TETRAPODS OF THE RED HILLS ROAD CAVE, JAMAICA (LATE PLEISTOCENE)

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Samenvatting

In 1988 ontdekten twee studenten, Anita Godwin en Marlene Britton, de Red Hills Road Cave (RHRC) nabij Kingston, Jamaica. Grotten zijn een veel voorkomend verschijnsel in het verkarste kalkstenen landschap van Jamaica. Fossiele tetrapoden zijn bekend uit het Eoceen, waarna het eiland 40 miljoen jaar lang onder water verdween. Toen het eiland ongeveer 10 miljoen jaar geleden weer boven de zeespiegel steeg, werd het opnieuw gekoloniseerd door vliegende tetrapoden (vogels, vleermuizen) of soorten die via 'sweepstake routes' Jamaica wisten te bereiken (amfibieën, reptielen, kleine zoogdieren). Fossiel bewijs van deze taxa is alleen gevonden in grotten en is gewoonlijk minder dan 100.000 jaar oud. De rijkste vindplaats is de Red Hills Road Cave in de gemeente St. Andrew, nabij Kingston. De opvulling heeft een rijke verscheidenheid opgeleverd aan landslakken (62 soorten) en zeldzame, goed geconserveerde geleedpotigen, zoals duizendpoten en pissebedden. Vertebraten worden bewaard als een 'Irish Stew' van ongearticuleerde botten. Amfibieën zijn zeldzaam, maar de kaken van hagedissen komen vaak voor. Vogels, minstens acht soorten, worden vertegenwoordigd door de uitgestorven vleugelloze ibis *Xenicibis xympithecus* Olson & Steadman, de Jamaicaanse tody en leden van ten minste vijf andere groepen. Het enige landzoogdier is het knaagdier *Geocapromys brownii* (Fischer). Vier soorten vleermuizen getuigen van uitstervens aan het eind van het Kwartair.

Abstract

Two students, Anita Godwin and Marlene Britton, found the Red Hills Road Cave (RHRC) near Kingston, Jamaica, in 1988. Caves are a common feature of the karstified limestone landscape of Jamaica. Fossil tetrapods are known from the Eocene, after which the island was inundated for 40 million years. The tetrapods that have recolonized the island after its re-emergence about 10 million years ago are dominated by those that can fly (birds, bats) and small taxa that could travel across wide expanses of sea on floating 'sweepstake routes' (amphibians, reptiles, small mammals). Fossil evidence of these taxa is limited to caves and are commonly less than 100,000 years old. The most fossiliferous of these sites is the Red Hills Road Cave in the parish of St Andrew, near Kingston. This has yielded a diversity of land snails (62 species), and rare, well-preserved arthropods such as millipedes and isopods. Vertebrates are preserved as an 'Irish Stew' of disarticulated bones. Amphibians are rare, but the mandibles of lizards are common. Birds, at least eight species, include the extinct flightless ibis *Xenicibis xympithecus* Olson & Steadman, the Jamaican tody and members of at least five other groups. The only land mammal is the rodent *Geocapromys brownii* (Fischer). Four species of bat provide evidence of extirpation and extinction.

This account begins with the slightly strange tale of the two students who made an unexpected discovery of some palaeontological importance, but who walked away from it. In 1988, Ms Anita Godwin, a Ph.D. student from the University of Liverpool, was in Jamaica collecting Recent and Pleistocene land snails for her geochemical research into shell chemistry. On the day in question, she was accompanied by Ms Marlene Britton, a final year undergraduate at the University of the West Indies, Mona, Kingston (UWI), majoring in geology. And what these ladies found that morning was what we now call the Red Hills Road Cave (RHRC) (Donovan & Gordon, 1989).

At that time S.K.D. was a lecturer in the Department of Geology at UWI. The girls appeared in the Department in time for lunch, bursting into Steve's office with tales of a shallow cave full of red sediment, shells of land snails and what were thought to be infilled, lithified burrows (trace fossils).

Lunch came first and then the three made a return trip to the cave. The red sediment was there, as were the snails, but not the trace fossils. Rather, these were misidentified bones, mainly ribs and elements of limbs. I have not seen a more fossiliferous terrestrial site before or since.

THE GEOLOGY OF JAMAICA IN BRIEF

The Caribbean Plate is a basaltic province that was emplaced between North and South America in the Mesozoic from the Pacific, long before the formation of the Central American land bridge (Pindell, 1994; Donnelly, 1994). Jamaica is situated close to the northern margin of this plate, within the North Caribbean Plate Boundary Zone, and drifting eastwards. Draper (1987) recognised a four-fold division of the island's geological evolution, briefly summarised as follows.

- Cretaceous island arc volcanism with associated limestone deposition.
- Late Cretaceous to Paleogene uplift and intrusion.
- Mid-Cenozoic quiescence, with the island forming a submerged carbonate bank for about 40 million years.
- Neogene uplift and renewed deformation in the North Caribbean Plate Boundary Zone.

