



Late Cenozoic Land Mammals from Grenada, Lesser Antilles Island-Arc

Authors: MacPHEE, R.D.E., SINGER, RONALD, and DIAMOND, MICHAEL

Source: American Museum Novitates, 2000(3302) : 1-20

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2000\)3302<0001:LCLMFG>2.0.CO;2](https://doi.org/10.1206/0003-0082(2000)3302<0001:LCLMFG>2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3302, 20 pp., 6 figures, 4 tables

October 16, 2000

Late Cenozoic Land Mammals from Grenada, Lesser Antilles Island-Arc

R.D.E. MACPHEE,¹ RONALD SINGER,² AND MICHAEL DIAMOND³

ABSTRACT

We report on a small collection of late Cenozoic fossil vertebrates recovered from a lahar (mudflow) deposit at Locality 12° North on the southern coast of Grenada.* ⁴⁰K/⁴⁰Ar-dated hornblende concentrate from the lahar deposit yielded age estimates of 2.6–3.7 Ma (Late Pliocene). Although these estimates date crystallization of the hornblende and not the lahar event, the latter is unlikely to be substantially younger. The contained fauna is here regarded as latest Pliocene or slightly younger.

Dental specimens in the collection are readily referable to Hydrochaeridae (Rodentia, Caviida) and Megalonychidae (Xenarthra, Phyllophaga), groups heretofore unknown on this island. The capybara, *Hydrochaeris gaylordi*, new species, differs from extant *Hydrochaeris hydrochaeris* in the conformation of the maxillary second molar. The sloth teeth (two caniniforms, one molariform) notably differ from one another in size, but whether they represent one species or two cannot be decided on this evidence. Because of the limitations of the material, attribution of the specimens to subfamily or tribe within Megalonychidae is also uncertain. Megalonychid sloths have never been found previously on any of the Lesser Antilles, although they formed part of the terrestrial vertebrate fauna of most of the Greater Antilles. Curaçao is the only other island in the Caribbean Sea that has yielded sloth and capybara fossils. Sloths and capybaras might have reached that island as well as Grenada by short-distance over-water transport, perhaps during a time of lowered sea level. A late land connection with South America is perhaps possible, but this would need to be confirmed with suitable geological evidence.

INTRODUCTION

The land mammal fauna of Grenada is typically viewed as being highly depauperate,

like that of the other Lesser Antilles (Allen, 1911). Its extant fauna comprises 19 species, 11 of which are bats (table 1). The remainder consists of species that were probably or pos-

*Contribution 3 in the series "Origin of the Antillean Land Mammal Fauna."

¹ Curator, Division of Vertebrate Zoology (macphee@amnh.org); Adjunct Senior Research Scientist, CERC, Columbia University.

² Professor of Anatomy and of Anthropology; Robert R. Bensley Professor of Biology and Medical Sciences, Department of Organismal Biology and Anatomy, University of Chicago, 1027 E. 57th St., Chicago IL 60637.

³ 3100 37th St., Rock Island IL 61201-6532.

TABLE 1
Known Land Mammal Fauna of Grenada^a

Didelphimorphia	Rodentia
Didelphidae	Muridae
<i>Marmosa robinsoni</i> ^b	Murinae
<i>Didelphis marsupialis</i> ^c	<i>Rattus rattus</i>
Chiroptera	<i>Mus musculus</i>
Emballonuridae	Sigmodontinae
<i>Peropteryx macrotis</i>	†oryzomyin sp. A
Noctilionidae	†oryzomyin sp. B
Noctilio leporinus	Dasyproctidae
Mormoopidae	<i>Dasyprocta leporina</i> ^e
<i>Pteronotus davyi</i> ^d	Hydrochaeridae
Phyllostomidae	† <i>Hydrochaeris gaylori</i> , new species
<i>Micronycteris megalotis</i>	Primates
<i>Glossophaga longirostris</i>	Cercopithecidae
<i>Carollia perspicillata</i>	<i>Cercopithecus mona</i>
<i>Artibeus cinereus</i>	Edentata
<i>Artibeus jamaicensis</i>	Dasypodidae
<i>Artibeus lituratus</i>	<i>Dasypus novemcinctus hoplites</i>
Vespertilionidae	Megalonychidae
<i>Myotis nigricans</i>	† <i>Megalonychidae</i> , gen. & sp. indet.
Molossidae	Carnivora
<i>Molossus molossus</i>	Viverridae
	<i>Herpestes auropunctatus</i>

^aNew discoveries in bold; list otherwise based on Varona (1974), Groome (1970), Pregill et al. (1994), and other sources. Domesticated species not included.

^bIdentical nominal subspecies on Tobago (*M. r. grenadae*).

^cIdentical nominal subspecies (*D. m. insularis*) found in Tobago, St. Vincent, Dominica, and Martinique.

^dSee fn. 7.

^eThis is the valid species, of which *D. aguti* is a synonym (Woods, 1989). This widespread South American species was introduced extensively into the Lesser Antilles as far north as St. Thomas, in some cases aboriginally (Allen, 1942).

sibly introduced by human agency (Varona, 1974; Eisenberg, 1989). At the species level, no Grenadian mammal is an exclusive endemic,⁴ a fact that has been used (e.g., by Groome, 1970) to argue that this island was never connected to South America (but see Discussion and Conclusions). Until the recent discovery of two unnamed species of oryzomyin sigmodontines in very late Qua-

⁴An exclusive endemic is a species-level taxon that originated in, and whose primary natural distribution is limited to, a single continuous area (usually small). In principle, origin could be allopatric or sympatric, although for obvious reasons allopatric endemics are easier to document. Endemics can, of course, secondarily disperse, but by definition they remain endemic in their area of origin until and unless extinction occurs therein. Island endemics are exclusive only when sufficiently differentiated from mainland parent populations/species (= allopatry). Until there is differentiation there is no exclusive endemism, only range extension.

ternary contexts (Pregill et al., 1994), no extinct land mammals of any sort were known from Grenada.

This report adds two more entries to the Grenadian faunal list: *Hydrochaeris gaylori*, new species, and Megalonychidae, gen. & sp. indet., material of which was recovered by one of us (RS) from a lahar deposit on the south end of the island. The capybara, represented by a partial maxillary dentition, is similar but not identical to living *Hydrochaeris hydrochaeris* from the South American mainland. The sloth material is scanty: little can be said about it beyond the fact that the specimens are megalonychid. A few fragments of bone belonging to smaller vertebrates (?lizards) were found in matrix samples, but none is complete enough to identify. Whatever their limitations as specimens, these finds are important because they pro-

vide faunal records that are essential for reconstructing the historical biogeography of the Caribbean region (cf. Iturralde-Vinent and MacPhee, 1999).

ACKNOWLEDGMENTS

Pat and Joseph Gaylord, owners of the 12° North Hotel, generously facilitated Singer's work on their property in many ways, including permitting him to hire two of their staff, David Adolphus and Neville James, for part-time excavating. Mr. Gaylord kindly donated all of the specimens recovered by Singer to the American Museum of Natural History, to ensure their availability to scientific workers. We thank Susan Philip (AMNH) for assisting with this matter.

Singer thanks St. George's University School of Medicine for invitations to teach anatomy at their campus on several occasions, which permitted the fieldwork described in this paper. Singer's fieldwork in Grenada was supported by a grant from the Marion R. and Adolph J. Lichtstern Fund of the Department of Anthropology, University of Chicago. Financial support for preparation of this paper was provided by a grant from Mr. Robert Liberman (to RDEM).

This paper benefitted from anonymous reviews and the advice of Brian J. Crother (Southeastern Louisiana University) on herpetological matters. The authors additionally thank Lorraine Meeker (specimen photography), Patricia J. Wynne (maps), and Clare Flemming (editing) for their usual excellent services.

ABBREVIATIONS

Anatomical

BL	buccolingual width
CA	cross-sectional area (BL × MD)
CF	caniniform (i.e., anteriormost tooth in megalonychid dentition)
m1, m2, m3	mandibular first, second, third molar
M1, M2, M3	maxillary first, second, third molar
MD	mesiodistal length
MF	molariform (i.e., any postcaniniform tooth in megalonychid dentition)
M × W	labioexternal to proximointernal angles (CF), greatest distance

Other

AMNH-VP	American Museum of Natural History, Division of Paleontology (Vertebrate Paleontology)
bsl	below sea level
GIUA	Geological Institute of the University of Amsterdam
⁴⁰ K/ ⁴⁰ Ar	potassium-argon (dating technique)
Ma	millions of years (ago)
UF	Florida Museum of Natural History, University of Florida

GEOGRAPHICAL AND GEOLOGICAL SETTING OF GRENADA

Geographically and geologically, Grenada (12°N, 61°W; 310 km²) is associated with the Grenadines, the spray of ~40 small islets lying south of St. Vincent (figs. 1, 2). Grenada and the Grenadines are the subaerial components of the Grenadines Bank, a large (180 km × 25 km) submarine structure extending NE-SW and having an average water depth of 20–40 m. Regional slope of the top of the bank is 1:300, indicating that it is nearly horizontally disposed (Dey and Smith, 1989). The bank drops off abruptly E and W into the Tobago and Grenada troughs.

In the larger regional picture (fig. 1), Grenada is situated 125 km from the closest point on the South American mainland and 115 km from Tobago, the closest non-Antillean island. Measuring from the –200 m isobath, however, island and continent are even closer: only ~40 km separate the southern end of the Grenadines Bank from the edge of the continental shelf. However, seafloor depth in this short interval reaches 600 m bsl (fig. 1).

