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LARVAL DEVELOPMENT OF THE LAND CRAB *GECARCINUS LATERALIS LATERALIS* (FRÉMINVILLE, 1835) (BRACHYURA: GECARCINIDAE) REARED IN THE LABORATORY

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ABSTRACT

The complete larval development of *Gecarcinus lateralis lateralis* (Fréminville, 1835), a gecarcinid land crab from Bermuda, is described and illustrated based on larvae reared in the laboratory. The species passes through six (possibly five) zoeal stages and one megalopal stage. The development through six zoeal stages to the young crab stage takes at least 29 days.

Morphological characters of *G. l. lateralis* larvae are compared with gecarcinid species of which the complete larval development is known, i.e., *Cardisoma guanhumi* and *C. carnifex*.

RÉSUMÉ

Description du développement larvaire de *Gecarcinus lateralis lateralis*, un crabe terrestre de Bermuda, cultivé en laboratoire. L'espèce est caractérisée par six (ou cinq) stades zoé et une mégalope, qui sont décrits et figurés. Le développement larvaire depuis l'éclosion jusqu'au premier stade crabe, dure au moins 29 jours.

Les caractères morphologiques sont comparés avec d'autres espèces des Gecarcinidae, dont le développement complet est connu, i.e., *Cardisoma guanhumi* et *C. carnifex*.

The land crab *Gecarcinus lateralis lateralis* (Fréminville) occurs on the Atlantic coast from Florida to Guyana and throughout the West Indies (Rathbun, 1918; Türkay, 1970). It inhabits almost the whole island of Bermuda and causes substantial damage to valuable crops (Dustan, 1959).

Until now no description of the complete larval development of *G. lateralis lateralis* has been available, although the general biology and physiology of this species have been thoroughly studied (Klaassen, 1975; Bliss *et al.*, 1978). Descriptions of the larval stages of the Gecarcinidae are few. Only in *Cardisoma guanhumi* Latreille (Costlow and Bookhout, 1968; Moreira, 1913, first zoea only) and *Cardisoma carnifex* (Kannupandi *et al.*, 1980) is the complete larval development known. In addition, only the first zoeae of *Cardisoma armatum* Herklots (Cannon, 1923) and *Gecarcinus lateralis* (Cabrera, 1966), and the first and second zoeae of *G. planatus* Stimpson (Erhardt and Niaussat, 1968) have been described.

This paper provides a detailed morphological description of the complete larval development of *G. lateralis lateralis* based on laboratory reared specimens. A comparison is made with described species in the family, especially *Cardisoma guanhumi*, in order to facilitate the identification of the different stages which may co-occur in the plankton.

All specimens have been deposited at the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 31, B-1040 Brussels, Belgium: n° I.G. 26258.

METHODS

Ovigerous females of *Gecarcinus lateralis lateralis* were collected during their seaward migration at John Smith's Bay, Bermuda, on 29 July 1978. Hatching occurred when the female crabs were placed in a jar filled with seawater. Part of the hatched larvae were fixed immediately.

In the laboratory the larvae were segregated into groups of 10 and 20 zoeae per bowl (ϕ: 4 cm; h: 2 cm) filled with sea water (salinity 35.9‰) from Ferry Reach. Recently hatched nauplii of *Artemia*

(San Francisco Bay Brand, Newark, California 94560, USA) were given as food. Air conditioning kept the room temperature at 25°C and no differences in air and water temperatures were observed. Owing to electrical failure at the Biological Station temperature rose to 27°C after the 17th day of culture. The larvae were reared under normal room illumination. They were transferred into fresh sea water and fed daily after examination for exuviae and dead larvae. Megalopae were kept separately after cannibalism had been observed.

Larvae and exuviae were preserved in 7% formaldehyde. After dissection in glycerine, specimens were mounted and stained with Turtox CMCP-9AB mounting medium. Morphological descriptions are based on killed specimens and exuviae. At least five specimens of each stage were used, except for the sixth stage, of which only three specimens were studied. Illustrations were made with the aid of a camera lucida. Carapace length, the distance from the tip of the dorsal spine to the tip of the rostral spine, and the length of the dorsal spine were measured in lateral profile. Carapace length was measured from the base of the rostrum just above the ocular peduncle to the posterior extremity of the lateral margin. Carapace length of the megalopa was measured from the tip of the rostral spine to the posterior margin of the carapace, and the carapace width was measured across the widest part of the carapace. The distance from tip to tip of the lateral carapace spines was measured in frontal view.

RESULTS

Description

There are six zoeal stages and one megalopa stage in the larval development of *G. lateralis lateralis*. The main characteristics are as follows:

Zoea I

Size.—Carapace length (C.L.): 0.68–0.71 mm; length of dorsal spine (D.L.): 0.42–0.48 mm; length of rostral spine (R.L.): 0.29–0.32 mm; tip of dorsal to tip of rostral spine: 1.29–1.35 mm; tip to tip of lateral carapace spines: 0.88–0.95 mm.

Eyes.—Sessile.

Carapace (Fig. 1A, B).—1 dorsal, 1 rostral, and 2 lateral spines present, bare; rostral spine clearly exceeding antenna in length; no other armature present except for 2 spinules near base of dorsal spine.

Antennule (Fig. 1C).—Conical, uniramous; 2 terminal aesthetascs of equal length, 2 unequal terminal setae.

Antenna (Fig. 1D).—Spinous process, with 2 rows of minute spines; exopod 1-segmented, with 2 unequal terminal setae, terminal edge with spinules; exopod-protopodal spine ratio (exp./pr.): 0.40–0.46.

Mandible (Fig. 1E).—As shown; without palp.

Maxillule (Fig. 1F).—Endopod 2-segmented, proximal segment with 1 seta, distal segment with 2 terminal, 2 subterminal, and 1 lateral setae; basal and coxal endites with 5–6 and 6 processes respectively; endopod setation unchanged until sixth stage.

Maxilla (Fig. 1G).—Basal and coxal endite, proximal lobe with 5, distal lobe with 4 processes; scaphognathite with 4 plumose (featherlike) marginal setae, terminal process, pointed, hairy, with 1 seta; endopod unsegmented, slightly bifurcated, with 4 setae: 2 terminal and 2 subterminal; this endopod arrangement consistent for all zoeal stages; endopod, basal endite and coxal endite hairy.

First Maxilliped (Fig. 1H).—Exopod indistinctly 2-segmented, with 4 articulated natatory setae; endopod 5-segmented, setal arrangement: 2, 2, 1, 2, 4 + 1 dorsal,

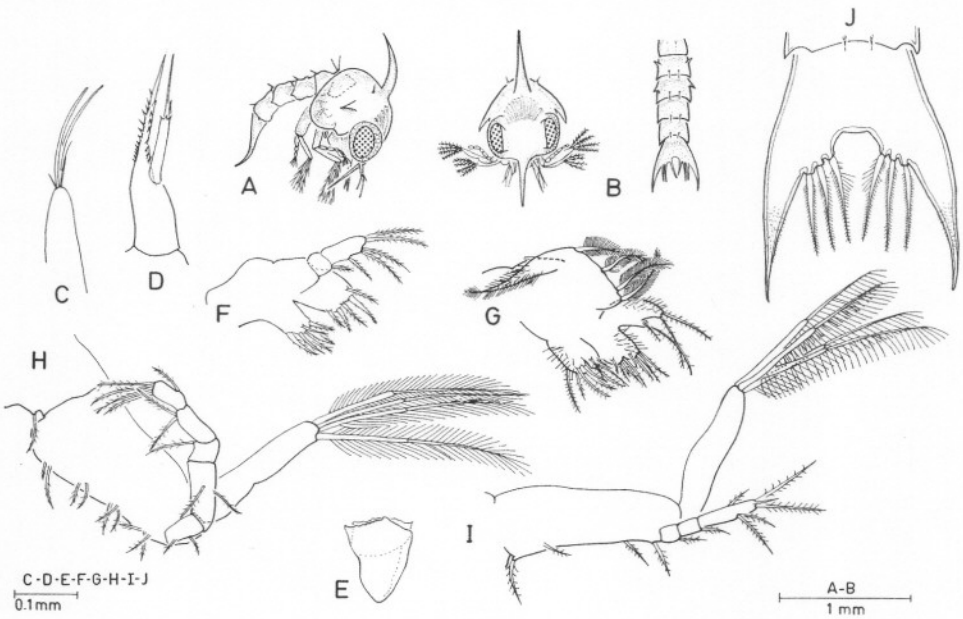

Fig. 1. *Gecarcinus lateralis lateralis*, first zoea: A, Lateral view; B, Frontal view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, Maxilliped I; I, Maxilliped II; J, Telson.

progressing distally; basipodite with 10 medial setae, placed: 2 + 2 + 3 + 3 progressing distally; coxa with single seta.

Second Maxilliped (Fig. 1I).—Exopod indistinctly 2-segmented, with 4 articulated natatory setae; endopod 3-segmented, setal pattern: 1, 1, 6; basipodite with 4 setae, placed: 1 + 1 + 1 + 1.

