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Larval development and first crab of *Mithraculus sculptus* (Decapoda: Brachyura: Majoidea: Mithracidae) described from laboratory-reared material

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The present work describes the complete larval development of *Mithraculus sculptus* (two zoeal stages, the megalopa) and the first crab instar from laboratory cultured material. The larval morphology is compared with other descriptions currently available for the *Mithrax–Mithraculus* complex: *Mithraculus coryphe*, *M. forceps*, *Mithrax hispidus*, *M. pleuracanthus*, *M. spinosissimus* and *M. verrucosus*. Although the different species of the *Mithrax–Mithraculus* complex display uniform morphological characters, the first zoeal stage of *M. sculptus* differs from other species in the setal meristics of the carapace and the number of aesthetascs of the antennule. The second zoeal stage differs in the number of aesthetascs of the antennule and the number of setae in the distal margin of the coxal endite of the maxillule. The megalopa of *M. sculptus* can be distinguished by the presence of 3–4 aesthetascs and a simple seta in the distal segment of the antennule. The morphological differences between the larvae from the genus *Mithrax* and *Mithraculus* are insufficient to support the separation of the two genera using adult morphology. Future studies should address in detail setal meristics.

INTRODUCTION

In recent years, brachyuran decapods have become popular in commercial aquaria. Although many species are sold for their ornamental value (e.g. *Lybia* spp. and *Stenorhynchus* spp.), most are traded for algae control as members of 'clean-up crews' (e.g. *Percnon* spp. and *Mithraculus* spp.) (see Calado et al., 2003a). Despite the absence of accurate reports, *Mithraculus sculptus* (Lamarck, 1818) commonly known as the emerald crab, is probably the most heavily traded brachyuran in the marine aquarium industry. This small mithracid majoid crab is abundant in shallow waters of the tropical western Atlantic Ocean, from as far north as Miami, throughout the Bahamas and Caribbean, and south to northern Brazil (Williams, 1984). Due to its popularity and economic value, researchers have started to develop suitable culture protocols that may allow, in the short term, the replacement of wild caught specimens by captive cultured emerald crabs in the aquarium trade (Calado et al., 2003b; Rhyne et al., 2005).

However, as pointed out by Calado et al. (2004), the insufficient knowledge on cultured species larval development and morphology can become a serious obstacle to the establishment of commercial scale culture protocols. Additionally, the collection of such data can be of extreme value for phylogenetic studies on decapod crustaceans, since larval morphology is a valuable tool to support a phylogenetic hypothesis (Pohle & Marques, 2000; Marques & Pohle, 2003a). The genus *Mithrax* Desmarest, 1825, *sensu lato*, comprises about 30 species traditionally divided into the subgenera *Mithrax* and *Mithraculus* established by Rathbun (1925). However, Wagner (1990) recognized *Mithrax* and *Mithraculus* as separate genera (*sensu stricto*), only using adult morphology to support his decision. Although the information on the complete larval development of several species of the *Mithrax–Mithraculus* complex is currently available, the inaccuracy of most of this information still impairs the use of larval features to support or refute the validity of Wagner's separation (Santana et al., 2003).

The present work describes the complete larval development of *M. sculptus*, and compares it with other descriptions currently available for the *Mithrax–Mithraculus* complex: *Mithraculus coryphe* (Herbst, 1801), *M. forceps* (A. Milne-Edwards, 1875), *Mithrax hispidus* (Herbst, 1790), *M. pleuracanthus* Stimpson, 1871, *M. spinosissimus* (Lamarck, 1818) and *M. verrucosus* H. Milne-Edwards, 1832.

MATERIALS AND METHODS

Ovigerous females of *Mithraculus sculptus* were hand collected from *Porites* sp. coral patches in Florida Bay, north of Grassy Key, Florida (June, 2003). Females were kept in aerated 18-l buckets, at 28°C and 35 salinity, and were checked daily for late stage embryos. Females carrying embryos close to hatching were transferred to the larval rearing system. Larviculture of *M. sculptus* was conducted using the rearing methods developed and

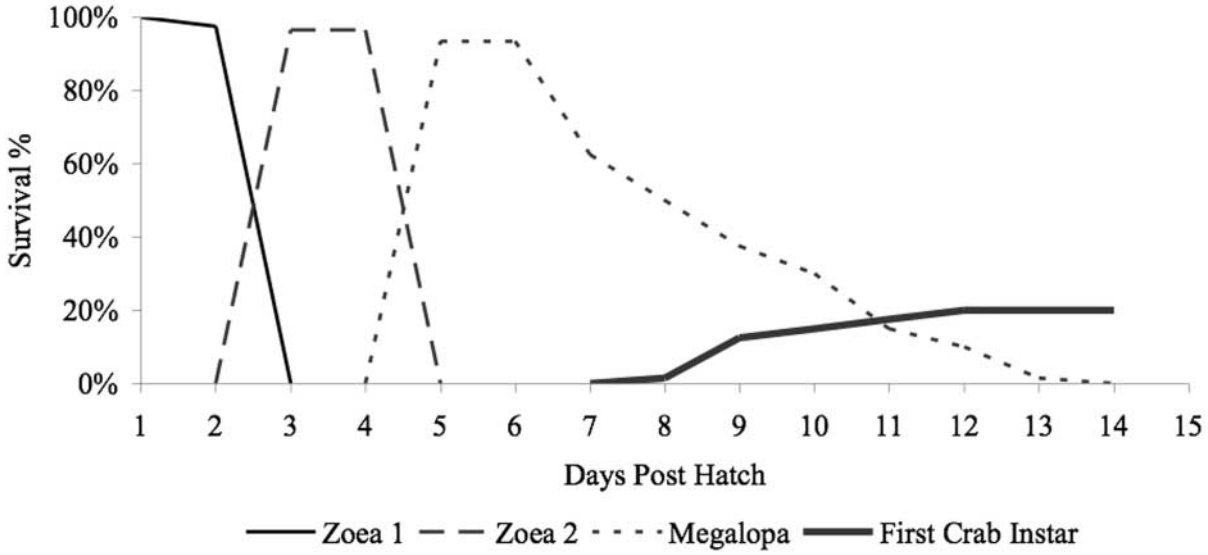

Figure 1. Survival (%) and stage duration of *Mithraculus sculptus* larvae cultured under laboratory conditions.

described in detail by Calado et al. (2003b) and Rhyne et al. (2005). The most active larvae (the ones displaying pronounced positive phototactic responses) of three different females were selected and stocked at a density of about 20 larvae l^{-1}. Larvae were fed newly hatched *Artemia* nauplii at a density of 5000–7000 nauplii l^{-1}. A salinity of 35, temperature of 28–29°C, pH of 8.0–8.2, and photoperiod of 14 h light:10 h dark was maintained. Ammonia, nitrite, and nitrate were maintained below detectable levels. Uneaten food was flushed from the culture tanks and replaced with fresh nauplii daily.

Ten randomly selected larvae were sampled daily and staged to determine stage duration. The sampled larvae were fixed in 5% formalin and some specimens subsequently transferred to 50% ethylene glycol for morphological observation. The observations and drawings were made using a Nikon Optiphot-2 binocular microscope equipped with a *camera lucida*. Descriptions were based on dissections of at least five specimens of each zoeal stage, megalopae, and juveniles. Larval description followed the method proposed by Clark et al. (1998) and setal terminology is according to Ingle (1991). Setal counts refer to proximal–distal sequence. The carapace length was measured for both zoeal stages, in lateral view, from the base of the rostrum to the most posterior margin. The carapace length was measured for the megalopa and first crab instar, both in dorsal view, from the small rostrum to the posterior margin. The spent females, complete larval series and first crab instar (undissected samples) have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

RESULTS

The larval development of *Mithraculus sculptus* consisted of two zoeal stages and one megalopa. Both zoeal stages lasted two days. Moulting occurred just after darkness and no mark-time or delayed moulting was observed in zoeal stages (as defined by Gore, 1985; Anger, 2001). Survival to the megalopa stages was extremely high and mortality normally began on the second or third day of megalopa (Figure 1). The duration of the megalopa was more variable, lasting from three to nine days until metamorphosing to the first crab instar (Figure 1). The morphometrics of the different larval stages of *M. sculptus* are described in Table 1.

The first zoeal stage, megalopa and first crab instar are completely described, while only the main differences of the second zoeal stage are referred to in detail.

