

Decapod crustaceans from the Neogene of the Caribbean: diversity, distribution and prospectus

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Collins, J.S.H., Portell, R.W. & Donovan, S.K. Decapod crustaceans from the Neogene of the Caribbean: diversity, distribution and prospectus. *Scripta Geologica* **138**: 55-111, 4 pls., 1 fig., 5 tables, Leiden, March 2009.

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Key words – Neogene, Caribbean, Crustacea, Decapoda, crabs, systematics, biogeography.

The Neogene decapod crustaceans are reviewed from Aruba, Bonaire and Curaçao, Anguilla, Barbados, Carriacou, Costa Rica, Cuba, Florida, Hispaniola (Haiti and Dominican Republic), Jamaica, Mexico, Panama, Puerto Rico, St. Kitts, Tintamare Island, Trinidad and Venezuela. The most widely distributed taxa, both stratigraphically and geographically, are callianassids and *Calappa* (both with easily identifiable dactyli), and portunids. The latter include eleven genera in the study area; of these, *Callinectes*, *Euphyllax* and *Portunus* are known from the Miocene, Pliocene and Pleistocene of the Caribbean. The two occurrences of scleractinian-inhabiting crab faunas, the Lower Miocene Montpelier Formation of Jamaica and the Pleistocene Coral Rock of Barbados, show limited affinities with most other formations. The Upper Pliocene Bowden shell bed and Upper Pleistocene Port Morant Formation, both of Jamaica, include 26 and 27 genera, respectively, and generally show good generic similarities with other Neogene formations throughout the Caribbean. New species include the pagurid *Dardanus squamatus* Collins sp. nov., the calappid *Tutus granulatus* Collins gen. et sp. nov., the hepatid *Hepatus guraboensis* Collins sp. nov., and the portunids *Rathbunella pentaspinosus* Collins gen. et sp. nov. and *Psygmodthalmus bifurcatus* Collins sp. nov.

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Introduction

Although Rathbun (1919a, b, 1920a, b, 1923) made known a great number of fossil decapods from the Neogene (*sensu* Lourens *et al.*, 2004, that is, including the Quaternary) of the West Indies and summarized previous work, only a fraction of the species concerned were recorded from Plio-Pleistocene deposits, the majority coming from Miocene. Two species, one of doubtful provenance from Florida, were added later (Rathbun, 1935).

This situation remained unchanged until Collins & Morris (1976) recorded twelve species of crabs in seven genera from the Pleistocene Coral Rock of Barbados and included species from the Miocene of Trinidad. However, by far the greatest known occurrence of fossil crabs from any one of the Antillean islands hails from Jamaica (Morris, 1993; Collins *et al.*, 1997, 2001, 2009a, b; Collins & Portell, 1998; Collins & Donovan, 1998; Donovan & Dixon, 1998), from whence 28 Pliocene and 48 Pleistocene species (Plio-Pleistocene combined total = 58) have been reported (Donovan *et al.*, 2003b; Collins *et al.*, 2009a, b). An evaluation of the Lower Miocene species from that island (Portell & Collins, 2004) revealed 16 new species assigned to 14 genera (three were new).

Although limited in number, it is inevitable that these various publications, concerning localities ranging from Barbados westerly to Costa Rica and the Panama Canal Zone, and from Florida southerly to Trinidad, should contain some reports of the same species recorded from different Neogene deposits (Table 1). Whereas Rathbun did not hesitate to confirm specific designation on isolated claws, later authors took a more flexible approach using open nomenclature, being more inclined to record forms simply as "*Agenus* [aff. or cf.] *aspecies*." Thus, specimens showing superior preservation or, perchance, associated carapace remains, as in the case of *Eurytium crenatum* (Rathbun, 1919a), would undoubtedly influence the taxonomic designation of many species hitherto based on claws alone, either 'firmly established' or provisionally placed in genera. By far the greatest number of Miocene decapods from the Caribbean region was described by Rathbun (1919b, 1920b, 1923) from Costa Rica, Panama and Hispaniola. Among these was the first notice of fossil macrura, *Nephrops costatus* Rathbun, 1919a, from the Panama Canal Zone, followed by *Nephrops maoensis* Rathbun, 1920b, and *Nephrops aequus* Rathbun, 1920b, from the Caribbean; Rathbun considered the former to be akin to the Recent *Nephrops norvegicus* Linnaeus, 1758.

Low figures from some localities may well be attributed to collecting bias or adverse ecological factors (see 'Discussion,' below). Sparse though regional data may be, it is possible to recognise small trends in fossil distribution compared with Recent occurrences. Correlation with extant occurrences is impeded by recent and continuing revision of taxonomy, and subsequent amendments of long established faunal lists. To these early records can be added the results of subsequent collecting from various localities exposing deposits ranging from Early Miocene to Late Pleistocene of Florida, the Dominican Republic, Jamaica and Central America, and associated Caribbean faunas of Mexico and Venezuela. Principal formations referred to herein are summarised in Table 1.

Despite this wealth of decapod taxa, their geographic distributions are patchy, stratigraphic distributions have (not uncommonly) been poorly defined and no complete synthesis of the data on Neogene crabs from the region has been attempted hitherto. The purpose of the present paper is to review the Miocene, Pliocene and Pleistocene decapod crustaceans of the Antillean region and adjacent areas, providing a synthesis of the available information on their taxonomic diversity and geographic distribution. Factors influencing our knowledge of these crustaceans will be discussed where appropriate, as will possible ways to forward their study in the Antilles. New taxa described herein (Appendix 1) are deposited in The Natural History Museum, London (BMNH) and the Naturhistorisches Museum Basel (NMB). Collections listed under "R.W.P. *et al.*, research in progress" are deposited in the Florida Museum of

Table 1. Principal Neogene lithostratigraphic formations containing fossil decapod crustaceans discussed in this paper, with stratigraphic positions and locations.

Formation	Position	Location
Lares Formation	Upper Oligocene to Lower Miocene	Puerto Rico
Canimar Formation	Miocene	Cuba
Imías Formation	Miocene	Cuba
Lagunitas Formation	Miocene	Cuba
Anguilla Formation	Lower Miocene	Anguilla
Lowlands Formation	Lower Miocene	Tintamare Island
Chattahoochee Formation	Lower Miocene	Florida, USA
Chipola Formation	Lower Miocene	Florida, USA
Marks Head Formation	Lower Miocene	Florida, USA
Parachucla Formation	Lower Miocene	Florida, USA
Penney Farms Formation	Lower Miocene	Florida, USA
Montpelier Formation	Lower Miocene	Jamaica
Thomonde Formation	Lower Miocene	Haiti
Castilla Formation	Lower Miocene	Venezuela
Brasso Formation	Lower to Middle Miocene	Trinidad
Grand Bay Formation	Middle Miocene	Carriacou
Coosawhatchie Formation	Middle Miocene	Florida, USA
Shoal River Formation	Middle Miocene	Florida, USA
Tuxpan Formation	Middle Miocene	Mexico
Ponce Limestone	Middle to Upper Miocene	Puerto Rico
Tuira Formation	Middle to Upper Miocene	Panama
Cercado Formation	Upper Miocene	Dominican Republic
`Gatun Formation`	Upper Miocene	Costa Rica
Choctawhatchee Formation	Upper Miocene	Florida, USA
Nancy Point Formation	Upper Miocene	Panama
Tobabe Sandstone	Upper Miocene	Panama
Gurabo Formation	Upper Miocene to Lower Pliocene	Dominican Republic
Guanajibo Formation	Upper Miocene or Pliocene	Puerto Rico
Intracoastal Formation	Pliocene	Florida, USA
Jackson Bluff Formation	Pliocene	Florida, USA
Tamiami Formation	Pliocene	Florida, USA
Rio Banano Formation	Lower Pliocene	Costa Rica
Penito Formation	Lower Pliocene	Costa Rica
Mao Formation	Lower Pliocene	Dominican Republic
Cayo Agua Formation	Lower Pliocene	Panama
Moin Formation	Upper Pliocene	Costa Rica
Bowden Formation	Upper Pliocene	Jamaica
Hopegate Formation	Upper Pliocene	Jamaica
Escudo de Veraguas Formation	Upper Pliocene	Panama
Seroe Domi Formation	Upper Pliocene to Lower Pleistocene	ABC Islands
Caloosahatchee Formation	Upper Pliocene to Lower Pleistocene	Florida, USA
Nashua Formation	Upper Pliocene to Lower Pleistocene	Florida, USA
Manchioneal Formation	Lower Pleistocene	Jamaica
Bermont Formation	Lower to Middle Pleistocene	Florida, USA
Coral Rock	Middle to Upper Pleistocene	Barbados
Anastasia Formation	Upper Pleistocene	Florida, USA
Fort Thompson Formation	Upper Pleistocene	Florida, USA
Miami Limestone	Upper Pleistocene	Florida, USA
Falmouth Formation	Upper Pleistocene	Jamaica
Port Morant Formation	Upper Pleistocene	Jamaica
Jaimanitas Formation	Upper Pleistocene	Cuba

Natural History, University of Florida, Gainesville. Our philosophy of open nomenclature follows Bengtson (1988).

Geographic and stratigraphic distributions

ABC Islands (Aruba, Bonaire and Curaçao) – Fossil decapods have not formally been reported from the Netherlands Antilles. However, a suite of fossil carapaces and disarticulated appendages (Raninidae, Calappidae, Leucosiidae and Majidae) were recently collected in Curaçao from the carbonate rocks of the Plio-Pleistocene Seroe Domi Formation (Harper *et al.*, 2003; R.W.P. *et al.*, research in progress).

Anguilla – Attention was drawn to fossil crabs of Anguilla by Rathbun (1919b), who described three species which were all assigned to the Upper Oligocene. The Anguilla Formation of Anguilla is now recognised to be Lower Miocene (Poddubiuk & Rose, 1985; Wadge, 1994, p. 169). This small fauna, consisting of *Callianassa pellucida*, *Callianassa anguillensis* and *Lyreidus fastigatus* (founded on a partially exposed merus), was referred to by Withers (1924) who, from additional material, enlarged upon the description of '*C.* *anguillensis* and opined that this species appeared to be very close to '*C.* *latidigitata* Rathbun, 1919a, from the Early Miocene of the Dominican Republic. Withers (1924) also added another four taxa from Anguilla: *Calappa earlei* Withers, 1924 (partial carapace and disassociated chela); *Scylla costata* Rathbun, 1919b (claws); an unnamed merus assigned to *Panopeus* sp.; and another to *Parthenope* sp. which was said to agree well with *Parthenope affinis* (A. Milne-Edwards, 1872). *Calappa earlei* was distinguished from (extant) *Calappa flammea* in having more prominent and extra tubercles on both carapace and chela. Withers (1924) was of the opinion that the (unfigured) dactyli recorded as *C.* *flammea* by Rathbun (1919b) from the Early Miocene of the Dominican Republic may belong to *C.* *earlei*. In a systematic survey of *Lyreidus*, Feldmann (1992) removed *L.* *fastigatus* on grounds of incompatibility of generic characters, although no alternative taxonomic position was suggested.

Further specimens from the Anguilla Formation are documented herein (see Appendix 1). A hitherto undescribed species included in *Psygomophthalmus* Schweitzer *et al.*, 2006, extends the geographic range from a more or less contemporary deposit in Puerto Rico. An unnamed *Calappa* sp. (Pl. 1, fig. 9), represented by an associated dactylus and fixed finger, retains characters in common with the extant species *Calappa springeri* (Rathbun, 1931) and *C.* *flammea*, both of which have been recorded in the fossil record of the Caribbean.

Barbados – The series of fossil decapods obtained from the Pleistocene Coral Rock of Barbados by C.T. Trechmann *circa* 1920-1964 contains some of the finest preserved carapace material known from the late Cenozoic of the Antilles; more recent fieldwork by S.K.D. has failed to find further specimens of comparative quality. Trechmann (1937, p. 358) considered that aspects of the macrofauna of the basal Coral Rock presented a "pre-Pleistocene aspect," but the modern view is that this unit is limited to the Pleistocene (Speed, 1994; Donovan, 2003).

One of the extinct forms, mentioned above, occurs in the Coral Rock. *Herbstia exserta* Collins & Morris, 1976, a well preserved carapace, is quite unlike other Atlantic

members of this genus, but is undoubtedly analogous to the extant Pacific species *Herbstia pyriformis* (Bell, 1836) which ranges from the Galapagos Islands. Rathbun (1925) recognised only one other pair of analogous *Herbstia* on opposite sides of America, *Herbstia depressa* Stimpson, 1860 (Atlantic), and *Herbstia tumida* (Stimpson, 1871) (Pacific). Among extant members of the Mithracidae from Barbados, *Mithrax caribbaeus* Rathbun, 1920a, *Mithrax spinosissimus* (Lamarck, 1818) and *Mithrax verrucosus* H. Milne Edwards, 1832, are all common in the Pleistocene of the island. *Mithrax caribbaeus* has been tentatively recorded (Morris, 1993) from the Upper Pleistocene Falmouth Formation of Jamaica together with *M. spinosissimus*, while *M. verrucosus* and *Mithrax hispidus* (Herbst, 1790) occur in the Upper Pleistocene Port Morant Formation of Jamaica (Collins *et al.*, 1997; Collins & Donovan, 1998). *Mithrax spinosissimus* is also tentatively recorded on the basis of claw fragments from Haiti, where it represents the only Pleistocene crab known from Hispaniola (Rathbun, 1923). As far as is known, the fossil status of *Mithrax hemphilli* Rathbun, 1892, is confined to the Pleistocene of Barbados (Collins & Morris, 1976). The species was not recorded by Rathbun (1925) among the extant crabs of that island, although its modern range is from the Florida Keys to Rio de Janeiro.

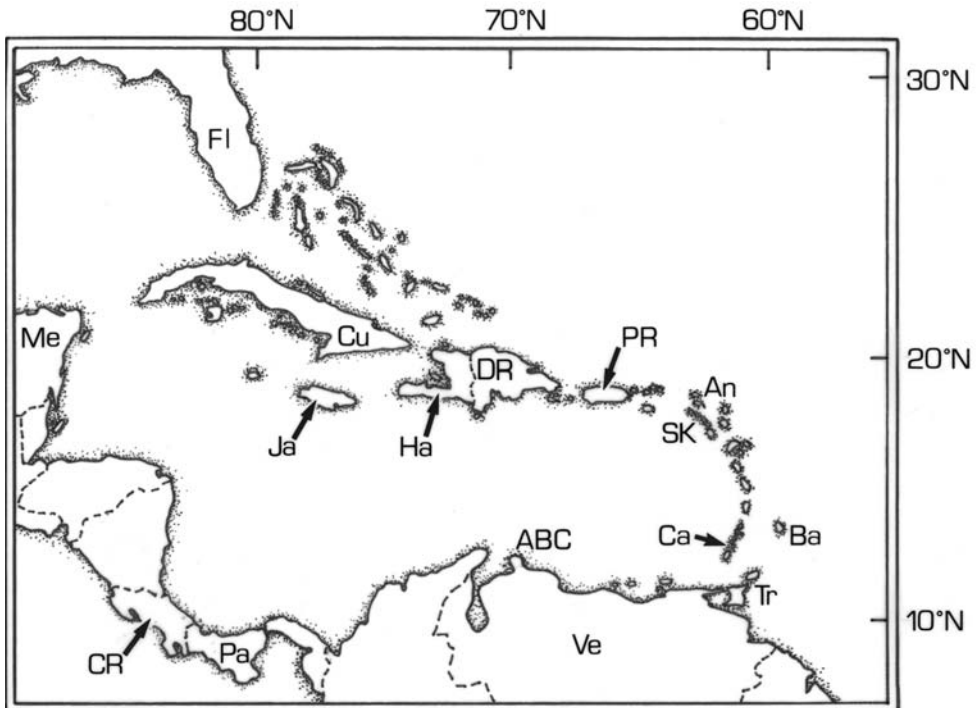


Fig. 1. Outline map of Caribbean region, labelling all islands and countries whose fossil decapod crustaceans are discussed in text (adapted from Jackson, 1996, fig. 1). Key: An = Anguilla and Tintamare Island, St. Martin; ABC = Aruba, Bonaire and Curaçao; Ba = Barbados; Ca = Carriacou; Cu = Cuba; CR = Costa Rica; DR = Dominican Republic; Fl = Florida; Ha = Haiti; Ja = Jamaica; Me = Mexico; Pa = Panama; PR = Puerto Rico; SK = St. Kitts; Tr = Trinidad; Ve = Venezuela.

The remaining brachyuran known from the Coral Rock is a well-preserved carapace of *Mithraculus ruber* Stimpson, 1871. The specimen from Barbados differs (Collins & Morris, 1976) from that described by Rathbun (1925, p. 432) in little more than having comparatively less prominent dorsal tubercles. The modern distribution is from Cuba to Barbados and Curaçao. The only other species from the Pleistocene of Barbados to be recorded elsewhere is *Carpilius corallinus* (Herbst, 1783) which also occurs in the Upper Pleistocene Port Morant Formation of Jamaica (Collins *et al.*, 1997, 2009a). It was not recorded as a Recent species from Barbados by Rathbun (1930), who stated the range to be from the Bahamas to Brazil.

