

The first zoeal stages of *Grapsus grapsus* (Linnaeus) and *Geograpsus lividus* (H. Milne Edwards) (Decapoda, Brachyura, Grapsidae) from the western Atlantic.

Guerao¹, G.; Schubart^{2,3}, C. D. and Cuesta², J. A.

¹ Department de Biologia Animal, Secció de Zoologia (Artròpodes), Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal, 645, 08028 Barcelona, Spain. e-mail: guilleg@porthos.bio.ub.es

² Department of Biology, Laboratory for Crustacean Research, University of Louisiana at Lafayette, P.O. Box 42451, Lafayette, LA 70504-2451, USA. e-mail: jac4813@louisiana.edu

³ Biologie I, Universität Regensburg, D-93040 Regensburg, Germany. e-mail: christoph.schubart@biologie.uni-regensburg.de

Abstract

The first zoeal stages of *Grapsus grapsus* (Linnaeus, 1758) and *Geograpsus lividus* (H. Milne Edwards, 1837) were obtained from laboratory-hatched material originating from the Gulf of Mexico (Veracruz, Mexico). The zoeae are described and illustrated in detail. Comparisons are made with previous larval descriptions of both genera. Morphological differences found between the first zoeal stage of *Grapsus grapsus* and *G. adscensionis* (Osbeck, 1765) confirm the validity of both taxa and give evidence for the isolating effect of the Atlantic Basin. The first zoea of *Geograpsus lividus* from the present study presents marked morphological differences when compared to the same zoeal stage of *G. lividus* from the Pacific coast of Panama. These differences are at a level of distinction normally found between congeneric species, and support a possible taxonomic separation between these trans-isthmian populations, as suggested previously.

Key words: larval morphology, taxonomy, zoea, *Grapsus grapsus*, *Geograpsus lividus*

Introduction

Despite the fact that knowledge on larval morphology of the family Grapsidae *s. str.* (previous subfamily Grapsinac; taxonomy according to Schubart *et al.*, 2000; 2002) is far from complete, Cuesta *et al.* (1997) and Cuesta and Schubart (1999) showed that the first zoeal stage of all known grapsid genera presents a combination of consistent morphological characters that allows distinction from the rest of grapsoid families.

There are only few larval morphological descriptions of *Grapsus*, the type genus of the Grapsidae *s. str.* The first zoea of *G. adscensionis* was described in detail by Cuesta *et al.* (1997). Brief and incomplete descriptions are also known for the first zoea of *G. grapsus* (see Lebour, 1950), and *G. tenuicrustatus* (Herbst) (see Aikawa, 1937), as well as for the zoea I, IV, V and the megalopa of *G. strigosus* (Herbst) (see Gohar and Al-Kholi, 1957). The megalopa of *G. longitarsis* Dana was incompletely described and illustrated by Chen (1995).

Until recently, *Grapsus grapsus* was considered to have a wide distribution throughout the tropical Atlantic as well as the tropical eastern Pacific. Türkay (1982) was the first to suggest that east and west Atlantic populations of this species are distinct and he referred to the African populations as *G. webbi* H. Milne Edwards, 1853. Manning and Chace (1990) pointed out that the oldest available name for the east Atlantic form of *G. grapsus*, including the oceanic islands of Ascension and St. Helena, would be *G. adscensionis* (Osbeck, 1765). Separation at species level was not accepted by d'Udekem d'Acoz (1999) who suggested that the two forms should be considered at most closely related subspecies. The present description of the first zoeal stage of *G. grapsus* and its comparison with the first zoea of *G. adscensionis* provides a new set of morphological characters to be used for testing the taxonomic status of these potential species.

The first zoeal stage of *Geograpsus lividus* has recently been described by Cuesta and Schubart (1999) based on material from the Pacific coast of Panama. The same larval stage of this species from the Gulf of Mexico was now examined taking into account that Atlantic and Pacific populations have been isolated during the uplift of the Panama Isthmus, between 3 and 3.5 million years ago (Keigwin, 1982; Knowlton and Weigt, 1998) and that many other trans-isthmian pairs are recognized as good species (Lessios, 1981; Abele and Kim, 1989; Knowlton and Weigt, 1998).

Material and Methods

Ovigerous crabs of *Grapsus grapsus* and *Geograpsus lividus* were collected at Punta Delgada, Veracruz (Mexico) on 18 April 1998. First stage zoea larvae hatched during the transport to the laboratories of the University of Louisiana at Lafayette, where larvae were preserved in 70% ethanol. Larval appendages were dissected under a Wild MZ8 binocular microscope, and drawings were made using an Olympus BH-2 microscope equipped with Nomarski interference contrast and an attached *camera lucida*. Semipermanent mounts were made of whole larvae and dissected appendages were stained using CMC 10 (Turtox Ltd.) and lignin pink. Permanent mounts were made using polyvinyl lactophenol, and cover slips were sealed with nail varnish. All measurements were made by an ocular micrometer. Drawings were based on five larvae and measurements on 10 larvae. The following measurements were taken: rostro-dorsal 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 distance between the tips of the lateral spines. Descriptions and figures are arranged according to the standard proposed by Clark *et al.* (1998). Parental vouchers and samples of larvae of the two species have been deposited at the Colección Nacional de Crustáceos del Instituto de Biología de la Universidad Nacional Autónoma de México, CNCR 19218 and CNCR 19219.

Results

Grapsus grapsus (Linnaeus, 1837)

Grapsus grapsus: Lebour, 1950: 377, figure 7F-H (zoea I).

