

New specimens of *Amblyrhiza inundata* (Rodentia: Caviomorpha) from the Middle Pleistocene of Saint Barthélemy, French West Indies

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ABSTRACT. The extinct Pleistocene giant rodent *Amblyrhiza inundata* is reported here for the first time from the island of St Barthélemy. Bracketing uranium-thorium dates provide an age of ~ 500 ka for the specimens, making these the oldest known examples from any of the islands of the Anguilla bank. As with con-familial heptaxontids on Jamaica, and probably Puerto Rico and Hispaniola, *Amblyrhiza* appears to have become extinct in the late Middle Pleistocene, long before anthropogenic impacts that correlate with the loss of several smaller West Indian endemic rodents.

Le rongeur géant disparu du Pléistocène *Amblyrhiza inundata* a été signalé ici pour la première fois sur l'île de St Barthélemy. La datation par uranium-thorium sous et au dessus de la sample donnent un âge de ~ 500 ka pour ces spécimens, ce qui fait d'eux les plus anciens spécimens connus des îles du banc d'Anguille. Comme les heptaxontids, membres de la même famille, à la Jamaïque, et probablement à Porto Rico et Hispaniola, *Amblyrhiza* semble avoir disparu à la fin du Pléistocène Moyen, bien avant les impacts anthropogéniques qui sont en corrélation avec la disparition de plusieurs petits rongeurs endémiques des Antilles.

Keywords: Rodent; Extinction; West Indies; Uranium series dating.

1. INTRODUCTION

A distinctive component of the Quaternary mammal fauna of the northern West Indies was the radiation of large caviomorph rodents that comprise the nominal family Heptaxodontidae (an exhaustive review by MacPhee, 2011 strongly suggests that the Heptaxodontidae may not be monophyletic, and that *Amblyrhiza*, in particular, may be more taxonomically distinctive than previously supposed – but the term is used as a matter of convenience here). The endemic genera *Clidomys*, *Quemisia*, and *Elasmodontomys* are represented by single species on Jamaica (we follow MacPhee, 1984, in subsuming the Jamaican *Spirodontomys*, *Speoxenus* and *Alterodon* in the genus *Clidomys*, but note that only a single, sexually dimorphic species, *C. osborni*, is now plausible, c.f. discussion in Morgan and Wilkins, 2003), Hispaniola and Puerto Rico. A second Puerto Rican taxon, *Tainotherium*, has been tentatively assigned to the Heptaxodontidae (Turvey et al., 2006) but in the absence of any cranial or dental material, its familial relationships must remain conjectural. Extensive investigations into the Quaternary palaeontology of Cuba have not produced heptaxodontids. Given the Greater Antillean distribution of most of the family, it is therefore notable that another, monotypic genus,

Amblyrhiza, occurs only in the northernmost Lesser Antilles. Moreover, *Amblyrhiza inundata* Cope is the most spectacular example of its family, reaching truly megafaunal size of ~200 kg body mass (Biknevicius et al., 1993).

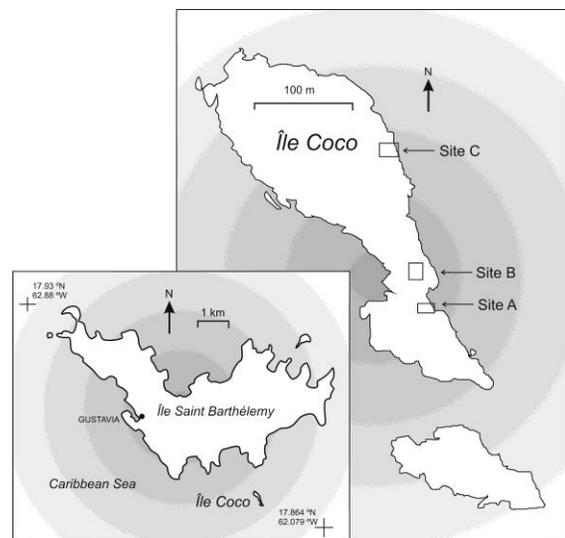


Figure 1. Location of cave sites on Île Coco and location of Île Coco in relation to St. Barthélemy.



