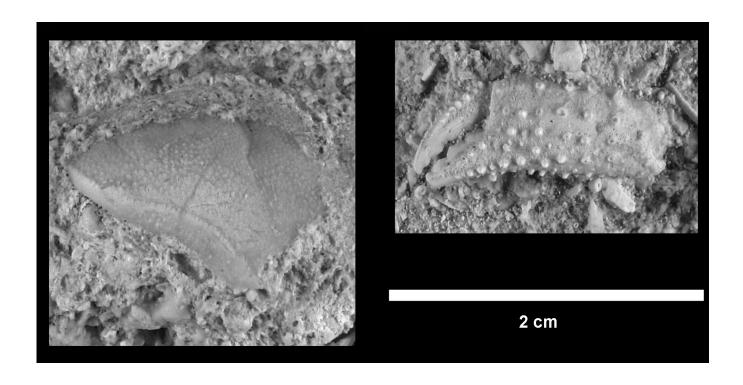


# BULLETIN

of the Florida Museum of Natural History

## DECAPOD CRUSTACEANS OF THE SEROE DOMI FORMATION OF CURAÇAO

Ashleigh M. Sload, Rodney M. Feldmann, Carrie E. Schweitzer, Roger W. Portell, and Stephen K. Donovan



Vol. 56, No. 2, pp. 49–82 ISSN 2373-9991 July 7, 2018

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ISSN: 2373-9991

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Publication Date: July 7, 2018

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Editor of the Bulletin; Florida Museum of Natural History; University of Florida; P.O. Box 117800; Gainesville, FL 32611-7800 USA

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# DECAPOD CRUSTACEANS OF THE SEROE DOMI FORMATION OF CURAÇAO

Ashleigh M. Sload<sup>1</sup>, Rodney M. Feldmann<sup>2</sup>, Carrie E. Schweitzer<sup>3</sup>, Roger W. Portell<sup>4</sup>, and Stephen K. Donovan<sup>5</sup>

#### **ABSTRACT**

A new collection of brachyuran decapod crustaceans (crabs) from the Mio-Pliocene Seroe Domi Formation of Curaçao totals 284 specimens. They exhibit excellent preservation of fine details, including fragile spines and delicate surface textures; however, the majority of the specimens are fragmented and disarticulated. Seven genera are identified from six families; Raninidae, Calappidae, Aethridae, Leucosiidae, Mithracidae, and Portunidae. The decapod fauna from the Pliocene portion of the Seroe Domi Formation was compared to coeval Caribbean brachyuran faunas to judge the relative diversity. Jamaica hosts the largest concentration of Pliocene brachyurans in the Bowden Member of the Layton Formation. Other localities, in Costa Rica, Panama, Florida, and the Dominican Republic, were similar in generic diversity to that of the Seroe Domi Formation. Following uplift of the Central American Isthmus and the end of genetic exchange between the Pacific and Atlantic, crab species that previously spanned both oceans evolved into distinct Pacific and Atlantic forms. The Pliocene crabs of the Seroe Domi Formation all belong to species that represent Atlantic forms.

**Key words:** Decapoda, Curação, Pliocene, Seroe Domi Formation, biogeography, sedimentology.

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#### INTRODUCTION

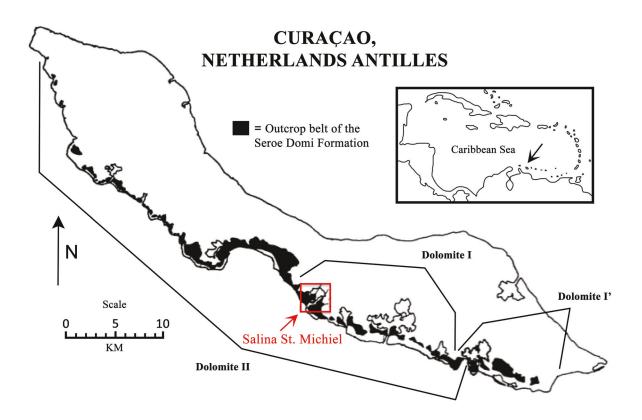
The purpose of this study is to identify, describe, and illustrate the crabs of the Seroe Domi Formation of Curaçao, as well as to compare their diversity to that in surrounding, coeval Caribbean localities. Curaçao is located in the southern Caribbean approximately 70 km from the northern coast of Venezuela (Fig. 1, inset). It is an east-west trending island about 60 km long. The Seroe Domi Formation crops out along the leeward coast of Curaçao, as well as on Aruba and Bonaire, the two closest islands (= the ABC Islands). The three islands are part of the Aruba-La Blanquilla island archipelago, which spans approximately 500 km.

The Seroe Domi Formation consists of siliciclastic and calcareous sandstones with abundant skeletal fragments and corals. The unit has undergone dolomitization, but not all of the formation has been diagenetically altered (Fouke, 1994; Fouke et al., 1997).

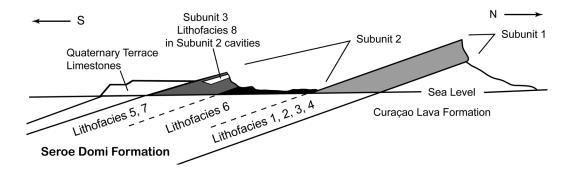
Previous studies of the ABC Islands have

focused on the general geology of the islands (de Buisonje, 1974), the dolomitization and chronostratigraphy of the Seroe Domi Formation (Fouke, 1994; Fouke et al., 1997), and the reef corals (McNeill et al., 1997; Budd et al., 1998). Collins and Donovan (2004) described several new decapods from the Seroe Domi Formation of Aruba, but no studies have mentioned the decapods of this unit from Curação.

The decapods of the Seroe Domi Formation are important because they occur in an early Pliocene portion of the formation that represents an important time in the Caribbean, following uplift of the Central American Isthmus earlier in the Pliocene (O'Dea et al., 2016). After uplift occurred, two faunas that were previously open to genetic exchange between the western Atlantic and eastern Pacific were geographically isolated from one another, leading to the development of distinct Atlantic and Pacific populations, and eventually species (Abele, 1976).



**Figure 1.** Outcrop map of the Seroe Domi Formation along the leeward coast of Curação, Salina St. Michiel collection locality highlighted (modified from Fouke et al., 1997:fig. 1.8).



**Figure 2.** Geologic cross section showing the stratigraphic relationship of the overlying Quaternary terrace limestones and the underlying Curação Lava Formation with the Seroe Domi Formation at the St. Michiel locality (after Fouke et al., 1997:fig. 2.1).

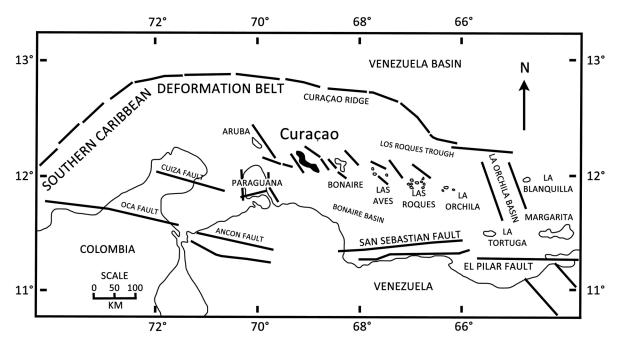


Figure 3. Tectonic map of the southern Caribbean (after Fouke et al., 1997:fig. 1.2).

#### GEOLOGIC SETTING

The Seroe Domi Formation is a middle Miocene to early Pliocene unit that crops out along the leeward coast of Curaçao (Fig. 1) in the southern Caribbean. The unit dips seaward at angles ranging from 5°–30° (Fig. 2). The Seroe Domi Formation unconformably overlies the Curaçao basement rock, which is formed by Cretaceous basalts of the Curaçao Lava Formation (Fig. 2) (de Buisonje, 1974; Pindell and Barrett, 1990). The island is located on the Bonaire Block, between the Caribbean and South American plates (Fig. 3) and has a complex tectonic history of extension and uplift

that began in the Oligocene (Fouke, 1994; Fouke et al., 1997). The Seroe Domi Formation in particular has undergone hundreds of meters of uplift since deposition began in the middle Miocene (Herweijer and Focke, 1978). Approximately 60 m of late Pleistocene lagoon and reef deposits known as the Quaternary Limestone Terraces overlie the formation (Herweijer and Focke, 1978).

The Seroe Domi Formation is 350 m thick and consists of three lithologically distinct subunits, all representing different times and modes of deposition. The general lithology of the unit is siliciclastic and calcareous sandstones, which have gone through several episodes of dolomitization (Table 1) (Fouke, 1994; Fouke et al., 1997; McNeill et al., 1997; Budd et al., 1998). Reef corals are abundant in the formation and have been the focus of past studies.

The basal portion of the formation, Subunit 1 (S1), is a 30–100 m thick sequence of grainstones and packstones interbedded with wackestones and allochthonous blocks representing a middle Miocene, deep water environment dominated by gravity flows (Fouke, 1994). The weakly lithified skeletal sandstones that make up parts of the subunit are derived from fragmented corals, coralline algae, pelagic foraminifera, molluscs, benthic foraminifera, and echinoderms. Subunit 1 is further divided into Lithofacies 1, 2, 3, and 4, each representing a

separate stage of deposition in the subunit.

Subunit 2 (S2) represents a fore-reef talus slope to reef-front environment ranging in age from late Miocene to early Pliocene (Fouke, 1994; Fouke et al., 1997). It comprises coralgal grainstones, packstones, and boundstones in the upper 250–300 m of the Seroe Domi Formation. Subunit 2 contains bivalve molluscs, calcareous algae, echinoderms, corals, foraminifera, and extensively leached skeletal sandstones. Subunit 2 also contains a high proportion of siliciclastic material derived from the basement rock. This material is thought to be a result of weathering of the basement rock during subaerial exposure upslope of the Subunit 2 depositional basin. This subunit is further divided into Lithofacies 5, 6, and 7 (Fouke,

**Table 1.** Lithostratigraphy of the Subunits and Lithofacies of the Seroe Domi Formation (modified from Fouke et al., 1997;fig. 2.1).

