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Redetermination of Holotype of *Isolobodon portoricensis* (Rodentia, Capromyidae), with Notes on Recent Mammalian Extinctions in Puerto Rico*

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ABSTRACT

While examining material of the Antillean capromyid *Isolobodon portoricensis*, we discovered that the specimen designated by Allen (1916) as the holotype of this species has been consistently misidentified in the literature (e.g., Lawrence, 1993). In this paper we correct this error and make some observations on Allen's (1916) designated type series in the AMNH-M collections. Additionally, we analyze information bearing on the extinction date of *I. portoricensis* and its purported utilization by humans as a food resource.

INTRODUCTION

As measured by the number of specimens in collections, the Puerto Rican hutia *Isolobodon* ranks as one of the best known members of the extinct Quaternary mammal fauna of the West Indies. The systematic history of this taxon and its contents is somewhat confusing. Three species have been named: *portoricensis*, *montanus*, and

levir (the last two originally placed in different monotypic genera by Miller [1922]). Reynolds et al. (1953) doubted the validity of *levir*, and it now seems to be generally accepted that this nomen is a synonym of *portoricensis* (Woods, 1993). Samples assigned to *montanus* and *portoricensis* also differ very little when ontogenetic and clinal variation is taken into account (Reynolds et al., 1953; Woods, 1993), but most authors

* We respectfully dedicate this paper to the memory of our friend and colleague, Karl F. Koopman (1922–1997).

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continue to separate the two species. Varona (1974) followed Mohr (1939) in considering *Isolobodon* a subgenus of *Plagiodontia*. However, all *Isolobodon* can be readily distinguished from other capromyids, including *Plagiodontia*, by derived features of cheek-tooth cementum, warranting a genus-level distinction (Woods, 1989a; MacPhee and Iturralde-Vinent, 1995). As *Isolobodon montanus* has been recognized from Hispaniolan localities only, referral of all Puerto Rican specimens discussed here to *I. portoricensis* is not controversial.

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ABBREVIATIONS

AMNH-M	American Museum of Natural History, Department of Mammalogy
AMNH-VP	American Museum of Natural History, Department of Vertebrate Paleontology
AMS ¹⁴ C	accelerator mass spectrometry radiocarbon dating
Beta	Beta Analytic, Coral Gables, FL (radiocarbon dating lab)
cal-AD	solar years AD (used with calibrated dates)
rcyrbp	radiocarbon years before present (radiometric datum AD 1950)
yrbp	years before present

REDETERMINATION OF HOLOTYPE OF *ISOLOBODON PORTORICENSIS*

The first scientific collection of the Puerto Rican hutia was made in 1915 at Cueva de la Ceiba by the anthropologist Franz Boas, who sent his faunal collection to J. A. Allen with the notation that

[t]he remains were found in a heavy deposit of ashes in a cave in the Jobo district, between Utuado and Arecibo. In the same deposit was the burial of a child. A very large number of shells of crabs and of various kinds of snails were found. The deposit was undoubt-

edly artificial. I do not believe that it was purely an accumulation of kitchen refuse. It seems more likely that it was made for some other purpose. There is no indication of post-Columbian disturbance of the deposit, but I do not presume that it is more than a few hundred years old (F. Boas, in litt., cited by Allen, 1916: 18).

Allen (1916) immediately recognized that prominent among the ash-encrusted bones sent to him by Boas were the remains of a previously unknown capromyid—the first extinct mammal species to be discovered in Puerto Rico. Boas' material included more than a dozen skulls and large cranial fragments. Allen selected one of the more complete specimens among these remains as the *portoricensis* holotype (fig. 1), describing it as follows (Allen, 1916: 19 and pl. 1, figs. 3–5):

Isolobodon portoricensis gen. et sp. nov.

Type, No. 38409a, from the Cuerva de la Seiba [i.e., Cueva de la Ceiba], near Utuado, Porto Rico; coll[ector], Dr. Franz Boas. The type skull has the nasals and entire upper dentition complete, but lacks part of one zygoma and the braincase posterior to the fronto-parietal suture.

Allen (1916: 19) also made a critical comparison to other material in the collection from the type locality: "type skull [is] fully adult but smaller and evidently younger than [paratype] No. 38409b."

