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## First Tertiary Land Mammal from Greater Antilles: An Early Miocene Sloth (*Xenarthra*, *Megalonychidae*) From Cuba

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### ABSTRACT

Parts of the Greater Antilles have been continuously subaerial since the beginning of the Late Eocene, and therefore have been potentially open to colonization by land vertebrates for more than 40 million years. However, documentation for the timing of Antillean colonization(s) is very poor, partly because of the paucity of fossils. Here we report the first discovery, in the Greater Antilles, of skeletal remains of a land mammal in a securely dated Tertiary context. The remains are those of a heretofore unknown megalonychid sloth, from Lagunitas Formation sediments at the locality of Domo de Zaza, province of Sancti Spiritus, south-central Cuba. Lagunitas sediments were deposited in a coastal environmental setting late in the Lower Miocene, perhaps around 17.5–18.5 mya.

This and other recent discoveries establish that the Greater Antilles possessed a terrestrial vertebrate fauna by early Neogene, but how this fauna was emplaced (by vicariance or by dispersal) remains controversial. One possibility is that emplacement occurred during the Oligocene, when lowered sea level and the paleogeographical configuration of the Greater Antilles may have provided conditions particularly favorable for dispersal across then-subaerial parts of the Aves Ridge. By contrast, patterns of species distribution in the Quaternary could have a strictly vicariant historical explanation, if, as seems likely, they are the result of Neogene tectonic fragmentation of the Greater Antilles Ridge.

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## RESUMEN

Una parte de las Antillas Mayores ha permanecido emergida desde el comienzo del Eoceno Superior y por lo tanto ha estado potencialmente abierta a la colonización por los vertebrados terrestres durante más de 40 millones de años. Sin embargo, la verificación del fechado de la, o las, colonizaciones es muy pobre, debido a la escasez de restos fósiles. Aquí se reporta el primer descubrimiento en las Antillas Mayores, de restos esqueléticos de un mamífero terrestre en un contexto Terciario bien datado. Los restos fósiles corresponden con un perezoso megalonychido antes desconocido, encontrado en los depósitos del Mioceno Inferior (alrededor de 17.5–18.5 Ma) en la localidad que aquí denominamos Domo de Zaza, situada en Cuba sur central (Provincia de Sancti Spiritus).

Este descubrimiento, junto a otros muy recientes,

permiten afirmar que las Antillas Mayores poseían su propia fauna de vertebrados terrestres en el Mioceno Inferior. Pero la manera en que esta fauna se estableció (si por vicarianza o dispersión) es un asunto aun controvertido. Una posibilidad es que el establecimiento haya ocurrido durante el Oligoceno, cuando el bajo nivel del mar y la configuración geológica de las Antillas Mayores pudieron ofrecer condiciones mas favorables para la dispersión a través de partes entonces emergidas de la Dorsal de Aves. En contraste con la anterior, los patrones de distribución de las especies en el Cuaternario pueden tener una explicación estrictamente por vicarianza histórica, si, como todo parece indicar, ellos son el resultado de una fragmentación tectónica de las Antillas Mayores durante el Mioceno.

## INTRODUCTION

The Greater Antilles have had complicated tectonic, paleogeographic, and faunal histories, the outlines of which are still poorly understood and the subject of much controversy (e.g., Matthew, 1915; Barbour, 1916; Darlington, 1938; Rosen, 1975<sup>3</sup>, 1985; MacFadden, 1980; Borhidi and Muñiz, 1980; Borhidi, 1985; Pregill, 1981; Sykes et al., 1982; Iturralde-Vinent, 1982, 1988; Burke et al., 1984; Buskirk, 1985; Guyer and Savage, 1986; Pindell et al., 1988; Kluge, 1988; Williams, 1989; MacPhee and Wyss, 1990; Hedges et al., 1992). One of the least understood aspects of biotic history concerns how and when Cenozoic land vertebrates—particularly mammals—became part of the fauna of these islands. Biogeographers have tended to concentrate on the question of how this occurred because of its relevance to assessing whether dispersal or vicariance was the major mode of faunal formation in the West Indies. Knowing the timing of faunal formation, however, is also critically impor-

tant because time supplies a constraint for likelihood models of Caribbean biogeography (see discussion by MacPhee and Wyss, 1990). Fossils supply temporal information, but at present the Tertiary paleontological record for the Greater Antilles is woefully inadequate for testing purposes (Williams, 1989). Any substantial amplification of this record is therefore of great potential importance. In this report we describe the first land mammal recovered so far from a Tertiary context within the Greater Antilles—a late Early Miocene megalonychid sloth from Domo de Zaza, south-central Cuba (Sancti Spiritus).

