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FIRST ZOEAL STAGES OF *GEOGRAPSUS LIVIDUS* AND *GONIOPSIS PULCHRA* FROM PANAMA CONFIRM CONSISTENT LARVAL CHARACTERS FOR THE SUBFAMILY GRAPSINAE

(CRUSTACEA: BRACHYURA: GRAPSIDAE)

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ABSTRACT

The first zoeal stages of *Geograpsus lividus* (H. Milne Edwards, 1837) and *Goniopsis pulchra* (Lockington, 1876), both obtained from laboratory hatched material in Panama, are described and illustrated. *Geograpsus* was one of the few genera of Grapsinae for which larval data were unavailable. Zoeal features are compared with those of other genera included in Grapsinae, and several shared morphological characters are established for the subfamily. A combination of six characters, one of them newly recognized, seems to be diagnostic for the Grapsinae and allows recognition of planktonic material. Zoea I larvae of the eastern Pacific *Goniopsis pulchra* and the western Atlantic *G. cruentata* (Latreille, 1803) exhibit differences in size, morphometrics, and setation of the antennule and telson, rendering support to the taxonomic distinction of this trans-isthmian species pair.

INTRODUCTION

Cuesta et al. (1997) found consistent morphological characters for the first zoeal stage in the grapsid subfamily Grapsinae. They stated that in addition to the need of describing more species and later stages, larvae of two genera, *Geograpsus* Stimpson, 1858 and *Grapsodius* Homes, 1900, were still unknown. Description of larvae of these genera and of *Leptograpsodes* Montgomery, 1929, also belonging in this subfamily, is essential for a complete understanding of larval morphology of the Grapsinae.

The type material of the monotypic genus *Grapsodius* was destroyed during an earthquake. No one has found any specimen that matches the description since then. From its morphology, it is most likely that *G. eximius* Holmes, 1900, was an aberrant specimen of *Pachygrapsus* Randall, 1840 or *Planes* Bowdich, 1825 (Mary Wicksten pers. comm. 1996). In consequence, *Grapsodius* is here not considered a valid genus of Grapsinae.

Geograpsus and *Leptograpsodes* thus remain as the only genera of Grapsinae with undescribed larval stages. Pautsch (1965) raised larvae of *G. lividus* for chromatophore studies, but did not describe them. With the present description and illustration of the first zoeal stage of *G. lividus*, first zoea larvae of an additional grapsine genus become available for comparison. *Geograpsus lividus* has a wide distribution and is found on rocky shores of the African (from Senegal to Angola) and American (from Florida to Brazil) Atlantic as well as along the East Pacific coast from Baja California (Mexico) to Chile.

In addition, the first zoeal stage of another grapsine crab from Panama, *Goniopsis pulchra*, is described. This species inhabits mangrove swamps and estuaries in the tropical eastern Pacific from Baja California to Peru and is taxonomically separated from congeneric species of the Atlantic, *G. pelii* (Herklots, 1851) (East Atlantic) and *G. cruentata* (Latreille, 1803) (West Atlantic).

This study is an important step towards completing our knowledge of first stage zoeal morphology in the subfamily Grapsinae, which will provide the framework for comprehensive comparative and phylogenetic studies.

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MATERIAL AND METHODS

Ovigerous specimens of *Geograpsus lividus* and *Goniopsis pulchra* were collected at different localities along the Pacific coast of Panama: *G. lividus* between rocks at Isla Culebra (35 PSU ambient salinity, 28 February 1996) and *G. pulchra* under stones at the Miraflores Locks Spillway (1 PSU ambient salinity, 1 March 1996) and from between mangrove roots at Diablo Heights (4 March 1996).

At the Naos laboratories of the Smithsonian Tropical Research Institution (STRI), ovigerous crabs were maintained in a compartmented plastic dish filled with filtered sea water, and immersed in a large outdoor water tank, thus exposed to ambient temperature and light regimes. Two hatches were obtained for both species: larvae of *G. lividus* hatched on March 8 and 10, those of *G. pulchra* on March 2 and 26. The last brood of *G. pulchra* hatched after transport of an ovigerous female to Cádiz (Spain), where larvae were cultured in the laboratories of the Instituto de Ciencias Marinas de Andalucía.

