Larval development of *Acanthonyx lunulatus* (Brachyura, Majidae, Epialtinae)

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**Abstract.** The two zoeal stages and the megalopa of the majid crab *Acanthonyx lunulatus* are described and illustrated from laboratory-reared material. The morphology of the larvae is compared to previous descriptions of larvae of other majid crabs of the subfamily Epialtinae.

**Introduction**

*Acanthonyx lunulatus* (Risso, 1816) is a small majid crab known from the Mediterranean Sea and eastern Atlantic waters from Portugal to Namibia, including the Azores (Zariquiey-Álvarez, 1968; Manning and Holthuis, 1981). It lives attached to algae at depths of between ~0 and 20 m (Zariquiey-Álvarez, 1968). Some aspects of its biology are known, including its life cycle (Chaix, 1979; Sanz, 1989), relative growth and biometry (Sanz, 1986), and physiology (Chaix et al., 1976; Chaix, 1984; Laugier and Chaix, 1984, 1985). However, the knowledge of its larval development was, to date, incomplete.

Cano (1893) was the first author to illustrate a larval stage attributed to *A. lunulatus*. Bourdillon-Casanova (1960) reported limited descriptions of the first and second zoeae from plankton material. Heegaard (1963) described a first zoea from laboratory-hatched material. The megalopa stage was, as yet, unknown.

The larval development of other species of the genus *Acanthonyx* is only known for *A. petiverii* (see Hiyodo et al., 1994), whereas complete descriptions of other species of the subfamily Epialtinae (=Acanthonychinae) are only available for four species: *Epialtus dilatatus* (see Yang, 1968), *Taliepus dentatus* (see Fagetti and Campodonico, 1971), *Dehaanius limbatus* (see Kakati and Sankolli, 1975), and *Epialtus brasiliensis* (see Negreiros-Fransozo and Fransozo, 1991). Partial or incomplete descriptions are known for *Menaethius monoceros* (see Gohar and Al-Kholy, 1957), *Puggetia quadridens* (see Kurata, 1969; Iwata, 1970), *P. incisa* (see Kurata, 1969), *P. gracilis* (see Forss and Coffin, 1960), and *Huenia proteus* (see Aikawa, 1937; Kurata, 1969).

The present study aimed to describe the complete larval development (two zoeal stages and the megalopa) of the majid crab *A. lunulatus*, and to compare its larval features with other species of the Epialtinae.

**Method**

An ovigerous *A. lunulatus*, 14 mm carapace length, was collected near Tarragona (41°06.4 N, 1°17.1 E, western Mediterranean) from a depth of 0 m in June 1995 and was associated to the alga *Pterocladia capillacea.*
The crab was placed in an aquarium (60 x 35 x 30 cm) containing filtered and well-aerated sea water at a salinity of 37 p.p.t. and maintained at 21 ± 1°C until larvae hatched. The zoeae were placed in individual compartments of 30 cm³ and checked daily for evidence of moulting. The larvae were fed fresh Artemia nauplii and were maintained under the same constant conditions of temperature and salinity. Exuviae and specimens of each developmental stage were preserved in 7% buffered formalin.

An Olympus phase contrast microscope was used in the dissection and observation of the setal structures of the appendages. Measurements were taken with a Wild binocular microscope equipped with an ocular micrometer, and are based on measurements of five individuals within each stage. The following measurements were taken: distance between tips of dorsal and rostral spines (TT); carapace length (CL), from the base of the frontal spine to the posterior margin of the carapace. For the megalopa, carapace width (CW) was measured as the greatest distance across the carapace, and carapace length (CL) as the distance from the tip of the rostrum to the posterior margin of the carapace.

All drawings were made with the aid of a camera lucida. The number of individuals of each stage examined to describe the morphology varied between four and five.

The adult female from which the present larvae were obtained is deposited in the Biological Collections of Reference of the Institut de Ciències del Mar (CSIC) in Barcelona (Registration Number: ICMD-341995).

Results

Acanthonyx lunulatus (Risso, 1816)

Cano, 1893: 582, Plate 35, Figs 60–63 (zoea II); Bourdillon-Casanova, 1960: 214, Fig. 73 (zoeae I–II); Heegaard, 1963: 482–484, Figs 112–118, Plate 17, Fig. 21 (zoea I).

