Fossil hermit and land crabs (Decapoda: Anomura, Brachyura) from the Quaternary of Antigua and Bermuda

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(Received 31 August 2016; accepted 17 November 2016)

ABSTRACT
Uncatalogued fossil crabs from Antigua and Bermuda deposited in the Department of Paleobiology, Smithsonian Institution, National Museum of Natural History (USNM) includes the remains of the hermit crab Coenobita Latreille, 1829 and the land crabs Gecarcinus Leach, 1814 and Cardisoma Latreille, in Latreille, Le Peletier, Serville & Guérin, 1828. Fossil remains of terrestrial crabs are uncommon in the fossil record due to a number of preservation biases, thus, even isolated or fragmentary, their fossils aid in our understanding of the evolution and geographic distribution of these taxa through time. The remains of Cardisoma and presumably Gecarcinus from the late Pleistocene of Bermuda represent the first record of fossil crustaceans from the island, and one of the only fossil records of the genera known to date, whereas the fossil hermit crab remains from the Holocene of Antigua represent the second record of fossil Coenobita worldwide.

Key Words: Cardisoma, Coenobita, Caribbean Basin, Gecarcinus, Holocene, Pleistocene

INTRODUCTION
A small parcel of crab remains from the Quaternary of Antigua and Bermuda was discovered among uncatalogued fossil decapod crustaceans at the collections of the Department of Paleobiology, Smithsonian Institution, National Museum of Natural History (USNM) in November 2015. The studied material constituted of a few dozen disarticulated or fragmented podomeres, mostly cheliped dactyli and pollices, represents at least three taxa of terrestrial to semi-terrestrial hermit crabs: the left-handed hermit crab Coenobita Latreille, 1829, and the land crabs Cardisoma Latreille, in Latreille, Le Peletier, Serville & Guérin, 1828, and Gecarcinus Leach, 1814.

The material from Bermuda consists of a few cheliped dactyli and pollices of “Gecarcinus” collected by William Beebe (1877–1962), from presumably Pleistocene rocks in association with petrel bones at Crystal Cave. Although the exact date of collection is uncertain, one specimen that was originally stored at the American Museum of Natural History, New York was later donated by H. Ernestine Bulger Ripley to the USNM in May 1944, and a few more specimens from the New York Zoological Society were donated in November 1946 (D. Levin, personal communication).

The material from Antigua is represented by pollices and dactyli of Coenobita, Cardisoma, and Gecarcinus collected during the early 1980s from Late Holocene sediment cropping out at the Burma Quarry. Little or no information is fortunately associated with the material. The collector is unknown (D. Levin, personal communication). The only mention of fossil crabs from Antigua so far comes from Pregill et al. (1988), who reported a diverse vertebrate assemblage from unconsolidated Quaternary sediments as a fissure infill on Late Oligocene limestones at the Burma Quarry, including amphibia (frogs), squamates (iguans), a colubrid, and boid snakes, birds (dues, owls, and hummingbirds), and mammals (rodents, bats). The authors also reported the presence of over a dozen species of molluscs, including bivalves and prosobranch gastropods, associated with some plant remains (Ulmacea), and remains of the terrestrial crabs Coenobita, Cardisoma, and Gecarcinus (Pregill et al., 1988). Radiocarbon dates from the fossiliferous fracture infills indicate a late Holocene age between 4,300 and 2,500 ybp (Pregill et al., 1988). Although the vertebrate material reported by Pregill et al. (1988) was illustrated and assigned catalogue numbers, the crustacean samples were not illustrated and there is no mention of a catalogue number or where they were deposited. Given that to date there are no Quaternary fossil crabs known from Antigua other than those reported by Pregill et al. (1988), that their vertebrate material from Burma Quarry is deposited at the USNM collections, their reported crab taxa coincide with the material in the uncatalogued parcel, and that the collection dates on some of the labels associated with the specimens coincide with the collection dates reported by the authors, I therefore conclude that the previously uncatalogued crab samples studied here...
correspond to the original specimens to which Pregill et al. (1998) referred to. It has been brought to my attention that nearly six hundred samples of Quaternary crabs from Bermuda are deposited at the invertebrate collections of Florida Museum of Natural History, Gainesville (FLMNH) (R. Portell, personal communication). The FLMNH online database (http://www.flnmh.ufl.edu/collections/databases/) indicates that the material, although not classified to the species level, could be referred to Geocarcinus sp.