## ACKNOWLEDGMENTS

Fieldwork at Domo de Zaza was conducted under the auspices of an agreement between the Museo Nacional de Historia Natural (La Habana) and the American Museum of Natural History, and was financed by the Philip McKenna Foundation and National Science Foundation (BSR 900002). We thank the MNHNH and the Academia de Ciencias de Cuba for permission to collect and describe the specimens discussed in this paper.

We are grateful to all of the individuals, Cuban and American, who made our joint venture possible. Our special thanks go to

<sup>3</sup> Rosen's paper is frequently cited as "Rosen, 1976" because this is the date that appears at the head of the abstract and agrees with the actual distribution date (6 April 1976) of the "December 1975" number of volume 24 of *Systematic Zoology*. However, for information retrieval purposes the use of actual time of distribution rather than volume/number is problematic and ought to be avoided.

Gilberto Silva Taboada (MNHNH) and Michael L. Smith (Center for Marine Conservation), who labored hardest to create the MNHNH-AMNH agreement; and to Reynaldo Rojas (MNHNH), Luis Olmo (then of the Museo de Historia Natural, Sancti Spiritus), Alejandro Emperador (Grupo "Sama," Sociedad Espeleológica de Cuba, Sancti Spiritus), and Michael L. Smith, all of whom helped with the fieldwork. We also thank A. Areces-Mallea for pollen analysis of Lagunitas sediments; S. Algar, O. Arredondo, T. W. Donnelly, D. Grimaldi, V. MacPhee, R. Rojas, M. L. Smith, S. D. Webb, and E. E. Williams for helpful discussions concerning issues raised in this paper; L. Meeker, E. Heck, and C. Tarka for illustrations; and C. Fleming for specimen preparation.

#### ABBREVIATIONS

a1/a2/a3	first/second/third molariform (alveoli)
AMNH	American Museum of Natural History
f	fossa in advance of alveolus of first molariform
Fm	formation
ims	intermaxillary suture
MNHNH	Museo Nacional de Historia Natural (La Habana)
MNHNH P	Paleontological Collection, MNHNH
mya	million years ago
pc	palatine canal(s)
tims	torus on intermaxillary suture

#### SYSTEMATIC PALEONTOLOGY

Genus and species diagnoses for the new sloth are the same and are therefore efficiently presented together, as follows:

Order Xenarthra  
 Infraorder Phyllophaga  
 Family Megalonychidae

#### IMAGOCNUS ZAZAE, NEW GENUS AND SPECIES

**HOLOTYPE:** Edentulous partial palate, MNHNH P 3014 (fig. 1), found in lag deposits.

**ETYMOLOGY:** Roots are *imago*, "image, likeness" (Latin) + *ocnus*, "delay, slowness"

(latinized Greek); gender of combination is masculine. Root "-ocnus" is traditional combining form used in propounding names for Antillean megalonychids. Species name is derived from Domo de Zaza, the type locality.

**REFERRED MATERIAL:** Molariform tooth, MNHNH P 3013 (fig. 2); caudal vertebra, MNHNH P 3050; partial pelvis (uppermost part of sacrum and adjoining ilia), MNHNH P 3021. The pelvis was found in situ within lagoonal clay resting on sand; the other specimens were found in lag deposits.

**TYPE LOCALITY AND LOCAL FAUNA:** Holotype and referred specimens were collected at Domo de Zaza (approximately 21°45'N, 79°30'W, 18 km SE of the town of Sancti Spiritus) in lagoonal/near-shore sediments of Lagunitas Fm (see Study Area). Associated vertebrate fauna, as currently known, includes an unidentified bird, pelomedusid turtles, crocodiles, sharks, sirenians, and a small odontocete. These fossils will be described in a separate report (MacPhee et al., in prep.).

**AGE:** Late Early Miocene, based on invertebrate assemblage recovered from related marine facies (see Study Area).

**DIAGNOSIS:** The type species (and only known member) of genus *Imagocnus* is *I. zazae*. The holotype palate of *I. zazae* is distinctively slothlike, being narrow but thick in profile, and bearing subparallel rows of large, closely spaced alveoli (fig. 1). Subparallel, anteriorly diverging cheektooth rows are considered derived within Phyllophaga by us, but are not exclusive to Megalonychidae (cf. Fischer, 1971; Engelmann, 1985). However, attribution to this family is warranted because the partly preserved fossae in front of the first molariform are steep-walled and inwardly concave, unlike anything seen in megatheriids and mylodontids. (These comments assume that these conventional sloth families are monophyletic; on this point see Engelmann, 1985.) We do not wish to base any part of this diagnosis on inferential evidence, but for the record we note that we also recovered what appears to be a natural cast of a megalonychid upper caniniform, in a biocalcarenite near the top of the sequence at Domo de Zaza. The "tooth" is quasitriangular in section—an earmark of megalonychid caniniforms (Webb and Perrigo, 1985). However, the cast (if that is what it is) is

