Larval morphology of the spider crab *Leurocyclus tuberculosus* (Decapoda: Majoidea: Inachoididae)

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Abstract

Within the recently resurrected family Inachoididae is *Leurocyclus tuberculosus,* an inachoidid spider crab distributed throughout the Western Atlantic of South America from Brazil to Argentina (including Patagonia), and along the Eastern Pacific coast of Chile. The larval development of *L. tuberculosus* consists of two zoeal stages and one megalopa. We observed that the larval morphology of *L. tuberculosus* conforms to the general pattern found in Majoidea by having two zoeal stages, in which the first stage has nine or more seta on the scaphognatite of the maxilla, and the second zoeal stage present well developed pleopods. Here, we describe the larval morphology of *L. tuberculosus* and compare with other inachoidid members for which we have larval information.

Key words: Larval development, Majidae, Zoeal stages, Megalopa, Crustacea, *Leurocyclus.*

Introduction

Few decades ago, the family Inachoididae Dana, 1851 was resurrected by Drach and Guinot (1983; see also Drach and Guinot, 1982), who considered that the morphological modifications on the carapace and endophragmal skeleton among some majoid genera granted to a set of them the status of a higher taxon – the family Inachoididae. Originally, Inachoididae was proposed as a subfamily of Majidae to accommodate only the genus *Inachoides* H. Milne Edwards and Lucas, 1843 (Dana, 1851:432). However, at the present, Inachoididae is represented by 35 species included in ten genera that assembles taxa once included in Inachidae McLeay, 1838 and Pisidae Dana, 1851 (Rathbun, 1925; Garth, 1958; Drach and Guinot, 1983; Williams, 1984; Guinot and Richer de Forges, 1997).

The knowledge on the larval morphology of members of Inachoididae is incipient. Within over 30 recognized species in Inachoididae only three of them have had their larval morphology described. Larval stages of *Anasimus latus* Rathbun, 1894 was the first one to be described by Sandifer and Van Engel (1972). Following, Webber and Wear (1981) and Terada (1983) described the first zoeal stage of *Pyromaia tuberculata* (Lockington, 1877), which was completely described by Fransozo and Negreiros-Fransozo (1997) and re-described by Luppi and Spivak (2003). Lately, the complete larval development of *Paradasygyius depressus* (Bell, 1835) was described by Pohle and Marques (2000).

Members of Inachoididae are endemic from the Americas, being found in both sides of the continent. In the Southwestern Atlantic Ocean we found *Leurocyclus,* a monotypic genus (see Guinot, 1984; Guinot and Cleva, 2002; Santana, 2008) occurring from Brazil (Rio de Janeiro to Rio Grande do Sul), through Argentina including Patagonia. *Leurocyclus tuberculosus* (H. Milne Edwards and Lucas, 1843) is generally found in mud and shell bottoms, from 10 to 170 m (Melo, 1996).

The purpose of our contribution is to present a detailed description of all larval stages of *Leuro-*

cyclus tuberculosus, for which, although some larval characters have been coded in previous phylogenetic studies (Marques and Pohle, 2003), the larval morphology remain undescribed. Based on our description, we compare the larval morphology of *L. tuberculosus* with larval stages of inachoidid members present in the literature.

Material and Methods

Larval development and description – Specimens of *Leurocyclus tuberculosus* were collected in October 2001, in the Bay of Ubatuba, northern São Paulo State, (24°43'S, 23°32'W), Brazil. The specimens were held in an aquarium in a temperature controlled room (24° ± 2°C) until hatching, which occurred at night. After hatching, 50 of the most active, positively phototactic larvae were individualized into 100 ml acrylic jars containing 50 ml of filtered seawater. The remaining larvae were kept in mass culture as additional specimens to be used in morphological descriptions.

Newly hatched larvae were fed *ad libitum* with *Artemia* nauplii. Sea water was changed, and specimens inspected and fed daily. All acrylic jars were washed in freshwater and air-dried before reuse with fresh seawater in the following day. Average salinity was 32. A natural photoperiod was maintained (14L:10D).

Whenever possible, a minimum of five specimens of each stage were dissected for morphological description. For slide preparations polyvinyl lactophenol was used as mounting medium with Acid Fuchsin and/or chlorazol black stains. The description of setae generally followed Pohle and Telford (1981), but here includes only analysis by light microscopy (LM), using an Olympus BX51 microscope with Nomarski Differential Interference Contrast and camera lucida. Some of the setae designated as plumose herein may be plumodenticulate setae due to the lower resolution limits of LM as compared to scanning electron microscopy (SEM). Description guidelines of Clark *et al.* (1998) were generally followed. Taxonomic rankings follow Ng *et al.* (2008) in which some majid subfamilies were raised to the family level and included within the Majoidea.

Specimens of larval stages and a spent female crab have been deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo State, Brazil, under MZUSP 19910.

Results

Larval development and description – Larval development of *Leurocyclus tuberculosus* consists of two zoeal stages and one megalopa. The duration of each zoeal stage was 4-6 days (3.9 ± 0.3) for Zoea I, 5-12 days (5.0 ± 0.6) for Zoea II, the megalopa appearing 10-18 days after hatching. Only morphological changes are described for the second zoea.

