JOURNAL OF CRUSTACEAN BIOLOGY, 22(1): 28–44, 2002

GLYPTOGRAPSIDAE, A NEW BRACHYURAN FAMILY FROM CENTRAL AMERICA: LARVAL AND ADULT MORPHOLOGY, AND A MOLECULAR PHYLOGENY OF THE GRAPSOIDEA

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A B S T R A C T

During an ongoing systematic revision of the Decapoda Grapsoidea (here defined as including the families Gecarcinidae, Grapsidae *s. str.,* Plagusiidae, Sesarmidae, and Varunidae; see Schubart *et al.,* 2000a), it became evident that adult and larval morphology of two Central American genera, *Glyptograpsus* and *Platychirograpsus,* differs greatly from that of all other genera within this superfamily. Several important morphological characters are shared by these two genera and represent synapomorphies when compared to the other grapsoids. Both of these genera lack a pleurobranch on the sixth thoracic segment. Adult males of *Glyptograpsus* and *Platychirograpsus* are all strikingly heterochelous with the major chela being conspicuously flattened anteriorly and showing a subproximal articulation with the carpus. The distal portion of the male gonopod is uncinate, with a narrowed, elongate terminus. The anteriormost portion of the sternum consists of a narrow, fused sternite terminated in a distinctly flanged tip inserted between the mouth appendages. The male abdomen exhibits immobility in the joints between segments 3 to 5 and very limited mobility in the joint between segments 1 and 2. Zoeae of the two genera show a 1,2 setation pattern on the maxillar endopod. A molecular phylogeny of the Grapsoidea, based on 16S mtDNA and including type genera of the five recognized families, confirms that the species of *Glyptograpsus* and *Platychirograpsus* together form a well-defined monophyletic unit that is distinct from all other taxa within the Grapsoidea. We therefore describe a new family, the Glyptograpsidae, to accommodate these two genera of crabs.

The Grapsidae *s.l.* has been one of the few brachyuran families that has experienced almost no taxonomic change during the past hundred years. It was Alcock (1900) who established the long-accepted subdivision of the Grapsidae *s.l.* by adopting three subfamilies of Dana (1851) (Grapsinae, Plagusiinae, Sesarminae) and adding the redefined Varuninae (previously introduced by H. Milne Edwards (1853) as a tribe). A large number of grapsid species have been described since then, but the subdivision of this family and the distribution of genera among the four subfamilies has remained unchanged until very recently. This is especially surprising as most subfamilies were defined by single adult morphological characters that often seemed weak in terms of their phylogenetic value.

For a long time, adult morphology has been the only instrument for carrying out crustacean systematics and taxonomy. With increasing numbers of descriptions available for larval stages of the Grapsidae *s.l.*, an additional tool became available for the study of phylogenetic relationships (Rice, 1980). However, larval morphologists rarely challenged the taxonomic system of the Grapsidae, despite the fact that incongruencies with groupings based on larval characters were noticed (Wear, 1970; Wilson, 1980; Terada, 1982; Pereyra Lago, 1993; Cuesta and Schubart, 1997; Schubart and Cuesta, 1998). This is mostly because larval descriptions were not available for most of the species and many genera, and it was thus not possible to provide a complete picture. Furthermore, many larval descriptions, especially older ones, are incomplete or erroneous when specifying setation patterns, which are essential for larval morphological comparisons.

The recent application of molecular techniques to grapsoid phylogenetics has corrob-

orated results form larval morphology and prompted proposals for taxonomic changes within the Grapsoidea (see Schubart *et al.,* 2000a). These changes are additionally supported by adult morphological characters that had not been considered to date (see Discussion). As part of the new taxonomy, the four grapsid subfamilies (*sensu* Alcock, 1900) have been raised to family level, in order to better reflect the phylogenetic relationship to the Gecarcinidae. Two genera formerly included in the Sesarmidae (*Chasmagnathus* and *Cyclograpsus*) have been transferred to the Varunidae, and it has been suggested that this might also be necessary for some other genera (*Helice s.l., Helograpsus, Metaplax,* and *Paragrapsus*) (Schubart *et al.,* 2000a). Furthermore, it has been observed that some genera need to be removed from the Varunidae in order to make this family a monophyletic taxon. While *Euchirograpsus* appears to be the sister genus of *Plagusia* and thus a member of the Plagusiidae (see Cuesta and Schubart, 1997; d'Udekem d'Acoz, 1999; Schubart *et al.,* 2000a), two other genera, *Glyptograpsus* and *Platychirograpsus,* are closely related to each other, but do not seem to belong to any of the current grapsoid families (Cuesta and Schubart, 1997; Schubart *et al.,* 2000a).

Here we present new results on adult and larval morphology of *Glyptograpsus* and *Platychirograpsus*. Several shared morphological characters that are unique among grapsoid crabs were found in adults of the three species belonging to these genera. The description of the first zoea of *Platychirograpsus spectabilis* and its comparison with the same stage of *Glyptograpsus impressus* revealed two additional important morphological synapomorphies. Distinct characters in adult and larval morphology are corroborated by a molecular phylogeny, showing a monophyletic and independent lineage of *Glyptograpsus* and *Platychirograpsus*. On the basis of this evidence, we describe a new family, Glyptograpsidae, to accommodate these two genera of grapsoid crabs.

Materials and Methods

Material for this study was collected in Jamaica, Panama, Florida, and Mexico between 1993 and 1999. In addition, several specimens were donated from colleagues or obtained as a loan from the United States National Museum of Natural History, Washington, D.C. (USNM), and the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de Mexico (CNCR). New specimens were deposited at the University of Louisiana at Lafayette Zoological Collection, Lafayette (ULLZ); the Senckenberg Museum, Frankfurt a.M. (SMF); the Muséum national d'Histoire naturelle, Paris (MNHN-B); and the Zoological Reference Collection of the National University of Singapore (ZRC). Ovigerous females of *Platychirograpsus spectabilis* were collected in April 1998 in Veracruz (Mexico) and maintained in freshwater aquaria until eggs hatched. One female released zoea larvae on 1 May 1998. Actively swimming zoeae were fixed in 4% Formalin. First zoeae of *Glyptograpsus impressus* obtained and previously described by Cuesta and Schubart (1997) were re-examined.

Drawings and measurements of larvae were based on 20 zoeae examined with Wild MZ6, Olympus BH-2, and Zeiss Axioskop compound microscopes (latter both equipped with Nomarski DIC), all equipped with a *camera lucida*. All measurements were made by 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 distance between the tips of the lateral spines. 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. The parental female of *Platychirograpsus spectabilis* and samples of zoea I were archived as USNM 309788.

Genomic DNA of *Glyptograpsus, Platychirograpsus* and various other crab species including the type genera of the five currently recognized families (see Table 1) was isolated from muscle tissue of walking legs by phenol-chloroform extraction (Kocher *et al.,* 1989). An aliquot of genomic DNA from *Varuna litterata* was obtained from Sara Fratini (University of Florence). Selective amplification of a fragment from the mitochondrial large subunit rRNA gene (16S mtDNA) was carried out by polymerase-chain-reaction (PCR) with the primers 16Sar (5′-CGCCTGTTTATCAAAAACAT-3′), 16Sbr (5′-CCGGTCTGAACTCAGATCACGT-3′), and 1472 (5′-AGATAGAAACCAACCTGG-3′) (see Schubart *et al.,* 2000b: Table 3), as well as the newly designed primer 16L2 (5′-TGCCTGTTTATCAAAAACAT-3′). The PCR products were purified with Microcon 100® filters prior to sequencing with the ABI BigDye® terminator mix in an ABI Prism 310 Genetic Analyzer®. Sequences were aligned manually with the multisequence editing program ESEE (Cabot and Beckenbach, 1989), taking into account the secondary structure of the gene (Schubart *et al.,* 2000a: App. 1). Variable regions that could not be aligned with complete certainty, as well as positions with compensatory mutations in stem regions, were excluded from phylogenetic analyses. The DNA-sequence of the palicid crab *Palicus obesus* (see also Schubart *et al.,* 2000a) was used as an outgroup. We applied Kimura 2-parameter distances (s+v) and neighbor joining (NJ) to analyze distance matrices of sequence divergence with the program MEGA (Kumar *et al.,* 1993). Statistical significance of groups within inferred trees was evaluated by the interior branch method (Rzhetsky and Nei, 1992). Maximum parsimony (MP) trees were obtained through a heuristic search with random sequence addition and tree-bisection and reconnection as branch swapping option with the program PAUP (Swofford, 1993). Gaps were always treated as missing. Confidence values were ob-

Table 1. Grapsoid crab species used for phylogeny reconstructions, with locality of collection, museum catalogue number, and genetic database (EMBL) accession number. MZUF: Museo Zoologico Universitá di Firenze; SMF: Senckenberg Museum, Frankfurt a.M.; ULLZ: University of Louisiana at Lafayette Zoological Collection, Lafayette; USNM: Smithsonian Institution and National Museum of Natural History, Washington.