The fate of the holotype and type collection of *Isolobodon portoricensis* from this point onward is obscure. Although the taxon was certainly not forgotten (e.g., Miller, 1929a), Goodwin (1953) failed to include the holotype of *portoricensis* in his catalog of the AMNH-M type collection. Lawrence's (1993: 149) later catalog rectified this omission. However, her account of the holotype and its condition is at variance with Allen's: in her paper, the accession number of the *portoricensis* holotype is listed as AMNH-M 38409, rather than as 38409a, and the condition report reads "Cranium partial (nasals, occiput, basiocciput, incisors, both P4, M1s, and left M2, M3 missing)." One might assume that Lawrence's description differs from that of Allen because of postaccession damage to the holotype, but this is not the case: Allen's (1916) holotype specimen exists in the same state as when he described it, but to the confusion of subsequent investigators, it was placed in the general AMNH-

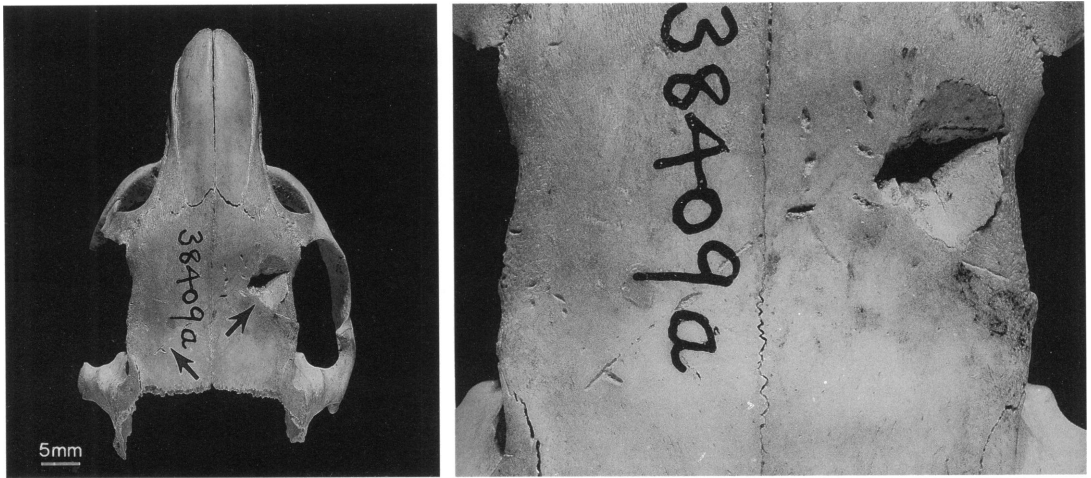


Fig. 1. *Isolobodon portoricensis* holotype cranium: AMNH-M 38409a (showing suffix as corrected by authors). **Left**, dorsal view, showing premortem damage (arrows). **Right**, closeup of frontal bones of same specimen. Punctures and cracks are still filled with gray ash (possibly from cooking fires) from the deposit in which the specimen was found (see text).

M collections bearing another accession suffix (38409b).

It is easy to determine that the specimen described by Lawrence is one of the paratype skulls, as it is illustrated by Allen on the same plate as the true holotype (Allen, 1916: pl. 1, figs. 6–8; our fig. 2). Evidently, substitution in the collections occurred when the numbers were physically written on the spec-

imens, whenever that took place; it had certainly happened at or before the time that H. E. Anthony (1918) had several *Isolobodon* specimens photographed for his monograph on Puerto Rican mammals. Three skulls having similar accession numbers (i.e., AMNH-M 38409a, 38409b, and 38409c) are depicted on Anthony's (1918) plate 62. Of these, his AMNH-M 38409a, listed as the type in the

