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Zoeal stages of *Pseudomicippe varians* Miers, 1879 (Decapoda: Brachyura: Majoidea: Majidae) and a comparison with other Majidae larvae

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Abstract

Pseudomicippe varians Miers, 1879 is a majid crab recorded from Western Australia (Shark Bay) and northern Queensland. The zoeal stages are described from laboratory reared material. The zoeal stages of *P. varians* can be easily distinguished by the absence of carapace spines and extremely large mandibles. These characters are likely diagnostic among majoideans in general. Additionally, recent phylogenetic studies of majoids using larval characters showed the Majidae as one of the few families for which there is larval support for its monophyly. Furthermore, based on the monophyly of Majidae and the morphology of *P. varians*, a set of characters is established that could be used as a diagnostic for majids in general.

Keywords: Larval development, Majidae, Pseudomicippe varians

Introduction

The family Majidae (sensu Martin and Davis 2001), previously considered as the subfamily Majinae, includes 20 genera, with the majority of 70 species occurring in the Indo-west Pacific, the remaining members consisting of two monotypic genera in the east Pacific, and three genera with few species in Atlantic waters (Griffin & Tranter 1986). However, knowledge on the larval morphology of this family is restricted to 11 species. Larval accounts for Majidae are available for species of Maja Lamarck, 1801 (Couch 1843; Bell 1844; Claus 1876; Cano 1893; Schlegel 1911; Lebour 1927; Bourdillon-Casanova 1960; Heegaard 1963; Terada 1981; Paula 1985, 1988; Clark 1986; Ingle 1991; Rodriguez 2002), Schizophrys White, 1848 (Kurata 1969; Kakati & Nayak 1979; Tirmizi & Kazmi 1987), Notomithrax Griffin, 1963 (Webber & Wear 1981), Jacquinotia Rathbun, 1915 (Webber & Wear 1981), and Leptomithrax Miers, 1876 (Kurata 1969; Webber & Wear 1981).

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Within this family, the genus *Pseudomicippe* Heller, 1861 is represented by 11 species distributed throughout the Indo-west Pacific region. *Pseudomicippe varians* Miers, 1879 occurs in Western Australia (Shark Bay), and northern Queensland (Griffin & Tranter 1986).

The purpose of this is to describe the zoeal stages of *P. varians*, which comprise the first larval description for the genus. In addition, the zoeal information available in the literature is used to compare the findings of this study with those of other species previously described for this family.

Materials and methods

Larval development and description

A single ovigerous specimen of *Pseudomicippe varians* was collected in August 2001 on seaweed beds, in Heron Island, Queensland, Australia $(23^{\circ}27'S, 151^{\circ}55'E)$. The specimen was held in an aquarium in a temperature-controlled room $(24\pm1^{\circ}C)$ until hatching, which occurred at night. After hatching, 50 of the most active, positively phototactic larvae were placed individually into 100 ml acrylic jars containing 50 ml of filtered seawater. The remaining larvae were kept in mass culture as extra specimens to be used for morphological description.

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

Whenever possible, a minimum of five specimens of each stage were dissected for morphological description. For slide preparations polyvinyl lactophenol was used as the mounting medium with acid fuchsin and/or chlorazol black stains. The description of setae follows Pohle and Telford (1981), but here includes only analysis by light microscopy (LM), using an Olympus BX-51 microscope with Differential Interference Contrast and drawing tube. Some of the setae designated as plumose herein may be plumodenticulate setae because of the lower resolution limits of LM as compared to scanning electron microscopy (SEM). Description guidelines of Clark et al. (1998) were generally followed.

Specimens of larval stages and a spent female crab have been deposited at the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil, accession number 17281.

Results

Larval development and description

Zoeal development of *Pseudomicippe varians* consists of two zoeal stages. The duration of the first zoeal stage was 4-11 days (3.9 ± 0.3) , 5-12 days (5.0 ± 0.6) for the second stage. It was not possible to obtain megalop stages because of fungus infection in our culture that arrested the development of the second zoeal stage leading to death. Only morphological changes are described for the second zoea.

Description

Pseudomicippe varians Miers, 1879 First zoea (Figure 1)

Carapace (Figure 1A). Dorsal, rostral, and lateral spines absent. Ventral margin posterior to scaphognathite notch with small plumodenticulate seta preceding densely plumose

