

OLIGOCENE AND MIOCENE DECAPODS (THALASSINIDEA AND BRACHYURA) FROM THE CARIBBEAN

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ABSTRACT

Oligocene and Miocene fossil decapods from Puerto Rico and Cuba have been poorly known; new collections from these regions as well as from the Dominican Republic have now yielded several new reports. One new genus, *Psygmophthalmus*, and several new species (*Neocallichirus aetodes*, *Neocallichirus? quisquellanus*, *Calappa pavimenta*, *Necronectes collinsi*, *Portunus yaucoensis*, and *Psygmophthalmus lares*) are named herein. New combinations include *Euphylax domingensis* (Rathbun 1919), *Megokkos feldmanni* (Nyborg et al. 2003), and *Neocallichirus vaughni* (Rathbun 1918). Specimens of a callianassoid and brachyuran indeterminate at the family, genus, and species level are also described and illustrated, and emended descriptions are provided for *Euphylax domingensis* and *Megokkos feldmanni*. *Scylla costata* Rathbun, 1919, and three indeterminate species of *Portunus* are also reported. *Ceroneustes* De Angeli and Beschin, 1998, is a member of the Cancridae, not the Portunidae as originally reported. Most of the Caribbean taxa reported herein belong to tropical or subtropical extant genera that inhabit both carbonate and siliciclastic, soft, shallow marine substrates, supported by the occurrence of most of the fossils in clastic units. The Cenozoic genera reported herein exhibited either a Tethyan or North Pacific distribution, typical of Eocene and Oligocene decapods of the region. The open Caribbean Seaway facilitated dispersal of fauna throughout the region between the Atlantic and Pacific oceans.

KEY WORDS: Decapoda, Thalassinidea, Brachyura, paleogeography, paleobiogeography, Oligocene, Miocene, Caribbean

INTRODUCTION

Fossil decapod crustaceans have been reported from the Caribbean region for over 100 years. Caribbean, east coastal Mexican, and Central American occurrences from the Cretaceous through Miocene were recently summarized (Schweitzer et al. 2002b). Jamaican decapod occurrences have been extensively summarized in recent years as well (Morris 1993; Donovan et al., 2003; Portell and Collins 2004). Numerous Pliocene and Pleistocene decapods previously have been reported from the Caribbean (Collins and Morris 1976; Collins et al. 1996; Collins and Donovan 1995, 1997, 2004; Collins and Portell 1998). New decapod fossils are herein reported from localities in Puerto Rico, the Dominican Republic, and Cuba. Rathbun (1919, 1920) had previously reported a large Cenozoic decapod fauna from what is now the Dominican Republic and later from Haiti (Rathbun 1923). Fossil decapods from Cuba have not previously been reported. Only one previous published report of Cenozoic decapods from Puerto Rico (Gordon 1966) included notices of two portunid taxa, *Necronectes proavitus* (Rathbun 1918) and *Portunus* cf. *P. oblongus* Rathbun, 1920 from the San Sebastián and Lares formations and the Ponce Formation, respectively. Thus, we here report on decapods from Cenozoic Caribbean localities that previously have been underrepresented or lacking in the

fossil record and discuss their paleoecology and paleobiogeography.

GEOLOGICAL SETTING

Upper Cenozoic stratigraphic sections (Oligocene, Miocene, and Pliocene) are well developed on-shore and off-shore in the Caribbean realm. They have been generally correlated with one another, both lithologically and chronologically, during the course of a paleogeographic characterization of the area (Iturralde-Vinent and MacPhee 1999; Iturralde-Vinent 2001, 2003). In the present paper, this general stratigraphic and paleogeographic scheme will be adopted in order to place the decapod-bearing sites of Cuba, Hispaniola (including Haiti and Dominican Republic), and Puerto Rico into context.

The decapod-bearing sites described in this paper belong to the Oligocene and Miocene (Juana Díaz and Lares formations) of Puerto Rico, the Miocene (Yanigua Formation) of Hispaniola, and the Miocene (Canimar, Lagunitas, and Imías formations) of Cuba (Figs. 1 and 2). Most of these collecting sites were located during joint paleontological expeditions in the search for land vertebrates by the National Museum of Natural History

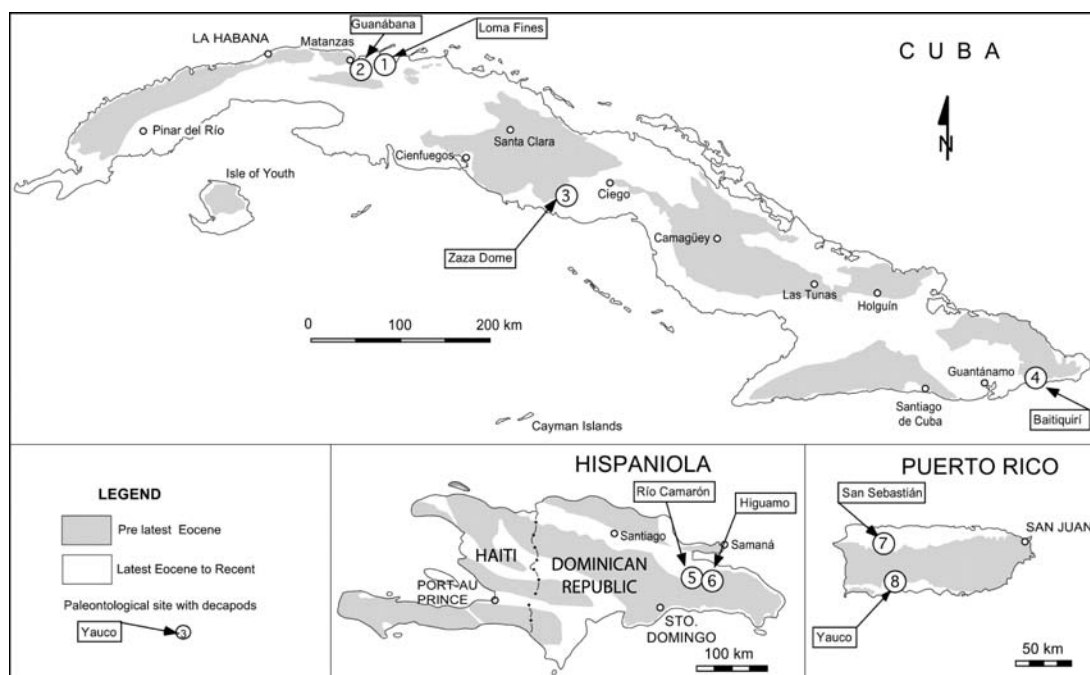


Fig. 1.—Location map of the decapod-bearing rocks in Puerto Rico, Hispaniola, and Cuba. Latitude and longitude are given in the text. Stratigraphic position of localities in Figure 2.

(Havana) and the American Museum of Natural History (New York) (MacPhee and Iturralde-Vinent 1994, 1995; MacPhee et al. 2003; Iturralde-Vinent and MacPhee 1999; Iturralde-Vinent 2001). Decapods have been collected over several years in Puerto Rico by one of us (JV-J); furthermore, a special search for decapods took place in Puerto Rico by a joint expedition of Kent State University and the University of Puerto Rico at Mayagüez.

Institutional abbreviations.—**CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; **MNHNCu-P**, National Museum of Natural History, Paleontological collection, Havana, Cuba; **MGSB**, Museo Geológico del Seminario de Barcelona, Spain; **UPRMP**, Paleontology Collection, Department of Geology, University of Puerto Rico, Mayagüez, Puerto Rico, United States Territory; **R**, Muséum National d'Histoire Naturelle, Paris, France; **USNM**, United States National Museum, Smithsonian Institution, Washington, DC, USA.

PALEONTOLOGICAL SITES

Yauco, Puerto Rico.—The Yauco paleontological site was described by MacPhee and Iturralde-Vinent (1995, p. 13) as a road-cut section located south of Yauco on highway 3334 (18° 01' 17.5" N–66° 51' 16.8" W) (Figs. 1 and 2). At the Yauco site, the Juana Díaz Formation (*sensu* Frost et al. 1983) crops out, represented by lower Oligocene (*Globigerina ampliapertura* Zone, P20) terrestrial to inshore shelf facies represented by sandy clay, sandstone, and conglomerate with a few calcareous intercalations that yield abundant large foraminifera. Overlying this section, separated by an erosional unconformity of

short duration, are coralgal marine limestone and marl (so called Unnamed Formation of Frost et al. 1983), which have been dated as late Oligocene (*Globigerina angulisurens*–*Globorotalia opima opima* Zone, P20–P21) (MacPhee and Iturralde-Vinent 1995). The decapod-bearing horizon is located within the lower Oligocene sandy clay of the Juana Díaz Formation, 6 to 10 m below the top of the unit, where the decapods are associated with a variety of other marine invertebrates (mollusks, echinoderms, corals, foraminifera, ostracods) and fish remains. From this locality were recovered specimens UPRM 2640, 2641, 2642 and 2643, and USNM 527048, 527049, 527051, 527057, 527058, 527059, 527067, 527068, 527074, and 527075 during collecting trips between 1993 and 2004.

San Sebastián, Puerto Rico.—The decapod-bearing section is exposed near the town of San Sebastián (18° 19' 58.5" N–66° 56' 47.5" W) (Figs. 1 and 2). The rocks belong to the upper part of the Lares Formation (Monroe 1980) composed mainly of indurated, very pale orange, fine- to medium-grained calcarenite stratified in beds from 10 cm to 1 m thick. According to Seiglie and Moussa (1984), the formation is late Oligocene to early Miocene in age and represents a back-reef complex and coral bioherm. The age of the decapod-bearing site is early Miocene based on the occurrence of the foraminiferan *Miosorites americanus*, which does not occur in the Oligocene (Wilson Ramírez, pers. comm., 2003). From this locality, specimens USNM 527050,

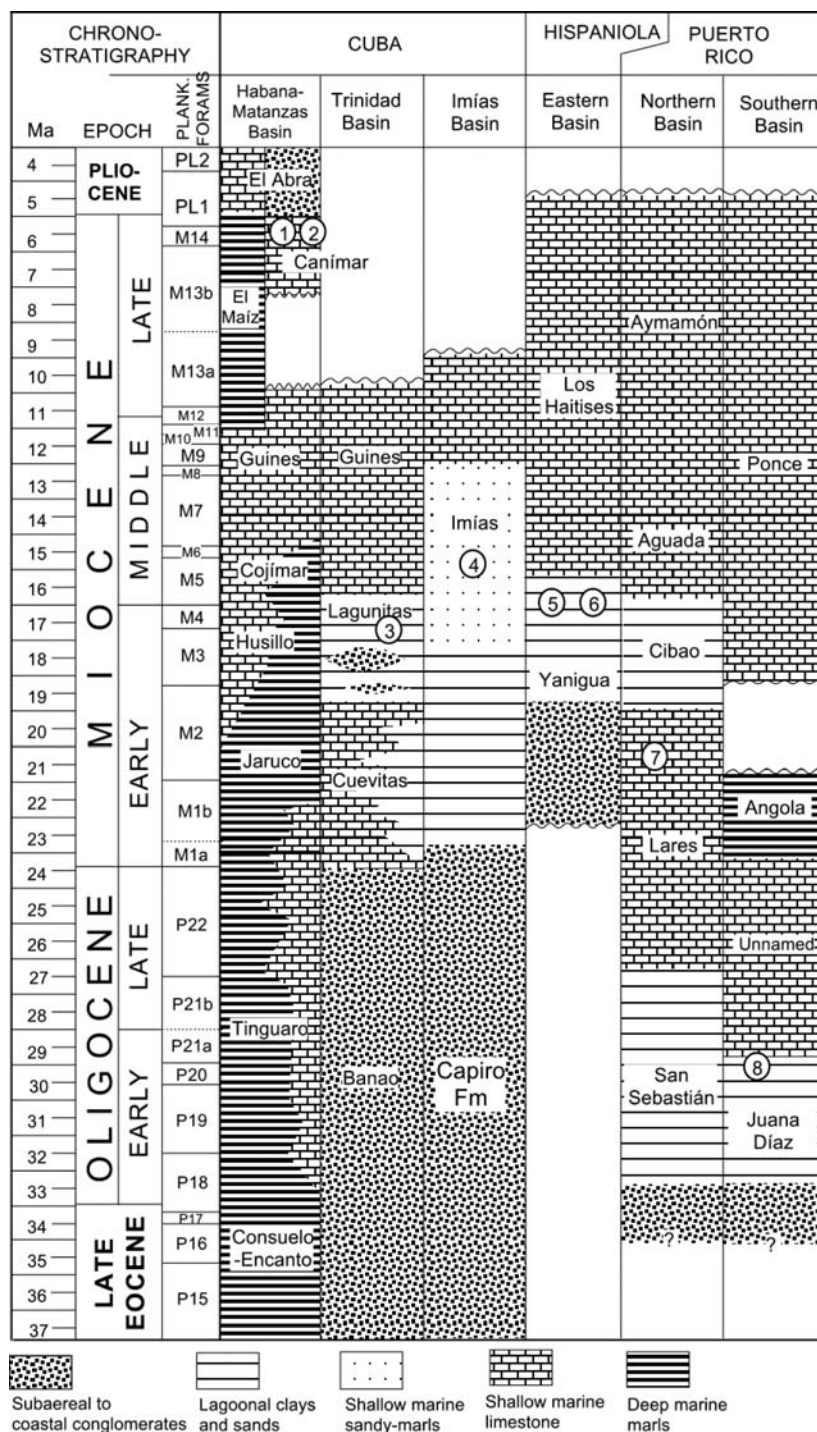


Fig. 2.—Late Cenozoic columnar sections of the basins where the collecting sites are located. Adapted and updated from Iturralde-Vinent and MacPhee (1999). Paleontologic sites in Cuba (1—Loma Fines, 2—Guanábana, 3—Zaza Dome, 4—Baitiquirí); Dominican Republic (5—Río Camarón, 6—Higuamo); and Puerto Rico (7—San Sebastián, 8—Yauco). Approximate location in Figure 1.

527069, 527070, 527071, 527072, and 507076 were recovered.

Higuamo, Dominican Republic.—The Higuamo decapod-bearing site is located on the Higuamo (also spelled Iguamo) River banks, approximately 300 m west-southwest from Colonia San Rafael (approximately 18° 52' N–69° 21' W) (Figs. 1 and 2). The rock section belongs to the top lower to basal middle Miocene Yanigua Formation, composed mainly of dark gray, shallow marine clay, sandy clay, and marl, intercalated with horizons of alluvial sandstone, lignite, and conglomerate that can be locally abundant toward the base of the section. The decapod remains (MNHN Cu-P5117) were recovered during 1998 from gray, indurated, shallow, near-shore lagoonal marl that contains abundant remains of invertebrates (mollusks, echinoderms, foraminifera, corals) and fish, probably a back-reef lagoonal environment (Iturralde-Vinent 2001).

Río Camarón, Dominican Republic.—The Río Camarón decapod-bearing site is located on the Camarón River banks, near Camarón, approximately 15 km north of Bayaguana (approximately 18° 50' N–69° 41' W) (Figs. 1 and 2). The rock section belongs to the top lower to basal middle Miocene Yanigua Formation, near the contact with the overlying Haitises Limestone. Specimens MNHN Cu-P5116 and 5181 were collected in 1998 from gray, sandy clays with calcareous cement, associated with abundant marine invertebrates, suggesting a shallow, near-shore, marine lagoonal environment (Iturralde-Vinent 2001).