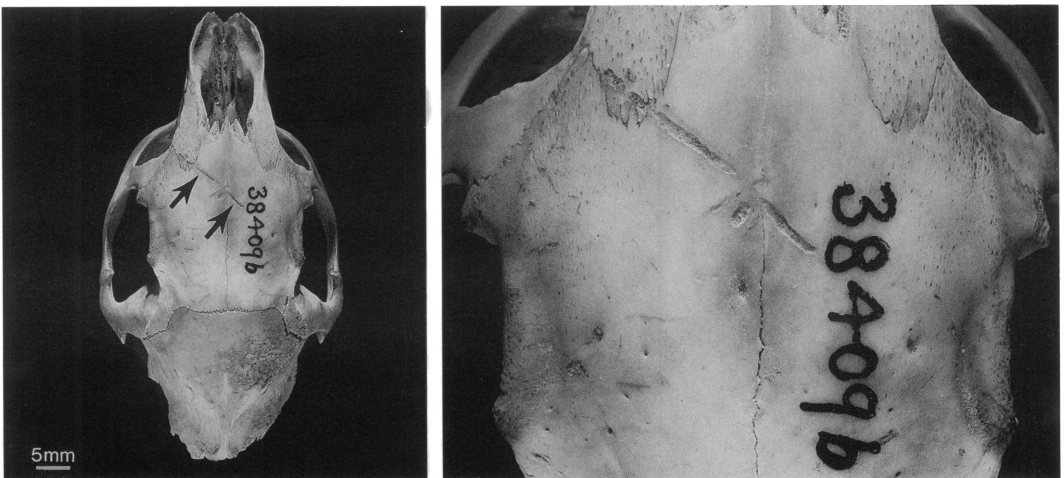


Fig. 2. *Isolobodon portoricensis* paratype cranium: AMNH-M 38409b (showing suffix as corrected by authors). **Left**, dorsal view, showing possible premortem damage (arrows). **Right**, closeup of frontal bones of same specimen. This specimen has been consistently misidentified as the holotype of this species since publication of Anthony's (1918) monograph on Puerto Rican land mammals.

figure caption, actually conforms to Allen's paratype *b*. Anthony identified another specimen as AMNH-M 38409*b*, but this corresponds to a *third* member of Allen's paratype series. The true holotype is in fact illustrated in Anthony's monograph, but as AMNH-M 38409*c*.

Some additional mixups must have occurred, because Allen's paratype *b* was eventually inscribed with the number 38409*a* and placed in the type collection; the real holotype was deposited with the remaining paratypes. Anthony's confusion of specimens required that he use language different from Allen's when redescribing the holotype (e.g., Anthony, 1918, 1926), which is the description on which Lawrence (1993) relied.

These errors have now been repaired, and the proper holotype is now installed in the AMNH-M type collection. We correct the relevant entry in the Lawrence (1993) catalog to read:

Isolobodon portoricensis J. A. Allen
Ann. New York Acad. Sci. 27: 19, 1916.
HOLOTYPE: **38409a**. Cranium only.
LOCALITY: Puerto Rico; Jobo; Cueva de la Ceiba, near Utuado.
COLLECTOR: F Boas. Original number unknown.
CONDITION: Cranium partial (nasals and entire upper dentition complete).

DISTRIBUTION AND CULTURAL UTILIZATION OF *ISOLOBODON*

Remains of *I. portoricensis* have been discovered at late Holocene occupation sites on many islands in the northeastern Caribbean (La Gonave, Ile de la Tortue, Hispaniola, Mona, Puerto Rico, Vieques, St. Thomas, St. Croix). No other endemic West Indian rodent species enjoyed such an extensive distribution. Indeed, on some islands (e.g., Virgin Islands), hutias have been recovered *only* within human occupation horizons, which strongly suggests they could not have been endemic and had to have been introduced by humans (Miller, 1918; Woods, 1996).³ For

this reason, the question has been raised frequently whether Puerto Rican hutias were kept in a state of captivity or even quasi-domestication by Amerindians (cf. J. A. Allen, 1916; Anthony, 1918; Miller, 1916, 1918; G. M. Allen, 1942; Woods, 1996).

Larger land mammals (various species of sloths and other rodents) also existed in Hispaniola and Puerto Rico during the late Quaternary. Oddly, none of these has turned up in any undisturbed archeological contexts; by contrast, manatees (*Trichechus manatus*) and even monk seals (*Monachus tropicalis*) have been found in middens and other coastal sites (Rainey, 1940; personal obs.). One explanation for this might be that larger land mammals disappeared so rapidly after human colonization of the Greater Antilles in the early to mid-Holocene that their remains have simply not yet been found in archeological contexts (Martin and Steadman, 1999; but see Burney et al., 1994; Flemming et al., 1998). However, explanations of extinction that do not involve overhunting also exist (MacPhee and Marx, 1997).