Figure 2. *Amblyrhiza inundata*, diagnostic incisor tooth (centre; molar to upper right, embedded in terra rosa matrix).

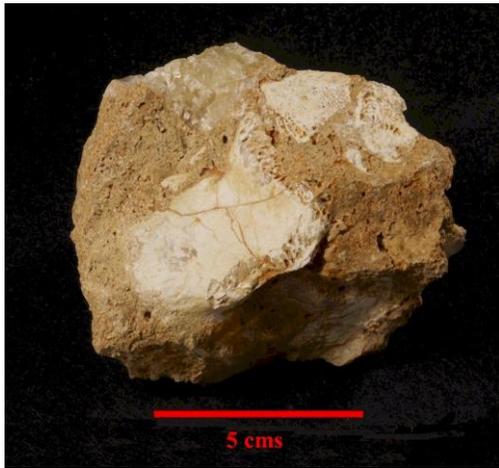


Figure 3. *Amblyrhiza inundata*, vertebra. (MNHN.F.ANC.2).

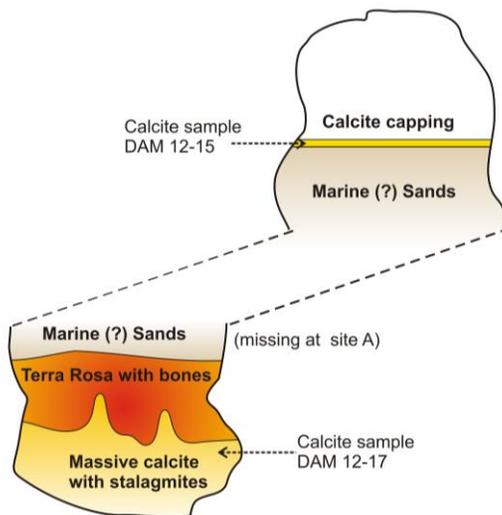


Figure 4. Stratigraphy of the Île Coco deposits.

Amblyrhiza inundata first came to scientific attention in 1869 (Cope, 1869), when its remains were described from a shipment of phosphatic cave earth mined from a cave in Anguilla, probably the site now known as Cavannah Cave (18.211 °N, 63.071 °W; McFarlane and MacPhee, 1989, 1993). Subsequent investigations recovered additional material from a cave, or caves, at Simson's Bay (believed to be at Meschrine Hill, 18.029 °N, 63.090 °W.), St. Maarten (Holthuis, 1959). *Amblyrhiza* has never before been reported from the island of St. Barthélemy, although its former presence there was expected on palaeogeographic grounds.

Recent work by one of us (GM) has recovered material of *A. inundata* from several sites on Île Coco, a satellite island of St. Barthélemy (Figure 1). In each case, the palaeontological material is preserved in an indurated, lateritic matrix which fills fissures in the host Middle Eocene limestone of the Flamand Member of the Saint Bartholomew Formation (Christman, 1953).

ST. BARTHÉLEMY SPECIMENS

Sites 'A', 'B' and 'C' are fissures on the islet of Ile Coco, lying 4.5 km southeast of Gustavia, St. Barthélemy (17.873 °N, 62.812 °W), and 800 m off the southern coast of the main island. These fissures are apparently the remains of former vadose cave passages, heavily invested with speleothem calcite, that were subsequently unroofed by erosion.

Diagnostic Specimens

Two small blocks of fossiliferous material have been accessioned into the collections of the Muséum national d'Histoire naturelle (Paris, France): *Amblyrhiza inundata*, incisor tooth [MNHN.F.ANC.1] (Figure 2); and *Amblyrhiza inundata*, vertebra [MNHN.F.ANC.2] (Figure 3).

A more extensive collection of material, including additional teeth and fragmentary long bones has been deposited with the Préfecture of St. Barthélemy, and is awaiting a decision on final disposition.

