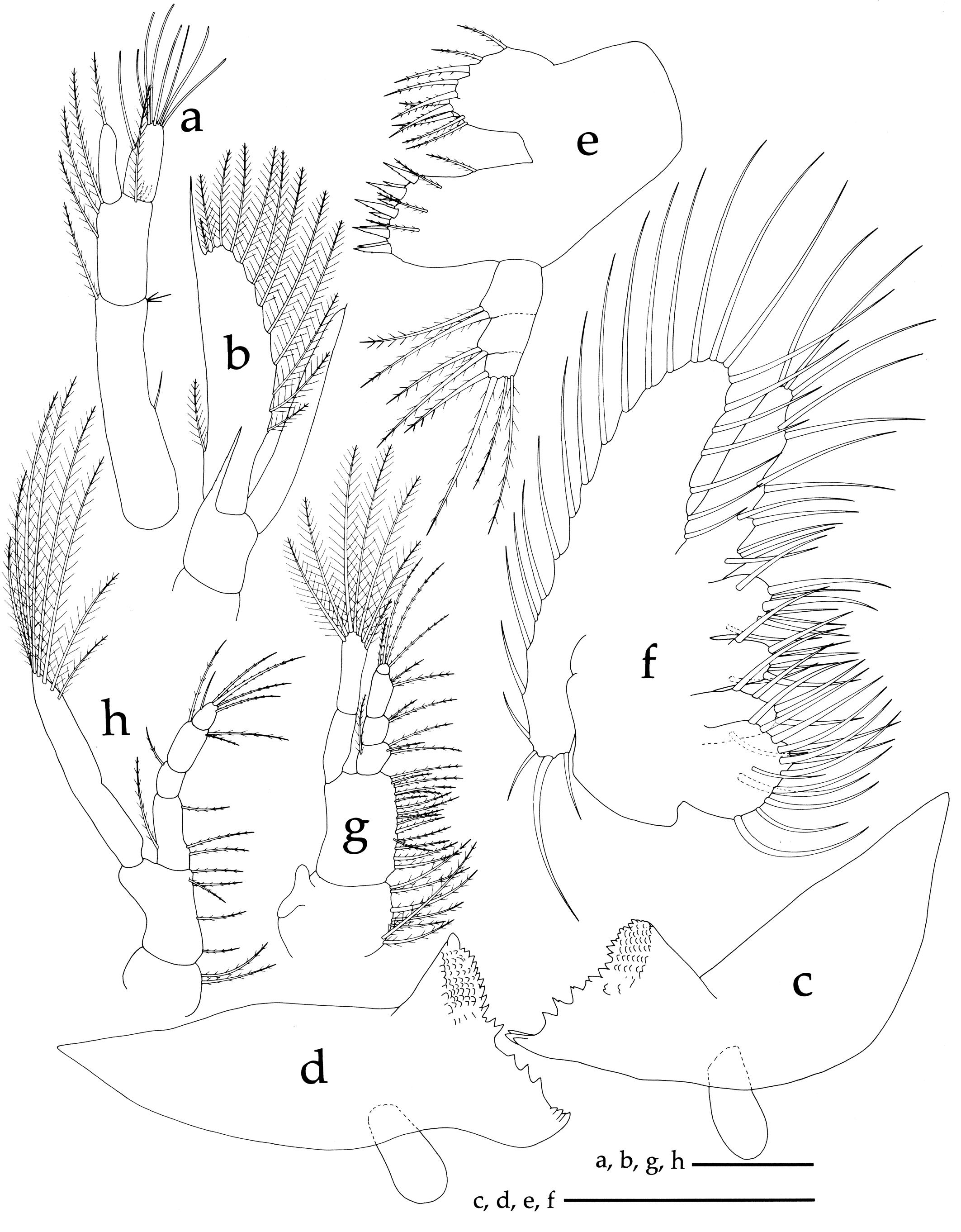

Fig. 5. *Callichirus islagrande,* ZIII stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2. All setae on the maxilla were plumose. Scales = 0.2 mm.

Maxilliped 3 (Fig. 6a).—Coxa with 0 or 1 seta; basis with 1–3 setae; endopod 4-segmented, (1 or 2), 2, (2–4), (4 or 5) setae; exopod unsegmented, 7 or 8 setae on distal margin; all setae plumose.

Pereiopod 1 (Fig. 6b).—Chelate and biramous; coxa without setae; basis with 0 or 1 seta; endopod 4-segmented, 0, (1 or 2), (2–4), 2 setae; exopod with 6 or 7 setae on distal margin.

