Larval Stages Of Paradasygyius Depressus (Bell, 1835) (Crustacea : Decapoda : Brachyura : Majidae) And A Phylogenetic Analysis For 21 Genera Of Majidae

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Larval stages of *Paradasygyius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae

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Abstract.—All larval stages and the first crab instar of *Paradasygyius depressus* (Bell) were obtained in laboratory culture. Larval development consists of two zoeal stages, followed by the megalopa. Each larval stage is described in detail. Beginning with the first zoea, the duration of each stage was 4–7 (4.5 ± 0.7), 4–5 (4.5 ± 0.5), and 7 days, the megalopa and first crab instar appearing 11 ± 1 and 15 days after hatching, respectively. A phylogenetic analysis of 21 genera of Majidae is provided based on 34 zoeal and three megalopal characters. The phylogenetic analysis resulted in four equally parsimonious trees 173 steps long (CI = 0.66, RI = 0.71, and RC = 0.47) supporting the monophyly of Oregoniinae, Majinae, and Inachinae (with the exclusion of *Macrocheira* De Haan incertae sedis). Based on general agreement of sister-group hypotheses, we provide sets of larval characters that define Oregoniinae, Majinae, and Inachinae. Our phylogenetic hypothesis suggests that Oregoniinae is the most basal clade within the Majidae, and Majinae and the clade (*Epialtus* H. Milne Edwards + Inachinae [excluding *Macrocheira* incertae sedis]) are sister taxa. Within Inachinae, all trees suggest that *Inachus* Weber and *Macropodia* Leach are sister taxa nested as the most derived clade, followed by *Achaeus* Leach, *Pyromaia* Stimpson, *Paradasygyius* Garth, *Anasimus* A. Milne-Edwards, and the most basal *Stenorhynchus* Lamarck. The sister-group relationships of the clade (*Pisa* Leach (*Taliepus* A. Milne-Edwards + *Libinia* Leach)), *Mithrax* Latreille and *Microphrys* H. Milne Edwards remained unresolved.

Paradasygyius depressus (Bell, 1835) is an eastern Pacific majid crab known from the Gulf of California to Colombia (Garth 1958). Members of this genus were considered to belong to the Inachinae (Rathbun 1925), Inachidae sensu Guinot (1978). However, recent morphological evidence of the skeleton from adults suggests that *Paradasygyius* Garth, 1958 and the nine other American inachine genera *Inachoides* H. Milne Edwards & Lucas, 1842, *Collodes* Stimpson, 1860, *Euprognatha* Stimpson, 1871, *Batrachonotus* Stimpson, 1871, *Arachnopsis*, Stimpson, 1871, *Pyromaia* Stimpson, 1871, *Anasimus* A. Milne-Edwards, 1880, *Leurocyclus* Rathbun, 1897, and *Aepinus* Rathbun, 1897 differ significantly from the remaining Inachinae (Drach & Guinot 1982, Guinot & Richer de Forges 1997). Accordingly, Drach & Guinot (1983) resurrected the family Inachoididae Dana, 1851 to include these genera which here are considered as Inachoidinae for placement within the still widely recognized Majidae (e.g., Griffin & Tranter 1986, Ingle 1992, Melo 1996). Few larvae of in-

achoidines are presently known. The aim of the present paper is to describe the zoeal stages and the megalopa of *Paradasygyius depressus*, to compare them to those of other inachoidines and majids, and to provide a phylogenetic hypothesis for 21 genera of Majidae based on zoeal and megalopal characters.

Materials and Methods

Larval development and description.—Specimens of *Paradasygyius depressus* were collected 2 July 1992 while trawling at about 70 m depth on the Pacific coast of Costa Rica near Dominical, Puntarenas (9°13′N, 83°48′W). Ovigerous specimens were held in separate aquaria until hatching, which always occurred at night. On 4 July 1992 a numbered series consisting of 50 of the most active, positively phototactic larvae were separated into acrylic jars (2 larvae per jar). Each jar held about 40 ml of filtered sea water with 0.2 mg/ml potassium benzylpenicillin (Squib Brazil Inc.) to prevent bacterial infection. Rearing of this series of larvae was discontinued 17 days after hatching. Larvae from different females were also reared under mass culture conditions to provide additional specimens for analysis.

Newly hatched larvae were fed ad libitum with *Artemia* nauplii. Sea water was changed, and specimens were inspected and fed daily. All acrylic ware was washed in fresh water and air-dried before re-use with fresh sea water the following day. Mean daily water temperature in the tank was 28°C, within about 1°C of the natural environment fluctuation. Average salinity was 32‰. A 12L:12D photoperiod was maintained.

Whenever possible, a minimum of ten specimens was measured and at least five specimens of each stage were dissected for morphological description. For slide preparations polyvinyl lactophenol mounting medium was used with CMC (Turtox) or chlorazol black stain. Morphometric data were obtained using a microscope-mounted high resolution video camera to a computer equipped with image analysis (OPTIMAS vers. 5.2) and spreadsheet (Microsoft EXCEL 6.0) software. Measurements (±7 μm) of zoeal stages include carapace length measured in lateral view from the base of the rostrum to the most posterior margin; carapace width in frontal view at its widest point; the dorsal spine in lateral view from the posterior basal margin to the tip; 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 vestigial rostrum to the posterior margin, and at its widest point, respectively.

The description of setae follows Pohle & Telford (1981), but here includes only analysis by light microscopy (LM), using an Olympus BH-2 microscope with Nomarski Differential Interference Contrast and camera lucida. Some of the setae designated as plumose herein may be plumodenticulate setae due to the lower resolution limits of LM as compared to scanning electron microscopy (SEM). Denticulettes sensu Pohle & Telford (1981) are generally only visible by SEM but were recorded here when occurring in dense clusters. Description guidelines of Clark et al. (1998) were generally followed. We followed the conventional taxonomic ranking of spider crabs as a single family divided into a series of subfamilies (Rice 1983, Griffin & Tranter 1986, Negreiros-Fransozo & Fransozo 1991, Melo 1996). Specimens of larval stages and a spent female crab have been deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 259645, 291488). Slide preparations were banked 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 numbers NEBECCDLC 00003.1–23.

Phylogenetic analysis.—The data matrix

from Marques & Pohle (1998) for 15 genera of Majidae was implemented with additional data from the larval descriptions of *Achaeus cranchii* Leach, 1817 (cf. Paula 1987), *Anasimus latus* Rathbun, 1894 (cf. Sandifer & Van Engel 1972), *Macropodia* sp. (cf. Paula 1987), *Pyromaia tuberculata* (Lockington, 1877) (cf. Fransozo & Negreiros-Fransozo 1997), *Stenorhynchus* spp. (cf. Yang 1976), and *Epialtus brasiliensis* Dana, 1852 (cf. Negreiros-Fransozo & Fransozo 1991) and *E. bituberculatus* H. Milne Edwards, 1834 (cf. Negreiros-Fransozo & Fransozo 2000). Modifications in coding and character argumentation of new characters follow.

An examination of intra- and interspecific variability of antennal morphology among all taxa led to a simplified coding of character states, reduced to four from the original eight states used by Clark & Webber (1991). Character 4, exopod morphology of the antenna: The spinulose tip or spine varies in length relative to a pair of setae. State 0, terminal spine minute, less than half length of smaller apical seta; state 1, terminal exopod spine half or more length of apical setae but not extending beyond tip of setae; state 2, exopod tip extending beyond setae, latter inserted distally to proximal half of shaft; state 3, exopod tip extending much beyond setae, latter inserted on proximal half of shaft.

Six new characters were added to the data matrix in an attempt to resolve sister-group relationships within the Inachinae. Character polarization was inferred with reference to the states observed in *Callinectes* spp. and *Cancer* spp. using the outgroup comparison method (Watrous & Wheeler 1981, Maddison et al. 1984). The following new characters were added to the analysis of Marques & Pohle 1998 (see Table 2):

(32) Posterolateral carapace margin of zoeal stages ornamented with serrulations: Within Inachinae sensu lato, *Inachus*, *Macropodia*, and *Achaeus* are serrulated on the posterolateral margin of the carapace. In other inachines, as well as oregoniines and the outgroups, the posterolateral margin of the carapace is smooth. According to the outgroup comparison, serrulation on the posterolateral margin of the carapace was considered derived within Inachinae. Character states were coded as: 0, ornamentation absent; 1, ornamentation present.

Character polarization: 0 → 1

(33) Distinct paired acicular (sensu Webber & Wear 1981) curved processes on abdominal somite of zoeal stages: Within Inachinae sensu lato, *Paradasygyius*, *Anasimus*, and *Pyromaia* possess a conspicuous lateral pair of acicular cuved processes on somite 2. In other inachines as well as oregoniines and the outgroups, the lateral process on somite 2, although present, is nonacicular. Thus, we considered the presence of acicular processes as derived within Inachinae. Character states were coded as: 0, acicular process absent; 1, acicular process present.

