

# New Cretaceous and Cenozoic Decapoda (Crustacea: Thalassinidea, Brachyura) from Puerto Rico, United States Territory

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## Abstract

A large number of recently collected specimens from Puerto Rico has yielded two new species including *Palaeoxanthopsis tylotus* and *Eurytium granulosum*, the oldest known occurrence of the latter genus. Cretaceous decapods are reported from Puerto Rico for the first time, and the Cretaceous fauna is similar to that of southern Mexico. Herein is included the first report of Pleistocene decapods from Puerto Rico, which were previously known from other Caribbean localities. The Pleistocene *Cardisoma guanhum* is a freshwater crab of the family Gecarcinidae. The freshwater crab families have a poor fossil record; thus, the occurrence is noteworthy and may document dispersal of the crab by humans.

*Key words:* Decapoda, Thalassinidea, Brachyura, Puerto Rico, Cretaceous, Paleogene, Neogene.

## Introduction

Fossil decapod crustaceans have long been well known from the Caribbean but were essentially unknown from Puerto Rico until recently (see summary in Schweitzer *et al.*, 2006). Eleven named species and four indeterminate species are now known from Puerto Rico, including the specimens reported herein (Table 1). Decapod occurrences range in age from Cretaceous to Pleistocene, reflecting essentially the entire geologic and depositional history of the island.

## Geological Setting and Localities

During the Cretaceous and the early part of the Paleogene, the island of Puerto Rico was part of an island-arc system divided into three main volcanic provinces: Southwestern Igneous Province (SIP), Central Igneous Province (CIP), and Northeastern Igneous Province (NIP) (Jolly *et al.*, 1998; Schellekens, 1998). During the Cretaceous, the CIP and NIP were united into one block; later, in the Eocene, the SIP collided with this block forming the island of Puerto Rico (Jolly *et al.*, 1998; Schellekens, 1998). These three provinces are separated by the Southern Puerto Rico Fault Zone and the Northern Puerto Rico Fault Zone. However, rocks younger

than Eocene are not separated by these fault zones and even overlie parts of the fault zones in some areas (Jolly *et al.*, 1998). Here we briefly discuss the age and environment of the formations from which fossil crustaceans were collected, which range in age from Upper Cretaceous to Pleistocene, and the corresponding localities (Fig. 1).

*Botijas Limestone Member of the Pozas Formation:* The Pozas Formation is exposed between the towns of Jayuya and Coamo in the CIP (Jolly *et al.*, 1998; Schellekens, 1998). The formation consists of volcanic breccia, tuff, volcanic sandstone interbedded with ash-flow tuff, lava, and limestone lenses, one of which is the Botijas Limestone Member consisting of massive to thick-bedded limestone and calcarenite (Krushensky and Schellekens, 2001). The Botijas Limestone Member was deposited in a shallow marine environment containing abundant rudists of middle Campanian age (S. Mitchell, pers. comm., 2005). The decapods were collected from an outcrop on a secondary road out of road 568, near Orocovis, Puerto Rico, lat. 18°14'18.8" N; long. 66°22'29.5" W.

*Melones Limestone:* The Melones Limestone is exposed in the town of Cabo Rojo in the SIP (Jolly *et al.*, 1998; Schellekens, 1998). The formation is composed of volcanic sandstone

Table 1. All fossil decapods currently known from Puerto Rico. See Schweitzer *et al.* (2006) for details not in this paper.

Order Decapoda Latreille, 1802	Genus <i>Necronectes</i> A. Milne Edwards, 1881
Infraorder Thalassinidea Latreille, 1831	<i>Necronectes collinsi</i> Schweitzer <i>et al.</i> , 2006
Superfamily Callianassoidea Dana, 1852	Genus <i>Portunus</i> Weber, 1795
Family Callianassidae Dana, 1852	<i>Portunus yaucoensis</i> Schweitzer <i>et al.</i> , 2006
Subfamily Callichirinae Manning and Felder, 1991	Genus <i>Scylla</i> de Haan, 1833
Genus <i>Neocallichirus</i> K. Sakai, 1988	<i>Scylla costata</i> Rathbun, 1919
<i>Neocallichirus aetodes</i> Schweitzer <i>et al.</i> , 2006	Subfamily Podophthalminae Dana, 1851b
? <i>Neocallichirus? quisquellanus</i> Schweitzer <i>et al.</i> , 2006	Genus <i>Psygmophthalmus</i> Schweitzer <i>et al.</i> , 2006
Callianassoidea family, genus, and species indeterminate	<i>Psygmophthalmus lares</i> Schweitzer <i>et al.</i> , 2006
(2 species)	Superfamily Carpilioidea Ortmann, 1893
Infraorder Brachyura Latreille, 1802	Family Palaeoxanthopsidae Schweitzer, 2003
Superfamily Raninoidea de Haan, 1839	Genus <i>Palaeoxanthopsis</i> Beurlen, 1958
Family Raninidae de Haan, 1839	<i>Palaeoxanthopsis tylotus</i> new species
Subfamily Ranininae de Haan, 1839	Superfamily Xanthoidea MacLeay, 1838
Genus <i>Lophoranina</i> Fabiani, 1910	Family Panopeidae Ortmann, 1893
<i>Lophoranina cf. L. precocious</i> Feldmann <i>et al.</i> , 1996	Genus <i>Eurytium</i> Stimpson, 1862
Superfamily Calappoidea H. Milne Edwards, 1837	<i>Eurytium granulolum</i> new species
Family Calappoidea H. Milne Edwards, 1837	Xanthoidea family, genus and species indeterminate
Genus <i>Calappa</i> Weber, 1795	Superfamily Grapsoidea MacLeay, 1838
<i>Calappa pavimenta</i> Schweitzer <i>et al.</i> , 2006	Family Gecarcinidae MacLeay, 1838
Superfamily Portunoidea Rafinesque, 1815	Genus <i>Cardisoma</i> Latreille, 1828
Family Portunidae Rafinesque, 1815	<i>Cardisoma guanhummi</i> Latreille, 1828
Subfamily Portuninae Rafinesque, 1815	

