Invertebrate Reproduction and Development, 44:1 (2003) 17–32
Balaban, Philadelphia/Rehovot
0168-8170/03/$05.00

Zoeal stages and megalopa of *Mithrax hispidus* (Herbst, 1790) (Decapoda: Brachyura: Majoidea: Mithracidae): a reappraisal of larval characters from laboratory cultured material and a review of larvae of the *Mithrax–Mithraculus* species complex

WILLIAM SANTANA[1*], GERHARD POHLE[2] and FERNANDO MARQUES[3]
[1]*Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Botucatu, São Paulo State, Brazil, 18618-000*
Tel. +55 (14) 68 02 62 68; Fax +55 (14) 68 02 60 52; email: williamsantana@terra.com.br
[2]*Huntsman Marine Science Centre, St. Andrews, New Brunswick, Canada, E5B 2L7*
[3]*Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, 05422-970 São Paulo, SP, Brazil*

Received 7 January 2003; Accepted 19 May 2003

Summary

Mithrax hispidus (Herbst, 1790) is a mithracid majoid crab occurring on sand, corals and rocks in waters of the western Atlantic. Larval development consists of two zoeal stages and a megalopa. All larval stages are described in detail based on multiple cultures. Prior to this study, larvae of *M. hispidus* were considered to be different and grouped separately from most other larvae of *Mithrax*, primarily based on setation. A detailed morphological examination, based on the same specimens used for the first description, revealed that the inclusion of *M. hispidus* in a separate group is not valid as zoeae now fully agree with the morphological characteristics defined for the other group of five *Mithrax* species, including *M. pleuracanthus*, *M. verrucosus*, *M. caribbaeus*, *M. coryphe*, and *M. forceps*. This illustrates the importance of precisely recording morphological details such as setation, which may otherwise lead to incorrect interpretations with regard to perceived taxonomic affinities. A comparison of larvae of the *Mithrax–Mithraculus* species complex does not support separation into two genera. Larval evidence supports the recently suggested adult-based synonymization of *M. caribbaeus* with *M. hispidus*.

Key words: Larval development, systematics, Majoidea, Mithracidae, *Mithrax hispidus*

Introduction

Among the Majoidea (*sensu* Martin and Davis, 2001) the family Mithracidae Balss, 1929, is represented by 17 genera, of which ten occur along the Brazilian coast. This includes the genus *Mithrax* Desmarest, 1823, *sensu lato*, comprising approximately 30 known species within the subgenera *Mithrax* and *Mithraculus* established by Rathbun (1925). Most authors follow this ranking, but others such as Wagner (1990) and Melo (1996) recognize *Mithrax* and *Mithraculus* as separate genera (*sensu stricto*). In Brazilian waters ten species of *Mithrax* (*sensu lato*) are

*Corresponding author.

recognized, including *M.* (*Mithraculus*) *coryphe* (Herbst, 1801), *M. forceps* (A. Milne Edwards, 1875), *M. sculptus* (Lamarck, 1818), *M.* (*Mithrax*) *braziliensis* Rathbun, 1892, *M. caribbaeus* Rathbun, 1920, *M. hemphilli* Rathbun, 1892, *M. tortugae* Rathbun, 1920, *M. verrucosus* H. Milne Edwards, 1832 and *M. hispidus* (Herbst, 1790).

Larval information is available for *M. spinosissimus* (cf. Provenzano and Brownell, 1977), *M. pleuracanthus* (cf. Goy et al., 1981), *M. verrucosus* (cf. Bolaños and Scelzo, 1981), *M. caribbaeus* (cf. Bolaños et al., 1990), *M. coryphe* (cf. Scotto and Gore, 1980), *M. forceps* (cf. Wilson et al., 1979) and *M. hispidus* (cf. Fransozo and Hebling, 1982). The latter five species are found in Brazilian waters (Melo, 1996), of which *M. hispidus* is the largest species, approaching a 15 cm carapace width (Williams, 1984). It seems to have a disjunct distribution near the equator with apparently separate populations in the southern and northern hemisphere of the Atlantic. North of the equator it is known from Delaware south to the Gulf of Mexico and the West Indies, while south of the equator it has only been reported in Brazilian waters from the states of Pará to São Paulo. However, if as Wagner (1990) suggests, *M. caribbaeus* and *M. pleuracanthus* are synonymous taxa, than the distribution of *M. hispidus* is continuous from the North to South Atlantic. *M. hispidus* is generally found on rough or sandy bottoms, in shallow water up to 65 m deep (Melo, 1996; Williams, 1984).

Existing larval information on *M. hispidus* (cf. Fransozo and Hebling, 1982) was to be incorporated into a study of mithracid phylogeny as part of an ongoing effort to investigate the evolution of majoid crabs based on larval characters. However, the description was found to be inadequate for this purpose, in lacking certain zoeal and megalopal characters; in needing reevaluation of other characters in light of information from additional species; and in not conforming to more recent standards of larval description (Clark et al., 1998), particularly with regard to setation. Thus the purpose of the present paper is to present a detailed description of all larval stages of *M. hispidus* and to compare them with other species within the *Mithrax–Mithraculus* species complex.

Material and Methods

The larval material used for the present study was obtained from two sources: specimens from the same hatch as used by Fransozo and Hebling (1982) and more recent material obtained from a mass culture in 2000 from São Sebastião, São Paulo State, Brazil, at a location very close to material collected by Fransozo and Hebling in 1979.

Whenever possible, a minimum of ten larval specimens was measured and at least five specimens of each stage were dissected for morphological description. Slide preparations were made using polyvinyl lactophenol mounting medium with Acid Fuchsin and/or chlorazol black stains. Measurements (±7 μm) of zoeal stages include carapace length, measured in lateral view from the base of the rostrum to the most posterior margin; the dorsal spine in lateral view from the posterior basal margin to the tip; and antenna length in lateral view from the base of the eye to the tip. For the megalopa, carapace length and width were measured in dorsal view from the small rostrum to the posterior margin, and at its widest point, respectively.

The description of setae follows Pohle and Telford (1981), but includes here only analysis by light microscopy (LM), using an Olympus BH-2 microscope with Nomarski Differential Interference Contrast and camera lucida. Setation formulae are presented progressing proximally to distally. 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). Denticulettes [*sensu* Pohle and Telford (1981)] are generally only visible by SEM but were recorded when occurring in dense clusters. Description guidelines of Clark et al. (1998) were generally followed.

The larval stages of *M. hispidus* have been deposited at the NEBECC Decapod Larval Collection, Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos, Department of Zoology IB, Universidade Estadual Paulista, Botucatu, São Paulo, Brazil, accession number NEBECCLC # 00014; larvae from mass cultures have been deposited at the Museum of Zoology, University of São Paulo, accession number MZUSP 15775.

Results

Larval development and description

Larval development of *M. hispidus* consists of two zoeal stages and one megalopa. Larval morphometrics are given in Table 1. Only morphological changes are described for the second zoea.

Description of *Mithrax hispidus* (Herbst, 1790)

First zoea (Fig. 1)

Carapace (Fig. 1A): Dorsal spine bearing minute spinules; bare rostral spine greatly reduced relative to

Table 1. Dimensions (mm) of larval structures of *Mithrax hispidus* (Herbst, 1790)

Species	Rostral spine length	Dorsal spine length	Carapace length	Carapace width	Antenna length
Zoea 1	0.16 ± 0.02 (0.14–0.20)	0.43 ± 0.01 (0.41–0.45)	0.92 ± 0.04 (0.86–1.0)	—	0.60 ± 0.01 (0.57–0.63)
Zoea 2	0.27 ± 0.03 (0.24–0.34)	0.42 ± 0.03 (0.39–0.47)	1.07 ± 0.04 (1.02–1.12)	—	0.65 ± 0.08 (0.53–0.72)
Megalopa	—	—	1.10 ± 0.18 (0.87–1.37)	0.86 ± 0.09 (0.75–1.02)	0.86 ± 0.15 (0.68–1.01)

Note: Values are given as the mean ± standard deviation, with range in parentheses.

dorsal spine, lateral spines absent. Ventral margin with densely plumose "anterior seta" (Clark et al., 1998) posterior to scaphognathite notch, followed by 3 plumose and 2 plumodenticulate 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). One 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 two long, two shorter aesthetascs, and short seta.

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

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

Maxillule (Fig. 1E): Coxal endite bearing 7 setae, 4 terminal setae, 1 plumodenticulate and 3 graded plumodenticulate; subterminally with 3 setae, 1 plumose, 2 plumodenticulate. Basial endite with 4 apical plumodenticulate cuspidate setae and 3 subterminal setae, 2 plumodenticulate and 1 plumose. Two-segmented endopod with proximal segment bearing sparsely plumodenticulate seta, distal segment bearing three pairs of plumodenticulate setae, one subapically and two apically. Exopod seta absent.

