

# Neogene and Quaternary crabs (Crustacea, Decapoda) collected from Costa Rica and Panama by members of the Panama Paleontology Project

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## Abstract

Crabs of Middle Miocene to Early Pleistocene age collected by members of the Panama Paleontology Project are described from the (Caribbean) Southern Limón Basin of Costa Rica and the Canal and Bocas del Toro basins of Panama, the (Isthmian) Chucunaque-Tuira Basin of Panama, and the (East Pacific) Osa-Burica, Parrita and Tempisque basins of Costa Rica. Thirty taxa are identified to species level, of which 25 are described in detail. Of these twelve species are new: *Ctenocheles falciformis* sp. nov., *Dardanus biordines* sp. nov., *Hepatus bififormis* sp. nov., *Hepatus lineatinus* sp. nov., *Thoe asperoides* sp. nov., *Platylambrus spinulatus* sp. nov., *Speleophorus subcircularis* sp. nov., *Persephona enigmatica* sp. nov., *Persephona manningi* sp. nov., *Iliacantha panamanica* sp. nov., *Euphyllax maculatus* sp. nov., *Lophopanopeus maculoides* sp. nov. Two new combinations are proposed; *Glypturus toulai* nov. comb. for *Callianassa toulai* Rathbun, 1919a, and *Neocallichirus scotti* nov. comb. for *Callianassa scotti* Brown and Pilsbry, 1913. A lectotype is designated for *Callianassa toulai* Rathbun, 1919a. As well as allowing description of new species, the new material includes the first fossil records of the extant genus *Speleophorus* and the extant species, albeit tentatively identified, *Raninoides benedicti* Rathbun, 1935a and *Panopeus chilensis* A. Milne Edwards and Lucas, 1844. The occurrence of *Petrochirus bouvieri* Rathbun, 1919a, *in situ* in domicile gastropod shells is recorded for the first time. The disproportionate abundance of carapaces and articulated specimens in coterminous mid-Pliocene strata of the Escudo de Veraguas and Cayo Agua formations of the Bocas del Toro Basin (Caribbean Panama) dated to 3.5–3.6 Ma suggests burial of whole crabs in gravity flows. Of the crabs described herein, nine of the 30 identified species have a trans-isthmian fossil record and five of these apparently became extinct during the Pleistocene of the East Pacific, suggesting a period of elevated extinction in this ocean after complete emergence of the Isthmus of Panama.

**Key words:** Decapoda, Systematics, Neogene, Costa Rica, Panama, Panama Paleontology Project, Pleistocene Extinction

## Introduction (JSHC and JAT)

As far as can be ascertained, the earliest description of a fossil crab from Panama or Costa Rica was of *Calappa zurcheri* by Bouvier, 1899, from a well-preserved carapace of Miocene age, which remains unique. In 1911 Toulou described and figured chelae of *Petrochirus* cf. *granulatus* Olivier, 1818, as well as an unnamed chela. This was followed, in 1913, by Brown and Pilsbry's description of *Callianassa scotti* from Oligocene strata of the Panama Canal Zone. But by far the largest contribution was made by Rathbun, 1919a, when (including earlier records), she made known nineteen species from Panama and eleven from neighbouring Costa Rica. At the same time (1919a) she described (but did not figure) *P.* cf. *granulatus* as a new species, *Petrochirus bouvieri*.

Over sixty years after Rathbun's (1919a) major contribution to our knowledge of fossil decapods of Panama and Costa Rica, a few speci-

mens were collected by Peter Jung, Peter Baumgartner and collaborators in the 1980s, prior to the many obtained during extensive fieldwork campaigns initiated in 1986 by the Panama Paleontology Project (PPP). Until now these decapod collections have remained unstudied. The international and multidisciplinary PPP was established to study the effect of the emergence of the Isthmus of Panama and associated environmental change on the composition of marine faunas of the region over the past 12 My; for a summary of project objectives and preliminary results, see Collins and Coates (1999a). A major component of this continuing research programme consists of systematic, large-scale collecting and documentation of macro- and microfaunas from marine sediments of Costa Rica and Panama – the area containing the last trans-isthmian marine corridors prior to complete division of Caribbean waters from the East Pacific at around 3.5–3.1 Ma (Coates and Obando, 1996). Collecting and sediment sampling has been tightly coupled with the establishment of an increasingly fine-scaled litho-



Fig. 1. Map of Costa Rica and Panama showing locations of depositional basins mentioned in text; The following peninsulas are indicated by single letters: B = Burica; N = Nicoya; O = Osa; V = Valiente.

bio-, chrono- and magnetostratigraphic framework (Coates *et al.*, 1992; Coates, 1999a; b; c; and papers in Collins and Coates, 1999b; McNeill *et al.*, 2000; Coates *et al.*, 2003; 2004a, b) for what were previously poorly studied, though generally richly fossiliferous, deposits. Although crabs have not been focal organisms for study or collection, they have proved to be well preserved and locally abundant in a number of formations from which large-scale collections have been made, particularly in the Southern Limón Basin of Costa Rica and the Canal and Bocas del Toro basins of Panama (see Fig. 1). As a result, the PPP crab collection housed in the Naturhistorisches Museum, Basel, Switzerland - supplemented by additional material in the Department of Palaeontology, The Natural History Museum, London - has substantially increased the known decapod material from this region available for study.

From the PPP collections eight new species are founded on carapace material, while another four are described from chelae remains deemed sufficiently distinctive. It has also become possible to ascribe, with confidence, a hitherto unknown carapace from the Plio-Pleistocene of Costa Rica, to previously described chela elements. Nevertheless, field observations by one of us (JAT) indicate that the decapod fauna of certain strata, for example the Moin (Southern Limón Basin), Cayo Agua, and Escudo de Veraguas (both Bocas del Toro Basin) formations, would likely be much enlarged were new collecting expeditions to focus more attention on the crabs rather than them being a 'by-catch' of malacofaunal studies.

The palaeogeographic range of 22 genera and/or species has been extended from other Caribbean islands. Notable among these is a carapace of *Sandomingia yaquiensis* Rathbun, 1919b, formerly described from a single carapace from the Early? Miocene of Haiti. The new carapace from the Pliocene Cayo Agua Formation of Caribbean Panama retains details of the ventral surface not available to Rathbun (1919b) and confirms Rathbun's surmise of portunid affinities of the genus, which is here transferred to the Podophthalminae. A fragment of a merus from the Late Pliocene Moin Formation of Caribbean Costa Rica is also assigned to this species as it corresponds to that accompanying the type specimen. The extant genus *Speleophorus* is newly recorded as fossil (*Speleophorus subcircularis* sp. nov.) as are the extant species *Raninoides* [cf.] *benedicti* Rathbun, 1935a and

*Panopeus* [cf.] *chilensis* A. Milne Edwards and Lucas, 1844.

Among abundant callianassid remains in the new collections from the Middle Miocene through to Early Pleistocene of Costa Rica and Panama, and from the Late Miocene Cercado Formation of the Dominican Republic, are similar and better preserved chelae elements displaying characters common to five previously described *Callianassa* species. By and large, these components correspond with the variety in form displayed by males, females and juveniles - as demonstrated by Manning and Felder, 1995 - of any one of a single species presently inhabiting the Caribbean. With the new comparable material to hand, *Callianassa scotti* Brown and Pilsbry, 1913 is here considered the senior taxon of synonymized *Callianassa crassimana* Rathbun, 1919a, *C. miocenica* Rathbun, 1919b, *C. vaughani* Rathbun, 1919a, and *C. rathbunae* Glaessner, 1929. Furthermore, all the material possesses characters fundamental to the genus *Neocallichirus* Sakai, 1988 and *Callianassa scotti* is here referred to that genus. *Neocallichirus* is an extant genus common in the Caribbean and *N. scotti* shares morphological features with *Neocallichirus guassuntingus* (Rodrigues, 1971) and the nominal taxon *Sergio mericeae* (Manning and Felder, 1995) that was subsequently synonymized under the former species by Sakai (1999). Other callianassid claws from Panama and Costa Rica allow redescriptions of *Callianassa moinensis* Rathbun, 1919a and *Callianassa toulai* Rathbun, 1919a; the latter is transferred to the genus *Glypturus* Stimpson, 1866. All these species are distinguished by their comparatively large size.

Although previously recorded from the Pliocene Bowden shell bed of Jamaica, the thalassinoid *Ctenocheles* makes its first appearance in the fossil record of the southwest Caribbean; it has been recognised from Pliocene Cayo Agua and Escudo de Veraguas formations of Caribbean Panama, the Early Pleistocene Moin Formation of Caribbean Costa Rica and the similar-aged Montezuma Formation of Pacific Costa Rica. The genus is presently represented in North American West Atlantic waters by four species (Manning and Felder, 1991).

The Paguridae contains additional material of *Petrochirus bouvieri* Rathbun, 1919a, the range of which can be confidently extended to the Late Miocene to Late Pliocene of isthmian and Caribbean Panama and Costa Rica and several examples are preserved within domicile gastropod shells belonging to the genera *Malea* and *Strombus*. *Dardanus biordines* sp. nov., established upon a propodus and pereopod dactylus from the Early Pliocene Cayo Agua Formation of Caribbean Panama, has much in common with corresponding elements figured as *Pagurus striatus petersi* A. Milne Edwards and Bouvier, 1880 which presently occurs in the Gulf of Mexico, west of Florida, and with *Dardanus insignis* Saussure, 1858 (in Verrill, 1908).

Raninids are rare fossils in Central America and the Caribbean and partial carapaces, from the Late Miocene Tobabe Sandstone of Caribbean Panama and Early? Pleistocene Armuelles Formation of Pacific Costa Rica, are 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 in the Caribbean fossil

record only from a partial carapace of *Raninoides louisianensis* Rathbun, 1933 from the Pleistocene of Jamaica (Collins *et al.*, 1997).

Propodi, one with an associated carpus, mark the first appearance of the extant *Cryptosoma bairdii* (Simpson, 1860) in the fossil record of Central America and extends the palaeogeographical range of this species previously described (as *Cycloes bairdii*) from the Early Miocene of the Dominican Republic (Rathbun, 1919b; Collins *et al.*, in prep.) to the Pliocene of Caribbean Panama and Early Pliocene of Pacific Costa Rica. The species presently ranges in the East Pacific from the west coast of Mexico southwards to Ecuador and the Galapagos Islands; and in the West Atlantic from North Carolina and the Bermudas southwards to the Caribbean (Rathbun, 1937).

The previous fossil record for *Hepatus* Latreille, 1802 in the region, hitherto represented by *Hepatus chiliensis* Rathbun, 1919a, described from a dactylus from the Pleistocene of Mount Hope, Colón, Panama, is extended to include a well preserved suite of carapaces, some retaining chelae and another with a well developed bopyriform infestation, which allows a new species, *Hepatus lineatinus*, to be described. This species ranges from the Middle Miocene basal Gatun Formation to Late Pliocene Escudo de Veraguas Formation of Caribbean Panama and it also occurs in the Late Pliocene Rio Banano Formation of Caribbean Costa Rica. It is present, too, on the Pacific side of the isthmus in the Early Pleistocene Montezuma Formation of Costa Rica. Whereas this new species has much in common with *Hepatus lineatus* Rathbun, 1898, presently ranging in the East Pacific from Mexico to Peru (Rathbun, 1937), a second species, *Hepatus biformis* sp. nov., found in the Late Miocene Tobabe Sandstone of Caribbean Panama and the Early Pliocene Peñita Formation of Pacific Costa Rica, more closely resembles *Hepatus kossmanni* Neumann, 1878, another East Pacific species. The genus is known fossil elsewhere in the Caribbean from the Miocene of Trinidad and the Dominican Republic, and from the Pleistocene of Jamaica (Collins *et al.*, 1996; Collins and Portell, 1998).

Within the Leucosiidae, *Leucosilia bananensis* Rathbun, 1919a, formerly represented by a few cheliped meri from the Rio Banano Formation (Late Pliocene) of Caribbean Costa Rica, has its stratigraphic range extended back through the Early Pliocene Cayo Agua Formation to the Late Miocene Tobabe Sandstone Formation and Middle Miocene basal Gatun Formation of Caribbean Panama. Also to this family can be added *Speleophorus subcircularis* sp. nov. (Late Pliocene, Cayo Agua Formation, Caribbean Panama), which has a superficial resemblance to *Speleophorus digueti* (Bouvier, 1898a), presently occurring in the East Pacific from the coast of Mexico southwards to Panama (Rathbun, 1937). Furthermore, *Iliacantha panamamica* sp. nov., described from a partial carapace from the Late Miocene Tobabe Sandstone of Caribbean Panama appears to be only distantly related to two widespread Recent Caribbean species and enlarges the palaeogeographical range of the genus, previously known from only the Dominican Republic (Collins pers. obs.). Two new species of *Persephona* are also described from carapaces from the Late Pliocene Cayo Agua and Escudo de Veraguas formations of Caribbean Panama. Whereas one of these, *Persephona manningi* sp. nov., does not appear

to have a close relationship with any other fossil or Recent species, the other, *Persephona enigmatica* sp. nov., although described as a new species, shares many morphological features with both *Persephona punctata* (Linné, 1758) and *Persephona townsendi* (Rathbun, 1893) that range from the Gulf of California to Ecuador. These species were 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.

New to the Portunidae of the region are claw elements of *Portunus gabbi* Rathbun, 1919b and *Portunus (Achelous)* cf. *tenuis* Rathbun, 1919b. *Portunus gabbi* was described from the Early? Miocene of Haiti; here its geographic and stratigraphic range is extended to the Middle–Late Miocene Tuira Formation of Darien, Panama through the Late Miocene Tobabe Sandstone of Bocas del Toro, Panama to the early Late Pliocene Rio Banano Formation of Southern Limón Basin, Costa Rica. Previously known from a fixed finger from the Early Miocene of the Dominican Republic; *Portunus (Achelous) tenuis* Rathbun is represented by a provisionally referred chela (as *P. (A.) cf. tenuis*), that much extends its stratigraphical and geographical range to the Armuelles Formation (Pleistocene) of the Pacific coast of Panama, and also allows description of an associated dactylus. A new *Euphyllax* species, *Euphyllax maculatus* sp. nov. (Middle/Late Miocene to Late Pliocene of Caribbean Panama and Costa Rica and Early Pleistocene of Pacific Costa Rica), is described from a carapace retaining partial chelipeds and other carapace material which, as well as being in a better state of preservation, has distinct dorsal characters separating it from *Euphyllax callinectias* Rathbun, 1919a, and indicating a closer relationship to *Euphyllax domingensis* (Rathbun, 1919b).

Recently discovered in the Dominican Republic Miocene (Collins pers. obs.), chelae fragments of *Eurypanopeus* and *Platyxanthus* species both make their appearance among the new material. *Eurypanopeus* sp. occurs in the Early Pleistocene of Caribbean Costa Rica (Moin Formation) and *Platyxanthus* species, of similar age (Late Pliocene–Early Pleistocene Moin Formation), also occur in the Late Miocene (Nancy Point Formation) of Caribbean Panama. A more doubtfully identified specimen (as cf. *Platyxanthus* sp.) occurs in the Early Pleistocene Montezuma Formation of Pacific Costa Rica. *Lophopanopeus maculoides* sp. nov., described from a partial carapace and attributable chelae from the Late Pliocene Moin Formation of Caribbean Costa Rica, is close to the East Pacific *Lophopanopeus maculatus* Rathbun, 1898. The extant xanthid *Heteractea lunata* (A. Milne Edwards and Lucas, 1843), a taxon previously known from the Moin Formation of Costa Rica by a partial propodus and dactylus, is represented by further chelae remains from the Plio–Pleistocene Moin Formation of Costa Rica and the Late Pliocene Escudo de Veraguas Formation (Caribbean Panama). Claws tentatively assigned to *Micropanope* (as cf. *Micropanope* sp.) from the Late Pliocene of Caribbean Costa Rica and Panama may extend the palaeogeographic range of the genus from the Miocene of Jamaica from whence it is also recorded from Pliocene deposits (Collins *et al.*, 1996; Portell and Collins, 2004). Claw fragments tentatively assigned to *Pilumnus* (as cf.

*Pilumnus*) are recorded from basins on both the Caribbean and Pacific sides (Caribbean: Cayo Agua Formation, Panama (Pliocene); East Pacific: Armuelles Formation, Burica Peninsula, Panama (Pleistocene)). None is sufficiently definitive to be treated at species level. Rathbun (1919a) did not record the genus from the isthmian region, but she described a new species, *Pilumnus subequus*, of Early Miocene age from the Dominican Republic (Rathbun, 1919b). Claw elements assigned to *Pilumnus* aff. *pannosus* Rathbun, 1896 and *Pilumnus* aff. *spinossimus* Rathbun, 1897 were recorded from the Pliocene Bowden shell bed of Jamaica (Collins and Portell, 1998), while *Pilumnus* cf. *sayi* Rathbun, 1897 is known from the Pleistocene Port Morant Formation of that island (Collins *et al.*, 1997). Of the 26 extant species described from the American coasts (Rathbun, 1930), 17 are Atlantic forms and nine are East Pacific; of these, three Atlantic species have Pacific 'analogues' (= proposed geminate species).

As in other parts of the Caribbean region, oxyrhynchs are poorly represented. A carapace, *Thoe asperoides* sp. nov., from the Late Miocene Tobabe Sandstone Formation of Caribbean Panama has many morphological features in common with *Thoe aspera* Rathbun, 1900, presently occurring off Puerto Rico (Rathbun, 1925), while dactyli reminiscent of *Hyas* Leach, 1814 from the Late Miocene Tuirá Formation of the Darien, Panama are described, but left in open nomenclature as aff. *Hyas* sp. A dactylus recorded as aff. *Hyas* sp. was described from the Bowden shell bed of Jamaica (Collins and Portell, 1998). A fixed finger tentatively assigned to *Pitho* sp. from the Late Pliocene Escudo de Veraguas Formation of Panama represents the only known fossil occurrence of this genus in Central America and extends its known fossil range from the Pliocene Bowden shell bed of Jamaica and Miocene of the Dominican Republic. *Mithrax*, from Moin Formation sediments of Plio–Pleistocene boundary age, is newly recorded from Costa Rica from two specimens including a fixed finger closely resembling *Mithrax caribbaeus* Rathbun, 1920a, Recent, Caribbean, and *Mithrax orcutti* Rathbun, 1925, which is found on both sides of the Isthmus of Panama today.

### Palaeoecology and taphonomy (JAT)

Neogene strata of the region have only recently been accurately delimited, described and dated, consequently detailed sedimentological, palaeoecological, or taphonomic studies are currently lacking. However, a few comments can be made based on field observations made by JAT in the Canal (Gatun Formation), Bocas del Toro (Cayo Agua and Escudo de Veraguas formations) and Southern Limón (Moin Formation) basins between 1994 and 1999.

#### Basal Gatun Formation

Propodi of *Neocallichirus scotti* (Rathbun) are found commonly in pervasively bioturbated silts comprising units 3 and 4 of the Gatun Formation at Sand Dollar Hill, Sabanita (Colón Province, Panama), less than 1.5 m above the first transgressive marine deposits comprising this formation (Todd, in prep.). The macrofauna is wholly marine and dominated by small gastropods, includ-

ing *Olivella* (which today typically lives on low intertidal and shallow subtidal sandflats, e.g., Aruda and Amaral, 2003), naticids, turritellids and bivalves. Higher in the same section (unit 21), abundant *Neocallichirus* propodi with rarer articulated chelae and carapace fragments, are found in a pebbly indurated silty sandstone with rolled and broken molluscs and angular sand dollar fragments. This represents a storm deposit containing shoreline taxa that have been eroded and transported shelfwards into slightly deeper water (A. Gale, pers. comm.). Extending down from the base of this unit into underlying sandy silts are large *Ophiomorpha* burrows, which are likely to have been produced by *Neocallichirus scotti*, though we could not prove a direct association.

Today, the smaller (in propodal dimensions) *Neocallichirus guassutingus* (Rodrigues) (described as *Sergio mericeae* Manning and Felder, 1995), of the Atlantic coast of Florida and northern Gulf of Mexico lives in intertidal muddy sand flats to shallow subtidal (13 m) depths, in mud-lined burrows with or without a surrounding sand mound (Manning and Felder, 1995). Evidently *Neocallichirus scotti* inhabited similar very shallow subtidal palaeoenvironments around the Central American Seaway some 12 million years earlier.

#### Cayo Agua and Escudo de Veraguas formations

The partly coeval Cayo Agua and Escudo de Veraguas formations represent onshore and offshore siliciclastic shelf sediments deposited at palaeobathymetries of 10–80 m and 100–150 m respectively (Appendix 1 in Jackson *et al.*, 1999). These formations yield a disproportionate number of articulated crab carapaces and the ratio of these to limbs and other fragments is high in comparison to that occurring within other formations of similar age and palaeobathymetry in the same region, for example the Moin, Shark Hole Point and basal Nancy Point formations.

In 1998, at Punta Norte, Cayo Agua, JAT collected crab carapaces from large eroded blocks of shelly, pebbly, mollusc-rich, silty sandstone of the Cayo Agua Formation. These lacked discernible bedding, with molluscs being preserved in all orientations. A carapace of *Euphyllax maculatus* sp. nov. (Pl. 4, Fig. 1 herein) with articulated legs and propodi, that was probably buried in its entirety, was found directly next to a dicotyledonous leaf that was embedded apparently almost vertically in the sediment and bent abruptly through its 5 cm+ length. Nearby in the same block was found a fragmentary carapace of *Hepatus lineatinus* sp. nov. The lack of bedding and random orientation of contained fossils may have been due to either pervasive bioturbation (certainly present in these formations; see Coates, 1999b) or the collected horizon representing a slump deposit. The preservation of whole crabs buried either alive or as corpses is more in accord with the latter interpretation; indeed, abundant bioturbating organisms probably would have scavenged upon and disarticulated any corpses present. Furthermore, dead crabs may become disarticulated within two weeks after death in tropical shelf settings, chiefly due to scavengers (Plotnick *et al.*, 1988), and complete burial would had to

have been both very rapid and to a depth that excluded them. This strongly implies the rapid burial of living or dead crabs within masses of slumped sediment.