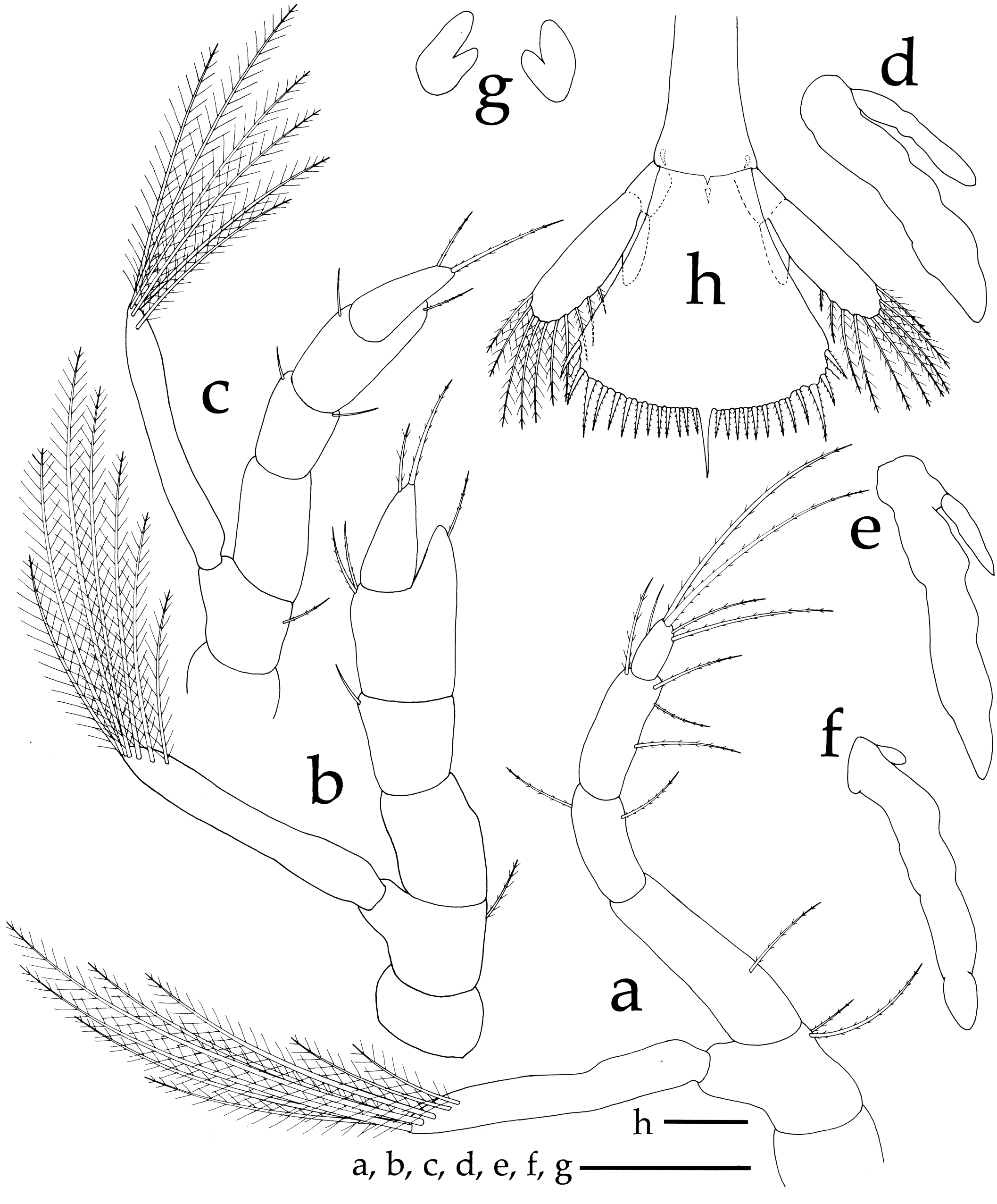

Fig. 6. *Callichirus islagrande,* ZIII stage: a, maxilliped 3; b, pereiopod 1; c, pereiopod 2; d, pereiopod 3; e, pereiopod 4; f, pereiopod 5; g, pleopods from fourth abdominal somite; h, telson. Scales = 0.2 mm.

Pereiopod 2 (Fig. 6c).—Chelate and biramous; coxa without setae; basis with 0 or 1 seta; endopod 4-segmented, 0, (0–2), (0–4), 2 setae; exopod with 5–7 setae on distal margin.

Pereiopods 3–5 (Fig. 6d, e, f).—Without setae.

Pleopods (Figs. 1c, 6g).—Bilobed buds on abdominal segments 2–5, first pair smaller than others.

Telson and Uropods (Fig. 6h).—No change in arrangement of posterior telsonal processes; uropods biramous, endopod without setae, exopod with 10 or 11 marginal plumose setae, ventral spine near base of protopod.

Zoea IV
Figs. 2d, 7a–h, 8a–i

Size.—CL = 1.92 ± 0.09 mm, range 1.69–2.15 mm; TL = 4.82 ± 0.25 mm, range 4.24–5.36 mm.

Carapace (Fig. 2d).—No marked change from ZIII.

Abdomen (Fig. 2d).—No marked change from ZIII.

Antennule (Fig. 7a).—Biramous, peduncle 2-segmented; with 1+(1–4) short setae on outer margin, and 0 or 1 plumose seta on inner margin of proximal segment; distal segment with 3–5 plumose setae on inner margin, 1 plumose seta between rami, and 0–3 short setae on outer margin; endopod with 1 or 2 plumose setae; exopod with 6 or 7 terminal, and 2 subterminal aesthetascs.

Antenna (Fig. 7b).—Protopod with 1 distal spine on outer margin; endopod with 0–2 setae; scaphocerite armed with 1 strong distolateral spine, 12–14 plumose setae on inner margin, and 1 plumose seta on outer margin.

Mandible (Fig. 7c, d).—Incisor process with 8 teeth on right mandible, 6–8 teeth on left mandible; molar process denticulate on both mandibles; palps present.

Maxillule (Fig. 7e).—Coxal endite with 12–14 marginal plumose setae; basal endite with 3 plumose setae, 5 or 6 large dentate spines, and 5 or 6 smaller dentate spines, inner margin with 1 plumose seta; endopod 3-segmented, distinction between segments sometimes obscure, 2, 2, (3 or 4) setae; protopod without setation.

Maxilla (Fig. 7f).—Coxal endite bilobed, 14–19 setae on proximal lobe, 5 setae on distal lobe; basal endite bilobed, 6–10 setae on proximal lobe, 8 or 9 setae on distal lobe; endopod with 5 lobes, 3+(2 or 3)+2+2+3 setae; scaphognathite with 27–32 setae; all setae plumose.