Character polarization: 0 → 1

(34) Separated sixth abdominal somite in the second zoea: Within Inachinae sensu lato, *Inachus*, *Macropodia*, and *Achaeus* do not show a separated sixth abdominal somite. In other inachines, as well as Oregoniinae, the sixth abdominal somite is defined. Unlike Majidae, the outgroups are characterized by more than two zoeal stages. In the latter, the sixth abdominal somite appears in the third zoeal stage. Using Oregoniinae and *Macrocheira* as functional outgroups, we considered the presence of a separated sixth abdominal somite in the second zoeal stage as derived within Inachinae. Character states were coded as: 0, sixth abdominal somite differentiated; 1, sixth abdominal somite not differentiated.

Character polarization: 0 → 1

(35) Megalopa uropods: Pleopods may be present or absent on abdominal somite 6. These uropods are present in the outgroups, while being present or absent in different genera of the ingroup. The absence of uropods was considered as the derived state within the ingroup. Character states

were coded as: 0, uropods present; 1, uropods absent.

Character polarization: 0 → 1

(36) Megalopa antenna exopod process: This lateral, sometimes spine-like process on the basal segment may be present or absent. Within the outgroups, *Cancer* spp. and *Callinectes sapidus* Rathbun, 1896 lack this process, whereas it is present in *Callinectes similis* Williams, 1966. According to the Maddison et al. (1984) algorithm, the presence of the process is considered as the derived state. Character states were coded as: 0, exopod process absent; 1, exopod process present

Character polarization: 0 → 1

(37) Megalopa antennal flagellum: There are a number of articles distal to the basal peduncular segments. In the outgroups there are eight articles, whereas in Majidae the number of articles may range from 3–5. Within the latter fusion of articles 2–3 and/or 4–5 occurred in different genera (Rice 1988). This multistate transformation series was left unordered as the character state observed in the outgroups is not present within the ingroup, and because there are many character states within the ingroup. Character states were coded as: 0, eight flagellar articles; 1, five flagellar articles; 2, articles 4–5 fused; 3, articles 2–3 fused; 4, articles 2–3 and 4–5 fused.

Phylogenetic analysis was performed with PAUP* (version 4.0b1, Swofford 1998) using the heuristic search with 50 replicates and Tree-Bisection-Reconnection (TBR) as the branch-swapping algorithm, and ACCTRAN optimization. Multistate transformation series were considered unordered, characters were equally weighted, and trees were rooted by specifying *Cancer* and *Callinectes* as outgroups, as used by Marques & Pohle (1998). A NEXUS format PAUP* input file containing the data matrix is provided in Appendix 1.

Results

Larval development and description.—Larval development of *Paradasygyius depressus* consists of two zoeal stages and one megalopa. Figure 1 shows the rearing record for the three stages cultured at ambient temperature (28°C). Beginning with zoea I, the duration of each stage was 4–7 (4.5 ± 0.7), 4–5 (4.5 ± 0.5), and 7 days, the megalopa and first crab instar appearing 11 ± 1 and 15 days after hatching, respectively. Larval morphometrics are given in Table 1. Only morphological changes are described for the stages following the first zoea.

Description

Paradasygyius depressus (Bell, 1835)

First zoea (Fig. 2)

Carapace (Fig. 2A).—With long, naked dorsal spine; lacking rostral and lateral spines. On ventral margin with densely plumose "anterior seta" (Clark et al. 1998) posterior to scaphognathite notch, followed by 3 additional sparsely plumose setae. Eyes sessile, with small papilla on peduncle. Small but distinct median ridge frontally between dorsal spine and eyes and a median tubercle on posterodorsal margin. Two pairs of simple or sparsely plumose setae present, one flanking dorsal spine, another longer pair just dorsal to median ridge.

Antennule (Fig. 2C).—Unsegmented, smooth, conical. Terminally bearing two long aesthetascs, 1 shorter aesthetasc and short seta.

Antenna (Fig. 2D).—Biramous, protopod very long and pointed, bearing 2 rows of sharp spinules, increasing in size distally; endopod bud present; one-segmented exopod with long spinulated distal process and pair of serrulate setae about ⅓ from tip.

Mandible (Fig. 2E).—With medial toothed molar process and enlarged lateral incisor process bearing about 10 circularly arranged marginal teeth. Palp absent.

Maxillule (Fig. 2F).—Coxal endite bearing 7 setae, 3 terminal graded plumodenticulate and subterminally 3 plumodenticulate and 1 plumose. Basial endite with 3 terminal plumodenticulate cuspidate setae

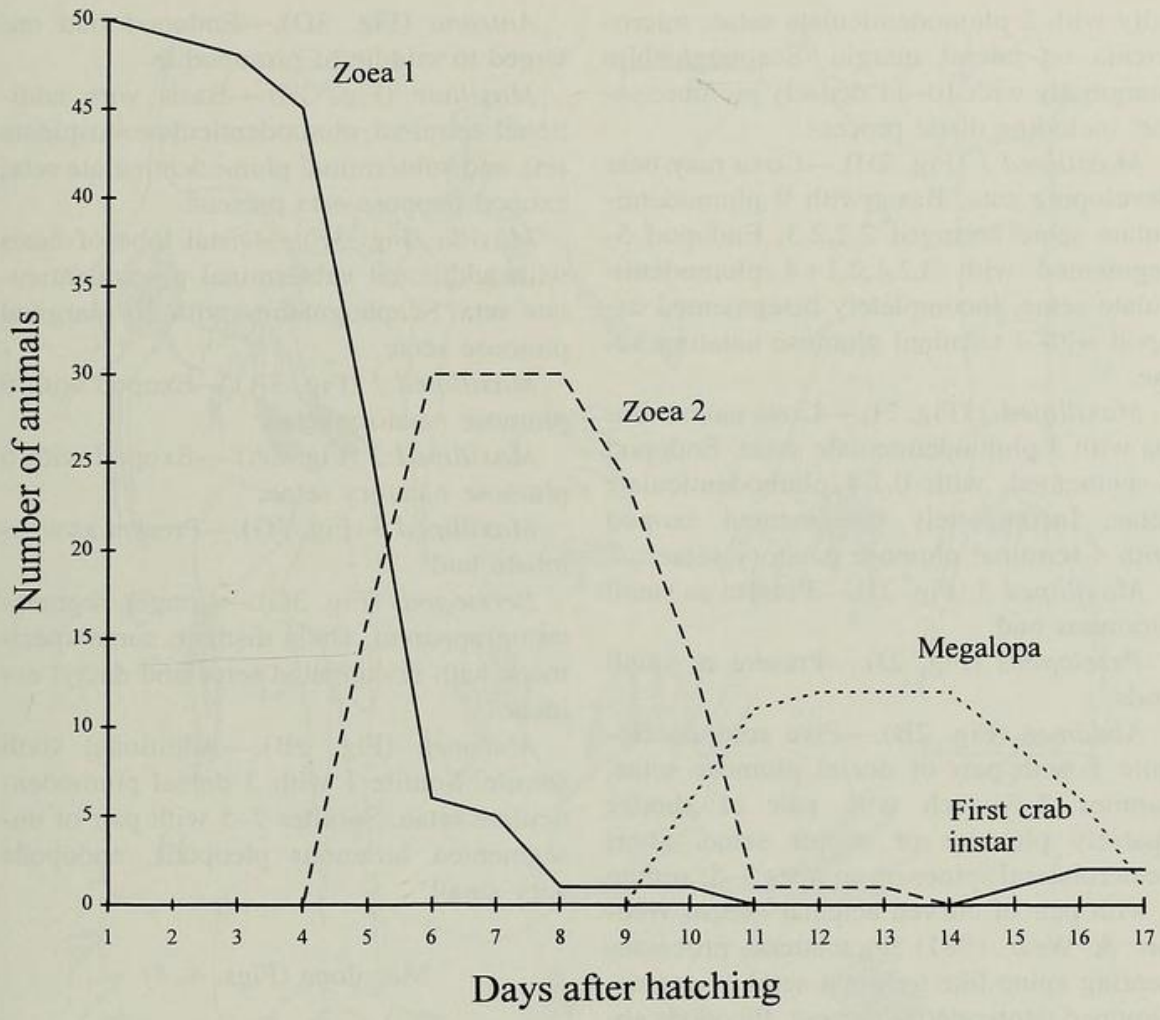

Fig. 1. Rearing record of larval stages of *Paradasygyius depressus* at ambient temperature (28 ± 1°C) and salinity (32‰).

and 4 subterminal setae, 3 plumodenticulate and 1 plumose. Two-segmented endopod with naked proximal segment, distal segment bearing 2 pairs of plumodenticulate setae apically. Exopod seta absent.