Description

***Leurocyclus tuberculosus* (Milne Edwards and Lucas, 1843)**
First zoea (Figure 1A-J)

Carapace (Fig. 1A) – With dorsal spine, rostral and lateral spines absent. Ventral margin with densely plumose "anterior seta" (Clark *et al.,* 1998) posterior to scaphognathite notch, followed by 3 plumose setae. Eyes sessile. Small indistinct median ridge frontally between dorsal spine and eyes and a small median tubercle on posterodorsal margin, each bearing cuticular dorsal organ (sensu Martin and Laverack, 1992). Pair of simple setae present anteriorly to dorsal spine and a pair of sparsely plumose setae posterolaterally to dorsal spine.

Antennule (Fig. 1B) – Unsegmented, smooth, conical. Terminally bearing 2 long, 2 shorter aesthetascs, and a short simple setae.

Antenna (Fig. 1C) – Biramous, protopod long and pointed, bearing 2 rows of sharp spinules; endopod bud present; one-segmented exopod shorter than protopod with long spinulated distal process and pair of serrulate setae about 1/3 from tip.

Mandible (Fig. 1D) – With medial toothed molar process and enlarged lateral incisor processes; marginal teeth between molar and incisor processes. Palp absent.

Maxillule (Fig. 1E) – Coxal endite with 4 terminal setae, 1 plumodenticulate and 3 graded plumodenticulate; and 3 subterminal plumodenticulate setae. Basial endite with 3 terminal plumodenticulate cuspidate setae and 4 subterminal setae, 3 plumodenticulate and 1 plumose. Two-segmented endopod, proximal segment smooth, distal segment bearing 2 pairs of plumodenticulate setae apically. Exopod seta absent.

Maxilla (Fig. 1F) – Coxal endite bilobed, proximal lobe with 4 setae, 3 plumose and 1 plu-