Maxilla (Fig. 1F): Coxal endite bilobed, proximal lobe with 5 setae, 4 plumose and 1 plumodenticulate; distal lobe with 4 setae, 3 plumose and 1 plumodenticulate. Basial endite bilobed, proximal and distal lobe with 5 and 4 plumodenticulate setae, respectively. Microtrichia present on both endites. Unsegmented endopod unilobed, with 5 apical plumodenticulate setae; microtrichia on lateral margin. Scaphognathite marginally with 13 densely plumose setae, including distal process.

Maxilliped 1 (Fig. 1G): Coxa with simple seta. Basis with 10 plumodenticulate setae arranged 2,2,3,3. Endopod 5-segmented with 3,2,1,2,4+1 plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 2 (Fig. 1H): Coxa naked. Basis with 3 plumodenticulate setae. Endopod 3-segmented, with 0,1,5 plumodenticulate setae of different types, 1 proximal, 2 medial, 3 apical. 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 defined.

Abdomen (Fig. 1A,J): Five somites. Somite 1 with pair of middorsal plumodenticulate setae, somites 2–5 each with pair of shorter posterolateral simple setae. Posterolaterally, somite 2 with blunt process, somites 3–5 with spines, longest on somite 5; somite 2 with pair of dorsolateral processes. Grouped denticulettes present. Pleopods absent.

Telson (Fig. 1J): Bifurcated, very shallow median arch, 3 pairs of plumodenticulate setae on inner margin; each furcal shaft proximally bearing lateral spine, furcal shafts and spines covered in rows of spinules to just below tips. Grouped denticulettes present.

Second zoea (Fig. 2)

Carapace (Fig. 2A): Eyes mobile. Two additional pairs of simple setae at base of dorsal spine, two more pairs above the eyes on frontal region. Posterolateral margin with 7–8 setae of plumose and plumodenticulate type.

Antennule (Fig. 2B): With 8 long aesthetascs and short seta; endopod bud present.

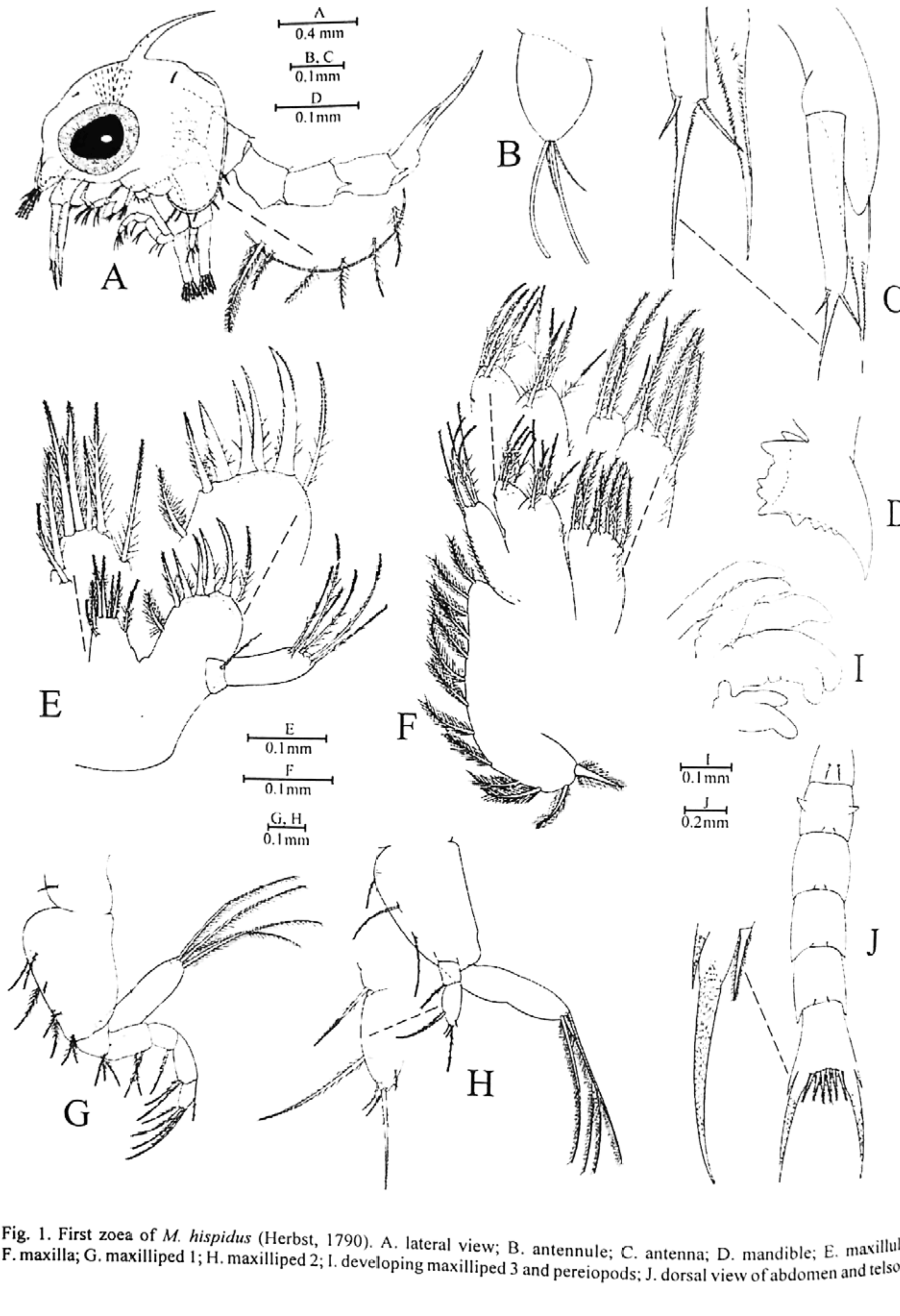

Fig. 1. First zoea of *M. hispidus* (Herbst, 1790). A. lateral view; B. antennule; C. antenna; D. mandible; E. maxillule; F. maxilla; G. maxilliped 1; H. maxilliped 2; I. developing maxilliped 3 and pereiopods; J. dorsal view of abdomen and telson.