Species	Collection site	Catalogue number	EMBL number
GECARCINIDAE Macleay, 1838			
Gecarcinus lateralis (Fréminville, 1835)	Mexico: Veracruz	ULLZ 3722	AJ130804
GLYPTOGRAPSIDAE fam. nov.			
Glyptograpsus jamaicensis (Benedict, 1892)	Jamaica: Portland	SMF 25987	AJ308420
Glyptograpsus impressus Smith, 1870	Panama: Farfán Beach	USNM 284160	AJ250646
Platychirograpsus spectabilis de Man, 1896a	Florida: Tampa Bay	SMF 24567	AJ250645
GRAPSIDAE Macleay, 1838			
Grapsus grapsus (Linnaeus, 1758)	Mexico: Veracruz	ULLZ 3709	AJ250650
Pachygrapsus transversus (Gibbes, 1850)	Mexico: Tamaulipas	ULLZ 3723	AJ250641
PLAGUSIIDAE Dana, 1851			
Euchirograpsus americanus A. Milne Edwards, 1880	Louisiana: Sackett Bank	ULLZ 3626	AJ250648
Plagusia dentipes de Haan, 1835	Japan: Banda Tateyana	SMF 24559	AJ308421
SESARMIDAE Dana, 1851			
Armases ricordi (H. Milne Edwards, 1853)	Mexico: Veracruz	ULLZ 3697	AJ250637
Chiromantes haematocheir (de Haan, 1835)	Japan: Samusaura	SMF 25989	AJ308414
Sesarma reticulatum (Say, 1817)	Delaware: Woodland Beach	ULLZ 3835	AJ130799
VARUNIDAE H. Milne Edwards, 1853			
Brachynotus atlanticus Forest, 1957	Spain: Cabo de Trafalgar	SMF 25706	AJ278831
Chasmagnathus granulatus Dana, 1851	Argentina: Mar Chiquita	SMF 24547	AJ250640
Cyclograpsus integer (H. Milne Edwards, 1837)	Mexico: Veracruz	ULLZ 3704	AJ250639
Cyrtograpsus affinis (Dana, 1851)	Argentina: Rio de la Plata	SMF 24545	AJ130801
Eriocheir sinensis (H. Milne Edwards, 1853)	California: San Francisco	ULLZ 4175	AJ250642
Helice crassa (Dana, 1851)	New Zealand: Christchurch	SMF 25988	AJ308416
Helograpsus haswellianus (Whitelegge, 1899)	Australia: Brisbane River	SMF 25996	AJ308417
Hemigrapsus oregonensis (Dana, 1851)	Washington: Friday Harbor	ULLZ 3794	AJ250644
Metaplax elegans de Man, 1888	Vietnam: Haiphong: Cam River	SMF 25992	AJ308415
Paragrapsus laevis (Dana, 1851)	Australia: Stradbroke Island	SMF 25986	AJ308418
Varuna litterata (Fabricius, 1798)	Kenya: Gazi	MZUF 2503	AJ308419

tained by running 2,000 bootstrap replicates. New sequences were deposited in the genetic database EMBL (AJ308414–AJ308421).

RESULTS

Systematic Account

Glyptograpsidae, new family

Type Genus.—*Glyptograpsus* Smith, 1870.

Included Genera.—*Glyptograpsus, Platychirograpsus*.

Diagnosis.—Cephalothorax subgloboid; front undulated, four-lobed, median groove deep; anterolateral margin with three pairs of teeth; buccal cavity covered almost completely by third maxillipeds; deep transverse sclerotized suture demarcating narrow anterior fused components of sternum, which terminates between mouth appendages in acuminate, flanged tip. Ischium and merus of third maxillipeds very broad, with longitudinal sulci; chelipeds of adult males markedly heterochelous, articulation of carpus and palm of major cheliped distal to proximal end of palm; fingers spoon-tipped, short; third pair of walking legs longest. Pleurobranch lacking on sixth thoracic segment. Male abdomen completely covering space between last pair of pereiopods; joints between segments 3 to 5 inflexible though marked by distinct sutures, flexibility between segments 1 and 2 very limited, greater in joints between segments 5 to 7; first gonopods with subterminal tufts of setae, distal portion uncinate, terminus elongate, narrowed.

Description.—Cephalothorax subgloboid, greatest width at base of third pereiopods. Front undulated and relatively narrow, with deep median groove, two conspicuous frontal lobes, and two smaller posterior lobes. Anterolateral margin with three pairs of teeth (not counting exorbital angle), fourth pair often present as prominent tubercles. Buccal cavity covered almost completely by third maxillipeds. Anteriormost sternites vestigial, narrow, demarcated by deep transverse furrow marking sclerotized suture, sternum terminated anteriorly in fused acuminate, flanged tip extending deeply between oral appendages. Ischium and merus of third maxillipeds very broad (merus wider than long), ischium with two and merus with three longitudinal sulci (Fig. 1). Chelipeds of adult males markedly heterochelous, in females homochelous. Articulation of carpus and palm of male major cheliped distal to proximal end of palm (Figs. 2, 3). Chelae spoon-tipped and, except major male claw, small; fingers short. Third pair of walking legs longest. Branchiae consisting of 1 podobranch (but no arthrobranch) on second maxilliped, 1 podobranch and 2 arthrobranchs on third maxilliped, 2 arthrobranchs on first pereiopod, and 1 large pleurobranch on second pereiopod; no branchiae on third pereiopod or on adjacent pleuron of sixth thoracic somite. Male abdomen completely covering space between coxae of the last pair of pereiopods; joints between segments 3 to 5 inflexible but retaining distinct uncalcified sutures, flexibility between segments 1 and 2 very limited; sutures at joints of segments 5 to 6 and 6 to 7 flexible. First gonopods with subterminal tufts of setae, distal portion uncinate, terminus narrowed, elongate and corneous (Fig. 4).

Remarks.—The Glyptograpsidae are comprised of two genera, *Glyptograpsus* Smith, 1870, and *Platychirograpsus* de Man, 1896a (descriptions in Rathbun, 1918: 275, 278), and three species.

Glyptograpsus impressus Smith, 1870.

Glyptograpsus impressus Smith, 1870: 154 [type locality: El Salvador: Acajutla].—Rathbun, 1918: 275, pl. 72: figs. 1, 2.

Glyptograpsus spinipes Cano, 1889: 241, pl. 7: fig. 15 [type locality: Panama: Perlas Archipelago].

Material Examined.—1 male, 3 females (USNM 268838), Panama: Perlas Archipelago: Isla Mina, 13 June 1973, *leg*. L. G. Abele; 5 males (USNM 268843), Panama: Perlas Archipelago: Isla Viveros, 13 June 1973, *leg*. L. G. Abele; 7 males, 1 female (USNM 268847), Panama: Perlas Archipelago: Saboga, 5 January 1975, *leg*. L. G. Abele; 11 males, 14 females (USNM 268848), Panama: Perlas Archipelago: Lanas, 18 January 1973, *leg*. L. G. Abele; 1 male (USNM 268849), Panama: Perlas Archipelago: I. San Jose, 20 May 1973, *leg*. L. G. Abele; 4 males, 3 females (USNM 268856), Panama: Perlas Archipelago: Isla Rey, 19 May 1973, *leg*. L. G. Abele; 2 males, 2 females (USNM 44174), Panama: Taboga Island, 11 May 1915, *leg*. Meek and Hildebrand; 1 female, first zoea larvae (USNM 284160), Panama: Farfán Beach (under log near stream bed), 29 February 1996, *leg*. J. A. Cuesta and C. D. Schubart (DNA voucher); 2 males (USNM 169682), Mexico: Guerrero: Ixtapa (old stream bed), 10 December 1975, *leg*. D. Pletsch; 3 males, 1 female, 2 juveniles (USNM uncat.), Mexico: Jalisco: Tenacatita Bay, 15 February 1932, *leg*. J. Garth.

Description.—Rathbun, 1918: 276.