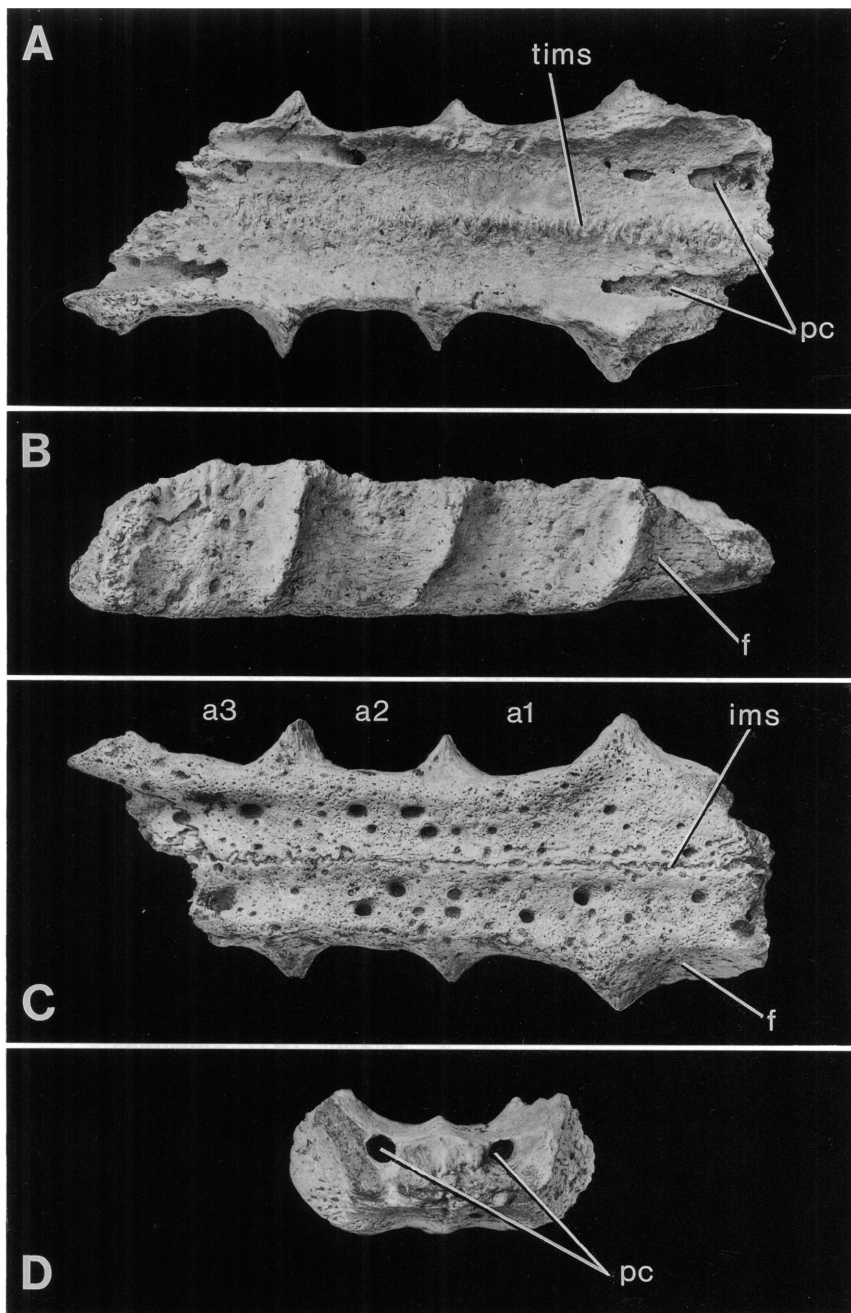


Fig. 1. The holotype palate (MNHNH P 3014) of *Imagocnus zazaе* in dorsal (A), right lateral (B), ventral (C), and rostral (D) aspects. Same scale as in figure 2.

imperfect on one side, and, as no part of the original object remains, we cannot responsibly include this specimen in the hypodigm. (However, for future reference the specimen is cataloged as MNHNH P 3015.)

