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Late Quaternary Fossil Mammals and Last Occurrence Dates from Caves at Barahona, Puerto Rico

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ABSTRACT.—Puerto Rico supported at least five genera of endemic terrestrial mammals in the late Quaternary, all of which are extinct. Whether these animals died out in the late Pleistocene, the mid-Holocene, or in post-Columbian time has not been established. This paper is the first attempt at radiometrically dating the 'last occurrences' of these taxa, together with the first unambiguous descriptions of localities reported by previous workers. Last occurrence dates for *Nesophontes*, *Elasmodontomys* and *Heteropsomys* are shown to be mid-Holocene and overlap with Amerindian occupation of the island. *Acratocnus* is known only from the late Pleistocene. No Puerto Rican taxon has been shown to have survived into the historic (European) era, which contrasts with the situation on some other islands of the West Indies.

RESUMEN.—Durante el cuaternario tardío Puerto Rico tenía por lo menos cinco géneros endémicos de mamíferos terrestres, todos extintos. No se ha determinado si estos animales se extinguieron durante el pleistoceno tardío, el holoceno medio o luego de la llegada de los colonizadores. Este artículo es el primer intento de establecer por medio de pruebas radiométricas la última presencia de estos géneros, así como de proveer la primera descripción precisa de las localidades informadas por otros investigadores. La última presencia de *Nesophontes*, *Elasmodontomys* y *Heteropsomys* corresponde al Holoceno medio y coincide con la ocupación indígena de la isla. *Acratocnus* se conoce solamente del pleistoceno tardío. No se ha demostrado que alguno de los taxones puertorriqueños hayan sobrevivido durante la era histórica (europea), lo que contrasta con la situación en algunas de las otras islas de las antillas.

INTRODUCTION

The late Quaternary endemic mammal fauna of Puerto Rico as currently recognized consists of 15 species of bats (Koopman, 1989) and 5 terrestrial genera representing 3 orders. All of the terrestrial taxa have been extinct since at least the early historic period, defined here as beginning in AD 1500. The earliest investigations of the extinct mammals were undertaken in 1916 by Harold E. Anthony, as part of a wider investigation of the island sponsored by the New York Academy of Sciences (Anthony, 1916, 1918, 1925, 1926), and were followed by workers from the University of Kansas in 1957, the Smithsonian Institution in 1976-77, and the University of Kansas again in 1978 (Pregill, 1981). Following Anthony's success, each expedition focused on a group of caves southwest of Barrio Barahona, near Morovis in north-central Puerto

Rico. The purpose of this paper is to definitively characterize these sites for the first time, and to place the faunal remains in a radiometric context.

A remarkable characteristic of the endemic terrestrial mammal fauna of the West Indies is the severity of the wave of extinctions that decimated it in late Quaternary time. MacPhee and Flemming (1997) noted that 38% of all historic-era mammalian extinctions worldwide impacted the West Indies, even though these islands account for only 1.4 % of the global land area and less than 3 % of recent global terrestrial mammalian genera. In the Lesser Antilles and in Puerto Rico, this extinction toll reaches 100% (Table 1). The causes of these extinctions have been widely speculated upon, and typically include climate change (Pregill and Olson, 1981), habitat loss (Morgan and Woods, 1986), introduced diseases (MacPhee and Marx, 1997), introduction of

TABLE 1. Extinction statistics for West Indian terrestrial mammals, by island.

Island Group	Late Pleistocene	
	Diversity (genera)	% Extinction
Lesser Antilles	3	100
Puerto Rico	5 ^a	100
Jamaica	5	80
Cuba	11	82
Hispaniola	12 ^b	83
Cayman Islands	2	100

^aexcludes the extinct *Isolobodon portoricensis*, generally considered to be an Amerindian introduction.

^bexcludes two nominal taxa of undescribed extinct sloths, whose validity is undetermined.

feral or exotic predators and competitors (especially rats and the Indian mongoose; Woods et al., 1985), and direct extermination by humans (Martin, 1984). The quality of evidence used to account for these extinctions varies tremendously, but in only a few cases can it be considered conclusive. The introduction of rats (*Rattus rattus*, *R. norvegicus*, *R. exulans*) and the Indian mongoose (*Herpestes auropunctatus*) onto tropical islands is a case in point. The impact of *Rattus* and *Herpestes* on ground-nesting birds is well established (Atkinson, 1985), but their impact on other terrestrial vertebrates is much less so. For example, the Antigua Racer *Alsophis* has survived (barely) on Antigua in the presence of *Rattus*, *Herpestes*, and almost total clearance of the native habitat, and yet is extinct on Barbuda, where *Herpestes* is absent and the vegetation largely uncleared. On Christmas Island (Indian Ocean), the extinction of two native species of rats is tied closely to the arrival of *R. rattus* and, possibly, the introduction of rat-borne disease (Andrews, 1909; Flannery, 1990). The impact of introduced *Rattus* on native Caribbean rodents has not been properly addressed.