About ⅔ of the surface rock outcrop of Jamaica is limestones (Fig. 1), which have endured tropical temperatures and rainfall since the island was uplifted about 10 million years ago. In consequence, Jamaica has developed a widespread karst topography (Sweeting, 1958; Donovan, 2002), including over 1,000 recognised caves (Fincham, 1998). Although there are a diverse range of Quaternary deposits on the island (Bertrand, 1987), it is only in the fills of certain caves that the terrestrial macrofossil record is recognised.

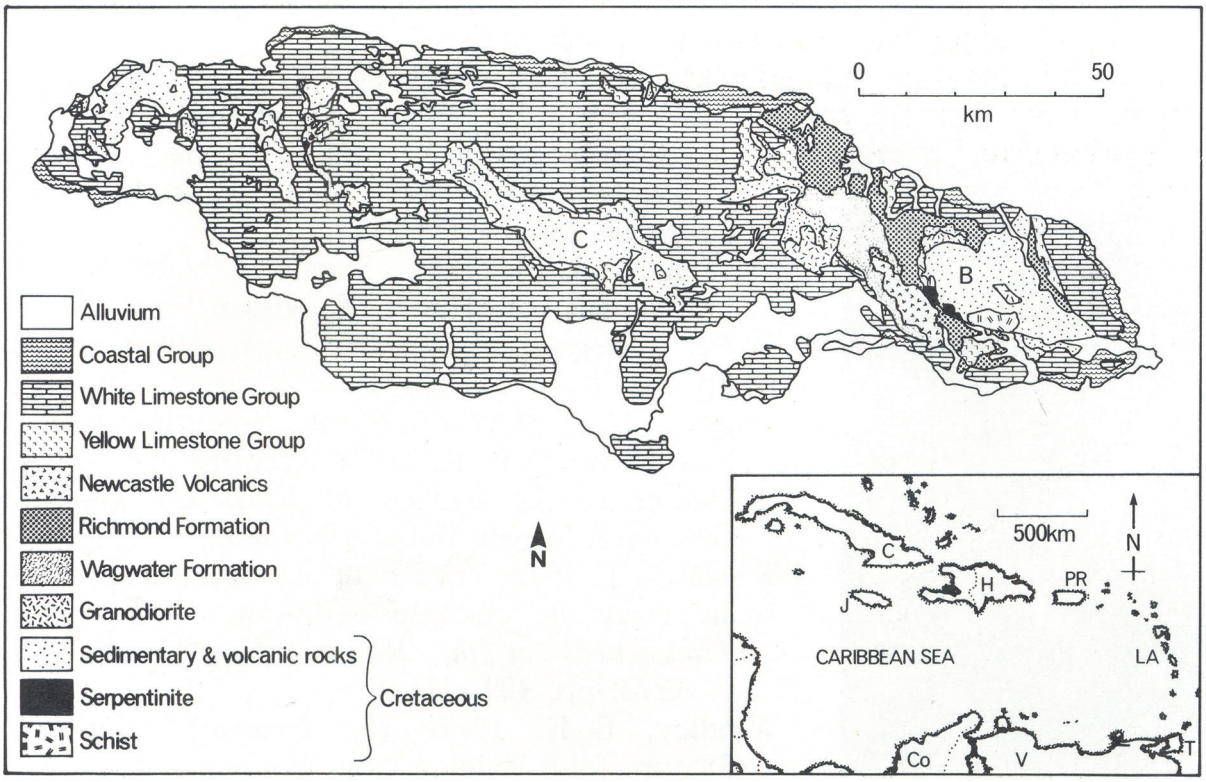

Figure 1. Simplified geological map of Jamaica, showing the principal stratigraphical units (after Donovan, 1993, fig. 1; based on Geological Survey of Jamaica, 1959). B: Blue Mountain inlier; C: Central inlier.
Ages of principal Cenozoic units: Granodiorite = Upper Cretaceous to Paleocene; Wagwater Formation, Newcastle Volcanics = Paleocene; Richmond Formation = Paleocene to Lower Eocene; Yellow Limestone Group = Lower to Middle Eocene; White Limestone Group = Middle Eocene to Upper Miocene; Coastal Group = Upper Miocene to Quaternary; alluvium = Quaternary.
The inset map shows the position of Jamaica in the Caribbean. Key (clockwise from Jamaica): J: Jamaica; C: Cuba; H: Hispaniola (Haiti + Dominican Republic); PR: Puerto Rico; LA: Lesser Antilles; T: Trinidad; V: Venezuela; Co: Colombia.