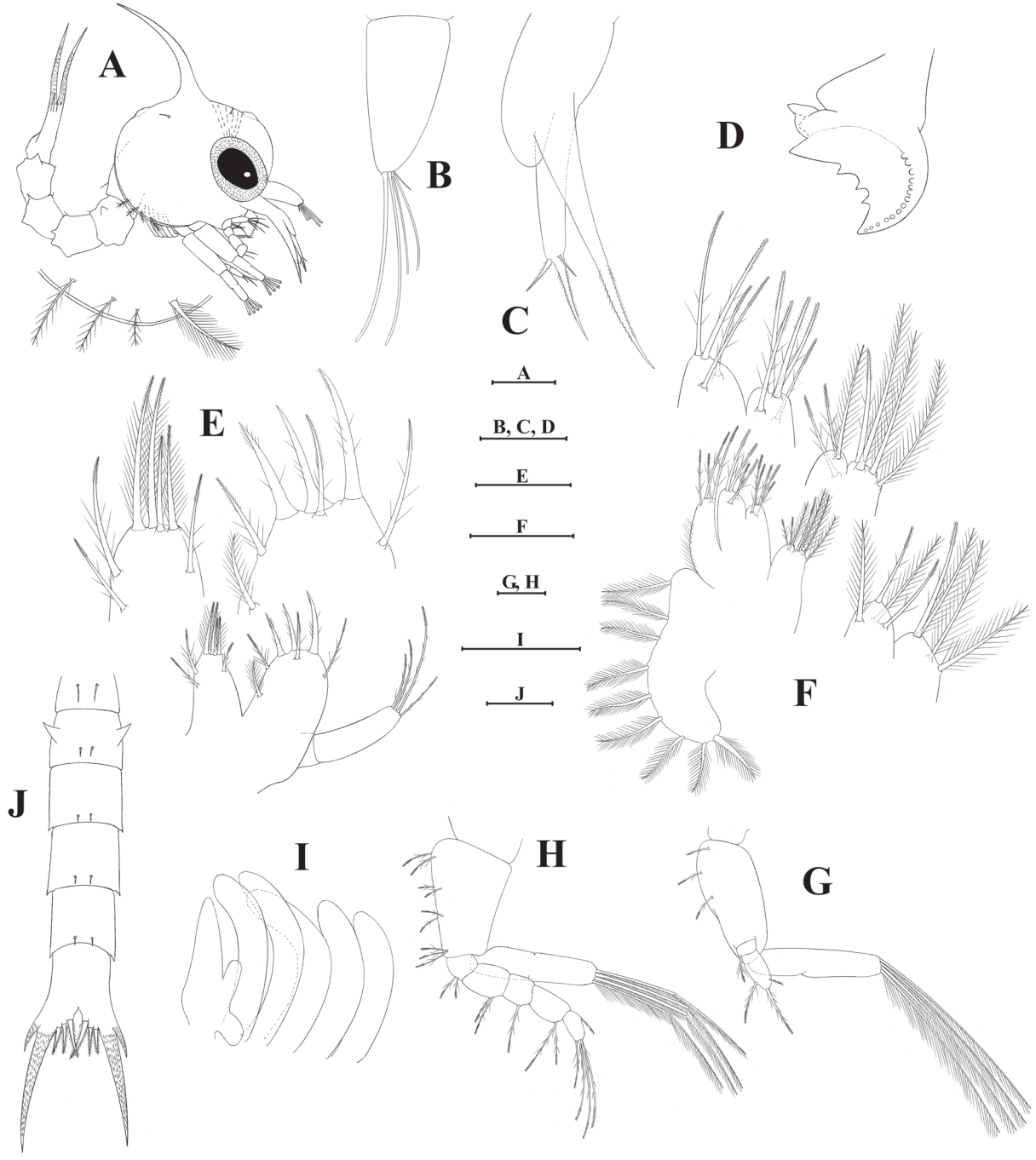

Figure 1. First zoea of *Leurocyclus tuberculosus* (H. Milne Edwards and Lucas, 1843). A, lateral view; B, antennule; C, antenna; D; mandible; E, maxillule; F, maxilla; G, maxilliped 2; H, maxilliped 1; I, developing maxilliped 3 and pereiopods; J, dorsal view of abdomen and telson. Scales A, 0.4 mm; B-I, 0.1 mm; J, 0.2 mm.

modenticulate; distal lobe with 3-4 setae, 1-2 plumose and 2 plumodenticulate. Basial endite bilobed, proximal and distal lobes with 5 and 4 plumodenticulate setae respectively. Unsegmented endopod unilobed, with 4 apical plumodenticulate setae; microtrichia on lateral margin. Scaphognathite marginally with 9-11 densely plumose setae, including distal process.

Maxilliped 1 (Fig. 1A, H) – Coxa without seta. Basis with 9 plumodenticulate setae arranged 2,2,2,3. Endopod 5-segmented with 2,2,1,2,4+1 plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 2 (Fig. 1A, G) – Coxa without seta. Basis with 3 plumodenticulate setae. Endopod three-segmented, with 0,1,3 plumodenticu-

late setae of different types, 2 medial, 1 apical on terminal segment. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 3 (Fig. 1I) – Present as small endo-, exo- and epipod buds.

Pereiopods (Fig. 1I) – Present as small buds, chela indistinct.

Abdomen (Fig. 1A, J) – 5 somites. Somite 1 with pair of middorsal setae, somites 2-5 each with pair of shorter posteromedial simple setae. Somite 2 with blunt process posterolaterally, somites 3-5 with spines; somite 2 with pair of dorsolateral processes. Grouped microtrichia present. Pleopods absent.

Telson (Fig. 1J) – Bifurcated, distinct median notch, 3 pairs of plumodenticulate setae on inner margin; each furcal shaft proximally bearing lateral spine, furcal shafts and spines covered with rows of spinules to just below tips. Grouped microtrichia present.

Second zoea (Figure 2A-H)

Carapace (Fig. 2A) – Eyes mobile. Ventral margin with densely plumose anterior seta followed by 5 plumose setae

Antennule (Fig. 2B) – With 8 long aesthetascs and a short simple setae, endopod bud present.

Antenna (Fig. 2C) – Endopod bud enlarged to just beyond middle of protopodite.

Mandible (Fig. 2D) – Palp bud present

Maxillule (Fig. 2E) – Coxal endite bearing optional additional plumodenticulate setae subterminally; basial endite with 2 additional setae, 1 plumodenticulate cuspidate, and 1 plumodenticulate seta terminally; exopod pappose seta present.

Maxilla (Fig. 2F) – Coxal endite with 4-5 setae on proximal lobe, 4 setae on distal lobe; basial endite with 5-6 plumodenticulate setae on proximal lobe, 5 plumodenticulate setae on distal lobe; Scaphognathite with 16-19 marginal plumose setae.

Maxilliped 1 (Fig. 2A) – Exopod with 6 plumose natatory setae.

Maxilliped 2 (Fig. 2A) – Exopod with 6 plumose natatory setae.

Maxilliped 3 (Fig. 2G) – Lobes of exo-, endo- and epipod enlarged.

Pereiopods (Fig. 2G) – Longer, chela apparent.

Abdomen (Fig. 2A, H) – Additional sixth somite. Posterolaterally, somites 1 and 6 with blunt processes, somites 2-5 with enlarged spines. Pair of unsegmented biramous pleopods on somites 2-5, endopods very small.

Megalopa (Figures 3A-G; 4A-G)

Carapace (Fig. 3A, B) – Slightly longer than wide, rounded, rostral spine very short, insipiently bilobed; 2 knob-like projections laterally in the hepatic region, 2 knob-like elevations just posterior to eyes with dorsal organ (Martin and Laverack, 1992) in the middle, and 2 additional pairs of dorsolateral protuberances near border of gastric area. A pronounced tubercle on the cardiac area. Posterolateral margin with series of 4 plumodenticulate setae, surface covered with mostly simple setae as shown.

