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A Middle Pleistocene Age and Biogeography for the Extinct Rodent *Megalomys curazensis* from Curaçao, Netherlands Antilles

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The extinct oryzomyine rodent *Megalomys curazensis* has been known from abundant but fragmentary remains on the island of Curaçao since 1959. Here we demonstrate an age of 130 000 to 400 000 years before present based on geomorphological context, and propose a biogeographical model for the genus.

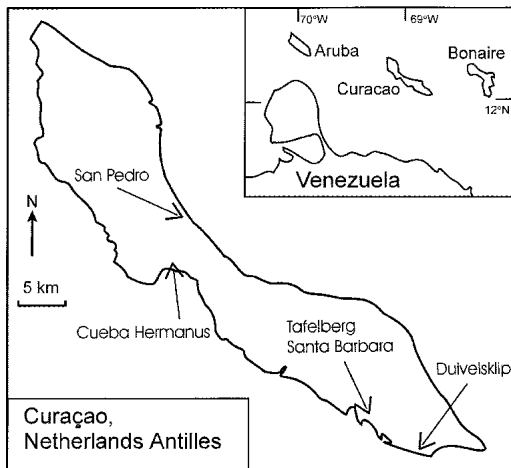


FIG. 1. Map of Curaçao, showing site localities.

The island of Curaçao lies only 70 km off the coast of Venezuela (Fig. 1), but is separated from the mainland by a major tectonic feature, the Bonaire basin, with a maximum water depth of 1344 m. The origin of this basin predates the sub-aerial exposure of the Quaternary carbonates that encircle Curaçao, so that the terrestrial fauna is depauperate and constrained by over-water dispersal. The modern native terrestrial mammal fauna consists of a single species of rodent, Hummelinck's vesper mouse *Calomys hummelincki* (Musser and Carleton, 1993), but fossil remains of three additional rodent taxa and a ground sloth have been reported from caves and limestone fissures on the island: the extinct 'giant rice rat' *Megalomys curazensis* (Hooijer, 1959), the extinct rice rat *Oryzomys curasoae* (McFarlane and Debrot, 2001), the locally extirpated capybara *Hydrochaeris hydrochaeris* (Hooijer, 1959), and the enigmatic sloth *Paulocnus petrificans* (Hooijer, 1962). *Oryzomys curasoae* is a late Pleistocene/Holocene form that occurs commonly in superficial contexts in the caves of Curaçao (McFarlane and Debrot, 2001) but the probable ages of the remaining fossil mammals are unknown; they occur only in a hard, indurated, 'phosphatic breccia' exposed as a fissure fill in the walls of caves and cliffs at Duivelsklip, Tafelberg Santa Barbara (e.g. Cueba Seru Boka; Pors and Debrot, in prep.), Hermanus and other sites at the same elevations (Fig. 1). Here we discuss a major exposure of *Megalomys curazensis* 'breccia' from Cueba di Hermanus (UTM ¹⁹495896, ¹³48720; also 'Cueba Hermanus') whose probable age (and thus the ages of the other fossil mammals in the same deposit) can be estimated because it is constrained by its geomorphological setting.

GEOLOGICAL AND GEOMORPHOLOGICAL SETTING

The Neogene and Quaternary limestones of the northern coast of Curaçao are exposed in an ascending series of five well-defined depositional terraces; Top-most (150-196 m), Highest (90-110 m), Higher (50-80 m), Middle (15-45 m) and Lower (0-10 m) (terminology follows de Buissonjé, 1974, and Stienstra, 1983). Along the south coast, three distinct erosional terraces (Lower, Middle, and Higher) are cut into the Seroe Domi Formation of Upper Miocene through Pliocene limestones (Jackson and Robinson, 1994). The erosional terraces are clearly associated with the depositional terraces (de Buissonjé, 1974; Herweijer and Focke, 1978): on the northern side of the island Late Quaternary high sea levels produced extensive reefal and coastal deposits; on the southern side of the island the same high sea levels produced wave cut platforms (Fig. 2). In each of the three lowermost terraces, erosion by the subsequent high sea level produced a cliff face with a distinct intertidal notch. In addition, the associated high groundwater levels produced distinct episodes of karstification and speleogenesis that are apparent in all the terraces. The red breccia cave and fissure fills bearing the mammalian fossils are located in the Middle and Higher erosional terraces of the south coast; Cueba di Hermanus, the study site, is located in the face of the erosional Middle Terrace (Fig. 2).

