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A New Megalonychid Sloth from the Late Wisconsinan of the Dominican Republic

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ABSTRACT.—An unusually well preserved skull, mandible, and indisputably associated post-cranial elements of new sloth, *Acratocnus* (*Miocnus*), were recovered from a cave in Jaragua National Park, Dominican Republic. The animal died lying in a rimstone pool and was rapidly coated with a thin calcite patina. We have documented a late Wisconsinan age for this specimen by inorganic ¹⁴C radiometric dating of the patina, with supporting data on the carbon systematics of the speleothems in this cave. This sloth is described as a new species on the basis of the distinctive morphology and relative size of cranial and mandibular features. We consider the close relationship between *Acratocnus* of the Dominican Republic and Puerto Rico to constitute clear evidence for late Tertiary inter-island dispersal of this lineage, congruent with similar evidence from other West Indian terrestrial mammal orders.

INTRODUCTION

Hispaniola has been recognized as a center of diversity for the late Quaternary terrestrial mammal fauna of the Greater Antilles (Woods, 1989) and is a critical test case for comparing competing hypotheses for the origin of these lineages. Nevertheless, the megafaunal and mesofaunal component of this diversity—an eclectic assemblage of megalonychid sloths—remains poorly understood, even at the level of simple alpha taxonomy. MacPhee et al. (2000) and White and MacPhee (2001) have added four new taxa, raising to six the nominal megalonychid alpha diversity. The specimen described below is as morphologically distinct as previously erected taxa assigned to the genus *Acratocnus*.

The specimen under consideration, hereafter the 'Jaragua sloth', was recovered from Cueva del Perezoso, UTM 1988498N 219938E, Jaragua National Park, southwestern Dominican Republic (Fig. 1). The animal died in a shallow rimstone pool and its bones were coated with a thin (~1 mm)

patina of speleogenic calcite sufficiently rapidly that many elements remained in approximate articulation. The preservation quality of much of the post-cranial skeleton was variable, but the skull, mandible, and both scapulae escaped complete immersion and were recovered in near-perfect condition. Other elements recovered include the distal right femur, femoral head, right calcaneus, over a dozen intact vertebrae and fragments of additional vertebrae, ilium, radius, ulna, and ribs. The mandible was first noted by the 1986 National Speleological Society Expedition to the Dominican Republic (Veni et al., 1987) but was collected in June 1999.

DATING

The extremely superficial context of the specimen seemed to favor a late Holocene age, but laboratory analysis determined that the post-cranial bone lacked recoverable quantities of macromolecular collagen. We therefore chose to date the specimen by

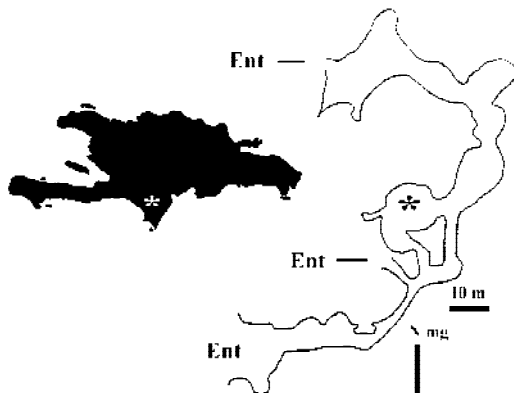


FIG. 1. Location map. Position of cave within the Dominican Republic shown with a white asterisk. Location of sloth within cave shown with a black asterisk.

the novel application of inorganic radiocarbon dating of the calcite patina, exploiting the serendipitous co-occurrence of modern calcite-rafts (Hill and Forti, 1986) to experimentally determine the carbon systematics of the site.

The ^{14}C activity of the calcite patina was measured by conventional beta counting at Beta Analytic laboratories, Florida, yielding a result in percent modern carbon (pMC). However, interpretation of radiocarbon data from speleogenic carbonates is complicated because the carbon may originate from different sources, each with different initial ^{14}C activity (Genty and Massault, 1999). The two main sources are 1. biological activity of roots and soil organisms producing CO_2 with a ^{14}C activity close to that of the atmosphere; and 2. weathering/dissolution of inorganic fractions of the soil and/or the host rock, at zero ^{14}C activity ("dead carbon"). The proportion of atmospheric C to rock C varies with biological activity, rock thickness, and the type of dissolutional system (Holmgren et al., 1994). In an "open" system percolation waters remain in contact with soil CO_2 during rock dissolution and the ^{14}C activity remains close to atmospheric. In a "closed" system, percolation waters are isolated from soil CO_2 during rock dissolution and the ^{14}C activity is only 50 % of atmospheric. The initial ^{14}C activity of CaCO_3 precipitated in a cave from dripping percolation thus var-