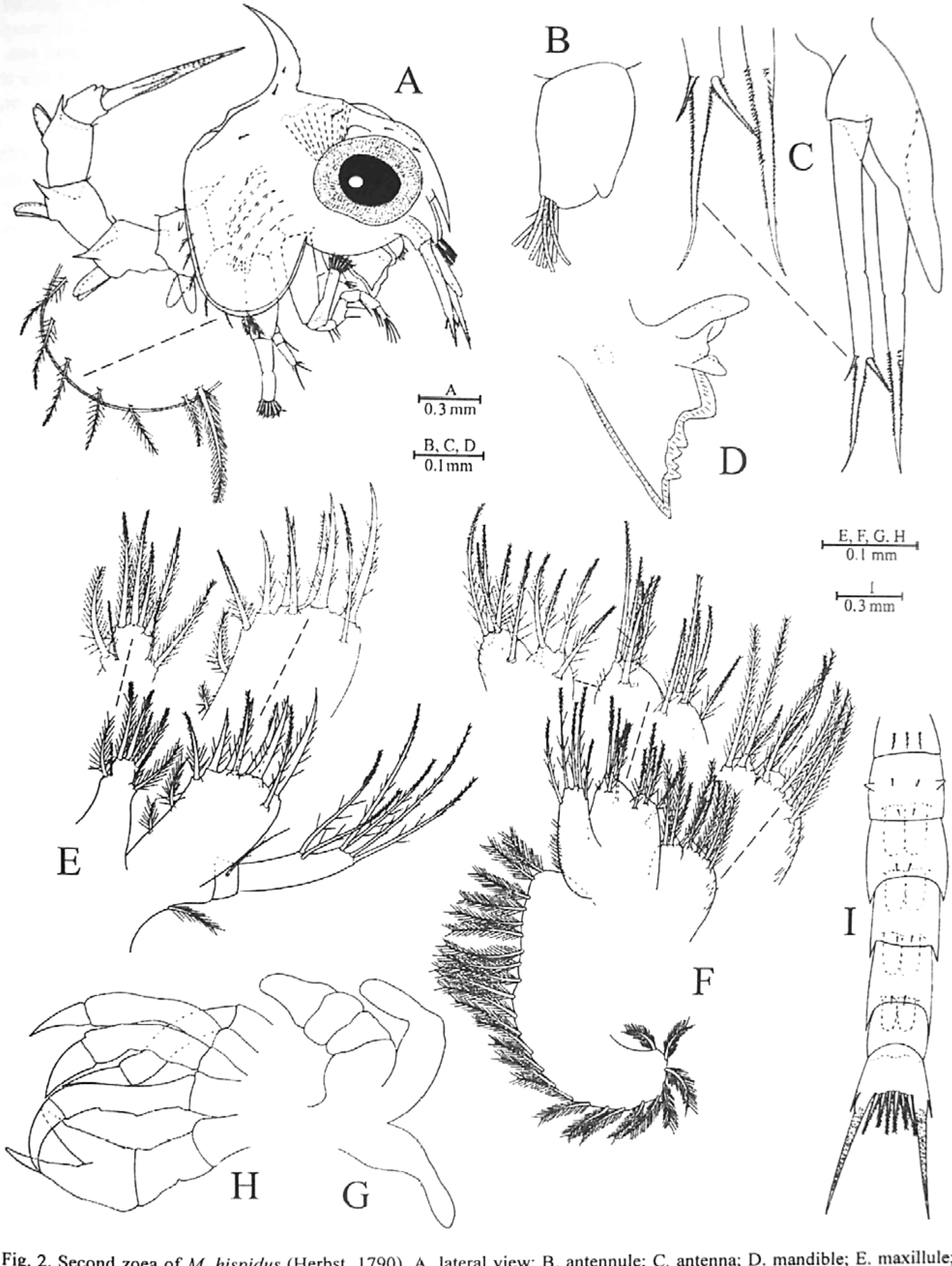

Fig. 2. Second zoea of *M. hispidus* (Herbst, 1790). A. lateral view; B. antennule; C. antenna; D. mandible; E. maxillule; F. maxilla; G. developing maxilliped 3; H. pereiopods; I. dorsal view of abdominal somites 1–6 showing ventral pleopods as stippling.

Antenna (Fig. 2C): Endopod bud lengthened, reaching to just beyond middle of protopodite.

Mandible (Fig. 2D): Palp bud present.

Maxillule (Fig. 2E): Coxal endite with additional plumodenticulate seta on distal margin. Basial endite apically with additional terminal plumodenticulate cuspidate seta and subterminal plumodenticulate seta, and additional plumose seta proximally; exopod pappose seta present.

Maxilla (Fig. 2F): Basial endite with additional plumodenticulate seta on distal lobe; proximal lobe with 4 or 5 plumodenticulate setae. Scaphognathite with 24–25 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, endopod segmentation apparent.

Pereiopods (Fig. 2H): Longer, segmentation apparent, chela distinct.

Abdomen (Fig. 2A,I): Additional sixth somite. Somite 1 with 3 dorsal plumodenticulate setae. Somite 2 with additional pair of simple setae on middorsal region; pair of unsegmented biramous pleopods on somites 2–5, endopods very small.

Megalopa (Figs. 3 and 4)

Carapace (Fig.3A): Longer than wide, narrowing anteriorly, with small rostral spine; lateral and dorsolateral ridge extending from eyes to branchial area, each with two knob-like elevations, and two additional pairs of dorsal protuberances either side of gastric area; intestinal area with blunt medial process near posterior margin. Posterolateral margin with series of four setae, surface otherwise covered with mostly simple setae as shown.

Antennule (Fig. 3B): Three-segmented peduncle with two simple setae on middle segment, 1 on distal segment; endopod with 1 subterminal and 2 terminal simple setae; 3-segmented exopod with middle segment bearing 8 aesthetascs arranged in three tiers, and distal segment with 4 basal aesthetascs and 1 aesthetasc-like apical seta.

Antenna (Fig. 3C): Segments 1–7, progressing proximally to distally, each with 1 or 3,2,3,0,0,4,3 simple setae, respectively; 3 terminal setae long. Basal segment with small exopod process.

Mandibles (Fig. 3D): Asymmetric, scoop-shaped process with cutting edge and 2-segmented palp bearing 5 plumodenticulate setae.

Maxillule (Fig. 3E): Coxal endite with 5 graded plumodenticulate, 3 plumodenticulate and 2 plumose setae, plus single basal plumodenticulate epipod seta. Basial endite distal to endopod with 13 or 15 apical plumodenticulate setae and 3 plumose setae on proximal margin. Endopod with 2 reduced setae.

Maxilla (Fig. 3F): Coxal endite proximal lobe with 1 plumodenticulate and 6–7 plumose setae, distal lobe bearing 1 plumodenticulate seta and 2 plumose setae; basial endite with 6 plumodenticulate setae on proximal lobe, 5–6 on distal lobe. Endopod reduced, indistinctly bilobed, without setae, but with microtrichia on distal lobe. Scaphognathite with 27–31 marginal plumose setae; blade with 3 simple setae.

Maxilliped 1 (Fig. 4A): Coxa with 7–8, basis bearing 10–11 plumodenticulate setae; endopod naked; exopod with pappose seta distally on proximal segment and 4 plumose setae on distal segment; epipod with 3–5 plumodenticulate setae.

Maxilliped 2 (Fig. 4B): Coxa and basis not clearly differentiated; endopod proximally without setae, carpus, propod and dactyl with 1, 2–3 and 5–6 plumodenticulate setae, respectively; exopod with naked proximal segment and 4 plumose setae on distal segment.

Maxilliped 3 (Fig. 4C): Coxa with 6–7 plumose setae, basis not differentiated; endopod proximally to distally with 12, 8–9, 5, 5 and 4 plumodenticulate and simple setae; basischium with protuberances indicative of crista dentata; bisegmented exopod with naked proximal segment, distal segment bearing 4 reduced plumose setae apically, two subterminally; epipod with 1 plumodenticulate seta proximally, 3–4 distally.

Pereiopods (Fig. 4D,E): Cheliped with mostly simple setae, except for plumose setae on coxa; pereiopods 2–5 mostly with simple setae, some serrulate setae near tip of dactyls; basischial seg-ment with distinct spine only on second pereiopod; dactyls of pereiopods 1–4 with rows of spinules as shown.

Sternum (Fig. 4F): Anterior sternal segment with 1 pair of simple setae and 2 pairs of plumodenticulate setae as shown, remaining segments naked.

Abdomen (Fig. 4G,H): Somites 1–6 proximally to distally with 2,8,6,8,8,2 simple setae dorsally and laterally; somite 1 with two additional pairs of distinct plumose setae ventrolaterally. Five pairs of pleopods; exopod of pleopods 1–5 with 11, 11, 10, 9 and 5 plumose setae, respectively; endopod of pleopods 1–4 with 2 cincinnuli each, pleopod 5, i.e., uropod, lacking endopod.