Carriacou – The first fossil decapod crustaceans from Carriacou were briefly discussed by Portell in Donovan *et al.* (2003a). All remains are from the Middle Miocene Grand Bay Formation. Specimens are fragmentary, mostly of fingers that are highly corroded (pitted) and commonly coated with a thin veneer of calcite. Only *Calappa* cf. *springeri* (Rathbun, 1931) and *Platyxanthus* sp. could be identified confidently to generic level. Both taxa are established in the fossil record of the Caribbean.

Cuba – Prior to Schweitzer *et al.* (2006), no fossil decapods had been reported from Cuba. The Miocene Canimar, Lagunitas and Imías formations have between them yielded a meager fauna comprising only *Euphyllax domingensis* (Rathbun, 1919b) and *Portunus* sp. (Schweitzer *et al.*, 2006). Recently, decapod material (Callianassidae, Paguridae, Calappidae and Panopeidae) has been excavated from the Upper Pleistocene Jaimanitas Formation (R.W.P. *et al.*, research in progress) from coastal deposits at the U.S. Guantanamo Bay Naval Station (Portell *et al.*, 2008).

Florida – Portell (2004) reviewed all reported Eocene through Miocene crabs derived from deposits around the state. Most Miocene occurrences came from the Lower Miocene Chipola Formation and consisted of *Callianassa floridana* Rathbun, 1935, *Paguristes chipolensis* Rathbun, 1935, *Petrochirus inequalis* Rathbun, 1919b, *Calappa flammea* (Herbst, 1794), *Callinectes sapidus* Rathbun, 1896, *Portunus sayi* (Gibbes, 1850), *Menippe nodifrons* Stimpson, 1859, and *Eurytium limosum* (Say, 1818). The majority of the Chipola Formation specimens are preserved as disarticulated appendages; however, rare carapaces have been found. Additionally, *Scylla floridana* Rathbun, 1935, and *Portunus* sp. are recorded from the Lower Miocene Chattahoochee Formation (formerly considered Tampa Limestone by Rathbun, 1935), chela elements of *Neocallichirus matsoni* (Rathbun, 1935) (see Schweitzer & Feldmann, 2002, p. 942) were described from the Lower Miocene Penney Farms and Parachucla formations (formerly considered Chipola Formation by Rathbun, 1935) and *Calappa flammea* was reported from the Middle Miocene Shoal River Formation (Portell, 2004). Jones & Portell (1988) also identified *Callianassa* cf. *floridana* from the Middle Miocene Coosawhatchie and Marks Head formations based on isolated chela. Many of these species appear to be peculiar to Florida, exceptions being *Eurytium limosum*, also known from the Plio-Pleistocene of Jamaica and, most distant, *Calappa flammea* from the Dominican Republic (Early Miocene of Rathbun, 1919b) and Pleistocene of Panama.

Portell & Agnew (2004) summarized all Pliocene through Pleistocene crab occurrences in Florida. The lower Tamiami Formation (Pliocene) has yielded exceptionally

well-preserved porcelain crab carapaces attached to beautifully articulated sun stars (*Heliaster microbrachius*). Bishop & Portell (1989) named these porcelain crabs *Petrolisthes myakkensis* and documented one of the few known fossil occurrences of crab-asteroid commensalism. Only one other Tamiami Formation decapod has been reported as *Calappa* sp. (Portell & Agnew, 2004). Another Florida Pliocene unit, the Intracoastal Formation (found in the state's panhandle), has yielded over 500 whole-bodied *Ranilia* sp. and chela segments of *Calappa* sp. This deposit was reported by Portell *et al.* (2003a) and the description of the new *Ranilia* species awaits publication. Rathbun (1935, pp. 105, 112) listed two taxa as occurring in the "upper Miocene." These were *Petrochirus bouvieri* Rathbun, 1919a (an extinct hermit crab originally described from the Gatun Formation of Panama), and a spider crab, *Euprognatha* sp. With refined stratigraphy for the area in which these specimens were collected, it seems most probable that both taxa were derived from the Pliocene Jackson Bluff Formation. The only other crabs recorded from the Jackson Bluff Formation are *Calappa* sp. (Portell & Agnew, 2004) and *Menippe floridana* Rathbun, 1935 (listed by Rathbun as derived from the Choctawhatchee Formation). Both the *Calappa* and *Menippe* are based on isolated fingers.

From numerous shell pits and river banks in the southern part of the state (those areas in which the Caloosahatchee and Bermont formations are exposed) come the bulk of the known decapod taxa. Typically, only disarticulated elements (meri, dactyli and propodi) are found. Portell & Agnew (2004) listed twelve taxa from the Plio-Pleistocene Caloosahatchee Formation. These are *Callichirus major* (Say, 1818), *Neotrypea* sp., *Sergio trilobatus* (Biffar, 1970), *Petrochirus bouvieri*, *Calappa* sp., *Persephona mediterranea* (Herbst, 1794), *Libinia* sp., *Parthenope charlottensis* Rathbun, 1935, *Ovalipes stephensoni* Williams, 1976, *Portunus gibbesii* (Stimpson, 1859), *Menippe mercenaria* (Say, 1818) and *Menippe nodifrons*. Additionally, Portell & Agnew (2004) listed 19 decapods from the Lower to Middle Pleistocene Bermont Formation. Many of these are the same species that occur in the Caloosahatchee Formation. Taxa recognized from the Bermont Formation are *Callichirus islagrande* (Schmitt, 1935), *Callichirus major*, *Neocallichirus* sp., *Neotrypea* sp., *Sergio trilobatus*, *Ctenocheles* sp., *Upogebia affinis* (Say, 1818), *Petrochirus diogenes* (Linnaeus, 1758), *Calappa* sp., *Hepatus* sp., *Persephona mediterranea*, *Libinia* sp., *Ovalipes stephensoni*, *Portunus depressifrons* (Stimpson, 1859), *Portunus gibbesii*, *Portunus spinimanus* Latreille, 1819, *Pilumnus* sp., *Pinnixa* sp. and *Uca* sp. As mentioned above, most of the taxa from these formations occur as chela elements and carapace fragments only, but sometimes in huge abundance. It is quite possible that some of these high density deposits of decapod remains are the result of shore bird predation (see Cadée, 2007).

Coastal areas with exposed Late Pleistocene rocks have yielded some of Florida's most exceptional crab occurrences. Near Tampa, on the west coast of the state, Portell & Schindler (1991) reported collecting nearly 100 articulated *Menippe mercenaria* from the Upper Pleistocene Fort Thompson Formation. Additionally, they reported chela elements of *Callianassa* sp. and diogenid hermit crabs as well as carapace fragments of *Persephona* sp. Near Melbourne on Florida's east coast, Portell *et al.* (2003b) recorded hundreds of fossil *Ocypode quadrata* (Fabricius, 1787), commonly eroded from the Late Pleistocene Anastasia Formation along Brevard County beaches. Portell *et al.* (2003b) investigated two questionable occurrences, one reported by Rathbun (1935, p. 118) of *Ocypode albicans* (now *O. quadrata*) listed as "Florida (probably)" and the other by Bishop (1986, p. 340) of "casts of ?stone crabs (*Menippe*?)" from the Florida Anastasia Formation,

that they confirmed as *O. quadrata*. Portell & Agnew (2004) also listed *Calappa* sp. from the Anastasia Formation. Lastly, Rathbun (1935, p. 117) listed *Cancer irroratus* Say, 1817, from the Pleistocene of Florida based on “two fingers” collected on Miami Beach. Given the location, these specimens were most likely derived from the Upper Pleistocene Miami Limestone.

Hispaniola – Subsequent to Rathbun’s (1919b) reference to Santo Domingo, some confusion has arisen concerning which country, Haiti or Dominican Republic, was intended. Disregarding reference to species assigned to Crangonidae and Eryonidae gen. et spp. indet., all of the 23 taxa (including the Xanthidae gen. et sp. indet.) recorded from Hispaniola by Rathbun (1919b) are from the Lower Miocene of the Dominican Republic. Thus, five references made by Rathbun to Haiti are spurious. Later, Rathbun (1920b) described three more taxa from the Dominican Republic, including two species of *Nephrops* remarked upon in the introduction. In 1923 Rathbun recorded *Mithrax* sp. from the Pleistocene and four Lower Miocene Thomonde Formation species from Haiti. These four taxa were recorded by Woodring *et al.* (1924, p. 190) from the Las Cahobas of the Thomonde Formation. No species is common to both countries and, of the 21 genera involved, only three are common to both countries.

Hispaniola: Haiti – With the exception of *Portunus haitensis* Rathbun, 1923, the Early Miocene fossil record of crabs from Haiti is based on limb fragments recorded as *Parthenope?* sp. and *Panopeus?* sp. A small portion of carapace of *Mithrax* sp. was reported from a Pleistocene deposit (Rathbun, 1923).

Hispaniola: Dominican Republic – The earliest descriptions (Rathbun, 1919b) of crabs were recorded simply as from the Lower Miocene. The sculpture of *Petrochirus inequalis* Rathbun, 1919b, from the Dominican Republic, described from incomplete chelae only, was said to be nearest to *Petrochirus californiensis* Bouvier, 1895, an extant species presently found from Lower California to Ecuador. This species is also present in the Lower Miocene Chipola Formation of Florida. *Cryptosoma bairdii* (Stimpson, 1860) (as *Cycloes bairdii*) was admitted to the fossil fauna of the Dominican Republic on the strength of a fragmentary chela which Rathbun (1919b) averred complied, as far as could be judged, with Recent forms occurring from Bahamas to the West Indies and Lower California to Panama. The species was not referred to by Schweitzer & Feldmann (2000). Nor did those authors recognise *Calapella* sp. of Rathbun, 1919a, in the Calappidae, in which family it was originally described from fragmentary material from the Oligocene of Panama, and recorded, tentatively, from the Dominican Republic from limb fragments and possible carapace spines. Indeed, the poor quality of the material renders taxonomic placement controversial. Of other Dominican Republic species, *Calappa flammae*, represented by limb fragments only, makes its earliest appearance as a fossil in the Caribbean (Rathbun, 1919b), but, as noted above, Withers (1924) averred the possibility of the material belonging to *C. earlei*. However, *C. flammae* has been determined from Miocene to Plio-Pleistocene deposits among recently collected material from Panama and Costa Rica (Todd & Collins, 2006). As noted above, fingers have also been found in some Early and Middle Miocene formations of Florida. The species presently ranges throughout the Caribbean, from southwestern Massachusetts to Brazil, Cape of Good

Hope and possibly the Indian Ocean (Rathbun, 1919b, 1937). The latter record possibly substantiates chelae of uncertain age among the newly collected material from the Pacific side of Panama and Costa Rica.

The Early Miocene parthenopid, *Mesorhoea mauryae* Rathbun, 1919b, also marks the earliest known appearance of the genus. Its fossil record is continued into the Upper Pliocene Bowden shell bed of Jamaica with *Mesorhoea* aff. *sexspinosa* Stimpson, 1871, an extant species with a range extending from southeast Cape Lookout, North Carolina, to the Virgin Islands (Collins & Portell, 1998). Another parthenopid, *Parthenope obscura* Rathbun, 1919b, was said to resemble *Parthenope serrata* H. Milne Edwards, 1834, an extant Caribbean species. Based on a fragmentary propodus, the presence of this genus from the Thomonde Formation of Haiti was queried by Rathbun (1923). A partial fixed finger, attributed to *Platylambrus* sp., was recorded from the Upper Pliocene Bowden shell bed of Jamaica (Collins & Portell, 1998).

Ecological conditions during the Miocene in Hispaniola appear to have been favourable to an unusually high percentage of swimming crabs (Portunidae) being preserved when compared with other Miocene faunas of this region (Schweitzer *et al.*, 2006, p. 132). Five of the six named species concerned occur in the Dominican Republic. *Portunus oblongus* Rathbun, 1920b, also has been tentatively recorded from Puerto Rico, Trinidad and Venezuela (Schweitzer *et al.*, 2006). The carapace of *Portunus gabbi*, from the Dominican Republic, is close to *Portunus pelagicus* Linnaeus, 1758, but that it also had characters linking it with *Callinectes*. *Callinectes declivis* Rathbun, 1919a, was originally described from a propodus from the Gatun Formation of Costa Rica and, later (Rathbun, 1919b), was identified from the Lower Miocene of the Dominican Republic and the Pirabas Formation of Para, Brazil (Beurlen, 1958). Founded on claws, *Portunus tenuis* Rathbun, 1919b, (= *P. (Achelous) tenuis* of Todd & Collins, 2006, p. 75), was said to resemble *Portunus spinicarpus* Stimpson, 1871. No comparative or regional comments were passed on *Portunus haitensis* Rathbun, 1923. A carapace and costate propodi distinguish *Scylla costata* from the more or less smooth chelae of the extant *Scylla serrata* (Forskål, 1775), a wide-ranging Indo-Pacific species. A second Miocene species, *Scylla floridana*, is known from Florida. This genus no longer exists in the Caribbean region. The stratigraphic position of *Podophthalmus domingensis* (Rathbun, 1919b) is uncertain and, although regarded as possibly Lower Miocene by Rathbun (1919b), was considered to be Oligocene or Lower Miocene by Collins *et al.* (2001). Transferred to *Euphyllax* by Todd & Collins (2006), this species has since been recorded from the latest Miocene of Cuba (Schweitzer *et al.*, 2006). Nevertheless, although somewhat older than either *Euphyllax callinectias* Rathbun, 1919a, or the questionable *Euphyllax fortis* Rathbun, 1919a, from the Gatun Formation of Costa Rica, it has characters more in common with *Euphyllax fortispinosus* Collins *et al.*, 2001, from the Lower Pleistocene Old Pera Beds, Manchioneal Formation, of Jamaica. This genus, represented by two Recent species, is confined to the Pacific coast of tropical Central America and the eastern tropical Pacific (Jerde, 1967). One genus, *Sandomingia* Rathbun, 1919b, from the Dominican Republic occurs also in the Lower to Upper Pliocene Cayo Agua Formation of Panama and Moin Formation, Upper Pleistocene of Panama (Todd & Collins, 2006).

In sharp contrast, the Xanthoidea contains only two species. *Pilumnus subequus* Rathbun, 1919b, was founded on a single dactylus from the Dominican Republic and no comparative data was given. Extant *Pilumnus* spp. range throughout the Caribbean

and Rathbun (1930) listed two Atlantic species with Pacific analogues. The extinct genus *Lobonotus* was described from the Early Miocene of the Dominican Republic as *Archaeopilumnus caelatus* Rathbun, 1919b, a junior synonym of the type species *Lobonotus sculptus* A. Milne-Edwards, 1864 (Schweitzer *et al.*, 2007, p. 280), from the Upper Oligocene of Haiti (see also Feldmann *et al.*, 1995). Schweitzer *et al.* (2006) described *Neocallichirus? quisquellanus* from the upper Lower to lower Middle Miocene of Rio Camarón.

Hispaniola: Dominican Republic - a new collection – With the exception of the two *Nephrops* species and half a dozen taxa, all other crabs listed by Rathbun (1919b, 1920b, 1923) from the Miocene of the Dominican Republic are present within a hitherto undocumented collection in the Naturhistorisches Museum Basel (NMB). This material, from the Cercado (Upper Miocene), Gurabo (uppermost Miocene to Lower Pliocene) and Mao formations (Lower Pliocene), consists mostly of claws and not only enhances the findings of Rathbun, but also clarifies the stratigraphic position of much of the crab fauna. It includes three new species and a further seven species either recorded as fossil elsewhere or new to the fossil record of the Caribbean (Appendix 1).

Species formerly described (Rathbun, 1919b, 1923) from neighbouring Haiti include *Scylla costata* (carapace and chelae fragments), known from all three formations mentioned above and also the Lower Miocene of Anguilla (Withers, 1924), and occurs in the Miocene Pirabas Formation of Para, Brazil (Beurlen, 1958). *Lobonotus sculptus* (carapace) and *Portunus gabbi* (right propodus) occur in the Cercado Formation, *Euphyllax dominicensis* (claw fragments) is from the Gurabo Formation.

Of note among new material is a section of cheliped merus with associated carpus which, by comparison with a fragment from the Plio-Pleistocene of Panama, can safely be attributed to *Sandomingia yaquiensis* Rathbun, 1919b (Pl. 2, fig. 3). This species, again by comparison with a well-preserved Panamanian carapace, was included in the Podophthalmidae (Appendix 1) by Todd & Collins (2006).