*Imagocnus zazaе* differs from all adequately described Antillean sloths except species of *Acratocnus* and *Mesocnus* in lacking large, paired palatal palatine foramina at the transverse level of the first molariform teeth. (Pal-

atal palatine foramina may have opened at a more rostral transverse level, or, if there were no discrete apertures, vasculature and nerves passed through the host of "nutrient" foramina perforating the ventral surface.) Holotype palate differs from equivalent portion of palate of *Acratocnus odontrigonus* (and *A. major*, if distinct) in being much larger, possessing distinct midsagittal torus on intermaxillary suture, and lacking sharp medial borders on alveoli. Differs from palate of *Mesocnus browni* (and *M. torrei*, if distinct) in being larger and in having greater interalveolar breadth at the level of first molariform due to slight rostral divergence of tooththrows.

Additional information concerning the systematic position of *Imagocnus* can be gleaned from MNHNH P 3013 (fig. 2). This referred tooth is fragmentary, and both the occlusal surface and root end are missing. However, it is a molariform of a megalonychid sloth because of its shape (reniform in section) and composition (thick core of vascular dentine successively enwrapped by much thinner shells of compact dentine and cementum). In mylodontids, tooth shape is more lobular and the layer of compact dentine tends to be relatively thicker, while megatheriids typically have lophodont, distinctly prismatic molariforms (Fischer, 1971; Englemann, 1978, 1985). In morphology the tooth closely resembles mandibular molariforms of the Quaternary Cuban species *Mesocnus torrei*, but in size it is intermediate between this species and *Megalocnus rodens*, the largest Antillean Quaternary sloth (Fischer, 1971). Other Zaza specimens referable to *I. zaza*—a caudal vertebra and a fragmentary pelvis—are seriously incomplete and in any case do not provide characters useful for differential diagnosis.

## DISCUSSION

### STUDY AREA

Río Zaza (fig. 3) drains the eastern and southern flanks of highland masses in central Cuba (Alturas de Santa Clara, del Nordeste de Las Villas, and de Sancti Spíritus). In recent years outflow through the lower Zaza basin has been substantially modified through the construction of a dam (Presa de Zaza) on this river and diversion of water through a newly built artificial channel, the Canal de

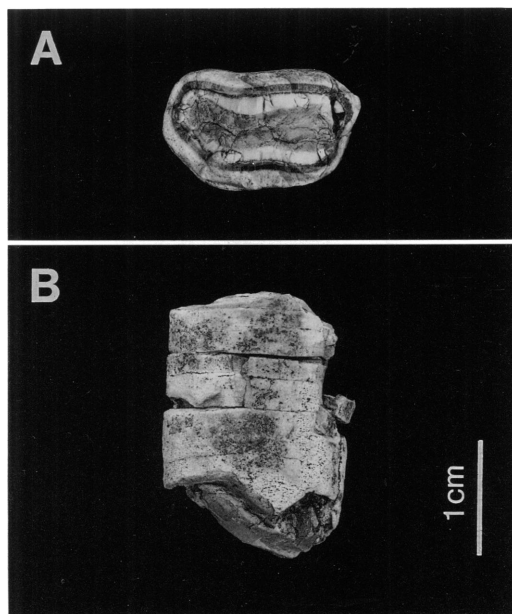


Fig. 2. Presumed lower molariform (MNHNH P 3013; 17.0 × 10.4 mm in section) referred to *Imagocnus zaza*, in cross-sectional (A) and lateral (B) aspects. Occlusal surface and root end are both missing. In morphology the tooth closely resembles mandibular molariforms of the Quaternary Cuban species *Mesocnus torrei*, but in size it is intermediate between this species and *Megalocnus rodens*, the largest Antillean Quaternary sloth.

Zaza. In order to direct the canal toward the irrigation works that it was designed to serve, it was necessary to transect a low, domelike hill (Domo de Zaza) located about 1 km S of the dam site and 18 km SE of the city of Sancti Spíritus. This transection provides one of the very few glimpses of the underlying stratigraphy of this region, which is otherwise almost devoid of relief and thickly covered by late Pleistocene-Recent sediments (MacPhee et al., in prep.). Unexpectedly, this cut revealed the first mid-Tertiary terrestrial depositional environments so far identified in central Cuba, the first fossil land vertebrate from which is described in this report. The locality consists of approximately 3 km of exposures, on both sides of the water channel, with a maximum exposure of 10–15 m.

