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MICROPHRYS BICORNUTUS (LATREILLE, 1825): THE COMPLETE LARVAL DEVELOPMENT UNDER LABORATORY CONDITIONS WITH NOTES ON OTHER MITHRACINE LARVAE (DECAPODA: BRACHYURA: MAJIDAE)

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ABSTRACT

The complete larval development, consisting of two zoeal stages and a megalopa, and the first crab stage is described for the shallow-water western Atlantic spider crab *Microphrys bicornutus*. Data from laboratory cultures indicate that the species can complete its planktonic development in less than a week, and is able to attain first crab stage in as few as 10 days. The zoeal stages of *M. bicornutus* show a great many similarities to known zoeae in other genera within the subfamily Mithracinae, including species of the American genus *Mithrax*, and to *Macrocoeloma*, and to a lesser extent the Indo-West Pacific genera *Tiarinia* and *Micippa*. Morphological features shared among both the zoeal and megalopal stages of the various mithracine genera are compared, and phylogenetic relationships within *Microphrys*, *Mithrax*, and *Macrocoeloma* are proposed.

Microphrys bicornutus is a small (*ca.* 30–40 mm carapace width, cw) intertidal and shallow subtidal spider crab in the subfamily Mithracinae, which occurs from Bermuda and North Carolina, southward to Brazil (Williams, 1965; Markham and McDermott, 1981). The species is ovigerous throughout the year over a large part of its range, but in spite of its abundance and the ease of its collection there has been no complete study published on the larval development of this crab. Lebour (1944) gave an abbreviated description and illustration of 2 zoeal stages from Bermuda, and Hartnoll (1964) provided an expanded description and illustration of the prezoea and 2 zoeal stages from Jamaica. Neither author's study is sufficiently detailed to allow meaningful comparison with larval stages of other mithracine crabs. Ironically, the complete larval development had been worked out for *Microphrys bicornutus* by Yang (1967), but the study forms part of a voluminous dissertation which is not readily available, and has remained unpublished. Inasmuch as several discrepancies in description and illustrations occur between the publications of Lebour and Hartnoll and that of Yang, we recultured the larvae of *M. bicornutus* and compared our material with the detailed study provided by Yang. In this paper we redescribe and illustrate the zoeal, megalopal, and first crab stage of *M. bicornutus*. We compare the larvae of this species with those known from other genera and species in the Mithracinae, pointing out possible relationships among them.

Methodology and Rearing Experiment Results

An ovigerous female crab was collected from near Bodden Town, Grand Cayman Island, on 15 July 1980. The specimen was returned to the laboratory at Fort Pierce, and maintained in a 19 cm diameter bowl with nonflowing seawater (34‰ salinity) until hatching occurred on 17 July. A total of 96 larvae were cultured at 20° and 25°C in controlled temperature units using methodology described by Gore (1968). Measurements follow those proposed by Yang (1967) and are the arithmetic means for the number of specimens examined. Specimens and/or molts of the two zoeal stages are deposited in the National Museum of Natural History,

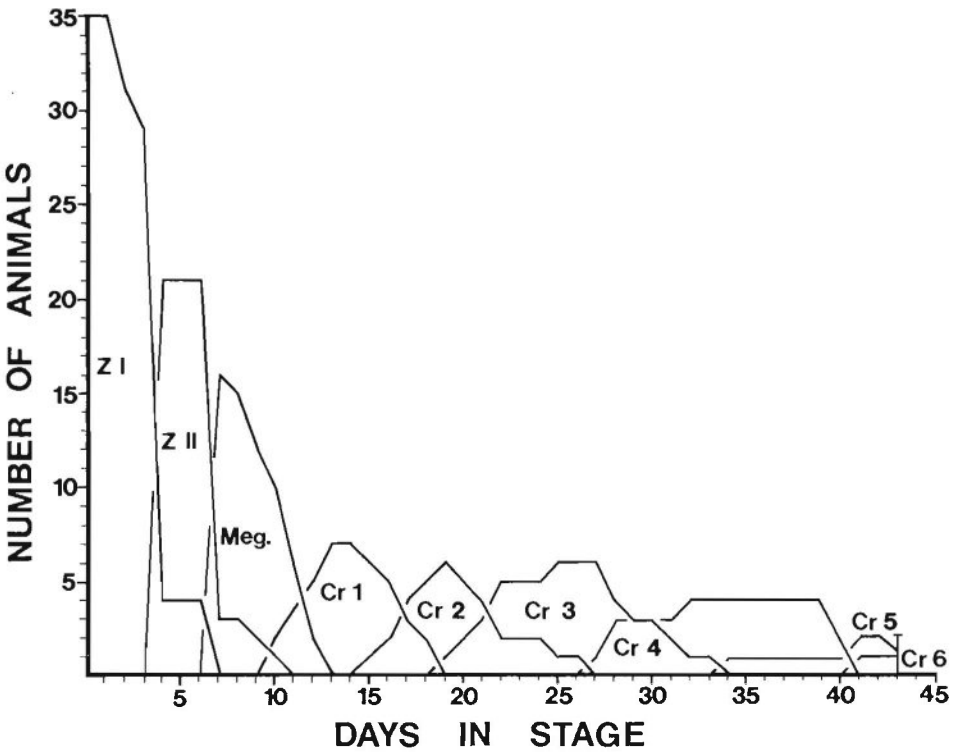

Fig. 1. Number of animals and stage duration of *Microphrys bicornutus* reared at 25°C. (After Yang, 1967.)

Washington, D.C., (USNM 190705), the British Museum (Natural History), London (1982-136), and the Indian River Coastal Zone Museum, Fort Pierce, Florida (IRCZM 89-5223).

As noted by Hartnoll (1964), *Microphrys bicornutus* possesses one prezoeal and two zoeal stages. Data from this study, and previous studies by Yang (1967), show that a single megalopal stage occurs approximately 1 week after hatching.

Zoeae usually lasted 3, rarely 4, days in stage I at 25°C, and from 5–6 days at 20°C before molting to stage II. The sole megalopal stage in this study was obtained after 3 days in stage II at 25°C; other larvae that survived for longer than 3 days died without molting. In this study we used *Artemia* nauplii as food, but the zoeae may not have fed very well on this, a fact also noted by Hartnoll (1964) in his attempt to rear *M. bicornutus*. However, Yang (1967) also used newly hatched *Artemia* nauplii and was considerably more successful in his culture experiment, obtaining sixth crab stage before terminating his study (Fig. 1). In Yang's program at 25°C, both first and second stages required a minimum of 3 days, and the megalopal stage lasted at least 4 days before attaining first crab stage. Results from these 2 culture programs suggest that *Microphrys bicornutus* is able to complete its planktonic development in as few as 10 days. The survival curve illustrated in Fig. 1 is similar to others obtained for majid crabs in laboratory culture (see e.g., Yang, 1967; Wilson *et al.*, 1979; Scotto and Gore, 1980). In Yang's study approximately 60% of first stage larvae reached stage II, and nearly

50% of the initial population developed to megalopa, a stage with a mean duration of 5 days. Greatest mortality occurred either in stage I or megalopa, a situation similar to that observed in our study. Crab stages showed enhanced survival, and lasted varying lengths of time from 4–11 days within each instar (Yang, 1967). Yang stated that lowering of water temperatures immediately prior to hatching would at least prolong the prezoeal stage, suggesting that Hartnoll's (1964) observation of lengthy prezoeal development might have been a consequence of lower water temperatures. On the other hand, we tend to agree with Hartnoll's statement that most *Artemia* nauplii are simply too large a food item for the rather small first zoeae of *M. bicornutus* (carapace length, cl 0.66–0.75 mm). Yang's successful culturing of this species is apparently a result of obtaining newly hatched *Artemia* filtered through a stainless steel sieve (105 × 105 mesh, 0.003 wire) thus producing a food item more easily ingested by the majid zoeae.

Description of Zoeal, Megalopa, and First Crab Stages

The following description is based primarily on larvae cultured from the ovigerous female collected at Grand Cayman Island. Descriptive text and illustrations of these zoeae and megalopae were compared with those provided by Yang (1967) from specimens cultured from females collected in Biscayne Bay, Florida. Important variation is noted under the appropriate appendage description. The description and illustration of the first crab stage is rewritten from that of Yang (1967). All setal formulas in the following descriptions progress proximally to distally unless otherwise stated.

First Zoea

Carapace length, 0.66 mm; 5 specimens examined.