By far the majority of callianassid remains are of *Neocallichirus scotti* (Brown & Pilsbry, 1913), which is common in the Cercado Formation and present in the Mao Formation. This species is discussed in detail under 'Panama and Costa Rica - new collections' (see below). A few remaining callianassid fragments not applicable to any of Rathbun's species may well represent absent parts from the figured material.

The sculpture of three pagurid fixed fingers differs from that described by Rathbun (1919b, pl. 9, figs. 13-15) as *Petrochirus inequalis* and more closely resembles that of *Dardanus* spp. They form the first members of the genus to be recorded as fossils from the Antilles and are described herein as *Dardanus squamatus* Collins sp. nov. (Appendix 1). The genus *Dardanus* is known elsewhere from North America, particularly the Eocene and Pliocene of California (Rathbun, 1926). The surface of *P. inequalis* from the Chipola Formation of Florida is abraded, producing an irregularly tessellated appearance (Rathbun, 1935, pl. 23, fig. 6). Similarly preserved fixed fingers and dactyli occur in the present collection (Pl. 1, figs. 1, 2), but, when well-preserved, the sculpture consists of irregular rounded-pentagonal nodes of varying sizes capped with a rounded granule and interspersed with small nodes. The right dactyl occludent surface is composed of flattened cusps, becoming medially bisected, and alternately large and small distally. The left dactylus has a median groove flanked by small rounded granules on

either side, they are slightly larger along the outer margin and granules extend the length of the occludent margin (locality NMB 16923).

Among the xanthoid taxa new to the Dominican Republic is a dactylus from the Cercado Formation assigned to *Eurytium* sp. This genus is present as *Eurytium* aff. *limosum* in the Lower Miocene Chipola Formation of Florida, the Plio-Pleistocene of North Carolina and the Plio-Pleistocene of Jamaica, and as *Eurytium crenulatum* Rathbun, 1919a, from the Pleistocene of Panama. The new record from the Dominican Republic minimally increases the geographic range of this genus. The geographic and stratigraphic ranges are also extended to encompass *Pilumnus* aff. *spinosissimus* and *Panopeus herbstii* H. Milne Edwards, 1834. The former is present in the Upper Pliocene Bowden shell bed of Jamaica, and the latter, tentatively known from the Bowden shell bed, is more confidently identified from the Pleistocene Port Morant and Falmouth formations of Jamaica. A right chela from the Gurabo Formation is attributed to *Eurypanopeus* aff. *crenatus* H. Milne Edwards, 1834, and marks the oldest fossil occurrence of that genus in the Caribbean; the present range of the species is from Ecuador to the Straits of Magellan. The genus is present elsewhere as *Eurypanopeus* sp. in the Pliocene of Jamaica; as *Eurypanopeus* cf. *depressus* Smith, 1869, and *Eurypanopeus abbreviatus* (Stimpson, 1860) in the Pleistocene of that island; and in the Upper Pliocene to Lower Pleistocene of Costa Rica. A large fixed finger attributable to *Platyxanthus* marks the oldest appearance of that genus in the Caribbean; the genus is also recorded from the Upper Miocene of Panama and Costa Rica, as well as the Upper Pliocene/Lower Pleistocene of Costa Rica (Todd & Collins, 2006).

Of particular note is a leucosiid propodus from the Gurabo Formation confidently referable to *Iliacantha liodactylus* Rathbun, 1898 (Pl. 4, fig. 8), which represents the first fossil record of this genus from the Dominican Republic. The species, presently occurring off Florida and the West Indies, has *Iliacantha hancocki* Rathbun, 1935, as a Pacific analogue. A carapace is known from the Pliocene of Panama (see below, 'Panama and Costa Rica - new collections'). Also worthy of attention is a broken right propodus (Pl. 1, fig. 3) retaining the fixed finger and a broken left propodus (Cercado Formation). These are remarkably similar to those parts of *Persephona punctata punctata* Linnaeus, 1758, to which species Rathbun (1919b) compared meral fragments of *Persephona prepunctata* Rathbun, 1919b (common in the present collection). Also present and equably ascribable to *P. prepunctata* are typical persephonid female 6th and 4th/5th male abdominal somites (Pl. 3, figs. 3, 4).

Spiny meral fragments close to those of the oxyrhynch *Stenocionops* (Pl. 1, fig. 4) (Cercado Formation and other unrecorded horizons) constitute the first fossil appearance of this extant genus which is common to both the Pacific coast of North America and the Caribbean. A right fixed finger with affinities to *Libinia setosa* Lockington, 1877, an extant genus confined to lower California (Rathbun, 1926), is the first Caribbean fossil record of this genus.

Chelae fragments from the Cercado Formation and unrecorded horizons augment the fossil record of *Mesorhoea mauryae* Rathbun, 1919b (Pl. 1, fig. 5). Other parthenopid limb fragments, from the Gurabo Formation and unrecorded horizons, more closely resemble those of the extant Caribbean *Parthenope serrata* (Pl. 1, fig. 6) than they do to *Parthenope obscura* Rathbun, 1919b, a species Rathbun compared with *P. serrata*.

Previously recorded from the Dominican Republic and from the Pleistocene of

Panama, chelae fragments of *Calappa flammea* form a dominant part of the present collection, occurring in the Cercado and Mao formations, and unrecorded horizons. The single left propodus fragment of *Cryptosoma bairdii* known to Rathbun (1919b) is supplemented by two more specimens from the same side, together with an almost entire left propodus (Pl. 4, figs. 3, 4), establishing the fossil range of the species from the Cercado to Mao formations. A carapace and carapace fragments, together with a growth series of claws, of a new *Hepatus* and a carapace of a new portunid genus and species, both from the Gurabo Formation, are described in Appendix 1.

Jamaica - Miocene – The coral-associated crab fauna of the Lower Miocene of the Montpelier Formation at Duncans Quarry, parish of Trelawny, is comprised of 16 species in 14 genera. Three of the genera, *Actaeops*, *Pseudoachelous* and *Duncania*, were new (Portell & Collins, 2004). Of the remaining eleven genera, *Lophopanopeus* is known from both older and younger deposits in North America; and *Daira*, *Dynomene*, *Teleophrys*, *Chlorodiella* and *Trapezia* are extant taxa that were recorded from the fossil record of the Caribbean for the first time. With the exception of *Teleophrys*, all are present in the Upper Miocene coral-associated deposits of Europe and similar Middle Miocene beds from Japan, from whence *Leptodius*, represented in the Montpelier Formation by *L. granulatus* Portell & Collins, 2004, has also been described (Müller, 1984; Karasawa, 1993). Only three extant genera, *Micropanope*, *Panopeus* and *Mithrax*, have previously been recorded in younger deposits from Jamaica and the last is also known from the Pleistocene Coral Rock of Barbados (Collins & Morris, 1976).

The commonest species in the Montpelier Formation is undoubtedly the parthenopid *Daira vulgaris* Portell & Collins, 2004, which is well represented by over 100 carapaces of various growth sizes, and numerous isolated elements of chelae corresponding to Recent species that can safely be attributed to this fossil species. The genus includes two Recent species, one of which, *Daira americana* Stimpson, 1860, ranges from Lower California to Ecuador.

The family Portunidae is represented by a fragmentary carapace, *Pseudoachelous schindleri* Portell & Collins, 2004. The anterolateral spines of this species follow the alternate wide and narrow arrangement common to North American species of *Achelous*.

It is evident that, in common with the above-mentioned occurrence, oxyrhynchs comprise a reasonably high percentage (20%) of the Miocene coral associated assemblage of Jamaica. Two species of *Mithrax* were determined. *Mithrax donovani* Portell & Collins, 2004, has characters in common with the more pyriform members of the genus such as *Mithrax acuticornis* (Stimpson, 1870) and *Mithrax spinipes* Bell, 1835; the former is widespread in the Caribbean, while the latter is a Pacific coast species. *Mithrax unguis* Portell & Collins, 2004, on the other hand, has some characters in common with extant *Mithrax hispidus*, a taxon known from the Pleistocene of Barbados. *Teleophrys acornis* Portell & Collins, 2004, has characters in common with *Teleophrys ornatus* Rathbun, 1901, presently recorded from Yucatan and the West Indies to Brazil (Rathbun, 1925).

Dynomene variabilis Portell & Collins, 2004, closely resembles *Dynomene emiliae* Müller, 1984, from the Miocene of Austria. The genus is represented by seven living species (Ng et al., 2008). Another taxon, *Kromtitis spinulata* Portell & Collins, 2004, has much in common with Recent coral-associated species of Paradynomeninae (Guinot, 2008, p. 21).

Trapezia prisca Portell & Collins, 2004, closely resembles Upper Miocene *Trapezia glaessneri* Müller, 1984, and Middle Miocene *Trapezia brevipennis* Karasawa, 1993. The three extant North American species of *Trapezia* are found off the Pacific coast, although two extend their range far beyond; of these, *T. prisca* is closest to *Trapezia cymodoce feruginea* Latreille, 1825. It also shares characters with *Quadrella nitida* Smith, 1869 (Hickmann & Zimmerman, 2000, p. 23) and could possibly be ancestral to that genus. Unlike *Trapezia cymodoce feruginea*, *Quadrella nitida* is presently confined to the Pacific coast of the Americas from southern California to Panama. Müller (1984) and Schweitzer (2005) noted the commensal relationship of trapeziids to acroporid and pocilloporid corals. *Trapezia* is unknown from the post-Miocene of the Caribbean.

The earliest appearance of *Lophopanopeus* in North America, from the Oligocene of Alaska, was recorded by Rathbun (1926), who also noted three species in the Pleistocene of California. The genus has subsequently been recognised, tentatively, from the Cercado Formation of the Dominican Republic and a new species from the Plio-Pleistocene Moin Formation of Costa Rica (Todd & Collins, 2006). *Chlorodiella* is another North American genus restricted to a single extant species, *Chlorodiella longimana* (H. Milne Edwards, 1834), which differs from *Chlorodiella occidentalis* Portell & Collins, 2004, in having more continuous transverse ridges; those of *C. occidentalis* are shorter and confined closely to the lateral margins, and thereby is more closely allied to the diminutive *Chlorodiella juglans* Müller, 1984, from the Upper Miocene of Hungary.

Although more Jamaican genera (32.6%) occur in the Middle Miocene of Japan than the Tethyan Upper Miocene (26.7%), there is a greater affinity of the Jamaican species to Tethyan taxa. This reflects the conclusion of Blow & Manning (1996, p. 1) that the crabs of the Eocene Castle Hayne and Santee formations of North and South Carolina have greater affinities "... with the fauna of the Eocene of Hungary, Italy and Spain" (see also Schweitzer *et al.*, 2002).

Jamaica - Pliocene-Pleistocene – Crabs from this time interval have been described from four formations and some cave deposits, each defined by a distinctive sedimentary facies or facies association: the Upper Pliocene Bowden shell bed of the (basal) Bowden Formation, and the Pleistocene Manchioneal (including Old Pera beds), Port Morant and Falmouth formations. To this must be added an undescribed collection of crab carapaces and appendages (Majidae, Panopeidae, Xanthidae) from the Upper Pliocene Hopegate Formation (R.W.P., research in progress). The total number of species is over 90. However, that number is undoubtedly influenced by preservation and/or collecting bias, as well as difficulties arising from determining closely allied limb fragments. It will likely be modified by future collecting. Nevertheless, the present total of known species from these deposits is little more than half the number of extant decapod species (130) recorded from the island by Rathbun (1897, 1899) and later authors. Nevertheless, it is sufficient to allow limited palaeoecological statistics to be drawn, as well as wider aspects concerning distribution.

Twenty-eight taxa are recognised (mostly from dactyli and fixed fingers) from the Bowden shell bed. However, the generic position of one of these, aff. *Eurypoda* sp. (Collins & Portell, 1998, p. 116, pl. 2, fig. 3) was in error. Subsequent re-examination indicates the finely crenulated opposing margin and rimmed basal margin of the fixed finger is close to that of *Tetraxanthus bidentatus* (A. Milne-Edwards, 1880) (Cape Fear, North

Carolina to Brazil) and the taxon is here revised as *Tetraxanthus* sp. Of these 28 Bowden taxa, nine genera persist from the Miocene, but no species coincide. At the current state of our knowledge, it may be said that, if species in open nomenclature are accepted, with but two exceptions much of this fauna represents the earliest known specific appearance of extant Caribbean crabs. Only two species, '*Callianassa*' sp. and *Micropanope* aff. *spinipes* (A. Milne-Edwards, 1880) are in common with the Upper Pleistocene Falmouth Formation. *Mithrax* sp. and, tentatively, *Petrochirus bahamensis* (Herbst, 1791), *Calappa springeri*, *Persephona punctata punctata*, *Eurytium limosum* and *Panopeus herbstii* are fully recorded from the Port Morant Formation.

The two exceptions, mentioned above, are the presence of dactyli tentatively determined as aff. *Cancer* sp. and aff. *Hyas* sp., both genera now occurring in cooler waters. According to Nations (1975), *Cancer* species are sensitive to water temperature and the distribution of Recent eastern North American species extends only to the Bahamas. Similarly, *Hyas* occurs in more northerly waters. The latter genus, also in open nomenclature, is known from the Port Morant Formation of Jamaica and the Upper Miocene of Caribbean Panama.

Taxa (all determined from limb fragments) of particular importance in the Bowden shell bed include a partial dactylus of *Chlorilia* sp., a genus now inhabiting waters off the Pacific coast of Japan and North America, from Alaska to San Diego, and *Rochinia* sp., a widely distributed genus on both the Atlantic and Pacific coasts of North America, although not now known among Recent crabs of Jamaica. The parthenopid *Mesorhoea* aff. *sexspinosa* Stimpson, 1871, presently ranging from southeast Cape Lookout, North Carolina, to the Virgin Islands, is not only the youngest known fossil species of the genus, but has characters in common with *Mesorhoea maurya* from the Miocene of the Dominican Republic.

The Port Morant Formation, which has produced some carapace remains, has only one species, *Panopeus herbstii*, in common with the Falmouth Formation. An extinct callianassid, *Neocallichirus peraensis* Collins et al., 1997, has affinities with *Neocallichirus grandimana* (Gibbes, 1850); a propodus, regarded as *Leptopthalmus jamaicense?* (Schmitt, 1935), represents the earliest known occurrence of this genus in the fossil record. A partial carapace of *Hepatus praecox* Collins et al., 1997, has characters in common with the Atlantic form *Hepatus pubibundus* (Herbst, 1785) and with *Hepatus kossmanni* Neuman, 1878, its Pacific analogue, while a fixed finger assigned to *Callinectes* cf. *toxodes* Ordway, 1863, was considered by Collins et al. (1997) more closely to resemble *Callinectes bocourti* A. Milne-Edwards, 1897, its Caribbean analogue. Also known as a fossil, but absent from present day Jamaican waters, is *Raninoides louisianensis* Rathbun, 1933, now restricted to the Gulf of Mexico.

Two extant species that are relatively common in the Port Morant Formation, *Petrochirus bahamensis* and *Calappa springeri*, are tentatively recorded from the Bowden shell bed. Claws of *P. bahamensis* reach a large size and remains of the gastropod *Lobatus gigas* (Linnaeus, 1758), a preferred domicile, are not uncommon in the Port Morant Formation (Pickerill & Donovan, 1997; Donovan, 2002); a particularly complete specimen retaining associated pereopods has survived the aragonite dissolution of such a shell (Collins et al., 2009a). Another extant pagurid, *Paguristes lymanni* A. Milne-Edwards & Bouvier, 1893, is known from a tentatively assigned propodus (Collins et al., 2009a). Claws tentatively assigned to *Eriphia* by Collins & Portell (1998) are complemented by

Eriphia gonagra xaymacaensis Collins & Donovan, 1998, from the Port Morant Formation. This species has characters in common with *Eriphia squamosa* Rathbun, 1930, the Pacific analogue of the nominate species.

Although common in the Caribbean at the present time, the Majidae are rare in the fossil record of Jamaica. *Chlorilia* and *Rochinia* have been mentioned above, and are the only known fossil representatives of those genera throughout the Caribbean. *Pitho* sp. is also known from the Bowden shell bed (Collins & Portell, 1998), a damaged carapace of *Pitho anisodon* (von Martens, 1872) is from the Port Morant Formation, and the genus is also present as tentatively assigned dactyli from the Escudo de Veraguas and Moin formations of Panama. *Mithrax*, recorded simply as *Mithrax* sp. from the Bowden shell bed, is represented in the Port Morant Formation by carapaces of *Mithrax acuticornis* Stimpson, 1870; by claws of *Mithrax hispidus* Herbst, 1790, and *Mithrax verrucosus* H. Milne Edwards, 1832; and a chela-merus resembling *M. pilosus* Rathbun, 1892. *Mithraculus forceps* A. Milne-Edwards, 1875, is known from a chela-carpus. The last three species have also been recorded from the Falmouth Formation (Morris, 1993). A similar concentration of species is known only from the Pleistocene of Barbados.