In Puerto Rico, the loss of one ground sloth, at least two native rodents, and an insectivore has not been evaluated radiometrically and thus could not hitherto be reasonably assigned to a cause or causes. The new last-occurrence dates reported here begin to establish the necessary radiometric framework.

STUDY SITES AND RESULTS

Quaternary Mammal Localities at Barahona

The Quaternary vertebrate sites of interest are a group of several dozen caves and rockshelters cut into the cone karst of the Lares Limestone, 2.5 kms northwest of the town of Ciales (Fig 1). Four of these caves have yielded sufficient fossil vertebrate material during this study to warrant further discussion. Topographic coordinates refer to the Universal Transverse Mercator Grid (North 19), and were obtained with a differentially-corrected global positioning satellite system to a precision of < 1m.

Cueva Del Perro 2030686 N; 769482 E.
(Fig. 2)

J. W. Bee of the University of Kansas first investigated this cave in 1957, screening some "4 cubic yards of sediment to a depth of four feet." The bats and insectivore material were described by Choate and Birney (1968; see Table 2). Unfortunately, Bee did not excavate by stratigraphic unit and his collection represents a time-transgressive sequence.

Examination of the site in 1996 revealed that a significant portion of undisturbed sediment remains in the cave. The section exposed in the face of Bee's pit consists of approximately 10 cm of sediment with sparse vertebrate remains, underlain by a distinctive 10 cm thick layer ('layer B') of land snails and vertebrate bones. Below, the sediment continues to the floor at approximately 1.2 meters with occasional vertebrate remains. Layer B is clearly an owl-pellet accumulation dominated by small birds with smaller quantities of rodent (including *Heteropsomys* and occasional *Elasmodontomys* remains) and reptile material, all of which may have been transported from the entrance chamber. An accelerator radiocarbon date of 5410 ± 80 radiocarbon years before present (rcyrbp) (Beta Analytic, Coral Gables, Florida, #60893) was obtained on bird bone collagen from the middle of layer B.

Cueva Clara 2030126 N; 769400 E. (Fig 3.)