Stratigraphy and Age of the specimens

Three sites on Île Coco expose remains of *Amblyrhiza* in the form of broken long bone fragments and teeth, embedded in a hard, indurated lateritic residuum, which has survived in formerly-protected vadose cave passages that are now exposed as unroofed fissures. However, no single site preserves the entire stratigraphic sequence that is illustrated in composite form in Figure 4. The

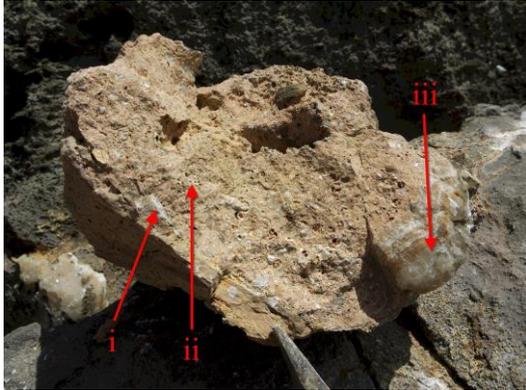


Figure 5. Indurated fossiliferous residuum at Site A, showing *Amblyrhiza* bone fragments (i) and gastropods (ii). The incorporated, broken flowstone block (iii) is “Unit 1”. Tip of geological hammer (bottom) provides scale.



Figure 6. The remnant flowstone floor, “Unit 2”, at Site B, resting above marine sands.

basal deposit in the cave remnants is a very thick, massive laminated flowstone, ‘Unit 1’. This is overlain by the fossiliferous residuum, well displayed at Site A (Figure 5). Elsewhere (e.g., Site B), the fissures and cave remnants are infilled with marine sands and capped by a thin (~ 2 cm) flowstone floor, ‘Unit 2’ (Figure 6). The calcite layers, units 1 and 2, were dated by the uranium series disequilibrium method. Site C consists of a former narrow fissure in what was probably an ancient cave floor that is now infilled with calcite.

Geochronological Methods

Samples of calcite from units 1 and 2 were collected under permit. Each sample was inspected by binocular microscope and any crack, vug or detrital particle avoided. Samples were analyzed according to standard U-Th disequilibrium techniques (e.g., Ivanovich et al., 1992; Cheng et al., 2000). All chemical preparation was done in ultraclean conditions. Samples were ultrasonically cleaned, heated for 5 hours at 875 °C to remove

organics, dissolved in HNO₃, and spiked with ²³³U-²³⁶U-²²⁹Th tracer (calibrated by analysis of uraninite in secular equilibrium). U and Th were co-precipitated with iron hydroxide, and purified twice on anion exchange columns (Dowex AG1-X 200-400 mesh). Measurement of U and Th isotopic ratios was done using the Triton TIMS at the Isotope Geochemistry and Geochronology Research Centre, Carleton University, Ottawa, Ontario. Instrumental reproducibility is 0.06% for ²³⁴U/²³⁸U and 0.11% for ²³⁰Th/²³⁴U. The high ²³⁰Th/²³²Th ratios obviated the need for adjustment for detrital content.

Results

Results of U-Th dating are shown in Table 1. With U concentrations of only ~0.15 ppm, these samples are very close to the limit of the method. The lowermost material gave a good date, and, while the upper material yielded a finite age, the error was high and it cannot be distinguished from the first date. The ages on both flowstone samples are consistent with a ‘Cromerian’ (MIS 13-17) origin.

Discussion

The island of St. Barthélemy, and its satellite islet of Ile Coco, lie at the southern end of the Anguilla Bank, a shallow (<50 m) carbonate bank of some 2,500 km² extent. During episodes of glacially-driven sea level depression, which were in excess of 100 m during each of the five low-stands of the past 500 ka, the modern islands of Anguilla, St. Martin/St. Maarten, St. Barthélemy and their satellites were fused into a single large island, and therefore, provided habitat for a single population of *Amblyrhiza*. The +13 m high sea-level highstand of MIS 11 at ~410 ka (Roberts et al., 2012) would have inundated most of the modern island of Anguilla, so it might be expected that St. Martin and St. Barthélemy, with their higher relief, probably acted as refugia for the species.

