RE-EXAMINATION OF THE ZOEAL MORPHOLOGY OF *CHASMAGNATHUS GRANULATUS*, *CYCLOGRAPSUS LAVAUXI*, *HEMIGRAPSUS SEXDENTATUS*, AND *H. CRENULATUS* CONFIRMS CONSISTENT CHAETOTAXY IN THE VARUNIDAE (DECAPODA, BRACHYURA)

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ABSTRACT

The morphology of first stage zoea larvae of four species of grapsoid crabs (viz., *Chasmagnathus granulatus* Dana, 1851, *Cyclograpsus lavauxi* H. Milne Edwards, 1853, *Hemigrapsus crenulatus* (H. Milne Edwards, 1837), and *H. sexdentatus* (H. Milne Edwards, 1837)) from Argentina and New Zealand was re-examined. Special attention was given to those characters that have been recently recognized to separate larvae of the families Sesarmidae and Varunidae. In all species studied, the setation of several appendages differed from that presented in the original descriptions of the larvae. The new chaetotaxy agrees well with expectations based on a recent taxonomic classification. The shared 2,2 setal pattern on the endopod of the maxilla and the same type of antenna and telson in all of these species, confirm a close phylogenetic relationship among them and their placement within the family Varunidae.

ZUSAMMENFASSUNG

Die Morphologie des ersten Zoea-Larvalstadiums von vier Arten grapsoider Krabben (viz., *Chasmagnathus granulatus* Dana, 1851, *Cyclograpsus lavauxi* H. Milne Edwards, 1853, *Hemigrapsus crenulatus* (H. Milne Edwards, 1837) und *H. sexdentatus* (H. Milne Edwards, 1837)) aus Argentinien und Neuseeland wurde erneut untersucht. Besondere Aufmerksamkeit galt dabei den Charakteren, die kürzlich als trennende Merkmale für Larven der Familien Sesarmidae und Varunidae erkannt wurden. In allen untersuchten Arten unterschied sich die Beborstung mehrerer Extremitäten von der Originalbeschreibungen der Larven. Die neue Chaetotaxie stimmt mit Erwartungen überein, die auf einer kürzlich aufgestellten Taxonomie beruhen. Der 2,2-Beborstungstyp des Endopods der zweiten Maxille und die gleiche Form von Antenne und Telson in allen Arten bestätigt eine nahe phylogenetische Verwandtschaft dieser Arten und deren Zuordnung zur Familie Varunidae.

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INTRODUCTION

Over the last thirty years, many great larval morphologists had to realize that it was impossible to define morphological characters that would allow distinction of zoea larvae of the grapsid subfamilies Sesarminae and Varuninae (Wear, 1970; Rice, 1980; Wilson, 1980; Pereyra Lago, 1993a). Within the Sesarminae, two major groups of genera could be distinguished based on zoeal morphology. These two groups differed from each other in the setation pattern of several appendages (Wear, 1970; Rice, 1980; Wilson, 1980; Terada, 1982; Pereyra Lago, 1993a; Schubart & Cuesta, 1998). The zoeal chaetotaxy characterizing one of these groups (comprising the genera *Chasmagnathus*, *Cyclograpsus*, *Helice* s.l., *Helograpsus*, and *Metaplax*) showed striking similarity to the one found in most zoeae of the Varuninae (Cuesta, 1999; Cuesta et al., 2000). In a revision of larval morphology of American Sesarminae, Schubart & Cuesta (1998) emphasized the clear-cut differences between *Sesarma*, *Armases*, and *Aratus* on the one hand and *Cyclograpsus* and *Chasmagnathus* on the other, and suggested that the last two genera "should not remain within the Sesarminae, being much closer to species currently included in the subfamily Varuninae..." (Schubart & Cuesta 1998: 82). The need to shift several genera from the Sesarminae to the Varuninae was confirmed by subsequent molecular phylogenies of many grapsoid genera and additional evidence from adult morphological characters (Schubart et al., 2000; Schubart et al., in press). Furthermore, all former grapsid subfamilies were raised to family level to make taxonomy congruent with phylogenetic relationships to the Gecarcinidae as well as to some Ocypodoidea (Schubart et al., 2000; Schubart et al., 2002). One of the consequences of the reclassification of genera is, that it is now easy to establish diagnostic characters that define zoeae as well as megalopae of the Sesarmidae and Varunidae (see Cuesta, 1999; Cuesta et al., 2000).