It seems remarkable that many of the most complete articulated specimens within the PPP collections, for example the holotypes of *Hepatus lineatinus* sp. nov. and *Euphyllax maculatus* sp. nov. (Pl. 3, fig. 12; Pl. 4, fig. 1), as well as an articulated specimen of *Sandomingia yaquiensis* Rathbun (Pl. 4, fig. 4), are from strata within the two formations dated to 3.5 to 3.6 Ma (Coates *et al.*, 1992; Appendix 1 in Jackson *et al.*, 1999) or that contain these dates within a longer bracketed range. In the absence of detailed sedimentological data we feel that it is likely that both the Cayo Agua and Escudo de Veraguas formations contain a number of slumped horizons dating to this interval. Based on observations of the molluscan faunal assemblages in the Cayo Agua Formation to the east of Punta Níspero (sediments subsequently dated to 3.5–3.6 Ma), Vermeij and Collins (1988) invoked post-mortem transport of molluscs in the production of mixed assemblages indicative of very different palaeoenvironments. It may not be coincidental that subduction of the Cocos Ridge beneath the southern margin of the Panama microplate was initiated at 3.6 Ma and led to the rapid emergence of the Burica Peninsula (L. Collins *et al.*, 1995). It seems possible that across the isthmus in the Bocas del Toro Basin, earthquakes linked to this or other coterminous tectonic events produced mass sediment slides that today may be highlighted by their decapod-rich horizons.

#### Basal Moin Formation mudstones

The stratigraphically most basal mudstones within the Moin Formation were extremely well exposed in 1998 across a large and slightly weathered bulldozed surface, exposing a few bedding planes, west of Pueblo Nuevo, Limón, Costa Rica (= PPP site 03255). These Late Pliocene shelly mudstones lie upon the shallow water Pueblo Nuevo Sand Member (see McNeill *et al.*, 2000; Coates, 1999c, p. 345; stratigraphic section 36) and contain an abundant, highly diverse and well-preserved molluscan fauna (Jackson *et al.*, 1999, pp. 205, 222; comprising part of Lower Lomas del Mar East faunule) and are dotted with small, zooxanthellate coral mounds a few metres across, with a distinct molluscan assemblage containing the worm-snails *Tenagodus* (that today lives commensally inside sponges) and vermetids, as well as cemented bivalves (*Chama*, *Spondylus* etc.). From the mudstones separating these mounds at least 10 genera of crabs were collected as ‘molluscan by-catch’ in less than an hour, representing probably the most diverse fauna among those studied herein. Almost all specimens consist of disarticulated claws and propodi. Of these, by far the most abundant examples were accumulations of propodi of *Callianassa moinensis* Rathbun, sometimes cemented together in small nodules. No other large body parts of this species were found. Lack of time precluded detailed observations on these accumulations. Many of the larger molluscan shells were bored and encrusted by abundant forams, bryozoans, serpulid worm

tubes, and vermetid gastropod tubes; many gastropods and bivalves show *Oichnus* (naticid and muricid) feeding traces, and larger gastropods are frequently peeled and fragmented (predation traces left by arthropods and perhaps fish). The sediment contains numerous encrusted and bored molluscan shell fragments, forams, abundant fragments of arborescent and frequent free-living lunuliform bryozoan colonies, and serpulid tubes. Herbivorous microgastropods such as caecids and rissoids are common. Together, the fauna and sediment strongly suggest a nearshore, probable lagoonal, palaeoenvironment with the bottom consisting of intensely reworked shelly and gritty muds with macroalgae and perhaps seagrass, separating small coral patches with erect sponges, and deposited in a few metres to no more than a few tens of metres water depth. Fossil *Callianassa moinensis* seems to have had similar habitat requirements to those living callianassids that burrow in intertidal vegetated sand flats and sandbars, for example in Florida and the Gulf of Mexico (Felder and Manning, 1995).

#### Species distributions, extinctions and the closure of the Central American Seaway (JAT)

Twenty-nine taxa have been identified confidently, or slightly more tentatively, to species-level. Of these; 17 (59%) are known as fossils only from ‘Caribbean’ basins (Canal, Bocas del Toro and Southern Limon); one (3%) is known only from the East Pacific (Osa-Burica Basin); one (3%) from solely an ‘Isthmian’ basin (Chucunaque-Tuira Basin) (Fig. 1); two (7%) from basins in all three regions: Caribbean, East Pacific and Isthmian; seven (24%) from Caribbean and East Pacific basins; and two (7%) from Caribbean and Isthmian basins (see Table 1). Occurrence of the majority of taxa in Caribbean basins is unsurprising as this reflects both the intensiveness of PPP sampling in this region and the disproportionate abundance of articulated carapaces in the Pliocene of the Bocas del Toro Basin.

The co-occurrence of nearly one-third (31%) of all identified species in deposits on both sides of the isthmus may be related to long species durations in these taxa; as represented by the studied material, 6 of the 10 trans-isthmian species have estimated minimum durations of between 7.1 and 23.1 My (mean = 9.1 My). Six trans-isthmian species are present in deposits that clearly postdate final isthmian emergence at 3.1–3.5 Ma in the Late Pliocene (Coates and Obando, 1996) and the complete separation of the East Pacific from the Caribbean. Additionally, one extant species may be inferred to have been present in the East Pacific based on its stratigraphically earlier records in the region, and one extant East Pacific species is known only from ‘Caribbean’ fossils. Surprisingly, five of the nine ‘post-uplift’ East Pacific species appear to be extinct and all of these have their last occurrence in the Armuelles or Montezuma formations (Early Pleistocene) of the Pacific Panama and Costa Rica. Although these are among the youngest, well dated, crab-bearing deposits in Central America documented herein, this pattern of last recorded occurrence in the

Taxon	Pre- Middle Miocene	Middle Miocene	Late Miocene	Early Pliocene	Late Pliocene	Pleistocene and Plio-Pleistocene boundary	Recent
<i>Glypturus toulai</i> (Rathbun)	–	–	C	–	–	–	–
<i>Callianassa moinensis</i> Rathbun	–	–	–	–	–	L	–
<i>Neocallichirus scotti</i> (Brown & Pilsbry)	C, DR	C, P	C, P	–	B	T	–
“ <i>Callianassa</i> ” sp(p).		C	C	B, O	B	L, O, T	N/A
<i>Ctenocheles falciformis</i> sp. nov.	–	–	–	B	B	L, T	–
<i>Dardanus biordines</i> sp. nov.	–	–	–	B	–	–	–
<i>Petrochirus bouvieri</i> Rathbun	–	–	C, D, B	–	B	L, (?O)	–
<i>Raninoides benedicti</i> Rathbun	–	–	B (cf.)	–	–	O (cf.)	CAR, TEP
<i>Cryptosoma bairdii</i> (Stimpson)	–	–	–	B	–	T	CAR, TEP
? <i>Cryptosoma</i> sp(p).	–	–	–	B	B	–	N/A
<i>Hepatus lineatinus</i> sp. nov.	–	C	C	B	B, L	T	–
<i>Hepatus bififormis</i> sp. nov.	–	–	B	O	–	–	–
<i>Calappa flammea</i> (Herbst)	–	–	C	B	B, L	B, L, T	CAR, TEP
<i>Calappa</i> sp.	–	–	–	–	B	–	N/A
<i>Speleophorus subcircularis</i> sp. nov.	–	–	–	–	B	(?T)	–
<i>Persephona enigmatica</i> sp. nov.	–	–	–	–	B	–	–
<i>Persephona manningi</i> sp. nov.	–	–	–	–	B	–	–
<i>Persephona</i> sp(p.) meri	–	–	–	–	–	L, O, T	N/A
<i>Iliacantha panamanica</i> sp. nov.	–	–	B	–	–	–	–
<i>Leucosilia bananensis</i> Rathbun	–	C	B	B	B, L	–	–
<i>Callinectes declivis</i> Rathbun	–	–	–	–	L	L	–
<i>Mithrax</i> sp.	–	–	–	–	–	L	N/A
<i>Thoe asperoides</i> sp. nov.	–	–	B	–	–	L	–
Majidae, gen. and sp. indet.	–	–	–	–	–	L	N/A
aff. <i>Hyas</i> sp.	–	–	D	–	–	–	–
<i>Pitho</i> sp.	–	–	–	–	B	–	N/A
Oxyrhyncha, family, gen. and sp. indet.	–	–	–	–	–	L	N/A
<i>Parthenope</i> sp.	–	–	–	–	–	T	N/A
<i>Platylambrus spinulatus</i> sp. nov.	–	–	–	B	B	L	–
<i>Platylambrus</i> sp(p).	–	–	–	–	B	–	N/A
<i>Portunus gabbi</i> Rathbun	–	D	B, D	–	L	–	–
<i>Portunus (Achelous) tenuis</i> Rathbun	–	–	DR	–	–	O (cf.)	–
<i>Euphyllax maculatus</i> sp. nov.	–	D	C, D	B	B	T	–
<i>Sandomingia yaquiensis</i> Rathbun	Haiti	–	–	B	B	L	–
Portunidae, gen. and sp. indet.	–	C	C	B	L	L, T	N/A
<i>Heteractea lunata</i> (A. Milne Edwards & Lucas)	–	–	–	–	B	L	TEP
<i>Platyxanthus</i> sp.	–	–	DR(?), B	–	–	L	N/A
cf. <i>Platyxanthus</i> sp.	–	–	–	–	–	T	N/A
<i>Eurytium crenulatum</i> Rathbun	–	–	–	L	–	L	–
<i>Panopeus antepurpureus</i> Rathbun	–	D	B, C, D	B	B	B, L, O	CAR, TEP
<i>Panopeus chilensis</i> A. Milne Edwards & Lucas	–	–	–	–	–	B (cf.)	TEP
<i>Panopeus tridentatus</i> Rathbun	–	–	–	–	B	B	–
<i>Panopeus</i> spp.	–	–	–	B	B	O, T	N/A
<i>Eurypanopeus</i> sp.	–	–	–	–	–	L	N/A
<i>Lophopanopeus maculoides</i> sp. nov.	–	–	–	–	–	L	–
cf. <i>Micropanope</i> sp.	–	–	–	–	B	L	N/A
cf. <i>Pilumnus</i> sp.	–	–	–	B	B	O	N/A

**Table 1**

Stratigraphic and geographic distribution of taxa in PPP collections.

**Bold** type indicates an East Pacific distribution, normal type an “Isthmian” or Caribbean distribution. “Isthmian” refers to basins that existed within the region of the Central American Seaway and that are now more or less centrally positioned within the uplifted Isthmus of Panama. “Caribbean” indicates a depositional basin on the eastern (Caribbean) side of the Central American Seaway prior to complete isthmian uplift, and Caribbean refers to a post-uplift basin. Plio–Pleistocene boundary refers to Moin Formation sediments that straddle the boundary in the Southern Limón Basin, Costa Rica.

Abbreviations:

B = Bocas del Toro Basin, Panama (“Caribbean” and Caribbean)

C = Canal Basin, Panama (“Caribbean”)

CAR = Recent Caribbean

DR = Dominican Republic (“Caribbean”)

L = Southern Limón Basin, Costa Rica (“Caribbean” and Caribbean)

N/A = not applicable; used for taxa not identified to species level

O = Osa-Burica Basin, Costa Rica and Panama (East Pacific)

P = Punta Judas, probable Middle to Late Miocene, Parrita Basin, Costa Rica (East Pacific)

D = Chucunaque-Tuira Basin, Darien, Panama (“Isthmian”)

T = Tempisque Basin, Costa Rica (East Pacific)

TEP = Recent Tropical East Pacific

Early Pleistocene of the East Pacific is unlikely to be solely an artefact. Although it might reflect inadequate taxonomy or sampling, possibly with some or all of these species remaining alive in the East Pacific, this seems unlikely. More intriguingly, it might indicate that there was a period of elevated extinction in the East Pacific after the closure of the Central American Seaway by the rising isthmus. The survival in the East Pacific – post isthmian uplift – of taxa that disappeared in the Caribbean is a particularly well-known phenomenon in molluscs, where the survivors have been termed ‘paciphiles’ (Woodring, 1966; Vermeij and Petuch, 1986). Differential extinction across the isthmus has long been accounted for by elevated extinction rates in the Caribbean through an extended period of oceanographic change and ecological reorganization in the (?) Late Pliocene, that resulted in the development of a distinct, oligotrophic, oceanographic realm (e.g., Jackson & Johnson, 2000; Todd *et al.*, 2002). Oceanographically, the tropical East Pacific today with its local seasonal upwelling and high productivity is thought to be much more similar to that of the Central American Seaway during the Middle to Late Miocene. Amongst marine molluscs there has been thought to be a post-uplift burst of speciation in the tropical East Pacific (e.g., Jackson *et al.*, 1996) and a significant level of “post-Pliocene” extinction (Vermeij and Petuch, 1986) but no detailed studies of the latter have been undertaken. In particular, the detailed timing and severity of faunal turnover episodes in the East Pacific Neogene remain poorly understood. The crab record documented herein suggests a major regional extinction that is not older than the Early Pleistocene and potentially may be much younger. Future, robust, large-scale palaeofaunal analyses of abundant taxa, as undertaken by the PPP for SW Caribbean molluscan diversity dynamics (e.g. Jackson *et al.*, 1993; 1999), or studies of individual clades with a rich fossil record (e.g. Todd and Rawlings, 2003), are required to

test our suggestion.

### Materials and Methods (JAT)

All of the larger specimens, including carapaces and claws, were discovered at outcrop. Much of this material is preserved in a moderate to excellent condition, often with cuticle present. A few specimens such as those from the Tuira Formation of Darien, Panama, are preserved within hard sandstone nodules and required preparation with steel dental tools. Many carapaces from the Gatun, Cayo Agua, and Escudo de Veraguas formations were easily prepared from slightly to moderately lithified siltstone nodules. Much other material is preserved in, at most, weakly lithified sediments and required just gentle cleaning. Smaller claws and other limbs were obtained when bulk sediment samples were washed down to 500  $\mu\text{m}$  and picked under a Wild M-5 stereomicroscope as part of routine PPP macrofaunal sampling procedures (see Jackson *et al.*, 1999); much of this material has remained unidentified. All digital images are of uncoated material.

### Systematic palaeontology (JAT & JSHC)

Open nomenclature follows the recommendations of Bengtson (1988).

#### Institutional and collection abbreviations:

ANSP: Academy of Natural Sciences, Philadelphia, PA, U.S.A.

(NMB) F: specimens with this prefix are deposited in Naturhistorisches Museum Basel, (Basle), Switzerland.

(BMNH) PI IC: specimens with this prefix are deposited in the Department of Palaeontology, The Natural History Museum, London, U.K.

MNHN: Muséum National d’Histoire Naturelle, Paris, France.

USNM: United States National Museum of Natural History,

Smithsonian Institution, Washington DC, U.S.A.

### Stratigraphy and localities:

Because formal stratigraphic names for the deposits studied herein have recently been revised and their assigned ages have changed markedly since Rathbun's (1919a) study (see discussion in Coates *et al.*, 1992), we have taken the opportunity to provide detailed locality and stratigraphic details and references upon first mention. A number of formations extend across stage or epoch boundaries and so, where possible, we give detailed ages for the sampled strata. The subdivision of the Gatun Formation into Lower, Middle and Upper parts (Woodring, 1957) is not considered to have a clear lithostratigraphic basis and these are treated as informal units in lower case (following Coates *et al.*, 1992; Coates, 1999a).

Brief details are given for Naturhistorisches Museum Basel collection locality numbers; these are in the form NMB xxxxx (5 numerals). Correspondences with PPP collection numbers (see below) are given wherever possible.

Locality numbers in the form JT year-numeral-numeral refer to collections made by JAT and now housed in the Department of Palaeontology, Natural History Museum, London. Full locality details remain to be published but may be obtained from the author upon request.

Numbers given for Panama Paleontology Project collections as PPP xxxxx (5 numerals) are PPP Site-Visit numbers (**not** Project numbers). Brief information is given in the text for localities (= PPP Site-Visits), which includes stratigraphic units, age, and the collectors and collection date. More detailed information including GPS-derived latitude and longitude, position on compiled stratigraphic sections (see Coates 1999b, p. 299–348), sample and subsample information including collection, processing and repository data, and selected palaeoenvironmental interpretations are available in the current PPP database downloadable from <http://www.fiu.edu/~collinsl/pppimagemapnew.htm>. Maps showing positions of collecting sites in Bocas del Toro, Canal and Southern Limón basins have been published by Coates (1999a, p. 287–298 and Coates *et al.*, 2003) and are also available at the PPP site at <http://www.fiu.edu/~collinsl/pppmaps.html>.

For locations of sites in the Chucunaque-Tuira Basin of Darien, Panama, see Coates *et al.* (2004b, Maps. A, B). Jung (1995) provided a location map for Punta Judas, the single locality in the Parrita Basin, Pacific Costa Rica.

### Excluded material :

Many limb elements (including possible pereopod dactyli) remain at the 'gen. et sp. indet.' level. This decision is due largely to their being in a fragmentary condition; or the possible juvenile stage, wherein reliable diagnostic characters distinguishing genera are not developed. Such material comprises 62 lots in total and was excluded from further consideration.

### Listed material:

The following taxa, listed in alphabetical order, are present in the collections studied, but are not treated further, as the new material

either adds nothing to earlier descriptions or is considered inadequate for detailed description. Within taxa, sites are ordered stratigraphically, oldest first. Numbers of specimens are given in parentheses (x) after the site number. This material comprises a total of 88 lots comprising 182 specimens. Abbreviated collection details or summaries of occurrences are provided. To prevent repetition, if the collection site is listed later in the main systematic section, then we give a reference to the taxon under which that information can be found.

### *Calappa flammea* (Herbst, 1794)

NMB F1717 (NMB 17638, PPP 00220) (1); see details under *Neocallichirus scotti*.

BMNH PI IC 319–338 (JT-98-2-PJ) (20); PI IC 339–355 (JT 98-2-7) (17); PI IC 356–358 (JT 99-13-3 Spec. sample) (3), PI IC 359–384 (JT 99-13-3),(26); PI IC 385–386 (JT 99-13-4 Spec. sample), (2); (no PPP numbers yet assigned); all from middle Gatun Formation, Upper Miocene; Las Lomas Suites, 1.2 km SW of Cativa, Colón Province, Panama.

F1718 (NMB 18665, PPP 02166) (1) middle Gatun Formation, Upper Miocene; Quarry at San Judas Tadeo, about 1.5 km SW of Cativa, Colón Province, Panama.

F1719 (NMB 18687, PPP 02188) (2) see details under.

### *Neocallichirus scotti*.

F1720 (NMB 18373, PPP 01188) (1) Cayo Agua Formation, Early Pliocene; SE coast of Cayo Agua, Bocas del Toro Province, Panama.

F1721 (NMB 18734, PPP 02237) (1) Cayo Agua Formation, Early Pliocene; 300 m WNW of Punta Piedra Roja, Bocas del Toro Province, Panama.

F1722 (NMB 17809, PPP 00294) (1) Cayo Agua Formation, early Late Pliocene; Bocas del Toro. Cayo Agua, E coast ca 300 m W of Punta Tiburón, Bocas del Toro Province, Panama.

F1723 (NMB 17451, PPP 01732) (2) Rio Banano Formation, Late Pliocene; Río Banano at Bomba, S of Limón, Costa Rica.

F1724 (NMB 18744, PPP 02247) (1) Unnamed formation, ?Pliocene; Ground Creek, Isla Colón, Bocas del Toro Province, Panama.

F1725 (NMB 18277, PPP 00950) (2) Details under *Ctenocheles falciformis*.

F1726 (NMB 18080, PPP 00631) (1) Details under *Ctenocheles falciformis*.

F1727 (NMB 19075, PPP 03641) (1) Armuelles Formation, Early Pleistocene; 1.8 km S of tanker dock, east coast of Burica Peninsula, Chiriqui Province, Panama (see Coates *et al.*, 1992).

F1728 (NMB 18486, PPP 00271) (1) Armuelles Formation, Early Pleistocene, Quebrada El Higo, 2300 m downstream from 2nd waterfall, Golfo Dulce, Chiriqui Province, Panama.

### *Calappa* sp.

F1729 (NMB17626, PPP 00178) (1 dactylus) Escudo de Veraguas

Formation, Late Pliocene; Long Bay Point, NW coast of Escudo de Veraguas, Bocas del Toro Province, Panama.

F1730 (NMB 17810, PPP 00295) (1) Cayo Agua Formation, early Late Pliocene; Cayo Agua, W of Punta Tiburón, Bocas del Toro Province, Panama.

“*Callianassa*” spp.

Fifteen lots comprising 27 specimens (BMNH PI IC 387–391; NMB F1731–F1741) of unidentified or indeterminate callianassid limb fragments from the ‘Caribbean’: lower and middle Gatun Formation (Middle to Late Miocene) of the Canal Basin; Cayo Agua and Escudo de Veraguas formations of the Bocas del Toro Basin (Pliocene); Moin Formation of the Southern Limón Basin (Plio–Pleistocene); and East Pacific: Peñita (Early Pliocene) and Armuelles (Early Pleistocene) formations of Burica Peninsula, Costa Rica and Panama respectively; and the Montezuma Formation (Early Pleistocene) of Nicoya Peninsula, Costa Rica.

*Callinectes declivis* Rathbun, 1919a

F1742 (NMB 17454, PPP 01734) (1) Río Banano Formation, early Late Pliocene (Jackson *et al.*, 1999); Río Banano at Quitaría, Limón Province, Costa Rica.

Doubtfully identified: F1743 (NMB 18080, PPP 00631) (1) Details under *Ctenocheles falciformis*.

? *Cryptosoma* sp(p).

F1744 (NMB 18446, PPP 00194) (1) Cayo Agua Formation, Early Pliocene; S of Punta Norte, Cayo Agua, Bocas del Toro Province, Panama.

F1745 (NMB 18670, PPP 02171) (1) Escudo de Veraguas Formation, Late Pliocene; NW coast of Escudo de Veraguas, Bocas del Toro Province, Panama.

*Eurypanopeus* sp.

F1746 (NMB 18080, PPP 00631) (1) Details under *Ctenocheles falciformis*.

*Leucosilia bananensis* Rathbun, 1919a

PI IC 392 (JT 98-1-20 #2, no PPP number) (1) Basal Gatun Formation, Middle Miocene, Sabanita, Colón Province, Panama.

F1747 (NMB 18687, PPP 02188) (1) Tobabe Sandstone Formation, Late Miocene (late Tortonian-Messinian), Plantain Cays, Valiente Peninsula, Bocas del Toro Province, Panama.

F1748 (NMB 18740, PPP 02243) (1) Cayo Agua Formation, Pliocene; Cayo Zapatillo, Cayo Agua, Bocas del Toro Province, Panama.

F1749 (NMB 18373, PPP 01188) (2) Cayo Agua Formation, Early Pliocene, SE coast of Cayo Agua, Bocas del Toro Province, Panama.

F1750 (NMB 18734, PPP 02237) (2) Cayo Agua Formation, Early Pliocene, Punta Piedra Roja, Cayo Agua, Bocas del Toro Province, Panama.