Measurements.—Males up to 22 mm carapace length (cl), ~26 mm carapace width (cw) (Abele and Blum, 1977), females up to 18.4-

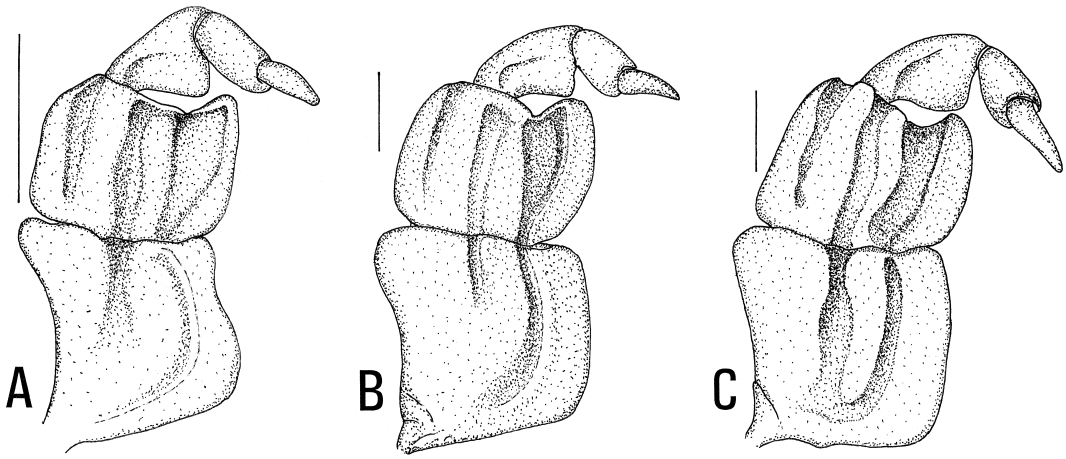

Fig. 1. Right third maxillipeds, external surface of endopod: A, *Glyptograpsus impressus* USNM 268848, 17.8-mm cw male; B, *Glyptograpsus jamaicensis* USNM 17226, 37.2-mm cw male; C, *Platychirograpsus spectabilis* USNM 23761 (paratype of junior synonym, *P. typicus* Rathbun, 1914) 42.9-mm cw male. Scale bars = 2.0-mm.

mm cl, 21.2-mm cw (Cuesta and Schubart, 1997), records of ovigerous females 17.6–21.2-mm cw.

First Zoeal Description.—Cuesta and Schubart, 1997: 292–294 (and as amended, present paper).

Ecological Remarks.—Abele and Blum, 1977: 246; Cuesta and Schubart, 1997: 292.

Distribution.—Tropical eastern Pacific: Panama–Mexico.

Glyptograpsus jamaicensis (Benedict, 1892)

Areograpsus jamaicensis Benedict, 1892: 77 [type locality: Jamaica: Kingston Harbour].

Glyptograpsus jamaicensis.—Rathbun, 1897: 27.—Rathbun, 1918: 277, fig. 140, pl. 72: fig. 3.—Chace and Hobbs, 1969: 171, figs. 52 *l,* 53.

Material Examined.—1 male (USNM 17226, holotype), Jamaica: Kingston Harbour, don. T. H. Morgan; 1 male (collection CDS), Jamaica: Portland: Christmas River mouth, March 1996, *leg*. C. D. Schubart; 1 male, 1 female (MNHN-B 27715), Jamaica: Portland: Reach Falls, 27 June 1992, *leg*. M. Schuh; 1 male (SMF 25987), Jamaica: Portland: Non Such pumphouse (3.5 km from sea), 21 March 1997, *leg*. R. Diesel, J. Reimer, and C. D. Schubart (DNA voucher); 1 male (USNM 120627), Jamaica: Portland: Swift River tributary at Elysium, 8 April 1959, *leg*. C. W. Hart and G. Thomas; 1 male (USNM 74518), Jamaica: Hanover: Flint River, *leg*. W. G. Lynn.

Description.—Rathbun, 1918: 277, 278; Chace and Hobbs, 1969: 171, 172.

Measurements.—Males up to 37.1-mm cl, 42.9-mm cw (Christmas River), females up to 34.9-mm cl, 39-mm cw (Reach Falls).

Ecological Remarks.—Unlike its Pacific congener, *G. jamaicensis* prefers fast flowing calcareous rivers. Several specimens have a thick calcium carbonate layer covering their carapaces. This species is often found on submerged logs or in pools under waterfalls in depths of up to 2 m. Occasionally, *G. jamaicensis* has been found in rivers with seasonally closed mouths (e.g., Portland: Christmas River). Only after heavy rainfall does water break a passage through the obstructing sand. This can be important for the timing of larval release (if the adults do not migrate over land). Most records (except holotype) are from the Jamaican north coast at distances of 100 m to 3.5 km from the sea.

Distribution.—Endemic to Jamaica.

Platychirograpsus spectabilis de Man, 1896a

Platychirograpsus spectabilis de Man, 1896a: 292 [type locality: West Africa: Gaboon (questionable)].—de Man 1896b: 97, pl. 2: figs. 4, 4a, 4b, 4d, pl. 3: fig. 4c.—Rathbun, 1900: 279.—Buitendijk, 1950: 280.—Monod, 1956: 426, figs. 584–588 (questioning African type locality).

Aspidograpsus typicus Krøyer, MS, Copenhagen Museum [type locality: Gulf of Mexico].

Platychirograpsus typicus Rathbun, 1914: 122, fig. 3, pl. 5 [type locality: Mexico: Tabasco: Macuspana River].— Rathbun, 1918: 278, figs. 141–143, pl. 73.—Bolivar Pieltain, 1945: 267, figs. 1–5.—Marchand, 1946: 97, figs. 1, 2.— Rickner, 1977: 833.

Material Examined.—1 male (USNM 19863), Mexico (Mexican exhibit at World's Columbian Exposition 1893); 2 males (USNM 23761, holotype *Platychirograpsus typicus* Rathbun, 1914), Mexico: Tabasco: Río Macuspana, Montecristo (225 km from sea, >100 ft), 7 May 1900, *leg*. Nelson and Goldman; 1 female (ULLZ 1454), Mexico: Tabasco: Río González, Chiltepec (1 km from sea), 6

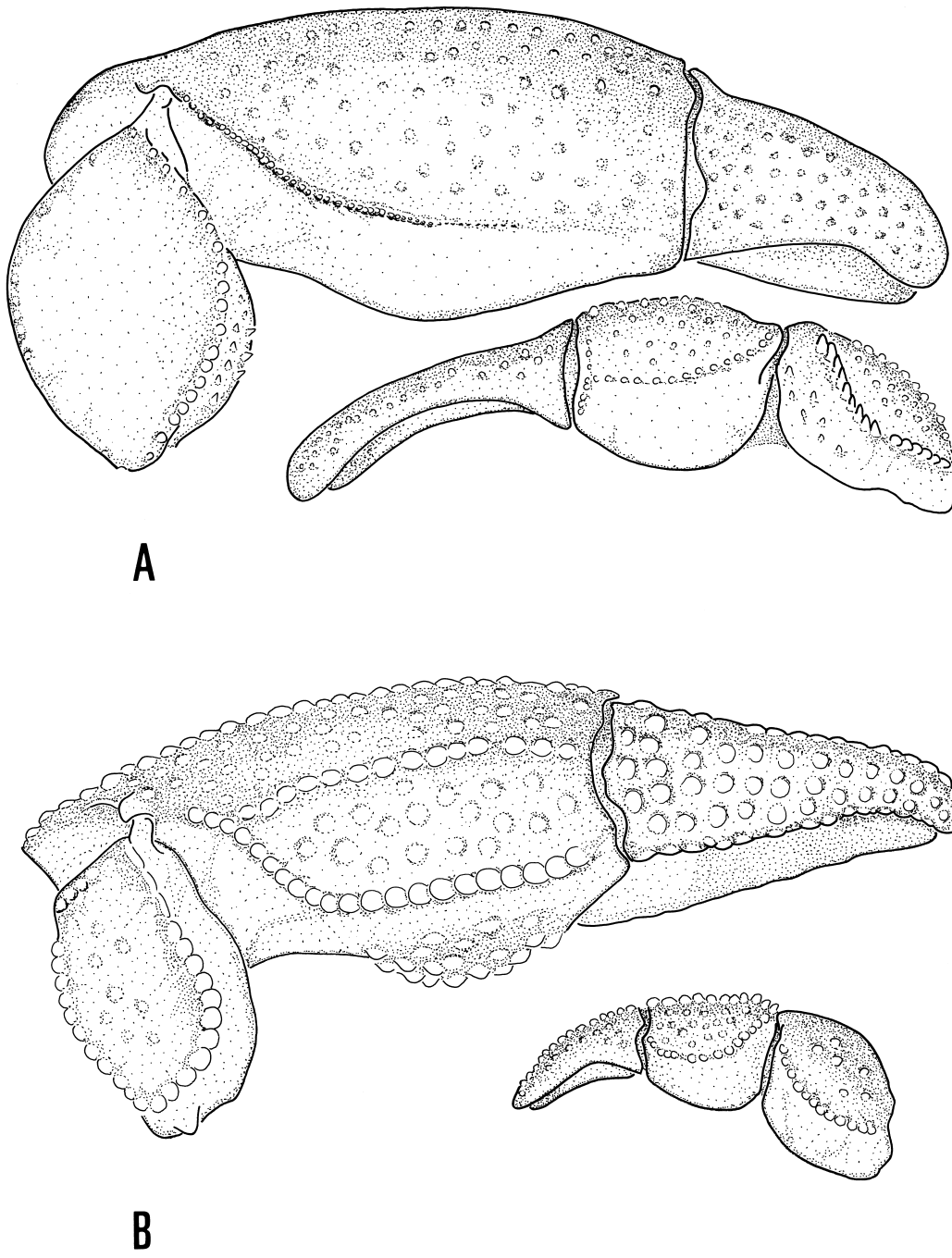

Fig. 2. Chelipeds: A, *Glyptograpsus impressus* USNM 268849, 13.7-mm cw male; B, *Glyptograpsus jamaicensis* (modified after Chace and Hobbs, 1969) 39.0-mm cl male.