Speed et al. (1993) have summarized a wealth of data on the stratigraphy, magmatism, depositional environments, and deformation of the southern Lesser Antilles arc platform, or SLAAP. According to these authors, the SLAAP, which forms the core of the Grenadines Bank, is a half-horst that was uplifted early in the Miocene. Neogene volcanism was widespread in this area, beginning about 12 Ma or shortly before, and it continues into the present day. The only active submarine volcano in the region is Kick-

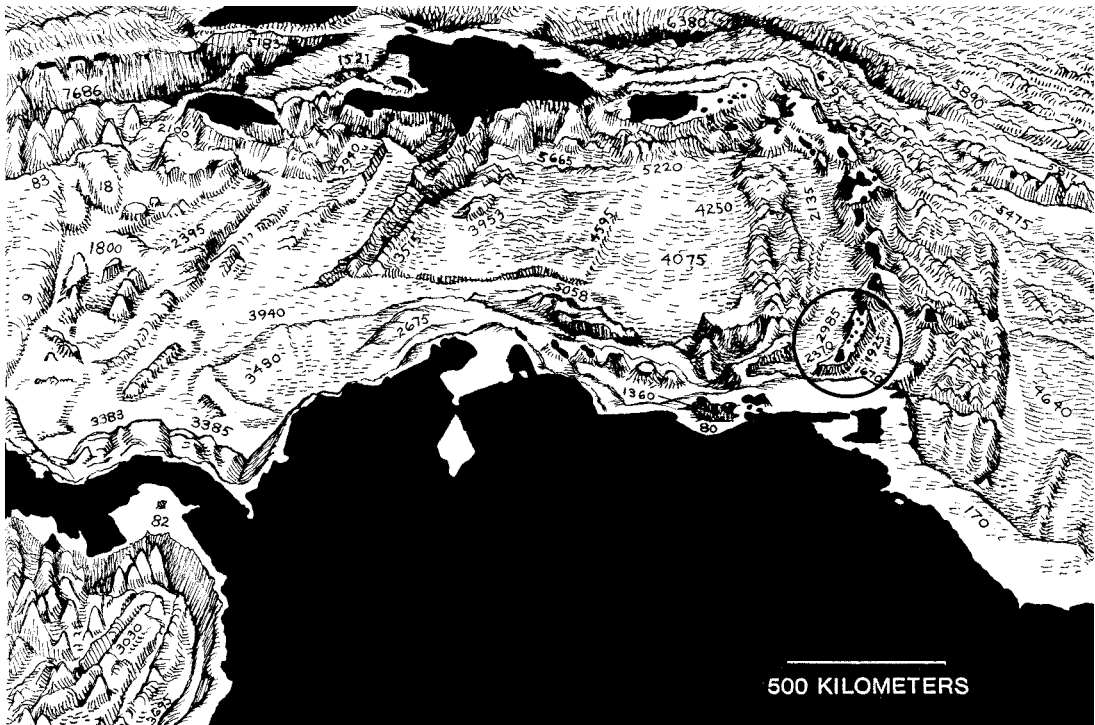


Fig. 1. Physiographic diagram of Caribbean basin and contiguous part of Atlantic (adapted from maps by B. Heezen and M. Tharp); depths are in meters. The Grenadines Bank (encircled) terminates a comparatively short distance (~ 40 km) north of the continental slope of South America, but the sea floor between bank and slope is < 600 m bsl.

'em-Jenny (Donnelly et al., 1990), located immediately north of Grenada (fig. 2).

The basement of Grenada is a volcanic unit of Middle Eocene age, succeeded by a series of tuffs of distinctive composition interbedded with limestones and marls ranging in age from Middle Eocene (50 Ma) to Middle Miocene (13 Ma) (Martin-Kaye, 1969; Maury et al., 1990; Wadge, 1994). There is only one recognized substantial unconformity, provisionally dated to the interval between Late Oligocene and Middle Miocene and possibly as much as 10 Ma long. This lacuna has so far been detected only on Carriacou in the Grenadines (Speed et al. 1993).

For the southern Lesser Antilles, Speed et al. (1993) identified three "generally sequential" sedimentary depositional environments (pelagic basin, turbidite basin, platform) from Middle Eocene onward. Volcanic platforms with some subaerial exposure were in existence in the area to the west from the

Middle Eocene onward, as suggested by the nature of deposits in the turbidite basins. However, neither the location nor the longevity of these earlier islands can be estimated from the data available. Extensive carbonate platform conditions, associated with uplift of the half-horst, came into being in the late Early/Middle Miocene. This is of importance because it is the first indication of extensive shallow marine and intertidal environments. Plio-Pleistocene reef limestones occur patchily among the Neogene volcanics in various parts of the island, indicating the continuing presence of land in more recent epochs (Maury et al., 1990; Wadge, 1994).

LOCALITY 12° NORTH

The area of interest is the toelike southwestern terminus of the island, which is continued for another 30 km as the shallowly submerged southern end of the Grenadines

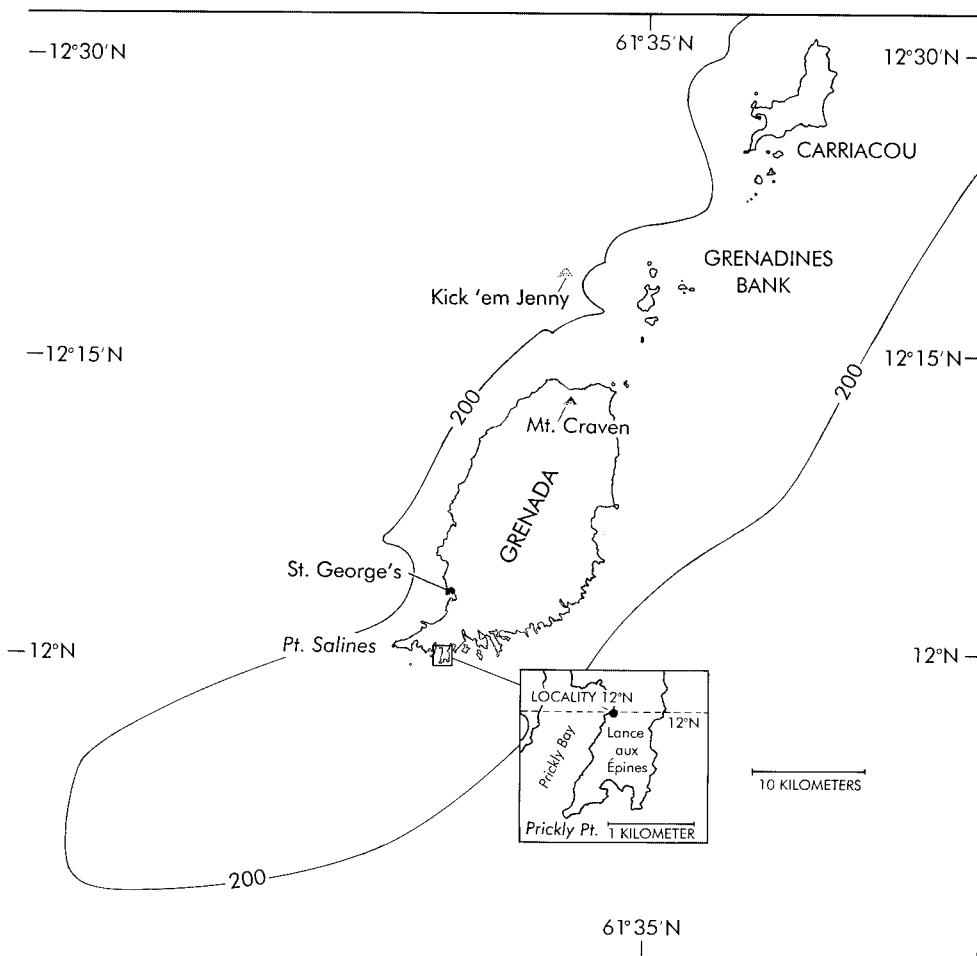


Fig. 2. Southern portion of Grenadines Bank, Lesser Antilles island-arc, showing the island of Grenada and major geographical features mentioned in text. Inset: Position of Locality 12° North, west side of Lance aux Épines peninsula on extreme southern coast.

Bank (figs. 1, 2). Composed of a series of weathered tuffs (Tomblin, 1970), the promontory is strikingly indented by a series of narrow embayments typical of a subsiding coastline. The most westerly subaerial projection is Point Salines; Lance aux Épines, 5 km to the east, is the most southerly projection. Locality 12° North is positioned on the latter's west side, facing into Prickly Bay.

In 1982, Mr. Joseph Gaylord, co-owner of the 12° North Hotel, pointed out to RS the existence of small bony fragments in the tuffaceous cliff face below the resort's garden. The cliff is entirely composed of a massive, homogenous yellow-brown clay (fig. 3),

from which pebbles, shells and other inclusions (other than teeth and bones) are virtually absent. On initial inspection, RS noted the sloth molariform (AMNH-VP 132714) and larger caniniform (AMNH-VP 132715) described below, as well as several unidentifiable fragments of bone (fig. 3B). These elements were removed in a single block of matrix and prepared in Chicago. Further efforts to secure fossils were made in subsequent years by exploration of the cliff face. This effort was rewarded in 1989 by the discovery of another sloth caniniform (AMNH-VP 132716) and somewhat later (in 1991) by recovery of a partial maxillary dentition of a



Fig. 3. View of Locality 12° North, southern coast of Grenada, from a photo taken in 1989 by R. Singer. Measuring rod held by man is approximately 120 cm long; approximately 5 m of cliff face is exposed at low tide. The deposit, composed of massive, homogeneous yellow-brown clay with virtually no inclusions derives from a lahar event that probably occurred in late Pliocene or early Pleistocene. Foot of measuring rod rests on spot where initial fossil discoveries—the sloth molariform and larger caniniform—were made (circled area in inset shows teeth and bone fragments in situ before their removal). *Capybara* maxilla was found two years later at approximately the same level as the other teeth, but some 15 m further to the right (off margin of photograph).

capybara (AMNH-VP 132713). These last finds were located about 15 m from the position of the 1982 finds, suggesting that the area around Locality 12° North ought to yield many more specimens if properly excavated.