Table 1. *Average carapace length (mm) measured for both zoeal stages, in lateral view, from the base of the rostrum to the most posterior margin of the carapace and for the megalopa and first crab instar, in dorsal view, from the small rostrum to the posterior margin of species from the* Mithrax–Mithraculus *complex.*

Species	First zoea	Second zoea	Megalopa	First crab instar
Mithraculus coryphe[1]	0.70	0.82	1.06	n.d.
Mithraculus forceps[2]	0.67	0.83	1.15	1.3[7]
Mithraculus sculptus[3]	0.68	0.79	1.14	1.26
Mihrax hispidus[4]	0.92	1.07	1.10	n.d.
Mithrax pleuracanthus[5]	0.96	1.10	1.40	n.d.
Mithrax spinosissimus[6]	1.10	1.15	1.30	1.5

n.d., data not described. Data from: [1], Scotto & Gore, 1980; [2], Wilson et al., 1979; [3], Present work; [4], Santana et al., 2003; [5], Goy et al., 1981; [6], Provenzano & Brownell, 1977; [7], Rhyne et. al., 2004.

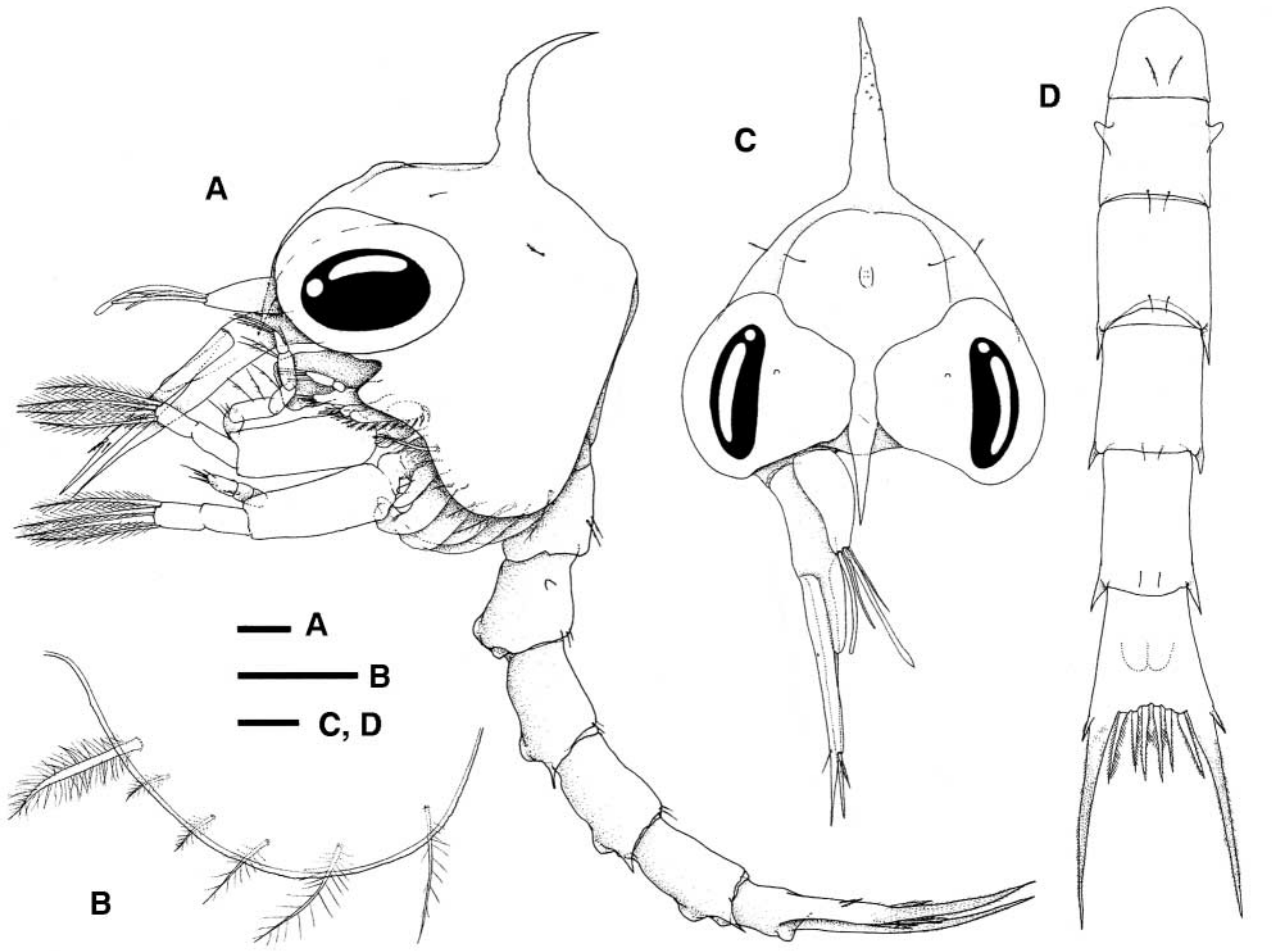

Figure 2. *Mithraculus sculptus*. First zoea: (A) entire animal, lateral view; (B) posteroventral margin of carapace, lateral; (C) anterior view of carapace, left side of antennule and antenna omitted; and (D) abdomen and telson, dorsal view. Scale bars: 0.1 mm.

Mithraculus sculptus (Lamarck, 1818)
Figures 2–9

First zoea (Figures 2 & 3)

Carapace (Figure 2A–C): globose, smooth; rostral spine bare and much shorter than antennular protopod; dorsal spine bearing minute spinules, posteriorly deflected and sharply pointed; lateral spines absent; anterodorsal region of carapace with a pair of short simple setae; posterodorsal with a pair of setae; each ventral margin with six plumose setae on inside of carapace, the anterior one much longer than the others; eyes sessile.

Antennule (Figure 3A): uniramous; endopod absent; exopod unsegmented, smooth, with conical appearence, and terminally bearing three aesthetascs and one simple seta.

Antenna (Figure 3B): biramous; protopodal process long and sharply pointed, with two rows of marginal spinules; endopod much shorter than exopod; exopod elongated, approximately three times longer than endopod, with one serrate and one simple setae at distal one-third, distal margin with two rows of spinules.

Mandible (Figure 3C): left and right mandibles asymmetrically dentate; incisor and molar processes distinct, incisor processes each with large teeth, molar processes with some tubercles; palp absent.

Maxillule (Figure 3D): coxal endite with seven setae (4 terminal plumodenticulate setae and 1 plumose and 2 plumodenticulate subterminal setae); basial endite with two small protuberances and seven setal processes (3 cuspidate and 4 plumose/plumodenticulate); endopod 2-segmented, with proximal segment bearing one simple seta, distal segment with six (2 subterminal and 4 terminal plumodenticulate) setae; exopod and epipod seta absent.

Maxilla (Figure 3E): coxal endite bilobed, with 5+4 simple/plumodenticulate setae; basial endite bilobed, with 5+4 plumodenticulate setae; microtrichia present on both endites; endopod not bilobed, with five terminal simple/plumodenticulate setae, microtrichia on lateral margin; exopod (scaphognathite) with 12–14 marginal densely plumose setae and microtrichia.

First maxilliped (Figure 3F): epipod present; coxa with one simple seta; basis with ten simple/plumodenticulate setae arranged 2+2+3+3; endopod 5-segmented, with 3, 2, 1, 2, 5(1 subterminal and 4 terminal) plumodenticulate setae; exopod incompletely 2-segmented, terminally bearing four long plumose natatory setae.

Second maxilliped (Figure 3G): epipod absent; coxa without setae; basis with three simple setae arranged 1+1+1; endopod 3-segmented, with 0,1,5 simple/serrate setae; exopod incompletely 2-segmented, terminally bearing four long plumose natatory setae.

Figure 3. *Mithraculus sculptus*. First zoea: (A) antennule; (B) antenna; (C) mandibles (r, right side; l, left side); (D) maxillule; (E) maxilla; (F) first maxilliped; (G) second maxilliped; (H) third maxilliped; and (I) pereiopods. Scale bars: 0.1 mm.

Third maxilliped (Figure 3H): biramous; epipod present; endopod and exopod as unsegmented buds.

Pereiopods (Figure 3I): first pereiopod with cheliped bilobed, gill buds present; the others as small, unsegmented buds.

Abdomen (Figure 2A,D): five segments; segment 1 with pair of mediodorsal plumose setae; segments 2–5 each with pair of posterodorsal simple setae; segment 2 with pair of dorsolateral processes directed anteriorly; segments 3–5 each with pair of posterolateral spines. Pleopods not distinct, but posteroventral margin of segments 2–5 slightly bulged as further pleopod buds.