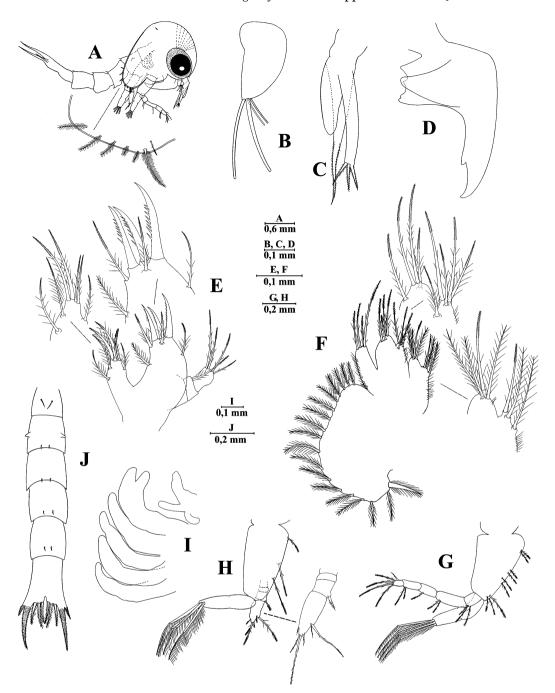


Figure 1. First zoea of *Pseudomicippe varians* Miers, 1879. A, lateral view; B, antennule; C, antenna; D; mandible; E, maxillule; F, maxilla; G, maxilliped 1; H, maxilliped 2; I, developing maxilliped 3 and pereiopods; J, dorsal view of abdomen and telson.

"anterior seta", followed by five plumose setae. Eyes sessile. Small indistinct median ridge frontally and a small median tubercle on posterodorsal margin, each bearing cuticular dorsal organ (*sensu* Martin and Laverack 1992). Pair of simple setae present on posterodorsal margin.

Antennule (Figure 1B). Unsegmented, smooth, conical. Terminally bearing two long, two shorter aesthetascs.

Antenna (Figure 1C). Biramous, spinous process of the protopod pointed, bearing two rows of sharp spinules; endopod bud present with half of the exopod length; one-segmented exopod shorter than protopod with two subterminal setae with similar size.

Mandible (Figure 1D). With medial toothed molar process and much enlarged lateral incisor processes, as long as antenna. Palp absent.

Maxillule (Figure 1E). Epipod seta absent. Coxal endite bearing seven setae, four terminal setae (two plumodenticulate and two graded plumodenticulate), subterminally with three plumodenticulate setae. Basial endite with three terminal cuspidate setae and four subterminal setae, three plumodenticulate and one plumose. Two-segmented endopod with proximal segment bearing plumodenticulate seta, distal segment bearing two pairs of plumodenticulate setae apically. Exopod seta absent.

Maxilla (Figure 1F). Coxal endite bilobed, proximal lobe with three setae, two plumose and one plumodenticulate; distal lobe with four setae, three plumose and one plumodenticulate. Basial endite bilobed, proximal and distal lobes with four to five and four plumodenticulate setae, respectively. Microtrichia present on both endites. Unsegmented endopod unilobed, with four apical plumodenticulate setae; microtrichia on lateral margin. Scaphognathite with 18 marginal densely plumose setae, including distal process.

Maxilliped 1 (Figure 1A, G). Coxa naked. Basis with nine plumodenticulate setae arranged 2,2,2,3. Endopod five-segmented with 3,2,1,2,5 (one subterminal, four terminal) plumodenticulate setae. Bisegmented exopod with four terminal plumose natatory setae.

Maxilliped 2 (Figure 1A, H). Coxa naked. Basis with three plumodenticulate setae. Endopod three-segmented, with 0,1,6 plumodenticulate setae of different types, two anterior, two medial, two apical on terminal segment. Bisegmented exopod with four terminal plumose natatory setae.

Maxilliped 3 (Figure 1I). Biramous. Endopod, exopod and epipod present

Pereiopods (Figure 11). Present with bilobed chela.

Abdomen (Figure 1A, J). Five somites. Somite 1 with pair of middorsal plumodenticulate setae, somites 2–5 each with pair of shorter posteromedial simple setae. Posterolaterally, somites 2, 4 and 5 with blunt process, somite 3 with spine; somite two with pair of dorsolateral processes. Grouped denticulettes present. Pleopods absent.

Telson (Figure 1J). Bifurcated, distinct median notch, three 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 (Figure 2)

Carapace (Figure 2A). Eyes stalked. Posterolateral margin with nine setae, one densely plumose followed by eight plumose setae.

Antennule (Figure 2B). With four long aesthetascs and one short simple seta, endopod bud present.

Antenna (Figure 2C). Endopod bud enlarged to beyond middle of protopodite.

Mandible (Figure 2D). Palp bud absent.

Maxillule (Figure 2E). Basial endite now with eight setae, three terminal cuspidate setae and five subterminal setae, four plumodenticulate and one plumose. Exopod pappose seta present.

Maxilla (Figure 2F). Scaphognathite with 28 marginal plumose setae.

Maxilliped 1 (Figure 2A). Exopod with six plumose natatory setae.

Maxilliped 2 (Figure 2A). Exopod with six plumose natatory setae.

Maxilliped 3 (Figure 2H). Developing. Endopod showing segmentation.

Pereiopods (Figure 2H). Longer, chela enlarged. Some segmentation apparent.

Abdomen (Figure 2G). Additional sixth somite. Somites 2–5 with posterolateral spines, a pair of unsegmented biramous pleopods on somites 2–5, endopods very small.