Carapace (Fig. 2A).—Cephalothorax smooth, globose, with short ventrally directed rostrum, posteriorly curved dorsal spine, median dorsal tubercle; pair of minute setae posterior to tubercle, second pair posterolateral to dorsal spine; posteroventral border with 6 setae, first stoutest (=anterior seta); pterygostomial region produced as bluntly rounded tooth; frontal organ on eyestalk extremely minute (often indiscernible in preserved specimens); eyes sessile.

Abdomen (Fig. 2A, B).—Five somites; first with 2 dorsomedial setae; second with 2 posterodorsal setae, 2 lateral anteriorly curved knobs; third to fifth with 2 posterodorsal setae plus pair of short posteroventral spines.

Telson (Fig. 2A, B, b).—Trapezoidal; elongate furcae covered with fine hairs, pair of movable lateral spines; posterior margin bearing 6 spines armed with spinules.

Antennule (Fig. 2C).—Conical rod, 2 long, stout, 2 short, thinner aesthetascs plus 1 hair (3 aesthetascs, Yang, 1967).

Antenna (Fig. 2D).—Protopodite an elongate tapered process armed with 2 rows of spinules; exopodite similar in form, equal to or slightly longer than protopodite with 2 rows of spinules on distal one-third, 1 naked seta and 1 serrate spine at base of spinules; endopodite bud one-third length of protopodite.

Mandibles (Fig. 2E).—Asymmetrically scoop-shaped, dentate processes; left with 3 bluntly rounded teeth on posterior margin, right with 1 tooth; incisor margins evenly and bluntly dentate; molar processes irregularly dentate.

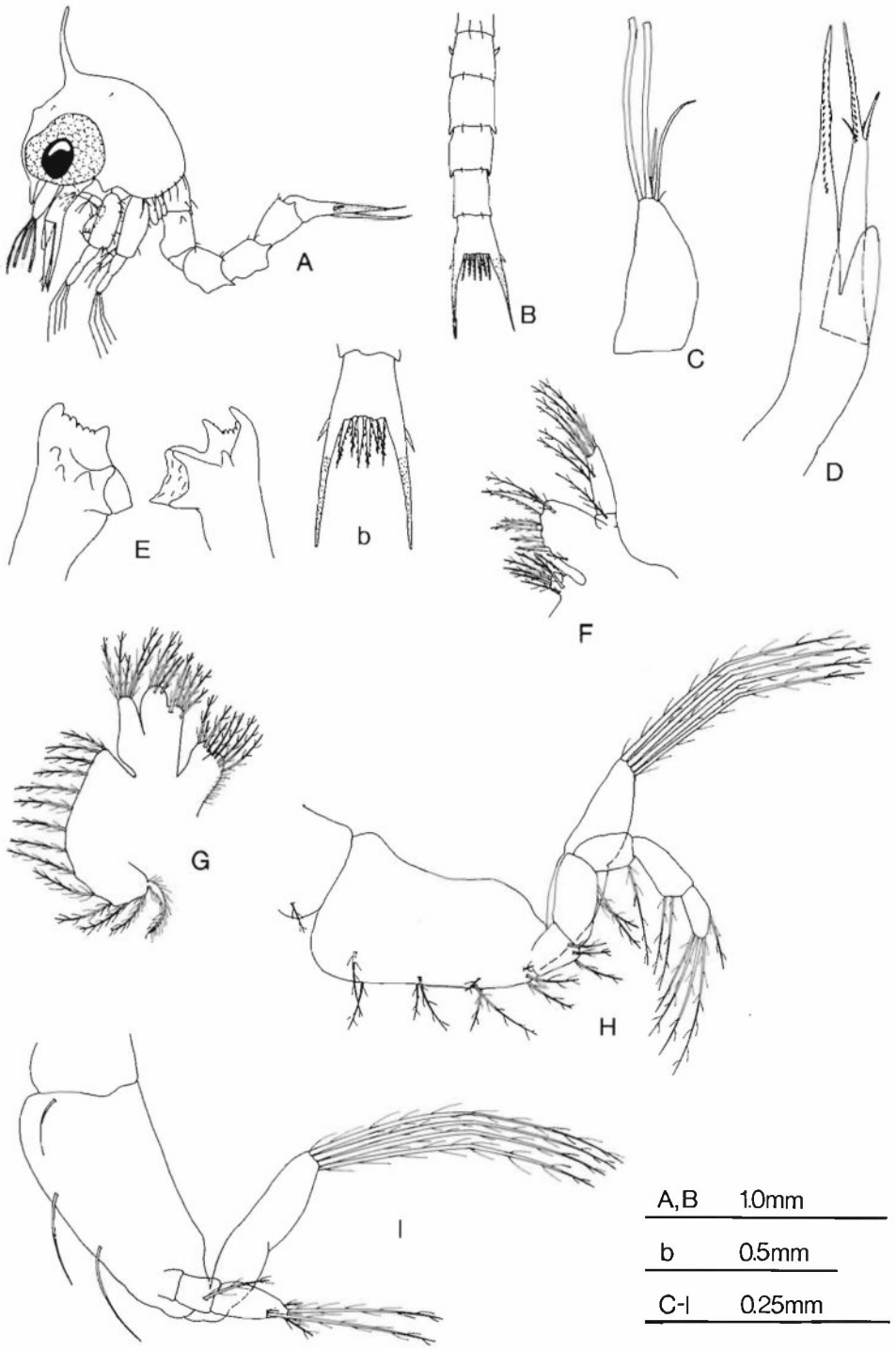

Fig. 2. *Microphrys bicornutus,* first zoea: A, Lateral view; B, Abdomen; b, Telson; C, Antennule; D, Antenna; E, Mandibles; F, Maxillule; G, Maxilla; H, Maxilliped 1; I, Maxilliped 2.

Maxillule (Fig. 2F).—Endopodite 2-segmented, short proximal article with 1 seta, longer distal article with 2 subterminal, 4 terminal setae; basal endite bearing 5 spines, 2 setae; coxal endite with 7 processes.

Maxilla (Fig. 2G).—Unilobate endopodite with 5 setae; bilobed basal and coxal endites each with 5, 4 processes progressing distally; scaphognathite bearing 12 or 13 thin, plus 1 stout, apical plumose setae; pubescence as illustrated.

Maxilliped 1 (Fig. 2H).—Coxopodite with 1 seta; basipodite ventral setae 2,2,3,3; endopodite 5-segmented, 3,2,1,2,4 + I (Roman numeral denoting dorsal seta); exopodite with 4 natatory setae.

Maxilliped 2 (Fig. 2I).—Coxopodite naked; basipodite with 3 naked ventral setae; endopodite 3-segmented 0,1,5 setae (2 long, 1 medium, 2 very short); exopodite with 4 natatory setae.

Color.—Carapace, basipodites of first and second maxillipeds, and abdomen, lime green. Single melanophore on mandibles, basipodites of first and second maxillipeds, paired melanophores distoventrally on abdominal somites 2–5. Gastric region and intestine to abdominal somite 3 shaded with black. Orange rose chromatophore above eyes, on surface of carapace at posteroventral angle, at base of antenna, on proximal portion of basipodite of maxilliped 2, and on distoventral margins of somites 3–5.

Second Zoea

Carapace length, 0.82 mm; 5 specimens examined.

Carapace (Fig. 3A).—Cephalothorax inflated; rostrum elongate; additional setae as follows, 2 pairs anterolateral to dorsal protuberance, 1 pair at base of dorsal spine, single seta on posteroventral border; buds of pereopods and gills well developed; eyes stalked, minute frontal organ on peduncle.

Abdomen (Fig. 3A, B, b).—Six somites; first with 3 dorsomedial setae, second now with additional pair of setae dorsomedially, sixth naked; otherwise as in stage I; unsegmented pleopods with exopod buds on somites 2–5, uropod buds on sixth somite.

Telson (Fig. 3A, B, b).—Similar in form and setation to first stage.

Antennule (Fig. 3C).—Endopodal bud present; 7 unequal aesthetascs, plus 1 hair terminally.

Antenna (Fig. 3D).—Similar in form and armature to first stage; endopodal bud now one-half length of protopodite.

Mandibles (Fig. 3E).—Palp bud present on anterior surface of each.

Maxillule (Fig. 3F).—Endopodite and coxal endite setation unchanged; basal endite with 10 processes plus plumose basal seta.

Maxilla (Fig. 3G).—Endopodite and coxal endites unchanged; basal endites with 5, 5 processes; scaphognathite with 23–25 plumose setae.

Maxillipeds 1 and 2 (Fig. 3H, I).—Exopodite with 6 natatory setae, all other setation unchanged.

Maxilliped 3 (Fig. 3J).—Naked, trilobed, rudimentary process.

Color.—Lime green now extends to antennae, antennules, and mandibles; additional single melanophores ventrally on basipodites of maxillipeds 1 and 2.