Shortly after hatching and active natatory behavior were observed, samples of zoea I larvae were fixed in 70% ethanol. No larva survived longer than 8 days and no successful molt to the second zoeal stage was observed, probably due to the failure of the small zoeae to ingest the offered *Artemia* sp. nauplii (or rotifers *Brachionus plicatilis* in Cádiz). Larvae of both species were dissected and their morphology compared with that of other crab species belonging to the subfamily Grapsinae. For comparative purposes, zoea I larvae of *Goniopsis cruentata* (Latreille, 1830) from Rio Escuro and Rio Comprido mangroves (23°S, 45°W, Ubatuba, Brazil) described by Fransozo et al. (1998) were newly dissected and measured.

Drawings and measurements were based on 20 larvae for each of 4 hatches with a Wild MZ6 and Zeiss compound DIC (Nomarski) microscope, both equipped with a camera lucida. All measurements were made by an ocular micrometer. Rostrodorsal length (rdl) was measured 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 margin, carapace width (cw) as the greatest distance across the carapace, dorsal spine (ds) from the base to the tip of the dorsal carapace spine, rostral spine (rs) from the base to the tip of the rostral carapace spine, and antenna (ant) from the base to the tip of the antenna. Semipermanent mounts of whole larvae and dissected appendages were stained using CMC 10 and lignin pink. Parental females of *Geograpsus lividus* and *Goniopsis pulchra* as well as samples of zoea I for both species were deposited at the United States National Museum of Natural History, Washington under the catalog numbers USNM 260890 and 260891 respectively.

RESULTS

Geograpsus lividus (H. Milne Edwards, 1837)

Zoea I (Figs 1-3)

(Pautsch 1965: figs 1-2)

Dimensions. – rdl: 0.75 ± 0.03 mm; cl: 0.42 ± 0.02 mm; cw: 0.32 ± 0.01 mm; ds: 0.16 ± 0.01 mm; rs: 0.22 ± 0.02 mm; ant: 0.24 ± 0.01 mm.

Carapace (Fig. 1A). – Globose, smooth, and without tubercles. Rostral and dorsal spine short and stout. Lateral spines minute, visible as rounded knob-like projections. A pair of dorsolateral simple setae near base of dorsal spine. Ventral margin without setae. Eyes sessile.

Antennule (Fig. 1B). – Uniramous. Endopod absent. Exopod unsegmented with 2 unevenly sized aesthetascs and 1 thin simple seta.

Antenna (Fig. 1C). – Well-developed protopod, slightly longer than rostral spine, bearing two longitudinal rows of long denticles, and one long denticle near distal end. Endopod absent. Exopod present as a small protuberance with 1 simple seta.

Mandible. – Palp absent.

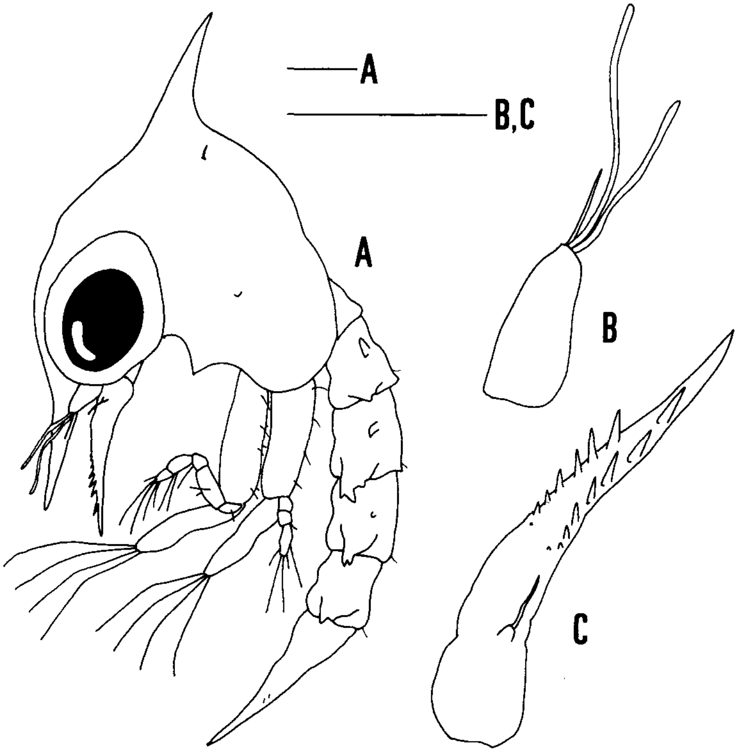

Fig. 1. *Geograpsus lividus* (H. Milne Edwards, 1837) from Pacific coast of Panama, zoea I: A, lateral view; B, antennule; C, antenna. Scale bars = 0.1 mm.