Although Allen (1916) made reference to cultural modification of *Isolobodon* bones recovered at the type locality, his remarks are very brief and need some amplification to put them into a useful perspective. Allen's (1916) most perceptive remark was that all skulls recovered from the type locality were found broken: "... none of them [is] quite complete, the occipital and parietal regions and the nasals being usually lacking, while many consist of only the middle portion of the skull." This last type of breakage pattern is arguably not natural, and suggests human preparation to get at the brain, rhinarium, neck musculature, and other soft tissues.

Allen (1916: 17) did not provide a faunal analysis of the Cueva de la Ceiba material, and his paper contains little quantitative information. It is evident that remains of *Isolobodon* constituted most of the faunal sample, although a few bird bones ("a pigeon and a parrot, the latter probably referable to the genus *Amazona*") were also recovered. Remarkably, the *Isolobodon* material consists mostly of hemimandibles (150) and skulls (20), or 43% of the "nearly 400 piec-

³ *Isolobodon* may have evolved originally in Hispaniola, as this is the only context in which it has been found in nonanthropogenic settings (Woods, 1996; but see Anthony, 1918). This point could be settled conclusively by finding and directly dating hutia material that is truly old (i.e., > 10,000 yrbp), but this project has yet to be undertaken.

es" identified by Allen to element.⁴ Postcranial bones are thus proportionately underrepresented, but the reason for this bias is not known. Bias resulting from butchering techniques seems unlikely since the animal's body size was relatively small (see below). Allen (1916) noted that "several hundred fragments of little or no scientific value" were also collected—possibly indicating that postcranials were broken up or cracked open during preparation or consumption.

A few skulls display unambiguous evidence of human manipulation. On the holotype skull (AMNH-M 38409a) there is a clear indication of premortem (or immediate postmortem) damage in the form of a circular, depressed fracture area on the right frontal, approximately 5 mm in diameter (fig. 1). The center of the impact site bears a small puncture wound. The frontals are incised by a linear cut mark which appears to terminate in or just before the puncture.

In mammals, a sandwich of dense connective tissues, consisting of scalp, periosteal, and dura mater, sheathes the tabular bones comprising the cranial vault. A forceful blow delivered to the vault of a living individual or intact cadaver will result in radial fracturing around the site, but the broken pieces of skull will tend to remain more or less in place thanks to the surrounding dense connective tissues. If the head is left undisturbed, the pieces will likely retain their relative positions after soft tissues disappear, allowing determination of the time of injury (Brothwell, 1965). Conversely, in skulls broken long after death and decay, there is nothing to keep small fragments in their proper relative positions so they tend to simply fall away. In the *portoricensis* holotype, the position of fractured pieces at the impact site is consistent with premortem injury.

We infer from this that the depressed fracture and perforation in AMNH-M 38409a were caused by an implement that terminated in a sharp point or spike. Both cut mark and

puncture wound may have been caused by the instrument being dragged across the cranial roof with some force (perhaps while skinning the animal, or stabbing it to kill it). Limestone pebbles are unlikely to cause this kind of damage under any circumstances, whether natural or anthropogenic. A similar linear cut mark is seen on the frontals of another paratype skull, AMNH-M 38409b (fig. 2). The feature begins just above the edge of the right orbit and slices obliquely over to the rim of the left infraorbital foramen.

Mandibles also show some signs of manipulation. Allen (1916: 18) stated that "in many [of the jaws] the condylar portion is defective or wholly lacking," although we saw nothing on any jaw that could be considered an unambiguous cut mark. If the condyles were removed by human agency, they were evidently snapped off rather than cut off—not a difficult undertaking given the gracility of this part of the mandible in these rodents.