In order to use larval morphology data for systematics, it is essential to rely on descriptions with accurate drawings and especially setal counts. In the past, optical instruments used for larval descriptions did not easily offer the same kind of resolution as modern instruments. Furthermore, exact numbers of setae did not appear as crucial as nowadays since the grouping of larvae based on their setation patterns was rather uncommon. Consequently, we find that many older descriptions of larvae lack the accuracy that we would like to see in modern ones (see Rice, 1979 and Clark et al., 1998 for standards). Larval descriptions with incorrect setal counts blur the picture that we may obtain from the evolution of larval appendages and make possible conclusions on phylogenetic relationships among taxa difficult. Recent re-examinations of larval material have helped to clarify setation patterns that seemed atypical for the taxonomic groups to which these taxa were ascribed (Fransozo et al., 1997; Schubart & Cuesta, 1998; Cuesta & Rodríguez, 2000).

In this study, we describe the results of a re-examination of first zoeal stages that we were able to carry out for the following species: *Chasmagnathus granulatus* Dana, 1851 (often incorrectly referred to as *C. granulata*) from Argentina and *Cyclograpsus lavauxi* H. Milne Edwards, 1853, *Hemigrapsus crenulatus* (H. Milne Edwards, 1837), and *H. sexdentatus* (H. Milne Edwards, 1837) (senior synonym of *H. edwardsii* (Hilgendorf, 1882)) from New Zealand. Our larvae differed in several important details from the original descriptions of these species (Boschi et al., 1967; Wear, 1970; Wear & Fielder, 1985). Corrected setal counts confirm that these species agree perfectly with other varunid larvae in their larval morphology and give additional support to the hypothesis of Schubart & Cuesta (1998) and Schubart et al. (2000) that the genera *Chasmagnathus* and *Cyclograpsus* should be considered members of Varunidae.

MATERIAL AND METHODS

One ovigerous *Chasmagnathus granulatus* was collected at Laguna de Mar Chiquita (Argentina) by Eduardo Spivak on 15 March 1999. First zoeae were reared at the laboratory of the Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de Mar del Plata (Argentina). Ovigerous crabs of *Cyclograpsus lavauxi*, *Hemigrapsus sexdentatus*, and *H. crenulatus* were collected by R. Diesel in the vicinity of Christchurch (New Zealand) in January 1998 and the larvae reared in the laboratories of the Zoology Department of the University of Canterbury.

Observations on larval characteristics were based on ten zoea I of each species. Appendages were dissected under a Wild MZ6 binocular microscope. Semipermanent mounts of whole larvae and dissected appendages were stained using CMC 10 and lignin pink. Permanent mounts were made using polyvinyl lactophenol, and cover slips were sealed with nail varnish. Drawings were made using an Olympus BH-2 and a Zeiss Axioskop compound microscope, both equipped with Nomarski's interference contrast and an attached camera lucida. The few zoeae of *H. crenulatus* obtained were all used for dissection. Samples of zoea I larvae of *Chasmagnathus granulatus*, *Cyclograpsus lavauxi*, and *Hemigrapsus sexdentatus* are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM 310333, 310334, and 310338, respectively).

RESULTS

First zoeal stages of *Chasmagnathus granulatus*, *Cyclograpsus lavauxi*, *Hemigrapsus sexdentatus*, and *H. crenulatus* were reared under laboratory conditions. Only the zoeae I were reared and fixed in 4% formalin; complete developmental sequences were not attempted. The description of these first stage zoeae is given

TABLE I

Differences between the setation pattern of the first zoeal stage of *Chasmagnathus granulatus* Dana, 1851 described by Boschi et al. (1967) and the first zoea described in the present study. Abbreviations used in tables I-IV: s., setation; ?, no data; sp., spines; a, aesthetascs; dlp, dorsolateral process

	Boschi et al. (1967)	Present description
Carapace		
Posterodorsal s.	?	2
Antenna		
Exopod s.	1	2
Maxillule		
Basial endite s.	6	5
Maxilla		
Coxal endite s.	6	4 + 3
Basial endite s.	8 + 2 sp.	5 + 4
First maxilliped		
Basis s.	7	2, 2, 3, 3
Endopod s.	1, 2, 1, 2, 5	2, 2, 1, 2, 5
Second maxilliped		
Endopod s.	0, 1, 5	0, 1, 6

TABLE II

Differences between the setation pattern of the first zoeal stage of *Cyclograpsus lavauxi* H. Milne Edwards, 1853 described by Wear (1970) and the first zoea described in the present study. For abbreviations, see table I

	Wear (1970)	Present description
Antennule		
Exopod s.	2a, 1s	3a, 1s
Maxillule		
Coxal endite s.	4	5
Maxilla		
Coxal endite s.	4 + 2	4 + 3
Basial endite s.	3 + 3	5 + 4
First maxilliped		
Basis s.	2, 2, 1, 1	2, 2, 3, 3
Endopod s.	1, 2, 1, 2, 5	2, 2, 1, 2, 5

below. In tables I-IV the differences found between the present descriptions and previous ones are shown. Descriptions are based on the malacostracan somite plan and described from anterior to posterior. Setal armature on appendages is described from proximal to distal segments and from endopod to exopod.