Maxilliped 1 (Fig. 7g).—Coxa with 2–8 setae; basis with 16–19 marginal setae; endopod 4-segmented, (3 or 4), 2, 2, 4 setae; exopod 2-segmented, proximal segment without setae, distal segment with 6 or 7 setae on distal margin; bilobed epipod without setae; all setae plumose.

Maxilliped 2 (Fig. 7h).—Coxa with 0–3 setae; basis with 4–6 setae; endopod 4-segmented, (5–8), 1, (3–5), (4 or 5) setae; exopod unsegmented, 7 or 8 setae on distal margin; all setae plumose.

Maxilliped 3 (Fig. 8a).—Coxa with 0 or 1 seta; basis with 2–4 setae; endopod 4-segmented, (1 or 2), 2, (3–5), (3 or 4) setae; exopod unsegmented, 7 or 8 setae on distal margin; all setae plumose.

Pereiopod 1 (Fig. 8b).—Biramous, cheliform; coxa without setae; basis with 0–2 setae; endopod 4-segmented, (0 or 1), (1 or 2), (2–4), (1 or 2) setae; exopod with 5–7 setae on distal margin.

Pereiopod 2 (Fig. 8c).—Biramous, cheliform; coxa without setae; basis with 0 or 1 seta; endopod 4-segmented, 0, (1 or 2), (3–5), (2 or 3) setae; exopod with 5–7 setae on distal margin.

Pereiopod 3 (Fig. 8d).—Biramous, coxa and basis without setae; endopod 4-segmented, 0, (0–2), (3 or 4), 2 setae; propodus bladelike; exopod with 4 or 5 terminal setae.

Pereiopod 4 (Fig. 8e).—Biramous, coxa and basis without setae; endopod 4-segmented, (0 or 1), (0–2), (2–4), 2 setae; exopod with 0–2 setae.

Pereiopod 5 (Fig. 8f).—Uniramous, 2 setae on terminal segment, 4 or 5 setae on adjacent segment.

Pleopods (Fig. 8g, h).—Larger than at ZIII, still without setae.

Telson and Uropods (Fig. 8i).—Telson triangular, narrow anteriorly; no anal spine; posterior margin with (12–15)+1+(13 or 14) processes arranged as (I, II, III, IV, III, II, I), (I) outermost process a plumodenticulate seta, (II) second process "anomuran hair," (III) 10–13 plumodenticulate setae, and (IV) naked spine; uropods biramous, endopod with 7–11 marginal plumose setae, exopod with 1 naked distolateral spine, 12–14 marginal plumose setae.