Antennule (Fig. 3C) – Three-segmented peduncle with a simple seta on distal segment; endopod unsegmented with 1 subterminal and 2 terminal simple setae; three-segmented exopod with second segment bearing 8 aesthetascs and simple seta, distal segment with 4 aesthetascs and aesthetasc-like apical seta.

Antenna (Fig. 3D) – Segments 1-7, progressing proximally to distally, each with 1,2,3,0,0,4,4 simple setae, respectively; 2 terminal setae long and 2 shorter on the distal segment. Basal segment with much reduced exopod process.

Mandibles (Fig. 3E) – Asymmetric, scoop-shaped process with cutting edge and small tooth; two-segmented palp bearing 5-6 plumodenticulate setae on the distal segment.

Maxillule (Fig. 3F) – Coxal endite with 4 graded plumodenticulate apically, 5 plumodenticulate setae, and a plumose seta subterminally. Basial endite distal to endopod with 15 plumodenticulate setae and 2 plumose setae on proximal margin, exopod seta plumodenticulate. Epipod plumodenticulate seta present; unsegmented endopod smooth.

Maxilla (Fig. 3G) – Coxal endite proximal lobe with 2 plumodenticulate and 4-5 plumose setae, distal lobe bearing 1 plumodenticulate and 2 plumose setae; basial endite with 6 plumodenticulate setae on proximal lobe and 6-7 on distal lobe. Endopod with a subterminal plumose setae, and microtrichia on distal margin. Scaphognathite with 31-34 marginal plumose setae; blade with 3 simple setae.

Maxilliped 1 (Fig. 4A) – Coxa with 6 plumodenticulate setae, basis bearing 12-13 plumodenticulate setae; endopod naked; exopod with pappose seta distally on proximal segment and 4 plumose setae on distal segment; epipod with 5 plumodenticulate setae.

Maxilliped 2 (Fig. 4B) – Coxa and basis not clearly differentiated; four endopod segments proximally to distally with 1,1,2-3 and 4 plumodenticulate setae, respectively; exopod with naked proximal segment and 4 plumose setae on distal segment; epipod not present on examined specimens.

Maxilliped 3 (Fig. 4C) – Coxa with 3-4 plumodenticulate setae, basis not clearly differentiated, with 2 plumodenticulate setae; endopod proximally to distally with 11, 7, 4-5, 5-6 and 4 plumodenticulate setae; ischium with protuberances indicative of crista dentata; bisegmented exopod with naked proximal segment, distal segment bearing 4 plumose setae apically; epipod with 2 plumodenticulate setae proximally, 3 distally.