Zoea I (figures 1-4)

Dimensions: rdl: 0.92 ± 0.02 mm; cl: 0.50 ± 0.01 mm; cw: 0.37 ± 0.01 mm.

Cephalothorax (figure 1A,B): globose, smooth and without tubercles. Dorsal and rostral spines short and stout. Lateral spines minute, only present as rounded knob-like projections. Pair of dorsolateral simple setae present. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (figure 1C): uniramous. Endopod absent. Exopod unsegmented with 4 aesthetascs (2 long and 2 thin and short) and 1 simple seta.

Antenna (figure 1D): well developed protopod, slightly longer than rostral spine and bearing 2 rows of well developed spines. Endopod absent. Exopod present as a minute bud with a terminal simple seta.

Mandible: endopod palp absent.

Maxillule (figure 2A): coxal endite with 6 plumose setae. Basial endite with 5 setae (2 plumodenticulate cuspidate and 3 plumodenticulate). Endopod two-segmented with 1 plumodenticulate seta on the proximal segment and 1 medial, 2 subterminal and 2 terminal plumodenticulate setae on the distal segment. Exopod absent.

Maxilla (figure 2B): coxal endites bilobed with 5 (2 plumodenticulate, 3 plumose) + 4 (1 plumodenticulate, 3 plumose) setae. Basial endites bilobed with 5 (2 plumodenticulate, 3 plumose) + 4 (1 plumose, 3 plumodenticulate) setae. Endopod unsegmented, bilobed with 2 long plumodenticulate setae on each lobe. Scaphognathite with 4 marginal plumose setae and 1 long setose posterior process.

First maxilliped (figure 3A): coxa with 1 plumodenticulate seta. Basis with 8 medial setae arranged 2,2,2,2 (longer first pair of setae plumodenticulate, other 3 pairs with 1 sparsely plumose and 1 simple seta each). Endopod five-segmented with 1,2,1,2,5 setae (setae on segments 1-3 sparsely plumose, setae on segment 4 plumodenticulate, and 4 terminal plumodenticulate and 1 subterminal simple setae on

distal segment). Exopod two-segmented, with 4 long terminal plumose natatory setae on the distal segment.

Second maxilliped (figure 3B): coxa without seta. Basis with 4 medial setae arranged 1,1,1,1 (a first longer plumodenticulate seta, a second sparsely plumose seta, and two last simple setae). Endopod three-segmented with 0,1,5 setae (1 plumodenticulate setae on segment 2, 1 simple and 1 plumodenticulate subterminal setae and 1 simple and 2 long plumose terminal setae on distal segment). Exopod two-segmented, with 4 long terminal plumose natatory setae on distal segment.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (figure 4A,B): five abdominal somites. Somites 2-5 with one pair of dorsolateral processes, those of somites 4 and 5 smaller. Somites 2-5 with conspicuous posterolateral processes. Somites 2-5 with a pair of posterodorsal simple setae. Pleopods absent.

Telson (figure 4A,B): bifurcated with three pairs of stout spinulate setae on posterior margin. Each furcal arm covered in spinules on central and distal part. Two lateral spines on outer margin of each furcal arm.

Geograpsus lividus (H. Milne Edwards, 1837)

Geograpsus lividus: Cuesta and Schubart, 1999: 165, figures 1-3 (zoea I).

Zoea I (figure 5)

Dimensions: rdl: 0.81 ± 0.02 mm; cl: 0.45 ± 0.01 mm; cw: 0.34 ± 0.01 mm.

Cephalothorax: globose, smooth and without tubercles. Dorsal and rostral spines short and stout. Lateral spines minute, visible as rounded knob-like projections. Pair of dorsolateral simple setae present. Anterodorsal region, posterior and ventral margin without setae. Eyes sessile.

Antennule (figure 5A): uniramous. Endopod absent. Exopod unsegmented with 3 aesthetascs (2 long and 1 thin and short) and one simple seta.

Antenna (figure 5B): well developed protopod, slightly longer than rostral spine and bearing 2 rows of well developed spines, increasing in size distally. Endopod absent. Exopod present as a minute bud with a terminal simple seta.

Mandible: endopod palp absent.

Maxillule: coxal endite with 6 plumose setae. Basal endite with 5 setae (2 plumodenticulate cuspidate and 3 plumodenticulate). Endopod two-segmented with 1 plumodenticulate seta on the proximal segment and 1 medial, 2 subterminal and 2 terminal plumodenticulate setae on the distal segment. Exopod absent.

Maxilla: coxal endites bilobed with 5 (2 plumodenticulate, 3 plumose) + 4 (1 plumodenticulate, 3 plumose) setae. Basal endites bilobed with 5 (2 plumodenticulate, 3 plumose) + 4 (1 plumose, 3 plumodenticulate) setae. Endopod unsegmented, bilobed with 2 long plumodenticulate setae on each lobe. Scaphognathite with 4 marginal plumose setae and 1 long setose posterior process.

First maxilliped: coxa with 1 plumodenticulate seta. Basis with 8 medial setae arranged 2,2,2,2 (longer first pair of setae plumodenticulate, other 3 pairs with 1 sparsely plumose and 1 simple seta each). Endopod five-segmented with 1,2,1,2,5 setae (setae on segments 1-3 sparsely plumose, setae on segment 4 plumodenticulate, and 4 terminal plumodenticulate and 1 subterminal simple setae on distal segment). Exopod two-segmented, with 4 long terminal plumose natatory setae on the distal segment.