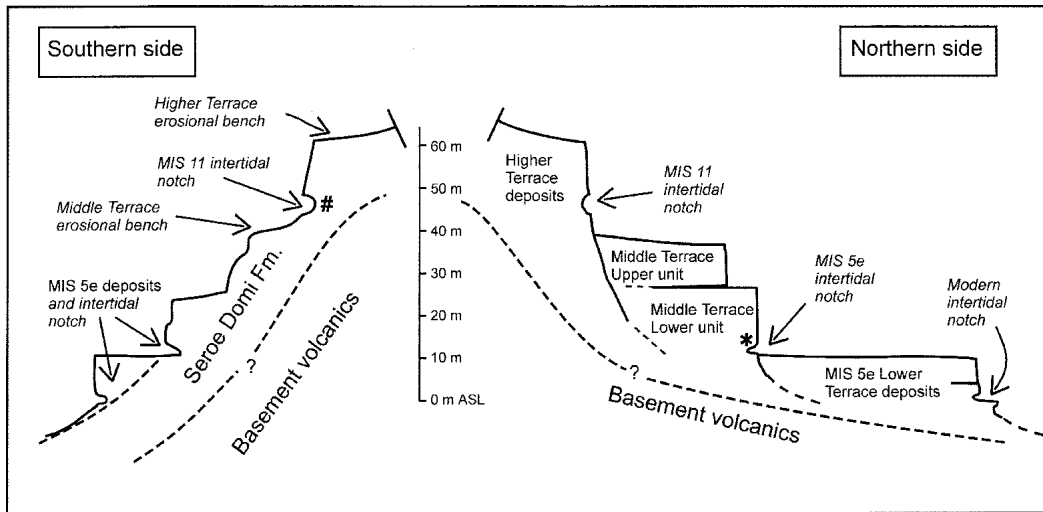


FIG. 2. Diagrammatic cross-sections of southern and northern sides of Curaçao, showing geomorphologic relationships of erosional (indicated in italics) and depositional terraces related to sea level high-stages of Marine Isotope Stages 11, 5e and 1. The location of the dated coral from the Middle Terrace, northern side, is shown with an asterisk *; the location of the Kueba di Hermanus site, southern side, is shown as the number sign #.

TABLE 1. Data from U-Th analysis on *Montastraea annularis* sample from base of Middle Terrace deposit, near San Pedro.

Sample age (ka)	Init $^{234}\text{U}/^{238}\text{U}$	U ppm	Th ppm	Act. Rat. $^{234}\text{U}/^{238}\text{U}$	Act. Rat. $^{230}\text{Th}/^{234}\text{U}$	Act. Rat. $^{230}\text{Th}/^{232}\text{Th}$
405 + 40 - 29	1.207 ± .009	1.98	0.005	1.07 ± 0.77	1.06 ± 0.69	42937

Isotopic ratios measured by NU MC-ICP-MS; Activity ratios calculated using half lives for ^{234}U and ^{230}Th from Cheng et al. (2000).