March 1981, *leg*. Felder, Snatic, and Forman; 1 male (CNCR 17037) Mexico: Tabasco: Mpio. Nacajuca: Río Gonzales (18°22.298′N–92°58.455′W), 24 January 1998, *leg*. J. L. Villalobos, R. Robles, and F. Alvarez (DNA voucher); 1 female (CNCR 1246) Mexico: Puebla: Arroyo de María Andrea, 10 August 1953, *leg*. J. L. Villalobos; 1 female (CNCR 7768) Mexico: Hidalgo: San Sebastián: Río Chitlán, 7 November 1986, *leg*. O. Meave; 1 male (CNCR 17041) Mexico: Veracruz: San José Las Choapas: Río Tonalá (17°52.28′N–94°05.04′W), 11 June 1997, *leg*. J. L. Villalobos and R. Robles; 1 male (CNCR 17238) same locality as previous, 24 March 1998, *leg*. J.

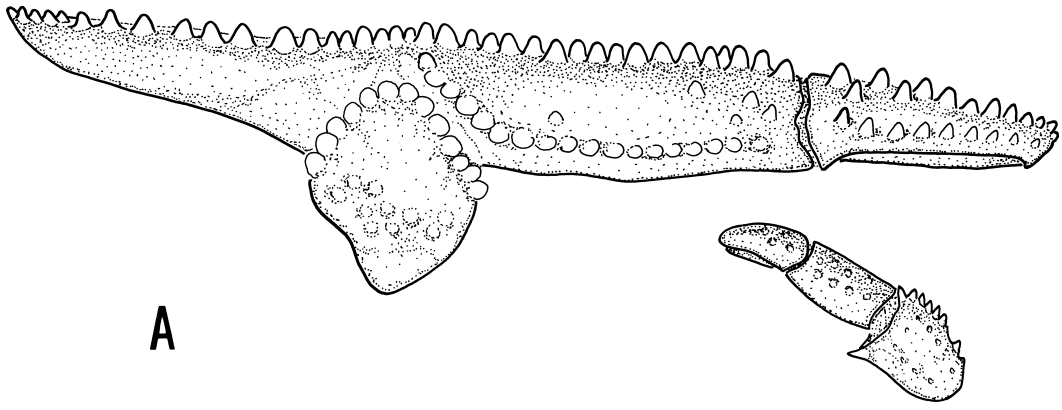

Fig. 3. Chelipeds: *Platychirograpsus spectabilis* USNM 23761 (holotype of junior synonym, *P. typicus* Rathbun, 1914, modified after Rathbun, 1918) 51.1-mm cw male.

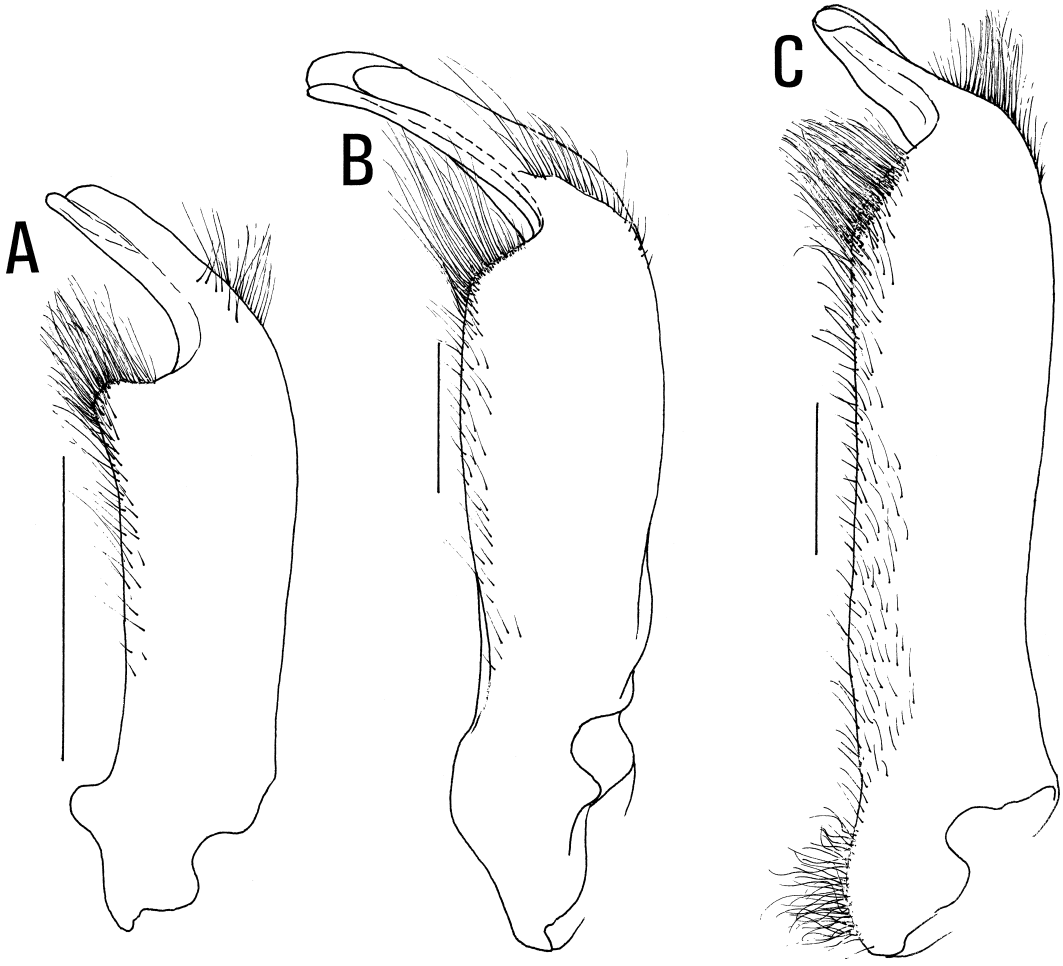

Fig. 4. Right male gonopods, mesial surface: A, *Glyptograpsus impressus* USNM 268848, 17.8-mm cw male; B, *Glyptograpsus jamaicensis* USNM 17226, 37.2-mm cw male; C, *Platychirograpsus spectabilis* USNM 23761 (paratype of junior synonym, *P. typicus* Rathbun, 1914) 42.9-mm cw male. Scale bars = 2.0-mm.

L. Villalobos and R. Robles; 1 male (CNCR 16115) Mexico: Veracruz: Río Tuxpan (43 km from river mouth), 25 October 1965, *leg*. E. A. Chávez; 1 male, 1 female (CNCR 4779) Mexico: Veracruz: Mpio. San Andrés Tuxtla: Río Máquinas between Los Tuxtlas and Montepío, 26 October 1985, *leg*. A. Cantú, J. C. Nates, and J. L. Villalobos; 1 juv. female (USNM 125807), Mexico: Veracruz: Río Chiquito (arm of Río Coatzacoalcos), near Tenochtitlan, 28 January 1968, *leg*. R. R. Miller, M. B. Lockey *et al*.; 1 male (USNM 123453), Mexico: Veracruz: river S of Nautla, 3 August 1967, *leg*. M. Tandy; 1 male and 1 female (USNM 82104), Mexico: Veracruz: El Raudal (3 km from mouth), near Nautla, 20 September 1945, *leg*. C. Bolívar; 26 males, 8 females (ULLZ 4376), Mexico: Veracruz: stream near Punta Delgada, under boulders from brackish mouth to about 80 m upstream, between Nautla and Palma Sola, 28 June 1978, *leg*. D. L. Felder, J. W. Martin, and R. Rodenbough; 2 females, first zoea larvae (USNM 309788), Mexico: Veracruz: stream near Punta Delgada in forest under boulders (150 m from mouth), between Nautla and Palma Sola, 18 April 1998, *leg*. D. L. Felder, C. D. Schubart *et al*. (DNA and parental voucher); 1 male (exuvium only), 1 female (ULLZ 4375), Mexico: Veracruz: Rancho Nuevo, between Nautla and Punta Delgada, under bridge of Hwy. 180, 30 December 1976, *leg*. D. L. Felder *et al.;* 2 males, 1 female (USNM 82105), Mexico: Veracruz: Río Tecolutla (12 km from mouth), near Gutiérrez Zamora, 2 November 1945, *leg*. C. Bolívar; 1 male (USNM 64514), Mexico: Veracruz: Rio de los Hules, 11 mi SW Tantoyuca, 5 May 1930, *leg*. E. P. Creaser, Gordon, and Ostos; 1 male, 2 females (ULLZ 4374), Mexico: Veracruz: stream about 13 mi N Boquilla de Piedras, *leg*. D. L. Felder, J. W. Martin, and R. Rodenbough; 1 male, 1 female (SMF 24567), Florida: Tampa Bay: Alafia River, May 1996, *leg*. P. Smith and E. Harris (DNA voucher); 1 female (ZRC 2000.1781) same data as previous.