This cave was first investigated by Anthony in 1916, and re-worked by Bee in

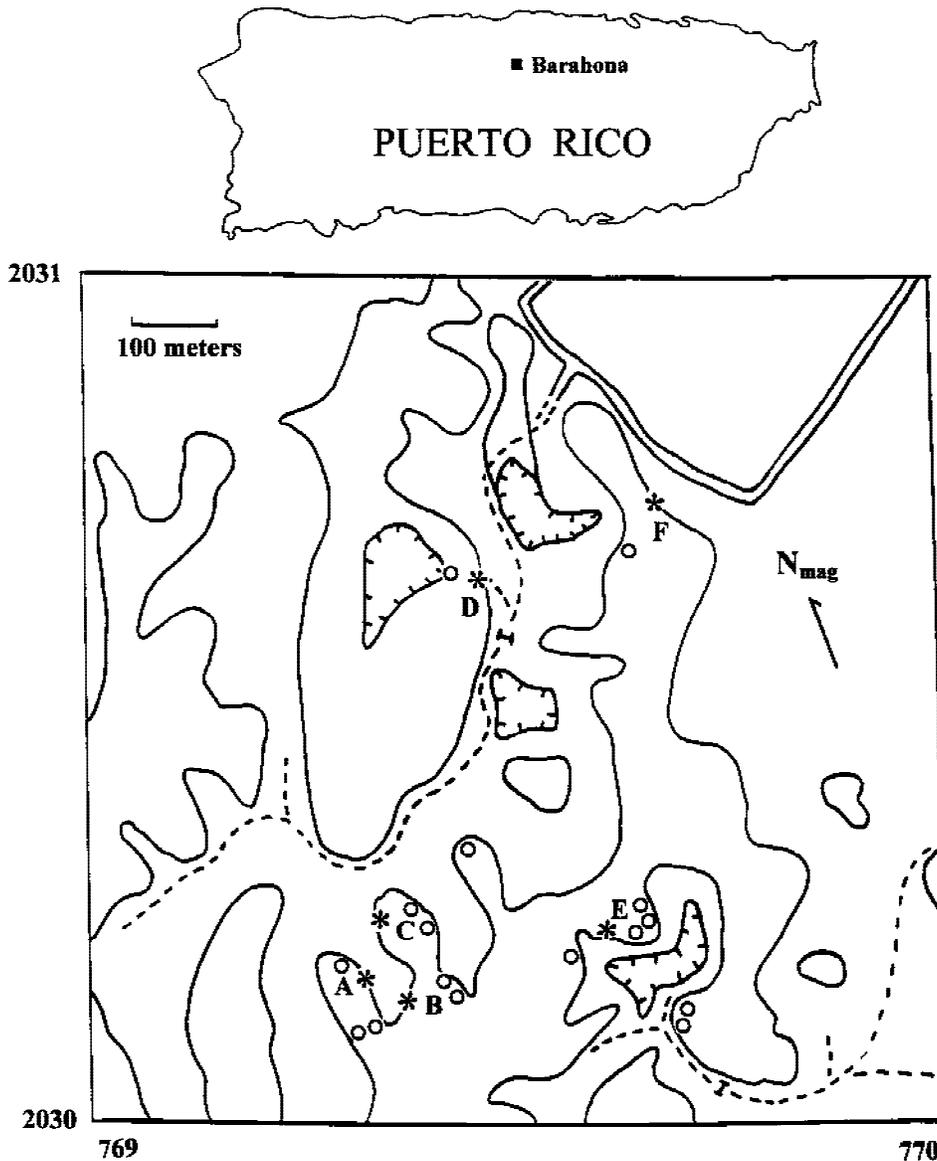


FIG. 1. Location map of the Barahona caves. Area mapped is the 1 km² UTM grid whose coordinates are shown. Cave entrances are shown as open circles and asterisks. A: Cueva de la Vaca, B: Cueva Clara, C: Cueva del Perezoso, D: Cueva del Perro, E: *Nesophontes* Cave (c.f. Pregill, 1981), F: Blackbone Cave (c.f. Pregill, 1981).

1957. Fossils of bats, the insectivore *Nesophontes*, the rodents *Elasmodontomys* and *Heteropsomys*, and the ground sloth *Acratocnus* were recovered from different parts of the cave without stratigraphic control. When examined in 1996, very little original sediment remained, but excavation of an undisturbed pocket yielded well preserved

material of rodents and bats (Table 2). A radiocarbon date on *Pluerodonte* shell carbonate from a depth of 30 cm and immediately adjacent to *Elasmodontomys* material yielded an 'infinite' age of >34,650 rcyrbp (Beta # 94478). Previous work has demonstrated that *Pluerodonte* exhibit a 'limestone effect' (Goodfriend and Stipp, 1983) of the