Lithostratigraphic Designation	Lithology	Extent of Dolomitization
Subunit 1		
Lithofacies 1	coralgal grainstones	partial
Lithofacies 2	foraminiferal wackestones	partial
Lithofacies 3	coralgal grainstone	partial
Lithofacies 4	red algal packstones	complete
Subunit 2		
Lithofacies 5	coralgal grainstones and boundstones	complete
Lithofacies 6	coralgal packstones	none
Lithofacies 7	coralgal grainstones and boundstones	partial
Subunit 3		
Lithofacies 8	siliciclastic sandstones	none

1994; Fouke et al., 1997). Subunit 2 Lithofacies 6 is the specific portion of the Seroe Domi Formation where the decapods in this study were collected. Fouke (1994) determined that the depth of deposition of Subunit 2 Lithofacies 6 would have been <100 m, lying along the shallow slope off the coral reef platform.

Subunit 3 (S3) is composed of siliciclastic sandstones deposited in crevices that penetrated S2 during the early Pliocene. The infill constitutes the final lithofacies, Lithofacies 8. It contains calcareous algae, bivalve molluscs, echinoderms, and corals (Fouke, 1994; Fouke et al., 1997).

Overall, the three subunits represent a shallowing upward sequence of siliciclastics and carbonates deposited discontinuously along the edge of the Curaçao horst from the Miocene to Pleistocene. The Neogene was a period of gradual uplift for the island and this trend is supported by the sequence seen in the formation (de Buisonje, 1974; Fouke, 1994). The depositional environment changed from a deep water, reef slope to a shallow water reef-front to reef environment that was periodically above sea level toward the later stages of deposition.

#### METHODS AND MATERIALS

Decapod specimens are deposited in the Florida Museum of Natural History (FLMNH), University of Florida (UF) in Gainesville. Roger W. Portell and associates (see Acknowledgments) excavated the material during three field trips to Curaçao in 2003, 2005, and 2011. The decapod material was carefully collected (mostly *in situ*) from the Salina St. Michiel area (Fig. 1) using small chisels and rock hammers.

Specimens were photographed using a Leica Z6 APO binocular microscope with camera attached and a Sony DSC-R1 camera. After initial digital photographs were taken, the specimens were prepared using Murray Engineering Micro-Jacks. This method efficiently cleans the matrix better exposing the fossils within the rocks. Once the specimens were exposed, they were re-photographed and systematic identifications were completed.

#### SIEVE PROCEDURES

A sediment analysis was conducted to better understand the depositional environment of the fossil site. Sediments removed from rocks associated with the decapod fossils were disaggregated and sieved. The material for disaggregation was cut from the weathered rind on the exterior of the samples. The cut pieces were then put into a container, covered with water, and allowed to sit for three weeks. One piece of cut material was placed in a container with Quaternary O detergent and water, and then placed in an ultrasonic bath for several hours. This was done to determine the best method for disaggregating the sedimentary rocks. After most of the rock pieces had disaggregated, the sediments were washed, dried, and sieved.

The sieve set consisted of three stacked screens of nos. 18, 40, and 80, from coarse to fine. After the screens were cleaned, the sediments were washed through the screens using water and gentle manual agitation. Once the sediments had been washed through, the screens were separated and the sediments from each were poured onto separate clean paper towels. The sediments were then placed in a drying oven overnight. Each screen residue was examined and microfossils were picked using a binocular microscope.

#### THIN SECTION PROCEDURES

A thin section of the rock was prepared by trimming off the friable outer material so that only well-cemented material from the interior of the rock remained for thin sectioning. The chip was then impregnated with epoxy using a vacuum chamber and allowed to cure overnight. The impregnated chip was removed from the epoxy tub and polished on a lap wheel using 80, 220, and 600 grit, successively. After polishing, the chip was dried overnight in a drying oven, mounted to a 1" x 2" glass slide and then cured under a UV lamp for 16 minutes. After the glue had cured fully overnight, the chip was cut and ground using a Hilquist thin section machine. After achieving the correct thickness, the slide was polished using 600 grit on a lapidary wheel to remove scratches. The thin section was then analyzed and described using a petrographic microscope.

#### CARBONATE DISSOLUTION PROCEDURE

The carbonate in the rock was dissolved in order to determine the approximate siliciclastic percentage of the rock. Two chips of the bulk rock were disaggregated with a rock hammer, then weighed on a scale to determine the initial weight of the sample. The sample was then placed in a glass container and covered with 10% HCl. Additional 10% HCl was added to the container until the reaction visibly slowed. Using a paper filter placed in a funnel, the sample was washed using de-ionized water. The sample was allowed to dry overnight in a drying oven and then placed back into the glass container, making sure to get all of the sample into the jar. The sample was once again covered with 10% HCl in order to ensure that all of the carbonates were dissolved. The sample was then washed once more, using the filter and funnel set up, and dried overnight. Once fully dried, the sample was reweighed to determine the mass of the siliciclastic materials in the rock. The percentage of siliciclastics was determined using the equation: % siliclastics = (weight of sediment)/(weight of total)  $\times$  100

## SEDIMENTOLOGY OF THE SEROE DOMI FORMATION

Previous Work

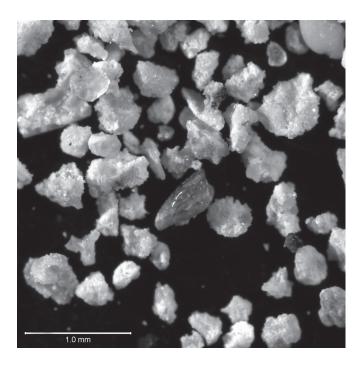
The Seroe Domi Formation has a complex depositional and diagenetic history. De Buisonjé (1974) originally subdivided the formation into the Older, Middle and Younger Seroe Domi Formation when he described the Neogene and Quaternary geology of Aruba, Curação, and Bonaire. He noted that the dip of the Seroe Domi Formation was original to the depositional environment and not post-depositional. He interpreted the depositional environment of the unit as representing a series of slumps of detrital material from a shallow-water coral platform up slope; therefore, the dip is a result of the angle of the slope. De Buisonjé (1974) described the sedimentology of the formation as reef detritus consisting of calcareous algae, corals, and varying amounts of detrital material from the weathered basement rock.

Later, studies on the Seroe Domi Formation examined the depositional and diagenetic history

of the unit. For example, Fouke (1994) modified de Buisonjé's original subdivisions by creating a more complex set of divisions, including three subunits and eight lithofacies based on the distinct sedimentology and depositional environments represented by the subunits/lithofacies.

#### SEDIMENT ANALYSIS

Bulk Rock Lithology. The lithology of the rock in which the decapod fossils are preserved is a coralgal packstone with a moderate percentage (17.3%) of siliciclastic materials. The rock is buff to tan in color, and contains coarse-grained bioclasts of fragmented echinoids, corals, foraminifera, and calcareous algae, and finer grained material made up of small, very fragmented bioclasts, and siliciclastic and carbonate sand (Fig. 4). The algae and foraminifera are visible in thin section, but not in hand sample. Due to exposure on the surface, the rock shows significant weathering and there are many void spaces filled with fine-grained lime mudstone. There is a weathering rind around the exterior of the exposed portion of the rock. The inner portion is not as weathered and is more wellcemented than the exterior of the rock. Some small



**Figure 4.** Seroe Domi sediments including calcareous and siliciclastic sand. Olivine grain from basement rock present.

dolomite crystals can be seen in void spaces of the rock, but overall the rock has not been diagenetically altered to dolostone.

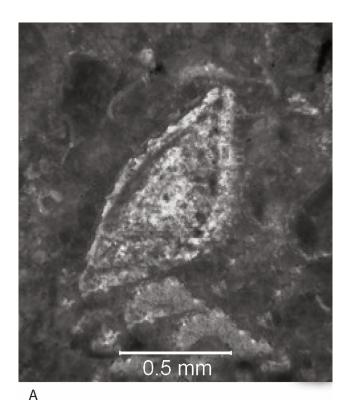
Thin Section Analysis. The thin section showed the presence of foraminifera (Fig. 5), algae and skeletal fragments, but, due to the friable nature of the rock, creating the thin section was difficult. Although impregnated with epoxy, the chip lost grains when put on the lap wheel and grinding the thin section to proper thickness was not successful. A sieve analysis was then conducted to get a better idea of the micro-grains present.

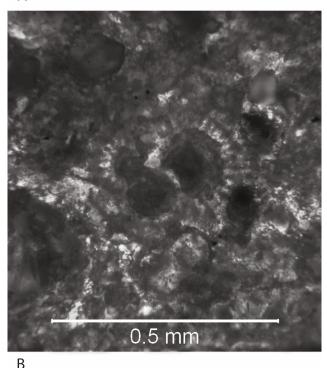
Sieve Analysis. The No. 18 sieve sediments consisted of broken shell material, echinoid spines and clusters of grains. The sieve size was too coarse to catch individual microfossils in the sediment. Foraminiferans recovered at this sieve size were coated with other grains and were not identifiable.

The sediments recovered from the No. 40 sieve contained some microfossils, but, due to dissolution and abrasion, these were unidentifiable. The majority of the sediment from this sieve size included fragments of shells and echinoderm spines, and siliciclastic and carbonate sediments.

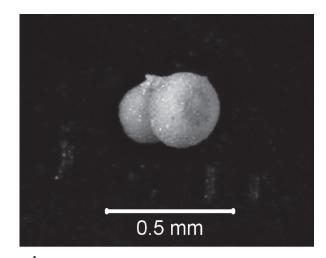
The sediments collected from the finest sieve (No. 80) contained pelagic foraminifera identified as *Globigerina* (Fig. 6A), an ostracode (Fig. 6B), echinoderm spines, fragmented shell material, unidentifiable biologic material thought to be calcareous algae (Fig. 6C), and both calcareous and siliciclastic grains. The material picked from the No. 80 sieve contained many more microfossils than the other sieve sizes.