Second maxilliped: coxa without seta. Basis with 4 medial setae arranged 1,1,1,1 (a first longer plumodenticulate setae, a second sparsely plumose setae, and two last simple setae). Endopod three-segmented with 0,1,5 setae (1 plumodenticulate seta on segment 2, 1 simple and 1 plumodenticulate subterminal seta and 1 simple and 2 long plumose terminal setae on distal segment). Exopod two-segmented, with 4 long terminal plumose natatory setae on distal segment.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (figure 5C): five abdominal somites. Somites 2-5 with one pair of dorsolateral processes, those of somites 4 and 5 smaller. Somites 3-5 with conspicuous posterolateral processes. Somites 2-5 with a pair of posterodorsal setae. Pleopods absent.

Telson (figure 5C): bifurcated with three pairs of stout spinulate setae on posterior margin. Each furcal arm covered in spinules to just below tip. Three lateral spines on outer margin of each furcal arm.

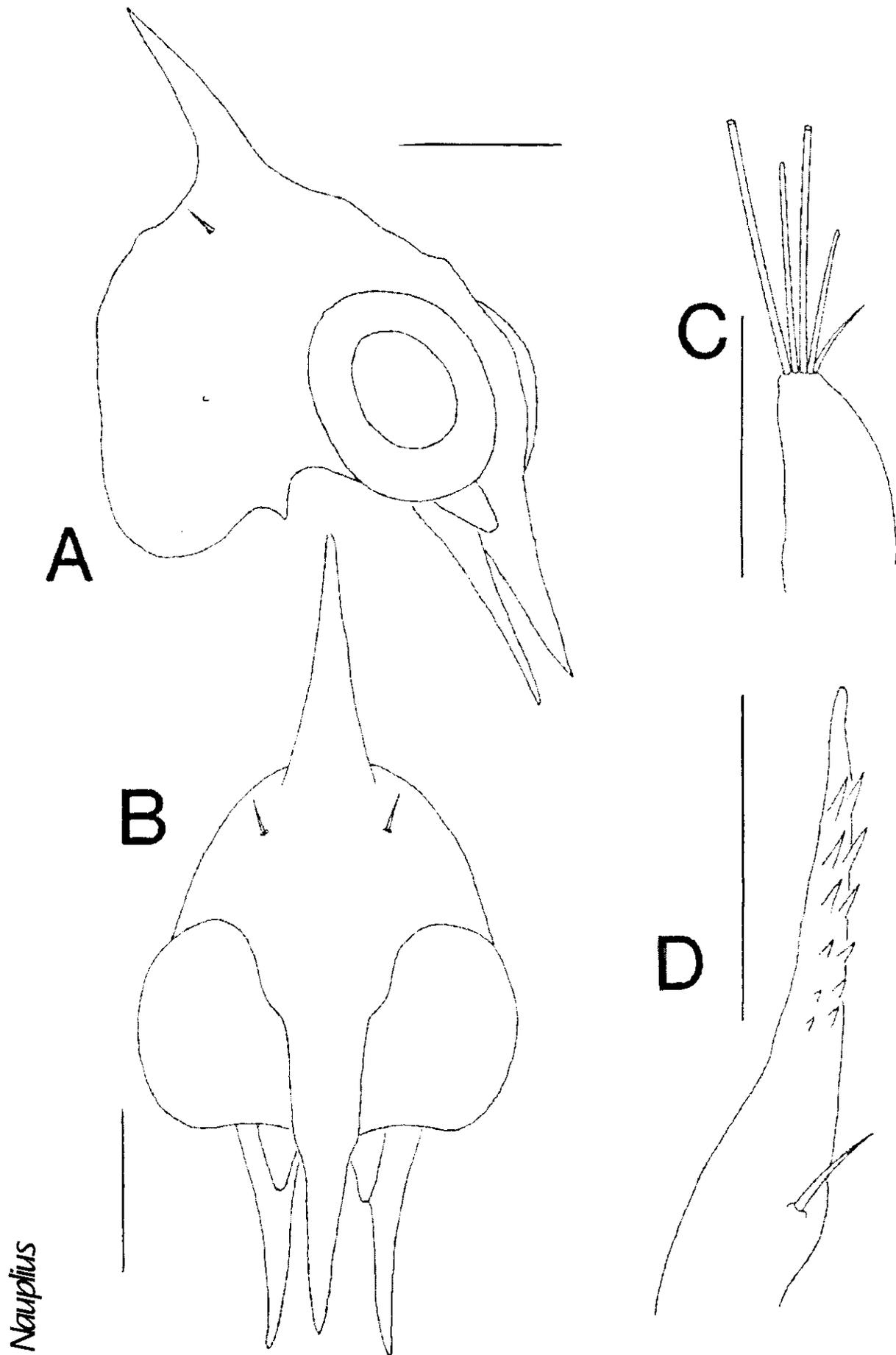


Fig. 1: *Grapsus grapsus* (Linnaeus, 1758), zoea I. A, carapace, lateral view; B, carapace, frontal view; C, antennule; D, antenna. Scale bars: 0.1 mm.