Zaza Dome, Cuba.—Zaza Dome is a site located in south-central Cuba, 17 km southeast of the city of Sancti Spiritus, just south of the Zaza artificial lake (approximately 21° 45' N–79° 30' W) (Figs. 1 and 2), which is described in greater detail by MacPhee and Iturralde-Vinent (1994) and MacPhee et al. (2003). At this locality, the early and early middle Miocene Lagunitas Formation is well exposed on both channel walls, represented by terrestrial sand and gravel intercalated with lagoonal clay and shallow marine limestone and calcarenite beds.

TABLE 1. Measurements (in mm) taken on specimens of *Neocallichirus aetodes* new species and their handedness. (H) indicates holotype; all other specimens are paratypes.

Specimen No.	Length of Manus	Height of Manus	Handedness
USNM 527058 (H)	16.7	16	L
USNM 527061	12.1	10.4	R
USNM 527062	—	—	L
USNM 527063	—	—	L
USNM 527064	10.5	9.1	L
USNM 527065	16.3	14	R
CM 45816-1	18.2	15.1	R
CM 45816-2	16.8	15.5	R
USNM 527066-4	17.8	13.4	R
USNM 527066-5	17	15	R
USNM 527066-6	16.1	13.2	R
USNM 527066-7	15.8	13.2	R
USNM 527066-8	15	14	R
USNM 527066-9	16.4	14.1	R
USNM 527066-10	17.5	13.7	R
USNM 527066-11	15	12.8	R
USNM 527066-12	15.5	13	R
USNM 527066-13	12.2	10.7	R
USNM 527066-14	14.4	11.1	R
USNM 527066-15	14.4	11	R
USNM 527066-17	12.9	10	R
USNM 527066-18	11.8	10.2	R
USNM 527066-19	11.5	9.1	R
USNM 527066-20	10.4	9.6	R
USNM 527066-21	11.3	9.4	R
USNM 527066-22	11.1	9.5	R
USNM 527066-23	10.5	8.9	R
USNM 527066-24	11.6	8.7	R
USNM 527066-25	11.5	8.8	R
USNM 527066-26	9.2	8.7	R
USNM 527066-27	7.7	7.1	R
USNM 527066-29	17.5	15.1	L
USNM 527066-30	17.3	14.8	L
USNM 527066-31	17.2	13.2	L
USNM 527066-32	15.8	13.2	L
USNM 527066-33	15.7	13	L
USNM 527066-34	15.1	12.7	L
USNM 527066-35	14.5	11.5	L
USNM 527066-36	13.8	11.7	L
CM 45816-37	15.4	11.8	L
CM 45816-38	14	11.8	L
CM 45816-39	13.4	11.4	L
CM 45816-40	14.4	11	L
USNM 527066-41	13.8	10.5	L
USNM 527066-42	12.6	10.3	L
USNM 527066-43	14.1	11	L
USNM 527066-44	10.4	9.2	L
USNM 527066-45	11.9	10	L
USNM 527066-46	11.9	9.6	L
USNM 527066-47	13	—	L
USNM 527066-48	10.8	8.9	L
USNM 527066-50	12.4	9.7	L
USNM 527066-51	10.7	9.5	L
USNM 527066-52	10.4	8.5	L
USNM 527066-55	10.4	8.1	L
USNM 527066-56	10.6	8.5	L
USNM 527066-57	10.2	8.1	L
USNM 527066-58	9.3	7.2	L
Specimen No.	Length of Carpus	Height of Carpus	Handedness
USNM 527059	11.6	>10.8	R
USNM 527060	6.8	7	L

Many small fragments of crustacean fingers are common in the limestones, but large decapod specimens were obtained from the so-called “calcarene bed,” which probably can be correlated with the 17.5–18.3 Ma onlap event (Haq et al. 1987; MacPhee et al. 2003). The decapods were recovered from the calcarenite (MNHNCu-P3564, MNHNCu-P3565) between 1990 and 2001 and were associated with marine invertebrates, fish remains, and other vertebrates (MacPhee et al. 2003).

Baitiquirí, Cuba.—This site is located in southeastern Cuba, represented by a quarry named “Mina de Yeso” (Gypsum Mine), located north of Baitiquirí (approximately 20° 02' 30" N–74° 49' 30" W) (Figs. 1 and 2). At this site the Imías Formation is well exposed and represented by a section of well-bedded, gray-greenish sandstones and lutites, with intercalated marls and limestone beds and some layers of gypsum. The marls and limestone contain an abundant association of marine invertebrates, including a decapod. The microfossils in the marls and limestones, identified by Sánchez-Arango (1975), include ostracods and foraminifera of middle Miocene age. This assemblage is characteristic of shallow, warm, hypersaline water, probably due to deposition in a local embayment (Sánchez-Arango 1975). The decapod MNHNCu-P921 was recovered from the calcarenite.

Loma Fines, Cuba.—The late Miocene Canimar Formation is well developed in the area north of Matanzas province, between the cities of Matanzas and Cárdenas (Iturralde-Vinent 1969). The Loma Fines site, located SW of the city of Cárdenas, is a large quarry at Loma Fines (approximately 23° 01' N–81° 08') (Figs. 1 and 2), where loosely cemented marine calcarenites occur. The portunid decapods are associated with many marine invertebrates and fish remains, and specimen MNHNCu-P1822 was recovered from this matrix.

Guanábana, Cuba.—The Guanábana site is a quarry located southeast of the city of Matanzas, near and west of the village of Guanábana (approximately 22° 59' N–81° 30' W) (Figs. 1 and 2). The upper Miocene Canimar Formation crops out here, where specimen MNHNCu-P844 was collected in 1996.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802
 Infraorder Thalassinidea Latreille, 1831
 Superfamily Callianassoidea Dana, 1852
 Family Callianassoidea Dana, 1852
 Subfamily Callichirinae Manning and Felder, 1991
 Genus *Neocallichirus* K. Sakai, 1988

Type species.—*Neocallichirus horneri* K. Sakai, 1988.

Included fossil species.—*Neocallichirus aetodes* new species; *N. bona* (Imaizumi 1958) as *Calliax* (see Karasawa 1993); *N. fortisi* Beschin,

Busulini, De Angeli, and Tessier, 2002; *N. grandis* Karasawa and Goda, 1996; *N. matsoni* (Rathbun 1935), as *Callianassa*; *N. nishikawai* (Karasawa 1993) as *Callianassa*; *N. okamotoi* (Karasawa 1993) as *Calliax*; *N. peraensis* Collins, Donovan, and Dixon, 1996; *N. rhinos* Schweitzer and Feldmann, 2002; *N. sakiae* Karasawa and Fudouji, 2000; *N. vaughni* (Rathbun 1918), **new combination**, as *Callianassa*; *N. wellsi* Schweitzer, Feldmann, and Gingerich, 2004; *N. ? quisquellanus* new species.

Discussion.—Schweitzer and Feldmann (2002) and Schweitzer et al. (2004) recently reviewed the genus and discussed key characters of the genus. Rathbun (1918) described *Callianassa vaughni* from Miocene rocks of Panama; that species has the serrate distal margin swelling and the heavily ornamented movable finger often seen in *Neocallichirus*. Thus, it is herein transferred to *Neocallichirus*. The genus has already been reported from the fossil record in the Caribbean (Collins et al. 1996), and other fossil occurrences span the Tethyan Realm of the Eocene through Pleistocene (Schweitzer et al. 2004). Thus, *N. vaughni* and the new species described below fall within the known geographic distributional pattern and geologic range of the genus.

Neocallichirus aetodes, new species

(Fig. 3A–C)

Types.—Holotype, USNM 527058 and paratypes USNM 527059–527067, 527074–75, CM 45816. Paratype USNM 527066 is a lot of over 60 specimens.

Diagnosis.—Carpus about as long as high, lower margin markedly serrate. Manus longer than high, highest proximally, narrowing distally; distal margin with serrated, bulbous swelling; fixed finger slender, with teeth proximally on occlusal surface; movable finger stout, with large teeth on occlusal surface, tip hooked downward, reminiscent of an eagle's beak.

Description.—Carpus of cheliped about as long as high, almond-shaped in cross-section; proximal margin with short projection at upper corner for articulation with merus, projection followed by smoothly concave indentation, margin then becoming convex and markedly serrate; proximal margin confluent with lower margin, lower margin weakly convex, serrate; upper margin nearly straight; distal margin weakly concave, at about 90 degrees to upper margin.

Manus of cheliped longer than high, highest just distal to proximal margin, narrowing distally; manus thin, almond-shaped in cross-section; proximal margin concave near upper and lower margins with long, ovate projection centrally for articulation with carpus; upper margin weakly convex; lower margin finely serrate, weakly convex initially, becoming weakly concave near base of fixed finger. Distal margin initially perpendicular to upper margin; then extending at about 100 degree angle to upper margin, central area of distal margin bulbous, bulbous area followed by small, concave reentrant just above fixed finger. Outer surface of manus smooth; inner surface smooth, with bulbous swelling parallel to distal margin, row of anteriorly-directed setal pits parallel to upper margin.

Fixed finger circular in cross-section, directed downward and inward, with small teeth on occlusal surface proximally.

Movable finger stout proximally and remaining stout for most of its length, appearing to have had bulbous, flattened teeth on occlusal surface; tip narrowed, strongly hooked downward at tip, like an eagle's beak.

Remainder of appendages and carapace unknown.

Measurements.—Measurements (in mm) and handedness data are presented in Table 1.

Etymology.—The trivial name is the Greek word *aetodes*, meaning eagle-like, in reference to the tip of the movable finger, which is reminiscent of an eagle's beak.

Occurrence.—Specimens were collected from the upper lower Oligocene at Yauco, Puerto Rico (Figs. 1, 2).

Discussion.—The new species is referable to *Neocallichirus* based upon its arcuate, serrate carpus; manus that narrows distally; serrate distal and lower margins of the manus; narrow, circular movable finger; and stout fixed finger. These features are diagnostic for the genus (Schweitzer and Feldmann 2002). The material upon which the new species is based lacks the merus, which bears one of the key features of the genus, meral serrations (Manning and Felder 1991); however, all of the features listed above taken together permit referral of the species to *Neocallichirus*.

Neocallichirus aetodes is most similar to *N. rhinos* from the Eocene of California; however, the fixed finger of *N. rhinos* has better-developed occlusal teeth and a narrower carpus than does *N. aetodes*. The fingers of the Eocene *N. wellsi* are more gracile than those of *N. aetodes*, and the serrations of the carpus of *N. aetodes* are much larger than those of *N. wellsi*. The extant *N. cacahuete* Felder and Manning, 1995, is very similar to the new species but the carpus is narrower and the movable finger is less stout in that species than in *N. aetodes*.

Neocallichirus ? quisquellanus, new species

(Fig. 3D)

Type.—Holotype, MNHNCu-P5116.

Diagnosis.—Manus of major chela rectangular, about three-quarters as high as long; outer surface with scattered tubercles in lower distal corner; lower margin sinuous; distal margin with bulbous, serrate swelling; fixed finger with blunt teeth on proximal half.

Description.—Manus of major chela rectangular, longer than high, height about three-quarters length; maintaining height along entire length. Proximal margin with rim, weakly convex. Upper margin nearly straight. Lower margin rimmed, initially straight, becoming weakly concave about two-thirds the distance distally along manus, then becoming convex; remaining convex as it merges with lower margin of fixed finger. Distal margin broken along upper margin; serrate, bulbous area oriented at about 90 degrees to upper margin, bulbous region with scattered tubercles on lower half; very shallow notch just above fixed finger. Outer surface moderately vaulted longitudinally and from upper to lower margins, with scattered tubercles in lower distal corner.

Fixed finger curved markedly inward, downturned with respect to manus; outer surface smooth, with row of setal pits parallel to occlusal surface. Occlusal surface with small, blunt teeth proximally; large, blunt tooth at midlength, smooth for remainder of length.

Measurements.—Measurements (in mm): length of manus and fixed fin-

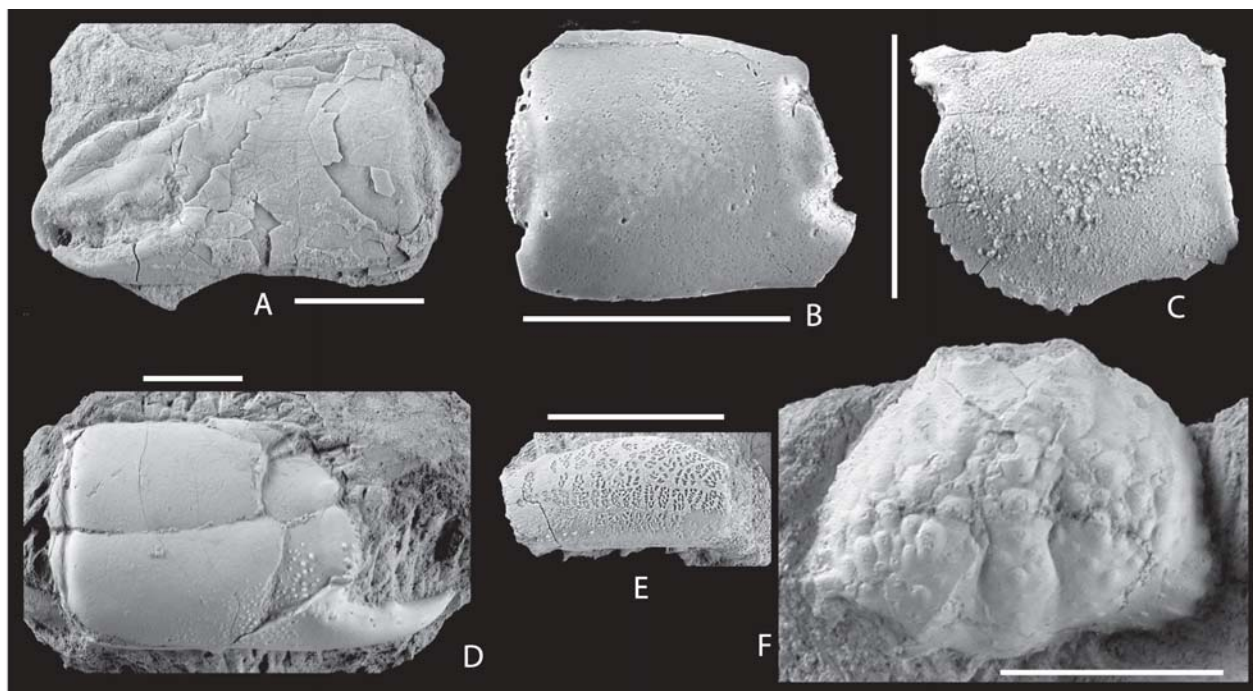


Fig. 3.—Thalassinoidea and Brachyura. **A**, *Neocallichirus aetodes* new species, holotype, USNM 527058, outer surface of major chela; **B**, *Neocallichirus aetodes*, paratype, USNM 527061, outer surface of manus of major chela showing inflated area along distal margin and reentrant above fixed finger; **C**, *Neocallichirus aetodes*, paratype, USNM 527059, outer surface of carpus of major cheliped showing serrations on lower proximal margin; **D**, *Neocallichirus? quisquellanus* new species, holotype, MNHNCu-P5116, outer surface of major chela; **E**, Callianassoidea (family, genus, and species indeterminate), USNM 527068, outer surface of merus of cheliped, lower margin with three spines, note reticulate cuticular pattern; **F**, *Calappa pavimenta* new species, holotype, USNM 527069, dorsal carapace. Scale bars = 1 cm.

ger = 38.0; length of manus = 27.6; height of manus = 20.3.