TABLE III

Differences between the setation pattern of the first zoeal stage of *Hemigrapsus sexdentatus* (H. Milne Edwards, 1837) (as *H. edwardsii* (Hilgendorf, 1882)) described by Wear (1970) and the first zoea described in the present study. For abbreviations, see table I

	Wear (1970)	Present description
Antennule		
Exopod s.	2a, 1s	3a, 1s
Maxillule		
Coxal endite s.	4	5
Maxilla		
Coxal endite s.	4 + 2	4 + 3
Basial endite s.	4 + 4	5 + 4
Scaphognathite s.	5	4
First maxilliped		
Basis s.	3, 3, 3, 3	2, 2, 3, 3
Endopod s.	2, 2, 2, 2, 6	2, 2, 1, 2, 5
Second maxilliped		
Endopod s.	1, 1, 6	0, 1, 6
Abdomen		
3rd. somite dlp	absent	present

TABLE IV

Differences between the setation pattern of the first zoeal stage of *Hemigrapsus crenulatus* (H. Milne Edwards, 1837) described by Wear (1970) and the first zoea described in the present study. For abbreviations, see table I

	Wear (1970)	Present description
Antennule		
Exopod s.	2a, 1s	3a, 1s
Maxillule		
Coxal endite s.	4	5
Maxilla		
Coxal endite s.	4 + 2	4 + 3
Basial endite s.	3 + 3	5 + 4
Scaphognathite s.	3	4
First maxilliped		
Basis s.	3, 3, 3, 3	2, 2, 3, 3
Endopod s.	1, 1, 1, 2, 5	2, 2, 1, 2, 5
Second maxilliped		
Endopod s.	1, 1, 6	0, 1, 6
Abdomen		
3rd. somite dlp	absent	present

Chasmagnathus granulatus Dana, 1851
Zoea I (fig. 1A-C)

Chasmagnathus granulata; Boschi et al., 1967: 28, figs. 9a, 10a, 11a, 12a, 13a, 15a.

Carapace. Globose, smooth and without tubercles. Dorsal and rostral spines long and straight. Dorsal spine slightly longer than rostral spine. Lateral spines short and directed downwards. One pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

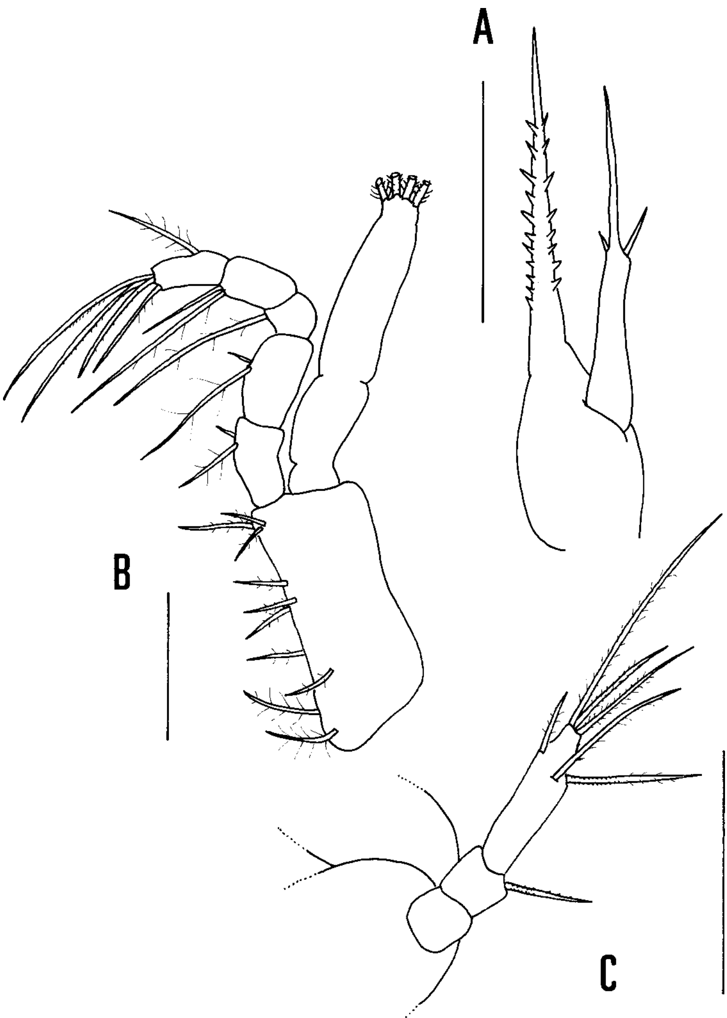

Fig. 1. *Chasmagnathus granulatus* Dana, 1851, zoea I. A, antenna; B, first maxilliped (long natatory setae truncated); C, second maxilliped endopod. Scale bars: 0.1 mm.