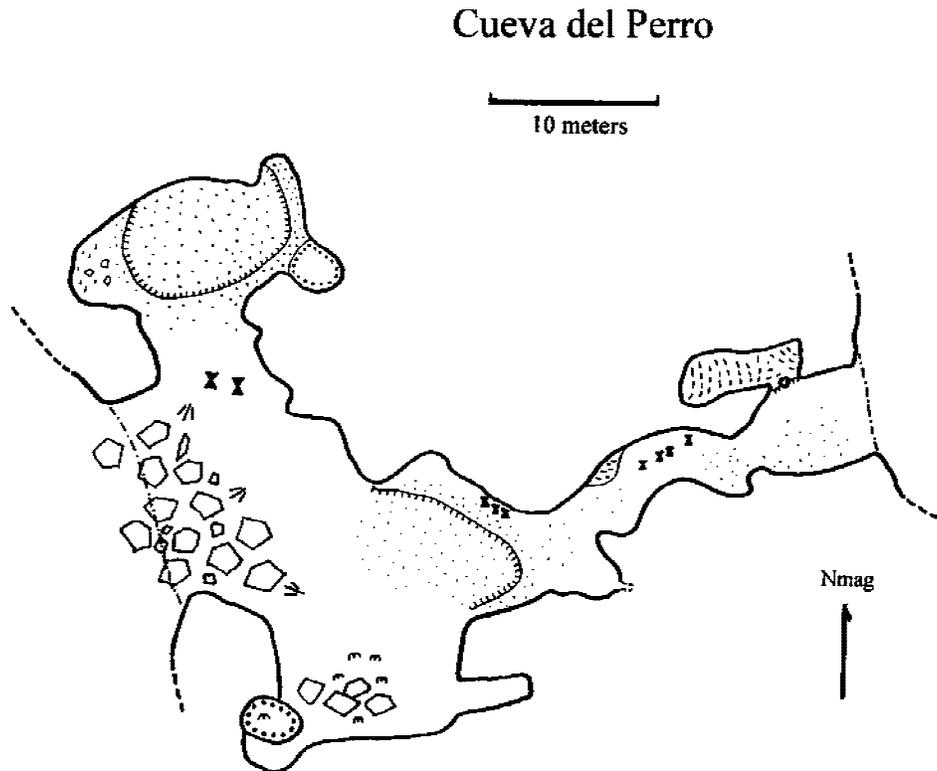


FIG. 2. Plan view of Cueva del Perro. Map symbols and conventions follow Dasher (1994).

order of 0-3000 excess rcyrbp, or less than 10% of the radiocarbon ages reported here.

Cueva de la Vaca 2030161 N; 769331 E.
(Fig 4.)

This cave was apparently not excavated by either Anthony or Bee. It may have been one of the caves visited by the Smithsonian party in 1976-77, but no adequate site documentation of this work exists. Several cubic meters of sediment had previously been removed from this site, but undisturbed sediment remains around the periphery. During work in 1996 and 1998, *Elasmodontomys*, *Heteropsomys*, *Nesophontes* and *Acratocnus*, together with two species of bat, were recovered from the upper 45 cm of the deposit (Table 2). The commonest taxon, *Elasmodontomys*, occurs to within 5 cm of the surface. A radiocarbon date on *Pluerodonte* shell carbonate from 12 cm depth gave an age of 33,670 370 rcybp (Beta # 95854).

Cueva Del Perezoso 2030224 N; 769302 E.

This is a previously unworked site located in 1996. A calcite-indurated cave mud, some 15-25 cm thick, overlies the floor of a shallow cave at its mouth, and is protected by large slabs of limestone roof fall. Excavation at this site yielded *Acratocnus* and *Elasmodontomys* remains (Table 2). Acid-dissolution of a bone fragment yielded no collagen residue and the site remains undated.

DISCUSSION

It is an axiom of paleontology that the fossil record is unlikely to yield the last individuals of a lineage, so extinction dates must be inferred from 'last occurrence' dates. Where a sequence of independent dates is available, it may be possible to estimate the statistical confidence limits around an inferred extinction date (McFar-

TABLE 2. Paleofaunal recoveries from Barahona caves.

	CC	CP	CV	CPZ
EDENTATA				
<i>Acratocnus</i>				
<i>odontrigonus</i>	X		X	X
INSECTIVORA				
<i>Nesophontes</i>				
<i>edithae</i>	X	X	X	
CHIROPTERA				
<i>Monophyllus</i>				
<i>plethedon</i>		X		
<i>Brachyphylla</i>				
<i>cavernarum</i>	X	X	X	
<i>Artibeus</i>				
<i>jamaicensis</i>		X		
<i>Stenoderma</i>				
<i>rufum</i>	X	X		
<i>Phyllonycteris</i>				
<i>major</i>	X	X		
<i>Eptesicus</i>				
<i>fuscus</i>	X	X	X	
RODENTIA				
<i>Elasmodontomys</i>				
<i>obliquus</i>	X	X	X	X
<i>Heteropsomys</i>				
<i>insulans</i>	X	X	X	

CC = Cueva Clara, CP = Cueva del Perro, CV = Cueva de la Vaca, CPZ = Cueva del Perezoso.

lane, 1999), but in no case is the West Indian mammal record currently adequate for statistical treatment.