McFarlane et al. (1998) reported on 11 known *Amblyrhiza* sites from Anguilla and 3 from St. Martin/St. Maarten. Three of these sites, all from Anguilla, have yielded bracketing U-Th dates consistent with pre-MIS 5e (128 ka) tenure. Here we add three additional sites from the middle Pleistocene of St. Barthélemy. Decades of research in the caves of these islands has failed to unearth any post-MIS5e, ¹⁴C-datable specimens, which adds support to the hypothesis (c.f. McFarlane et al., 1998) that *Amblyrhiza* was a Last Interglacial high-sea-level casualty. The minimum bracketing age on *Amblyrhiza* from Anguilla’s ‘Cave-No-Cave’ site is 200 +52/-38 ka (McFarlane et al., 1998), so that the

Table 1. U-Th isotopic data and ages

Sample	Age ka $\pm 2\sigma$	U conc $\mu\text{g/g}$	$^{230}\text{Th}/^{234}\text{U}$	$^{234}\text{U}/^{238}\text{U}$	$^{230}\text{Th}/^{232}\text{Th}$	$^{234}\text{U}/^{238}\text{U}$ initial
SB-17	583+75/-44	0.169	0.997 \pm 0.002	1.004 \pm 0.002	1084	1.022 \pm 0.001
SB-15	678+409/-78	0.142	1.003 \pm 0.002	1.012 \pm 0.001	1067	1.081 \pm 0.001

taxon must have survived the MIS 11+13 m sea level highstand; thereafter, the MIS 5e+6 m highstand is the only plausible terminus for the species. The Île Coco specimens are currently the oldest known specimens of *Amblyrhiza*.

Several recent publications have focused on late Holocene West Indian mammalian extinctions, including Puerto Rico taxa (Turvey et al., 2007), and Greater Antillean ground sloths (Steadman et al., 2005), and these authors have generally emphasized the overlap of last occurrence dates with the anthropogenic era (~6000 yr B.P. in the West Indies; Curet, 2005). The loss of small (<1 kg) mammals, like *Heteropsomys* (Puerto Rico) with last occurrence ages of ~1200 yr B.P., and insectivores, such as *Nesophontes* (590 +/-50 yrs B.P., Dominican Republic; MacPhee et al., 1999) very plausibly resulted from catastrophic interactions with black rats (*Rattus rattus* Linnaeus) whose remains co-occur with them. The fate of the ground sloths is more enigmatic – the last occurrence dates to the middle Holocene, arguably having an overlap with the arrival of Amerindians, but none of these megafaunal species have so far emerged from unambiguously archaeological contexts, in spite of extensive excavations in both Puerto Rico and Hispaniola. The giant heptaxodontid rodents stand in marked contrast to these other taxa, with no Holocene last occurrence ages reported from Hispaniola (*Quemesia*), Jamaica (*Clidomys*) or the islands of the Anguilla bank (*Amblyrhiza*). Only

Elasmodontomys (Puerto Rico) is securely dated to the Holocene (McFarlane, 1999; Turvey et al., 2007). The late Pleistocene endemic West Indian capromyid rodents (e.g., *Geocapromys* of Jamaica and *Plagiodontia* of Hispaniola, etc.) have not yet been found to co-occur in the heptaxodontid-bearing Middle Pleistocene deposits, and may represent a post-heptaxodontid radiation on these islands.

Île Coco is remarkable for its extensive calcite deposition and level of karstification associated with Middle Pleistocene interglacial periods. While no extensive intact cave has been found, the coast is dotted with many examples of un-roofed former cave passages, lined with substantial thicknesses of calcite flowstone and the characteristic indurated red cave fill. The palaeoclimatic implications are that the Middle Pleistocene (~MIS 13-17) in this region was considerably wetter than any of the subsequent interglacials, including the present one. Presumably this was reflected in a more-mesic plant community with correspondingly higher productivity, soil development and underlying speleothem deposition.

Acknowledgements. We thank the Prefect of St. Barthélemy, M. Philippe Chopin, for permission to work on Île Coco, and Anne-Marie Fourteau-Bardaji, Ministry of Cultural Affairs, Guadeloupe for oversight of fieldwork. Pascal Ledee, Odile Ledee-Maincent, Olivier and Sylviane Brin, Philippe Barbé, Helene Bernier, Patrick Marechal and Michel Magras generously provided their time, resources and support without which this fieldwork could not have been done.