Here, I provide some remarks on the Quaternary records of anomaluran and brachyuran crabs from Bermuda and Antigua deposited at the USNM, and discuss their significance for the fossil record of terrestrial crabs. For practical reasons, I refer to the studied material through the manuscript as “fossils”, regardless of whether they represent true fossil or sub-fossil remains. A summary of all fossil anomaluran and brachyuran crabs known to date from Antigua and Bermuda is also provided.

SYSTEMATIC PALEONTOLOGY

Decapoda Latreille, 1802
Anomura MacLeay, 1838
Paguroidea Latreille, 1802
Diogenidae Ortmann, 1892
Coenobita Latreille, 1829
Coenobita sp. cf. C. clypeatus (Fabricius, 1787)

Material examined: Dactylus of right pereiopod 2, fragments of dactyli of pereiopods 2 or 3, remains of cheliped dactylus. USNM 618302, Late Holocene, Burma Quarry, Antigua.

Remarks: Following Bracken-Grissom et al. (2013). Coenobita is herein included under Diogenidae. A total of 17 valid species of extant Coenobita have so far been described, mostly from the Indo-West-Paciﬁc region (McLaughlin et al., 2010; Rahayu et al., 2016).

No fossil species of Coenobita are known. The only mention of fossil remains of Coenobita is for the extant C. rugosus Bouvier, 1890 (see Schweitzer et al., 2010). The ichnogenus Coenobichnus Walker, Holland & Gardiner, 2003 from early Holocene deposits of San Salvador, Bahamas, is considered to have been produced by a putative coenobitid land crab. No fossil body remains were unfortunately found in association with the deposits. The only other fossil remains attributable to Coenobita are those from Antigua (Fig. 1A–E), which likely belong to C. clypeatus, which is the only extant coenobitid in the Western Atlantic region, including the Caribbean Sea.

Brachyura Latreille, 1802
Eubrachyura de Saint Laurent, 1980
Thoracotremata Guinot, 1977
Grapsoidea MacLeay, 1838
Gecarcinidae MacLeay, 1838
Cardisoma Latreille, in Latreille, Le Peletier, Serville & Guérin, 1828
Cardisoma sp. cf. C. guanhumi Latreille, in Latreille, Le Peletier, Serville & Guérin, 1828 (Fig. 1F–I, K, L)

Material examined: One cheliped dactylus, USNM 618303, Late Holocene, Burma Quarry, Antigua; a cheliped dactylus, USNM 618301, late Pleistocene?, Crystal Cave, Bermuda.

Remarks: The only known occurrences of Cardisoma in the fossil record are attributed to C. guanhumi from Pleocene-Holocene deposits through the Caribbean (Rathbun, 1918; Türkay, 1978; Collins & Donovan, 1997; Donovan & Dixon, 1998; Schweitzer et al., 2008; Collins et al., 2009b), and C. crassum Smith, 1870, from the Holocene of the Paciﬁc coast of Panama (Portell et al., 2012; Luque et al., 2015; Luque et al., unpublished). Cardisoma guanhumi (see Fig. 3A, B) is the only extant species of the genus on the island, and the remains from the Burma Quarry likely belong to this species.