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

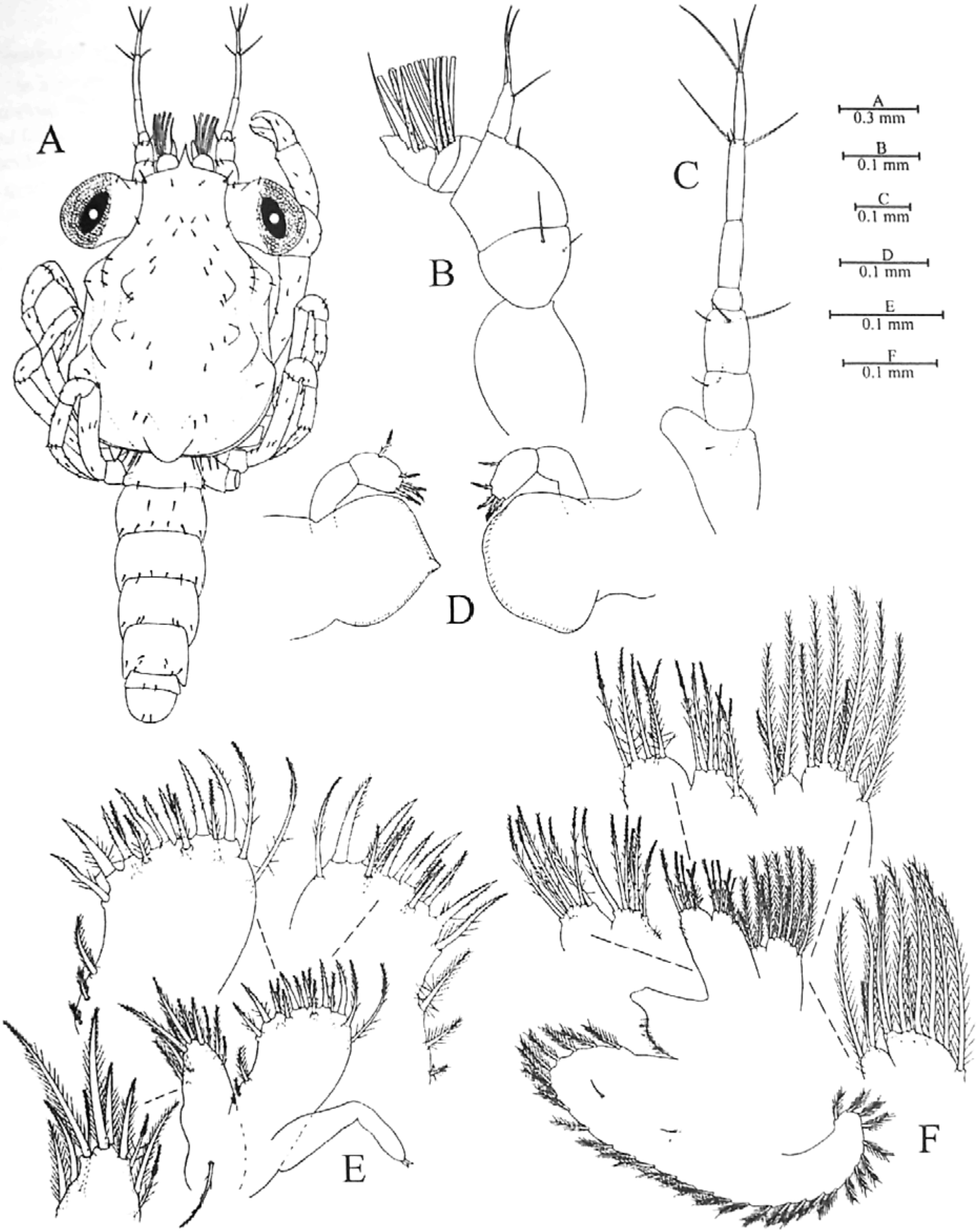

Fig. 3. Megalopa of *M. hispidus* (Herbst, 1790). A. dorsal view; B. antennule; C. antenna; D. mandible; E. maxillule; F. maxilla.

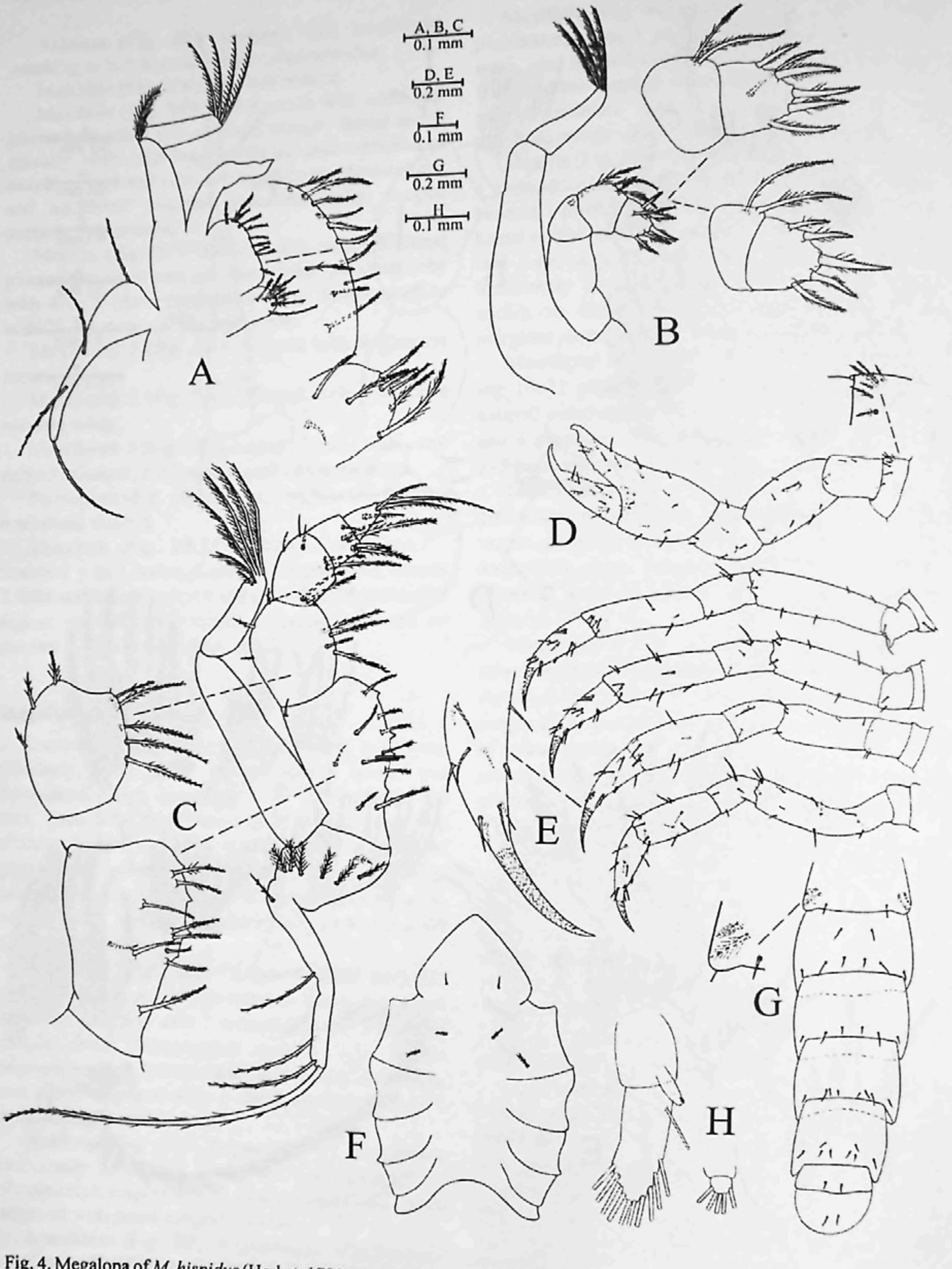

Fig. 4. Megalopa of *M. hispidus* (Herbst, 1790). A. maxilliped 1; B. maxilliped 2; C. maxilliped 3; D. cheliped; E. pereiopods; F. sternum; G. dorsal view of abdomen and telson; H. first and fifth pleopods.

Discussion

Taxonomic status and ranking

In a recent updated classification, elevating some previous majid subfamilies to the family level, Martin and Davis (2001) did not include the Plantogeridae by Števčić, (1994) nor Macrocheiridae and Oregoniidae suggested by Clark and Webber (1991). While the monophyletic status of the first two taxa may not yet be clear (Marques and Pohle, 1998), separation of the Oregoniidae as a basal group is supported based on larval evidence (Pohle and Marques, 2000) and this assemblage is also recognized as a distinct adult group (Griffin and Tranter, 1986). We therefore suggest that the Oregoniidae be included as a valid family-level taxon. The remaining families that are recognized by Martin and Davis (2001) include the Epialtidae, Inachidae, Inachoididae, Majidae, Pisidae, Tychidae and the Mithracidae. This approach is followed here.

The characters of larval stages of *M. hispidus* agree with those proposed by Rice (1980, 1983) for the Majidae, now Majoídea, in having nine or more setae on the scaphognathite in zoea I and well developed pleopods in zoea II. Also, the characters described for *M. hispidus* correspond to those shared by Group I of Mithracinae, now Mithracidae of Ingle (1979), that includes *Mithrax*, *Microphrys* and *Tiarinia*.

Comparison with previous description of **M. hispidus**

The larval description for the present study included specimens from the same hatch as used by Fransozo and Hebling (1982). A comparison shows that the older description omitted some diagnostic characters such as the setation of the carapace and abdomen, zoeal setation of the coxa of first and second maxillipeds, and the presence of the third maxilliped in zoeal stages.

In addition there are differences in the setal types, meristics and positioning between descriptions (Tables 2–4). In the first zoeal stage, setal counts differ for the antennule; coxal endite of the maxillule; coxal and basial endites and endopod of the maxilla (Table 2). For the second zoeal stage differences were found in the number of setae on the antennule, coxal endite and exopod of the maxillule, coxal and basial endites and scaphognathite of maxilla, and basis of first maxilliped (Table 3). For the megalopa stage we found differences in the number of segments and setae of the antennule and mandible, number of setae on the antenna, all endites and podites of the maxillule, maxilla, first and third maxillipeds, endopod of the second maxilliped and third pleopod (Table 4).