Megalopa

Carapace length × width, 1.19 × 1.13 mm; one specimen examined (description supplemented from Yang, 1967).

Carapace (Fig. 4A, B).—Cephalothorax subquadrate, well-developed hepatic and supraocular lobes; rostral spine elongate, declivate, forming large hook; gastric region with 2 pairs of transverse tubercles in tandem; cardiac region with single pair of small transverse tubercles; intestinal region exhibiting large posteriorly directed lobe; other setation as illustrated; minute frontal organ plus pair of setae anteroventrally on eyestalk.

Abdomen and Telson (Fig. 4A, B, C–G).—Six somites; posteroventral margins of 1–5 produced into rounded lobes, sixth subquadrate, setation as illustrated; telson semicircular, 2 dorsomedial setae. Exopodites and endopodites of segmented pleopods on somites 2–5 carrying 10 + 1, 10 + 1, 9–10 + 1, 7–9 + 1 setae, respectively, plus appendix interna with 2 hooks; uropods on somite 6 with 5 setae.

Antennule (Fig. 4H).—Biramous; peduncle 3-segmented, basal naked, second and third with 1 distal seta; lower ramus 2-segmented, 1 subterminal, 2 terminal setae on distal segment; upper ramus incompletely 3-segmented, armed progressing distally (0), (3 + 4 aesthetascs + 1 short anterodorsal seta), (4 subterminal, 1 thin terminal aesthetascs).

Antenna (Fig. 4I).—Basal article of peduncle expanded distally into lateral lobe bearing 1 seta, gland aperture present; remaining peduncular and flagellar setal formula 2,3,0,0,4,3 + 1 hair.

Mandible (Fig. 4J).—Incisor process truncately spatulate; palp incompletely 2-segmented, 0,5 setae.

Maxillule (Fig. 4K).—Endopodite naked, segmentation obscure; basal and coxal endites with 18 and 10 processes, respectively.

Maxilla (Fig. 4L).—Endopodite unsegmented, naked; basal endites with 6,6, coxal endites with 7,3 processes; scaphognathite with 28–31 plumose marginal setae, plus 3 on blade surface.

Maxilliped 1 (Fig. 4M).—Endopodite naked, obscurely segmented; exopodite 2-segmented, setation 1,4; basal endite with 9–11, coxal endite with 6–7 setae; epipodite fringed with at least 5 setae, latter appearing naked but with extremely fine setules under high magnification.

Maxilliped 2 (Fig. 4N).—Exopodite 2-segmented, setation 0,4; endopodite 4-segmented, setal formula 0,1,3,6, progressing distally.

Maxilliped 3 (Fig. 4O).—Exopodite 2-segmented, setation 0,6; endopodite 5-segmented, setal formula 12,9,5,6,4, ischium mesial margin dentate; protopodite bearing 6, epipodite fringed with 5, setae plus small laminated gill (future posterior arthrobranch) as illustrated.

Pereopods (Fig. 4P–U).—General setation as illustrated; chelipeds equal, not much inflated, slightly gaping, propodus dentate on cutting edge, tip slightly hooked, dactyl smooth; pereopod 2 armed with single spine on both coxa and

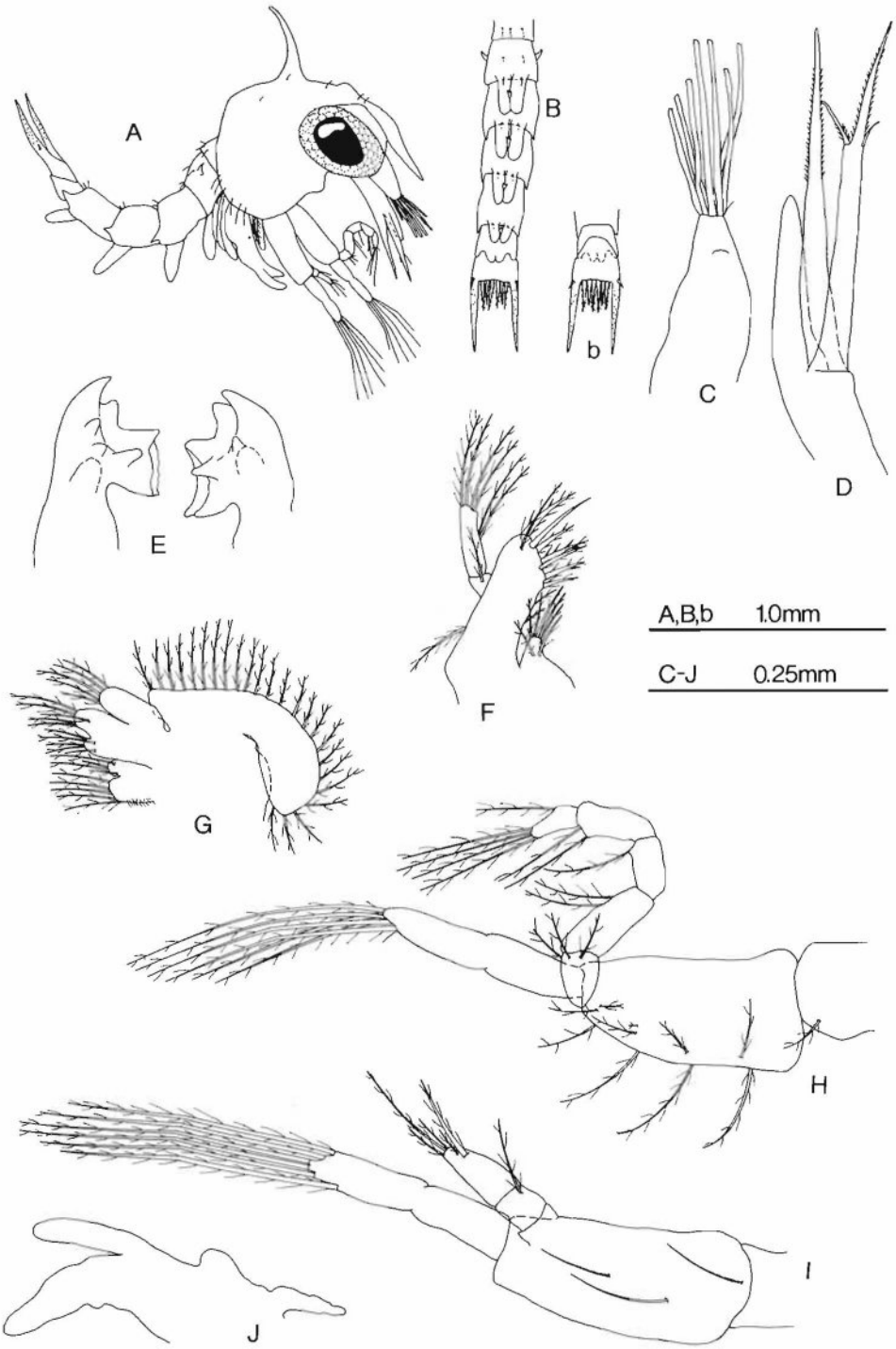

Fig. 3. *Microphrys bicornutus*, second zoea: A, Lateral view; B, Abdomen; b, Telson; C, Antennule; D, Antenna; E, Mandibles; F, Maxillule; G, Maxilla; H, Maxilliped 1; I, Maxilliped 2; J, Maxilliped 3.