Dr. Richard Hazlett (Joint Sciences Department, Claremont Colleges) has kindly examined samples of the matrix in which the fossils were found. He reported that the matrix is mostly composed of smectite, a clay derived from the weathering of volcanic ash. Small, diffusely bordered white lumps within the matrix are pumice; these pieces show little sign of weathering and are therefore suggestive of rapid burial. Also present in some abundance are lapilli and small crystals of gabbro, pyroxene, olivine, and augite (see

similar observations by Tomblin, 1970). The simplest scenario for the origin of the deposit at Locality 12° North is that it derives from a lahar, possibly triggered by an eruptive event. It seems probable that the lahar swept down valley from its point of origin, picking up older, weathered material as it went and rapidly burying pumice generated by the eruption. The ash may have been reworked to a minor extent after deposition. In any case, the few skeletal elements recovered were incomplete at the time of discovery, and no associated bones were encountered.

DATING

Here we report two $^{40}\text{K}/^{40}\text{Ar}$ age estimates for Locality 12° North, based on hornblende

TABLE 2
 Locality 12° North, Grenada: Potassium-Argon Age Determinations

Lab No.	Material analyzed	⁴⁰ Ar (ppm, average) ^a	⁴⁰ K (ppm)	⁴⁰ Ar/ ⁴⁰ K	Calculated age (Ma) ^b
Geochron A-7070	Hornblende	.000060	0.386	.000155	2.7 ± 0.3
Geochron A-8759	Hornblende	.000084	0.400	.000211	3.6 ± 0.4

^a ⁴⁰Ar refers to radiogenic ⁴⁰Ar; entry is the average of three analyses.

^b For standard constants and calculation, see Geyh and Schleicher (1990).

concentrates extracted from fresh matrix collected at fossiliferous locations approximately 15 m apart. The dates— 2.7 ± 0.3 and 3.6 ± 0.4 Ma (table 2)—are reasonably concordant and overlap at two standard errors. However, some caution is necessary in interpreting very young ⁴⁰K/⁴⁰Ar dates (Geyh and Schleicher, 1990), especially when the potassium content of the dated material is low, as it is in the present case.

The simplest interpretation of the age estimates for Locality 12° North is that they date the time of crystallization of hornblende within the original tephra matrix. The lahar is not directly dated thereby; it was certainly somewhat later, because there is no evidence that the fossils were exposed to high temperatures. On the other hand, the lahar event is unlikely to have been very much later, given the appearance of the matrix. We provisionally conclude that the mudflow and its contained mammal fossils were deposited no earlier than 2–3 Ma, most probably in the terminal Pliocene, or perhaps as late as the Early Pleistocene.

This conclusion is in good agreement with Tomblin's (1970) weathering-profile evidence that the tuffaceous sediments forming Point Salines are "not older than Pliocene," as well as the very young ⁴⁰Ar/³⁹Ar dates recently published by Speed et al. (1993) for the Mt. Craven volcanic center at the north end of the island. These dates, based on magmatic hornblende, cluster between 1.4 and 1.7 Ma and suggest that the present volcanogenic surface of Grenada may be very recent indeed. (Older work suggested that the Mt. Craven center was in excess of 21 Ma, which now appears to be invalid.) Although the Mt. Craven event was evidently somewhat later than lahar deposition at the far southern end of the island, the relative youth

of much of the island's geomorphology is certainly consistent with the young dates and light weathering of fossiliferous matrix at Locality 12° North.

A NEW HYDROCHAERINE RODENT FROM GRENADA

Maxillary M1–M3 (AMNH-VP 132713):

This specimen is unquestionably a hydrochaerid caviidan (fig. 4).⁵ It is a partial maxillary dentition (M1–M3) of an adult animal, held together by a few remnant patches of maxillary bone (fig. 4; table 3). Hypsodont, multilamellar tooth organization of the kind seen in this specimen is diagnostic of Hydrochaeridae (Kraglievich, 1930; Woods, 1989) and requires no special comment. The M1 and M2 are substantially intact except for minor abrasions and cracks. However, the M3 is clearly incomplete: distally the tooth ends abruptly, in the middle of an enamel-dentine lamella (or "prism").

Three subfamilies of Hydrochaeridae are generally recognized: Cardiatheriinae, Protohydrochaerinae, and Hydrochaerinae, with the last two being the more closely related (Mones, 1984; but see McKenna and Bell, 1997). According to Mones (1984), cardiatheriines have fewer lamellae (6–10) on maxillary M3s than do hydrochaerines (10–17) or protohydrochaerines (12–18). As noted, the Grenadian specimen is broken and its true count is therefore not known (but was surely higher than the nine that remain). The Grenadian specimen is trivially similar to Cardiatheriinae in that the major lamellae on maxillary M2 are united buccally (fig. 4D, F). However, there are no other features that can be viewed as specifically cardiatheriine.

⁵ For spelling of names based on *hydrochaer-*, see Woods (1989).

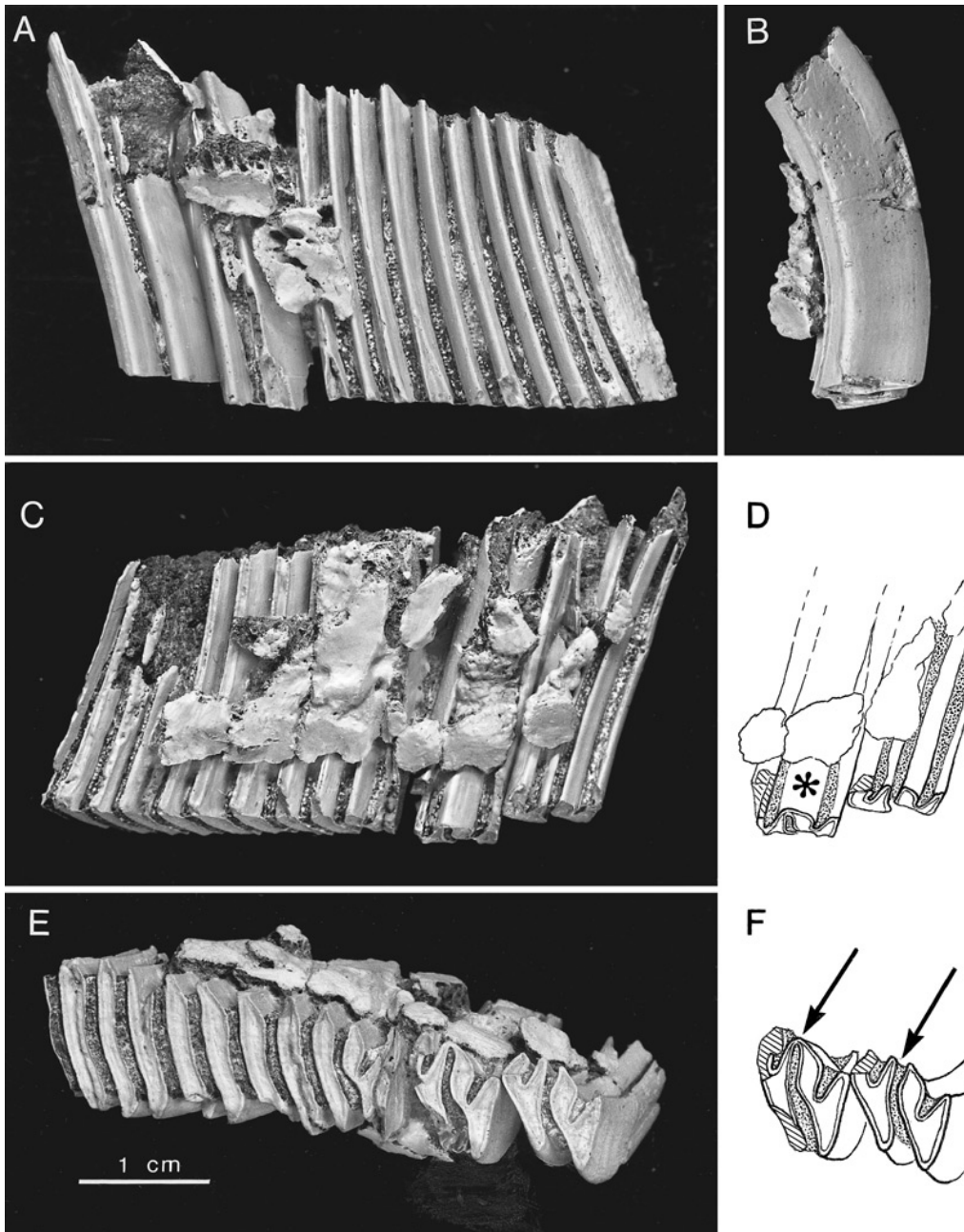


Fig. 4. *Hydrochaeris gaylordi*, new species, AMNH-VP 132713 (holotype, partial right maxillary dentition) from Locality 12° North, Grenada: **A**, lingual aspect; **B**, mesial aspect (of M1); **C**, buccal aspect; **D**, drawing of buccal aspect of M1 and M2 (asterisk on M2 identifies buccally conjoined lamellae); **E**, occlusal aspect; **F**, drawing of occlusal aspect of M1 and M2, showing effect on occlusal pattern of buccally conjoined lamellae (present in M2, left arrow; absent in M1, right arrow). By contrast, in extant *H. hydrochaeris*, lamellae are buccally separate in both M1 and M2.