ies with the ^{14}C activity of the percolation water. In addition to the calcite, a flowstone may contain some detrital material, at zero ^{14}C activity. The percentage of dead carbon causes an uncorrected ^{14}C date to be falsely old. A way to correct this is by calibration against the apparent age of a modern calcite sample of true zero age. On the assumption that the paleo-sample and the modern sample formed under comparable initial conditions, the percentage of dead carbon can be calculated and the paleo-sample age corrected.

For this study we measured the ^{14}C activity of a modern calcite raft forming on the surface of a nearby pool. Our use of such rafts for the determination of the carbon systematics of the system derived from the fact that these speleothems form in time frames of weeks to months and can be confidently recognized as modern. However, we acknowledge that raft calcite carbon systematics may not be exactly comparable with those of the patina calcite. Evaporation may cause excessive loss of $^{12}\text{C}^{16}\text{O}_2$ over $^{14}\text{C}^{18}\text{O}_2$ resulting in some enrichment in ^{14}C in the raft material; this error would make the sloth sample appear falsely young, but the error would be small in a sample of this age.

Results for the calcite patina and calcite-raft from Cueva del Perezoso appear in Table 1. There are two ways to view these numbers: 1. If a conventional pre-1950 "modern" carbon value of 1.00 is used, then a dead carbon contribution of 59 % is required to explain the low measured pMC and convert the measured activity level to 1.000 and the age to zero. 2. If the modern sample is assumed to have formed since 1950 and the true modern (post-bomb) carbon value of 1.17 is used, then the measured activity is 0.3548 percent of true modern carbon and a dead carbon contribution of 64 % is required to explain the apparent age.

The resultant values (see Table 2), expressed in the conventional form as 95 % confidence limits, yield a corrected age of the calcite patina of 18 499 to 21 491 radio carbon years before present (rcybp).

As previously stated, much of the skeleton of the Jaragua sloth, especially the cra-

TABLE 1. Modern calcite raft data.¹

$\delta^{13}\text{C}_{\text{PDB}}$	Percent modern carbon ²	Conventional radiocarbon age ³	Correct age
-0.5	0.4151 \pm 0.0084	7060 \pm 160 rcybp	0

Radiocarbon dates include 1-sigma error

¹There are two ways to view these numbers. If a conventional “modern” carbon value of 1.00 is used, then a dead carbon contribution of 59% is required to explain the low measured percentage of modern carbon and convert the measured activity level to 1.000 and the age to zero. If the modern sample is assumed to have formed since 1950 and the true modern (post-bomb) carbon value of 1.17 is used, then the measured activity is 0.3548 percent of true modern carbon and a dead carbon contribution of 64% is required to explain the apparent age.

²“Modern” represents the pre-1950s atmospheric value. Measured activity is normalized to the measured $\delta^{13}\text{C}$, which represents the carbon isotopic fractionation for the material.

³Conventional radiocarbon age is reported as rcybp (radiocarbon years before present, “present” representing AD 1950) calculated using the Libby ¹⁴C half life.

TABLE 2. Old calcite flowstone data.

$\delta^{13}\text{C}_{\text{PDB}}$	Percent modern carbon	Conventional radiocarbon age	Corrected age using 59% dead carbon	Corrected age using 64% dead carbon
-2.7	0.03185 \pm 0.0011	27687 \pm 280 rcybp	20622 \pm 440 rcybp	19368 \pm 440 rcybp

Radiocarbon dates include 1-sigma error

nium and mandible, is covered with a layer of calcite of varying thickness. Therefore, many observations and measurements of features have been done with the aid of medical computer axial tomography scans (CAT scans).

