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The first zoeal stage of *Glyptograpsus impressus*, with comments on the subfamilial arrangement of Grapsidae (Crustacea: Brachyura).

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Abstract: The first zoeal stage of the brackish-water crab *Glyptograpsus impressus* is described and illustrated from laboratory hatched material. This is the first description of a larval stage from the Central American genus *Glyptograpsus* which is traditionally placed within the grapsid subfamily Varuninae. Comparison of zoeal setation patterns revealed common features with the Varuninae, while other features are more typical for the Grapsinae and Plagusiinae. Furthermore, zoeae of *G. impressus* are distinct in the setation of the maxillar endopod, which is unique within the Grapsidae and makes the inclusion of the genus *Glyptograpsus* within one of the presently recognized grapsid subfamilies questionable.

Résumé : Le premier stade zoé du crabe d'eau saumâtre *Glyptograpsus impressus* est décrit et illustré à partir de matériel éclos en laboratoire. Ceci représente la première description d'un stade larvaire d'un genre de l'Amérique centrale, *Glyptograpsus*, qui est traditionnellement placé dans la sous-famille des Varuninae. Une comparaison des soies des zoés révèle des structures communes avec les Varuninae, tandis que d'autres caractères sont plus typiques des Grapsinae et des Plagusiinae. De plus les zoés de *G. impressus* sont différentes par les soies de l'endopodite maxillaire, unique parmi les Graspidae, ce qui remet en question la place du genre *Glyptograpsus* dans l'une des sous familles de Grapsidae.

Keywords : larval morphology, zoea, systematics, phylogeny, crabs.

Introduction

The brachyuran family Grapsidae is presently subdivided into 4 subfamilies: Grapsinae Dana, 1851, Plagusiinae Dana, 1851, Sesarminae Dana, 1851 and Varuninae Alcock, 1900. This taxonomic classification goes back to Alcock (1900) and has been adopted in subsequent systematic reviews of this family. The Varuninae comprise 22 morphologically and ecologically very diverse crab genera. Several morphological characters used by Alcock (1900) to describe this subfamily are ambiguously defined and it is widely believed that the Varuninae represent an artificial grouping (P. Davie, D. Guinot, M. Türkay, R. Manning personal communications 1997).

The present taxonomy of the Brachyura is mostly based on adult morphological characters. Rice (1980) emphasized the relevance of larval morphology for phylogenetic studies within the Brachyura, which gained further evidence by recent studies (*e.g.* Clark & Webber, 1991; Marques & Pohle, 1995). In the Grapsidae, larval morphological characters have occasionally been related to their taxonomic classification (Bourdillon-Casanova, 1960; Wear, 1970; Wilson, 1980; Pereyra Lago, 1993) and allowed to show

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diagnostic characters for the subfamily Grapsinae (Cuesta *et al.*, 1997). Within the Sesarminae and Varuninae, most genera are also very homogeneous in their larval morphology, while others show marked differences (Rice, 1980; Pereyra Lago, 1993; Schubart & Cuesta, in press).

Out of the 51 genera presently recognized within the Grapsidae, larval stages have been examined only in 33 genera. The lack of knowledge applies particularly to the Varuninae for which larval descriptions are only available for 8 out of 22 genera. Thus, to elaborate a taxonomic system for the Grapsidae based on both adult and larval morphology, it would be necessary to obtain descriptions of larvae from many more genera.

In this study, a larval stage of the grapsid genus *Glyptograpsus* is described for the first time. This genus is currently placed within the Varuninae and consists of two species which are restricted to Central America. The morphology of the first zoeal stage of *G. impressus* Smith, 1870 is compared with that of other Grapsidae. Based on these findings, the systematic position of the genus *Glyptograpsus* is discussed.