The age of the Lower Terrace has been firmly established by U-Th dating of the reef deposits as marine isotope stage (MIS) 5e (~130 ka; Schubert and Szabo, 1978). Attempts to date the Middle Terrace had been unsuccessful due to problems with coral diagenesis but we have dated by uranium-thorium disequilibrium methods an unaltered *Montastraea annularis* in growth position, collected from the base of the Middle (depositional) Terrace near San Pedro (Fig. 1; Fig. 2-sample site shown by asterisk). This sample yielded an age of 405 +40, -29 ka (by multi-collector, inductively-coupled mass spectrometry; Table 1) and securely places the Middle Terrace (lower unit) in the Isotope Stage 11 interglacial.

These ages on the depositional terraces allow interpretation of the associated erosional terraces, cliff-notch erosion, and speleogenesis. The cliff and intertidal notch in the Lower Terrace of MIS 5e sedimentary rocks is cut by the modern sea; the cliff and intertidal notch in the Middle Terrace of MIS 11 sedimentary rocks is cut by the 5e high sea level, and the Upper Terrace is cut by the former Stage 11 high sea level. Each of these high sea levels has also been associated with cave genesis roughly at the elevation of the former water table and at the intersection of the salt and fresh water following the flank margin model

of development (Myroie and Carew, 2000). The relationships are most obvious on the northern depositional terrace sequences: e.g., speleogenesis during the MIS 5e high sea level produced caves in the face of the Middle Terrace MIS 11 deposits. On the southern coast the erosional terraces cut into the Seroe Domo Formation have a similar relationship to former sea levels; thus, speleogenesis during the MIS 5e high sea level produced caves at the same level. Similarly, speleogenesis during the MIS 11 high sea level produced caves in the Higher Terrace.

KUEBA DI HERMANUS STRATIGRAPHY

Deposits of 'phosphatic breccia' containing remains of the extinct giant rice rat *Megalomys* occur as a fill in pockets and cavities in the entrance of Kueba di Hermanus, a shallow cave cut into the face of the Upper Terrace (the erosional cliff cut into Seroe Domo deposits that matches the intertidal notch and cliff cut into Higher Terrace deposits by the MIS 11 sea on the northern side of the island), and in the adjacent cliff face. Within the entrance of the cave, the deposit was exposed by blasting during 19th Century phosphate mining activity. This exposure reveals a thick flow-

stone capping the breccia, which in turn buries a substantial stalagmite. Three attempts to determine the age of these speleothems by uranium-thorium disequilibrium dating were unsuccessful, the calcite having been thoroughly leached.

Fortunately, the age of the *Megalomys*-bearing phosphatic breccias is bracketed, albeit rather broadly, by geomorphological considerations. The deposits do not occur in caves and fissures of the Lower Terrace, and must therefore predate the Last Interglacial, MIS 5e, at ~128 ka. It can be difficult to distinguish the remains of a flank-margin halocline cave from the remains of a fossil inter-tidal notch; however, both occur at the same elevation (sea level-halocline) and both develop at the same time. The breccia deposits are emplaced within the presumptive isotope Stage 11 inter-tidal notch at Kueba di Hermanus (or perhaps halocline cave chamber), so that they must postdate the ~400 ka high sea level stand. The *Megalomys* deposits must have therefore originated between ~130 ka and ~400 ka.

The relationship of the Kueba di Hermanus breccia to the deposits that contained the ground sloth *Paulocnus* and the capybara *Hydrochaeris hydrochaeris* is unknown. The type locality for *Paulocnus* was a fissure-fill exposed by quarrying at an altitude of 150 m above sea-level on the Tafelberg Santa Barbara and it was subsequently destroyed. The capybara site was also on Tafelberg Santa Barbara, at an altitude of 160 m (Hooijer, 1959). Since these sites lay ~100 m higher than the Hermanus site, we presume tentatively that they were not contemporaneous with the *Megalomys* breccia.