TABLE 3
Dental Dimensions of New Grenadian
Fossil Mammals^a

1. AMNH-VP 132713 (capybara maxillary dentition)		
M1 MD		7.7
BL		8.2
M2 MD		6.8
BL		8.9
M3 MD		26.5 ^b
BL		11.8
2. AMNH-VP 132714 (sloth molariform)		
MD		11.3
BL		15.3
CA (mm ²)		172.9
3. AMNH-VP 132715 (sloth caniniform)		
M × W		10.4
4. AMNH-VP 132716 (sloth caniniform)		
M × W		8.1

^aMeasurements in millimeters, unless otherwise indicated.

Acronyms are:

BL, buccolingual width;

CA, cross-sectional area (BL × MD);

MD, mesiodistal length;

M × W: labioexternal to proximointernal angles (CF), greatest distance.

^bMeasured as is, without accounting for loss due to breakage.

Importantly, buccal union of all M3 lamellae (when viewed in occlusal aspect), a feature distinctive of *Cardiatherium* itself (Kraglievich, 1930), is absent in the Grenadian specimen.

It is equally easy to distinguish the Grenadian specimen from the truly gigantic taxa comprising subfamily Protohydrochoerinae (cf. Paula Couto, 1979). Deep longitudinal incisures (infolds) on the buccal aspects of the middle lamellae of M3 are a distinguishing feature of *Protohydrochoerus* (Kraglievich, 1930). This feature is lacking in other subfamilies and in the Grenadian specimen. M1 and M2 of *Protohydrochoerus* are similar in occlusal pattern to their homologs in extant *Hydrochaeris*, but the lingual borders of their lamellae are less sharply angled than in living capybaras.

In general aspect and in the shape of individual lamellae making up each represented tooth, the Grenadian specimen is overwhelmingly similar to members of subfamily Hydrochaerinae. Hydrochaerine species are principally distinguished by small differences in the number of lamellae comprising M3/

m3, the angles formed by lamellae as seen medially or laterally, and other minor characters.

Dental measurements of AMNH-VP 132713 are within the size range of mid-sized extant *Hydrochaeris hydrochaeris* (Hooijer, 1959; Ojasti, 1973). The only obvious difference between the Grenadian specimen and extant capybaras is the condition of the M2. In extant capybaras, both the M1 and the M2 consist of two independent lamellae with well-marked infolds that are completely separated by intervening cementum. In the Grenadian specimen, by contrast, this description applies only to M1; in M2, the lamellae are united buccally by a narrow band of enamel and dentine (see asterisk and arrows in fig. 4C–F).

In the M3 of *H. hydrochaeris* the first and last lamellae are bilobate; the rest (usually 10) are entire. In this specimen the bilobate first lamella is followed by eight others, which suggests that the last three are missing (assuming same total count).

Discussion: Today, capybaras are commonly found in many parts of northern South America and, for that matter, throughout the continent north of the southern cone (Mares and Ojeda, 1982). However, until the discovery reported here, Curaçao was the only West Indian island where they were known to have existed during the Quaternary (on the basis of fossil evidence only). Hooijer (1959) described a series of teeth, apparently referable to a juvenile member of the living species, recovered from a hard oolitic phosphate matrix in the eastern part of the island. The origin of these deposits, found on several West Indian islands, is controversial but there is no reason to suspect that they are of any great antiquity (Robert Halley, pers. oral commun.). Indeed, Hooijer (1959) even raised the question whether the capybara from eastern Curaçao represented an animal introduced by humans. He seems to have been driven to this rather unlikely possibility because this island has a markedly xeric aspect at present, and was therefore not, in his estimation, fit habitat for water-loving *H. hydrochaeris*.

Kraglievich (1940a, 1940b) noted that, in extant *Hydrochaeris*, individual teeth vary ontogenetically in the degree to which la-

mellae are angled, separated, or joined. In the unerupted or little-worn cheek teeth of neonates, lamellae are frequently joined buccally. As wear progresses, such connections are quickly lost, yielding occlusal patterns typical of adults. This would seem to provide a simple basis for the existence of conjoined lamellae in adult dentitions, and Kraglievich documented a number of examples of persistent connections between lamellae in lower teeth. However, he also specifically noted that maxillary P4–M2 show relatively few variations as compared to M3. In fact, M1 and M2 appear to be essentially invariant except for the presence of slight compression or smoother reentrant angles (as seen on occlusal surfaces).

It is therefore of some systematic importance that Kraglievich (1940a) did not notice the occurrence, in extant *Hydrochaeris*, of buccal union of M2 lamellae, the one clearly distinctive feature of the Grenadian specimen. (As no M2s of the Curaçao capybara have been found, morphologies cannot be compared.) Indeed, the only group in which this conformation is regularly seen is the cardiatheres, and AMNH-VP 132713 from Locality 12° North differs in numerous details from any recognized member of this subfamily. Although this is a fairly narrow basis on which to found a new species, the unusual nature of the M2 warrants it.

Systematic Paleontology: We name, diagnose, and classify the new species as follows:

MAGNORDER EPITHERIA MCKENNA, 1975
 ORDER RODENTIA BOWDICH, 1821
 SUBORDER HYSTRICOGNATHA WOODS, 1976
 INFRAORDER HYSTRICOGNATHI
 TULLBERG, 1899
 PARVORDER CAVIIDA
 BRYANT AND MCKENNA, 1995
 SUPERFAMILY CAVIOIDEA
 FISCHER DE WALDHEIM, 1817
 FAMILY HYDROCHAERIDAE GRAY, 1825
 SUBFAMILY HYDROCHAERINAE GRAY, 1825

Hydrochaeris gaylordi, new species

HOLOTYPE: AMNH-VP 132713 (fig. 4), partial maxilla retaining M1–M3.

DISCOVERER AND DATE OF DISCOVERY: Ronald Singer and party, 1991.

TYPE LOCALITY AND AGE: Locality 12° North, Lance aux Épines, Grenada (Lesser Antilles); probably Late Pliocene, less likely Early Pleistocene ($^{40}\text{K}/^{40}\text{Ar}$ age estimate on hornblende in matrix, 2.7–3.6 Ma).

ETYMOLOGY: For Mr. Joseph Gaylord, in recognition of his many kindnesses to RS over many years.

DISTRIBUTION: Known only from Grenada in the southern Lesser Antilles.

DIAGNOSIS: A small hydrochaerine that can be distinguished from all other named hydrochaerines, including extant *Hydrochaeris hydrochaeris*, by its unique occlusal pattern, in which buccal connection of maxillary M2 lamellae is never lost during ontogeny.

DISCUSSION: Although in unerupted cheek teeth of *Hydrochaeris hydrochaeris* the summits of individual lamellae are typically joined, reflecting the earliest stage of crown ontogeny, these connections are lost with wear. By the young juvenile stage, the notably hypodont cheek teeth of capybaras appear to be made up of separate enamel-dentine lamellae of complicated shape, united by plaques of cementum. Although M3 may be somewhat variable in that some interlamellar connections may be preserved into later life, observational evidence indicates that M1 and M2 do not vary in this regard. Thus, preservation of a buccal connection between M2 lamellae in the Grenadian specimen appears to be a derived (albeit neotenic) feature within *Hydrochaeris*, justifying recognition of *H. gaylordi*. This feature is absent or unrecorded in the other species of *Hydrochaeris* recognized by Mones (1984): Lujanian *H. ballesterensis* (Rusconi, 1934) and extant *H. isthmus* (Goldman, 1912), sometimes regarded as a valid species (cf. Mares and Ojeda, 1982).

MEGALONYCHID FOSSILS FROM
 GRENADA

As noted in greater detail in subsequent paragraphs, the three teeth described in this section are referable to Megalonychidae, gen. & sp. indet. The homologs of phyllophagan teeth in other placentals are not certain, and we shall follow the convention of identifying the highly trenchant first tooth as the cani-

niform (CF), and the flat-wearing teeth that follow it as the molariforms (MFs).

In this section we will use the phylogenetic framework recently developed by White and MacPhee (in press). Although the grouping “Antillean members of Megalonychidae” has been used as a taxonomic as well as a biogeographical concept in the past, island sloths actually fall into two subfamilies, each with two contained tribes: Megalocninae, containing Megalocnini (*Megalocnus*) and Mesocnini (*Parocnus*); and Choloepodinae, containing Acratocnini (*Acratocnus*) and Cubanocnini (*Neocnus*). Extant *Choloepus*, the two-toed sloth, is the sister group of *Acratocnus*; the placement of *Paulocnus* from Curaçao is still unsettled, although it is definitely a choloepodine (and probably an acratocnin).

MAXILLARY MOLARIFORM (AMNH-VP 132714): The root end of this specimen is incomplete, and there is a small amount of damage evident on its occlusal surface (fig. 5A, B). On the whole, however, the tooth is well preserved and is immediately recognizable as a right maxillary MF of a megalonychid sloth. Although the specimen was found very close to the larger caniniform (fig. 3, inset), they are actually isolated finds and for this reason we cannot be certain that they represent the same individual.