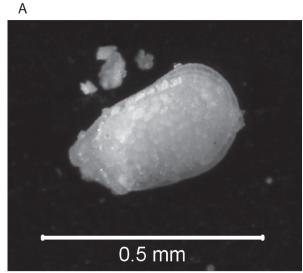
Analysis of the sedimentology and related data of each of the subunits suggests that the fossils were found in Subunit 2 Lithofacies 6. This subunit contains few to no *in situ* coral heads, has not undergone dolomitization, and contains a high proportion of basement-derived siliciclastic materials. The silica content is variable throughout the subunits. Fouke (1994) reported the average silica content for S2:L6 as 25–30%, which is higher than what was found for the rock associated with the fossils, but all of the other subunits from which the fossils could have come have much lower silica contents. Not all parts of the subunit have uniform

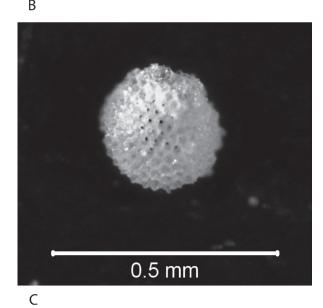




**Figure 5.** Thin section of Seroe Domi sediment. A. Benthic foraminiferan, *Quinqueloculina*? sp. B. Planktic foraminiferan, *Globigerina* sp.







**Figure 6.** Microfossils recovered from sieve No. 80 sample. A. Planktic foraminiferan, *Globigerina* sp. B. Ostracode. C. Calcareous algae?

silica content. The fossils may occur in a portion with less than average silica. The variable silica content could also be a result of differential weathering of the outcrops.

The proposed depositional environment of the subunit and lithofacies is typical of the sediments associated with the fossils. A shallow carbonate shelf talus slope would have been an environment typical of many of the crabs in the collections, which all live within a depth range similar to the <100 m water depth proposed by Fouke (1994). The skeletal fragments associated with the fossils are likely derived from upslope, nearer to the reef. The more fragmentary pieces of decapod material were likely a result of transport from the reef as well.

#### SYSTEMATIC PALEONTOLOGY

Order DECAPODA LATREILLE, 1802
Infraorder BRACHYURA LINNAEUS, 1758
Section RANINOIDA AHYONG et al., 2007
Superfamily RANINOIDEA DE HAAN, 1839
[in 1833–1850]
Family RANINIDAE DE HAAN, 1839 [in 1833–1850]
Subfamily NOTOPODINAE SERÈNE AND UMALI, 1972
Genus RANILIA H. MILNE EDWARDS, 1837

Type Species.—*Ranilia muricata* H. Milne Edwards, 1837 [in 1834–1840], by monotypy.

[in 1834–1840]

Diagnosis.—"Carapace ovate rostrum sharp, needle-like, frontal margin concave on either side of rostrum; upper orbital margin oblique; triangular inner orbital spines followed by smaller, triangular intra- and outer orbital spines, outer margins of spines serrate; small, needle-like anterolateral spine placed about one-quarter the distance posteriorly, anterolateral margin weakly serrate; postfrontal region scabrous; lateral margins parallel, very weakly serrate anteriorly; posterolateral margin weakly concave, sinuous; sternites 1–3 fused, caplike, sternite 4 wide, with short anterolateral projections, with tufts of short setae, concave laterally; posterior portion of sternite 5 narrow; notopodine-type chelae present (chelae very high, with

very reduced fixed finger and long movable finger, large gap between two fingers), ornamented with tufts of short setae" (Karasawa et al., 2014:262).

## RANILIA CONSTRICTA (A. MILNE-EDWARDS, 1880) Figure 7 A-C

Raninops constrictus A. Milne-Edwards, 1880b:35.
Ranilia constricta (A. Milne-Edwards, 1880). Rathbun, 1937:20; Pequegnat, 1970:180; Williams, 1984:265; Manning and Chace, 1990:44; Garassino and De Angeli, 2008:11; Schweitzer et al., 2010:73.

Notopus (Raninoides?) atlanticus Studer, 1883:17. Ranilia atlantica (Studer, 1883). Monod, 1956:47.

Diagnosis.—Carapace oval, fronto-orbital margin sloping toward outer anterolateral spine at about 30°. Rostrum slender, sharp, extending beyond inner orbital spines; four spines along anterior, fourth spine defining distal most point of anterior margin. Small, inclined, single spines along post-frontal region of dorsal surface, followed by rows of wider than long, inclined nodes each bearing six spines, followed by rows of pits.

Description of Material.—Carapace ovate, anterolateral margin serrate, anterolateral spine needle-like; rostrum extends past inner orbital spines, concave on either side of rostrum. Postfrontal region scabrous, small inclined spines and rows of pits (Fig. 7C). Sternum and appendages only partially preserved on one specimen, chelipeds scabrous, granulose (Fig. 7B).

Description.—"Resembling Ranilia muricata. Carapace oval, strongly convex from side to side, drawn to a midsagittal peak anteriorly but more arched posteriorly, slightly convex from front to back; smooth posteriorly but microscopically granulate and with numerous faint, transverse, lightly granulose wrinkles anteriorly. Rostrum slender, extending beyond innermost anterior spine; beaded anterior border of carapace with 4 spines, innermost overhanging base of orbit and fourth slightly behind external angle of front strongest, second and third reduced. Eyestalks strong about 4 times as long as rostrum and capable of being turned back into deep, oblique orbits. Antennules small. Antennae directed forward, slightly longer than eyestalks.

Bases of legs grouped behind midlength of

carapace, arranged in a dorsally curving arc on each side with fifth anterodorsal to fourth. First pair of legs subchelate, stout, flattened dorsally; merus squamous denticulate above with strong spine on superodistal margin; palm almost smooth above; distal margin of hand perpendicular, toothed; dactyl strong, smoothly curved; articles except dactyl with granulose wrinkles laterally. Dactyl of second and third pairs of legs flattened triangular, of fourth legs irregularly falciform, and of fifth narrowly and asymmetrically ovate. Abdomen short and narrow" (Williams, 1984:265).

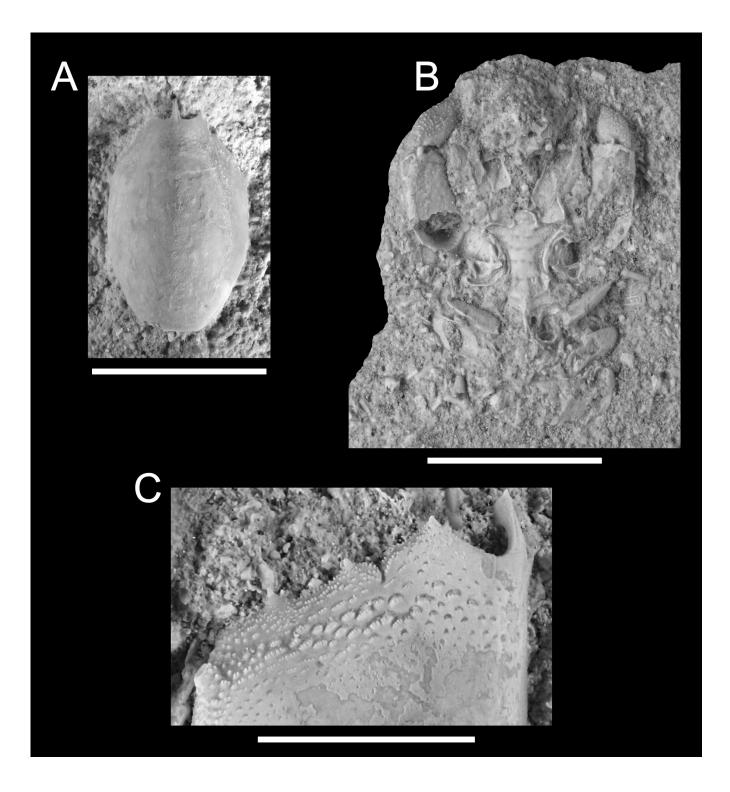
Discussion.—Ranilia constricta most closely resembles Ranilia muricata, but differs in that the rostrum extends past the inner-orbital spines. The angle of the slope along the anterolateral margin from the rostrum to the anterolateral spine is less inclined on R. constricta ( $\sim$ 30°), than on R. muricata ( $\sim$ 40°).

Only carapace material and a single sternum of *Ranilia constricta* are preserved. Raninids are the most common crabs throughout the collection, including the ten carapaces of *R. constricta*.

Ranilia constricta was originally named by A. Milne-Edwards as Raninops constrictus in 1880. Rathbun (1937) later moved the species to the genus Ranilia. Monod (1956) placed Notopus (Raninoides) atlanticus Studer, 1883, within Ranilia, which was considered a junior synonym of R. constricta by Williams (1984).

Modern *Ranilia constricta* inhabit shallow water reef environments up to 365 m (Williams, 1984). *Ranilia constricta* occurs throughout the western (Florida, Gulf of Mexico, Antilles, Colombia, and Brazil), central (Ascension Island) and eastern Atlantic Ocean (from Senegal to Congo) (Garassino and De Angeli, 2008). Fossil occurrences of the species are noted by Garassino and De Angeli (2008) from the Pleistocene of Italy. This occurrence of *R. constricta* in the Pliocene of Curaçao extends both the geographic and age range of the species.

Material.—Ten carapaces, UF 230023, UF 229669, UF 230227, UF 229699, UF 230228, UF 229956, UF 229463, UF 227321, UF 230224, UF 229667. Sternum, UF 227324.



**Figure 7.** *Ranilia constricta* (A. Milne-Edwards, 1880). A. Carapace, UF 227321. B. Sternum, UF 227324. C. Detail of cuticular pattern along the anterior dorsal surface of carapace, UF 230228. Scale bars A, B = 2 cm; scale bar C = 1 cm.

## SUBFAMILY RANINOIDINAE LŐRENTHEY IN LŐRENTHEY AND BEURLEN, 1929 GENUS *RANINOIDES* H. MILNE EDWARDS, 1837 [IN 1834–1840]

Type Species.—*Ranina laevis* Latreille, 1825:268, by monotypy.

Diagnosis.—Carapace longer than wide, rostrum triangular with triangular inner orbital and intra-orbital spines laterally, outer orbital spine bifid, single anterolateral spine. Fissures of varying depth between orbital spines.

## RANINOIDES LAMARCKI A. MILNE-EDWARDS AND BOUVIER, 1923 Figure 8

Raninoides laevis var. lamarcki A. Milne-Edwards and Bouvier, 1923:299.

Raninoides lamarcki (A. Milne-Edwards and Bouvier, 1923). Rathbun, 1937:13; Chace, 1940:5; Pequegnat et al., 1971:pl. 1; Goeke, 1980:146; Soto, 1986; Felder and Camp, 2009:1073.