Materials and methods

Adult *Glyptograpsus impressus* were obtained from Farfán (Panama) in February 1996, without encountering any ovigerous female in the field, and transported to the University of Bielefeld (Germany). Two females and two males were kept in a 30 x 20 cm aquarium with access to brackish water (1-5 PSU) and to rotting wood which was used as food and shelter. Temperatures ranged from 21 to 24° C and the light : dark cycle was 14 : 10 hours. In 1996, females were placed in a separate aquarium following egg extrusion and were offered small containers with water of 0 and 16 PSU salinity for larval release. After hatching, approximately 300 larvae were maintained in groups of 5 individuals and in mass-culture conditions (> 50 individuals). Light and temperature regimes were the same as described above. Differential survival was tested in salinities of 16 and 32 PSU. Samples of larvae were fixed in either 5% formalin or 70% ethanol.

Drawings and measurements were based on 20 larvae and made using a Wild MZ6 and Zeiss compound microscope with Nomarski interference, both equipped with a camera lucida. All measurements were made through an ocular micrometer and refer to the following distances: rostro-dorsal spine length (rd): from the tip of the rostral spine to the tip of the dorsal spine; carapace length (cl): from the base of the rostrum to the posterior carapace margin; carapace width (cw): distance between the tips of the lateral spines; dorsal spine length (ds): from the base to the tip of the dorsal spine; rostral spine length (rs): from the base to the tip of the rostral spine; lateral spine length (ls) from the base to the tip of the lateral spines; antennal length (al) from the base to the tip of the spinous process. Semipermanent mounts were made of whole larvae and dissected appendages were stained using CMC 10 and lignin pink. Due to the unusual setation pattern, more than 50 larvae were dissected for confirmation. One female crab and a sample of larvae were deposited in the United States National Museum of Natural History under the catalog number USNM cat. 284160.

Results

Several observations on the reproductive biology of *Glyptograpsus impressus* were obtained during 18 months of captivity. In 1996, prolonged copulations of the larger male with the two females were observed without previous molts of the females (*i.e.* in hard condition) from July to September. In July 1997, the surviving male and female remained in copula for two weeks. Females always became ovigerous 1 to 3 days after copulations. They carried eggs for 3 to 4 weeks. In 1996, the larger female of 20.6 mm carapace width (cw) copulated and carried eggs twice within the same molting cycle, while the smaller female (17.6 mm cw) only produced one brood. In 1997, the larger female (21.2 mm cw) released larvae only once, before molting in September. This last hatch consisted of approximately 3000 larvae. Fresh water was preferred for larval release in 2 out of 3 cases. In 1996, many larvae died as prezoeae. There were no significant differences in survival of first zoeal stage maintained in salinities of 16 or 32 PSU. Unfortunately no larva lived longer than eight days and no successful molt to the second zoeal stage was achieved. The small size of the larvae apparently did not allow them to feed on *Artemia* sp. nauplii. Detritus enriched water or rotifer cultures (in 1997) also failed to extend survival.

Description

Glyptograpsus impressus Smith, 1870
Zoea I (Figs. 1, 2)

Dimensions: rd: 0.66 ± 0.03 mm; cl: 0.37 ± 0.01 mm; cw: 0.48 ± 0.01 mm; ds: 0.21 ± 0.02 mm; rs: 0.16 ± 0.01 mm; ls: 0.08 ± 0.01 mm; al: 0.16 ± 0.02 mm.

Carapace (Fig. 1A). Globose and smooth. Dorsal spine slightly curved, thin rostral spine straight, both well developed. Lateral spines slightly curved and directed anteriorly. Pair of dorso-lateral simple setae near base of dorsal spine. No setae on lateral margin. Eyes sessile.

Antennule (Fig. 1C). Uniramous. Endopod absent. Exopod unsegmented with two unevenly sized aesthetases and two thin simple setae.