Several authors have attempted to 'shoehorn' West Indian extinctions into a single (or at least preminent) interval, based on global or continent-wide events. The most popular events have been terminal Pleistocene climate change and human immigration. Thus, Pregill and Olson (1981) suggested that the spread of mesic habitat during the Holocene may have led to the extinction of a xeric-adapted Pleistocene fauna, an explanation also adopted by Woods (1989a). As a reliable database of radiometric dates has begun to accumulate, it has become apparent that the late Quaternary extinction crisis cannot be attributed to a single phenomenon (Flemming et al., 1998). Last occurrence dates for West Indian late Quaternary mammals are distributed between at least three intervals (Table 3; Fig. 5): the Sangamonian interglacial (or its immediate aftermath), the mid-

Holocene, and the historic era (post AD 1500). The mid-Holocene extinctions are particularly poorly constrained by a shortage of radiometric dates and may prove to be illusory as additional dates become available.

Acratocnus

The Puerto Rican ground sloth, *Acratocnus odontrigonus* (including Anthony's *A. major*), is known from numerous poorly documented cave excavations in northwestern Puerto Rico. No single sloth or precisely defined 'sloth stratum' has been radiometrically dated. However, the animal has not been found in superficial contexts, nor has it been found in archaeological deposits that are otherwise common in caves of the Barahona district and elsewhere. Anthony recovered "one or two fragments of the sloth" from excavations in Cueva Clara (field notes in the Department of Mammalogy, American Museum of Natural History, 1916); although the stratigraphy of these finds cannot be reconstructed, it is unlikely that the specimens postdate the age of >34,650 rcyrbp reported here for the -30 cm stratum. *Acratocnus* was present in the Cueva de la Vaca excavation at 33,670 ± 370 rcyrbp. No date is available for the Cueva Del Perezoso specimens, but *Acratocnus* is absent from the Cueva Del Perro 'Layer B' at 5410 ± 80 rcyrbp, despite the presence of *Elasmodontomys*. The evidence available, though inadequate, is consistent with the view that *Acratocnus* survived into the late Pleistocene but disappeared from northwestern Puerto Rico before the mid-Holocene, without trace of anthropogenic contact.

Elasmodontomys

Elasmodontomys obliquus was recovered from Cueva Clara, Cueva del Perezoso, Cueva de la Vaca at 33,670 ± 370 rcyrbp, and Cueva del Perro at 5410 ± 80 rcyrbp. This large bodied (mean body mass = 13.7 kg, maximum = 17.6 kg, minimum = 9.4 kg; based on regression equation from Biknevicius et al., 1993, using 65% distal femur anterior-posterior diameter, n = 33) rodent

Cueva Clara

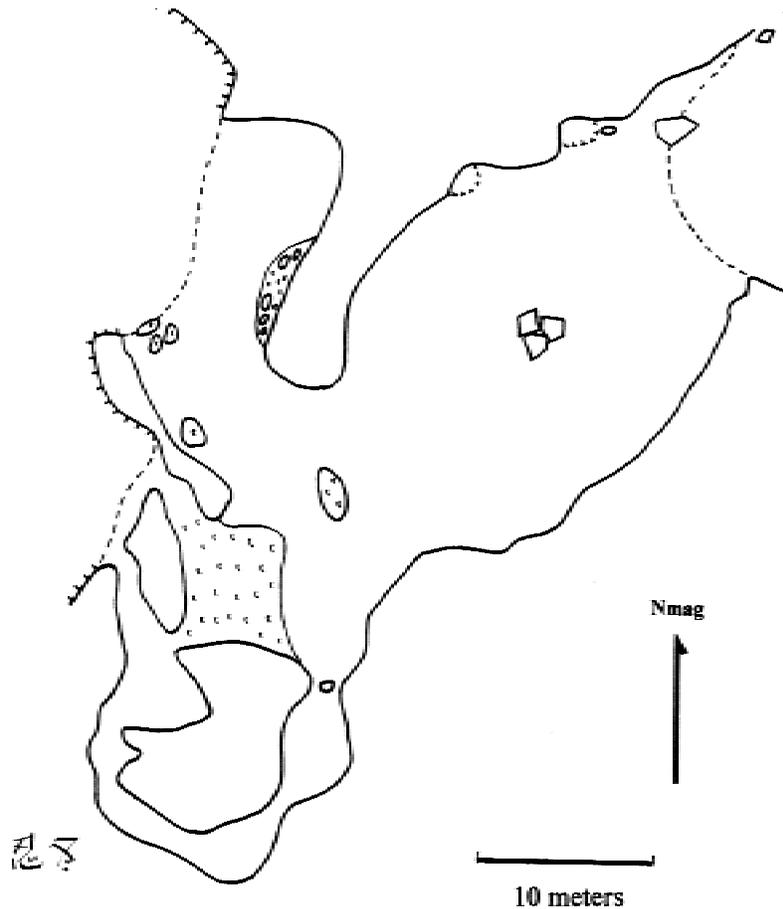


FIG. 3. Plan view of Cueva Clara. Map symbols and conventions follow Dasher (1994).

has never been found in Amerindian middens or other anthropogenic associations, even though the smaller rodent *Isolobodon*, believed to be an Amerindian introduction from Hispaniola (Woods, 1989b), is a common Amerindian dietary element and appears in middens from caves in the Barahona district.