F1751 (NMB 17454, PPP 01734) (2) Río Banano Formation, early Late Pliocene, Río Banano at Quitaría, S of Limón, Limón Province, Costa Rica.

F1752 (NMB 17451, PPP 01732) (3); NMB 17466, PPP 01774 (2) both from Río Banano Formation, Late Pliocene, Río Banano at Bomba, S of Limón, Limón Province, Costa Rica.

Majidae genus and species indet.: limb

F1753 (NMB 19069, PPP 03255) (1) Details as for *Callianassa moinensis*.

Oxyrhyncha family, genus and species indet.

F1754 (NMB 18080, PPP 00631) (1) Details under *Ctenocheles falciformis*.

*Panopeus antepurpureus* Rathbun, 1919a

F1755 (NMB 18510, PPP 01723) (1) Tuirá Formation, Middle-Late Miocene (late Serravillian/early Tortonian) (Coates *et al.*, 2004a, figs. 5, 7; 2004b, Map A); Río Tuquesa, between village Marragantí and Boca de Marragantí, Darien Province, Panama.

F1756 (NMB 17618, PPP 01973) (2) Gatun Formation, Late Miocene; cliffs 1.2 km E of Miguel de la Borda, Colón Province, Panama.

F1757 (NMB 18711, PPP 02212) (1) basal Nancy Point Formation, Late Miocene; “Finger Island”, W of S tip of Cayo Toro, Valiente Peninsula, Bocas del Toro Province, Panama.

F1758 (NMB 18398, PPP 00060) (1) Cayo Agua Formation, Early Pliocene; E side of Punta Norte, Cayo Agua, Bocas del Toro Province, Panama.

F1759 (NMB 18683, PPP 02184) (2) Escudo de Veraguas Formation, Early Late Pliocene; SE coast of Escudo de Veraguas, Bocas del Toro Province, Panama.

F1760 (NMB 18274, PPP 00948) (1) Details as for *Thoe asperoides*.

F1761 (NMB 17840, PPP 00368) (3) Details as for *Heteractea lunata*.

F1762 (NMB 18747, PPP 02250) (1) Unnamed formation, ? Plio-Pleistocene; Ground Creek, Isla Colón, Bocas del Toro Province, Panama.

F1763 (NMB 18277, PPP 00950) (1) Details as for *Ctenocheles falciformis*.

F1764 (NMB 18485, PPP 00260) (1) Armuelles Formation, Early Pleistocene, Quebrada El Higo, Golfo Dulce, Chiriqui Province, Panama.

*Panopeus tridentatus* Rathbun, 1919a

F1765 (NMB 18670, PPP 02171) (1) Escudo de Veraguas Formation, Late Pliocene; NW coast of Escudo de Veraguas, Bocas del Toro Province, Panama.

F1766 (NMB 18747, PPP 02250) (1) Unnamed formation, ? Plio-Pleistocene; Ground Creek, Isla Colón, Bocas del Toro Province, Panama.

F1767 (NMB 18743, PPP 02246) (3) Swan Cay Formation, Early Pleistocene; Swan Cay, N of Isla Colón, Bocas del Toro Province, Panama.

*Panopeus* spp.

Comprises six lots with seven specimens (F1768–1775) of fragmentary claws from the ‘Caribbean’; Cayo Agua and Escudo de Veraguas formations (Pliocene) of Bocas del Toro, Panama; and the East Pacific: Plio–Pleistocene of the Burica Peninsula (Panama) and Montezuma Formation (Early Pleistocene) of Nicoya Peninsula, Costa Rica.

*Parthenope* sp.

F1776 (NMB 17471, PPP 01738) (1) Details under *Cryptosoma bairdii*.

*Persephona* sp. (p.) : unattributable meri

F1777 (NMB 18274, PPP 0948) (1) Details under *Thoe asperoides*.

F1778 (NMB 18486, PPP 00271) (1) Armuelles Formation, Early Pleistocene; Quebrada El Higo, Chiriqui Province, Panama.

F1779 (NMB 17471, PPP 01738) (4) Details under *Cryptosoma bairdii*.

cf. *Pilumnus* sp(p).

F1780 (NMB 18598, PPP 00355) (1) Cayo Agua Formation, Pliocene, unnamed promontory between Puntas Tiburón and Piedra Roja, Cayo Agua, Bocas del Toro Province, Panama.

F1781 (NMB 18416, PPP 00091) (2); NMB 18435, no PPP number (1) both Armuelles Formation, Early Pleistocene, Río Rabo de Puerco, Burica Peninsula, Chiriqui Province, Panama.

*Pitho* sp.

F1782 (NMB 17832, PPP 00358) (1) Details under *Hepatus lineatus*.

*Platylambrus* sp(p).

F1783 (NMB 17831, PPP 00350) (1) Cayo Agua Formation, early Late Pliocene; E coast of Cayo Agua, Bocas del Toro Province, Panama.

F1784 (NMB 18670, PPP 02171) (1) Escudo de Veraguas Formation, Late Pliocene; NW coast of Escudo de Veraguas, Bocas del Toro Province, Panama.

cf. *Platylambrus* sp.

F1785 (NMB 17471, PPP 01738) (1), Montezuma Formation, Early (?) Pleistocene; Playa Cocalito, ENE Montezuma Village, Nicoya Peninsula, Puntarenas Province, Costa Rica.

Portunidae genus and species indet.

Comprises fragmentary claws (10 lots, 11 specimens: PI IC 393–394; F1786–1793) from the ‘Caribbean’; lower and middle Gatun

Formation (Middle–Late Miocene) of the Canal Basin, Cayo Agua Formation (Early Pliocene) of Bocas del Toro; the Rio Banano (early Late Pliocene) and Moin (latest Pliocene) formations of Limón; and, from the East Pacific; Montezuma Formation (Early Pleistocene) of Nicoya Peninsula, Costa Rica.

**Described material :**

Below, this consists of 90 lots comprising over 250 specimens. Under each taxon specimens are listed in stratigraphic order, oldest first.

**Systematic Descriptions (JSHC and JAT)**

Order DECAPODA Latreille, 1802

Infraorder THALASSINIDEA Latreille, 1831

Superfamily CALLIANASSOIDEA Dana, 1852

Family CALLIANASSIDAE Dana, 1852

Subfamily CALLIANASSINAE Dana, 1852

Genus *CALLIANASSA* Leach, 1814

*Type species: Cancer (Astacus) subterraneus* Montague, 1808, by monotypy.

*Range:* Late Cretaceous to Recent.

***Callianassa moinensis* Rathbun, 1919a**

(Pl. 1, Figs. 2–8, 10–12)

1919a *Callianassa moinensis* Rathbun, p. 142, pl. 60, figs. 1–3.

*Holotype:* A right propodus USNM 324287, from the “Miocene” (now Moin Formation, Late Pliocene to Early Pleistocene) of “Moin Hill, near Limon, Costa Rica” (Rathbun, 1919a, p. 142).

*New material:* 3 lots; 1) Figured, five left propodi, (Pl. 1, Figs. 2–6, F1613–1617); three right propodi, (Pl. 1, Figs. 7, 8, 12, F1618–1620); two left dactyli, (Pl. 1, Figs. 10, 11, F1621–1622); and unfigured, 88 propodi (including 44 left + 4 right) (F1624 1–88), all from (locality NMB 19069, PPP 03255), N of Route 32, N of a bulldozed site for a container depot, 1.5 km west of Pueblo Nuevo, Limón, Limón Province, Costa Rica. ‘Mollusc mudstone’, basal Moin Formation, Late Pliocene (McNeill *et al.*, 2000). Collected by J. A. Todd and H. Fortunato, 05/02/1998. 2) PI IC 396–400 (IBA-3-1, PPP 03641), 4 left, 1 right propodi from the ‘Mollusc mudstone’ of the basal Moin Formation, Late Pliocene; locality details as above. Collected by J. A. Todd, 05/02/1998. 3) F1625 1-8 (locality NMB 19075, PPP 03641) 4 left + 4 right propodi, details as for IBA-3-1.

*Remarks:* New, well preserved, material not only coincides both in size and basic description of Rathbun’s species, founded on a decorticated right propodus and an impression of a broken dactylus, but allows a more concise description of the right, as well as the first record of the left propodus and dactylus to be made.

*Emended description:* Left (major) propodus: subquadrate, height of manus a little longer than length, subglobose in transverse section. The upper margin is weakly convex, highest medially, the upper edge subcarinate. The lower margin is a little more

convex with a slight depression before the fixed finger; a subcarinate basal ridge continuing along the fixed finger may be either smooth or finely beaded; a ridge on the outer surface above the depression continues to the tip of fixed finger. The inner surface has a strong median ridge and a finer, granulated one lines the occludent margin. The carpal margin is at 90° to basal margin; the interdigital margin curves obliquely to the articulating facet and is vertical above.

The incurved fixed finger is a little shorter than, and in line with, the manus, the tip is upturned. A strong ridge bounds the occludent margin, three proximal cusps – the third sometimes conical – increasing in size distally, are followed by a ridge, either lined proximally with minute granules or smooth; setal pores line the grooves either side of the upper ridge.

Right (minor) propodus: similarly subglobose in transverse section; height/length proportions of the manus are much the same as the left manus, but only about half the size. The distal curvature of the upper margin is more acute, the depression before the fixed finger is deeper; the fixed finger is proportionally longer and straighter with more prominent ridges. Proximal cusps on the occludent margin are not so prominent and are preceded by a finely granulated ridge; distal granules are stronger with one, well developed, closer to the tip. The outer and inner surfaces have a similar ornament to the left propodus.

Left dactylus: height about one-third the length; a ridge on the outer surface lines the evenly curved upper margin, another shorter ridge lines the occludent margin, the area between is weakly concave. The upper edge is oblique to a weak ridge, which like one lining the occludent margin, becomes absorbed in a strong median ridge. A proximal cusp on the occludent margin is followed by a gap before a row of more or less even-sized granules. Setal pores are prominent between the ridges.

Subfamily CALLICHIRINAE Manning and Felder, 1991

Genus *GLYPTURUS* Stimpson, 1866

*Type species: Glypturus acanthochirus* Stimpson, 1866, by monotypy.

*Range:* Miocene to Recent.

***Glypturus toulai* (Rathbun, 1919a) Collins and Todd nov. comb.**

(Pl. 1, Fig. 1)

1911 ‘Krabbenscheren’ Toulai, p. 512 [26], pl. 30 [1], fig. 14.

1919a *Callianassa toulai* Rathbun, p. 146.

*Lectotype:* In the absence of a nominated holotype by Rathbun (1919a), the chela figured by Toulai (1911, pl. 30 [1], fig. 14) from the Gatun Formation of the Panama Canal is here selected as lectotype.

*New material:* Left propodus, PI IC 395 (JT 98-2-7, no PPP number), eastern end of graded quarry floor at Las Lomas Suites, 1.2 km SW of Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene. Collected by P. Jeffery, 08-11/08/1998.

*Remarks:* Rathbun (1919a) based the new species *Callianassa*

*toulai* on a description and figure by Toulai (1911) of a cheliped and a propodus lacking the fixed finger. The three ‘spinelike projections’ (represented as basal scars on the present material) on the upper margin as described by Rathbun (1919a) are criteria for the genus *Glypturus* as diagnosed by Manning and Felder (1991).

*Glypturus acanthochirus* Stimpson, 1866 has been described from the Pleistocene Port Morant Formation of Jamaica (Collins *et al.*, 1997); granules lining the interdigital margin of *G. toulai* are less numerous and coarser than those on *G. acanthochirus*. However, the expanse of granules on the latter is a variable feature; with discovery of better-preserved specimens from Panama, *G. toulai* may be found to be synonymous with *G. acanthochirus*.

Genus *NEOCALLICHIRUS* Sakai, 1988

*Type species: Neocallichirus horneri* Sakai, 1988, by original designation.

*Range:* Campanian, Late Cretaceous to Recent.

***Neocallichirus scotti* (Brown and Pilsbry, 1913)**

**Collins and Todd nov. comb.**

(Pl. 1, Figs. 9, 13–16; Pl. 2, Fig. 1)

1913 *Callianassa scotti* Brown and Pilsbry, p. 503, pl. 22, figs 1, 3 *non* fig. 2.

1919a *Callianassa scotti* Brown and Pilsbry; Rathbun, p. 140, pl. 60, figs. 9–12.

1919a *Callianassa vaughani* Rathbun, p. 148, pl. 63, figs. 10–13.

1919a *Callianassa crassa* Rathbun, p. 152, pl. 61, figs. 1–3 [*non C. crassa* A. Milne Edwards, 1870].

?1919a *Callianassa* sp. Rathbun, p. 153, pl. 64, fig. 10.

1919a *Callianassa crassimana* Rathbun, p. 141, pl. 141, figs. 15–17.

1919b *Callianassa miocenica* Rathbun, p. 166, pl. 2, figs. 1–6.

1929 *Callianassa rathbunae* Glaessner, 1929 (new name for *C. crassa* Rathbun 1919a, *non* A. Milne Edwards, 1870).

*Remarks:* According to Rathbun (1919a), *Callianassa scotti* Brown and Pilsbry was founded on specimens belonging to three species. As first reviser Rathbun restricted the name to three left propodi from the Culebra Formation (Oligocene) of the Las Cascadas section, Gaillard Cut, Panama Canal. Of the two species figured by Brown and Pilsbry under this name, Rathbun selected two figures (pl. 22, figs. 1, 3) to represent *Callianassa scotti* with the original specimen of fig. 1 (ANSP 2259) chosen as the (lecto-) type. Another specimen mentioned by Brown and Pilsbry (1913), ANSP 2255, labelled ‘Miocene’ (probably of Pliocene or Pleistocene age) from Costa Rica was considered by Rathbun (1919a) to belong to *C. scotti*. Also in 1919a, Rathbun described two left dactyli as *Callianassa crassimana* from both the same horizon and locality as *C. scotti* and from nearby younger strata of the Culebra Formation, and *Callianassa vaughani*, described from a portion of a right propodus retaining fixed finger and dactylus and two partial left propodi (all USNM 3242845) from the Gatun Formation (Late Miocene) of the Panama Canal Zone. *Callianassa rathbunae* Glaessner, 1929 (= *C. crassa* Rathbun, 1919a *non* Milne Edwards, 1870; see Karasawa, 2004) was described from two left

dactyli (holotype and paratype: USNM 324276) from the lower Gatun Formation, Middle? Miocene of Panama. Later, Rathbun (1919b) described a partial left propodus from the Miocene of Haiti as *Callianassa miocenica*. Visual differences between all are slight, amounting to no more than minor variation in length to width ratios and slight distal divergence of the upper and lower margins. A possible distinction is the presence or absence of setal pores. While the serrated digital 'plate' (the oblique edge of the propodus which overlaps the dactylus, Rathbun, 1919a, p. 149) present in Rathbun's material of *C. vaughani* is not preserved in that of *C. scotti*, both species possess the three tubercles on the outer surface proximal to the gape between the fingers and which are rather more numerous on the inner surface.

Apart from setal pores – which at best are seen only on better preserved material – these combined characters of the propodi and fingers, supported by corresponding features on the new material, not only fall within the diagnosis of the extant genus *Sergio* Manning and Felder, 1994, (subsequently synonymized under *Neocallichirus* by Sakai, 1999) but would encompass typical variation between left and right chelae and possible sexual dimorphism within a species, as demonstrated by Manning and Felder (1994).

It seems logical, therefore, that the four species considered should be regarded as synonymous and they are here recorded under the senior name as *Neocallichirus scotti* (Brown and Pilsbry). As reinterpreted herein, this species ranges from the Oligocene Culebra Formation through to the Late Pliocene Cayo Agua Formation of Caribbean Panama, probable Plio-Pleistocene deposits of Caribbean Costa Rica ("Oligocene, labelled 'Miocene'" according to Rathbun, 1919a, pp. 125, 141), and the Early Pleistocene of Pacific Costa Rica. The fragmentary propodus figured (as a merus fragment) by Rathbun (1919a, pl. 64, fig. 10; USNM 324280) from a horizon just above the type horizon of *N. scotti* at Las Cascadas, Gaillard Cut has all the aspects of the material discussed above and could also be included in *Neocallichirus scotti*. Material from the Late Miocene of the Dominican Republic (all from the Cercado Formation, except one lot less confidently assigned to this formation, see Saunders *et al.*, 1986) housed in the collections of the NMB, Basel has been used in the following redescription and is cited under its NMB site numbers.

**Diagnosis:** Propodus subquadrate upper and lower margins slightly divergent distally, upper margin smooth, margin finely granulate; outer surface very convex; three granules proximal to gape on outer surface, rather more on inner surface; 'digital plate' crenulated on both surfaces. Dactylus of adults with a proximal rectangular tooth followed by a recurved tooth and then a curved cutting edge distally, with fine, variably developed comb-like serrations, or nearly smooth.

**Lectotype:** By subsequent designation of Rathbun, 1919a, p. 141, the specimen figured by Brown and Pilsbry, 1913, p. 503, pl. 22, fig. 1 (ANSP 2259); paralectotype, specimen figured by Brown and Pilsbry, 1913, pl. 22, fig. 3.

**New material:** 11 lots; 1) Left propodus & carpus (PI IC 401; Pl.

1, Fig. 15) + 2 fragmentary left propodi (PI IC 402–403 and F1627–1628; Pl. 1, Figs. 13, 16); 2) fragmentary propodi + 3 left + 2 right dactyli PI IC 401–410 (no PPP number), just N of junction of road to Portobello with Boyd-Roosevelt Highway, Sabanita, Colón Province, Panama; lower Gatun Formation, Middle Miocene (Serravillian). Collected by S. Nielsen. 2) Two left propodi + 3 fragmentary propodi PI IC 411–415 (JT 99-14-5, no PPP number), graded surface just E of 'Sand Dollar Hill', 200 m NW of junction of road to Portobello with Boyd-Roosevelt Highway, Sabanita, Colón Province, Panama; unit 3 (Todd unpublished data), lower Gatun Formation, Middle Miocene (Serravillian) (Coates *et al.*, 2004a, fig. 7). Collected by J. A. Todd, July 1999. 3) Right propodus, fragmentary propodus + 2 left + 2 right dactyli + broken fixed finger PI IC 416–422 (JT 98-1-20#2, no PPP number), locality as above, units 3–5 (undivided) (Todd unpublished data), lower Gatun Formation, Middle Miocene (Serravillian). Collected by J. A. Todd, 03/08/1998. 4) Left propodus & carpus and carapace fragments + fragmentary left propodus PI IC 423–424 (JT 98-1-14, PPP 03381), locality as above; unit 21 (Todd unpublished data), Collected by J. A. Todd and P. Jeffery, 10/08/1998. 5) 1 dactylus (F1629; Pl. 2, Fig. 1) and 4 fixed fingers (F1630 1–4) (locality NMB 17638, PPP 00220); hill SE of houses, Residencial Dr. Martin Luther King, 1.2 km NW of Sabanita, Colón Province, Panama; lower Gatun Formation, Middle (?) Miocene. Collected by P. Jung, A. Foster, K. Johnson and T. Stemann, 19/08/1987. 6) 1 fragmentary propodus + 1 dactylus (F1631 1–2) (locality NMB 17796, PPP 00283); about 1 km W of Esterillos Oeste, Punta Judas, ca 40 km WNW of Quepos, Puntarenas Province, Costa Rica; unnamed formation, probably Middle to Late Miocene (Jung, 1995), Parrita Basin (see Coates and Obando, 1996, fig. 2.2). Collected by A. G. Coates and J. B. C. Jackson, 21/03/1988. 7) 1 dactylus (Pl. 1, Fig. 9) (F1632) (locality NMB 18541, PPP01163) downstream from Boca de Tigre, Río Chico, Darien Province, Panama; Tuirá Formation, early Late Miocene (early Tortonian) (see Coates *et al.*, 2004b, Map B). Collected A. G. Coates and J. B. C. Jackson, 06/05/1993. 8) 3 fragmentary left propodi, 1 right propodus and finger fragments, PI IC 425–431 (JT 98-2-7, no PPP number), E end of graded quarry floor at Las Lomas Suites, 1.2 km SW of Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene. Collected by P. Jeffery, 08-11/08/1998. 9) 1 dactylus (F1633) (locality NMB 18687, PPP 02188) from the westernmost island of Plantain Cays, off Tobabe Point, N side of Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene (late Tortonian–Messinian) (see Coates *et al.*, 2003, fig. 6). Collected by P. Jung, A. Heitz and J. A. Todd, 15/09/1995. 10) 1 left propodus (F1634; Pl. 1, Fig. 14) + 1 right propodus (F1635) (locality NMB 18737, PPP 02240) Punta de Níspero, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 25/09/1995. 11) 1 dactylus (F1636) (locality NMB 17771, PPP 00291) from the WSW end of Playa Cocalito, SE Coast of Nicoya Peninsula, Puntarenas

Province, Costa Rica; Montezuma Formation, Early Pleistocene (Coates *et al.*, 1992, p. 819). Collected by P. Jung, R. Panchaud and Y. Ventocilla, 23/03/1988.

*Emended description:* To the original description of *Callianassa vaughani* and the synonymized species, which consisted largely of fragmentary propodi and disassociated fixed fingers, the new material allows description of other elements of the chelipeds.

Left propodus with associated carpus: carpus length about two-thirds of height, upper margin nearly straight, forming a thin, smooth carina; lower proximal margin broadly rounded, upper proximal margin with deep articulating facet. Propodus a little longer than carpus, upper margin straight, smooth and narrowly rounded; lower margin nearly straight with a vague depression before the (broken) fixed finger; interdigital margin sigmoid, the upper part ('digital plate') boldly rounded and serrate; lower part smooth and bounded by a row of three granules. The inner surface is weakly concave before the fixed finger; there is a row of seven granules and a granulated 'digital plate'. The quadrate aspect of the propodus resembles that of the male chela of *Sergio mericeae* (Manning and Felder, 1995) (Fig. 1b) (synonymized under *Neocallichirus guassutingus* (Rodrigues) by Sakai, 1999).

Contrastingly, the upper margins of left and right propodi (F1634–1635) are markedly down-curved distally and there is a noticeable depression before the fixed finger. The upper and lower edges are sharp, with setal pores along the upper inner margin and lower outer margin, while the inner lower margin is finely granulated.

Left dactylus: elongate, length almost four times proximal height; upper margin sharply down-curved in its distal half and gently curved inwards. On the occludent margin a broad, rectangular cusp is followed by a smaller, rectangular cusp and a thin, sinuous cusp that, according to development may be smooth or weakly serrate, extends to the rounded tip. These serrations are generally more obvious on the inner surface. As preserved, three setal pores on the outer surface of the manus extend from the upper proximal angle, and a line of six extends along the upper margin; there are two pores on the larger rectangular tooth, one on the smaller and two between this and the tip; two pores occur near and six line the upper margin.