Telson (Figure 2A,D): bifurcated, displaying a shallow median arch, with three pairs of stout, plumodenticulate

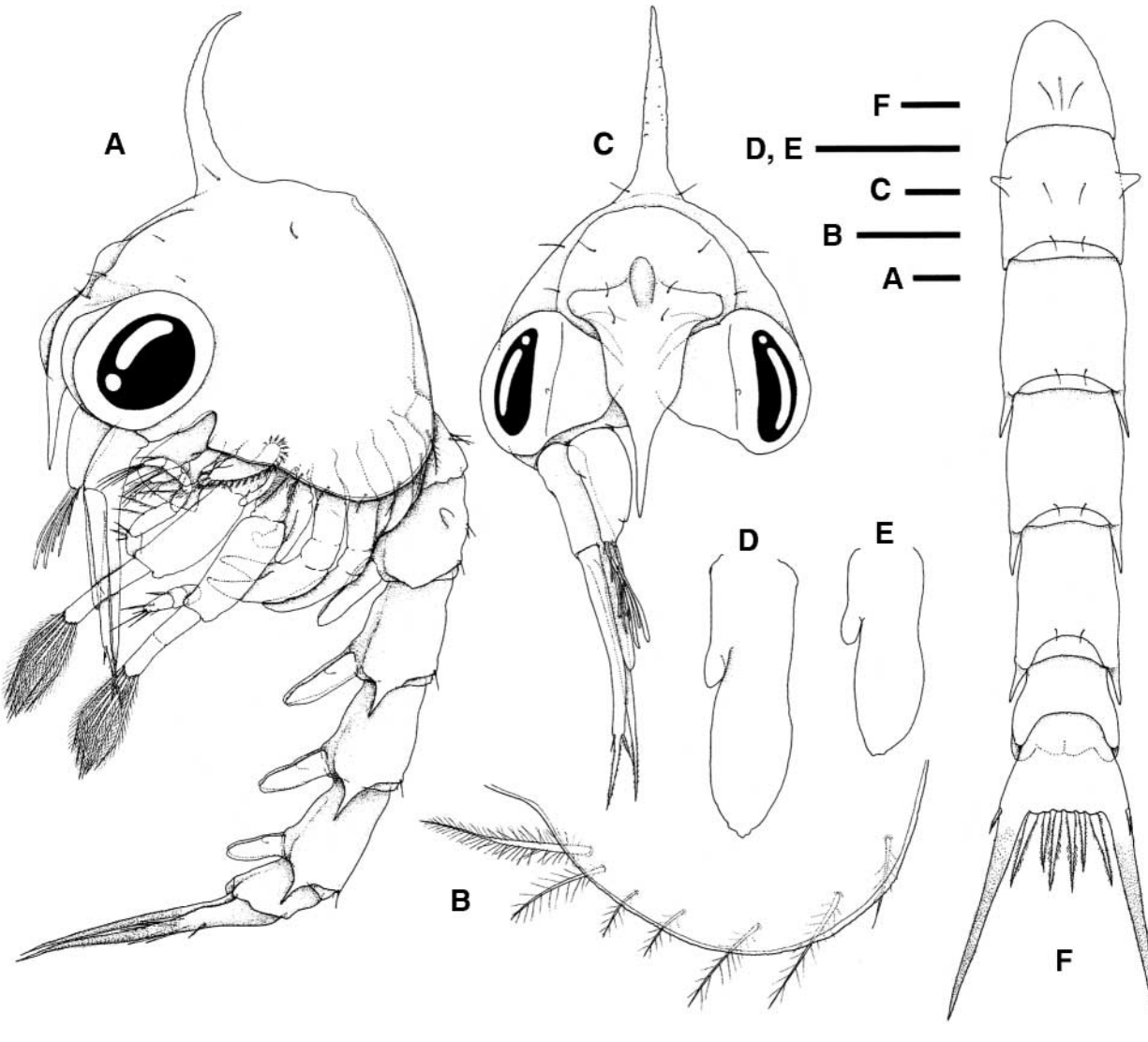

Figure 4. *Mithraculus sculptus*. Second zoea: (A) entire animal, lateral view; (B) posteroventral margin of carapace, lateral; (C) anterior view of carapace, left side of antennule and antenna omitted; (D) first pleopod, ventral view; (E) fourth pleopod, ventral view; and (F) abdomen and telson, dorsal view. Scale bars: 0.1 mm.

setae on the inner margin; both furcal shafts bearing a lateral spine proximately, with the shafts and spines being covered with rows of spinules.

Colour in life: body and limbs semitransparent, with a greenish hue at the centre of the body.

Second zoea (Figures 4 & 5)

Carapace (Figure 4A–C): anterodorsal region now with four pairs of setae; a pair of simple setae at the base of the dorsal spine; ventral margin now with seven plumose setae; eyes stalked; otherwise unchanged besides size.

Antennule (Figure 5A): now biramous; endopod bud present; exopod with eight long aesthetascs and one short seta terminally otherwise unchanged besides size.

Antenna (Figure 5B): endopod now reaching to middle part of exopod; otherwise unchanged besides size.

Mandible (Figure 5C): palp bud present; otherwise unchanged besides size.

Maxillule (Figure 5D): basial endite with nine or ten setal processes (5 cuspidate and 4–5 plumose/plumodenticulate setae); exopod pappose seta present; otherwise unchanged besides size.

Maxilla (Figure 5E): distal lobe of basial endite with five plumodenticulate setae; scaphognathite with 24–26 marginal plumose setae; otherwise unchanged besides size.

First maxilliped (Figure 5F): epipod more developed than in previous stage; exopod with six plumose natatory setae; otherwise unchanged besides size.

Second maxilliped (Figure 5G): exopod with six plumose natatory setae; otherwise unchanged besides size.

Third maxilliped (Figure 5H): unchanged with the exception for the larger size of the lobes of the exo-, endo- and epipod.

Pereiopods (Figure 5I): gill bud present on pereiopods 1–3; otherwise unchanged, except for the larger size.

Abdomen (Figure 4A,D–F): additional sixth segment present; somite 1 with three mediodorsal plumose setae; segment 2 with additional pair of simple dorsal setae on mid-dorsal area; otherwise unchanged besides size.

Pleopods (Figure 4D,E): present on segments 2–5, biramous and with small endopods.

Telson (Figure 4A&F): unchanged besides size.

Colour in life: body and limbs semi-transparent, with a greenish hue at the centre of the body.