Telson (Figure 2G) Unchanged.

Discussion

Taxonomic grouping

The zoeae of *Pseudomiccipe varians* conform to previous characterizations of this phase for Majoidea (Rice 1980, 1983) in having nine or more setae on the scaphognatite of the maxilla, and well-developed pleopods in the second zoeal stage. However, *P. varians* does not share the characters proposed by Ingle (1979) for the family Majidae, which he divided into two groups according to morphological resemblance. Ingle's (1979) larval classification of the Majidae (i.e. his Majinae) included species of the genera *Maja* and *Schyzophrys*. The zoeae of the group I taxa are diagnosed by the presence of lateral carapace spines; a dorsal spine that is often well developed and usually of moderate length; a prominent rostral spine; dorso-lateral processes on abdominal segments two and three; and posterolateral processes on abdominal somites 3–5 that are prominent and sometimes

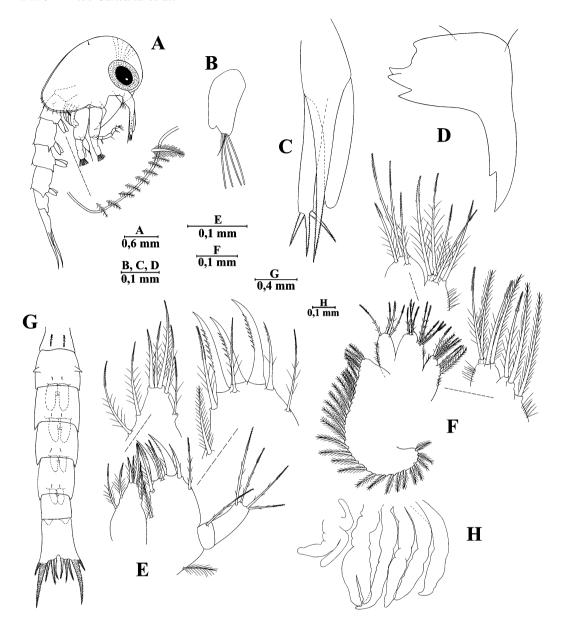


Figure 2. Second zoea of *Pseudomicippe varians* Miers, 1879. A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, developing maxilliped 3 and pereiopods; H, dorsal view of abdominal somites 1–6, showing ventral pleopods as stippling.

long. The group II, which comprises the genera *Leptomithrax* and *Acanthophrys*, is characterized in zoeal stages by the absence of lateral carapace spines; dorsal spine sometimes reduced or absent; rostral spine sometimes reduced; dorso-lateral processes only on abdominal somite two; and posterolateral processes on abdominal somites 3–5 that are not prominent and sometimes short. The zoeal stages of *P. varians* agree with Group II in having no dorsal or lateral carapace spines; a dorsolateral process that is restricted to

abdominal somite 2; posterolateral processes on abdominal somites 3–5 being short; the basal segment of maxilliped 2 with no more than three marginal setae; and the antennal exopod having terminal setae. However, *P. varians* differs substantially in lacking a rostral spine and in having only one spine on each telson fork (Tables I and II).

Among the Majidae the zoeal stages of *Pseudomiccipe varians* can be easily distinguished by lacking rostral, dorsal, and lateral spines, the relative size of the mandible that is as long as the antenna, and the number of furcal spines (Tables I and II). The absence of carapace spines and very large mandible are especially distinctive and likely diagnostic among majoideans in general.

Larval comparison and taxonomic affinities among species of Majidae

Within Majidae, a considerable number of workers have addressed the larval descriptions for species of Maja, Schizophrys, Jacquinotia, Notomithrax, and Leptomithrax. However, some of these accounts are not suitable for comparisons because they lack descriptions of appendages or stages, as is the case for the descriptions of Schizophrys aspera (Milne-Edwards, 1834) (cf. Kurata 1969; Tirmizi & Kazmi 1987), Leptomithrax edwardsi (de Haan, 1839) and L. bifidus Ortmann, 1893 (cf. Kurata 1969), and L. longimanus Miers, 1876 (cf. Webber & Wear 1981). Descriptions of the three species of majids by Kurata (1969) lack zoeal information such as on the maxillule, maxilla and other possibly distinctive appendages. The description of Tirmizi and Kazmi (1987) for S. aspera was included in Tables I and II, but the data should be viewed with caution because of considerable disparities between illustrations and descriptions. Due to the inaccurate or incomplete nature of these older descriptions, the comparisons we make are based on the most recent larval descriptions or those we consider to provide adequate morphological information.