A right dactylus (Dominican Republic [DR hereafter], Cibao Valley, Río Cana; Cercado Formation, Late Miocene: locality NMB 16844) is robust, its length (18.5 mm) about three times the proximal height (5.5 mm) and curved inwards. On the rounded outer surface are 4 setal pores close to the upper margin, the most proximal twinned, the 2<sup>nd</sup>–4<sup>th</sup> diminishing in size distally. The upper articulating socket protected by a horn-like process, from its base a row of 6 pores, the first minute, curves to the base of a sharp, thorn-like cusp on the opposing margin. Proximal to this cusp is a broad, quadrate process, minutely granulated along the proximal margin. Distal to this cusp is a minute granule, after which the margin is sharp and convex with rounded serrations distally and concave to the rounded tip. There are two, oblique setal

pores before the cusp and 7 line the upper margin. The flattened inner surface is weakly concave distally along the upper margin; there are 2 pores proximally and one together with a granule on the rectangular occludent process.

The proportions and setal pores of this dactylus approximate that of the right dactylus of a mature male of *Sergio mericeae* Manning and Felder, 1995 (fig. 1) (= *Neocallichirus guassutingus* (Rodrigues, 1971); Manning and Felder, 1991, p. 779; Sakai, 1999, p. 90), it differs in the distal cusp being more densely serrate.

A damaged right dactylus (DR, Cibao Valley, Río Cana; Cercado Formation, Late Miocene: locality NMB 16844), not so incurved as the above, has a length of 16.0 mm and proximal height of 4.4 mm; no thorn-like cusp has developed and the succeeding sinuous cutting edge is smooth. This arrangement is close to that of the minor cheliped of *Neocallichirus guassutingus* (Rodrigues).

Right dactylus (DR, Cibao Valley, Río Gurabo; Cercado Formation, Late Miocene: locality NMB 15912) (Length: 10.8 mm, Height: 3.0 mm), possibly that of a female, is gently incurved, has a sharper, slightly carinate, upper margin less curved in side view, and a setal pore above the 'thorn tooth'. In contrast, from the same locality, a small, robust left dactylus (L.: 10.0 mm, H.: 3.0 mm) has the characters of the type species of *Sergio* (synonymized with *Neocallichirus* by Sakai, 1999). A second left dactylus (DR, Cibao Valley, Río Gurabo; Cercado Formation, Late Miocene: locality NMB 15900), with much the same proportions as that of the type species, has similarly arranged setae pores.

A broken fixed finger (DR, Cibao Valley, Río Mao at mouth of Arroyo Bajón, ?Cercado Formation, ?Late Miocene: locality NMB 16915) (L.: 19.0 mm; H.: 7.0+ mm) is weakly incurved, has a convex-concave outer surface, with 4 setal pores within the concave part; the opposing margin has one pore about mid-length and there are 3 proximally. The basal margin, subcarinate proximally, becoming rounded, has at least 4 setal pores. It may be compared with the fixed finger of the female specimen (Manning and Felder, 1995, fig. 3) of *S. mericeae* (= *N. guassutingus*), which has serration only on the proximal part of the opposing margin. This degree of serration agrees with variation figured in Manning and Felder (1995) as examples of growth-stage development.

The length of a left fixed finger (F1630) is a little more than twice the proximal height, the lower margin is moderately curved upwards; the outer surface is flattened to gently rounded in its lower half, and chamfered towards the occludent margin. The occludent margin has three evenly spaced spinules, a lower, sub-bifurcated spinule and a row of granules; the distal third forms a sharp cutting edge. On the inner surface the chamfer is concave. There is a row of six setal pores on the lower margin.

*Discussion:* The distribution of setal pores on both the above left and right dactyli agrees in all respects with Rathbun's figured (1919a, pl. 63, fig. 13) right dactylus, which is rather more robust, thus comparing favourably with that of a male individual of *Sergio mericeae* (= *Neocallichirus guassutingus*; according to Sakai, 1999)

figured by Manning and Felder (1995). The small rectangular tooth of *C. vaughani* is developed into a short thorn-like process and the serrations on the distal cusp are developed similarly or distinctly comb-like. Both propodi (F1634–1635) share similar proportions, the distinct depression before the fixed finger is closest to that of a female of *S. mericeae* (Manning and Felder, 1995). The fixed finger (F1630) is altogether more slender than that of the type and is comparable to that of *N. guassutingus*, which differs in having more evenly formed granules on the occludent margin (Manning and Felder, 1995). Unfortunately, the nominal fossil species were named from different limb segments, some in poor state of preservation, some exposing inner or outer surfaces, others from opposite hands of the cheliped. These provide no reliable constants for measurements or ratios from which to draw comparisons with the new material.

Following recent investigation into the geographical range of extant species, Manning and Felder (1995) concluded that *Sergio guassutinga* was essentially a Brazilian species, while *S. mericeae* occupies intertidal sand-flats off the Atlantic coasts of Florida and could possibly range into the Gulf of Mexico. Sakai (1999, p. 90–91) synonymized the two species, regarding the described differences as reflecting individual variation. It is evident from comparisons of the dactyli of *N. scotti* that this is a sister species to the Recent species.

Family CTENOCHELIDAE Manning and Felder, 1991

Subfamily CTENOCHELINAE Manning and Felder, 1991

Genus *CTENOCHHELES* Kishinouye, 1926

*Type species: Ctenocheles balssi* Kishinouye, 1926, by monotypy.

*Range:* Late Cretaceous to Recent.

***Ctenocheles falciformis* Collins and Todd sp. nov.**

(Pl. 2, Fig. 2)

*Diagnosis:* Fixed finger slender, length about six times proximal height, slightly inturned; occludent margin pectinate.

*Type material:* Holotype: right fixed finger (F1637; figured) (locality NMB 17830; PPP 00345), small island off E coast of Cayo Agua, ca 1.2 km SE of Punta de Tiburón, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene. Collected by P. Jung, R. Panchaud and D. Geary, 03/06/1988. Two paratypes, both right fixed fingers; 1) F1638, (locality NMB 17809; PPP 00294), Cayo Agua: E coast, ca 300 m W of Punta de Tiburón, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung and R. Panchaud, 30/05/1988. 2) F1639 (locality NMB 17767; PPP 00288); Playa Cocalito, NE of Montezuma, SE coast of Nicoya Peninsula, Puntarenas Province, Costa Rica; Montezuma Formation, Early Pleistocene (Coates *et al.*, 1992, p. 819). Collected by P. Jung, R. Panchaud and Y. Ventocilla, 22/03/1988.

*Attributed material:* 3 lots: 1) 2 finger fragments (F1640 1–2) (locality NMB 17847; PPP 00431), cliffs on S coast of Escudo de

Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, early Late Pliocene. Collected by R. Panchaud, D. Geary and L. Anderson, 04/06/1988. 2) Small, broken finger fragment (F1641) (locality NMB 17825; PPP 00340), E coast of Cayo Agua, S of Punta de Tiburón, Bocas del Toro Province, Panama. Cayo Agua Formation, early Late Pliocene. Collected by P. Jung, R. Panchaud and D. Geary, 02/06/1988. 3) 2 finger fragments (F1642 1–2) (locality NMB 18277; PPP 00950), bulldozed area SW of Bella Vista and S and SE of Lomas del Mar, Limón, Limón Province, Costa Rica; Moin Formation, Early Pleistocene. Collected by Peter Jung and others, 09/01/1992.

*Questionably assigned material:* 2 left minor dactyli (F1643 1–2) (locality NMB 18080, PPP 0631) from a hill behind the cemetery on Route 32, Pueblo Nuevo, west of Limón, Limón Province, Costa Rica; Moin Formation, Early Pleistocene (see Jackson *et al.*, 1999, p. 212). Collected by P. Jung, R. Panchaud and others, 03/04/1989.

*Derivation of name:* With reference to the scythe-like nature of the fixed finger.

*Description:* Right fixed finger length (18.0 mm) rather more than six times proximal height (2.8 mm), weakly sinuous, curving inwards, tip moderately upturned, lower margin weakly convex after proximal constriction. The occludent margin is lined with thorn-like denticles – invariably broken off. Basal scars indicate erratic arrangement of large and small denticles generally leading to a 1 3 2 2 3 1 arrangement, giving way distally to 1 3 2 3 1 arrangement. Fine setal pores along the inner and outer basal margins alternate with a row along the basal edge. Left dactylus length (12.7 mm) about six times proximal height (2.2 mm), almost circular in section, slightly inturned and weakly downturned at the tip. Occludent margin with two large proximal cusps followed by small bluntly rounded triangular cusps with larger ones scattered between. A juvenile form (F1640) has a more regular arrangement of about 6 small granular cusps between larger ones. The same juvenile has a single setal pore just distal to the articulating boss; larger forms have 8 more or less regular rows of evenly spaced pores: 3 on the outer and 5 on the inner surface. A smaller, fragmentary, less robust form (F1643) has a more regular arrangement of occludent cusps; this questionably attributed form may indicate sexual dimorphism.

*Discussion:* The geographical and geological distribution of *Ctenocheles* has been discussed by Schweitzer and Feldmann (2001) and was augmented by the same authors in 2002. Manning and Felder (1991) recorded four Recent North American species, all from the Western Atlantic and ranging into the Caribbean Sea. Two, known only from chelae from the Caribbean, were described as *Ctenocheles A & B* by Holthuis (1967); one, *Ctenocheles holthuisi* Rodrigues, 1978, was described from a specimen taken off Rio São Francisco, Brazil and the fourth, *Ctenocheles leviceps* Rabalais, 1979 comes from Port Arkansas, Texas. Of these species, the major claw of *C. holthuisi* together with Species A & B of Holthuis differ radically in the arrangement of the denticles,

while that of *C. leviceps* has the 1 3 2 2 3 1 as well as the 1 3 2 3 1 arrangement of denticles and is probably morphologically closest to *C. falciformis*.

Infraorder ANOMURA MacLeay, 1838  
 Superfamily PAGUROIDEA Latreille, 1802  
 Family DIOGENIDAE Ortmann, 1892  
 Genus *DARDANUS* Paul'son, 1875

*Type species: Dardanus helleri* Paul'son, 1875, by original designation (on Official List ICZN).

*Range:* Eocene to Recent.

***Dardanus biordines* Collins and Todd sp. nov.**

(Pl. 2, Figs. 3, 4)

*Diagnosis:* Right propodus; manus subquadrangular with two rows of spines along upper margin; outer surface with regular rows of spines and scales. Left 2<sup>nd</sup> pereopod dactylus; outer surface with chevron ornament, margins spinose, inner surface with median and basal ridges.

*Type material:* Holotype, a right propodus (F1644; Pl. 2, Fig. 4), (locality NMB 18373, PPP 01188) from the southeast coast of Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene. Collected by P. Jung, A. Heitz and others, 02 & 04/08/1993. Paratype, a left 2<sup>nd</sup> pereopod dactylus, F1645 (Pl. 2, Fig. 3), from the same collection.

*Derivation of name:* Referring to the two rows of spines along upper margin.

*Description:* Manus subquadrangular, outer surface moderately curved longitudinally and transversely; inner surface weakly rounded. Distal height about equal to length of manus. Upper (inner) margin weakly convex with two rows of five alternating sharp spines; lower (outer) margin weakly concave; carpal margin vertical; interdigital margin slightly oblique. The fixed finger, worn at the tip, is a little under half the length of the manus. The occludent surface is weakly spooned with four setal pores, reduced in diameter proximally, the cusps reduced in diameter proximally. The outer surface is ornamented with scale-like tubercles, arranged in six vertical rows and horizontally with four basal rows developing from two rows of spines, the lower three rows continuing onto the fixed finger. All tubercles have a minute distal setal pore and pores line the occludent margin.

A 2<sup>nd</sup> pereopod left dactylus (F1645) attributable to this species has the outer surface chevroned by grooves leading from marginal spines to a median furrow lined with setal pores. On the inner surface blunt spines line the upper margin, and there is a strong median ridge bounded by a sharp ridge. Setal pores open from the bases of all the spines.

*Discussion:* Assuming that the above limb elements are conspecific, the characteristic *Dardanus*-like form of the dactylus has influenced placement of *biordines* in that genus. The attributed left pereopod dactylus has much in common with that figured by A. Milne Edwards and Bouvier (1893, p. 11, fig. 27) as *Pagurus*

*striatus petersi* (A. Milne Edwards, 1880) and with *Dardanus insignis* Saussure, 1858 (in Verrill, 1908). In contrast, the propodus differs considerably in ornament and the downward curvature of the fixed finger from the corresponding propodus of the above species.

Genus *PETROCHIRUS* Stimpson, 1859

*Type species: Pagurus granulatus* Olivier, 1811 (= *Cancer bahamensis* Herbst, 1791), by monotypy.

*Range:* Miocene to Recent.

***Petrochirus bouvieri* Rathbun, 1919a**

(Pl. 2, Fig. 6)

1911 *Petrochirus* cf. *granulatus* Olivier sp.; Toula, p. 511, pl. 30 [1], fig. 13.

1919a *Petrochirus bouvieri* Rathbun, p. 153.

*Lectotype:* The specimen figured by Toula, 1911, pl. 30 [1], fig. 13 from the Gatun Formation of the Panama Canal.

*New material:* 8 lots; 1) Right propodus (figured) (F1646) (locality NMB 18987; PPP 03221); cliff section at Morro Hueco, about 1 km NE of village of Gobeia (c. 5 km E of Miguel de la Borda), coast W of Colón, Colón Province, Panama; Rio Indio facies, Chagres Formation, Late Miocene (Messinian). Collected by J. A. Todd, P. Jung, A. G. Coates, H. Fortunato and O. Aguilera, 17/01/1998. 2) Finger tips, in gastropod *Malea ringens* (Swainson) (currently subject to further study) (F1647), (locality NMB 18657, PPP 01525); Río Tuira, near junction with Río Cube, Darien Province, Panama; Tuira Formation, early Late Miocene (Tortonian) (see Coates *et al.*, 2004b, Map B). Collected by A. G. Coates and J. B. C. Jackson, 26/02/1994. 3) Left fixed finger (F1648) (locality NMB 18711; PPP 01504); "Finger Island", about 50 m W of S tip of Cayo Toro, S side of Valiente Peninsula, Bocas del Toro Province, Panama. Nancy Point Formation (lowest part), Late Miocene (Messinian). Collected by P. Jung, J. A. Todd and H. Fortunato, 18/09/1995. 4) Right fixed finger (F1649) (locality NMB 18730, PPP 02232), W end of Punta de Níspero, Cayo Agua, Bocas del Toro Province, Panama. Cayo Agua Formation, early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 22/09/1995. 5) Finger tips, in a gastropod, *Strombus* (*Strombus*) sp. (F1650) (and indeterminate fragments probably belonging to this crab in two others) (F1651–1652) (locality NMB 17813, PPP 00476); just S of Punta de Níspero, east coast of Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung and R. Panchaud, 31/05/1988. 6) Right fingers in 2 specimens of *Strombus* (*Strombus*) sp. (F1653–1654) (locality NMB 18736, PPP 02239), Punta de Níspero, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 25/09/1995. 7) Left dactylus (F1655) (locality NMB 18681, PPP 02212), four easternmost islets off the E tip of Escudo de Veraguas, Bocas del Toro Province; Escudo de Veraguas Formation, early Late Pliocene.

Collected by P. Jung, A. Heitz, J. A. Todd, H. Fortunato and J. B. C. Jackson, 14/09/1995. 8) Right propodus + associated dactylus (F1656) (locality NMB 19069, PPP 03255), N of Route 32, N of a bulldozed site for a container depot, 1.5 km W of Pueblo Nuevo, Limón, Limón Province, Costa Rica. 'Mollusc mudstone', basal Moin Formation, Late Pliocene. Collected by J. A. Todd and H. Fortunato, 05/02/1998.

*Questionably assigned material:* Finger tips, in gastropod *Malea* sp. (F1657) (locality NMB 17745, PPP 0436); Quebrada El Higo, 5 km NE of Punta Banco, Golfo Duce shore of Burica Peninsula, Puntarenas Province, Costa Rica; Armuelles Formation, Early Pleistocene? (see Coates *et al.*, 1992, p. 819). Collected by P. Jung and others, 17/03/1988.

*Remarks:* Rathbun (1919a), in her discussion of *P. bouvieri*, drew attention to the ornament of the chela combining that of two Recent species; namely the similarity of the left chela to that of *Petrochirus bahamensis*, an eastern Caribbean form, and that of *Petrochirus californiensis* Bouvier, 1895, which ranges from Lower California to Ecuador. While only one left fixed finger is present in the new material, the contrast in ornament fully upholds Rathbun's observation. As noted above, some specimens are preserved in their domicile gastropod shell and these specimens will be described elsewhere; this material was mistakenly referred to as being from the Gurabo Formation [sic] of Panama by Collins and Jakobsen (2003, p. 64).

Fossil remains of *P. bahamensis* have been recorded, tentatively from the Pliocene Bowden shell bed and from the Pleistocene Port Morant Formation of Jamaica (Collins and Portell, 1998) and from the Pleistocene of St. Kitts (specimens in Dept of Palaeontology, The Natural History Museum, London) (Collins, unpublished data).

The Panamanian and Costa Rican range of the new material extends from the Tuira Formation (Tortonian, Late Miocene) of the isthmian Chucunaque Basin, Darien to the basal Moin Formation of Late Pliocene age of the Southern Limón Basin, Costa Rica. A specimen from the probable Early Pleistocene Armuelles Formation of the Nicoya Peninsula of Pacific Costa Rica (F1657) is small, largely embedded in matrix, and is not confidently assigned to this species. It appears likely that *P. bahamensis* appeared in the Caribbean after isthmian uplift, either in the Late Pliocene or Pleistocene.

Infraorder BRACHYURA Latreille, 1802

Section EUBRACHYURA de Saint Laurent, 1980

Subsection RANINOIDA de Haan, 1839

Superfamily RANINOIDEA de Haan, 1839

Family RANINIDAE de Haan, 1839

Subfamily RANINOIDINAE Lórenthey in Lórenthey and Beurlen, 1929

Genus *RANINOIDES* H. Milne Edwards, 1837

*Type species:* *Ranina loevis* Latreille 1825, by monotypy.

*Range:* Late Eocene to Recent.

### *Raninoides cf. benedicti* Rathbun, 1935a

(Pl. 2, Fig. 5)

cf. 1935a *Raninoides benedicti* Rathbun; Rathbun, p. 9, figs 4, 5; pl. 1, figs. 7, 8 (see also for prior synonymy).

*New material:* 2 lots; 1) a male carapace lacking front (F1658; figured) (locality NMB 17794, PPP 00269), Quebrada El Higo, Golfo Duce shore of Burica Peninsula, Puntarenas Province, Costa Rica; Armuelles Formation, ?Early Pleistocene (see Coates *et al.*, 1992, p. 819). Collected by A. G. Coates and J. B. C. Jackson, 18/03/1988. 2) Anterior portion of carapace (F1659) (locality NMB 18687, PPP 02188), from the westernmost island comprising Plantain Cays, off Tobabe Point, N side of Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene (late Tortonian–Messinian) (see Coates *et al.*, 2003, fig. 6). Collected by P. Jung, A. Heitz, J. A. Todd, J. B. C. Jackson and H. Fortunato, 15/09/1995.

*Remarks:* Both specimens lack vital details of the front (emphasized by Rathbun, 1937) that aid their distinction from the closely allied *Raninoides loevis* (Latreille, 1825), presently occurring off the Pacific coast of Panama and Colombia. However, an influencing feature towards tentative placement in *R. benedicti* is the closer agreement (as far as can be judged) between the anterolateral spine and carapace midline with Rathbun's (1937) figures.

Sufficient of the lateral spines remain on both the new carapaces to obtain an angle of c. 52.5 degrees. The angle obtained from *R. loevis* (*vide* Rathbun, 1937, pl. 1, fig. 2) is 59.0 degrees, whereas that for *R. benedicti* (Rathbun, 1937, pl. 1, fig. 7) is 53.5 degrees.

Today, *R. benedicti* occurs on the Pacific coast of Panama and the Caribbean north coast of South America and Barbados (Rathbun, 1937).

Subsection HETEROTREMATA Guinot, 1977

Superfamily CALAPPOIDEA de Haan, 1833

Family CALAPPIDAE de Haan, 1833

Genus *CRYPTOSOMA* H. Milne Edwards, 1837

*Type species:* *Cryptosoma dentatum* Brullé, 1840, by subsequent designation of Rathbun, 1924.

*Range:* Early Miocene to Recent.

### *Cryptosoma bairdii* (Stimpson, 1860)

(Pl. 2, Fig. 13)

1919b *Cycloes bairdii* Stimpson; Rathbun, p. 169, pl. 9, fig. 8 (see also for prior and intermediate synonymy).

1937 *Cycloes bairdii* Stimpson; Rathbun, p. 225, pl. 69, figs. 3, 4.

1998 *Cryptosoma bairdii* (Stimpson); Bellwood, p. 464.

*New material:* 2 lots: 1) Left propodus and associated carpus (F1660; figured) (locality NMB 17630; PPP 00197) 350 m SW of Punta Norte, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, late Early Pliocene. Collected by P. Jung and Y. Ventocilla, 11/08/1987. 2) A partial left propodus (F1661) (locality NMB 17471, PPP 01738) from Playa Cocalito, SE coast of Nicoya Peninsula, ENE of Montezuma village, Puntarenas Province, Costa

Rica; Montezuma Formation, Early Pleistocene (see Coates *et al.*, 1992, p. 819). Collected by P. Jung, P. Baumgartner and C. Mora, 12/04/1984.

*Remarks:* Recorded from the Lower Miocene of the Dominican Republic on the evidence of a fragmentary left propodus, this extant species was omitted by Schweitzer and Feldmann (2000) in their summary of fossil calappid species. Better-preserved material from the Cayo Agua Formation of Panama, supported by newly identified material from the Dominican Republic (Collins, pers. obs.), conforms in all respects with Recent specimens in the Department of Zoology, The Natural History Museum, London, and firmly reinstates this species in the fossil record of the Caribbean region. The additional propodi from the Dominican Republic reach a larger size and the tubercles on the outer surface are more conspicuous, but are considered to represent no more than typical growth variation.

The present range of *C. bairdii* in the East Pacific is from the west coast of Mexico southwards to Ecuador and the Galapagos Islands; and in the Western Atlantic from North Carolina and the Bermudas south to the Caribbean Sea (Rathbun, 1937).