SYSTEMATIC PALAEOLOGY

MAGNORDER XENARTHRA COPE,
1889
ORDER PILOSA FLOWER, 1883
SUBORDER PHYLLOPHAGA OWEN,
1842
SUPERFAMILY MEGATHERIOIDEA
GRAY, 1821,
FAMILY MEGALONYCHIDAE GERVAIS,
1855
SUBFAMILY CHOLOPODINAE GRAY,
1871
TRIBE ACRATOCNINI VARONA, 1974
Acratocnus Anthony, 1916

Generic placement and diagnosis

The cranial features of the Jaragua sloth are consistent with those defining the genus *Acratocnus* (MacPhee et. al., 2000), including a domed cranium, marked sagittal crest, pronounced medio-lateral

flare of rostrum, trigonal and curved first maxillary tooth, and a convex last mandibular molariform which is narrowest lingually. The post-orbital constriction is present but moderate—this dimension is broader than in other species of *Acratocnus* (Table 3). The first two mandibular teeth are missing but the triangular shape of the intact alveoli is consistent with generic assignment to *Acratocnus*. The Jaragua sloth can be distinguished from *Neocnus* by the presence of robust jugals, which are absent or reduced in the latter (MacPhee and White, 2001), rostral flaring, post-orbital constriction, and its larger overall size. The Jaragua sloth is distinguished from *Parocnus* by its overall smaller size, its short and pointed symphyseal spout, and the small size of the first maxillary tooth relative to the rest of the toothrow. The trigonal cross-sectional shape of the first maxillary tooth also distinguishes the Jaragua sloth from *Parocnus browni*, where this tooth is oval.

A postcranial feature consistent with placement in *Acratocnus* is the straight femoral shaft, which at its distal end narrows antero-posteriorly and widens medio-laterally. A narrow intercondylar notch (Table 4) and sub-equal femoral condyles terminating distally at the same level also separate the Jaragua sloth from *Neocnus*.

TABLE 3. Comparison of selected cranial measurements of *Acratocnus*.

Measurement (mm)	<i>Acratocnus simorhynchus</i>	Adjusted <i>A. simorhynchus</i> ¹	<i>A. ye</i> UF170533	Adjusted <i>A. ye</i> ¹	Mean <i>A. odontrigonis</i> ²
Maximum skull length	132.3	134.3	123.3	134.3	134.4
Maxillary diastema length	22.6	22.9	24.8	27.0	25.0
Maximum maxillary width at caniniform	42.5	43.1	40.6	44.2	42.5
Minimum width of palate	14.6	14.8	11.7	12.9	14.9
Total length of maxillary molariform tooth row	39.4	40.0	33.2	36.1	33.1
Posterior maximum palate width	32.6	33.1	23.8	25.9	25.8
Length infraorbital canal—rostrum	39.3	40.0	38.8	42.3	37.8
Midline total palate length	59.2	60.1	56.4	61.4	59.8
Maximum sagittal crest height	6.6	6.7	8.3	9.0	7.6
Sagittal crest length	48.5	49.2	N/A	N/A	64.5
Minimum width of post-orbital constriction	31.5	32.0	22.3	24.3	26.8
Maximum palate arch ³	4.8	4.8	3.6	3.9	4.2
Snout/palate angle ⁴	60°	60°	35°	35°	37.5°
Mand. buccolingual width at molariform 2	20.8	21.1	16.5	18.0	18.1
Mandibular height at molariform 2	33.3	33.9	27.5	30.0	31.1
Mandibular inter-caniform width	39.1	39.7	N/A	N/A	39.4
Distance mandibular caniform to spout tip	11.4	11.5	N/A	N/A	16.9
Width of spout at tip	6.3	6.3	N/A	N/A	7.4
Height of mandible parallel to mental suture including spout	43.2	43.9	N/A	N/A	42.4
Total mandibular toothrow length	34.4	34.9	N/A	N/A	27.8
Mandibular diastema length	10.3	10.5	N/A	N/A	13.4

All numbers in mm rounded to nearest tenth, unless otherwise noted.

¹Measurements of *A. ye* and *A. simorhynchus* are size-corrected to aid in comparison. The mean maximum cranial length was chosen as the most suitable proxy for overall size and metrics were adjusted so that the maximum cranial length of all specimens equals that of the mean of *A. odontrigonis*. The adjustment factors utilized are 1.09 and 1.015, respectively.

²The *A. odontrigonis* mean was determined from measurements taken by the first author on the following specimens: AMNH 17712, 17713, 17714, 17717, 17718, 17720, 17721, 17722, 17158.