The gravels, sands, clays, and rare limestone intercalations exposed on channel side-walls at Domo de Zaza are referable to the Lagunitas Fm, a unit defined by E. Popov in

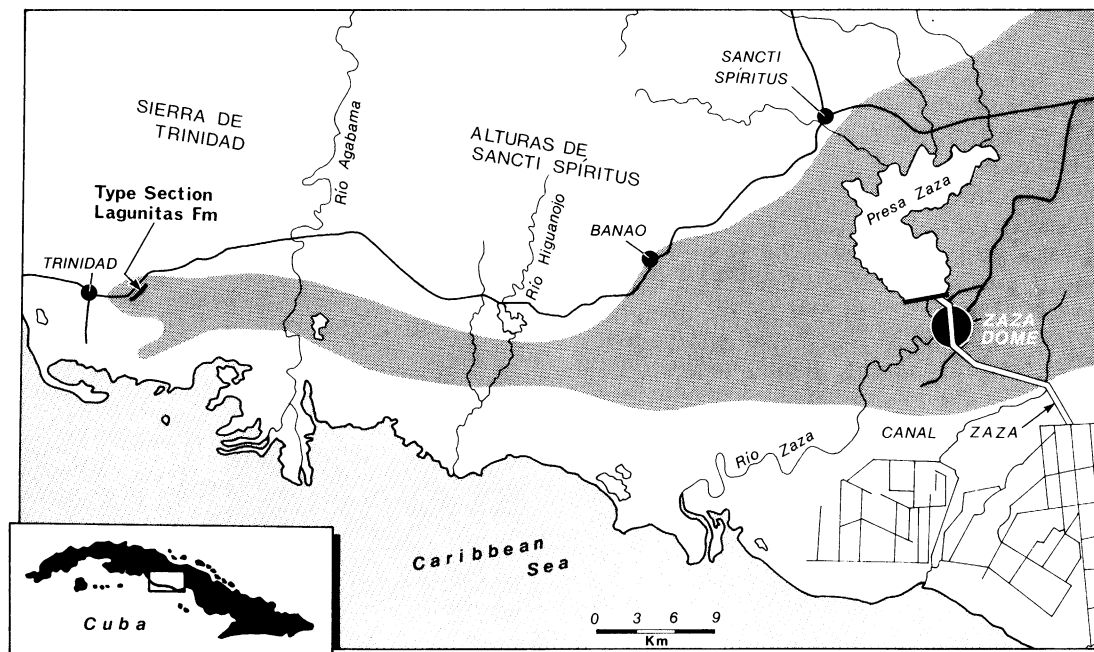


Fig. 3. Location map for Domo de Zaza, western part of Lagunitas Fm (shaded), and place names mentioned in text.

an unpublished geological survey conducted as part of the 1:250,000 scale mapping project of the former Las Villas province (Kantchev et al., ms). This formation, the western part of which is depicted in figure 3, will be more fully described in a related paper (MacPhee et al., in prep.). Here it is sufficient to note that the unit was deposited in a coastal plain environment, where conditions varied from terrestrial to shallow-water marine. The section exposed at Domo de Zaza is laterally and vertically complex, showing evidence of at least four different depositional regimes within the limited area of exposure. The sequence as a whole is composed of several transgressive cycles, beginning with lagoonal clays at base with thin limestones locally, and ending with a thick and ubiquitous limestone cap. However, within cycles there were clearly short phases of uplift. Alluvial deposits, soil development, and land-plant pollen (A. Areces-Mallea, personal commun.) occur in terrestrial facies, providing clear evidence of the periodic presence of emergent land.

The youngest lithostratigraphic unit overlain by Lagunitas Fm is Oligocene Las Cue-

vas Fm, in the type area near Trinidad (fig. 3). Lagunitas is in turn overlain by Middle Miocene Güines Fm and younger sediment. We note that the invertebrate faunal assemblage recovered from marine facies of Lagunitas Fm (table 1) corresponds in general content to the Lower Miocene Soritiidae-*Miogypsina* zone of Iturralde-Vinent (1969, 1971), because both nominate taxa of the zone are present in association with *Heterostegina antillea*. However, the earliest part of the Miocene is evidently not represented at Lagunitas, because the marker taxon *Lepidocyclina* is absent while *Sorites* and *Archaias* are present (last two taxa are never found near Oligocene/Miocene boundary or in association with *Lepidocyclina*). Additionally, the presence of *Procythereis* cf. *deformis* indicates that the Lagunitas is younger than zone N5 (*Catapsidrax dissimilis* zone), and probably fits biochronologically within N6-N7 (after last appearance of *C. dissimilis*, before first appearance of *Orbulina*). This information is consistent with Burdigalian age (approximately 16.9–19 mya). Furthermore, because Lagunitas is located at the base of a

thick Lower through Middle Miocene section (as represented by Lagunitas-Güines-Arabos Fms) in a transgressive interval, correlation with the 18.5–17.5 mya coastal onlap event of Haq et al. (1987) is highly likely. Elsewhere in Cuba, age and lithological partial equivalents of Lagunitas Fm have been described as Paso Real, Arabos, Rosario, and Magantilla Fms (Iturralde-Vinent 1969; Iturralde-Vinent et al., 1987).