Two zoal stages plus the megalopa were observed in the larval development of A. lunulatus. A prezoal stage was not observed and none of the specimens reached the first crab stage. The main morphological characteristics of each larval stage are given below.

First zoea

Size: TT: 0.60–0.68 mm; CL: 0.57–0.62 mm.

Duration: 4–6 days.

Carapace (Figure 1A,B): dorsal spine curved, smaller than the diameter of the eye but longer than rostral spine and distally armed with minute granular protuberances; rostral spine short, much shorter than the antennule protopod; lateral spines absent; 1 pair of anterodorsal and posterodorsal setae; majid spine present with 7 posterolateral subterminal setae on ventral margin of carapace; eyes sessile.

Antennule (Figure 1E): uniramous; endopod absent; exopod unsegmented with 3 terminal aesthetascs and a seta.
Antenna (Figure 1F,G): protopod (spinous process) distally spinulate and longer than rostral spine; endopod present; exopod almost equal in length to protopod, distally spinulate with two subterminal setae of unequal length.

Mandible: incisor and molar processes well developed; mandibular palp absent.

Maxillule (Figure 2A): coxal endite with 7 setae; basal endite with 7 setae, single seta absent on external margin; endopod 2-segmented, distal segmented with 4 terminal setae.

Maxilla (Figure 2B): coxal endite bilobed with 5+3 setae; basal endite bilobed with 5+4; endopod not bilobed with 5 terminal setae; exopod (scaphognathite) margin with 11 setae and 1 distal stout process.
First maxilliped (Figure 2C): basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,4+1 setae, respectively; exopod 2-segmented, distal segment with 4 terminal plumose natatory setae.

Second maxilliped (Figure 2D): basis with 2 setae; endopod 3-segmented with 0,1,4 setae, respectively; exopod 2-segmented, distal segment with 4 terminal plumose natatory setae.

Third maxilliped: present, rudimentary, bilobed.

Pereiopods: present, rudimentary; chela bilobed.

Abdomen (Figure 1B,C): 5 somites, somite 2 with 1 pair of lateral processes directed anteriorly; posterolateral processes absent from somites; somite 1 with one pair of dorsomedial setae; somites 2–5 with 1 pair of posterodorsal setae; pleopods absent.
Larval development of *Acanthonyx lunulatus*

Fig. 3. *Acanthonyx lunulatus*, second stage. (A) Frontal view; (B) lateral view; (C) abdomen, dorsal view; (D) half of telson, enlarged; (E) antennule; (F) antenna. Scale of A and B = 0.5 mm; scale of D–F = 0.1 mm.

Telson (Figure 1 B,C,D): each telson fork with a minute lateral spine and distally spinulate; posterior margin with 3 pairs of long plumodenticulate setae, medial notch absent.

*Second zoea*

Size: TT: 0.95–0.99 mm; CL: 0.69–0.75 mm.
Duration: 5–9 days.
Carapace (Figure 3A,B): carapace unchanged except dorsal spine now without distal protuberances; 3 pairs of anterodorsal setae (the third one longer), one pair
near the base of the dorsal spine, and one pair placed posterodorsally; majid spine
now with 9 posterolateral subterminal setae on ventral margin of carapace; eyes
stalked.

Antennule (Figure 3E): unchanged except endopod now present; exopod now
with 6 aesthetascs and 2 setae.

Antenna (Figure 3F): unchanged except endopod now almost half the length of
the protopod.

Mandible: unchanged except mandibular palp now present.

Maxillule (Figure 4A): coxal endite now with 8 setae; basial endite now with 10
setae, single plumose seta present on external margin; endopod unchanged.
Maxilla (Figure 4B): coxal endite bilobed with 5+3 setae; basial endite bilobed now with 5+5; endopod unchanged; exopod (scaphognathite) margin now with 22 setae and distal stout process now absent.

First maxilliped (Figure 4C): unchanged except exopod distal segment now with 6 terminal plumose natatory setae.

Second maxilliped (Figure 4D): unchanged except exopod distal segment now with 6 terminal plumose natatory setae.