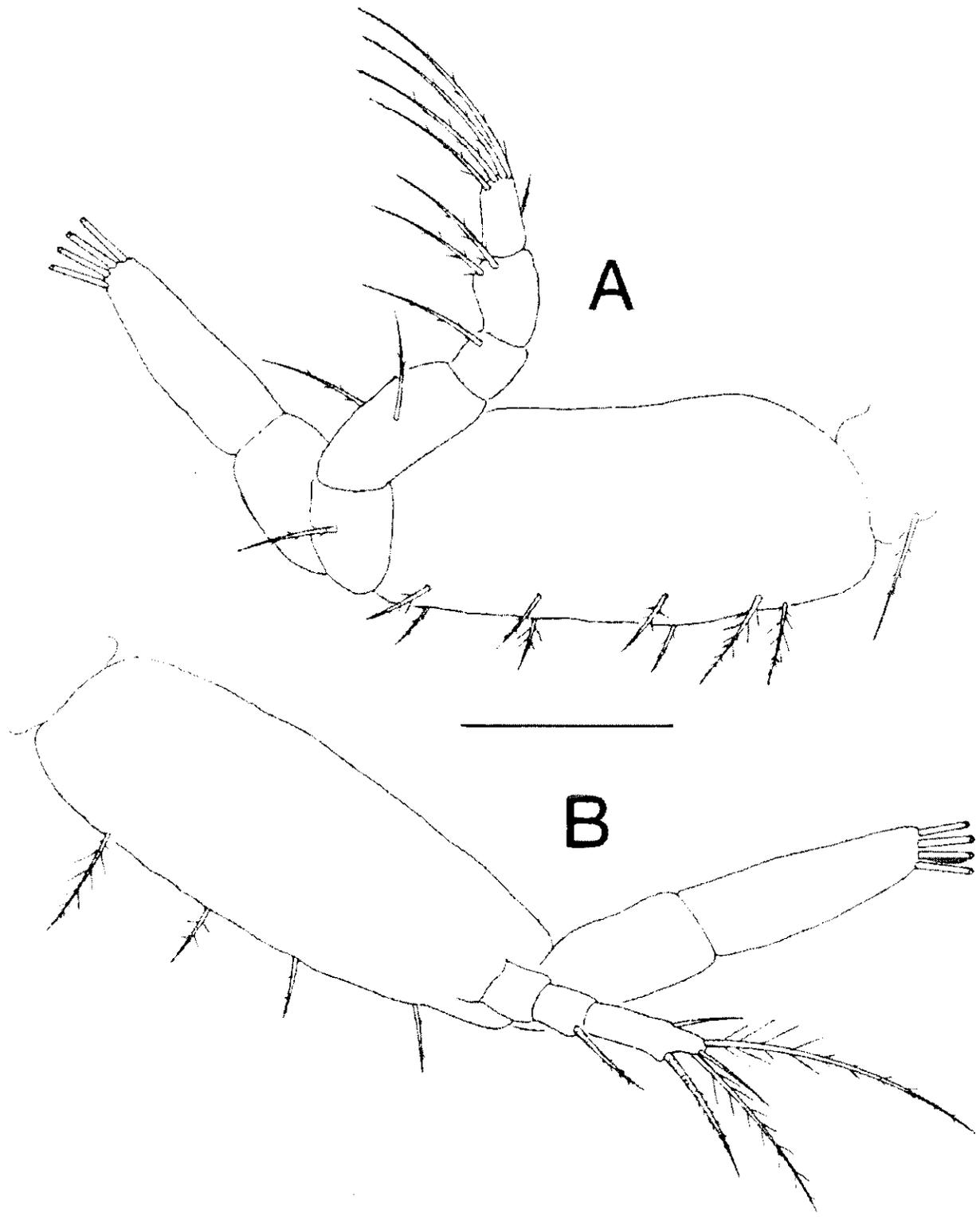


Fig. 3: *Grapsus grapsus* (Linnaeus, 1758), zoea I. A, first maxilliped; B, second maxilliped. Scale bar: 0.1 mm.