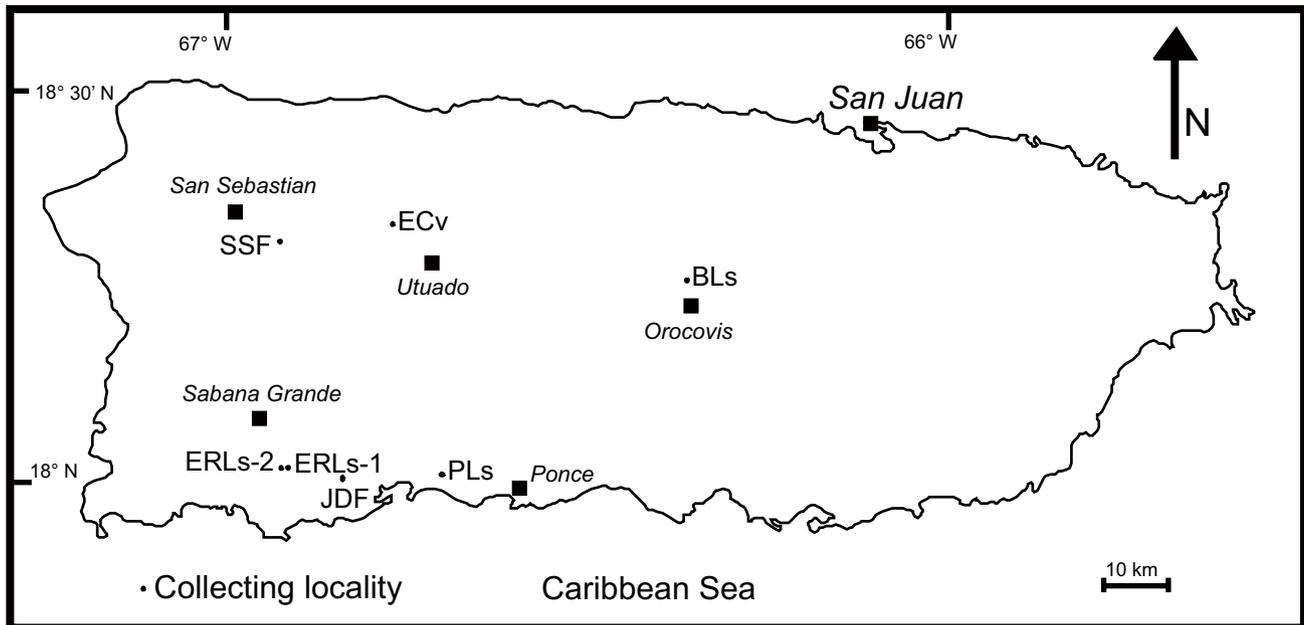


Fig. 1. Map of the island of Puerto Rico showing the localities where most fossil crustaceans were collected. Abbreviations: **BLS**, Botijas Limestone locality; **ECv**, Exit Cave locality; **ERLs-1**, **ERLs-2**, El Rayo Formation localities 1 and 2; **JDF**, Juana Diaz Formation locality; **PLS**, Ponce Limestone locality; **SSF**, San Sebastian Formation locality.

interbedded with limestone and mudstone, with skeletal calcarenite and cherty calcarenite higher in the section (Krushensky and Schellekens, 2001). The age of the Melones Limestone is late Campanian to middle Maastrichtian (Volckmann, 1983) or middle Campanian to late Maastrichtian (Jolly *et al.*, 1998). The decapod collecting locality is along road 301, after 7.3 km, near Sierra Melones, Barrio Corozo, Cabo Rojo, Puerto Rico, lat. 17°59'35.8"

N, long. 67°10'55.2" W.

*El Rayo Formation*: The El Rayo Formation is exposed between the towns of Lajas and Sabana Grande in the SIP (Jolly *et al.*, 1998, Schellekens, 1998). This formation is composed of basaltic to andesitic volcanic flows interbedded with volcanoclastic conglomerates, sandstones and limestones (Slodowski, 1956;

Mattson, 1960; Volckmann, 1983; Santos, 1999; Martínez, 2003). In general the limestone units are massive to bedded lenses interbedded with volcanoclastic breccia, conglomerate, and sandstone (Santos, 1999; Martínez, 2003). The limestone represents a carbonate platform/ramp developed over a volcanic surface during a Maastrichtian transgressive event.

Martínez (2003) divided the El Rayo Formation into two main subdivisions: the Lower and Upper El Rayo Formation. All of the fossil crustaceans from this formation were collected from the Upper El Rayo Formation which consists of thin-bedded to massive, bioclastic to volcanoclastic-rich limestone with minor breccia coupled with basalt flows; arkosic arenite; and paraconglomerate- and charophyte-bearing, reworked, weathered pyroclastics. The age of the El Rayo Limestone is early late Maastrichtian based upon the occurrence of the rudists *Parastroma guitarti* Palmer, 1933, and *Titanosarcolithes giganteus* (Whitfield, 1897) (Santos, 1999; Martínez, 2003). Decapods were collected from two localities in this unit: El Rayo Locality 1: outcrop on a dirt road in Barrio Arenas, Sabana Grande, Puerto Rico, lat. 18°01'32.3" N, long. 66°55'20.5" W; El Rayo Locality 2: outcrop on a hill west of El Rayo Locality 1, Barrio Arenas, Sabana Grande, Puerto Rico, lat. 18°01'32" N, long. 66°55'43" W.

*Juana Díaz Formation:* Several specimens were recovered from the early Oligocene Juana Díaz Formation, summarized previously (Schweitzer *et al.*, 2006), at lat. 18°01'45.40"N, long. 66°55'44.8" W, essentially the same outcrop as reported by Schweitzer *et al.* (2006).

*San Sebastian Formation:* The San Sebastian Formation is exposed in northern Puerto Rico between the towns of Moca and San Juan (Monroe, 1980). It generally overlies Cretaceous to Eocene rocks and was deposited in a basin that developed as a consequence of the subsidence of the Puerto Rico Trench (Monroe, 1980). Rivers draining the highlands present at that time supplied the clastic material deposited in the shallow marine environments, nearshore lagoons, and deltas (Monroe, 1980). Consisting mostly of clay and sandy clay, with some local conglomerates, its age has been determined as late Oligocene by Seiglie and Moussa (1984) based on its microfossils. Only one locality yielded fossil crustaceans, and it consists of carbonaceous clays and soft limestone found near the top of the formation, representing a transition into the overlying Lares Limestone. The general depositional environment of this formation consists of nearshore lagoonal facies; the occurrence of freshwater/brackish vertebrates supports this interpretation (MacPhee and Wyss, 1990; MacPhee and Iturralde-Vinent, 1995). The collecting locality is an outcrop on a south-facing road cut along road PR-111, before the bridge that crosses Collazo Creek, San Sebastian, Puerto Rico; lat 18°20'09"N; long. 66°56'57" W.

*Ponce Limestone:* This formation exposed in southern

Puerto Rico was deposited as fringing reefs in that region and consists mostly of pure limestone (Monroe, 1980). According to Krushensky and Monroe (1978), the Ponce Limestone consists of pale to orange, generally crystalline calcarenite with abundant internal molds of solitary corals and mollusks, echinoids, oysters, and foraminiferans. The locality from which fossils are collected represents a deepening-upward sequence. The lower-most units, where the decapod crustaceans were collected, represent mangrove/lagoonal deposits where rhizoliths and oysters with xenomorphic sculpture from attachment to branches or twigs are present. These units are overlain by reef facies. This change in facies represents a transition from low wave energy and high sedimentation to moderate to high energy, low sedimentation facies, a transition from back reef to fore reef. The age of this formation is middle to late Miocene based on its foraminiferal assemblage (Seiglie and Bermúdez, 1969). The collecting locality is an outcrop north of highway PR-2, Ponce, Puerto Rico; lat. 17°58'56.2"N; long. 66°40'03.3"W.

*Cave Deposit:* Cave deposits in Puerto Rico have been studied mostly for the extinct Quaternary vertebrates found in them (i.e. Anthony, 1916; McFarlane, 1999). Most of the fossils in these deposits are the result of natural traps or pelletal material deposited by owls (Pregill and Olson, 1981). The locality where the fossil decapod was collected contained remains of extinct mammals which can be used to determine the age of the deposit. Based on the last occurrence date of McFarlane (1999) for the extinct sloth *Acratocnus odontrigonus* Anthony, 1916, the deposit could be about 33 thousand years or older, giving a Pleistocene age. Locality: Exit Cave, northwest of Rio Tanama, Utuado, Puerto Rico; lat. 18°18'51" N, long. 66°46'52" W.