Maxilla (Fig. 2G).—Coxal endite bilobed, each lobe with 4 setae, 3 plumose, 1 plumodenticulate. Basial endite bilobed, proximal lobe with 5 plumodenticulate setae, distal lobe bearing 4 plumodenticulate setae. Unsegmented endopod distally slightly bilobed, proximally with single and dis-

Table 1.—Dimensions (mm) of larval structures of *Paradasygyius depressus* (Bell, 1835).

Species	Dorsal spine length	Carapace length	Carapace width	Antenna length
Zoea 1	0.67 ± 0.04	0.69 ± 0.04	0.53 ± 0.04	0.60 ± 0.04
	(0.57–0.76)	(0.60–0.69)	(0.49–0.60)	(0.50–0.68)
Zoea 2	0.48 ± 0.06	0.83 ± 0.05	0.67 ± 0.04	0.63 ± 0.04
	(0.44–0.53)	(0.79–0.88)	(0.64–0.70)	(0.59–0.67)
Megalopa	0.26 ± 0.01	1.14 ± 0.01	0.99 ± 0.00	0.88 ± 0.04
	(0.25–0.27)	(1.14–1.15)	(0.99–0.99)	(0.83–0.91)

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

tally with 2 plumodenticulate setae; microtrichia on lateral margin. Scaphognathite marginally with 10–11 densely plumose setae, including distal process.

Maxilliped 1 (Fig. 2H).—Coxa may bear developing seta. Basis with 9 plumodenticulate setae arranged 2,2,2,3. Endopod 5-segmented with 3,2,1,2,1+4 plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 2 (Fig. 2I).—Coxa naked. Basis with 3 plumodenticulate setae. Endopod 3-segmented, with 0,1,4 plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 3 (Fig. 2J).—Present as small biramous bud.

Pereiopods (Fig. 2J).—Present as small buds.

Abdomen (Fig. 2B).—Five somites. Somite 1 with pair of dorsal plumose setae, somites 2–5 each with pair of shorter sparsely plumose or simple setae. Short posterolateral spines on somites 3–5; somite 2 with pair of curved acicular (sensu Webber & Wear 1981) dorsolateral processes bearing spine-like terminal setal extension. Grouped denticulettes present. Pleopods absent.

Telson (Fig. 2B).—Bifurcated, shallow notch medially, 3 pairs of serrulate 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. 3)

Carapace (Fig. 3A).—Eyes mobile. Four additional pairs of simple or sparsely plumose setae, two pairs just above eyes, another two further dorsolaterally between dorsal spine and eyes. Lateral margin anteriorly to posteriorly with 5 plumose setae. Small lateral swelling dorsal to eyes.

Antennule (Fig. 3C).—With 6 long and 2 shorter aesthetascs and short seta; endopod absent.

Antenna (Fig. 3D).—Endopod bud enlarged to middle of protopodite.

Maxillule (Fig. 3E).—Basis with additional terminal plumodenticulate cuspidate seta and subterminal plumodenticulate seta; exopod pappose seta present.

Maxilla (Fig. 3F).—Distal lobe of basis with additional subterminal plumodenticulate seta. Scaphognathite with 20 marginal plumose setae.

Maxilliped 1 (Fig. 3A).—Exopod with 6 plumose natatory setae.

Maxilliped 2 (Fig. 3A).—Exopod with 6 plumose natatory setae.

Maxilliped 3 (Fig. 3G).—Present as a trilobate bud.

Pereiopods (Fig. 3G).—Longer, segmentation apparent, chela distinct; some specimens with invaginated setae and dactyl evident.

Abdomen (Fig. 3B).—Additional sixth somite. Somite 1 with 3 dorsal plumodenticulate setae. Somites 2–5 with pair of unsegmented biramous pleopods, endopods very small.

Megalopa (Figs. 4, 5)

Carapace (Fig. 4A).—Dorsally with median dromedary-shaped ridge flanked by short anterolateral spines; posteriorly a median spine; surface covered with many simple setae as shown, lateral margin with two clusters of sparsely plumose setae; area posterior to eyes laterally notched, posterior margin elevated middorsally.

Antennule (Fig. 4B).—Three-segmented peduncle with single simple seta on middle and distal segment; endopod with 1 subterminal and 2 terminal simple setae; three-segmented exopod with naked proximal segment, middle segment bearing 10–11 aesthetascs arranged in two tiers, and distal segment with 3–4 aesthetascs and 1 simple seta.

Antenna (Fig. 4C).—Segments 1–7, progressing proximally to distally, each with 1,2,3,0,0,4,4 simple setae, respectively; two

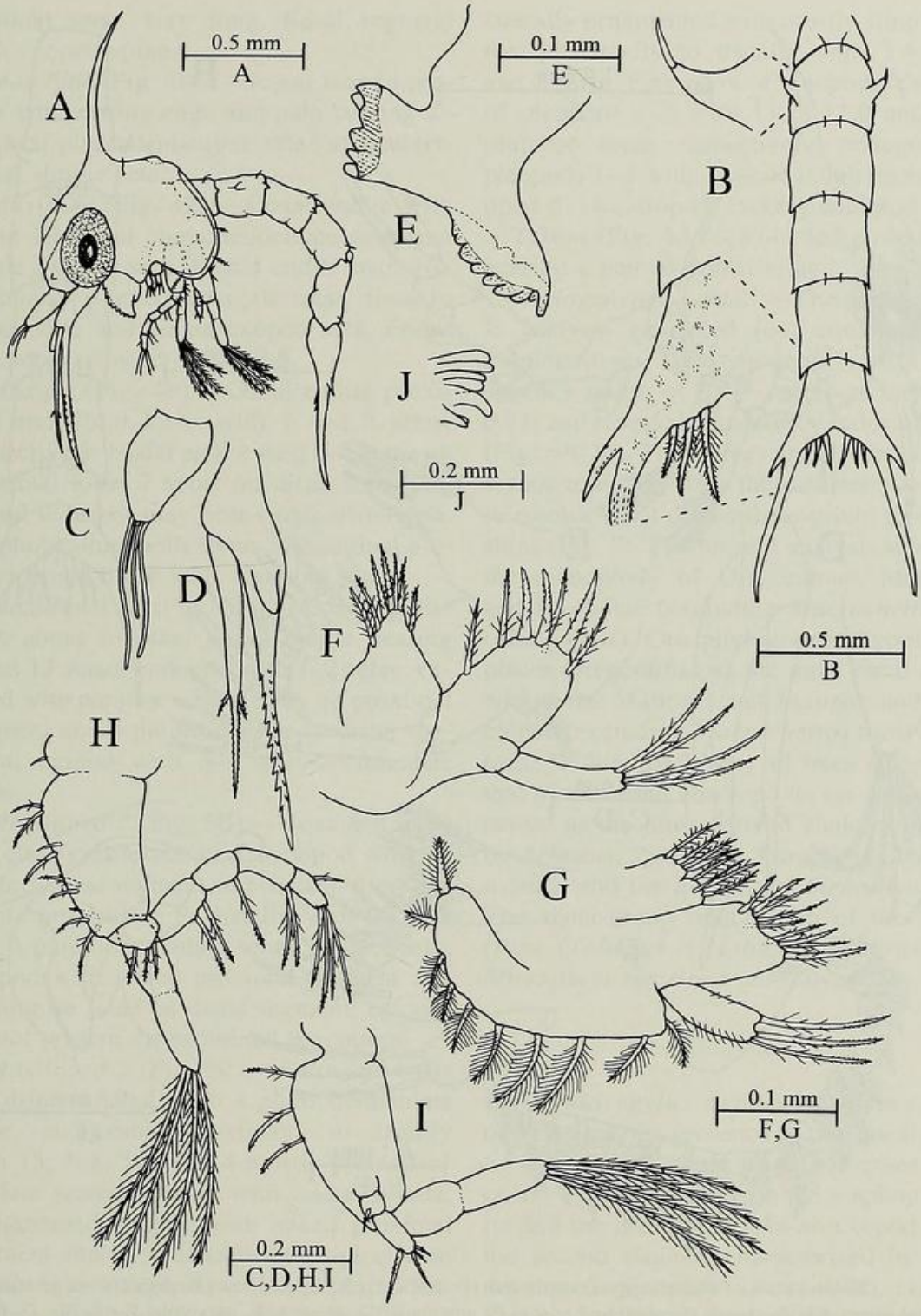

Fig. 2. First zoea of *Paradasygyius depressus* (Bell, 1835). A, lateral view; B, dorsal view of abdomen and telson, with enlargements of projection on somite 2 and proximal part of telson; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2; J, developing maxilliped 3 and pereiopods.