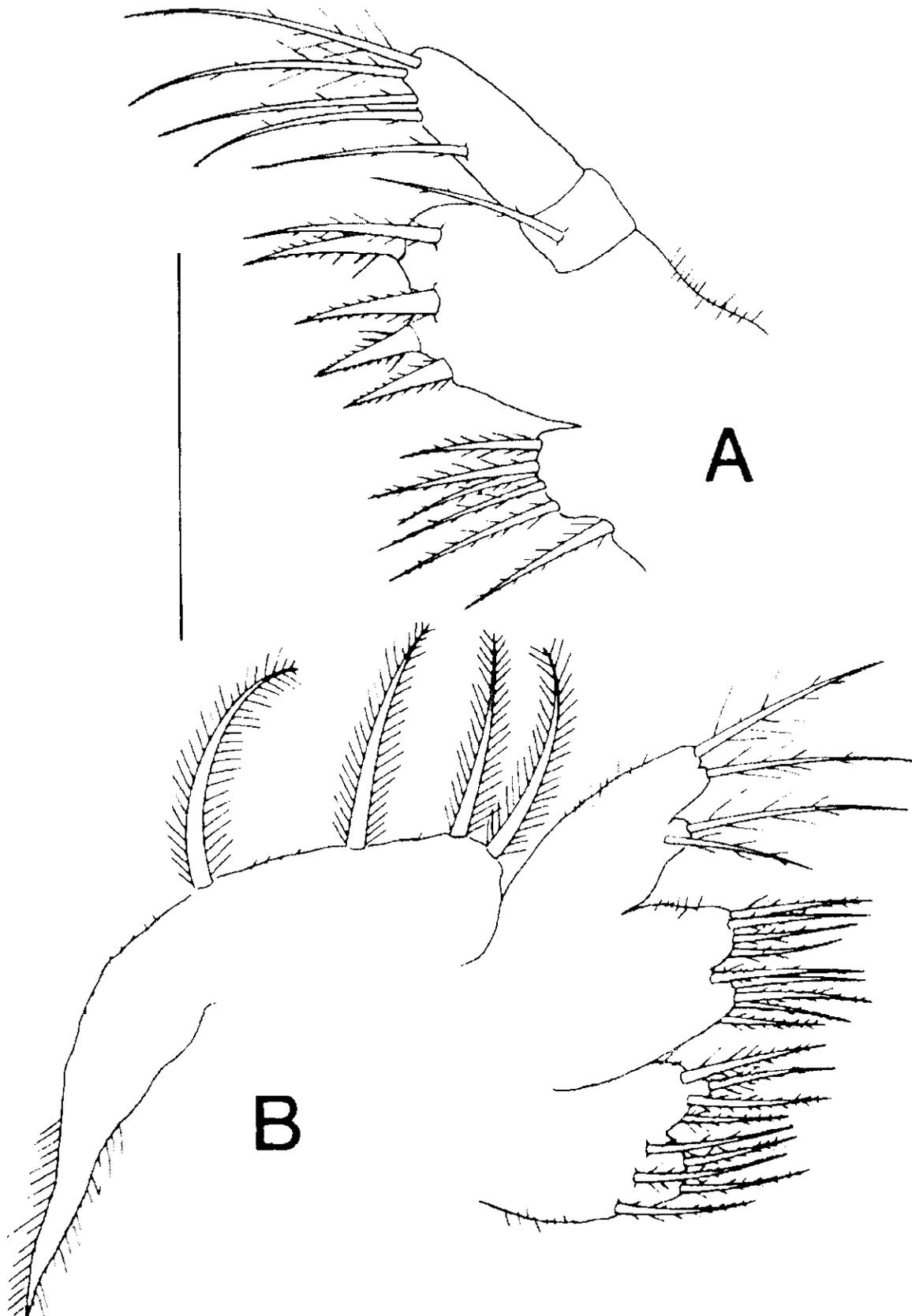


Fig. 2: *Cirripatus grapsus* (Linnaeus, 1758), zoea I. A, maxillule; B, maxilla. Scale bar: 0.1 mm.

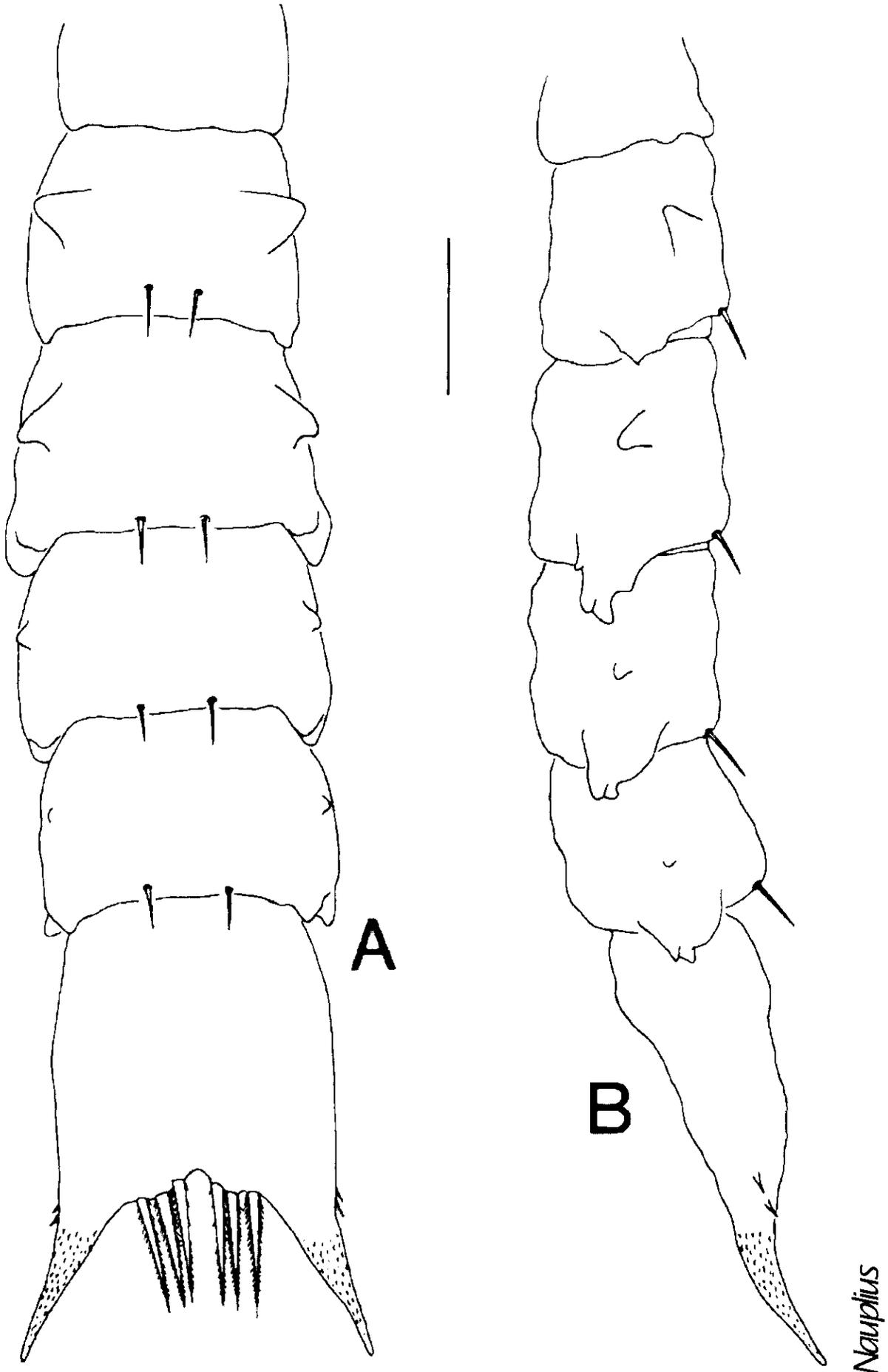


Fig. 4: *Grapsus grapsus* (Linnaeus, 1758), zoea I. A, abdomen, dorsal view; B, abdomen, lateral view. Scale bar: 0.1 mm.