Etymology.—The trivial name is derived from the occurrence of the specimen in the Dominican Republic, which was named Quisqueya by the aboriginal people.

Occurrence.—The specimen was collected from the upper lower–lower middle Miocene of Río Camarón, Dominican Republic (Figs. 1, 2).

Discussion.—The specimen consists of a very well-preserved manus and fixed finger; however, the merus and carpus are missing. The large size and robust nature of the manus suggests that it is the major chela. The features of the manus are very much like those of both fossil and extant *Neocallichirus*, including the rectangular manus shape, the downturned fixed finger, the serrate distal margin, and the shallow notch on the distal margin above the fixed finger. The manus does not narrow distally as seen in many other species of the genus, however, and the fixed finger has blunt teeth while other species have edentulous fixed fingers. Because of these differences and because the important features of the merus and carpus are lacking, we questionably assign the specimen to *Neocallichirus* until more complete material can be recovered. The large size and unique morphology are unlike any other taxa described from the region; thus, the new species name is warranted.

Callianassoidea Family, Genus, and Species Indeterminate

(Fig. 3E)

Material examined.—USNM 527068.

Description.—Merus of cheliped twice as long as high, arcuate, with blunt longitudinal keel on outer surface; proximal margin composed of two nearly straight segments, upper segment long, lower segment short and making approximately 150° angle with upper segment; upper margin convex, sinuous anteriorly; distal margin extending proximally at about 60° angle to upper margin. Lower margin straight, thickened; with three spines, increasing in size distally; first spine triangular, directed at about 90° to lower margin; second spine circular in cross-section, directed forward at about 45° angle to lower margin; third spine longest, attenuated, directed forward at about 30° to lower margin.

Measurements.—Measurements (in mm) on USNM 527068: length of merus, 14.0; height of merus, 7.0.

Occurrence.—The specimen was collected from the upper lower Oligocene of Yauco, Puerto Rico (Figs. 1, 2).

Discussion.—Although the specimen was collected from the same locality as the material referred to *Neocallichirus aetodes* new species, we do not refer it to that taxon. The merus of members of *Neocallichirus* is variable in shape but is always serrate along the lower margin; it lacks a meral spine or hook (Manning and Felder 1991). The spec-

imen described here as an indeterminate Callianassoidea not only possesses a meral spine, it has three. No other described callianassoid genus has such a feature. Because the merus is not articulated with any other segments of the cheliped, and because there is only one specimen, we refrain from creating a new taxon to accommodate it.

Infraorder Brachyura Latreille, 1802
 Section Heterotremata Guinot, 1977
 Superfamily Calappoidea H. Milne Edwards, 1837
 Family Calappidae H. Milne Edwards, 1837
 Genus *Calappa* Weber, 1975

Type species.—*Cancer granulatus* Linnaeus, 1758.

Confirmed fossil species.—*Calappa costaricana* Rathbun, 1919 (claw only); *C. earlei* Withers, 1924; *C. flammea* (Herbst 1794) (also Recent); *Calappa* cf. *C. gallus* (Herbst 1803) (also Recent); *C. granulata* (Linnaeus 1758) (also Recent); *C. heberti* Brocchi, 1883; *C. lanensis* Rathbun, 1926; *C. laraensis* Van Straelen, 1933; *C. lophos* (Herbst 1795) (also Recent); *C. marmorata* (Herbst 1790) (also Recent); *C. pavimenta* new species; *C. praelata* Lörenthey in Lörenthey and Beurlen, 1929; *C. protopustulosa* Noetling, 1901; *C. restricta* A. Milne-Edwards, 1873; *C. robertsi* Ross, Lewis, and Sclaro, 1964 (claws only); *C. sahelensis* Van Straelen, 1936; *C. springeri* Rathbun, 1931 (also Recent); *C. zinsmeisteri* Feldmann and Wilson, 1988 (claws only); *C. zurcheri* Bouvier, 1899.

Material examined.—*Calappa sahelensis*, holotype, R03768; *C. zurcheri*, holotype, R03770.

Diagnosis.—Carapace highly vaulted longitudinally, moderately vaulted transversely, ovate, wider than long, regions poorly defined, lateral margins of axial regions best defined; front triangular, bilobed, about as wide as an orbit; orbits circular, small, directed forward; supraorbital margin with two fissures; anterolateral margin arcuate and crenulate, dentate, or granular; posterolateral margin with expanded, crenulated, clypeiform flange posteriorly; branchial regions typically with large granules, often arranged into rows; chelipeds closely fitting to front of carapace, massive, subequal, manus triangular, usually with crest of spines on upper margin, movable finger with large basal tooth used to break open shells; male abdomen with somites 3–5 fused (after Rathbun 1926; Galil 1997).

Discussion.—The dorsal carapace of *Calappa* is quite distinctive. The granular ornament, narrow front, circular orbits, and posterolateral flange have historically been diagnostic and easily recognizable features of the genus. More recently, Galil (1997) erected the genus *Calappula*, which differs from *Calappa* in having only one supraorbital fissure instead of two, a trilobate front, and some other features of the chelae and venter that rarely fossilize. Unfortunately, in fossil Calappidae, the front and orbital areas of the carapace are often broken, so that it is not possible to observe those regions. Thus, it is difficult to differentiate between *Calappa* and *Calappula* in the fossil record. Through examination of the illustrations, descriptions, and in some cases, type material of the exclusively fossil species of *Calappa* represented by dorsal carapace material, only *C. lanensis* and *C. praelata* could be confirmed as having two orbital fissures and thus belonging to the genus for certain. *Calappa heberti* as illustrated in Lörenthey and Beurlen (1929) has at least one orbital fis-

sure, but the remainder of the orbit and frontal area is broken. Because *Calappa* is the older and much better-known generic name, it is likely that fossils with this general form and that are missing the front and orbital areas will continue to be referred to *Calappa*, as we do here. Thus far, there are only two known extant species of *Calappula* (Galil 1997) and numerous extant species of *Calappa*; thus, referral of fossils to *Calappa* with the general dorsal carapace form of *Calappa* and *Calappula* but that lack the orbital and frontal area seems the most parsimonious course of action in the absence of complete data. In any event, the two genera are clearly closely related, and recovery of fossils clearly referable to *Calappula* could help to determine the timing of the event leading to the two genera. Based upon confirmed fossil occurrences and the large number of extant species (Rathbun 1937; Galil 1997), at this time it seems likely that *Calappa* is the older genus.

Calappa was a speciose genus in the Caribbean during the middle and late Cenozoic; this should not be surprising because it is quite speciose in the region today (Rathbun 1937; Williams 1984) as well as in the Indo-Pacific (Galil 1997; Davie 2002). The genus has apparently been quite successful since it first appeared during the Eocene; these earliest occurrences are recorded from Antarctica (Feldmann and Wilson 1988) and Oregon (Rathbun 1926). As previously summarized (Schweitzer and Feldmann 2000a), it is interesting that these earliest records show an amphitropical distribution, because the later Oligocene, Miocene, Neogene, and Recent occurrences of the genus are nearly all subtropical to tropical. The new species from Puerto Rico does not resolve this apparent change in ecological preference over time within the genus.

Calappa pavimenta, new species

(Fig. 3F)

Types.—Holotype USNM 527069 and paratypes USNM 527070, 527072, CM 45817.

Diagnosis.—Carapace narrow for genus; tubercles on branchial regions large, closely spaced to form pavement, not arranged into rows.

Description.—Carapace ovoid, wider than long, L/W excluding the posterolateral flange about 0.85, widest at about midlength; carapace regions not well differentiated; carapace very strongly vaulted longitudinally, moderately vaulted transversely.

Front not well known, about 15 percent maximum carapace width measured excluding clypeiform posterolateral flange; orbits small, appearing to have been circular, directed forward, fronto-orbital width about 30 percent maximum carapace width measured excluding posterolateral flange. Anterolateral margin weakly convex, with blunt, broadly rounded projections; posterolateral margin initially with blunt, broadly rounded projections, followed by clypeiform crenulated flange typical of genus, flange not projecting much laterally, with about five major ridges and crenulations. Posterior margin convex, poorly known.

Protogastric regions small, weakly inflated, with at least two large, domed, flattened swellings centrally. Axial regions best defined of all carapace regions, especially their lateral margins; mesogastric region with

TABLE 2. All Caribbean fossil species referable to the Portunidae.

Taxon	Age	Location
<i>Portunus yaucoensis</i> new species	early Oligocene	Yauco, Puerto Rico
<i>Portunus atecuicilis</i> Vega et al., 1999	Miocene	Eastern Mexico
<i>Portunus gabbi</i> Rathbun, 1919	Miocene	Haiti
<i>Portunus haitensis</i> Rathbun, 1923	Miocene	Haiti
<i>Portunus oblongus</i> Rathbun, 1920	Miocene	Dominican Republic; Puerto Rico?
<i>Portunus</i> spp.	early-middle Miocene	Dominican Republic; Cuba
<i>Necronectes nodosus</i> Schweitzer et al., 2002b	Oligocene	Baja California Sur, Mexico
<i>Necronectes summus</i> Collins and Donovan, 1995	Oligocene	Antigua
<i>Necronectes proavitus</i> (Rathbun 1918)	Miocene	Panama; Puerto Rico
<i>Necronectes collinsi</i> new species	early Oligocene-early Miocene	Puerto Rico
<i>Necronectes tajinensis</i> Vega et al., 1999	Miocene	Eastern Mexico
<i>Scylla costata</i> Rathbun, 1919	early Oligocene; Miocene	Puerto Rico; Haiti
<i>Euphylax callinectias</i> Rathbun, 1918	Miocene	Panama
<i>Euphylax domingensis</i> (Rathbun 1919) new combination	Miocene	Haiti
<i>Euphylax fortis</i> Rathbun, 1918	Miocene	Panama
<i>Euphylax fortispinosus</i> Collins et al., 2001	Pleistocene	Jamaica
<i>Sandomingia yaquiensis</i> Rathbun, 1919	Miocene	Caribbean
<i>Psygmophthalmus lares</i> new species	Miocene	Puerto Rico

long, poorly defined anterior process, widened posteriorly, ornamented posteriorly with large, oblong swelling and anteriorly with smaller swellings; metagastric region rectangular, with central, broadly domed swelling; urogastric region with concave lateral margins, ornamented centrally with large swelling; cardiac region longitudinally elongate, widest at about one-third its length, ornamented with several domed tubercles, merging smoothly with intestinal region, which is ornamented with scattered, small tubercles.

Hepatic region flattened, ornamented with low, domed swellings. Branchial regions not differentiated, with large swellings anteriorly, arranged into a closely spaced pavement anteriorly, swellings becoming more sparse and smaller posteriorly.

Venter and appendages unknown.

Measurements.—Measurements (in mm) on the holotype, USNM 527069: maximum carapace width, excluding posterolateral flange, 15.3; maximum carapace length, 13.0; fronto-orbital width, 4.5; frontal width, 2.3.

Etymology.—The trivial name is derived from the Latin *pavimentum*, meaning “a floor of stones,” in reference to the closely spaced swellings on the dorsal carapace.

Occurrence.—Specimens were collected from the lower Miocene at San Sebastián, Puerto Rico (Figs. 1, 2).

Discussion.—Although none of the specimens is complete, they are clearly referable to a new species of *Calappa*. *Calappa pavimenta* differs from all other species of the genus in its relatively high length to width ratio, small clypeiform posterolateral flange, and dorsal carapace ornamentation arranged into a pavement instead of into distinct rows. None of the extinct Caribbean fossil species has such ornamentation on the dorsal carapace, and no species, living or fossil, exhibits this combination of characters. *Calappa zurcheri*, from the Miocene of Panama, has very distinctive rows of tubercles on the dorsal carapace, unlike *C. pavimenta*. *Calappa earlei* from the Oligocene of Anguilla has sharp tubercles on the dorsal carapace, while the ornamentation on *C. pavimenta* is composed of low, domed swellings. *Calappa larensis* from

the Oligocene and Miocene of Venezuela (Van Straelen 1933; Feldmann and Schweitzer 2004) possesses small and large tubercles arranged into discrete rows on the carapace, unlike *C. pavimenta*, and a serrate anterolateral margin, not seen in *C. pavimenta*. The other two extinct species known from the area, *C. robertsi* and *C. costaricana*, are known only from claws and cannot be directly compared with *C. pavimenta*.

Superfamily Portunoidea Rafinesque, 1815

Family Portunidae Rafinesque, 1815

Subfamily Portuninae Rafinesque, 1815

Genus *Portunus* Weber, 1795

Type species.—*Cancer pelagicus* Linnaeus, 1758.

Diagnosis.—Carapace much wider than long; carapace regions moderately developed; six frontal spines including inner-orbital spines which are usually present; orbit with two closed supraorbital fissures; nine anterolateral spines including outer-orbital spine; chelae keeled; male abdomen triangular with somites 3–5 fused.

Discussion.—Several Caribbean fossil species have been referred to the genus *Portunus* (Table 2). Referral of fossil specimens to genera within the Portuninae can be difficult, because genera within that subfamily have quite similar dorsal carapace morphologies. This process is made more difficult by the rather irregular descriptive terminology used to describe the front in *Portunus* and other genera. The front in *Portunus* is described as possessing four or six teeth or possessing three or four lobes (Rathbun 1930; Apel and Spiridonov 1998). Examination of illustrations of *Portunus*, *Scylla* de Haan, 1833, and other genera suggests that usually the front has six spines including the inner-orbital spine, with the middle four spines sometimes distinctly separated from the inner-orbital spines by a broad notch or projected forward somewhat more than the

inner-orbital spines. Almost all observed species within *Portunus*, *Callinectes*, and *Scylla* have an axial frontal notch.

The dorsal carapace morphology of species of *Portunus* and *Scylla* are quite similar to one another. Both have wider than long carapaces; long, attenuated, laterally-directed last anterolateral spines; frontal margins with six spines including the inner-orbital spines; and nine anterolateral spines including the outer-orbital spine. Apel and Spiridonov (1998), in a key to species of the two genera in the Arabian Gulf region, suggested that species of *Portunus* have better-defined regions of the carapace than do species of *Scylla*, and that species of *Scylla* have smooth, short, massive chelae while those of *Portunus* have keeled chelae. Examination of fossils, however, demonstrates that some species of *Scylla* have short, massive chelae with weak keels. Species of *Portunus* always have keels, but the chelae are elongate and more slender than those of *Scylla*. These seem to be the best features by which to distinguish the two genera, especially in fossils in which the dorsal carapace and chelae are quite common.