Diagnosis.—Carapace longer than wide; widest part of carapace just posterior to anterolateral spine and narrowing posteriorly. Outermost orbital and anterolateral spines reduced when compared to other species of *Raninoides*. No spine at base of dactyl on chelae.

Description of Material.—Only partial carapaces and chelae are preserved. Fronto-orbital region narrower than the widest point of carapace. Orbital spines short; fissures between orbital spines open, shallow, parallel; outer orbital spine bifid, longest of orbital spines; post frontal ridge present.

Description.—"Akin to *Raninoides louisian-ensis* Rathbun, 1933. The tooth on either side of the front, bounded by the sinuses, is devoid of a spine. The outer orbital spine and the hepatic spine are reduced. The arm lacks a spine. The dactyl of the third ambulatory is wider than in *R. louisianensis*" (Rathbun, 1937:13).

Emendation to the Description.—Carapace much longer than wide, widest point about one-quarter of the distance posteriorly, narrowing toward posterior margin. Carapace very similar to *R. louisianensis*, but with greatly reduced orbital spines.

Discussion.—Raninoides lamarcki closely



**Figure 8.** *Raninoides lamarcki* A. Milne-Edwards and Bouvier, 1923. Partial carapace, UF 230380. Scale bar = 2 cm.

resembles *R. louisianensis*, but the orbital spines are reduced in length in the former. Only specimens of *R. lamarcki* with partial carapaces and partial chelae are preserved in the Seroe Domi Formation. This is the first fossil occurrence of *R. lamarcki*, extending the age range of the species to the Pliocene. Modern members of the species are known to inhabit the southern Gulf of Mexico, Cuba, the Straits of Florida, and the Greater Antilles to Panama (Goeke, 1980; Soto, 1986; Felder and Camp, 2009). *Raninoides lamarcki* inhabits waters

between 46–366 m and prefers to live on rubble, shell hash, and unlithified sediments (Felder and Camp, 2009). The fossil specimens from Curação were found in sedimentary rocks that correspond to the modern environments of *R. lamarcki*.

Material.—Carapace, UF 230380. Two carapaces with partially articulated chelae, UF 229890.

## Section EUBRACHYURA DE SAINT LAURENT, 1980 Superfamily CALAPPOIDEA DE HAAN, 1833 [in 1833–1850] Family CALAPPIDAE DE HAAN, 1833 [in 1833–1850] Genus CALAPPA WEBER, 1795

Type Species.—Cancer granulatus Linnaeus, 1758, by the subsequent designation of Latreille (1810).

Diagnosis.—Carapace ovate, wider than long, widest near posterior margin of carapace; front narrow, triangular; orbits directed forward; anterolateral margin arcuate and crenulate, dentate or granular; posterolateral margin with spined posterolateral flange; carapace regions poorly defined; axial regions best defined of all regions; carapace ornamented with large tubercles often arranged into rows; chelae stout, narrowing proximally.

## CALAPPA GALLOIDES STIMPSON, 1859 Figure 9

Calappa galloides Stimpson, 1859:71. Manning and Chace, 1990:45; Almeida et al., 2007:12; Almeida and Coelho, 2008:190.

Calappa gallus (Herbst, 1803:18 and 46) (part). Rathbun, 1937:214; Monod, 1956:100; Fausto-Filho, 1974:10; Manning and Holthuis, 1981:51.

Diagnosis.—Deep grooves on carapace between hepatic and gastric region. Transverse, non-continuous, granulose rows on posterior third of carapace. Cheliped broad; outer and upper surface of palm tuberculate.

Description of Material.—Chelae high, tubercles covering outer surface of manus. Tubercles large along upper surface, decreasing in size toward fixed finger; movable finger with large curved tubercle at base.

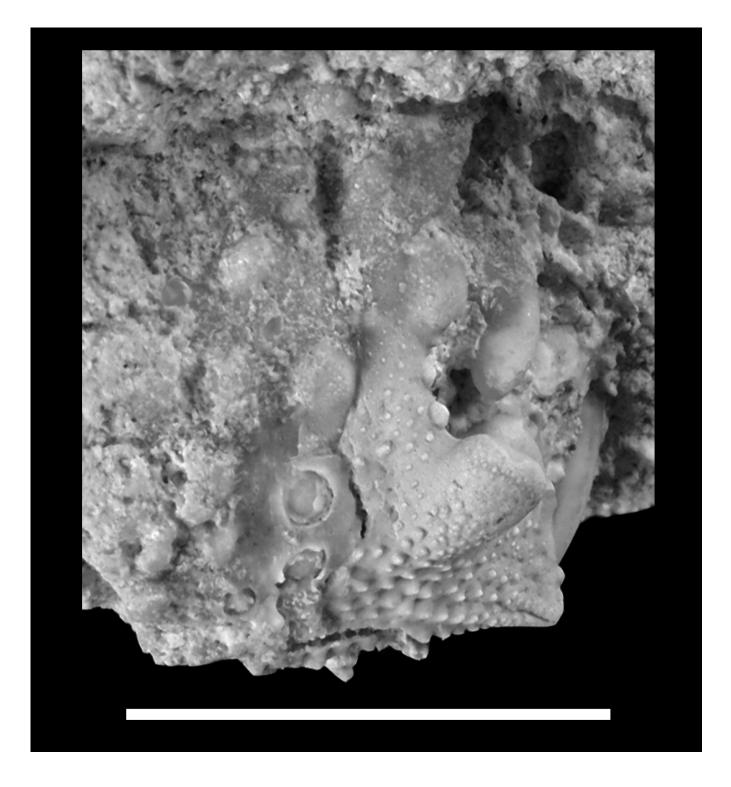
Description.—"Extreme length of carapace

varying from about three-fourths to five-sixths of breadth; anterior two-thirds covered with tubercles, posterior one-third with short, transverse, granulate ridges; anterolateral margin crenulate; posterior border slightly arcuate, finely beaded, unarmed; clypeiform expansions well developed, bearing six strong teeth with beaded edge, two teeth behind and three in front of posterolateral tooth. Orbits directed forward, only slightly upward. Rostrum wholly in advance of orbits, laminate, and with four sub-equal, blunt teeth. Hepatic region defined by furrows; a large median tubercle in front of cervical suture. Upper surface of wrist tuberculate. Wing-like expansion near end of arm 4-toothed, About 10 tubercles on upper half of outer surface of palm; on the lower half the tubercles widen into crenulate laminae; on and near the fixed finger are small, round, flat tubercles" (Rathbun, 1937:214, as Calappa gallus).

Discussion.—Rathbun (1937) referred specimens to *Calappa gallus* (Herbst, 1803), considering *C. galloides* to be a junior synonym. Manning and Chace (1990) considered the specimens referred to *C. gallus* by Rathbun (1937), Monod (1956), Fausto-Filho (1974), and Manning and Holthuis (1981) as being members of *C. galloides*. They maintained *C. gallus* as a separate species. The species are very similar, but possess slight differences in morphology and geographic distribution. *Calappa galloides* was described by Stimpson (1859:71) in his original description as, "Very closely allied to *C. gallus* of the Pacific, but is less convex, and less strongly tuberculated. The front or rostrum is distinctly quadridentate."

The fossil specimen was assigned to *Calappa galloides* because of the tuberculate nature of the cheliped that distinguishes *C. galloides* from many other *Calappa* species. The tubercles on the specimen are large and widely spaced. The chelipeds of *C. gallus* possess much more closely spaced, smaller tubercles than *C. galloides*.

Modern representatives of *Calappa galloides* occur throughout the Atlantic, in Bermuda, Florida, the Gulf of Mexico to Brazil, Ascension Island and the eastern Atlantic (Felder and Camp, 2009). They inhabit soft substrates, specifically rubble and shell



**Figure 9.** *Calappa galloides* Stimpson, 1859. Chela, UF 229672. Scale bar = 2 cm.

hash sediments up to 220 m water depth (Felder and Camp, 2009). No previous fossil occurrences of *C. galloides* have been reported.

Material.—Cheliped, UF 229672.

### Family AETHRIDAE DANA, 1851 Genus *HEPATUS* LATREILLE, 1802

Type Species.—*Calappa angustata* Fabricius, 1798:347, by monotypy (= *Cancer pudibundus* Herbst, 1785:199).

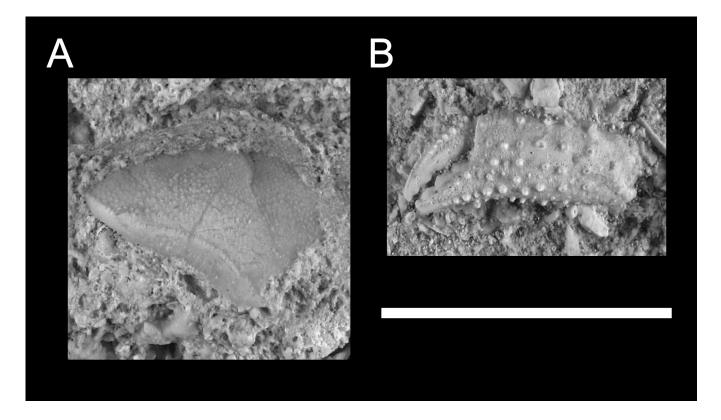
Diagnosis.—"Carapace broad, convex, regularly arcuate in front, strongly narrowing behind; hepatic regions very large, branchial regions very small. Front narrow, straight or nearly so, rather prominent, and situated above the level of the lateral border of carapace, which is prolonged beneath the orbits to join the margin of buccal cavity. Orbits small, circular, on a level with front. Antennulae very oblique. Antennae at inner angle of orbit. Buccal cavity very narrow forward and triangular, extending as far as level of lower border of orbits and entirely covered by outer maxillipeds, of

which the merus is triangular and has straight inner margin, under which are concealed the following segments. Chelipeds strong, and when flexed fit closely against lower surface of body. Hands with a superior crest, fingers inclined a little downward and inward. Ambulatory legs smooth, unarmed" (Rathbun, 1937:234).

## HEPATUS LINEATINUS COLLINS AND TODD IN TODD AND COLLINS, 2005 Figure 10

Diagnosis.—Carapace broad, granular; gastric region inflated. Posterolateral margins concave, beaded. Small spine at beginning of the concavity of posterolateral margin. Five rows of tubercles covering manus, lower two rows converge at distal propodus terminus, upper two rows converging at dactylus terminus. Occlusal surface serrated, dentate.