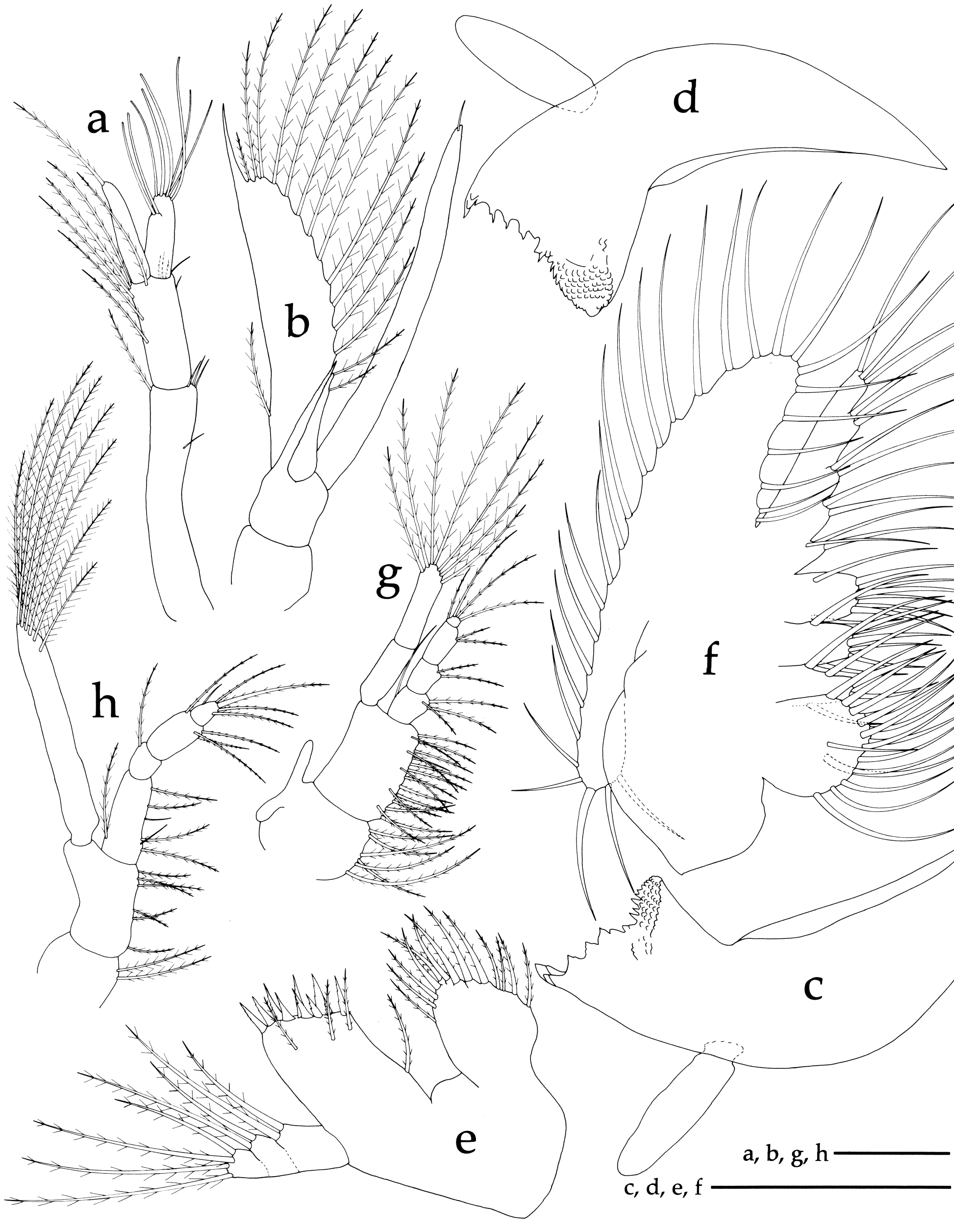

Fig. 7. *Callichirus islagrande,* ZIV stage: a, antennule; b, antenna; c, right mandible; d, left mandible; e, maxillule; f, maxilla (plumose condition not shown); g, maxilliped 1; h, maxilliped 2. All setae on the maxilla were plumose. Scales = 0.2 mm.

Decapodid (first postlarva)
Figs. 2e, 9c–j, l0a–i

Size.—CL = 1.33 ± 0.02 mm, range 1.29–1.38 mm; TL = 3.78 ± 0.11 mm, range 3.61–4.05 mm.

Carapace (Fig. 2e).—Shorter than abdomen, no anterolateral serrations, with pterygostomial projections; rostrum reduced, without serrations, sometimes bending down between eyes.

Abdomen (Fig. 2e).—Somites broad and flattened, posterior projections rounded with 0–7 setae, somite 2 rectangular, somites 3–5 oval.

Antennule (Fig. 9c).—Peduncle 3-segmented, proximal segment with 17–24 setae, 13–15 of

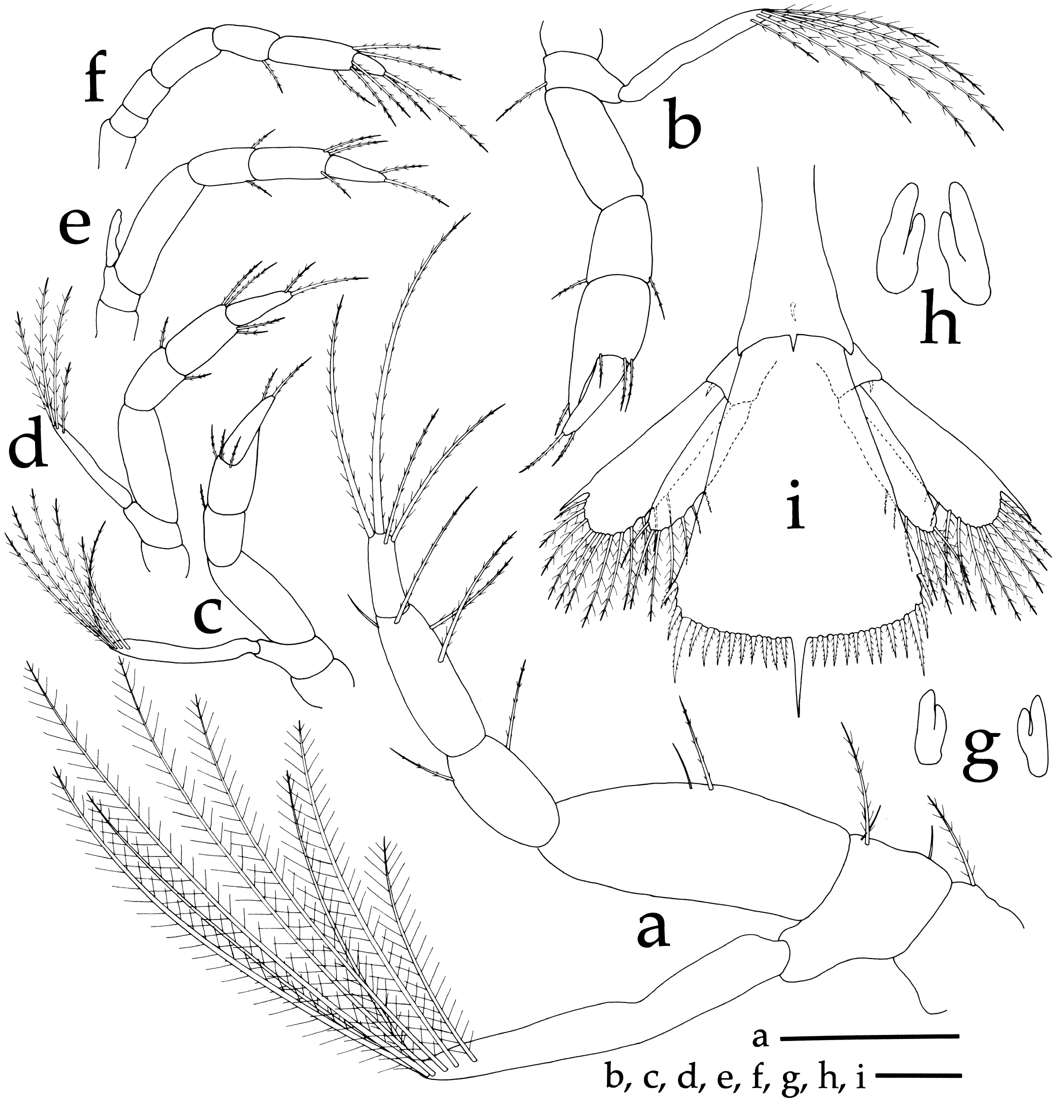

Fig. 8. *Callichirus islagrande,* ZIV stage: a, maxilliped 3; b, pereiopod 1; c, pereiopod 2; d, pereiopod 3; e, pereiopod 4; f, pereiopod 5; g, pleopods from first abdominal somite; h, pleopods from fourth abdominal somite; i, telson. Scales = 0.2 mm.