For much of the Tertiary, Cuba consisted of three main archipelagos distributed along an approximately east-west axis (Iturralde-Vinent, 1988: fig. 4). The middle group of islands was centered on the Cordillera del Escambray, existing as a high massif at least since the Late Paleogene (Iturralde-Vinent, 1982, 1988). We envisage the Escambray, in Early Miocene, as having formed a small but high island that was ringed by periodically inundated keys in shallow seas. The rivers draining the highlands would have formed extensive deltaic deposits in their lower reaches (future Lagunitas and related formations). During major regressions (late Middle Eocene, Late Oligocene, Late Miocene, and Plio-Pleistocene) these archipelagos were temporarily united; they became permanently so at the end of the Pliocene (Iturralde-Vinent, 1988). From a biogeographical standpoint, these periods of marked regression are of critical significance, because they would have both increased the total land area available for colonization and reduced distances between islands (see fig. 4).

SYSTEMATIC POSITION OF *IMAGOCNUS*

Although the material available for the diagnosis of *Imagocnus zaza* is limited, the basis for its allocation to Phyllophaga seems indisputable. A fragmentary, toothless palate of a very large caviomorph might be momentarily confused with that of a sloth, because caviomorphs also possess narrow interalveolar spaces defined by subparallel rows of closely spaced alveoli. However, caviomorph palates are never as thick as those of sloths, and moreover they lack fossae in advance of the anteriormost tooth.

Allocation to Megalonychidae also seems beyond question, for biogeographical as well as morphological reasons. Megalonychids are

TABLE 1  
Invertebrate Fauna, Lagunitas Formation<sup>a</sup>

Foraminifera	<i>Ammonia beccarii</i>
	<i>Amphistegina</i> aff. <i>A. taberana</i>
	<i>Amphistegina angulata</i>
	<i>Archaias aduncus</i>
	<i>Archaias angulatus</i>
	<i>Discorbis</i> sp.
	<i>Elphidium discoidale</i>
	<i>Elphidium nauitloideum</i>
	<i>Elphidium sagrei</i>
	<i>Heterostegina antillea</i>
	<i>Miogypsina antillea</i>
	<i>Pyrgo</i> sp.
	<i>Sorites marginalis</i>
	<i>Aurila</i> aff. <i>A. cicatricosa</i>
Ostracoda	<i>Bairdia antillea</i>
	<i>Bairdia bradyi</i>
	<i>Caudites</i> sp.
	<i>Costa (Rectotrachyleberis)</i> sp.
	<i>Cytheropteron</i> sp.
	<i>Haplocytheridea cubensis</i>
	<i>Haplocytheridea</i> sp.
	<i>Loxoconcha antillea nodosa</i>
	<i>Loxoconcha cubensis</i>
	<i>Procythereis</i> cf. <i>deformis</i>
Mollusca	<i>Quadracythereis antillea</i>
	<i>Crassostrea vaughani insularis</i>
	<i>Glycymeris acuticostatus</i> aff. <i>G. a. guaica</i>
	<i>Glycymeris jamaicanus</i>

<sup>a</sup> As reported for type section by Popov (in Kantshev et al., MS); for biochronological significance for Zaza vertebrate fauna, see text.

the only sloths known to have entered the West Indies, where they were widespread and diverse prior to their extinction in the late Quaternary (e.g., Arredondo, 1961; Mayo, 1969; Fischer, 1971). Their known distribution included Cuba, Hispaniola, Puerto Rico, and small islands close to northern South America (Anthony, 1918; Hoffstetter, 1955; Hooijer, 1962; White, 1992). A new Pliocene record for Antillean sloths, for Grenada, has not yet been formally published but seems secure (R. Singer, personal commun.).

Megalonychids, both continental and Antillean, are in need of cladistic analysis (cf. Webb and Perrigo, 1985) and there is little point in trying to specify the sister taxon of *Imagocnus* until revisionary treatments of this putatively monophyletic family have been undertaken. For the present it may be noted that strong torus development and mesial placement of the palatine foramina are also seen in various Miocene Patagonian mega-