Family HEPATIDAE Stimpson, 1871

Genus *HEPATUS* Latreille, 1802

*Type species:* *Cancer princeps* Herbst, 1794, by original designation.

*Range:* Oligocene to Recent.

***Hepatus lineatinus* Collins and Todd sp. nov.**

(Pl. 2, Figs. 8–12)

*Diagnosis:* Carapace transversely subovate, spines on anterolateral margins tridenticulate; dorsal lobes tumid, sharply to weakly defined according to growth size, with granulated summits. Chelae homochelous, with rows of tri-granulate nodes.

*Type material:* Holotype: a male carapace (F1662; Pl. 2, Fig. 8), (locality NMB 17832, PPP 00358), from the north-central coast of Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, Late Pliocene. Collected by P. Jung and A. G. Coates, 04/06/1988.

9 paratypes; 8 carapaces, 1 right propodus and dactylus:

1) Carapace (Pl. 2, Fig. 10) PI IC 440, (no PPP number) just N of junction of road to Portobello with Boyd-Roosevelt Highway, Sabanita, Colón Province, Panama; lower Gatun Formation, Middle Miocene (Serravillian). Collected by S. Nielsen. 2) Carapace, PI IC 441 (JT-99-14-3, no PPP number), 'Sand Dollar Hill', Sabanita, Colón Province, Panama; bed 4 (Todd MS), basal Gatun Formation, Middle Miocene (Serravillian) (Coates *et al.*, 2004a, fig. 7). Collected by J. A. Todd, 03/07/1999. 3) Carapace (Pl. 2, Fig. 12) PI IC 442, (JT-98-2-PJ, no PPP number), float from bulldozed surface at Las Lomas Suites, 1.2 km SW of Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene. Collected by P. Jeffery, 08-11/08/1998. 4) Right propodus and dactylus (F1663; Pl. 2, Fig. 11), (locality NMB 18373, PPP

01188); SE coast of Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene. Collected by P. Jung, A. Heitz and others, 02 or 04/08/1993. 5) Carapace (F1664) (locality NMB 18596, PPP 00352), unnamed promontory between Punta Tiburón and Punta Piedra Roja, N coast of Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene. Collected by A. G. Coates, 03/06/1988. 6) Carapace, largely embedded in matrix, with left and right propodi exposed (F1665) (locality NMB 18734, PPP 02237), 300 m WNW of Punta Piedra Roja, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 24/09/1995. 7) Carapace (F1666) (locality NMB 18739, PPP 02242), E side of Punta de Nispero, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by A. Heitz, O. Aguilera and H. Fortunato, 25/09/1995. 8) Carapace (F1667; Pl. 2, Fig. 9), (locality NMB 17784, PPP 00461), left bank of river, 700 m SW of bridge, Bomba, Río Banano, south of Limón, Limón Province, Costa Rica; type locality of Río Banano Formation, Late Pliocene. Collected by P. Jung, R. Panchaud and C. Mora, 29/03/1988. 9) Carapace (F1668) (locality NMB 17767; PPP 00288); Playa Cocalito, NE of Montezuma, SE coast of Nicoya Peninsula, Puntarenas Province, Costa Rica; Montezuma Formation, Early Pleistocene (Coates *et al.*, 1992, p. 819). Collected by P. Jung, R. Panchaud and Y. Ventocilla, 22/03/1988.

*Other material:* Right propodus, (F1669) (locality NMB 18730, PPP 02232), W end of Punta Nispero, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 22/09/1995. Fragmentary carapace, PI IC 443, (no PPP number), Punta Norte, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by J. A. Todd, 06/02/1998.

*Derivation of name:* From a similarity to the Recent *Hepatus lineatus* Rathbun, 1898.

*Description:* Carapace length about four-fifths of the width (holotype, 70.4 percent), widest at spinule cluster before lateral angle, strongly arched longitudinally and moderately so transversely, becoming thin towards the margins. Anterolateral margin evenly rounded and lined with 16 or 17 tridenticulate spines, gradually increasing in size from behind the orbit to the lateral angle. Even-sized granules, with larger ones interspersed, line the strongly convex posterolateral margins and continue above the posterior margin which is also granulate and narrower than the orbitofrontal margin. The orbitofrontal margin, occupying about one-third of the carapace width (30.0 – 37.7 percent, according to growth size) is raised above the level of the anterolateral margins; the front is weakly bilobed with a faint median sinus, thickened and granulated. Small, subovate orbits are directed slightly upwards. Bent, truncated orbital peduncles are densely pitted. Smooth upper orbital margins are fairly thick, pierced by two closed notches and coarsely granulated laterally round to the lower margin. The lower margin

of the suborbital cavity is coarsely beaded and clearly visible from above. The regions and lobes are mostly well-defined, tumid in younger forms, the tumidities dispersing as growth advances. The cervical furrow, obscured by prominent uro/cardiac depression, curves gently across the midline, broadens round the mesogastric lobe and becomes obsolete before reaching the margin. Proto gastric, mesogastric, epibranchial and metabranchial lobes are all more sharply defined in young individuals; in older forms the proto gastric lobes are merely tumid. All tumidities are crowned with a cluster of coarse and fine granules, those on the epibranchial and metabranchial lobes become linear, curving latero-posteriorly. A subrectangular urogastric lobe is weakly separated from a large, elongate shield-shaped cardiac region. Pits of several diameters crowd the dorsal surface.

The male abdominal trough is widest at 6<sup>th</sup> somite; 1<sup>st</sup>–4<sup>th</sup> sternites fused, although defined by grooves, 1<sup>st</sup>/3<sup>rd</sup> sternites triangular, 1<sup>st</sup>/2<sup>nd</sup> separated from 3<sup>rd</sup> by a low, weakly granulate to smooth ridge, base of 3<sup>rd</sup> overlaps head of 4<sup>th</sup> sternite and separated from it by an oblique groove; 4<sup>th</sup> sternites subquadrilateral, thickened along the coxigeal margin. ‘Press-buttons’ (Guinot and Bouchard, 1998) to secure the abdomen on the pentagonal 5<sup>th</sup> sternites; 6<sup>th</sup> sternites are rather more rounded. Large, subtriangular episternites extend half the length of the preceding sternites. The (male) abdomen extends to 3<sup>rd</sup>/4<sup>th</sup> sternites, the ‘trough’ extending as a suture to the 1<sup>st</sup> sternites. The telson is as long as the 4<sup>th</sup> sternite; there is a transverse pair of nodes on the 4<sup>th</sup> somite and thin spurs from a ridge lining its posterior margin embrace the articulating node of the 4<sup>th</sup> coxae.

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

A juvenile specimen (Pl. 2, Fig. 10) from the lower Gatun Formation of Panama is remarkable in having a well developed bopyriform swelling occupying the entire left metabranchial region; granules topping the original node are disturbed, otherwise no distortion of carapace outline occurs.

*Discussion:* There is a close resemblance of *H. lineatus* to the

Recent *Hepatus lineatus* Rathbun, 1898, in which species the anterolateral margins are lined with fewer (14–15) tridentate granules; the suborbital cavities are not visible from above and the granules surmounting the nodes are concentrated around a larger one, not in evidence on *H. lineatus*. The node on the 4<sup>th</sup> (male) abdominal somite of *H. lineatus* is lacking in *H. lineatus*.

### *Hepatus biformis* Collins and Todd sp. nov.

(Pl. 2, Fig. 7)

*Diagnosis:* Anterolateral margin tridentate; regions vaguely nodose; epi- and metabranchial and cardiac nodes crossed by single rows of granules; tubercles on outer surface of chelae in open semicircle; dorsal surface punctate.

*Derivation of name:* Indicating a resemblance to two *Hepatus* species.

*Type material:* Holotype, a male carapace (F1670; figured), (locality NMB 18715, PPP 02216) from the NW end of Cayo Toro, S coast of Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene (late Tortonian–Messinian) (Coates *et al.*, 2003, fig. 6). Collected by P. Jung, A. Heitz and J. A. Todd, 19/09/1995. Paratype, a broken carapace (F1671), (locality NMB 18054, PPP 00746) from Quebrada La Peñita, 200 m upstream from junction with eastern tributary, Burica Peninsula, Puntarenas Province, Costa Rica; Peñita Formation, probably Early Pliocene (Coates *et al.*, 1992). Collected by P. Jung and R. Panchaud, 16/01/1989.

*Description:* Carapace similar in outline to *H. lineatus* sp. nov. (L/W. est. 78.2 percent) but distinguished in being rather more arched in longitudinal section, by having almost smooth gastric lobes and only short lines of weak granules on the metabranchial and cardiac lobes; granules on the hepatic side of the epibranchial lobe are reduced to a single sinuous row directed antero-medially. Little remains of the front; the upper margin of the suborbital cavity forms a regular curve with the anterolateral margins and only the beaded edge of the lower margin is visible from above. The orbitofrontal margin occupies about 34.7 percent of the carapace width. Spinules flanking the anterolateral spines are not strongly developed. The dorsal surface is minutely punctate.

Male subtriangular 3<sup>rd</sup> sternites, extending beyond the head of the 4<sup>th</sup> sternites, have a granule either side of the midline flanked by four smaller ones; ‘press-buttons’ are present on the 5<sup>th</sup> sternites. The tip of the abdomen extends fractionally beyond the 3<sup>rd</sup> sternites.

Right chela: propodus a little less than half carapace width. The 1<sup>st</sup> and 2<sup>nd</sup> tubercular rows on the manus are similar to *H. lineatus*; row 3 has six single, isolated tubercles; row 4 comprises 16 distinct tubercles and numerous granules extending from the fixed finger are barely distinguishable. The fixed finger is about half propodus height and lacks the upper ridge seen on *H. lineatus*.

*Discussion:* Although the carapace outline of *H. biformis* has much in common with *H. lineatus*, particularly in retaining the tridentate anterolateral spines, well-developed in the latter; it dif-

fers in having a more steeply arched carapace and a smoother dorsal surface on which the granules are reduced to single rows across the epi- and metabranchial and cardiac lobes. The rounded, more delicate ornament of the chelae is in sharp contrast to that of *H. lineatus* and similar subtle differences distinguish both the new species from chelae from the Miocene of the Dominican Republic, wherein only one tubercle occupies row 1, row 2 has four or five tubercles, row 3 has four and tubercles on rows 4 and 5 are more or less run together; the fixed finger is almost smooth. In having a steeper longitudinal section, sparse and lineal granular ornament, *H. biformis* closely approaches *Hepatus kossmanni* Neumann, 1878 (vide Rathbun, 1937, pl. 72, fig. 3), but the finely denticulate anterolateral margins readily distinguish that species. *Hepatus kossmanni* presently ranges from the west coast of Mexico to Ecuador (Rathbun, 1937).

Superfamily LEUCOSIOIDEA Samouelle, 1819

Family LEUCOSIIDAE Samouelle, 1819

Subfamily EBALIINAE Stimpson, 1871

Genus *SPELEOPHORUS* A. Milne Edwards, 1865

*Type species: Oreophorus nodosus* Bell, 1855, by monotypy;  
Recent, provenance unknown.

*Range:* Late Pliocene (herein) to Recent.

***Speleophorus subcircularis* Collins and Todd sp. nov.**

(Pl. 3, Figs. 1, 2)

*Diagnosis:* Carapace subhexagonal with two pairs of orifices; a deep furrow isolates the hepatic region; a tubercle on prominent subhepatic region not visible from above.

*Type material:* Holotype (F1672; Pl. 3, Fig. 1), a carapace, (locality NMB 18731, PPP 02234), from 400 m W of Punta Nispero, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 22/09/1995.

*Questionably assigned material:* A cheliped merus (F1673; Pl. 3, Fig. 2), (locality NMB 17471, PPP 01738) from Playa Cocalito, SE coast of Nicoya Peninsula, ENE of Montezuma village, Puntarenas Province, Costa Rica; Montezuma Formation, Early Pleistocene (see Coates *et al.*, 1992, p. 819). Collected by P. Jung, P. Baumgartner and C. Mora, 12/04/1984.

*Derivation of name:* From the outline of the upper orifices.

*Description:* Carapace subhexagonal in outline, a little wider than long (L.: 17.8 mm, W.: 21.0 mm) and widest at mid-length. The orbitofrontal margin, occupying one-fourth of the carapace width, is shortly produced; the antennary fossae and orbits are subcircular and deep. The weakly upturned front is broadly V-shaped, from its rounded outer angles the upper orbital margin is gently curved to a rounded angle and continues as a beaded ridge defining short, concave anterolateral margins from conspicuous subhepatic lobes, the ridge crosses subconical hepatic regions. Lateral angles and posterolateral margins are broadly rounded to a constriction at the posterior angle. The margin bordering the large, round outer

orifices is coarsely beaded and runs above prominent conical tubercles at the posterior angles. Behind the front a median ridge leads back to a narrow mesogastric region. On either side of the ridge, deep, rounded pits lead to a narrow channel encircling the hepatic regions, then recurve around tumid mesobranchial lobes and become obsolete. The cardiac region is weakly defined and tumid, a node at each end forms the highest part of the carapace. Separated by a thin septum, the inner orifices are subcircular and granule bounded. The wider septum between the inner and outer orifices is transversely divided at the junction with the large, tumid pentagonal intestinal region.

Numerous, but well spaced granules of several diameters cover the tumid areas; weaker granules in the anterior grooves become sparse posterolaterally.

A cheliped merus (Pl. 3, Fig. 2) from the Montezuma Formation, dated to Early Pleistocene, of the Nicoya Peninsula, Costa Rica, approximating the length/width proportions of *Speleophorus digueti* (Bouvier, 1898a), yet with tri-nodular ornament closer to that of *Speleophorus nodosus* (a species with only one pair of orifices) may belong to *Speleophorus subcircularis*.

*Discussion:* Of the five species in the genus described by Rathbun (1937) the new species bears a superficial resemblance only to *S. digueti* which differs in being longer than wide, in having a more produced front, less tumid mesobranchial regions and circular inner orifices. This would appear to be a scarce species presently occurring off the coasts of Gulf of California and Pacific Panama (Rathbun, 1937).

Subfamily PHILYRINAE Leach, 1817

Genus *PERSEPHONA* Leach, 1817

*Type species: Persephona latreillii* Leach, 1817 = *Cancer punctatus* Linné, 1758 (partim). by subsequent designation of Rathbun (1922).

*Range:* Miocene to Recent.

***Persephona enigmatica* Collins and Todd sp. nov.**

(Pl. 3, Fig. 4)

*Diagnosis:* Three posterior spines, those at the posterior angles flattened; a weak subhepatic tubercle and a coarse granule terminating anterolateral margin.

*Type material:* Holotype, a carapace (F1674), (locality NMB 17630, PPP 00197) from 350 m SW of Punta Norte, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung and Y. Ventocilla, 11/08/1987.

*Derivation of name:* A puzzle – indicating possible synonymy with *Persephona prepunctata* Rathbun, 1919b.

*Description:* Carapace almost as wide as long, globular, with three spines, one median above and overhanging the posterior margin, and one, flattened and apically rounded at each posterior angle. The front, occupying a quarter of the carapace width, is weakly upturned; the short, triangular rostrum is directed steeply downward and sulcate. Antennal and orbital fossae are round and

almost in line; there is a closed notch in the upper orbital margin, a longer one lateral to it, together with another at the side, extends to a circular postfrontal depression. The anterolateral margin, bounded by the prominent subhepatic region, is convex above a blunt tubercle on the subhepatic and excavated to an enlarged marginal granule before the posterolateral margin. The posterolateral margin is coarsely granulated anteriorly and minutely so posteriorly. Coarser granules line the posterior margin, which is about half the width of the front. The regions are ill defined; the hepatic region is weakly tumid and a vague groove entirely isolates the intestinal region. Granules of several diameters covering the entire surface are denser on the subhepatic, hepatic and intestinal regions. There is a pit below the subhepatic region and a shallow depression between that region and the branchial region.

*Discussion:* Rathbun (1919b), when discussing *Persephona prepunctata* Rathbun, 1919b, described from a number of meri from the Lower Miocene of the Dominican Republic, drew attention to characters of that species in common with the Recent *P. punctata* and *P. townsendi* (Rathbun, 1893) (East Pacific). The new species, in having characters in common with those species, yet retaining distinguishing features, could ideally be the hitherto unknown carapace of *P. prepunctata*, particularly so when meri in the present collection could be attributed to *Persephona prepunctata*. However, the occurrence in the present collection of another persephonid species, together with *Iliacantha* negates specific identification of possible attributable meri and their assignment to respective carapaces.

*Persephona enigmatica* differs from *P. punctata* in having blunter, flatter, less divergent spines at the posterior angles, in the latter respect being closer to *P. townsendi*. The blunt tubercle on the subhepatic region is closer to that of *P. punctata*, as is the coarser dorsal ornament and more clearly defined intestinal lobe. Neither of the two Recent species appears to have the coarse granule before the posterolateral margin (*vide* Rathbun, 1937).

A fragmentary carapace (F1675) from the basal Moin Formation, latest Pliocene (1.5 km W of Pueblo Nuevo, Limón, Costa Rica; locality NMB 19069, PPP 03255) is too incomplete for positive identification and is identified as *Persephona cf. enigmatica* sp. nov.

***Persephona manningi* Collins and Todd sp. nov.**

(Pl. 3, Fig. 3)

*Diagnosis:* Carapace longer than wide; three upturned posterior spines, those at posterior angles flattened, lateral traces of cervical furrow; a weak subhepatic tubercle; dorsal granules concentrated laterally and posteriorly.

*Type material:* Holotype, a fragmentary carapace free from matrix (F1676), (locality NMB 17838, PPP 00365); small island off N coast of Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, early Late Pliocene. Collected by P. Jung and A. G. Coates, 04/06/1988.

*Derivation of name:* In recognition of the late R. B. Manning's,

Smithsonian Institution, contribution to our knowledge of decapod crustaceans.

*Description:* Carapace subglobose, wider than long, with three upwardly directed spines, one median above and overhanging the posterior margin and one, stouter, flattened at each posterior angle. Orbitofrontal margin missing, but with indications of being upturned. The anterolateral margin, bounded by the subhepatic region, is convex and terminates in a broad notch. The lateral margins are sharp and beaded to the widest part of carapace, then rounded to the posterior angles. Above and slightly median to the marginal notch a trace of the cervical furrow is seen between the granules; broadening, it turns back and obliquely medially at a sharp angle. The regions are poorly defined. A sharp, forwardly directed spine and a much smaller, blunter one anterior to it on the subhepatic region are clearly visible from above. The median dorsal area appears smooth and glossy, but is covered in worn, or undeveloped, granules, similar to those crowding the rest of the surface; those on the intestinal region encircle the median spine.

*Discussion:* *Persephona manningi* differs from *P. enigmatica* in dorsal ornament, in having elements of the cervical furrow, size and shape of the posterior spines and presence of the distal 'tubercle' on the subhepatic region. This additional 'tubercle' distinguishes *P. manningi* from other *Persephona* species, among which *Persephona lichtensteinii* Leach, 1817 also has a partially developed cervical furrow.

Subfamily LEUCOSIINAE Samouelle, 1819

Genus *ILIACANTHA* Dana, 1871

*Type species:* *Iliacantha globosa* Stimpson, 1871, by original designation.

*Range:* Miocene; Late Miocene (herein) to Recent.

***Iliacantha panamanica* Collins and Todd sp. nov.**

(Pl. 3, Fig. 5)

*Diagnosis:* Carapace subglobose, finely granulated; subhepatic pit shallow; spine at posterior angle flattened, bluntly rounded.

*Type material:* Holotype, a carapace (F1677), (locality NMB 18687, PPP 02188) lacking orbitofrontal area, from the westernmost island comprising Plantain Cays, off Tobabe Point, N side of Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene (late Tortonian-Messinian) (Coates *et al.*, 2003, fig. 6). Collected by P. Jung, A. Heitz and J. A. Todd, 15/09/1995.

*Derivation of name:* From Panama.

*Description:* Carapace subovate, longer than wide (L.: incomplete, 20.6 mm/W.:18.0 mm), smoothly and evenly subglobose. The frontal area is missing, its sides rounded at base into short anterolateral margins barely distinguishable from prominent subhepatic regions clearly visible from above. There is a slight indentation before rounded lateral margins which are sharp edged for half their length and rounded to a flattened, bluntly rounded spine above the posterior angle. A prominent, rounded median spine

extends beyond the posterior margin. Vague furrows define the cardiac region and the intestinal lobe is weakly tumid. A shallow pit bounds the subhepatic lobe posteriorly. The dorsal surface is finely granulated, denser laterally.

*Discussion:* Although close in general outline to *Persephona*, the prominent subhepatic lobe, well separated from the branchial region, and flattened spines above the posterior angles more typically conform to *Iliacantha*. As far as preservation allows comparison, *I. panamanica* is close to the Recent *Iliacantha subglobosa* Stimpson, 1871, an eastern Caribbean species – although the posterolateral spines more closely resemble those of *Iliacantha sparsa* Stimpson, 1871, with much the same distribution as *I. subglobosa*, which is distinguished by the presence of a subhepatic spine.

A left propodus lacking the fixed finger and with articulated carpus (F1678; Pl. 3, Fig. 6), from the Cayo Agua Formation of the western side of Punta Norte, Cayo Agua (locality NMB 18401, PPP 00063: early Late Pliocene), can be attributed to *Iliacantha* sp. The carpus is slightly ovoid in section, about one-third the length of the manus. The manus is very short compared with other Caribbean members of the genus; its proximal height is about two-thirds the length, the upper margin is nearly straight, and the lower margin is boldly convex to the base of the fixed finger where there is a marked constriction; the surface is smooth; a proximal groove on the inner surface of the fixed finger may have extended the length of that digit.

Superfamily MAJOIDEA Samouelle, 1819

Family MAJIDAE Samouelle, 1819

Subfamily MITHRACINAE Balss, 1929

Genus *MITHRAX* Desmarest, 1823

*Type species:* *Cancer aculeatus* Herbst, 1790 (= *Mithrax pilosus* Rathbun, 1892), by subsequent designation of H. Milne Edwards, 1837.

*Range:* Miocene to Recent.

#### ***Mithrax* sp.**

*Material:* 2 lots; 1) A left fixed finger, F1679 (locality NMB 18278, PPP 00963), bulldozed area SW of Bella Vista and S and SE of Lomas del Mar, Limón, Limón Province, Costa Rica; Lomas del Mar Reef Member, Moin Formation, Late Pliocene to Early Pleistocene (see McNeill *et al.*, 2000). Collected by P. Jung and others, 09/01/1992. 2) Pereiopod manus, F1680 (locality NMB 19069, PPP 03255), bulldozed site for a container depot, N of Route 32, 1.5 km W of Pueblo Nuevo, Limón, Limón Province, Costa Rica. 'Mollusc mudstone', basal Moin Formation, Late Pliocene. Collected by J. A. Todd and H. Fortunato, 05/02/1998.