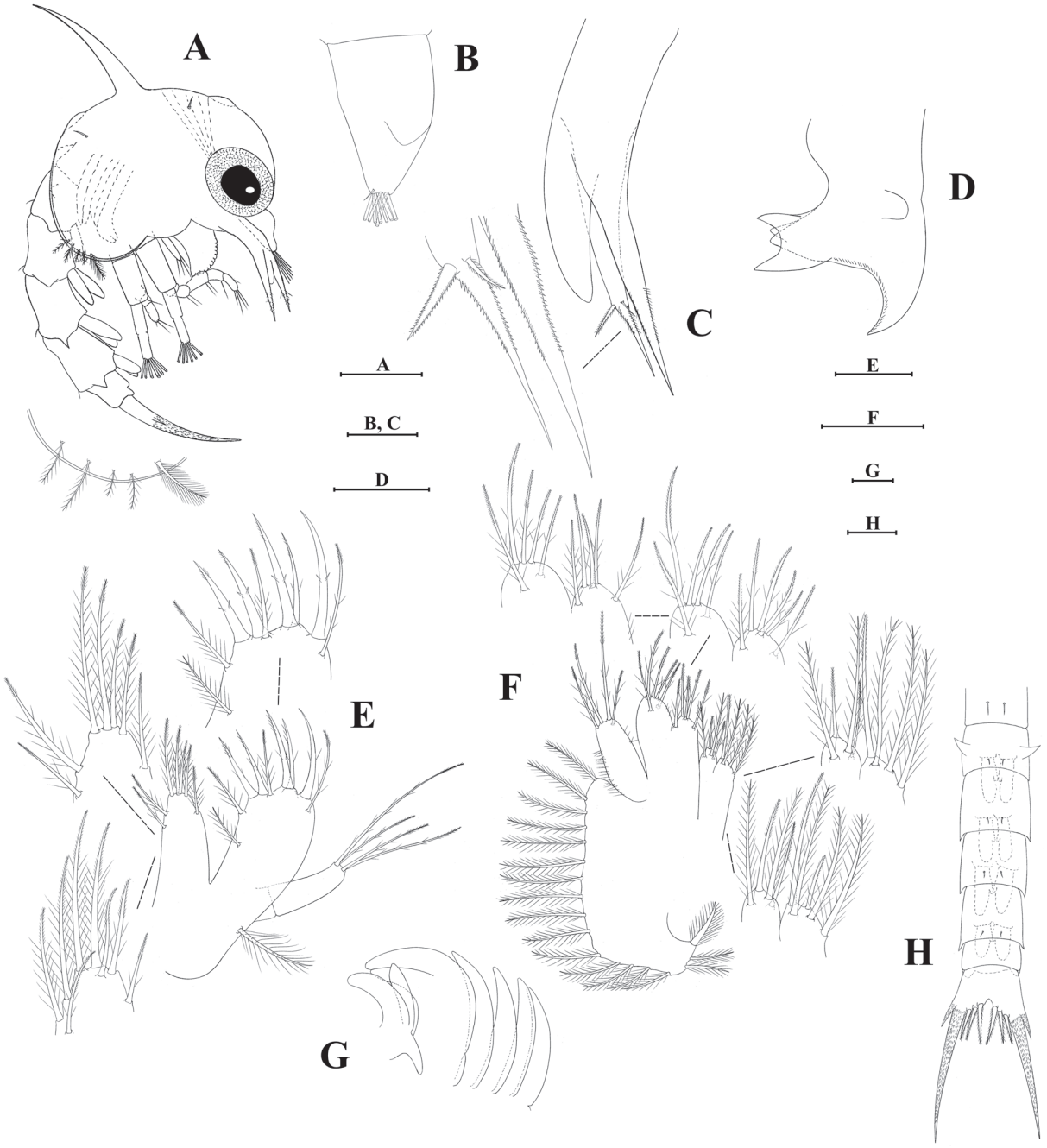

Figure 2. Second zoea of *Leurocyclus tuberculosus* (H. Milne Edwards and Lucas, 1843). A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, developing maxilliped 3 and pereiopods; H, dorsal view of abdominal somites 1-6, showing ventral pleopods as stippling. Scales A, 0.4 mm; B-G, 0.1 mm; H, 0.2 mm.

Pereiopods (Fig. 4D-E) – Cheliped with mostly simple setae, except for plumodenticulate setae on coxa; pereiopods 2-5 mostly with simple setae, some serrulate setae near tip of dactyls; basischial segments without spines; dactyls of pereiopods 1-4 with rows of spinules as shown.

Sternum (Fig. 4F) – Segments 1-3 fused, 2 pairs of simple setae as shown; segment 4 with 1 pair of simple setae; subsequent segments without setae.

Abdomen (Fig. 4G) – Somites 1-5 proximally to distally with 2,4,4,8,8 simple setae dorsally and laterally, sixth somite smooth; somite 1 with an additional pairs of distinct plumodenticulate setae ventrolaterally. 4 pairs of pleopods, exopod with 11, 11, 10, 9 and 2 plumose setae, endopod with 3-2 cincinnuli each; uropod very reduced, with 2 plumose setae distally, endopod absent.