Antennule. Uniramous. Endopod absent. Exopod unsegmented with 3 aesthetascs (2 long, 1 thin and short) and 1 seta.

Antenna (fig. 1A). Well developed protopod shorter than rostral spine and bearing two rows of spines. The exopod is elongated and acute in its distal half, with 1 long seta and 1 midlateral spine.

Mandible. Endopod palp absent.

Maxillule. Coxal endite with 5 plumodenticulate setae. Basial endite with 5 setae (2 cuspidate, 3 plumodenticulate). Endopod 2-segmented with 1 plumodenticulate seta on the proximal segment and 1 subterminal and 3 terminal plumodenticulate setae on the distal segment. Exopod absent.

Maxilla. Coxal endite slightly bilobed with 4 + 3 plumodenticulate setae. Basial endite bilobed with 5 + 4 plumodenticulate setae. Endopod unsegmented, bilobed with 2 long plumodenticulate setae on each lobe. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

First maxilliped (fig. 1B). Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (1 subterminal + 4 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Second maxilliped (fig. 1C). Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (3 subterminal + 3 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Third maxilliped. Absent.

Pereiopods. Absent.

Abdomen. Five abdominal somites. Somites 2 and 3 with one pair of dorsolateral processes each. Somites 2-4 with one pair of posterodorsal setae. Pleopods absent.

Telson. Bifurcated with 3 pairs of serrulate setae on posterior margin. A row of teeth (4 terminal longer than the rest) on the inner distal part of each furcal arm.

Cyclograpsus lavauxi H. Milne Edwards, 1853
Zoea I (fig. 2A-F)

Cyclograpsus lavauxi; Wear, 1970: 18, figs. 34-41; Wear & Fielder, 1985: 72, figs. 186-187.

Carapace (fig. 2A). Globose, smooth and without tubercles. Dorsal spine long and curved backwards at its medial part. Dorsal spine twice the length of rostral spine. Lateral spines well developed and directed posteriorly. One pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (fig. 2B). Uniramous. Endopod absent. Exopod unsegmented with 3 aesthetascs (2 long, 1 thin and short) and 1 seta.