Third maxilliped: present, rudimentary, bilobed.

Pereiopods: present, rudimentary; chela bilobed.

Abdomen (Figure 3B,C): unchanged except now with 6 somites; somite 6 without setae; somite 1 now with 3 dorsomedial setae; somites 2–3 now with 1 pair of dorsomedial setae; pleopods now present with endopod buds.

Telson (Figure 3C, D): unchanged.

Megalopa

Dimensions: CL 1.18–1.26 mm; CW 0.82–0.96 mm.

Carapace (Figure 5A,B): longer than broad, narrowing anteriorly and without spines; rostrum acute, well developed and straight; front with acute corners each one bearing a seta in its tip.

Antennule (Figure 5D): peduncle 3-segmented with 2,1,1 setae; endopod 2-segmented with 0,1+2 setae; exopod 4-segmented with 0,8,4,0 aesthetascs and 0,1,0,1 setae, respectively.

Antenna (Figure 5E): protopod 3-segmented with 0,2,2 setae; segment 1 with a dorsal protuberance; flagellum 4-segmented, with 0,0,4,4 setae.

Mandible (Figure 5F): mandibular palp 3-segmented with 0,0,4 setae.

Maxillule (Figure 6A): coxal endite with 8 setae; basal endite with 17 setae; endopod unsegmented without setae.

Maxilla (Figure 6B): coxal endite slightly bilobed with 6+3 setae; basal endite with 6+6 setae; endopod unsegmented with one seta; exopod (scaphognathite) with 36 setae and 2 medial setae.

First maxilliped (Figure 6C): coxal endite with 4 setae; basal endite with 9 marginal setae; epipod with 8 long setae; endopod unsegmented; exopod 2-segmented, proximal segment with one plumose terminal seta, distal segment with 4 long plumose terminal setae.

Second maxilliped (Figure 6D): endopod 4-segmented with 0,1,3,6 setae; exopod 2-segmented, distal segment with 4 terminal plumose setae.

Third maxilliped (Figure 6E): coxa with 7 setae; epipod with 3 long setae and 2 small setae; endopod 5-segmented with 9,8,5,5,4 setae; exopod 2-segmented, distal segment with 4 plumose setae.

Pereiopods (Figure 7A–I): pereiopod 2 with spine on ischium; dactylus of pereiopods 2–5 distally spiculated with 4,4,5,5 small spines on their inner margin; pereiopods 1–5 setose as shown.

Abdomen (Figure 5C): abdomen with 6 somites plus telson; posterolateral margins of segments 1–3 rounded; somite 1 with 1 pair of posterolateral setae; somites...
2 and 3 with 1 pair of dorsal and 3 pairs of posterodorsal setae; somite 4 with 4 pairs of posterodorsal setae; somite 5 with 3 pairs of posterodorsal setae; somite 6 with 1 pair of posterodorsal setae.

Pleopods (Figure 7J–M): present on segments 2–6; endopods with 2,3,2,2 coupling hooks; exopod of segments 1–4 with 12,12,12,10 long plumose natatory setae; uropods with 5 plumose setae.

Telson (Figures 5C, 7N): slightly broader than long; posterior margin almost straight; dorsal surface with 2 median setae and 2 terminal spines.
Fig. 6. Acanthonyx lunulatus, megalopa. (A) Maxillule; (B) maxilla; (C) 1st maxilliped; (D) 2nd maxilliped; (E) 3rd maxilliped. Scale of A and B = 0.05 mm; C–E = 0.1 mm.

Discussion

Zoeal stages of A. lunulatus were previously described by Cano (1893), Bourdillon-Casanova (1960), and Heegaard (1963). Cano (1893) described the second zoeal stage of Acanthonyx sp., attributed to A. lunulatus by Bourdillon-Casanova (1960) and Heegaard (1963). Bourdillon-Casanova described incompletely two zoeal stages taken from plankton samples which were attributed to A. lunulatus. Heegaard (1963) described the first stage from laboratory-hatched material. These descriptions are limited and there are some discrepancies between them. For example, Bourdillon-Casanova (1960) illustrated some small protuberances on the
dorsal spine, while Heegaard (1963) showed it as smooth. The former author mentioned a small spine on the base of the telson fork whereas the latter did not mention its occurrence. Cano (1893) also showed the telson fork without a spine.