Fourteen xanthoid species are reported from the Port Morant Formation and four from the Falmouth Formation (Morris, 1993; Collins *et al.*, 1997, 2009a; Collins & Donovan, 1998). Two genera and only one species, *Panopeus herbstii*, are common to both formations.

The first mention of crabs from the Lower Pleistocene Manchioneal Formation (Morris, 1993) was of an 'indeterminate fragment' and a 'galatheid fragment'. To this meagre sample Collins *et al.* (2001) added the description of *Euphyllax fortispinosus* from the Old Pera beds of this formation, a unit that has otherwise failed to produce crab remains. It is the youngest known fossil member of the genus; *Euphyllax callinectias* and *Euphyllax fortis* were described from the Miocene of Costa Rica, and *Euphyllax domingensis* (as *Podophthalmus*) from the Oligocene or Lower Miocene of Haiti. *Euphyllax septendentatus* Beurlen, 1958, has been described from the Miocene of Brazil, and *Euphyllax maculatus* Collins & Todd (*in* Todd & Collins, 2006) was described from the Upper Miocene and Lower Pliocene of Caribbean Panama. At present, the genus is confined to the Pacific coast of tropical Central America and the eastern tropical Pacific (Jerde, 1967). The closely related *Psygmodthalmus bifurcatus* Collins sp. nov. is only known from the Pliocene of Anguilla (Appendix 1).

Another taxon peculiar to the Falmouth Formation and recorded by Morris (1993) is a claw attributed to *Petrolithes* sp., a genus represented otherwise in the fossil record of the Caribbean region only by *Petrolithes avitus* Rathbun, 1919a, from the Pliocene of Costa Rica and by *Petrolithes myakkensis* described from the Pliocene Tamiami Formation of Florida (Bishop & Portell, 1989). A carapace of a leucosiid, *Uhlias* cf. *limbatus* Stimpson, 1871, which presently ranges from Florida to Jamaica, a claw ascribed to *Albunea* sp., and, in the Grapsidae, claws assigned to *Pachygrapsus* sp. and *Varuna?* sp. also occur. These, together with the xanthid *Cyclodius maculatus* (Stimpson, 1860), make their first appearance in the fossil record of the Caribbean region in the Falmouth Formation. Propodi of *Callianassa* sp. figured by Morris (1993, fig. 3:7, 3:8) may more correctly be assigned to *Neocallichirus*.

Attention was drawn by Rathbun (1919b) to the presence of claws of *Cardisoma guanhumii* Latreille, 1825, in the Pliocene of Costa Rica. The species was further recorded

from the Port Morant Formation of Jamaica by Collins & Donovan (1998), but the only instance of this essentially land crab occurring in a terrestrial deposit, a (Late?) Pleistocene fissure fill, was reported from eastern Jamaica by Donovan & Dixon (1998). Similarly, the species was recorded by Schweitzer *et al.* (2008) from a Late Pleistocene cave deposit in Puerto Rico. *Sesarma primagenium* Collins *et al.*, 2009b, described from numerous propodi from cave deposits, has characters in common with extant, indigenous *Sesarma* spp. of Jamaica.

Leeward Islands – A fragmentary carapace, *Tutus* gen. nov., from the Lower Miocene Lowlands Formation of Tintamare Island, St. Martin, is described in Appendix 1. It is similar to, and possibly derived from, *Stenodromia* A. Milne-Edwards, 1873, which ranges from the Middle Eocene to Middle Oligocene of France and Spain.

Mexico (Gulf Coast and Caribbean Sea) – Apart from references to “callianassid” and *Mursia?* sp. limb and/or carapace fragments (Vega *et al.*, 1999, p. 411), the only crabs described from the Middle Miocene Tuxpan Formation of the eastern coastal region of Mexico appear to be *Callinassa pellucida* Rathbun, 1919b, first known from the Oligocene of Anguilla (Rathbun, 1919b), and *Raninoides mexicanus* Rathbun, 1930. *Portunus ateuicutilis* Vega *et al.*, 1999, was likened to the Miocene Burdigalian *Portunus viai* Secretan, 1971, of France, whereas *Necronectes tajinensis* Vega *et al.*, 1999, was said to rather closely resemble *Necronectes proavitus* which ranges eastward to Puerto Rico.

Panama and Costa Rica - Miocene – The earliest description of a fossil crab from Panama appears to have been a well-preserved carapace of *Calappa zurcheri* by Bouvier (1899) from the Miocene. This species was recently reported from the Lower Miocene of Chiapas, Mexico (Vega *et al.*, 2009). Toulou (1911) described and figured chelae of *Petrochirus* cf. *granulatus* Olivier, 1811, as well as an unnamed chela. Brown & Pilsbry (1913) described *Neocallichirus* (as *Callianassa*) *scotti* from the ‘Oligocene’ (= Miocene) Gatun Formation of the Panama Canal Zone. By far the largest contribution was by Rathbun (1919a), when she documented 19 species from Panama and eleven from neighbouring Costa Rica (including earlier records). At the same time she described (but did not figure) *P.* cf. *granulatus* as *Petrochirus bouvieri*.

Descriptions and/or references to 14 nominal Miocene species, probably from the Gatun Formation, were included by Rathbun (1919a) in her treatment of decapods from Panama and Costa Rica. Six species were callianassids, one of which is from Costa Rica. *Callianassa moinensis* Rathbun, 1919a, is tentatively recorded from the Miocene Gatun Formation. This distinctive species may be referred to *Neocallichirus*.

Comparative data is included only for *Callianassa hilli* Rathbun, 1919a, consisting of limb fragments, one of which was said to be “much like the corresponding member of *Callianassa stimpsoni* Smith,” a Recent Atlantic species (Rathbun, 1919a, p. 148). *Callianassa toulou* Rathbun, 1919a, was not figured, although it was described as having three spines on the upper margin. This character would suit the requirement for *Glypturus* Stimpson, 1866, to which *C. toulou* is here referred. This genus is represented in the Pleistocene Port Morant Formation of Jamaica by *Glypturus acanthochirus* Stimpson, 1866 (Collins *et al.*, 1997), a western Atlantic species. *Callianassa crassa* Rathbun, 1919a, was described from two left cheliped dactyli. *Neocallichirus scotti* Brown &

Pilsbry, 1913, and *Callianassa vaughani* Rathbun, 1919a, are discussed below.

Of the other four taxa from Costa Rica, two *Euphyllax* species have been dealt with under Jamaica (see above). *Leucosilia bananensis* Rathbun, 1919a, is represented by limb fragments that were compared with a Recent species, *Leucosilia jurinii* (Saussure, 1853), otherwise known from limb fragments from the Pleistocene of the Panama Canal Zone. The present range of *L. jurinii* extends from Matzatlán, Mexico to Peru and the Galapagos Islands (Rathbun, 1937).

From Panama, *Petrochirus bouvieri* (figured in Toulou, 1911, pl. 30, fig. 13) shares characters with two Recent species, *Petrochirus californiensis* Bouvier, 1895, a Pacific form, and *Petrochirus bahamensis*, common to the Caribbean and known also from the Pleistocene of Jamaica. *Calappa zurcheri*, described from a well-preserved carapace, was said to be close to the Recent Mediterranean species *Calappa granulata* Linnaeus, 1758. No comparative data was included for *Mursillia ecristata* Rathbun, 1919a, described from an associated carpus and propodus.

Panama and Costa Rica - new collections – Since Rathbun's (1919a) contribution to the crabs of Panama and Costa Rica, intensive collecting from various localities by members of the Panama Palaeontological Project substantially increased the known decapod material. This was studied by Todd & Collins (2006), wherein extensions to the ranges recorded by Rathbun (1919a) are also detailed. From these collections eight new species were founded on carapace material, while another five were described from chelae remains deemed sufficiently distinctive. It was also possible to ascribe, with confidence, a carapace from the Pliocene/Pleistocene of Costa Rica to previously described chela elements. The species concerned, *Eurytium crenatum* Rathbun, 1919a, more closely shares characters of *Eurytium tristani* (Rathbun, 1906) (Pacific) than to *Eurytium limosum* (Caribbean), also referred to by Rathbun (1919a). The geographic range of 17 genera and/or species was extended from other Caribbean localities.

Among abundant callianassid remains in the new collections from the Miocene through Lower Pleistocene of Costa Rica and Panama, and from the Cercado and Mao formations of the Dominican Republic, similar and better preserved chelae were found to have characters common to four previously described *Callianassa* species. By and large, these components corresponded with the variety in form displayed by males, females and juveniles, as demonstrated by Manning & Felder (1995), of any one of a single species presently inhabiting the Caribbean. With the new comparable material to hand, *Callianassa scotti* was considered the senior taxon of synonymized *Callianassa crassimana* Rathbun, 1919a, *Callianassa vaughani* and *Callianassa miocenica* Rathbun, 1919b. Furthermore, all the material possesses characters fundamental to the genus *Neocallichirus* Sakai, 1988, and *C. scotti* was referred to that genus. Likewise, *Callianassa toulou* (Rathbun, 1919a), from the middle Gatun Formation, Late Miocene of Panama, was referred to *Glypturus*.

The thalassinoid *Ctenocheles falciformis* Collins & Todd (*in* Todd & Collins, 2006) was described from the Pliocene Cayo Agua and Escudo formations of Caribbean Panama, the Lower Pleistocene Moin Formation of Caribbean Costa Rica and the coeval Montezuma Formation of Pacific Costa Rica. The genus is also known from the Pliocene Bowden shell bed of Jamaica and is presently represented in North American western Atlantic waters by four species (Manning & Felder, 1995).

The range of *Petrochirus bouvieri* was extended from the Upper Pliocene to Lower Pleistocene of isthmian and Caribbean Panama and Costa Rica; examples are preserved within domicile gastropod shells of several species. *Dardanus biordines* Collins & Todd (*in* Todd & Collins, 2006) was established upon a propodus and pereopod dactylus from the Lower Pliocene Cayo Agua Formation of Caribbean Panama. It has much in common with corresponding elements figured as *Pagurus striatus petersi* by A. Milne-Edwards & Bouvier (1893), which presently occurs to the west of Florida, and with *Dardanus insignis* Saussure, 1858 (*in* Verrill, 1908).

Partial carapaces, from the Upper Miocene Tobabe Sandstone of Caribbean Panama and Lower(?) Pleistocene Armuelles Formation of Pacific Costa Rica, were tentatively identified as the extant *Raninoides benedicti* Rathbun, 1935, presently found on both sides of the isthmus (Rathbun, 1937). These records make a significant contribution to the fossil record of the genus, previously known only from a partial carapace of *Raninoides louisianensis* from the Pleistocene of Jamaica (Collins *et al.*, 1997).

The appearance of the extant *Cryptosoma bairdii* from the Lower Pliocene of Panama and Plio-Pleistocene boundary of Costa Rica extends the fossil geographical range of this species, previously described from the Lower Miocene of the Dominican Republic (Rathbun, 1919b). The species presently ranges from the west coast of Mexico to Ecuador and the Galapagos Islands, North Carolina to the Caribbean sea and the Bermudas (Rathbun, 1937).

Hepatus chiliensis H. Milne Edwards, 1837, was described from the Pleistocene of Mount Hope, Colon, Panama. *Hepatus lineatinus* Collins & Todd (*in* Todd & Collins, 2006) ranges from the Middle Miocene basal Gatun Formation to Upper Pliocene Escudo de Veraguas Formation of Caribbean Panama, and also occurs in the Lower Pliocene Penito and Rio Banano formations of Caribbean Costa Rica. It has much in common with *Hepatus lineatus* Rathbun, 1898, presently ranging on the west coast of Mexico to Peru (Rathbun, 1937); one carapace has a well developed bopyriform infestation. *Hepatus biformis* Collins & Todd (*in* Todd & Collins, 2006), found in the Tobabe Sandstone of Caribbean Panama and the Lower Pliocene Peñita Formation of Pacific Costa Rica, more closely resembles *Hepatus kossmanni* Neumann, 1878, another East Pacific species. The genus is known as a fossil elsewhere in the Caribbean from the Miocene of Trinidad and the Dominican Republic, and from the Pleistocene of Jamaica (Collins *et al.* 1997; Collins & Portell, 1998).

Leucosilia bananensis Rathbun, 1919a, formerly recorded from the Lower Pliocene Rio Banano Formation of Caribbean Costa Rica and the Lower Pliocene Cayo Agua Formation, was extended back to the Upper Miocene Tobabe Sandstone and Upper Miocene basal Gatun Formation of Caribbean Panama. Also from the Tobabe Sandstone of that region, *Iliacantha panamanica* Collins & Todd (*in* Todd & Collins, 2006) appears to be distantly related to two widespread Recent Caribbean species and extends the geographical range of the genus from the Dominican Republic. *Speleophorus subcircularis* Collins & Todd (*in* Todd & Collins, 2006) from the Upper Pliocene Cayo Agua Formation, Caribbean Panama, has a superficial resemblance to *Speleophorus digueti* (Bouvier, 1898), presently occurring off the west coast of Mexico to Panama (Rathbun, 1937). Of two species of *Persephona* described by Collins & Todd (*in* Todd & Collins, 2006), *Persephona manningi*, low Upper Pliocene Escudo de Veraguas Formation of Bocas del Toro Province, Panama, does not appear to have a close relationship with other fossil or Recent

species. In contrast, *Persephona enigmatica*, low Upper Pliocene Cayo Agua Formation of Panama, although described as a new species, shares characters with both *Persephona punctata punctata* and *Persephona townsendi* (Rathbun, 1893) from the Gulf of California to Ecuador, species referred to by Rathbun (1919b) when describing *Persephona prepunctata* from meri from the Miocene of the Dominican Republic. Because of the presence of more than one species, persephonid meri in the new collections cannot with confidence be ascribed to any of them.

The geographic and stratigraphic range of *Portunus gabbi*, described from the Lower(?) Miocene of Hispaniola, was extended to the Middle to Upper Miocene Tuirá Formation through to the Upper Miocene Tobabe Sandstone of Panama and the Lower Pliocene Rio Banano Formation of Costa Rica. *Euphyllax maculata* Collins & Todd (*in* Todd & Collins, 2006), described from the Middle/Late Miocene to Late Pliocene of Caribbean Panama, has distinct characters separating it from *Euphyllax callinectias*, Lower Pliocene Rio Banano Formation (originally considered as Miocene by Rathbun, 1919a) of Costa Rica, and indicate a closer relationship to *Euphyllax domingensis*. Also included in the Podophthaminae by Todd & Collins (2006), the geographic and stratigraphic range of *Sandomingia yaquiensis* Rathbun, 1919b, formerly described from the Lower(?) Miocene of Haiti, was extended to the Cayo Agua Formation of Panama and basal Moin Formation of Costa Rica.

Also recorded herein from the Dominican Republic, *Eurypanopeus* and *Platyxanthus* species both make their appearance in this region. *Eurypanopeus* sp. occurs in the Lower Pleistocene Moin Formation of Caribbean Costa Rica, while *Platyxanthus* sp., of similar age from Costa Rica, is also known from the Upper Miocene Nancy Point Formation of Panama. *Lophopanopeus maculoides* Collins & Todd (*in* Todd & Collins, 2006), of the Upper Pliocene Moin Formation of Caribbean Costa Rica, is close to the Pacific coast form *Lophopanopeus maculatus* Rathbun, 1898. The extant xanthid *Heteractaea lunata* (H. Milne Edwards & Lucas, 1843), previously known from the Moin Formation of Costa Rica (Rathbun, 1919a), occurs in the Upper Pliocene Escudo de Veraguas Formation of Caribbean Panama (Todd & Collins, 2006).

Claws tentatively assigned to genera and/or species include *Micropanope* (as cf. *Micropanope* sp.) from the Upper Pliocene of Caribbean Costa Rica and Panama, thereby extending the generic fossil range from the Miocene of Jamaica from whence it is also recorded from Pliocene deposits. *Pilumnus* (listed as cf. *Pilumnus* sp.) from the Pliocene Cayo Agua Formation of Panama and Pleistocene Armuelles Formation (Todd & Collins, 2006) extends the range of the genus from the Pliocene of Jamaica (Collins & Portell, 1998). *Eurypanopeus* sp. occurs in the Lower Pleistocene Moin Formation of Caribbean Costa Rica as does *Platyxanthus* sp., also known from the Upper Miocene of Panama.

As in other parts of the Caribbean region, oxyrhynchs are poorly represented. A carapace, *Thoe asperoides* Collins & Todd (*in* Todd & Collins, 2006) from the Pleistocene Swan Clay Formation of Panama, has characters in common with *Thoe aspersa* Rathbun, 1901, presently occurring off Puerto Rico (Rathbun, 1925), while dactyli reminiscent of *Hyas* Leach, 1814, left in open nomenclature as aff. *Hyas* sp., as is the genus, were also recorded from the Bowden shell bed of Jamaica (Collins & Portell, 1998). *Pitho* sp. from the Upper Pliocene Escudo de Veraguas Formation of Caribbean Panama represents the only known fossil occurrence of the genus in Central America (Todd & Collins, 2006). *Mithrax* sp. from the Moin Formation of Costa Rica has characters

closely resembling the Recent Caribbean species *Mithrax caribbaeus* Rathbun, 1920a, and *Mithrax orcutti* Rathbun, 1925, which is found on both sides of the Isthmus of Panama today. The fossil range of the genus extends from the Miocene of Haiti to the Upper Pliocene Bowden Shell Bed of Jamaica (Collins & Portell, 1998).