these associated with statocyst; intermediate segment with 6–10 setae; distal segment of peduncle with 2 vertical rows of setae, one with 4 or 5 setae, other with 2–4 setae, 1–3 additional setae on outer margin, and 3–5 short setae on distal margin; endopod 4–6 segmented, (1–3), (0 or 1), (1–4), (1–4), (3–6), (3–6) setae; exopod 3–5-segmented, 0, (0–4), (0–4), (1–4) setae +2 asthetascs, (5–8) asthetascs (?).

Antenna (Fig. 9d).—Peduncle 2-segmented, proximal segment with 0 or 1 seta, distal segment with 1–3 setae on inner margin, spine present in some; flagellum ranging from 14–18 segments, (0 or 1), (2–4), variable region (1–3 articles, with 0–2 setae), (0–4), (0–2), (2–5), (1–4), (3–6), (0–3), (2–5), (3–6), (0–3), (3–6), (0 or 1), (1–7), (4–9) setae; exopod reduced to small lobe with 0–5 setae.

Mandible (Fig. 9e, f).—Both mandibles similar, incisor process with 5–8 teeth; molar process smooth or with small ridges; palp 3-segmented, 0, (0 or 1), (8–12) setae.

Maxillule (Fig. 9g).—Coxal endite with 15–22 marginal setae, and 0 or 1 submarginal

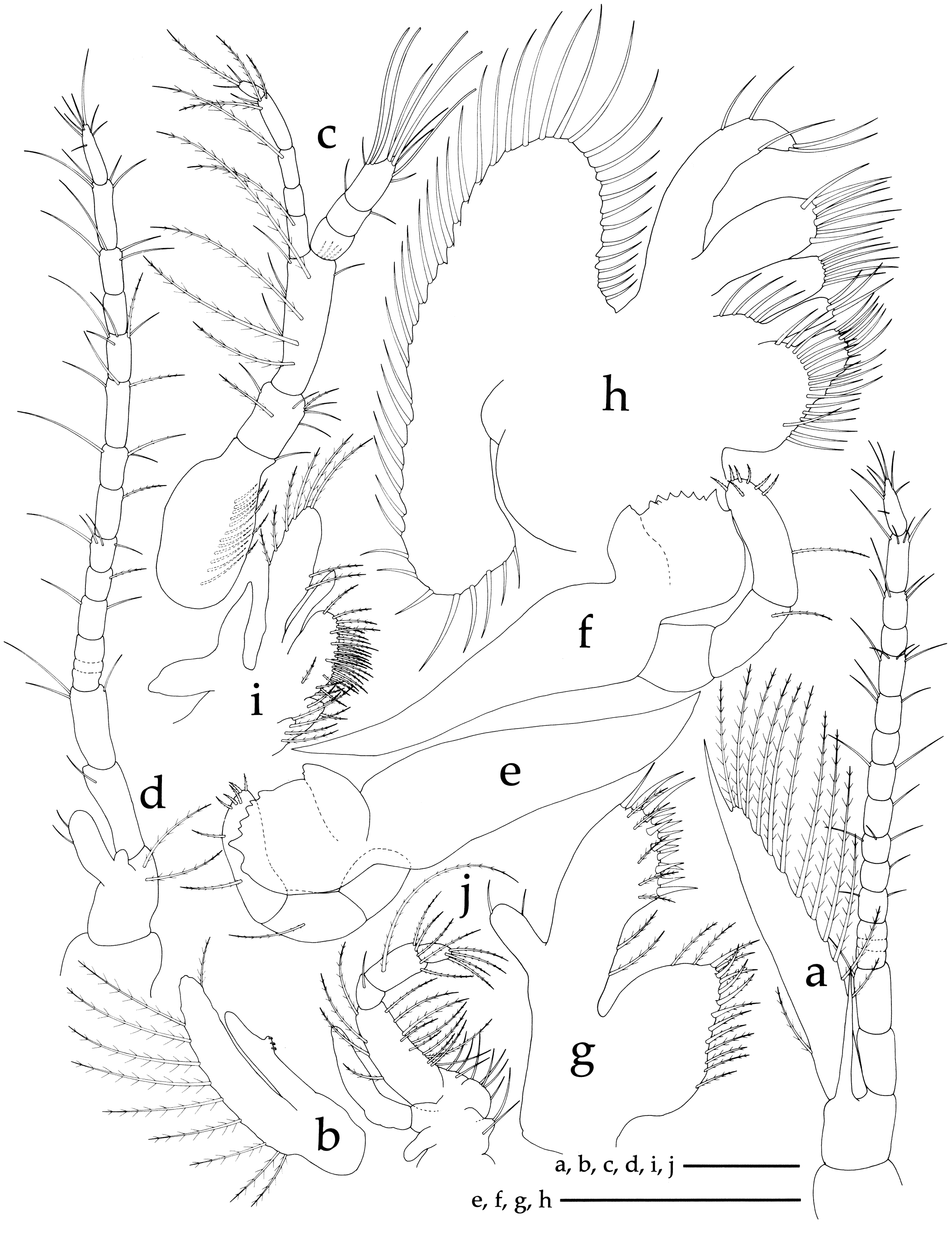

Fig. 9. *Callichirus islagrande,* ZV stage: a, one example of the antenna; b, one example of pleopods. Decapodid stage: c, antennule; d, antenna; e, right mandible; f, left mandible; g, maxillule; h, maxilla (plumose condition not shown); i, maxilliped 1; j, maxilliped 2. Scales = 0.2 mm.

seta; basal endite with 3–5 plumose setae, 14–19 dentate spines, 0–2 plumose setae on inner margin; endopod reduced, unsegmented with 0–8 setae.