Description of Material.—Carapace partially preserved, broad, granular. Posterolateral margins concave, beaded, posterolateral spine broken.



**Figure 10.** *Hepatus lineatinus* Collins and Todd *in* Todd and Collins, 2005. A. Left lateral side of carapace showing the beaded posterolateral margin, UF 227322. B. Chela, UF 229673. Scale bar = 2 cm.

Rows of tubercles on cheliped converging distally on propodus. Large serrations on occlusal surfaces of both fingers.

Description.—"Carapace length about fourfifths of the width (holotype, 70.4 percent), widest at spinule cluster before lateral angle, strongly arched longitudinally and moderately so transversely, becoming thin towards the margins. Anterolateral margin evenly rounded and lined with 16 or 17 tridenticulate spines, gradually increasing in size from behind the orbit to the lateral angle. Even-sized granules, with larger ones interspersed, line the strongly convex posterolateral margins and continue above the posterior margin which is also granulate and narrower than the orbitofrontal margin. The orbitofrontal margin, occupying about one-third of the carapace width (30.0-37.7%, according to growth size) is raised above the level of the anterolateral margins; the front is weakly bilobed with a faint median sinus, thickened and granuated. Small, subovate orbits directed slightly upwards. Bent, truncated orbital peduncles densely pitted. Smooth upper orbital margins fairly thick, pierced by two closed notches and coarsely granulated laterally round to the lower margin. The lower margin of the suborbital cavity is coarsely beaded and clearly visible from above. The regions and lobes are mostly well-defined, tumid in younger forms, the tumidities dispersing as growth advances. The cervical furrow, obscured by prominent uro/cardiac depression, curves gently across the midline, broadens round the mesogastric lobe and becomes obsolete before reaching the margin. Protogastric, mesogastric, epibranchial and metabranchial lobes are all more sharply defined in young individuals; in older forms the protogastric lobes are merely tumid. All tumidities crowned with a cluster of coarse and fine granules, those on the epibranchial and metabranchial lobes become linear, curving latero-posteriorly. A subrectangular urogastric lobe weakly separated from a large, elongate shield-shaped cardiac region. Pits of several diameters crowd the dorsal surface.

The male abdominal trough is widest at 6<sup>th</sup> somite; 1<sup>st</sup>–4<sup>th</sup> sternites fused, although defined by grooves, 1<sup>st</sup>/3<sup>rd</sup> sternites triangular, 1<sup>st</sup> /2<sup>nd</sup> sepa-

rated from 3<sup>rd</sup> by a low, weakly granulate to smooth ridge, base of 3<sup>rd</sup> overlaps head of 4<sup>th</sup> sternite and separated from it by an oblique groove; 4<sup>th</sup> sternites subquadrilateral, thickened along the coxigeal margin. 'Press-buttons' (Guinot and Bouchard, 1998) to secure the abdomen on the pentagonal 5<sup>th</sup> sternites; 6<sup>th</sup> sternites are rather more rounded. Large, subtriangular episternites extend half the length of the preceding sternites. The (male) abdomen extends to 3<sup>rd</sup>/4<sup>th</sup> sternites, the 'trough' extending as a suture to the 1<sup>st</sup> sternites. The telson is as long as the 4<sup>th</sup> sternite; there is a transverse pair of nodes on the 4<sup>th</sup> somite and thin spurs from a ridge lining its posterior margin embrace the articulating node of the 4<sup>th</sup> coxae.

The chelipeds are more or less homochelous; merus is about as long as the manus, coarsely granulated distally along the lower and carpal margins; the triangular outer surface of the carpus has three rows of granules, the lower two united proximally. The distal height of the propodus is a little more than half its length, five or six triangular spines line the upper margin. On the right manus the outer surface is lined with five rows of tubercles; the upper row consists of four tubercles extending from the base of the dactylus; the 2<sup>nd</sup> row has four of five tubercles in a distinct curve; the 3<sup>rd</sup> row consists of seven separated tubercles, the median 3 tripartite; the 4<sup>th</sup> row, continuing the upper ridge on the fixed finger, has seven or eight tripartite groupings running together; 5th row continues the lower, granulated ridge on the fixed finger as a continuous row of nine, still vaguely grouped, tubercles joining the 4<sup>th</sup> row proximally. The robust fixed finger is about one-third the length of the propodus and weakly deflexed. There are brief lines of tubercles on the dactylus. Details of the buccal margin correspond to those of *H. lineatus*.

A juvenile specimen from the lower Gatun Formation of Panama is remarkable in having a well-developed bopyriform swelling occupying the entire left metabranchial region; granules topping the original node are disturbed, otherwise no distortion of carapace outline occurs" (Todd and Collins, 2005:69–70).

Discussion.—Only a partial carapace and a

cheliped are preserved, but the posterior portion of the carapace closely resembles the illustrations of *Hepatus lineatinus* in Todd and Collins (2005:pl. 2, figs. 8–12). The cheliped matches the description of the chelipeds of *H. lineatinus*, covered in granules, which are more widely spaced proximally and converge toward the distal end of the cheliped.

The range of *Hepatus lineatinus* is from the middle Miocene to the early Pleistocene of Costa Rica and Panama (Todd and Collins, 2005), and the early Pliocene of Curaçao (herein). It is known only from fossil occurrences.

Material.—Partial carapace, UF 227322. Cheliped, UF 229673.

## Superfamily LEUCOSIOIDEA SAMOUELLE, 1819

### Family LEUCOSIIDAE SAMOUELLE, 1819 Genus *MYROPSIS* STIMPSON, 1871

Type Species.—*Myropsis quinquespinosa* Stimpson, 1871:157, by monotypy.

Diagnosis.—"Carapace subglobular, narrowed anteriorly; cardiac and intestinal regions defined; five posterior spines. The anterior extremity of the septa of the branchial channels does not extend beyond orbits. Basal article of antennules indurated and crested. Chelipeds very long and slender. Male abdominal segments 3–6 fused" (Rathbun, 1937:164).

## MYROPSIS QUINQUESPINOSA STIMPSON, 1871 Figure 11

Myropsis quinquespinosa Stimpson, 1871:157. A. Milne-Edwards, 1880b:21; A. Milne-Edwards and Bouvier, 1902:110; Rathbun, 1937:164; Chace 1940:24; Williams, McCloskey, and Gray, 1968:46; Pequegnat, 1970:179; Felder, 1973:39; Powers, 1977:38; Williams, 1984:287.

*Myropsis constricta* A. Milne-Edwards, 1880b:21. A. Milne-Edwards and Bouvier, 1902:110.

Myropsis goliath A. Milne-Edwards, 1880b:21. A. Milne-Edwards and Bouvier, 1902:111.

Diagnosis.—Carapace subspherical, granular, narrowing anteriorly and posteriorly; five spines posteriorly, two pairs on posterolateral margins, one at posterior tip of carapace; one pair of spines located on the posterolateral margin of the branchial region, the second pair of spines located

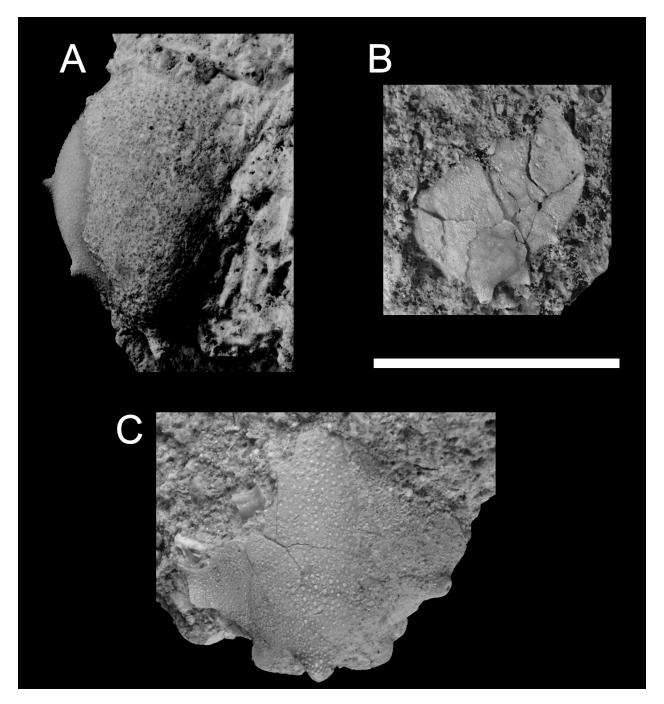
centrally on posterolateral margin on either side of the fifth spine, which is located at posterior tip of carapace.

Description of Material.—Only carapaces preserved. Carapace rounded, subspherical, granulose. Five spines on posterior half of carapace, outer spines on posterolateral branchial margin, posterior pair of spines located on posterolateral margin, fifth spine in center of posterior margin, intestinal region, conical, upturned. Posterior pair of spines frame central spine when viewed from above.

Description.—"Body and appendages everywhere granulated except the ambulatory dactyls. Carapace, exclusive of spine, a little longer than wide; intestinal and cardiac regions defined by rather deep furrows on either side; hepatic region slightly swollen; cervical sulcus partially defined at hepatic region; granules of surface distant from one another by spaces equal to two or three times their diameter; anterolateral margin slightly sinuous. Of the five posterior spines, the median one is intestinal; the intermediate pair is marginal and in the adult equally long and more evenly conical; the outer pair very small, with tip strongly upturned, is situated on the branchial region over the insertion of the posterior legs. There is a tubercle at middle of lateral margin and another on the hepatic margin; also between the two and directly behind the hepatic suture a small granulated tubercle. Frontal teeth elevated, tips subacute.

Merus of chelipeds cylindrical, longer than carapace exclusive of spine, granules densely crowded; granules of hand smaller, also crowded; hand broader than thick, upper face nearly three times as long as wide; fingers longer than palm, armed within with minute and acute teeth varying in size. Ambulatory feet naked (except dactyli), cylindrical, and microscopically granulated; those of first pair one and two-thirds times as long as carapace; dactyli with two fringes of hair on upper and outer surface" (Rathbun, 1937:166).