Callinectes Stimpson, 1860, is also quite similar to *Portunus* in terms of dorsal carapace and chela morphology. There are some notable differences, however, that are useful for paleontologists. *Callinectes* is described as possessing five keels on the outer surface of the manus (Rathbun 1930), but examination of illustrations suggests that only two or three are on the outer surface (Williams 1984), similar to *Portunus*. A more noticeable difference is that species of *Portunus* have longer and more slender meri, mani, and fingers of the major cheliped than do species of *Callinectes* (illustrations in Rathbun 1930). Species of *Portunus* also appear to be somewhat less wide with respect to the length than species of *Callinectes*, but there is considerable variation among species within each genus. The best means of distinguishing species of *Callinectes* is use of the male abdomen, which is T-shaped (Rathbun 1930; Williams 1984), while in *Portunus*, it is triangular (Williams 1984). *Lupella* Rathbun, 1897, is very similar to *Portunus*, but in the former there is only one supraorbital fissure (Rathbun 1930, pl. 57). Species of *Arenaeus* Dana, 1851, have two open supraorbital fissures, and the male abdomen is narrower than that of *Portunus* spp. but not T-shaped as in *Callinectes* spp. (Rathbun 1930, p. 134). An exclusively fossil genus, *Necronectes* A. Milne Edwards, 1881, is distinguishable from other genera in possessing eight anterolateral spines including the outer-orbital spine and large, smooth chelae. Species of *Necronectes* also lack transverse ridges on the dorsal carapace (Glaessner 1969).

Portunus yaucoensis, new species

(Fig. 4A, B)

Types.—Holotype UPRMP 2642, and paratypes UPRMP 2640, 2641, and 2643, and USNM 527048, 527049; CM 45818, 45819.

Diagnosis.—Carapace small, regions well-defined for genus, cardiac region distinctly fan-shaped; carapace weakly vaulted longitudinally and transversely.

Description.—Carapace wider than long, L/W = 0.63, widest at position of last anterolateral spine; regions moderately developed; carapace weakly vaulted longitudinally and transversely.

Front with six spines including inner-orbital spines, axially notched, about 23 percent maximum carapace width. Middle four frontal spines separated from inner-orbital spines by deep, broad, U-shaped reentrant; inner-most two spines blunt, separated by shallow axial notch; outer pair of spines blunt, separated from inner pair by broad, shallow notch; inner-orbital spines directed forward. Orbits broad; with two fissures, one at mid-width of orbit, other just proximal to outer-orbital spine; weakly rimmed; outer-orbital spine much stronger than inner-orbital spine; fronto-orbital width about 68 percent maximum width.

Anterolateral margins weakly convex, with nine spines including outer-orbital spine; last spine very large, attenuated, directed laterally; remainder of spines excluding outer-orbital spine triangular, directed anterolaterally, becoming somewhat smaller posteriorly. Posterolateral margin concave just posterior to last anterolateral spine, becoming convex posteriorly. Posterior margin nearly straight, about 34 percent maximum carapace width.

Epigastric regions weakly tumid; protogastric regions about as wide as long, weakly tumid; mesogastric region widened and tumid posteriorly, bounded posteriorly by deep grooves, with long anterior process; urogastric region reduced, short, depressed below level of mesogastric and cardiac regions; cardiac region fan-shaped, anterior margin convex, broadest anteriorly, narrow distally, lateral margins very concave; intestinal region poorly developed, flattened. Hepatic region much wider than long, depressed proximally and weakly inflated distally parallel to anterolateral margin. Epibranchial region tumid, arcuate, extending from last anterolateral spine axially, terminating in large swelling adjacent to anterior-most cardiac region and urogastric regions. Remainder of branchial region inflated axially, flattening toward posterolateral margin.

Measurements.—Measurements (in mm) taken on the dorsal carapace of *Portunus yaucoensis*: UPRMP 2642 (holotype): maximum length (L) = 17.2; maximum width (W) = 28.2; fronto-orbital width (FOW) = 18.0; frontal width (FW) = 6.4; posterior width (PW) = 9.5. UPRMP 2640 (paratype): L = 17.8; W = 28.0; FOW = 19.6. UPRMP 2641 (paratype): L = 31.0. USNM 527049 (paratype): W = 32.8; L = 20.5; FOW = 22.4. USNM 527048 (paratype): W = 22.0; FOW = 15.4.

Etymology.—The trivial name is derived from the town near which the specimens were collected.

Occurrence.—All of the specimens were collected from the upper lower Oligocene at Yauco, Puerto Rico (Figs. 1, 2).

Discussion.—The new material differs from all other species in the genus; thus, a new species must accommodate it. The moderately well-developed regions, fan-shaped cardiac region, and small size in *Portunus yaucoensis* new species differentiate it from most other species within the genus. *Portunus yaucoensis* is most similar to *P. oblongus* Rathbun, 1920. However, *Portunus oblongus* is much wider than long and too wide to accommodate the new material. In addition, although specimens of *P. oblongus* are quite small and have moderately developed regions, (Feldmann and Schweitzer 2004, pl. 2, fig. 1), the last anterolateral spine is positioned very far posteriorly and directed posteriorly, not seen in *P. yaucoensis*. The protogastric regions of *P. oblongus* are larger proportionally than those of *P. yaucoensis*.

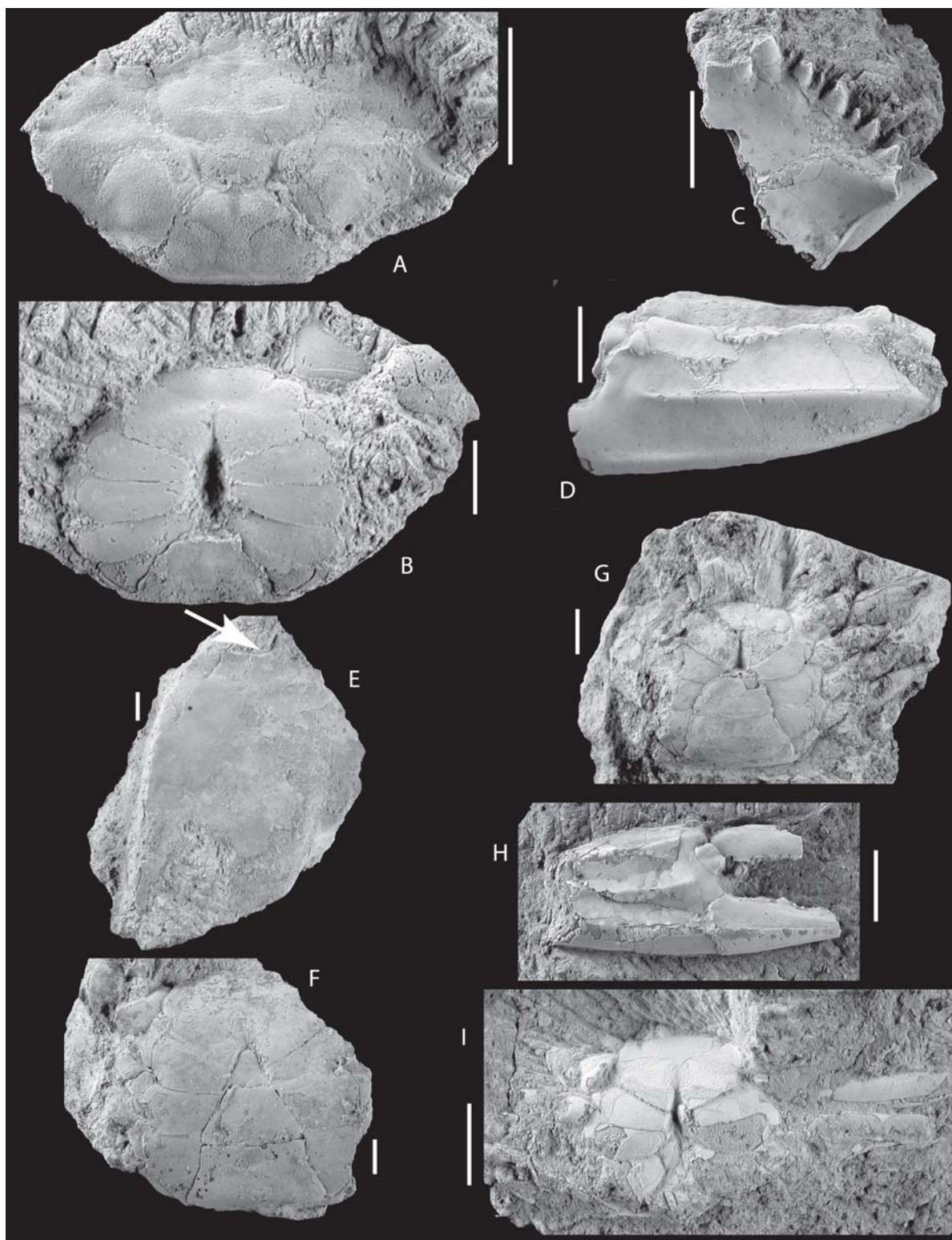


Fig. 4.—*Portunus* spp. **A–B**, *Portunus yaucoensis* new species, holotype, UPRMP 2642, dorsal surface (A) and ventral surface (B); **C–D**, *Portunus* sp. 1, MNHNCu-P5117, portion of anterolateral margin and orbit (C) and outer surface of chela (D); **E–F**, *Portunus* sp. 2, MNHNCu-P3564, male, partial dorsal carapace, arrow indicates position of orbit (E) and male abdomen (F); **G**, *Portunus* sp. 2, MNHNCu-P3565, female abdomen; **H–I**, *Portunus* sp. 3, MNHNCu-P5181, outer surface of chela (H) and partial sternum, apparently male (I). Scale bars = 1 cm.

Gordon (1966) reported a specimen that he referred to *Portunus* cf. *P. oblongus*. Only the ventral aspect of that specimen (USNM 638810) was illustrated (Gordon 1966, fig. 1), and the dorsal carapace was described as badly preserved. Thus, a direct comparison of that specimen with the material referred to *P. yaucoensis* is not possible here, but it may belong to *P. yaucoensis*. The frontal spines in *P. ateuicicilis* Vega et al., 1999, are much reduced as compared to those of *P. yaucoensis*. Thus, the new species is easily differentiated from other Caribbean species.

Portunus sp. 1

(Fig. 4C, D)

Material examined.—MNHNCu-P5117.

Occurrence.—The material was collected from the upper lower–lower middle Miocene of Higuamo, Dominican Republic (Figs. 1, 2).

Discussion.—The material is assignable to *Portunus* based upon its possession of nine anterolateral spines including the outer-orbital spine which alternate in size and of keeled chelae. The material is too fragmentary to assign to a species, several of which are known from Hispaniola. The new material is relatively small in size (carapace length about 30 mm), as is *P. yaucoensis*. *Portunus haitensis* is depicted as having anterolateral spines of the same size excluding the ninth (Rathbun 1923, pl. 1, fig. 3), a condition not seen in the new material. However, the incomplete nature of the material makes it difficult to compare it to other species from the region, *P. oblongus*, *P. ateuicicilis*, and *P. yaucoensis*. More complete material will be necessary to make a species-level placement.

Portunus sp. 2

(Fig. 4E–G)

Material examined.—MNHNCu-P3564, 3565.

Occurrence.—The specimens were collected from the upper lower–lower middle Miocene at Zaza Dome, Cuba (Figs. 1, 2).

Discussion.—The specimens referred to *Portunus* sp. 2 are much larger than those assigned to *Portunus* sp. 1; the carapace length of MNHNCu-P3564 exceeds 75 mm. Unfortunately, the dorsal carapace of the specimens referred to *Portunus* sp. 2 is either missing or incomplete. The specimens are clearly portunids based upon the broad, ovate sternum and fused male abdominal somites 3–5, and are referred to *Portunus* based upon the apparently spined anterolateral margins and the large posterolateral reentrant. No other portunid genera known from the fossil record of the area have such a large posterolateral reentrant; in addition, as previously discussed, *Portunus* spp. are well known from Miocene of the Caribbean region

(Table 2). More complete material is needed to make a species-level placement.

Portunus sp. 3

(Fig. 4H, I)

Material examined.—MNHNCu-P5181.

Occurrence.—The specimens were collected from the upper lower–lower middle Miocene of Río Camarón, Dominican Republic (Figs. 1, 2).

Discussion.—The material referred to *Portunus* sp. 3 consists of a partial sternum and most of a chela. The sternum is ovate and the sternites have long episternal projections, typical of species of *Portunus* illustrated by Rathbun (1930). The chela exhibits a keeled manus, and the fingers each possess blunt teeth on the occlusal surface, all of which are typical of the genus. Dorsal carapace material will be needed to place these specimens within a species.

Genus *Necronectes* A. Milne Edwards, 1881

Necronectes A. Milne Edwards, 1881, p. 1, pl. 21, fig. 1.

Gatunia Rathbun, 1918, p. 168, pls. 54–56.

Type species.—*Necronectes vidalianus* A. Milne Edwards, 1881, by original designation.

Included species.—*Necronectes beaumonti* (A. Milne Edwards 1864), as *Cancer*; *N. collinsi* new species; *N. drydeni* Rathbun, 1935; *N. nodosus* Schweitzer et al., 2002b; *N. proavitus* (Rathbun 1918), as *Gatunia*; *N. schafferi* Glaessner, 1928; *N. summus* Collins and Donovan, 1995; *N. tajinensis* Vega et al., 1999; *N. vicksburgensis* (Stenzel 1935), as *Portunites*, = *N. vauhani* Rathbun, 1935 (fide Rathbun 1936); *N. vidalianus*.

Diagnosis.—Carapace wider than long; axial regions generally well developed; protogastric region defined by two circular swellings; mesogastric region broad posteriorly, narrowing anteriorly, well defined by grooves posteriorly and laterally, more poorly defined anteriorly; cardiac region circular, elevated.

Frontal margin with six spines including inner-orbital spine; spines small, blunt-tipped. Anterolateral margin generally longer than posterolateral margin; eight spines on anterolateral margin including outer orbital spine; spines increasing in size posteriorly except for eighth spine which is generally smaller than adjacent spine; spines triangular, with pointed tips; moving posteriorly spines become increasingly curved anteriorly. Posterior border thickly rimmed. First four sternites fused, triangular; sternites five through eight curving posteriorly, decreasing in size posteriorly. Telson triangular; abdominal somites rectangular, wider than long.