³The maximum palate arch was measured as the perpendicular distance from the top of the maxillary palate to a chord connecting the anterior maxillary alveolus to the palatine bones.

⁴Snout-palate angle was measured using a goniometer. The base rested on the hard palate, along a cord spanning the anterior-most (maxillary) and posterior-most (palatine) points. The angle was then determined by adjusting the arm tangential to the snout so that the maximum contact with the frontal and nasal bones was achieved. Because it is a shape measure, snout-palate angle is not size adjusted.

Although the distal humerus is damaged, clear evidence of an entepicondylar foramen precludes assignment to *Parocnus*. The elongate dimension of the vertebral border of the scapula and the relative angle of the scapular spine also support assignment to *Acratocnus* and exclude *Megalocnus*.

ACRATOCNUS (MIOCNUS) SIMORHYNCHUS
NEW SPECIES

Holotype: Skull, mandible and unambiguously associated postcranial skeleton,

including distal right femur, femoral head, right calcaneus, left and right scapulae, over a dozen intact vertebrae and fragments of additional vertebrae, acetabulum, ilium, radius, ulna, and ribs.

(ALF 7194) collected June 1999 by Keith Christenson and Donald A. McFarlane.

Type locality: Cueva del Perezoso, Jaragua National Park, Pedernales Province, Dominican Republic (UTM 1988498N 219938E).

Age: 18 499 to 21 491 rcybp (95% confi-

TABLE 4. Selected postcranial measurements of *Acratocnus simorhynchus*.

Element measured	(mm)
Calcaneus:	
• Maximum length	53.5
• Maximum width	33.3
Scapula:	
• Vertical scapular glenoid height	26.3
• Vertebral border length	90.7
• Cranial border length	82.1
• Axillary border length	81.7
Femur:	
• Maximum head diameter	23.3
• Medio-lateral diameter at midshaft, 4.5 cm proximal to condyles	34.9
• Anterior posterior diameter at midshaft, 4.5 cm proximal to condyles	16.0
• Maximum bicondylar breadth	46.3
• Medial condyle length (anterior-posterior)	31.5
• Lateral condyle length (anterior-posterior)	31.4
• Intercondylar notch (proximal posterior dimension)	4.6
• Intercondylar notch (distal dimension)	8.5

dence interval), based on inorganic ^{14}C dating of the calcite patina on the bones, calibrated against modern carbon systematics of the cave.

Synonyms and referred specimens:

None.

Etymology: Specific epithet from Latin *simo-* meaning flattened or snub and *rhynchus* meaning ‘nose or snout’. Recommended vernacular name: “Hispaniolan snub-nosed sloth”.

Distribution: Type locality.

Diagnosis: A megalonychid sloth distinguishable from other species of *Acratocnus* by prominently enlarged frontal sinuses resulting in the appearance of a foreshortened snout angled approximately 60 degrees relative to the anterior-posterior plane of the palate, only moderate postorbital constriction, flared rostrum, relatively short symphyseal spout, deep mandibular corpus and lengthed molariform toothrow in both the maxilla and mandible with correspondingly shortened diastema.

Description

The greatly enlarged frontal sinuses (Fig. 2) are the most prominent diagnostic cranial feature. Anterior projection of maxilla and associated nasal bones broadly similar to other *Acratocnus*, including *A. odontrigonus*

(Puerto Rico). When scaled for size (Table 3), snout length (anterior margin of infra-orbital canal on maxilla to anterior-most portion of rostrum) falls between that of *A. odontrigonus* and *A. ye* (Hispaniola). “Snub-nosed” appearance mainly due to pronounced dome shape of frontal bones due to marked frontal sinus enlargement, which makes snout appear much shorter (Fig. 3). Enlargement of frontal sinus far exceeds that of *A. ye* (observable because it is exposed by breakage in UF 170533; see MacPhee et al., 2000). Cranial dome in parietal region far more sharply angled along sagittal crest relative to facial skeleton than in *A. ye* or *A. odontrigonus*. Examination of coronal section CT scans reveals large mastoid, sphenoid, and ethmoid sinuses (such examination of other *Acratocnus* species is warranted to evaluate significance of these features).