Of the few long bones represented, none shows obvious signs of butchering on shafts or articular ends. A few specimens in the collection are deeply calcined, suggesting that hutias were cooked, at least on occasion. Capromyids are relatively large rodents and therefore a potentially significant source of meat (cf. Anthony [1920] concerning hutia hunting in 20th century Jamaica). Allen (1916) estimated the size of *Isolobodon portoricensis* to have been roughly comparable to that of Desmarest's hutia (*Capromys pilorides*), an extant Cuban capromyid (adult weight, ~ 2.6 kg; Silva and Downing, 1995). This compares favorably to guinea pigs (*Cavia*, 0.25–0.75 kg) and agoutis (*Dasyprocta*, 2.0–3.8 kg), both of which were introduced to various West Indian islands by Amerindians (Miller, 1930), although later introductions are known to have occurred as well (DeVos et al., 1956). Because of its substantial size the Puerto Rican hutia would have been an animal worth hunting or transporting, especially in smaller island contexts where few or no endemic mammals other than bats would have been available. On a final note, it is worth recording that the Cueva de la Ceiba sample included a tibia with a healed fracture and a mandible with an abraded molar. This is not an unusual amount

⁴ Allen (1916) listed the following elements of *I. portoricensis* as coming from the same collection as the holotype skull: 20 skulls, 150 mandibular rami, 15 scapulae, 1 "clavicle" [= juvenile radius], 15 humeri, 30 ulnae, 10 radii, 25 femora, 40 tibiae, 5 fibulae, 1 sacrum, 50 ribs, 50 innominate bones, and "several hundred fragments."



Fig. 3. Reconstruction of *Isolobodon portoricensis*. The cord around the animal's hind leg need not necessarily imply domestication as such. For example, in reference to the anthropogenically influenced distribution of *I. portoricensis*, animals would have to have been caught and kept alive before being transported to other islands, whether or not they were kept "in captivity" thereafter.

of pathology to encounter in a natural population, of course, but it is commonplace that injuries such as these are less likely to be mortal in animals that are kept (and cared for) in captivity.

It must be admitted on this evidence that it is not possible to conclude that *Isolobodon* was husbanded (as opposed to hunted) in Puerto Rico. Nor does there appear to be any independent archeological evidence that can be recruited to support this notion. If hutias were actually kept, they would have to have been housed in structures that would not allow their escape. Quadrilateral areas defined by borders of piled or erected stones (usually described as *juegos de bola* or ball courts even though there is no definitive evidence that most of them were used as such) have been identified at a number of Puerto Rican archeological sites (e.g., Rainey, 1940; Mason, 1941). However, the areas enclosed by these features are usually quite large, and it therefore seems rather unlikely that they could have functioned as pens or hutches.

Wing (1991) reported a high incidence of dental mutilation (evulsion of fourth premolars) in dogs at Sorcé, a Saladoid site (~2000–1500 yrbp) on Vieques Island, east of Puerto Rico. She thinks the mutilation may have been practiced in order to insert a muzzle of some sort, so as to prevent the dogs from preying on hutias and ground-nesting birds that humans wanted themselves.

As to the matter of the unusually wide distribution of hutias, perhaps the best inference

is that *Isolobodon* individuals were occasionally trapped alive by Amerindians, who then used them to stock any nearby islands lacking this convenient resource (cf. similar utilization of *Dasyprocta* in aboriginal West Indies [Allen, 1942]; cf. also rabbits and hares (*Oryctolagus* and *Lepus*) on islands elsewhere [Nowak, 1999]). This scenario would explain the distribution and frequent utilization of Puerto Rican hutias by humans without requiring that the latter husbanded them to any significant degree (see fig. 3).

EXTINCTION OF *ISOLOBODON PORTORICENSIS*

EARLY LOSS OR LATE SURVIVAL?

Whatever its relationship with humans, the Puerto Rican hutia became extinct nevertheless, as did two dozen other species of endemic Antillean land mammals (MacPhee and Flemming, 1999). Indeed, from one perspective Puerto Rico was hit the hardest of all the larger islands of the West Indies, as it lost 100% of its endemic nonvolant mammals.

In Anthony's (1926: 146) view, *I. portoricensis* was likely to have been "the last mammal to become extinct on Porto Rico," although he cited no decisive evidence for this beyond its occurrence in human occupation sites. It has frequently been assumed that *I. portoricensis* survived into the early 16th century or later, perhaps until the introduction of the mongoose in the late 19th cen-

ture (Hoagland et al., 1989; Woods et al., 1985). Recently, Woods (1993: 804) has gone further and stated that "this species survived in Hispaniola and Puerto Rico until the last few decades, and may still survive in certain remote areas [such as] La Tortue island off the north coast of Haiti." However, as there has been no net increase in the evidence supporting late survival (see below), the question of when and under what circumstances the Puerto Rican hutia disappeared remains open.