Puerto Rico – Until Gordon (1961, p. 610) listed “fragments of crustacean pincers” from the “late Miocene or possibly Pliocene Guanajibo formation,” no fossil decapods were known from Puerto Rico. Later, Gordon (1966, pp. 184, 185) reported *Necronectes proavitus* (Rathbun, 1919a) as occurring in the Lower Miocene “San Sebastian formation or basal Lares limestone” and *Portunus* cf. *oblongus* Rathbun, 1920b, from the Lower Miocene “Ponce limestone, probably lower member.” The taxonomic designation of the latter was deemed unacceptable by Feldmann & Schweitzer (2004) based on the outline of sternites and overall form of the abdomen. Refinements to stratigraphic determinations of the formations (Larue, 1994), however, now place the San Sebastian Formation in the Lower to Upper Oligocene and the basal Lares Formation in the Upper Oligocene. Therefore, only the portunid (formerly considered *P.* cf. *oblongus*) should be considered to occur in the Neogene of Puerto Rico. To this single Neogene record, Schweitzer *et al.* (2006) described, from the upper Lares Formation near San Sebastian, two new portunids (*Necronectes collinsi* and *Psymophthalmus lares*) and one new calappid (*Calappa pavimenta*). The upper Lares Formation, based on the occurrence of *Miosorites americanus*, is Lower Miocene (Schweitzer *et al.*, 2006). *Eurytium granulatum* Schweitzer *et al.*, 2008, from the Miocene Ponce Limestone, is the earliest known member of the genus, which is known elsewhere in the Caribbean from the Plio-Pleistocene of Jamaica (Collins *et al.* 1997; Collins & Portell, 1998) and the Plio-Pleistocene of Panama (Rathbun, 1919b; Todd & Collins, 2006). Furthermore, the land crab *Cardisoma guanhumii* was reported by Schweitzer *et al.* (2008) from an Upper Pleistocene cave deposit.

St. Kitts – A worn chela in the BMNH, labelled as *Petrochirus bouvieri*, is from the Pleistocene of Brimstone Hill, which has given a radiocarbon age of 44 ± 1.2 ka (Westermann & Kiel, 1961, *loc. cit.* Maury *et al.*, 1990, p. 159). The nature of the sculpture is better regarded as *Petrochirus bahamensis* (compare with Collins *et al.*, 1997).

Trinidad – Mention has been made above (see Puerto Rico) of *Necronectes proavitus* and *Portunus oblongus*. Also described from the Brasso Formation of Trinidad (for stratigraphy, see Donovan, 1994) are *Hepatus nodosus* Collins & Morris, 1976 (overlooked by Schweitzer & Feldmann, 2000, in their survey of included calappoids), a species that has similarities to the extant *Hepatus lineatus* which ranges from Mexico to Peru(?) (Rathbun, 1937). A well-preserved carapace, recorded by Collins & Morris (1976) as *Persephona* cf. *punctata punctata*, compares reasonably well with Rathbun’s (1937) description and figures. No persephonid limb fragments were among the C.T. Trechmann collection in the BMNH, but the Trinidad carapace has certain affinities to *Persephona townsendi*, the Pacific analogue of *P. punctata punctata*, to which Rathbun (1937, p. 152) referred when discussing *Persephona prepunctata*. The Trinidad specimen may thus be synonymous with *P. prepunctata*.

Palaeopinnixa intermedia (Collins & Morris, 1976) was considered to have affinities to *Palaeopinnixa eocenica* (Woods, 1922) and to closely resemble the Panamanian Oligocene

species *Palaeopinnixa prima* (Rathbun, 1919a). All three species, formerly placed in *Thaumastoplax*, were transferred to *Palaeopinnixa* (Hexapodidae) in a re-evaluation of that genus by Schweitzer & Feldmann (2001). With origins in the Maastrichtian-Danian of Argentina, the geographical distribution of this extinct genus includes North and South America, the Caribbean and Spain.

The remaining known Early Miocene crab from Trinidad is the raninid *Ranina cuspidata* Guppy (1909).

Venezuela – Feldmann & Schweitzer (2004) summarized the work of other authors (whose opinions regarding the age of the material varied from Late Eocene to Early Miocene), and recognized a total of nine species and at least two indeterminate taxa from the Lower Miocene Castillo Formation. Limb fragments were assigned to *Callianassa* sp. and *Petrochirus* sp., genera widespread in the Caribbean. *Eoinachoides senni* Van Straelen, 1933, is unique to Venezuela. *Raninoides rathbunae* Van Straelen, 1933, *Calappa laraensis* Van Straelen, 1933, and *Parthenope venezuelensis* Van Straelen, 1933, are known only from Venezuela, although the genera are all well distributed throughout the Caribbean. *Eriosachila rathbunae* (Maury, 1930), likewise known only from Venezuela, is the youngest member of an essentially Eocene genus. *Falconoplax kugleri* Van Straelen, 1933, has characters in common with *Falconoplax bicarinella* Collins & Morris, 1976, an Eocene species from Barbados, whereas *Palaeopinnixa perornata* (Collins & Morris, 1976), was first described from the Lower or Middle Eocene Scotland Beds of Barbados. The most widespread of the species recorded by Feldmann & Schweitzer (2004) was *Portunus oblongus* Rathbun, 1920b, known elsewhere from the Dominican Republic, Puerto Rico and Trinidad.

Discussion

Much of the generic data presented herein are summarised in Tables 2-4; specific data can be cross referenced from the text. These, in turn, are examined using a simple index of similarity at the level of genus in Table 5, only including those formations with ten or more species. These data are very preliminary; the known diversity of seven out of fourteen horizons is less than 15 and some (Cal, Chi, Low, Upp_p, Upp_M) are composites of approximately coeval formations from one area.

Three groups of decapod crustaceans are apparently particularly diverse throughout the Neogene, the callianassids, *Calappa* and the portunids. Their diversity, as presence per total number of formations, can be summarised from Tables 2-4 thus:

	Miocene	Pliocene	Pleistocene
callianassids	8/16	5/7	6/12
<i>Calappa</i>	9/16	6/7	4/12
portunids	14/16	4/7	4/12

The reasons for this pattern may be taphonomic and collector bias, in part. Callianassids have propodi that are easily identifiable to family level, commonly as '*Callianassa*,' but in only relatively few cases has this been extended to accurate generic determinations, due to the inherent difficulty of the taxonomy of their fragments. The broad

	Cub	Lar	Ang	Chi	Mon	Tho	Cas	Bra	Coo	Tux	Gra	Mid	Pon	Cer	Upp	Gur
Family Inachidae																
<i>Eoinachoides</i>							1									
Family Majidae															1	
<i>Thoe</i>																
Family Mithracidae																
<i>Mithrax</i>					2											
<i>Teleophrys</i>				1												
Family Pisidae																
aff. <i>Hyas</i>															1	
<i>Libinia</i>														1		
Family Dairidae																
<i>Daira</i>					1											
Family Parthenopidae																
<i>Mesorhoea</i>														1		
<i>Parthenope</i>			1			1?	1									
Family Portunidae																
<i>Callinectes</i>				1										1		
<i>Euphylax</i>	1											1			1	
<i>Necronectes</i>		1						1		1						
<i>Portunus</i>	1			2		1	1	1		1		1	1		1	
<i>Pseudoachelous</i>					1											
<i>Psygmophthalmus</i>		1	1													
<i>Rathbunella</i>																1
<i>Sandomingia</i>																1
<i>Scylla</i>			1	1										1		
portunid sp.											1					
Family Goneplacidae																
<i>Falconoplax</i>							1									
Family Hexapodidae																
<i>Palaeopimixa</i>							1	1								
Family Menippidae																
<i>Menippe</i>				1												
Family Panopeidae																
<i>Lophopanopeus</i>					2									1		
<i>Micropanope</i>					1											
<i>Panopeus</i>			1		1	1?						1		1	1	
Family Pilumnidae																
<i>Pilumnus</i>														2		
Family Platyxanthidae																
<i>Platyxanthus</i>											1				1	
Family Trapeziidae																
<i>Trapezia</i>					1											
Family Xanthidae																
<i>Actaeops</i>					1											
<i>Chlorodiella</i>					1											
<i>Eurytium</i>				1									1	1		
<i>Leptodius</i>					1											
Total species	2	3	9	11	16	3	10	6	2	5	2	8	2	19	16	6
Total genera	2	3	7	9	14	3	10	6	2	5	2	8	2	17	15	6

Table 3. Pliocene decapod crustaceans of the Caribbean region (compiled mainly from Rathbun, 1919a, b, 1920a, b, 1923; Collins & Portell, 1998; Portell & Agnew, 2004; Todd & Collins, 2006; herein). Numbers indicate number of species; totals include species and genera. Key: Bow = Bowden shell bed, Bowden Formation, Upper Pliocene of Jamaica; Cal = Caloosahatchee and Nashua formations, Upper Pliocene to Lower Pleistocene of Florida; Flo = Intracoastal, Jackson Bluff and Tamiami formations, Pliocene of Florida; Low = Lower Pliocene, Costa Rica and Panama; Mao = Mao Formation, Lower Pliocene of Dominican Republic; Sdo = Seroe Domi Formation, Upper Pliocene to Lower Pleistocene of ABC Islands; Upp = Upper Pliocene, Costa Rica and Panama. Numbers indicate number of species of each genus known from horizon; uncertainties are indicated by '1?' or 'aff.' (Bengtson, 1988).

	Flo	Low	Mao	Upp	Bow	Sdo	Cal
Infraorder Thalassinidea							
Family Callianassidae							
<i>'Callianassa'</i>		1	1	1	1		
<i>Callichirus</i>							1
<i>Neocallichirus</i>				1			
<i>Neotrypea</i>							1
<i>Sergio</i>			1				1
Family Ctenochelidae							
<i>Ctenocheles</i>		1	1	1	1		
Infraorder Anomura							
Family Porcellanidae							
<i>Petrolisthes</i>	2						
Family Diogenidae							
<i>Dardanus</i>		1					
<i>Paguristes</i>					1		
<i>Petrochirus</i>				1	1		1
Infraorder Brachyura							
Family Raninidae							
<i>Ranilia</i>	1						
raninid sp.						1	
Family Calappidae							
<i>Calappa</i>	1	1	1	2	1		1
<i>Cryptosoma</i>		2	1	1?			
calappid sp.						1	
Family Hepatidae							
<i>Hepatus</i>		2		1	1		
Family Leucosiidae							
<i>Leucosilia</i>		1		1			
<i>Persephona</i>				2	1		1
<i>Speleophorus</i>				1			
leucosiid sp.						1	
Family Majidae							
<i>Euprognatha</i>	1						
<i>Libinia</i>							1
majid sp.						1	
Family Mithracidae							
<i>Mithrax</i>					1		
Family Pisidae							
aff. <i>Chlorilia</i>					1		
aff. <i>Hyas</i>					1		
aff. <i>Rochimia</i>					1		

	Flo	Low	Mao	Upp	Bow	Sdo	Cal
Family Tychidae							
<i>Pitho</i>				1	1		
Family Parthenopidae							
<i>Mesorhoea</i>					1		
<i>Parthenope</i>							1
<i>Platylambrus</i>		1		2	1		
Family Cancridae							
aff. <i>Cancer</i>					1		
Family Portunidae							
<i>Callinectes</i>				1	1		
<i>Euphylax</i>		1		1			
<i>Portunus</i>				1	1		1
<i>Sandomingia</i>		1		1			
portunid sp.		1		1			
Family Carcinidae							
<i>Ovalipes</i>					aff.		1
Family Eriphiidae							
<i>Eriphia</i>					1		
Family Menippidae							
<i>Menippe</i>	1						2
Family Panopeidae							
<i>Eurypanopeus</i>					1		
<i>Eurytium</i>		1			1		
<i>Micropanope</i>				1	2		
<i>Neopanope</i>					1		
<i>Panopeus</i>		2		3	1		
Family Pilumnidae							
<i>Pilumnus</i>		1		1	2		
Family Xanthidae							
<i>Heteractea</i>				1			
<i>Tetraxanthus</i>					1		
Total species	6	17	5	26	28	4	12
Total genera	5	14	5	21	26	4	11

claws of *Calappa*, the 'shame faced crab,' are easily identifiable to generic level. More interestingly, portunids are very diverse. The following are all listed in Tables 2-4 - *Achelous*, *Callinectes*, *Euphylax*, *Necronectes*, *Ovalipes*, *Portunus*, *Pseudoachelous*, *Psygmothalmus*, *Rathbunella*, *Sandomingia*, *Scylla* and the eponymous portunid sp. Of these, *Callinectes*, *Euphylax* and *Portunus* are known from the Miocene, Pliocene and Pleistocene of the study area; *Portunus* notably occurs at multiple localities.

The overall pattern apparent in Table 5 is that Miocene and Pliocene formations generally show greater similarity than those of the Miocene and Pleistocene, as would be anticipated. There are some high generic similarities. For example, that between the Caloosahatchee plus Nashua formations (Cal) and the Bermont Formation (Ber) is 82%, but all are in Florida, from the Upper Pliocene to Lower Pleistocene and Lower to Middle Pleistocene, respectively. Similarly, the Lower (Low) and Upper (Upp_p) Pliocene of Costa Rica and Panama show 86% similarity over a limited stratigraphic range and geographic area.

Table 4. Pleistocene decapod crustaceans of the Caribbean region (compiled from Rathbun, 1919a, b, 1920a, b, 1923; Collins & Morris, 1976; Morris, 1993; Collins *et al.*, 1997, 2009a; Collins & Donovan, 1998; Donovan *et al.*, 2003b; Portell & Agnew, 2004; herein). Numbers indicate number of species (if any); totals include species and genera. Key: Ana = Anastasia Formation, Upper Pleistocene of Florida; Ber = Bermont Formation, Lower to Middle Pleistocene of Florida; Cor = Coral Rock, Middle to Upper Pleistocene of Barbados; Cub = Jaimanitas Formation, Upper Pleistocene of Cuba; Fal = Falmouth Formation, Upper Pleistocene of Jamaica; Fth = Fort Thompson Formation, Upper Pleistocene of Florida; Hai = Pleistocene of Haiti; Man = Manchioneal Formation (including Old Pera beds), Lower Pleistocene of Jamaica; Mls = Miami Limestone, Upper Pleistocene Florida; Pmo = Port Morant Formation, Upper Pleistocene of Jamaica; Pue = Upper Pleistocene of Puerto Rico; Ski = Upper Pleistocene of St. Kitts; Rhr = Red Hills Road Cave, Upper Pleistocene of Jamaica. Numbers indicate number of species of each genus (if any) known from horizon; uncertainties are indicated by '1?' or 'aff.' (Bengtson, 1988).