The genus Jacquinotia, represented by J. edwardsii (Jacquinot 1853), was considered as a member of the family Mithracidae by Webber and Wear (1981). However, Griffin and Tranter (1986) placed this monotypic genus within the family Majidae based on several adult characters, and we followed this taxonomic placement here since the larval characters for this genus match the pattern observed for Majidae. Additionally, the genus Eurynome Leach, 1814, traditionally viewed as a member of the family Pisidae (Sakai 1965, 1976; Griffin 1966; Ingle 1980, 1991; Salman 1982; Aiyun & Siliang 1991; Santana et al. 2004), was placed in the family Majidae by Hale (1927–1929) and by Griffin and Tranter (1986). In this case we do not follow Hale's or Griffin and Tranter's approach, leaving the genus as a member of Pisidae based on the differences with the majid larval characters. This is largely based on the setation of the maxilla, first maxilliped, and other appendages (Tables I and II). The genus Acanthophrys A. Milne-Edwards, 1865, traditionally considered as a majid (Griffin 1966; Kurata, 1969; Ingle 1979; Clark 1986), was placed in the family Pisidae by Griffin and Tranter (1986). However, due to the lack of larval information we could not make any assertion on the position of the genus, and we do not include Acanthophrys in the comparisons.

Based on morphological comparisons (Tables I and II), several characters appear to be diagnostic for some majid genera. For species of *Maja*, the presence of rostral, dorsal and lateral spines (also in *Leptomithrax longipes* (Thomson 1902)), and dorsolateral processes on the second and third abdominal somites in both zoeal stages are diagnostic for this genus. For *Schizophrys*, the setation of the basial endite of the maxillule in zoea I, and the setation of the basis of the first maxilliped, and basial endite of the maxilla in both zoeal stages are

Table I. Comparison of larval characters of the first zoeal stage for Majidae genera.

Zoea 1	Pseudomicippe varians Present study	Maja crispata Rodriguez (2002)		Maja squinado Clark (1986)	Schizophrys aspera Tirmizi and Kazmi (1987)	Notomithrax peronii Webber and Wear (1981)	Notomithrax ursus Webber and Wear (1981)	Notomithrax minor Webber and Wear (1981)	edwardsii Webber and	Leptomithrax longipes Webber and Wear (1981)
carapace	RS: absent;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;
	DS: absent;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;
	LS: absent;	LS: present;	LS: present;	LS: present;	LS: present;	LS: absent;	LS: absent;	LS: absent;	LS: absent;	LS: present;
	7 s ventral	6 s ventral	6 s ventral	7 s ventral	6 s ventral	7 s ventral	5 s ventral	5 s ventral	6 s ventral	5 s ventral
	margin	margin	margin	margin*	margin	margin	margin	margin	margin	margin
antennule	4 aes	4 aes	4 aes, 1 s	4 aes, 2 s	4 aes	5 aes	4 aes	5 aes	4 aes	6 aes
antenna	exo <pro< td=""><td>exo>pro</td><td>exo≤pro</td><td>exo:</td><td>exo<pro;< td=""><td>exo=pro</td><td>exo≤pro*</td><td>exo=pro</td><td>exo≤pro*</td><td>exo≤pro*</td></pro;<></td></pro<>	exo>pro	exo≤pro	exo:	exo <pro;< td=""><td>exo=pro</td><td>exo≤pro*</td><td>exo=pro</td><td>exo≤pro*</td><td>exo≤pro*</td></pro;<>	exo=pro	exo≤pro*	exo=pro	exo≤pro*	exo≤pro*
maxillule	cox: 7;	cox: 7;	cox: 7;	cox: 7;	cox: 7;	cox: 7*;	cox: 7*;	cox: 6;	cox: 6*;	cox: 7;
	bas: 7;	bas: 7;	bas: 7;	bas: 7;	bas: 8;	bas: 7*;	bas: 7*;	bas: 7;	bas: 7*;	bas: 7;
	end: 1, 4	end: 1, 6	end: 1, 6	end: 1, 6	end: 1, 5	end: 1, 5*	end: 1, 5*	end: 1, 3	end: 1, 6*	end: 1, 6*
maxilla	cox: 3, 4;	cox: 3, 4;	cox: 3, 4;	cox: 3, 4;	cox: 3, 4;	cox: 3, 3*;	cox: 3, 4*;	cox: 3, 3;	cox: 3, 4*;	cox: 3, 4;
	bas: 4-5, 4;	bas: 5, 4;	bas: 5, 4;	bas: 5, 4;	bas: 3, 5;	bas: 5, 4*;	bas: 5, 4*;	bas: 5, 4;	bas: 5, 4*;	bas: 4, 4;
	end: 4;	end: 5;	end: 5;	end: 5;	end: 4;	end: 5*;	end: 5*;	end: 4;	end: 5*;	end: 5;
	sca: 18	sca: 12-13	sca: 15	sca: 12	sca: 14	sca: 11-12	sca: 11-12	sca: 10-11	sca: 16	sca: 13
mxpd 1	cox: 0;	cox: 1;	cox: n/a;	cox: n/a;	coxa 0;	cox: 1*;	cox: 1*;	coxa 0;	cox: 1*;	cox: 1*;
	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,
	2, 3;	2, 3;	2, 3;	2, 3;	2, 2;	2, 3*;	2, 2*;	2, 3*;	2, 3*;	2, 3*;
	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 1, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,
	1, 2, 4	1, 2, 5	1, 2, 5	1, 2, 5	1, 4, 4*	1, 2, 5*	1, 2, 5*	1, 2, 5*	1, 2, 5*	1, 2, 5*
mxpd 2	bas: 3;	bas: 3;	bas: 3;	bas: 3;	bas: 3;	bas: 3*;	bas: 3*;	bas: 3*;	bas: 3*;	bas: 3*;
	end: 0, 0, 5	end: 0, 1, 6	end: 0, 1, 6	end: 0, 1, 4	end: 4	end: 0, 7*	end: 0, 7*	end: 0, 7*	end: 0, 7*	end: 0, 7*
abdomen	S1-5: 2;	S1: 4;	S1-5: 2;	S1-5: 2;	setation: n/a	S1-5: 2*;	S1-5: 2*;	S1-5: 2*;	S1-5: 2*;	S1-5: 2*;
	dlp: S2	S2-5: 2;	dlp: S2-3	dlp: S2-3		dlp: S2*	dlp: S2*	dlp: S2*	dlp: S2*	dlp: S2*
	-	dlp: S2-3	-	-		-	-	-	-	-
telson	furca: 1 sp;	furca: 3 sp;	furca: 3 sp;	furca: 3 sp;	furca: 1 sp;	furca: 3 sp*;	furca: 3 sp*;	furca: 3 sp*;	furca: 3 sp*;	furca: 3 sp*;
	spi present;	spi present;	spi absent*;	spi present*;	6 s	spi present*;	spi present*;	spi present*;	spi present*;	spi present*;
	6 s	6 s	6 s	6 s		6 s*	6 s*	6 s*	6 s*	6 s*