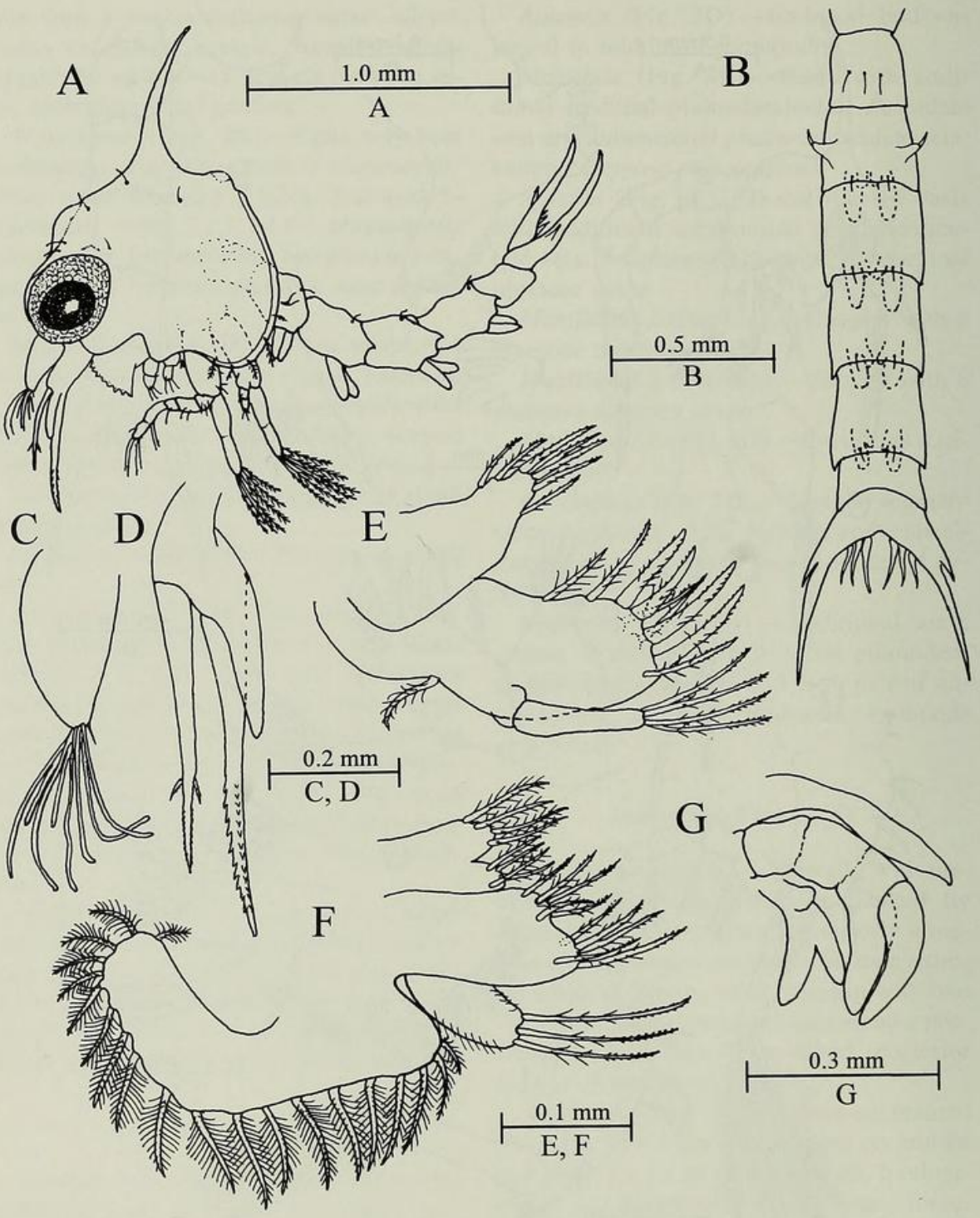

Fig. 3. Second zoea of *Paradasygyius depressus* (Bell, 1835). A, lateral view; B, dorsal view of abdomen (ventral pleopod buds shown stippled) and telson; C, antennule; D, antenna; E, maxillule; F, maxilla; G, developing maxilliped 3, cheliped and pereiopod 2.

terminal setae very long. Basal segment with exopod spine.

Mandible (Fig. 4D).—Scoop-shaped process with cutting edge and palp bearing 2–4 apical plumodenticulate setae and subterminal simple seta.

Maxillule (Fig. 4E).—Coxal endite with about 10 apical plumodenticulate setae and single exopod seta. Basial endite with 16–17 mostly plumodenticulate setae distal to endopodite and single exopod seta. Endopod setae reduced or lacking.

Maxilla (Fig. 4F).—Coxal endite proximal and distal lobes with 7 and 5 setae, respectively; basial endite with 6–7 setae on proximal lobe, 7 setae on distal lobe. Endopod reduced, may bear single distal seta. Scaphognathite with about 35 marginal plumose setae; blade with 4 simple setae.

Maxilliped 1 (Fig. 5A).—Coxal endite with about 6 setae, basial endite bearing about 12 setae; endopod with 1–2 setae; exopod with pappose seta distally on proximal segment and 4 plumose setae on distal segment; epipod with 3–4 plumodenticulate setae.

Maxilliped 2 (Fig. 5B).—Coxa and basis not clearly differentiated; endopod with indistinct basal segment, subsequent four segments proximally to distally with 0–1,1,3 and 4 plumodenticulate setae, respectively; exopod with naked proximal segment and 4 plumose setae on distal segment; epipodite not present on examined specimens.

Maxilliped 3 (Fig. 5C).—Coxa and basis not differentiated, with 4 plumodenticulate setae; endopodite proximally to distally with 13, 7–8, 5, 5 and 4 mostly plumodenticulate setae; ischium with crista dentata; bisegmented exopod with naked proximal segment and 4–5 reduced setae apically on distal segment; epipod with 1–2 plumodenticulate setae proximally and 3 distally.

Pereiopods (Fig. 5D–H).—Covered with mostly serrulate setae; coxa and ischium of pereiopods 1–5 with single spine, merus of cheliped with additional spine; dactyl of pereiopods 1–4 with spinules as shown.

Abdomen (Fig. 4A, 5I).—Dorsally and laterally ornamented with mostly simple setae, proximally to distally with 3,4,4,6,6 and 2 setae. Five pairs of pleopods, exopod of pleopods 1–5 with 11,11,11,9 and 2–3 plumose setae, respectively; endopod of pleopods 1–4 with 2–3 cincinnuli each, pleopod 5, i.e., uropod, lacking endopod.

Telson (Fig. 4A).—Rounded posteriorly, bearing a pair of dorsal setae

Phylogenetic analysis.—The phylogenetic analysis generated four equally parsimonious trees 173 steps long, with a consistency index of 0.66, retention index of 0.71, and rescaled consistency index of 0.47 (Fig. 6A–D). These trees and the strict consensus tree show that the data set was able to resolve most of the sister-group relationships (Fig. 7). The present analysis supports the monophyly of Oregoniinae, Majinae, and Inachinae (excluding *Macrocheira* incertae sedis). Our phylogenetic hypothesis places Oregoniinae as the most basal clade within the Majidae, and Majinae and Inachinae (excluding *Macrocheira*) form sister taxa. Within Inachinae, all trees suggested that *Inachus* and *Macropodia* are sister taxa nested as the most derived clade, followed by *Achaeus*, *Pyromaia*, *Paradasygyius*, *Anasimus*, and the most basal *Stenorhynchus*. The sister-group relationship of the clade (*Pisa* (*Taliepus* + *Libinia*), *Mithrax* and *Microphrys* remained unresolved (Fig. 7).

Discussion

Paradasygyius depressus shares with other majids the presence of two zoeal stages, in which the first stage possesses nine or more marginal setae on the scaphognathite and the maxillule lacks an exopod seta; the second stage is characterized by well developed pleopods (Rice 1980, 1988). Some of these characters are thought to support the monophyly of this family (Rice 1983). However, although the monophyly of Majidae seems to be well supported, the sister-group relationships within the family remain uncertain (Rice 1980, Griffin & Tranter 1986, Clark & Webber 1991,