Antenna (Fig. 1D). Well developed protopod, almost equal in length to rostral spine, proximally bearing two rows

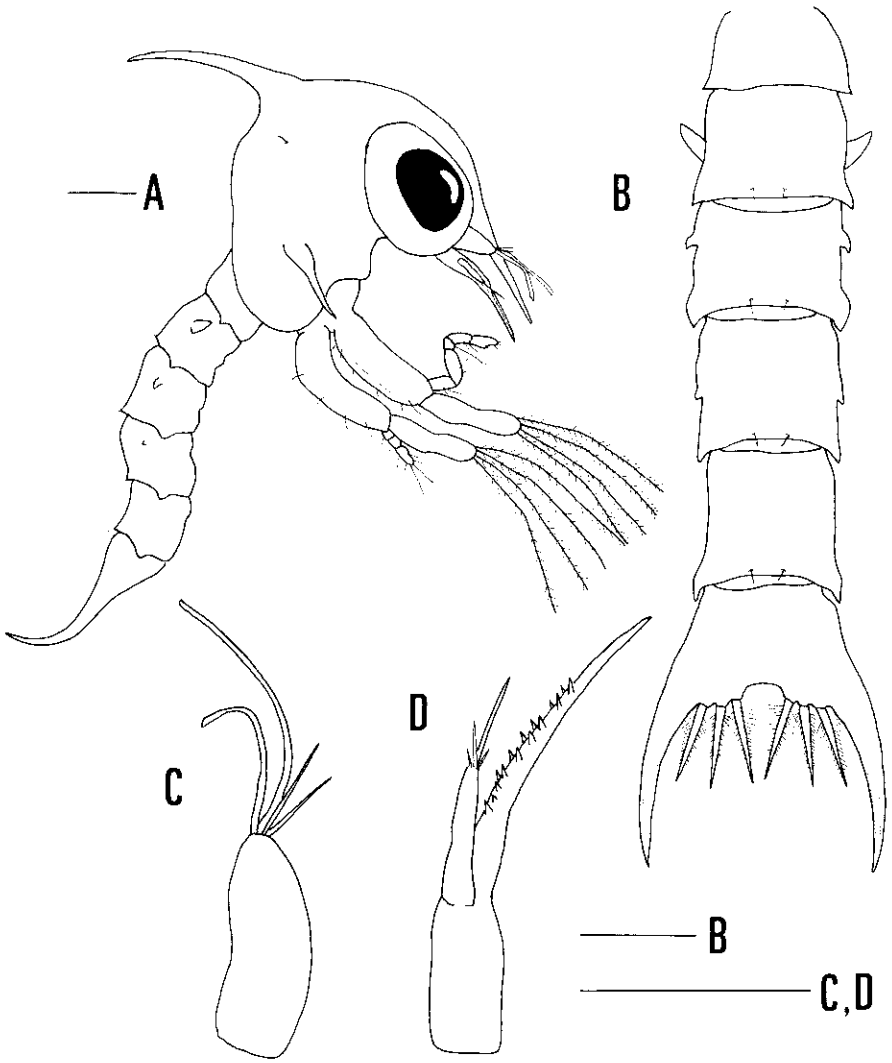

Figure 1. *Glyptograpsus impressus*, zoea I. A, lateral view; B, abdomen, dorsal view; C, antennule; D, antenna. Scale bars = 0.1 mm.
Figure 1. *Glyptograpsus impressus*, zoé I. A, vue latérale ; B, abdomen, vue dorsale ; C, antennule ; D, antenne. Échelles = 0.1 mm.

of denticles. Endopod absent. Exopod elongated about 3/4 the length of protopod, with three unequal simple setae and one longer terminal seta.

Maxillule (Fig. 2A). Coxal and basial endites each with five plumodenticulate setae; no seta on external margin of basis. Endopod 2-segmented, proximal segment with one simple seta, distal segment with one subterminal and four terminal plumodenticulate setae.

Maxilla (Fig. 2B). Coxal endite bilobed with 5+3 plumodenticulate setae on the outer and inner lobe respectively. Basial endite bilobed with 4+4 on the inner and outer lobe. Endopod unsegmented, bilobed with one long plumodenticulate seta on the inner lobe and two long setae (outer simple and inner plumodenticulate) on the outer lobe. Scaphognathite with four plumose marginal setae and long stout posterior process.

First maxilliped (Fig. 2C). Basis with eight medial plumodenticulate setae arranged 2,2,2,2. Endopod 5-segmented with 12 plumodenticulate or simple setae arranged 2,2,1,2,5. Exopod slightly constricted with four long terminal plumose natatory setae.