RS: rostral spine; DS: dorsal spine; LS: lateral spine; dlp: dorsolateral process; cox: coxa or coxal endite; bas: basis or basial endite; end: endopod; exo: exopod; sca: scaphognathite; epi: epipod; pro: protopod; ped: peduncle; S: somite; s: setae; aes: aesthetasc; sp: spine; spi: spinules, * observation from figure, n/a: not available.

Table II. Comparisons of larval characters of second zoeal stage for Majidae genera; see Table I for definition of abbreviations.

Zoea 1	Pseudomicippe varians Present study	Maja crispata Rodriguez (2002)		Maja squinado Clark (1986)	Schizophrys aspera Tirmizi and Kazmi (1987)	Notomithrax peronii Webber and Wear (1981)	ursus Webber and	minor	edwardsii Webber and	Leptomithrax longipes Webber and Wear (1981)
carapace	RS: absent;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;	RS: present;
	DS: absent;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;	DS: present;
	LS: absent;	LS: present;	LS: present;	LS: present;	LS: present;	LS: absent;	LS: absent;	LS: absent;	LS: absent;	LS: present;
	9 s ventral margin	7 s ventral margin	7 s ventral margin	8 s ventral margin*	6 s ventral margin	7 s ventral margin*	6 s ventral margin	6 s ventral margin	7 s ventral margin*	6 s ventral margin
antennule	4 aes, 1 s	8 aes	7 aes, 2 s	6 aes, 3 s	5 aes	8 aes*,	8 aes	8 aes	7 aes	8 aes
antenna	exo <pro< td=""><td>exo>pro</td><td>exo≤pro</td><td>exo:</td><td>exo<pro;< td=""><td>exo=pro</td><td>exo≤pro*</td><td>exo≤pro*</td><td>exo≤pro*</td><td>exo≤pro*</td></pro;<></td></pro<>	exo>pro	exo≤pro	exo:	exo <pro;< td=""><td>exo=pro</td><td>exo≤pro*</td><td>exo≤pro*</td><td>exo≤pro*</td><td>exo≤pro*</td></pro;<>	exo=pro	exo≤pro*	exo≤pro*	exo≤pro*	exo≤pro*
maxillule	cox: 7;	cox: 7;	cox: 7;	cox: 7;	cox: 7;	cox: 7*;	cox: 7;	cox: 6;	cox: 8;	cox: 7*;
	bas: 8;	bas: 9;	bas: 9;	bas: 9;	bas: 8;	bas: 10;	bas: 8;	bas: 8;	bas: 8;	bas: 9*;
	end: 1, 4;	end: 1, 6;	end: 1, 6;	end: 1, 6;	end: 1, 1, 4;	end: 1, 5*;	end: 1, 6;	end: 1, 3;	end: 1, 6*	end: 1, 6*;
	exo: 1	exo: 1	exo: 1	exo: 1	exo: n/a	exo: 1	exo: 1	exo: 0	exo: 1*	exo: 1*
maxilla	cox: 3, 4;	cox: 3, 4;	cox: 3, 4;	cox: 3, 4;	cox: 3, 4;	$\cos 3, 4*;$	$\cos 3, 4*;$	$\cos 3, 3*;$	cox: 3, 4;	$\cos 3, 4^*;$
	bas: 5, 4;	bas: 5, 5;	bas: 5, 5;	bas: 5, 5;	bas: 4, 4;	bas: 5, 5*;	bas: 5, 5*;	bas: 5, 5*;	bas: 5, 5;	bas: 5, 5*;
	end: 4;	end: 5;	end: 5;	end: 5;	end: 4;	end: 5*;	end: 5*;	end: 4;	end: 5*;	end: 6;
	sca: 28	sca: 21-23	sca: 27	sca: 21	sca: 26	sca: 22	sca: 21	sca: 19	sca: 28	sca: 23*
mxpd 1	cox: 0;	cox: 1;	cox: n/a;	cox: n/a;	coxa 0;	cox: 1*;	cox: 1*;	coxa 0;	cox: 1*;	cox: 1*;
	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,	bas: 2, 2,
	2, 3;	2, 3;	2, 3;	2, 3;	2, 2;	2, 3*;	2, 2*;	2, 3*;	2, 3*;	2, 3*;
	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,	end: 2, 2,	end: 3, 2,	end: 3, 2,	end: 3, 2,
	1, 2, 4	1, 2, 5	1, 2, 5	1, 2, 5	2, 1, 4*	1, 2, 5*	1, 2, 5*	1, 2, 5*	1, 2, 5*	1, 2, 5*