Third Maxilliped.—Not developed.

Abdomen (Fig. 1A, B, J).—Five somites and telson; somite 1 with 2 well-developed setae on middorsal surface; somites 2–5 with pair of small spinules near posterodorsal margin, posterolateral margins laterally extended as short spines, overlapping next segment; somites 2 and 3 with dorsolateral knobs; telson with 3 + 3 processes on posterior margin, dorsal and ventral surface of forks ornamented with tiny spinules. Patterns of chromatophores identical with that of Cabrera (1966), but not studied further.

Zoea II

Size.—C.L.: 0.74–0.81 mm; D.L.: 0.65–0.71 mm; R.L.: 0.50–0.61 mm; tip of dorsal to tip of rostral spines: 1.77–1.94 mm; tip to tip of lateral carapace spines: 1.03–1.15 mm.

Number of setae on appendages increased, a tendency continuing in later larval stages. Third maxilliped appearing as bud.

Eyes.—Stalked.

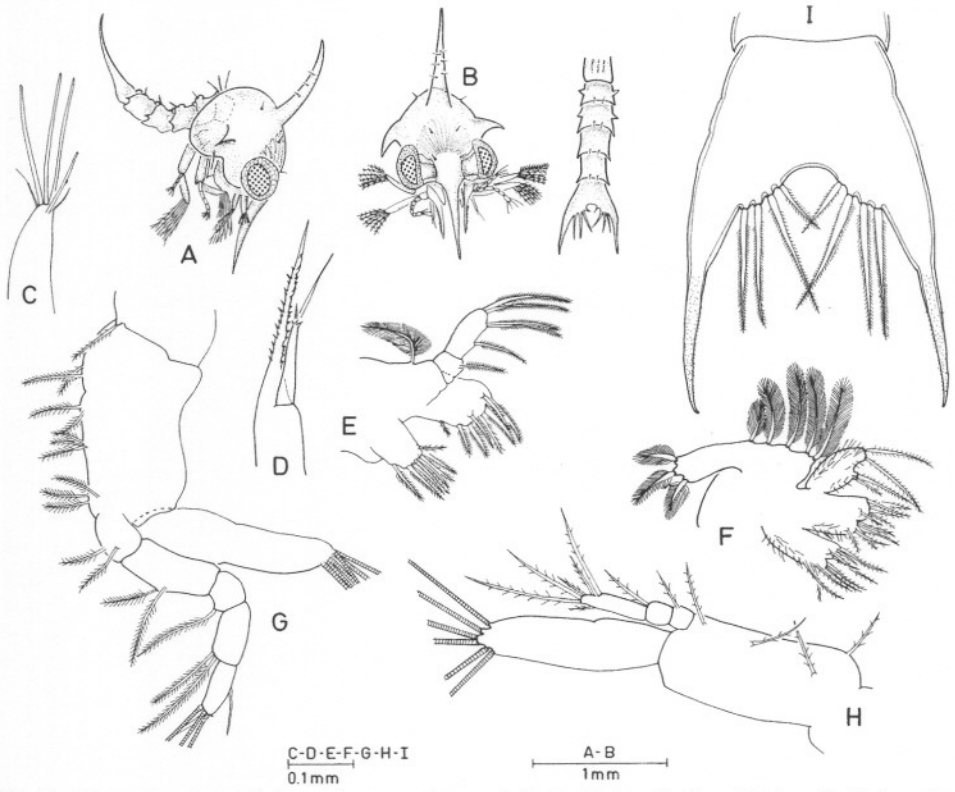

Fig. 2. *Gecarcinus lateralis lateralis*, second zoea: A, Lateral view; B, Frontal view; C, Antennule; D, Antenna; E, Maxillule; F, Maxilla; G, Maxilliped I; H, Maxilliped II; I, Telson.

Carapace (Fig. 2A, B).—With 6 spinules: 2 dorsolateral, 4 frontal; lateral margin with seta; dorsal spine with 3 pairs of spinules.

Antennule (Fig. 2C).—Unchanged in form, now with 4 aesthetascs and 2 setae.

Antenna (Fig. 2D).—No significant change; exp./pr.: 0.39–0.45.

Mandible.—Without palp.

Maxillule (Fig. 2E).—Endopod as in stage I; basal endite with 8 processes, 1 plumose seta present on outer margin; coxal endite with 7–8 processes.

Maxilla (Fig. 2F).—Endopod, basal and coxal endite hairy; basal endite, proximal lobe with 5, distal lobe with 4–5, processes; coxal endite, proximal lobe with 5, distal lobe with 4, processes; scaphognathite with 5–7 plumose setae, 3 setae at apical tip.

First Maxilliped (Fig. 2G).—Exopod with 6 natatory setae; setal pattern as stage I.

Third Maxilliped.—Present as small, nonfunctional bud.

Abdomen (Fig. 2A, B, I).—Somite 1 with 2–3 setae on middorsal surface; posterior margin of telson with 4 + 4 processes, innermost smaller; distal part of forks with tiny spinules.

Zoea III

Size.—C.L.: 0.90–0.96 mm; D.L.: 0.90–0.94 mm; R.L.: 0.74–0.77 mm; tip of dorsal to tip of rostral spine 2.33–2.50 mm; tip to tip of lateral carapace spines 1.35–1.46 mm.

Apart from increase in size, principal differences from preceding stages are: development of endopod bud on antenna, thoracopod buds, and differentiation of sixth abdominal somite. This last somite, however, devoid of posterolateral extensions present in somites 2–5.

Eyes.—Stalked.

Carapace (Fig. 3A, B).—With 8 spinules: 2 dorsolateral, 6 frontal; dorsal spine with 4–5 pairs of spinules; lateral margin with 4–5 setae.

Antennule (Fig. 3C).—With 4 aesthetascs and 3 terminal setae.

Antenna (Fig. 3D).—Protopodite with slight swelling in basal region, representing unsegmented endopod bud; exp./pr.: 0.46–0.54; endopod-exopod ratio (endp./exp.): 0.24–0.34; endopod-protopodal spine ratio (endp./pr.): 0.11–0.17.

Mandible.—Unchanged.

Maxillule (Fig. 3E).—Endopod as in preceding stages; basal endite with 9–11 processes; coxal endite with 8 processes.

Maxilla (Fig. 3F).—Basal endite, proximal lobe with 6, distal lobe with 5, processes; coxal endite, proximal lobe with 5–7, distal lobe with 4, processes; scaphognathite with 10–12 marginal setae, 4–5 setae on apical tip.

First Maxilliped (Fig. 3G).—Exopod with 8 natatory setae; setal pattern as in preceding stages.

Second Maxilliped (Fig. 3H).—Exopod with 8 natatory setae; setal pattern as before.

Third Maxilliped.—Nonfunctional bud.

Thoracopods.—Nonfunctional buds.

Abdomen (Fig. 3A, B, I).—Now 6 somites; somite 6 without posterodorsal spinules and posterolateral extensions; somite 1 with dorsal transverse row of 4–5 setae; telson with 4 + 4 equally long processes, most specimens with additional (1 + 1) minute processes.

Zoea IV

Size.—C.L.: 1.13–1.32 mm; D.L.: 1.23–1.42 mm; R.L.: 1.00–1.13 mm; tip of dorsal to tip of rostral spine: 3.19–3.35 mm; tip to tip of lateral carapace spines: 1.76–1.94 mm.

Increase of number of processes; appearance of chelate pereopod 1 and pleopod buds.

Carapace (Fig. 4A, B).—With 8 spinules; dorsal spine now with 8–9 pairs of spinules; lateral margin with 8 setae.

Antennule (Fig. 4C).—With 5 aesthetascs: 4 terminal + 1 subterminal, and 3 terminal setae.

Antenna (Fig. 4D).—Endopod bud further developed; exp./pr.: 0.49–0.57; endp./exp.: 0.56–0.61; endp./pr.: 0.28–0.33.

Fig. 3. *Gecarcinus lateralis lateralis*, third zoea: A, Lateral view; B, Frontal view; C, Antennule; D, Antenna; E, Maxillule; F, Maxilla; G, Maxilliped I; H, Maxilliped II; I, Telson.

Mandible.—Without palp.

Maxillule (Fig. 4E).—Endopod as in preceding stages; basal endite with 12–14 processes, coxal endite with 8–11 processes; protopodal margin with 2 setae, 1 featherlike, 1 normal.

Maxilla (Fig. 4F).—Basal endite, proximal lobe with 6–7, distal lobe with 6–7, processes; coxal endite, proximal lobe with 7–8, distal lobe with 4 processes; scaphognathite with 22–27 processes.

First Maxilliped (Fig. 4G).—Exopod with 10 natatory setae; endopod setal arrangement now: 2, 2 + 1 dorsal, 1 + 1 dorsal, 2, 5 + 1 dorsal; coxa now with 2 setae.

Second Maxilliped (Fig. 4H).—Exopod with 10 natatory setae; setal arrangement unchanged.