## Systematic Paleontology

Order Decapoda Latreille, 1802

Infraorder Thalassinidea Latreille, 1831

Superfamily Callianassoidea Dana, 1852

### **Callianassoidea family, genus, and species indeterminate**

*Material examined:* UPRMP 2830, 2865, 2872, 2881.

*Occurrence:* UPRMP 2881 and 2872 were collected from the Melones Limestone, UPRMP 2865 from El Rayo Formation Locality 1, and UPRMP 2830 from the Botijas Limestone Member of the Pozas Formation.

*Discussion:* Four claws that appear to be referable to the Callianassoidea were recovered from Late Cretaceous deposits. Unfortunately, none of these claws was found articulated with the proximal elements of the cheliped. None of the claws are referable to the typical Cretaceous callianassoid genus *Protocallianassa* Beurlen, 1930, as that genus is typified by possessing the proximal margin of the manus at a high angle (approximately 120 degrees) to the lower margin of the manus. The specimens herein referred

to Callianassoidea family, genus, and species indeterminate possess proximal margins at nearly right angles to the lower margin. However, the incomplete nature of the material makes it impossible to more narrowly restrict the identification of the Cretaceous callianassoid chelae. We note that there appear to be two different types, one an order of magnitude larger than the other. It is not possible to determine whether these differences are systematic or due to sexual dimorphism.

Family Callianassidae 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* Schweitzer et al., 2006; *N. allegranzii* Beschin et al., 2005; *N. bona* (Imaizumi, 1958) as *Calliax* (see Karasawa, 1993); *N. borensis* Beschin et al., 2006; *N. fortisi* Beschin et al., 2002; *N. grandis* Karasawa and Goda, 1996; *N. matsoni* (Rathbun, 1935a), as *Callianassa*; *N. manningi* Schweitzer et al., 2003; *N. nishikawai* (Karasawa, 1993) as *Callianassa*; *N. okamotoi* (Karasawa, 1993) as *Calliax*; *N. peraisensis* Collins et al., 1996; *N. rhinos* Schweitzer and Feldmann, 2002; *N. sakiae* Karasawa and Fudouji, 2000; *N. vaughni* (Rathbun, 1918a), as *Callianassa*; *N. wellsii* Schweitzer et al., 2004; *N. ? quisquellanus* Schweitzer et al., 2006.

*Discussion:* Schweitzer and Feldmann (2002), Schweitzer et al. (2004), and Schweitzer et al. (2006) have recently reviewed the genus; we have nothing new to add here.

**?*Neocallichirus*? *quisquellanus* Schweitzer, Iturralde-Vinent, Hetler, and Velez-Juarbe, 2006**

(Fig. 2)

*Material examined:* USNM 533970 – 533973. USNM 533973 is a large lot containing numerous specimens.

*Occurrence:* The specimens were collected from the Oligocene

Juana Diaz Formation locality.

*Discussion:* The large specimens are badly weathered and not particularly well preserved. They are, however, quite large in size for callianassids, and possess a large reentrant on the distal margin above the position of the fixed finger and a rectangular manus. These features are characteristic of *Neocallichirus*? *quisquellanus*, described from the Miocene of the Dominican Republic (Schweitzer et al., 2006). Because the new specimens are so poorly preserved, they are questionably referred to that species until more and better material can be collected to confirm the placement.

Infraorder Brachyura Latreille, 1802

Section Podotremata Guinot, 1977

Superfamily Raninoidea de Haan, 1839

Family Raninidae de Haan, 1839

Subfamily Ranininae de Haan, 1839

Genus *Lophoranina* Fabiani, 1910

*Type species: Ranina marestiana* König, 1825, by original designation.

*Included species: Lophoranina aculeata* (A. Milne Edwards, 1881); *L. aldrovandi* (Ranzani, 1820); *L. bakerti* (A. Milne Edwards, 1872); *L. barroisi* (Brocchi, 1877); *L. bishopi* Squires and Demetron, 1992; *L. bittneri* (Lörenthey, 1902); *L. cristaspina* Vega, Cosma et al., 2001; *L. georgiana* (Rathbun, 1935a); *L. kemmelingi* Van Straelen, 1924; *L. laevifrons* (Bittner, 1875); *L. levantina* Lewy, 1977; *L. marestiana*; *L. maxima* Beschin et al., 2004; *L. persica* Withers, 1932; *L. porifera* Woodward, 1866; *L. precocious* Feldmann et al., 1996; *L. quinquespinosa* (Rathbun, 1945); *L. raynora* Blow and Manning, 1996; *L. rossi* Blow and Manning, 1996; *L. soembaensis* Van Straelen, 1938; *L. straeleni* Vía, 1959; *L. tchihatcheffi* (A. Milne Edwards, 1866); *L. toyosimai* Yabe and Sugiyama, 1935.

*Diagnosis:* as in Vega, Cosma et al. (2001).

*Discussion:* The composition and distribution of *Lophoranina*



Fig. 2. ?*Neocallichirus*? *quisquellanus* Schweitzer, Iturralde-Vinent, Hetler, and Velez-Juarbe, 2006. 1, outer surface of left manus, USNM 533970; 2, outer surface of left manus showing large indentation in distal margin above fixed finger, USNM 533971. Scale bars = 1 cm.

were discussed in detail fairly recently (Feldmann *et al.*, 1996; Vega, Cosma *et al.*, 2001). The occurrence of a Maastrichtian specimen of *Lophoranina* in Puerto Rico is one of the oldest occurrences of the genus and follows the general distribution patterns of the genus as discussed below.

***Lophoranina* cf. *L. precocious* Feldmann, Vega, Tucker, Garcia-Barrera, and Avendaño, 1996**

(Fig. 3)



Fig. 3. *Lophoranina* cf. *L. precocious* Feldmann, Vega, Tucker, Garcia-Barrera, and Avendaño, 1996, dorsal carapace, USNM 533969. Scale bar = 1 cm.

**Description of material:** Carapace longer than wide, maximum carapace width = 28.1; length > 40.0; carapace narrowing posteriorly. Carapace badly damaged, entire anterior portion and posterior margin missing; lateral margins rimmed. Terraces of dorsal carapace wide, broadly spaced, nine terraces visible on left side of carapace; terraces with broken bases of spines; terraces of branchial region appearing to have been continuous across carapace; hepatic regions of carapace appear to have been differentiated.

**Material examined:** USNM 533969.

**Occurrence:** The specimen was collected from the upper part of the El Rayo Formation.

**Discussion:** The specimen is incomplete but bears numerous similarities to *Lophoranina precocious*, including the broad, widely spaced, continuous terrace lines; the differentiated hepatic region; the marked lateral rim; and the posteriorly narrowing carapace. Because the anterior portion of the carapace is missing, which bears the rostrum, orbits, and orbital spines, considered very important for the identification of raninid crabs, we only tentatively refer the specimen to the species.

*Lophoranina precocious* is known from early Maastrichtian rocks of Chiapas, Mexico (Feldmann *et al.*, 1996), making it

about the same age as the Puerto Rican specimen. Feldmann *et al.* (1996) noted that older species of *Lophoranina* tend to exhibit broad, widely spaced terrace lines and the Puerto Rican specimen is no exception. The occurrence of the Puerto Rican specimen in the Maastrichtian of Puerto Rico makes it one of the oldest known occurrences of *Lophoranina*. Its Caribbean occurrence, along with the older *Lophoranina precocious*, strongly suggest that the genus evolved in that region and subsequently dispersed via an Atlantic and Tethyan dispersal route to localities in east coastal North America, Europe, the Middle East, and the Indo-Pacific, where it is known in Eocene through Miocene rocks (Vega, Cosma *et al.*, 2001).