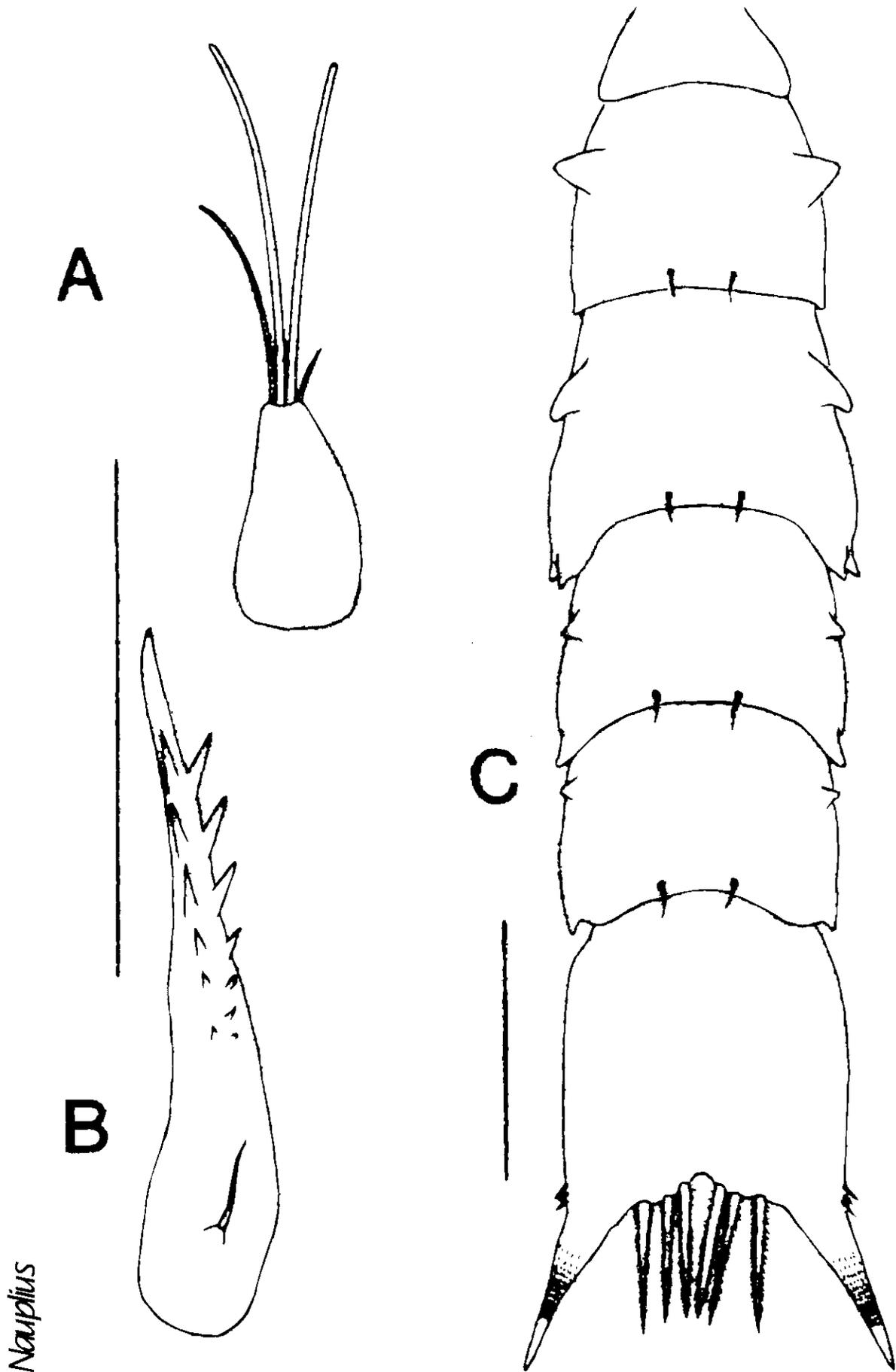


Fig. 5: *Geopsus lividus* (H. Milne Edwards, 1837). A, antennule; B, antenna; C, abdomen, dorsal view. Scale bars: 0.1 mm.

Discussion

Morphological features of the first zoeal stages of *Grapsus grapsus* and *Geograpsus lividus* correspond to those that define the zoeae of Grapsidae *s. str.* according to Cuesta *et al.* (1997) and Cuesta and Schubart (1999). Comparisons with the first zoeal stage of *Grapsus grapsus* described by Lebour (1950) are not possible because this description is brief and incomplete and the illustrations are not detailed enough. When comparing zoeae of *G. grapsus* with those of its putative sister species *G. adscensionis* (see Cuesta *et al.*, 1997), the only important differences found are in the morphology of the abdomen. Both species present dorsolateral processes in somites 2-5, but those of somites 4 and 5 are clearly less developed in *G. grapsus*. Differences can also be found in the shape of the posterolateral processes and in the number of minute outer spines on the furcal arms, two in *G. grapsus* vs. three in *G. adscensionis*.