mxpd 2	bas: 3;	bas: 3;	bas: 3;	bas: 3;	bas: 2;	bas: 3*;	bas: 3*;	bas: 3*;	bas: 3*;	bas: 3*;
	end: 0, 0, 5	end: 0, 1, 6	end: 0, 1, 6	end: 0, 1, 4	end: 1, 0, 2, 2	end: 0, 7*	end: 0, 7*	end: 0, 7*	end: 0, 7*	end: 0, 7*
abdomen	S1-5: 2;	S1: 5;	S1: 3;	S1: 3;	setation: n/a	S1-5: 2*;	S1-5: 2*;	S1-5: 2*;	S1-5: 2*;	S1: 3
	dlp: S2	S2-5: 2;	S2: 4;	S2: 4;	with 5 S	dlp: S2*	dlp: S2*	dlp: S2*	dlp: S2*	S2: 4
		dlp: S2-3	S3–5: 2 dlp: S2–3	S3–5: 2 dlp: S2–3						S3–5: 2 dlp: S2–3
telson	furca: 1 sp; spi present; 6 s	furca: 3 sp; spi present; 6 s	furca: 3 sp; spi absent*; 6 s	furca: 3 sp; spi present*; 6 s	furca: 1 sp; 6 s	furca: 3 sp*; spi present*; 6 s*	furca: 3 sp*; spi present*; 6 s*	furca: 3 sp*; spi present*; 6 s*	furca: 3 sp*; spi present*; 6 s*	furca: 3 sp*; spi present*; 6 s*

unique characters of the genus (Tables I and II). However, these apparent diagnostic characters of *Schizophrys* need to be verified since we found discrepancies between descriptions based on text and figures. Species of *Notomithrax* are the only majoids with 11 setae on the scaphognathite of the maxilla in the first zoeal stage, and setal meristics of the maxillule are distinctive in both stages (Tables I and II). Finally, species of *Leptomithrax* have six aesthetascs on the antennule of the zoea I, and six setae on the endopod of the maxilla on the zoea II (Tables I and II).

Phylogenetic relationships

In recent phylogenetic analyses of majoids using larval characters (Marques & Pohle 1998; Pohle & Marques 2000), the family Majidae appears to be one of the few families that have larval support for its monophyly. The authors base the monophyly of Majidae on the 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 the setae in the zoea; proximal coxal lobe of the maxilla in zoea II bearing three setae; scaphognathite of maxilla bearing 21–28 setae in zoea II; and the fork of the telson bearing three lateral spines (Tables I and II). Except for the presence of one rather than three telson furcal spines in *P. varians* and *S. aspera*, and the number of setae on the scaphognathite of the maxilla of zoea II in *N. minor* (Filhol 1885), the other majid species are in agreement with the synapomorphies determined by Marques and Pohle (1998, 2003), and Pohle and Marques (2000) for Majidae. So we believe that those characters cited above, based on a cladistic analysis, could better define this family, and should be used instead of the Ingle's (1979) groups.

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References

Aiyun D, Siliang Y. 1991. Crabs of the China Seas. Beijing, China: China Ocean Press.

Bell T. 1844–1852. A history of the British stalk-eyed Crustacea. London.

Bourdillon-Casanova L. 1960. Le méroplancton du Golfe de Marseille: Les larves de crustacés décapods. Recueil des Travaux de la Station Marine D'Endoume 30:1–286.

Cano G. 1893. Sviluppo e Morfologie degli Oxyrhynchi. Mitteilungen aus der Zoologischen Station zu Neapel 10:527–583.