JAMAICAN CENOZOIC TETRAPODS

Fossil tetrapods are locally common in only two parts of the Cenozoic rock record of Jamaica: the Eocene Yellow Limestone Group in the western part of the island, and Late Pleistocene caves, such as the RHRC, which are widespread and can be richly fossiliferous (Fincham, 1997). The Eocene occurrences were first reported from a straight-snouted sirenian (sea cow), *Prorastomus sirenoides* Owen, 1855, found in a float boulder in the Quashies River. Over a hundred years later, this was supplemented by the crocodilian *Charactosuchus*? *kugleri* Berg, 1969, from the Dump Limestone. It was only beginning in 1989 that a research team under the fervent leadership of Professor Daryl P. Domning (Howard University, Washington, D.C.) started the search for primitive sea cows in Jamaica, following the lead of Owen's species. In particular, excavations centred on the Seven Rivers site near Montego Bay, discovered that same year by Roger W. Portell (Florida Museum of Natural History, Gainesville). Sirenians such as the extraordinary walking *Pezosiren portelli* Domning, 2001, rubbed shoulders with amphibious and terrestrial taxa such as crocodilians, lizards, turtles and a rhinoceros (Domning *et al*., 1997; Fig. 2 herein). A complete appraisal of this site is in preparation (Domning & Portell, editing in progress).

The importance of the Seven Rivers site is in confirming the accuracy of what hitherto had been a theoretical determination. It had been assumed that the Antillean islands were populated by terrestrial tetrapods in the Paleogene, called the Stage I terrestrial vertebrate fauna (Donovan *et al*., 2007), but that these were subsequently wiped out by the subsequent inundation of the islands. The Stage II fauna (post-inundation) populates the islands at the present day and is presumed to be very different from that of Stage I (Williams, 1989). Jamaica, as one example, was entirely submerged for about 40 million years in the mid-Cenozoic (Draper, 1987; Robinson, 1994). Upon re-emergence, Jamaica was repopulated by tetrapods from nearby land areas (= Stage II fauna). The Seven Rivers site yielded the first diverse members of the Stage I fauna, including at least three species of primitive, walking, but amphibious sirenians and a lizard. Most particularly, the rhinoceros could have walked from North America to Jamaica because in the earlier part of the Eocene the island was adjacent to the Yucatan Peninsula. Forty million years later, Jamaica had been carried further east by the movement of the Caribbean Plate. Jamaica's Stage II terrestrial vertebrate fauna is thus dominated by birds and bats, with small non-flyers (amphibians, reptiles, a few mammals) arriving by sweepstake routes (MacPhee *et al*., 1983; Morgan, 1993). No large terrestrial tetrapods were able to walk or swim to the island, now distant from major land masses. And the only fossil Stage II vertebrates are found in caves in the highly karstified limestones of Jamaica; most of these cave deposits are less than 100,000 years old (MacPhee *et al*., 1989).

THE RED HILLS ROAD CAVE

The RHRC is a cave or fissure deposit exposed on the south side of the Red Hills Road (Fig. 3) in the parish of St. Andrew, Jamaica, north-west of Kingston, and about 3.3 km west from the lookout between mileposts 9 and 10 (Donovan & Veltkamp, 1994). The cave is flask-shaped and exposed in vertical section, with a narrow opening at the apex. It was presumably exhumed and truncated when the road was built (Donovan & Gordon, 1989). The cave was dissolved into well-lithified limestones of the mid-Tertiary White Limestone Group. It is partially infilled with dripstones, fallen limestone boulders and clastic sediment; it was probably completely filled, but much of the sediment must have been removed when the Red Hills Road was blasted through. Sediment is probably largely derived from the *terra rosa* soils that are prevalent in this area (hence the name Red Hills). Where lithified, the red sediment is cemented by calcite. The range of ages of this deposit is uncertain, preliminary dating by amino acid racemisation suggested a range in the order of 20,000-40,000 years (Goodfriend in Paul & Donovan, 2006, p. 110). This agrees well with the (uncorrected) radiocarbon date from a large *Pleurodonte* snail shell of 31,960 ± 1220 yr BP (McFarlane & Blake, 2005) (adapted from Baalbergen & Donovan, 2013, p. 629).

The invertebrates of the RHRC are unusually diverse. Other Jamaican caves have yielded bones, land snails, and the claws and fingers of land crabs. The extant land snails of the island are particularly diverse – over 500 native species – so they are not unexpected in caves, probably washed in during storms. The RHRC has the richest fossil land snail fauna known from a Jamaican cave, including 62 species (Paul & Donovan, 2006). These are associated with the fingers of land crabs (*Sesarma* sp.) and, uniquely for the Antilles, a range of other arthropods, including millipedes and isopods preserved in three dimensions, ostracodes and rare insect remains (Donovan & Veltkamp, 1994; Baalbergen & Donovan, 2013; Donovan *et al*., 2013).