Consistent morphological differences could also be observed between the first zoeal stages of the two populations of *Geograpsus lividus*. The abdomen of the larvae from the Atlantic coast of Mexico presents dorsolateral processes on somite 5, which are absent in the Pacific population (Cuesta and Schubart, 1999). The same processes on somite 4 are also more developed in Atlantic specimens than in their Pacific counterparts. Atlantic zoeae of *G. lividus* present three outer minute spines on the furcal arms of the telson, while there are only two in the Pacific population. Furthermore, in *G. lividus* differences are also found in the setation of antennules and antennae. *G. lividus* from the Atlantic coast of Mexico presents one more aesthetasc on the antennule and does not have the last unpaired terminal spine on the protopod of the antenna.

We also observed differences in zoeal size between the two pairs of species / populations. In both cases the larvae from the Gulf of Mexico were larger than the previously described from Canary Island (East Atlantic) and Panama (East Pacific). However, this type of morphological difference has to be considered with care, because it is known that differences in size can be observed between geographically separated populations of the same species and are most likely related to water temperature (Christiansen, 1973) and food supply.

It is normally difficult to encounter marked larval morphological differences between first zoeal stages of congeneric species. In several studies no differences at all could be found between closely related species (see Christiansen, 1973; Rice and Ingle, 1975; Clark, 1984). There are even cases in which important morphological differences can be absent between zoeae of genera within the same family (Spivak and Cuesta, 2000). Differences at lower taxonomic levels (intrageneric and intraspecific) are normally restricted to antennular setation and the morphology of the carapace, antennae, and / or abdomen. Differences can also be observed in size and ratios between distinct morphometric parameters (e.g. Cuesta and Schubart, 1998). In contrast, in the present study we show important morphological differences between congeneric species and even within species, depending on the taxonomic interpretation. This is opposed to Clark *et al.*'s (2001: 300) statement that "the expectation that differences in zoeal morphology provide support for species-level discrimination is unfounded". We agree that important characters of the mouthpart setation probably only change at higher taxonomic levels (e.g. family level in Grapsoidea, Cuesta *et al.* in prep.). However, this and previous studies (e.g. Ko and Kim, 1991; Cuesta and Rodríguez, 1994; Schubart and Cuesta, 1998) have shown that there are a number of cases in which larvae of congeneric species can be separated by their morphology.

We consider that larval morphological differences as established in this study between *Grapsus grapsus* and *G. adscensionis*, and *Geograpsus lividus* from the Atlantic and the Pacific can be used to support a distinct taxonomic status (species or subspecies) for each of the studied forms. In the case of the Atlantic populations of *Grapsus*, Manning and Chace (1990) mentioned colour, shape of the female gonopores, and tuberculation of the ventral margin of the front (coarser and fewer tubercles in *G. adscensionis*) as separating characters. D'Udekem d'Acoz (1999) challenged the apparent differences in colour by citing published examples of eastern Atlantic specimens of *Grapsus* that fit Manning and Chace's (1990) colour description from the west Atlantic. We agree with d'Udekem d'Acoz (1999) that a

more detailed and geographically more comprehensive study, with illustration of distinct characters, will be necessary to confirm morphological differences between the adults. However, the present study adds new separating larval characters between these two geographic forms, thereby providing additional evidence for the existence of two distinct taxa.

Stimpson (1860: 230) noted that Pacific *Geograpsus lividus* from Cabo San Lucas, Baja California, Mexico "are darker in color than West Indian examples, being more closely reticulated with purplish. Should they prove distinct, we propose to call the new species *G. occidentalis*". This name would therefore be available if the Pacific populations are considered a distinct species or subspecies. Results of DNA-sequencing of approximately 540 basepairs of 16S mtDNA have shown that Atlantic and Pacific populations of *Geograpsus lividus* have a sequence divergence of 3.7%, while *Grapsus grapsus* from the Caribbean and *G. adscensionis* are separated by a sequence divergence of 1.7% (Schubart, unpublished). These molecular results show that the level of divergence is actually greater between Atlantic and Pacific populations of *Geograpsus* than between the two (sub)species of *Grapsus*. On the basis of this and the larval morphological evidence, we suggest recognition of *Geograpsus occidentalis* Stimpson, 1860 as a valid species from the eastern Pacific, despite the current absence of morphological characters (other than colour and morphometric data, Schubart *et al.* in prep.) to separate it from the Atlantic *Geograpsus lividus*.

Acknowledgements

Thanks are due to Darryl Felder from the University of Louisiana at Lafayette for facilitating a field trip to Mexico and for comments on the manuscript, and to Gerald Pohle and Fernando Marques for their comments and criticism as reviewers of the manuscript. This study was partially funded by the 'U.S. Department of Energy' (Grant DE-FG02-97ER12220 to D.L. Felder) (CDS and JAC) and the 'Subprograma General de Perfeccionamiento de Doctores en el Extranjero, Ministerio de Educación y Cultura', Spain (JAC). This is the contribution 95 of the Laboratory of Crustacean Research of the University of Louisiana at Lafayette.