The colonization date of Puerto Rico by Amerindians is uncertain, with the oldest secure radiocarbon date being 3010 ± 70 rcyrbp (Rouse, 1992). Burney et al. (1994) argued that the sudden appearance of

abundant charcoal in the sediment record of a Puerto Rican lake at ~ 5300 cal-BP is the signature of Amerindian colonization but this remains speculative. It is likely that *Elasmodontomys* persisted at least up to, and perhaps beyond, Amerindian first contact.

Heteropsomys

Anthony (1926) described three taxa of rodents from his Puerto Rican collections; *Isolobodon portoricensis* Allen 1916, which was considered by Anthony and all subse-

Cueva de la Vaca

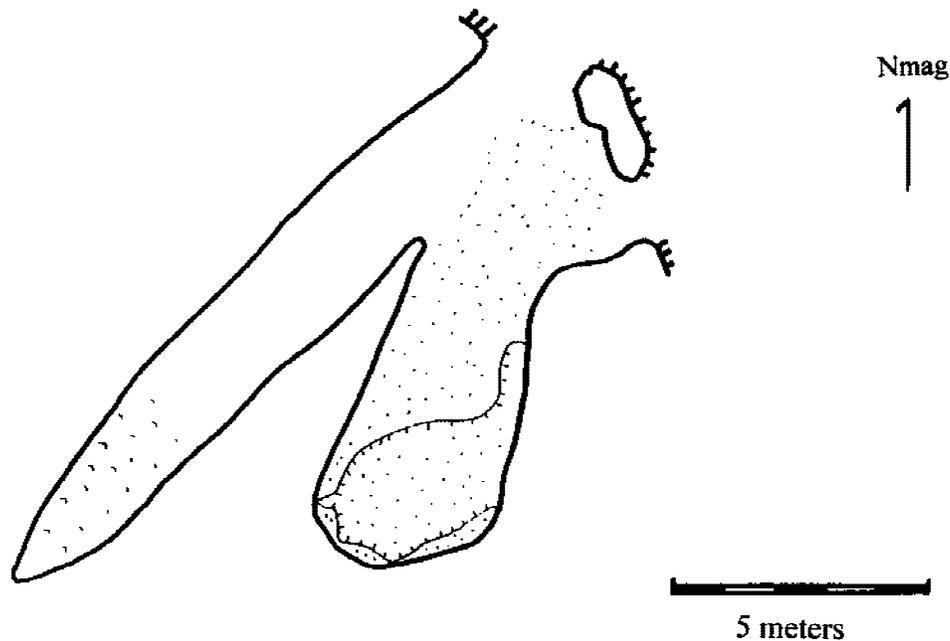


FIG. 4. Plan view of Cueva de la Vaca. Map symbols and conventions follow Dasher (1994).

quent workers to be an Amerindian introduction; *Heteropsomys insulans* Anthony 1916, and *Homopsomys antillensis* Anthony 1917. Anthony noted that the latter two genera were very closely related, and "it may be that the two forms should be considered congeneric" (Anthony, 1926: p151). Varona (1974) treated *Heteropsomys* and *Homopsomys* as congeneric, without elaboration, whereas Woods declared them generically distinct (1989b) and then synonymous (1993). I follow Woods (1993) in referring all late Pleistocene and Holocene Puerto Rican echimyid material to *Heteropsomys*.

Heteropsomys was recovered from Cueva Clara, Cueva de la Vaca, and 'layer B' of Cueva del Perro; the latter demonstrating the survival of the taxon into the mid-Holocene. The limited postcranial material available for *Heteropsomys* suggests that the animal closely matched *Isolobodon* in size, and thus the absence of this animal from Amerindian associations strongly suggests a non-anthropogenic extinction.