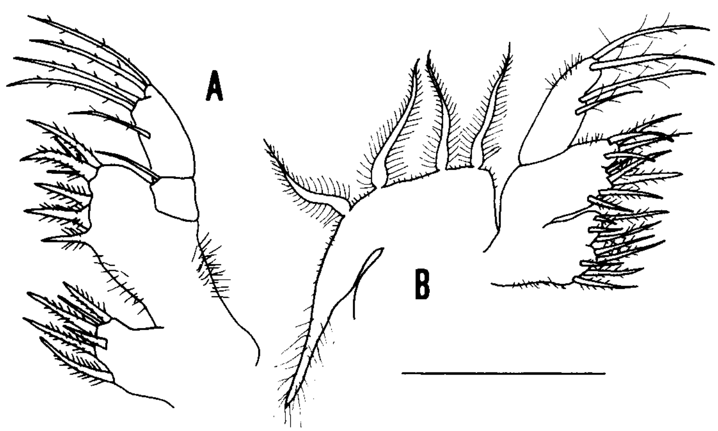

Fig. 2. *Geograpsus lividus* (H. Milne Edwards, 1837) from Pacific coast of Panama, zoea I: A, maxillule; B, maxilla. Scale bar = 0.1 mm.

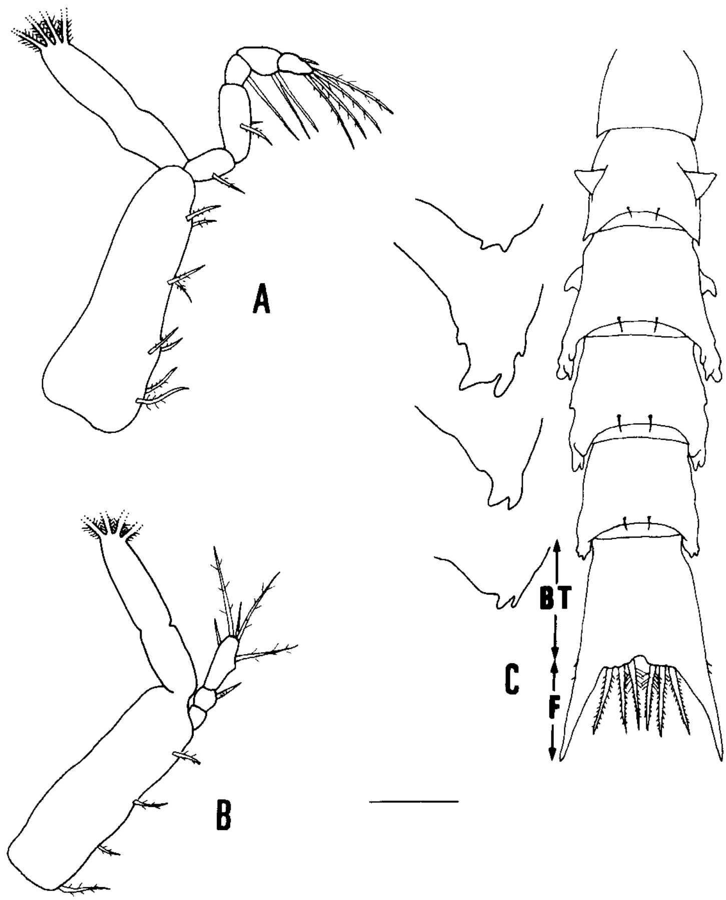

Fig. 3. *Geograpsus lividus* (H. Milne Edwards, 1837) from Pacific coast of Panama, zoea I: A, first maxilliped; B, second maxilliped; C, dorsal view of abdomen (with magnification of posterolateral margins of abdominal somites 2-5). Long natatory setae on the distal exopod segments of the first and second maxilliped are truncated. Abbreviations: F: length of furcal arms; BT: length of basal telson. Scale bar = 0.1 mm.