Maxillary and mandibular diastema relatively and absolutely shorter than in other *Acratocnus* (Table 3). These characters are related to total length of molariform toothrows, which are longer in *A. simorhynchus*. Principal features defining the species appear to relate functionally to the masticatory apparatus, including expanded frontal sinuses and relatively deep mandibular corpus. Change in frontal shape could be an adaptation to counter addi-

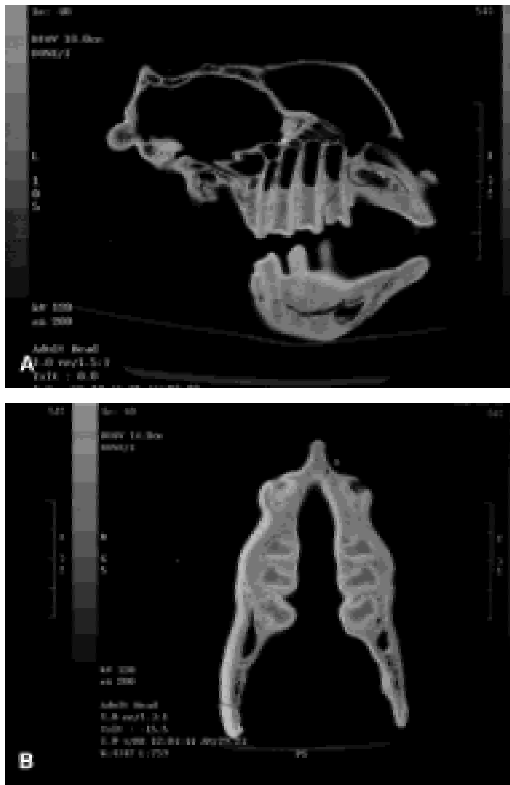


FIG. 2. *Acratocnus simorhynchus* n. sp. (ALF 7194) A. Mid-sagittal CAT scan of holotype. Note the greatly enlarged frontal sinus (at arrow). The paranasal and other sinuses are clearly visible in other "slices" and are distinct from the frontal sinus. The mandible is slightly off mid-sagittal in this section, so the symphyseal spout is not shown in its full anterior projection. B. Horizontal section of mandible through alveoli showing anterior projection of symphyseal spout.

tional bending and/or torsion, since this area is vital in transmitting bite force. Several other mandibular features distinguish *A. simorhynchus*, including a short, narrow and spatulate symphyseal spout. Height of mandibular corpus at the second molar greater than that of *A. ye* and mean of *A. odontrigonus* (Table 3). Anterior edge of ascending ramus, where it intersects mandibular corpus, overlaps second molariform tooth by one half its mesio-distal diameter.

Femoral shaft (Fig. 4c) straight, with a highly reduced third trochanter notably smaller than in *A. odontrigonus*, but similar to *A. ye*. Femoral condyles roughly sub-

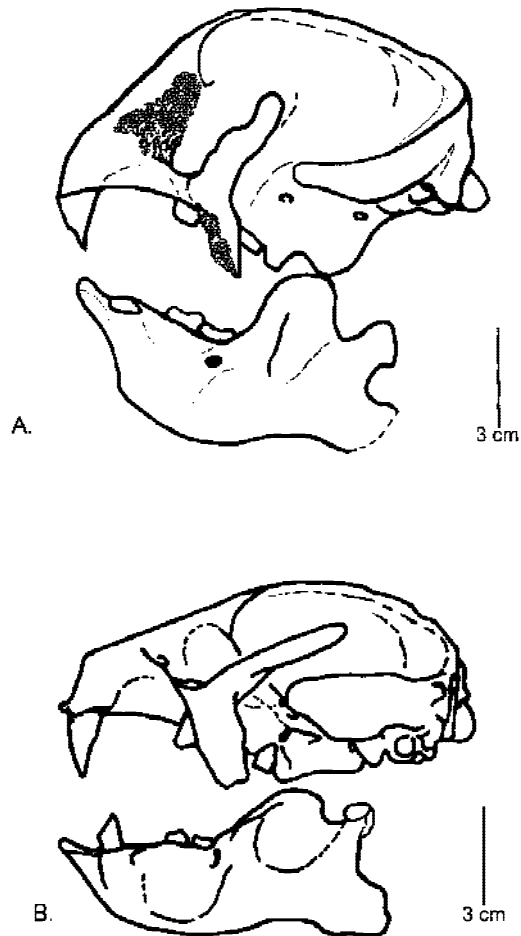


FIG. 3. (ALF 7194) Comparative line drawings. A. *Acratocnus simorhynchus* n. sp. Dark stippling and dashed line at posterior of mandible indicate areas of breakage. B. *Acratocnus ye*, lateral view composite (after MacPhee, et. al. 2000).