The differences in the number of setae on the antennule and scaphognathite may be natural intra-specific variation as this has been observed in other species (Marques et al., 2003.). However, other meristic differences on endites of the maxillule and maxilla may be errors related to problems in dissection, e.g., broken setae, slide mounting, overlapping setae, or observation. Certainly the number of setae on the maxillipeds of majoid zoeae is very consistent within a stage, and usually also between stages. Thus, we strongly suspect that in this case setae were not completely reported. The usage of an inadequate microscope may have been a contributing factor (Clark et al., 1998); thus we recommend the use of a microscope with differential interference contrast.

In the megalopa, variation in setal counts is known from the antennule, endites of maxillule, marginal setae on the scaphognathite, endopod of the third maxilliped and pleopods (Marques et al., 2003). However, the basal epipod seta on the maxillule, setae on the blade of the scaphognathite and microtrichia on maxillary endopod reported here were likely omitted by Fransozo and Hebling (1982).

Aside from setal meristics, setal types have also been widely used in differentiating species and stages of crustacean larvae (Clark et al., 1998). A wide variety of distinct setal types (Pohle and Telford, 1981) provide important diagnostic characters that are discernible with light microscopy and are applicable to a wide variety of crustaceans (Bookhout and Costlow, 1974, 1977; Shinkarenko, 1979). Surprisingly, Fransozo and Hebling (1982) described only three types of setae for larvae of *M. hispidus*, consisting of plumose, simple and aesthetasc setae. Other usually common setae, such as various types of plumodenticulate setae or pappose setae, were not recorded. The re-examination of specimens from the same hatch now makes it apparent that larvae of *M. hispidus* bear more setal types than previously reported, including plumodenticulate setae.

Comparison of **M. hispidus** *with other species of the* **Mithrax–Mithraculus** *complex*

A comparison of larvae with other species of *Mithrax* (*sensu lato*) is relevant in view of larval information now being available for seven species (Tables 2–4) and because in a recent revision, based on findings of comparative adult morphology (Wagner, 1990), *M. pleuracanthus* and *M. caribbaeus* were synonymized with *M. hispidus*. Larval information is available for all these taxa.

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

Zoea I	Carapace	Antennule	Maxillule	Maxilla	Mxpd 1	Mxpd 2	Abdomen	Telson
Mithrax hispidus Fransozo & Hebling (1982)	n/d	3+2 ae	cox: 6 pl; bas: 7 pl; end: 7 pl	cox: 5 pl, 3 pl; bas: 4 pl, 4 pl; end: 1 pl; sca: 13	cox: n/d; bas: 10 pl; end: 3,2,1,2,5 pl	bas: 3 pl; end: 0,1,5 pl	n/d	6 pl
Mithrax hispidus Present study	2 s, 2 pl, 4 pl, 2 pld	2+2 ae, 1 s	cox: 6 pld + 1 pl; bas: 6 pld + 1 pl; end: 7 pld	cox: 4 pl + 1 pld, 3 pl + 1 pld; bas: 5 pld, 4 pld; end: 5 pld; sca: 13	cox: 1 s; bas: 10 pld; end: 3,2,1,2,5 pld	bas: 3 pld; end: 0,1,5 pld	S1: 2 pld; S2–5: 2 s	6 pld
Mithrax pleuracanthus Goy et al. (1981)	4 s, 6 pl	2+1 ae, 1 s	cox: 7 pld; bas: 7 pld; end: 7 pld	cox: 5 pld, 4 pld; bas: 5 pld, 4 pld; end: 5 pld; sca: 13	cox: 1 pld; bas: 10 pld; end: 3,2,1,2,5 pld	bas: 3 s; end: 0, 1 pld, 2 pld + 3 s	S1–5: 2 s	6 pld
Mithrax caribbaeus Bolanos et al. (1990)	2 s, 2 pld, 7 pld	2+2 ae, 2 s	cox: 7 pld; bas: 7 pld; end: 2 s, 5 pld	cox: 5 pld, 4 pld; bas: 5 pld, 4 pld; end: 5 pld; sca: 13	cox: 1 s; bas: 10 pld; end: 3,2,1,2,5 pld	bas: 2 pld, 1 s; end: 0,1 pld, 1 pld + 4 s	S1–5: 2 pld	6 spr
Mithraculus forceps Wilson et al. (1979)	4 s, 6 pl?*	2+2 ae, 1 s	cox: 7 pld?*; bas: 7 pld?*; end: 7 pld?*	cox: 5 pld?*, 4 pld?*; bas: 5 pld?*, 4 pld?*; end: 5 pld?*; sca: 13	cox: 1 pld?*; bas: 10 pld?*; end: 3,2,1,2,5 pld?*	bas: 3 pld?*; end: 0,1,5 pld?*	S1–5: 2 s	6 ?
Mithraculus coryphe Scotto and Gore (1980)	4 s, 6 pl?*	2+2 ae; 1 s	cox: 7 pld?*; bas: 7 pld?*; end: 7 pld?*	cox: 5 pld?*, 4 pld?*; bas: 5 pld?*, 4 pld?*; end: 5 pld?*; sca: 13	cox: 1 pld?*; bas: 10 pld?*; end: 3,2,1,2,5 pld?*	bas: 3 pld?*; end: 0,1,5 pld?*	S1–5: 2 s	6 ?
Mithrax verrucosus Bolanos and Scelzo (1981)	3 ?	4 ae ?, 2 ?	cox: 6 ?; bas: 7 ?; end: 7 ?	cox: 5 ?, 4 ?; bas: 5 ?, 4 ?; end: 5 ?; sca: 13	cox: 1 ?; bas: 10 ?; end: 3,2,1,2,5 ?	bas: 3 ?; end: 0,1,5 ?	n/d	n/d
Mithrax spinosissimus Provenzano and Brownell (1977)	n/d	3+2 ae	cox: 5 s; bas: 6 s; end: 2 s	cox: 1 s, 1 s; bas: 3 s, 3 s; end: 1 s; sca: 30	cox: 0 *; bas: 0 *; end: 0,1,1,2,3-4 s	bas: 0 *; end: 1 or 3 s	n/d	6 pld?*

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; pl: plumose setae, s: simple setae, pld: plumodenticulate setae, pap: pappose setae, ae: aesthetascs, spr: spinulose processes, n/d: not described, ?: setal type or number not specified, *: observation from figure.

Table 3. Comparisons of larval characters of second zoeal stage for species of the *Mithrax–Mithraculus* complex (see Table 2 for abbreviations)