Maxillule (Fig. 2A). – Coxal and basial endites with 6 and 5 plumodenticulate setae respectively; no seta on external margin of basis. Endopod 2-segmented, proximal segment with 1 simple seta, distal segment with 1 subterminal and 4 terminal plumodenticulate setae.

Maxilla (Fig. 2B). – Coxal and basial endite distally bilobed with 4 + 5 and 5 + 4 plumodenticulate setae on the inner and outer lobes respectively. Endopod unsegmented, distally bilobed with 1 long plumodenticulate seta and 1 short (half length) plumodenticulate seta on inner lobe and 2 long plumodenticulate setae on outer lobe. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

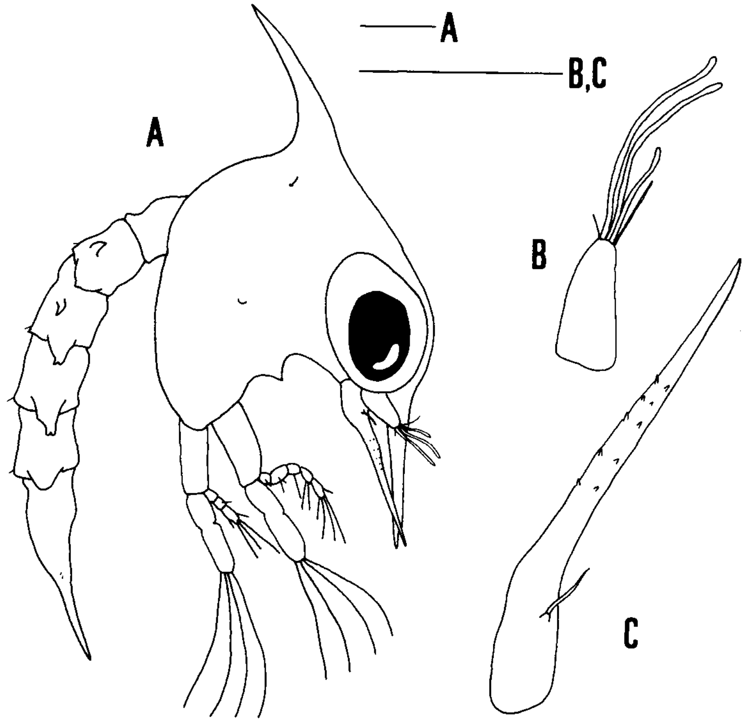

Fig. 4. *Goniopsis pulchra* (Lockington, 1876) from Pacific coast of Panama, zoea I: A, lateral view; B, antennule; C, antenna. Scale bars = 0.1 mm.

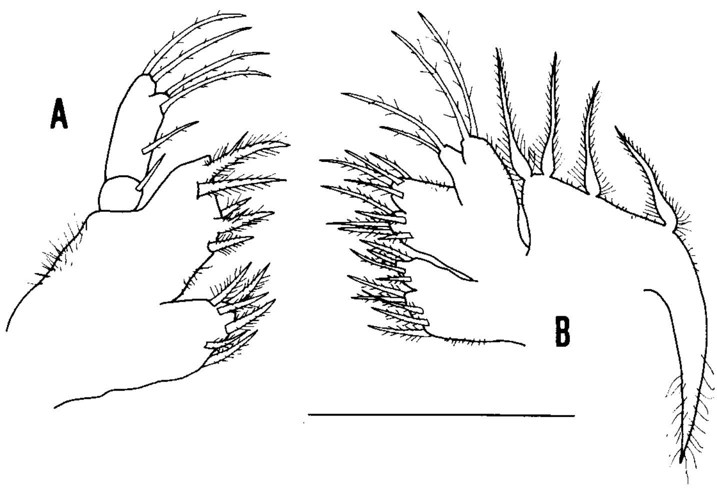

Fig. 5. *Goniopsis pulchra* (Lockington, 1876) from Pacific coast of Panama, zoea I: A, maxillule; B, maxilla. Scale bar = 0.1 mm.

First maxilliped (Fig. 3A). – Basis with 8 medial plumodenticulate setae arranged 2,2,2,2. Endopod 5-segmented with 11 plumodenticulate or simple setae arranged 1,2,1,2,5 (1 subterminal and 4 terminal). Exopod slightly constricted with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 3B). – Basis with 4 medial plumodenticulate setae arranged 1,1,1,1. Endopod 3-segmented with 6 plumodenticulate or simple setae arranged 0,1,5 (2 subterminal and 3 terminal). Exopod slightly constricted with 4 long terminal plumose natatory setae.