The first and the last of the four upper MFs of Antillean megalonychids tend to be subtriangular to ovoid in cross section, while the middle teeth tend to be reniform or meniscoid. In details of shape the Grenadian tooth strongly recalls MF2s/MF3s of the Late Quaternary Cuban megalocnines *Megalocnus rodens* and *Parocnus* (= *Mesocnus*) *browni*. The new specimen’s smooth-walled shaft is convex on its mesial surface and concave on its distal; the latter surface is, however, interrupted by a longitudinal groove that parallels the shaft’s mesiobuccal margin (fig. 5A). The semiserrate wear pattern on the tooth is precisely like that seen in other Antillean sloths. As in the latter, the softer dentine at the center of the tooth is hollowed out by wear, producing a central basin that deepens distolingually.

AMNH-VP 132714 is comparatively large (table 3), and its measurements are close to those cited by Matthew and Paula

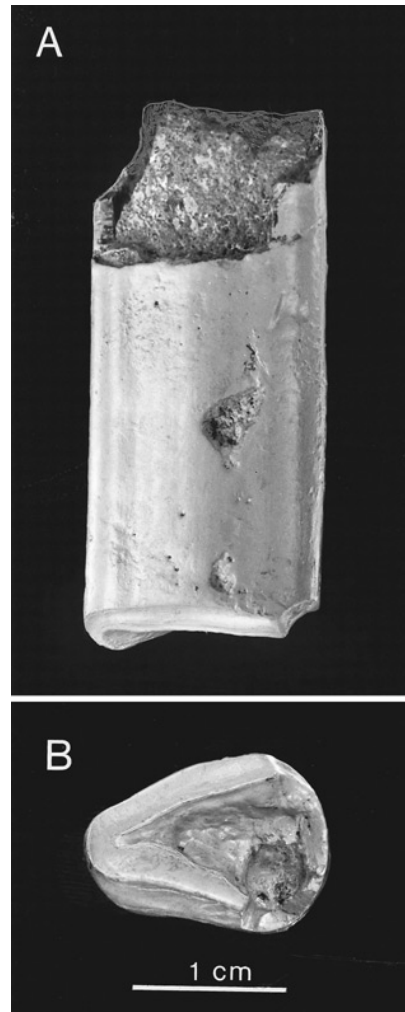


Fig. 5. Megalonychid molariform (AMNH-VP 132714; maxillary, right side) from Locality 12° North, Grenada: **A**, mesial aspect (mesiobuccal margin faces left); **B**, occlusal aspect (distal surface faces bottom of page).

Couto (1959) for MF2s/MF3s of *Parocnus browni*. *Paulocnus petrifactus* from Curaçao is also fairly large for an Antillean sloth (Hooijer, 1962, 1964), but the MF2 and MF3 of this species are not known. The Grenadian specimen is seemingly too large to belong to any recognized species of Acratocnini or Cubanocnini as reorganized by White and MacPhee (in press).

MAXILLARY CANINIFORMS (AMNH-VP 132715 and 132716): There are two maxillary caniniforms (both from the right side) in

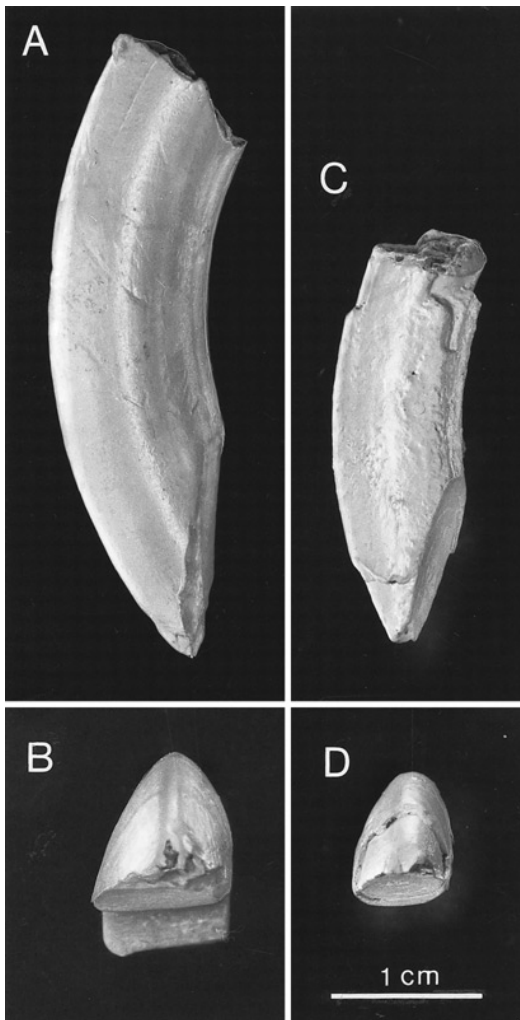


Fig. 6. Megalonychid caniniforms (maxillary, right side) from Locality 12° North, Grenada: “large” caniniform (AMNH-VP 132715), medial (A) and (B) adoral aspects; “small” caniniform (AMNH-VP 132716), medial (C) and (D) adoral aspects. (In B and D, occlusal surfaces face distally, i.e., toward the bottom of page.)

the sample from Locality 12° North (fig. 6A–D). These teeth are typically megalonychid in being trigonal, stout, and trenchant, with lengthy wear facets on distal surfaces. However, they differ greatly in size (table 3). The larger caniniform is the size of that of a large *Acratocnus* (e.g., *A. odontrigonus* AMNH-VP 17715, $M \times W = 11.1$ mm) while the small tooth is more like that of *Neocnus* (e.g., *N. comes* UF 76356, $M \times W = 7.7$ mm).

The teeth of extinct megalonychids were nonreplacing and ever-growing, and the evidence is clear that they increased in size during life in conformity with jaw growth (cf. Simpson in Matthew and Paula Couto, 1959: 54). Accordingly, it is often difficult or impossible to decide, when examining isolated megalonychid teeth of different sizes, whether the specimens represent different species or merely different growth stages of the same species. As there is no evidence either way in the present case, we must leave the question undecided.

In discrete features, the CFs from Locality 12° North are rather nondescript, although they are primitive and thus most similar to those of acratocnins and cubanocnins. They were obviously protruding; Naples (1982) has pointed out that CFs extending well beyond the occlusal plane are generally primitive for sloths. The angles at which the three faces meet are slightly rounded, the one bordering the mesial side of the occlusal surface being the most rounded. The tips are sharply pointed rather than chisel-edged, and the large honing facet produced by wear with the lower caniniform faces directly caudad. The Grenadian specimens lack the slight longitudinal groove seen on the external surface of the upper CF of *A. odontrigonus* (Anthony, 1918) as well as the “longitudinal ribbing” said to be distinctive of the upper CF of *A. antillensis* (Matthew and Paula Couto, 1959: pl. 27).

A relevant question is whether the large CF represents the same species as the MF from the same locality. Although the large CF compares well with the equivalent tooth of *Acratocnus* specimens from the Greater Antilles, the MF is much larger than those of any recognized member of that genus. In all Antillean sloths described to date, the maxillary caniniform is the largest tooth in the entire dentition. This is also true in living *Choloepus*, suggesting that the living two-toed sloth retains the symplesiomorphous condition. However, given the large size of the Grenadian MF, one would expect an even larger CF to be associated with it. As already noted, within-species ontogenetic variation in tooth dimensions is known to be marked in Antillean sloths (cf. Matthew and Paula Couto, 1959; Paula Couto, 1967), making it dif-

ficult to set taxonomic boundaries on dental grounds alone (White, 1993). Obviously, the question of how many species are represented in the existing sample must await the recovery of more and better material.

Comparisons to *Paulocnus* from Curaçao are extremely relevant, because this island is closer to Grenada than are any of the Greater Antilles, and because both of these small islands are situated approximately the same distance from the South American continental shelf. Only one maxillary CF of the Curaçao sloth has been described, from a quarry block containing portions of the skull and mandible of one individual (GIUA X 4781; Hooijer, 1964). Hooijer's maximum-width measurement of the maxillary CF of this specimen is 11 mm, which compares well with the size of the larger CF from Grenada.

A seeming bar to further comparisons, however, is Hooijer's (1964) assertion that the CF of *Paulocnus* is widest on its mesial face (as distinct from its external face, widest in all other Antillean sloths except *Megalocnus* whose CF is differently derived). Hooijer particularly emphasized this feature in distinguishing *Paulocnus* from both *Acratocnus* and *Parocnus*, which it otherwise resembles. Close study of a photographic illustration of GIUA X 4781 (Hooijer, 1964: pl. X) indicates that Hooijer's interpretation of caniniform morphology and dimensions cannot be correct. In this plate, the fragmentary upper jaw (essentially corresponding to a palatal fragment with three teeth) rests on the lower jaw, with the first MFs in occlusion. However, the conformation of the occlusal surfaces of the depicted MFs indicates that it is the *left* lower first molariform that is in occlusion with the *right* upper, i.e., the palate has been displaced and is not in correct occlusal relationship with the mandible. That being the case, the preserved upper CF is evidently not a left, as Hooijer claimed, but instead a right, and the surface facing the viewer is not the mesial but the external. Although this clarification does not solve the problem of the phylogenetic relationships of the large Grenadian specimen, it does mean that *Paulocnus* is not barred from being a close relative on the basis of caniniform morphology. Indeed, in view of their metrical similarities, it is possible that they may even

represent the same taxon. Once again, further resolution must await new material.