Maxilla (Fig. 9h).—Coxal endite trilobed, (17–21)+(7–10)+(6–9) setae; basal endite bilobed, 8–10 setae on proximal lobe, 8–15 setae on distal lobe; endopod reduced with

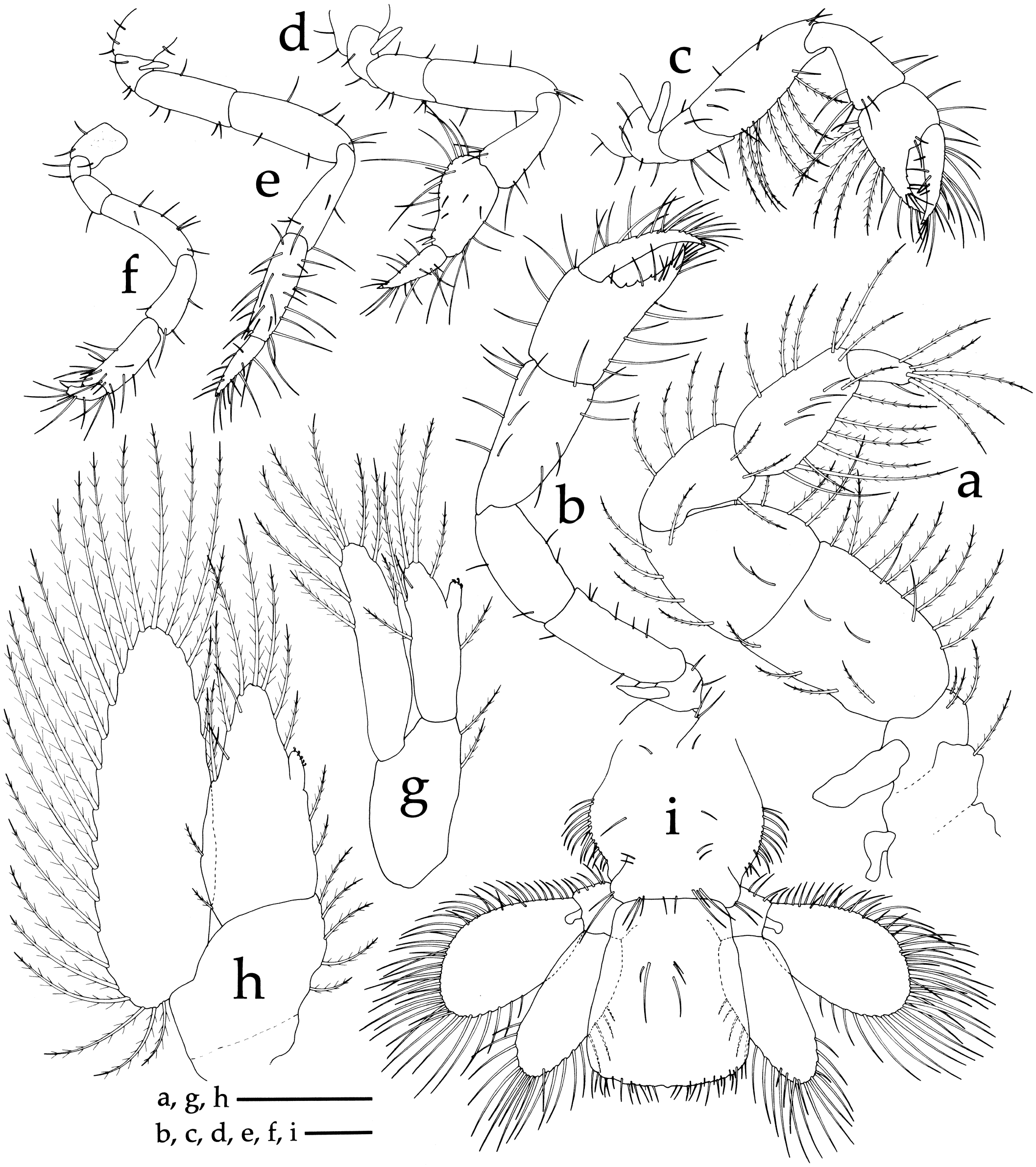

Fig. 10. *Callichirus islagrande*, decapodid stage: a, maxilliped 3; b, pereiopod 1; c, pereiopod 2; d, pereiopod 3; e, pereiopod 4; f, pereiopod 5; g, pleopods from first abdominal somite; h, pleopods from fourth abdominal somite; i, telson. Scales = 0.2 mm.

5–11 setae; scaphognathite with 37–45 setae; all setae plumose.

Maxilliped 1 (Fig. 9i).—Coxa with 8–12 setae; basis highly setose, with 27–39 setae; endopod reduced, with 0–11 setae; exopod unsegmented, 6–14 setae; bilobed epipod without setae.

Maxilliped 2 (Fig. 9j).—Coxa partially fused to basis, with 1–4 setae; basis with 3–5 setae; endopod 4-segmented, (16–23), (0 or 1), (6–11), (4–8) setae; exopod with 0–8 setae; epipod present but without setae.

Maxilliped 3 (Fig. 10a).—Coxa partially fused to basis, with 0–3 setae; basis with 1–4 setae; endopod 5-segmented, (11–19), (9–15), (7–11), (8–21), (5–11) setae; exopod usually reduced and without setae, occasionally with 2–9 setae; epipod present.