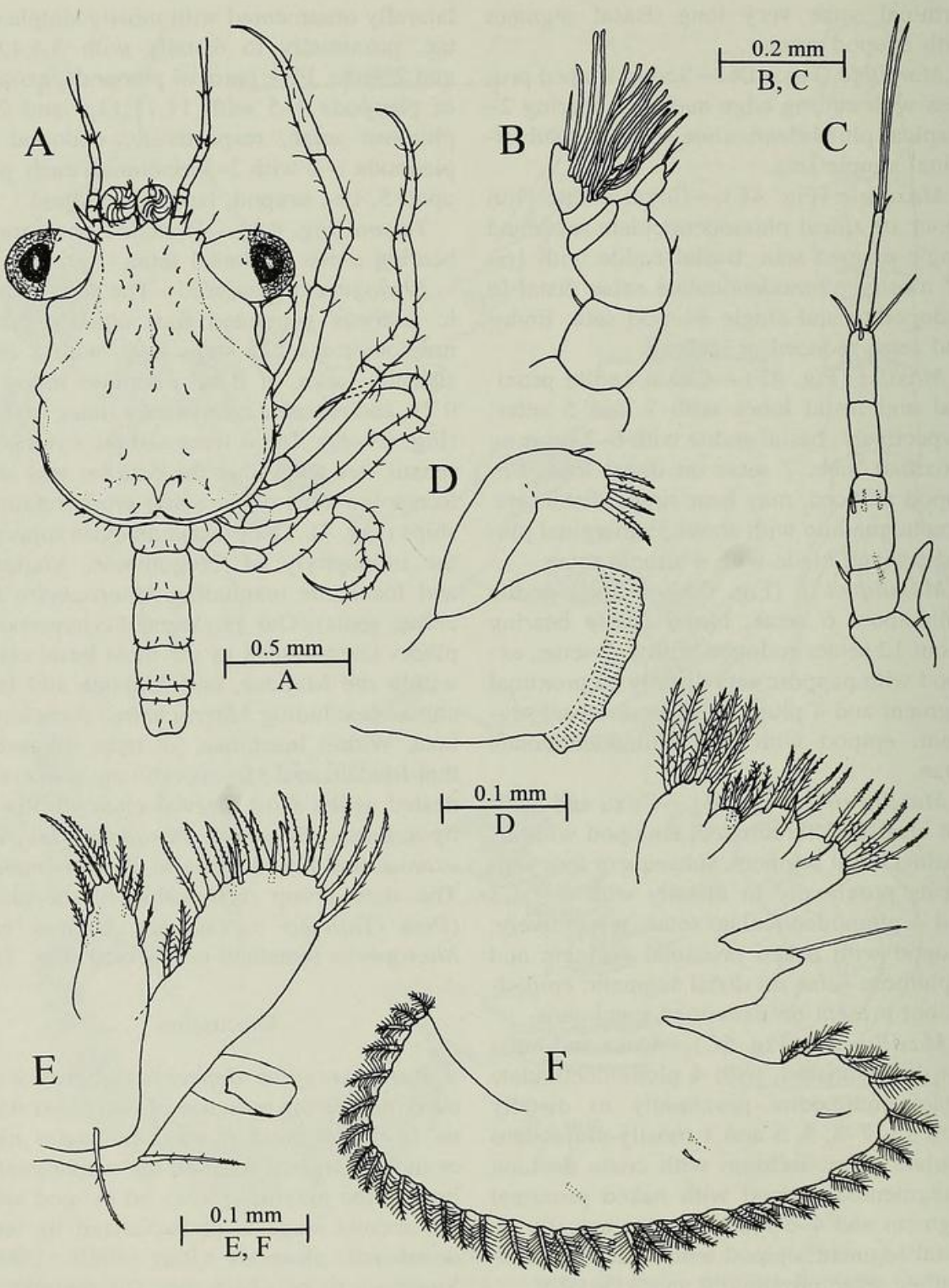

Fig. 4. Megalopa of *Paradasygyius depressus* (Bell, 1835). A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla.

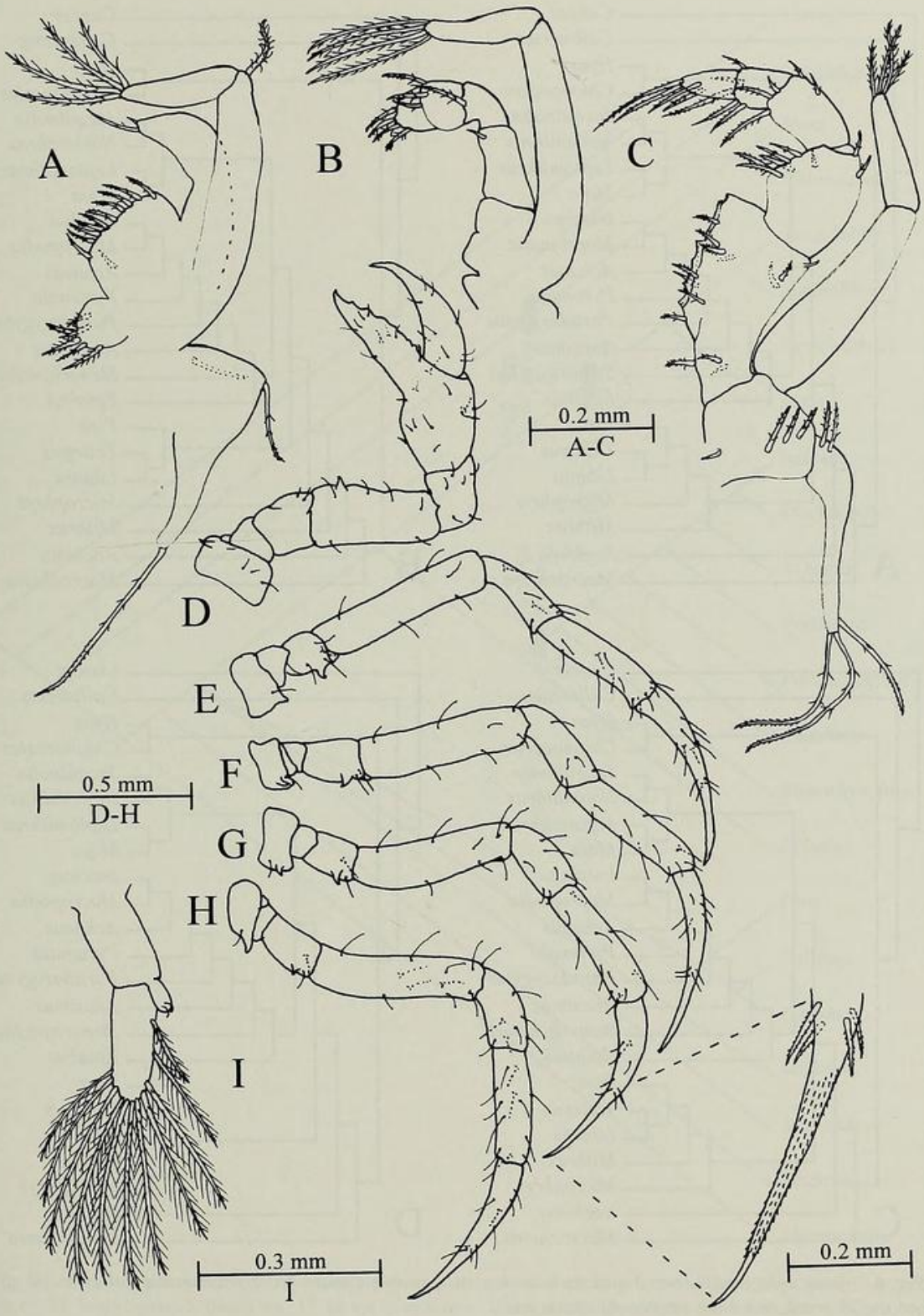

Fig. 5. Megalopa of *Paradasygyius depressus* (Bell, 1835). A, maxilliped 1; B, maxilliped 2; C, maxilliped 3; D, cheliped; E, pereiopod 2; F, pereiopod 3; G, pereiopod 4 with enlargement of distal part of dactyl; H, pereiopod 5; I, pleopod of third abdominal somite.