The peculiarity of preservation in the RHRC is noteworthy. Certain arthropods that we rarely encounter as fossils, such as millipedes and isopods, are preserved in three dimensions with delicate structures such as legs and antennae *in situ*, yet tetrapods are invariably disarticulated. The reason for this taphonomic discordance can be explained by visualizing the environment of the RHRC 30,000 years ago (Donovan, 2017; Fig. 4 herein). The cave or fissure was a hole in the ground into which crumbling sediment and soil, leaves and errant animals dropped in. Although the cave fill includes a diversity of animal remains, it is unknown if many or even any were obligate cave taxa (we suspect the latter). Rather, they were likely victims of the cave's shape, like a section through a beer bottle (cave) or a fissure, open only at the apex. It is reminiscent in shape to the 'bottle' dungeons found in some ancient castles (Fig. 4A; see <http://uncover.travel/st-andrews-castles-bottle-dungeon-the-grimmest-of-scotlands-many-castle-dungeons>). Most sediment and organic remains probably accumulated in the RHRC during tropical storms and hurricanes, when large volumes of water as surface runoff flowed over the land surface and sank into the fractured, karstified limestones, filling the cave (Fig. 4B). Animals washed in would have drowned. After the storm the water level of the cave would drop, slowly, by flowing away through the limestone aquifer and by evaporation (Fig. 4C). Evaporation would have concentrated dissolved calcium carbonate in the slightly acidic cave waters, which then precipitated as lime on the walls of the cave and on

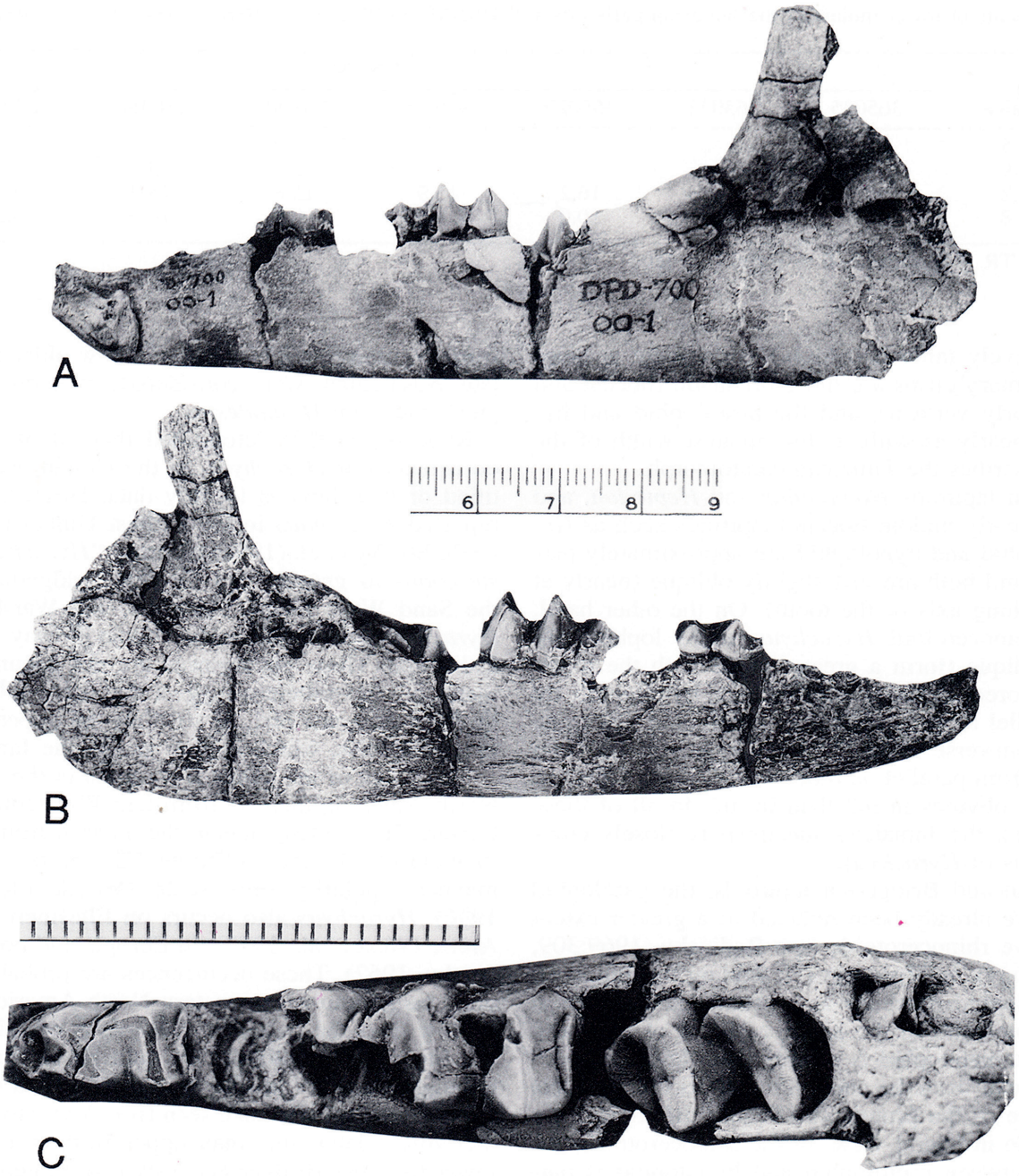

Figure 2. Right dentary and dp3-m3 of the rhinocerotoid Hyrachyus *sp. (USNM 489191) from the Early or Middle Eocene of Jamaica, in medial (A), lateral (B), and occlusal views (C) (after Domning* et al.*, 1997, fig. 1). Scales in cm (A, B) and mm (C).*