Pereiopod 1 (Fig. 10b).—Chelate, biramous, 7-segmented; coxa with 0–6 setae; basis with 2–5 setae; ischium with 4–7 setae and 0–3 spines; merus with 5–8 setae; carpus with 10–14 setae; propodus with 27–37 setae and 3–4 spines on inner margin of immovable finger; dactylus with 21–33 setae; exopod usually reduced and without setae, occasionally with 4–7 setae.

Pereiopod 2 (Fig. 10c).—Chelate, biramous, 7-segmented; coxa with 2–5 setae; basis with 1–5 setae; ischium with 4–10 setae; merus with 15–20 setae; carpus with 8–12 setae; propodus with 30–40 setae and 1–4 spines on inner margin of immovable finger; dactylus with 21–30 setae; exopod usually reduced, 0–7 setae.

Pereiopod 3 (Fig. 10d).—Biramous, 7-segmented; coxa with 2–5 setae; basis with 1–3 setae; ischium with 5–8 setae; merus with 6–9 setae; carpus with 7–11 setae; propodus bladelike with 25–34 setae, 1 spine on inner distal margin; dactylus with 15–21 setae; exopod usually reduced, 0–5 setae.

Pereiopod 4 (Fig. 10e).—Biramous, 7-segmented; coxa with 2–7 setae; basis with 1–4 setae; ischium with 3–8 setae; merus with 5–11 setae; carpus with 4–9 setae; propodus with 27–38 setae, 1 spine on inner distal margin; dactylus with 15–19 setae; exopod usually reduced, with 0–2 setae.

Pereiopod 5 (Fig. 10f).—Cheliform, uniramous, 7-segmented; coxa with 2–6 setae; basis with l or 2 setae; ischium with 2–5 setae; merus with 5–9 setae; carpus with 4–7 setae; propodus with 22–30 setae, 1 spine on immovable finger; dactylus with 6–10 setae; exopod absent.

Pleopods (somite 2) (Fig. 10g).—Biramous, coxa partially fused to basis, without setae; basis with 0–3 setae; endopod with 3–5 hooked setae on appendix interna, 10–17 marginal plumose setae, 0–2 submarginal naked setae; exopod with 21–27 marginal, plumose setae and 0–1 submarginal, naked seta.

Pleopods (somites 3–5) (Fig. 10h).—Biramous, coxa without setae; basis with 3–6 marginal, plumose setae; endopod with 3–6 hooked setae on appendix interna, 10–18 marginal, plumose setae, and 0–3 naked, submarginal setae; exopod with 20–29 marginal, plumose setae and 0 or 1 submarginal, naked seta.

Telson and Uropods (Fig. 10i).—With 24–36 processes on posterior margin, median process usually absent or reduced; uropods biramous, endopod with 19–25 plumose setae, exopod with 35–58 plumose setae, protopod with 3–5 setae.

Discussion

As in other species of *Callichirus* (see Rodrigues, 1976; Aste and Retamal, 1983; Strasser and Felder, in press b), larval development of *C. islagrande* included four or five zoeal stages before metamorphosis to the decapodid. ZI larvae may be identified by the presence of an elongate, rounded rostrum, sessile eyes, and a lack of pereiopods, pleopods, or uropods (Fig. 1a). At ZII, larvae acquired biramous buds of pereiopods 1 and 2, eyes were separated from the carapace, and the rostrum became flattened and serrated laterally (Fig. 1b). Buds of pleopods on abdominal segments 2–5, pereiopods 3–5, and uropods were developed at ZIII (Fig. 1c). In addition to further development of structures mentioned thus far, ZIV larvae could be distinguished by presence of a distal spine on the exopod and setae on the endopod of each uropod (Fig. 1d). When it occurred, ZV typically resembled ZIV, but varied widely in morphology. Appendages at ZV resembled those of ZIV, the decapodid stage, or some gradation between the two (see Figs. 9a, b for examples). The decapodid stage was similar to other species of *Callichirus* in the reduction of larval characters such as the elongate rostrum, dorsal spines on the abdomen, and exopods of the pereiopods (Fig. le). Acquisition of fan-like pleopods marked the transition to a primarily abdominal mode of swimming at this stage.

In the Florida Atlantic population of *C. major,* both salinity and presence of putative settlement cues at ZIV impacted the observed number of zoeal stages and the duration of ZIV (Strasser and Felder, in preparation, 1999c). In *C. islagrande,* the percentage of larvae that passed through five versus four zoeal stages varied (9–89%) between parental females, but was not shown to depend on salinity or presence of various putative settlement cues (Strasser and Felder, 1998, in preparation). Larvae that molted from ZIV to ZV were usually normal morphologically and had mortality similar to those that molted directly from ZIV to D. In contrast, larvae of the Florida Atlantic *C. major* that molted to ZV had a higher incidence of mortality and deformity at D than did those that had bypassed ZV (Strasser and Felder, 1999a, c).