	Hai	Man	Ber	Cor	Ana	Fth	Mls	Fal	Pmo	Cub	Pue	Ski	Rhr
Infraorder Thalassinidea													
Family Callianassidae													
' <i>Callianassa</i> '		1				1				1			
<i>Callichirus</i>			2										
<i>Glypturus</i>									1				
<i>Lepidophthalmus</i>									1				
<i>Neocallichirus</i>			1					1	1				
<i>Neotrypea</i>			1										
<i>Sergio</i>			1										
Family Ctenochelidae													
<i>Ctenocheles</i>			1										
Infraorder Anomura													
Family Upogebiidae													
<i>Upogebia</i>			1										
Family Galatheidae													
galatheid sp.		1											
Family Porcellanidae													
<i>Petrolisthes</i>								1					
Family Albuneidae													
<i>Albunea</i>								1					
Family Diogenidae													
<i>Petrochirus</i>			1					1	1			1	
diogenid sp.						1							
Family Paguridae													
<i>Paguristes</i>									1				
pagurid sp.										1			
Infraorder Brachyura													
Family Raninidae													
<i>Raninoides</i>									1				
Family Calappidae													
<i>Calappa</i>			1		1			1	1				
calappid sp.										1			
Family Hepatidae													
<i>Hepatus</i>			1						1				
Family Leucosiidae													
<i>Persephona</i>			1			1			1				
<i>Uhlias</i>								1					

	Hai	Man	Ber	Cor	Ana	Fth	Ms	Fal	Pmo	Cub	Pue	Ski	Rhr
Family Majidae													
<i>Herbstia</i>				1									
<i>Libinia</i>			1										
Family Mithracidae													
<i>Mithraculus</i>				1				1	1				
<i>Mithrax</i>	1			5				2	3				
Family Pisidae													
aff. <i>Hyas</i>									1				
Family Tychidae													
<i>Pitho</i>									1				
Family Cancridae													
<i>Cancer</i>							1?						
Family Portunidae													
<i>Achelous</i>									1				
<i>Callinectes</i>									1				
<i>Euphylax</i>		1											
<i>Portunus</i>			3	2					1				
Family Carcinidae													
<i>Ovalipes</i>			1										
Family Carpiliidae													
<i>Carpilius</i>				1					1				
Family Pseudorhombilidae													
<i>Nanoplax</i>									1				
Family Eriphidae													
<i>Eriphia</i>									1				
Family Menippidae													
<i>Menippe</i>						1							
Family Panopeidae													
<i>Eurypanopeus</i>								1	1				
<i>Eurytium</i>									1				
<i>Hexapanopeus</i>									1				
<i>Micropanope</i>								2	1				
<i>Panopeus</i>								1	2				
paneopeid sp.										1			
Family Pilumnidae													
<i>Pilumnus</i>			1	1					1				
Family Xanthidae													
<i>Actaea</i>				1					2				
<i>Cyclodius</i>								1					
Family Pinnotheridae													
<i>Pinnixia</i>			1										
Family Ocypodidae													
<i>Ocypode</i>					1								
<i>Uca</i>			1					1					
Family Gecarcinidae													
<i>Cardisoma</i>									1		1		
Family Grapsidae													
<i>Pachygrapsus</i>								1					
Family Sesarmidae													
<i>Sesarma</i>													1
Total species	1	3	19	12	2	4	1	16	31	4	1	1	1
Total genera	1	3	16	7	2	4	1	14	27	4	1	1	1

Table 5. Similarity of the decapod crustacean genera of Neogene decapod crustacean localities of the Caribbean region that have yielded at least ten species (n = number of genera). Sites with 0% similarity are emphasized by bold type. Similarity calculated using Simpson's Index, where

$$\text{Similarity (\%)} = \frac{(\text{number of genera in common})}{(\text{number of genera in smaller fauna})} \times 100\%$$

Cas n=10	Chi n=9	Mon n=13	Cer n=16	Upp_M n=15	Low n=14	Upp_P n=21	Bow n=26	Cal n=11	Ber n=16	Cor n=7	Fal n=14	Pmo n=27	
---	44	0	30	50	20	40	40	40	30	14	30	40	Cas
	---	0	56	44	33	56	78	44	33	14	33	67	Chi
		---	15	8	8	15	23	0	0	14	23	23	Mon
			---	40	57	56	56	36	44	14	29	56	Cer
				---	36	53	47	27	33	14	29	60	Upp_M
					---	86	57	9	29	0	21	43	Low
						---	62	36	56	29	36	48	Upp_P
							---	45	50	43	50	62	Bow
								---	82	14	18	36	Cal
									---	29	21	44	Ber
										---	29	86	Cor
											---	50	Fal
												---	Pmo

Key to Miocene localities: Cas = Castilla Formation, Lower Miocene of Venezuela; Chi = Lower Miocene formations of Florida; Mon = Montpelier Formation, Lower Miocene of Jamaica; Cer = Cercado Formation, Upper Miocene of Dominican Republic; Upp_M = Upper Miocene of Costa Rica and Panama (after Todd & Collins, 2006).

Key to Pliocene and Plio-Pleistocene localities: Low = Lower Pliocene, Costa Rica and Panama; Upp_P = Upper Pliocene, Costa Rica and Panama; Bow = Bowden shell bed, Bowden Formation, Upper Pliocene of Jamaica; Cal = Caloosahatchee and Nashua formations, Upper Pliocene to Lower Pleistocene of Florida.

Key to Pleistocene localities: Ber = Bermont Formation, Lower to Middle Pleistocene of Florida; Cor = Coral Rock, Middle to Upper Pleistocene of Barbados; Fal = Falmouth Formation, Upper Pleistocene of Jamaica; Pmo = Port Morant Formation, Upper Pleistocene of Jamaica.

Only two units demonstrate 0% similarity with other formations (Table 5), the Lower Miocene Montpelier Formation of Jamaica (four times) and the Pleistocene Coral Rock of Barbados (once). As noted by Portell & Collins (2004), these two units include the only assemblages of coral-inhabiting decapod crustaceans in the Caribbean. The Montpelier Formation, although consisting of deeper water chalks, includes slide blocks of scleractinian limestones derived from shallower water and presumably a reef. Its decapod fauna includes a number of genera that are otherwise unknown from the region; indeed, three out of 13 are only known from the Montpelier Formation (Portell & Collins, 2004, fig. 1). In contrast, the Pleistocene Coral Rock is autochthonous and includes the lowest generic diversity of the units considered (n = 7); of the twelve included species, five are *Mithrax* and two *Portunus* (Collins & Morris, 1976). Like the Montpelier Formation, it includes rare genera; however, it shows an 86% similarity (six out of seven genera) to the slightly younger Port Morant Formation of Jamaica. But, with only seven included genera, it would be expected to show a marked dissimilarity to some formations even if it didn't represent a rarely encountered palaeoenvironment. Attempts to find a similar fauna in the raised reef of the Pleistocene Falmouth Formation at east Rio Bueno Har-

bour, parish of St. Anne, have been unsuccessful (Donovan & Collins, 1997).

Two Jamaican horizons have yielded 26 genera, the Upper Pliocene Bowden shell bed, Bowden Formation, and the Upper Pleistocene Port Morant Formation. As might be expected, these show high similarities with less diverse formations, even from other series (Table 5). For example, both have 23% similarity with the Lower Miocene Montpelier Formation, among the highest found with that horizon. Most notably, the Port Morant Formation has 86% similarity (six out of seven genera) with the slightly older Coral Rock of Barbados. Exceptionally for a Pleistocene unit, the Port Morant Formation shows 50% or more similarity with three out of five Miocene sites, presumably due to its own high generic diversity.

The youngest record for Caribbean species of Pacific forms is Upper Pleistocene, which does not affect other opinions of closure date, but could suggest that the species concerned in earlier deposits have not yet been found elsewhere or could have continued to survive in the Caribbean after closure.

Acknowledgements

Mrs Pat Christopher (formerly BMNH) is thanked for her considerable efforts in typing an early incarnation of this paper, Dr. R.-P. Carriol (Muséum national d'Histoire naturelle) for supplying relevant literature, Dr. P. Clark (BMNH) for providing access to Recent comparative material, Ms Claire Mellish (BMNH) for checking registration numbers and Dr. W. Etter (NMB) for providing registration numbers. We thank the Photographic Unit of the BMNH for supplying the images used herein and the Naturhistorisches Museum Basel for loaning specimens for description. Detailed review comments by Drs Francisco J. Vega (Ciudad Universitaria, Coyoacán, Mexico) and Carrie E. Schweitzer (Kent State University, Ohio) are very gratefully acknowledged. This is University of Florida Contribution to Paleobiology 563.

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Appendix 1

Systematic palaeontology

J.S.H. Collins

Order Decapoda Linnaeus, 1758
Infraorder Anomura H. Milne Edwards, 1832
Superfamily Paguroidea Latreille, 1802
Family Paguridae Latreille, 1802
Genus *Dardanus* Paulson, 1875

Type species – *Dardanus helleri* Paulson, 1875, by original designation (after Glaessner, 1969, p. R480).

Diagnosis – (Adapted from Glaessner, 1969.) “Carapace elongate, widened and weakly calcified posteriorly, rostrum very short, abdomen uncalcified and coiled or secondarily symmetrical externally” (p. R479). “Chelipeds (with few exceptions) dissimilar and unequal, left being much larger than right; finger tips corneous, blackened and somewhat spooned, especially those of smaller chelae” (p. R480).

Range – Eocene to Recent.

***Dardanus squamatus* Collins sp. nov.**

Pl. 1, figs. 7, 8.

Derivation of name – Latin, *squamosus*, scaly, for the appearance of the surface sculpture.

Diagnosis – Fixed finger with scale-like ornament and weakly spooned occludent surface.

Material – Holotype, a right fixed finger, Naturhistorisches Museum Basel (NMB) collection, NMB F1467, locality 15907. Paratypes, two fixed fingers in the NMB (localities 15878 and 16913, respectively).

Locality and horizon – The holotype is from the Upper Miocene Cercado Formation at Río Gurabo. The paratypes are from the Upper Miocene-Lower Pliocene Gurabo Formation at Río Gurabo (locality NMB 15878) and Río Mao (locality NMB 16913). All specimens are from the Dominican Republic.

Description – Fixed finger, moderately curved inwards, length a little more than twice the proximal height and about one third longer than the occludent surface. The ornament is composed of subrhomboidal scales composed of three lines each divided

into four or five rows. On the outer surface a shallow groove lined with setal pores runs parallel with the cutting edge; the edge itself is lined with four or five granules which give way to a smooth edge round the tip; setal pores line a furrow behind the ridge. The vaguely spooned occludent surface has three medial pores and two more at the distal inner margin. A small area preserved of the inner margin of the propodus is smooth.

Discussion – Recent *Dardanus venosus* (H. Milne Edwards, 1848), strictly from the tropical western Atlantic (Biffar & Provenzano, 1972), differs in having fewer lines and rows of scale-like ornament. Fossil occurrences in the Caribbean are rare; *Dardanus bi-ordines* Collins & Todd in Todd & Collins, 2006, from the Lower Pliocene of Panama, has fewer rows of tubercles on the fixed finger and the lower margin is straighter than that of *D. squamatus*.

Section Eubrachyura Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Calappoidea De Haan, 1833
Family Calappidae De Haan, 1833
Genus *Calappa* Weber, 1795

Type species – *Cancer granulatus* Linnaeus, 1758, by subsequent designation of Latreille (1810).

Diagnosis – (After Glaessner, 1969, p. R494.) “Carapace strongly convex, expanded to maximum width posterolaterally, front and orbits small, chelipeds very large, fitting front of carapace, dactylus of one hand with strongly curved basal tooth.”

Range – Middle Eocene(?) to Recent.

***Calappa* sp.**
 Pl. 1, fig. 9.

Material, locality and horizon – An associated right dactylus and fixed finger, BMNH In. 63682, from the Lower Miocene Anguilla Formation, near Cathedral Cave, western Anguilla.

Description – The dactylus (L, 32.2+ mm; H, proximal, 16.00+ mm) is weakly sinuous along the upper edge, the tip overlapping the fixed finger; triangular tubercles becoming granulose distally are bounded on the outer surface by distally converging granules. Granules extend half the height of the outer surface. A robust articulating boss curves into a corresponding notch in the fixed finger. The occludent margin, chamfered on the inner and outer surfaces, has three or four elongated, weakly rounded cusps. The inner surface is smooth and weakly convex in its upper part. The full depth of the fixed finger is not preserved, but can be estimated as more than half the length. There is a broad excavation before the occludent margin and an elongate, weakly bifid boss. The basal margin has a marked depression before the rounded tip. On the smooth inner surface a sharp distal ridge curves towards the tip.

Remarks – *Calappa* sp. agrees with *Calappa flammea* in having a weakly bifid boss on the fixed finger, but the latter has a straighter basal margin lacking the depression before the tip. The upper margin of the dactylus of *C. flammea* has a single, conspicuous proximal elevation followed by granules rather than the low, triangular ornament of *Calappa* sp. On the other hand, whereas the margin of the boss on the fixed finger of *Calappa springeri* is uninterrupted, the basal margin is broadly curved with a distinct distal depression. Although suggestive of an early ancestral form of the two Recent species, the scanty evidence allows no finite conclusions to be drawn.

Genus *Tutus* gen. nov.

Type species – *Tutus granulatus* sp. nov.

Derivation of name – Latin *tutus*, a safe place, with reference to ‘Leeward’.

Diagnosis – Carapace pyriform, long, narrow, very convex, no transverse median grooves, outer course of cervical furrow weak; median and lateral rows of tubercles, inner posterior tubercle well developed as a spine; posterior margin triangular.

Range – Lower Miocene of the Leeward Islands.

***Tutus granulatus* Collins sp. nov.**

Pl. 2, figs. 4, 5.

Derivation of name – With reference to the secondary dorsal ornament.

Material, locality and horizon – Holotype, a partial carapace, BMNH In. 63675, from the Lower Miocene Lowlands Formation (= Anguilla Formation), St. Martin, Tintamare Island, Leeward Islands. The only specimen known.

Diagnosis – As for the genus.

Description – Carapace pyriform, longer than wide (L, c. 23.5 mm; W, 19.4 mm), greatest width in the anterior fourth; transversely and longitudinally steeply arched, the posterior margin slightly upturned. Details of front not preserved. Anterolateral margins are broadly rounded and finely granulated, with three evenly-spaced coarser granules. From the hindmost of these, a line of minute granules curves up to the hindmost inner lateral tubercle which, as indicated by a basal scar, was robust and produced as a spine. The posterolateral margin extends below the granules to a granule at the posterior angle, and the posterior margin forms an acute triangle with rounded apex and edge. The dorsal surface is divided longitudinally by furrows, the median, gastric part narrowest. There is a well developed tubercle on each of the mesogastric and urogastric lobes. A constriction separates the urogastric lobe from a long, lingulate cardiac region. In the furrows on either side of the mesogastric tubercle, conspicuous gastric pits mark the cervical furrow, only the extreme lateral course of which is weakly developed. The inner lateral row of tubercles consists of one, obscure, on the protogastric,

one mesobranchial and three on the metabranchial lobes increasing in size to the fourth, spinose one. The outer row is formed by one tubercle on the epibranchial lobe and two on the metabranchial lobes.

More or less even-sized granules on the dorsal surface forming a network of round, shallow craters anteriorly, become more numerous posteriorly. A pair of more prominent granules occurs on the mesogastric lobe between the protogastric tubercles.

Remarks – Evidently close to, and possibly derived from *Stenodromia* A. Milne-Edwards, 1873 (Middle Eocene (Spain) to mid Oligocene (France)), *Tutus granulosus* differs in the absence of posterolateral spines and a flattened, slightly upturned posterior margin, only the lateral aspects of the cervical furrow are present, and there are more numerous dorsal tubercles.

Posterolateral damage to the left side could suggest a compressive distortion of the carapace towards a mursiid or calapiliid appearance. This is illusory; the bilateral distance of the gastric and epi/metabranchial tubercles are equidistant to the midline, and which the merest distortion would displace. The pointed posterior margin is undamaged and, in its entirety, quite dissimilar to the posterior margins of both *Calapilia* and *Mursia* species, more closely resembling that of *Stenodromia*.

Family Hepatidae Stimpson, 1871
Genus *Hepatus* Latreille, 1802

Type species – *Cancer pubibundus* Herbst, 1785, p. 199 (= *Hepatus princeps* Herbst, 1794, p. 325).

Diagnosis. – (After Feldmann *et al.*, 2005, p. 433.) “Carapace relatively smooth, much broader than long, broadly obovate, vaulted; rostrum bilobed, extending well beyond orbits, elevated; extremely convex, crenulated or serrated anterolateral margins; posterolateral margin concave, margin beaded, complete; posterior margin narrow.”

Range. – Oligocene to Recent (Todd & Collins, 2006, p. 69).

***Hepatus guraboensis* Collins sp. nov.**
Pl. 3, figs. 1, 2; Pl. 4, figs. 5-7.

Etymology – From the Gurabo River, Dominican Republic.

Types – Holotype, NMB F1468, a carapace from NMB locality 16835. Paratypes, three carapaces, NMB collection, from localities NMB 15903, 15906 and 16835. Attributed chelae are from localities NMB 15903, 15906, 15907 and 15910 (Saunders *et al.*, 1986, pl. 1, fig. 1), 15911 and 16923, including specimen NMB F1474 (Pl. 4, fig. 6).

Diagnosis – Carapace transversely subovate, front slightly produced; spines on anterolateral margins granulose, becoming triangular posteriorly; a granule on dorsal lobes encircled by smaller ones.

Locality and horizon – The holotype is from the Upper Miocene Cercado Formation, Río Cana, Dominican Republic. Most specimens are from the same formation, Río Gurabo, Dominican Republic. The exception is from the Río Mao at NMB 16923.

Description – The carapace is about one fifth broader than long, the gastric and branchial regions are protuberant and granulose. The front is slightly advanced beyond the outer orbital angles and takes up rather more than half the orbitofrontal margin, which occupies a little under half the carapace width (c. 44%); the front is weakly granulated and weakly sulcate with a dorsal swelling on either side (epigastric regions). Small, rounded orbits are forwardly directed. The anterolateral margins are lined with 16/17 spines, granular behind the orbit, becoming triangular and larger posteriorly; the largest, at the lateral angle, is followed by a smaller spine and fine granules line the posterolateral margins to a prominent spinule at the posterior angle. The posterior margin is about as wide as the front, finely beaded and bounded by a narrow flange extending from the branchiostegites. A thin cervical furrow curves broadly across the midline anterior to greatest carapace width and becomes obsolete before reaching the margin. The dorsal lobes are crowned by a granule surrounded by smaller ones, the mesogastric protuberance is the largest; the one on the cardiac and on each of the slightly more advanced metabranchial lobes are linear, while those on the epibranchial lobes taper laterally and curve towards the spinule on the posterior angle.