Discussion.—*Necronectes* is an extinct, speciose genus within the Portuninae. Numerous species have been referred to it over the years (Glaessner 1929, 1933; De Angeli and Marangon 1992), some of which do not appear to belong within it. Schweitzer et al. (2002) reviewed the genus recently and removed *N. boeckhi* Lőrenthey in Lőrenthey and Beurlen, 1929, from it, placing it within the Cancridae Latreille, 1802. De Angeli and Beschin (1998) placed *N. boeckhi* in a new genus created for it,

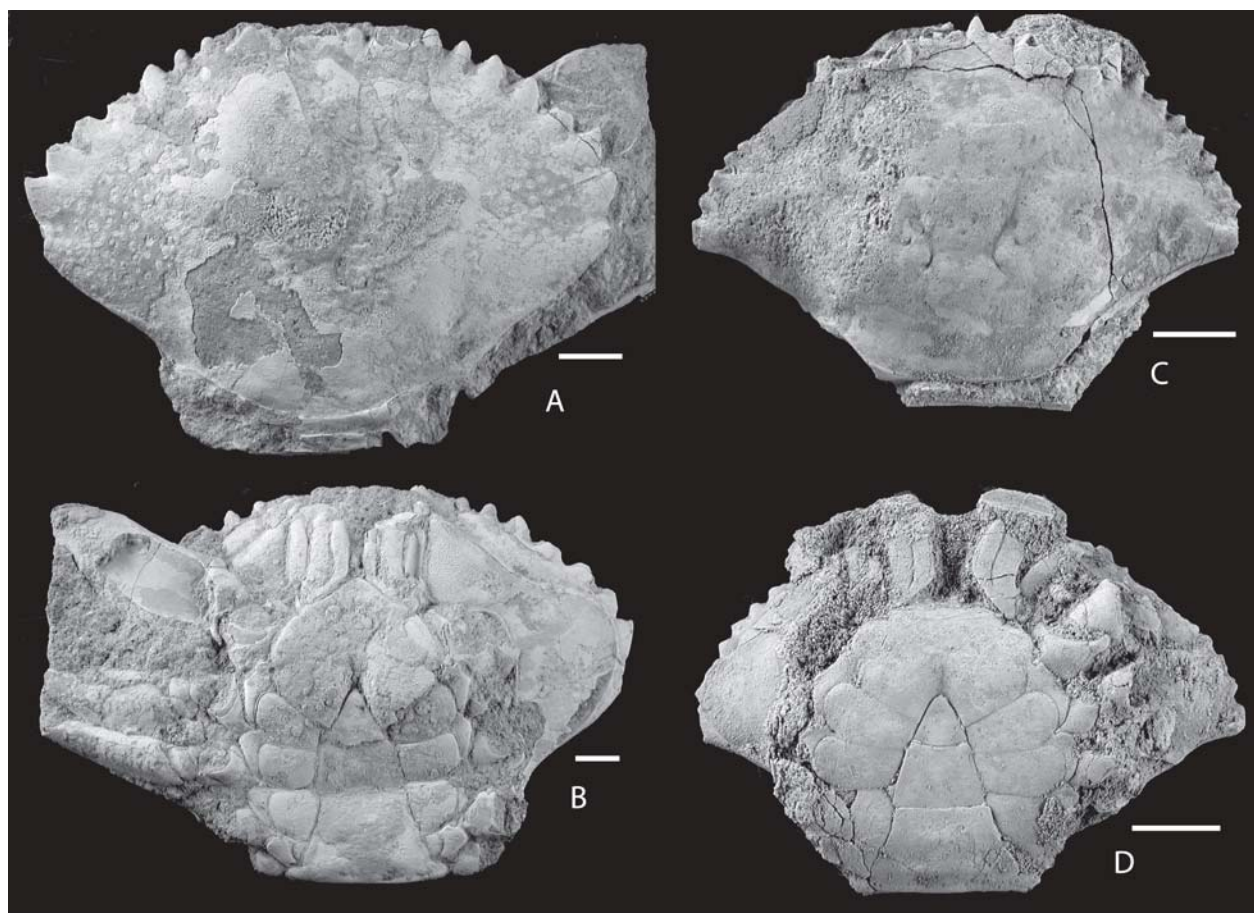


Fig. 5.—Portunidae. **A–B**, *Necronectes collinsi* new species, holotype, USNM 527050, dorsal carapace (A) and male sternum and abdomen (B); **C–D**, *Scylla costata* Rathbun, 1919, USNM 527057, dorsal carapace (C) and male sternum and abdomen (D). Scale bars = 1 cm.

Ceronnectes, which they considered to be a member of the Carcininae MacLeay, 1838, of the Portunidae. We herein place *Ceronnectes* within the Cancridae, closely allied with *Romaleon* Gistel, 1848, and *Anisospinos* Schweitzer and Feldmann, 2000c, based upon the overall carapace shape, paired anterolateral spines, and carapace groove patterns. De Angeli and Marangon (1992) questionably referred *Scylla michelini* to *Necronectes*. That species is represented only by a smooth, fragmentary chela; thus, its generic identity is difficult to ascertain. Herein we leave that species within *Scylla*, which is characterized by large, typically smooth chelae.

Species of *Necronectes* are known from the Oligocene and Miocene of the Tethyan Realm. Oligocene occurrences include *Necronectes nodosus*, *N. summus*, and *N. vicksburgensis*, from Pacific coastal Mexico, the Caribbean, and the North American Gulf Coastal Plain respectively (Rathbun 1935; Collins and Donovan 1995; Schweitzer et al. 2002b). *Necronectes nodosus* was mistakenly reported as Eocene (Schweitzer et al. 2002b); that occurrence is in fact Oligocene in age. The remainder of the occurrences of the genus are Miocene in age, from

Central America, the Caribbean, east coastal North America, and Tethyan Europe. The genus appears to have dispersed via a Tethyan distribution route, apparently from west to east, based upon its first occurrences in North America.

Necronectes collinsi, new species

(Fig. 5A, B)

Types.—Holotype USNM 527050 and paratypes USNM 527051–527055, CM 45820.

Diagnosis.—Carapace wider than long. Frontal margin with six spines including inner-orbital spines. Orbits shallow, with two orbital fissures. Anterolateral margin with eight spines including outer-orbital spine. Weak ridge extending onto carapace from eighth spine; posterolateral reentrants well formed.

Description.—Carapace wider than long, maximum width 1.4 times maximum length; dorsal surface finely granular, more coarsely granular near anterolateral margins; carapace moderately convex transversely, weakly convex longitudinally.

Frontal margin about 25 percent maximum width, with six spines

including inner-orbital spines; spines triangular with rounded tips, separated by shallow grooves. Orbits shallow, each about seven percent maximum width, with two fissures; intra-orbital spine reduced; fronto-orbital width about 40 percent maximum width. Anterolateral margin flared upward, with eight triangular spines including outer-orbital spine; spines increasing in size posteriorly except for eighth spine, which is smaller than seventh; spines one and two with rounded tip and wide base; third spine with wide base, directed slightly anteriorly; fourth through seventh spines increasingly curved, with sharp triangular tip, wide base; eighth spine triangular, more narrow than adjacent spine, curving slightly anteriorly but not as markedly as spines six and seven; posterolateral margin about as long as anterolateral margin; posterior margin with thick, sinuous rim, about 28 percent maximum carapace width.

Carapace regions not well preserved; frontal region slightly depressed; weak ridge extending axially onto carapace from eighth spine; carapace slightly depressed near posterolateral margin toward well-formed posterolateral reentrants.

Male sternum narrow, straight sided; first four sternites fused, slightly elevated above others, triangular; fifth sternite curving anterolaterally, narrowing axially; sternites six through eight directed slightly anterolaterally, remaining wide towards axis, decreasing in size posteriorly; shallow groove extending anteriorly from sterno-abdominal cavity.

Telson of male triangular; situated partially on fourth and partially on fifth sternites; sixth somite rectangular, wider than long; somites three to five fused, forming trapezoid-shaped unit; other somites not well preserved. Exopod, ischium, and merus of third maxilliped present; finely granular ventrally near exopod.

Coxa, basis, and ischium present on right cheliped; coxa and basis small, rounded; ischium robust, longer than wide. Pereiopods 1 and 2 present; coxa, basis, ischium small, rounded; merus longer than wide, extremely convex; coxa of third pereopod small, rounded; fourth not present. Coxa of left cheliped and all four left pereiopods present; all small, rounded.

Measurements.—Measurements (in mm) taken on the dorsal carapace of the holotype (USNM 527050) and sole complete specimen of *Necronectes collinsi*: L = 73.0; W = 103.2; FOW = 42.0; FW = 25.8; PW = 29.0. Paratype CM 45820: L = 79.7; W = 119.8.

Etymology.—The trivial name honors Joe S.H. Collins, London, UK, a preeminent decapod paleontologist who has contributed much to our understanding of Caribbean, European, African, and Asian fossil decapod crustaceans.

Occurrence.—The holotype, USNM 527050, was collected from the lower Miocene of San Sebastián, Puerto Rico. All paratypes were collected from the upper lower Oligocene at Yauco, Puerto Rico (Figs. 1, 2).

Discussion.—*Necronectes collinsi* clearly belongs to *Necronectes* but several differences allow it to be considered a new species. In *Necronectes proavitus*, the orbits are bordered by long inner- and outer-orbital spines; the orbits also exhibit a small, blunt intra-orbital spine (Rathbun 1918). *Necronectes vidalianus* has a sub-orbital and intra-orbital spine on each orbit, and the inner-orbital spines are blunt and poorly formed (A. Milne Edwards 1881). *Necronectes tajinensis* has a small, triangular, intra-orbital spine, and the outer-orbital spine is elongate and slender (Vega et al. 1999). The orbits of *N. drydeni* also have a blunt intra-orbital spine (Rathbun 1935). *Necronectes nodosus* has only one orbital fissure (Schweitzer et al. 2002b). By contrast, the inner- and outer-orbital spines of *N. collinsi* are not long, the orbits contain no sub-orbital spine, and there are two orbital fissures.

There are other distinctive features. *Necronectes dry-*

deni shows less well-formed posterolateral reentrants than *N. collinsi* (Rathbun 1935). Similarly, *N. schafferi* also has less developed reentrants, and the posterior border is more rounded than that of the new species (Glaessner 1928; De Angeli and Marangon 1992). The spines on the frontal margin project further forward in *N. vicksburgensis*, and the anterolateral margin is positioned further anteriorly and is less convex (Stenzel 1935) than in *N. collinsi*. The spines on the anterolateral margin of *N. beaumonti* are wide and blunt tipped, and there appear to only be seven spines (A. Milne Edwards 1864). In addition, the posterolateral reentrants on *N. beaumonti* are not well-developed (A. Milne Edwards 1864); they are quite well developed in *N. collinsi*. All of the spines on *N. vauhani* are much more elongate than those of *N. collinsi* (Rathbun 1935). The anterolateral margin is longer than the posterolateral margin in *N. tajinensis* (Vega et al. 1999), whereas the reverse is true for *N. collinsi*. The carapace of *N. nodosa* has a row of nodes across the branchial region (Schweitzer et al. 2002b), whereas there is no evidence of this on the carapace of *N. collinsi*. It is difficult to make a comparison when considering *N. summus* because only the right and left chela were described (Collins and Donovan 1995).

The occurrences of *Necronectes collinsi* in the lower Oligocene Juana Díaz Formation and the lower Miocene Lares Formation fall within the known age distribution of the genus and make it one of the oldest known species. The early occurrence in the Caribbean also supports the hypothesis that the genus dispersed from west to east in the Tethyan Realm.

Genus *Scylla* de Haan, 1833

Type species.—*Cancer serratus* Forskål, 1775, by subsequent designation (Rathbun 1922).

Included species.—*Scylla costata* Rathbun, 1919 (fossil); *S. olivacea* (Herbst 1796) (Recent); *S. ozawai* Glaessner, 1933 (fossil); *S. paramamosain* Estampador, 1949 (Recent); *S. serrata* (fossil and Recent); *S. tranquebarica* (Fabricius 1798), as *Portunus* (Recent).

Fossil species known only from chelae.—*Scylla floridana* Rathbun, 1935; *S. hassiaca* Ebert, 1887; *S. laevis* Böhm, 1922.

Diagnosis.—Carapace about twice as wide as long, ovate, maximum width just over half the distance posteriorly; regions poorly defined, carapace smooth; front with six spines including inner-orbital spines; orbits directed forward, with two fissures; fronto-orbital width about half maximum carapace width; anterolateral margins with nine spines including outer-orbital spines, last spine longest; gastric grooves strong; chelipeds unequal; carpus with 1–3 spines on lower margin; mani of chelipeds massive, with two distal spines on upper margin, sometimes with very weak keels on outer surface; male abdominal somites 3–5 fused, entire abdomen triangular in shape; sternum rather narrow for family, about as long as wide (after Ng 1998; Apel and Spiridonov 1998).

Discussion.—Apel and Spiridonov (1998) diagnosed *Scylla* as possessing stout, smooth chelae. As mentioned above, some fossil species of *Scylla* that also have pre-

served dorsal carapace material (*S. costata*, *S. ozawai*) have very weak keels on the outer surface of the manus of the major cheliped. In other regards, however, these fossil species referred to the genus fit the diagnosis well, so they are placed there with confidence. The fossil species known only from chelae are all quite fragmentary and until they are described in conjunction with dorsal carapace material, their generic placement cannot be confirmed.

The four extant species of the genus are known only from the Indo-Pacific (Ng 1998). Confirmed fossil species are known from the lower to middle Miocene of Japan (Karasawa 1993); lower Oligocene and lower Miocene rocks of the Caribbean (Rathbun 1919; this paper); Miocene rocks of India (Das-Gupt 1925); and Pliocene, Pleistocene, and subfossil occurrences of the Indo-Pacific and South Africa (Etheridge and McCulloch 1916; Van Straelen 1928; Cooper and Kensley 1991). Withers (1924) reported *Scylla costata* from the upper Oligocene of Anguilla, but that occurrence is based only upon broken chelae; the other unconfirmed reports based solely on chelae are from Europe and the Indo-Pacific (A. Milne-Edwards 1860; Ebert 1887; Böhm 1922) and range in age from Eocene to Miocene. Thus, based upon confirmed occurrences, the genus appeared during the late Oligocene or early Miocene and exhibited a Tethyan distribution early in its history, as evidenced in its occurrences in circum-tropical and equatorial regions during the Miocene. Even if the older chelae were to be confirmed as members of the genus, the distribution pattern would still clearly be a Tethyan one; this genus seems to prefer warm climes. The current range in the Indo-Pacific is a relict of this once broader distribution.

Scylla costata Rathbun, 1919

(Fig. 5C, D)

Scylla costata Rathbun, 1919, p. 170, pl. 4, pl. 5, pl. 6, figs. 3–5.
Withers, 1924, p. 229, pl. 6, figs. 1, 2.

Material examined.—USNM 527057.

Emendation to description.—Front with six spines including inner-orbital spines, inner four appearing to have been more closely spaced to one another than to the inner-orbital spines, about one-quarter maximum carapace width; inner-orbital spines stout, directed forward; orbits broad, circular, directed forward, with two orbital fissures; fronto-orbital width a little over half maximum carapace width. Anterolateral margins with nine spines including outer-orbital spines, last spine largest. Second and third male abdominal somites with transverse keels. Upper distal corner of carpus with distally directed spine, a few blunt spines on outer surface.

Measurements.—Measurements (in mm): carapace length, 37.4; carapace width, >56.3; fronto-orbital width, 30.7; frontal width, 13.1; posterior width, 17.6; length to position of maximum width, 21.4.

Occurrence.—The specimen was collected from the upper lower Oligocene at Yauco, Puerto Rico (Figs. 1, 2).

Discussion.—The specimen conforms in all regards except one to the description and specimens illustrated by Rathbun (1919). Rathbun (1919) described the ninth anterolateral spine as being diminished in size basally, while in the new specimen and in her illustration of the dorsal carapace (pls. 4, fig. 1), that spine is robust. The keels on Rathbun's (1919) specimens seem to be more robust than in the new specimens, but the outer surface of the manus in the new specimen appears to have been weathered. The front and orbits were not visible in the original material; thus, the new material permits that portion of the carapace to be described as well as some details of the carpus and male abdomen.