Systematic Paleontology: The three sloth teeth recovered from Locality 12° North are classifiable as follows:

MAGNORDER XENARTHRA COPE, 1889

ORDER PILOSA FLOWER, 1883

SUBORDER PHYLLOPHAGA OWEN, 1842

SUPERFAMILY MEGATHEROIDEA GRAY, 1821

FAMILY MEGALONYCHIDAE GERVAIS, 1855

The teeth are difficult to classify below the family level because they display fairly primitive morphologies. Although the molariform (AMNH-VP 132714) is generally similar to maxillary MF2s/MF3s of megalocnines, this is hardly decisive evidence that its owner was phylogenetically a megalocnine rather than a choloepodine. At the tribal level, megalocnin affiliations can be ruled out for the caniniforms because megalocnin CFs are distinctively oval or crescent-shaped in cross-section. However, a relationship with mesocnines (i.e., *Parocnus*) is not so easily dismissed, since CFs are trigonal in the latter tribe as in other Antillean tribes. As already noted, because sloth cheek teeth vary conspicuously in size with ontogenetic age, it is quite possible that all three specimens represent the same species, although the presence of more than one phyllophagan in the sample cannot be ruled out based on this argument alone. In the absence of diagnostic characters, for classificatory purposes it is appropriate to consider all three teeth as Megalonychidae, gen. & sp. indet.

OTHER FOSSIL MATERIAL FROM LOCALITY 12° NORTH

A number of fragments of postcranial bones have been collected at the site, but their condition is such that no positive systematic identifications can be made. A few are clearly rib fragments belonging to large vertebrates (largest fragment, 23.7 mm wide). They may well represent the megalonychid(s) or the capybara already known from the site, or they may relate to some other large vertebrate not yet discovered. (Sirenians are ruled out because the rib fragments are not osteosclerotic.) A few tiny long bone

sections, unfortunately lacking articular ends, are provisionally regarded as belonging to small lizards. Their presence indicates that there is also a microfaunal component at Locality 12° North that remains completely unknown.

DISCUSSION AND CONCLUSIONS

The presence of at least two kinds of large mammals on Grenada during the late Cenozoic raises some intriguing biogeographical questions. Was this island physically attached to South America at some point, permitting an influx of terrestrial species? Was there only one connection, or were there several over time? How long has the connection been severed? Alternatively, can the presence of land mammals in the fauna be interpreted as the result of passive rafting? If so, were some timespans more likely than others for over-water travel? None of the questions just posed can be answered at present, and may in fact be unanswerable. However, some observations about comparative likelihoods can be made (cf. Crother and Guyer, 1996).

Recently, Iturralde-Vinent and MacPhee (1999) undertook a comprehensive examination of possible Cenozoic connections between and among the islands in the Caribbean basin and their adjacent continental mainlands. They hypothesized that a landspan—that is, a transitory connection between a continent and one or more off-shelf islands—briefly connected the northern part of South America with the Greater Antilles via the Aves Rise around the time of the Eocene–Oligocene transition (~35–33 Ma). The appearance of the GAARlandia (i.e., Greater Antilles/Aves Rise) landspan is correlated with a phase of general tectonic uplift more or less coincident with a major sea-level drawdown (Haq et al., 1987; Miller et al., 1996). As a result, subaerial exposure within the Caribbean region was greater than at any other time in the Cenozoic, including the late Quaternary. GAARlandia was probably in existence as a corridor or set of closely spaced large islands for only a short period; with sea-level recovery and tectonic subsidence later in the Oligocene, the landspan became defunct (Iturralde-Vinent and MacPhee, 1999).

In the present case, however, there are significant mismatches in space and in time that make it unlikely that Grenada received its fauna over the hypothesized GAARlandia landspan. Iturralde-Vinent and MacPhee (1999) argued that the landspan's axis ran along the Aves Rise, an extinct island-arc lying considerably to the west, rather than along the line of the more recent Lesser Antilles, the paleogeography of which is very poorly understood (Holcome and Edgar, 1990). As noted earlier, the southern part of the Lesser Antilles island-arc is essentially a Neogene magmatic structure that developed transversely to the older (Paleogene) island arc, probably as a consequence of a major reconfiguration of the Caribbean-American plate boundary zone (Pindell et al., 1988; Speed et al., 1993; Iturralde-Vinent and MacPhee, 1999). On this evidence, GAARlandia is probably too old and too far to the west to have relevance for interpreting the terrestrial biogeography of lands emergent on the SLAAP, although much depends on the accuracy of the timetable adopted by Iturralde-Vinent and MacPhee (1999).

There are other interpretative problems as well. In the Lesser Antilles, marine rocks often occur within volcanic sequences, indicating that their paleogeographical history has been complicated by alternating phases of emergence, subsidence, and migration of topographic highs (Iturralde-Vinent and MacPhee, 1999). Evanescent islands have no doubt existed along the axis of this island-arc since the Eocene, but their form, position, and continuity cannot be reconstructed from the evidence now available. Thus the mid-Cenozoic depositional hiatus on Carriacou, noted earlier, has the correct age to correlate with the appearance of the GAARlandia landspan. However, it has not yet been identified elsewhere in the southern Lesser Antilles, and therefore its regional significance as a paleogeographical land indicator remains uncertain. In any case, given that the early Cenozoic history of the SLAAP was dominated by pelagic and turbidite depositional environments (see above), it would seem unlikely that Grenada as a subaerial entity has persisted as such from the Eocene/Oligocene onward. Accordingly, the GAARlandia landspan, whether or not it acted as a

conduit for vertebrate migration 30 Ma, probably came and went too early to be relevant in explaining how terrestrial vertebrates entered Grenada. We therefore need to consider the possibility of a much more recent time of mammalian entry and successful colonization.

The Plio-Pleistocene was an interval that witnessed great alterations in eustatic sea level (Haq et al., 1987). During significant drawdowns (> 100 m), such as the ones that occurred during the late Pliocene and repeatedly during the Pleistocene, the Grenadines Bank would have formed a relatively large island (ca. 4,000–4,500 km², or about half the current size of Puerto Rico). Also, during drawdowns tens of thousands of square kilometers of the South American continental shelf would have been exposed in the region between Margarita and Tobago (cf. fig. 1). Although modern bathymetry indicates that there would always have been a narrow but deep water gap to cross, theoretically the shorter the distance, the higher the potential success rate.

Several factors would have affected the likelihood of a successful crossing, the most important probably being the autecology of the propagules themselves. Here it is useful to consider the evidence provided by mammalian distributions in the relevant parts of the Neotropics, past and present.

As previously noted, Curaçao, like Grenada, possessed a capybara, although one apparently indistinguishable from *Hydrochaeris hydrochaeris* (Hooijer, 1959; Husson, 1960). If the conventional view that Curaçao has not been connected to the mainland in recent times is correct, capybaras must have colonized it over water.⁶ Given their reputation as highly aquatic mammals—the ecological vicars of pygmy hippos according to some authors (Mares and Ojeda, 1982)—capybaras seem to be good candidates for over-water dispersal. However, extant capy-

baras are not known to frequent marine waters, and, although quite capable in swamps and streams, they perform most maintenance activities on land (Schaller and Cranshaw, 1981). Be that as it may, if one island could be reached by a swimming capybara, it seems reasonable to infer that another could as well. It would be interesting to know if capybaras managed to reach any of the islands comprising the Venezuelan Antillas Menores; at present there is no published evidence that they did. (It is of tangential interest that the only published record of South American *Crocodylus intermedius* in the Lesser Antilles is a 1910 Grenadian record of a beached individual that, according to Barbour [1914], must have traveled from the Orinoco; see table 4.)

These points strike a chord with reference to sloth distributions. By the late Neogene, megalonychid sloths were already well distributed in New World landmasses lying north of South America (cf. Webb, 1985b). Megalonychids were in North America 9 Ma at least (Webb, 1985a), and sloths—presumably but not certainly megalonychid by relationship—reached the Greater Antilles even earlier, at least 32 Ma (MacPhee and Iturralde-Vinent, 1995). How they managed these feats has been the subject of much speculation (Webb, 1985b; Iturralde-Vinent and MacPhee, 1999). It has also been argued, from taphonomic considerations and ambiguous morphological evidence, that some phyllophagans may have been truly aquatic (e.g., Peruvian Pliocene nothrothere *Thalassocnus natans*; de Muizon and McDonald, 1995). There is no evidence, taphonomic or otherwise, that *Paulocnus* was aquatic; yet it is obviously of interest that freshwater-preferring *Hydrochaeris* was the only large mammal other than a sloth known to have lived in Curaçao, forming a strong parallel to the Grenadian case.

Finally, it is significant that the existing mammal fauna of Grenada can be described as “strictly South American,” essentially lacking any exclusively endemic species (Eshelman and Morgan, 1985). Even more remarkable is the fact that the Grenadian fauna is not just South American in some vague general sense; it is explicitly and pervasively similar to that of Tobago. According to Esh-

⁶ Three much smaller rodents are known from Curaçao—recently extinct *Megalomys curazensis*, an unnamed *Oryzomys*, and *Calomys hummelincki* (Hooijer, 1959; Husson, 1960; see Carleton and Musser, 1993). The latter two are presumably still extant (Koopman, 1959). Sigmodontines enjoyed a wide distribution in the Lesser Antilles, suggesting over-water transport (Pregill et al., 1994).