Figure 1. Fossil Quaternary terrestrial crabs from Antigua and Bermuda. A–E: Coenobita sp. cf. C. clypeatus (Fabricius, 1787) (Anomura: Paguroidea: Diogenidae), USNM 618302, dactylus of pereiopods 2 and 3, Late Holocene, Burma Quarry, Antigua. F–G, K–L: Cardisoma sp. cf. C. guanhumi Latreille, in Latreille, Le Peletier, Serville & Guérin, 1828 (Brachyura: Grapsoidea: Gecarcinidae), USNM 618303, Late Holocene, Burma Quarry, Antigua, cheliped dactylus, inner (F) and outer (G) views; K, L, USNM 618301, Pleistocene?, Crystal Cave, Bermuda, dactylus fragment outer (K) and inner (L) views. H–J: Geocarcinus sp. cf. G. lateralis (Guérin, 1832), USNM 618303, Late Holocene, Burma Quarry, Antigua, cheliped dactylus outer (H) and inner (I) views; cheliped pollex slightly curved downwards (J) bearing more than 10 well-developed teeth on occlusal surface. M, N: unidentified gecarcinoid?, pollex inner (M) and outer (N) views.
FOSSIL HERMIT AND LAND CRABS FROM ANTIGUA AND BERMUDA

Geocarcinus Leach, 1814

Geocarcinus sp. cf. G. lateralis (Guérin, 1832) (Fig. 1H–J)

Material examined: Two short, disarticulated, fragmented dactyli and pollices, USNM 618303, late Holocene, Burma Quarry, Antigua.

Remarks: Geocarcinus is an extant genus of land crabs from tropical America comprised of three species: G. lateralis (Guérin, 1832), from the Bahamas to Venezuela, including the Florida Keys, Gulf of Mexico, and the West Indies; G. quadratus Saussure, 1853, from the Eastern Tropical Pacific (Mexico to Peru) and some parts of the Caribbean; and G. ruricola (Linnaeus, 1758), from the Bahamas, Florida Keys, and throughout the West Indies (Bright & Hogue, 1972; Sherman, 2002; Ng et al., 2008). No exclusively fossil species of Geocarcinus have been described (Schweitzer et al., 2010) and practically nothing is known about fossil or subfossil records from any of the extant species. A presumed fossil of Geocarcinus cf. ruricola was reported by Collins (in Donovan & Dixon, 1998: 825) from the Pleistocene Red Hills Road Cave of Jamaica, but later recognized as a species of Sesarma Say, 1817, first as S. primigenium Collins, Mitchell & Donovan, 2009 (Collins et al., 2009a), and more recently as Sesarma sp. cf. S. cookei Hartnoll, 1971 (Baalbergen & Donovan, 2013; Donovan, in press). A handful of late Holocene cheliped remains attributed to Geocarcinus sp. were reported by Locatelli (2013) from San Salvador, Bahamas, but most of the material disintegrated due to weathering before it could be described. Pregill et al. (1980) reported the occurrence of late Holocene Geocarcinus remains from the Burma Quarry in Antigua. Donovan, in a personal communication to Locatelli (2013) commented that “such occurrences are likely rare in Antigua, as no other crab fossils have been recovered since, and Pregill’s original quarry has been quarried away” (Locatelli, 2013: 865). The gecarcinid remains from the Burma Quarry (Fig. 1H–N) are most likely conspecific with G. lateralis (Figs. 2S–X, 3C, D), which until now is the only extant species of Geocarcinus in Bermuda.