equal, with only a slight bicondylar angle. Intercondylar notch of distal femur narrow (Table 4). Femoral angle cannot be assessed because head is detached from shaft. Acetabular fossa open, with moderate pit for insertion of ligamentum fovea capitis femoris. Femoral head small, half width relative to medio-lateral diameter of distal femur compared with two-thirds in *A. ye*. Femoral head with shallow but distinct fovea capitis femoris, thus differentiating it from afoveate femoral head of *A. ye*. Humerus smaller and more slender than in *A. odontrigonus*. Distal humerus damaged but with clear evidence of an entepicondylar

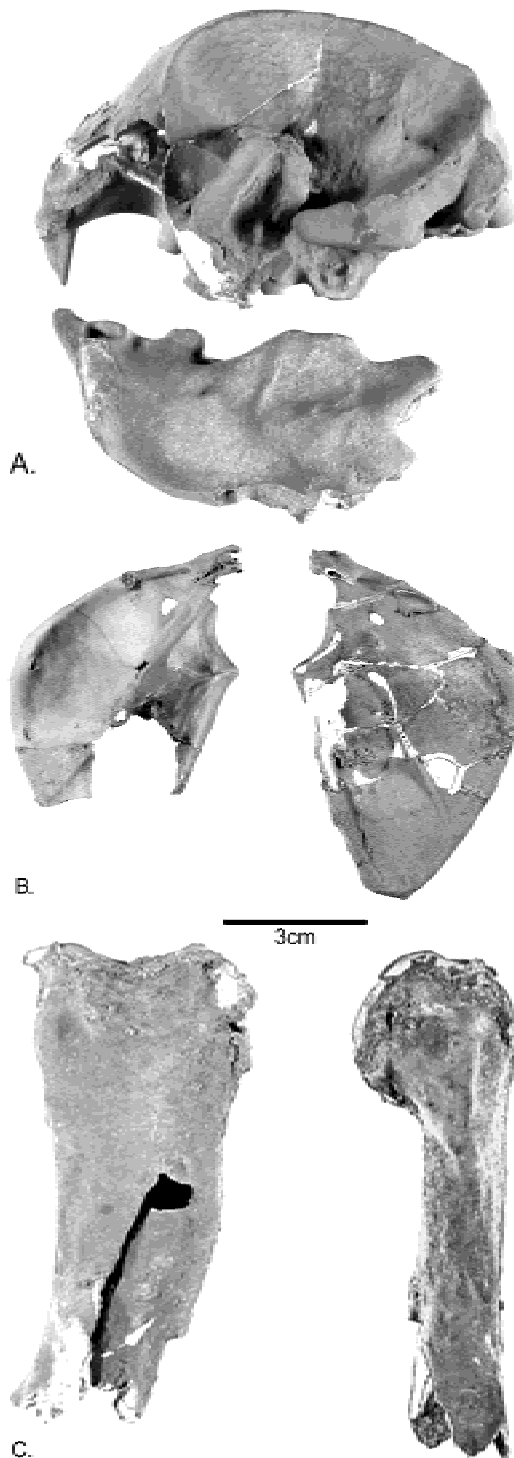


FIG. 4. (ALF 7194) *Acratocnus simorhynchus* n. sp., selected elements. A. Lateral view of skull and mandible. B. Right and left scapula, dorsal aspect; C. Anterior and lateral views of distal right femur.

foramen. Scapula without markedly elevated second scapular spine demarcating caudal origin of teres major. A small (remnant?) spur present near vertebral border only (Fig. 4). Selected postcranial metric features are listed in Table 4.