Zoea II	Carapace	Antennule	Maxillule	Maxilla	Mxpd 1	Mxpd 2	Abdomen
Mithrax hispidus Fransozo and Hebling (1982)	n/d	6 ae	cox: 6 pl; bas: 10 pl; end: 7 pl; exo: n/d	cox: 4-5 pl, 6 pl; bas: 5 pl, 4 pl; end: 5 pl; sca: 25-27	cox: n/d; bas: 9 pl; end: 3,2,1,2,5 pl; exo: 6 pl	bas: 3 pl; end: 0,1,5 pl; exo: 6 pl	n/d
Mithrax hispidus Present study	10-12 s; 7-8 pl+pld	8 ae; 1 s	cox: 6 pld + 2 pl; bas: 8 pld + 2 pl; end: 7 pld; exo: 1 pap	cox: 4 pl + 1 pld, 3 pl + 1 pld; bas: 4-5 pld, 5 pld; endo: 5 pld; sca: 24-25	cox: 1 s; bas: 10 pld; end: 3,2,1,2,5 pld; exo: 6 pl	bas: 3 pld; end: 0,1,5 pld; exo: 6 pl	S1: 3 pld; S2: 4 s
Mithrax pleuracanthus Goy et al. (1981)	10 s; 8 pl	7 ae; 1 s	cox: 7 pld; bas: 11 pld; end: 7 pld; exo: 1 pld ?*	cox: 5 pld, 5 pld; bas: 5 pld, 5 pld; end: 5 pld; sca: 24	cox: 1 pld; bas: 10 pld; end: 3,2,1,2,5 pld; exo: 6 pl	bas: 3 s; end: 0,1,1 s + 3 pld; exo: 6 pl	S1: 3 s; S2: 4 s
Mithrax caribbaeus Bolanos et al. (1990)	12 pld; 8 pld	8 ae; 2 s	*cox: 8 pld;* bas: 10 pld; end: 7 pld; *exo: 1 pld*	*cox: 5 pld, 4 pld;* bas: 5 pld, 5 pld; end: 5 pld; *sca: 24*	*cox: 1 s;* bas: 10 pld; end: 3,2,1,2,5 pld; *exo: 6 pl*	*bas: 2 pld, 1 s;* end: 0,1 pld, 1 pld + 4 s; exo: 6 pl	*S1: 3 pld;* S2: 4 s
Mithraculus forceps Wilson et al. (1979)	10 s?*; 7 pl?	7 ae; 1 s	cox: 7 pld?*; bas: 10 pld?*; end: 7 pld?*; exo: 1 pld?*	cox: 5 pld?*, 4 pld?*; bas: 5 pld?*, 5 pld?*; end: 5 pld?*; sca: 24	cox: 1 pld?*; bas: 10 pld?*; end: 3,2,1,2,5 pld?*; exo: 6 pl?*	bas: 3 pld?*; end: 0,1,5 pld?*; exo: 6 pl?*	S1: 3 s?; S2: 4 s?
Mithraculus coryphe Scotto and Gore (1980)	10 s?*; 7 pl?	8 ae; 1 s	cox: 7 pld?*; bas: 10 pld?*; end: 7 pld?*; exo: 1 pld?*	cox: 5 pld?*, 4 pld?*; bas: 5 pld?*, 5 pld?*; end: 5 pld?*; sca: 24	cox: 1 pld?*; bas: 10 pld?*; end: 3,2,1,2,5 pld?*; exo: 6 pl?*	bas: 3 pld?*; end: 0,1,5 pld?*; exo: 6 pl?*	S1: 3 s?; S2: 4 s?
Mithrax verrucosus Bolanos and Scelzo (1981)	6 ?	8 ae ?; 1 ?	cox: 7 ?; bas: 9 ?; end: 7 ?; exo: n/d	cox: 5 ?, 4 ?; bas: 5 ?, 5 ?; end: 5 ?; sca: 24	cox: 1 ?; bas: 10 ?; end: 3,2,1,2,5 ?; exo: 6 pl?	bas: 3 ?; end: 0,1,5 ?; exo: 6 pl?	n/d
Mithrax spinosissimus Provenzano and Brownell (1977)	n/d	3+2 ae	cox: 5 s; bas: 7 s; end: 2 s?* exo: 0 *	cox: 1 s?*, 1 s?*; bas: 2 s?*, 2 s?*; end: 2 s?*; sca: 31	cox: 0 *; bas: 0 *; end: 1,1,1,1,3-4 s?*; exo: 5-6 pl	bas: 0 *; end: 2 s; exo: 5-6 pl	n/d

Table 4. Comparisons of larval characters of megalopa stage for species of the *Mithrax–Mithraculus* complex (see Table 2 for abbreviations)

Megalopa	Antennule	Antenna	Mandible	Maxillule	Maxilla
Mithrax hispidus Fransozo and Hebling (1982)	ped: 0,0,1 s; end: 3 s; exo: 7+5 ae	seg 1-7: 0,1,2,0,0,3,3 s	palp: 6 s	cox: 7-8 pl; bas: 17-19 pl; end: 0; epi: 0	cox: 6-7 pl, 3 pl; bas: 6 pl, 8-9 pl; end: 2 pl; sca: 28-31, 0
Mithrax hispidus Present study	ped: 0,2,1 s; end: 3 s; exo: 8 ae, 5 ae	seg 1-7: 1 or 3,2,3,0,0,4,3 s	palp: 5 pld	cox: 8 pld, 2 pl; bas: 13 or 15 pld, 3 pl; end: 2 s; epi: 1 pld	cox: 6-7 pl + 1 pld, 2 pl + 1 pld; bas: 5-6 pld, 6 pld; end: 0; sca: 27-31, 3 s
Mithrax pleuracanthus Goy et al. (1981)	ped: 0,2,1 pld; end: 3 pld; exo: 8 ae + 1 pld; 5 ae	seg 1-7: 0,2,3,0,0,4,2 pld + 1 s	palp: 5 pld	cox: 10 pld; bas: 15 pld; end: 2 s; epi: 0	cox: 7 pl, 3 pl; bas: 6pld, 6 pld; end: 2 s; sca: 28-39, 7 pld ?*
Mithrax caribbaeus Bolanos et al. (1990)	ped: 0,2,1 s; end: 3 s; exo: 9 ae + 1 s; 5 ae	seg 1-7: 1,2,3,0,0,4,4 s	palp: 5 pld	cox: 10 pld; bas: 15 pld, 3; end: 2 s; epi: 1 pl	cox: 7 pld, 3 pld; bas: 6 pld, 6 pld; end: 0; sca: 32, 2 s
Mithraculus forceps Wilson et al. (1979)	ped: 0,2,1 pld?*; end: 3 pld?*; exo: 7 ae + 1 s?*; 5 ae	seg 1-7: 1,2,3,0,0,4,4 s?*	palp: 5 pld	cox: 10 pld?*; bas: 18 pld?*; end: 0; epi: 1 pld?*	cox: 7 pld?*, 3 pld?*; bas: 6 pld?*, 6 pld?*; end: 0; sca: 26-30, 3 pld?*
Mithraculus coryphe Scotto and Gore (1980)	ped: 0,2,1 pld?*; end: 3 pld?*; exo: 7 ae + 1 s?*; 5 ae	seg 1-7: 1,2,3,0,0,4,4 s?*	palp: 5 pld	cox: 10 pld?*; bas: 18 pld?*; end: 0; epi: 1 pld?*	cox: 7 pld?*, 3 pld?*; bas: 6 pld?*, 6 pld?*; end: 0; sca: 29-33, 3 pld?*
Mithrax verrucosus Bolanos and Scelzo (1981)	ped: ?; end: ?; exo: 7 ae ?; 5 ae ?	seg 1-7: ?,2,3,0,0,4,4 ?	palp: 5 ?	cox: 10 ?; bas: 17 ?; end: 2 ?; epi: 1 ?	cox: 7 ?, 3 ?; bas: 5 ?, 6 ?; end: 0; sca: 31 ?
Mithrax spinosissimus Provenzano and Brownell (1977)	ped: 0,0,1 s?*; end: 3 s?*; exo: 5 ae + 1 s?*; 4 ae*	seg 1-6: 2,2,2,0,4,3 s?*	palp: 5 s	cox: 8 s?*; bas: 12-15 s?*; end: 0; epi: 0 *	cox: 3-5 s?*, 3-5 ?*; bas: 5-6 s?*, 5-6 s?*; end: 1s?*; sca: 33-37, 0

Table 4 (continued)

Megalopa	Mxpd 1	Mxpd 2	Mxpd 3	Abdomen	Pleopods	Pereiopods
Mithrax hispidus Fransozo and Hebling (1982)	cox: 7pl; bas: 9 pl; endo: 0; exo: 1 pl, 3 pl; epi: 5 s	end: 0,0,4,5 pl; exo: 0, 4 pl	cox: 3 pl; end: 9-10, 6,4,6,4 pl; exo: 4 pl; epi: 4	n/d	P1-5: 11,11,11,9,5 pl	setae: s
Mithrax hispidus Present study	cox: 7-8 pld; bas: 10-11 pld; end: 0; exo: 1 pap, 4 pl; epi: 3-5 pld	end: 0,1,2-3,5-6 pld; exo: 0, 4 pl	cox: 6-7 pl; end: 11-12, 8-9,5,5,4 pld; exo: 6 pl; epi: 4-5 pld	S1-6: 2,8,6,8,8,2 s; S1: 4 pl	P1-5: 11,11,10,9,5 pl	setae: mostly s
Mithrax pleuracanthus Goy et al. (1981)	cox: 3 pld; bas: 10 pld; end: 1 pld, 1 s; exo: 1pld, 4 pl; epi: 4 s, 1 pld	end: 1,1,4,6 pld; exo: 0, 4 pl	cox: 10 pld; end: 12, 7,4,6,4 pld; exo: 6 pl; epi: 5	S1-6: 2,4,4,4,4,2 s; S1: 0 pl	P1-5: 11,11,10,9,5 pl	setae: pld
Mithrax caribbaeus Bolanos et al. (1990)	cox: 8 pld; bas: 11 pld; end: 0; exo: 1 pl, 4 pl; epi: 7 pld	end: 0,1,3,6 pld; exo: 0, 4 pl	cox: 7 pld; end: 12, 9,5,6,4 pld; exo: 6 pl; epi: 5 pld	S1-6: 2,8,6,8,8,2 s; S1: 4 pl	P1-5: 11,11,11,9,5 pl	setae: mostly s
Mithraculus forceps Wilson et al. (1979)	cox: 5-7 pld?*; bas: 9-11 pld?*; end: 0; exo: 1 pl?*, 4 pl?*; epi: 6 pld?*	end: 0,1,3,6 pld?*; exo: 0, 4 pl?*	cox: 5-7 pld?*; end: 12, 9,5,4-6,3-4 pld?*; exo: 6 pl?*; epi: 5-6 pld?*	?	P1-5: 11,11,11,9,5 pl?*	setae: pld?*
Mithraculus coryphe Scotto and Gore (1980)	cox: 5-7 pld?*; bas: 9-11 pld?*; end: 0; exo: 1 pl?*, 4 pl?*; epi: 6-7 pld?*	end: 0,1,3,6 pld?*; exo: 0, 4 pl?*	cox: 5-7 pld?*; end: 12, 9,5,4-6,3-4 pld?*; exo: 6 pl?*; epi: 4-6 pld?*	?	P1-5: 11,11,11,9,5 pl?*	setae: pld?*
Mithrax verrucosus Bolanos and Scelzo (1981)	cox: 7 ?; bas: 10 ?; end: 2 ?; exo: 1 ?, 5 ?; epi: 7 ?	end: 0,1,3,6 ?; exo: 0, 4 ?	cox: 6 ?; end: 10,7,5,5,4 ?; exo: 6 ?; epi: 4 ?	n/d	P1-5: 11,11,11,9,5 ?	n/d
Mithrax spinosissimus Provenzano and Brownell (1977)	cox: 8 s?*; bas: 8 s?*; end: 0; exo: 0 *, 4-6 pl; epi: 4 s?*	end: 0,1,3,6 s?*; exo: 0, 4-6 pl	cox: 4 pld?*; end: 12, 5,5,3,4 pld?*; exo: 4 pl; epi: 4-6 s?*	n/d	P1-5: 9-10,11,10-11,9,5-6 pl?*	setae: s?*