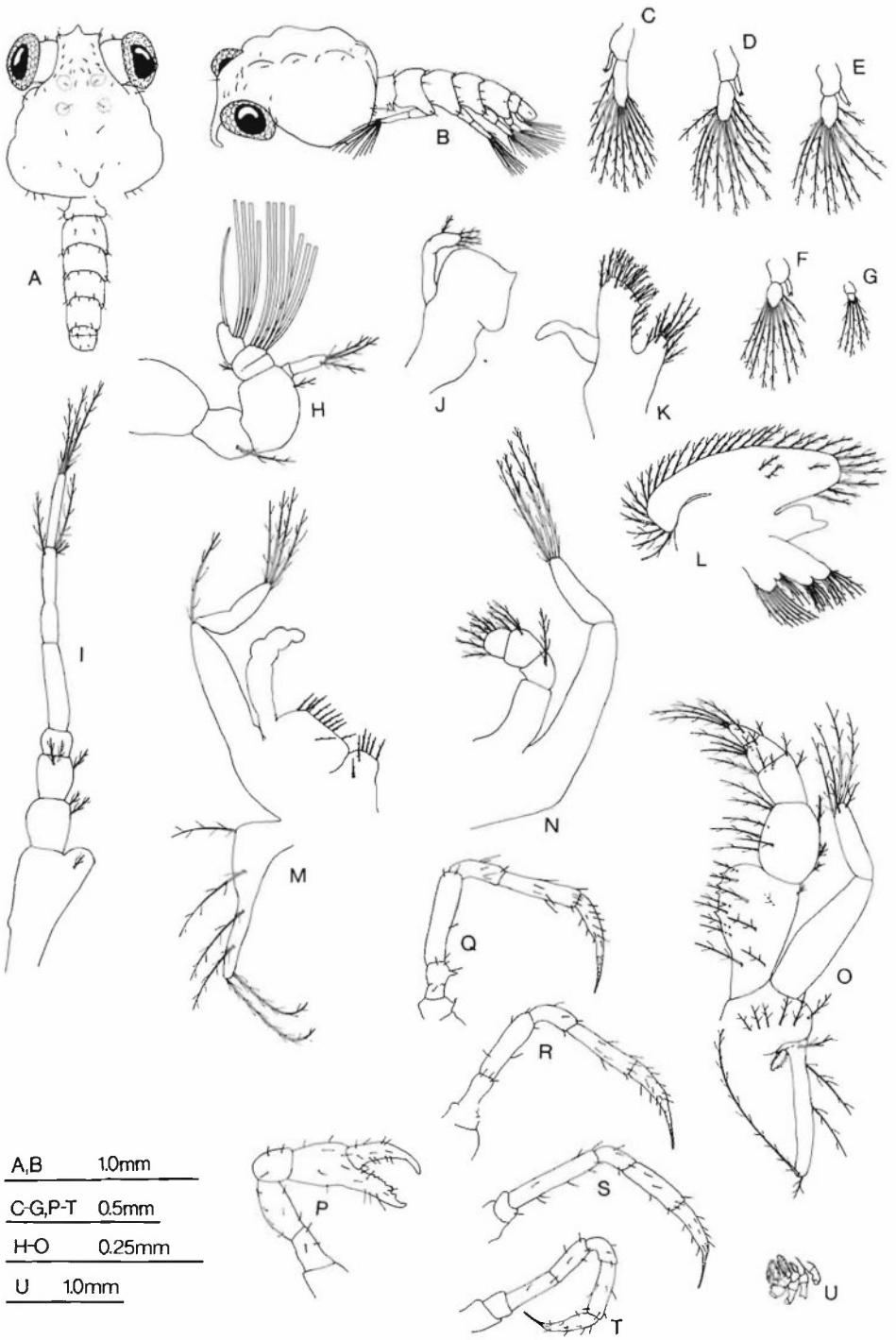

Fig. 4. *Microphrys bicornutus*, megalopa: A, Dorsal view; B, Lateral view; C–G, Pleopods 1–5; H, Antennule; I, Antenna; J, Mandible; K, Maxillule; L, Maxilla; M–O, Maxillipeds 1–3; P–T, Pereopods 1–5; U, Gills.

ischium, pereopods 3–5 lacking spine, but with setation as illustrated. Four laminated gills on each side of pereopods; 2 arthrobranchs (1 small anteriorly, 1 large posteriorly) above cheliped, 1 large pleurobranch above pereopod 2, and 1 small pleurobranch above pereopod 3.

Color.—Rostral spine, intestinal region of carapace and pereopods olive yellow; red chromatophores on ventral surface of last 3 abdominal somites, interiorly and laterally on intestinal region, and distally on merus and propodus of pereopods 2–5; gastric region with scattered black pigmentation; small melanophores on eye peduncle, rostrum, basal article of antenna, lateral surface of carapace, and dorsal surface of abdominal somites and telson; small light orange chromatophores on basal article of antenna and penultimate segment of antennular peduncle.

First Crab

Carapace length × width at branchial region, 1.35 × 0.81 mm.

Carapace (Fig. 5A, B).—Lateral aspect of cephalothorax convex, depth slightly greater at gastric region than cardiac; carapace moderately covered with hooked hairs; gastric, cardiac, intestinal, branchial, hepatic, and rostral regions faintly marked with grooves; divergent rostral horns somewhat parallel and pointed, median notch rounded; peduncle of eye well calcified with small front-organlike structure plus few apical hairs anterodistally; hemispherical hepatic lobe continuous with large postorbital spine and with spine on ventrolateral side of lobe; small spine on pubescent posterolateral margin of supraorbital margin; interorbital region of rostrum depressed, series of minute protuberances on each side; gastric region posterior to hepatic lobe moderately truncate.

Abdomen.—Six somites plus telson; socket on lateral margin of somite 6 locked into hook on fifth thoracic sternum; pleopods present.

Pereopods (Fig. 5C–E).—Sparsely covered with hairs; distal inner margin of fingers of chelipeds serrate with about 4 teeth, coxopodite with several setae anteriorly; dactyl of pereopods 3–5 with 2 large teeth on ventral margin, posterodistal margin of propodus of pereopods 2–5 dilated into shield covering proximal portion of dactyl. Cheliped with 2 arthrobranchs, anterior slightly smaller than posterior and closer to coxopodite; pereopods 2 and 3 each with pleurobranch (much smaller in pereopod 3).

Antennule (Fig. 5F).—Peduncle 3-segmented, setation 2,1,2; lower ramus 2-segmented, setation 0,4; upper ramus 4-segmented, setal and aesthetascs formula progressing distally: (0), (7 aesthetascs plus 1 anterodorsal seta), (4 aesthetascs), (1 long terminal seta plus 2 short dorsal and 1 long ventral seta).

Antenna (Fig. 6A–C).—First 3 segments fused, continuous with epistome, gland aperture at distal base of basal article, distolateral process bifurcate; distolateral knob present fitting into socket on ventral base of rostrum (illustrations showing structure after removal of antennule from fossa), basal article serving as ventral floor of orbit; 2 distal segments of peduncle movable, with several setae; flagellum 6-segmented, setation as illustrated.

Mandible (Fig. 5G).—Palp 2-segmented with 5 stout setae on distal segment.

Maxillule (Fig. 5H).—Endopodite 2-segmented with terminal seta on distal segment; basal endite with 18, coxal endite with 11 processes plus small plumose seta basally.