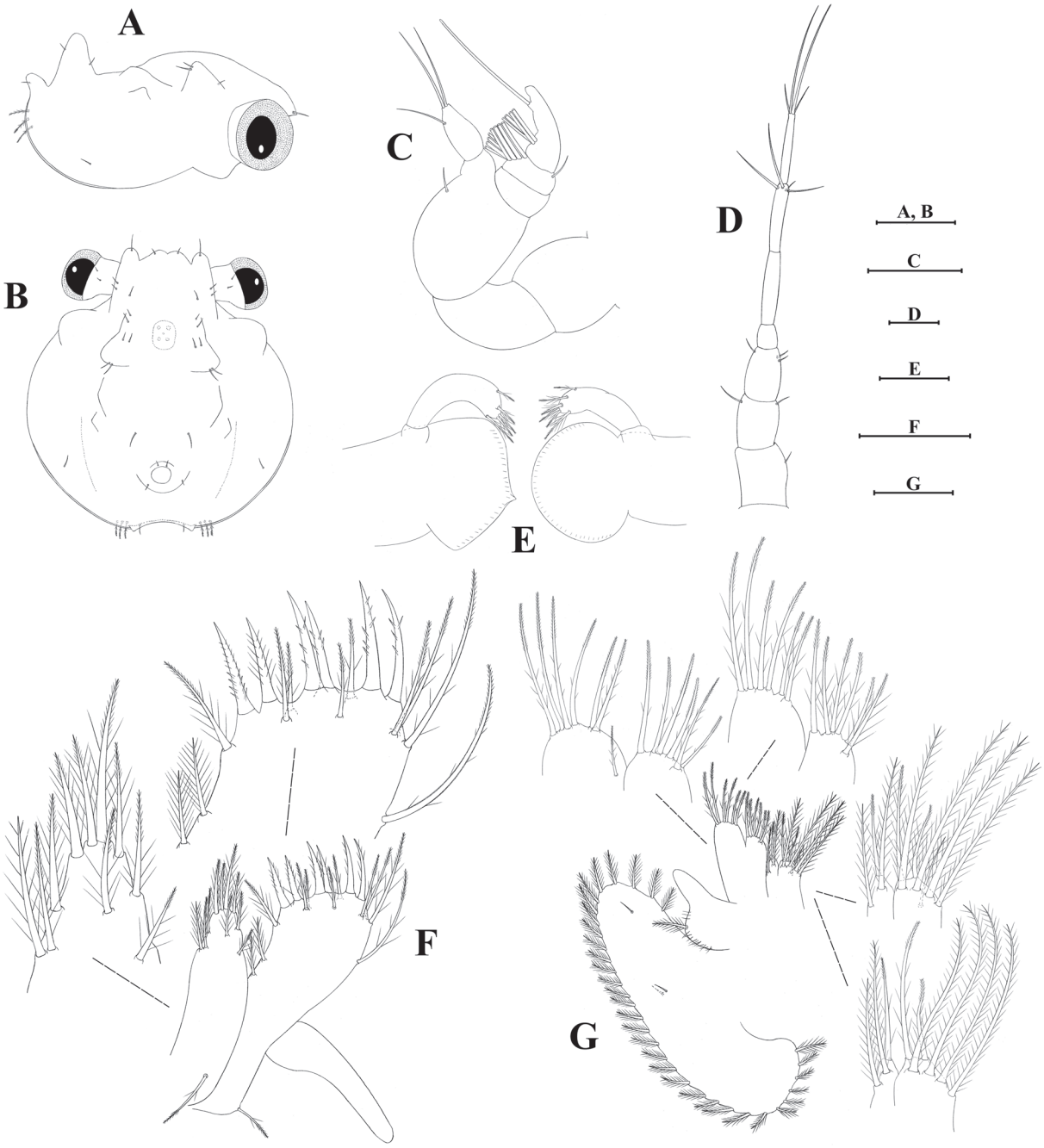

Figure 3. Megalopa of *Leurocyclus tuberculosus* (H. Milne Edwards and Lucas, 1843). A, dorsal view, B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla. Scales A-B, 0.4 mm; C-G, 0.1 mm.

Telson (Fig. 4G) – Rounded posteriorly, bearing 1 pair of simple middorsal setae.

Discussion

There are three inachoidid species with complete larval development described, *Anasimus latus* (cf. Sandifer and Van Engel, 1972), *Pyromaia tuberculata* (cf. Webber and Wear, 1981; Terada, 1983; Fransozo and Negreiros-Fransozo, 1997; Luppi and Spivak, 2003), and *Paradasygyius depressus* (cf. Pohle and Marques, 2000) (Tables I-III). All these species, including *L. tuberculosus,* conform to the general pattern found for Majoidea characterized by two zoeal stages, in which the first stage has nine or more seta on the scaphognatite of the maxilla, and the second zoeal stage