TABLE 4
Geographical Distributions of Grenadian Herp Species^a

Distributional Category I	
<i>Eleutherodactylus euphronides</i>	GR ^b
<i>Leptodactylus validus</i>	GR, GS, SV ^c
<i>Mastigodryas bruesi</i>	GR, GS, SV
<i>Typhlops tasymicris</i>	GR ^d
Distributional Category II	
<i>Anolis aeneus</i>	GR, GS; ?I (TR, nSAM [Guyana]) ^e
<i>Ameiva ameiva</i>	GR, GS, SV; TO, TR; sCAM, nSA
<i>Anolis richardi</i>	GR, GS; TO
<i>Bachia heteropus</i>	GR, GS; TO, TR; nSAM (Venezuela)
<i>Clelia clelia</i>	GR, SV, DO; CAM, nSAM
<i>Corallus enydris</i>	GR, GS, SV; TO, TR; CAM, nSAM
<i>Gymnophthalmus speciosus</i>	GR; CAM, nSAM
<i>Liophus melanotus</i>	GR, TO; nSAM
<i>Pseudoboa neuweidi</i>	GR; nSAM, sCAM ^f
Distributional Category III	
<i>Eleutherodactylus johnstonei</i>	wWI (incl. GR) ^g
<i>Hemidactylus mabouia</i>	wWI (incl. GR); nSAM
<i>Iguana iguana</i>	wWI (incl. GR); CAM, nSAM, cSAM ^h
<i>Mabuya mabouya</i>	wWI (incl. GR); nSAM
Distributional Category IV	
<i>Bufo marinus</i>	I
<i>Crocodylus intermedius</i>	V
<i>Geochelone carbonaria</i>	wWI (incl. GR)

^aDistributions, based largely on information in Schwartz and Henderson's (1991) catalog, grouped as discussed in text; order of taxa within categories is alphabetical. Key to insular designations: **DO**, Dominica; **GR**, Grenada; **GS**, Grenadines; **SV**, St. Vincent; **TO**, Tobago; **TR**, Trinidad; **wWI** (incl. GR), widespread in West Indies, including Grenada. Key to continental designations: **CAM**, Central America (undifferentiated); **sCAM**, southern part of Central America; **cSAM**, middle part of South America; **nSAM**, northern periphery of South America. Key to other abbreviations: **I**, introduced; **V**, vagrant.

^b Previously regarded as a subspecies of *E. urichi* (see Censky and Kaiser, 1999). According to Schwartz and Thomas (1975), distribution of *E. urichi* (all subspecies) is GR, SV; To, Tr; nSAM (Guianas).

^c Regarded as a synonym of *L. wagneri* by Schwartz and Thomas (1975), who give distribution of species as GR, GS, SV; To, Tr; cSAM, nSAM.

^d Closely related to *T. trinitatus* and *T. lehneri* from northeastern South America (Thomas, 1989: 422).

^e Possibility that Trinidadian and Guyanese records for this species are natural cannot be excluded.

^f Possibly now extirpated in Grenada (Schwartz and Henderson, 1991).

^g This taxon does not occur in South America.

^h Distribution significantly influenced by human transportation.

elman and Morgan (1985), all 11 chiropterans⁷ known from Grenada also occur in Tobago, as do four of the terrestrial mammals. (This last datum is of uncertain value because an aboriginal role in influencing distributions cannot be discounted.) Yet while Grenada lacks endemic mammals, the existing diversity is an exact aliquot of that of South America's northern margin, which is

⁷ The Tobagan species of *Pteronotus*, *P. parnelli*, evidently does not occur in Grenada, where only *P. davyi* is found (Varona, 1974).

puzzling if there has never been a land connection between them. (Compare complete identity of mammalian faunas of Margarita and northeastern Venezuela [Eisenberg, 1989], which were without question connected during recent sea-level lowstands.)

The aliquot argument can also be applied to the existing herpetofauna of Grenada, although the biogeographical correspondence with Tobagan taxa is somewhat less exact. Table 4 divides the total Grenadian herpetofauna (21 species) into four distributional

categories. Categories I and II are restricted to species that are either exclusive to Grenada and nearby islands (Grenadines, St. Vincent), or are found both there and in adjacent parts of South America but nowhere else in the West Indies. Category III includes taxa widely distributed in the West Indies, including the southern Windwards, while category IV covers species introduced to or vagrant in Grenada. Taxa in the last two categories are not informative as to the biogeographical connection between the southern Windwards and northeastern South America and will not be considered further here. (An additional reason is that several of the taxa in these categories have anthropogenically influenced distributions.)

Only the four taxa listed in category I can be regarded as endemic and exclusive to the southern Windwards, in the sense that they are plausible minimally diagnosable units and occur there and nowhere else (see table 4, footnotes). Censky and Kaiser (1999, table 6.1) apparently used a wider definition, claiming that Grenada supports six endemic species (not named). Possibly they regarded *Anolis aeneus* and *A. richardi* as Grenadian endemics, although the first has been recovered from northeastern South America (where it is allegedly introduced rather than native) and the second also occurs in Tobago. By any measure, however, the number of endemics relative to the size of the island is small.

It is particularly noteworthy that all four exclusive endemics are very closely related to taxa whose distribution includes, or is restricted to, northeastern South America. Thus the endemic Grenadian leptodactylids *Lepidodactylus validus* and *Eleutherodactylus euphronides* are extremely similar to mainland *L. wagneri* and *E. urichi*, within which they were formerly included (cf. Schwartz and Thomas, 1975; Censky and Kaiser, 1999); the colubrid *Mastigodryas bruesi* is apparently closely related to mainland South American forms (Stuart, 1941), although there is no recent phylogenetic investigation of this taxon; and the typhlopod *Typhlops tasymericis* was characterized by its describer as being "obviously an insular derivative of *trinitatus* and *lehneri* of northeastern South America" (Thomas, 1989: 422). These facts

underline the continuity that exists between category I and II taxa: category II elements are simply those taxa whose Grenadian populations are not yet sufficiently differentiated to be recognized as minimally diagnosable units (and therefore to place in category I).

Looked at from a taxon/area standpoint, all of these dyads (each Grenadian endemic + its sister species) narrowly converge on the axis defined by southern Windwards/Tobago/Trinidad/northeastern South America. So do the "proto"-endemics of category II; at least six of the nine listed taxa are known to have populations on Trinidad or Tobago (or both). From this evidence it would appear that Grenada has received a very recent infusion of herps from the immediately contiguous part of northeast South America, particularly the latter's insular component.

Returning to the mammalian evidence, it is also relevant to point out that, although Tobago is similar in size and general ecological parameters to Grenada, its extant land mammal fauna is twice as large. This disparity could, of course, be radically lessened by new fossil discoveries, as the present paper illustrates. Eshelman and Morgan (1985) found that 50% of the total number of mammals (26 species) identified paleontologically in Tobago have disappeared from that island. They relate this to late Quaternary climate change and a final severing of the connection between Tobago and the mainland via Trinidad. It remains to be seen whether a similar faunal crash also occurred in Grenada (?due to excessive volcanic activity). In this context it would be of great interest to know if any of the Grenadines, with their similar faunal complement, also have a datable fossil record awaiting discovery.

In summary, the 12° North faunule includes a capybara and at least one kind of megalonychid sloth, representing groups that are well known from late Cenozoic Neotropical contexts. However, there is no direct evidence that mammals experienced a lengthy tenure in Grenada; indeed, the lack of endemic species would ordinarily suggest the reverse (or, in the alternative, that a complete faunal turnover has taken place, for which there is no evidence either). The only other fossil land mammals so far discovered in Grenada are sigmodontine rodents, a group

known to have enjoyed a wide and presumably natural distribution in the eastern Caribbean. In contrast to the Greater Antilles, in which overland dispersal (and subsequent island-island vicariance) seems necessary to plausibly explain the biogeographical facts, the circumstances of Grenada do not seem to require it, although many ambiguous points remain to be resolved. Further work on this island is definitely indicated.