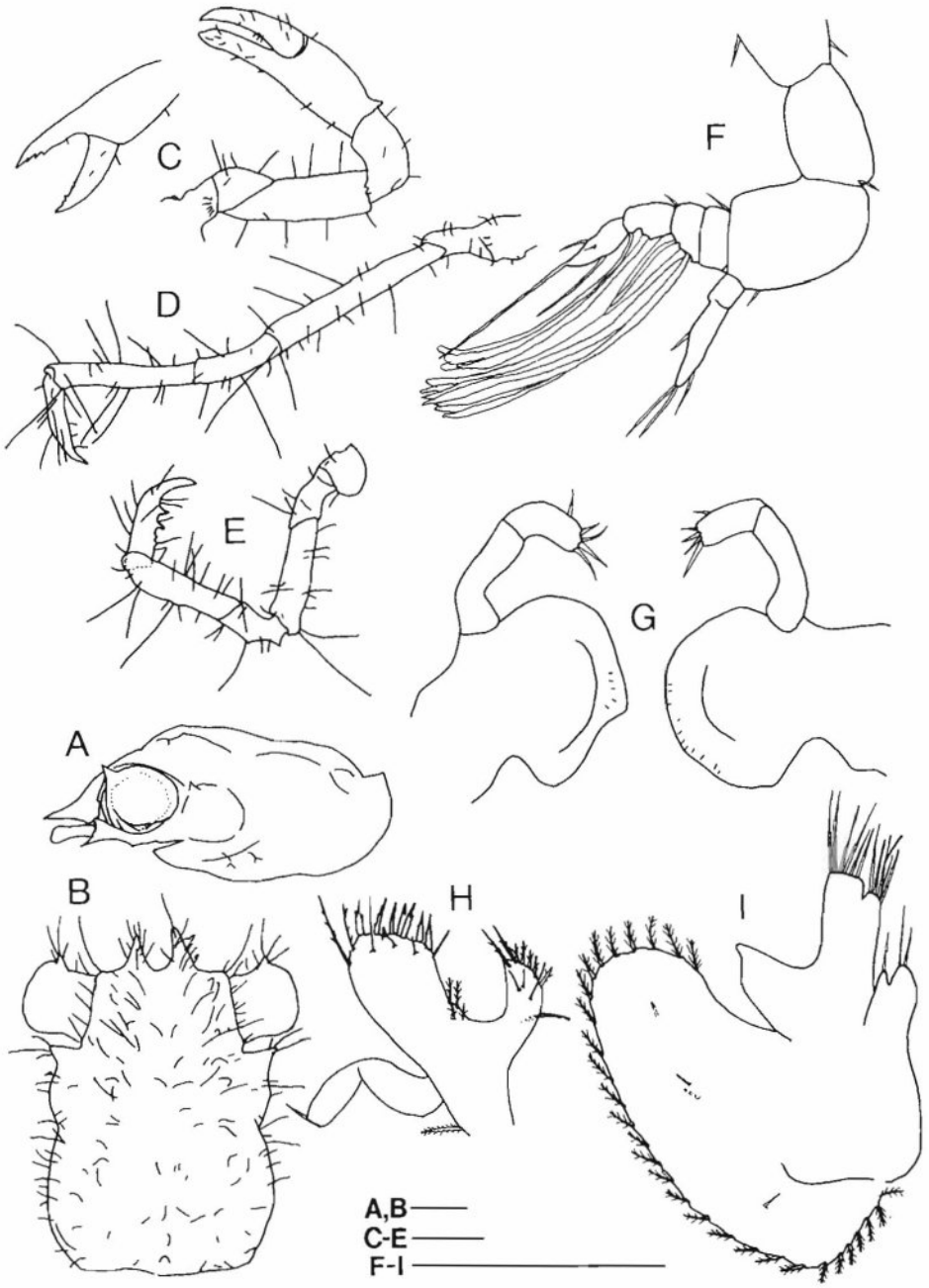

Fig. 5. *Microphrys bicornutus*, first crab: A, Lateral view; B, Dorsal view; C–E, Pereopods 1, 2, 5; F, Antennule; G, Mandibles; H, Maxillule; I, Maxilla. (After Yang, 1967.)

Maxilla (Fig. 5I).—Scaphognathite with 29 or 30 bushy plumose setae along margin; endopodite much reduced, lateral margin faintly lobate; bifurcated basal endite with 6,6, small coxal endite with 2,1 processes.

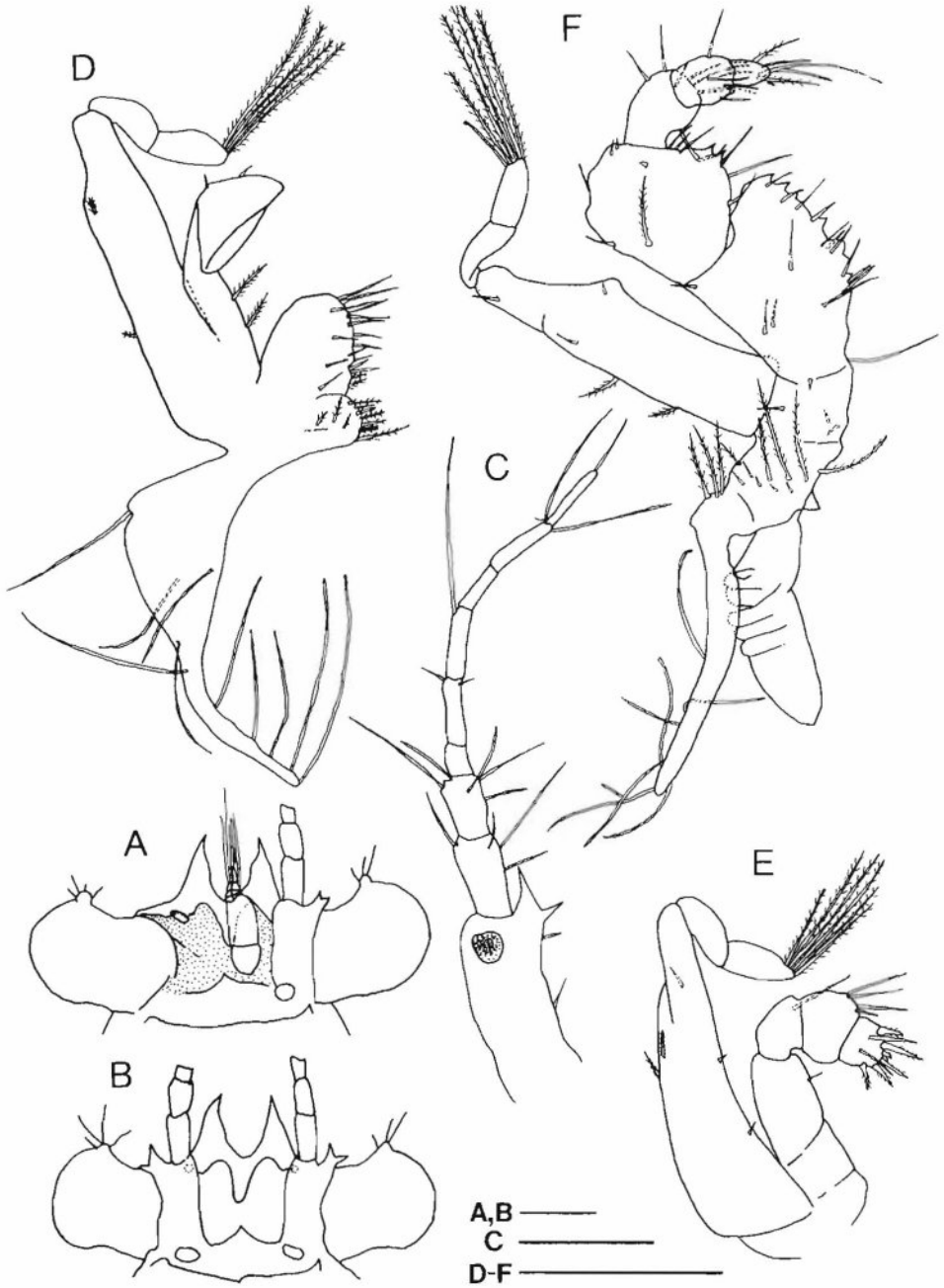

Fig. 6. *Microphrys bicornutus*, first crab: A,B, Carapace anterior, ventral view, without left antennule and antenna, and without antennules, respectively; C, Antenna; D, Maxilliped 1; E, Maxilliped 2; F, Maxilliped 3. (After Yang, 1967.)

Maxilliped 1 (Fig. 6D).—Endopodite obscurely 2-segmented, distal segment hatchet-shaped with 2 setae on distal margin, proximal segment with 2 plumose setae on medial margin; exopodite 3-segmented with 4 plumose terminal setae on distal segment, 2 small setae on lateral margin of proximal segment; basal endite with 17–21 naked and plumose setae; coxal endite usually with 12 plumose setae; epipodite fringed with about 10 smooth hairs.

Maxilliped 2 (Fig. 6E).—Endopodite 5-segmented, process formula progressing distally 0,1,1,4,6 spines + 2 setae; exopodite 3-segmented, distal segment with 6 plumose terminal setae, proximal with 5 small setae.

Maxilliped 3 (Fig. 6F).—Separation between basi-ischium of endopodite faintly marked, mesial margin of ischium strongly serrate, margin of merus with 2 dilated teeth; exopodite 3-segmented, setal formula progressing distally 6,0,1 smooth plus 5 plumose; coxopodite with 10 setae (5 small, 5 long plumose); epipodite with 3 long plumose setae on proximal portion, fringed with hairs on distal half. One laminated posterior arthrobranch, slightly laminated bud of podobranch, and bud of anterior arthrobranch on maxilliped 3.

Color.—Dorsal surface of carapace stippled with minute melanophores, more densely spotted anteriorly than posteriorly; punctate melanophores on eye peduncle and chelipeds; large melanophore on distal posterior margin of merus, carpus, and propodus of pereopods 2 and 3; melanophore on coxopodite of chelipeds and ischium of maxillipeds, rostral horns, and basal article of antenna. Small red chromatophores on interorbital groove of rostrum, red chromatophore on lateral surface of cardiac region. (Above from Yang, 1967).

Discussion

Comparison of Mithracine Zoeal Stages

The zoeal stages of *Microphrys bicornutus* resemble very closely those belonging to other members of the subfamily Mithracinae, including all *Mithrax* species but *Mithrax spinosissimus* (Lamarck, 1818), at least 2 species of *Macrocoeloma,* the sole known *Micippa* larva, as well as the zoeae of *Tiarinia cornigera* (Latreille, 1825) described by Kurata (1969) but not those of Aikawa (1937; see below). Zoeae of *M. bicornutus* can be distinguished from other mithracine larvae by using a combination of features, summarized in Table 1, which include carapacial spines, antennular and antennal setation, meristic data, and setal formulae of the various mouthparts, but separation and identification of larvae in the plankton will undoubtedly prove difficult without dissection of mouthparts.