Section Heterotremata Guinot, 1977

Superfamily Portunoidea Rafinesque, 1815

Family Portunidae Rafinesque, 1815

Subfamily Portuninae Rafinesque, 1815

Genus *Necronectes* A. Milne Edwards, 1881

*Necronectes* A. Milne Edwards, 1881, p. 1, pl. 21, fig. 2.

*Gatunia* Rathbun, 1918a, 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* Schweitzer *et al.*, 2006; *N. drydeni* Rathbun, 1935a; *N. nodosus* Schweitzer *et al.*, 2002; *N. proavitus* (Rathbun, 1918a), 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. vaughani* Rathbun, 1935a (*vide* Rathbun, 1936); *N. vidalianus*.

**Occurrence:** Oligocene and Miocene of the Tethys (Schweitzer *et al.*, 2006).

**Discussion:** Schweitzer *et al.* (2006) recently diagnosed and summarized the genus. *Necronectes* is distinguished from all other members of the Portuninae by possessing eight anterolateral spines, including the outer-orbital spines. The number of anterolateral spines has long been held as an important distinguishing characteristic within the Portuninae (Glaessner, 1969; Apel and Spiridonov, 1998).

***Necronectes collinsi* Schweitzer, Iturralde-Vinent, Hetler, and Velez-Juarbe, 2006**

(Fig. 4.1)

*Necronectes collinsi* Schweitzer, Iturralde-Vinent, Hetler, and Velez-Juarbe, 2006, p. 12, figs. 5A, B.

**Material examined:** USNM 533975–533978.

**Occurrence:** Juana Diaz Formation locality. The species is known from the late early Oligocene to early Miocene of Puerto Rico (Schweitzer *et al.*, 2006).

**Discussion:** The new specimens are each incomplete; however, they possess eight anterolateral spines including the outer-orbital spines. This feature is unique among the Portuninae, and in fact, the Portunidae, and places them within *Necronectes* with

confidence. The specimens also possess other typical portunine characters such as a wider than long carapace which is widest at the position of the last anterolateral spine; a frontal margin with six spines including the inner-orbital spines; an ovate sternum; and male abdominal somites 3–5 fused and somite 3 with a transverse keel.

Genus *Scylla* de Haan, 1833

*Type species: Cancer serratus* Forskåi, 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, 1935a; *S. hassiaca* Ebert, 1887; *S. laevis* Böhm, 1922.

*Discussion: Schweitzer et al.* (2006) recently diagnosed the genus and provided a means by which to distinguish *Scylla* from *Portunus* Weber, 1795, a closely related genus.

***Scylla costata* Rathbun, 1919**

(Figs. 4.2, 4.3)

*Scylla costata* Rathbun, 1919, p. 170, pl. 4, pl. 5, pl. 6, figs. 3–5; Withers, 1924, p. 229, pl. 6, figs. 1–2; Schweitzer et al., 2006, p. 14, figs. 5C, D. *Material examined:* USNM 533974.

*Occurrence:* The specimen was collected from the late Oligocene San Sebastian Formation.

*Discussion:* The specimen is herein referred to *Scylla costata* based upon its possession of a longer than wide carapace; nine anterolateral spines; six frontal spines; broad orbits with two orbital fissures; a carpus of the major cheliped with upper and lower marginal spines; a manus of the major cheliped with weak keels on the outer margin and at least one spine on the upper margin; and a movable finger with a large, proximal tooth. All of these are either described or illustrated features of the species (Rathbun, 1919; Schweitzer et al., 2006); in addition, the species is previously known from early Oligocene to early Miocene rocks of the Caribbean, including the early Oligocene of Puerto Rico. Thus, this occurrence is from a new locality in Puerto Rico but does not extend the geologic range of the species.

Superfamily Carpilioidea Ortmann, 1893

Family Palaeoxanthopsidae Schweitzer, 2003

Genus *Palaeoxanthopsis* Beurlen, 1958

*Palaeoxanthopsis* Beurlen, 1958, p. 11, pl. 1; Schweitzer et al., 2002, p. 36; Schweitzer, 2003, p. 1122, figs. 5.4, 5.5.

*Paraxanthopsis* Vega, Feldmann et al., 2001, p. 323, fig. 4.

*Type species: Xanthopsis cretacea* Rathbun, 1902, by original designation.

*Included species: Palaeoxanthopsis cretacea; P. meyapaquensis* (Vega, Feldmann et al., 2001), as *Paraxanthopsis*; *P. tylotus* new

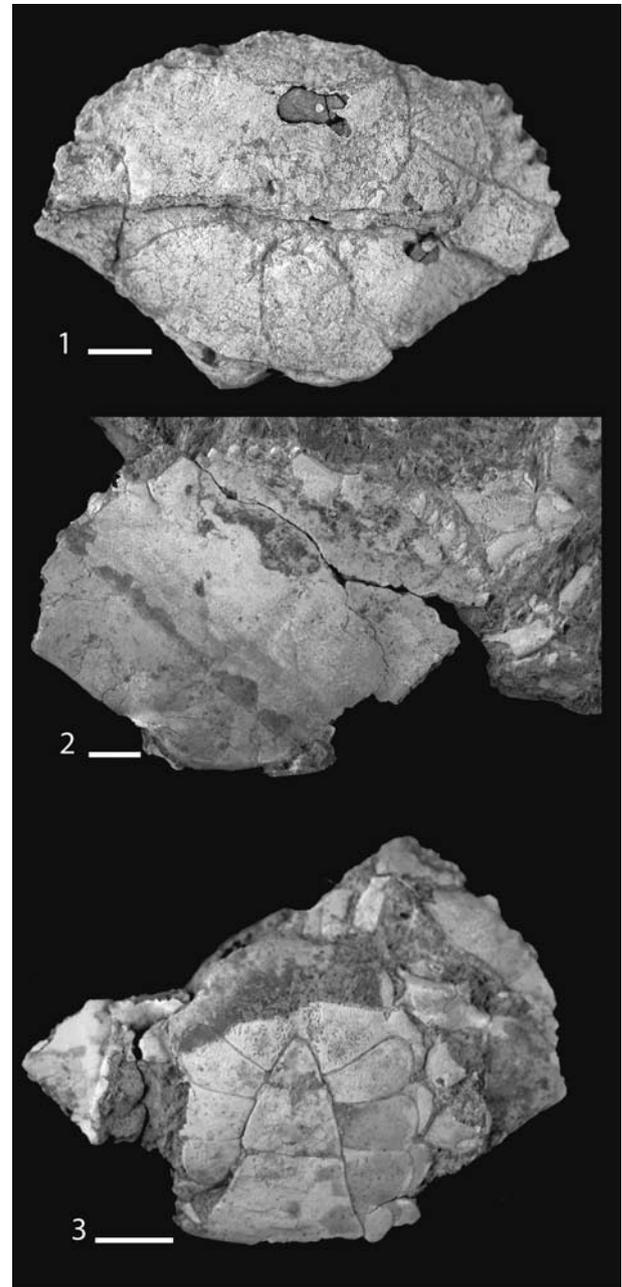


Fig. 4. Family Portunidae, Subfamily Portuninae. 1, *Necronectes collins* Schweitzer et al., 2006, USNM 533976, dorsal carapace; 2–3, *Scylla costata* Rathbun, 1919, USNM 533974, dorsal (2) and ventral (3) surface of carapace. Scale bars = 1 cm.

species.