Chelae: a small propodus (locality NMB 15906) of appropriate size (L, 5.0 mm; H, 5.0 mm) may confidently be attributed to *Hepatus guraboensis* sp. nov.; it forms the first of a growth series, from the same locality, which ranges in size to L, 17.0 mm - H, 11.0 mm. A carpus and dactylus are attached to one propodus, and a dactylus to another. There are five spines along the upper margin as opposed to four as stated by Rathbun (1937, p. 246) for *H. lineatus*, otherwise there is no appreciable difference between the two species.

Carapace measurements – Paratype, NMB collection (NMB locality 15906): length, 10.0 mm; width, 12.8 mm; orbitofrontal margin, 5.6 mm.

Remarks – This species has much in common with the Recent Caribbean *Hepatus lineatus*, both in carapace proportions and distributions of carapace protuberances. *Hepatus guraboensis* is comparatively wider and the anterolateral spines are more equitriangular rather than tridentate as in *H. lineatus* and more numerous (16/17-14/15). The summits of the cardiac and metabranchial protuberances of *H. guraboensis* are linear, whereas in *H. lineatus* they are rounded. The advanced frontal region of *H. guraboensis* and *H. lineatus* distinguishes both species from other Recent and fossil Caribbean species within the genus.

Hepatus guraboensis fits well within section 2 of the diagnostic characters required by Schweitzer & Feldmann (2000, p. 246). There are superficial similarities to *Hepatebella amazonica* Beurlen, 1958, from the Miocene of Brazil, but the anterolateral margins are proportionally shorter than those of *H. guraboensis*, there is a noticeable anteromesogastric process and the cervical furrow reaches the anterior third of the anterolateral margins, rather than nearly half the length in *H. guraboensis*. *Hepatus lineatinus* Collins & Todd in Todd & Collins, 2006, from the Upper Pliocene of Panama, has

similar front and dorsal protuberances, but they are less prominent than in *H. guraboensis*; both are likened to *Hepatus lineatus* Rathbun, 1898. The rostrum of both *H. guraboensis* and *H. lineatus* extends only a little further than that of *H. lineatus* (*vide* Rathbun, 1937, pl. 76, fig. 1); in these species it is embraced in a continuous arc with the anterolateral margins, whereas in *H. amazonica* and *Hepatella amica* Smith, 1869, the arc is elliptical.

Superfamily Portunoidea Rafinesque-Schmaltz, 1815

Family Portunidae Rafinesque-Schmaltz, 1815

Subfamily Portuninae Rafinesque-Schmaltz, 1815

Genus *Rathbunella* Collins gen. nov.

Etymology – In recognition of the work of M.J. Rathbun.

Type species – *Rathbunella pentaspinosa* sp. nov.

Diagnosis – Carapace broadly subpentagonal (L/W about 0.85); orbitofrontal margin wide (76%); front slightly produced; inner orbital spine rounded, outer orbital spine sharp, directed forwards; upper orbital margin slightly receding; five pairs of anterolateral spines. Dorsal surface smooth, lobes poorly defined.

Range – Upper Miocene.

***Rathbunella pentaspinosa* Collins sp. nov.**

Pl. 3, figs. 5, 6.

Etymology – From the five pairs of anterolateral spines.

Diagnosis – As for the genus.

Material, locality and horizon – Holotype, NMB F1417, carapace with damaged front, from NMB locality 16821, Upper Miocene-Lower Pliocene Gurabo Formation, Río Cana, Dominican Republic. The only specimen known.

Description – Carapace broadly subpentagonal, moderately convex in both longitudinal and transverse sections with the lateral part of the metabranchial lobes deeply excavated; carapace length about three quarters of the width. The orbitofrontal margin occupies about three quarters of the carapace width; of this, the slightly produced front takes up the median third and follows the general curvature of the anterolateral margins. Details of the front are not preserved; it is separated by a notch from a rounded inner orbital angle and there is another notch close by. The upper orbital margin is weakly raised, recedes slightly and terminates in a broad triangular spine. Of five triangular spines (excluding the outer orbital spine) lining the anterolateral margin, the 1st is the smallest and, together with the 2nd - 4th, curves forwards; the 5th, the largest, situated at the lateral angle just anterior to carapace midlength, is more laterally di-

rected and slightly thickened. Convergent posterolateral margins are almost straight to a prominent notch and curve round deep, oblique coxigeal incisions. The weakly concave (male) posterior margin is rather more than half the orbitofrontal margin and bounded by a broad, flat ridge.

The lobes are weakly defined. The cervical furrow is broadly V-shaped across the carapace midline level with the 5th marginal spine and the short urogastric lobe is barely separated from the cardiac region. There is a line of three minute granules on the mesogastric lobe, others border the cervical furrow and a few occur in the uro-cardiac depression.

The 4th male sternites are broadly heart-shaped, and all sternites are sparsely and minutely punctate. The abdomen is isosceles triangular, weakly concave margins of the fused 4th - 5th somites are weakly ridged and the telson is as long as the 6th somite.

Measurements – Carapace length about 34.0 mm; width (between 3rd and 4th spines) 40.7 mm; orbitofrontal margin 30.5 mm.

Remarks – The five pairs of anterolateral spines extending beyond mid-carapace length, comparatively wide orbitofrontal margin and virtually smooth dorsal surface of this species, occurring together, immediately differentiate it from all other known por-tunids.

Subfamily Podophthalminae Rafinesque-Schmaltz, 1815
Genus *Sandomingia* Rathbun, 1919b

Type species – *Sandomingia yaquiensis* Rathbun, 1919b, p. 179, by original designation.

Diagnosis – (After Glaessner, 1969, p. R531.) “Carapace wide, anterior margin arcuate, anterolateral angle with extraorbital and lateral teeth, lateral margins converging; orbits long, shallow, extending whole width of carapace from front which is 0.85 width of carapace; chelipeds large, equal.”

Range – Lower Miocene (Glaessner, 1969, p. R531) to Plio-Pleistocene (Todd & Collins, 2006, p. 58).

***Sandomingia yaquiensis* Rathbun, 1919b**
Pl. 2, fig. 3.

1919b *Sandomingia yaquiensis* Rathbun, p. 179-180, pl. 8, figs. 1, 2.

Sandomingia yaquiensis Rathbun; Glaessner, p. R531.

2006 *Sandomingia yaquiensis* Rathbun; Todd & Collins, p. 77.

2008 *Sandomingia yaquiensis* Rathbun; Karasawa *et al.*, p. 107, fig. 9.

Material, locality and horizon – The new material illustrated herein is a partial left merus, NMB F1460, and associated carpus, NMB collection, from NMB locality 16825, Upper Miocene-Lower Pliocene Gurabo Formation, Río Cana, Dominican Republic.

Description of new material – The carpus of the new material is one third longer than high, outer surface boldly rounded, upper margin is a little more than one third the length of the basal margin; the meral margin is straight and oblique; basal scars of two or three tubercles line the propodal margin. The partially preserved merus is rounded triangular in section, more rounded across the lower and lateral angles. The sharper upper margin broadens slightly, a double row of granules terminates in a hooked spine distally; a row of ten (some seen only as basal scars) tubercles progresses from beside the granules towards a rounded ‘column’ extending obliquely to the articulating facet. All three surfaces are weakly concave.

Remarks – While placing this species in the Ocypodidae, based on dorsal characteristics that seemed to be closest to *Uca*, Rathbun (1919b) also considered the possibility of it being a portunid allied to *Podophthalmus* or *Euphyllax*. The position of *Sandomingia* in the Ocypodinae was questioned by Glaessner (1969), who placed the genus in “subfamily uncertain.” Comparison of the sternites preserved with *Euphyllax callinectias* and *Euphyllax maculatus* (Todd & Collins, 2006) from the Miocene of Panama convinced those authors that *Sandomingia* should be transferred to the Podophthalminae.

As figured by Rathbun (1919b, pl. 8, figs. 1, 2), the cheliped meri occur as two short lengths, each of about 15 mm and exposing the upper surface. They were described as being “stout, triangular in cross-section, upper surface concave and smooth, posterior and inferior margins blunt and granulate, anterior margin subacute and furnished with tubercles arranged in two irregular rows” (Rathbun, 1919b, p. 180). This description adequately serves the proximal portion, absent from the present specimen, but is supported by an almost identical-sized length to those figured, of a right merus from the Plio-Pleistocene Moin Formation of Panama (itself supported by a carapace from the Pliocene Cayo Agua Formation from a further Panamanian locality). This small fragment clearly shows the double line of tubercles along the upper margin and, additionally, has the basal scars of three larger tubercles slightly towards the inner face of the summit, the distalmost indicating a downward curve.

The present merus bears a superficial resemblance to those of some species within the parthenopid genera *Leiolumbrus* and *Solenolumbrus* of the Caribbean. However, these differ radically in having sharper angles, providing a distinctly triangular section with all margins coarsely beaded; those beads on the upper margin are restricted to the summit.

Genus *Psygmophthalmus* Schweitzer, Iturralde-Vinent, Hetler & Velez-Juarbe, 2006

Type species – *Psygmophthalmus lares* Schweitzer *et al.*, 2006, pp. 127-128, fig. 6D, by original designation.

Diagnosis – (After Schweitzer *et al.*, 2006, p. 128.) “Carapace hexagonal, length about 60 percent maximum width, widest slightly more than half the distance posteriorly; front narrow proximally, proximal portion about 10 percent maximum carapace width, broadening distally into crenulated T-shape, with central projection and lateral projections on either side; fronto-orbital width about 80 percent maximum carapace width; orbits with two notches; anterolateral margin with five spines including outer-orbital spine; epibranchial ridge arcuate.”

Range – Lower Miocene.

Psygmothalmus bifurcatus Collins sp. nov.

Pl. 2, figs. 1, 2.

Etymology – Referring to the bifurcated appearance of the lateral spines.

Material, locality and horizon – Holotype, an internal cast of carapace. BMNH In. 63681, from the Lower Miocene Anguilla Formation, Betty Hill Quarry, Anguilla.

Diagnosis – Carapace broadly sub-hexagonal, length about half maximum width, width rather more than half distant from the front; base of T-shaped rostrum one tenth of orbitofrontal margin, orbitofrontal margin about three fourths of carapace width; anterolateral margin with five short spines (not including outer orbital spine) before the cervical notch and two, at the lateral angle, give rise to a short transverse epibranchial ridge.

Description – Carapace broadly sub-hexagonal, length a little more than the total width (87.7%). The orbitofrontal margin occupies about 76.4% of the width and terminates in a slender, upstanding, forward curving outer orbital spine. The T-shaped rostrum, apparently produced, is in line with the arc of the anterolateral margins. The frontal edge is weakly biconcave and sulcate above, the sides curving in a deep ocular constriction to a wide base occupying 10.0% of the orbitofrontal margin. Thin, raised upper orbital margins are straight and oblique to a short notch at midlength and, interrupted by the outer notch, curve to the outer orbital spine. The preserved length of the third maxillipeds indicates the lower orbital margin extended the length of rostrum. Short anterolateral margins are lined with five more or less even sized triangular spines, separated by U-shaped notches before the cervical notch. Two larger spines at the lateral angle are almost bifurcate and give rise to a short, transverse, epibranchial ridge. The cervical furrow is deep and transverse across the midline, sharply upturned along the broadly ovate mesogastric lobe, curves forwards and outwards almost to the margin then recurves behind the hepatic lobe; there is a pair of gastric pits close to the midline and even sized pits line its lateral arc. Rounded posterolateral margins obscured. A thickening round a coxigeal incision continues along the posterior margin which is less than half the orbitofrontal margin. The epigastric lobes, forming a shallow triangle into the rostrum, are thickened basally. A broad post-orbital depression leads directly to depressed subrhomboidal hepatic regions. Weakly tumid protogastric lobes are separated by an obscure parallel-sided anteromesogastric process. The urogastric region forms a narrow bar depressed between the mesogastric and very wide subpentagonal cardiac region, the basilateral angles of which intrude between tumid metabranchial lobes.

Male sternites (further developed after photography) are moderately wide (about 54% of carapace width) and widest at sternite 7. Sternites 1 and 2 not preserved. Sternites 3 are weakly curved anteriorly, terminating in a notch developing into a curving groove; sternites 4 sub-rhomboidal with rounded anterolateral angles terminating in a closed notch leading to a curved ridge reaching the groove on preceding sternites and

marking the limit of the abdominal trough; sternites 5 and 6 regularly petaloid; the lower margin of sternites 7 is more strongly rounded than the upper; sternites 8 as long as sternites 7, isocetes triangular, with convex margins, the hindmost corner distinctly overlapping sternite 3, indicating that the specimen is that of a corpse. Sternites 5, 6 and 7 bounded by regularly curved episternites, each with a narrow periopod-articulating notch.

The much damaged abdomen lacks the telson, the margins are weakly sinuous and a low median ridge on somite 4 does not reach the margins.

Remarks – The broad-based rostrum and carapace proportions of *Psygmophthalmus bifurcatus* Collins sp. nov. agree by and large with the diagnostic requirements of *Psygmophthalmus* as defined by Schweitzer *et al.* (2006), and by the same degree distinguish it from the superficially similar species of *Euphylax*. Differences from the type species, *P. lares*, lay in the greater number (five rather than four) and more delicate anterolateral spines – normal to variations accommodated in *Euphylax* – and smooth rather than nodose frontal margin of the rostrum.

Appendix 2

Collecting stations of the Naturhistorisches Museum Basel that yielded decapod crustaceans from the Dominican Republic

The following list of site numbers are those applied by the Naturhistorisches Museum Basel (NMB) in the 1970s to the numerous exposures (=collecting stations) on or near the banks of six major river systems in northern Hispaniola (Dominican Republic). Further data can be obtained from Saunders *et al.* (1986).

Collecting stations in the Dominican Republic

Formations and NMB localities of figured specimens (Pls. 1-4) are listed below.

- 15878 Gurabo Formation, Río Gurabo.
- 15906, 15907, 15910 Cercado Formation, Río Gurabo.
- 16821, 16825 Gurabo Formation, Río Cana.
- 16835 Cercado Formation, Río Cana.
- 16923, 16929 formation uncertain, Río Mao.
- 16986 formation uncertain, Río Cana.

Dominican Republic 'New Collection'

This is presented as a supplement to Rathbun's (1919a) original list. Formations and NMB localities of determined specimens are listed below.

Río Gurabo, Mao Formation – 15828 - *Ctenocheles* sp.

Río Gurabo, Gurabo Formation - 15878 - *Dardanus squamatus* Collins sp. nov., *Calappa* sp., *Iliacantha* cf. *liodactyla* Rathbun, leucosiid sp.

Río Gurabo, Cercado Formation - 15898 - *Lobonotus sculptus* A. Milne-Edwards.

15900 - *Neocallichirus scotti* (Brown & Pilsbry), *Calappa flammea* (Herbst), *Persephona prepunctata* Rathbun.

15903 - *Neocallichirus scotti* (Brown & Pilsbry), '*Callianassa*' sp., *Petrochirus inequalis* Rathbun, *Calappa flammea* (Herbst), *Hepatus guraboensis* Collins sp. nov., *Persephona prepunctata* Rathbun, *Callinectes declivis* Rathbun.

15904 - *Neocallichirus scotti* (Brown & Pilsbry), *Calappa flammea* (Herbst), *Persephona prepunctata* Rathbun.

15906 - *Neocallichirus scotti* (Brown & Pilsbry), *Petrochirus inequalis* Rathbun, Paguridae sp. (agrees with Rathbun, 1919b, pl, 9, figs. 6, 7), *Calappa flammea* (Herbst), *Hepatus guraboensis* Collins sp. nov., *Cryptosoma bairdii* (Stimpson), *Persephona prepunctata* Rathbun, *Eurytium* sp.

15907 - *Neocallichirus scotti* (Brown & Pilsbry), *Petrochirus inequalis* Rathbun, Paguridae sp. (comments as for locality 15906), *Dardanus squamatus* Collins sp. nov., *Calappa*

flammea (Herbst), *Hepatus guraboensis* Collins sp. nov., *Cryptosoma bairdii* (Stimpson), *Persephona prepunctata* Rathbun, *Callinectes declivis* Rathbun, *Panopeus* cf. *herbsti* H. Milne Edwards, *Pilumnus* sp. 1.

15910 - *Neocallichirus scotti* (Brown & Pilsbry), '*Callianassa*' sp., *Petrochirus inequalis* Rathbun, *Calappa flammea* (Herbst), *Hepatus guraboensis* Collins sp. nov., *Persephona prepunctata* Rathbun, *Libinia* aff. *setosa* Lockington.