The only contemporary reference to hutia-like mammals living in Hispaniola occurs in the *Historia general y natural de las Indias* of Oviedo y Valdés (1535). According to Miller (1929b), the relevant passage in the *Historia* may have referred with about equal probability to (still extant) *Plagiodontia* as to (extinct) *Isolobodon*. Although Oviedo y Valdés (1535) made reference to the gustatory excellence of several of Hispaniola's endemic rodents (identified as *hutia*, *cori*, and *muhoy*), his text does not state or even imply that Amerindians kept any of them in confinement. While his report may be said to confirm the survival of some native Hispaniolan species into the early part of the 16th century, its value is otherwise limited.

Specimen-based evidence for late disappearance of the Puerto Rican hutia is equally limited, and possibly contradictory. There are a few reported associations with introduced *Rattus rattus* (see below), but this establishes only that the "last occurrence" of *Isolobodon portoricensis* evidently occurred subsequent to AD 1500. Radiocarbon dating of critical samples can potentially provide much finer resolution of extinction times (cf. Steadman et al., 1991). Using this approach, MacPhee et al. (1999) tried to determine a "last occurrence" date for the Antillean island-shrew *Nesophontes*, thought to have survived into the 20th century. The latest direct date on *Nesophontes* material retrieved in the course of that investigation was 590 ± 50 rcyrbp (cal-AD 1295–1430, with 2-sigma envelope), based on a sample from a Cuban cave site. All other dated material was older, even though some specimens were reported as having been found in association with *Rattus*. Radiometric dating provides an independent test of age which, in this instance,

was incompatible with the hypothesis of very recent survival of the target taxon. When an adequate sequence of independent dates is available, it may be possible to estimate the statistical confidence limits around an inferred extinction date (McFarlane, 1999). The next section discusses our effort to begin to place the "last occurrence" of *I. portoricensis* on such a basis.

METHODS

Isolobodon specimens selected for dating are from collections made at two localities—Cueva de la Ceiba, described above, and an unnamed cave on Hacienda Jobo near Utuado, where H. E. Anthony worked briefly in 1916. The Hacienda Jobo specimen selected for dating (a mandible) comes from a box of uncatalogued AMNH-VP specimens that also included the bones of the Puerto Rican sloth (*Acratocnus odontrigonus*) and another extinct, endemic rodent (*Elasmodontomys obliquus*). Judging from paper slips in the box and Anthony's fieldnotes (Anthony, MS), this collection probably came from the "No. 2 cave" on Hacienda Jobo, which he excavated during the period June 30–July 2, 1916.

Specimens selected were submitted for accelerator mass spectroscopy (AMS) dating (table 1). The $^{13}\text{C}/^{12}\text{C}$ ratios as reported by the lab are normal for recent bone and suggest that no contamination has taken place (Geyh and Schleicher, 1990). The ^{13}C -adjusted ^{14}C dates for these localities (1120 ± 50 and 620 ± 60 rcyrbp, respectively) neither prove nor disprove that Puerto Rican hutias were still extant at the beginning of European entry into the West Indies. However, the 2-sigma calibrated age range (cal-AD 1280–1425) for the Hacienda Jobo jaw is not far removed from that climacteric, and shows that the extinction of *Isolobodon* could not have occurred earlier than the 14th century (cf. Flemming et al., 1998).

In order to test for contemporaneity of extinct species, 0.5 kg of *Elasmodontomys* bone from the same box as the *Isolobodon* jaw was submitted for dating. Although the pretreatment appearance of the *Isolobodon* jaw was identical to that of the *Elasmodontomys* material (i.e., a thin rind of calcium

TABLE 1
AMS ¹⁴C Dates: *Isolobodon portoricensis* from Puerto Rico, West Indies

Accession lab number (locality)	Material	Measured ¹⁴ C age, in rcyrbp	¹³ C/ ¹² C ratio (‰)	Conventional ¹⁴ C age, in rcyrbp (calibrated age intercept, in yr AD) ^a		Calibrated age range, 1 σ (68% probability), in yr AD		Calibrated age range, 2 σ (95% probability), in yr AD	
AMNH-M 38409c Beta-108155 (Cueva de la Ceiba)	2 molars and 1 incisor	1080 \pm 50	-22.5	1120 \pm 50 (cal-AD 960)		885-990		800-1015	
AMNH-VP (uncataloged) Beta-108156 (cave near Hacienda Jobo)	1 hemimandible with teeth	620 \pm 60	-24.5	620 \pm 60 (cal-AD 1315; cal-AD 1345; cal-AD 1390)		1295-1410		1280-1425	