Third Maxilliped.—Unchanged.

Thoracopods.—Thoracopod bud 1 chelate.

Abdomen (Fig. 4A, B, I).—Somites 2–5 with small pleopod buds; somite 1 with row of 5–6 setae; telson with 5 + 5 processes, innermost smaller, plumose.

Zoea V

Size.—C.L.: 1.84–1.94 mm; D.L.: 1.73–1.77 mm; R.L.: 1.32–1.50 mm; tip of dorsal to tip of rostral spine: 4.29–4.68 mm; tip to tip of lateral carapace spines: 2.28–2.42 mm.

Increased setation; thoracopods and pleopods segmented.

Carapace (Fig. 5A, B).—Dorsal spine with 10 pairs of setules; carapace with 8 setules; lateral margin with 12 setae.

Antennule (Fig. 5C).—Inflated in basal region; indistinctly 3-segmented; 9 aesthetascs arranged: 5 + 1 + 3 and 3 terminal setae.

Antenna (Fig. 5D).—Endopod 2-segmented; exp./pr.: 0.53–0.59; endp./exp.: 0.83–1.36; endp./pr.: 0.46–0.74.

Mandible (Fig. 5E).—Palp present as small bud.

Maxillule (Fig. 5F).—Terminal segment of endopod indistinctly 2-segmented; basal endite with 15–16, coxal endite with 11–13, processes.

Maxilla (Fig. 5G).—Basal endite, proximal lobe with 8–9, distal lobe with 8–9, processes; coxal endite, proximal lobe with 11–14, distal lobe with 5, processes; scaphognathite now with 34–37 processes.

First Maxilliped (Fig. 5H).—Exopod with 11–12 natatory setae; endopod setation as in stage IV.

Second Maxilliped (Fig. 5I).—Exopod with 12–13 natatory setae; setal arrangement unchanged.

Third Maxilliped (Fig. 7A).—Five-segmented, bare; exopod bud present.

Thoracopods (Fig. 7B, C, D).—Now segmented.

Abdomen (Fig. 5A, B, J).—Posterolateral spines somites 3–5 almost covering entire next somite; somite 1 with row of 7–9 setae on dorsal surface; pleopods

Fig. 4. *Gecarcinus lateralis lateralis*, fourth zoea: A, Lateral view; B, Frontal view; C, Antennule; D, Antenna; E, Maxillule; F, Maxilla; G, Maxilliped I; H, Maxilliped II; I, Telson.

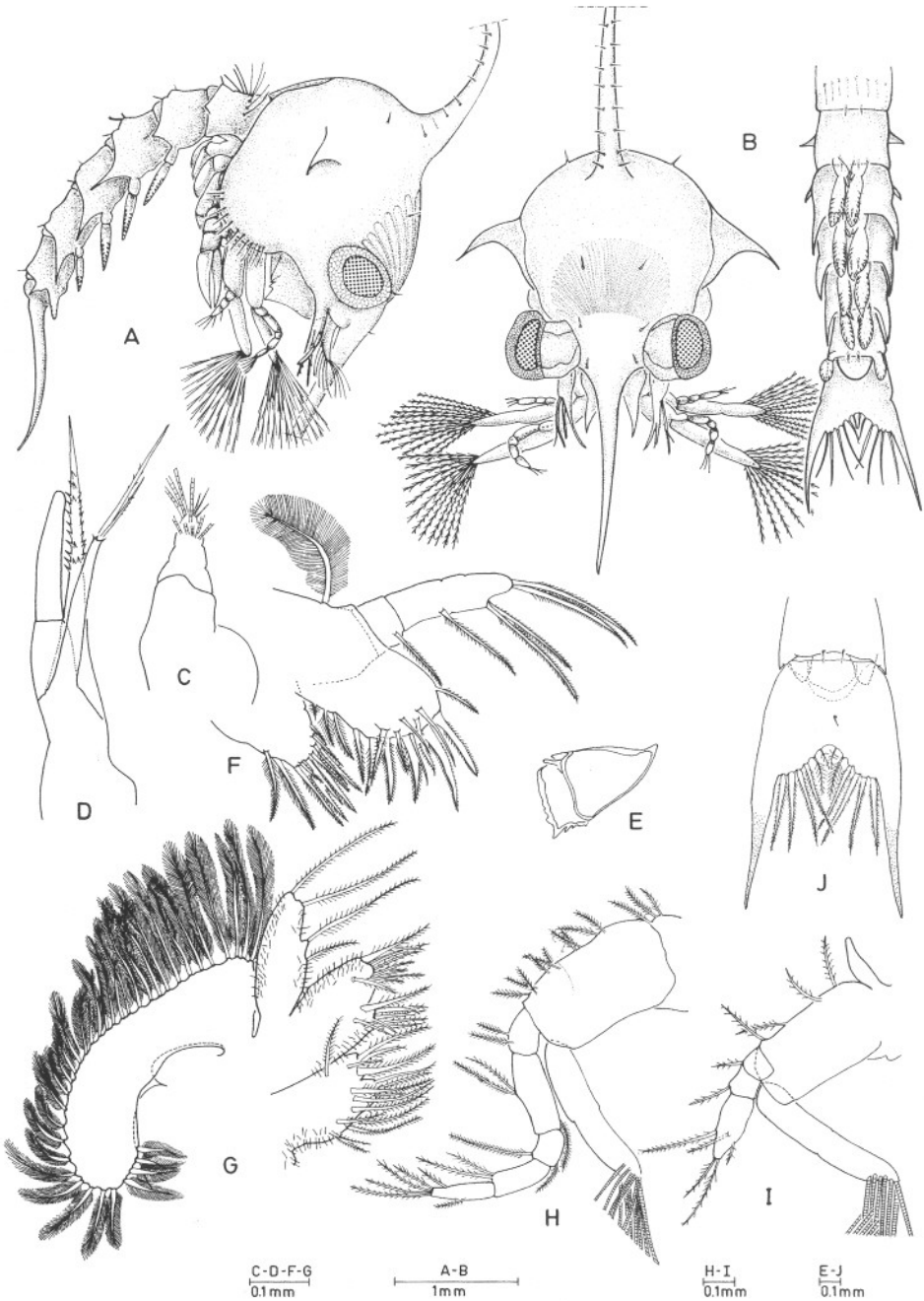

Fig. 5. *Gecarcinus lateralis lateralis*, fifth zoea: A, Lateral view; B, Frontal view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, Maxilliped I; I, Maxilliped II; J, Telson.

somites 2–5 biramous, small setal buds present; somite 6 now with 2 spinules near posterodorsal margin; posterior margin of telson with 6 + 6 processes, 2 innermost smaller and plumose.

Zoea VI

Size.—C.L.: 2.08–2.14 mm; D.S.: 2.16 mm (n = 1); R.S.: 1.55 mm (n = 1); tip of dorsal to tip of rostral spine: not measured; tip to tip of lateral carapace spines: 2.52–2.65 mm.

Sixth zoeal stage changing drastically in most respects in comparison to previous larval stages; increased setation and segmentation.

Carapace (Fig. 6A, B).—Dorsal spine with 10 pairs of setules; lateral margin with 14–16 setules.

Antennule (Fig. 6C).—Exopod 3-segmented with 4 groups of aesthetascs arranged according to segments: 6 + 1 seta, 6 + 1 seta, 4 + 3 setae; endopod present as amorphous bud.

Antenna (Fig. 6D).—Endopod 3-segmented with setae on second segment; terminal endopod segment as well as exopod weakly segmented; exp./pr.: 0.54–0.66; endp./exp.: 1.51–1.83; endp./pr.: 0.95–1.06.

Mandible (Fig. 6E, F).—Palp unsegmented, well developed.

Maxillule (Fig. 6G).—Endopod 2-segmented, setal pattern unchanged; basal endite with 21–26, coxal endite with 16–20, processes.

Maxilla (Fig. 6H).—Basal endite, proximal lobe with 11, distal lobe with 11–13, processes; coxal endite, proximal lobe with 16–19, distal lobe with 8–9, processes; scaphognathite with 46–57 processes with 1–2 setae on surface.

First Maxilliped (Fig. 6I).—Exopod 2-segmented with 13–14 natatory setae on distal segment, proximal segment with 2 setae on distal surface; endopod setation unchanged; basipodite now with 14 setae: 2 + 2 + 5 + 5; coxa with 9 setae.

Second Maxilliped (Fig. 6J).—Exopod 2-segmented, proximal segment with 3 setae on distal surface, distal segment with 14–15 natatory setae; endopod 5-segmented, with proximal 2 segments distinct, distal 3 less so; setal formula 1, 1, 0, 2–4, 8–9.

Third Maxilliped (Fig. 7E).—Armed.

Thoracopods (Fig. 7F, G, H).—Clearly 5-segmented, weakly armed except thoracopod 5.