Color patterns of live zoeae may also be of aid. *Microphrys* is predominantly lime or olive green, with scattered melanophores, whereas *Mithrax* larvae generally are transparent, highlighted by yellow, gold, red orange or rose coloration, and scattered melanophores. In *M. bicornutus* a prominent black chromatophore occurs distally on the first, and proximally on the second, of each of the lime green maxillipedal basipodites. In *Mithrax forceps* (A. Milne Edwards, 1875) and *M. coryphe* (Herbst, 1801) the basipodites are clear or rose orange, respectively, and the melanophore is more diffuse and located medioventrally in the former, and distally in the latter, species. A similar pattern is seen in *M. pleuracanthus* Stimpson, 1871, but the zoea has "a great deal of yellow" on the carapace and abdomen (Goy *et al.,* 1981). In *M. verrucosus* H. Milne Edwards, 1832, 3 orange chromatophores appear on the carapace, at the posterior base of the rostral spine, and on the posterolateral and posterodorsal areas, respectively (*cf.* Yang, 1967;

Table 1. Comparison of morphological characters in first zoeal stages of Mithracinae.

	Carapace spines		Antennule	Antenna	Maxillule	Maxilla	Maxilliped setae	
	Dorsal	Rostral	aesthetascs	exo : protopod	endopod	endopod	Endopod (1)	Basipod (2)
Microphrys bicornutus	0.6 carapace ht.; slightly curved	>½ of antennule	4 + 1 seta	Exo ≥ protopod	1,2 + 4 setae	5 setae	3,2,1,2,4 + I	3, naked
Mithrax forceps	0.7 carapace ht.; moderately curved	*ca.* ½ of antennule	4 + 1 seta	Exo ≳ protopod	1,2 + 4 setae	5 setae	3,2,1,2,4 + I	3, naked†
Mithrax pleuracanthus	0.6 carapace ht.; falcate	*ca.* ½ of antennule	3 + 1 seta	Exo = protopod	1,2 + 4 setae	5 setae	3,2,1,2,4 + I	3, naked
Mithrax coryphe	0.5 carapace ht.; strongly curved	>½ of antennule	4 + 1 seta	Exo = protopod	1,2 + 4 setae	5 setae	3,2,1,2,4 + I	3, plumose
Mithrax spinosissimus	0.4 carapace ht.; slightly hooked	≈⅓ of antennule	5, no seta	Exo < protopod	2 terminal setae	1 setae	0,1,1,2,3 + I	No setae
Macrocoeloma camptocerum	0.8 carapace ht.; oblique	<½ of antennule	3 + 1 seta	Exo = protopod	1,1 + 4 setae	5 setae	3,2,1,2,4 + I	3, naked
Macrocoeloma diplacanthum	0.4 carapace ht.; vertical, undercut anteriorly	¾ of antennule	3 + 1 seta	Exo ≲ protopod	1,1 + 4 setae	4 setae	3,2,1,2,4 + fixed spine	3, naked (proximal serrated)
Tiarinia cornigera	0.4 carapace ht.; strongly hooked	<⅓ of antennule	3 + 1 seta?*	Exo < protopod	No data	3 setae	0,0,1,1,4*	None figured
Micippa thalia	Absent; lateral spines present	2× antennule	3 + 1 seta?*	Exo > protopod	1,2 + 4 setae	6 setae	3,2,1,2,4 + I*	None figured

* Interpolated from illustration.
† Erroneously figured as plumose in Wilson *et al.* (1979).

Bolaños and Scelzo, 1981). The carapacial chromatophores are red in the other *Mithrax* zoeae.

In *Macrocoeloma* zoeae (Yang, 1967) the general color is either red orange in *M. diplacanthum* (Stimpson, 1860) or light yellow green in *M. camptocerum* (Stimpson, 1871), with no melanophores in the former, but several on the mandible, basipodite of maxilliped 1, and the gastric area of the latter. In *Micippa thalia* (Herbst, 1803) the zoea is "a deep dark yellow color" with melanophores on the posterolateral carapace region, the medioventral bases of the maxillipeds, and abdominal somite 3 (Kurata, 1969). In the same paper, Kurata stated that the first zoea of *Tiarinia cornigera* was "red-orange scattered with yellow" with yellow chromatophores on the antenna, "mouth" (=mandibles), the posterolateral region of the carapace and along abdominal somites 1–5, and the telson (translated from original Japanese and verified in Kurata, 1969: 114, figs. 24, 26).

Slight differences occur in maxillipedal 2 basipodal setae of known mithracine larvae. Goy *et al.* (1981) separated zoeae of *M. pleuracanthus* from *M. forceps* according to whether these setae were plumose or simple (i.e., nonplumose or naked). Regrettably, this perpetuates an erroneous observation in the study by Wilson *et al.* (1979), in which these setae were illustrated as being plumose when, in fact, they are naked (Gore, unpublished data). The character may, nevertheless, have some value, because the only mithracine larva presently known to have plumose setae on the maxillipedal basipod is *Mithrax coryphe* (Scotto and Gore, 1980; see Table 1 this study). Although neither Lebour (1944) nor Hartnoll (1964) figured basipodal setae on the maxillipeds of *Microphrys bicornutus,* consequently leading Ingle (1979) to incorporate this error in his synopsis of mithracine larval stages (see below), we found these setae always present in larvae we cultured.

Comparison of Mithracine Megalopal Stages

The megalopal stages of known mithracine species are all dissimilar and should be less of a problem in identification. Two of the species, *Micippa thalia* and *Tiarinia cornigera,* are primarily Indo-West Pacific in distribution, but the megalopa is known only from *Micippa*. The remaining megalopae are known from western Atlantic species. According to Rathbun (1925) the genus *Macrocoeloma* occurs "sparingly in the Indo-Pacific region," apparently referring to A. Milne Edwards's (1873) record from the Fiji Islands. The easiest features allowing separation appear to be the morphology of the rostrum, the aesthetasc formula on the antennule, the presence or absence of endopodal setae or a basal seta on the maxillulary coxal endite, and the occurrence of coxal and ischial spines on the second pereopod, and a dactylar tooth on pereopods 2–4. These, and carapacial characters, including general color pattern among the known megalopae, are summarized in Table 2.

Numbers of Larval Stages in the Mithracinae

With the exception of *Paranaxia serpulifera* (Guérin, 1829), all mithracine genera pass through two zoeal stages and one megalopal stage in their larval development, thus agreeing with other Majidae. However, Rathbun (1914) stated that *Naxioides serpulifera* (Guérin, 1829) from the Monte Bello Islands, Australia, had direct development. Rathbun placed this species in the Pisinae near the genus *Lissa*. She later (1924) erected a new genus, *Paranaxia,* to contain this species, and Balss eventually (1929) assigned it to the Mithracinae. Data from Kurata

Table 2. Comparison of morphological characters in megalopal stages of Mithracinae.

	Carapace armature				Antennule formula	Antenna formula	Maxillule setae		Maxilliped 3		Pereopod spines			Telson seta
	Rost.	Gst.	Crd.	Int.			Cxl end.	Endopod.	Proto.	Endo.	Coxa	Isch.	Dact.	
Microphrys bicornutus	Declivate hooked	4	2	1	(0) (3 + 4A + 1S)(4 + 1A)	2,3,0,0,3 + hair	Absent	None; 1-segmented	6 setae	Dentate	P2+	P2+	None	2 dorsomedial
Mithrax forceps	Deflexed spiniform	5	5	1	(0) (1,2,2,2A + 1S)(4 + 1A)	2,3,0,0,4,3 + hair	Present	None; 2-segmented	5–7 setae	Dentate*	P2+	P2+	None	2 dorsomedial
Mithrax pleuracanthus	Oblique pointed tooth	5	1	1	(0) (2,2,2,2A + 1S)(4 + 1A)	2,3,0,0,4,2 + hair	Absent	2 terminal; 2-segmented	8 setae	Nondentate	P2+	P2+	P2–P4+	2 dorsomedial
Mithrax coryphe	Deflexed spiniform	6	4	1	(0) (1,2,2,2, 2A +1S) (4 + 1A)	2,3,0,0,4,3 + hair	Present	None; 2-segmented	6 setae	Dentate*	P2+*	P2+*	None	2 dorsomedial
Mithrax spinosissimus	Deflexed bladelike	5	3	1	(3 + 2A) (3A + 1S)	2,2,0,4,3†	Absent	None; 1-segmented	4 setae	Dentate	?	?	None	2 dorsomedial
Macrocoeloma camptocerum	Deflexed bladelike	3	2	0	(0) (5A) (3A + 1S)	1,2,0,0,4,3 + hair	Absent	3 + 1 distally; 2-segmented	4 setae	Dentate	None	P2+	P2–5 fine spinules	4 dorsomedial
Macrocoeloma diplacanthum	Deflexed 90°, acute	6 ridgelike only on gastric region			(0) (6A) (4A + 1 seta)	2,3,0,0,3 + hair, 3 + hair	Absent	3 + 1 distally; 2-segmented?	6 setae	Dentate	None	P2+	P2–5 (2–3 spines + spinules)	4 dorsomedial
Micippa thalia	Slightly oblique, toothlike	10	3	1	No data	2,1,0,0,2§	No data	No data	No data	No data	P1+ P2+	P1+ P2+	— P2–5 3 spinules§	4 dorsomedial

M. bicornutus	*M. forceps*	*M. pleuracanthus*	*M. coryphe*	*M. spinosissimus*	*M. camptocerum*	*M. diplacanthum*	*M. thalia*
Olive yellow	golden brown	yellowish orange	rose orange	No data	light brown?	red orange	yellow brown

* Correction of erroneous previous data. † Flagella fused. § Data from illustration only.