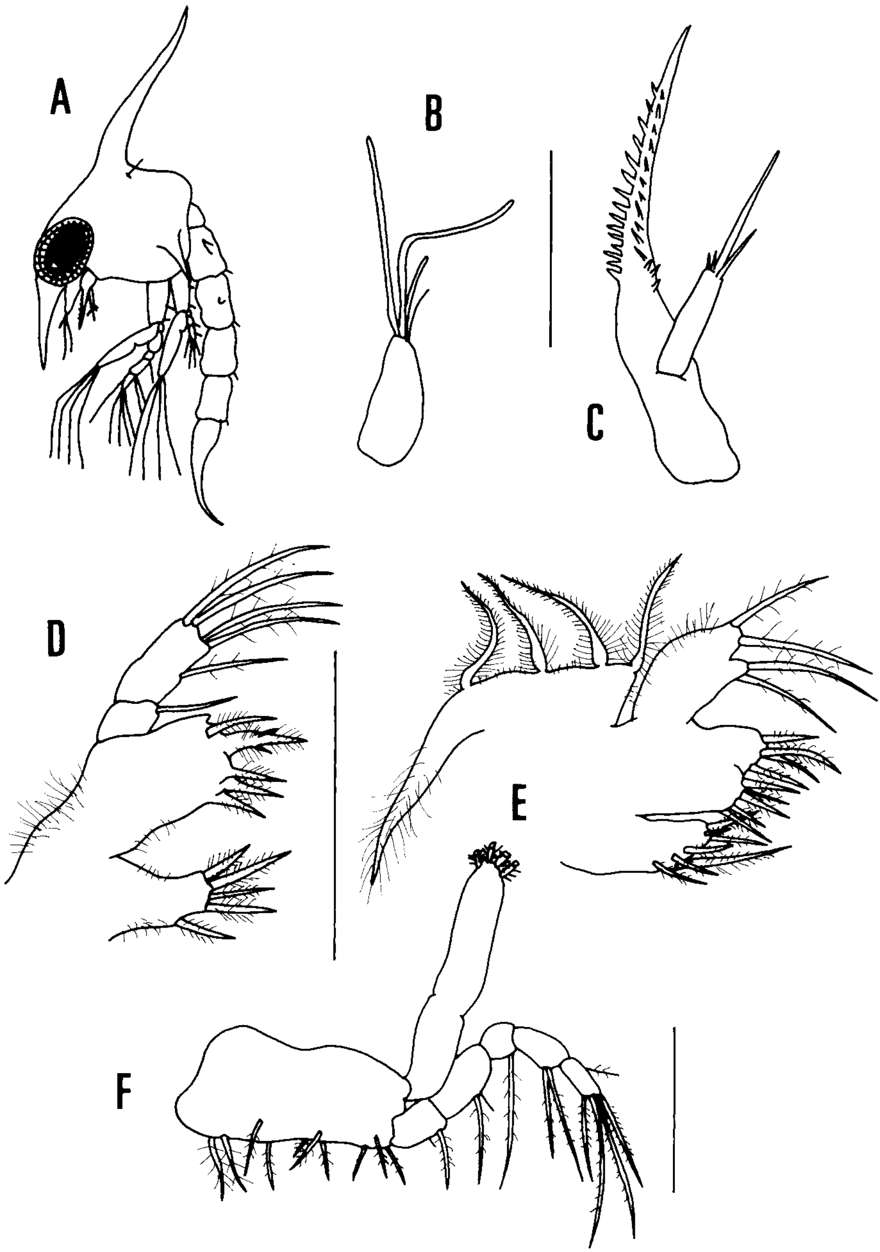

Fig. 2. *Cyclograpsus lavauxi* H. Milne Edwards, 1853, zoea I. A, lateral view (after Wear, 1970); B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped (long natatory setae truncated). Scale bars: 0.1 mm.

Antenna (fig. 2C). Well developed protopod not reaching the middle of rostral spine length and bearing two rows of spines. The exopod is elongated and acute in its distal half, with 1 long seta and 2 midlateral spines.

Mandible. Endopod palp absent.

Maxillule (fig. 2D). Coxal endite with 5 plumodenticulate setae. Basial endite with 5 setae (2 cuspidate, 3 plumodenticulate). Endopod 2-segmented with 1 plumodenticulate seta on the proximal segment and 1 subterminal and 3 terminal plumodenticulate setae on the distal segment. Exopod absent.

Maxilla (fig. 2E). Coxal endite slightly bilobed with 4 + 3 plumodenticulate setae. Basial endite bilobed with 5 + 4 plumodenticulate setae. Endopod unsegmented, bilobed with 2 long plumodenticulate setae on each lobe. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

First maxilliped (fig. 2F). Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (1 subterminal + 4 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Second maxilliped. Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (3 subterminal + 3 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Third maxilliped. Absent.

Pereiopods. Absent.

Abdomen. Five abdominal somites. Somites 2 and 3 with one pair of dorsolateral processes each. Somites 2-4 with one pair of posterodorsal setae. Pleopods absent.

Telson. Bifurcated with 3 pairs of serrulate setae on posterior margin. A row of teeth (4 terminal longer than the rest) on the inner distal part of each furcal arm.

Hemigrapsus sexdentatus (H. Milne Edwards, 1837)
Zoea I (fig. 3A-H)

Hemigrapsus edwardsi; Wear, 1970: 14, figs. 28-33; Wear & Fielder, 1985: 68, figs. 177-178.

Carapace (fig. 3A). Globose, smooth and without tubercles. Dorsal spine long, slightly curved on its base and straight over distal half. Dorsal spine more than twice the length of rostral spine. Rostral spine short and straight. Lateral spines well developed and directed ventrally. One pair of posterodorsal setae. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (fig. 3B). Uniramous. Endopod absent. Exopod unsegmented with 3 aesthetascs (2 long, 1 thin and short) and 1 seta.

Antenna (fig. 3C). Well developed protopod shorter than rostral spine and bearing two rows of spines. The exopod is elongated and acute in its distal half, with 1 long seta and 2 midlateral spines.