Clark PF. 1986. The larval stages of *Maja squinado* (Herbst, 1788) (Crustacea, Brachyura, Majidae) Reared in the Laboratory. Journal of Natural History 20:825–836.

Clark PF, Calazans DK, Pohle GW. 1998. Accuracy and standardization of brachyuran larval description. Invertebrate Reproduction and Development 33:127–144.

Claus C. 1876. Unteruchugen zur Erforschung der genealogischen Grundlage des Crustaceen-Systems. Wien, Austria.

Couch RQ. 1843. On the metamorphosis of the decapod crustaceans. Report of the Royal Cornwall Polytechnic Society, Falmouth 11:28–43.

- Filhol H. 1885. Considérations relatives à la faune des Crustacés de la Nouvelle-Zélande. Bibliothèque de l'École des Hautes Études, Section des Sciences Naturelles 30:3–60.
- Griffin DJG. 1963. *Notomithrax* gen. nov. and the status of the Genus *Paramithrax* H. Milne Edwards (Crustacea, Brachyura, Majidae). Transactions of the Royal Society of New Zealand, Zoology 3:229–231 [233].
- Griffin DJG. 1966. The marine fauna of New Zealand: spider crabs, family Majidae (Crustacea, Crachyura). New Zealand Department of Scientific and Industrial Research Bulletin 172:1–112.
- Griffin DJG, Tranter HA. 1986. The Decapoda Brachyura of the Siboga Expedition. Part VIII. Majidae. Siboga-Expeditie. Leiden Monograph 39, C4, Livraison 148.
- de Haan W. 1833–1850. Crustacea. In: von Siebold FP, editor. Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japonicum, Jussu et Auspiciis Superiorum, que Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit, i–xxxi, ix–xxi, 1–243, plates A–J, L–Q 1–55, circ. tab. 2. Lugdumi-Batavorum. (Leiden). [Dates of publication in Holthuis and Sakai, 1970:77.].
- Hale HB. 1927-1929. The crustaceans of South Australia, Parts I & II. South Australia: Government Printer.
- Heegaard P. 1963. Decapod larvae from the Gulf of Napoli, hatched in captivity. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening I Kjøbenhaun 125:449–493.
- Heller C. 1861. Beitrage zur Crustaceen-Fauna des Rothen Meeres, 1. Sitzungsbericht der Akademie der Wissenschaften. Wien. Mathmatisch-Naturwissenschaftliche Classe 43(1):297–374.
- Ingle RW. 1979. The larval development of the spider crab *Rochinia carpenteri* (Thomson) [Oxyrhyncha: Majidae] with a review of majid subfamilial larval features. Bulletin of the British Museum of Natural History (Zoology) 37:47–66.
- Ingle RW. 1980. British Crabs. British Museum Natural History. Oxford: Oxford University Press.
- Ingle RW. 1991. Larval stages of northeastern Atlantic crabs. An illustrated key. Natural History Museum Publications. London: Chapman & Hall.
- Jacquinot H, Lucas H. 1853. Crustacea. In: Voyage au Pole Sud et dans l'Oceanie sur les corvettes l'Astrolabe et la Zelée execute pendant 1837–40. sous le Commandement de M.J. Dumont d'Urville. Zoologie 3, 107 p. Atlas (1842–1853) pl. 1–9. Paris.
- Kakati VS, Nayak VN. 1979. Larval history of the spider crab, *Schizophrys aspera* (H. Milne Edwards) (Brachyura, Majidae) as observed in the laboratory. Journal of the Bombay Natural History Society, Bombay 76:259–267.
- Kurata H. 1969. Larvae of decapod Brachyura of Arasaki, Sagami Bay. IV. Majidae. Bulletin of the Tokai Regional Fisheries Research Laboratory 57:81–127.
- Lamarck JB. 1801. Système des Animaux sans vertèbres, ou Tableau général des classes, des ordres et des genres de ces animaux; présentant leurs caractères essentiels et leur distribution d'après les considérations de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire naturelle, parmi leurs dépouilles conservées; précédé du Discours d'ouverture de l'an VIII de la République. Paris: Déterville. VIII+432 p.
- Leach WE. 1814. Crustaceology. In: Brewster's Edinburgh Encyclopedia. Edinburgh: Blackwood 7. p 383–437.
 Lebour MV. 1927. Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity with a description of the larval stages of *Inachus dorsettensis*, *Macropodia longirostris* and *Maia squinado*. Journal of the Marine Biological Association of the United Kingdom, Plymouth 14:795–820.
- Marques F, Pohle G. 1998. The use of structural reduction in phylogenetic reconstruction of decapods and a phylogenetic hypothesis for fifteen genera of Majidae: testing previous hypotheses and assumptions. Invertebrate Reproduction and Development 33:241–262.
- Marques F, Pohle G. 2003. Searching for larval support for majoid families (Crustacea: Brachyura) with particular reference to Inachoididae Dana, 1851. Invertebrate Reproduction and Development 43:71–82.
- Martin JW, Davis GE. 2001. An updated classification of the recent Crustacea. Science series. Natural History Museum of L.A. County 39:1–124.
- Martin JW, Laverack MS. 1992. On the distribution of the crustacean dorsal organ. Acta Zoologica 73:357–368. Miers EJ. 1876. Descriptions of some new species of Crustacea, chiefly from New Zealand. Annals and magazine of natural history 17:218–229.
- Miers EJ. 1879. An Account of the petrological, botanical, and zoological collections made in Kerguelen's Land and Rodriguez during the transit of Venus Expeditions, carried out by order of Her Majesty's Government in the Years 1874–75. Philosophical Transactions of the Royal Society of London 168:200–214.
- Milne-Edwards A. 1865. Description de quelques crustacés nouveaux appartenant à la tribu des Maiens. Anales de la Societe Entomologique de France 4 série 5:133–147.
- Milne-Edwards H. 1834. Histoire naturelle des Crustacés, comprenant lánatomie, la physiologie et la classification de ces animaux. Vol. 1, XXV+468pp. Atlas, Paris: Librarie Roret.