*Remarks:* The fixed finger closely resembles that of the larger members of the genus, e.g. *Mithrax caribbaeus* Rathbun, 1920a, and *Mithrax orcutti* Rathbun, 1925 (Mazatlan, Mexico to Panama and West Indies to the northern coasts of South America - Rathbun, 1925) whose fixed fingers have a continuous line of granules around the cupped occludent margin.

Subfamily MAJIINAE Samouelle, 1819

Genus *THOE* Bell, 1836

*Type species:* *Thoe erosa* Bell, 1835 (1836), by monotypy.

*Range:* ?Miocene; Late Miocene (herein) to Recent.

#### ***Thoe asperoides* Collins and Todd sp. nov.**

(Pl. 3, Fig. 7)

*Diagnosis:* Regions well marked and tumid; tubercles on mesogastric, epibranchial, and cardiac lobes.

*Type material:* Holotype, a fragmentary carapace (F1681; figured), (locality NMB 18687; PPP 02188) from the westernmost island comprising Plantain Cays, off Tobabe Point, north side of Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene (late Tortonian–Messinian) (Coates *et al.*, 2003, fig. 6.). Collected by P. Jung, A. Heitz and J. A. Todd, 15/09/1995.

*Attributed material:* A fixed finger (F1682), (locality NMB 18274, PPP 0948) from a bulldozed area for extension of the Lomas del Mar subdivision, SW of Bella Vista and S and SE of Lomas del Mar, Limón, Limón Province, Costa Rica; Lomas del Mar Reef Member, Moin Formation, Late Pliocene–Early Pleistocene. Collected by P. Jung and others, 09/01/1992.

*Derivation of name:* Indicating a likeness to *Thoe aspera* Rathbun, 1900.

*Description:* Only the slight upturned posterior margin is discernable; it curves narrowly round the cardiac region and there is a low node at the right-hand angle. The mesogastric, mesobranchial and cardiac lobes are tumid. The cervical furrow is deep and U-shaped across the midline and extends to the base of the anteromesogastric process before curving towards the margin in two loops. The flask-shaped mesogastric lobe has a blunt tubercle anteriorly, another blunt tubercle occurs anteriorly on the ovoid cardiac region, and there is a smaller one behind in the furrow separating the cardiac from the metabranchial lobe. In contrast, there is a conical one on the epibranchial lobe. Coarse granules crowding the dorsal surface tend to a 'circular' pattern round the cardiac tubercle.

*Thoe vanuaensis* Rathbun, 1945 from the Miocene? of Vanua Mbalavu, Fiji, was described from a partial left chela. A fixed finger, here attributed to *Thoe asperoides*, in the present collection, closely resembles that figured by Rathbun (1945, pl. 57D), but differs in having a more continuous row of granules along the occludent margin and in this respect is close to *Thoe sulcata* Stimpson, 1860, a Recent Caribbean species.

*Discussion:* Although fragmentary, the present specimen retains characters pertaining to *Thoe* sufficient to be included in that genus. There is a particular similarity to *Thoe aspera* in the shape of the mesogastric lobe and course of the cervical furrow, also the tumid mesobranchial lobes and tubercle-bearing cardiac region, together with the secondary tubercles behind and lateral to it, also sufficient remains of the posterior angle node to be compatible.

*Thoe aspera*, presently occurring off Puerto Rico (Rathbun, 1925), lacks the tubercle on the epibranchial lobe.

Subfamily OREGONIINAE Garth, 1958

Genus *HYAS* Leach, 1814

*Type species*: *Cancer araneus* Linné, 1758, by Cmonotypy.

*Range*: Miocene to Recent.

**aff. *Hyas* sp.**

(Pl. 3, Fig. 8)

*Material*: Two right dactyli (one worn) (F1683; figured: F1684), (locality NMB 18490, PPP 01171), from the Chico River about 5 km NE of Comun, Darien Province, Panama; Tuira Formation, Late Miocene (early Tortonian) (Coates *et al.*, 2004b, Map B). Collected by A. G. Coates, 06/05/1993.

*Description*: The proximal height is about half the length, weakly intumed. The upper margin is gently concave; a strong median ridge on the outer surface has four setal pores, a similar number line the concave area between the ridges of the upper margin and five or six line the occludent margin. The occludent margin has a low, linear proximal cusp followed by a row of even-sized granules. A few pores are scattered on either side of a ridge on the inner surface.

*Discussion*: The dactylus has characters in common with that of the Recent *Hyas coarctatus* Leach, 1815 *sensu lato* which has a dactylus length of about four times the height; the groove lining the upper margin and positioning of the setal pores is much the same, but the upper edge of *H. coarctatus* is rounded rather than grooved. A male *H. coarctatus* figured by Rathbun (1925, pl. 96) has a proximal linear cusp on the occludent margin, whereas a right dactylus tentatively ascribed to *Hyas* (as aff. *Hyas*) from the Early Pliocene Bowden shell bed of Jamaica (Collins and Portell, 1998, pl. 1, fig. 7) has a more continuous line of even-sized granules along the occludent margin more consistent with that of a female (Collins, pers. coll.). The present range of *Hyas* in North America is confined to more northerly latitudes, extending from the Bering Sea southwards to Washington State, USA in the East Pacific, and from the North Atlantic (Iceland, Norway) southwards to Cape Hatteras, North Carolina, USA in the West Atlantic (Rathbun, 1925, p. 252; Ingle, 1980).

Superfamily PARTHENOPOIDEA MacLeay, 1838

Family PARTHENOPIIDAE MacLeay, 1838

Genus *PLATYLAMBRUS* Stimpson, 1871

*Type species*: *Lambrus serratus* H. Milne Edwards, 1834; *non Lambrus serratus* White, 1847, by subsequent designation of Rathbun, 1924.

*Range*: ?Miocene to Recent.

***Platylambrus spinulatus* Collins and Todd sp. nov.**

(Pl. 3, Figs. 9, 10)

*Diagnosis*: Propodus: margins a little expanded distally; lower

surface smooth, outer margin with 5 spines separated by spinules, all with spinulated margins.

*Type material*: Holotype, a right propodus (F1685; Pl. 3, Fig. 9), (locality NMB 18080, PPP 00631) from a hill behind the cemetery on Route 32, Pueblo Nuevo, W of Limón, Limón Province, Costa Rica; Moin Formation, Early Pleistocene (see Jackson *et al.*, 1999, p. 212). Collected by P. Jung, R. Panchaud and others, 03/04/1989. 3 paratypes: a right merus and two right dactyli. 1, 2) Two right dactyli (F1686–1687; Pl. 3, Fig. 10a, b), (locality NMB 18373, PPP 01188), the SE coast of Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene. Collected by P. Jung, A. Heitz and others, 02 & 04/08/1993. 3) Right merus (F1688), (locality NMB 18736, PPP 02239) from Punta Nispero, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 25/09/1995.

*Derivation of name*: With reference to spinules lining major spines.

*Description*: Propodus subtriangular in section, height about one-third the length; margins more or less parallel, becoming only a little expanded at the interdigital margin. Lower surface is smooth, inner margin finely beaded, upper margin with five long spines and three small distal spines curve towards the outer margin. On the outer margin five (proximal three broken) large spines – the distal one overhanging the dactylus – are separated from one another by two spinules; the basal margins of the larger spines are minutely spinulate. The strongly deflexed finger is about one-third the length of the manus; there is a small medial granule on the occludent margin and a smaller one mid-distance from the tip.

Right dactylus moderately curved, length about half proximal height; outer surface with broad triangular elevation bounded by a chamfered surface to upper and occludent margins. Basal scars indicate two strong proximal spines between several smaller ones on upper margin, a spine before mid-length followed by spinules. The occludent margin is lined with more or less even-sized, or alternate large and small cusps. The inner surface is flattened.

Right merus, although about twice the size of the propodus, agrees with it in relative length/width proportions. Subtriangular in cross-section, highest at about mid-length. Basal surface flat, basal margin granulated. The outer surface is smooth, its upper margin coarsely granulate; the upper surface is angled by a conspicuous row of short, sharp to bluntly rounded, conical granules, the margin is lined with flattened spines, the proximal three broken, probably small, followed by a large, three small, a large and three alternately large and small spines – all with finely spinulate margins.

*Discussion*: Both the merus and propodus of *P. spinulatus* appear to share characters with the Recent *Platylambrus pourtalesii* (Stimpson, 1870) (eastern Caribbean) and the more widespread *Platylambrus serratus* (H. Milne Edwards, 1834). The alternate arrangement of marginal spines is more obvious in *P. pourtalesii*, which in that species have spinulate edges, and the fixed finger is

rather more sharply deflected than that of *P. serratus*. The upper dactyl margin of *P. pourtalesii* is broader and spinulate, rather than smooth as in *P. spinulatus*.

Superfamily PORTUNOIDEA Rafinesque, 1815

Family PORTUNIDAE Rafinesque, 1815

Subfamily PORTUNINAE Rafinesque, 1815

Genus *PORTUNUS* Rafinesque, 1815

*Type species*: By subsequent designation of Rathbun, 1926; *Cancer pelagicus* Linné, 1758 [ICZN Opinion 394]; from Recent, type locality not known. The International Commission of Zoological Nomenclature in reaching its decision on the type species appears to have overlooked the selection by H. Milne Edwards (July 1840) of *Portunus puber* (Linné, 1767).

Range: ?Miocene; Middle/Late Miocene (herein) to Recent.

***Portunus gabbi* Rathbun, 1919b**

(Pl. 4, Fig. 3)

1919b *Portunus gabbi* Rathbun, p. 172, pl. 13, figs. 2–7; pl. 6, figs. 1, 2.

*Holotype*: Female carapace, ANSP 2256.

*New material*: Three fragmentary propodi: 1) F1689 (figured), (locality NMB 18534, PPP 01138), Río Tuquesa, between Charco Chivo and Marragantí village, Darien Province, Panama; Tuira Formation, Middle–Late Miocene (late Serravillian/early Tortonian) (Coates *et al.*, 2004a, figs. 5, 7). Collected by A. G. Coates and J. B. C. Jackson, 04/05/1993. 2) F1690, (locality NMB 18714, PPP 02215) from NW end of Cayo Toro, off W side of Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene (late Tortonian–early Messinian) (see Coates *et al.*, 2003, fig. 6.). Collected by P. Jung, A. Heitz, J. A. Todd, J. B. C. Jackson and H. Fortunato, 19/09/1995. 3) F1691, (locality NMB 17477, no PPP number) Bomba on the Río Banano, Limón Province, Costa Rica; Rio Banano Formation, early Late Pliocene. Collected by P. Baumgartner and students, June 1982.

*Remarks*: The new material conforms well with figures of *Portunus gabbi* (Rathbun, 1919b, pl.13, figs. 2–7; pl. 6, figs. 1, 2) from probable Miocene deposits of the Dominican Republic and considerably increases the geographical and stratigraphical range of the species.

While superficially similar to *P. gabbi*, propodi of *Euphylax maculatus* differ in having a sharper ridged and straight, lower margin, the ridge continuing along the fixed finger where it is bounded by a groove, and the lower surface is granulated. The basal surface of the fixed finger is flatter and the occludent margins are tricuspid. The propodi of *Necronectes proavitus* (as *Gatunia*) (Rathbun, 1919a) are devoid of longitudinal ridges.

***Portunus (Achelous) cf. tenuis* Rathbun, 1919b**

(Pl. 3, Fig. 11)

cf. 1919b *Portunus tenuis* Rathbun, p. 173, pl. 7, fig. 7.

*Holotype*: A fixed finger, USNM 324478.

*New material*: Distal portion of a right chela (F1692), (locality NMB 18074, PPP 00613), from Río Rabo de Puerca, Burica Peninsula, Chiriqui Province, Panama; Armuelles Formation, Pleistocene. Collected by P. Jung, R. Panchaud and others, 22/01/1989.

*Remarks*: The new material not only extends the probable range of this species from the Early Miocene of the Dominican Republic to the Pleistocene of the Pacific coast of Panama but also, if conspecific, permits description of the dactylus and distal part of the propodus. The present fixed finger is about three times the size of the holotype; there is a minor difference in the shape of the 2<sup>nd</sup> proximal cusp, which in the Pleistocene material is about twice the length and where there are fewer large granules prior to the median ridge, the inter-ridge area is minutely granulate; otherwise the ‘squamous spines’ extend along the basal ridge as depicted by Rathbun (1919b, pl. 7, fig. 7).

The distal part of the propodus indicates the lowest ridge on the outer surface of the fixed finger to be extended, and the upper ridges to continue as weak granular rows. The interdigital margin is concave and there is an oval plate under the articulating facet. A sharp spine on the upper margin overhangs the dactylus. On the inner surface, granules line the median ridge, those lining the lower margin become denser. The incurving dactylus is virtually an image of the fixed finger without granules; a large, posteriorly directed cusp on the occludent margin precedes tridentate cusps engaging with those on the fixed finger.

The new material supports Rathbun’s comparison of *P. tenuis* with *Portunus spinimanus* Latreille, 1819 – a rare eastern Caribbean Recent species – in which the distal propodal spine is set further back. Rathbun (1930, p. 67) referred to age variation in *P. (A.) spinimanus* and this may account for the slight differences in the fossil forms.

Subfamily PODOPHTHALMINAE Dana, 1851

Genus *EUPHYLAX* Stimpson, 1860

*Type species*: *Euphylax dovii* Stimpson, 1860, by monotypy.

Range: Eocene to Recent.

***Euphylax maculatus* Collins and Todd sp. nov.**

(Pl. 3, Figs. 12–14; Pl. 4, Fig. 1)

*Diagnosis*: Carapace subhexagonal with deep corneal depressions; upstanding outer orbital spines larger than any of 4 pairs of anterolateral spines, 4<sup>th</sup> pair largest, directed forwards; a weak epigastric ridge and stronger, almost transverse epibranchial ridge. Homochelate, fingers flattened, tricuspid, dactylus ridged medially, fixed finger ridged along basal margin.

*Type material*: Holotype: a carapace retaining parts of both chelipeds (F1693; Pl. 3, Fig. 12), (locality NMB 18671, PPP 02172) from the NW coast of Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, Late Pliocene. Collected by J. A. Todd, 12/09/1995.

7 paratypes: 4 carapaces, 2 right propodi and 1 broken fixed fin-

ger; 1–3) 3 carapaces with limb fragments, preserved in sandstone nodules, one showing underside (F1694: figured, Pl. 3, Fig. 13; F1695 1–2), (locality NMB 18535, PPP 1138), Río Tuquesa, between Charco Chivo and Marragantí village, Darien Province, Panama; Tuira Formation, Middle–Late Miocene (late Serravillian/early Tortonian) (Coates *et al.*, 2004a, figs. 5, 7). Collected by A. G. Coates and J. B. C. Jackson, 04/05/1993. 4) Right propodus (Pl. 3, Fig. 14) PI IC 444, (JT-98-2-PJ, no PPP number), float from bulldozed surface at Las Lomas Suites, 1.2 km SW of Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene. Collected by P. Jeffery, 08-11/08/1998. 5) Broken right propodus (F1696), (locality NMB 18734, PPP 02237) from 300 m WNW of Punta Piedra Roja, SE coast of Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene to early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 24/09/1995. 6) Carapace preserving underside and limb fragments carapace (Pl. 4, Fig. 1), PI IC 445, (no PPP number), Punta Norte, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene. Collected by J. A. Todd, 06/02/1998. 7) Broken fixed finger (F1697), (locality NMB 17471, PPP 1738) from Playa Cocalito, SE coast of Nicoya Peninsula, ENE of Montezuma village, Puntarenas Province, Costa Rica; Montezuma Formation, Early Pleistocene (see Coates *et al.*, 1992, p. 819). Collected by P. Jung, P. Baumgartner and C. Mora, 12/04/1984.

*Other material:* 3 lots: 1) 6 propodus and fixed finger fragments PI IC 446–451, (JT-98-2-PJ, no PPP number), float from bulldozed surface at Las Lomas Suites, 1.2 km SW of Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene. Collected by P. Jeffery, 08-11/08/1998. 2) A broken fixed finger (F1698), (locality NMB 18732; PPP 02235), Punta de Tiburón, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 23/09/1995. 3) A broken fixed finger, F1699, (locality NMB 18671, PPP 02172) from NW coast of Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, Late Pliocene. Collected by J. A. Todd and A. Heitz, 12/09/1995.

*Questionably assigned material:* Juvenile? dactylus, F1700, (locality NMB 17835; PPP 00362); north-central coast of Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, Late Pliocene. Collected by P. Jung and A. G. Coates, 04/06/1988.

*Derivation of name:* From the spotted preservation on some specimens suggesting colour preservation.

*Description:* Carapace transversely subovate, length about two-thirds the width (taken anterior to lateral spines), gently arched transversely, in longitudinal section it rises to rounded protogastric lobes, becomes almost flat medially and slopes down to the posterior margin; cardiac and branchial regions highest and tumid. The orbitofrontal margin occupies almost the entire carapace width; the rostrum is broad, T-shaped and deeply constricted at its base.

Granulated upper orbital margins, gently curved for three-fourths of their length, are sharply deflected into deep corneal depressions and terminate in a strong, upstanding triangular spine. The fore-edge of the well-advanced suborbital margin is sharp and deeply deflected under; its upper surface is granulated and the peduncular cavity is rather narrow. Almost straight anterolateral margins are much shorter than sinuous posterolateral margins that converge by shallow coxigeal embayments to a gently rounded, finely ridged and beaded posterior margin. The first of 4 pairs of anterolateral spines is the smallest and emerges from the base of the outer orbital spine. Triangular, even-sized 2<sup>nd</sup> and 3<sup>rd</sup> spines are apically hooked forwards, their base occupying the median third between the outer orbital spine and the more strongly hooked spine at the lateral angle which terminates in a thin, but conspicuous epibranchial ridge. A fine, steep-fronted epigastric ridge (more obvious in younger specimens) crossing the anteromesogastric process inclines laterally forwards. The epibranchial ridge is bounded distally by a double row of granules and progresses medially and forwards. The hepatic, mesogastric and lateral parts of the metabranchial lobes are depressed, other lobes weakly tumid.

Triangular male sternites 1–2 are almost vertically inclined between the third maxillipeds, becoming spinose apically, thickened medially and along the basal margin; steep-fronted, sub-hexagonal 3<sup>rd</sup> sternites are weakly concave anteromedially, the sides sloping back to a shallow notch before elevated subcircular anterolateral corners of 4<sup>th</sup> sternites; anteromedial margin of 4<sup>th</sup> sternites straight, bounded by an oblique chamfered ridge. Peltoid 5<sup>th</sup>–8<sup>th</sup> sternites are each embraced by episternites. The dorsal surface is densely and evenly pitted. Little is known of the carpus except for a long spine at the inner distal angle. Distal height of right manus almost two-thirds the length, reducing to about half proximally. Upper and lower margins are gently convex with just a slight indentation before the fixed finger. Of four ridges on the outer surface, the second is coincident with that on the dactylus and the third with the occludent margin of the fixed finger; the fourth runs along the basal margin and fixed finger. The fixed finger is slightly longer than the manus, the occludent margin being similar to that of the dactylus. On the inner surface, a short, weak ridge parallel to the upper margin terminates in a spine; the median ridge is possibly spinose and a weak basal ridge extends to the fixed finger. The lower edge is flatly oblique. Right dactylus sharp along the upper margin; a sharp ridge extends the length of the outer surface; the inner surface is concave. Five or six sets of large tridentate cusps, each set separated by a smaller cusp, line the occludent margin.

*Discussion:* The length/width ratio (61.1 percent) of *E. maculatus* compares favourably with that of the Recent species *E. dovii* (58.3 percent) which has four pairs of weakly developed anterolateral spines and (as far as preservation allows comparison) the upper orbital margin of *E. maculatus* agrees, apart from the beading, with that of *E. dovii*. The latter differs in the absence of an epigastric ridge and a less well-defined epibranchial ridge.

*Euphylax maculatus* has much in common with *Euphylax dominicensis* (Rathbun, 1919b), Miocene of Hispaniola, particularly in the arrangement of the anterolateral spines, but that species differs in having deeper, poorly defined ocular depressions, and a weaker epigastric ridge. Anterolateral margins are not preserved in *Euphylax callinectias* Rathbun, 1919a, from the Río Banano Formation, Early Pliocene (originally dated as Miocene by Rathbun, 1919a) of Río Banano, Costa Rica, that is further distinguished by a broadly curved epigastric ridge and an obscure epibranchial ridge. Closer agreement occurs between the similarly shaped 3<sup>rd</sup> sternites and their union with the 4<sup>th</sup> sternites. *Euphylax fortis* Rathbun, 1919a, also from the Río Banano Formation (again redated to Early Pliocene) of Río Banano, Costa Rica, was described from a single specimen preserving parts of the underside and a cheliped. The union of the 3<sup>rd</sup>/4<sup>th</sup> sternites in this species is distinctly oblique; the ridges crossing the 4<sup>th</sup> sternites are much the same in all three species. With the various discrepancies noted – perhaps due to preservation – it is nonetheless considered prudent to erect *E. maculatus* as a distinct species. A large and robust broken right propodus (F1701; Pl. 4, Fig. 2) from the Río Banano Formation (Late Pliocene) of Río Banano, Costa Rica is much more inflated than that of *E. maculatus* sp. nov. Compared with *E. fortis* Rathbun (p. 167, pl. 64, figs. 11–13), this specimen lacks the basal groove described by Rathbun, whereas for the other Río Banano Formation *Euphylax*, *E. callinectias* Rathbun (p. 165–166), appendages remain unknown. Consequently we identify the new specimen as *Euphylax* sp.

Four pairs of anterolateral spines are present in the youngest known fossil species, *Euphylax fortispinosus* Collins *et al.*, 2001, from the Pleistocene Port Morant Formation of Jamaica and attention was drawn to the similarity of the arrangement of the anterolateral spines with those of *E. dominicensis*. This is reflected in *E. maculatus*, otherwise the disposition of the epigastric and epibranchial ridges readily distinguishes the two species. The remaining Miocene species, *Euphylax septendentatus* Beurlen, 1958, Bahia, Brazil is distinguished by the greater number of anterolateral spines.

The Late Eocene *Euphylax feldmanni* Nyborg *et al.*, 2003 (Washington, USA) is immediately distinguished from *E. maculatus* sp. nov., in having a more angular carapace, a more triangular rostrum with shallower ocular constrictions, an apparent absence of a lower orbital ledge, and robust, smooth chelae, as well as other important characters at variance with other known members of the genus.