Subfamily Podophthalminae Dana, 1851

Included genera.—*Euphyllax* Stimpson, 1860 (Recent and fossil); *Podophthalmus* Lamarck, 1801 (Recent and fossil); *Psygmophthalmus* new genus (fossil only); *Sandomingia* Rathbun, 1919 (fossil only); *Saratunus* Collins, Lee, and Noad, 2003 (fossil only).

Diagnosis.—Carapace much broader than long, widest about one-quarter to one-half the distance posteriorly on carapace; front extremely narrow at base and broadening distally to form a "T-shape;" orbits extremely broad, occupying about 80 percent to nearly entire anterior margin of carapace, entire or with fissures or notches; eyestalks very long, sometimes wider than carapace; anterolateral margin with two to five spines including outer-orbital spine; carapace often with transverse ridges on protogastric and branchial regions; "antennules not completely retractile in fossae beneath front" (Davie 2002, p. 456); basal article of antennae short and flagellum slender and long; chelipeds very long, merus, carpus, and manus with spines, manus sometimes with keels; fifth pereopod with paddle-like dactylus; gonopod 1 of male with subterminal spines (modified after Ng 1998; Apel and Spiridonov 1998; Davie 2002).

Discussion.—*Saratunus* Collins et al. (2003) was originally referred to the Portunidae, subfamily uncertain. The very long, beaded orbits; fronto-orbital width occupying about 80 percent of the maximum carapace width; transverse ridges on the hepatic and branchial regions; and short anterolateral margin with spines all suggest placement in the Podophthalminae. The front is not well preserved in the sole species of the genus, but appears to be narrow anteriorly and to widen distally (Collins et al. 2003, pl. 5, fig. 4). Thus, placement into the subfamily is done with relative confidence.

Rathbun (1919) erected the new genus *Sandomingia* and placed it with the fiddler crabs; however, she did note the similarity in form with *Podophthalmus* and *Euphyllax*. Later workers maintained her placement (Glaessner 1969; Schweitzer et al. 2002b). Herein, we move *Sandomingia* to the Podophthalminae based upon the clear similarities of the dorsal carapace with species of *Podophthalmus*, including extremely long orbits, short anterolateral margins; convex anterior margin of the carapace, and transverse dorsal carapace ridge.

The Podophthalminae does not have a lengthy fossil record, occurrences being limited to the upper Paleogene and Neogene, where individual taxa may be quite com-

mon. *Euphyllax* is known from fragmentary Oligocene occurrences and robust Miocene and later occurrences, whereas *Podophthalmus* is known only from the Pliocene and Pleistocene of the Indo-Pacific (Schweitzer et al. 2002a). *Psygmophthalmus* new genus is reported herein from lower Miocene rocks of Puerto Rico, and *Sandomingia* is reported as being “probably lower Miocene” (Rathbun 1919, p. 180). *Saratunus* is known only from middle to upper Miocene deposits of Sarawak in the Indo-Pacific (Collins et al. 2003). The limited and relatively recent occurrences in the fossil record may be due to the apparently very specialized orbits and eyestalks of the subfamily, which appear to have evolved rather late within the Portunidae. Many of the other portunid subfamilies appeared in the Eocene or earlier, including the Portuninae, Polybiinae Ortmann, 1893, and Psammocarcininae Beurlen, 1930 (Glaessner 1969; Feldmann et al. 1995).

Genus *Euphyllax* Stimpson, 1860

Type species.—*Euphyllax dovii* Stimpson, 1860, by original designation.

Included species.—*Euphyllax callinectias* Rathbun, 1918; *E. dominicensis* (Rathbun 1919) new combination, as *Podophthalmus*; *E. dovii* (extant only); *E. fortis* Rathbun, 1918; *E. fortispinosus* Collins et al., 2001; *E. robustus* A. Milne Edwards, 1874 (extant only); *E. septendentatus* Beurlen, 1958; *Euphyllax* sp. in Idris, 1989; *Euphyllax* sp. in Karasawa and Fudouji, 2000. All are extinct unless otherwise noted.

Diagnosis.—Carapace hexagonal, wider than long, length about two-thirds maximum width, widest about half the distance posteriorly; front *T*-shaped, often with sharp central spine; fronto-orbital width about 80 percent maximum carapace width; orbit with granular rim, sometimes with two closed fissures positioned near distal end, sometimes with concave reentrant near outer-orbital angle to embrace eye; anterolateral margin usually with three to five spines including outer-orbital spine; transverse ridge extending from last anterolateral spine axially on dorsal carapace; transverse ridges often on protogastric and hepatic regions.

Discussion.—Nyborg et al. (2003) recently provided an overview of the genus. Karasawa and Kato (2003) included *Ommatocarcinus zariquieyi* Vía, 1959, in *Euphyllax*. However, that species belongs neither in *Ommatocarcinus* White, 1852, nor *Euphyllax* based upon examination of the holotype (MGSB 20.097) which exhibits a narrow carapace, continuous transverse carapace ridges, lack of a *T*-shaped front, and unusual anterior margins. Work on that species is ongoing by one of us (CS) and others (P. Artal and B. van Bakel, pers. comm.).

Rathbun (1919) erected the new species *Podophthalmus domingensis*. That species is herein moved to *Euphyllax* due to its possession of broad orbits that do not occupy the maximum carapace width, numerous anterolateral spines, and multiple dorsal carapace ridges (Rathbun 1919, pl. 2, figs. 7, 8), all characteristic of *Euphyllax* and not *Podophthalmus*.

Nyborg et al. (2003) described *E. feldmanni*, a new

species of *Euphyllax* from the Eocene Hoko River Formation of Washington, USA. That species is not a member of the genus or the subfamily for several reasons. Members of *Euphyllax* and the Podophthalminae possess a very distinctive front that is extremely narrow proximally and that widens distally into an elongate, narrow element, making the entire front “*T*-shaped.” The tip of the front may be ornamented with a tiny spine. The antennules are folded horizontally beneath this *T*-shaped front, and the bases of the eyestalks are placed just alongside the narrow proximal element of it (Rathbun 1930, p. 143, pls. 65-67). These are important morphological features that control the mobility of the antennules and eyestalks and that provide a very distinctive, constrained subfamilial and generic definition. *Euphyllax feldmanni* possesses a much broader front that is not “*T*-shaped.” The front in that species is concave proximally, widens slightly distally, and narrows again at the distalmost end to form a sharp tip (Nyborg et al. 2003, figs. 2.1, 2.3). In addition, the orbital margin of *E. feldmanni* is concave and sinuous, while in most species of *Euphyllax* and the Podophthalminae, it is nearly straight along most of its length. Species of *Euphyllax* have a single orbital fissure near the outer-orbital spine; the orbits of *E. feldmanni* are described as having two fissures, neither of which are visible in the illustrations (Nyborg et al. 2003, figs. 2, 3). The chelae of *E. feldmanni* have mani with smooth outer surfaces; those of other *Euphyllax* and the Podophthalminae have sharp spines and often have sharp, marked keels on the outer surfaces. Thus, *E. feldmanni* is neither a member of the genus nor of the subfamily. We herein place *E. feldmanni* in a different genus in another portunid subfamily, as discussed below.

Euphyllax was much more speciose during the past; only two extant species, which Rathbun (1930) supposed might be conspecific, are known. Confirmed members of the genus are known primarily from the Miocene, when the genus was apparently most speciose, of the Caribbean and Central America (Nyborg et al. 2003). One Miocene occurrence is known from the Indo-Pacific (Idris 1989). The only Oligocene occurrence is a poorly preserved specimen referred to *Euphyllax* sp. from Japan (Karasawa and Fudouji 2000). Interestingly, the only occurrences outside of North and Central America are so poorly preserved that they were not referred to a species (Idris 1989; Karasawa and Fudouji 2000), suggesting that collection of better material may preclude placement of these taxa in *Euphyllax*. All of the extant occurrences are along the Pacific coastal Americas. Considering all of the taxa now referred to the genus, it appears that the genus evolved in the western Pacific and dispersed eastward to the Americas. If the western Pacific occurrences were to be excluded, the genus would have a solely American distribution throughout its geologic range.

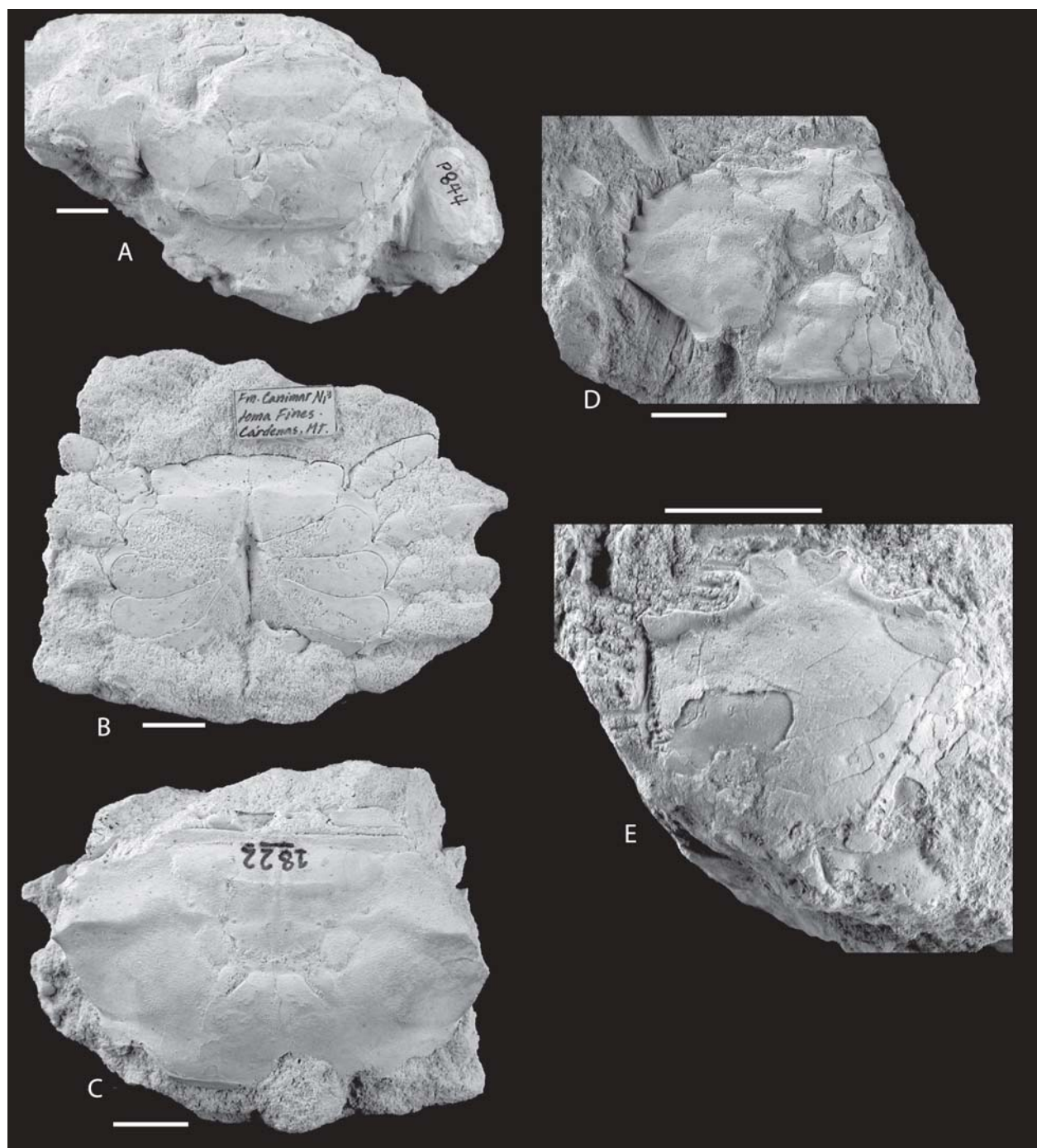


Fig. 6.—Portunidae and Brachyura. **A**, *Euphylax domingensis* (Rathbun 1919), MNHCu-P844, dorsal carapace; **B–C**, *Euphylax domingensis* (Rathbun 1919), MNHCu-P1822, male sternum and abdomen (**B**) and dorsal carapace (**C**); **D**, *Psymphthalmus lares*, new genus and species, USNM 527076, dorsal carapace; **E**, Brachyura (family, genus, and species indeterminate), USNM 527073, partial dorsal carapace. Scale bars = 1 cm.

Euphylax domingensis (Rathbun, 1919),
new combination

(Fig. 6A–C)

Material examined.—Specimens MNHCu-P844 and P1822.

Diagnosis.—Carapace trapezoidal, wider than long. Front *T*-shaped, ending in a reduced medial spine. Orbits wide, directed forward. Eyestalks long, possessing an outer surface with small, triangular spines. Anterolateral margin shorter than posterolateral margin, bearing two small and one well-developed spine. Carapace regions well defined. Protogastric region transversely oval and inflated, with trans-

verse ridge; mesogastric region narrow, widening distally; cardiac region elevated, widening distally.

Emendation to description.—Carapace trapezoidal, weakly vaulted transversely, more so longitudinally, wider than long, length about 60 percent maximum width, widest about 43 percent the distance posteriorly; carapace regions well defined. Front narrow, projected beyond orbits, base about 3 percent maximum width; *T*-shaped, ending in a reduced medial spine. Orbits wide, each about 41 percent maximum width, directed forward, shallow, weakly rimmed; fronto-orbital width about 85 percent maximum width. Eyestalks long, convex, with rounded tip, outer margin with small, triangular teeth.

Anterolateral margin short, bearing two small spines, one well-developed spine, and a probable outer-orbital spine that has been broken; spine one and two similar in size, closely spaced, separated by shallow, *U*-shaped indentation; third spine larger, not as closely spaced to second spine as spines one and two are to one another; margin weakly convex. Posterolateral margin slightly more than twice as long as anterolateral margin; concave, well-defined posterolateral reentrants; ridge parallel to posterior margin; posterior width about 40 percent maximum width.

Carapace regions well defined; protogastric region transversely oval and inflated, well-defined transverse ridge parallel to posterior margin of protogastric region; hepatic region relatively flat and undifferentiated; mesogastric region narrow anteriorly, widening distally, defined by shallow grooves along lateral and posterior margins, bounded by small, rounded, elevated epibranchial swellings posteriorly; cardiac region elevated, widening distally, well-defined by deep grooves at lateral margins, defined by shallow groove anteriorly; branchial region weakly inflated centrally, sloping to concave posterolateral margin; epibranchial ridge extending from mesogastric region, curving to anterolateral margin, extending beyond margin as well developed third spine; intestinal region long.

Male sternum broad, transversely rectangular; second sternite depressed; sternite 3 more elevated; sternite 4 narrow axially, broadening while curving toward anterior, longest of fused sternites with rounded ends; groove between sternites 2 and 3; fourth sternite elevated above others, with central transverse ridge; sternites 1–4 fused, transversely rectangular; sternites 5–8 narrowing axially, widening distally while curving anterolaterally; sternite 5 directed anterolaterally; sternite 6 directed laterally; sternite 7 directed posterolaterally; sternites 5–7 progressively increasing in size; eighth sternite smallest.

Abdomen unknown.