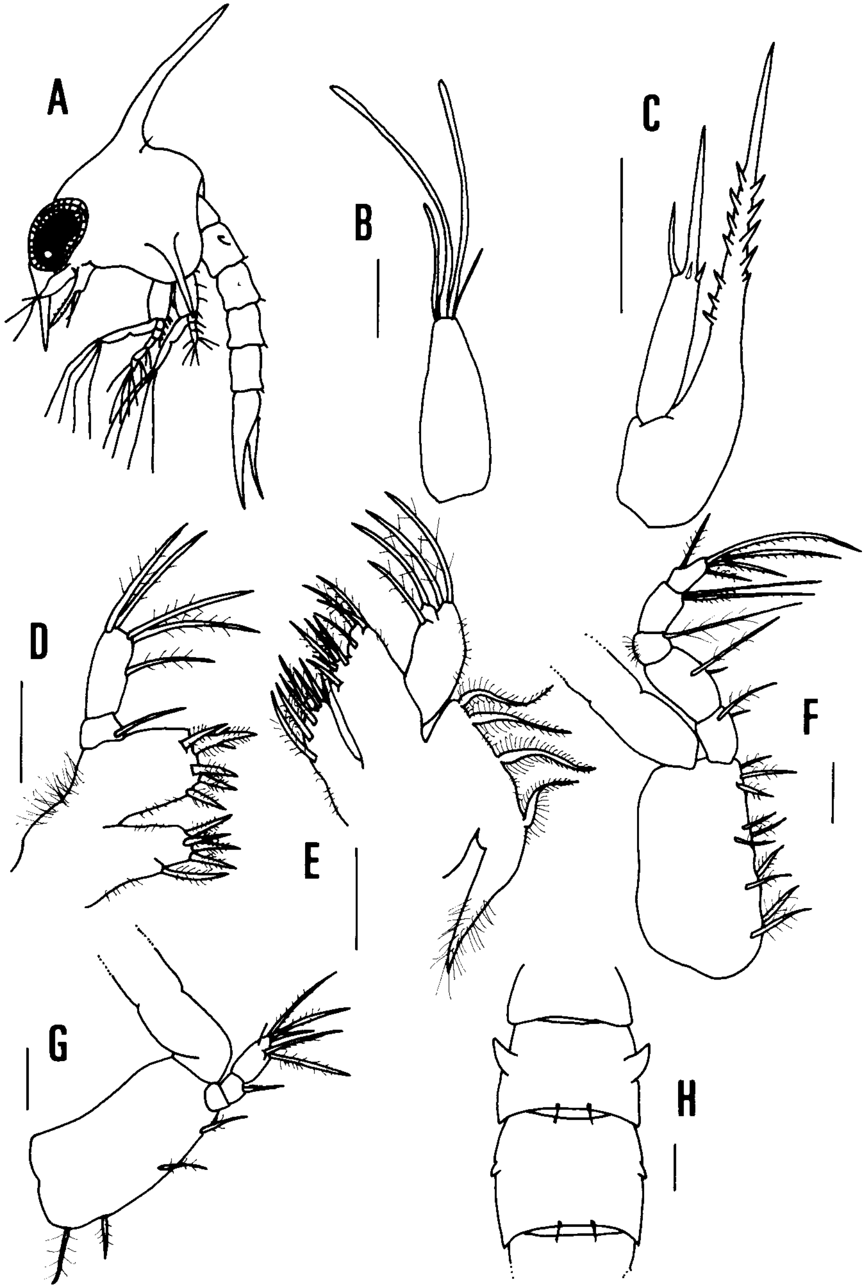

Fig. 3. *Hemigrapsus sexdentatus* (H. Milne Edwards, 1837), zoea I. A, lateral view (after Wear, 1970); B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, abdominal somites 2 and 3. Scale bars: 0.1 mm.

Mandible. Endopod palp absent.

Maxillule (fig. 3D). Coxal endite with 5 plumodenticulate setae. Basial endite with 5 setae (2 cuspidate, 3 plumodenticulate). Endopod 2-segmented with 1 plumodenticulate seta on the proximal segment and 1 subterminal and 3 terminal plumodenticulate setae on the distal segment. Exopod absent.

Maxilla (fig. 3E). Coxal endite slightly bilobed with 4 + 3 plumodenticulate setae. Basial endite bilobed with 5 + 4 plumodenticulate setae. Endopod unsegmented, bilobed with 2 long plumodenticulate setae on each lobe. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

First maxilliped (fig. 3F). Basis with 10 medial setae arranged 2,2,3,3. Endopod 5-segmented with 2,2,1,2,5 (1 subterminal + 4 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Second maxilliped (fig. 3G). Basis with 4 medial setae arranged 1,1,1,1. Endopod 3-segmented with 0,1,6 (3 subterminal + 3 terminal) setae. Exopod unsegmented, with 4 long terminal plumose natatory setae.

Third maxilliped. Absent.

Pereiopods. Absent.

Abdomen (fig. 3H). Five abdominal somites. Somites 2 and 3 with one pair of dorsolateral processes each. Somites 2-4 with one pair of posterodorsal setae. Pleopods absent.

Telson. Bifurcated with 3 pairs of serrulate setae on posterior margin. A row of teeth (4 terminal longer than the rest) on the inner distal part of each furcal arm.

Hemigrapsus crenulatus (H. Milne Edwards, 1837)
Zoea I

Hemigrapsus crenulatus; Wear, 1970: 11, figs. 19-25; Wear & Fielder, 1985: 69, figs. 180-181.

This zoea I presents only two minor differences in comparison with the zoea I of *H. sexdentatus* described above. The dorsal spine is slightly curved from base to tip, and the rostral spine is proportionally longer than that of *H. sexdentatus*, with the dorsal spine of *H. crenulatus* only being 1.3 times longer than the rostral one. For the rest of the appendages, only minor differences in size are appreciated. We therefore do not repeat here the description, and the appendages are not figured.