15911 - *Hepatus guraboensis* Collins sp. nov., *Persephona prepunctata* Rathbun, *Pilumnus* sp. 2, *Eurytium* sp.

15912 - *Neocallichirus scotti* (Brown & Pilsbry), Paguridae gen. et sp. nov., *Persephona prepunctata* Rathbun, aff. *Lophopanopeus* sp., *Mesorhoea mauryae* Rathbun.

15915 - *Scylla costata* Rathbun.

15916 - *Calappa flammea* (Herbst).

Río Gurabo, formation uncertain - 16810 (= 16155) - *Pilumnus* sp. 3.

16817 - *Pilumnus* sp. 4.

Río Cana, Cercado Formation - 16821 - *Rathbunella pentaspinosa* Collins gen. et sp. nov.

16825 - *Portunus oblongus* Rathbun, *Sandomingia yaquiensis* Rathbun.

16830 - *Scylla costata* Rathbun.

16831 - *Oxyrhyncha* sp.

16835 - '*Callianassa*' sp., *Petrochirus inequalis* Rathbun, *Hepatus guraboensis* Collins sp. nov., *Persephona prepunctata* Rathbun.

16839 - *Neocallichirus scotti* (Brown & Pilsbry).

16842 - *Calappa flammea* (Herbst), aff. *Stenocionops* sp.

16857 - *Neocallichirus scotti* (Brown & Pilsbry).

16858 - *Mesorhoea mauryae* Rathbun.

Río Mao - 16913 (Saunders et al., 1986, pl. 7, fig. 4) - *Dardanus squamatus* Collins sp. nov., *Calappa flammea* (Herbst), *Scylla costata* Rathbun.

16915 - *Neocallichirus scotti* (Brown & Pilsbry), *Calappa flammea* (Herbst), *Calappa* sp., *Persephona prepunctata* Rathbun.

16916 - '*Callianassa*' *miocenica* Rathbun, *Persephona prepunctata* Rathbun.

16917 - *Neocallichirus scotti* (Brown & Pilsbry), *Petrochirus inequalis* Rathbun, *Persephona prepunctata* Rathbun, *Scylla costata* Rathbun.

16918 - '*Callianassa*' sp., *Persephona prepunctata* Rathbun, *Callinectes declivis* Rathbun, *Scylla costata* Rathbun.

16922 - *Neocallichirus scotti* (Brown & Pilsbry), '*Callianassa*' sp., *Calappa flammea* (Herbst), *Calappa* sp., *Persephona prepunctata* Rathbun, *Callinectes declivis* Rathbun.

16923 - *Neocallichirus* aff. *peraensis* Collins et al., *Petrochirus inequalis* Rathbun, Paguridae sp., *Hepatus guraboensis* Collins sp. nov., *Cryptosoma bairdii* (Stimpson), *Mesorhoea mauryae* Rathbun, *Scylla costata* Rathbun, *Portunus (Achelous) tenuis* Rathbun.

16924 - *Petrochirus inequalis* Rathbun, *Persephona prepunctata* Rathbun, *Scylla costata* Rathbun, *Callinectes declivis* Rathbun.

16926 - '*Callianassa*' sp., *Calappa flammea* (Herbst), *Persephona prepunctata* Rathbun, *Callinectes declivis* Rathbun, Parthenopidae sp.

16827 - *Calappa flammea* (Herbst), *Persephona prepunctata* Rathbun, *Callinectes declivis* Rathbun.

16828 - *Calappa flammea* (Herbst), *Persephona prepunctata* Rathbun, *Scylla costata* Rathbun, *Callinectes declivis* Rathbun, aff. *Stenocionops* sp., *Pilumnus* aff. *spinosissimus* Rathbun.

16929 - '*Callianassa*' sp., *Persephona prepunctata* Rathbun, *Parthenope* sp., *Mesorhoea mauryae* Rathbun, *Portunus gabbi* Rathbun, *Scylla costata* Rathbun.

16932 - '*Callianassa*' sp., *Persephona prepunctata* Rathbun, *Scylla costata* Rathbun, *Portunus* sp.

Río Cana, formation uncertain – 16935 - '*Callianassa*' sp.

16936 - *Neocallichirus scotti* (Brown & Pilsbry), *Psygmodphthalmus bifurcatus* Collins sp. nov., *Platyxanthus?* sp.

16938 - *Persephona prepunctata* Rathbun.

16970 - *Eurypanopeus* aff. *crenatus* (H. Milne Edwards).

16986 - aff. *Stenocionops* sp.

Río Yaque del Norte, formation uncertain – 17269 - Calappidae sp., *Callinectes declivis* Rathbun.

17823 - *Neocallichirus scotti* (Brown & Pilsbry).

Plate 1

Fossil decapod crustaceans from Anguilla (Fig. 9 only) and the Dominican Republic (Figs. 1-8). All specimens are in the collection of the Naturhistorisches Museum, Basel, unless stated otherwise.

Figs. 1, 2. *Petrochirus inequalis* Rathbun, 1919b, NMB locality 16923, Río Mao, formation uncertain. (1) NMB F1461, occludent surface of left fixed finger. (2) NMB 1462, left dactylus, outer surface.

Fig. 3. *Persephona prepunctata* Rathbun, 1919b, NMB F1463, locality 15907, Río Gurabo, Cercado Formation. Distal part of manus and fixed finger.

Fig. 4. *Stenocionops* sp., NMB F1464, locality 16986, Río Cana, formation uncertain. Inner surface of left propodus.

Fig. 5. *Mesorhoea maurayae* Rathbun, 1919b, NMB F1465, locality 16929, Río Mao, formation uncertain. Inner surface of left dactylus.

Fig. 6. *Parthenope* aff. *serrata* H. Milne Edwards, 1834, NMB F1466, NMB locality uncertain. Outer surface of left dactylus.

Figs. 7, 8. *Dardanus squamatus* Collins sp. nov., holotype, NMB F1467. NMB locality 15907, Río Gurabo, Cercado Formation. (7) Occludent surface of left fixed finger. (8) Inner surface of left fixed finger.

Fig. 9. *Calappa* sp., BMNH In. 63682. Lower Miocene Anguilla Formation, near Cathedral Cave, western Anguilla. Associated right dactylus and fixed finger.

All scale bars represent 10 mm.



Plate 2

Fossil decapod crustaceans from the Cenozoic of Anguilla (Figs. 1, 2), the Dominican Republic (Fig. 3) and Tintamare Island (Figs. 4, 5). All specimens are in the collection of the Naturhistorisches Museum, Basel, unless stated otherwise.

Figs. 1, 2. *Psygmophthalmus bifurcatus* Collins sp. nov., BMNH In. 63681, holotype, carapace. Lower Miocene Anguilla Formation, Betty Hill Quarry, Anguilla. (1) Dorsal view. (2) Ventral view.

Fig. 3. *Sandomingia yaquiensis* Rathbun, 1919b, NMB F1460, locality 16825, Upper Miocene-Lower Pliocene Gurabo Formation, Río Cana, Dominican Republic. Partial left merus and associated carpus.

Figs. 4, 5. *Tutus granulatus* Collins gen. et sp. nov., BMNH In. 63675, holotype, carapace. Lower Miocene Lowlands Formation (= Anguilla Formation), Tintamare Island, St. Martin. (4) Right lateral view. (5) Dorsal view.

All scale bars represent 10 mm.

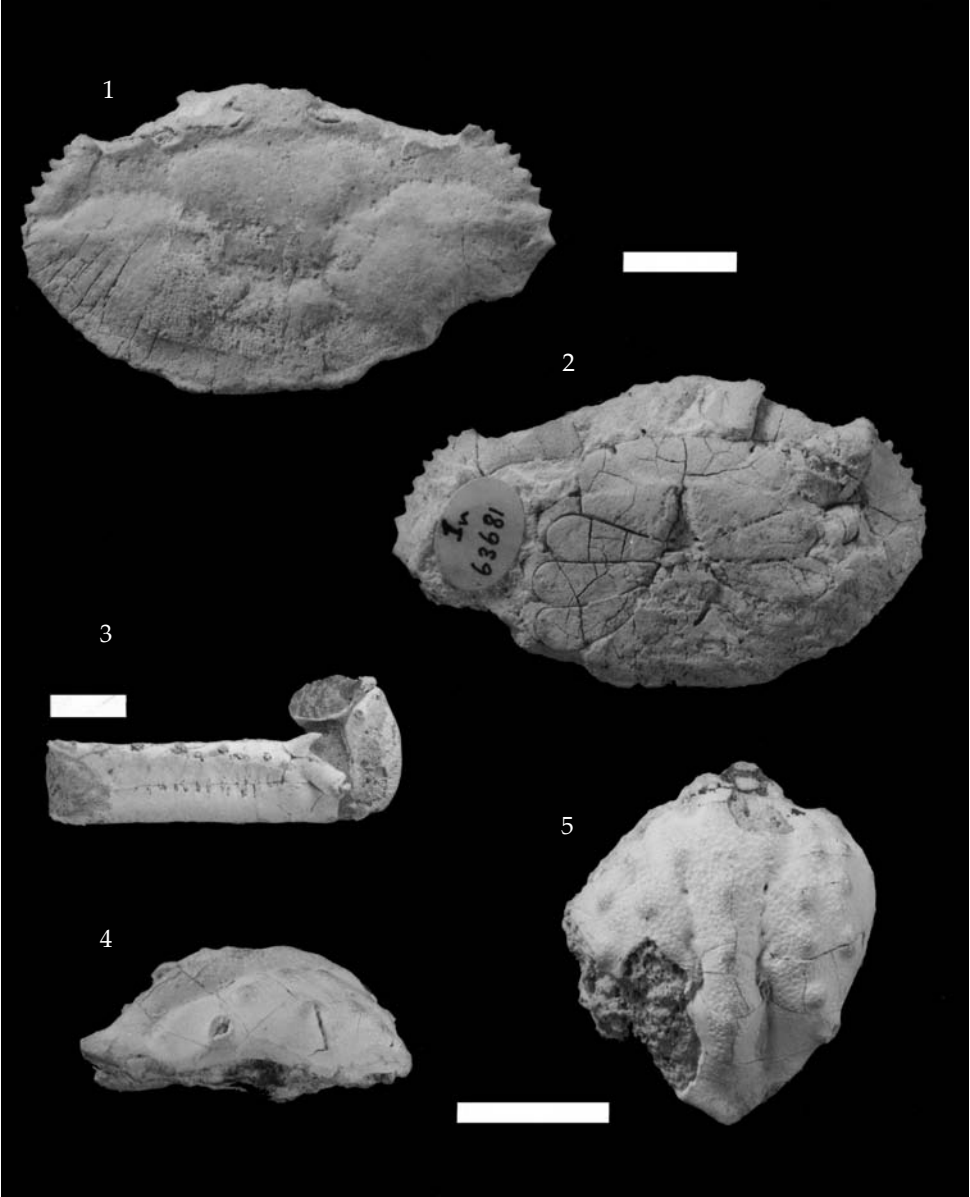


Plate 3

Fossil decapod crustaceans from the Dominican Republic, all Upper Miocene Cercado Formation unless stated otherwise. All specimens are in the collection of the Naturhistorisches Museum, Basel.

Figs. 1, 2. *Hepatus guraboensis* Collins sp. nov., holotype, carapace, NMB F1468, locality 16835, Río Cana. (1) Dorsal view. (2) Frontal view.

Fig. 3. *Persephona prepunctata* Rathbun, 1919b, NMB F1469, locality 15910, Río Gurabo. Sixth female abdominal somite.

Fig. 4. *Persephona prepunctata* Rathbun, 1919b, NMB F1470, locality 16835, Río Cana. Fused male 3/4/5 abdominal somites.

Figs. 5, 6. *Rathbunella pentaspinosa* Collins gen. et sp. nov., holotype, carapace, NMB F1417, locality 16821, Upper Miocene-Lower Pliocene Gurabo Formation, Río Cana. (5) Posterior view. (6) Dorsal view.

All scale bars represent 10 mm.

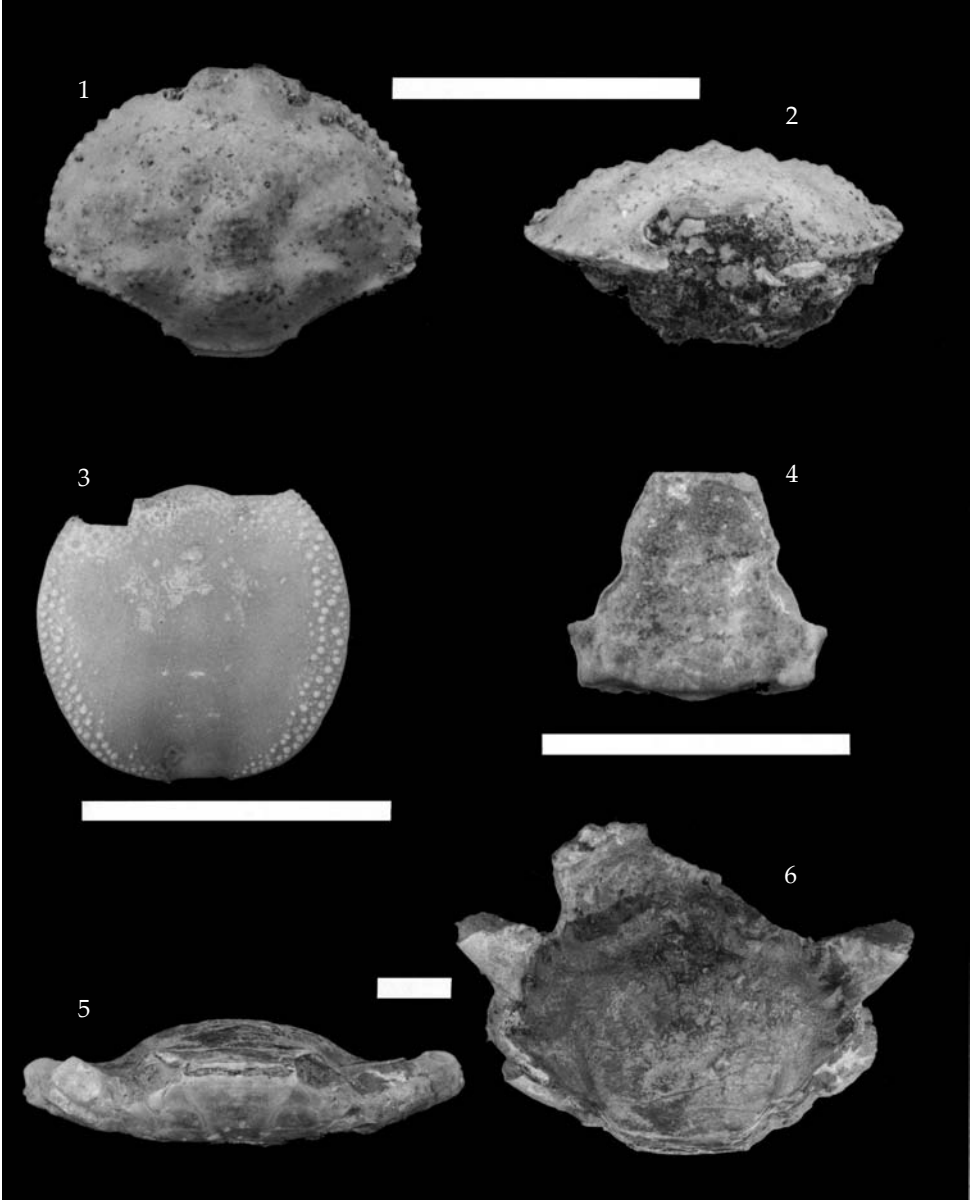


Plate 4

Fossil decapod crustaceans from the Dominican Republic, Upper Miocene Cercado Formation unless stated otherwise. All specimens are in the collection of the Naturhistorisches Museum, Basel, unless stated otherwise.

Figs. 1, 2. *Petrochirus inequalis* Rathbun, 1919b. NMB locality 16923, Río Mao, formation uncertain. (1) NMB F1462, left fixed finger, inner surface. (2) NMB F1461, left dactylus, inner surface. See also Pl. 2, figs. 1, 2.

Figs. 3, 4. *Cryptosoma bairdii* (Stimpson, 1860), NMB F1472, locality 15906, Río Gurabo. Outer (3) and inner (4) surfaces of left propodus.

Figs. 5-7. *Hepatus guraboensis* Collins sp. nov. NMB locality 15906, Río Gurabo. Paratypes. (5) NMB F1473, outer surface of right chela and carpus. (6, 7) NMB F1474 (6) and F1475 (7), outer surfaces of left chelae.

Fig. 8. *Iliacantha liodactylus* Rathbun, 1898, NMB F1475, locality 15878, Río Gurabo, Upper Miocene-Lower Pliocene Gurabo Formation. Left inner surface of propodus.

All scale bars represent 10 mm.