Yang (1968), and Kakati and Sankolli (1975), who worked on other species of the subfamily Epialtinae, suggested that, since Bourdillon-Casanova’s material was obtained from the plankton, her identification must be suspect, especially since other features of her larvae did not correspond to those described by Heegaard. However, the present laboratory-reared material clearly confirms the results of Bourdillon-Casanova (1960): the first zoeal stage of *A. lunulatus* possesses minute protuberances on the dorsal spine and a very small lateral spine on
Larval development of *Acanthonyx lunulatus*

**Table I.** Comparison of the characteristics of the first zoeae of *Acanthonyx lunulatus*, as given by the drawings of Heegaard (1963), with those obtained in the present study

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Heegaard (1963)</th>
<th>Present work</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Antennule setation:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. S</td>
<td>2.1</td>
<td>3.1</td>
</tr>
<tr>
<td><strong>Maxillule setation:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S on endopod</td>
<td>0.3</td>
<td>0.4</td>
</tr>
<tr>
<td>S on basal endite</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>S on coxal endite</td>
<td>5</td>
<td>7</td>
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<tr>
<td><strong>Maxilla setation:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S on endopod</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>S on basal endite</td>
<td>3+3</td>
<td>5+4</td>
</tr>
<tr>
<td>S on coxal endite</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Pl on scaphognathite</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td><strong>Maxilliped 1 setation:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S on endopod</td>
<td>1.2.1.1.4</td>
<td>3.2.1.2.5</td>
</tr>
</tbody>
</table>

S = setae; A = aesthetascs; PI = plumose seta.

Each telson fork. These spines are very small and rather difficult to see so they were probably missed by Heegaard and Cano. Hiyodo *et al.* (1994) also observed a small lateral spine on each telson fork of the zoeae of *Acanthonyx petiverii* which were also not recorded in the first description of this species by Lebour (1944). Moreover, there are many differences (Table I) between the present descriptions and the drawings of the appendages of the first zoea illustrated by Heegaard (1968).

The zoeal stages of *A. lunulatus* are very similar to those of *A. petiverii* (Hiyodo *et al.*, 1994). Differences between the larvae of the two species appear to be limited to the setation of the appendages (Table II), since no granular round protuberances on the dorsal spine are mentioned in the descriptions of the zoeal stages of *A. petiverii*.

The species of the subfamily Epialtinae may be divided into three subgroups depending on the degree of development of the dorsal spine. Subgroup I includes species whose zoeae have a long dorsal spine on their carapace (longer than the eye diameter), such as *Pugettia* spp. and *Taliepus dentatus*. Subgroup II includes the species whose zoeae have a short dorsal spine (shorter than the eye diameter), such as *Acanthonyx* spp., *Epialtus* spp., *Dehaanius limbatus* and *Huenia proteus*. Subgroup III includes only one species, so far, which lacks a dorsal spine: *Menaethius monoceros*.

*Taliepus dentatus* differs from all the other Epialtinae of subgroup I (*Pugettia* spp.), and also from those of subgroup II, in the presence of knobs in the third abdominal somite.