The number of zoeal stages appears to be less variable in *Callichirus garthi* and the Gulf of Mexico population of *C. major* than in congeneric populations studied to date. *Callichirus garthi* was reported to have five zoeal stages and a long larval duration, reaching the decapodid stage 48 days after hatching (Aste and Retamal, 1983). Development of the Gulf population of *C. major* was shorter in duration (decapodid reached about 10 days after hatching) and typically included four zoeal stages (Strasser and Felder, 1999a); animals rarely passed through three or five zoeal stages before the molt to the decapodid. Although the number of stages is reduced from that observed in *C. garthi,* development in the Gulf population of *C. major* cannot be classified as abbreviated. There are species in both the Callianassinae (*Callianassa* s.l. *kraussi* Stebbing, *C.* s.l. *kewalramanii,* and *C.* s.l. *tyrrhena* (Petagna)) and Callichirinae (*Sergio mirim, Lepidophthalmus sinuensis,* and *L. louisianensis*) that have only two zoeal stages before the molt to the decapodid (Forbes, 1973; Sankolli and Shenoy, 1975; Rodrigues, 1984; Thessalou-Legaki, 1990; Nates *et al.*, 1997).

Compared to other species of the genus *Callichirus, C. islagrande* is morphologically closer to *C. garthi* (from Chile) than to the Gulf of Mexico population of *C. major,* which overlaps in distribution with *C. islagrande*. In the zoeal phase of *C. islagrande* and *C. garthi*, the telson is concave and the outermost process on the ventral margin is articulated. In both *C. major* and *Callichirus* sp. the posterior margin of the telson is straight and the outermost process is unarticulated during the zoeal stages (Rodrigues, 1976; Strasser and Felder, 1999a). There are also differences in spination of the abdomen. In zoeae of *C. islagrande* and *C. garthi* the dorsal spine of abdominal segment 3 is not longer than those found on segments 4 and 5 (Aste and Retamal, 1983). In contrast, the dorsal spine of abdominal segment 3 is approximately twice as long as the dorsal spines on segments 4 and 5 in early zoeal stages of *C. major* and *Callichirus* sp. (Rodrigues, 1976; Aste and Retamal, 1983; Strasser and Felder, 1999a). The greatest difference between these groups is the number of pleopod pairs at zoeal and decapodid stages. *Callichirus islagrande* and *C. garthi* have pleopods on abdominal segments 2–5, while pleopods are present only on abdominal segments 3–5 in *C. major* and *Callichirus* sp. (Rodrigues, 1976; Aste and Retamal, 1983; Strasser and Felder, 1999a). Although *Callichirus islagrande* and *C. garthi* are similar morphologically, there are differences between these two species. *Callichirus islagrande,* as well as *C. major* and *Callichirus* sp., develops pleopod buds and chelate pereiopods at ZIII, whereas *C. garthi* does not acquire these characters until ZIV.

There are few callianassid species for which the larval development has been described (Sankolli and Shenoy, 1975; Rodrigues, 1976, 1984; Aste and Retamal, 1983, 1984; Konishi *et al.,* 1990; Nates *et al.*, 1997; Strasser and Felder, 1999a), all of which are members of the Callichirinae and Callianassinae. Among species, there is a great deal of overlap in larval characters, making it difficult to draw distinctions between these subfamilies. At present, information on larval development of species in the Callichirinae is limited to larval descriptions of *Callichirus major, C. garthi, Callichirus* sp., *C. islagrande, Sergio mirim, Lepidophthalmus louisianensis,* and *L. sinuensis* (see Rodrigues, 1976, 1984; Aste and Retamal, 1983; Nates *et al.,* 1997; Strasser and Felder, 1999a). As mentioned above, species of *Callichirus* have been shown to have four to five zoeal stages, while the other members exhibit abbreviated development that consists of only two zoeal stages. The most obvious difference between larvae of the species of Callichirinae with abbreviated development is the number of pleopod pairs. Larvae of *S. mirim* have pleopods on abdominal segments 3–5, whereas *L. louisianensis* and *L. sinuensis* have pleopods on segments 2–5 (Rodrigues, 1984; Nates *et al.,* 1997).

Ghost shrimps of the genus *Callichirus* may be distinguished from other genera of the Callianassidae by the cuticular pattern on the dorsal surface of the abdomen and by the strap-like shape of the uropodal endopods (Manning and Felder, 1991). Whereas these characters may be used to distinguish adults of the genus *Callichirus,* they are not present at zoeal and decapodid stages. Larvae may be distinguished from all other callianassid genera by having four to five zoeal stages and numerous processes (12–25+1+12–25) on the posterior margin of the telson during the early zoeal stages. Larvae of *Callichirus* may also differ from other callianassids with extended development by the retention of the anomuran hair as the second process on the posterior margin of the telson in the late zoeal stages. Whereas this process is converted to a spine in *Neotrypaea uncinata* at ZV and *Callianassa* s.l. *petalura* at ZIV, the anomuran hair is retained at ZIV in *Callichirus major* and *C. islagrande* (see Rodrigues, 1976; Strasser and Felder, 1999a). Although not mentioned specifically in the descriptions, the anomuran hair appears to be present in illustrations of *Callichirus* sp. at ZIII and *C. garthii* at ZV (Rodrigues, 1976: fig. 35; Aste and Retamal, 1983: fig. 8Q). A bilobed epipod on the first maxilliped of ZI is consistently found in *Callichirus*, but is also present at ZI in *Lepidophthalmus sinuensis* (see Nates *et al.,* 1997). Other callianassids acquire this character at ZII (*L. louisianensis,* Nates *et al.*, 1997; *Callianassa* s.l. *kewlramanii*, Sankolli and Shenoy, 1975), at ZV (*Neotrypaea uncinata,* Aste and Retamal, 1984), or at the decapodid stage (*Sergio mirim,* Rodrigues, 1984; *C.* s.l. *petalura* Konishi *et al.,* 1990). Thus, the number of zoeal stages and setation of the telson may serve as the best characters to distinguish larvae of *Callichirus* from other genera. However, since larval descriptions are lacking for many callianassid species, it is unknown if these characters (in combination) will prove to be diagnostic until descriptions for other species are published.

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