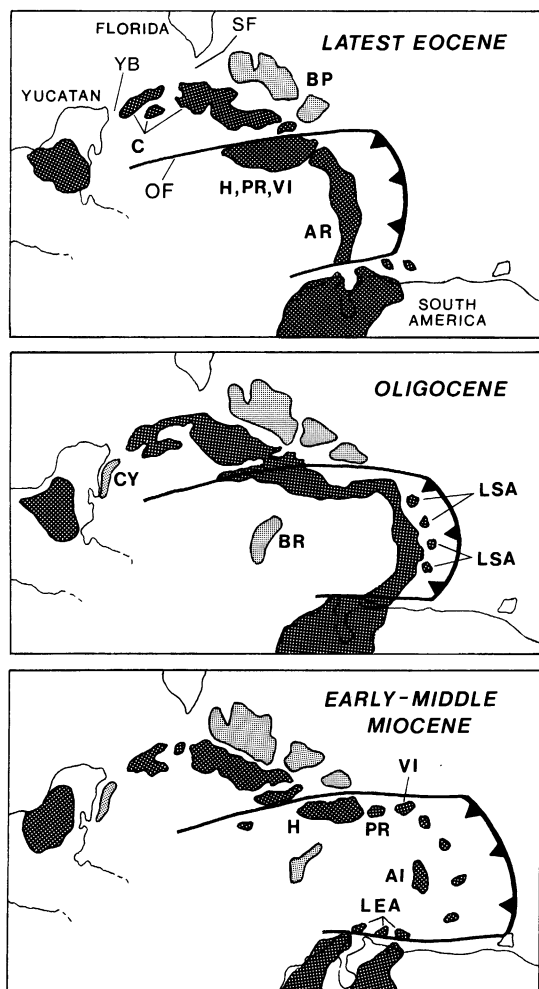


Fig. 4. Paleogeographic maps of Caribbean area, 38–16 mya, based mainly on Ross and Scotese (1988) with various modifications (cf. Iturralde-Vinent, 1988). *Latest Eocene*: Cuba (designated as C) has been approximately stationary since “docking” against Bahamas Platform (BP) in late Middle Eocene. For much of the Tertiary, Cuba consisted of several archipelagos rather than a single large

landmass. To the southeast, the Greater Antilles magmatic arc (future Hispaniola [H], Puerto Rico [PR], and Virgin Islands [VI]) is continued southward by another arc, the Aves Ridge (AR), in collision with South America. Yucatan Basin (YB) is already in existence, as is Straits of Florida (SF). *Oligocene*: Grenada Basin, probably formed by intra-arc spreading, began to split old Aves Ridge from new Lesser Antilles Arc (LSA) after the close of the Eocene. Two important events occurred after termination of island arc volcanic activity at end of Eocene: (1) substantial tectonic uplift took place along the Greater Antilles Ridge and Aves Ridge, and (2) sea level dropped ~160 m at ~30 mya. Substantial emergence of land along these ridges, indicated by latest Eocene-Oligocene depositional hiatuses in many West Indian stratigraphic sequences (Iturralde-Vinent, 1988; Maurrasse, 1990), was probably sufficient to create continuous land or groups of very closely spaced islands from western Cuba through to northern South America. However, they were insufficient to create connectors between the Greater Antilles and the Beata Rise (BR) or Cozumel-Yucatan Ridge (CY). Conditions for overland dispersion to the Greater Antilles from South America were less propitious by Late Oligocene (27 mya) because of rising sea level. *Early/Middle Miocene*: Topographic highs in various parts of future Cuba, Hispaniola, and Puerto Rico remained subaerial for rest of Neogene. Aves Ridge eventually subsides 600–1200 m (Holcombe and Edgar, 1990), leaving Aves Island (AI) and Venezuelan Leeward Islands (LEA) as sole subaerial portions. Volcanic activity continues in parts of Lesser Antilles Arc until present. Reorganization of stress fields within Caribbean Plate, beginning in late Paleogene, had by this time caused significant disruption of formerly compact Greater Antilles Ridge along left lateral faults. Lateral displacements of major blocks and creation of concomitant deep water gaps (e.g., Windward Passage between Cuba and Hispaniola, along rejuvenated Oriental Fault [OF]) led to vicariant separations of formerly continuous populations.

lonychids with suspected ties to better-known *Acratocnus* and *Mesocnus* (Pascual et al., 1990). On the basis of postcranial features, White (1992, 1993) has recently argued that Antillean sloths may be most closely related to Santacrucian *Eucholoeops*. Megalonychids entered North America well before the completion of the Panamanian landbridge ca. 3 mya (Webb and Perrigo, 1985), but at present there is no indication that they did so via the

Greater Antilles, or that Antillean sloths share a more recent ancestry with North American than with South American taxa. White (1993) presented some evidence for the proposition that two different clades of megalonychids colonized the northern Greater Antilles, although the difference in tree length between this solution and slightly less parsimonious ones providing for a single initiator lineage is small.