The zoeae of the genus *Acanthonyx* differ from the other known Epialtinae of subgroup II in the setation of the maxillule endopod (Table II), the very small size of the outer telson spines, and in the absence of postero-lateral processes on the abdominal somites, although this last characteristic is also shared by *Epialtus brasiliensis*. They resemble those of *Dehaanius limbatus* in their possession of minute protuberances on the dorsal spine (Kakati and Sankolli, 1975), and differ in their lack of dorso-lateral processes in the abdominal somites, together with some...
<table>
<thead>
<tr>
<th>Reference</th>
<th>Taliepus dentatus</th>
<th>Epialtus brasiliensis</th>
<th>Epialtus dilatatus</th>
<th>Acanthonyx petiveri</th>
<th>Acanthonyx hamatus</th>
<th>Delaenus limbatus</th>
<th>Pugettia quadridens</th>
<th>Menaethius monoceros</th>
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<tbody>
<tr>
<td>Zoea I</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Carapace:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Dorsal spine</td>
<td>long</td>
<td>short</td>
<td>short</td>
<td>short</td>
<td>short</td>
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<td>ND</td>
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<tr>
<td>Antennule setation:</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>A. S</td>
<td>4+2</td>
<td>3+1</td>
<td>2+1</td>
<td>3+1</td>
<td>3+1</td>
<td>2+1</td>
<td>ND</td>
<td>2?</td>
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<td></td>
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<tr>
<td>S on endopod</td>
<td>1.5</td>
<td>0.6</td>
<td>6 (unseg.)</td>
<td>0.4</td>
<td>0.4</td>
<td>1.6</td>
<td>1.4</td>
<td>0.4</td>
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<tr>
<td>S on basal endite</td>
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<td>7</td>
<td>7</td>
<td>6</td>
<td>6 (7)</td>
<td>6</td>
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<td></td>
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<td></td>
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<td>S on endopod</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
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<td>4 (2–3)*</td>
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<td>5+3</td>
<td>5+4</td>
<td>5+4</td>
<td>5+4</td>
<td>4+4 (4+5)*</td>
<td>3+3</td>
<td></td>
</tr>
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<td>S on coxal endite</td>
<td>5+4</td>
<td>5</td>
<td>6</td>
<td>5+3</td>
<td>5+3</td>
<td>4+4</td>
<td>4+4 (2+4)*</td>
<td>4+4</td>
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<td>Sp on scaphognathite</td>
<td>10</td>
<td>12</td>
<td>12</td>
<td>11</td>
<td>11</td>
<td>13</td>
<td>9 (5)</td>
<td>10–12</td>
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</table>
Maxilliped 1 setation:
S on basis  2,2,2,3  3,1,2,3 ?  2,2,2,3  2,2,3,3  2,2,3,3  2,2,2,2  (2,2,2,3)?  ND
Maxilliped 2 setation:
S on basis  3  2(3)  2  3  2  3  (3)?  3
Pleon:
Knobs on somite 3  present  absent  absent  absent  absent  absent  absent  present
Zoea II
Antennule setation:
A. S  7  7+1  6  6+2  6+2  6+2  ND  4?
Maxillule setation:
S on endopod  1,5  0,6  5 (unseg.)  0,4  0,4  1,6  1,4  0,4
S on basal endite  10  9  9  10  10  10  9  8
S on coxal endite  8  5  7  7  8  7  9  3
Maxilla setation:
S on endopod  4  6  5  5  5  5  4  5
S on basal endite  5+5  3(4)+3(4)  5+5  5+4  5+5  5+5  5+5  3+4
Sp on scaphognathite  20 approx.  19(20)  22 approx.  22  22  24  20-25
Maxilliped 1 setation:
S on basis  2,2,2,3  3,2,2,2 ?  2,2,2,3  2,2,3,3  2,2,3,3  2,2,2,2  ND  ND
Maxilliped 2 setation:
S on basis  3  4  2  3  2  3  ND  ND
Abdomen setation  3,2+2,2+2,2,2,0  ND  3,2+2,2,2,0  ND  3,2+2,2+2,2,2,0  ND  ND

S = setae; A = aesthetascs; Sp = plumose setae; ND = no data.
Table III. Morphological differences in the megalopa of seven species of Epialtinae. Abbreviations and remarks in Table II