Pereiopods not well preserved; coxa, basis, and ischium present; coxa quadrate, basis triangular, ischium subquadrate; all small and convex.

Occurrence.—Specimens were collected from the upper upper Miocene at Loma Fines (MNHN Cu-P1822) and at Guanábana (MNHN Cu-P844), Cuba (Figs. 1, 2).

Discussion.—The specimens under consideration closely resemble *Euphyllax domingensis*, which is known from the same region, and are therefore referred to that species. As a result of poor preservation, there are two superficial differences that suggest that these specimens are not referable to *E. domingensis*. One is the lack of granules on the carapace, which are present in *E. domingensis*, but which are present as ridges in the new specimens. The other is the absence of an outer-orbital spine in the new specimens, which is present in the type material of *E. domingensis*. Upon close examination of the new specimens, it is probable that the outer layers of the cuticle have been lost, which would account for the missing granules. Cuticle loss often leads to loss of ornamentation and other fine detail of the dorsal carapace of decapods (Feldmann and Gaździcki 1998). The area where the outer orbital spines were

located has been broken on the new specimens, although it is most likely that they were present. The protogastric ridge, epibranchial ridge, wide orbits, *T*-shaped front, and number of anterolateral spines constitute the similarities between these specimens and *E. domingensis*; thus, we are confident in the specific placement.

A few characteristics allow this species to be distinguished from all other *Euphyllax* species. First are the regions of the carapace. The gastric region on *E. dovii* (illustrations in Rathbun 1930) is much less distinct than that of *E. domingensis*. *Euphyllax callinectias* has a well-defined transverse protogastric ridge, much more striking than the ridge on *E. domingensis*. The roundness and steepness of the margins also sets *E. callinectias* apart from *E. domingensis*. Next is the absence of orbital fissures on *E. domingensis*; there are small orbital fissures present on *E. dovii* and *E. septendentatus* (Rathbun 1930; Beurlen 1958). Lastly is the shape and number of spines present on the anterolateral margin. The spines of *E. robustus* are more prominent than those of *E. domingensis*, and *E. fortispinosus* has slender and elongate spines (Collins et al. 2001), unlike those of *E. domingensis*, which are reduced. *Euphyllax septendentatus* has seven spines on the anterolateral margin, whereas there are only three present on *E. domingensis*.

An accurate comparison of *E. domingensis* to *Euphyllax fortis* cannot be made due to the absence of the carapace in the latter species (Rathbun 1918). It is also difficult to make a direct comparison with *Euphyllax* sp. in Karasawa and Fudouji and *Euphyllax* sp. in Idris due to the poor preservation of the specimens. It can, however, be noted that there is evidence of only one anterolateral spine on *Euphyllax* sp. in Karasawa and that the carapace shape of *Euphyllax* sp. in Idris is more ovate than that of *E. domingensis*. Thus, we are confident that the new specimens may be placed within *E. domingensis*. The collection of more complete material than was available to Rathbun (1919) permits a more detailed description of the species.

Psygmophthalmus, new genus

Type species.—*Psygmophthalmus lares* new species, by monotypy.

Diagnosis.—As for species.

Description.—As for species.

Etymology.—The genus name is derived from the Greek words *psygma*, meaning fan, and *ophthalmos*, meaning eye, referring to the fan-shaped, or crenulated, front and to the long orbits in this taxon. The gender is masculine.

Discussion.—The new genus is clearly referable to the Podophthalminae based upon its *T*-shaped front, broad orbits, wider than long carapace, spined anterolateral margins, and overall portunoid countenance. However, the crenulated *T*-shaped front, two open orbital notches, and lack of straight, well-developed transverse carapace ridges

distinguish it from the other genera within the subfamily. *Psygmophthalmus* is much more similar to *Euphylax* than to *Podophthalmus*, but the two genera are readily distinguished based on the features just mentioned. In addition, the front on *Euphylax* is much narrower proximally, occupying about three percent of the maximum carapace width, than on *Psygmophthalmus*, in which it occupies about ten percent of the maximum carapace width. The anterolateral spines of *Saratunus* are much longer and better developed than in *Psygmophthalmus*, and *Psygmophthalmus* lacks the transverse ridges on the hepatic and branchial regions characteristic of *Saratunus*.

The only other genera with which *Psygmophthalmus* might be confused are *Ommatocarcinus* White, 1852 and *Icriocarcinus* Bishop, 1988, of the Goneplacidae MacLeay, 1838. Both of those genera have extremely broad orbits as in *Psygmophthalmus*; however, they each achieve their maximum width very close to the anterior margin of the carapace and lack a defined anterolateral margin. Those two genera are, however, very similar in dorsal carapace morphology to *Podophthalmus*. Those similarities are still in need of investigation, which is beyond the scope of this paper.

Psygmophthalmus new genus is one of the oldest known members of the Podophthalminae; only a few occurrences of *Euphylax* are older.

Psygmophthalmus lares, new species

(Fig. 6D)

Type.—Holotype USNM 527076.

Diagnosis.—Carapace hexagonal, length about 60 percent maximum width, widest slightly more than half the distance posteriorly; front narrow proximally, proximal portion about 10 percent maximum carapace width, broadening distally into crenulated T-shape, with central projection and lateral projections on either side; fronto-orbital width about 80 percent maximum carapace width; orbits with two notches; anterolateral margin with five spines including outer-orbital spine; epibranchial ridge arcuate.

Description.—Carapace hexagonal, wider than long, length about 60 percent maximum width, widest a little over half the distance posteriorly; regions moderately defined; weakly vaulted longitudinally and transversely.

Front narrow proximally, about 10 percent maximum carapace width, broadening distally to form a "T-shape;" axially sulcate, with broad central, down-turned spine; a broad projection on either side of axial spine; surface of front ridged at position of flanking spines such that entire front appears crenulated.

Fronto-orbital width about 80 percent maximum carapace width, occupying entire anterior margin of carapace. Orbits broad, each about 42 percent maximum carapace width; upper margin sinuous, with thickened rim axially; two small orbital notches, one positioned at not quite half the distance distally from inner-orbital angle, second positioned about two-thirds the distance distally from inner-orbital angle; outer-orbital spine small, sharp, triangular, directed forward.

Anterolateral margin short, with four spines excluding outer-orbital spine; first smallest, triangular, directed forward; second larger, triangular, directed anterolaterally; third smaller than second but larger than first, triangular, directed anterolaterally; fourth about as large as second, more

attenuated than others, directed laterally. Posterolateral margin much longer than anterolateral margin, entire, initially weakly ridged. Posterior margin nearly straight, rimmed.

Protogastric regions broadly ovate, weakly inflated; urogastric region depressed below level of cardiac region; cardiac region with two broad swellings anteriorly; hepatic regions depressed below level of protogastric regions; epibranchial ridge arcing anteriorly, terminating along mesogastric region; branchial region with broad central swelling.

Base of eyestalk robust.

Remainder of carapace, venter, and appendages unknown or crushed.

Measurements.—Measurements (in mm) taken on the dorsal carapace: maximum carapace width, 62.0; maximum carapace length, 35.7; fronto-orbital width, 50.8; frontal width (at base), 5.9; posterior width, 22.5; orbital width, 25.1; length to position of maximum width, 33.2.

Etymology.—The trivial name is derived from the Lares Formation, from which the holotype and sole specimen was collected.

Occurrence.—USNM 527076 was collected from the lower Miocene at San Sebastián, Puerto Rico (Figs. 1, 2).

Discussion.—Only a single partial specimen is known; however, the front and anterolateral margins are very well preserved. The chelae appear to have been quite long, as is typical for members of the family.

Subfamily Polybiinae Ortmann, 1893 *sensu lato*

Included fossil genera.—*Falsiportunites* Collins and Jakobsen, 2003; *Liocarcinus* Stimpson, 1871; *Maeandricampus* Schweitzer and Feldmann, 2002; *Megokkos* Schweitzer and Feldmann, 2000b; *Minohellenus* Karasawa, 1990; *Ovalipes* Rathbun, 1898; *Parathranites* Miers, 1886; *Portunites* Bell, 1858; *Proterocarcinus* Feldmann et al., 1995.

Diagnosis.—Carapace moderately broad; fronto-orbital width usually from about half to three-quarters maximum carapace width; orbits usually moderate sized, often with two fissures; front spined, number and size of spines variable; anterolateral margins with three to five spines including outer-orbital spine; epibranchial ridge arcuate, extending from last anterolateral spine to axial regions; usually with longitudinal branchial ridges parallel to axis; some pereopods as long as chelipeds; dactylus of fifth pereopod paddle-like (after Glaessner 1969; Davie 2002).

Discussion.—As discussed above, *Euphylax feldmanni* cannot be accommodated within *Euphylax* or the Podophthalminae. It is thus placed within the Polybiinae, and as discussed below, *E. feldmanni* is herein referred to *Megokkos*. The only subfamily to which *Megokkos* may be referred is the Polybiinae. Members of the Caphyrinae Paulson, 1875, and the Carcininae MacLeay, 1838, are not much broader than long; have small, semi-circular orbits; and have four or five anterolateral spines. In addition, the Carcininae lack a paddle-like dactylus of the fifth pereopod. The Carupinae Paulson, 1875, usually lack a paddle-like dactylus of the fifth pereopod and usually have small, semi-circular orbits. Members of the Portuninae have a long anterolateral margin with 4–9 spines, usually have from 4–6 frontal spines, and possess small orbits. The Thalamininae Paulson, 1875, have a very broad front, small orbits placed on the anterior corners of the carapace,

and 4 to 7 anterolateral spines. The extinct Psammocarininae have extremely elongated last anterolateral spines. The Podophthalminae have extremely elongated orbits and eyestalks and a “T-shaped” front.

A problem with referral of *Megokkos* to the Polybiinae is that extant genera within the group are typified by carapaces that are moderately wider than long and that have relatively small orbits and well-formed anterolateral spines. *Megokkos* has a much broader than long carapace, broad orbits, and small anterolateral spines. Other fossil genera with features similar to that of *Megokkos* are also placed within the Polybiinae, including *Minohellenus* and *Proterocarcinus*. When these genera are taken together with other fossil genera (*Portunites* and *Maeandricampus*) and representative extant genera, such as *Ovalipes*, *Liocarcinus*, and *Parathranites*, each of which also have fossil records (Jenkins 1972; Müller 1984; Karasawa 1993, respectively), it is clear that this is a heterogeneous group united by a “typical” portunoid carapace (eliminating the Caphyrinae and Carupinae, often described as “aberrant” portunids) that is not as elongate as in some subfamilies (Portuninae and Thalamitinae) and that possess paddle-like fifth pereopods (eliminating Carcininae) and that lack a very long last anterolateral spine (eliminating Psammocarcininae). Clearly, more work needs to be done on this subfamily, which is beyond the scope of this paper. It is probable that the Polybiinae as currently understood is polyphyletic, as already suggested by von Sternberg and Cumberlidge (2001) and H. Karasawa (pers. comm.).

Genus *Megokkos* Schweitzer and Feldmann, 2000b

Included species.—*M. alaskensis* (Rathbun 1926), as *Portunites*; *M. feldmanni* (Nyborg et al. 2003), as *Euphyllax*; *M. hexagonalis* (Nagao 1932), as *Portunites*; *M. macrospinus* (Schweitzer et al. 2000), as *Portunites*.

Emended diagnosis.—Carapace wider than long, hexagonal, length about 65 percent maximum width; regions moderately defined by shallow grooves; front broad, nearly straight, with central, triangular, blunt protuberance or four blunt protuberances; orbits very wide; fronto-orbital width two-thirds to three-quarters maximum carapace width but may reach 90 percent maximum carapace width; orbits very wide, deep, sometimes with small intraorbital spine and notch, two orbital fissures or notches (one of which is notch adjacent to intraorbital spine if present); anterolateral margin short, with three or four spines excluding outer-orbital spine, last spine usually longest; protogastric and hepatic regions with transverse ridges; epibranchial region arcuate; branchial regions weakly inflated; posterolateral reentrant large, well-developed; chelipeds heterochelous, stout; fingers with large, blunt denticles on occlusal surface; dactyl of fifth pereopod paddle-like (after Schweitzer and Feldmann 2000b).

Discussion.—Both *Euphyllax feldmanni* and species of *Megokkos* exhibit paddle-like fifth pereopods; broad, ovate, typically portunoid sterna; carapace length about two-thirds the maximum width; broad orbits with two indistinct orbital fissures; a nearly straight front with small protuberance(s); an arcuate epibranchial swelling;

a transverse ridge on the hepatic region; a ridge on the branchial region parallel to the axial regions; well-developed posterolateral reentrants; and heterochelous, stout chelae with large blunt denticles on the occlusal surface of the fingers (Schweitzer and Feldmann 2000b; Nyborg et al. 2003). This strongly suggests that *E. feldmanni* should be referred to *Megokkos*.

Some aspects of *E. feldmanni* differ from other species of *Megokkos*. The fronto-orbital width ratio in *E. feldmanni* is higher, about 90 percent, than in typical *Megokkos*, in which it is about 75 percent. The fronts of other *Megokkos* have four very small, blunt protuberances, while *E. feldmanni* has a single, blunt, central frontal protuberance. This same range of variation in frontal ornamentation is seen in other brachyuran families, such as the Carpiliidae Ortmann, 1893. The anterolateral spines of *E. feldmanni* are certainly smaller than in other *Megokkos*, but there is significant range of variation in spine size even among individuals within a species of *Megokkos* (Schweitzer and Feldmann 2000b). The development of the carapace ridges is more subdued in *E. feldmanni* than in other species of *Megokkos*. However, the size of the anterolateral spines, the development of carapace ridges, and the nature of the spines on the frontal margin were in fact all cited as means of differentiating species within the genus. The only drawback to referral of *E. feldmanni* to *Megokkos* is the fronto-orbital width to maximum width ratio. We do not believe that this one difference warrants the creation of a new genus; thus, *E. feldmanni* is herein placed within *Megokkos*.

Species of *Megokkos* are only known from Eocene and Oligocene rocks of the North Pacific Ocean. *Megokkos macrospinus* is the oldest known member of the genus, from the middle to upper Eocene of Washington (Schweitzer et al. 2000). Late Eocene species include *M. feldmanni* and *M. hexagonalis* from Washington, USA, and Japan, respectively (Nagao 1932; Nyborg et al. 2003). *Megokkos alaskensis* is known from Oligocene rocks of Alaska, Washington, and Oregon, USA, and British Columbia, Canada (Rathbun 1926; Tucker and Feldmann 1990; Schweitzer and Feldmann 2000b; Schweitzer et al. 2003). The genus exhibited a North Pacific distribution (Schweitzer 2001).

Megokkos feldmanni (Nyborg, Berglund, and Goedert 2003), **new combination**

Euphyllax feldmanni Nyborg, Berglund, and Goedert, 2003, p. 325, figs. 2, 3.

Emendation to diagnosis.—Front broad, nearly straight, with central, triangular, blunt protuberance. (Remainder of diagnosis as in Nyborg et al. 2003).

Emendation to description.—Front broad, nearly straight, with central, triangular, blunt protuberance. (Remainder of description as in Nyborg et al. 2003.)