Genus *SANDOMINGIA* Rathbun, 1919b

*Type species: Sandomingia yaquiensis* Rathbun, 1919b, by monotypy, from the ?Lower Miocene of Haiti.

*Geologic range:* Miocene to Pliocene.

### *Sandomingia yaquiensis* Rathbun, 1919b

(Pl. 4, Figs. 4, 5)

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

*New material:* 2 specimens; 1) A carapace retaining underside (F1702; Pl. 4, Fig. 4), (locality NMB 18734, PPP 02237) from 300 m WNW of Punta Piedra Roja, SE coast of Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene to early Late Pliocene. Collected by P. Jung, A. Heitz, J. B. C. Jackson and H. Fortunato, 24/09/1995. 2) Cheliped merus fragment (F1703; Pl. 4, Fig. 5), (locality NMB 19069, PPP 03255), bulldozed site for a container depot, N of Route 32, 1.5 km W of Pueblo Nuevo, Limón, Limón Province, Costa Rica. ‘Mollusc mudstone’, basal Moin Formation, Late Pliocene. Collected by J. A. Todd and H. Fortunato, 05/02/1998.

*Remarks:* The male? carapace which is a little smaller (L.: 20.0 mm / W.: 35.0 mm) than the holotype (L.: 23.0 mm / W.: c. 42 mm) from the ?Lower Miocene of Haiti, considerably extends both the geological and geographical range of the taxon, but adds little to the description of the dorsal surface, except it retains an obscure outline of a triangular rostrum continuing the longitudinal curvature of the front. The steep anterior margin of the 3<sup>rd</sup> sternites is weakly concave to vague notches near weakly produced, slightly elevated, rounded outer angles of subtrapezoidal 4<sup>th</sup> sternites. The 5<sup>th</sup> sternites are peltoid; the 6<sup>th</sup>, subrectangular, with a sigmoidal basal margin and the reniform 7<sup>th</sup> sternites emphasises this outline. The abdominal trough extends to the 3<sup>rd</sup> sternites where there is a weak transverse depression. The telson is as long as the 6<sup>th</sup> somite; 4<sup>th</sup> & 5<sup>th</sup> and possibly 3<sup>rd</sup> somites are fused. Coarse, even sized punctae crowd the 4<sup>th</sup>–6<sup>th</sup> sternites, other sternites are almost smooth.

The depressed, steep fronted 3<sup>rd</sup> sternites, partly embraced by the 4<sup>th</sup> sternites of *S. yaquiensis* closely resemble the corresponding members of *Euphylax* species. However, the anterior margin of the three Panamanian/Costa Rican species *Euphylax fortis*, *Euphylax callinectias*, and *Euphylax maculatus*, is extended beyond the rounded lateral angles of the 4<sup>th</sup> sternites, rather than more or less in line as in *Sandomingia*, in which the 3<sup>rd</sup> sternites are not so steeply depressed. The oblique 3<sup>rd</sup> sternites and undivided 4<sup>th</sup> sternites of *S. yaquiensis* are closer to those of *E. callinectias*.

The merus, described by Rathbun (1919b, p. 180) as being, “triangular in section, upper surface concave, smooth, posterior and inferior margins blunt and granulate, anterior margin subacute and furnished with tubercles of varying size arranged in two irregular rows”, agrees in all respects with a (?left) meral fragment from the basal Moin Formation (Late Pliocene) of Costa Rica, albeit the tubercles being largely represented by basal scars.

There is a superficial resemblance to the left merus of *Parthenope panamensis* Rathbun, 1919a (p. 178; pl. 66, figs 10, 11) from the Emperador Limestone Member, Culebra Formation (Oligocene) of Las Cascadas section, Panama Canal, which is described as being quadrilateral in cross section, whereas that of the present fragment is distinctly rounded triangular.

Family XANTHIDAE MacLeay, 1838

Genus *HETERACTAEA* Lockington, 1876(1877)

*Type species: Heteractaea pilosus* Lockington = *H. lunata* A. Milne Edwards and Lucas, 1843, by original designation.

*Range:* Late Pliocene (herein) to Recent.

***Heteractaea lunata* (A. Milne Edwards and Lucas, 1843)**

(Pl. 4, Fig. 6)

1919a *Heteractaea lunata* (A. Milne Edwards and Lucas); Rathbun, p. 171, pl. 63, figs. 7–9.

1930 *Heteractaea lunata* (A. Milne Edwards and Lucas); Rathbun, p. 532 (see also for synonymy), pl. 214, figs. 1–3.

*New material:* 3 right fixed fingers: 1, 2) F1704 1–2, (locality NMB 17840, PPP 00368), N coast of Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, early Late Pliocene. Collected by P. Jung and A. G. Coates 04/06/1988. 3) F1705 (figured), (locality NMB 18274, PPP 00948), a bulldozed area for extension of the Lomas del Mar subdivision, SW of Bella Vista and S and SE of Lomas del Mar, Limón, Limón Province, Costa Rica; Lomas del Mar Reef Member, Moin Formation, Late Pliocene–Early Pleistocene. Collected by P. Jung and others, 09/01/1992.

*Remarks:* Hitherto described as fossil from a partial propodus and dactylus (USNM 324265) from the “Port Limon formation. Pliocene series” (Rathbun, 1919a, p. 171), now known as the Moin Formation of Late Pliocene to Early Pleistocene age (Coates *et al.*, 1993; McNeill *et al.*, 2000), of Limón, Costa Rica, the attributed fixed fingers agree with the Recent specimen figured by Rathbun, 1919a (pl. 63, fig. 9). The larger size of the figured specimen is more in keeping with the specimens figured by Rathbun, 1930 (pl. 214, figs. 1–3). Today, this species is confined to the East Pacific (Rathbun, 1930).

Family PLATYXANTHIDAE Guinot, 1977

Genus *PLATYXANTHUS* A. Milne Edwards, 1863

*Type species: Xantho orbignyi* H. Milne Edwards and Lucas, 1844, by original designation.

*Range:* Late Miocene (herein) to Recent.

***Platyxanthus* sp.**

(Pl. 4, Figs. 8, 9)

*Material:* 3 specimens; 1) Left fixed finger (F1706), (locality NMB 18690, PPP 02191), S of Nancy Point, W side of Valiente Peninsula, Bocas del Toro Province, Panama; Nancy Point Formation, Late Miocene (Messinian). Collected by P. Jung, A. Heitz, J. A. Todd, J. B. C. Jackson and H. Fortunato, 16/09/1995. 2) Right dactylus (F1707; Pl. 4, Fig. 9), (locality NMB 19069, PPP 03255), N of Route 32 and N of a bulldozed site for a container depot, 1.5 km west of Pueblo Nuevo, Limón, Limón Province, Costa Rica; ‘Mollusc mudstone’, basal Moin Formation, Late Pliocene. Collected by J. A. Todd and H. Fortunato, 05/02/1998. 3)

A right propodus lacking extremity of fixed finger (F1708; Pl. 4, Fig. 8) and a carpus fragment (F1709), (locality NMB 18080, PPP 00631) from a hill behind the cemetery on Route 32, Pueblo Nuevo, W of Limón, Limón Province, Costa Rica; Moin Formation, Early Pleistocene (see Jackson *et al.*, 1999, p. 212). Collected by P. Jung, R. Panchaud and others, 03/04/1989.

*Remarks:* Tentatively identified from the Miocene of the Dominican Republic (Collins, pers. obs.), this genus is new to the fossil record of Costa Rica and Panama. The propodus closely resembles that of Recent *Platyxanthus* species in length/height proportions (L.:17.00 mm; H.:13.3 mm); the slight proximal curvature of the upper margin and weak inflection before the fixed finger; the pit-lined groove extending onto the fixed finger and the weakly concave plate below the articulating facet of the dactylus, are particularly reminiscent of the Recent Western Atlantic species *Platyxanthus crenulatus* A. Milne Edwards, 1873 which ranges from Uruguay to Patagonia. The proposed geminate species to this, *Platyxanthus cokeri* Rathbun, 1930 from the Caribbean, has the fixed finger inclined to the manus basal margin.

? Family PILUMNIDAE Samouelle, 1819

Genus *EURYTIUM* Stimpson, 1859

*Type species: Cancer limosa* Say, 1818, by monotypy.

*Range:* Late Pliocene (herein) to Recent.

***Eurytium crenulatum* Rathbun, 1919a**

(Pl. 4, Figs. 10, 11)

1919a *Eurytium crenulatum* Rathbun, p. 174, pl. 64, fig. 8 (*non* fig. 9 = *Callianassa* sp., p. 183).

*Holotype:* A right dactylus, USNM 324253.

*Remarks:* This species was originally founded on a right dactylus of Pleistocene age from near Mount Hope, Colón, Panama (Caribbean coast). A partial carapace and additional chelae parts so resemble the Recent species referred to by Rathbun (1919a) in connection with *E. crenulatum*, that given their geographical and temporal proximity we consider them to be conspecific.

*Diagnosis:* Carapace moderately convex, front slightly in advance of external orbital angle; a transverse sinus separating epigastric lobes from smooth frontal region.

*New material:* 2 specimens: 1) Right dactylus (F1710; Pl. 4, Fig. 11), (locality NMB 17455, PPP 01735), Quitaría, 2.3 km S of railway bridge over Río Banano at Bomba, Limón Province, Costa Rica; lower part of Río Banano Formation, late Early Pliocene (Coates, 1999a, text-fig. 6; Aubry and Berggren in Coates, 1999a, p. 40). Collected by P. Jung, 06/08/1984. 2) A partial carapace (F1711; Pl. 4, Fig. 10), (locality NMB 19069, PPP 03255), N of Route 32, N of a bulldozed site for a container depot, 1.5 km W of Pueblo Nuevo, Limón, Limón Province, Costa Rica; ‘Mollusc mudstone’, basal Moin Formation, Late Pliocene. Collected by J. A. Todd and H. Fortunato, 05/02/1998.

*Remarks:* The figure numbers given by Rathbun, 1919a, relating to plate 64 are not represented on the legend on p. 183; no mention

is made to fig. 8, and fig. 9 is referred to *Callianassa* sp.

The tip of the right dactylus, F1710, is broken, the position of the basal cusp agrees with that of type material, as does the larger size of the succeeding 2<sup>nd</sup> and 4<sup>th</sup> cusps in relation to the distal ones, of which three or four remain. The attributed carapace has much in common with *Eurytium tristani* Rathbun, 1906 (*vide* 1930, pl. 176) and *Eurytium limosus* Say, to both of which species Rathbun referred in her description of *E. crenatum*.

**Description:** Carapace length about two-thirds of width, moderately arched in longitudinal section and rather flatter transversely. The orbitofrontal margin takes up about five-sixths of the carapace width and of this, the weakly produced front occupies the median third. The front is gently convex either side of a V-shaped median notch; the inner orbital angle curves sharply down to the upper orbital margin which terminates in a sharp angle, rather than a spine, almost level with the base of the front. The raised orbital margin is emphasized by a groove extending from close to the inner orbital angle. The margin from the outer orbital angle is weakly concave to the first, largest, of four equidistant, upwardly directed, blunt, triangular spines; the smallest spine (broken) is at the lateral angle. Regions and lobes well defined; the median notch continues as a sinus and divides to embrace the tip of a tapering anteromesogastric process extending as far as a shallow depression bounding the epigastric lobes. The cervical furrow, faint and straight across the midline, turns sharply forwards to the angle of the mesogastric lobe, runs forwards and outwards to the union with the hepatic furrow and curves round a weak prominence on the epigastric region. The hepatic furrow continues to the orbital margin. The hepatic lobe, rather more tumid than the proto-gastric, has a weak tumidity opposite the third anterolateral spine. Dorsal, frontal and lateral areas extending onto the spines are minutely granulated.

**Discussion:** The orbitofrontal margin of *E. crenatum* is almost identical with that of the Recent East Pacific species *Eurytium tristani* Rathbun, 1906 (*vide* 1930, pl. 176) which otherwise differs in having flatter anterolateral spines and a shorter, parallel sided anteromesogastric process. The carapace of *Eurytium limosum* Say, 1818, tentatively recorded from the Pliocene of Jamaica (Collins and Portell, 1998), differs in having a straighter front with less deeply incised orbits, and a greater width/length ratio.

The Recent distribution of *E. tristani* ranges from Costa Rica to Peru, and that of the Western Atlantic species *E. limosum* from New York, Bermuda, and Bahamas to São Paulo State, Brazil (Rathbun, 1930).

Family PANOPEIDAE Ortmann, 1893

Genus PANOPEUS H. Milne Edwards, 1834

**Type species:** *Panopeus herbstii* H. Milne Edwards, 1834. ICZN Opinion, p. 10, 1282, 1924.

**Range:** Early Eocene to Recent.

***Panopeus cf. chilensis* H. Milne Edwards and Lucas, 1844**

(Pl. 4, Fig. 7)

*cf.* 1930 *Panopeus chilensis* H. Milne Edwards and Lucas; Rathbun, p. 346, pl. 158, fig. 3; pl. 160, figs. 1–3 (see also for previous synonymy).

**Type material:** 3 co-types (=syntypes): USNM 20264, NMNH and ANSP, all from Chile.

**New material:** A right fixed finger (F1712; figured), (locality NMB 18372, PPP 01995) from Swan Cay, 1.7 km north of Isla Colón, Bocas del Toro Province, Panama; Swan Cay Formation, Early? Pleistocene. Collected by P. Jung, A. Heitz, J. Schneider and H. Noda, 01 or 06/08/1993.

**Remarks:** This robust fixed finger closely resembles that of Rathbun's figure (1930, pl. 160, fig. 1) of a male major cheliped, belonging to an individual a little smaller than the present specimen. The proximal part of the occludent margin is eroded, but sufficient remains distally to show rounded cusps before a smooth, hooked tip. If this specimen belongs to the Recent East Pacific species *Panopeus chilensis*, which ranges from Sinaloa, Mexico southwards to Chile (Rathbun, 1930), then this Caribbean specimen will represent its first fossil record. Rathbun (1919a, p. 174) discussed *Panopeus chilensis* when describing a distinct species represented by a right dactylus and identified as *Panopeus* sp., from the Oligocene Culebra Formation of the Panama Canal.

Genus LOPHOPANOPEUS Rathbun, 1898

**Type species:** *Xantho bella* Stimpson, 1860 by original designation.

**Range:** Miocene to Recent.

***Lophopanopeus maculoides* Collins and Todd sp. nov.**

(Pl. 4, Figs. 12–14)

**Diagnosis:** Carapace rounded hexagonal, front slightly produced with median notch; 2<sup>nd</sup> and 3<sup>rd</sup> anterolateral spines larger than 1<sup>st</sup> and 4<sup>th</sup>, dorsal and particularly lateral areas and spines densely granulated.

**Type material:** Holotype: a fragmentary carapace (F1713; Pl. 4, Fig. 12), (locality NMB 19069, PPP 03255), N of Route 32, N of a bulldozed site for a container depot, 1.5 km W of Pueblo Nuevo, Limón, Limón Province, Costa Rica; 'Mollusc mudstone', basal Moin Formation, Late Pliocene. Collected by J. A. Todd and H. Fortunato, 05/02/1998.

**Attributed material:** Two left articulated propodi (one figured, F1714; Pl. 4, Fig. 14; other, F1715) and one right articulated propodus (F1716; Pl. 4, Fig. 13) with same collection details as holotype.

**Derivation of name:** Indicating a likeness to the Recent *Lophopanopeus maculatus* Rathbun, 1898.

**Description:** Carapace rounded hexagonal, length (c. 8.8 mm) about four-fifths of width (c. 10.8 mm) between 3<sup>rd</sup>/4<sup>th</sup> spines. The front is straight, slightly produced with a shallow median notch, the outer angles almost uninterrupted into weakly sinuous, upturned, upper orbital margins, damaged medially, allowing clear

view of only one notch near a truncated outer orbital spine. Lateral to the spine, the margin is slightly concave to the 1<sup>st</sup> (broken) anterolateral spine. Frontal, orbital margins and margin to 1<sup>st</sup> anterolateral spine are finely beaded. 1<sup>st</sup> anterolateral margin spine with a long, straight, margin leading to a u-shaped notch before 2<sup>nd</sup> spine. Equal sized 2<sup>nd</sup> and 3<sup>rd</sup> spines are triangular, rounded in section and separated by a rounded v-shaped notch; base of 4<sup>th</sup> spine indicates it to have been half that of 3<sup>rd</sup>.

Regions moderately delineated, a shallow sinus runs back from the frontal notch across a narrow postfrontal depression and divides behind slightly tumid protogastric lobes at the tip of the parallel-sided anteromesogastric process. A transverse ridge fronting the protogastric lobes is well developed as a cast on the left hand side. The cervical furrow curves to its junction with an obscure hepatic furrow, then curves sharply round a tumid hepatic region to the margin. A short, almost parallel, depression runs between the 3<sup>rd</sup> and 4<sup>th</sup> spines and isolates a narrow epibranchial lobe; the mesobranchial lobe is tumid. Granules covering the dorsal surface become larger and denser in the lateral areas and over the anterolateral spines.

The attributed left and right carpi and propodi are robust, the left the major. Carpus about as long as high with a distal groove, the right has two distal spines on the upper margin. Distal height of propodus about three-fourths the length; the right proportionally thinner in section. The lower margin has a distinct depression before the fixed finger. Surface densely granulated, with a row of coarser granules along the upper margin. Fixed finger about half the length of the manus; a ridge, granulated on the left, extends slightly onto the manus. Remains of an arched right dactylus indicate a gape between the fingers.

*Discussion:* The carapace has much in common with that of the Recent East Pacific species *Lophopanopeus maculatus*. The frontal margin of *L. maculoides* is slightly produced and straighter than depicted for *L. maculatus* by Rathbun (1930, fig. 51) and more closely resembles the figure included in Hickmann and Zimmermann (2000, p. 113). No mention is made by Rathbun (1930) of prominent dorsolateral granular ornament in the Recent species.

The genus has been tentatively identified from the Miocene Cercado Formation of the Dominican Republic (Collins, pers. obs.). Both of the Oligocene species described from Alaska, *Lophopanopeus olearis* Rathbun, 1926 and *Lophopanopeus baldwini* Kooser and Orr, 1973, were referred to *Panopeus* by Schweitzer, 2000.

Genus *MICROPANOPE* Stimpson, 1871

*Type species:* *Micropanope scultipes* Stimpson, 1871, by original designation.

*Range:* Pliocene to Recent.

**cf. *Micropanope* sp.**

(Pl. 4, Fig. 15)

*Material:* 5 specimens; 1–3) Three finger fragments (F1626 1–3), (locality NMB 17841, PPP 00365), NE coast of Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, early Late Pliocene. Collected by P. Jung and A. G. Coates, 04/06/1988. 4) Right propodus (F1627), (locality NMB 19069, PPP 03255), N of Route 32, N of a bulldozed site for a container depot, 1.5 km W of Pueblo Nuevo, Limón, Limón Province, Costa Rica; ‘Mollusc mudstone’, basal Moin Formation, Late Pliocene. Collected by J. A. Todd and H. Fortunato, 05/02/1998. 5) Left propodus (F1628; figured), (locality NMB 18282, PPP 0949) bulldozed area SW of Bella Vista and S and SE of Lomas del Mar, Limón, Limón Province, Costa Rica; Lomas del Mar Reef Member, Moin Formation, Late Pliocene to Early Pleistocene (see McNeill *et al.*, 2000). Collected by P. Jung, 10/01/1992.

*Remarks:* The left propodus closely resembles that of the right-hand of *Micropanope polita* (Rathbun, 1893, pl. 80, figs. 3, 4) in having granules lining the entire length of the upper margin and rounded cusps on the occludent margin, which in F1628 is convex. There is also a considerable difference in size – Rathbun’s (1930, pl. 180, figs. 4, 5) being about half that of F1628. *Micropanope* aff. *nuttingi* (Rathbun, 1898) and *Micropanope* aff. *spinipes* A. Milne Edwards, 1880, on which granules are confined to the distal part of the upper margin, have been recorded by Collins and Portell, 1998 from the Early Pliocene Bowden shell bed of Jamaica, and *Micropanope* cf. *polita* from the Pleistocene Falmouth Formation (Morris, 1991) of the same island.