*Diagnosis:* See Schweitzer (2003).

*Discussion:* The new specimen exhibits many of the defining features of species of the genus *Palaeoxanthopsis*. The well-developed grooves and carapace regions, hexagonal carapace, and distinctive anterolateral spines are diagnostic characters of *Palaeoxanthopsis* (Schweitzer, 2003) and are present in the new specimens. In particular, the number (three) and arrangement of anterolateral spines and also the pattern of tubercles on the dorsal carapace are nearly identical among species of *Palaeoxanthopsis* and the new specimens.

Similar genera were examined before placing the new specimens

within *Palaeoxanthopsis*. Whereas *Verrucoïdes* Vega, Cosma *et al.*, 2001, also displays large dorsal carapace swellings, they differ from those of the new specimens in being small and exhibiting wart-like ornamentation. The carapace of *Verrucoïdes* has a more angular shape than that of the new specimens and also deviates in its acuminate spines that are more numerous than those of the new specimens, including four anterolateral, one posterolateral, four frontal, and one outer-orbital spine in *Verrucoïdes*. Minor disparities also prevent the new specimens from being placed in *Paraverrucoïdes*, in which the carapace is more ovoid with granular swellings and crispate margins. The cardiac region of *Paraverrucoïdes* is more inflated than that of the new specimens, and the epibranchial areas have a distinct swelling directly adjacent to the branchiocardiac groove which is absent in the new species. The orbits of *Paraverrucoïdes* are rimmed, and the frontal margin is quadrilobed. The anterolateral spines of *Paraverrucoïdes* lack the tiny serrations seen on those of the new specimen. *Jakobsenius* Schweitzer, 2005; *Lobulata* Schweitzer *et al.*, 2004; and *Rocarcarcinus* Schweitzer, 2005, each lack the large swellings on the carapace as seen in the new species. Thus, placement in *Palaeoxanthopsis* is warranted.

*Palaeoxanthopsis* is previously known from the Maastrichtian of Brazil (Beurlen, 1958) and Chiapas (Vega, Feldmann *et al.*, 2001). Other members of the family also have Cretaceous occurrences, including *Jakobsenius* from the late Cretaceous of Scandinavia; *Lobulata* and *Rocarcarcinus* from the Maastrichtian of Argentina (Feldmann *et al.*, 1995); and *Remia* Schweitzer, 2003, from the Maastrichtian of Sénégal (Remy and Tessier, 1954). The former three genera extend into the Danian in their respective areas of occurrence. The Palaeoxanthopsidae has been previously suggested to exhibit an Atlantic distribution (Schweitzer, 2003; Schweitzer *et al.*, 2004). The occurrence of the family in the Cretaceous of Mexico and the Eocene occurrence of *Paraverrucoïdes* in the North American Gulf Coastal Plain make the Maastrichtian occurrence in Puerto Rico unsurprising.

### ***Palaeoxanthopsis tylotus* new species**

(Figs. 5.3, 5.4)

**Diagnosis:** Carapace small for genus, regions defined by distinct but low swellings, orbits clearly rimmed; last anterolateral spine directed weakly anterolaterally.

**Description:** Carapace hexagonal; widened anteriorly and widest just over half the distance posteriorly at position of last and largest anterolateral spine; maximum carapace length about 80 percent maximum width excluding last anterolateral spines; carapace vaulted longitudinally, flattened transversely. Frontal margin narrow, about one-quarter maximum carapace width, axially notched. Orbits moderate sized, circular, directed forward, rimmed, fronto-orbital width about 60 percent maximum carapace width. Anterolateral margins weakly convex; four anterolateral spines including outer orbital spines; last anterolateral spine largest, triangular, at just over mid-length, directed weakly anterolaterally;

other spines follow outer-orbital spine after straight section, small, forward-directed with serrated edges. Posterolateral margins slightly convex; slightly longer than anterolateral margin. Posterior margin incomplete, appearing straight or slightly concave.

Carapace differentiated into well-defined regions indicated by swellings and shallow grooves; branchiocardiac grooves especially well defined; swellings with knobby rather than wart-like ornamentation. Protogastric regions weakly swollen, symmetrically divided centrally by anterior process of mesogastric region; mesogastric region with pentagonal posterior swelling and elongated triangular, anterior process; small, narrow, rectangular urogastric depression separates mesogastric region from hexagonal cardiac region; cardiac region weakly inflated; intestinal region present but incompletely known, strongly depressed compared to other regions, outlining posterior margin. Hepatic regions with anterior tubercle; length nearly equal to width. Epibranchial regions broad, indicated by central, broad swelling with sloping sides; swellings of epibranchial and mesogastric areas, along with last anterolateral spines, aligned at same linear level. Mesobranchial and cardiac swellings also aligned at same linear level. Mesobranchial regions and their swellings help define posterolateral margins, contributing to slightly convex posterolateral margins. Metabranchial region depressed, merging with intestinal region.

Remainder of carapace and appendages unknown.

**Measurements:** Measurements (in mm) taken on specimens of *Palaeoxanthopsis tylotus*: UPRMP 2673, holotype, maximum width excluding last anterolateral spines = 27.2; maximum length = 21.0; frontal width = 6.4; fronto-orbital width = 14.6; length to position of maximum width = 12.3; USNM 533968, paratype, maximum width excluding last anterolateral spines = 10.5; maximum length = 8.8; frontal width = 2.6; fronto-orbital width = 6.6; length to position of maximum width = 4.9.

**Etymology:** The trivial name is derived from the Greek word “tylotos,” meaning knobby, in reference to the ornamentation on the dorsal carapace swellings.

**Types:** The holotype, UPRMP 2673, and paratype UPRMP 2648 are housed in the collections of the University of Puerto Rico, Mayagüez. Paratypes USNM 533967 and 533968 are deposited in the United States National Museum, Smithsonian Institution, Washington, DC.

**Occurrence:** The holotype UPRMP 2673, and paratypes UPRMP 2648 and USNM 533967–533968 were collected from El Rayo Formation Locality 1.