<table>
<thead>
<tr>
<th>Reference</th>
<th>Talepus dentatus</th>
<th>Epialtus brasilienensis</th>
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<th>Acanthonyx petiverii</th>
<th>Acanthonyx humulus</th>
<th>Dehaanius lambatus</th>
<th>Gaetanus monoceros</th>
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<td>S on endopod</td>
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<tr>
<td>S on basal endite</td>
<td>17 approx.</td>
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<td><strong>Maxilla setation:</strong></td>
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<tr>
<td>S on basal endite</td>
<td>6+6</td>
<td>9</td>
<td>10</td>
<td>6+7</td>
<td>6+6</td>
<td>5+5</td>
<td>2+3</td>
</tr>
<tr>
<td>S on coxal endite</td>
<td>7+3</td>
<td>7</td>
<td>7</td>
<td>7+3</td>
<td>6+3</td>
<td>6+2</td>
<td>5+3</td>
</tr>
<tr>
<td><strong>Maxilliped 1 setation:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S on basal endite</td>
<td>12 approx.</td>
<td>8</td>
<td>7 approx.</td>
<td>10</td>
<td>9</td>
<td>8</td>
<td>11-15</td>
</tr>
<tr>
<td>S on coxal endite</td>
<td>6</td>
<td>3</td>
<td>5</td>
<td>7</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>S on exopod</td>
<td>1+4</td>
<td>1+2</td>
<td>1+4</td>
<td>1+4</td>
<td>1+4</td>
<td>1+4</td>
<td>3 (unseg.)</td>
</tr>
<tr>
<td><strong>Maxilliped 2 setation:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S on endopod</td>
<td>0,1,3,6</td>
<td>0,1,3,6</td>
<td>0,1,3,5</td>
<td>0,1,3,6</td>
<td>0,1,3,6</td>
<td>0,0,1,7</td>
<td>0,0,0,8</td>
</tr>
<tr>
<td>S on exopod</td>
<td>0,5</td>
<td>0,5</td>
<td>0,4</td>
<td>0,4</td>
<td>0,4</td>
<td>0</td>
<td>0,3</td>
</tr>
<tr>
<td><strong>Maxilliped 3 setation:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S on endopod</td>
<td>12,7,5,5,4</td>
<td>6,1,4,3,6</td>
<td>13,6,3,3,5</td>
<td>7,6,3,5,4</td>
<td>9,8,5,5,4</td>
<td>7,2,5,5,4</td>
<td>10-15,???,?</td>
</tr>
<tr>
<td><strong>Abdominal segments:</strong></td>
<td>6</td>
<td>6</td>
<td>7</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td><strong>Pleopod setation:</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S on exopod of PL 1</td>
<td>13</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>S on exopod of PL 2</td>
<td>13</td>
<td>12</td>
<td>11</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>S on exopod of PL 3</td>
<td>12</td>
<td>11(10)</td>
<td>11</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>S on exopod of PL 4</td>
<td>10</td>
<td>9(8)</td>
<td>9</td>
<td>8</td>
<td>10</td>
<td>10</td>
<td>4?</td>
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</table>
Larval development of *Acanthonyx lunulatus*

setation features (Table II). The zoeae of *Epialtus* resemble *Acanthonyx* and *Huenia proteus*, and differ from the rest of Epialtinae species in the absence of setae in the proximal segment of the maxillule endopod (segment absent in *Epialtus dilatatus*; Table II). The second zoeae of *Epialtus* differ from the other Epialtinae species in the absence of the outer plumose seta on the maxillule.

The megalopa of *A.lunulatus* shows some differences with those of *A.petiverii* and the other known megalopae of Epialtinae. The carapace of *A.lunulatus* narrows anteriorly in dorsal view; it is not sub-rectangular as in *A.petiverii*. The rostrum is acute and straight, not small and deflected. Other meristic and morphometric data of the different described megalopal stages of Epialtinae crabs are shown in Table III.

The morphological variability of the megalopal antenna in the family Majidae, and in particular within the subfamily Epialtinae, enables the differentiation between several genera (Rice, 1988). In *Acanthonyx, Taliepus, and Puggetia*, the antennae are similar to those of the typical Pisinae (Rice, 1988), with the size of their terminal article being more than half the length of the anterior article. However, the terminal article in the genus *Epialtus* is greatly reduced, and in *Dehaanius limbatus* it is absent (Kakati and Sankolli, 1975).

The relationships between *Acanthonyx* and *Dehaanius*, based on adult characters, are unclear (Tirmizi and Serène, 1971; Manning and Holthuis, 1981). Adults of *Acanthonyx* closely resemble *Dehaanius*, however, some features clearly separate *Dehaanius* larvae from those of *Acanthonyx*. Thus, the two complete larval developments described for species of *Acanthonyx* indicate that larvae of both species have a larger number of morphological characters in common than shared with *Dehaanius limbatus*. These features would support the validity of keeping *Dehaanius* as a distinct genus, as suggested by Kakati and Sankolli (1975).

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**References**


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