DISCUSSION

The use of larval characters as an additional systematic tool is being increasingly accepted and applied by taxonomists. It has helped to clarify phylogenetic relationships of several decapods (Rice, 1980; Clark & Webber, 1991; Marques & Pohle, 1995; Clark & Galil, 1998; Ng & Clark, 2000). However, accurate morphological

TABLE V

Morphology of first zoeal stages of selected species of each genus of Varunidae and Sesarmidae with known data on larval morphology. Telson type A refers to a telson with increasing number of posterior processes throughout the development; type B refers to a telson with constantly three posterior processes throughout the development. Antenna type A refers to an exopod equal to or longer than 2/3 of the protopod length, with 1-3 unequal-sized medial setae; type B refers to an exopod not reaching to 2/3 of the protopod length, with 2 unequal-sized terminal setae and 2-5 terminal short spines. Abbreviations: Fam, family; Mxll, maxillule; Mxl, maxilla; Mxpd, maxilliped; c/b, coxal and basial endites setation; V, Varunidae; S, Sesarmidae; endp, endopod

	Fam	Telson type	Antenna type	Mxll c/b	Mxl c/b	Mxl endp	Mxpd 1 basis	Mxpd 1 endp	Mxpd 2 endp	Reference
Acmaeopleura parvula Stimpson, 1858	V	A	A	5/5	7/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	Kim & Jang, 1987
Brachynotus sexdentatus (Risso, 1827)	V	A	A	5/5	6/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	Cuesta et al., 2000
Chasmagnathus granulatus Dana, 1851	V	A	A	5/5	8/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	present study
Cyclograpsus lavauxi H. Milne Edwards, 1853	V	A	A	5/5	7/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	present study
Cyrtograpsus affinis Dana, 1851	V	A	A	5/5	6/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	Spivak & Cuesta, 2000
Eriocheir sinensis H. Milne Edwards, 1853	V	A	A	5/5	6/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	Kim & Hwang, 1995
Gaetice depressus (De Haan, 1833)	V	A	A	5/5	6/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	Kim & Lee, 1983
Helice leachi Hess, 1865	V	A	A	4/5	5/7	2,2	2,2,3,3	2,2,1,2,5	0,1,6	Mia & Shokita, 1996
Helograpsus haswellianus (Whitelegge, 1899)	V	A	A	4/5	6/8	2,2	2,2,3,3	2,2,1,2,5	0,1,6	Fielder & Greenwood, 1984
Hemigrapsus crenulatus (H. Milne Edwards, 1837)	V	A	A	5/5	7/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	present study
Hemigrapsus sexdentatus (H. Milne Edwards, 1837)	V	A	A	5/5	7/9	2,2	2,2,3,3	2,2,1,2,5	0,1,6	present study

TABLE V
(Continued)

	Fam	Telson type	Antenna type	Mxll c/b	Mxl c/b	Mxl endp	Mxpd 1 basis	Mxpd 1 endp	Mxpd 2 endp	Reference
Metaplax distincta H. Milne Edwards, 1852	V	A	A	4/4	6/8	2,2	2,2,3,3	2,1,1,2,5	0,1,6	Krishnan & Kannupandi, 1989
Aratus pisonii (H. Milne Edwards, 1853)	S	B	B	5/5	8/9	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Fransozo et al., 1998
Armases miersii (Rathbun, 1897)	S	B	B	6/5	8/9	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Cuesta et al., 1999
Bresedium brevipes (De Man, 1887)	S	B	B	5/5	7/8	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Fielder & Greenwood, 1983
Chiromantes eulimene (De Man, 1895)	S	B	B	6/5	9/8	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Pereyra Lago, 1993
Nanosesarma andersoni (De Man, 1895)	S	B	B	5/5	8/9	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Vijayakumar & Kannupandi, 1986
Parasesarma tripectinis Shen, 1940	S	B	B	5/5	8/9	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Terada, 1976
Perisesarma guttatum (A. Milne-Edwards, 1869)	S	B	B	6/5	8/8	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Pereyra Lago, 1993
Selatium brockii (De Man, 1887)	S	B	B	5/5	8/10	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Vijayakumar & Kannupandi, 1987
Sesarma rubinofforum Abele, 1973	S	B	B	5/5	8/9	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Schubart & Cuesta, 1998
Sesarmops intermedium (De Haan, 1835)	S	B	B	5/5	8/9	2,3	2,2,3,3	2,2,1,2,5	0,1,6	Terada, 1976