**Discussion:** The new specimens exhibit distinct differences that strongly indicate that they belong to a new species. The carapace has a much stronger hexagonal shape than does *Palaeoxanthopsis cretacea*. Whereas *P. cretacea* is described as having its last, longest spine directed posterolaterally, that spine in *P. tylotus* new species is directed anterolaterally. The grooves dividing the protogastric regions are much less pronounced in the new species than in *P. cretacea*. No inner orbital spines are present in *P. tylotus*,

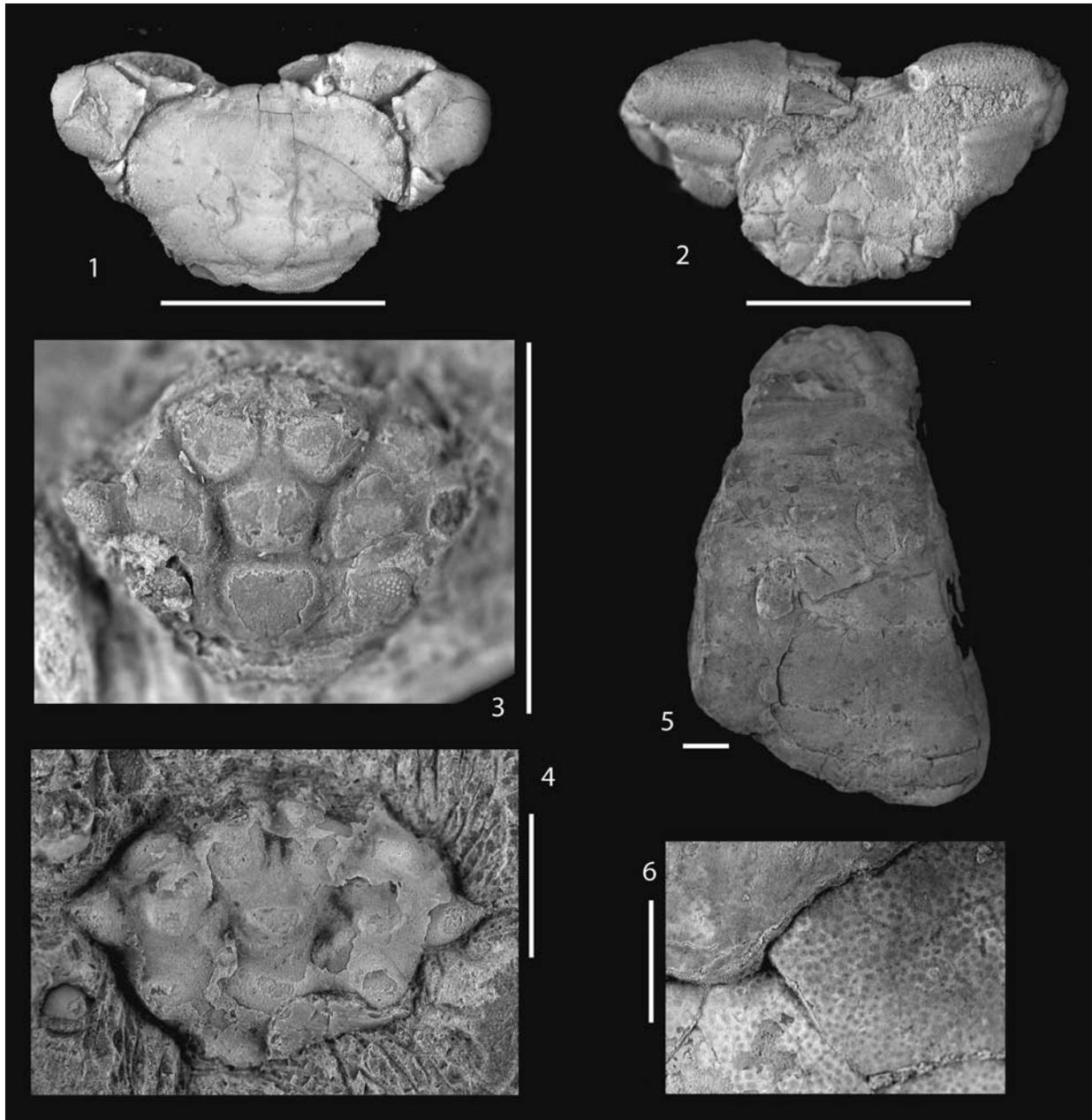


Fig. 5. Superfamilies Carpilioidea and Xanthoidea. 1–2, *Eurytium granulosum* new species (Panopeidae), holotype, UPRMP 2934, dorsal (1) and ventral (2) surface of carapace; 3, *Palaeoxanthopsis tylotus* new species (Palaeoxanthopsidae), paratype, USNM 533968, dorsal carapace; 4, *Palaeoxanthopsis tylotus* new species (Palaeoxanthopsidae), holotype, UPRMP 2673, dorsal carapace; 5–6, Xanthoidea family, genus, and species indeterminate, USNM 533979, female abdomen (5) and close-up of dorsal carapace cuticle ornamentation (6). Scale bars = 1 cm.

whereas *P. cretacea* possesses such spines. The anterolateral spines do not have connecting cuticular material between them in *P. tylotus*, whereas in *P. cretacea*, the spines appear partially fused by cuticular material.

As compared to *Palaeoxanthopsis meyapaquensis*, the only other species of the genus, *P. tylotus* is also distinct. *Palaeoxanthopsis meyapaquensis* exhibits an oval carapace with thin and crispate margins, whereas the new species has a strong hexagonal shape and stout margins. *Palaeoxanthopsis meyapaquensis* exhibits inner orbital spines and lacks the strong spines on the anterolateral margins, especially the distinct large anterolateral spine, seen in

*P. tylotus*. *Palaeoxanthopsis meyapaquensis* has more distinctive carapace regions that are defined by deeper grooves, possibly from erosion of the cuticle, and additional tubercles, especially on the protogastric region, which also is extremely elongated in comparison to the new species. *Palaeoxanthopsis meyapaquensis* also has a highly defined epigastric region which is emphasized by an extra, pronounced tubercle adjacent to the defining groove. Also, *P. meyapaquensis* has shallow and rimmed orbits which are also notably different from the new species, in which the orbits are widely rimmed.

Superfamily Xanthoidea MacLeay, 1838

Family Panopeidae Ortmann, 1893

*Diagnosis:* See Karasawa and Schweitzer (2006).

*Discussion:* The new species described below is represented by a single, moderately preserved specimen. It is referable to the Panopeidae based upon its possession of a hexagonal carapace that is about three-quarters as long as wide; a flattened carapace with moderately defined regions; a bilobed front occupying about 40 percent the maximum carapace width; orbits with two fissures; a fronto-orbital width of about 60 percent maximum carapace width; a lobate anterolateral margin with four spines excluding the outer-orbital angle; a moderately broadened sternum; a male abdomen with somites 3–5 fused; and moderately heterochelous chelipeds. All of these features are diagnostic for the family (Karasawa and Schweitzer, 2006) and are present in the new specimen. This combination of features also excludes the specimen from all other xanthoid families as diagnosed by Karasawa and Schweitzer (2006).

Members of the Panopeidae are common in waters of the Caribbean and the Atlantic coast of North America today (Rathbun, 1901; Williams, 1984). Thus, it is not surprising that the family would be present in Puerto Rico during the Miocene. Many extant brachyuran genera were present by Miocene times in many parts of the world (Schweitzer, 2001) and Puerto Rico is no exception; for example, the extant genera *Scylla* and *Portunus* Weber, 1795, have already been reported from the Miocene there (Schweitzer *et al.*, 2006).

Genus *Eurytium* Stimpson, 1862

*Type species:* *Cancer limosa* Say, 1818, by subsequent designation of Stimpson, 1862.

*Included species:* *Eurytium abbreviatum* (Stimpson, 1860), as *Panopeus*; *E. affine* (Streets and Kingsley, 1877), as *Panopeus*; *E. crenulatum* Rathbun, 1918a (fossil only); *E. granulosum* new species; *E. limosum*; *E. tristani* Rathbun, 1906.

*Diagnosis:* Carapace broad, ovate; regions weakly defined, lacking transverse ridges; fronto-orbital width a little over half maximum carapace width; front deflexed, bilobed, from one-quarter to one-third maximum carapace width; orbit with two fused fissures; anterolateral margins with five spines, the first two of which are fused together; male abdominal somites 3–5 fused (after Rathbun, 1930).