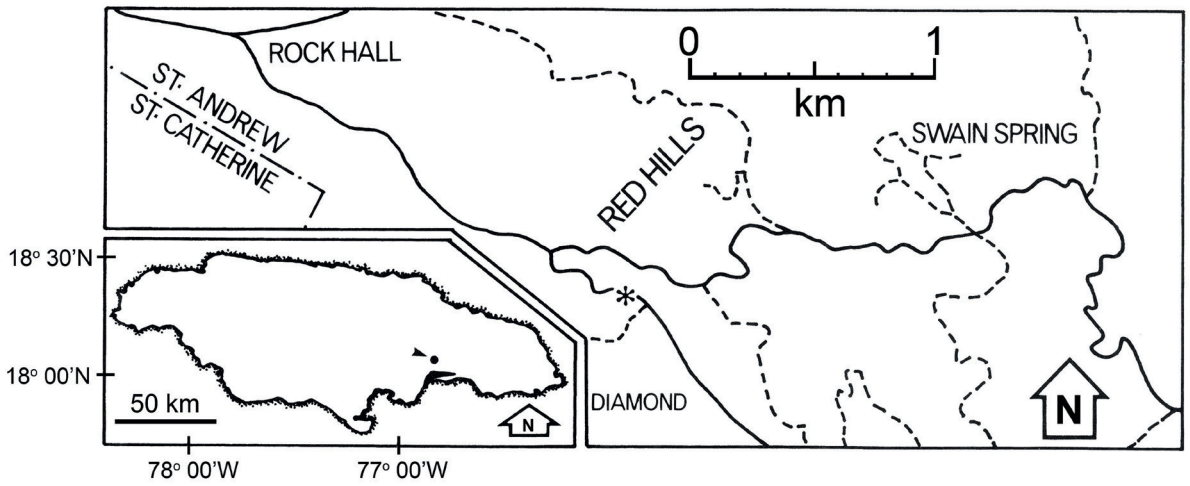

Figure 3. Locality map showing the position of the Late Pleistocene Red Hills Road Cave (*) on the south side of the Red Hills Road, near Diamond, parish of St. Andrew, Jamaica (modified after Donovan & Gordon, 1989, fig. 1A). Main (solid lines) and minor roads (dashed lines), and the boundary between the parishes of St. Andrew and St. Catherine are shown. Inset map of Jamaica shows the approximate position of the main map (arrowed).