Abdomen (Fig. 6A, B, K).—Somite 1 with row of 10–11 setae; posterodorsal edge of somites 1–5 with spinules; posterolateral extensions of somites with single small setule at base; pleopods, somites 2–5 biramous, endopods with 3–5 hooks, somite 6 uniramous, exopods with distinct setation: I: 23; II: 25; III: 23; IV: 21; V: 15–17; telson with 6 + 6 processes, 2 innermost smaller and plumose.

Megalopa

Size.—C.L.: 2.58–3.19 mm; carapace width: 2.06–2.90 mm; carapace length-width ratio: 1.10–1.25.

Carapace (Fig. 8A, B).—Rostrum terminating as single median process, projected downwards; carapace armed with setae and spinules, with dorsolateral knobs.

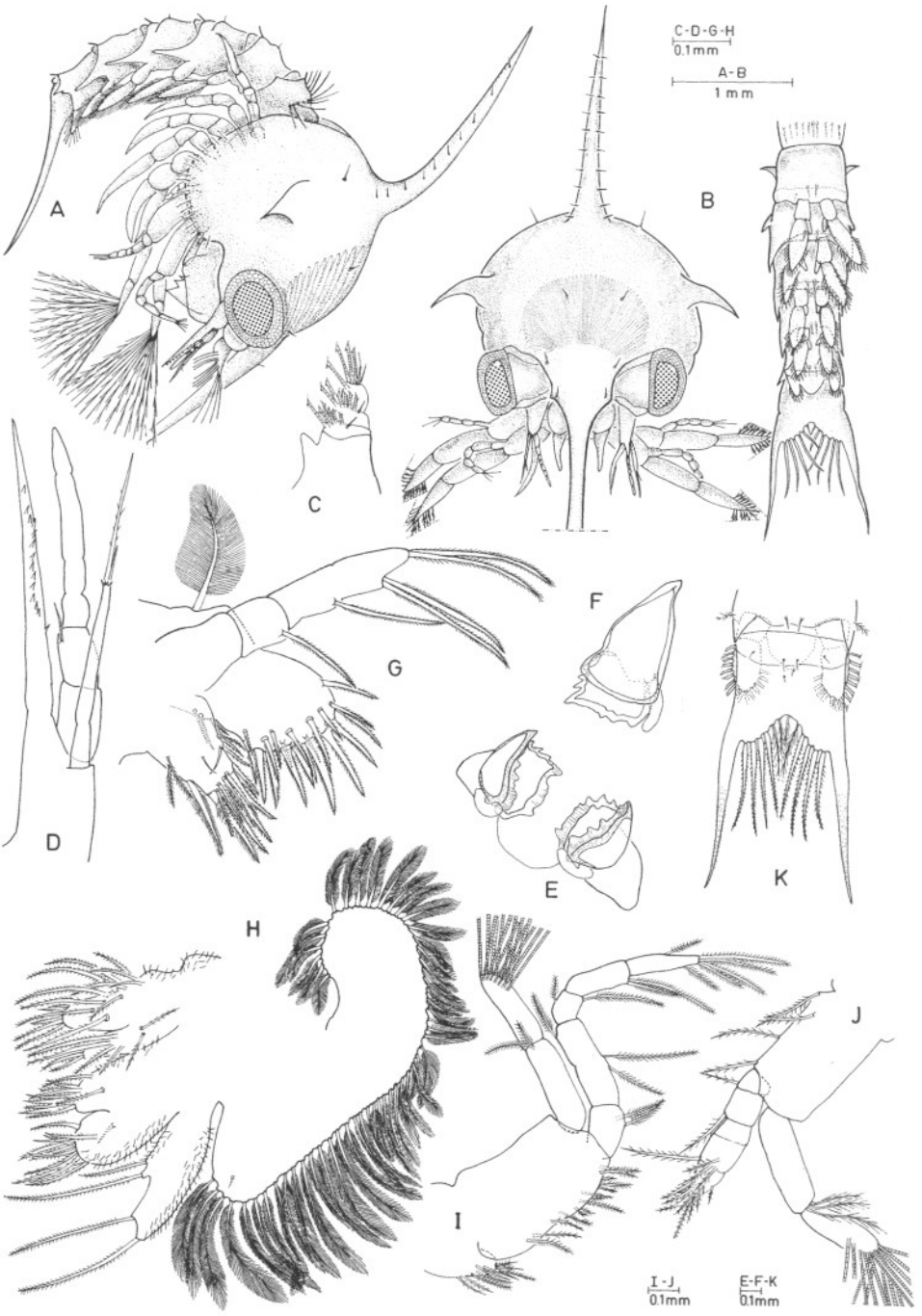

Fig. 6. *Gecarcinus lateralis lateralis,* sixth zoea: A, Lateral view; B, Frontal view; C, Antennule; D, Antenna; E, Mandible, ventral view; F, Mandible, dorsal view; G, Maxillule; H, Maxilla; I, Maxilliped I; J, Maxilliped II; K, Telson.

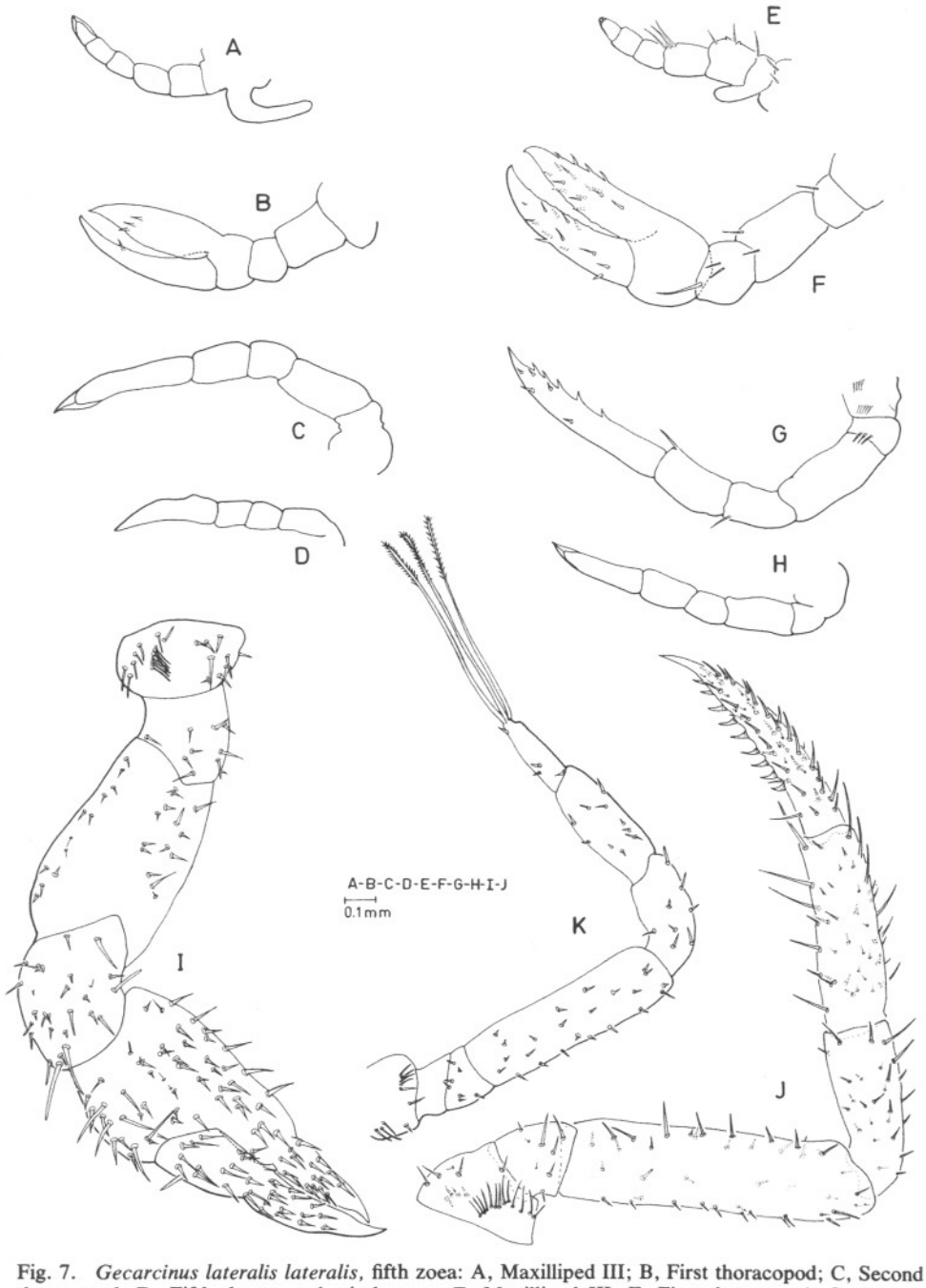

Fig. 7. *Gecarcinus lateralis lateralis,* fifth zoea: A, Maxilliped III; B, First thoracopod; C, Second thoracopod; D, Fifth thoracopod; sixth zoea: E, Maxilliped III; F, First thoracopod; G, Second thoracopod; H, Fifth thoracopod; megalopa: I, First thoracopod; J, Second thoracopod; K, Fifth thoracopod.