Third maxilliped. – Absent.

Pereiopods. – Absent.

Pleon (Fig. 3C). – Five abdominal somites; dorsolateral knobs on somites 2-4 (small on somite 4). Somites 2-5 with posterolateral projections and a pair of sparsely plumose setae near posterodorsal margin. Pleopods absent.

Telson (Fig. 3C). – Three pairs of serrulate setae on inner posterior margin of telson. Two minute lateral spines at outer base of each furcal arm.

Goniopsis pulchra (Lockington, 1876)

Zoea I (Figs 4-6)

Dimensions. – rdl: 0.75 ± 0.02 mm; cl: 0.30 ± 0.01 mm; cw: 0.28 ± 0.01 mm; ds: 0.22 ± 0.01 mm; rs: 0.21 ± 0.01 mm; ant: 0.23 ± 0.01 mm.

Carapace (Fig. 4A). – Globose and smooth. Dorsal spine slightly curved and rostral spine straight, both well-developed. Lateral spines minute, visible as rounded knob-like projections. A pair of dorsolateral simple setae near base of dorsal spine. Ventral margin without setae. Eyes sessile.

Antennule (Fig. 4B). – Uniramous. Endopod absent. Exopod unsegmented with 3 unevenly sized aesthetascs and 2 thin simple setae.

Antenna (Fig. 4C). – Well developed protopod, almost equal in length to rostral spine, proximally bearing two longitudinal rows of minute denticles. Endopod absent. Exopod present as a small protuberance with 1 simple seta.

Mandible. – Palp absent.

Maxillule (Fig. 5A). – Coxal endite with 6 plumodenticulate setae. Basial endite with 5 plumodenticulate setae; no seta on external margin of basis. Endopod 2-segmented, proximal segment with 1 simple seta, distal segment with 1 subterminal and 4 terminal plumodenticulate setae.

Maxilla (Fig. 5B). – Coxal and basial endites bilobed with 5 + 4 and 4 + 5 plumodenticulate setae on the outer and inner lobe respectively. Endopod unsegmented, bilobed with 1 long plumodenticulate seta and 1 short (half length) plumodenticulate seta on inner lobe and 2 long plumodenticulate setae on outer lobe. Scaphognathite with 4 plumose marginal setae and a long setose posterior process.

First maxilliped (Fig. 6A). – Basis with 8 medial plumodenticulate setae arranged 2,2,2,2. Endopod 5-segmented with 11 plumodenticulate or simple se-