Nesophontes

Insectivores of the genus *Nesophontes* are known from Cuba, Hispaniola, the Cayman Islands, and Puerto Rico; the latter supporting a single large form, *N. edithae*. The Cayman Islands form is reported to co-occur with *Rattus* (Morgan, 1994), implying a post AD1500 extinction. In the absence of direct radiocarbon date or a description of a closed stratigraphic context this should be considered probable but conjectural. Owl-pellet remains of *Nesophontes* from superficial contexts in Hispaniola were reported by Miller (1930) to retain tissue and hair, and have been considered as evidence that the animal was extant into the 20th century (e.g., Woods and Eisenberg, 1989). However, *N. hypomicrus* specimens preserving tissue and hair collected from Cueva Jurg, Parque Nacional Sierra de Baoruco, Dominican Republic, provided a direct accelerator radiocarbon date on bone collagen of 710 ± 50 rcyrbp, demonstrating that preser-

TABLE 3. Last occurrence dates for West Indian late Quaternary extinct mammals

Genus	Island	Last dated occurrence
<i>Clidomys</i>	Jamaica	174,000 ± 12,000 ^a
<i>Oryzomys</i>	Jamaica	AD 1877 ^{b*}
<i>Xenothrix</i>	Jamaica	1870 ± 50 ^k
Undescr. rodent	Jamaica	11,260 ± 80 ^l
<i>Nesophontes</i>	Puerto Rico	5410 ± 80 ^c
<i>Elasmodontomys</i>	Puerto Rico	5410 ± 80 ^c
<i>Heteropsomys</i>	Puerto Rico	5410 ± 80 ^c
<i>Acratocnus</i>	Puerto Rico	33,670 ± 370 ^c
<i>Nesophontes</i>	Cuba	490 ± 50 ^{h*}
<i>Megalocnus</i>	Cuba	6250 ± 50 ^{h*}
<i>Nesophontes</i>	Hispaniola	590 ± 50 ^{h*}
<i>Rhizoplagiodonita</i>	Hispaniola	3755 ± 175 ^f
<i>Antillothrix</i>	Hispaniola	3850 ± 135 ^j
<i>Brotomys</i>	Hispaniola	430 ± 60 ^{l*}
<i>Isolobodon</i>	Hispaniola	710 ± 50 ^{l*}
<i>Capromys</i>	Grand Cayman	375 ± 60 ^g
<i>Amblyrhiza</i>	Anguilla	91,000 ± 9800 ^d
<i>Megalomys</i>	St. Lucia	AD 1849 ^{l*}
<i>Megalomys</i>	Martinique	AD 1902 ^{b*}
<i>Megalomys</i>	Barbuda	750 ± 50 ^{e*}
<i>Megalomys</i>	Antigua	AD 1200-1260 ^e

*signifies direct date on bone collagen, or live-caught museum specimen. Other dates by stratigraphic association. ^aMcFarlane et al., 1998b; ^bMacPhee and Flemming, 1999; ^cThis paper; ^dMcFarlane et al., 1998a; ^eMcFarlane and Flemming, unpublished data; ^fWoods, 1989a; ^gMorgan, 1994; ^hMacPhee et al., 1999; ⁱAllen, 1942; ^jRimoli, 1977; ^kMacPhee, 1996; ^lunpublished data, this author.

vation of organic material is not a reliable indicator of very recent age (MacPhee et al., 1999). These authors provide a last-occurrence date of 680 ± 50 rcybp for *N. paramicus* on Hispaniola, consistent with a rapid extinction following the circa AD1500 introduction of *Rattus rattus* to the island.

Nesophontes has not been recovered from superficial contexts on Puerto Rico. The last-occurrence date for a tightly constrained stratum containing *N. edithae* is currently 5410 ± 80 rcyrbp from 'layer B' of Cueva Perro. A single *Nesophontes* femoral fragment was recovered from the overlying, more sparsely fossiliferous 'layer A.' Whether this specimen is substantially younger than the 'layer B' specimens cannot be answered on the basis of the available material. Morgan and Woods (1986) reported *Nesophontes* from an Amerindian site on Vieques, but this is difficult to evalu-

ate without a site description and stratigraphic details. A possible *Nesophontes* association with an Amerindian midden has also been reported from Mona Island (A. Nieves, pers. comm.). Presently, it is prudent to note the marked contrast between the superficial occurrence of *Nesophontes* on Hispaniola and the Cayman Islands, and its apparent absence from such contexts on mainland Puerto Rico.