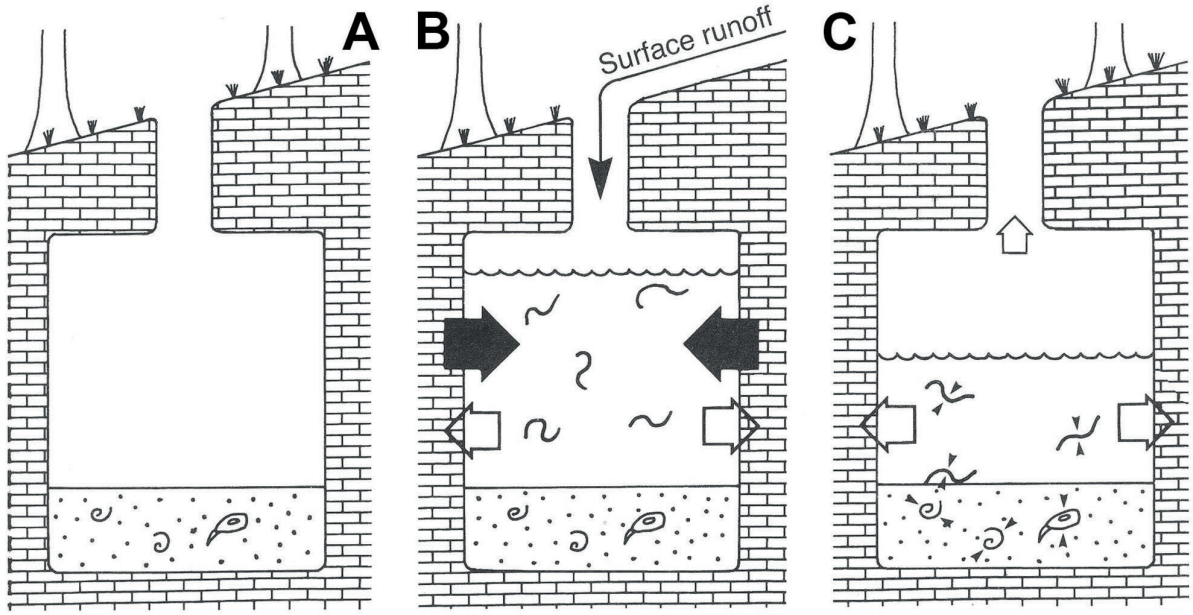

Figure 4. Postulated depositional sequence for calcitic preservation of millipedes in Red Hills Road cave (after Donovan & Veltkamp, 1994, fig. 7). (A) Dry/damp conditions. The cave acts as a bottle trap for any organisms, particularly terrestrial tetrapods that topple into the opening in the roof, but accumulation of infill is slow. Many of the invertebrates could come and go as they pleased. (B) Hurricane/tropical storm conditions. The cave fills with water from surface runoff and from the karstic aquifer (large black arrows; smaller open arrows indicate outflow into karst). Millipedes and other organisms washed in and drown. (C) After the storm. Water level drops by evaporation (small arrow) and karstic runoff. Calcareous skeletons in, on and floating above the sediment (mainly gastropods and some arthropods) act as substrates for calcite precipitation (small black arrows). Uncalcified organisms and soft tissues of tetrapods rot away.

calcium-rich fossil substrates. The latter would have included the exoskeletons of drowned arthropods, such as millipedes and isopods, which include up to 10% calcium carbonate. In contrast, recently drowned vertebrates could not be coated, as their skeleton is only exposed after rotting, by which time the cave waters would have fully subsided. The exposed skeletons would likely fully disarticulate before the next storm. Hence, millipedes can be beautifully preserved, but invertebrates and vertebrates together invariably occur as a sort of prehistoric 'Irish Stew'. A crunchy stew, as the disarticulated bones were often coated during a later drowning and evaporation stage.

The systematic diversity of the vertebrates of the RHRC has only been partly unravelled, mainly due to the disarticulated preservation of multiple individuals and taxa. Individual bones and teeth may be well preserved, but they are still fragments of incompletely known organisms and not attractive to systematists. The RHRC is a typical mixed vertebrate site, with bones of an indeterminate number of species, but no complete specimens. It is analogous to a box of mixed pieces from a number of jigsaw puzzles (how many we do not know) and with all the box lids thrown away. Savage (1990, p. 33) was the first to sum up the non-mammalian tetrapods of the RHRC, thus:

"The amphibians comprise only a few very small bones and no recognizable skull or dental material. The reptiles are small lizards and there is one mandibular ramus amongst the isolated bones. Birds are represented by several medium and small sized species: tarso-metatarsals are the most readily recognized limb bones."

Amphibians remain unstudied. Lizards are represented most commonly by dentary bones and eggs, although the latter should be dated in order to show if they are recent or ancient. Only the birds and mammals have received more than passing comment.

Soon after the RHRC was recognised, two easily recognised tetrapods were identified from its fill. One of these was a bird, the extinct Jamaican flightless ibis *Xenicibis xympithecus* Olson & Steadman, 1977. This taxon is particularly well known from its long leg bones (Fig. 5). Other bones, hollow or beaks, showed that birds were moderately common in the 'Irish Stew', but difficult to identify. The only systematic study of these bird bones was by Boot *et al*. (2015), based on Boot's undergraduate thesis at the University of Leiden. His list of taxa is diverse:

Corvus? sp. indet. (crow)
Todus todus Linnaeus, 1758 (Jamaican tody)
Xenicibis xympithecus Olson & Steadman, 1977 (extinct ibis)
trochilid gen. et sp. indet. (hummingbird)
cuculid gen. et spp. indet. (cuckoos)
scolopacid gen. et spp. indet. (snipes and sandpipers)
passeriforms gen. et spp. indet. (perching birds)

This list indicates at least eight species, yet could conceal as many as 37. This seems meagre when compared to an extant avifauna of about 320 known taxa, but nominal fossil birds from the island are few. Morgan (1993, table 2) listed only nine bird taxa "... identified from published Late Quaternary sites in Jamaica". Other species have since been added from Late Pleistocene and Holocene deposits (see, for example, McFarlane *et al*., 2002; Olson, 2006, 2008), but even the minimum estimate of eight taxa makes the RHRC the most diverse fossil bird site on the island. The list also shows that, where the flightless ibis is a clear instance of insular evolution, most birds did not lose the ability to fly. This is common on islands. We all know the Dodo as the typical flightless bird of Mauritius, but here too, the majority of (endemic) species had a lifestyle no different from their mainland counterparts.

The other prominent tetrapod is an extant rodent, the Jamaican hutia, *Geocapromys brownii* (Fischer, 1830), recognised from rare skulls, jaws and mandibles, and more common teeth (Fig. 5). Although quite sizable, we need to be careful not to automatically classify it as a case of insular gigantism. After all, South American rodents tend to be larger than their counterparts elsewhere in the world, and a body weight between one and two kg, as in the Jamaican hutia, is no exception in continental species. That *Geocapromys* is the only land mammal identified from the RHRC is not surprising. MacPhee *et al*. (1983, table 1) identified members of only four families of endemic mammals in Jamaica (excluding bats): the extinct pithecine atelid *Xenothrix mcgregori* Williams & Koopman, 1952; and various rodents, including *G. brownii*. This depauperate fauna indicates how unexpected the find of the Eocene rhinoceros was to palaeontologists used to bats, rodents and little else. Unlike nearby islands in the Greater Antilles, the Quaternary of Jamaica has yielded, at least to date, no sloths and no insectivores (Simpson, 1956, table 1; MacPhee *et al*., 1983; MacPhee *in* Fincham, 1997; Rega *et al*., 2002, table 5).