References

- Abele, L. G. and Kim, W. 1989. The decapod crustaceans of the Panama Canal. Smithsonian Contribution to Zoology, 482: 1-50.
- Aikawa, H. 1937. Further notes on brachyuran larvae. Records of the Oceanographic Works of Japan, 9: 87-162.
- Chen, W.-J. 1995. Studies on the taxonomy of the crab megalopae collected from Tungking coast. 1-137 pp. MS. Thesis, National Sun Yat-Sen University, Kaoshiung, Taiwan.
- Christiansen, M. E. 1973. The complete larval development of *Hyas araneus* (Linnaeus) and *Hyas coarctus* Leach (Decapoda, Brachyura, Majidae) reared in the laboratory. Norwegian Journal of Zoology, 21(2): 63-89.
- Clark, P. F. 1984. A comparative study of zoeal morphology in the genus *Liocarcinus* (Crustacea: Brachyura: Portunidae). Zoological Journal of the Linnean Society, 82: 273-290.
- Clark, P. F., Calazans, D. K. and Pohle, G. W. 1998. Accuracy and standardization of brachyuran larval descriptions. Invertebrate Reproduction and Development, 33: 127-144.
- Clark, P. F., Neale, M. and Rainbow, P. S. 2001. A morphometry analysis of regional variation in *Carcinus* Leach, 1814 (Brachyura: Portunidae: Carcininae) with particular reference to the status of the two species *C. maenas* (Linnaeus, 1758) and *C. aestuarii* Nardo, 1847. Journal of Crustacean Biology, 21(1): 288-303.
- Cuesta, J. A., González-Gordillo, J. I. and Rodríguez, A. 1997. First zoeal stages of *Grapsus adscensionis* (Osbeck) and *Planes minutus* (Linnaeus) (Brachyura: Grapsidae) described from laboratory hatched material with notes on larval characters of the Grapsinae. Journal of Natural History, 31: 887-900.
- Cuesta, J. A. and Rodríguez, A. 1994. Early zoeal stages of *Pachygrapsus marmoratus* (Fabricius), *P. transversus* (Gibbes) and *P. maunus* (Lucas) (Decapoda: Brachyura: Grapsidae) reared in the laboratory. Scientia Marina, 58: 323-327.
- Cuesta, J. A. and Schubart, C. D. 1998. Morphological and molecular differentiation between three allopatric populations of the littoral crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura: Grapsidae). Journal

- of Natural History, 32: 1499-1508.
- Cuesta, J. A. and Schubart, C. D. 1999. First zoeal stages of *Geograpsus lividus* and *Goniopsis pulchra* from Panama confirm consistent larval characters for the subfamily Grapsinae (Crustacea: Brachyura: Grapsidae). *Ophelia*, 51: 163-176.
- Gohar, H. A. F. and Al-Kholy, A. A. 1957. The larvae of some brachyuran Crustacea. Publications of the marine biological Station, Ghardaqa, 9: 145-176.
- Keigwin, L. 1982. Isotopic paleoceanography of the Caribbean and East Pacific: role of Panama uplift in late neogene time. *Science*, 217: 350-353.
- Knowlton, N. and Weigt, L. A. 1998. New dates and new rates for divergence across the Isthmus of Panama. *Proceedings of the Royal Society of London, B*, 265: 2257-2263.
- Ko, H. S. and Kim, C.H. 1991. The zoeal stages of *Ilyoplax tansuiensis* Sakai, 1939 (Decapoda, Brachyura, Ocypodidae) reared in the laboratory. *Crustaceana*, 61(1): 81-87.
- Lebour, M. V. 1950. Notes on some larval decapods (Crustacea) from Bermuda. *Proceedings of the Zoological Society of London*, 120(2): 369-379.
- Lessios, H. A. 1981. Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the Isthmus of Panama. *Evolution*, 35(4): 618-634.
- Manning, R. B. and Chace, F. A. Jr., 1990. Decapod and Stomatopod Crustacea from Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to Zoology*, 503.
- Rice, A. L. and Ingle, R. W. 1975. The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bulletin of the British Museum (Natural History)*, 28: 103-121.
- Schubart, C. D. and Cuesta, J. A. 1998. The first zoeal stages of four *Sesarma* species from Panama, with identification keys and remarks on the American Sesarminae (Crustacea: Brachyura: Grapsidae). *Journal of Plankton Research*, 20(1): 61-84.
- Schubart, C. D., Cuesta, J. A., Diesel, R. and Felder, D. L. 2000. Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogenetics and Evolution*, 15(2): 179-190.
- Schubart, C. D., Cuesta, J. A. and Felder, D. L. 2002. Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. *Journal of Crustacean Biology*, 22(1): 28-44.
- Spivak, E. D. and Cuesta, J. A. 2000. Larval development of *Cyrtograpsus affinis* (Dana) (Decapoda, Brachyura, Varunidae) from Rio de la Plata estuary, reared in the laboratory. *Scientia Marina*, 64: 29-47.
- Stimpson, W. 1860. Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. *Annals of the Lyceum of Natural History of New York*, 7: 177-246.
- Türkay, M. 1982. Marine Crustacea Decapoda von den Kapverdischen Inseln mit Bemerkungen zur Zoogeographie des Gebietes. *Courier Forschungs-Institut Senckenberg*, 52: 91-129.
- Udekem d'Acoz C. d'. 1999. Inventaire et distribution des Crustacés Décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25°N. Collection "Patrimoines Naturels" (Muséum National d'Histoire Naturelle / S.P.N.), Paris, vol. 40, 383 pp.

Received: 5th May 2001

Accepted: 15th Jan 2002