Discussion.—Eight carapaces are preserved that show the characteristic five posterior spines of *Myropsis quinquespinosa*. The species is known from the modern Atlantic Coast from Massachusetts to the Gulf of Mexico, throughout the Caribbean and southern Atlantic as far as Brazil, inhab-



**Figure 11.** *Myropsis quinquespinosa* Stimpson, 1871, A. Left lateral margin of carapace, UF 227323, B. Right lateral and posterior margin of carapace, UF 230586, C. Posterior margin of carapace, UF 229962. Scale bar = 2 cm.

iting depths of 84 to 521 m (Rathbun, 1937), and living on soft and broken shell substrates (Felder and Camp, 2009). No fossil specimens of the species or genus have been reported previously. The presence of *M. quinquespinosa* in the Seroe Domi

Formation extends the age range of the species and genus to the Pliocene.

Material.—Eight carapaces, UF 229424, UF 229885, UF 229963, UF 229659, UF 227323, UF 229962, UF 230029, UF 230586.

## Superfamily MAJOIDEA SAMOUELLE, 1819 Family MITHRACIDAE MACLEAY, 1838 Genus *MAGUIMITHRAX* KLOMPMAKER ET AL., 2015

Type Species.—*Maia spinosissima* Lamarck, 1818:241, by original designation.

Diagnosis.—Carapace convex, slightly longer than wide, covered in spines. Orbital margins with 4 or 5 upper spines and 4 suborbital spines; lateral margins with 6 spines; axial regions well-defined. Chelipeds long, strong; fingers with spoonlike tips. Pereiopods long, strong, spinose (adapted from Klompmaker et al., 2015:8).

### MAGUIMITHRAX SPINOSISSIMUS (LAMARCK, 1818) Figure 12

Maia spinosissima Lamarck, 1818:241.

Mithrax spinosissimus (Lamarck, 1818). H. Milne Edwards, 1832:9; White, 1847:6; Gibbes, 1850:172; Guerin Meneville, 1857:25; Stimpson, 1860:188; Desbonne and Schramm, 1867:4; von Martens, 1872:81; A. Milne Edwards, 1875:100; Kingsley, 1880:390; Miers, 1886:86: Aurivillius, 1889:57, Rathbun, 1892:261; Nutting, 1895:209; Rathbun, 1897:9; Rathbun, 1898:259; Torralbas, 1900; Rathbun, 1901:66; Rathbun, 1919:344; Rathbun, 1921:82; Rathbun, 1933:29; Jones, 1969:380; LaTourette, 1974:99, 125; Hazlett and Rittschoft, 1975:101–118; Voss, 1976:118, 119; Provenzano and Brownell, 1977:735–752; Colin, 1978:366, 368; Gore, Scotto and Yang, 1982:525; Valdes-Munoz, 1986:11, 15; Abele and Kim, 1986:522, 523; Wagner, 1990:14–17; Ng et al., 2008.

Maja (Mithrax) spinosissima (Lamarck, 1818). De Haan, 1837, pl. F in de Haan, 1833–1850.

Mithrax spinosissima (Lamarck, 1818). Gundlach, 1887:117. Mithrax hispidus Doflein, 1899:179.

Mithrax (Mithrax) spinosissimus (Lamarck, 1818). Young, 1900:88; Rathbun, 1925:383, pl. 135; Chace, 1940:67; Williams, 1965:254; Gómez and Ortiz, 1976:15; Powers, 1977:58; Williams, 1984:335.

Damithrax spinosissimus (Lamarck, 1818). Windsor and Felder, 2014:160.

Maguimithrax spinosissimus (Lamarck, 1818). Klompmaker et al., 2015:8.

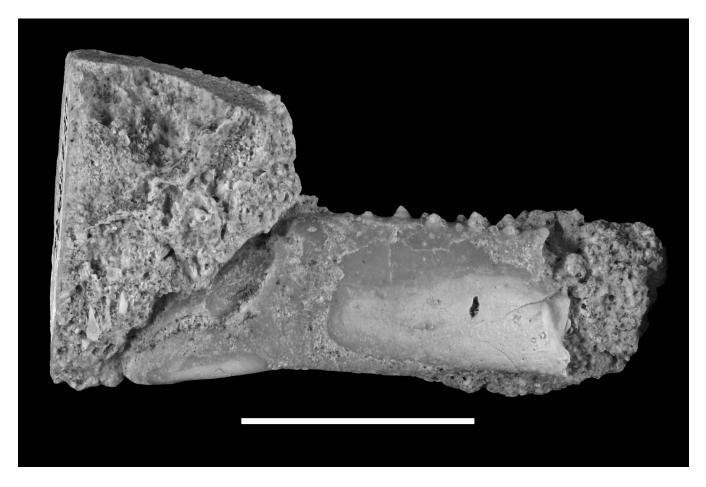
Diagnosis.—As for genus; monospecific.

Description of Material.—Chela long; manus of cheliped armed with spines along upper surface; spines irregularly spaced and shaped, not a single row. Tips of dactyl and propodus broken, spoon-

like tip missing. Tubercles covering chela.

Description.—"The carapace is about as broad as long. Its surface is rough with short tubercles, and it is nearly naked. Laterally the tubercles become more and more spine-like. The rostrum is bifid, relatively long, obliquely truncate and granulate. At the base of the two horns of the rostrum there are two stout spines present, and behind these two others but farther apart. Basal antennal segment with three spines of which the first, situated near the base of the first movable article, is so strongly reduced in adults that it seems absent at first sight; the second spine is largest and reaches as far forward as the rostrum, the third is half as long as the second. The antennae are one seventh of the carapace length in large specimens and laterally bordered by a few short hairs. The orbit is armed with one spine below (not counting the third basal antennal spine), one at the outer angle and five above. These five are formed by one preorbital spine, one postorbital spine, and three smaller spines in between. These spines sometimes are bifid at the tip. The carapace has five anterolateral spines and one posterolateral spine; the first two anterolateral spines, of which the first is situated on the hepatic region, are bifid. The last anterolateral spine and the posterolateral spine are smaller than the first four anterolateral spines.

The chelipeds of the male are stouter, and up to 1.5 times longer, than the first pair of ambulatory legs; the merus is armed with numerous spines of which up to ten are on the posterior margin, the others are irregularly disposed; the carpus is covered on the outer side with numerous unequal tubercles or spines, of which about five are on the inner margin; the palm is high, compressed, armed above with an irregular row of up to 11 tubercles or spines and on the inner surface with two to our spines in the proximal half; the fingers are curved, with a wide gape; only the distal half of their cutting edges is denticulate, and there is a larger denticle in the middle of the edge of the dactylus. In the female the chelipeds are as long as the first pair of ambulatory legs. The first pair of ambulatory legs is 1.5 times as long as the carapace (including the rostrum). The ambulatory legs are coarsely



**Figure 12.** *Maguimithrax spinosissimus* (Lamarck, 1818). Chela, UF 229982. Scale bar = 2 cm.

hairy and have two or three rows of spines on the upper border of the merus, carpus and propodus, the spines of the most anterior row are largest and all spines increase in size distally. There are two to four spines on the anterior side of the propodus.

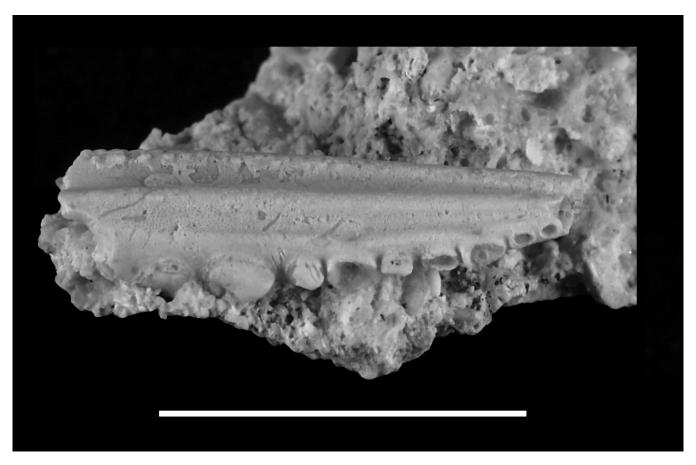
The male gonopod is long and stout. It is dorsoventrally flattened, slightly bent distally and tapers to a rather sharp point. The genital opening of the female is on the inner anterior part of the genital prominence" (Wagner, 1990:15–17).

Discussion.—This species was originally placed in *Maia* and subsequently has been referred to *Mithrax* Desmarest, 1823, for over 150 years (see synonymy above). More recently, the species was referred to *Damithrax* Windsor and Felder, 2014, and then to *Maguimithrax* Klompmaker et al., 2015. The identification of *Maguimithrax spinosissimus* was made from the chela which exhibits the

spines along the upper margin of the manus characteristic of the species. Many species of *Mithrax* do not have spines on the palm or have a regularly spaced, single row of spines. Only partial appendages are preserved of this species.

Modern members of *Maguimithrax spinosis-simus* are known from the Atlantic off the coast of North Carolina to southern Florida, and from the Caribbean (Felder and Camp, 2009). The species typically inhabits depths of 1 to 179 m and prefers shell hash beds and rubble bottoms (Felder and Camp, 2009). Fossil specimens of *M. spinosissimus* were reported by Donovan et al. (2003) from the Pleistocene of Jamaica. The occurrence of *M. spinosissimus* in the Seroe Domi Formation extends the known range of the species to the Pliocene.

Materials.—Cheliped, UF 229982. Pereiopod, UF 229423.



**Figure 13.** *Achelous sebae* (H. Milne Edwards, 1834 [in 1834-1840]). Dactyl, UF 229437. Scale bar = 1 cm.

## Superfamily PORTUNOIDEA RAFINESQUE, 1815 Family PORTUNIDAE RAFINESQUE, 1815 Subfamily PORTUNINAE RAFINESQUE, 1815 Genus *ACHELOUS* DE HAAN, 1833 [in 1833–1850]

Type Species.—*Portunus spinimanus* Latreille, 1819:47, by monotypy.

Diagnosis.—"Carapace narrow, the anterolateral margin being the arc of a circle with short radius, whose center is near center of cardiac region. Last spine of anterolateral margin usually not much if any larger than the others" (Rathbun, 1930:62).

Discussion.—Schweitzer and Feldmann (2015) discussed the usage of subgenera within *Portunus* Weber, 1795. *Achelous* has been used as a genus in its own right in recent publications;

however, it can be difficult to differentiate between *Achelous* and *Portunus* in fossils (Schweitzer and Feldmann, 2015).