(1969) show that the species in the genus *Naxioides* (Pisinae) are similar to other majids, passing through two zoeal stages.

Phylogenetic Relationships within the Mithracinae

The genus *Microphrys* has had a complicated taxonomic history, having been placed in several different subfamilies by various authors. Balss (1929) was the first to assign the genus (along with *Macrocoeloma*) to his subfamily Macrocoelominae, a classification accepted by some authors (e.g., Sakai, 1965; Stephenson, 1945). However, Garth (1958) incorporated the Macrocoelominae (and *Microphrys*) into the Mithracinae because of the inconsistent occurrence among the adults of several genera of the intercalated orbital-eave spine ("interkalardorn"), and because the morphological characteristics of the adult male gonopods within the two subfamilies were often similar. Indeed, as Garth pointed out, *Microphrys* must be considered a mithracine genus because it possesses an intercalated spine and because the gonopods are "typically mithracine." Along with *Microphrys* the subfamily Mithracinae presently comprises about 17 genera, occurring predominantly in the Americas, with a smaller group being found in the Indo-West Pacific (Rathbun, 1925). One genus, *Jacquinotia,* is endemic to New Zealand (Griffin, 1966a). The zoogeographic distribution of the subfamily itself raises interesting questions which lie beyond the scope of the present study.

Until recently, the zoeae of the Mithracinae had not been much studied. In the first detailed comparison of known larval stages within the subfamily, Yang (1967) noted that larvae of the genus *Mithrax* were closely related to those of *Microphrys*. At the time of his study the major differences were to be found in the relative length of the antennal exopod to the protopodal spine, and in chromatophore pattern. Although still valid today, recent studies have shown taxonomic groupings to be much more complex. As can easily be seen from Table 1, *Microphrys* zoeae appear to be almost identical in many characters to the larvae of at least 4 of the 5 known species of *Mithrax* in either the subgenus *Mithrax* (*M. pleuracanthus, M. verrucosus*) or *Mithraculus* (*M. forceps, M. coryphe*), thereby confirming Yang's observation that relationships apparently cross generic lines. But as Wilson *et al.* (1979) and Scotto and Gore (1980) have shown, similarity in larval features does not necessarily conform along subgeneric lines. For example, within the genus *Mithrax* larvae from two species in the subgenus *Mithraculus* (*M. forceps, M. coryphe*) show nearly identical characters to those seen in larvae from the subgenus *Mithrax* (*M. pleuracanthus*; see also Goy *et al.,* 1981) on the one hand, but exhibit distinct differences to larvae from another species in the same genus (*M. spinosissimus, cf.* Provenzano and Brownell, 1977). As pointed out by Ingle (1979) data such as these suggest multiple phylogenetic lineages within the Mithracinae.

Yang (1967) described the complete development of *Macrocoeloma diplacanthum* (Stimpson, 1860) and *M. camptocerum* (Stimpson, 1871). In discussing larval affinities he stated that *M. camptocerum* was most closely related to both *Mithrax* and *Microphrys,* but that larvae of both species of *Macrocoeloma* differed from all other mithracine larvae in having a single subterminal seta on the distal article of the maxillulary endopod, instead of two setae in this position. This character is also seen in larvae of the subfamily Pisinae. Moreover, *M. diplacanthum* zoeae differed from those of its congener in several important characters, including an undercut dorsal carapacial spine, and in possessing a remarkable immovable spine (instead of the usual simple seta) on the dorsal margin of the terminal endopodal article of maxilliped 2, thus indicating more distant

relationships between these two species. The setal formula of 1+4 on the maxillulary endopod and the endopodal spine in *M. diplacanthum* certainly differentiate the larvae of *Macrocoeloma* from all other mithracine larvae at present. But such characters seem insufficient to consider re-establishment of the Macrocoelominae, a subfamily originally erected on apparently variable adult characters (see below).

The larvae of *Tiarinia cornigera* (Latreille, 1825) form another interesting case. Both Aikawa (1937) and Kurata (1969) described first zoeae attributed to this species. However, the zoea of Aikawa differs from all other mithracine zoeae in several remarkable characters, including possession of a bifurcated endopodite on the maxilla, three spines on each telson furca (a large and a small lateral, plus a small dorsal spine), a single distoventral seta on the proximal segment of the endopodite in maxilliped 2, and only four plumose seta on the scaphognathite lateral margin. As noted by Aikawa (1937) these would be primitive or peculiar characters in the Majidae. Aikawa made no mention of an endopodal bud on the antenna, but stated that the antenna was type A-3, thus conforming to typical majid antennal morphology.

This, and more recent evidence, strongly suggests that Aikawa's larva was misidentified. Yang (1967), for example, felt that Aikawa's *T. cornigera* probably had more than two zoeal stages (the usual number within the Majidae) because pereopod and maxilliped 3 buds were absent, and the maxillary scaphognathite possessed only four plumose setae. In addition, recent studies on brachyuran scaphognathites (Van Dover *et al.*, 1982) indicate that Aikawa's zoea differs from typical majid zoeae not only in the general form of the maxillary scaphognathite, but in possessing an elongate spinelike apical seta thereon. Another majid larval character lacking in Aikawa's larva is the distinct anterior seta on the posterolateral carapace margin ("soie antérieur"; Bourdillon-Casanova, 1960). This seta is found in all Mediterranean (Bourdillon-Casanova, 1960), nearly all Japanese (Kurata, 1969), and in most American majid larvae (*auct. cit.*).

On the other hand, Kurata's (1969) brief description of first and second stage zoeae hatched from *T. cornigera* is sufficiently detailed in conjunction with his illustration of stage I to show that his larvae differ considerably from that of Aikawa, and are distinctly majid in all features. Although Kurata placed *Tiarinia* in the Macrocoelominae, adults of the genus presently are placed in the Mithracinae (Griffin, 1966b), and the general zoeal features differ very little from those of other mithracine larvae (Table I). Unfortunately, there are no data as to whether the maxillular endopod formula is 4 + 1 (macrocoelomine) or 4 + 2 (mithracine).

Synopsis of Mithracine Larval and Postlarval Characters

Using the studies of several authors previously mentioned, Ingle proposed a brief synopsis of mithracine larval characters, recognizing two zoeal groupings: (I), those without lateral carapace spines (*Microphrys, Mithrax, Tiarinia*), and (II), those possessing lateral spines (*Micippa*). Based on studies in Yang's (1967) dissertation we can now add *Macrocoeloma* to group I of Ingle. However, recent additional data on *Mithrax* larvae (*auct. cit.*) requires a revision of Ingle's synoptic characters delineated for his group I zoeae, as follows:

Mithracinae

Zoea (Group I): Carapace lateral spines absent; dorsal spine short to moderately long, 0.4–0.8 times carapace height; telson furcae with single lateral spine;

dorsolateral processes on abdominal somite 2; posterolateral angles on somites 3–5 armed, sometimes poorly developed; setal formula on maxilliped 2 basipodite 1,1,1; antennal exopodite generally subequal to, and rarely longer than the protopodite, subterminal seta and spine present.

Because *Micippa thalia* (see Kurata, 1969) is the only mithracine presently assigned to Ingle's group II, further consideration must await additional material. Griffin (1966b) discussed taxonomic problems in *Micippa* and *Tiarinia*.

Using recent data we may also modify Ingle's synopsis for the megalopal stage of group I, to wit: Rostrum present, slightly or noticeably declivate, may be hooked apically; submedian processes usually developed as tubercles; cardiac spine reduced or absent, an intestinal process may be present; pereopod 2 basis without, coxa and ischium often with spines; uropod present.