DISCUSSION

Terrestrial and semi-terrestrial crabs are uncommon in the fossil record due to a number of biotic and abiotic biases preventing their preservation (Locatelli, 2013; Luque et al., 2015). New occurrences, even if fragmentary, thus greatly help understand the evolution and geographic distribution through time of taxa with a patchy fossil record such as terrestrial crabs. Although the specimens from the late Pleistocene of Bermuda and the Holocene of Antigua are constituted by isolated podomeres of chelipeds and pereiopods 2 and 3, some of which are fragmented, weathered, and lacking coloration, they are among the only known fossil remains for Coenobita, Cardisoma, and Geocarcinus. Distinguishing among genera and species of land crabs based on isolated or fragmented fossil remains is nevertheless troublesome, and usually leads to inaccurate or unclear systematic placements. Cardisoma and Geocarcinus fortunately have quite distinctive anatomies, so although telling congeneric species apart may not be simple, the genera differ such that differentiating their chelipeds is relatively straightforward. Adult Cardisoma

Figure 2. Cheliped remains of the extant land crabs Cardisoma guanhumi Latreille, in Latrille, Le Peletier, Serville & Guérin, 1828, and Geocarcinus lateralis (Guérin, 1832), uncatalogued material, Bocas del Toro, Caribbean Coast of Panama. Cardisoma guanhumi, A–F: hypertrophied major right cheliped of large male; outer (A), inner (B), dorsal (C), ventral (D), dactyl occlusal (E), and pollex occlusal (F) views. G–L: G, H, normal major left cheliped of large male; outer (G), inner (H), dorsal (I), ventral (J), dactyl occlusal (K), and pollex occlusal (L) views. M–R: minor right cheliped of large female; outer (M), inner (N), dorsal (O), ventral (P), dactyl occlusal (Q), and pollex occlusal (R) views. Geocarcinus lateralis, right cheliped of large specimen, undetermined sex; outer (S), inner (T), dorsal (U), ventral (V), dactyl occlusal (W), and pollex occlusal (X) views.

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The dactylus is five times as long as high, one-fifth longer than the manus height, slightly curved upwards, about twice as long as high, bearing nearly a dozen small and evenly-spaced teeth on the occlusal surface (Fig. 2A–F). The dactylus is five times as long as high, nearly twice as long as the manus height, strongly deflected downwards, lacking conspicuous denticulation on the occlusal surface, but bearing about 10 rows of mineralized granules mainly on the upper, inner, and occlusal margins (Fig. 2A–F). The palm bears several granules scattered from the junction with the dactylus to near the junction with the carpus. The upper margin of the propodus is granular, with a posterior edge flattened near articulation with the upper articular condyle of the carpus. In both the “normal” and hypertrophied major chelipeds of Cardisoma, the junction between the palm and the pollex is marked by a conspicuous depression (Fig. 2B, D, H, J), which is not developed in Gecarcinus (Fig. 2T, V). Furthermore, the pollex and the lower margin of the manus are nearly in the same sub-horizontal plane (Fig. 2A, B, G, H, M, N).

The propodus length (manus + pollex) of the minor cheliped of Cardisoma male and female (Fig. 2M–R) is nearly three times the propodus height; the pollex is as long as the manus, nearly straight, three times as long as high, bearing conspicuous and well-developed denticulation on the occlusal surface, with about eight teeth varying in size (Fig. 2M, N, R). A few rows of granules or sub-parallel ridges cover the pollex (Fig. 2M, N). The dactylus is three and a half times as long as high, slightly less than twice as long as the manus height, nearly straight but slightly deflected downwards, bearing conspicuous and well-developed denticulation on the occlusal surface, with several small teeth (Fig. 2M, N, Q). The lower and upper margins of the propodus are coarsely granular, with a posterior edge flattened near the articulation with the lower articular condyle of the carpus.