DISCUSSION

The description of another *Acratocnus* species invites comments on the alpha diversity of sloths known from the late Quaternary of Hispaniola. As many as seven taxa are recognized (six in MacPhee *et al.*, 2000 plus *A. simorhynchus*), which is a remarkable diversification on an island 78 460 km². This radiation complements the extremely depauperate nature of other members of the Hispaniolan terrestrial mammal guild at the level of family and order. The entire Late Quaternary mammalian fauna of Hispaniola (excluding bats and Sirenians) comprises only 7 families in 4 orders, in stark contrast to the much smaller (4828 km²) continental-shelf island of Trinidad with 16 (extant) families in 6 orders (data from Eisenberg, 1989). The probability of the various subsets of the same six lineages (Table 5; we assume that Solenodontidae and Nesophontidae share a common ancestor in the Antilles), and no others, occurring on the four Greater Antillean islands as random extinction-winnowed representatives of a more diverse 'continental' assemblage of 16 lineages is calculated to be $p = 0.008$. Only two explanations are reasonable, scenarios corresponding to the much debated (e.g. Williams, 1989) 'overwater dispersal' versus 'land bridge' hypotheses for the colonization of the Antilles; either the original colonists of the islands were limited to very few ancestral stocks, or an early, more diverse fauna was culled very early by a Caribbean basin-wide wave of deterministic extinctions of unprecedented selectivity. There is no theoretical foundation in support of identical extinctions acting across multiple orders and ecologies of mammals.

Our goal here is not to review the considerable evidence for Pleistocene inter-island mammalian dispersal events. We

TABLE 5. Representation of endemic mammal lineages on the islands of the Greater Antilles.¹

	Jamaica	Puerto Rico	Hispaniola	Cuba
Capromyid rodents	present		present	present
Heptaxodontid rodents	present	present	present	
Echimyid rodents		present	present	present
Ceboid primates	present		present	present
Solenodontid insectivores		present	present	present
Megalonychid sloths		present	present	present

¹*Oryzomys antillarum*, a muroid rodent from Jamaica, is excluded because it is known to be a Late Wisconsinan arrival (McFarlane *et al. in press*) and not relevant to the early colonization of the islands. *Isolobodon portoricensis*, a capromyid rodent from Puerto Rico, is excluded because it is generally considered to an Amerindian translocation from Hispaniola.

simply note that multiple recoveries of mid-Tertiary Antillean mammals have added no new lineages to the Quaternary mammal roster, with the sole exception of an Eocene rhinocerotoid from Jamaica (Domning *et al.*, 1997) that predated the late Eocene submergence of the island and has no bearing on the late Tertiary-Quaternary faunas of Jamaica or the other Greater Antilles. Moreover, despite an exhaustive review of the paleogeography of the Caribbean Basin in precisely this context, Iturralde-Vinent and MacPhee (1999) could not confirm the presence of a continuous land bridge between mainland South America and the proto-Antilles, although they hypothesize its existence.

The Iturralde-MacPhee model was effectively challenged in a detailed critique by Hedges (2001). However, if we accept the time frame of the subdivision of the hypothesized "GAARlandia" landmass, the separation of Hispaniola and Cuba was complete 12 million years ago (cf. Iturralde-Vinent, 2001; much earlier in other models). The presence of a single genus on all three northern Greater Antilles requires that no more than species-level differentiation occur in these forms in the interval since the Miocene. Furthermore, since the separation of Cuba and Hispaniola preceded the separation of Hispaniola and Puerto Rico by several million years in the Iturralde-MacPhee model, a vicariant sloth model predicts a closer similarity between the Hispaniola-Puerto Rico sloth (and other mammal) faunas than between Cuba-Hispaniola. The reverse is, in fact, true.

The presence of representatives *Acratoc-*

nus on Cuba, Hispaniola, and Puerto Rico can only reasonably be interpreted as resulting from relatively late Quaternary inter-island movements of these animals. Given the narrow water barriers and the favorable ocean current and probable storm tracks, such dispersal in an easterly direction is not surprising. Similar late-Pleistocene dispersal patterns are seen in the endemic echimyid rodents of these three islands.

Our current understanding of the megalonychid radiation on Hispaniola is very limited, lacking as it does a meaningful understanding of the ecology of these animals. Differences between moist and xeric vegetation could have driven the speciation of *Acratocnus*, but this hypothesis is as yet untested. Most notably, we cannot yet determine why sloth diversification on Puerto Rico was so limited compared to Hispaniola. The most obvious hypothesis, that the arrival of *Acratocnus* on Puerto Rico was a rather recent event (i.e. late Pleistocene) can only be addressed by extending the mid and early Pleistocene radiometric record on Puerto Rico.

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