Second maxilliped (Fig. 2D). Basis with four medial plumodenticulate setae arranged 1,1,1,1. Endopod 3-segmented with 8 plumodenticulate or simple setae arranged 1,1,6 (three subterminal and three terminal). Exopod slightly constricted with four long terminal plumose natatory setae.

Third maxilliped. Absent.

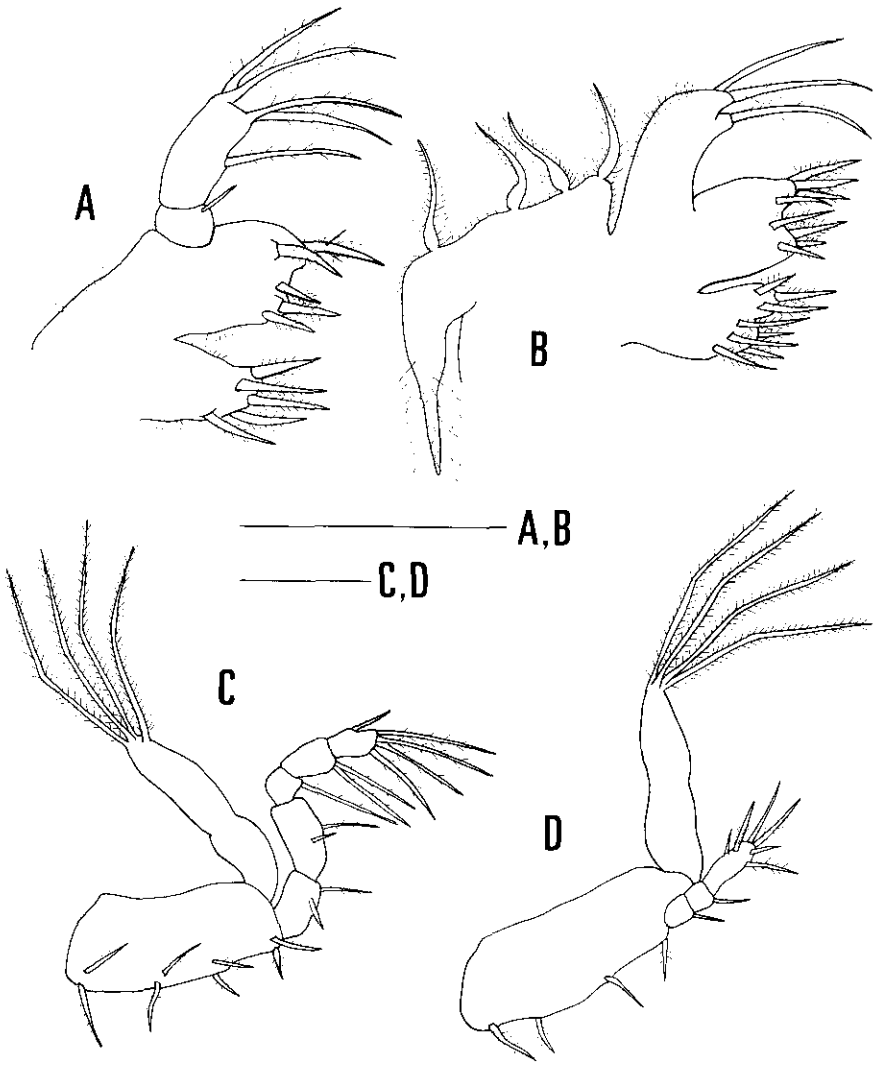

Figure 2. *Glyptograpsus impressus*, zoea I. A, maxillule; B, maxilla; C, first maxilliped; D, second maxilliped. Scale bars = 0.1 mm.
Figure 2. *Glyptograpsus impressus*, zoé I. A, maxillule ; B, maxille ; C, premier maxillipède ; D, second maxillipède. Échelles = 0.1 mm.

Pereiopods. Absent.

Abdomen (Fig. 1B). Five abdominal somites; dorso-lateral knobs on somites 2-4 (smaller on somite 4). Somites 2-5 with a pair of sparsely plumose setae on posterio-dorsal margin. Pleopods absent.