comparisons of minute larval appendages can only be based on detailed descriptions and precise setal counts, which are often missing in older studies. Therefore, there is a great need of larval re-descriptions for many species. In the Grapsoidea, larval features (especially antennal and telson types as well as mouthpart setation patterns) allow clear distinction of the constituent families as homogeneous groups (Schubart & Cuesta, 1998; Cuesta & Schubart, 1999; Cuesta, 1999; Cuesta et al., 2000). In several cases, in which this classification seemed to fail, i.e., larval descriptions did not present the features that would be expected according to the families into which they were placed, a re-examination of larval characters resulted in corrections of errors in the descriptions (Fransozo et al., 1997; Schubart & Cuesta, 1998; Cuesta & Rodríguez, 2000). In other cases, the found aberrations provided a good indication that some genera needed to be reclassified and prompted additional comparative studies. For example, zoeae of *Chasmagnathus*, *Cyclograpsus*, *Helice* s.l., *Helograpsus*, and *Metaplax*, present a 2,2 setal pattern on the endopod of the maxilla, and show the same type of antenna and telson, that characterize the zoeae of the Varunidae (Schubart & Cuesta, 1998; Cuesta et al., 2000). As a result, and with additional evidence from adult morphology and mtDNA, these genera were transferred from the Sesarmidae to Varunidae (see Schubart et al., 2000; Schubart et al., 2002).

Table V summarizes the most important first zoeal characters of the Varunidae and Sesarmidae. While some characters are shared by both families, as the setation pattern of the first maxilliped basis and the second maxilliped endopod, consistent differences are found in the antenna and telson type as well as in the setation of the maxillar endopod. These characters allow us to diagnostically distinguish larvae of these two grapsoid families. In the following, some of the unifying and separating characters are discussed in detail, highlighting the corrections that are proposed with the present study.

Antennal type. Varunidae antennae differ from Sesarmidae antennae in the morphology of the exopod. In Varunidae, the exopod is elongated, reaching farther than 2/3 of the total length of the protopod; it only bears 1-3 medial setae, and the distal half is acute. In Sesarmidae, the exopod is always shorter than 2/3 of the protopod length; it only bears terminal setae and spines in a variable number and is distally rounded. In their description of the first zoeal antenna of *Chasmagnathus granulatus*, Boschi et al. (1967) describe a short exopod with 2 terminal setae. This is different from our finding of a long exopod with medial setae as described and figured above and in fig. 1A.

First maxilliped. In Varunidae and Sesarmidae, all first zoeae present 10 setae on the basis, arranged 2,2,3,3. In the previous descriptions of *Chasmagnathus granulatus*, *Cyclograpsus lavauxi*, *Hemigrapsus sexdentatus*, and *H. crenulatus* none of these larvae showed this setation. The 3,3,3,3 pattern proposed for

H. sexdentatus and *H. crenulatus* was never reported for any other grapsoid larvae. The presence of only one seta on the proximal segment of the endopod, as described for *C. granulatus*, *C. lavauxi*, and *H. crenulatus*, would be a typical feature of Grapsidae s. str. (see Cuesta et al., 1998; Cuesta & Schubart, 1999), instead of the two setae that are commonly found in the Varunidae and Sesarmidae. For all these species we now find a 2,2,3,3 pattern on the basis and two setae on the proximal segment of the endopod.

Second maxilliped. The endopod presents a common setation of 0,1,6 (see table V) in Varunidae and Sesarmidae. In the older descriptions of *C. granulatus*, *H. sexdentatus* and *H. crenulatus*, several different setation patterns were described: 0,1,5; 1,1,6; 1,1,6, respectively. 0,1,5 pattern would be typical for Grapsidae s. str. and 1,1,6 for Plagusiidae and Gecarcinidae (see Cuesta & Schubart, 1997, 1999; Cuesta et al., in press). The present re-examination, confirms the expected 0,1,6 pattern of the Varunidae and Sesarmidae.

In several of the appendages described by Wear (1970) for three different species, there is a higher number of setae than expected or found in the present study. We refer to this uncommon phenomenon as "extra-setation". Normally, setae are overlooked and setal counts show smaller numbers than are actually present. The cases of extra-setation in Wear's (1970) descriptions could be explained by the method of preparation, e.g., overlaying of different appendages under the microscope, if they are not completely dissected from each other. Also for *Cyclograpsus insularum* Campbell & Griffin, 1966, Wear (1970) describes 3,3,3,3 setae on the first maxilliped basis and 0,2,6 setae on the second maxilliped. Even though we were unable to obtain larval material for this species, we assume that also in this case the larvae might present 2,2,3,3 and 0,1,6 setae as found in our present re-description of *Cyclograpsus lavauxi* and two species of *Hemigrapsus* from New Zealand.

For other mouthpart appendages, we have also found some differences in the setation pattern (see tables I-IV). However, in most cases, like the setation of coxal and basial endites, there is no taxonomic relevance, because variable numbers can already be found within genera (see table V).

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