Antennule (Fig. 8D).—Biramous, with 3-segmented pedunculus; dorsal ramus unsegmented, with 3 terminal setae; ventral ramus 3-segmented, aesthetasc setal formula: $2 \times 6 - 2 \times 1$ seta, $4 - 2$ setae, $1 + 3 - 2$ setae.

Antenna (Fig. 8E).—Flagellum 9-segmented, each segment with processes, except segment 3; exopod and protopodite still present.

Mandible (Fig. 8H).—Palp 3-segmented, terminal segment with 21–23 processes.

Maxillule (Fig. 8F).—Endopod 2-segmented, basal segment with 2 setae, terminal segment with 1 + 4 setae; armature of basal and coxal endites with 30–32 and 21–24 processes respectively.

Maxilla (Fig. 8G).—Unsegmented endopodite with 7–9 lateral and 1 terminal setae: 3 inner + 3–5 on outer margin; basal endite, proximal lobe with 14–18, distal lobe with 16–20, processes; coxal endite, proximal lobe with 20–24, distal lobe with 10–11, processes; scaphognathite with 62–69 processes with 4–7 spines on surface.

First Maxilliped (Fig. 9A).—Exopod 2-segmented with 4 setae on distal outer corner of basal segment, 7–8 setae on terminal segment; endopod indistinctly 2-segmented with 4 terminal setae: 3 well developed + 1 small, inner lateral margin with 7–10 processes: 2–3 + 2–3 + 1 + 2 + 0–1; basal and coxal endites each with 24–29 processes; epipodite triangular, with several processes as shown.

Second Maxilliped (Fig. 9B).—Exopod 2-segmented; terminal segment with 7–10 terminal setae; basal segment with 2–3 setae on inner and 0–2 setae on outer margin, 1–2 spines on outer margin; endopod 4-segmented, processes ranging: I: 2; II: 1–2; III: 9–11; IV: 12–14 from proximal to distal segments; basipodite with 5–7 processes.

Third Maxilliped (Fig. 9C).—Now well developed; endopod 5-segmented, each armed with spines: I: 31–33; II: 23–25; III: 15–17; IV: 12; V: 8–9; exopod 1-segmented, with 4–5 processes.

Thoracopods (Fig. 7I, J, K).—Armed; cheliped as shown; dactyls of pereopods 2–4 armed with strong serrated spines along inner edge; dactyl of pereopod 5 with 3 long curled terminal processes.

Abdomen (Figs. 8A, B, C; 9D, E, F).—Six somites plus telson; somite 1 with row of 13–14 setae on dorsal surface; posterodorsal margins with several spines as shown; segments 2–6 with pleopods, decreasing in size posteriorly, somite 2–5 biramous, somite 6 uniramous; exopods marginal setae: I: 28–30; II: 28–29; III: 26–27; IV: 22–24; V: 16–17; endopods with hooks: 6–7, 5, 4–5, 3–5; basal segment of uropods with 2 lateral setae; most (10 out of 11) megalopae had telson as shown in Fig. 9E: inner margin of telson with 7–8 processes, apical tips each with 3 terminal processes and arms of fork still present on lateral margin; Fig. 9F: telson with rounded tip and 4 processes on posterior margin, dorsal surface with several spinules and setae.

Larval Development

Quantitative data are based on four groups, each containing ten zoeae (Fig. 10). Three groups of 20 zoeae were used to collect additional data. The development of the larvae from hatching to megalopa was reached after 19–20 days. Some early megalopa stages occurred in group 4 on the 17th and 19th days, but

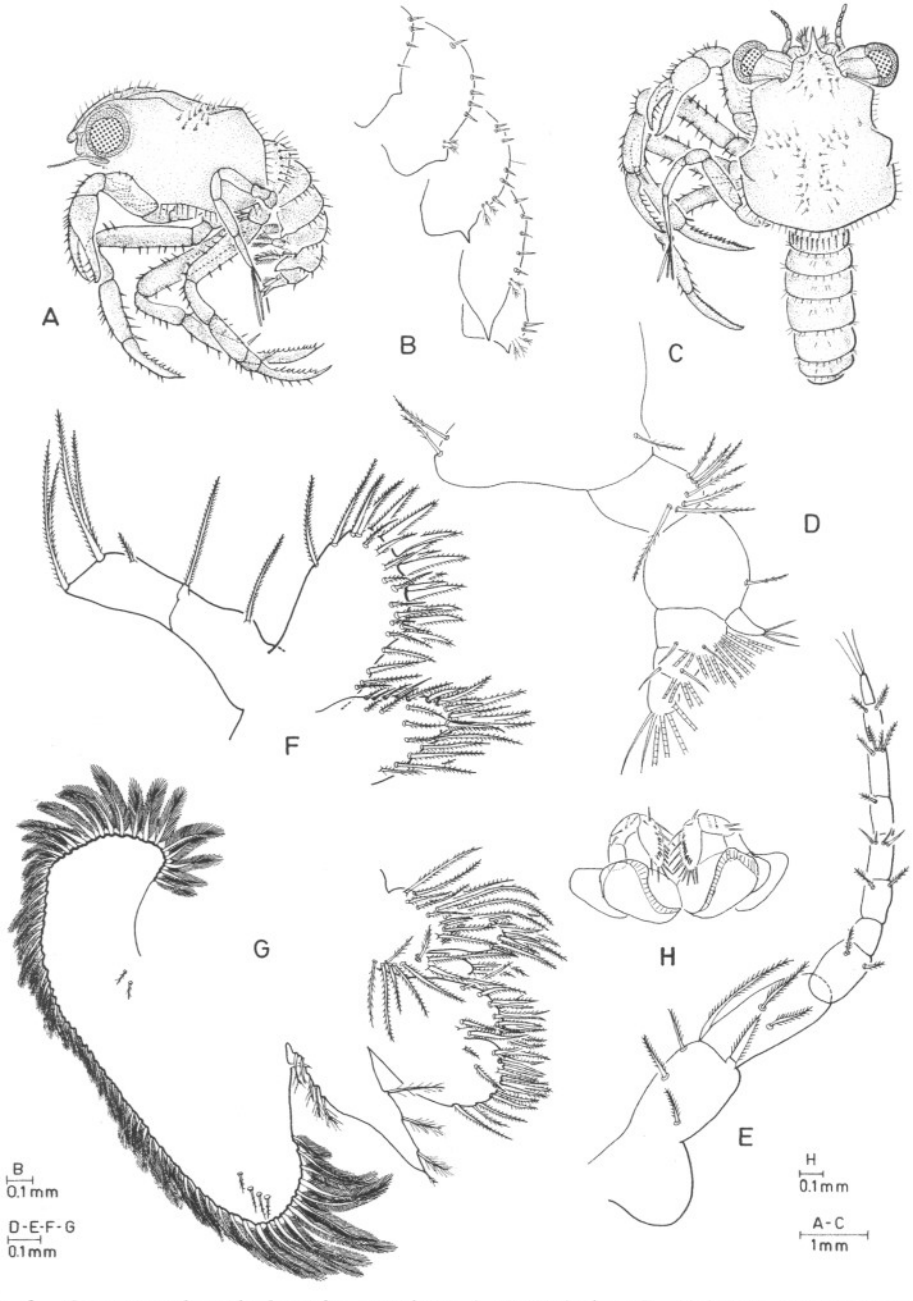

Fig. 8. *Gecarcinus lateralis lateralis*, megalopa: A, Lateral view; B, Abdomen, lateral view; C, Dorsal view; D, Antennule; E, Antenna; F, Maxillule; G, Maxilla; H, Mandible, ventral view.