Telson (Fig. 1B). Six serrulate setae on posterior margin of telson. No lateral spines on outer side of furcae. Furcae covered with two rows of small setules.

Discussion

First zoeal morphology of *Glyptograpsus impressus* does not allow to place this species in one of the existing subfamilies (see Bourdillon-Casanova, 1960; Wear, 1970; Wilson, 1980; Rice, 1980). Table 1 summarizes data on first zoeal features of all described Varuninae and Plagusiinae species (for comparison with Grapsinae see Cuesta *et al.* (1997) and with Sesarminae see Pereyra Lago (1993)). The first zoea of *G. impressus* shows two characteristics (type B of antenna and telson) which are consistently found in the Varuninae. The strongly developed antennal exopod is also characteristic for the Varuninae (and Sesarminae). On the other hand, *G. impressus* larvae differ from the Varuninae in several of the setation patterns. The 2,2,2,2-setation on the basis of the first maxilliped is typical of the Plagusiinae and Grapsinae, while the 1,1,6-setation on the second maxilliped

Table 1. First zoeal features of all known Varuninae, including *Glyptograpsus impressus* and Plagusiinae.
Tableau 1. Caractères des premières zoés de tous les Varuninae connus, y compris *Glyptograpsus impressus* et des Plagusiinae.

Species	No. of Zoeal Stages	Telson Type	Antenna Type	Lateral Carapace Spines	Maxilla Endopod	Maxilliped 1 Basis	Maxilliped 1 Endopod	Maxilliped 2 Endopod	Abdominal Knobs	References
Acmaeopleura parvula	5(6)	B	B (3)	-	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Kim & Jang, 1987
Gaetice depressus	5	B	B (3)	-	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Kim & Lee, 1983
Brachynotus atlanticus	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2	Rodríguez *et al.*, 1992
Brachynotus gemmellari	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Guerao *et al.*, 1995
Brachynotus sexdentatus	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Cuesta & Rodríguez, unpublished data
Cyrtograpsus altimanus	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Scelzo & Lichtschein de Bastida, 1979
Cyrtograpsus angulatus	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Boschi, 1981
Eriocheir leptognathus	5	B	B (2)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Lee, 1988
Eriocheir sinensis	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Kim & Hwang, 1995[1]
Eriocheir japonicus	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-4	Kim & Hwang, 1990
Eriocheir formosa	5	B	B (?)	+	?	?	1,1,1,1,4	5	2-4	Shy & Yu, 1992
Hemigrapsus nudus	5	B	B (3)	+	2,2	1,2,3,3	2,2,1,2,5	0,1,6	2-3	Hart, 1935
Hemigrapsus oregonensis	5	B	B (3)	+	2,2	1,2,3,3	2,2,1,2,5	0,1,6	2	Hart, 1935
Hemigrapsus penicillatus	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Terada, 1981; Hwang & Kim, 1995
Hemigrapsus sanguineus	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-3	Hwang *et al.*, 1993
Hemigrapsus sinensis	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2-4	Kim & Moon, 1987
Hemigrapsus longitarsis	5	B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,5	2-3	Terada, 1981
Hemigrapsus crenulatus	5	B	B (3)	+	2,2	3,3,3,3	1,1,1,2,5	1,1,6	2	Wear, 1970
Hemigrapsus edwardsi	5	B	B (3)	+	2,2	3,3,3,3	2,2,2,2,6	1,1,6	2	Wear, 1970
		B	B (3)	+	2,2	2,2,3,3	2,2,1,2,5	0,1,6	2	Cuesta *et al.* (unpublished)
Glyptograpsus impressus	?	B	B (4)	+	1,2	2,2,2,3	2,2,1,2,5	1,1,6	2-4	present study
Euchirograpsus americanus	5(6)	A[2]	C (2)	+!	2,3	2,2,2,2	2,2,1,2,5	1,1,6	2-5	Wilson, 1980
Plagusiinae ASM29	?	A	C (2)	+!	2,3	2,2,2,2	2,2,1,2,5	1,1,6	2-5	Rice & Williamson, 1977
Plagusia d. depressa	6?	B	C (2)	+!	2,3	2,2,2,2	2,2,1,2,5	1,1,6	2-5	Wilson & Gore, 1980
Plagusia dentipes	?	B	C (2)	+!	2,3	2,2,3,2	2,2,1,2,5	1,1,6[3]	2-5[4]	Aikawa, 1937; Terada, 1987
Plagusia chabrus	12[5]	A	C (3)	+!	2,3	?,2,3,2[6]	2,2,1,2,5	1,1,6	2-5	Wear, 1970; Wear & Fielder, 1985
Percnon gibbesi	6?	B	C (1)	+!	2,2[7]	2,2,3,2	2,2,1,2,5	1,1,5	2-5	Lebour, 1944; Paula & Hartnoll, 1989