Geocapromys brownii from the RHRC has been thoroughly examined by McFarlane & Blake (2005); for discussion of skeletal characteristics, see Anderson *et al*. (1983). This species is still extant, but rare and protected; its common and widespread fossils show that it was formerly widespread and common. The evidence from a growth series of *G. brownii* supports the supposition that the RHRC was a natural pit trap; for example, the fauna of the cave is not dominated by micromammals as would be expected if it were an accumulation produced by owls.

The other mammals reported from the RHRC are bats (Ouwendijk *et al*., 2014; Hoek Ostende *et al*., 2018). Chiropterans have been identified from their mandibles and determined to include four species (Fig. 6). The bats of Jamaica include about 21 extant species (Genoways *et al*., 2005), but the situation is rather more complex than simply four ancient members of the modern fauna. The fossil species are:

- *Stenoderma rufum* Desmarest, 1820, extirpated from Jamaica, but still extant in the eastern Greater Antilles.
- *Tadarida* sp. cf. *T. brasiliensis* I. Geoffroy St.-Hillaire, 1824; *T. brasiliensis* occupies all Greater Antillean islands and elsewhere.
- *Pteronotus trevorjacksoni* Van den Hoek Ostende, Van Oijen & Donovan, 2018, an extinct Jamaican endemic.
- chiropteran spp. indet.

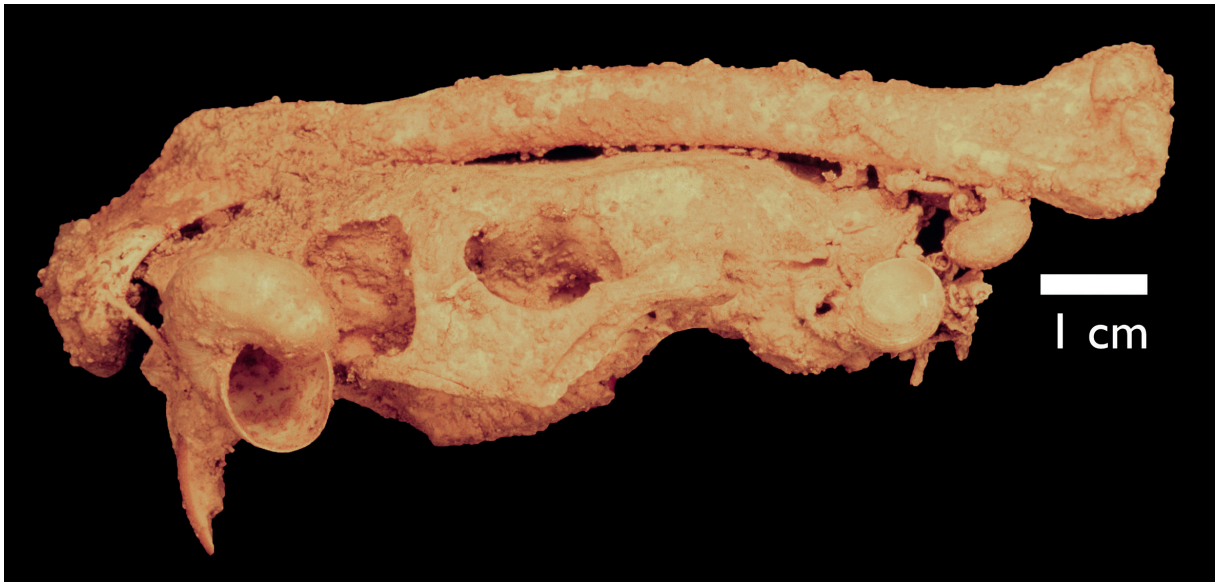

Figure 5. Some Late Pleistocene vertebrates of the RHRC, and a large gastropod on the lower left, Zaphysema tenerrimum *(C.B. Adams). The skull of the rodent* Geocapromys brownii *(Fischer) cemented to the right humerus of the flightless ibis* Xenicibis xympithecus *Olson and Steadman (compare with Morgan, 1993, fig. 2C; after Donovan & Paul, 2011, fig. 11). Specimen in Geology Museum, University of the West Indies.*