Description.—Rathbun, 1918: 279–281.

Measurements.—Males up to 44.5-mm cl, 51.1-mm cw (USNM 23761), females up to 34.8-mm cl, 40.6-mm cw (USNM 82105), records of ovigerous females 26.6–40.6-mm cw.

First Zoeal Description (Figs. 5, 6).—Size: rdl: 0.73 ± 0.03 mm; cl: 0.44 ± 0.01 mm; cw: 0.45 ± 0.01 mm.

Carapace (Fig. 5A): dorsal spine curved, spinulation or setation absent. Rostral spine shorter than dorsal spine, approximately equal in length to antennal protopod. Lateral spines present, directed anteriorly, curving ventrally. Anterodorsal setae absent. One pair of posterodorsal setae. Ventral and posterior margins without setae. Eyes sessile.

Antennule (Fig. 5B): uniramous. Endopod absent. Exopod unsegmented with 2 aesthetascs and 2 setae.

Antenna (Fig. 5C): well-developed protopod as long as rostral spine, with 2 rows of unequally sized denticles. Endopod absent. Exopod about two-thirds length of protopod, with 1 long and 1 short terminal setae and 2 short terminal spines.

Mandible: palp absent.

Maxillule (Fig. 5D): coxal and basial endites with 5 setae each. Endopod 2-segmented, proximal segment with 1 simple seta, distal segment with 5 setae (1 proximal, 2 subterminal and 2 terminal). Exopod setae absent.

Maxilla (Fig. 5E): coxal endite bilobed, with 5 + 3 setae. Basial endite bilobed with 5 (4 + 1 spine) + 4 setae. Endopod unsegmented, bilobed, with 1 seta on inner lobe and 2 (1 long + 1 short) setae on outer lobe. Exopod (scaphognathite) margin with 4 plumose setae and 1 long, thick process.

First maxilliped (Fig. 6A): coxa with 1 seta. Basis with 9 setae arranged 2,2,3,2; dorsally covered with minute spinules, stronger on basal part. Endopod 5-segmented, with 2,2,1,2,5 (1 subterminal, 4 terminal) setae respectively. Exopod 2-segmented, proximal segment dorsally covered with minute spinules, distal segment with 4 long, terminal, plumose natatory setae.

Second maxilliped (Fig. 6B): coxa without setae. Basis with 4 setae arranged 1,1,1,1; dorsally covered with minute spinules. Endopod 3-segmented with 0,1,6 (3 subterminal, 3 terminal) setae respectively. Exopod 2-segmented, proximal segment dorsally covered with minute spinules, distal segment with 4 long, terminal, plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Fig. 6C): five somites. Somite 2 with pair of dorsolateral processes directed anteriorly. Somites 3 and 4 each with pair of dorsolateral processes, directed posteriorly. Somites 2–5 each with pair of posterodorsal setae. Somites 1–5 without remarkable posterolateral processes. Pleopod buds absent.

Telson (Fig. 6C): furcal arms covered with 2 rows of small spinules on dorsal part. One minute lateral spine (scale-like) on outer side of each furcal arm. Three pairs of posterior processes.

Ecological and Behavioral Remarks.—These crabs occur in shallow freshwater streams, from brackish waters at stream mouths to up to several hundred kilometers inland. They are active at night, feeding on algae, diatomaceous mats, and dead fish. Males only

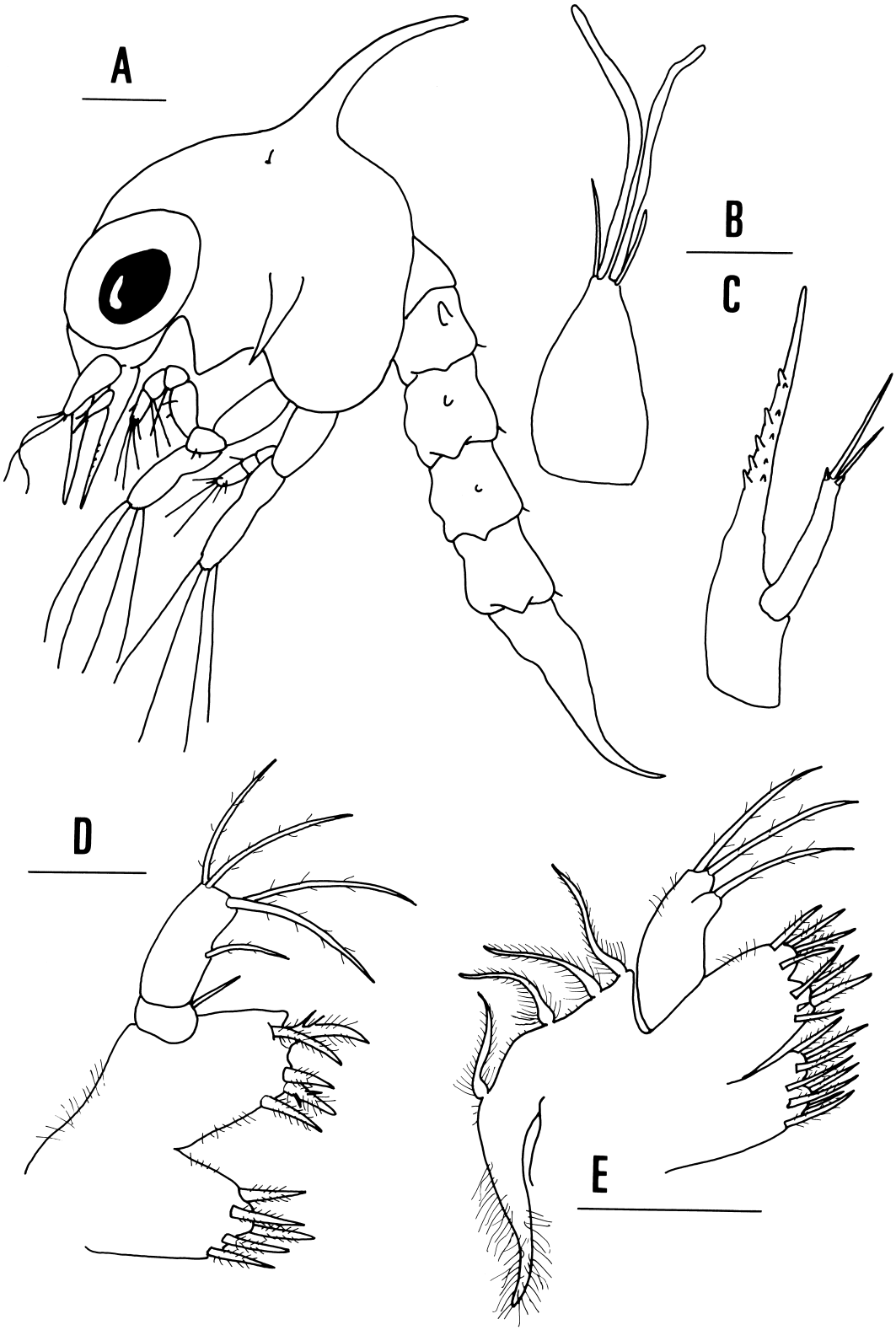

Fig. 5. *Platychirograpsus spectabilis*, zoea I: A, lateral view; B, antennule; C, antenna; D, maxillule; E, maxilla. Scale bars, A = 0.1-mm, B–E = 0.05-mm.