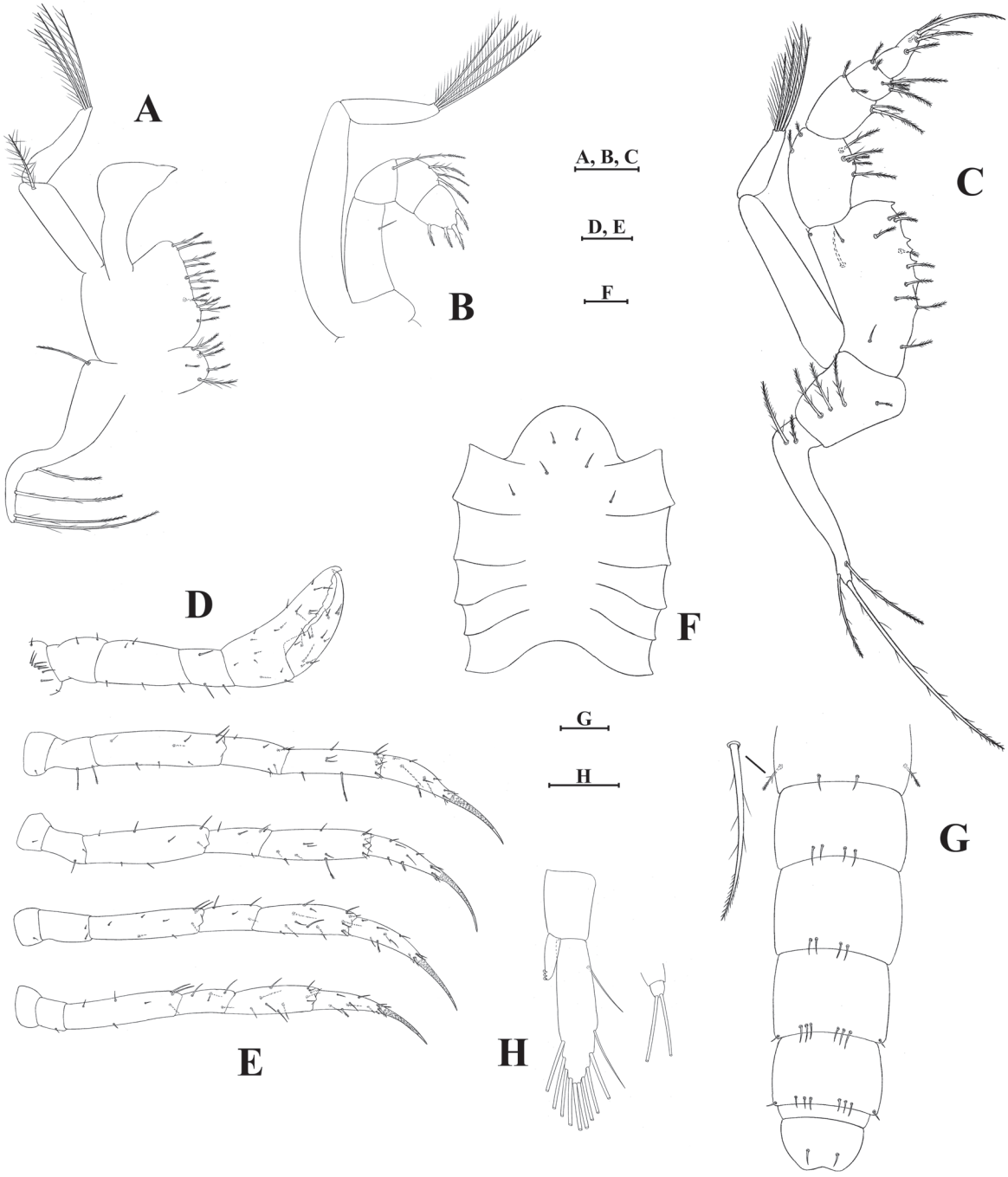

Figure 4. Megalopa of *Leurocyclus tuberculosus* (H. Milne Edwards and Lucas, 1843). A, maxilliped 1; B, maxilliped 2; C, maxilliped 3; D, cheliped; E, pereiopods; F, sternum; G, dorsal view of abdomen and telson; H, first and fifth pleopods. Scales A-C, 0.1 mm; D-E, 0.2 mm; F-H, 0.1 mm.

Table I. Comparison of the larval characters of the first zoeal stage for species of the family Inachoididae. Sca: scaphognathite, cox: coxa or coxal endite, bas: basis or basial endite, end: endopod, exo: exopod, epi: epipod, ped: peduncle, seg: segments, S: somites, P: pleopods; s: simple setae, ae: aesthetascs, n/d: not described, (*) observation from figure.

Zoea I	Carapace	Antennule	Maxillule	Maxilla	Mxpd 1	Mxpd 2	Abdomen
Leurocyclus tuberculosus Present study	4	2 + 2 ae, 1s	cox: 7 bas: 7 end: 4	cox: 4, 3-4 bas: 5, 4 end: 4 sca: 9-11	cox: 0 bas: 2,2,2,3 end: 2,2,1,2,4+1	bas: 3 end: 0,1,3	S1-S5: 2
Pyromaia tuberculata (Luppi and Spivac, 2003)	4	2 + 1 ae, 1s	cox: 7 bas: 7 end: 4	cox: 4, 4 bas: 5, 4 end: 3 sca: 11	cox: 0 bas: 2,2,2,3 end: 3,2,1,2,4+1	bas: 3 end: 0,1,4	S1-S5: 2
Paradasygyius depressus (Pohle and Marques, 2000)	4	2 + 1 ae, 1s	cox: 7 bas: 7 end: 4	cox: 4, 4 bas: 5, 4 end: 3 sca: 10-11	cox: 1 bas: 2,2,2,3 end: 3,2,1,2,4+1	bas: 3 end: 0,1,4	S1-S5: 2
Anasimus latus (Sandifer and Van Engel, 1972)	n/d	2 + 2 ae	cox: 7 bas: 7 end: 3	cox: 4, 4 bas: 5, 4 end: 5 sca: 11	cox: n/d bas: 2,2,2,3 end: 3,2,1,2,5	bas: 3 end: 0,1,4	S1-S5: 2

Table II. Comparison of the larval characters of the second zoeal stage for species of the family Inachoididae (see Table I for definition of abbreviations).

Zoea I	Carapace	Antennule	Maxillule	Maxilla	Mxpd 1	Mxpd 2	Abdomen
Leurocyclus tuberculosus Present study	5	8 ae, 1s	cox: 7-8 bas: 9 end: 4 exo: 1	cox: 4-5, 4 bas: 5-6, 5 end: 4 sca: 16-19	cox: 0 bas: 2,2,2,3 end: 2,2,1,2,4+1	bas: 3 end: 0,1,3	S1-S5: 2
Pyromaia tuberculata (Luppi and Spivac, 2003)	6	4+1 ae, 1s	cox: 9 bas: 7 end: 4 exo: 1	cox: 4, 4 bas: 5, 5 end: 3 sca: 20	cox: 0 bas: 2,3,2,3 end: 3,2,1,2,4+1	bas: 3 end: 0,1,4	S1: 3 S2-5: 2
Paradasygyius depressus (Pohle and Marques, 2000)	5	6 + 2 ae, 1s	cox: 9 bas: 7 end: 4 exo: 1	cox: 4, 4 bas: 5, 5 end: 3 sca: 20	cox: 1 bas: 2,2,2,3 end: 3,2,1,2,4+1	bas: 3 end: 0,1,4	S1: 3 S2-5: 2
Anasimus latus (Sandifer and Van Engel, 1972)	n/d	6 + 2 ae	cox: 7 bas: 9 end: 3 exo: 1	cox: 4, 4 bas: 5, 5 end: 5 sca: 20	cox: n/d bas: 2,2,2,3 end: 3,2,1,2,5	bas: 3 end: 0,1,4	S1-S5: 2

Table III. Comparison of the larval characters of the megalopa stage for species of the family Inachoididae (see Table I for definition of abbreviations).