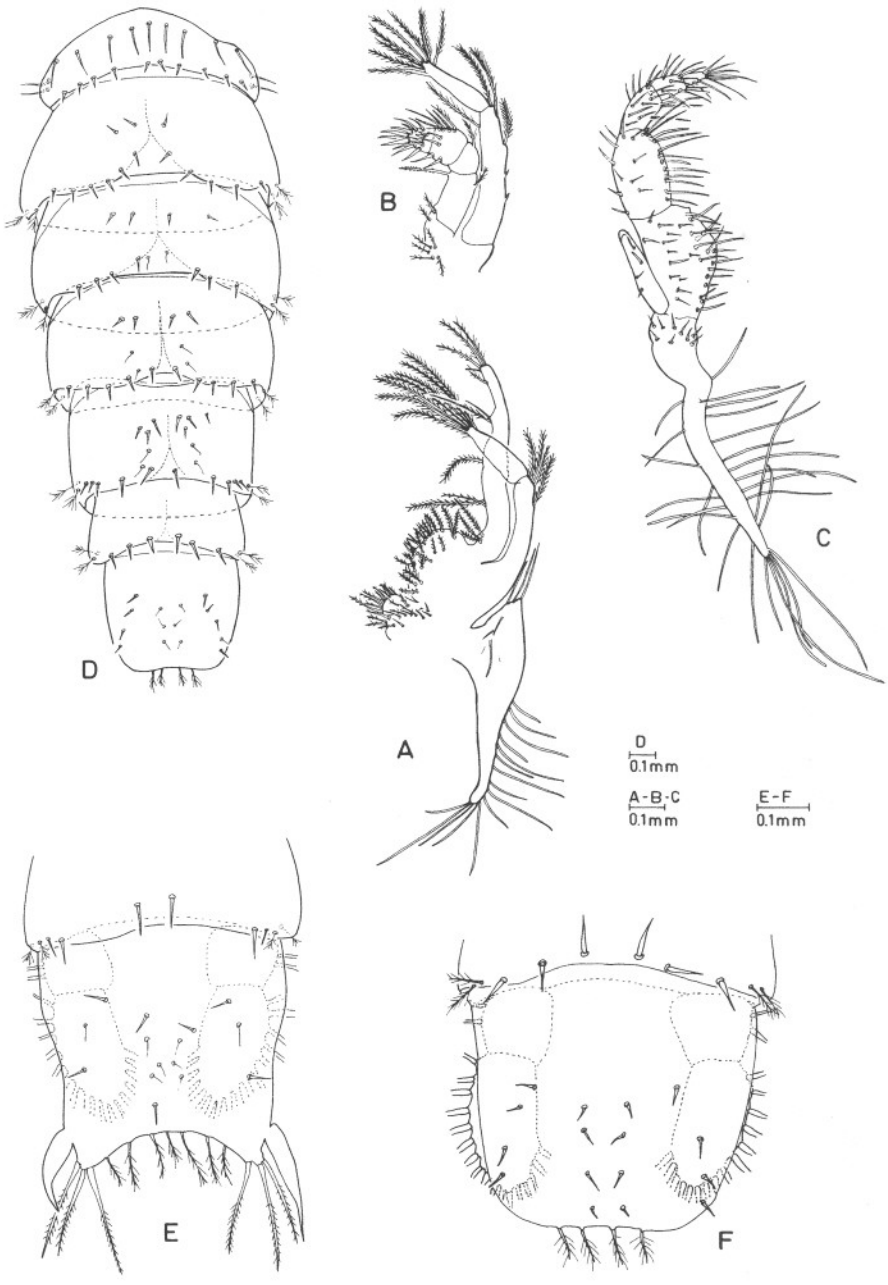

Fig. 9. *Gecarcinus lateralis lateralis*, megalopa: A, Maxilliped I; B, Maxilliped II; C, Maxilliped III; D, Abdomen and telson, dorsal view; E, Telson, abnormal; F, Telson, normal.

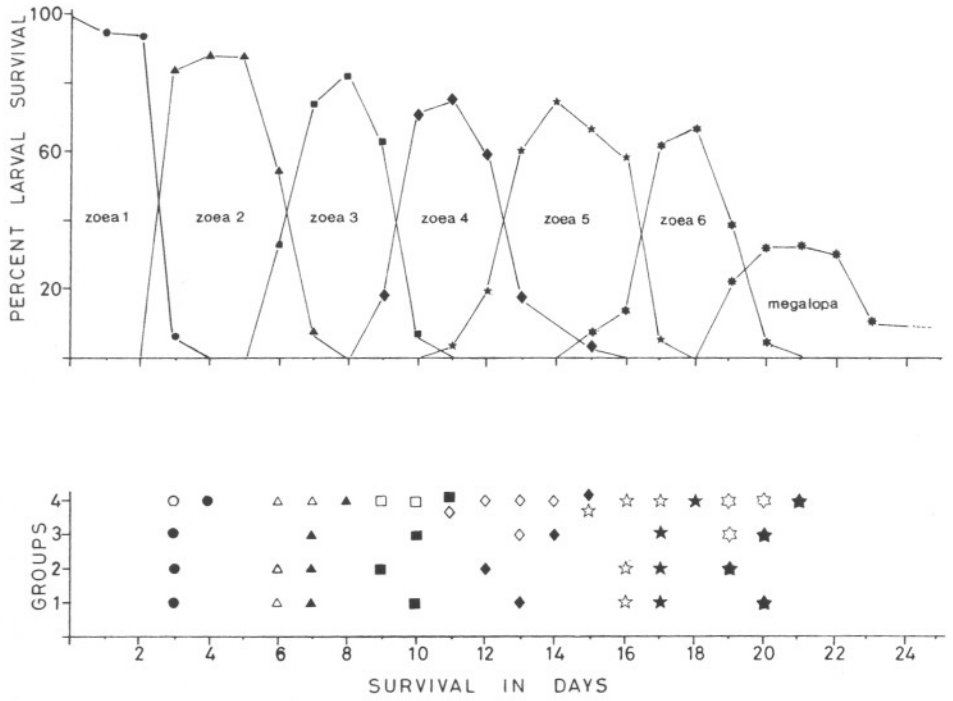

Fig. 10. Percentage survival and stage duration of *Gecarcinus lateralis lateralis* larvae reared under laboratory conditions; white = moulting activity; black = 100% moulted.

they all died during molting. Successive zoeal stages were reached after: 3–4 days for zoea II; 6–8 days for zoea III; 9–11 days for zoea IV; 11–15 days for zoea V; 15–18 days for zoea VI. Little information was obtained on the time required to reach the first crab stage since mortality was high in the megalopa stage and culturing was discontinued after 29 days. At that time only two specimens had reached the crab stage. No prezoeal exuviae were found among the larvae fixed immediately after hatching.

Discussion

Gecarcinus lateralis lateralis passes through six zoeal stages during its larval development, differing from *Cardisoma guanhumi* and *C. carnifex* in which only five zoeal stages were observed (Costlow and Bookhout, 1968; Kannupandi *et al.*, 1980). The larval development of *Gecarcinus lateralis lateralis* through six zoeal stages to the megalopa (20.0 days) takes about the same time as for *Cardisoma guanhumi* (22.5 days). The development time from megalopa to the first crab stage seems to be much shorter for *Gecarcinus lateralis lateralis*.

It must be recognized that "pseudomass" rearing does not allow individual larval life histories, which are essential in detecting intercalated or extra stages, to be followed. In view of much recent evidence (Gore *et al.*, 1981), the possible existence of intercalated stages should no longer be ignored for *G. l. lateralis*.

The presence of additional setae on the posterior telson margin, as observed in the third and fifth zoeae, can in combination with other differences, be an

Table 1. A comparison of the first zoeal stage in *Gecarcinus lateralis lateralis* and *Gecarcinus lateralis*.

	G. lateralis lateralis Present study	*G. lateralis* Cabrera, 1966
Carapace armature	2 spinules	absent
Antennule	2 aesthetascs + 2 setae	3 aesthetases + 1 seta
Maxillule, endopod	two-segmented ; 1, 1+2+2 setae	two-segmented ; 1, 1+2+2 setae
basal endite	5-6 processes	5 processes
coxal endite	6 processes	6 processes
Maxilla, endopod	4 setae : 2+2	4 setae : 2+2
basal endite, distal lobe	9 processes { 4	6-9 processes { 3-4
proximal lobe	5	3-5
coxal endite, distal lobe	9 processes { 4	6-9 processes { 2-4
proximal lobe	5	4-5
scaphognathite	4+1 plumose setae, pointed, plumose tip	4 plumose setae, pointed
First maxilliped, exopod	unsegmented, 4 natatory setae	unsegmented, 4 natatory setae
endopod	five-segmented : 2, 2, 1, 2, 4+1 setae	five-segmented : 2, 2, 1, 2, 4+1 setae
basipodite	10 setae : 2+2+3+3	8-10 setae : 2+2+2(3)+2(3)
Second maxilliped, exopod	unsegmented, 4 natatory setae	unsegmented, 4 natatory setae
endopod	three-segmented ; 1, 1, 6 setae	four-segmented ; 1, 1, 3, 3
basipodite	4 setae : 1+1+1+1	3-(4) setae : 1+1+1(+1)
Abdomen, somite 2-5	postero-dorsal spines	absent
Telson, fork armature	spinules	absent

indication of such stages (Gore *et al.*, 1981). However, comparison of the different specimens revealed no other variable features. Further evidence is found in the early development of megalopae that died during molting on the 17th and 19th days. Examination of exuviae of one individual, slightly damaged and still attached to the megalopa, revealed it to be a zoea V, differing from the other fifth zoeae in the well-developed mandibular palp (cf. zoea VI). No other differences could be detected. For this reason, the possibility of the fifth zoea molting directly to megalopa must be considered for *G. l. lateralis*.

All stages of *G. l. lateralis* observed in the present study show the rostral, dorsal, and lateral spines on the carapace, previously described for the zoeal stages of the different species within the Gecarcinidae (Cannon, 1923; Cabrera, 1966; Costlow and Bookhout, 1968; Erhardt and Niaussat, 1968; Kannupandi *et al.*, 1980). The lateral spines on somites 2 and 3 of *G. l. lateralis* are similar to *Cardisoma guanhumi* and *C. carnifex*. However, these species differ from *C. armatum* and *Gecarcinus planatus* which bear lateral spines on the second abdominal somite only. In his key to the brachyuran families Rice (1980) uses the lateral spines on the third somite as a diagnostic character for the Gecarcinidae. Thus, the latter two species should be re-examined.