## ACHELOUS SEBAE (H. MILNE EDWARDS, 1834) [IN 1834–1840] Figure 13

Lupea sebae H. Milne Edwards, 1834 [1834–1840]:455.

Neptunus sebae (H. Milne Edwards, 1834). A. Milne-Edwards, 1861:329.

*Achelous sebae* (H. Milne Edwards, 1834). Smith, 1869:34; Verrill, 1908:380; Mantelatto et al., 2009:561; Collins et al., 2009a; Donovan, 2011:48.

Lupa biocellata Forns in Torralbas, 1900:57.

Portunus (Achelous) sebae (H. Milne Edwards, 1834). Rathbun, 1901:46; Rathbun, 1930:79; Ng et al., 2008:151.

*Portunus sebae* (H. Milne Edwards, 1834). Felder and Camp, 2009:1080; Schweitzer et al., 2010:112.

Diagnosis.—Carapace broad, convex. Anterolateral margin serrate. Manus compressed,

deep longitudinal groove, spine at articulation with carpus.

Description of material.—Dactyl straight, ridges along longest dimension, merging toward terminus, rounded denticles along occlusal surface.

Description.—"Has much in common with P. (A.) ordwayi, namely, the elevations of the carapace, the shape of the front and orbit, the character of the lateral teeth, the fringes on the inner-upper margin of the cheliped, and the larger size; has relatively wider carapace, not including the lateral spine; a large red spot on the postero-lateral slope, which persists in alcohol; all the spines except those of the front and inner orbit have dark horny tip; the lateral spine is as long as the next  $2\frac{1}{2}$  teeth in the old; chelipeds more elongate, less enlarged at middle of merus and manus, one spine at extremity of ischium, six or five spines on inner margin of merus veiled by a fringe of long hair, posterior distal spine same length as proximal spine of manus; upper-outer surface of palm elongate, not enlarged or iridescent but bearing a granulated carina just below upper margin; all the carinae of the palm, 5 outside and 2 inside, more or less fringed with hair; two superior spines, one at distal third, a small one at extremity; on the basis of swimming paddles a curved spine directed upward, outward ad forward; a spine at postero-distal angle of merus, and a second smaller spine on the distal margin next to the articulation with the carpus" (Rathbun, 1930:79, as *P.* (*A*.) sebae).

Discussion.—The history of the naming and synonymies of *Achelous sebae* is complicated and remains to be fully resolved. The genus *Portunus* was at one point divided into many subgenera, *Portunus (Achelous)* being one of them. Many authors still use the name *P. (A.) sebae*, but the phylogenetic analysis of Mantellato et al. (2009) supported raising *Achelous* to the level of genus once more. Since then, several papers have referred to the species as *Achelous sebae* (Collins et al., 2009a; Donovan, 2011), which we follow here. The identification of this specimen was based on the similarity of the dactyl to that of *Achelous sebae* illustrated by Collins et al. (2009a, pl. 4, figs. 5, 6), identified from the Pleistocene Port Morant Formation of

Jamaica and the first report of a fossil of the species from the Caribbean

Achelous sebae is known from the Pleistocene of Jamaica, but no other fossil specimens of the species have been reported elsewhere in the Caribbean. The discovery of *A. sebae* in the Seroe Domi Formation extends the age range of the species to the Pliocene. Modern *A. sebae* inhabit the Gulf of Mexico, Bermuda, Cuba, the southern Antilles, and northern South America (Felder and Camp, 2009). They are demersal, living between 1 to 18 m water depth on soft and rubble substrates (Felder and Camp, 2009).

Material.—Two dactyls, UF 229437, UF 229436.

#### UNIDENTIFIED MATERIAL

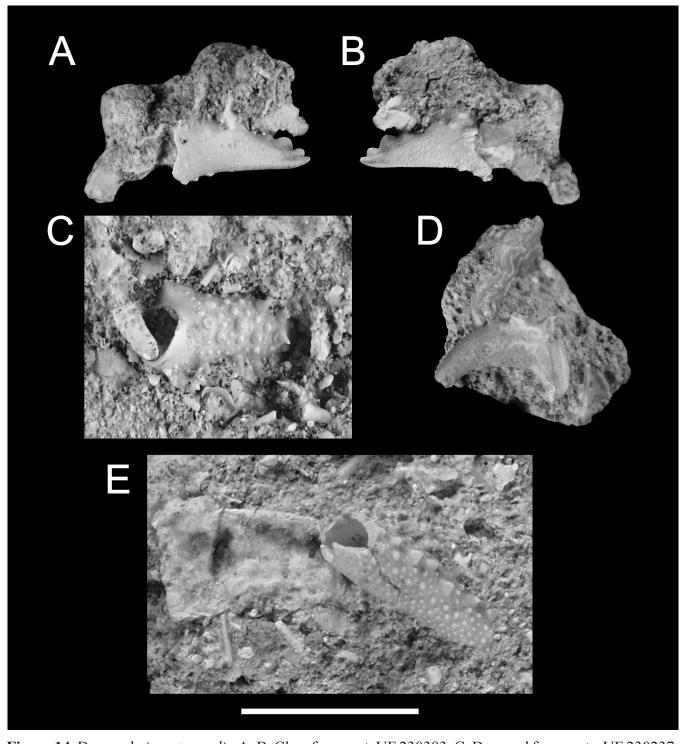
Much of the material in the collection exhibited excellent preservation, but was unidentifiable (e.g., Fig. 14A–E).

## CARIBBEAN DISTRIBUTION OF BRACHYURAN GENERA

The Caribbean and Gulf of Mexico have a high diversity of decapod crustaceans, both present and past. With a variety of habitats and oceanographic conditions present, a wide range of decapod species inhabit the region and can be found in the fossil record of many of the Caribbean Islands. The relative diversity of the brachyuran decapods from the Seroe Domi Formation of Curaçao has been compared to those of the Pliocene fossil record throughout the region.

Genera from the Caribbean and Gulf of Mexico were analyzed in order to determine areas of high diversity. These data were compared with the relative diversity of the decapods of the Seroe Domi Formation as compared to other deposits of similar age. Genera were used as a basis of comparison because many of the studies which have summarized decapods from Caribbean units include taxa/specimens that were fragmentary and identified only to this level.

Seventeen Caribbean and Gulf of Mexico Pliocene deposits were identified in a literature review of decapods in the region (Table 2). The formations vary in diversity, with the most diverse



**Figure 14.** Decapoda *incertae sedis*. A, B. Claw fragment, UF 230383. C. Decapod fragments, UF 230237. D. Small partial dactyl, UF 230525. E. Fragment of pereiopod with small spines preserved, UF 230392. Scale bar = 1 cm.

unit being the Layton Formation (Bowden Member) of Jamaica (Collins and Portell, 1998). The Bowden Member is characterized by fragmentary preservation of the decapod fossils, many of which

are represented by a single dactyl or cheliped. Of 26 genera of decapod crustaceanss preserved in the unit, 22 are brachyurans. The Bowden Member has yielded the most diverse fossil decapod fauna from

**Table 2.** Summary of Pliocene Caribbean brachyuran taxa. Compiled from Collins and Morris (1976), Collins and Portell (1998), Donovan et al. (2003), Collins and Donovan (2004), Portell and Collins (2004), Todd and Collins (2005), Collins et al. (2009a, b), Vega et al. (2009), Klompmaker et al. (2015), and Luque et al. (2017).

Location	Age	Formation	Genus
Aruba	upper Pliocene	Seroe Domi Fm.	Mursia Leach in Desmarest, 1822
Costa Rica	lower Pliocene	Rio Banano Fm.	Hepatus Latreille, 1802
Costa Rica	lower Pliocene	Rio Banano Fm.	Leucosilia Bell, 1855
Costa Rica	lower Pliocene	Rio Banano Fm.	Portunus Weber, 1795
Costa Rica	lower Pliocene	Rio Banano Fm.	Euphylax Stimpson, 1860
Costa Rica	lower Pliocene	Penito Fm.	Hepatus Latreille, 1802
Costa Rica	upper Pliocene	Moin Fm.	<i>Cryptosoma</i> Brullé in Barker-Webb and Berthelot, 1840
Costa Rica	upper Pliocene	Moin Fm.	Sandomingia Rathbun, 1919
Costa Rica	upper Pliocene	Moin Fm.	Lophopanopeus Rathbun, 1898
Costa Rica	upper Pliocene	Moin Fm.	Heteractaea Lockington, 1877
Costa Rica	upper Pliocene	Moin Fm.	Thoe Bell, 1836
Costa Rica	upper Pliocene	Moin Fm.	Micropanope Stimpson, 1871
Costa Rica	upper Pliocene	Moin Fm.	Persephona Leach, 1817
Costa Rica	upper Pliocene	Port Limon Fm.	Calappa Weber, 1795
Costa Rica	upper Pliocene	Port Limon Fm.	Cardisoma Latreille, 1825
Cuba	Pliocene	Canimar Fm.	Mithrax Latreille, 1817
Cuba	Pliocene-Pleistocene	Vedado Fm.	Mithrax Latreille, 1817
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Euphylax Stimpson, 1860
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Scylla De Haan, 1833
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Eurypanopeus A. Milne-Edwards, 1880
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Rathbunites Schweitzer, Dworschak, and Martin, 2011
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Sandomingia Rathbun, 1919
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Mesorhoea Stimpson, 1871
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Portunus Weber, 1795
Dominican Republic	upper Miocene-lower Pliocene	Gurabo Fm.	Iliacantha Stimpson, 1871
Dominican Republic	lower Pliocene	Mao Fm.	Calappa Weber, 1795
Dominican Republic	lower Pliocene	Mao Fm.	<i>Cryptosoma</i> Brullé in Barker-Webb and Berthelot, 1840
Dominican Republic	lower Pliocene	Mao Fm.	Hepatus Latreille, 1802

 Table 2. Continued.