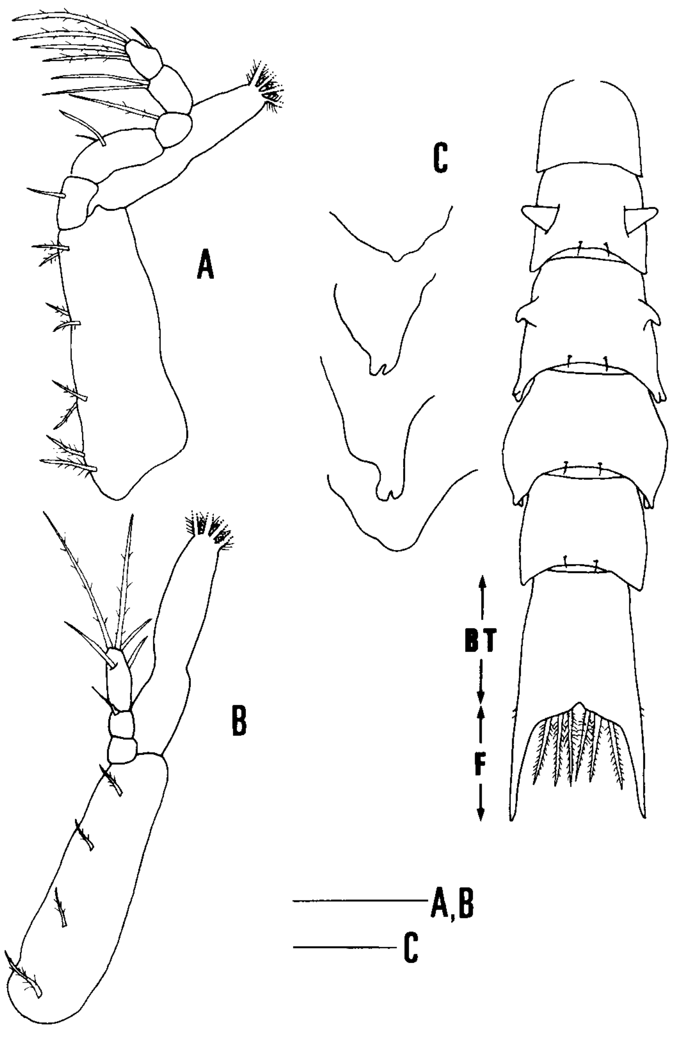

Fig. 6. *Goniopsis pulchra* (Lockington, 1876) from Pacific coast of Panama, zoea I: A, first maxilliped; B, second maxilliped; C, dorsal view of abdomen (with magnification of posterolateral margins of abdominal somites 2-5). Long natatory setae on the distal exopod segments of the first and second maxilliped are truncated. Abbreviations: F: length of furcal arms; BT: length of basal telson. Scale bars = 0.1 mm.

tae arranged 1,2,1,2,5 (1 subterminal and 4 terminal). Exopod slightly constricted with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 6B). – Basis with 4 medial plumodenticulate setae arranged 1,1,1,1. Endopod 3-segmented with 6 plumodenticulate or simple setae arranged 0,1,5 (2 subterminal and 3 terminal). Exopod slightly constricted with 4 long terminal plumose natatory setae.

Third maxilliped. – Absent.

Pereiopods. – Absent.

Pleon (Fig. 6C). – Five abdominal somites; dorsolateral knobs on somites 2-3. Somite 4 globose. Somites 2-5 with posterolateral projections and a pair of sparsely plumose setae near posterodorsal margin. Pleopods absent.

Telson (Fig. 6C). – Six serrulate setae on inner posterior margin of telson. Two minute lateral spines at outer base of each furcal arm.

DISCUSSION

The description of the first zoeal stage of *Geograpsus lividus* and *Goniopsis pulchra* corroborates the presence of morphological characters that are typical of zoea I larvae for the subfamily Grapsinae (see Cuesta et al. 1997). The validity of these characters is of importance for systematic purposes and plankton identifications. In the following, six morphological characters are listed, which in their combination are diagnostic for zoeae larvae of Grapsinae:

1) No lateral carapace spines in the zoea I, but instead knob-like or hooked projections (Figs 1A & 4A, Tab. 1), as precursors of lateral spines in following zoeal stages.

2) Antennal exopod absent or reduced (type C or D according to Aikawa 1929). Most genera show a rudimentary protuberance carrying a simple seta (type C; Figs 1C & 4C, Tab. 1). In *Metopograpsus* the protuberance and the seta are absent (type D).

3) The maxillar endopod is characterized by a 2,2 setal arrangement (Figs 2B & 5B, Tab. 1).

4) The first maxilliped bears eight medial setae on the basis (arranged 2,2,2,2) and always a single seta on the proximal segment of the endopod (overall setation in the first zoeal stage: 1,2,1,2,5) (Figs 3A & 6A, Tab. 1).

5) Basal part of telson (BT) elongated and always longer than furcal arms (F) in first stage zoeae (Figs 3C & 6C) so that $F/BT < 1$ (Tabs 1-2).

6) The setation pattern on the endopod of the second maxilliped is 0,1,5 (or 0,1,4), but never 0,1,6 (Figs 3B & 6B, Tab. 1).