Table 1 shows only slight differences between the first zoeae of *G. l. lateralis* from Bermuda and *G. lateralis* described from the Mexican coast by Cabrera (1966), who gives no further indication on the subspecies. His specimens have an antennule with three aesthetascs and one seta, but from his figure it is not clear whether the smaller process is an aesthetasc or a long seta. Furthermore, Cabrera's specimens show more variation in the number of processes of the basal and coxal endite of the maxilla and the basipodite setation of the first and second maxilliped. The maxilla also differs from the Bermuda specimens in the absence of both an apical process on the scaphognathite and tiny hairs on the apical tip, the endopod, and the basal and coxal endites. The description of the endopod of the second maxilliped as four-segmented is not clear from Cabrera's figure, where the distal part seems one-segmented or at most indistinctly two-segmented. The abdominal armature differs in the absence of the posterodorsal spinules on so-

mites 2–5 and the absence of tiny spinules on the telson fork. The spinules on the carapace are not mentioned and, like the abdominal armature, were possibly overlooked.

A comparison of the different characters among *G. l. lateralis, Cardisoma guanhumi* (Costlow and Bookhout, 1968), and *C. carnifex* (Kannupandi *et al.*, 1980) is presented in Table 2. In the zoeal phase all stages of *Gecarcinus lateralis lateralis* can be distinguished from both *Cardisoma* species by the following characters: the carapace armature; the antennule; the spinules on the distal edge of the exopod of the antenna; the setal arrangement of the endopod of the maxillule; the number and arrangement of the endopod setae of the maxilla; the featherlike character of the protopodal and scaphognathite setae of the maxillule and maxilla, respectively; the early development and segmentation of the third maxilliped and thoracopods; and the armature of the abdominal somites and telson forks.

The armature of the dorsal spine and carapace itself is not mentioned or figured by Costlow and Bookhout (1968) and Kannupandi *et al.* (1980). In particular the lateral processes on the carapace margin of stages II–VI also occur in some Catometopa and in most Cyclometopa (Rice, 1980).

The antennule differs among all stages of the three gecarcinid species in the number and arrangement of the processes. For the *Cardisoma* species the endopod of the antennule appears earlier than in *Gecarcinus lateralis lateralis*. Otherwise, the reverse holds for the antennal endopod. The mandibular palp appears in both genera in the fifth stage.

The total number of setae on the distal segment of the maxillule endopod is identical in all stages of the three species, but *G. l. lateralis* and *G. lateralis* (Cabrera, 1966) differ in the arrangement of the setae, which is an easily observed feature to distinguish both genera. Furthermore, the three species differ from each other in the pattern of the protopodal setae. Although no range of variance of the number of processes is available for both *Cardisoma* species, there do not seem to be important differences. Nevertheless, a slight increase in the number of the processes on the coxal endites is apparent in *G. l. lateralis*.

The three gecarcinid species also show differences in the endopod setation of the maxillae. According to Rice (1980) *Gecarcinus* has the most advanced arrangement (2 + 2) with decreasing order *Cardisoma guanhumi* (2 + 3) and *C. carnifex* (3 + 4). The latter represents the most primitive situation within the Gecarcinidae which is similar in some Calappidae, the primitive Cancridae, the Carcininae, and Goneplacidae (Rice, 1980). As for the maxillule no range of variation in the number of processes on the basal and coxal endites is given and thus evaluation of the differences is difficult. Based on the available information, no significant differences seem to exist. The featherlike character of one protopodal seta of the maxillule and the scaphognathite setae of the maxilla is rather exceptional for both anomuran and brachyuran larvae.

Except for the basal segment, the endopod setation of the first maxilliped differs among the three species. The exopod of *C. carnifex* can be distinguished from both other species by the early development of a two-segmented exopod. Based on the present study, however, it can be questioned whether these exopods are either in reality two-segmented or only indistinctly two-segmented. Furthermore, *C. guanhumi* differs from *C. carnifex* and *Gecarcinus lateralis lateralis* by the setation of the basipodite of the second maxilliped. However, it is difficult to decide on the distinguishing value of this feature since Cabrera (1966) found it to be variable. The endopod setation of *Cardisoma carnifex* differs in the number and arrangement of the setae, representing (if exact) a unique setal pattern within

Table 2. Summary of zoeal characters in gecarcinid species of which the complete larval development is known.

	Gecarcinus lateralis lateralis Present study	*Cardisoma guanhumi* Costlow & Bookhout, 1968	*Cardisoma carnifex* Kannupandi *et al.*, 1980
CARAPACE			
Length (mm), stages I-VI	0.68-0.71 ; 0.74-0.81 ; 0.90-0.96 ; 1.06-1.32 ; 1.84-1.94 ; 1.88-1.94	?	0.38 ; 0.45 ; 0.50 ; 0.74 ; 0.90 ; -
Dorsal, rostral, lateral spines	all stages well-developed	all stages well-developed	all stages well-developed
Dorsal spine, armature	stages II-VI only	absent	absent
Armature, spinules-latero-marginal setules, stages I-VI	2-0 ; 6-±1 ; 6-±5 ; 6-±8 ; 6-±12 ; 6-±16	absent	absent
ANTENNULE			
Segments, aesthetascs-seta formula	stage VI three-segmented only	all stages one-segmented	all stages one-segmented
Stages I-VI	2-2 ; 4-2 ; 4-3 ; 1+1+3-3 ; 5+1+3-3 ; (6-1)(6-1)(1+3-1)	2-2 ; 5-2 ; 5-2 ; 3-1+1+3 ; 5+1+3 -2 ; -	3-1 ; 5-0 ; 5-0 ; 2+5-0 ; 1+1+8-0 ; -
ANTENNA			
Protopodite, rows of spines, stages I-VI	2 ; 2 ; 2 ; 2 ; 2 ; 2	2 ; 2 ; 2 ; 2 ; 2 ; -	? ; 2 ; 2 ; 2 ; 2 ; -
Exopod, terminal processes	all stages two unequal setae + spinules	all stages two unequal setae	all stages two unequal setae
Endopod, segments-protopodal length, stages I-VI	n.d. ; n.d. ; 1-±1/5 ; 1-±1/3 ; 2->1/2 ; 4-equal	n.d. ; n.d. ; n.d. ; 1-±1/3 ; 1-equal ; -	n.d. ; n.d. ; n.d. ; 1-±1/2 ; 1-±3/4 ; -
MANDIBLE			
Mandibular palp	unsegmented bud in stages V-VI	unsegmented bud in stage V	unsegmented bud in stage V
MAXILLULE			
Endopod, seta-formula	all stages two-segmented : 1, 1+2+2	all stages two-segmented : 1, 1+4	all stages two-segmented : 1, 1+4
Basal endite, protopodal setae, stages I-VI	a ; 1 ; 1 ; 2 ; 2 ; 2	a ; a ; 1 ; 1 ; 2 ; -	all stages absent
processes, stages I-VI	5-6 ; 8 ; 9-11 ; 12-13 ; 15-16 ; 21-26	5 ; 6 ; 7 ; 10 ; 16 ; -	5 ; 8 ; 9 ; 12 ; 14 ; -
Coxal endite, processes, stages I-VI	6 ; 7-8 ; 8 ; 8-11 ; 11-14 ; 16-20	6 ; 6 ; 6 ; 7 ; 9 ; -	6 ; 6 ; 6 ; 6 ; 10 ; -
MAXILLA			
Endopod, seta-formula	all stages unsegmented : 4 : 2+2	all stages unsegmented : 5 : 2+3	all stages unsegmented : 7 : 3+4
Basal endite processes, stages I-VI, distal lobe	4 ; 4-5 ; 5 ; 6-7 ; 8-9 ; 11-13	4 ; 4 ; 4 ; 5 ; 7 ; -	2 ; 5 ; ? ; 6 ; ? ; ? ; -
proximal lobe	5 ; 5 ; 6 ; 6-7 ; 8-9 ; 11	5 ; 5 ; 5 ; 6 ; 7 ; -	2 ; 5 ; ? ; 5 ; ? ; ? ; -
Coxal endite processes, stages I-VI distal lobe	4 ; 4 ; 4 ; 4 ; 5 ; 8-9	4 ; 4 ; 4 ; 4 ; 5 ; -	3 ; 5 ; ? ; ? ; ? ; ? ; -
proximal lobe	5 ; 5 ; 5-7 ; 7-8 ; 11-14 ; 16-19	5 ; 5 ; 5 ; 6 ; 7 ; -	6 ; 5 ; ? ; ? ; ? ; ? ; -
Scaphognathite, processes, stages I-VI	4+1 ; 5-7+3 ; 10-12+4-5 ; 22-27 ; 34-37 ; 46-57	4+1 ; 5+3 ; 15 ; 23 ; 34 ; -	3+3 ; 5+3 ; 15 ; 27 ; 37 ; -
FIRST MAXILLIPED			
Basipodite, medial setae	all stages 10 : 2+2+3+3	all stages 4 : 1+1+1+1	stages I-IV 10 : (2+2+3+3)?
Endopod, seta formula	all stages five-segmented - stages I-III 2, 2, 1, 1, 4+1 stages IV-VI 2, 2+1, 1+1, 2, 5+1	all stages five-segmented - stages I-III 2, 2, 1, 2, 4+1 stages IV-V 2, 2, 1, 2, 5+1	all stages five-segmented - stages I-V 2, 2, 2, 2, 4+1
Exopod, natatory setae	stage VI two-segmented only 4 ; 6 ; 8 ; 10 ; 11-12 ; 13-14	all stages one-segmented 4 ; 6 ; 8 ; 9 ; 10 ; -	stages II-V two-segmented 4 ; 6 ; 8 ; 10 ; 11 ; -
SECOND MAXILLIPED			
Basipodite, medial setae	all stages 4 : 1+1+1+1	all stages 3 : 1+1+1	stages I-IV 4 : 1+1+1+1 ; stage V ?
Endopod, seta formula	all stages 3-segmented : 1, 1, 6	all stages three-segmented : 1, 1, 6	all stages three-segmented : 1, 3, 3
Exopod, natatory setae	stage VI two-segmented only, articulated, 4 ; 6 ; 8 ; 10 ; 12-13 ; 14-15	all stages one-segmented, 4 ; 6 ; 8 ; 10 ; 12 ; -	stages II-V two-segmented 4 ; 6 ; 8 ; 11 ; 14 ; -
THIRD MAXILLIPED			
Segments	stages II-IV small bud, stages V-VI five-segmented	stages IV-V small bud	stages IV-V small bud
THORACOPODS	stages III-IV small buds, stages V-VI four-five-segmented, stages IV-VI first thoracopod chelate	stages IV-V small buds	stages IV-V small buds
PLEOPODS	stage IV uniramous, stages V-VI biramous	stages IV-V uniramous	stages IV-V uniramous
ABDOMEN			
Dorso-lateral processes, somite 2-3	all stages	all stages	all stages
Postero-lateral extensions, somite 2-5	all stages	all stages	all stages
Dorsal setae, somite 1	all stages, 2 ; 2-3 ; 4-5 ; 5-6 ; 7-9 ; 10-11	absent	absent
Median spines, somite 1-6	absent	absent	all stages
Postero-dorsal spines, somite 2-5	all stages	absent	absent
somite 6	stages V-VI only	absent	absent
TELSON			
Posterior margin	3+3 ; 4+4 ; 4-5 + 4-5 ; 5+5 ; 5-6 + 5-6 ; 6+6	3+3 ; 3+3 ; 4+4 ; 5+5 ; 5+5 ; -	3+3 ; 3+3 ; 4+4 ; 5+5 ; 5+1+5 ; -