Based on available data (Provenzano and Brownel, 1977) larvae of *M. spinosissimus* are very different from other species of *Mithrax*. However, aspects of the description relating to reduction in setation and segmentation, e.g. maxillipeds and maxilla, are suspect, as discussed below. Thus, no detailed comparison is made here with that species. Similarly, the incomplete description of *M. verrucosus* larvae, in an abstract (Bolaños and Scelzo, 1981) and later as part of another species description (Bolaños et al., 1990), is also not suitable for comparative purposes. We believe that further examination of larvae of these two species is necessary before undertaking a comparison. Thus, while available data are listed in pertinent tables, we excluded these two species from the comparison. Furthermore, a detailed examination of differences in setal types was not undertaken due to incomplete pertinent descriptions in other species, including *M. forceps* (Wilson et al., 1979) and *M. coryphe* (Scotto and Gore, 1980).

Zoeal stages of the different species of *Mithrax* (*sensu lato*), with the exception of *M. spinosissimus*, have remarkably uniform morphological characters, as is apparently the case for many mithracid genera (Yang, 1967; Wilson et al., 1979). This makes it difficult to identify the larvae of these species. The only interspecific differences in the first zoeal stage are setal meristics on the posterolateral margin of the carapace and antennule of *M. caribbaeus* and the number of aesthetascs in *M. pleuracanthus* (Table 2). In the second zoeal stage, *M. caribbaeus* differs in the number of setae on the antennule; *M. pleuracanthus* in the number of aesthetascs, setae on coxal and basial endites of the maxillule, distal coxal endite of maxilla and endopod of second maxilliped; *M. forceps* in the number of aesthetascs, and *M. coryphe* and *M. forceps* in the coxal setation of the maxillule (Table 3).

There are more differences between species in the megalopa. *Mithrax caribbaeus* differs in the number of setae on the antennule, fifth segment of antenna, scaphognathite, epipod of first maxilliped, forth segment of third maxilliped and third pleopod (Table 4). In *M. pleuracanthus* there are meristic setal differences on the antennule, first segment of antenna, basial endite and epipod of maxillule, scaphognathite, coxa and endopod of first maxilliped, endopod of second maxilliped, coxa and merus of third maxilliped and on the abdomen (Table 4). Both *M. forceps* and *M. coryphe* differ in the setation of the antennule, fifth segment of antenna, endopod of maxillule, coxal endite and epipod of first maxilliped and third pleopod. There possibly is a difference between the latter two species in abdominal setation (Table 4).

This comparison shows that the morphological differences between larvae of *Mithrax* and *Mithraculus* (*sensu stricto*) are very small, as also observed by Yang (1967) and Bolaños et al. (1990). Tables 2 and 3 show that zoeal stages of *M. hispidus* resemble more those of *M. coryphe*, *M. forceps* and *M. caribbaeus* than to those of *M. pleuracanthus*. Similarly, the megalopa of *M. pleuracanthus* differs more from *M. hispidus* than other species (Table 4). Unfortunately, information on an important differentiating character relating to abdominal setation of the megalopa is not available for *Mithraculus* (Table 4). However, it is clear that larval characters do not support the separation of taxa into two distinct genera, as suggested by Wagner (1990) based on adult morphology. This reaffirms the importance of including larval evidence when reevaluating the status of these two genera (Wilson et al., 1979; Goy et al., 1981; Bolaños et al., 1990). The only consistent difference is in relative size, larvae of *M. forceps* and *M. coryphe* being relatively smaller than those of *Mithrax* (Table 5). However, this is not a justification for partitioning into separate genera.

In his recent revision based on adult morphology, Wagner (1990) also concluded that *M. pleuracanthus* and *M. caribbaeus* are synonyms with *M. hispidus*. Larval evidence agrees in *M. caribbaeus* being very similar to *M. hispidus*. In the megalopa (Table 4), there are only small differences in setal meristics such as on the antennule, scaphognathite and pleopds. These are known to be intraspecifically variable and may therefore represent natural variation. However, the megalopa of *M. pleuracanthus* presents more significant differences in comparison with *M. hispidus*, including setation of the basial endite of the maxillule, endopod of first maxilliped and particularly the abdomen (Table 4). Relative size of larvae (Table 5) indicates *M. hispidus* and *M. caribbaeus* are nearly identical while the megalopa of *M. pleuracanthus* is larger. Thus, while there seems to be justification in synonymyzing *M. hispidus* with *M. caribbaeus*, larval evidence does not support the same for *M. pleuracanthus*, as suggested by Wagner (1990). However, distinguishing characters of *M. pleuracanthus* should be verified in view of our findings.

Taxonomic grouping

Setal meristics and morphometrics of *M. hispidus* zoeae, as reported by Fransozo and Hebling (1982), differed extensively from most other species of *Mithrax*. In a review of the larvae of seven species of

Table 5. Comparison of carapace length in larval stages of the *Mithrax–Mithraculus* species complex

Carapace length	Zoea 1	Zoea 2	Megalopa
Mithrax hispidus	0.92 (0.86–1.0)	1.07 (1.02–1.12)	1.10 (0.87–1.37)
Mithrax caribbaeus	0.96 (0.87–1.10)	1.04 (0.96–1.18)	1.12 (0.90–1.29)
Mithrax pleuracanthus	0.96 (0.93–0.98)	1.10 (0.99–1.20)	1.40 (1.30–1.50)
Mithraculus forceps	0.67	0.83	1.15
Mithraculus coryphe	0.70	0.82	1.06
Mithrax spinosissimus	1.10 (1.0–1.20)	1.15 (1.10–1.20)	1.30 (1.20–1.50)

Note: Values are given in mean with range in parentheses.

Mithrax, Bolaños et al. (1990) noted that *M. caribbaeus*, *M. verrucosus*, *M. pleuracanthus*, *M. forceps* and *M. coryphe* all share the following characteristics: carapace with 3–7 marginal setae in zoea I, 6–8 in zoea II; antennule with 3–4 aesthetascs in zoea I, 7–8 in zoea II; antenna exopod as long or longer than protopod in zoea I and II; maxillule coxal endite with 7–8 setae in zoea II; maxilla of zoea I coxal and basial endites each with 5 and 4 setae on proximal and distal endite, respectively, endopodite with 5 setae, scaphognathite 13 setae.

These combined similarities, at that time apparently not shared with *M. hispidus,* have led Bolaños et al. (1990) to separate the latter species into a second group together with *M. spinosissimus*. However, as shown in Tables 1 and 2, our detailed re-examination of *M. hispidus* reveals that the inclusion of that species in the latter group is likely not valid since *M. hispidus* zoeae now agree with the first group of five *Mithrax* species in all of the characteristics listed by Bolaños et al. (1990). The suspicion of Bolaños et al. (1990) that larvae of *M. hispidus* may be incompletely or incorrectly described is thus validated. In light of these findings we agree with Bolaños et al. (1990) and Rice (1980) that larvae of *M. spinossisimus* should also be re-examined. This illustrates the importance of precisely recording morphological details such as setation, which may otherwise lead to incorrect interpretations with regard to perceived taxonomic affinities, and certainly will result in incorrect character coding for phylogenetic analyses.