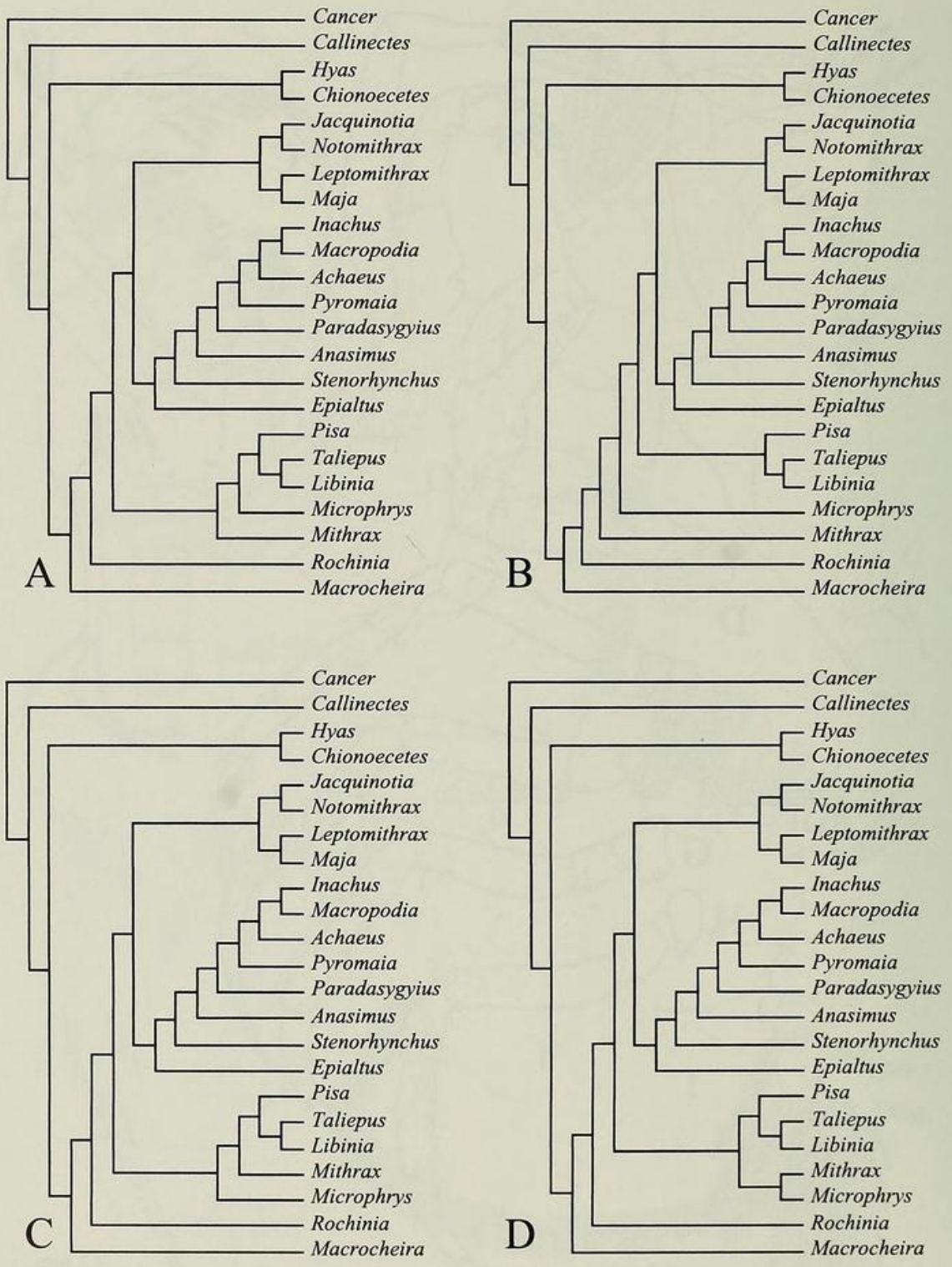

Fig. 6. Four most equally parsimonious trees depicting possible sister-group relationships of 21 majid genera based on 34 zoeal and three megalopal characters.

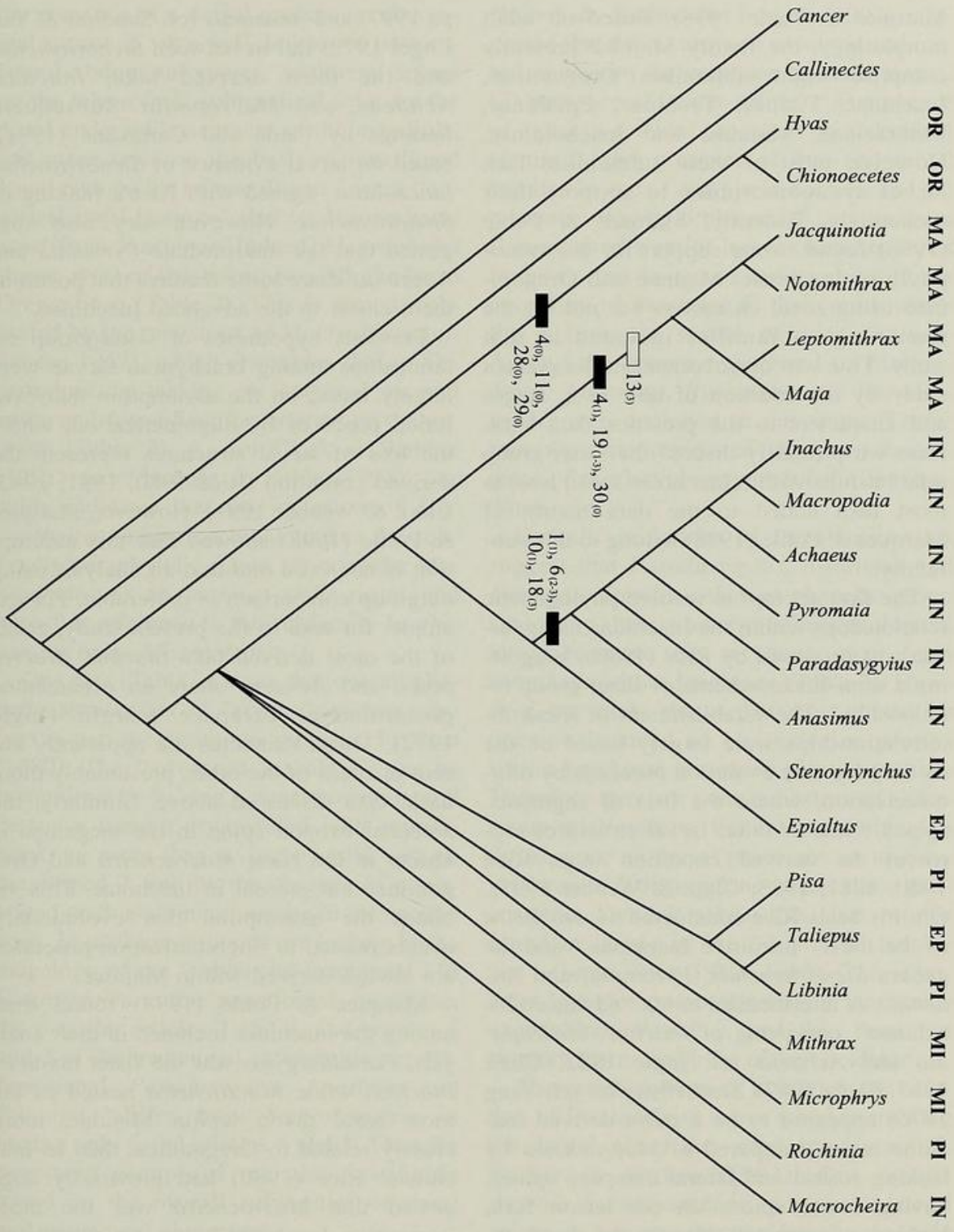

Fig. 7. Strict consensus tree of 4 equally parsimonious trees depicting hypothesized phylogenetic relationships of 21 majid genera based on 37 larval characters. Black rectangles represent character changes, open rectangles reversals. Large numbers represent a given character, small numbers enclosed within brackets represent a character state for a given character (see Marques & Pohle 1998 and materials and methods section of the present study for a detailed description of characters). EP, Epialtinae; IN, Inachinae, MA, Majinae; MI, Mithracinae; OR, Oregoniinae; PI, Pisinae.

Marques & Pohle 1998). Based on adult morphology, the family Majidae presently comprises eight subfamilies: Oregoniinae, Inachinae, Pisinae, Tychinae, Epialtinae, Mithracinae, Majinae, and Inachoidinae. However, most of these subfamilies lack larval synapomorphies to support their monophyly. Recently, Marques & Pohle (1998) found strong support for the monophyly of Inachinae, Majinae and Oregoniinae using zoeal characters but not for the remaining subfamilies included in that study. This was corroborated in the present study by the addition of new taxa, stages and characters to the previous data base. Here we primarily discuss the sister-group relationships within Inachinae sensu lato, as most taxa added to the data matrix of Marques & Pohle (1998) belong to this subfamily.

The first attempt to resolve phylogenetic relationships within the Inachinae using larvae was proposed by Rice (1980), suggesting a semi-linear scheme of sister-group relationships. The establishment of these interrelationships were largely based on the assumption that evolution proceeds by oligomerization, where the loss of segments, spines, setae or other larval structures represent the derived condition (e.g., Rice 1980, 1981, 1983; Clark & Webber 1991). On this basis Rice considered *Macrocheira* as the most "primitive Inachinae" and the genera *Stenorhynchus*, *Pyromaia*, and *Anasimus* as intermediate to his "advanced Inachinae" consisting of *Inachus*, *Macropodia* and *Achaeus* (cf. Ingle 1982, Clark 1983, Paula 1987). *Stenorhynchus* (cf. Yang 1976) appeared to be a more derived inachine taxon compared to *Macrocheira* by lacking rostral and lateral carapace spines, having fewer spines on the telson fork, lacking subterminal setae on the distal endopod segment of the maxillule, and the setation of the carapace margin and endopod of maxilliped 2 being intermediate in nature (Table 2). Rice (1980) further postulated that larvae of *Pyromaia* (cf. Webber & Wear 1981, Fransozo & Negreiros-Fransozo 1997) and *Anasimus* (cf. Sandifer & Van Engel 1972) fall in between *Stenorhynchus* and the most derived taxa, *Inachus*, *Achaeus*, and *Macropodia*. Subsequent findings by Paula and Cartaxana (1991), based on larval evidence of *Stenorhynchus lanceolatus*, agreed with Rice's ranking of *Stenorhynchus*. However, they also suggested that the intermediate *Pyromaia* and *Anasimus* share some features that positions them closer to the advanced Inachinae.