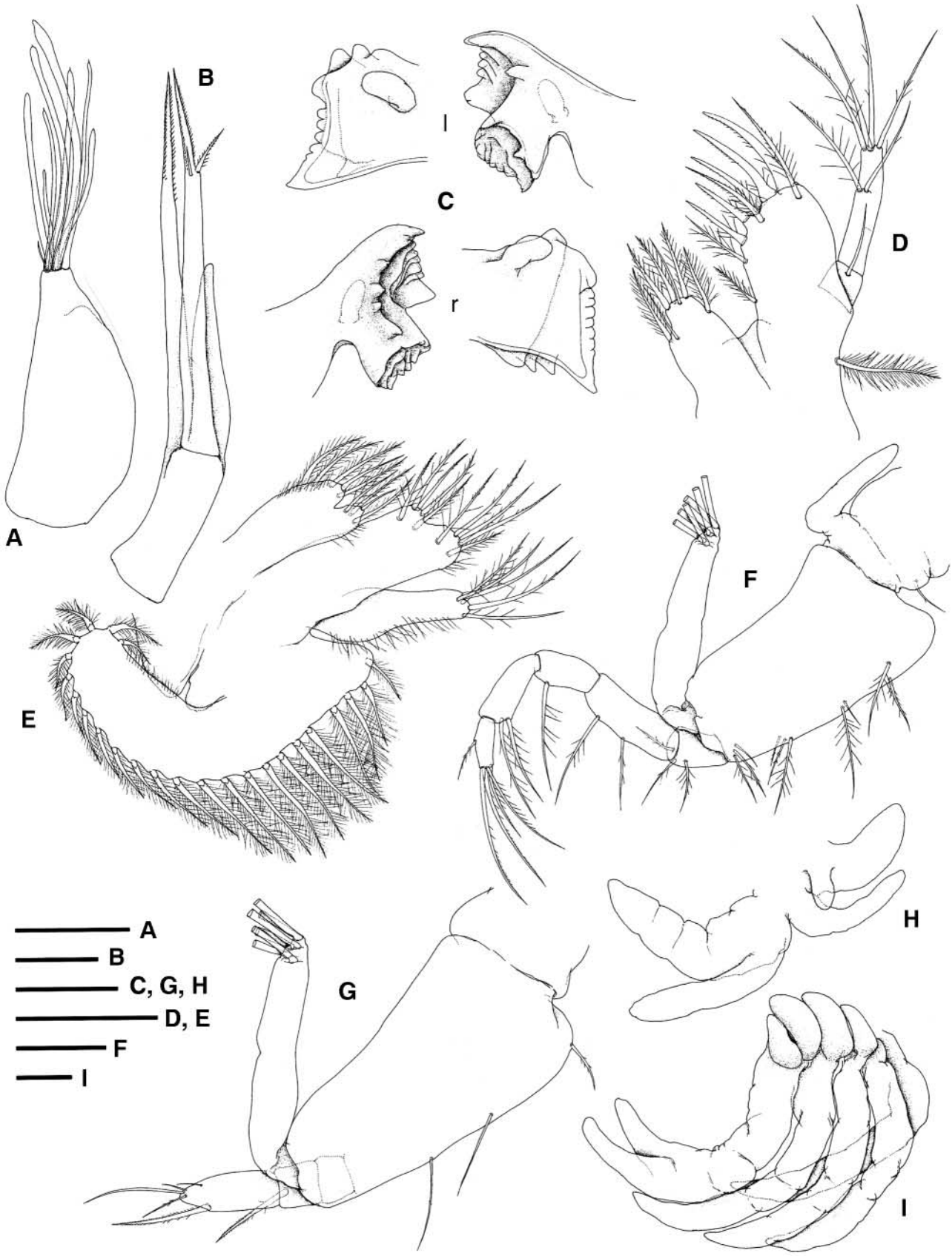

Figure 5. *Mithraculus sculptus*. Second zoea: (A) antennule; (B) antenna; (C) mandibles (r, right side; l, left side); (D) maxillule; (E) maxilla; (F) first maxilliped; (G) second maxilliped; (H) third maxilliped; and (I) pereiopods. Scale bars: 0.1 mm.

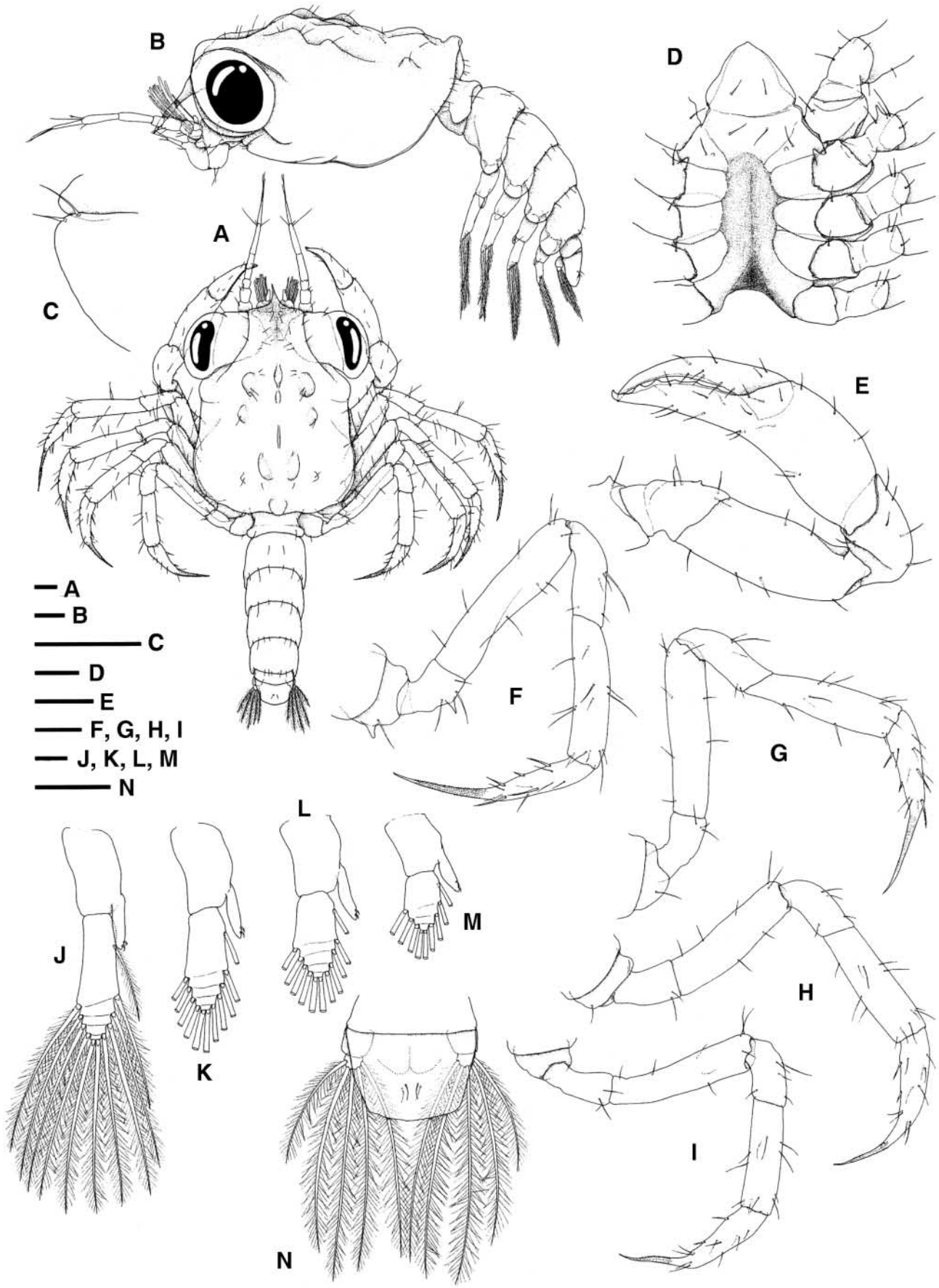

Figure 6. *Mithraculus sculptus*. Megalopa: (A) entire animal, dorsal view; (B) lateral view of carapace, abdomen and telson; (C) posteroventral margin of carapace, lateral view; (D) thoracic sternites, ventral view; (E) first pereiopod, ventral view; (F) second pereiopod, ventral view; (G) third pereiopod, ventral view; (H) fourth pereiopod, ventral view; (I) fifth pereiopod, ventral view; (J) first pleopod, ventral view; (K) second pleopod, ventral view; (L) third pleopod, ventral view; (M) fourth pleopod, ventral view; and (N) uropods and telson, dorsal view. Scale bars: 0.1 mm.