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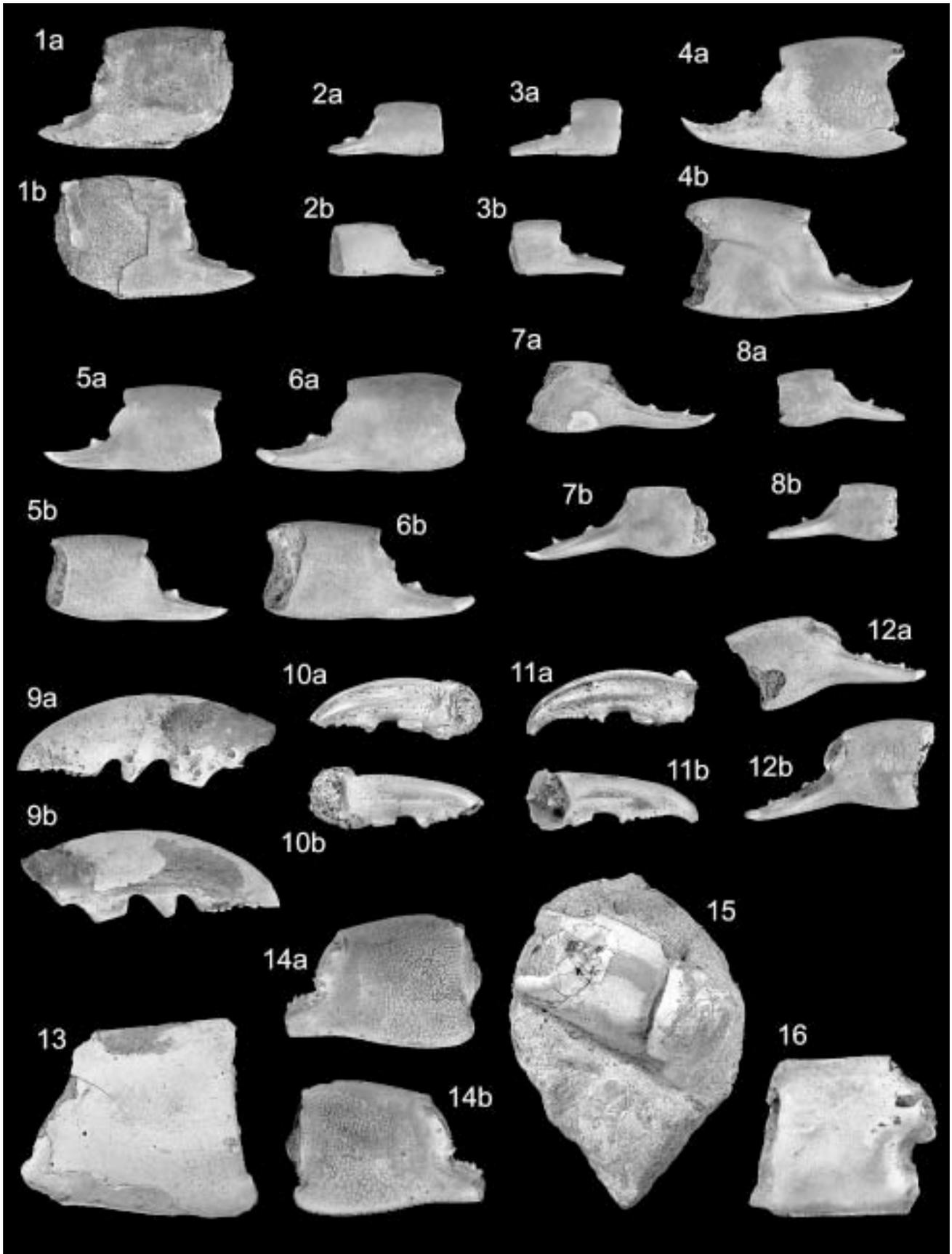
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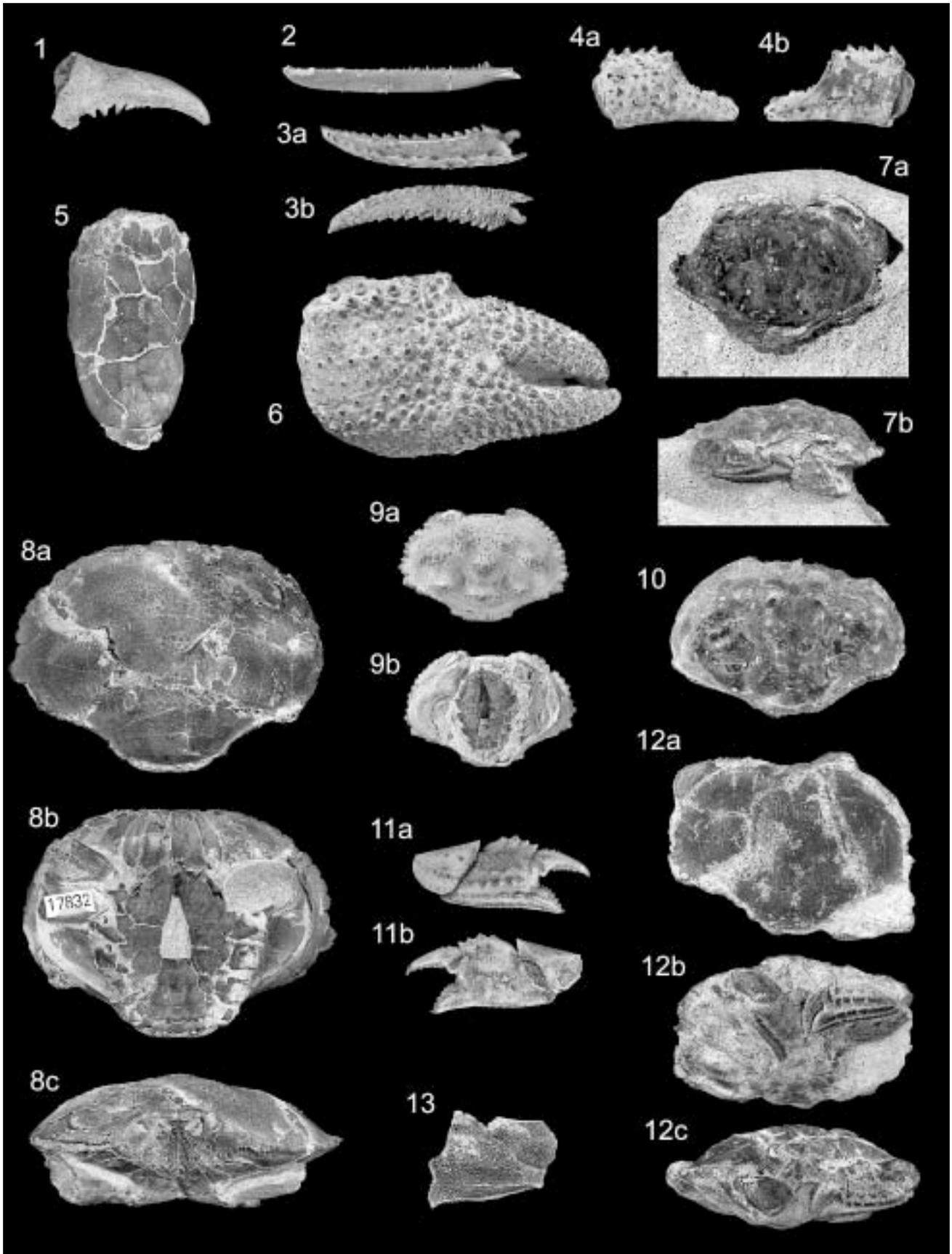
## Plate 1

- Fig. 1. *Glypturus toulai* (Rathbun). BMNH PI IC 395, no PPP number; Las Lomas Suites, near Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene; left propodus; a, outer; b, inner surface,  $\times 1.5$
- Figs. 2–8. *Callianassa moinensis* Rathbun. Locality NMB 19069 = PPP 03255, basal Moin Formation, latest Pliocene; 1.5 km west of Pueblo Nuevo, Limón, Costa Rica; Figs. 2 (F1613), 3 (F1614), 4 (F1615), 5 (F1616), 6 (F1617); left propodi; a, outer; b, inner surface. Figs 7, (F1618), 8 (F1619), right propodi; a, outer; b, inner surface, all  $\times 2$ .
- Fig. 9. *Neocallichirus scotti* (Brown and Pilsbry). NMB F1632; locality NMB 18541 = PPP 01163, Tuirá Formation, early Late Miocene; near Boca de Tigre, Río Chico, Darien Province, Panama; left dactylus; a, outer; b, inner surface,  $\times 1.5$ .
- Figs. 10–12. *Callianassa moinensis* Rathbun. Locality NMB 19069 = PPP 03255, basal Moin Formation, latest Pliocene; 1.5 km west of Pueblo Nuevo, Limón, Costa Rica; Figs. 10 (F1621); 11 (F1622); left dactyli; a, outer surface; b, inner surface; both  $\times 2.8$ . Fig. 12 (F1620), right propodus; a, outer; b, inner surface,  $\times 2$ .
- Fig. 13. *Neocallichirus scotti* (Brown and Pilsbry). BMNH PI IC 402, no PPP number; Sabanita, Colón Province, Panama; lower Gatun Formation, Middle Miocene; left propodus, outer surface,  $\times 1.5$ .
- Fig. 14. *Neocallichirus scotti* (Brown and Pilsbry). NMB F1634; locality NMB 18737 = PPP 02240; Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene; left propodus, a, outer; b, inner surface,  $\times 1.5$ .
- Fig. 15. *Neocallichirus scotti* (Brown and Pilsbry). BMNH PI IC 401, no PPP number; Sabanita, Colón Province, Panama; lower Gatun Formation, Middle Miocene; left propodus and carpus, outer surface,  $\times 1$ .
- Fig. 16. *Neocallichirus scotti* (Brown and Pilsbry). BMNH PI IC 403, no PPP number, Sabanita, Colón Province, Panama; lower Gatun Formation, Middle Miocene; inner surface of left propodus,  $\times 1$ .



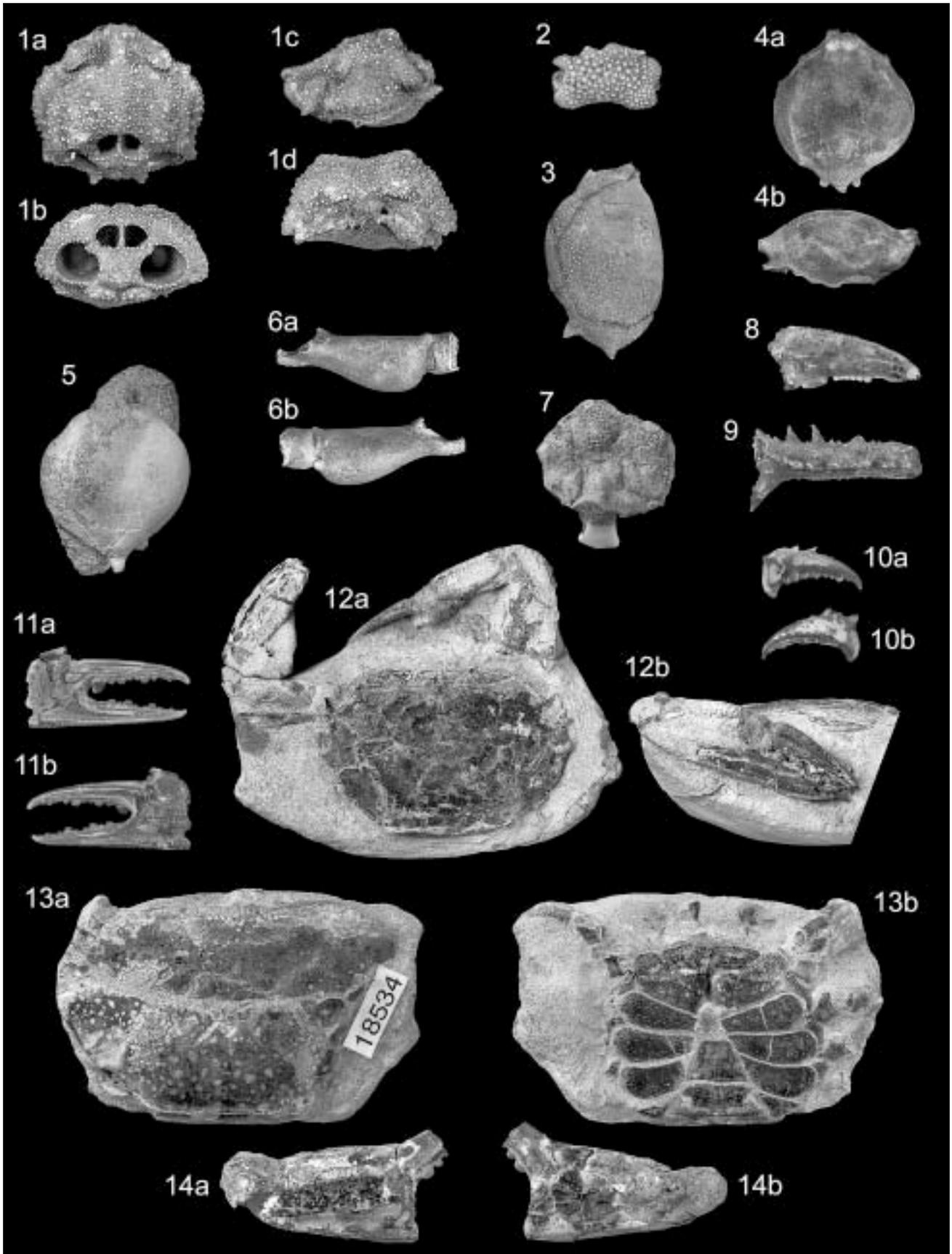
## Plate 2

- Fig. 1. *Neocallichirus scotti* (Brown and Pilsbry). NMB F1629; locality NMB 17638 = PPP 00220; Sabanita, Colón Province, Panama; lower Gatun Formation, Middle Miocene; right dactylus, outer surface,  $\times 2$ .
- Fig. 2. *Ctenocheles falciformis* sp. nov. Holotype. NMB F1637; locality NMB 17830 = PPP 00345; Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene; right fixed finger, inner surface,  $\times 1.5$ .
- Fig. 3. *Dardanus biordines* sp. nov. Paratype. NMB F1645; locality NMB 18373 = PPP 01188; Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene; left 2<sup>nd</sup> pereopod dactylus; a, inner surface; b, outer surface,  $\times 3$ .
- Fig. 4. *Dardanus biordines* sp. nov. Holotype. NMB F1644; locality NMB 18373 = PPP 01188; Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene; right propodus, a, outer; b, inner surface,  $\times 3$ .
- Fig. 5. *Raninoides* cf. *benedicti* Rathbun. NMB F1658; locality NMB 17794 = PPP 00269; Quebrada El Higo, Burica Peninsula, Costa Rica; Armuelles Formation, Early? Pleistocene; dorsal surface,  $\times 1.5$ .
- Fig. 6. *Petrochirus bouvieri* Rathbun. NMB F1646; locality NMB 18987 = PPP 03221, Gobeá, near Miguel de la Borda, Colón Province, Panama; Rio Indio facies, Chagres Formation, Late Miocene; outer surface of right propodus,  $\times 1.5$ .
- Fig. 7. *Hepatus bififormis* sp. nov. Holotype. NMB F1670; locality NMB 18715 = PPP 02216, Cayo Toro, Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene; male carapace; a, dorsal; b, frontal view,  $\times 1$ .
- Fig. 8. *Hepatus lineatinus* sp. nov. Holotype. NMB F1662; locality NMB 17832 = PPP 00358, Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, Late Pliocene; male carapace; a, dorsal; b, ventral; c, frontal views,  $\times 1$ .
- Fig. 9. *Hepatus lineatinus* sp. nov. Paratype. NMB F1667; locality NMB 17784 = PPP 00461, Bomba, Río Banano, Limón, Costa Rica; Rio Banano Formation, Late Pliocene; male carapace; a, dorsal; b, ventral views,  $\times 1.5$ .
- Fig. 10. *Hepatus lineatinus* sp. nov. Paratype. BMNH PI IC 440, no PPP number; Sabanita, Colón Province, Panama; lower Gatun Formation, Middle Miocene; dorsal view of carapace with bopyriform swelling of left branchial region,  $\times 1.5$ .
- Fig. 11. *Hepatus lineatinus* sp. nov. Paratype. NMB F1663; locality NMB 18373 = PPP 01188; Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene; right propodus and articulated carpus; a, outer; b, inner surface,  $\times 2$ .
- Fig. 12. *Hepatus lineatinus* sp. nov. Paratype. BMNH PI IC 442, no PPP number; Las Lomas Suites, near Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene; carapace; a, dorsal; b, oblique ventral; c, frontal views,  $\times 1$ .
- Fig. 13. *Cryptosoma bairdii* (Stimpson). NMB F1660; locality NMB 17630 = PPP 00197; Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, late Early Pliocene; outer view of left propodus and articulated carpus,  $\times 2$ .



### Plate 3

- Fig. 1. *Speleophorus subcircularis* sp. nov. Holotype. NMB F1672; locality NMB 18731 = PPP 02234, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene; carapace; a, dorsal surface elevated slightly forwards to show the orifices; b, rear view; c, left lateral view; d, frontal views,  $\times 1.5$ .
- Fig. 2. *Speleophorus subcircularis* sp. nov. NMB F1673; locality NMB 17471 = PPP 01738, Playa Cocalito, Montezuma, Nicoya Peninsula, Costa Rica; Montezuma Formation, Early Pleistocene; outer surface of an attributed cheliped merus,  $\times 3$ .
- Fig. 3. *Persephona manningi* sp. nov. Holotype. NMB F1676; locality NMB 17838 = PPP 00365, Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, early Late Pliocene, dorsal surface of carapace,  $\times 1.5$ .
- Fig. 4. *Persephona enigmata* sp. nov. Holotype. NMB F1674; locality NMB 17630 = PPP 00197, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene; carapace; a, dorsal; b, left lateral views,  $\times 1.5$ .
- Fig. 5. *Iliacantha panamanica* sp. nov. Holotype. NMB F1677; locality NMB 18687 = PPP 02188, Plantain Cays, Tobabe Point, Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene; carapace lacking orbitofrontal area,  $\times 1.5$ .
- Fig. 6. *Iliacantha* sp. NMB F1678; locality NMB 18401 = PPP 00063, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene; left carpus and associated propodus lacking fixed finger; a, outer surface; b, inner surface,  $\times 3$ .
- Fig. 7. *Thoe asperoides* sp. nov. Holotype. NMB F1681; locality NMB 18687 = PPP 02188, Plantain Cays, Tobabe Point, Valiente Peninsula, Bocas del Toro Province, Panama; Tobabe Sandstone Formation, Late Miocene; dorsal surface of a fragmentary carapace,  $\times 3$ .
- Fig. 8. aff. *Hyas* sp. NMB F1683; locality NMB 18490 = PPP 01171, Chico River, about 5 km northeast of Comun, Darien Province, Panama; Tuira Formation, Late Miocene; right dactylus, outer surface,  $\times 3$ .
- Fig. 9. *Platylambrus spinulatus* sp. nov. Holotype. NMB F1685; locality NMB 18080 = PPP 00631, Pueblo Nuevo, Limón, Costa Rica; Moin Formation, Early Pleistocene; right propodus, inner view,  $\times 3$ .
- Fig. 10. *Platylambrus spinulatus* sp. nov. Paratypes. Locality NMB 18373 = PPP 01188, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene; right dactyli; a, NMB F1686, outer surface; b, NMB F1687, inner surface of another specimen,  $\times 4$ .
- Fig. 11. *Portunus (Achelous)* cf. *tenuis* Rathbun. NMB F1692; locality NMB 18074 = PPP 00613, Río Rabo de Puerca, Burica Peninsula, Chiriquí Province, Panama; Armuelles Formation, Pleistocene; distal portion of right chela; a, outer; b, inner surface,  $\times 1.5$ .
- Fig. 12. *Euphylax maculatus* sp. nov. Holotype. NMB F1693; locality NMB 18671 = PPP 02172, Escudo de Veraguas, Bocas del Toro Province, Panama; Escudo de Veraguas Formation, Late Pliocene; carapace retaining parts of both chelipeds; a, upper surface of carapace; b, frontal view of articulated right propodus,  $\times 0.75$ .
- Fig. 13. *Euphylax maculatus* sp. nov. Paratype. NMB F1694; locality NMB 18535 = PPP 1138, Río Tuquesa between Charco Chivo and Marragantí, Darien Province, Panama; Tuira Formation, Middle–Late Miocene; a, dorsal; b, ventral views of male carapace,  $\times 1.5$ .
- Fig. 14. *Euphylax maculatus* sp. nov. Paratype. BMNH PI IC 444; no PPP number, Las Lomas Suites, near Cativa, Colón Province, Panama; middle Gatun Formation, Late Miocene; right propodus; a, outer; b, inner surfaces,  $\times 1$ .



## Plate 4

- Fig. 1. *Euphylax maculatus* sp. nov. Paratype. BMNH PI IC 445; no PPP number, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, early Late Pliocene; carapace with fragmentary limbs; a, dorsal; b, ventral; c, frontal views,  $\times 0.75$ .
- Fig. 2. *Euphylax* sp. NMB F1701; locality NMB 17479, no PPP number, Bomba, Río Banano, Limón, Costa Rica; Río Banano Formation, early Late Pliocene; right propodus; a, outer surface; b, inner surface,  $\times 1$ .
- Fig. 3. *Portunus gabbi* Rathbun. NMB F1689; locality NMB 18534 = PPP 01138, Río Tuquesa between Charco Chivo and Marragantí, Darien Province, Panama; Tuirá Formation, Middle–Late Miocene; a, outer surface; b, inner surface of right propodus,  $\times 1$ .
- Fig. 4. *Sandomingia yaquiensis* Rathbun. NMB F1702; locality NMB 18734 = PPP 02237, Cayo Agua, Bocas del Toro Province, Panama; Cayo Agua Formation, Early Pliocene to early Late Pliocene; male? carapace; a, dorsal; b, ventral view,  $\times 1.5$ .
- Fig. 5. *Sandomingia yaquiensis* Rathbun. NMB F1703; locality NMB 19069 = PPP 03255, 1.5 km west of Pueblo Nuevo, Limón, Costa Rica; basal Moin Formation, latest Pliocene; partial cheliped merus,  $\times 3$ .
- Fig. 6. *Heteractaea lunata* A. Milne Edwards and Lucas. NMB F1705; locality NMB 18274 = PPP 00948, near Lomas del Mar, Limón, Costa Rica; Lomas del Mar Reef Member, Moin Formation, latest Pliocene–Early Pleistocene; outer surface of right fixed finger,  $\times 3$ .
- Fig. 7. *Panopeus* cf. *chilensis* A. Milne Edwards and Lucas. NMB F1712; locality NMB 18372 = PPP 01995, Swan Cay, 1.7 km north of Isla Colón, Bocas del Toro Province, Panama; Swan Cay Formation, Early? Pleistocene; outer surface of right fixed finger,  $\times 2$ .
- Fig. 8. *Platyxanthus* sp. NMB F 1708; locality NMB 18080 = PPP 00631, Pueblo Nuevo, west of Limón, Costa Rica; Moin Formation, Early Pleistocene; outer surface of right propodus,  $\times 1.5$ .
- Fig. 9. *Platyxanthus* sp. NMB F1707; locality NMB 19069 = PPP 03255, 1.5 km west of Pueblo Nuevo, Limón, Costa Rica; basal Moin Formation, latest Pliocene; right dactylus; a, outer; b, opposing surface,  $\times 1.5$ .
- Fig. 10. *Eurytium crenulatum* Rathbun. NMB 1711; locality NMB 19069 = PPP 03255, 1.5 km west of Pueblo Nuevo, Limón, Costa Rica; basal Moin Formation, latest Pliocene; dorsal view of partial carapace,  $\times 3$ .
- Fig. 11. *Eurytium crenulatum* Rathbun. NMB F1710; locality NMB 17455 = PPP 01735, Quitaría, 2.3 km south of Bomba, Limón, Costa Rica; Río Banano Formation, late Early Pliocene; a) outer; b, inner surfaces of right dactylus,  $\times 3$ .
- Figs. 12–14. *Lophopanopeus maculoides* sp. nov. Locality NMB 19069 = PPP 03255, 1.5 km west of Pueblo Nuevo, Limón, Costa Rica; basal Moin Formation, latest Pliocene. Fig. 12. Holotype; NMB F1713; dorsal view of partial carapace,  $\times 4$ . Fig. 13. NMB F1716; right cheliped; a, outer; b, inner surface,  $\times 3$ . Fig. 14. NMB F 1717; left cheliped, inner surface,  $\times 3$ .
- Fig. 15. cf. *Micropanope* sp. NMB F1628; locality NMB 18282 = PPP 0949; near Lomas del Mar, Limón, Costa Rica; Lomas del Mar Reef Member, Moin Formation, Late Pliocene to Early Pleistocene; a, outer; b, inner views of left propodus,  $\times 3$ .