Table 1. Telson and antenna type according to Aikawa (1929). In column "Antenna Type", numbers in brackets correspond to the number of setae on the exopod. In column "Lateral Carapace Spines": + refers to presence, +! to presence with tubercles, spines and/or setae,- to absence. Signs ? = no data. Exponent numbers [1] to [7] mean: [1], Larval development also described by Montú *et al.* (1996) for a German population of *Eriocheir sinensis*, introduced early this century into Europe; several differences were found and here we prefer to use the description from the original Asian population; [2], type B in subsequent zoeal stages; [3], 1,1,5 in Aikawa's description; [4], 2-4 in Aikawa's description; [5], plankton-collected, instar number estimated from the sizes of the zoeae; [6], deduced from illustration, first group of setae not visible; [7], 2,3 in subsequent stages, with one plumose seta.

Tableau 1. Type de telson et d'antenne d'après Aikawa (1929). Dans la colonne "Type d'antenne", les nombres entre parenthèses correspondent au nombre de soies sur l'exopodite. Dans la colonne "Epines latérales de la Carapace": + signifie présence, +! présence avec tubercules, épines et/ou soies, - signifie absence, ? = pas de données. Les exposants [1] à [7] signifient : [1], développement larvaire également décrit par Montú *et al.* (1996), sur une population d'Allemagne, de *Eriocheir sinensis*, espèce introduite au début du siècle en Europe ; plusieurs différences ont été notées et ici nous préférons utiliser la description basée sur la population asiatique ; [2], type B dans les stades zoés suivants ; [3], 1, 1, 5 dans la description de Aikawa ; [4], 2-4 dans la description de Aikawa, [5], stades zoés récoltés dans le plancton, nombre de stades estimé d'après la taille des larves ; [6], déduit d'une illustration, premier groupe de soies non visible, [7], 2-3 dans les stades suivants, avec une soie plumeuse.

endopod is only found in *Plagusia*, *Euchirograpsus* and *Glyptograpsus*. Wear (1970) also described a 1,1,6-setation for two species of *Hemigrapsus* from New Zealand, *H. edwardsi* (Hilgendorf, 1882) and *H. crenulatus* (H. Milne-Edwards, 1837). However, recent re-examination of *H. edwardsi* first zoeal stage revealed the more typical 0,1,6-pattern (Table 1). The second species of this genus described by Wear (1970), *H. crenulatus*, is now the only *Hemigrapsus* with the questionable 1,1,6-setation and a re-examination of zoeae of this species needs to be done.

The first zoeal stage of *Glyptograpsus impressus* has a 1,2-setation on the endopod of the maxilla which is unique among all the known zoea larvae of the Grapsidae. While a setation of 2,3 is common for Plagusiinae and Sesarminae, Varuninae and Grapsinae have a 2,2-pattern (Rice, 1980). The 1,2-setation is otherwise only found in the families Leucosiidae, Pinnotheridae and Ocypodidae (Ocypodinae). This finding gives importance to *Glyptograpsus* in terms of systematics of the Grapsidae. Following the argumentation of Rice (1980), this genus should be one of the more advanced genera within the Grapsidae, since it shows reduction in the number of setae (e.g. on the endopod of the maxilla and the basis of the first maxilliped). On the other hand, the possible link to the Ocypodinae and Pinnotheridae would rather suggest a basal position of *Glyptograpsus* within the Grapsidae.