REFERENCES

- Curet, L. A. 2005. *Caribbean palaeodemography: population, culture, history and sociopolitical processes in ancient Puerto Rico*, Tuscaloosa; AL. Alabama University Press, 288 pp.
- Biknevicius, A. R., McFarlane, D. A., and MacPhee, R. D. E. 1993. Body size in *Amblyrhiza inuncta* (Rodentia: Caviomorpha), an extinct megafaunal rodent from the Anguilla Bank, West Indies: Estimates and implications. *American Museum Novitates* **3079**, 1-25.
- Cheng, H., Edwards, R. L., Hoff, J., Gallup, C. D., Richards, D. A. and Asmerom, Y. 2000. The half-lives of uranium-234 and thorium-230. *Chemical Geology*, **169**, 17–33.
- Christman, R. A. 1953. Geology of St. Bartholomew, St. Martin, and Anguilla, Lesser Antilles. *Bulletin of the Geological Society of America*, **64**, 65-96.
- Cope, E. D. 1869. Exhibition of bones and teeth of a large rodent from the cave deposits of Anguilla, one of the West India islands. *Proceedings Academy of Natural Sciences, Philadelphia*, 1868, p. 313.
- Holthuis, L. B. 1959. H.E. van Rijersma – a little-known naturalist of St. Martin (Netherlands Antilles). *Studies on the Fauna of Curacao and other Caribbean Islands*, **9**, 69-78.
- Ivanovich, M., Latham, A. G. and Ku, T.-I. 1992. Uranium-series disequilibrium applications in geochronology. In: M. Ivanovich and R. S. Harmon (Eds.), *Uranium-series Disequilibrium: Applications to Earth, Marine and Environmental Sciences*, 2nd edition, Clarendon Press, Oxford, pp. 62–89.
- MacPhee, R. D. E. 1984. Quaternary mammal localities and heptaxodontid rodents of Jamaica. *American Museum Novitates* **2803**, 1-34.
- MacPhee, R. D. E. 2011. Basicranial morphology and relationships of Antillean Heptaxodontidae (Rodentia, Ctenohipstrica, Caviomorpha). *Bulletin of the American*

- Museum of Natural History*, **363**, 1-70.
- MacPhee, R. D. E., Flemming, C. and Lunde, D. 1999.** “Last occurrence” of the Antillean insectivore *Nesophontes*: new radiometric dates and their interpretation. *American Museum Novitates* **3261**, 1-20.
- McFarlane, D. A. and MacPhee R. D. E. 1989.** *Amblyrhiza* and the Quaternary bone caves of Anguilla, British West Indies. *Cave Science*, **16**(1), 31-34.
- McFarlane, D. A. and MacPhee R. D. E. 1993.** *Amblyrhiza* and the vertebrate paleontology of Anguillan caves. *Boletín Society Venezolana Espeleología*, **27**, 33-38.
- McFarlane, D. A., MacPhee R. D. E. and Ford, D. 1998.** Body size variability and a Sangamonian extinction model for *Amblyrhiza*, a West Indian megafaunal rodent. *Quaternary Research*, **50**, 80-89
- Morgan, G. S. and Wilkins, L. 2003.** The extinct rodent *Clidomys* (Heptaxodontidae) from a Late Quaternary Cave Deposit in Jamaica. *Caribbean Journal of Science*, **39**(1), 34-41
- Roberts, D. L., Karkanias, P., Jacobs, Z., Marean, C. W. and Roberts, R. 2012.** Melting ice sheets 400,000 yr ago raised sea level by 13 m: past analogue for future trends. *Earth and Planetary Science Letters*, **357-358**, 226-237
- Turvey, S. T., Grady, F. V. and Rye, P. 2006.** A new genus and species of ‘giant hutia’ (*Tainotherium vlei*) from the Quaternary of Puerto Rico: an extinct arboreal quadruped? *Journal of Zoology*, **270**(4), 585-594.

Editorial Responsibility: Dr S. James-Williamson. Type setting: Prof. S. F. Mitchell

Accepted 14th September 2014