While the first four characters are derived from previous studies (Wear 1970; Rice 1980; Wilson 1980; Konishi & Minagawa 1990; Cuesta et al. 1997), the fifth character is here recognized for the first time as diagnostic for the Grapsinae (see Tab. 2). Konishi & Minagawa (1990) previously mentioned the 0,1,5 setation on the endopod of the second maxilliped (sixth character) of *Pachygrapsus, Planes,* and *Leptograpsus.* The 0,1,4 setation described by Pasupathi & Kannupandi (1986) for the endopod of the second maxilliped of *Metopograpsus lati-*

Table 1. Morphological features of first zoea larvae of eight genera presently included in the subfamily Grapsinae (most recent descriptions used). Telson and antenna type from the classification of Aikawa (1929). Abbreviations: **F**, length of furcal arms; **BT**, length of basal telson; **c.e.**, coxal endite; **b.e.**, basial endite; **Mxpd.**, maxilliped; ?, no data; Exponents: [1]Cuesta & Rodríguez, unpublished data; [2]based on Fukuda's (1978) statement that characters correspond to those found in Ocypodidae; [3]described as *M. maculatus* by Pasupathi & Kannupandi (1986).

Species	No of zoeal stages	Telson type (F/BT)	Antenna type	Lateral spines		Maxillule		Maxilla			Mxpd. I		Mxpd. II	References
				zoea I	later stages	c.e.	b.e.	c.e.	b.e.	endo-pod	basis	endo-pod	endo-pod	
Geograpsus lividus	?	A (0.9)	C	knob-like	?	6	5	9	9	2,2	2,2,2,2	1,2,1,2,5	0,1,5	present study
Grapsus adscensionis	?	A (0.8)	C	knob-like	?	6	5	10	9	2,2	2,2,2,2	1,2,1,2,5	0,1,5	Cuesta et al. 1997
Goniopsis pulchra	?	A (0.9)	C	knob-like	?	6	5	9	9	2,2	2,2,2,2	1,2,1,2,5	0,1,5	present study
Leptograpsus variegatus	?	A (0.7)	C	No	?	5	5	9	8	2,2	2,2,2,2	1,2,1,2,5	0,1,5	Wear 1970
Pachygrapsus marmoratus	6[1]	A (0.8)	C	knob-like[1]	II-VI	6	5	9	9	2,2	2,2,2,2	1,2,1,2,5	0,1,5	Cuesta & Rodríguez 1994
Metopograpsus latifrons[3]	5	B (0.6)	D	knob-like	II-V	5	5	6	7	2,2	2,2,2,2	1,2,1,2,5	0,1,4	Pasupathi & Kannupandi 1986
Planes minutus	?	A (0.8)	C	knob-like	?	6	5	9	9	2,2	2,2,2,2	1,2,1,2,5	0,1,5	Cuesta et al. 1997
Ilyograpsus paludicola	?	B[2] (?)	B[2]	No[2]	?	?	?	?	?	2,2[2]	2,2,3,2[2]	2,2,1,2,5[2]	0,1,6[2]	Fukuda 1978

Table 2. Ratio of furca and basal telson for first stage zoeae of the four subfamilies of Grapsidae. Measurements based on figures from 74 descriptions (n) of zoeae I.

		Furca / basal telson		
Subfamily	n	range	mean	sd
Grapsinae	17	0.5 - 0.91	0.76	0.13
Plagusiinae	4	1.18 - 1.75	1.47	0.27
Varuninae	16	1.66 - 3.5	2.41	0.46
Sesarminae	37	1.09 - 4.33	2.27	0.59

frons (Tab. 1) is questionable. In later stages the same authors found 0,1,5, but setation of the second maxilliped endopod is normally consistent during the course of zoeal development. Furthermore, Hashmi (1971) and Fielder & Greenwood (1983) found 0,1,5 in zoeae I of two other species of *Metopograpsus*.

Two other characters mentioned by Cuesta et al. (1997) were also confirmed for *Geograpsus lividus* and *Goniopsis pulchra*, but cannot be used for diagnostic purposes because they are not consistently present in all Grapsinae species:

1) Dorsolateral knobs on somites 2-3 and posterolateral projections on somites 3-5 (Figs 3C & 6C); exception: *Metopograpsus*.

2) Furcal arms of telson with one, two or three fine seta-like spines on the outer side; exceptions: *Metopograpsus*, *Goniopsis cruentata*, *Pachygrapsus crassipes*.