In adult morphology, the pronounced chelar dimorphism of *Glyptograpsus* is another character which is unique among grapsid crabs (with the only exception of *Platychirograpsus* for which no larval stages are known). A recent comparison of all American grapsid genera, based on mitochondrial DNA sequence, also suggests a position of these two genera clearly outside of the Varuninae and other grapsid subfamilies (Schubart *et al.*, unpublished). For a better understanding of the systematic position of *Glyptograpsus* within the Grapsidae, the description of larvae from *G. jamaicensis* (Benedict, 1892) and *Platychirograpsus* would be extremely useful.

Table 1 and Fig. 3 give evidence for a great morphological similarity between the first zoeae of the varunine species *Euchirograpsus americanus* A. Milne-Edwards, 1880 and those of the subfamily Plagusiinae (see also Wilson, 1980). The Plagusiinae presently consist of 16 species belonging to two genera (*Plagusia* and *Percnon*). Data on zoeal morphology are only available for one species of *Percnon* and three species of *Plagusia* (see Table 1). A prezoea of *Plagusia depressa tuberculata* has been described by Rajabai (1961) (as *P. d. squamosa*), but is not included in this table due to an incomplete development of setation patterns in that early phase. The description of "Plagusiinae ASM29", a first zoeal stage from the plankton of the eastern Atlantic (Rice and Williamson, 1977), most probably represents a zoea of *Euchirograpsus* as suggested by the morphology of the telson (Table 1; see also Paula, 1987). According to Rice (1980), the Plagusiinae larvae are characterized by: 1) a well-developed lateral spine which, like the rostral spine, carries tubercles, spinules or setae, 2) a short or rudimentary antennal exopod, 3) 2,3-setation on the maxillary endopod, and 4) basal segment of the second maxilliped endopod armed with a single seta. Wilson (1980) described small rounded protuberances on the dorsal carapace posterior to the dorsal spine (see Fig. 3) as an additional common character to the Plagusiinae. This character was also found in "Plagusiinae ASM29" - Rice and Williamson, 1977 and *Percnon gibbesi* (Lebour, 1944), but was not mentioned in the descriptions of Aikawa (1937), Wear (1970), Terada (1987) and Paula & Hartnoll (1989). Instead, the last two authors proposed the presence of dorso-lateral knobs on the abdominal somites 2-5 as an additional feature to distinguish Plagusiinae larvae. All these larval characters allow an easy distinction of Plagusiinae zoeae from other grapsid zoeae, with the only exception of *Euchirograpsus americanus* (see Wilson & Gore, 1980). In the case of the sympatric American species *E. americanus* and *Plagusia depressa* (Fabricius, 1775), only minor morphological features allow the identification of zoeae: two knob-like postero-lateral protuberances of *E. americanus* in addition to the small rounded protuberance mentioned above, the type of telson (only in the zoea I, being of the same type in later stages), and differences in setation of the coxal endite of the maxillae. These species are even identical in characteristics which are otherwise recognized as highly variable on an intrageneric level, as for example the number of abdominal knobs (Table 1) and the number of setae or aesthetases on the antennules. Also in this case, results from mitochondrial DNA sequencing corroborate findings from larval morphology and suggest a systematic position of *E. americanus* in close relationship to *P. depressa* and not linked to the main group of Varuninae (Schubart *et al.*, unpublished).

Results from this study strongly suggest that the grapsid subfamily Varuninae as defined by Alcock (1900) needs to be revised. Besides the possible exclusion of *Euchirograpsus* and *Glyptograpsus*, inclusion of other genera presently included within the Sesarminae are necessary (Schubart & Cuesta, in press) to give this subfamily a reliable phylogenetic basis. Larval morphology alone cannot be used to determine the systematic position of the genera *Euchirograpsus* and *Glyptograpsus*, but for the former it clearly suggests a close similarity to the Plagusiinae, while the latter, *Glyptograpsus*, cannot presently be attributed to any other grapsid subfamily and might be of special interest for future studies of grapsid subfamilial relationships.