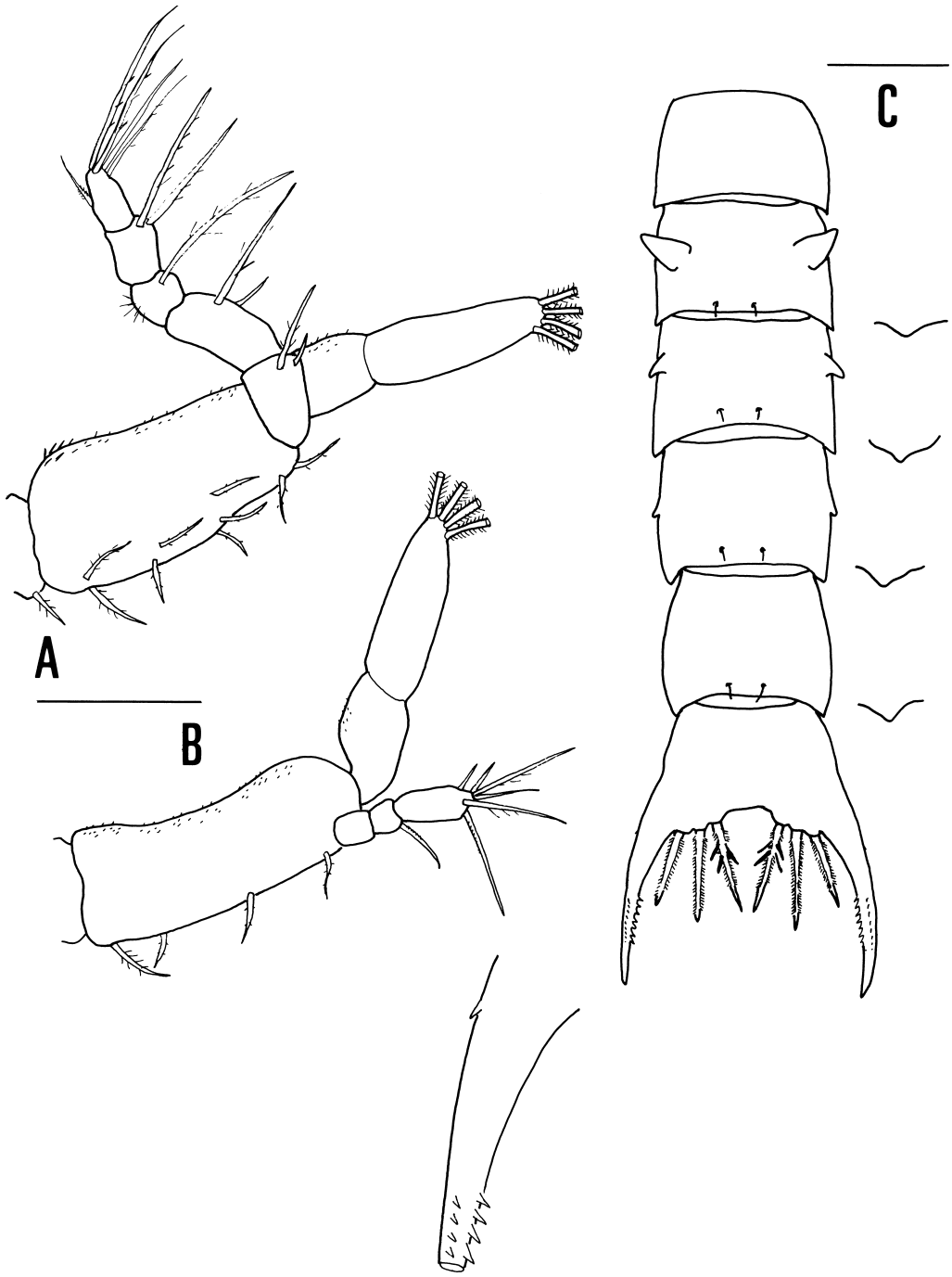

Fig. 6. *Platychirograpsus spectabilis,* zoea I: A, first maxilliped, B, second maxilliped; C, abdomen, dorsal view, part of telson with lateral spine enlarged. Scale bars = 0.1-mm.

use the small chela for feeding, the large chela is designed for competitive behaviors (Marchand, 1946: 94–97) or blocking of burrow apertures (see also Discussion). Actively mating animals and ovigerous females in Veracruz have been observed congregated in the mouth of a small stream near the sea alongside aggregated ovigerous females of the

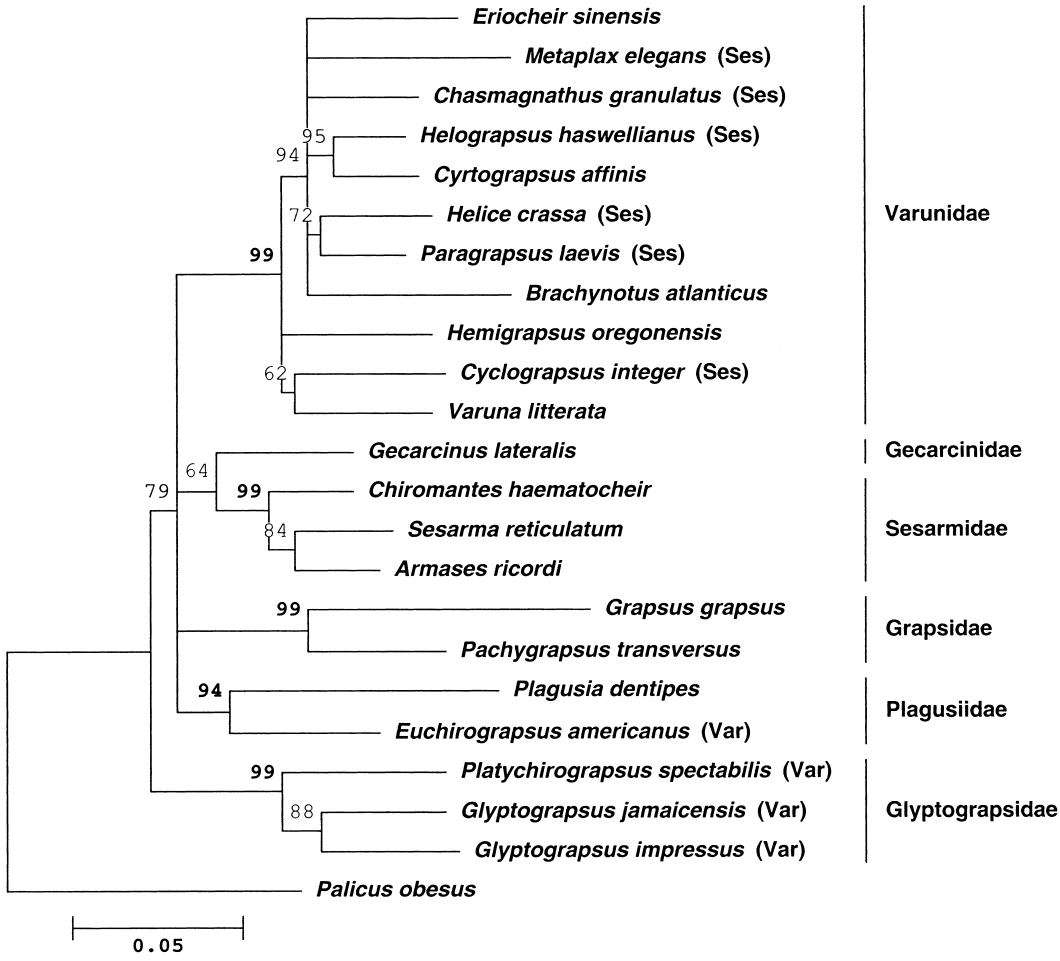

Fig. 7. Phylogenetic relationships of Grapsoidea including the three species of Glyptograpsidae as inferred from 529 conserved basepairs of 16S mtDNA and a neighbor joining analysis (Kimura 2-parameter distances, internal node test). Nodes are shown only if they are supported by confidence values above 50. Labels to the right reflect the current taxonomy; parenthesis after species names indicate previous classification of genera (Ses: Sesarminae; Var: Varuninae).

palaemonid shrimp *Macrobrachium carcinus* (Linnaeus, 1758) and *M. hobbsi* Nates and Villalobos, 1990.

Distribution.—Endemic to Gulf of Mexico: Mexico: Tabasco–Veracruz, Florida (probably introduced into Florida).

Vernacular Names.—Saber crab, Zapatera.

Molecular Phylogeny

The total alignment of 16S mtDNA sequences of 22 grapsoid crabs and one outgroup consisted of 587 positions, not including the primer regions. Of these, 529 homologous basepairs were used for phylogenetic analyses. They included 219 variable and 151 parsimony-informative positions. Pairwise comparisons of genetic differences revealed a transition to transversion ratio between 12 (closely related genera) and 0.53 (distant genera). In NJ, Kimura-2 parameter distances separate the two types of changes and account for the scaling of multiple-hits by correcting with distance. For MP, transversions were weighted three times greater than transitions, resulting in 5 most parsimonious trees, (length = 1,187; CI = 0.5; RI = 0.528) and a single consensus tree after bootstrapping with 2,000 replications.