Location	Age	Formation	Genus
Florida	upper Pliocene	Intracoastal Fm.	Ranilia H. Milne Edwards, 1837
Florida	upper Pliocene	Intracoastal Fm.	Calappa Weber, 1795
Florida	upper Pliocene	Jackson Bluff Fm.	Euprognatha Stimpson, 1871
Florida	upper Pliocene-lower Pleistocene	Tamiami Fm.	Calappa Weber, 1795
Florida	upper Pliocene-lower Pleistocene	Tamiami Fm.	Damithrax Windsor and Felder, 2014
Florida	upper Pliocene-lower Pleistocene	Tamiami Fm.	Menippe De Haan, 1833
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Calappa Weber, 1795
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Hepatus Latreille, 1802
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Persephona Leach, 1817
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Mithrax Latreille, 1817
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Chlorilia Dana, 1851
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Hyas Leach, 1814
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Rochinia A. Milne-Edwards, 1875
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Pitho Bell, 1836
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Mesorhoea Stimpson, 1871
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Platylambrus Stimpson, 1871
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Cancer Linnaeus, 1758
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Callinectes Stimpson, 1862
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Ovalipes Rathbun, 1898
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Eurypanopeus A. Milne-Edwards,
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	1878 Micropanope Stimpson, 1871
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Panopeus H. Milne Edwards, 1834
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Pilumnus Leach, 1816
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Eriphia Latreille, 1817
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Eurytium Stimpson, 1859
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Portunus Weber, 1795

 Table 2. Continued.

Location	Age	Formation	Genus
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Neopanope A. Milne-Edwards, 1880
Jamaica	upper Pliocene	Bowden Mbr., Layton Fm.	Tetraxanthus Rathbun, 1898
Panama	lower Pliocene	Cayo Agua Fm.	Cryptosoma Brullé in Barker-Webb and Berthelot, 1840
Panama	lower Pliocene	Cayo Agua Fm.	Leucosilia Bell, 1855
Panama	lower Pliocene	Cayo Agua Fm.	Pilumnus Leach, 1816
Panama	lower Pliocene	Cayo Agua Fm.	Speloeophorus A. Milne Edwards, 1865
Panama	lower Pliocene	Cayo Agua Fm.	Persephona Leach, 1817
Panama	lower Pliocene	Cayo Agua Fm.	Iliacantha Stimpson, 1871
Panama	lower Pliocene	Cayo Agua Fm.	Platylambrus Stimpson, 1871
Panama	lower Pliocene	Cayo Agua Fm.	Sandomingia Rathbun, 1919
Panama	upper Pliocene	Escudo de Veraguas Fm.	Hepatus Latreille, 1802
Panama	upper Pliocene	Escudo de Veraguas Fm.	Persephona Leach, 1817
Panama	upper Pliocene	Escudo de Veraguas Fm.	Euphylax Stimpson, 1860
Panama	upper Pliocene	Escudo de Veraguas Fm.	Micropanope Stimpson, 1871
Panama	upper Pliocene	Escudo de Veraguas Fm.	Heteractaea Lockington, 1877
Trinidad	Miocene-Pliocene	Brasso Fm.	Persephona Leach, 1817
Mexico	lower Pliocene	Agueguexquite Fm.	Eurytium Stimpson, 1859
Curaçao	upper Miocene - Pliocene	Seroe Domi Fm.	Hepatus Latreille, 1802
Curaçao	upper Miocene - Pliocene	Seroe Domi Fm.	Calappa Weber, 1795
Curação	upper Miocene - Pliocene	Seroe Domi Fm.	Myropsis Stimpson, 1871
Curação	upper Miocene - Pliocene	Seroe Domi Fm.	Achelous De Haan, 1833
Curação	upper Miocene - Pliocene	Seroe Domi Fm.	Raninoides H. Milne Edwards, 1837
Curação	upper Miocene - Pliocene	Seroe Domi Fm.	Ranilia H. Milne Edwards, 1837
Curaçao	upper Miocene - Pliocene	Seroe Domi Fm.	Maguimithrax Klompmaker et al., 2015

any one Pliocene locality in the region (Collins and Portell, 1998). The sedimentary rocks are representative of a submarine flow deposited in 100-200 m water depth (Pickerell et al., 1998). Due to the disarticulated and fragmentary nature of the material, it is likely not representative of a living assemblage; certainly, the gastropods of the same unit vary from terrestrial to deep water and planktic. Two genera of crabs found in the shell bed, Cancer Linnaeus, 1758, and Hyas Leach, 1814a, are typically found in cooler waters than presently occur in the Caribbean (Collins and Portell, 1998). This suggests that the Caribbean may have been cooler during the Pliocene than it is today or, perhaps more likely, that these genera had a wider range of environmental tolerance in the past.

Although the Bowden Member does not represent a life assemblage, it nonetheless yields an estimate of regional diversity that could be expected throughout the Caribbean in the Pliocene. No other Caribbean islands come close to the level of diversity of the Bowden Member at this time, but, with further collection and research, it is likely that other Pliocene deposits would have equal or higher numbers of genera.

Most of the Caribbean Pliocene genera are those found in the Caribbean today. Calappa is the most common genus among the fossil brachyurans of the islands. Some fossil occurrences from the Seroe Domi Formation are unique to Curação and have not previously been described as fossils from other Pliocene Caribbean localities, including Achelous, Myropsis, and Raninoides. Achelous was reported from the Pleistocene of Jamaica from the Port Morant Formation by Collins et al. (2009a). Raninoides was reported from the Pleistocene of Jamaica and the Miocene of Caribbean Panama (Collins et al., 2009b), but this study is the first to report Raninoides in the Pliocene of the Caribbean. Myropsis has never been described from the fossil record prior to this study.

The Seroe Domi Formation has a similar mode of deposition and type of preservation as that of the Bowden Member, but due to the fragmentary preservation of much of the material, identifications were limited. It is likely that many more gen-

era were present in Curaçao in the Pliocene. With increased study of the Seroe Domi Formation, it is possible that a level of diversity similar to or greater than the diversity of the Bowden Member would be found. Each of the deposits in the Caribbean is unique in that none of the localities share the exact same combination of genera. Because of this, it is difficult to make comparisons to identify which deposit is most similar to the Seroe Domi Formation. The Bowden Member of Jamaica contains most of the genera listed from the other Caribbean localities suggesting that the genera were common throughout other regions of the Caribbean during the Pliocene.

There are several possible explanations for the high level of diversity in Jamaica. Of the Caribbean islands, Jamaica is better studied than the other islands; it is centrally located and easily visited. Other islands, such as Cuba and Haiti, have very few decapod fossils reported due to lack of studies. Not only have the large number of studies in Jamaica likely biased the record, the numbers for Jamaica may be artificially inflated from identifications based only on single dactyls and fixed fingers. Another possibility could be time-averaging. The fragmentary material could have been accumulating in the depositional environment for a much longer period of time than is perceived by what is seen in the deposit. Most importantly, it must be remembered that the fossil biota of the Bowden Member is exceptional, including in excess of 850 nominal taxa (Donovan, 1998).

All of the species that were identified from the Seroe Domi Formation of Curação are known from the Atlantic Ocean. This is significant because it shows that the split between Pacific and Atlantic species could have occurred by this time. Increased study of the other Pliocene localities should likewise yield only Atlantic species. All of the species identified from the Seroe Domi Formation of Curação are extant forms. This suggests that the environments preferred by those species still remain in the Caribbean today.

The Seroe Domi Formation could be affected by preservational biases, as could any of the fossil deposits in the Caribbean. The fossils in

the Seroe Domi that are best preserved are the raninids, which are also the most common. Raninids are burrowing crabs; if the raninids were living along the depositional slope, they may have died *in situ*, whereas the other fossil material could have been transported from further up slope.

#### CONCLUSIONS

The Seroe Domi Formation is a middle Miocene to early Pliocene, southeast-northwest trending unit, which crops out along the coasts of Aruba, Curaçao, and Bonaire in the southern Caribbean. In Curaçao, the Seroe Domi Formation is divided into three distinct subunits, which are further divided into eight lithofacies. Through analysis of the sedimentary rocks and location of the collection site, it was determined that the decapods were collected from Subunit 2 Lithofacies 6. The sediments were deposited in a series of slumps along the fore-reef slope in <100 m water depth. The sedimentary rocks consist of fragmentary shell material, and carbonate and siliciclastic sands.

Not all fossil material could be identified due to the fragmentary nature of preservation of the material. The crabs that could be identified belong to Ranilia constricta, Raninoides lamarcki, Calappa galloides, Hepatus lineatinus, Myropsis quinquespinosa, Maguimithrax spinosissimus and Achelous sebae. Raninids were the most common and wellpreserved crabs in the collection. This is unusual due to the relative lack of abundance of raninids in the fossil record of the Caribbean. Because of their burrowing lifestyle, however, the raninids may have been buried alive in their burrows during a slumping event, leading to better preservation. Whether all the crabs were buried during a slumping event, or if some were transported in the slump, is uncertain. All of the preferred habitats of the species match the environment of a reef to forereef slope environment.

When compared to other Caribbean Pliocene deposits, the Seroe Domi Formation represents a moderate level of diversity. Jamaica possesses the most diverse decapod-bearing deposit of comparable age in the Caribbean (=Bowden Member) and none of the other units comes close to that level

of diversity. Because of the wealth of studies done in Jamaica, it is likely that there are more genera reported because of greater sampling. With an equal amount of study at the other Caribbean localities, it is possible that a similar number of genera would be found.

Overall, the Pliocene represents a vital time in the evolution of Caribbean brachyurans. After the closing of the Central American Isthmus, a cessation of genetic exchange occurred leading to the evolution of distinct Pacific and Atlantic species. By studying the diversity and types of Caribbean species in the Pliocene, we can evaluate the timing of the closure of the isthmus and the divergence of Atlantic species from Pacific species.

#### ACKNOWLEDGEMENTS

R.W.P. thanks A. Booth, D. A. T. Harper, B. A. Kittle, M. Savarese, J. K. Toomey, and M. Toomey for assistance in the field, and S. Roberts (FLMNH) for help with digital photography. Logistical support by former subdirector A. Debrot and Science Director M. Vermeij (both CARMABI Foundation) was greatly appreciated. Funding for travel and fieldwork was provided (in part) by brothers, J. K. and M. Toomey, the FLMNH-IP McGinty Endowment, and Nationaal Natuurhistorisch Museum, Leiden (now the Naturalis Biodiversity Center). Thoughtful reviews by Matúš Hyžný, Comenius University, Bratislava, Slovakia, an anonymous reviewer, and David Steadman, Florida Museum of Natural History, Gainesville, improved the manuscript. This is University of Florida Contribution to Paleobiology 836.

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