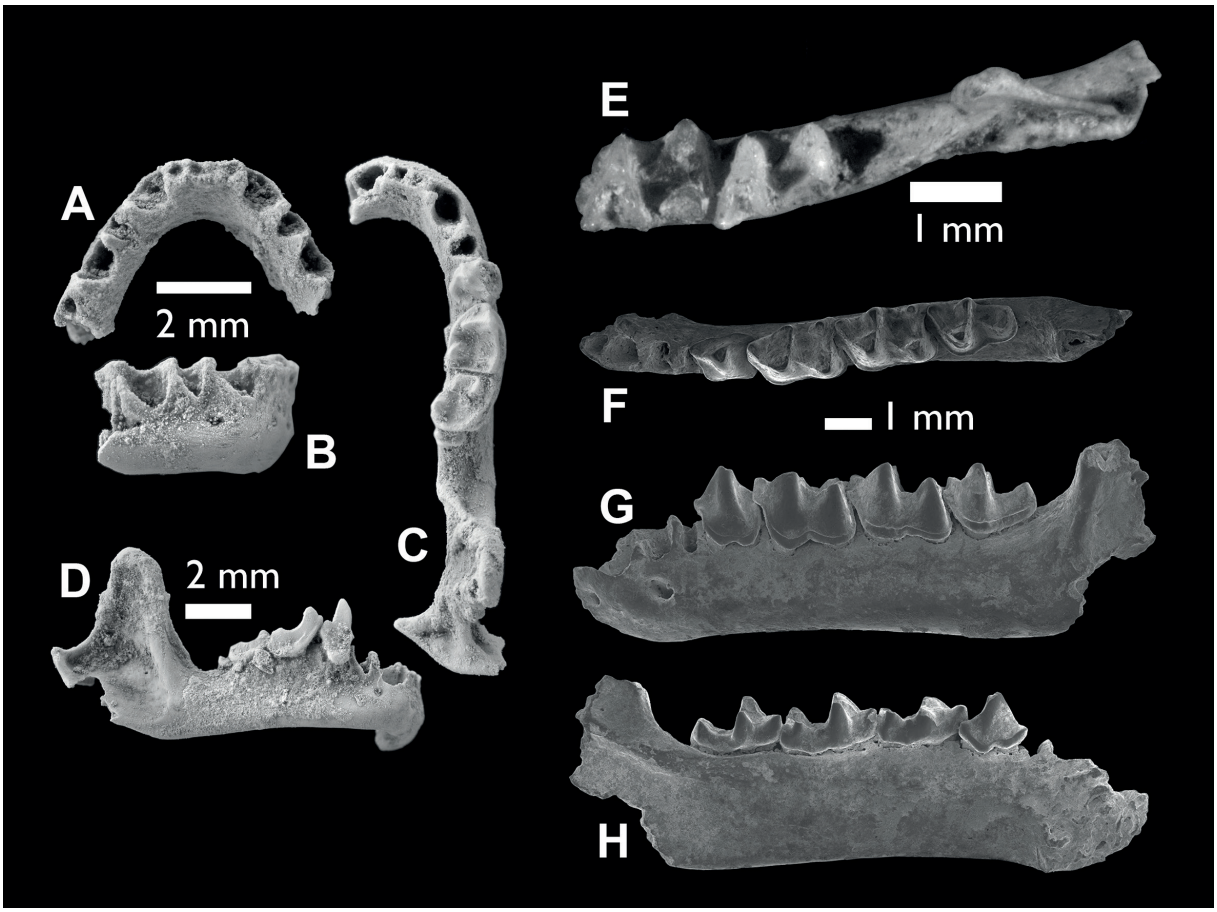

*Figure 6. Some Late Pleistocene bat (*Chiroptera*) mandibles of the RHRC.*
(A, B) Chiropteran *sp. indet., RGM 632 058, anterior of jaw (after Ouwendijk et al., 2014, fig. 2A, B). (A) Occlusal view. (B) Right lateral (labial) view. (C, D)* Stenoderma rufum Desmarest, *RGM 632 059, right mandible (after Ouwendijk et al., 2014, fig. 2C, D). (C) Occlusal view. (D) Right lateral (labial) view. (E)* Tadarida *sp. cf.* T. brasiliensis *I. Geoffroy St.-Hillaire, RGM 632 064, broken right mandible, occlusal view (after Ouwendijk et al., 2014, fig. 3A). (F-J)* Pteronotus trevorjacksoni *Van den Hoek Ostende et al. (after Van den Hoek Ostende et al., 2018, fig. 1a-c), RGM 1285849, holotype, left mandible with p4 - m3 (F) Occlusal view. (G) Labial view. (H) Lingual view. All specimens in the Naturalis Biodiversity Center, Leiden (prefix RGM).*

Thus, at least half of these taxa are no longer extant in Jamaica, although the sample is small. There is no reason to assume that further bat taxa will not be forthcoming.

In conclusion, Anita Godwin and Marlene Britton missed out on a scientific bonanza. Anita finished her Ph.D., but has not published it; Marlene became a missionary in Central America. We wish them both well, but can only be sad that they were not involved in any of the studies discussed herein. Their loss is somebody else's gain, and the story of the RHRC was written in part by other students, including Els Baalbergen, Marlous Ouwendijk and Arjan Boot. There is no doubt that the cave which Anita and Marlene discovered on that fateful morning 30 years ago has been a palaeontological bonanza. May it continue to produce new and exciting finds.

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