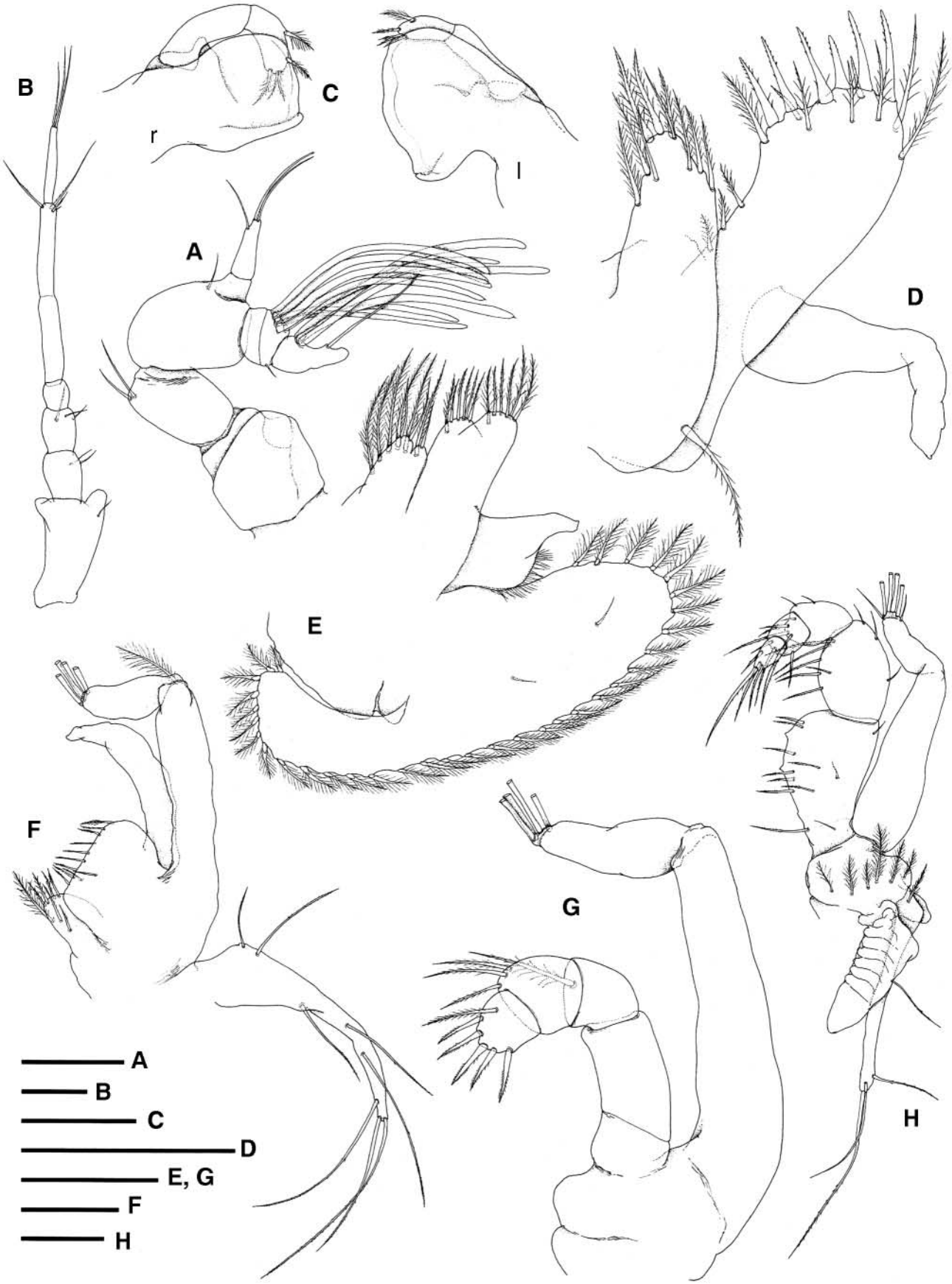

Figure 7. *Mithraculus sculptus*. Megalopa: (A) antennule; (B) antenna; (C) mandible (r, right side; l, left side); (D) maxillule; (E) maxilla; (F) first maxilliped; (G) second maxilliped; and (H) third maxilliped. Scale bars: 0.1 mm.

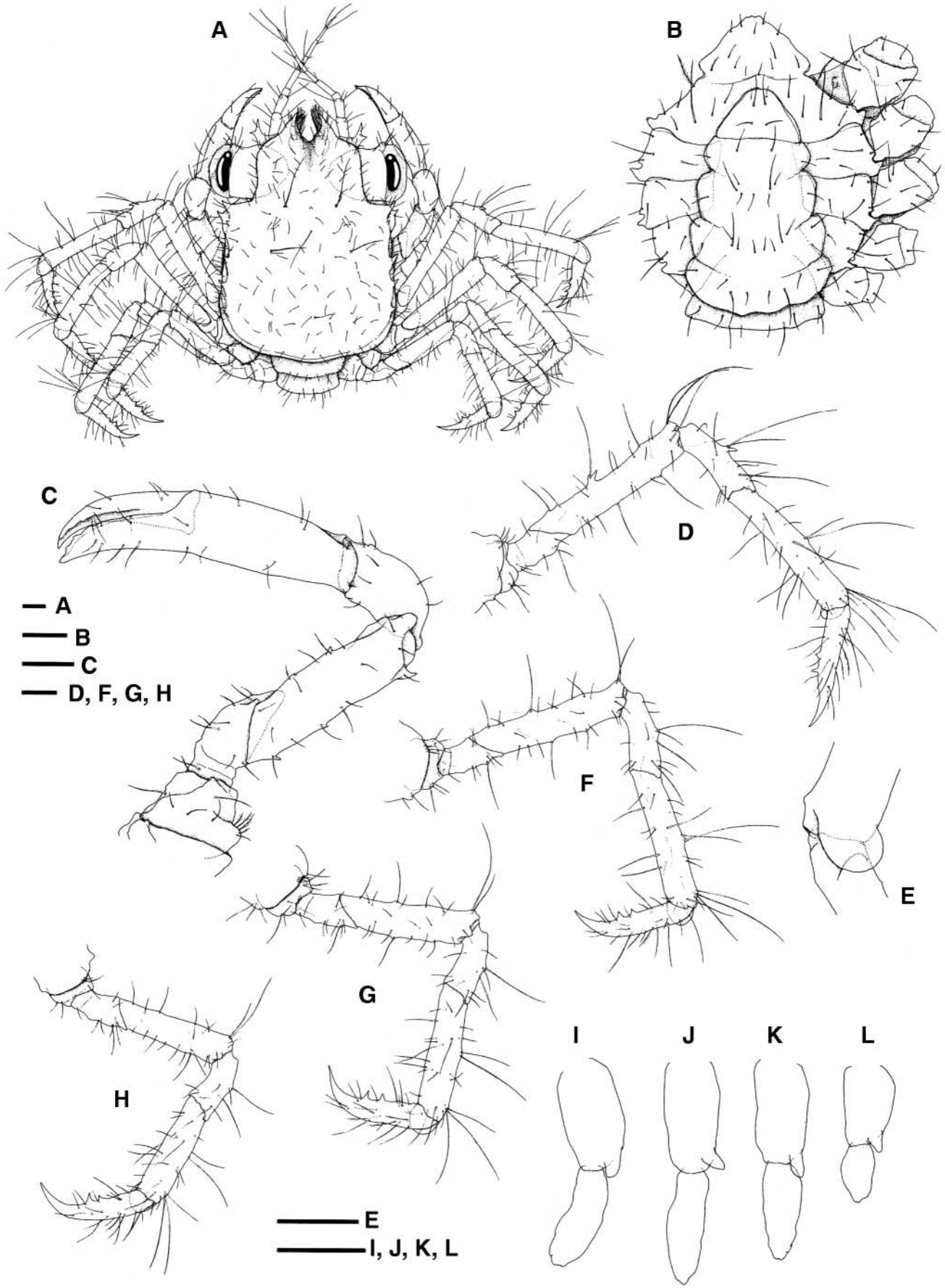

Figure 8. *Mithraculus sculptus*. First crab instar: (A) entire animal, dorsal view; (B) thoracic sternites, abdomen and telson, ventral view; (C) first pereiopod, ventral view; (D) second pereiopod, ventral view; (E) second pereiopod, posterior margin of propodus, dorsal view; (F) third pereiopod, ventral view; (G) fourth pereiopod, ventral view; (H) fifth pereiopod, ventral view; (I) first pleopod, ventral view; (J) second pleopod, ventral view; (K) third pleopod, ventral view; and (L) fourth pleopod, ventral view. Scale bars: 0.1 mm.