Megalopa	Antennule	Mandibule	Maxillule	Maxilla	Mxpd 1	Mxpd 2	Mxpd 3	Abdomen
Leurocyclus tuberculosus Present study	ped: 0,0,1 end: 3 exo:0, 8ae + 1s, 4ae+1s	palp: 5	cox: 10 bas: 17 exo: 1 epi: 1	cox: 6-7, 3 bas: 6, 6-7 end: 1 sca: 31-34	cox: 6 bas: 12-13 end: 0 exo: 5 epi: 5	end: 1,1,2-3,4 exo: 0,4	cox: 5-6 end: 11, 7, 4-5, 5-6, 4 exo: 0, 4 epi: 5	S1-6: 6,4,4,8,8,0
Pyromaia tuberculata (Luppi and Spivac, 2003)	ped: 0,1,1 end: 3 exo:0,9ae+1s, 4ae+1s	palp: 5	cox: 9 bas: 15 exo: 1 epi: 1	cox: 6, 3 bas: 4, 7 end: 0 sca: 28-30	cox: 6 bas: 10 end: 0 exo: 1, 4 epi: 5	end: 0,1,3,4 exo: 0,5	cox: 6 end: 12,8,5,5,4 exo: 0, 5 epi: 4	S1-6: 4,2,2,8,8,2
Paradasygyius depressus (Pohle and Marques, 2000)	ped: 0,1,1 end: 3 exo:0,10-11ae, 3-4ae+1s	palp: 3-5	cox: 10 bas: 16-17* exo: 1 epi: 1	cox: 7, 5 bas: 6-7, 7 end: 0-1 sca: 35	cox: 6 bas: 12 end: 1-2 exo: 1, 4 epi: 3-4	end: 0-1,1,3,4 exo: 0,4	cox: 4 end: 13,7-8,5,5,4 exo: 0, 4-5 epi: 4-5	S1-6: 3,4,4,6,6,2
Anasimus latus (Sandifer and Van Engel, 1972)	ped: 0,0,1 end: 3 exo:0,6ae+1, 4ae+1	palp: 6	cox: 10 bas: 17	cox: 4, 6-7 bas: 6, 6 end: 1 sca: 28-30	cox: 5-6 bas: 10-11 end: 0 exo: 1, 4 epi: 4	end: 1,1,3,4 exo: 0,4	cox: n/d end: 9,8,5,5,4 exo: 0, 4+1 epi: 3	S1-6: n/d

present well developed pleopods (Rice, 1980, 1983).

In the comparison with other inachoidids, *L. tuberculosus* show the following differences in the first zoeal stage: (i) the setal formula of the antennule presenting 4 aesthetascs and simple setae; (ii) the setal meristics of the endopod of the maxilla; (iii) and setation of the endopod of first and second maxillipeds (Table I). On the other hand, the setal formula of the basial endites of the maxillule, maxilla, and the setation of the abdomen are invariable among all known inachoidids (Table I). For the second zoeal stage, *L. tuberculosus* differs from other inachoidids in: (i) the number of setae on the endopod and scaphognatite of the maxilla; (ii) the setal formula of the endopod of first and second maxillipeds. Thus far, only the number of setae on coxa and basis of maxilla are consistent in all inachoidids in the second zoeal stage (Table II). Finally, diagnostic features for *Leurocyclus* megalopa stage include (i) the setal formula of the exopod of the antennule; (ii) the number of setae on the scaphognatite of the maxilla; (iii) the setal formula of the endopodite of the third maxilliped; (iv) and the setation of the abdomen. Despite of these differences, in the megalopa stage the endopod of the antennules, the coxa of the maxillule and first maxilliped are similar to those found in other inachoidids (Table III).

The zoeas of *L. tuberculosus* are distinguishable from other majoids by the setal formula of the first maxilliped. The only other majoid with similar formula is *Notomithrax ursus* Griffin, 1963 (cf. Webber and Wear, 1981) in the second zoea. However, this similarity should be viewed with caution since this is an observation from the figure provided by Webber and Wear (1981) (Santana *et al.,* 2006).

The identification of many majoid species from plankton material is a very hard task. Although the characters presented here for *L. tuberculosus* could be distinctive among inachoidids and other majoids, great part of them seems to be shared with other Majoidea. Examples are common as the setation of the endopod of the maxilla is the same as in *Achaeus* Leach, 1817, *Inachus* Weber, 1795, *Macropodia* Leach, 1814 and *Taliepus* A. Milne-Edwards, 1878. As far as we know, the only character that could distinguish larvae of *L. tuberculosus* from other majoids is the setal formula of the distal segment of the endopod of the second maxilliped in both zoeal stages.

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