REFERENCES

- Allen, G. M.
1911. Mammals of the West Indies. *Bull. Mus. Comp. Zool. Harvard Univ.* 54: 175–263.
1942. Extinct and vanishing mammals of the Western Hemisphere with the marine species of all the oceans. American Committee for International Wild Life Protection Spec. Pub. 11. New York: Cooper Square.
- Barbour, T.
1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. *Bull. Mus. Comp. Zool. Harvard Univ.* 44: 209–359.
- Carleton, M. D., and G. G. Musser
1993. Family Muridae. In D. E. Wilson and D. M. Reeder (eds.), *Mammal species of the world*, 2 ed.: 501–755. Washington, DC: Smithsonian Institution Press.
- Censky, E. J., and H. Kaiser
1999. The Lesser Antillean fauna. In B. I. Crother (ed.), *Caribbean amphibians and reptiles*: 181–221. New York: Academic Press.
- Crother, B. I., and C. Guyer
1996. Caribbean historical biogeography: was the dispersal–vicariance debate eliminated by an extraterrestrial bolide? *Herpetologica* 52: 440–465.
- Dey, S., and L. Smith
1989. Carbonate and volcanic sediment distribution patterns on the Grenadines Bank, Lesser Antilles Island Arc, East Caribbean. *Bull. Can. Petr. Geol.* 37: 18–30.
- Donnelly, T. W., D. Beets, M. J. Carr, T. Jackson, G. Klaver, J. Lewis, R. Maury, H. Schellenkens, A. L. Smith, G. Wadge, and D. Westercamp
1990. History and tectonic setting of Caribbean magmatism. In G. Dengo and J. E. Case (eds.), *The geology of North America*, vol. H, The Caribbean region: 339–374. Boulder, CO: Geological Society of America.
- Eisenberg, J.
1989. *Mammals of the Neotropics*, 1: The northern Neotropics. Chicago: Univ. Chicago Press.
- Eshelman, R. E., and G. S. Morgan
1985. Tobagan Recent mammals, fossil vertebrates, and their zoogeographical implications. *Natl. Geogr. Soc. Res. Rep.* 21: 137–143.
- Geyh, M. A., and H. Schleicher
1990. Absolute age determinations: physical and chemical dating methods and their application. New York: Springer.
- Goldman, E. A.
1912. New mammals from eastern Panama. *Smithson. Misc. Collect.* 60(2): 18 pp.
- Groome, J. R.
1970. A natural history of Grenada. Arima, Trinidad: Caribbean Printers Limited.
- Haq, B. U., J. Hardenbol, and P. R. Vail
1987. Chronology of fluctuating sea levels since the Triassic. *Science* 235: 1156–1166.
- Holcombe, T. L., and N. T. Edgar
1990. Late Cretaceous and Cenozoic evolution of Caribbean ridges and rises with special references to paleogeography. In A. Azzaroli (ed.), *Biogeographical aspects of insularity*. *Atti Convegno Lincei* 85: 611–626. Rome: Accademia Nazionale dei Lincei.
- Hooijer, D.
1959. Fossil rodents from Curaçao and Bonaire. *Stud. Fauna Curaçao & Other Caribb. Isl.* 9(35): 27 pp.
1962. A fossil ground sloth from Curaçao, Netherlands Antilles. *Proc. K. Ned. Akad. Wet. ser. B Phys. Sci.* 65: 46–60.
1964. The snout of *Paulocnus petrifactus* (Mammalia, Edentata). *Zool. Meded.* 39: 79–84.
- Husson, A. M.
1960. De Zoogdieren van de Nederlandse Antillen. Curaçao: Natuurwetenschappelijke Werkgroep Nederlandse Antillen.
- Iturralde-Vinent, M. A., and R.D.E. MacPhee
1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bull. Am. Mus. Nat. Hist.* 238: 95 pp.
- Koopman, K. F.
1959. The zoogeographical limits of the West Indies. *J. Mammal.* 40: 236–240.
- Kraglievich, L.
1930. Los mas grandes carpinchos actuales y

- fossiles de la subfamilia "Hydrochoerinae." *An. Soc. Cien. Argent.* 110: 233–250; 340–358. [Not successively paginated; reprinted in A. J. Torcelli and C. A. Marelli (eds.), Lucas Kraglievich: obras de geología y paleontología 2: 503–535. La Plata: Taller de Impresiones Oficiales.]
- 1940a. Morphología normal y morphogenesis de los molares de los carpinchos y caracteres filogenéticos de este grupo de roedores. [Posthumous work published in A. J. Torcelli and C. A. Marelli (eds.), Lucas Kraglievich: obras de geología y paleontología 3: 439–484. La Plata: Taller de Impresiones Oficiales. (Title page states part I of this work was written in collaboration with L. Parodi.)]
- 1940b. Monographía del gran carpincho corredor plioceno, *Protohydrochoerus* (Rovereto) y formas afines. [Posthumous work published in A. J. Torcelli and C. A. Marelli (eds.), Lucas Kraglievich: obras de geología y paleontología 3: 487–556. La Plata: Taller de Impresiones Oficiales.]
- MacPhee, R.D.E., and M. A. Iturralde-Vinent
1994. First Tertiary land mammal from Greater Antilles: an Early Miocene sloth (*Xenarthra*, *Megalonychidae*) from Cuba. *Am. Mus. Novitates* 3094: 13 pp.
1995. Origin of the Greater Antillean land mammal fauna, 1: New Tertiary fossils from Cuba and Puerto Rico. *Ibid.* 3141: 31 pp.
- Mares, M. A., and R. A. Ojeda
1982. Patterns of diversity and adaptation in South American hystricognath rodents. *In* M. A. Mares and H. H. Genoways (eds.), *Mammalian biology in South America*, Pymatuning Lab. Ecol., Univ. Pittsburgh, Spec. Publ. 6: 393–433.
- Martin-Kaye, P.H.A.
1969. A summary of the geology of the Lesser Antilles. *Overseas Geol. Miner. Res.* 10: 172–206.
- Matthew, W. D., and C. de Paula Couto
1959. The Cuban edentates. *Bull. Am. Mus. Nat. Hist.* 117: 1–56.
- Maury, R. C., G. K. Westbrook, P. E. Baker, P. Bouysse, and D. Westercamp
1990. Geology of Lesser Antilles. *In* G. Deno and J. E. Case (eds.), *The geology of North America*, vol. H, *The Caribbean region*: 141–166. Boulder, CO: Geological Society of America.
- McKenna, M. C., and S. K. Bell
1997. *Classification of mammals above the species level*. New York: Columbia Univ. Press.
- Miller, K. G., G. S. Mountain, Leg 150 Shipboard Party, and members of New Jersey Coastal Plain Drilling Project
1996. Drilling and dating New Jersey Oligocene–Miocene sequences: ice volume, global sea level, Exxon record. *Science* 271: 1092–1095.
- Mones, A.
1984. Estudios sobre la familia Hydrochoeridae, XIV. Revision sistemática (Mammalia: Rodentia). *Senckenb. Biol.* 65: 1–17.
- Muizon, C. de, and G. McDonald
1995. An aquatic sloth from the Pliocene of Peru. *Nature* 375: 224–227.
- Naples, V.
1982. Cranial osteology and function in tree sloths, *Bradypus* and *Choloepus*. *Am. Mus. Novitates* 2739: 41 pp.
- Ojasti, J.
1973. Estudio biológico del chigüire o capibara. Caracas: Fondo Nac. Invest. Agropec.
- Paula Couto, C. de
1967. Pleistocene edentates of the West Indies. *Am. Mus. Novitates* 2304: 55 pp.
1979. *Tratado de paleomastozoología*. Rio de Janeiro: Academia Brasileira de Ciências.
- Pindell, J. L., S. C. Cande, W. C. Pitman, D. B. Rowley, J. F. Dewey, J. LaBrequé, and W. Haxby
1988. A plate–kinematic framework for models of Caribbean evolution. *Tectonophysics* 155: 121–138.
- Pregill, G. K., D. W. Steadman, and D. R. Watters
1994. Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. *Bull. Carnegie Mus. Nat. Hist.* 30: 51 pp.
- Rusconi, C.
1934. Tercera noticia sobre los vertebrados fósiles de las arenas puelchenses de Villa Ballester. *An. Soc. Cient. Argent.* 117: 19–37.
- Schaller, G. B., and P. G. Cranshaw
1981. Social organization in a capybara population. *Säugetierek. Mitt.* 29: 3–16.
- Schwartz, A., and R. W. Henderson
1991. *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*. Gainesville: Univ. Florida Press.

- Schwartz, A., and R. Thomas
1975. A check-list of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist. Spec. Pub.* 1: 216 pp.
- Speed, R. C., P. L. Smith-Horowitz, K. S. Perch-Nielsen, J. B. Saunders, and A. B. Sanfilippo
1993. Southern Lesser Antilles Arc platform: pre-Late Miocene stratigraphy, structure, and tectonic evolution. *Geol. Soc. Am. Spec. Pap.* 277: 98 pp.
- Stuart, L. C.
1941. Studies on the Neotropical Colubrinae VIII. A revision of the genus *Dryadophis* Stuart, 1939. *Misc. Pub. Mus. Zool. Univ. Michigan* 49: 106 pp.
- Thomas, R.
1989. The relationships of Antillean *Typhlops* (Serpentes: Typhlopidae) and the description of three new Hispaniolan species. *In* C. A. Woods (ed.), *Biogeography of the West Indies*: 409–432. Gainesville: Sandhill Crane Press.
- Tomblin, J. F.
1970. Field guide to the Grenadines, Lesser Antilles. *Int. Field Inst. Guidebook Caribb. Island–Arc Syst.* 19. Washington, DC.
- Varona, L.
1974. *Catálogo de los mamíferos vivientes y extinguidos de las Antillas*. La Habana: Academia de Ciencias de Cuba.
- Wadge, G.
1994. The Lesser Antilles. *In* S. K. Donovan and T. A. Jackson (eds.), *Caribbean geology, an introduction*: 167–177. Kingston, Jamaica: Univ. West Indies Publishers' Assoc.
- Webb, S. D.
1985a. Late Cenozoic mammal dispersals between the Americas. *In* F. G. Stehli and S. D. Webb (eds.), *The great American biotic interchange*: 357–386. New York: Plenum Press.
1985b. The interrelationships of tree sloths and ground sloths. *In* G. G. Montgomery (ed.), *The evolution and ecology of armadillos, sloths, and vermilinguas*: 105–112. Washington, DC: Smithsonian Institution Press.
- White, J. L.
1993. Functional and phylogenetic implications of the postcranial skeleton of fossil sloths for the evolution of arboreality in tree sloths. Unpubl. Ph.D. diss., State Univ. New York, Stony Brook.
- White, J. L., and R. D. E. MacPhee
In press. The sloths of the West Indies: a systematic and phylogenetic review. *In* C. A. Woods (ed.), *West Indian Biogeography*. Boca Raton, FL: CRC Press.
- Woods, C. A.
1989. The biogeography of West Indian rodents. *In* C. A. Woods (ed.), *Biogeography of the West Indies*: 741–797. Gainesville, FL: Sandhill Crane Press.