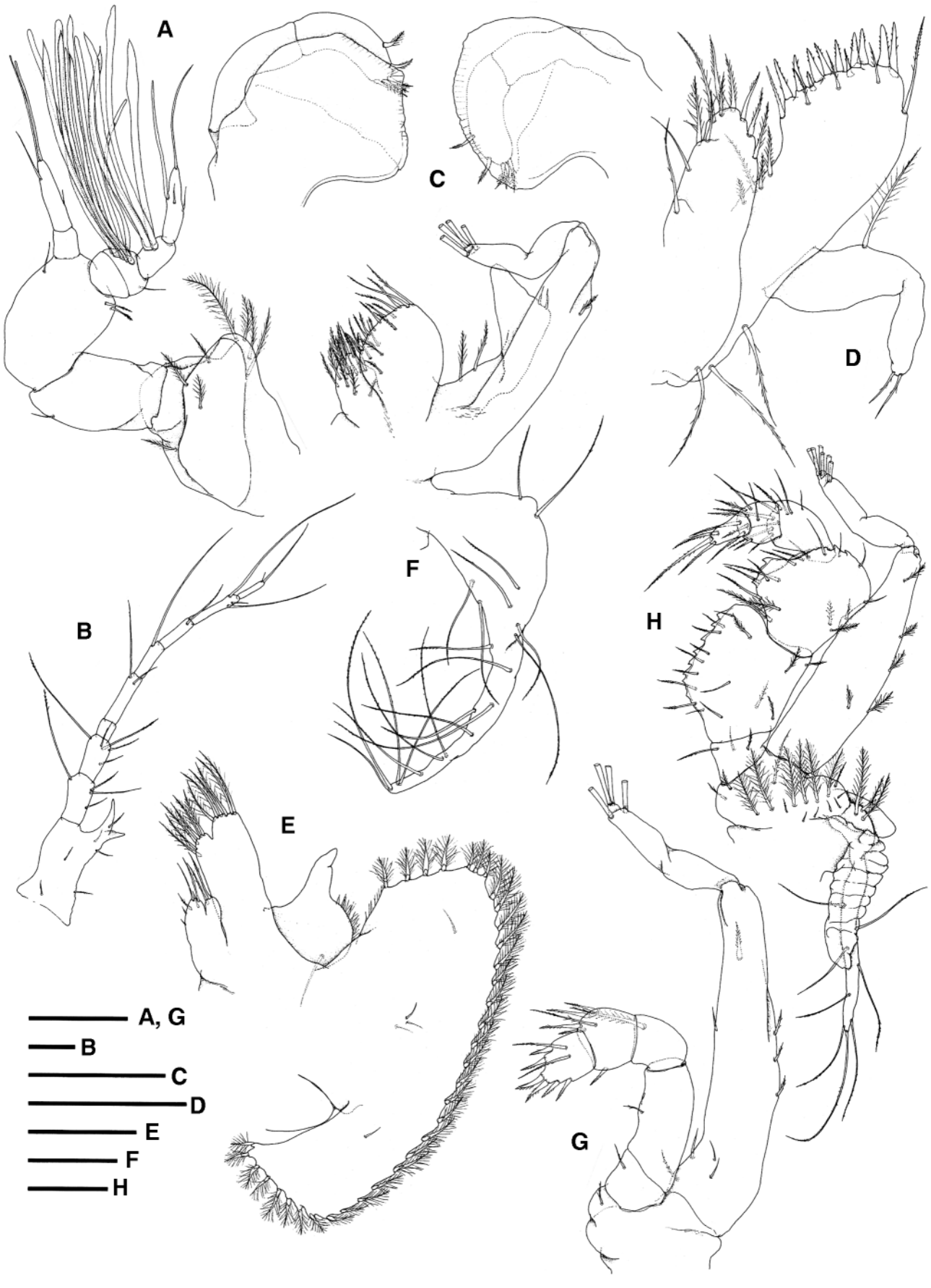

Figure 9. *Mithraculus sculptus*. First crab instar: (A) antennule; (B) antenna; (C) mandible (r, right side; l, left side); (D) maxillule; (E) maxilla; (F) first maxilliped; (G) second maxilliped; and (H) third maxilliped. Scale bars: 0.1 mm.

Table 2. *Comparison of relevant larval characters of the first zoeal stage of species from the* Mithrax–Mithraculus *complex*.

Species	*Mithraculus sculptus*	*Mithraculus coryphe*	*Mithraculus forceps*	*Mithrax hispidus*	*Mithrax pleuracanthus*	*Mithrax spinosissimus*	*Mithrax verrucosus*
Reference	Present study	(1)	(2)	(3)	(4)	(5)	(6)
Carapace:							
anterodorsal region	2s (1 pair)	2s (1 pair)*	2s (1 pair)*	2s (1 pair)	2s (1 pair)	no data	no data
posterodorsal region	2s (1 pair)	2s (1 pair)*	2s (1 pair)*	2s (1 pair)	2s (1 pair)	no data	no data
ventral margin	6ps	6ps*	6ps*	6ps	6ps	no data	4s
Antennule: exopod	3a+1s	4a+1s	4a+1s	4a+1s	3a+1s	5a	4a+2s
Maxillule:							
coxal endite	7s	7s*	7s*	7s	7s	5s	6s
basal endite	7s	7s*	7s*	7s	7s	6s	7s
endopod	1s, 6s	1s, 6s*	1s, 6s*	1s, 6s	1s, 6s	2s	1s, 6s
Maxilla:							
coxal endite	(5+4)s	(5+4)s*	(5+4)s*	(5+4)s	(5+4)s	(1+1)s	(5+4)s
basal endite	(5+4)s	(5+4)s*	(5+4)s*	(5+4)s	(5+4)s	(3+3)s	(5+4)s
endopod	5s	5s*	5s*	5s	5s	1s	5s
scaphognathite	(12–14)ps	13ps	13ps	13ps	13ps	30ps	13ps
First maxilliped:							
coxa	1s	1s*	1s*	1s	1s	naked*	1s
basis	(2+2+3+3)s	(2+2+3+3)s*	(2+2+3+3)s*	(2+2+3+3)s	(2+2+3+3)s	naked*	(2+2+3+3)s
endopod	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	0,1s,1s,2s,(3–4)s	3s,2s,1s,2s,5s
Second maxilliped:							
coxa	naked	naked	naked	naked	naked	naked	naked
basis	(1+1+1)s	(1+1+1)s*	(1+1+1)s*	(1+1+1)s	(1+1+1)s	0*	(1+1+1)s
endopod	0, 1s, 5s	0, 1s, 5s*	0, 1s, 5s*	0, 1s, 5s	0, 1s, 5s	1 or 3s	0, 1s, 5s

a, aesthetasc; s, seta except for ps; ps, plumose seta; sp, spine; *, data from figures observation. References: (1) Scotto & Gore (1980); (2) Wilson et al. (1979); (3) Santana et al. (2003); (4) Goy et al. (1981); (5) Provenzano & Brownell (1977); (6) Bolaños & Scelzo (1981).

Table 3. *Comparison of relevant larval characters of the second zoeal stage of species from the* Mithrax–Mithraculus *complex*.

Species	*Mithraculus sculptus*	*Mithraculus coryphe*	*Mithraculus forceps*	*Mithrax hispidus*	*Mithrax pleuracanthus*	*Mithrax spinosissimus*	*Mithrax verrucosus*
Reference	Present study	(1)	(2)	(3)	(4)	(5)	(6)
Carapace:							
dorsal region	12s	10s*	10s*	(10–12)s	10s	no data	6s
ventral margin	7ps	7ps*	7ps*	(7–8)ps	8ps	no data	4s
Antennule: exopod	8a+1s	8a+1s	7a+1s	8a+1s	7a+1s	5a	8a+1s
Maxillule:							
coxal endite	7s	7s*	7s*	8s	7s	5s	7s
basal endite	(9–10)s	10s*	10s*	10s	11s	7s	9s
endopod	1s, 6s	1s, 6s*	1s, 6s*	1s, 6s	1s, 6s	2s*	1s, 6s
exopod seta	present (1s)	present (1s)	present (1s)	present (1s)	present (1s)*	absent*	no data
Maxilla:							
coxal endite	(5+4)s	(5+4)s*	(5+4)s*	(5+4)s	(5+5)s	(1+1)s*	(5+4)s
basal endite	(5+5)s	(5+5)s*	(5+5)s*	(4–5+5)s	(5+5)s	(2+2)s*	(5+5)s
endopod	5s	5s*	5s*	5s	5s	2s*	5s
scaphognathite	(24–26)ps	24ps	24ps	(24–25)ps	24ps	31ps	24ps
First maxilliped:							
coxa	1s	1s*	1s*	1s	1s	naked*	1s
basis	(2+2+3+3)s	(2+2+3+3)s*	(2+2+3+3)s*	(2+2+3+3)s	(2+2+3+3)s	naked*	(2+2+3+3)s
endopod	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	3s,2s,1s,2s,5s	1,1s,1s,1s,(3–4)s*	3s,2s,1s,2s,5s
Second maxilliped:							
basis	(1+1+1)s	(1+1+1)s*	(1+1+1)s*	(1+1+1)s	(1+1+1)s	naked*	(1+1+1)s
endopod	0, 1s, 5s	0, 1s, 5s*	0, 1s, 5s*	0, 1s, 5s	0, 1s, 4s	2s*	0, 1s, 5s

a, aesthetasc; s, seta except for ps; ps, plumose seta; sp, spine; *, data from figures observation. References: (1) Scotto & Gore (1980); (2) Wilson et al. (1979); (3) Santana et al. (2003); (4) Goy et al. (1981); (5) Provenzano & Brownell (1977); (6) Bolaños & Scelzo (1981).

Table 4. *Comparison of relevant larval characters of the megalopa of species from the* Mithrax–Mithraculus *complex*.