^a Calibrated age ranges are not directly equivalent to "conventional" (¹³C-adjusted) ¹⁴C age \pm 1 or 2 sigmas; the span of a given calibrated range depends on the specific shape of the calibration curve as it crosses confidence envelope around radiocarbon age intercept. Calibrated age is the intercept of radiocarbon age with calibration curve, as reported by lab.

carbonate encased most bones in the collection prior to cleaning), only the *Isolobodon* mandible yielded a date. Evidently, collagen had been stripped from the *Elasmodontomys* bones after deposition, probably as a result of continuous immersion in water within the cave.

DISCUSSION

Before discussing dates for *Isolobodon* and their significance, we would like to sound a cautionary note concerning the importance of dating target taxa directly (and not relying on referential dates based on ¹⁴C dating of other taxa supposedly from the same layer or context). As noted above, the *Isolobodon* fossils from Hacienda Jobo were as encrusted and stained as material of other endemic taxa. If we had chosen to date only *Elasmodontomys* remains, we might have jumped to the conclusion that all fossils from this site were undatable and possibly very old. Conversely, if we had attempted to date *Isolobodon* only, we might have felt justified in using the resulting date to establish "last occurrence" times for *Acratocnus* and *Elasmodontomys* as well. Neither conclusion is warranted, especially in view of the fact that our attempt to date the last-named taxon directly was unsuccessful. When these other Puerto Rican land mammals became extinct is completely unresolved; it need not have been as late as ca. AD 1500 (Flemming et al., 1998). Anthony's (MS) sketchy fieldnotes are of little assistance in this regard, since no stratigraphic data are provided concerning the recovery points of individual specimens.

There are few dates to which those reported in table 1 can be usefully compared. Woods (1989b) reported a number of dates for faunas from cave sites in Hispaniola, many of which included *Isolobodon*. However, as he was not primarily interested in collecting evidence of "last occurrences" of now-extinct taxa, most of his dates are for levels well beneath the surface. All are much older than the ones reported here.

Somewhat more pertinent are dates recently reported by MacPhee et al. (1999) for Monte Culo de Maco, a rock shelter which yielded owl-pellet material (collected for G. S. Miller) containing *Nesophontes*, unidentified

fied mammal hair, *Rattus* bones, and the remains of several small extinct mammals, including *Isolobodon* (for taxon list see Miller, 1930). Despite Miller's (1930) belief that this material was very recent, specimens of the insectivoran *Nesophontes* from this site yielded a ^{13}C -adjusted ^{14}C age of 680 ± 50 rcyrbp, while Old World rats from the same site spanned a range of 480 ± 60 to 310 ± 40 rcyrbp (MacPhee et al., 1999). The disparity between the insectivore and rat dates implies that the owl-pellet remains at Monte Culo de Maco are not penecontemporaneous but were instead built up over several centuries. The message here is that one should always be cautious in accepting the validity of claimed associations between endemics and exotics in such contexts, and always attempt to date the target taxon directly.

The only conclusion that seems warranted from the chronometric evidence available at present is that, contra Miller (1929a, 1929b) and Woods et al. (1985), there is still no evidence to support the view that *Isolobodon portoricensis* survived long into the period of European occupation. The documentary indications are that these rodents were to be seen only very occasionally even in the earliest days of European colonization, and it is therefore entirely plausible that they were in precipitous decline by or even before AD 1500.

Finally, we note that it is somewhat puzzling that Puerto Rican hutias became extinct if in fact they were kept by pre-Columbian Amerindians. Human management (as opposed to overkill) of food animals is usually conceived to be a hedge against extinction. It is clear that much remains to be learned about the cause/effect relationships that resulted in the loss of so many island mammals during recent historic times (MacPhee and Marx, 1997; MacPhee and Flemming, 1999).

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