The trees obtained by NJ (Fig. 7) and MP (Fig. 8) both confirm the taxonomic groups suggested by Schubart *et al*. (2000a) and sup-

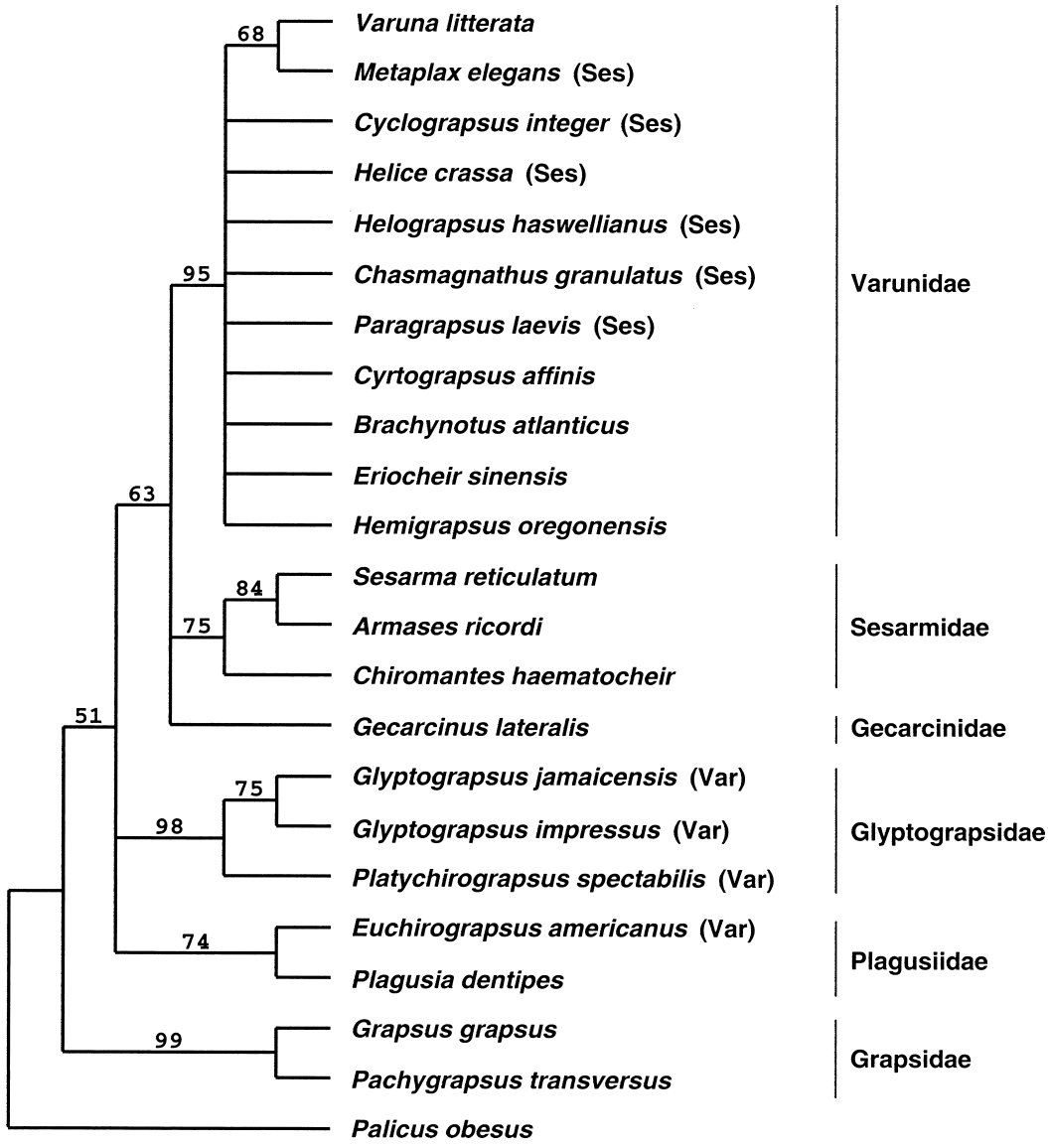

Fig. 8. Phylogenetic relationships of Grapsoidea including the three species of Glyptograpsidae as inferred from 529 conserved basepairs of 16S mtDNA and a maximum parsimony analysis (2,000 bootstraps of heuristic search, transversions weighted 3 times transitions). Nodes are shown only if bootstrap support was above 50. Labels to the right reflect the current taxonomy; parentheses after species names indicate previous classification of genera (Ses: Sesarminae; Var: Varuninae).

port the validity of the new family Glyptograpsidae as an independent taxon with confidence levels of 99 (NJ) and 98 (MP). Both phylogenetic methods strongly support the inclusion of the genera *Chasmagnathus, Cyclograpsus, Helice s.l., Helograpsus, Metaplax,* and *Paragrapsus* (previously Sesarminae) within the Varunidae and give evidence that the newly defined Varunidae (99/95) and Sesarmidae (99/75) are monophyletic. The genus *Euchirograpsus* is correctly placed within the Plagusiidae (94/74). Within the Glyptograpsidae, the separation into the genera *Glyptograpsus* and *Platychirograpsus* finds molecular support by grouping the two species of *Glyptograpsus* together (88/75). The different tree building methods are not consistent in the reconstruction of pos-

sible phylogenetic relationship among the grapsoid families: in NJ, the Glyptograpsidae form an outgroup to all other grapsoids included (79), while the MP keeps the Grapsidae *s. str.* at the base of the Grapsoidea (51). Possible phylogenetic subdivisions within the Varunidae are also poorly resolved and differ according to the tree building methods.

Discussion

The most conspicuous externally evident adult morphological character of the three species that comprise *Glyptograpsus* and *Platychirograpsus* is the unique heterochely shown by the males. The major chela is sometimes longer than the entire animal (e.g., in *Platychirograpsus*) and is more or less flattened on its anterior side. The fingers are short, comparatively weak, and spoon-tipped. One explanation for this chelar morphology is its use for mutual pushing as observed by Marchand (1946: 95): "two males, approaching one another from opposite sides of a stone, met and placed the flat surfaces of their chelae together, but after a few minutes of pushing against one another separated and went away." From observations by one of us (DLF) of several dozen males and females congregated near the mouth of a stream in Veracruz, Mexico, during June, 1978, it was also obvious that males, when in retreat from conflicts with other males or from our attempts to capture them, utilized the outer surface of the large chela as a tightly fitted operculum to seal the broad shallow burrows they had constructed beneath stream boulders. Our collective observations and those of Marchand (1946) provide no apparent evidence for the use of the major chela in feeding. A possible visual attraction to females in terms of a waving display as known for several genera of Ocypodoidea has not been reported to date. No such behavior was evident in our aforementioned observations of *P. spectabilis,* though males observed in shallow (< 10 cm deep) clear waters of the stream were clearly involved in competing for females, and several were holding females *in copula*. A similarly flattened chelar morphology is found in the west African sesarmid *Chiromantes buettikoferi* de Man, 1883, but in this case both chelae are of the same shape.

The two genera herewith assigned to the Glyptograpsidae also differ from a diverse sample of all other Grapsoidea in their unique gill formula. The three glyptograpsid species all lack a pleurobranch on the sixth thoracic pleuron, while we find this gill to be consistently present in *Plagusia, Chasmagnathus, Grapsus, Hemigrapsus, Goniopsis, Brachynotus, Aratus,* and *Armases*. While the glyptograpsid genera share the lack of this gill with the gecarcinid genera *Cardisoma* and *Gecarcinus,* we find that the gecarcinids have both an arthrobranch and podobranch on the second maxilliped, while glyptograpsids have only the podobranch.

Other features that are unique to the Glyptograpsidae are the morphology of the third maxillipeds, which are characterized by three longitudinal sulci on the merus (Fig. 1), and the uncinate distal portion of the gonopods (Fig. 4). Furthermore, all Glyptograpsidae are morphologically different from the Varunidae by the shape of the male abdomen, which completely covers the sternum and touches the coxae of the last pair of walking legs. Also, there is very limited flexibility between abdominal segments 1 and 2 in the Glyptograpsidae, while this joint is usually more mobile in the Varunidae. Conversely, the joint between abdominal segments 5 and 6, usually immobile in the Varunidae, is flexible in the Glyptograpsidae. The third pair of walking legs tends to be the longest or at least subequal to the second pair in the Glyptograpsidae, while the second pair is always longest in the Varunidae. In addition, the anteriormost elements of the sternum in the Varunidae appear to be comparatively larger than those of the Glyptograpsidae, and lack the distinct flanges of the sternal tip as characteristic of the latter family.

The zoea I stages of *G. impressus* and *P. spectabilis* show important synapomorphies within the Grapsoidea by having 1) a setation pattern of 1,2 on the maxillar endopod, whereas the rest of grapsoid families have a 2,2 or 2,3 setation on this appendage; and 2) four setae plus one short spiniform seta on the maxillar basial endite, whereas the rest of grapsoid families have five well-developed setae. In their general morphology, zoeae of these two species are very similar and have the same number and shape of cephalothoracic spines as well as the same type of abdominal processes and antennae (see also Cuesta and Schubart, 1997). However, there are clear differences in the setation of the maxillipeds (see Table 2). Such differences

Table 2. Differences in setation pattern of zoea maxillipeds (mxpd) in *Glyptograpsus impressus* and *Platychirograpsus spectabilis*.