Species	*Mithraculus sculptus*	*Mithraculus coryphe*	*Mithraculus forceps*	*Mithrax hispidus*	*Mithrax pleuracanthus*	*Mithrax spinosissimus*	*Mithrax verrucosus*
Reference	Present study	(1)	(2)	(3)	(4)	(5)	(6)
Antennule:							
peduncle	0, 2s, 1s	0, 2s, 1s*	0, 2s, 1s*	0, 2s, 1s	0, 2s, 1s	0, 0, 1s*	no data
endopod	3s	3s*	3s*	3s	3s	3s*	no data
exopod	0, (7–8)a+1s, (3–4)a+1s	0, 7a+1s, 5a*	0, 7a+1s, 5a*	0, 8a, 5a	0, 8a+1s, 5a	0, 5a+1s, 4a*	0, 7a, 5a*
Antenna:							
setation	1s, 2s, 3s, 0, 0, 4s, (3–4)s	1s, 2s, 3s, 0, 0, 4s, 4s*	1s, 2s, 3s, 0, 0, 4s, 4s*	(1–3)s, 2s, 3s, 0, 0, 4s, 3s	0, 2s, 3s, 0, 0, 4s, 3s	2s, 2s, 2s, 0, 4s, 3s*	?, 2s, 3s, 0, 0, 4s, 4s
Mandible: palp	0, 5s	0, 5s	0, 5s	0, 5s	0, 5s	0, 5s	0, 5s
Maxillule:							
coxal endite	10s	10s*	10s*	10s	10s	8s	10s
basal endite	(17–18)s	18s*	18s*	(16–18)s	15s	(12–15)s	17s
endopod	0	0	0	2s	2s	0	2s
epipod seta	present (1s)	present (1s)*	present (1s)*	present (1s)	absent	absent*	present (1s)
Maxilla:							
coxal endite	(7+2–3)s	(7+3)s*	(7+3)s*	(7–8+3)s	(7+3)s	(3–5+3–5)s*	(7+3)s
basal endite	(6+6)s	(6+6)s*	(6+6)s*	(5–6+6)s	(6+6)s	(5–6+5–6)s*	(5+6)s
endopod	0	0	0	0	2s	1s*	0
scaphognathite	(30–34)ps+2s	(26–30)ps+3s*	(29–33)ps+3s*	(27–31)ps+3s	(28–39)ps+7s	(33–37)ps	31ps
First maxilliped:							
coxa	(6–7)s	(5–7)s*	(5–7)s*	(7–8)s	3s	8s*	7s
basis	(10–11)s	(9–11)s*	(9–11)s*	(10–11)s	10s	8s*	10s
endopod	0	0	0	0	1s, 1s	0	2s
exopod	1ps, 4ps	1ps, 4ps	1ps, 4ps	1ps, 4ps	1ps, 4ps	0, (4–6)ps	1ps, 5ps
epipod	(6–9)s	(6–7)s	6s	(3–5)s	5s	4s	7s
Second maxilliped:							
endopod	0, 0, 1s, 3s, (6–7)s	0, 1s, 3s, 6s*	0, 1s, 3s, 6s*	0, 1s, (2–3)s, (5–6)s	1s, 1s, 4s, 6s	0, 1s, 3s, 6s*	0, 1s, 3s, 6s
exopod	0, 4ps	0, 4ps*	0, 4ps	0, 4ps	0, 4ps	0, (4–6)ps	0, 4ps
Third maxilliped:							
coxa/basis	(5–6)s	(5–7)s*	(5–7)s*	(6–7)s	10s	4s	6s
endopod	(12–13)s+ (2–3)t, 9s, 5s, 6s, 4s,	12s, 9s, 5s (4–6), (3–4)s*	12s, 9s, 5s (4–6), (3–4)s *	(11–12)s, (8–9)s, 5s, 5s, 4s	12s, 7s, 4s, 6s, 4s	12s, 5s, 5s, 3s, 4s*	10s, 7s, 5s, 5s, 4s
exopod	0, 6ps	0, 6ps*	0, 6ps*	0, 6ps	0, 6ps	0, 4ps	0, 6ps
epipod	(4–5)s	(4–6)s*	(5–6)s*	(4–5)s	5s	(4–6)s	4s
Abdomen:							
1st–6th segments	2s,10s,6s,8s, 8s,0	no data	no data	6s,8s,6s,8s,8s,2s	2s,4s,4s,4s, 4s,2s	no data	no data

a, aesthetasc; s, seta except for ps; ps, plumose seta; sp, spine; *, data from figures observation. References: (1) Scotto & Gore (1980); (2) Wilson et al. (1979); (3) Santana et al. (2003); (4) Goy et al. (1981); (5) Provenzano & Brownell (1977); (6) Bolaños & Scelzo (1981).

Megalopa (Figures 6 & 7)

Carapace (Figure 6A–C): sub-quadrate, narrowing anteriorly, approximately 1.5 times longer than broad, with small rostrum ventrally deflected and with medium cleft; dorsal surface with round tubercles and sparsely setose as in Figure; anteroventral margin rounded with two simple setae.

Antennule (Figure 7A): peduncle 3-segmented; first segment broad and naked; second and third segments with two and one simple setae, respectively; endopod unsegmented, with one subterminal and two terminal simple setae; exopod 3-segmented, proximal segment naked, middle segment with seven or eight aesthetascs and one short seta, distal segment with three or four aesthetascs proximally and one long seta subterminally.

Antenna (Figure 7B): peduncle 3-segmented, with one, two and three simple setae, respectively; flagellum 4-segmented, with 0, 0, 4, 3–4 terminal simple/serrate setae, respectively.

Mandible (Figure 7C): asymmetric, with subsymmetrical scoop-like processes with cutting edge; palp 2-segmented, proximal segment naked, distal segment with five stout serrate setae.

Maxillule (Figure 7D): coxal endite with ten plumose/plumodenticulate setae, lower part of coxal endite with one long plumodenticulate seta (=epipod seta); basial endite with 17 or 18 setal processes (7–8 cuspidate and 9–10 plumose/plumodenticulate setae); endopod unsegmented and without setae.

Maxilla (Figure 7E): coxal endite bilobed, proximal lobe with seven simple/plumose setae, distal lobe with 2–3

simple/plumose setae; basial endite bilobed, with six plumodenticulate setae on proximal lobe and six plumodenticulate setae on distal lobe; endopod unsegmented, proximal part swollen with microtrichia on distal lobe; scaphognathite with 30–34 marginal plumose setae, and with two simple lateral setae.

First maxilliped (Figure 7F): biramous; coxal endite with six or seven serrate/plumodenticulate setae; basial endite with 10 or 11 setae (including simple, serrate, plumodenticulate setae); endopod unsegmented, naked; exopod 2-segmented, with one plumose seta on proximal segment and with four plumose setae on distal segment; epipod with 6–9 long plumodenticulate setae.

Second maxilliped (Figure 7G): biramous; coxa and basis not clearly differentiated, naked; endopod 5-segmented, showing indistinct fusion of the two proximal segments, with setation of 0, 0, 1, 3, 6–7 (including plumodenticulate and stout serrate setae), respectively; exopod 2-segmented, with four terminal plumose setae.

Third maxilliped (Figure 7H): biramous; arthrobranch and podobranch gill buds present; coxa and basis not differentiated with five or six plumose setae; endopod 5-segmented, ischium with 12–13 simple/serrate setae and 2–3 crista dentata, remaining segments with 9, 5, 6, 4 simple/serrate setae; exopod with six terminal plumose setae; epipod with one proximal plumose and 3–4 distal long plumodenticulate setae.

Pereiopods (Figure 6A,E–I): all legs fully developed, segmented and sparsely setose as in Figure. Cheliped (first pereiopod) robust, cutting edge with 4–5 rounded teeth. Ambulatory legs (second to fifth pereiopods) subcylindrical; dactylus ending sharply pointed, covered with rows of spinules; coxa and ischium of pereiopods 1–2 each with one spine (sometimes reduced or absent).

Sternum (Figure 6D): thoracic sternites as illustrated; anterior part of the fourth sternite triangular, with two simple setae, and posterior area with four simple setae; remaining sternites naked.

Abdomen (Figure 6A,B): six segments; first segment with pair of posterior marginal simple setae; segment 2 with pair of dorsomedial simple setae and three pairs of posterior marginal simple setae; segments 3–5 with three pairs, four pairs and four pairs of posterior marginal simple setae, respectively; segment 6 naked.