Discussion.—*Megokkos feldmanni* has previously been well described and documented (Nyborg et al. 2003); only a few remarks need be added here. It is interesting to note that the species bears certain superficial resemblances to species of the goneplacid genus *Orbitoplax* Tucker and Feldmann, 1990, which were briefly acknowledged previously (Nyborg et al. 2003). Species of that genus have a hexagonal carapace, broad orbits, a nearly straight front, two orbital fissures, weakly developed anterolateral spines, and well-developed posterolateral reentrants, all present in *M. feldmanni*. Most interestingly, all species of *Orbitoplax* have well-preserved eyestalks, as does *M. feldmanni*, and Schweitzer (2000) suggested that this feature might be a generic level character for *Orbitoplax*. The many similarities between *Orbitoplax* and *M. feldmanni* suggest that further research into a possible relationship between *Megokkos* and *Orbitoplax* is warranted.

Brachyura Incertae Sedis
Family, Genus, and Species Indeterminate

(Fig. 6E)

Material examined.—USNM 527073.

Description.—Carapace appearing to have had poorly defined regions, weakly vaulted longitudinally and transversely.

Front axially notched, with six lobes; middle four on same plane, about equal to one another in size, triangular; outer lobes, which are inner-orbital spines, are situated slightly posterior to inner four, directed anterolaterally; front about 37 percent fronto-orbital width. Orbits very wide, each orbit about 31 percent fronto-orbital width; deeply excavated and smoothly convex axially, with blunt projection just axial to outer-orbital angle; outer-orbital angle projected into spine, directed laterally; orbital rim flared vertically; fronto-orbital width occupying entire width of carapace.

Measurements.—Measurements (in mm): fronto-orbital width, 22.6; frontal width, 8.3; orbital width, 7.1.

Occurrence.—The sole specimen was collected from the lower Miocene at San Sebastián, Puerto Rico (Figs. 1, 2).

Discussion.—The material is fragmentary and therefore cannot be referred to a taxon, although it may be a broken specimen of *Psymphthalmus lares*. The front and orbits are very well preserved, however, so we illustrate it here in the hope that more material will be found in the future, enabling a more complete identification.

DISCUSSION

Paleogeography.—The Caribbean realm was very active tectonically during the Late Cenozoic (Mann et al. 1990; Iturralde-Vinent and MacPhee 1999), and this is reflected in the paleogeographic evolution of the area, as illustrated in Fig. 7. At about the Eocene-Oligocene transition, there was a general uplift in the Caribbean realm and surrounding continental margins, but beginning in the latter half of

the early Oligocene, a general inundation took place, and many previously exposed areas were transgressed by shallow marine waters (Iturralde-Vinent and MacPhee 1999). As a consequence, the amount of land drastically reduced, and the marine environments were widely interconnected by both deep- and shallow-water channels (Fig. 7A). Within the continental margin areas surrounding the Caribbean, as well as within the shallow banks and island shelf areas, sea grass muddy plains, calcareous detrital and coralline environments, and siliciclastic ramps and deltas developed, which mutually intermingled in time and space (Iturralde-Vinent and MacPhee 1999). Some of these environments are exemplified by the stratigraphy of the paleontological sites described above (fig. 2 and columnar section in appendix 1 of Iturralde-Vinent and MacPhee 1999).

During the late early to late Miocene, with a spike in the middle Miocene, extensive carbonate platforms are recognized; thus, Caribbean coralline communities were widespread and increasing in areal development, probably due to a general warming process and the input of nutrients from the Central Atlantic. Likewise, surrounding emerged land areas and shallow sea grass plains developed, and extensive marginal lagoon environments are recorded in the stratigraphic sections (fig. 2 and columnar section in appendix 1 of Iturralde-Vinent and MacPhee 1999). After the middle Miocene, tectonic uplift dominated in almost every topographic high within the Caribbean area, a process that produced an increase of land areas and ultimately the present-day Caribbean islands (Iturralde-Vinent and MacPhee 1999; Iturralde-Vinent 2001).

During the Oligocene and Miocene, Atlantic, Caribbean and Pacific waters were united, and the Circum-Tropical Marine Current generally drifted westward (Fig. 7; Berggren and Hollister 1974; Droxell et al. 1998; Iturralde-Vinent 2003). This scenario lasted until the Pliocene, when the Isthmus of Panama progressively uplifted (Coates and Obando 1996), and eventually emerged as a barrier since the early Pleistocene (Beu 2001). As a result, since the Pliocene, and perhaps as early as the Miocene (Bice et al. 2000), the Atlantic-Caribbean and Pacific marine biotas were poorly connected only during sea level highs, but since the early Pleistocene have been completely separated (Beu 2001).

Paleobiogeography.—This late Cenozoic paleogeographic evolution (Fig. 7) provides the scenario for the dispersal and evolution of the Caribbean portunids and other decapods. Nearly all of the decapods reported herein from the Caribbean displayed a Tethyan distribution pattern during their history. In addition, nearly all required an open Caribbean Seaway for dispersal between the Atlantic and Pacific oceans. *Neocallichirus* and *Necronectes* have already been described as having a Tethyan distribution (Schweitzer and Feldmann 2002; Schweitzer et al. 2002b; Schweitzer et al. 2004), originating and dispersing throughout the Tethyan region, and the Caribbean occurrences described herein only confirm that pattern. Based

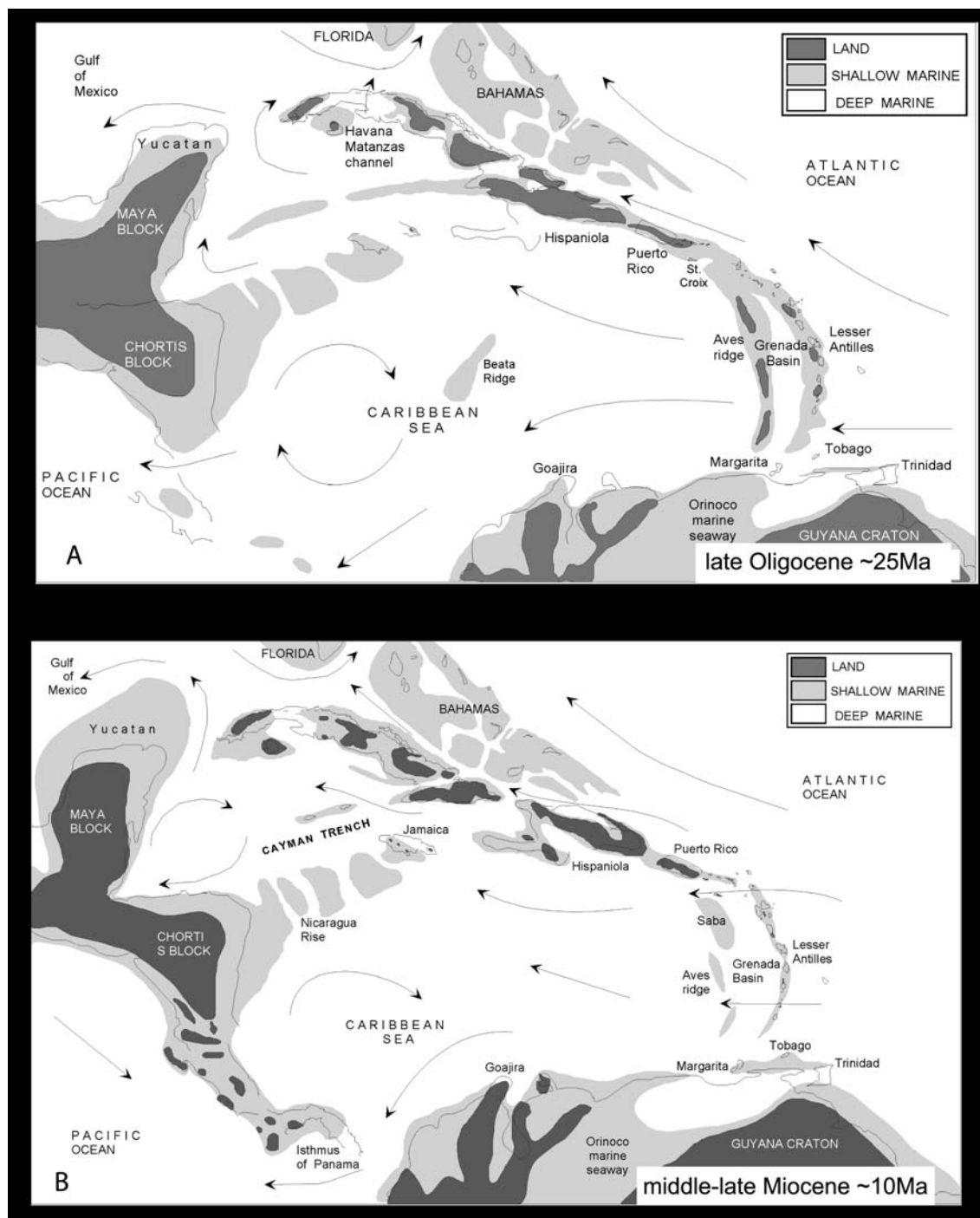


Fig. 7.—Late Oligocene (A) and middle-late Miocene (B) paleogeographic maps of the Caribbean. Arrows are hypothetical direction of surface marine currents. Adapted and updated from Iturralde-Vinent and MacPhee (1999).

upon the occurrences of *Portunus* spp. beginning in the Eocene, the genus appears to have originated in the Tethyan Realm and displayed a Tethyan distribution throughout the Cenozoic (Schweitzer et al. 2002b), and is today cosmopolitan in warm and temperate oceans

(Glaessner 1969). *Scylla* originally displayed a Tethyan distribution early in its history (Miocene), with some species reaching southern Africa by the Pleistocene (Cooper and Kensley 1991), and it now exhibits a relict Tethyan, Indo-Pacific distribution.

Because the Podophthalminae is a small subfamily (only five included genera), we have chosen to examine its paleobiogeography at the subfamily level as well as that of one of the included genera, *Euphylax*. *Euphylax* apparently originated in the North Pacific (Japan), not uncommon in the Cenozoic (Schweitzer 2001), and subsequently dispersed to the eastern Pacific and other Indo-Pacific localities. The subfamily as a whole displays a similar pattern; it appears to have originated in the North Pacific and subsequently dispersed to other Indo-Pacific locations and the Caribbean, probably following North Pacific currents or continental shelves. The group would have reached the Caribbean via the open Central American Seaway (Bice et al. 2000).

Calappa spp. displayed a broad geographic distribution in the fossil record. *Calappa* appears to have originated in the high southern latitudes during the Eocene (Feldmann and Wilson 1988), with subsequent dispersal to the Central Americas and Northern Hemisphere. It displays a cosmopolitan distribution in tropical modern oceans (Schweitzer and Feldmann 2000a).

Paleoecology.—From an ecological standpoint, extant members of the fossil genera represented herein from Cuba, the Dominican Republic, and Puerto Rico are largely typical of areas with substrates composed of clastic sediments, either siliciclastic or carbonate, although most are known from a broad range of habitats; all are typical of tropical and subtropical areas (Rathbun 1930; T. Sakai 1976; Williams 1984; Ng 1998). Most members of the Callianassidae are burrowers, constructing lengthy domicile galleries in nearshore or intertidal sediments (Manning and Felder 1991). Extant species of *Portunus* inhabit a broad range of environments, including clastic bottoms, mangroves, coral reefs, and pelagic areas in seaweed (Rathbun 1930; Williams 1984; Ng 1998). The clastic deposits in which the species of *Portunus* described herein were collected suggest that they preferred clastic bottoms. Although paleoecological data for extant *Euphylax* spp. are lacking (Rathbun 1930), extant *Podophthalmus*, the only other extant genus within the same subfamily as *Euphylax* and the extinct *Psygmodthalmus* described herein, inhabit clastic, offshore bottoms (T. Sakai 1976; Ng 1998). Extant *Scylla* spp. prefer offshore clastic bottoms or mangroves but may be found in rocky areas and near reefs (T. Sakai 1976; Ng 1998). Similarly, species of *Necronectes* have been described from a variety of sediments, ranging from coarse clastics to carbonates (Schweitzer et al. 2002b). Only extant *Calappa* spp. seem to prefer coral reef habitats, but they may also be found on various clastic substrates (Schweitzer and Feldmann 2000a).

The majority of the fossil decapods described herein are from clastic units. Most of the investigated rock units in this report are clastic in nature; the only exception being the San Sebastián locality, which is a coral-rich limestone (Lares Formation). Not surprisingly, it is from that local-

ity that two of the decapods most likely to be found associated with reefs were found, *Calappa pavimenta* and *Scylla costata*, in addition to a third species, *Psygmodthalmus lares*. The abundance of decapods inhabiting clastic bottoms is also congruent with the paleogeographic scenario described above, with a variety of clastic settings, including sea grass muddy plains, calcareous detrital environments, siliciclastic ramps, deltas, and quiet lagoons, present in the region during the Oligocene and through the late Miocene to the present.

Portunid diversity.—The vast number of portunid taxa known from the Oligocene and Miocene of the Caribbean is notable (Table 2). Not only were the portunids diverse, they also appear to have been one of the most abundant taxa in the fossil record of the region; for example, portunid samples account for the vast majority of brachyuran samples in this study. Based upon Oligocene through Pleistocene fossil species described from dorsal carapace material or well-preserved, complete cheliped material, there are a total of five named and three unnamed species of *Portunus*; five species of *Necronectes*; four species of *Euphylax*; and one species each of *Scylla*, *Sandomingia*, and *Psygmodthalmus*. This abundance and diversity is probably due to at least two major factors. First, portunid crabs in modern oceans are abundant and diverse in warm, tropical seas, inhabiting a broad variety of niches and habitats (Rathbun 1930; Williams 1984; Apel and Spiridonov 1998; Ng 1998). The Oligocene, Miocene, and Pliocene Caribbean clearly exhibited these climatic characteristics, and the family continues to be abundant and speciose in the region today (Rathbun 1930; Williams 1984). The Portunidae are currently most diverse in the Indo-Pacific (Davie 2002), and the open connection between the Pacific and Caribbean during the Oligocene and Miocene would have facilitated the dispersal of these crabs, perhaps leading to the high portunid diversity seen in the Caribbean during that time. Second, portunid crabs often inhabit soft, clastic bottoms but can also inhabit rocky or coral substrates or mangrove habitats. Based upon our paleogeographic reconstruction, it is likely that all of these habitats were abundant during the later Cenozoic, resulting in abundant suitable niches and therefore high diversity among the Portunidae.

ACKNOWLEDGMENTS

NSF grant INT-0003058 to Schweitzer and R. Feldmann, Department of Geology, Kent State University, funded research on decapod crustaceans in Baja California Sur, México; much of that research has informed this work. NGS Grants to M. Iturralde-Vinent funded paleontological expeditions to Puerto Rico, Dominican Republic, Haiti and Cuba. D. Waugh, Kent State University, assisted with the figures. A. Rage, Muséum National d'Histoire Naturelle, Paris, and S. Calzada and P. Artal, Museo Geológico del Seminario de Barcelona, Spain, facilitated access to the collections at their respective institutions; our thanks to these individuals. Feldmann read an earlier draft of the manuscript and improved it with his suggestions; he also assisted with photography and drafted the plates. H. Karasawa, Mizunami Fossil Museum, and two anonymous

reviewers provided helpful and complete reviews of the manuscript; our thanks to these individuals.

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