Table 3. Summary of megalopal characters in gecarcinid species of which the complete larval development is known.

	Gecarcinus lateralis lateralis Present study	*Cardisoma guanhumi* Costlow & Bookhout, 1968	*Cardisoma carnifex* Kannupandi *et al.*, 1980
CARAPACE			
Rostral spine	directed downwards	directed downwards	directed downwards
Lateral knobs	present	absent	absent
Armature	present	present	present
ANTENNULE			
Pedunculus	three-segmented, armed, middle segment with row of processes	three-segmented, middle segment bare	three-segmented, middle segment bare
Dorsal ramus	unsegmented, three terminal setae	unsegmented, two terminal setae	unsegmented, two terminal setae
Ventral ramus, aesthethase - seta formula	three-segmented : 6+6-2, 4+2, 1+3-2	three-segmented : 6, 7-1, 6	four-segmented : 6, 6, 6, 0-2
ANTENNA	nine-segmented, armed except segment 3	nine-segmented, armed except segments 4 and 6	nine-segmented, armed except segments 4 and 6
MANDIBLE			
Mandibular palp, spine formula	three-segmented : 1-2, 4-5, 21-23 spines	two-segmented : 11 spines : 1, 10	two-segmented : 11 spines : 1, 10
MAXILLULE			
Endopod, seta formula	two-segmented : 2, 1+4 setae	two-segmented : 2, 4 setae	two-segmented : 2, 4 setae
Basal endite	30-32 processes	? (± 21)	13 processes
Coxal endite	21-24 processes	? (± 14)	9 processes
MAXILLA			
Endopod, seta formula	unsegmented : 3+1+3-5 setae	unsegmented : 3+2+2+2 setae	unsegmented : 0+2+2+2 setae
Basal endite, distal lobe proximal lobe	30-38 processes : 16-20 / 14-18	? (± 14) processes : ? (± 9) / ? (± 10)	15 processes : ? (± 7) / ? (± 8)
Coxal endite, distal lobe proximal lobe	30-35 processes : 10-11 / 20-24	? (± 22) processes : ? (± 7) / ? (± 15)	19 processes : ? (± 3) / ? (± 16)
Scaphognathite	62-69 plumose setae + 4-7 spines	± 61 plumose setae + ±3 spines	± 60 plumose setae
FIRST MAXILLIPED			
Exopod, seta formula	two-segmented : 4, 7-8 setae	two-segmented : 3, 5 setae	two-segmented : 0, 5 setae
Endopod	unsegmented : 11-14 setae	unsegmented : 10 setae	unsegmented : 8 setae
Basipodite, basal lobe	24-29 processes	± 21 processes	12 processes
coxal lobe	24-29 processes	± 14 processes	7 processes
SECOND MAXILLIPED			
Exopod, seta formula	two-segmented : 3-5, 7-10 setae	two-segmented : 1, 5 setae	two-segmented : 0, 5 setae
Endopod, process formula	four-segmented : 2, 1-2, 9-11, 12-14 processes	three-segmented : 1, 7, 10 processes	three-segmented : 1, 4, 7 processes
Basipodite	5-7 processes	8 processes	7 processes
THIRD MAXILLIPED			
Exopod	one-segmented : armed	two-segmented : 0, 5 setae	two-segmented : 0, 5 setae
Endopod, process formula	five-segmented : 31-33, 23-25, 15-17, 12, 8-9 processes	five-segmented : 15, 12, 6, 10, 9 processes	five-segmented : 7, 5, 5, 7, 6 processes
THORACOPODS	armed, 5th dactylus with 3 processes	armed, 5th dactylus with 3 processes	armed, 5th dactylus with 3 processes
ABDOMEN			
Somites, postero-lateral extensions	somites 1-6	somites 2-5, somite 6 ?	somites 2-5 only
postero-dorsal spines	somites 1-6	absent	absent
mid-dorsal spines	somites 1-5	absent	absent
Somite 1, dorsal surface	14-16 setae	bare	bare
Pleopods, somites 2-5 exopods	28-30, 28-29, 26-27, 22-24 setae	?	?
endopods	hooks : 6-7, 5-5, 4-5, 3-5	?	3 hooks
somite 6 distal segment	16-17 setae	?	12
proximal segment	2 setae	?	bare
Telson, posterior margin	rounded, 4 processes	rounded, 6 processes	rounded, 5 processes

the brachyrhynch families (see Table XI; Rice, 1980). In both first and second maxillipeds the natatory setae are articulated in *Gecarcinus*, but no information is available on *Cardisoma*.

Gecarcinus lateralis lateralis can be distinguished from both *Cardisoma* species by the armature of the abdominal somites, particularly by the dorsal setae on the first somite. The latter were also noticed by Cabrera (1966) for *Gecarcinus lateralis*. He did not mention or figure posterodorsal spines. Furthermore, *Cardisoma carnifex* shows some peculiar dorsomedian spines not found in the other gecarcinid species. The tiny spinules on the distal part of the telson forks are present only in the zoeal stages of *Gecarcinus lateralis lateralis*. However, it is possible that these structures were overlooked in the other species.

A comparison between the known megalopae is given in Table 3. The megalopa of *G. l. lateralis* can easily be distinguished from both *Cardisoma* species by the following features: the dorsolateral knobs on the carapace; the number of processes on the middle segment of the pedunculus and dorsal ramus of the antennule; the setation of the antennal segments; the three-segmented mandibular palp; the increased number of processes on the maxillule, maxilla, and first and second maxilliped; the four-segmented exopod of the second maxilliped; the one-segmented exopod of the third maxilliped; and the armature of the abdomen and telson.

The primitive evolutionary level of the Gecarcinidae within the Catometopa (Rice, 1980) is further confirmed by the new information, particularly the number of zoeal stages and the spinules on the telson in *G. l. lateralis* and the new, more primitive pattern of endopod setation of the maxilla in *Cardisoma carnifex*. The number of zoeal stages (six) is recorded for the first time in the Catometopa, since none of them are known to have more than five zoeae (Rice, 1980).

It is clear that the family Gecarcinidae is a heterogeneous group probably in need of splitting. However, to decide on this matter, additional descriptions of larvae of the different species must be awaited.

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