Pleopods (Figure 6J–M): present on segments 2–5, decreasing in size posteriorly, biramous; each endopod with two cincinnuli; exopod of pleopods bearing marginal plumose natatory setae, numbering from proximal to distal end 11, 11, 11 and 9.

Uropods (Figure 6N): present on segment 6, endopod absent, two-segmented, distal segment with five marginal plumose natatory setae.

Telson (Figure 6A,B&N): sub-squared in shape; posterior margin slightly rounded, naked; dorsal and ventral surfaces with pair of short simple setae.

Colour in life: body and limbs semi-transparent, with a dark greenish hue at the centre of the body.

First crab instar (Figures 8 & 9)

Carapace (Figure 8A): longer than broad, lateral margin with six spines; dorsal surface heavily setose as in Figure; rostrum bifid, slightly deflected ventrally.

Antennule (Figure 9A): peduncle 3-segmented, with 7–8 plumose, 1–2 simple, 2–3 simple/serrate setae, respectively; endopod 2-segmented, proximal segment naked, distal segment with one proximal, one subterminal and two terminal simple setae; exopod 4-segmented, proximal segment naked, second segment with eight or nine (usually 9) aesthetascs and one short simple seta, third segment with four or five (usually 4) aesthetascs, distal segment with one or two subterminal aesthetascs, 1–2 short subterminal simple setae, and one long terminal seta.

Antenna (Figure 9B): peduncle 3-segmented, proximal segment broad, posterior angle ending with a bifid robust spine, with six short simple/serrate setae, second and third segments with four and five simple/serrate setae, respectively; flagellum 6-segmented, with 0, 2, 1, 1, 3, 1–2 (terminal) setae, respectively.

Mandible (Figure 9C): distal segment of palp with four or five (usually 5) stout, serrate setae.

Maxillule (Figure 9D): coxal endite with 11 simple/plumodenticulate setae, lower part of coxal endite with one long plumodenticulate seta (=epipod seta); basial endite with 18–20 setal processes (11–12 cuspidate and 7–9 plumose/plumodenticulate setae), lower part of basial endite with two long plumodenticulate setae (=exopod setae) present directly proximal to endopod; endopod unsegmented, with one long proximal plumodenticulate seta and two short terminal setae (terminal setae sometimes absent).

Maxilla (Figure 9E): coxal endite more reduced than in megalop stage, bilobed, with 5–7+2–3 simple/plumodenticulate setae; basial endite bilobed with 6+6 plumodenticulate setae; endopod with one simple seta proximally; scaphognathite with 30–35 marginal plumose setae, and 3–5 simple lateral setae.

First maxilliped (Figure 9F): coxal and basial endites with 12–15 and 17–19 setae (including simple, serrate, and plumodenticulate setae), respectively; endopod with 3–4 plumodenticulate setae; exopod with one short plumose on proximal segment and with four plumose setae on distal segment; epipod with 15–20 long plumodenticulate setae.

Second maxilliped (Figure 9G): coxa and basis not clearly differentiated, with one short seta; endopod 5-segmented, with 1,1,1,5–6,8–9 setae (including simple, serrate, plumodenticulate, setae); exopod 2-segmented, proximal segment with 7–11 short simple/plumodenticulate setae, distal segment with four terminal plumose setae.

Third maxilliped (Figure 9H): coxa with 12–17 (usually 14–17) simple/plumose setae; endopod 6-segmented, basis differentiated from ischium with three simple/serrate setae, ischium with 6–10 crista dentata and 14–16 simple/serrate setae, merus with 2–4 broad teeth and 12–15 setae (including simple, serrate, plumodenticulate setae), distal three segment with setation of 9–10, 8–9, 3–5 (including simple, serrate, plumodenticulate setae), respectiverly; exopod 2-segmented, proximal segment with five or six plumose setae, distal segment with six plumose setae; epipod with three proximal plumose setae and 6–8 distal long, plumodenticulate setae.

Pereiopods (Figure 8A–H): all legs heavily setose as in Figure; dorsoposterior margin of ambulatory propodi with rounded projection; ambulatory dactyli with two teeth on flexor margin.

Sternum (Figure 8B): heavily setose as in Figure.

Abdomen (Figure 8A,B,I–L): six segments, each segment not well differentiated, only recognized by notches and faint demarcations, sparsely setose as in Figure. First to fourth pleopods much reduced, biramous; distal cincinnuli of endopod absent; exopodal plumose natatory setae absent; uropod reduced, almost vestigal.

Telson (Figure 8B): subtriangular in shape, with six setae.

Colour in life: body and limbs semi-transparent, with a dark brown to black spot at the centre of the body.

DISCUSSION

The zoeal stages of *Mithraculus sculptus* described in the present work fully agree with characters proposed by Rice (1980, 1983) for the Majidae, now classed as Majoidea according to Martin & Davis (2001), with the first zoeal stage having nine or more setae in the scaphognathite and the second zoeal stage displaying well developed pleopods.

Despite the number of publications describing the larval development of *Mithrax–Mithraculus* species, and the list of such data in pertinent Tables in the present work, the inaccuracy of most of them according to modern standards (see Clark et al., 1998) makes the comparison of relevant morphological features a difficult task.

The different species of the *Mithrax–Mithraculus* complex display uniform morphological characters (obviously excluding *Mithrax spinosissimus*), an apparent common feature among mithracid genera (Yang, 1967; Marques et al., 2003b; Santana et al., 2004), making their identification a challenging task. In the first zoeal stage, *Mithraculus sculptus* can be distinguished from *M. coryphe*, *M. forceps*, *Mithrax hispidus* and *M. verrucosus* by the number of aesthetascs of the antennule. *Mithrax pleuracanthus* do not show any significant setal differences from *Mithraculus sculptus* in the first zoea. In the second zoeal stage, *M. sculptus* differs from *Mithrax pleuracanthus*, *Mithraculus forceps* and *Mithrax verrucosus* in the number of aesthetascs of the antennule, from *Mithraculus coryphe* in the number of carapace setae, and from *Mithrax hispidus* in the number of setae of the maxillular coxal endite (Table 3). Concerning the megalopa, *Mithraculus sculptus* has unique characters that the distal segment of the antennule presents 3–4 aesthetascs and a simple setan (while *M. coryphe*, *M. forceps*, *Mithrax pleuracanthus*, *M. verrucosus* and *M. hispidus* present five aesthetascs) and the maxilla scaphognatite bears two simple setae (while *Mithraculus coryphe*, *M. forceps* and *Mithrax hispidus* present three setae, and *M. pleuracanthus* presents seven setae). Other minor differences among the species of *Mithrax–Mithraculus* complex are summarized in Table 4.

As suggested by Yang (1967) and Bolaños et al. (1990), the morphological differences between the larvae from the genera *Mithrax* and *Mithraculus* are minor. If the problematic larval descriptions of *Mithrax spinosissimus* and *M. verrucosus* are excluded, the megalopa of the genus *Mithraculus* can be distinguished from those in the genus *Mithrax* by the higher number of setae in the epipod of the first maxilliped (6 or more) and by the absence of setation on the endopod of the maxillule. However, if the larval descriptions of *M. spinosissimus* and *M. verrucosus* are considered this division is no longer valid, since the first species presents no setae on the endopod of the maxillule and the latter presents seven setae in the epipod of the first maxilliped. Only a future study addressing the redescription of these two species of larvae, according to modern standards and using laboratory cultured material, can either confirm or refute this hypothesis for the separation of *Mithrax* and *Mithraculus* megalopa. Santana et al. (2003) referred the consistent differences in the size of larvae from the genus *Mithrax* and *Mithraculus*. The larvae of *M. sculptus* fit this criterion, with the first and second zoeal stages of *Mithrax* being smaller than those of *Mithraculus*. However, the megalopa cannot be separated according to size, since the dimensions of *Mithrax hispidus* megalopa are smaller than those of *Mithraculus forceps* and *M. sculptus* (Table 1).

In conclusion, the apparent differences among the larvae of the genera *Mithrax* and *Mithraculus* are currently insufficient to support the separation of taxa into distinct genera performed by Wagner (1990), and demonstrate the importance of using larval evidence to support such studies. Future work on the *Mithrax–Mithraculus* complex must address the larval development of species whose larval morphology is still unknown or poorly described, with special emphasis on setal meristics (e.g. abdomen setation of the megalopa). Only after pooling this important data can complete phylogenetic analyses be performed and taxonomic affinities established.

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