Previous hypotheses of sister-group relationships among brachyuran larvae were largely based on the assumption that evolution proceeds by oligomerization, where the loss of larval structures represent the derived condition (Rice 1980, 1981, 1983; Clark & Webber 1991). However, Marques & Pohle (1998) showed that this assumption is not valid and that an analysis using outgroup comparison is preferable. For example, for taxa in the present study, zoeas of the most derived taxa *Inachus*, *Macropodia* and *Achaeus* share an ornamented posterolateral carapace margin (Ingle 1992). These structures are apparently absent in zoeas of the other, presumably more basal taxa discussed above. Similarly, the antennal exopod spine in the megalopa is absent in the basal *Macrocheira* and Oregoniinae but present in Inachinae. This violates the assumption that evolutionary events related to oligomerization processes are always derived within Majidae.

Marques & Pohle (1998) found that, among the inachines included in their analysis, *Paradasygyius* was the sister taxon of *Inachus*, while *Macrocheira* nested as the most basal taxon within Majidae, more closely related to Oregoniinae than to Inachinae. Rice (1980) had previously suggested that *Macrocheira* was the most "primitive Inachinae", but he considered the subfamily to be monophyletic. It was Clark & Webber (1991) who first suggested that *Macrocheira* should not be included within Inachinae. They contend that the presence of rostral and lateral carapace spines, more submarginal carapace setae,

the presence of a dorsal process on abdominal somite 3, very well developed posterolateral abdominal spines, additional spines on the telson fork, subterminal setae on the distal endopodite segment of the maxillule, and more setae on the basis of maxilliped 1 and endopodite of maxilliped 2 were "ancestral zoeal features" that set *Macrocheira* apart from Inachinae. Indeed, *Macrocheira* shares most of these features with the basal Oregoniinae (Table 2). This is also corroborated by the megalopa of *Macrocheira* (cf. Tanase 1967), which resembles that of Oregoniinae in lacking an antennal exopod spine and fused flagellar articles on the antenna (Table 2). As for Clark & Webber (1991) and Marques & Pohle (1998), our study indicates that the inclusion of *Macrocheira* within Inachinae makes the subfamily paraphyletic. Thus, we consider *Macrocheira* as an *incertae sedis* taxon and hereafter reference to the subfamily Inachinae excludes *Macrocheira*.

Our data (Table 2) show that overall phenetic similarities of larval characters support in part the groupings proposed by Rice (1980). The "advanced Inachinae" can be recognized by having a zoeal posterolateral carapace margin ornamented with serrulations, no more than a single basial seta on maxilliped 2, and by the absence of a separated sixth abdominal somite in the second zoea. In addition, uropods are lacking in the megalopa of the "advanced Inachinae". In *Stenorhynchus*, the most basal Inachinae, the flagellar articles 2 and 3, and articles 4 and 5 of the megalopal antenna are not differentiated. *Paradasygyius*, *Anasimus* and *Pyromaia* differ from *Stenorhynchus* in having only fused articles 4 and 5. Thus the proposed groupings are also justifiable based on the overall similarities of zoeal and megalopal characters.

Drach & Guinot (1982, 1983) resurrected the family Inachoididae Dana, 1851, hereafter referred to as Inachoidinae, to include some American majids previously assigned to Inachinae and Pisinae, based on their distinct adult skeletal features. Subsequently, Guinot & Richer de Forges (1997) suggested that the (i) absence of lateral and rostral spines on the carapace of zoeal stages, (ii) presence of ocular spines, (iii) presence of a pair of acicular processes on abdominal somite 2, (iv) presence of five abdominal somites in zoea I and six in zoea II, and (v) presence of simple pleopodal buds in zoea II comprised a set of larval character states found in *Anasimus* and *Pyromaia* (with the exception of character ii) that could justify the taxomonic status of Inachoidinae. Among the genera transferred to Inachoidinae, *Anasimus*, *Pyromaia*, and *Paradasygyius* were included in our study. Therefore we can provide an improved assessment of the larval support for the Inachoidinae.

Overall similarities of larval characters suggest that *Paradasygyius*, *Anasimus* and *Pyromaia* form a coherent phenetic group since they share a number of morphological larval features that set them apart from some taxa within Inachinae (Table 2). However, our study shows that most characters previously used to characterize groups within Inachinae constitute plesiomorphies. Therefore they are poor indicators of sister-group relationships. For instance, although the absence of dorsal processes on abdominal somite 3 distinguishes these three genera from *Stenorhynchus*, this state is also found in larvae of the "advanced Inachinae" (sensu Rice 1980, 1983). This character is a synapomorphy for all inachinids except *Stenorhynchus*, and thus does not support the monophyly of Inachoidinae.

The same problem of justifying the erection of Inachoidinae arises when examining the larval characters used by Guinot & Richer de Forges (1997). Our results showed that character (i), the loss of lateral spines, is a synapomorphy for a large clade that encompasses members of all subfamilies except Oregoniinae. Also, the loss of rostral spines is a synapomorphy for Inachinae including taxa assigned to the Inachoidinae (character $1_{(1)}$, Fig. 7). We found that the presence of a distinct pair of acic-

Table 2.—Comparison of larval characters of selected taxa representing, left to right, presumably derived Inachinae (*Inachus, Macropodia, Achaeus*), Inachoidinae (*Paradasygyius, Anasimus, Pyromaia*), intermediate Inachinae (*Stenorhynchus*), ancestral Inachinae (*Macrocheira*), and Oregoniinae (*Hyas, Chionoecetes*), representing basal Majidae.

Taxon	Derived Inachinae	*Paradasygyius depressus*	*Anasimus latus*	*Pyromaia tuberculata*	Intermediate Inachinae	Ancestral Inachinae	Basal Majidae: Oregoniinae
Sources	Clark 1983; Ingle 1982, 1992; Paula 1987	present study	Sandifer & Van Engel 1972	Fransozo & Negreiros-Fransozo 1997	Yang 1976	Clark & Webber 1991; Tanase 1967	Pohle 1991
Character							
Zoea:							
Carapace spines	dorsal only	dorsal only	dorsal only	dorsal only	dorsal only	dorsal, rostral, lateral	dorsal, rostral, lateral
Carapace spines	smooth	smooth	smooth	smooth	smooth	smooth	spinulose
Carapace post. tubercle	absent?	present	none shown	indistinct	present	present	present
Posterolateral carapace margin	ornamented	smooth	smooth	smooth	smooth	smooth	smooth
Carapace margin zoea I	1–3 setae	3–4 setae	3 (+?) setae	3–4 setae	4–5 setae	8 setae	4–6 setae
Eye papilla or 'spine'	?	small	very distinct	small	present	?	present
Antenna 2 exopod setae	2, midpoint	2, ⅔ distance	2, ⅔ distance	2, midpoint	2, ⅔ distance	2, apically	2, apically
Maxillule endopod segment 1	unarmed	unarmed	unarmed	unarmed	unarmed	armed with seta	armed with seta
Maxillule endopod segment 2	3 (*Macropodia*) and 4 terminal setae	4 terminal setae	3 terminal setae	4 terminal setae	4 terminal setae	4 terminal setae	4 terminal setae
Maxillule endopod segment 2	no subterminal setae	no subterminal setae	no subterminal setae	no subterminal setae	no subterminal setae	with subterminal setae	with subterminal setae
Maxilliped 1 basis setation	2,2,2,3	2,2,2,3	2,2,2,3	2,2,2,3*	2,2,2,3	2,2,3,3	2,2,3,3
Maxilliped 2 basis	0 or 1 seta	3 setae	3 setae	3–4 setae**	3 setae	3 setae	4 setae
Maxilliped 2 endopod segments	3	3	3	2 or 3***	3	3	3
Maxilliped 2 endopod setation	0,0–1,4–5	0,1,4	0,1,4	1,4 or 0,1,4***	0,1,5	1,1,5	1,1,5

Table 2.—Continued.