The above-listed combination of characters allows precise determination of whether a zoea larva from plankton samples belongs to the Grapsinae. For only one genus currently assigned to the Grapsinae, *Ilyograpsus*, can these larval morphological characters not be confirmed (Tab. 1). The only larval description of this genus (*I. paludicola* by Fukuda 1978) lacks illustrations and detailed descriptions. However, the presence of an antenna type B (sensu Aikawa 1929) makes it unlikely that this genus belongs to the Grapsinae at all. This is supported by Fukuda's (1978) statement that the first zoea of *I. paludicola* shows a close affinity to larvae of the Ocypodidae rather than to the Grapsidae. *I. paludicola* was moved from the Ocypodidae (genus *Camptandrium*) to the Grapsidae after a case of taxonomic confusion. Barnard (1955) erected the genus *Ilyograpsus* for a new species, *I. rhizophorae*, which was later found to be a junior synonym of *Camptandrium paludicola* Rathbun. However, the monotypic genus *Ilyograpsus* remained valid and was attributed to the Grapsinae as originally suggested by Barnard (1955) (see Davie 1993). Redescription of zoeae of *I. paludicola* will be necessary to compare them with larvae of other grapsid species and to help to determine the best phylogenetic assignment of the genus *Ilyograpsus*.

Re-examination of the original larval material of *Goniopsis cruentata* from Brazil revealed two errors in a previous description by Fransozo et al. (1998). The coxa of the maxillule carries 6 setae (not 5) and the setation of the coxal endite of the maxilla is 5 + 4 (not 4 + 3). This corresponds to the setation found in the two species described in the present study and most other grapsine species (Tab. 1). The measurements of 20 larvae of *G. cruentata* were rdl: 0.88 ± 0.04 mm, cw: 0.32 ± 0.01 mm; ds: 0.26 ± 0.01 mm; rs: 0.25 ± 0.01 mm; ant: 0.25 ± 0.01 mm.

There is a striking morphological similarity between adults of the two trans-isthmian species of *Goniopsis* (*G. pulchra* and *G. cruentata*). Postulated differences in color patterns do not seem to hold as shown by von Sternberg (1994). Morphological differentiation and taxonomic status of these two species and the West African *G. pelii* have been addressed and questioned repeatedly (Rathbun 1918; Abele 1971; Manning & Holthuis 1981; von Sternberg 1994). Zoea I larvae of the two American species were found to differ in the following characters:

1) Larvae of *Goniopsis cruentata* were overall larger than those of both hatches of *G. pulchra* (e.g. rdl: 0.88 ± 0.04 mm vs. 0.75 ± 0.02 mm). However, the ratios of most measurements did not differ significantly. Only the antenna of *G. cruentata* turned out to be proportionally shorter than in both of the hatches of *G. pulchra* (ant/rs: 0.97 ± 0.05 vs. 1.06 ± 0.06).

2) The telson of *G. cruentata* does not carry any spines at the outer base of the furca, while two pairs of small spines are present in *G. pulchra.*

3) The antennule of *G. cruentata* bears 2 aesthetascs and 2 setae, while that of *G. pulchra* has 3 aesthetascs and 2 setae.

Different sizes of larvae can often be attributed to different climatic conditions under which they originate (e.g. Christiansen 1973). Shirley et al. (1987) showed that larval size can vary with incubation water temperature. However, differences in relative size of the antenna and setation of the antennule and telson are consistent among the studied hatches of *Goniopsis* and can possibly be used as diagnostic larval characters for the separation of the two species. Sequences of mitochondrial DNA of these species also showed genetic distances in a range which is normally found between species, but this also holds true for other trans-isthmian pairs which are at present considered single species (Cuesta & Schubart 1998; Schubart et al. unpublished data).

Among the Brazilian materials of *Goniopsis cruentata,* one larva was raised to a zoea II stage (Fransozo et al. 1998). The present study confirmed that lateral carapace spines are acquired in the second stage. The first zoeal stage of *G. cruentata* is characterized by rounded knob-like projections. Delayed development of lateral carapace spines is postulated to be a general phenomenon in the Grapsinae (see above list, character 1). The presence of lateral knob-like projections on the carapace of the zoea I of *Geograpsus lividus* and *Goniopsis pulchra* is therefore indicative that lateral carapace spines will be acquired in later zoeal stages, as already confirmed for *Pachygrapsus* (see Cuesta & Rodríguez

1994), and *Metopograpsus* (see Kakati 1982; Fielder & Greenwood 1983; Pasupathi & Kannupandi 1986), and as postulated for *Grapsus* and *Planes* (see Cuesta et al. 1997). This must be taken into account when identifying and quantifying later zoeal stages from the marine plankton.

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