Phylogenetic Position of the Mithracinae

Kurata (1969) summarized data he obtained from the larva of 15 species in 13 genera of Japanese spider crabs and provided a key for their determination. He attempted a classification by dividing the larvae into six major groupings (many of which crossed subfamilial boundaries), using the presence or absence of carapace spines as a basic plesiomorphic or apomorphic character, respectively (see his Fig. 27, p. 124). To this foundation he added antennal morphology, abdominal armature, and size and occurrence of the telsonal posterior notch. In Kurata's classification the Majinae, and some Inachinae (equivalent to Ingle's group II), were relatively more primitive than the remaining subfamilies, and the arrangement was clearly polyphyletic. Kurata's grouping showed some similarity to that proposed by Yang (1967), although both authors had considered genera unavailable to the other.

Rice (1980) provided an alternate classification to that of Kurata (1969), in which he derived the primitive Inachinae and Majinae from the Oregoniinae monophyletically, with a second line from the primitive Majinae giving rise to the Pisinae and Acanthonychinae. The Ophthalminae and Mithracinae were not included in his phylogenetic diagram because little information was available at the time. *Micippa* was, of course, also not considered, although Rice did enumerate several primitive and advanced characters which occur in the larvae of the genus. For our purposes we need consider only that section of Kurata's phylogeny in which an undefined, but apparently multispined ancestral form, gave rise to two sublineages, one leading via *Schizophrys* (Majinae) to the Oregoniinae, the other via *Camposcia* (Ingle's Inachinae group II) to *Micippa* in the Mithracinae. The latter zoea, which Ingle placed in his Mithracinae group II, exhibits allegedly primitive features in the multispined telsonal furcae, and in the retention of lateral carapace spines. As Kurata demonstrated, the loss of these two features apparently occurred in parallel over several subfamilies, and is not restricted to the Mithracinae. *Micippa* nevertheless remains unusual in several respects because it is the only majid zoea lacking the dorsal carapace spine but keeping the lateral spines, and it retains five abdominal somites in both zoeal stages. (In the megalopa a sixth somite is added, as well as setose uropods. Other majids with reduced abdominal segmentation in the second zoeal stage do not exhibit a sixth somite or uropods in the megalopal stage.) In most other majid zoeae the lateral spines are lost and the dorsal spine is retained, in some cases even after the rostral spine disappears. In a small number of forms both dorsal and lateral spines are wanting. The retention of five abdominal somites is otherwise known in zoeae of *Achaeus*,

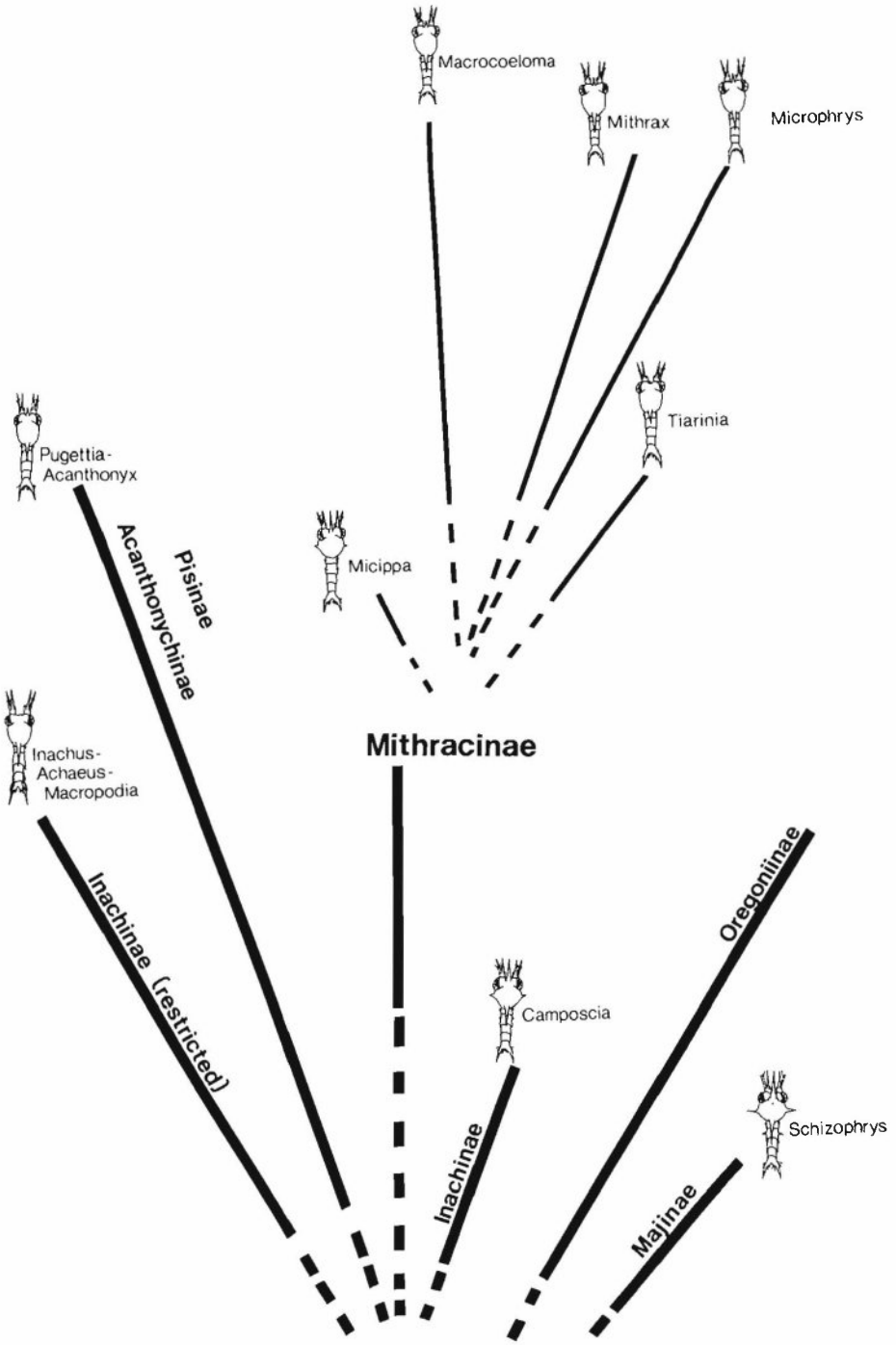

Fig. 7. Semidiagrammatic representation of inferred phylogenetic relationships among known larvae of the Mithracinae (modified from Kurata, 1969). Not all genera in which larvae are known are listed in the compared subfamilial lineages. No direct temporal progression is implied.

Inachus, and *Macropodia* in the Inachinae. However, this may be derived, rather than a primitive feature.

From somewhere near the *Micippa*-mithracine line we thus postulate a lineage giving rise to the zoeal form seen in *Mithrax, Microphrys, Macrocoeloma,* and *Tiarinia* (=Ingle's group I mithracines). In this scheme, this line would parallel Kurata's *Pugettia* line (Acanthonychinae) and lead eventually, either directly or via splitting, to the Pisinae. We would, however, remove *Tiarinia* (which Kurata classified as Macrocoelominae and placed near the apex of his phylogeny with *Pisa* and *Acanthonyx* zoeae) and place it instead near the zoeae of *Macrocoeloma* with which it shares closer relationships. This derivation is shown schematically in Fig. 7.

Do larval characters support the classification of the adults? The gross similarities seen among the larvae seem to have analogues in the adults. For example, although adults of both *Mithrax* and *Microphrys* are easily separated using simple carapacial characters, it cannot be denied that the two genera are closely related. In Rathbun's (1925) key the major difference between the two is whether the rostrum is small (leading to *Mithrax*) or of good size, usually with two strong horns (leading to *Microphrys*). Even these characters are not completely exclusionary, as a glance at the relative large rostrums of *Mithrax cornutus, M. spinipes,* or *M. acuticornis* will show. Several other generic characters also show overlap; the orbits are either not tubular (*Mithrax*) or at best only slightly projecting (*Microphrys*), and in both genera the basal antennal article is moderately broad and bears one or more large spines. The most easily distinguishable difference between the two genera appears to be the presence of a large, or at least distinctly isolate, spine at the lateral margin of the carapace in *Microphrys*. However, even this spine is lacking in the megalopa and early crab stages of the species. On the other hand, the monacanthid rostrum of the megalopa in *M. bicornutus* becomes distinctly bifid in the first crab stage. Moreover, the first crab stage of *Microphrys* shows a very strong superficial resemblance to adults of several species in the genus *Macrocoeloma*. It will be interesting to see if these relationships are supported, in turn, by larval characters in those species not yet cultured in the laboratory. We suspect that the larvae of additional species in *Microphrys, Mithrax, Macrocoeloma,* and even *Stenocionops* will eventually prove to be quite similar.

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