BIOGEOGRAPHY

The origin of the native West Indian terrestrial vertebrate fauna has been the subject of contentious debate for more than a century, and shows little sign of resolution (see arguments in Hedges, 2001). The West Indian oryzomyine rodents are unusual in this context because they can be unequivocally recognized as 'waif' dispersers. The Late Quaternary West Indian oryzomyine record includes nominally endemic Lesser Antillean species of *Megalomys* on Antigua/Barbuda, Guadeloupe, Martinique, and St Lucia; *Megalomys curazensis* from Curaçao; and at least three species of smaller oryzomyines—one each from Curaçao, St. Vincent, and Jamaica (Novak, 1999; Hooijer, 1959; Musser and Carleton, 1993). Additional, undescribed oryzomyines are known from sub-fossil deposits on Nevis, St. Kitts, Montserrat, and Barbados (Morgan and Woods, 1986). *Megalomys desmarestii* from Martinique survived at least until 1902 (Nowak, 1999), *O. antillarum* survived on Jamaica until at least 1880, and *M. luciae* lived on St. Lucia until at least 1849 (Nowak, 1999).

The two oryzomyines known from Curaçao show no evidence of being contemporary. *M. curazensis* is unknown from deposits younger than the breccia reported here and is thus of Illinoian age or older. The smaller *O. curasoae* is known only from very superficial contexts in caves and owl-pellet deposits, often intermingled with remains of introduced brown rats (*Rattus rattus*). We believe that *O. curasoae* arrived in Curaçao during the late Pleistocene or Holocene.

The evolutionary history of the oryzomyines in the West Indies is one of frequent, over-water colonization events. *Oryzomys antillarum* apparently entered Jamaica from Central America in the Late Wisconsinan (see Morgan, 1993 for a summary of the systematic relationships of *O. antillarum* and its mainland progenitor; McFarlane et al., 2002 provide radiometric evidence of Pleistocene age), requiring two water crossings via the Serranillo Bank. The Lesser Antillean *Megalomys* spp. required multiple 'island-hopping' dispersals to achieve their known distribution. Hershkovitz (1970) proposed that the closest living relative of the *Megalomys* spp. is *O. hammondi*, the largest member of that genus, noting a "cricetine with the size, skull, dentition, and arboreal habitats of *Oryzomys hammondi* could have given rise to all the species referred to *Megalomys*...". However, Hershkovitz's hypothesis is contraindicated by the geographic range of *O. hammondi*, which is limited to the Andes of northwestern Ecuador. Because Hershkovitz (1970) included the Galapagos giant oryzomyine in *Megalomys*, he further postulated that the ancestral taxon must have been "widely distributed on the South American mainland between northern Columbia and southwestern Ecuador", thereby including the modern range of *O. hammondi*. The Galapagos form has since been shown to be an evolutionarily convergent taxon and moved to its own genus, *Megaoryzomys* (Lenglet and Coppo, 1979), and no evidence has emerged to suggest that *O. hammondi* was ever significantly more widespread in its distribution. We therefore reject *O. hammondi* as the likely progenitor of the Lesser Antillean *Megalomys* spp., and suggest that the ancestral taxon was more likely to have been a small (~40-80 g; i.e. in the range of body masses for extant Caribbean margin *Oryzomys* given by Nowak, 1999) *Oryzomys*, which then evolved to the larger body size characteristic of *Megalomys* (~500 g?) in insular isolation. Current fossil evidence suggests that Curaçao hosted only one species of oryzomyine at a given time. We speculate that the presence of an established large 'megalomid' rodent on these islands may have resisted successful colonization by subsequent oryzomyine arrivals. On Curaçao, the extinction of the endemic *M. curazensis* opened the niche to a successful colonization by the ancestor of *O. curasoae* in the latest Pleistocene or early-mid Holocene, a process akin to the taxon cycles of Ricklefs and Cox (1972). One interpretation of this biogeographic scenario is that the *Megalomys* spp. of the Lesser Antilles are likely to have evolved from mainland oryzomyine ancestor or ancestors independently of events on Curaçao, in which case the genus *Megalomys* as currently recognized would have to be regarded as a polyphyletic construct.

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