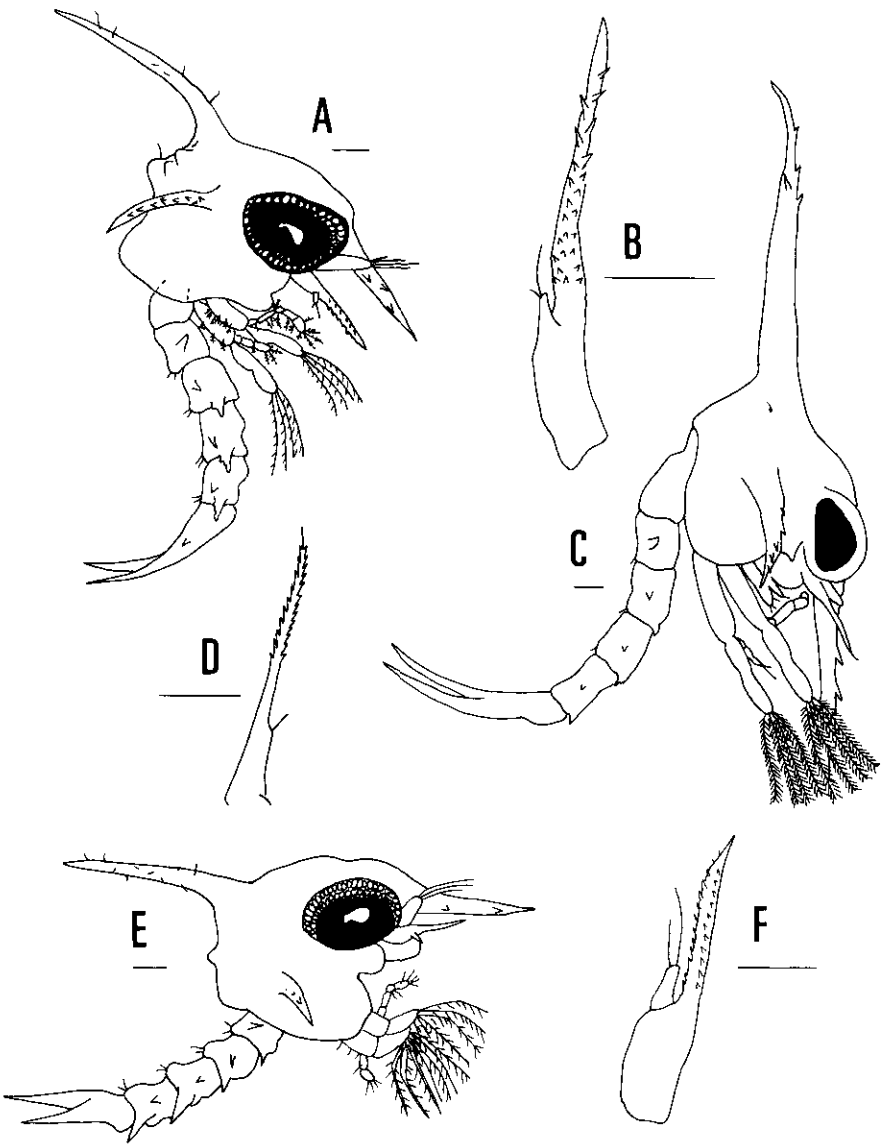

Figure 3. *Euchirograpsus americanus*, zoea I. A, lateral view; B, antenna (after Wilson, 1980). *Percnon gibbesi*, zoea I. C, lateral view; D, antenna (after Paula and Hartnoll, 1989). *Plagusia d. depressa*, zoea I. E, lateral view; F, antenna (after Wilson and Gore, 1980). Scale bars = 0.1 mm.

Figure 3. *Euchirograpsus americanus*, zoé I. A, vue latérale; B, antenne (d'après Wilson, 1980). *Percnon gibbesi*, zoé I. C, vue latérale ; D, antenne (d'après Paula et Hartnoll, 1989). *Plagusia d. depressa*, zoé I. E, vue latérale ; F, antenne (d'après Wilson et Gore, 1980). Échelles = 0.1 mm.

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