In the “normal” major chelipeds of male and female Cardisoma, the propodus length (manus + pollex) is nearly twice the propodus height; the pollex is as long as the manus, nearly straight, bearing conspicuous and well-developed denticulation on the occlusal surface, with about eight teeth varying in size, the largest positioned in the middle of the pollex, and preceded by two less-produced teeth towards the junction with the dactylus (Fig. 2G, H, I). Several rows of granules cover the pollex, mostly on the occlusal and lower margins (Fig. 2G, H, J). The dactylus is four times as long as high, one-fifth longer than the manus height, slightly deflected downwards, bearing conspicuous and well-developed denticulation on the occlusal surface, with about 10 or more teeth varying in size, the largest positioned in the middle of the dactylus, at about the same distance as the largest tooth is positioned in the pollex, and preceded by two or three less-produced teeth in the gape (Fig. 2G, H, K). The dactylus and pollex are highly granular, the lower margin of the propodus is coarsely granular, and the palm bears several granules scattered from the junction with the dactylus to near the junction with the carpus. The upper margin of the propodus is granular, with a posterior edge flattened near articulation with the upper articular condyle of the carpus. In both the “normal” and hypertrophied major chelipeds of Cardisoma, the junction between the palm and the pollex is marked by a conspicuous depression (Fig. 2B, D, H, J), which is not developed in Gecarcinus (Fig. 2T, V). Furthermore, the pollex and the lower margin of the manus are nearly in the same sub-horizontal plane (Fig. 2A, B, G, H, M, N).

The male and female chelipeds of Gecarcinus are mostly isochelous, equidimensional, short, with a stout propodus and more robust than those in Cardisoma (Fig. 2S–V), but can be quite unequal in larger males (Rathbun, 1918); the propodus length (manus + pollex) is nearly twice as long as the propodus height; the pollex is much shorter than the manus (Fig. 2S, T), noticeably deflected downwards, about twice as long as high, bearing nearly a dozen small and evenly-spaced teeth on the occlusal surface (Fig. 2S, T, X). The dactylus is two and a half times as long as high, as long as the manus height, directed downwards, bearing nearly a dozen small and evenly spaced teeth on the occlusal surface (Fig. 2W). The dactylus and propodus are smooth thorough and lacking conspicuous granulations. The chelipeds of Gecarcinus differ considerably from those of Cardisoma in 1) the much shorter dactylus and pollex ratios...
with respect to the manus height, 2) the stouter and more robust palm and manus, 3) the lower margin of the pollex is deflected downwards instead of being in a similar sub-horizontal plane as the lower margin of the manus, 4) the absence of granulations throughout the surface, 5) the denticulation patterns in the occlusal surfaces of dactylus and pollex, and 6) the lack of a conspicuous depression between the junction of the palm and the pollex.

The fossil hermit crab remains from the Holocene of Antigua represent the second record of fossil Coenobita worldwide, and one of the few records of fossil crabs from Antigua besides Cardisoma, Gecaricus, and a few Oligocene marine crabs (Collins & Donovan, 1995; 2002) (Table 1). Local extinction of land crabs in Antigua has been considered a consequence of overharvesting by humans during the last couple thousand years (Pregill et al., 1988).

ACKNOWLEDGEMENTS

Special thanks to Daniel Levin (Department of Paleobiology, USNM), for help accessing their collections; Laure Corbani and S. Lepricier (Muséum national d’Histoire naturelle, Paris) for the images of extant land crabs from Guadeloupe here illustrated and deposited at MNHN; the Autoridad Nacional del Ambiente (ANAM, Panama) and the Autoridad de los Recursos Acuáticos de Panamá (ARAP) for providing the necessary collection permits; Juan Maté (Smithsonian Tropical Research Institute, Panama) for valuable assistance with processing collection and export permits; Kecia Kerr (University of Alberta, Canada) for field assistance and improving the manuscript; A. Richard Palmer (University of Alberta, Canada) for support via the NSERC Canada Discovery Grant RGPIN 04863; Stephen K. Donovan (Naturalis Biodiversity Center, The Netherlands), Roger W. Portell (FLMNH); and Rodney M. Feldmann (Kent State University, USA), and the Editor-in-Chief for their reviews, comments, and suggestions for improving the manuscript. This work was possible thanks to a Natural Science and Engineering Research Council of Canada Graduate Scholarship (NSERC CGS-D) and an Izaak Walton Killam Memorial Scholarship (Canada) to the author.

REFERENCES