Acknowledgments

This work was supported through research grant A2313 to G. Pohle, from the Natural Sciences and Engineering Research Council, Canada; by grant JP 99/10407-1 and 99/08256-5 to F. Marques by the Fundação de Amparo à Pesquisa do Estado de São Paulo, State Government of São Paulo; and by fellowship 132962/2001-2 to William Santana by the CNPq (Conselho Nacional de Desenvolvimento Científico), Federal Government, Brazil. We thank Adilson Fransozo and Maria Lucia Negreiros-Fransozo (Universidade Estadual Paulista, Brazil) for making specimens of *Mithrax hispidus* available to us.

References

Balss, H., Decapoden des Roten Meeres. IV. Oxyrhyncha und Schlussbetrachtungen. (Expedition S.M. Schiff "Pola" in das Rote Meer. Zool. Ergeb. 36) Denkschr. Akad. der Wiss. Wien, Math.-Nat. Kl., 102 (1929) 1–30.

Bolaños, J.A., Lares, L.B. and Hernández, J.E., Desarrolo larval de *Mithrax caribbaeus* Rathbun, 1920 (Crustacea: Decapoda: Majidae) realizado en condiciones de laboratorio. Bol. Inst. Ocean. Venezuela, Universidad de Oriente, 29 (1990) 67–89.

Bolaños, J.A. and Scelzo, M.A., Larval development of the spider crab *Mithrax verrucosus* Milne Edwards, reared in the laboratory (Decapoda: Brachyura: Majidae). Am. Zool., 21 (1981) 989.

Bookhout, C.G. and Costlow Jr., J.D., Larval development of *Portunus spinicarpus* reared in the laboratory. Bull. Mar. Sci., 24 (1974) 20–51.

Bookhout, C.G. and Costlow Jr., J.D., Larval development of *Callinectes similis* reared in the laboratory. Bull. Mar. Sci., 27 (1977) 704–728.

Clark, P.F., De Calazans, D. and Pohle, G., Accuracy and standardization of brachyuran larval descriptions. Invert. Reprod. Develop., 33 (1998) 127–144.

Clark, P.F. and Webber, W.R., A redescription of *Macrocheira kaempferi* (Temminck, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura). J. Nat. Hist., 25 (1991) 1259–1279.

Desmarest, A.G., Malacostracés. In: Dictionnaire des Sciences Naturelles, Vol. 28, Paris, 1823, pp. 138–425.

Fransozo, A. and Hebling, N.J., Desenvolvimento pós-embrionário de *Mithrax hispidus* (Herbst, 1790) (Decapoda, Majidae) em laboratório. Ciên. Cult., 34(3) (1982) 385–395.

Goy, J.W., Bookhout, G. and Costlow, J., Larval development of the spider crab *Mithrax pleuracanthus* Stimpson reared in the laboratory (Decapoda: Brachyura: Majidae). J. Crust. Biol., 1(1) (1981) 51–62.

Griffin, D.J.G. and Tranter, H.A., The Decapoda Brachyura of the Siboga Expedition, Part VIII, Majidae. Siboga Expedite, Leiden (Monograph) 29, C4, Livraison 148, 1986.

Herbst, J.F.W., Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Berlin und Stralsund, Vol.1 (1782–1790), Vol. 2 (1791–1796), Vol. 3 (1799–1804).

Ingle, R.W., The larval development of the spider crab *Rochinia carpenteri* (Thomson) (Oxyrhyncha: Majidae) with a review of the majid subfamilial larval features. Bull. Br. Mus. Nat. Hist. (Zool.), 37 (1979) 47–66.

Lamark, J.B.P.A de M., Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leurs distributions, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent, précédee d'une introduction offrante la détermination des caractères essentiels de l'animal, sa distinction de végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie, Vol. 5, Paris, 1818.

Marques, F. and Pohle, G., The use of structural reduction in phylogenetic reconstruction of decapods and a phylogenetic hypothesis for fifteen genera of Majidae: testing previous hypotheses and assumptions. Invert. Reprod. Develop., 33 (1998) 241–262.

Marques, F.P.L., Pohle, G.W. and Vrbova, L., On the larval stages of *Macrocoeloma diplacanthum* (Stimpson, 1860) (Decapoda: Brachyura: Majidae), and a review of mithracine phylogenetic aspects. J. Crust. Biol., 23 (2003) 187–200.

Martin, J.W. and Davis, G.E., An updated classification of the recent Crustacea. Science series. Nat. Hist. Museum LA County, 39 (2001) 1–124.

Martin, J.W. and Laverack, M.S., On the distribution of the crustacean dorsal organ. Acta Zool., 73(5) (1992) 357–368.

Melo, G.A.S., Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. Editora Plêiade/ Fundação de Amparo à Pesquisa do Estado de São Paulo, São Paulo, Brazil, 1996.

Milne-Edwards, A., Études sur les Crustacés Podophthalmaries de la région méxicaine. In: Mission Scientifique du Mexique et dans l'Amerique Centrale. Recherches zoologiques pour servir a l'histoire de la faune de l'Amerique Centrale et du Mexique. Ministère de l'Instruction Publique, Vol. 5, Paris, 1875, pp. 57–120.

Milne-Edwards, H., Observations sur les crustacés du genre *Mithrax*. Mag. Zool., 2 (1832) 1–16.

Pohle, G.W. and Marques, F.P.L., Larval stages of *Paradasygyius depressus* (Bell, 1835) (Brachyura: Majidae) and a phylogenetic hypothesis for 21 genera of Majidae. Proc. Biol. Soc. Wash., 113(3) (2000) 739–760.

Pohle, G. and Telford, M., Morphology and classification of decapod crustacean larval setae: a scanning electron microscope study of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae). Bull. Mar. Sci., 31 (1981) 736–752.

Provenzano, A.J. and Brownell, W.N., Larval and early postlarval stages of the West Indian spider crab *Mithrax spinossisimus* (Lamarck) (Decapoda: Majidae). Proc. Biol. Soc. Wash., 90 (1977) 735–752.

Rathbun, M.J., Catalogue of the crabs of the family Periceridae in the U.S. National Museum. Proc. US Natl. Mus., 15 (1892) 231–277.

Rathbun, M.J., New species of spider crabs from the Straits of Florida and Caribbean Sea. Proc. Biol. Soc. Wash., 33 (1920) 23–24.

Rathbun, M.J., The spider crabs of America. US Natl. Mus. Bull., 129 (1925) 1–613 + pls. 1–283.

Rice, A.L., Crab zoeal morphology and its bearing on the classification of the Brachyura. Trans. Zool. Soc. Lond., 35 (1980) 271–424.

Rice, A.L., Zoeal evidence for brachyuran phylogeny. In: F.R. Schram (ed.), Crustacean Phylogeny, Crustacean Issues, Vol. 1, A.A. Balkema, Rotterdam, 1983, pp. 313–329.

Scotto, L.E. and Gore, R.H., Larval development under laboratory conditions of the tropical spider crab *Mithrax* (*Mithraculus*) *coryphe* (Herbst, 1801) (Brachyura: Majidae). Proc. Biol. Soc. Wash., 93 (1980) 551–562.

Shinkarenko, L., Development of the larval stages of the blue swimming crab, *Portunus pelagicus* Lamarck (Portunidae: Decapoda: Crustacea). Aust. J. Mar. Freshw. Res., 30 (1979) 485–503.

Števčić, Z., Contribution to the re-classification for the family Majidae. Periodicum Biologorum, 96 (1994) 419–420.

Wagner, H.P., The genera *Mithrax* Latreille, 1818 and *Mithraculus* Withe, 1847 (Crustacea: Brachyura: Majidae) in the western Atlantic Ocean. Zool. Verh. Leiden, 264 (1990) 1–65.

Williams, A.B., Shrimps, lobsters and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institute, Washington, DC, 1984.

Wilson, K.A., Scotto, L.E. and Gore, R.H., Studies on decapod Crustacea from the Indian River region of Florida. XIII. Larval development under laboratory conditions of the spider crab *Mithrax forceps* (A. Milne Edwards, 1875) (Brachyura: Majidae). Proc. Biol. Soc. Wash., 92 (1979) 307–327.

Yang, W.T., A study of zeal, megalopal, and early crab stages of some oxyrhynchus crabs (Crustacea: Decapoda). PhD Dissertation, University of Miami, 1967.