- Ortmann A. 1893. Abtheilung: Brachyura (Brachyura genuine Boas), I. Unterabtheilung: Majoidea and Concroidea, 1: Section Portuninea. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und z. Z. im Strassburger Museum aufbewahrten Formen, VI. Theil. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 7:23–88, plate 3.
- Paula J. 1985. The first zoeal stages of *Polybius henslowi* Leach, *Maja squinado* (Herbst), *Pachygrapsus marmoratus* (Fabricius), and *Uca tangeri* (Eydoux) (Crustacea, Decapoda, Brachyura). Arquivos do Museu Bocage, series B 2:137–147.
- Paula J. 1988. The larval development of the spider crab Maja goltziana d'Oliveira, 1888 (Crustacea, Decapoda, Majidae) reared in the laboratory. Journal of Natural History 22:1687–1708.
- Pohle GW, Marques FPL. 2000. Larval stages of *Paradasygius depressus* (Bell, 1835) (Brachyura: Majidae) and a phylogenetic hypothesis for 21 genera of Majidae. Proceedings of the Biological Society of Washington 113:739–760.
- Pohle GW, Telford M. 1981. Morphology and classification of decapod crustacean larval setae: a scanning electron microscope study of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae). Bulletin of Marine Science 31:736–752.
- Rathbun MJ. 1915. *Jacquinotia*, a new crab name. Proceedings of the Biological Society of Washington 28:142. Rice AL. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. Transactions of the. Zoological Society of London 35:735–752.
- Rice AL. 1983. Zoeal evidence for brachyuran phylogeny. In: Schram FR, editor. Crustacean Phylogeny, Crustacean Issues. vol. 1.A.A, Rotterdam: Balkema. p 313–329.
- Rodriguez A. 2002. Larval development of *Maja crispata* Risso 1827 (Crustacea, Decapoda, Majidae) reared in the laboratory. Journal of Natural History 36:1589–1600.
- Sakai T. 1965. Crabs of Sagami Bay. Tokyo, Japan: Maruzen Co. Ltd.
- Sakai T. 1976. Crabs of Japan and Adjacent Seas. Tokyo, Japan: Kodansha Ltd.
- Salman SD. 1982. Larval development of the spider crab *Eurynome aspera* (Pennant), reared in the laboratory, with a key to the known larvae of the subfamily Pisinae (Brachyura, Majidae). Crustaceana 43:78–88.
- Santana W, Pohle GW, Marques FPL. 2004. Larval development of *Apiomithrax violaceus* (A. Milne Edwards, 1868) (Decapoda: Brachyura: Majoidea: Pisidae) reared in laboratory conditions, and a review of larval characters of Pisidae. Journal of Natural History 38:1773–1797.
- Schlegel C. 1911. Sur le développement de *Maia squinado* Latr. Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris 153:480–482.
- Terada M. 1981. Zoeal development of five crabs (Brachyura, Majidae, Majinae) in the laboratory. Zoological Magazine 90:2283–2289.
- Thomson GM. 1902. On a new species of *Paramithrax* from New Zealand. Annals of the Magazine of Natural History 7:361–364.
- Tirmizi NM, Kazmi QB. 1987. Larval development of two spider crabs reared in the laboratory, families Hymenosomatidae and Majidae. Crustaceana 53:281–291.
- Webber WR, Wear RG. 1981. Life history studies on New Zeland Brachyura. 5A. Larvae of the family Majidae. New Zealand Journal of Marine and Freshwater Research 15:331–383.
- White A. 1848. Short descriptions of new or little-known Decapod Crustacea. In: November 23, 1847. William Yarell, Esq., Vice-Preseident, in the Chair. Proceedings of the Zoological Society of London 1847(XV), no. clxxix: 222–228, 2 text-figs.