The West Indian radiometric database is currently too coarse to confidently identify patterns in the vertebrate extinction record that have pan-West Indian utility. It should be noted that many of the larger-bodied taxa that have been uncritically assumed to be victims of Amerindian hunting lack any such demonstrable association. *Amblyrhiza*, the 100-200 kg giant rodent of the Anguilla Bank and its somewhat smaller sister taxon *Clidomys* of Jamaica, apparently disappeared a hundred millennia before human first-contact (McFarlane et al., 1998a; 1998b). The ~14 kg rodent *Elasmodontomys* of Puerto Rico provides an especially interesting case, because the 'last-occurrence' date of 5410 rcybp overlaps (within statistical confidence limits) the ~5300 rcybp date (Burney et al., 1994) for the appearance of potentially anthropogenic charcoal on the island. *Elasmodontomys* has not appeared in an archaeological context, even though the Taino are believed to have introduced the smaller rodent *Isolobodon* from Hispaniola and remains of the latter species are common in Puerto Rican midden deposits.

The insectivore *Nesophontes paramicus* may have survived on Hispaniola into the early historic era, but no comparable evidence of survival beyond the mid-Holocene has been found for *N. edithae* on mainland Puerto Rico. A similar problem exists for the Lesser Antillean *Megalomys*, 'giant rice rats' which appear to have disappeared very rapidly after European first-contact on Barbuda, but which persisted on St. Lucia into the late 19th century and on Martinique into the early 20th century (Flemming and McFarlane, 1997). These varied extinction chronologies show no obvious correlation with habitat destruction, the introduction of feral mongooses, or Amerindian exploitation. Given that 5 of

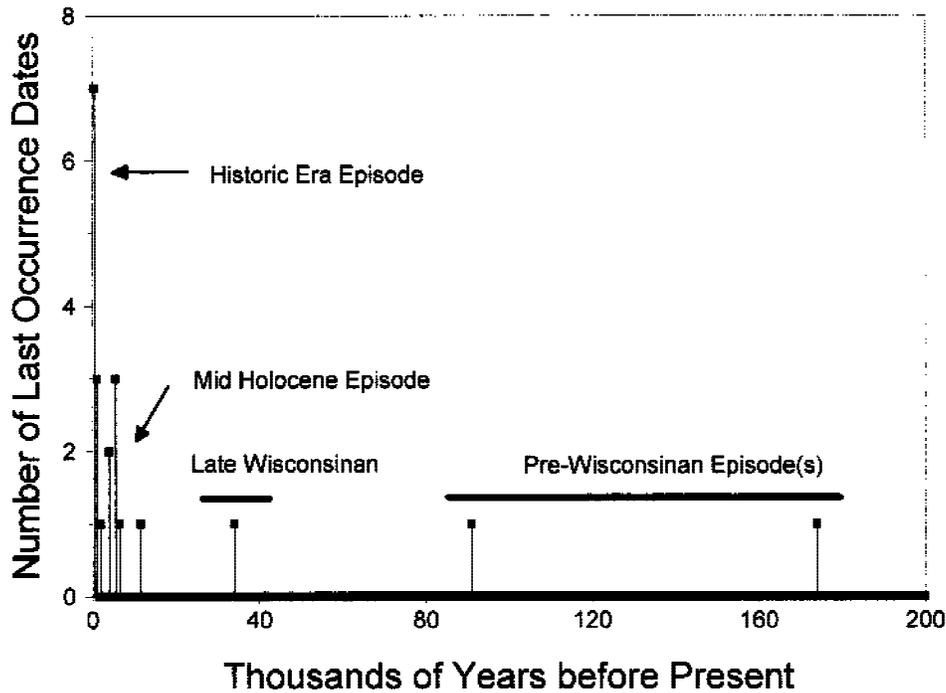


FIG. 5. Distribution of West Indian mammal 'last occurrence' dates.

the 8 global, genus-level rodent extinctions of the historic era have impacted West Indian taxa (data from MacPhee and Fleming, 1999), the difference of perhaps four centuries between different *Megalomys* species extinctions in the Lesser Antilles, and perhaps four millennia between different *Nesophontes* species extinctions in the Greater Antilles, demands explanation. The extinction of the entire suite of greater Antillean ground sloth genera is currently beyond explanation, due to the lack of radiometric dates. The solutions to these problems can only derive from the accumulation of a dense database of radiometric dates, with careful attention to stratigraphic control and the problems of taphonomy in caves.

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