	Glytograpsus impressus (see Cuesta and Schubart, 1997)	*Platychirograpsus spectabilis* (present study)
First mxpd basis	2, 2, 2, 2	2, 2, 3, 2
Second mxpd endopod	1, 1, 6	0, 1, 6

are not commonly found between genera of the same family in the Grapsoidea (see Cuesta, 1999), and indicate that there is an important separation between these two genera. Re-examination of first zoeae of *G. impressus* in polyvinyl lactophenol mounting medium revealed the presence of minute lateral scaliform spines on the outer side of each furcal arm. These were overlooked in the original description (Cuesta and Schubart, 1997). For a better understanding of the relationships between *Glyptograpsus* and *Platychirograpsus* and the position of the Glyptograpsidae among the Grapsoidea, larvae of *G. jamaicensis* as well as later zoeal stages and the megalopae of the three species will have to be studied.

Results from molecular phylogenetics based on the 16S mtDNA also clearly suggest that the Glyptograpsidae constitute a monophyletic unit and represent an independent lineage within the Grapsoidea (Figs. 7, 8; see also Schubart *et al.,* 2000a). The molecular findings also confirm the generic subdivision of the Glyptograpsidae. However, it remains unclear which group within the Grapsoidea or Thoracotremata might represent the closest relative to the Glyptograpsidae. The NJ analysis suggests that the Glyptograpsidae form an outgroup to all other grapsoids included in this study (Fig. 7). On the other hand, MP places the Glyptograpsidae within the Grapsoidea. A possible phylogenetic relationship between the Glyptograpsidae and Sesarmidae, as weakly suggested by the tree in Schubart *et al*. (2000a), was not confirmed in this study.

In addition to close morphological and molecular relationships, the three species encompassed by the Glyptograpsidae also share several ecological characteristics. All of them live in brackish or freshwater habitats as adults. *Platychirograpsus spectabilis* has been reported at a distance of 225 km from the sea (Rathbun, 1918). The small size of zoea larvae of *P. spectabilis* (this study) and *Glyptograpsus impressus* (see Cuesta and Schubart, 1997) and eggs of *G. jamaicensis* (see Diesel *et al.,* 2000) excludes a lecithotrophic development as found in other freshwater or brackish grapsoid crabs (Hartnoll, 1964; Schuh and Diesel, 1995a, b; Diesel *et al.,* 2000) and suggests that larval development takes place in the sea. The far-inland range of the adult habitat in *P. spectabilis* probably requires adult migration for larval release. Marchand (1946) found that adults of *Platychirograpsus* were hard to find from November to March and reported that one specimen of this species was collected from salt water in the Tampa, Florida, area. All of those adult females of this species from Mexico that were collected in close vicinity to the sea between November and April were ovigerous or showed evidence of having recently been ovigerous. The two species of *Glyptograpsus,* on the other hand, seem to prefer freshwater habitats in direct vicinity of the sea. It is unknown whether they undergo seasonal migration or the larvae are carried into the ocean by water currents as in some sesarmid crabs (Anger *et al.,* 1990; Diesel and Schuh, 1998). In captivity, females of *G. impressus* preferred fresh water for larval release in two of three cases, when given the choice between fresh water and salinities of 16 psu (Cuesta and Schubart, 1997).

The present recognition of the new brachyuran crab family Glyptograpsidae is strongly supported by its being based on three independent lines of evidence: adult morphological, larval morphological, and molecular. Separation at a family level is obviously better founded than for recognition of the Gecarcinidae, which has been treated as a distinct family (or superfamily) since Alcock (1900), even though the distinction from other grapsoid crabs was based only on carapacial shape. Having previously offered evidence that the Gecarcinidae evolved within the Grapsidae (*sensu* Alcock, 1900), it became necessary to raise all former grapsid subfamilies (or major lineages) to family level (Schubart *et al.,* 2000a). This also facilitates future comparisons with ocypodoid families (wherein a close relationship between Varunidae and Macrophthalminae, the latter itself a candidate for family status, is sus-

pected). Morphological (adult and larval) as well as genetic differences between Glyptograpsidae and the remaining grapsoid families clearly exceed differences between xanthoid families (e.g., Xanthidae, Panopeidae) (Schubart *et al.,* 2000c, unpublished).

The two genera encompassed by the Glyptograpsidae were previously placed within the grapsid subfamily Varuninae. It has been argued before that the Varuninae constitute a polyphyletic group (Jamieson *et al.,* 1996; von Sternberg and Cumberlidge, 1998; P. Davie, P. Ng, personal communication). However, Schubart *et al.* (2000a) showed that the Varuninae could be monophyletic if some genera from the Sesarminae were included and at least three genera (*Euchirograpsus, Glyptograpsus,* and *Platychirograpsus*) were removed. The taxonomic consequences of that study were to 1) consider *Euchirograpsus* a member of Plagusiidae, and 2) transfer the genera *Chasmagnathus* and *Cyclograpsus* from Sesarmidae to Varunidae. In the present study, two additional steps are taken to make the Varunidae monophyletic: 1) removal of the genera *Glyptograpsus* and *Platychirograpsus* to create a new family, Glyptograpsidae; 2) transfer of the genera *Helice s.l., Helograpsus, Paragrapsus,* and *Metaplax* from Sesarmidae to Varunidae. Both of these changes were anticipated in Schubart *et al.* (2000a). Here we provide the morphological evidence (adult and larval) that was necessary to recognize the Glyptograpsidae as a new family. Furthermore, DNA-sequences were added for the non-American genera that seemed morphologically close to *Chasmagnathus* and *Cyclograpsus* and did not fit into what we consider Sesarmidae *s. str.* These genera, despite having a hairy crest on the third maxilliped (previous definition for Sesarmidae), lack a fully developed reticulation on the pterygostomial region and have large lobules on the male suborbital ridge. Additionally, the proximal part of the male abdomen does not touch the coxae of the walking legs and the second pair of walking legs is the longest. In the Sesarmidae *s. str.,* on the other hand, the pterygostomial region is always covered by a well-defined reticulation of intercrossing lines and setae, the suborbital ridge is finely denticulate, the male abdomen touches the coxae of the walking legs, and the third pair of walking legs tends to be the longest or at least subequal to the second pair. The inclusion of *Helice, Helograpsus, Paragrapsus, Chasmagnathus, Cyclograpsus,* and *Metaplax* in the molecular analysis showed that these genera indeed must be considered Varunidae, because they form a monophyletic group with the type genus *Varuna* and not the Sesarmidae. Kitaura *et al.* (unpublished manuscript) also provide strong genetic evidence that *Helice s.l.* and *Metaplax* belong to the Varunidae and that this family might be the sister taxon to the Macrophthalminae (Ocypodoidea). These results are in accordance with findings from larval morphology that show several shared characters between zoeae and megalopae of *Chasmagnathus, Cyclograpsus, Helice, Helograpsus,* and *Metaplax* with the respective stages of the Varunidae (larvae of *Paragrapsus* are unknown) (Cuesta, 1999; Cuesta *et al.,* unpublished manuscript). They also explain Guinot's (1979) observation that the male genital openings in *Metaplax, Cyclograpsus,* and *Helice* correspond to the sternal position as found in the Varunidae.

For some genera of the Varunidae, larval and molecular characters remain to be defined. However, even in the absence of those data, a forthcoming thorough revision of this family (N. K. Ng and P. Davie, in preparation) should be of great value. It is likely that additional genera (e.g., *Miersiograpsus* and *Xenograpsus*) will have to be removed from the Varunidae to make it a monophyletic group, and it also seems appropriate to establish further subdivisions within this family. However, this study and that of Cuesta (1999) show that *Varuna* and many other genera (some of them previously included in the Sesarmidae) do form a monophyletic unit and that the Glyptograpsidae represents an independent lineage from all other grapsoid families.

ACKNOWLEDGEMENTS

We thank Dave Camp, Wayne Price, P. Smith, and E. Harris for their efforts to obtain *Platychirograpsus* from Tampa Bay waters. Klaus Anger, Peter Davie, Rudolf Diesel, Sara Fratini, Kathy Hieb, Jun Kitaura, Eduardo Spivak, and Shinji Tsuchida kindly provided specimens or DNA-aliquots for the molecular work. Additional material was made available from the USNM by Rafael Lemaitre, Janice Clark Walker, and Karen Reed, and from CNCR by Fernando Alvarez, José Luis Villalobos, and Rafael Robles. The DNA-sequences were obtained in the laboratories of Blair Hedges (Pennsylvania State University) and at the UL Lafayette Department of Biology sequencing facilities, where Joe Neigel was especially helpful in sharing his laboratory facilities. Clarissa

Schubart assisted with some of the figures. Our gratitude is extended to Danièle Guinot, Peter Ng, and two anonymous reviewers for comments on the manuscript. Research was partly funded by the DFG (grant Di 479-2/2), the 'Subprograma General de Perfeccionamiento de Doctores en el Extranjero, Ministerio de Educación y Cultura', Spain and the U.S. Department of Energy (grant no. DE-FG02-97ER12220 to D.L. Felder). Contribution No. 77 of the UL Lafayette Laboratory for Crustacean Research.

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RECEIVED: 26 October 2000.
ACCEPTED: 20 June 2001.