*Discussion:* The single specimen exhibits all of the diagnostic features listed by Rathbun (1930) for the genus that are visible on the dorsal carapace and abdomen. *Eurytium* was described by Rathbun (1930) as being smooth, whereas the new specimen is granular along the anterolateral and posterior margins. However, the specimen is not sufficiently preserved to erect a new genus, and in any event, displays all of the diagnostic characters of *Eurytium*. Importantly, the specimen lacks the transverse ridges on the dorsal carapace that are very common within the Panopeidae; thus, the placement in *Eurytium* seems justified. Two other species of *Eurytium* have been reported from the fossil record, the extant

*Eurytium cf. E. limosum* from the Pliocene and Pleistocene of Jamaica (Collins *et al.*, 1996; Collins and Portell, 1998) and *E. crenulatum* from the Pliocene and Pleistocene of Panama (Rathbun, 1918a; Todd and Collins, 2005). Extant species are known from both the east and west coastal Americas. Thus, the new species does not extend the geographic range of the genus but does mark the earliest geological notice.

#### *Eurytium granulosum* new species

(Figs. 5.1, 5.2)

*Diagnosis:* Carapace wider than long; front axially notched, downturned, beaded; orbits small, directed forward, with two fissures; anterolateral margins with four indistinct, granular lobes; posterolateral and posterior margins beaded; carapace regions poorly marked.

*Description:* Carapace wider than long, maximum length about three-quarters maximum width measured about 30 percent the distance posteriorly on carapace; regions moderately defined; carapace moderately vaulted longitudinally, flattened transversely.

Front appearing to have been very weakly convex, axially notched, downturned, beaded, about 40 percent maximum carapace width. Orbits small, circular, rimmed, directed forward, one closed fissure centrally, another closed fissure proximal to outer-orbital angle; fronto-orbital width about 55 percent maximum carapace width; eyestalks short, well calcified. Anterolateral margin beaded, crenulated, with four lobes; first lobe long, extending straight from outer-orbital angle; second lobe weakly convex; third lobe produced into blunt, weak spine; fourth lobe produced into weak spine at anteriormost tip. Posterolateral margin beaded, weakly convex; posterior margin with beaded rim.

Mesogastric region with long anterior process, widened distally. Protogastric and hepatic regions not well separated. Urogastric region narrow, short, weakly depressed, with two pits along anterior margin; cardiac region much broader than other axial regions, hexagonal; intestinal region depressed well below level of other axial regions. Epibranchial region arcuate, extending axially from last anterolateral lobe; remainder of branchial region inflated and beaded laterally, depressed to level of intestinal region posteriorly.

Male sternum moderately broad, ovate; sternites 3 and 4 separated by shallow groove. Sternite 4 long, directed anterolaterally. Sternite 5 directed anterolaterally, sternite 6 directed laterally, sternite 7 appearing to be longer than other sternites, directed posterolaterally, sternite 8 apparently not visible.

Male abdomen narrow, with concave sides, reaching to about middle of sternite 4; telson and somite 6 about equal to one another in length; somites 4 and 5 appearing to be fused, remainder of somites not preserved.

First pereopods heterochelate; merus very short, shorter than high; carpus equant; proximal articulation of manus with carpus with projected collar and interlocking blunt projections on upper proximal corners; manus short, widening distally; outer surface of

manus granular, lacking keels; fingers short.

*Measurements:* Measurements (in mm) taken on the sole specimen of *Eurytium granulosum*: maximum carapace length = 10.0; maximum carapace width = 13.1; fronto-orbital width = 7.4; frontal width = 5.0; length to position of maximum width = 4.0.

*Etymology:* The trivial name is derived from the Latin word “granosus,” meaning seedy, in reference to the granular ornamentation on the frontal, anterolateral, posterolateral, and posterior margins of the carapace.

*Type:* UPRMP 2934, holotype and sole specimen.

*Occurrence:* Near Ponce, Puerto Rico from the Miocene Ponce Limestone.

*Discussion:* The new species is distinguished from all other species in the genus by its granular anterolateral and posterior margins. It has less well-developed anterolateral spines than *Eurytium crenulatum*, the only other solely fossil species. The granular ornamentation seems to be a feature of the cuticle itself, as the cuticle is retained on the sole specimen of *Eurytium granulosum*.

#### Superfamily Xanthoidea incertae sedis

#### Family, genus, and species indeterminate

(Figs. 5.5, 5.6)

*Description of material:* Specimen large, incompletely preserved, length approximately 118 mm, width unknown; dorsal carapace apparently lacking well defined regions; posterior margin rimmed; cuticle obscurely beaded, exfoliated in posterior area of dorsal carapace; layer beneath exfoliated layer, probably the endocuticle, more obviously beaded.

Female abdomen broad, with concave lateral margins; telson poorly known; somite 6 long, more than twice the length of somites 4 or 5; somites 4 and 5 much shorter than wide. Large knob distal to articulation of telson and somite 6, possibly a swelling on the coxae of pereopod 1 or on sternum but not possible to determine.

Fingers of cheliped robust, with large denticles on occlusal surface, cuticle black.

*Material examined:* USNM 533979.

*Occurrence:* Melones Limestone.

*Discussion:* The specimen is referred to the Xanthoidea based upon its possession of robust fingers with large denticles and black cuticle. This type of finger is quite typical of xanthoid crabs, although not limited to that group. Better preserved material will be necessary to confirm this placement.

The specimen is very large, especially for a Cretaceous brachyuran. Unfortunately, it is insufficiently preserved to identify it beyond the superfamily level. Very few such large brachyuran taxa are known from Cretaceous rocks. *Ophthalmoplax triambonatus* Feldmann and Villamil, 2002, from the Cretaceous of Colombia possesses a very large dorsal carapace but is characterized by sharply defined ridges on the carapace which do not appear in the Puerto Rican specimen described here.

*Megaxantho zoque* Vega, Feldmann *et al.*, 2001, also referred to the Xanthoidea incertae sedis (Karasawa and Schweitzer, 2006) and known from the Maastrichtian of Chiapas, Mexico, is more similar to the Puerto Rican specimen discussed here. Both *M. zoque* and the new Puerto Rican specimen exhibit robust fingers of the chelipeds and dorsal carapaces without distinct regional development. However, the surface of *M. zoque* was described as pitted, not characteristic of the new specimen, and in any event, the new specimen is insufficiently preserved to further identify it. Recovery of more material may make a positive comparison with *M. zoque* possible.

Superfamily Grapsoidea MacLeay, 1838

Family Gecarcinidae MacLeay, 1838

Genus *Cardisoma* Latreille, 1828

*Type species:* *Cardisoma guanhumii* Latreille, 1828, p. 685, by original designation.

*Included species:* *Cardisoma armatum* Herklots, 1851; *C. carnifex* (Herbst, 1796); *C. longipes* (A. Milne Edwards, 1867); *C. guanhumii*. *Cardisoma hirtipes* Dana, 1851a, and *C. rotundum* (Quoy and Gaimard, 1824), traditionally assigned to the genus, have recently been reassigned to *Discoplax* A. Milne Edwards, 1867 (Davie, 2002).