Taxon	Derived Inachinae	*Paradasygyius depressus*	*Anasimus latus*	*Pyromaia tuberculata*	Intermediate Inachinae	Ancestral Inachinae	Basal Majidae: Oregoniinae
Abdomen somite 2	non-acicular curved processes	acicular curved processes	acicular curved processes	acicular curved processes	non-acicular curved processes	non-acicular curved processes	non-acicular curved processes
Abdomen somite 3	no dorsal processes	no dorsal processes	no dorsal processes	no dorsal processes	curved dorsal processes	curved dorsal processes	curved dorsal processes
Abdomen postero-lateral spines	well developed	small	small	absent	small	very well developed	very well developed
Abdomen somite 6, zoea 2	not separated	separated	separated	separated	separated	separated	separated
Zoea II endopod of pleopod	?	very small	very small	?	?	small	small
Telson fork	1 spine	1 spine	1 spine	1 spine	1 spine	3 spines	2 spines
Megalopa							
Uropods	absent	present	present	present	present	present	present
Antenna exopod spine	present	present	present	absent	present	absent	absent
Antenna fused flagellar articles	*Macropodia*: 2&3 *Inachus, Achaeus*: 2&3, 4&5	4&5	4&5	4&5	2&3, 4&5	none	none

* Webber & Wear (1981) illustrate 2,2,2,3 but state 2,2,2,2 in text, while Fransozo & Negreiros-Fransozo (1997) indicate 2,2,2,2 but now confirm 2,2,2,3 (in litt.); ** Fransozo & Negreiros-Fransozo (1997) indicate 4 setae, in litt. revealed 3–4 setae; *** discrepancy between Webber & Wear (1981) and Fransozo & Negreiros-Fransozo (1997), former claiming 2 segments with 1,4 setae, latter giving 3 segments with 0,1,4 setae.

ular curved processes on abdominal somite 2 (iii) could be a putative synapomorphy for the three genera included in Inachoidinae. However, this character did not hold as a synapomorphy for this group when the data were submitted to cladistic analysis. Our analysis suggested that an abdomen composed of five abdominal somites in zoea I and six somites in zoea II (iv) is plesiomorphic for the taxa included in Inachoidinae, since the absence of the 6th abdominal somite in zoea II supports the monophyly of (*Achaeus* (*Inachus* + *Macropodia*)). Finally, the presence of ocular papillae or spines (ii) and simple pleopodal buds in zoea II (v) should be considered in the phylogenetic analysis. However, we found that, among the taxa included herein, it was difficult to define the states of these characters since the taxa differed extensively in the degree of development of these structures or were inadequately described (Table 2).

The inclusion of additional taxa and characters in the matrix used by Marques & Pohle (1998) suggested that the phenetic agreement discussed above does not hold when the data is submitted to cladistic analysis (Figs. 5A–D, 7). Our phylogenetic hypothesis for 21 genera of Majidae supports Rice's (1980) contention that *Inachus*, *Macropodia*, and *Achaeus* are the most derived taxa within the subfamily Inachinae, and that *Pyromaia* and *Anasimus* are nested between the most derived taxa and the basal *Stenorhynchus* (Fig. 7). However, the inclusion of *Paradasygyius*, whose larvae were unknown to Rice, suggested that *Pyromaia* is relatively more derived than *Anasimus* (Fig. 7) (contra Rice 1980). Finally, we found no larval evidence to support the monophyly of Inachoidinae despite the phenetic similarities discussed above for three genera presently included within this subfamily (contra Drach & Guinot 1982, 1983; Guinot & Forges 1997).

The most relevant aspect of the phylogenetic hypotheses presented herein is that within Majidae the subfamilies Oregoniinae, Majinae, and Inachinae can be defined by sets of larval synapomorphies (Fig. 7). The monophyly of Oregoniinae is supported by four characters: zoea I exopod of the antenna bearing a minute terminal spine, less than half the length of smaller apical seta ($4_{(0)}$); distal basial lobe of the maxilla in zoea I with five setae ($11_{(0)}$); mid-dorsal region of the fourth and fifth abdominal somites with paired setae in zoea II ($28_{(0)}$–$29_{(0)}$). The subfamily Majinae is supported by the zoeal exopod of the antenna bearing a well developed terminal spine half or more the length of apical setae but not extending beyond the tip of setae ($4_{(1)}$); proximal coxal lobe of the maxilla in zoea II bearing three setae ($13_{(3)}$); scaphognathite bearing 21–28 setae in zoea II ($19_{(1-3)}$); and presence of three lateral spines on the fork of the telson ($30_{(0)}$). Finally, the subfamily Inachinae forms a monophyletic group based on the loss of a rostral carapace spine ($1_{(1)}$); presence of four or three setae on the distal portion of the endopodite of the maxillule ($6_{(2-3)}$); proximal coxal lobe of the maxilla in zoea I bearing four setae ($10_{(1)}$); and the scaphognathite bearing 11 setae in zoea I ($18_{(3)}$).

Our phylogenetic hypothesis showed no larval support for the monophyly of the subfamilies Epialtinae, Mithracinae, and Pisinae. Within Epialtinae, *Epialtus* nested basally to Inachinae, whereas, *Taliepus* nested as sister taxon of *Libinia*, member of Pisinae (Fig. 7). For the subfamily Mithracinae, represented by *Mithrax* and *Microphrys*, the analysis was unable to resolve the relationships between these taxa and other majids, since they nested in a polytomy with the clade (*Pisa* (*Taliepus* + *Libinia*)). However, one of the four most parsimonious trees suggested that *Mithrax* and *Microphrys* are sister taxa (Fig. 6D). Finally, there was no support to the monophyly of Pisinae since *Pisa* and *Rochinia* did not nest as sister taxa (Fig. 6) in any trees.

Three clades, including Oregoniinae, Inachinae, and Majinae, support the taxonomic arrangement based on adult morphology.

Although the taxonomy of Majidae is not based on a cladistic framework, the agreement between the larval phylogeny and adult taxonomy suggests that larval characters covary with adult morphology to the extend that both indicate, with a given degree of fidelity, the same nested groups. If that is true, the disagreement between the larval phylogeny and traditional taxonomy indicates that the adult characters used on the taxonomy of Epialtinae, Inachoidinae, Mithracinae, and Pisinae are poor indicators of sister-group relationships. Thus, some general recommendations can be drawn from our study. First, since larval information was useful to define nested sets, there is no reason to exclude larval data as diagnostic characters on any taxonomic level. However, because most of the characters supporting the monophyly of subfamilies are homoplastic, one cannot delimit these taxonomic groups on the basis of a single larval character. Instead sets of larval characters should be used in defining assemblages among Majidae or other Brachyura. Second, because no larval support was found for the monophyly of Epialtinae, Inachinoidinae, Mithracinae, and Pisinae, further evidence is required to resolve the taxonomic status of these groups. This can be achieved by re-examining adult characters and by using larval information of other genera to define these subfamilies within a phylogenetic framework. Finally, few megalopal characters have been used in phylogenetic analysis despite their high information content (Marques & Pohle 1995, Pohle & Marques 1998). This is mostly due to poor or lacking descriptions in the literature (Clark et al. 1998). If more attention is given to this larval stage by carcinologists working on larval descriptions, a higher number of megalopal characters can be analyzed cladistically to improve and/or test the monophyly of groups already established by zoeal and adult morphology.

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Appendix 1.—Input data matrix of 37 characters and 21 taxa of Majidae in NEXUS file format (Swafford 1998). Outgroups are the first two genera listed. Multistate characters are indicated by brackets and missing data as ?.

```
#NEXUS
[Pohle & Marques, phylogeny for 21 genera of Majidae]
BEGIN DATA;
DIMENSIONS NTAX=23 NCHAR=37;
FORMAT SYMBOLS= '' 0 1 2 3 4 5 6'' MISSING=? ;OPTIONS
MSTAXA=POLYMORPH;
MATRIX
Cancer                  001200(03)1(02)210(13)(01)(01)014(06)(01)?01?311111(01)00(01)000
Callinectes             00(01)?(01)0(03)2(03)210(03)(02)(02)014(06)1(01)010311111000(01)0(01)0
Hyas                    000000(01)11100200013300010200001000000l
Jacquinotia             01110021121131112011110121111101000???
Leptomithrax            00110011221131102221110010111101000???
Rochinia                00120001201001101220111121010121000012
Inachus                 11131221211221122351212131111121101114
Macrocheira             00010000011021100000100001111010000l
Maja                    00110011221131112231112010111010000(23)
Pisa                    01120011101111112340100120111212?0001(23)
Taliepus                01120101101211122321112010011210000l2
Notomithrax             01110021221131112131110121111010000(23)
Chionoecetes            00000001110020001l(01)000102000010000001
Libinia                 011201(01)1111121112(23)(45)011211001121000012
Mithrax                 01120001201111112120l1(12)11011121000012
Microphrys              0112000120111(12)(12)(12)(12)1(34)011111011121000012
Paradasygius            11121211213211313(34)111211111121010012
Macropodia              11131321211221122 3(56)121(12)12111121101113
Achaeus                 111312?????3?????360212121111121101114
Anasimus                11121311211121112341112121111121010012
Pyromaia                11131220111312232341(01)12121111?1010002
Stenorhynchus           11121211211121(12)123(45)111201111121000014
Epialtus                011210(01)2(01)20(01)222021?111211111121000012;
END;
BEGIN ASSUMPTIONS;
OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS;
ANCSTATES allzero = 0:ALL;
END;
```