*Discussion:* Considerable difference of opinion surrounds the date of authorship of the generic name. Typically, the genus is cited as having been named in 1825. However, Neave (1939) listed the genus as having been named in 1824, and Davie (2002) cited a date of 1828. Examination of Latreille (1825–28) does not clearly indicate dates of publication of sections within the large work. Indeed, the title page simply indicates a publication date of 1825, which probably explains the frequent citation of that date of naming. However, Sherborn and Woodward (1906) examined two sets of the encyclopedia, preserved in their original wrappers, which clarified the actual dates of publication of the various sections. The genus *Cardisoma* was described on p. 685, and the sole reference to *C. guanhumii* also appeared on that page. According to Sherborn and Woodward (1906, p. 578), that portion of the work was published in 1828. Therefore, 1828 should stand as the proper date of publication of the genus and the species. The source of the date 1824, cited in Neave (1939), remains a mystery as he correctly cites the volume number and page number for the reference. None of volume 10 of the Encyclopédie Méthodique was published until the following year.

#### *Cardisoma guanhumii* Latreille, 1828

(Fig. 6)

*Cardisoma guanhumii* Latreille, 1828, p. 685.

*Description of material:* Specimen with crushed, broken carpus, propodus, and dactylus of left cheliped.

Carpus crushed.

Propodus crushed proximally and with fixed finger broken and rotated outward. Hand about 13 mm long and 10 mm high; outline

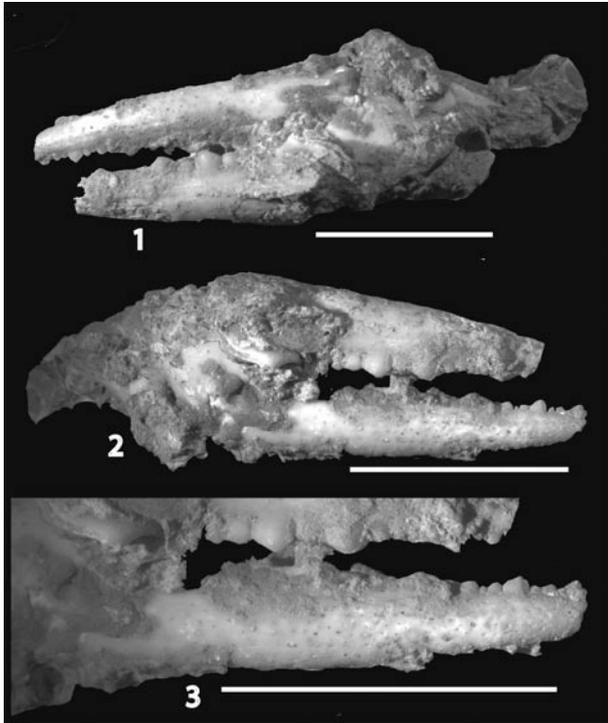


Fig. 6. *Cardisoma guanhumii* Latreille, 1828, UPRMP 3119. 1, Outer surface of left cheliped oriented to show fixed finger in the plane of the photograph; 2, inner surface of the left cheliped rotated to show dactyl in the plane of the photograph; 3, enlargement of fig. 6.2 highlighting the denticles on the occlusal surfaces of the fingers. Scale bars = 1 cm.

obscured; surface apparently smooth. Fixed finger >11.5 mm long, tip broken; slightly curved inward, tapered uniformly distally; inner surface apparently smooth; lower surface straight, weakly pustulose proximally and smooth distally; outer surface smooth, with at least two longitudinal rows of tiny setal pits; occlusal surface with more than nine closely spaced teeth separated by narrow fissures and terminated by sharp, acuminate surfaces, alternate teeth more elevated than intervening teeth.

Dactylus long, >17.5 mm, slender, curved inward, tip broken; inner surface mostly obscured, generally smooth, with setal pits; lower surface straight, smooth where visible; outer surface with densely spaced longitudinal rows of setal pits; occlusal surface with teeth morphologically similar to those on propodus but of at least three different sizes; largest teeth separated from one another by five? intermediate and small teeth.

**Material and Occurrence:** The sole specimen, UPRMP 3119, was collected from Exit Cave.

**Discussion:** The specimen referred to *Cardisoma guanhumii* conforms closely to the specimens illustrated by Rathbun (1918a, pl. 64, figs. 2–4) and Türkay (1978, pl. 1, figs. 1, 2). The fixed fingers illustrated by both Rathbun and Türkay are nearly straight along the lower margin, and arched inward; the occlusal teeth are closely spaced and vary in size in a manner similar to that seen in the Puerto Rico specimen. One of the characteristic features of the species is that the lower proximal surface of the fixed finger is covered by small protuberances bearing setal pits. The specimen

from Puerto Rico bears several abraded pustules in this region but the density of the structures is difficult to determine owing to abrasion of the exposed part of the surface. Much of that region is obscured by sediment. The pustulose nature of that region seems to be best expressed when the surface is decorticated; that is, when the exocuticle has been removed. This condition is well illustrated on a specimen collected from the Pleistocene of Jamaica (Collins and Donovan, 1997, figs. 11–13).

Fossil fragments referred to this species have been reported from the Pliocene of Panama (Rathbun, 1918a), the Pliocene of Costa Rica (Türkay, 1978), and the Pleistocene of Jamaica (Collins and Donovan, 1997; Donovan and Dixon, 1998; Collins, 1999). Türkay (1978) concluded that the specimen referred to the closely related species, *C. planum* Rathbun, 1945, from the Pliocene of Fiji, cannot be assigned to *Cardisoma*. We concur. The form of the fixed finger on the sole specimen of *C. planum* does not taper substantially, has a blunt termination, and exhibits teeth that are isolated and rounded, not acuminate.

Extant members of *Cardisoma guanhumii* are known from throughout the Caribbean region and along the coast of Brazil as far south as São Paulo (Rathbun, 1918b). Other extant species of the genus *Cardisoma* have been reported from the Caribbean, the west Atlantic Ocean, Brazil, and West Africa (Rathbun, 1935b; Türkay, 1973; Manning and Holthuis, 1981). Türkay (1974) and Davie (2002) document a circumtropical distribution for the genus based upon the occurrence of species in Australia and many Pacific islands. Türkay and Sakai (1976) documented the presence of *Cardisoma carnifex* in Japan. The extremely broad distribution of a terrestrial brachyuran species in remote, isolated locations introduces the possibility of dispersal by humans. Specimens of land crabs could have served as a food resource on oceanic voyages, providing a venue for introduction of the animals into otherwise inaccessible locales.

Rathbun (1918b) reported that the crabs live in a variety of terrestrial habitats ranging from swamps to forests, that they produce deep burrows, forage at night, and return to the sea to reproduce. The occurrence of the fossil specimen from Puerto Rico in a cave deposit and in association with fossils of terrestrial organisms is consistent with this interpretation. Their habit of returning to marine environments to reproduce is supported by the observation of Collins and Donovan (1997) that *Cardisoma guanhumii* has been collected from a marine unit, the Port Morant Formation in Jamaica.

### Acknowledgments

NSF grant EF 0531670 to Feldmann and Schweitzer funded travel to museums in Europe and to the United States National Museum, Smithsonian Institution, Washington, DC, where comparative material of the Xanthoidea and the Gecarcinidae was examined. We are grateful to A. Bonilla, T. Miller, R. Morales and M. Plaza-Toledo who provided help in the field. H. Karasawa

provided a helpful review of the manuscript.

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Accepted on January 27, 2007