TABLE 2  
Tertiary Freshwater and Terrestrial Vertebrates of the Greater Antilles<sup>a</sup>

Island	Age/formation/locality	Reference
Cuba <sup>b</sup>		
<i>Imagocnus zaza</i> (Megalonychidae, Xenarthra)	E. Miocene; Lagunitas Fm, Domo de Zaza, S. Spíritus	This paper
Unidentified bird	E. Miocene; Lagunitas Fm, Domo de Zaza, S. Spíritus	MacPhee et al., in prep.
Hispaniola <sup>c,d</sup>		
<i>Cichlasoma woodringi</i> (Cichlidae, Perciformes)	?M. Miocene; Las Cahobas Fm, Mirebalais	Cockerell, 1924
<i>Anolis dominicanus</i> (Iguanidae, Sauria)	?Miocene; amber deposits, Dominican Republic	Rieppel, 1980
<i>Sphaerodactylus dommeli</i> (Gekkonidae, Sauria)	?Miocene; amber deposits, Dominican Republic	Böhme, 1984
<i>Eleutherodactylus</i> sp. (Leptodactylidae, Anura)	?Late Eocene; amber deposits, Dominican Republic	Poinar and Cannatella, 1987
Unidentified mammal (?rodent)	?Miocene; amber deposits, Dominican Republic	Poinar, 1988
Puerto Rico <sup>b,e</sup>		
Boid (Ophida)	E. Miocene; Cibao Fm, Aguadilla	MacPhee and Wyss, 1990
?Iguanid (Sauria)	E. Miocene; Cibao Fm, Aguadilla	MacPhee and Wyss, 1990

<sup>a</sup> Sloth and caviomorph remains of Pliocene age from Grenada (R. Singer, personal commun.) are the only known Tertiary land vertebrate fossils from the Lesser Antilles.

<sup>b</sup> Miocene pelomedusid turtles from the Greater Antilles, known from Puerto Rico (Wood and Gaffney, 1989) and Cuba (MacPhee et al., in prep.) are possibly but not certainly freshwater. They are therefore omitted from this list.

<sup>c</sup> Some reported ages of Dominican amber deposits are controversial; listed ages follow authors' reports.

<sup>d</sup> Additional vertebrate inclusions in Dominican amber have been discovered in recent years (including additional examples of embedded hair, feathers) and are in the process of being described by various workers.

<sup>e</sup> Age of echimyd rodent *Puertoricomys corozalus* from Corozal is undetermined (MacPhee and Wyss, 1990), although Woods (1989) regarded it as possibly Tertiary.

BIOGEOGRAPHICAL SIGNIFICANCE OF  
*IMAGOCNUS*

The discovery of *Imagocnus zaza* marks an important milestone in efforts to recover the enigmatic biotic history of the Greater Antilles, but its significance needs to be judged in relation to other discoveries. Like *Imagocnus*, most of the small number of Tertiary land vertebrates known from the Greater Antilles are dated to Miocene (table 2). However, parts of Cuba and Hispaniola have been continuously subaerial since the beginning of the Late Eocene (Iturralde-Vinent, 1982, 1988), and palynological evidence (Graham and Jarzen, 1969) indicates that terrestrial environments with moderate plant diversity were already in existence in Puerto Rico by

Late Oligocene. Land vertebrates could therefore be older than the Early Miocene minimum date supplied by the majority of fossils. (The earliest attributed date for a vertebrate, ?Late Eocene for a frog referable to the extant Neotropical genus *Eleutherodactylus* [Poinar and Cannatella, 1987], is older than generally accepted dates for Dominican amber and needs to be confirmed.)

Some recent authors (e.g., Poinar and Cannatella, 1987) have argued that proof of the existence of land vertebrates in the Greater Antilles during the mid-Tertiary tends to support vicariist rather than dispersalist interpretations of Caribbean historical biogeography. However, all taxonomically identifiable land vertebrate taxa (including *Imagocnus*) can be comfortably nested, at

relatively low hierarchical levels, within clades that persisted into the Quaternary. (Specimens for which no reliable lower-level placement has yet been made, like the ?rodent hair reported by Poinar [1988] or the ?iguanid vertebra described by MacPhee and Wyss [1990], have no bearing on this observation.) In lacking any "unexpected" vertebrate taxa—that is, groups representing major clades not known to have existed on the islands in the Quaternary (MacPhee and Wyss, 1990)—the paleontological record can be interpreted to mean that Antillean diversity has always been limited to a few groups (Williams, 1989; Woods, 1989). Yet the failure to find "unexpected" taxa may simply mean that an originally more diverse fauna had already been reduced by the start of the Neogene, when the fossil record begins, to groups that would survive into the Quaternary. Or, alternatively, it may indicate that collection efforts have been inadequate to give a fair picture of previous diversity (Mayer and Lazell, 1988; Williams, 1989; MacPhee and Wyss, 1990). Several examples of "unexpected" terrestrial arthropods have been recovered from ?Miocene Dominican amber (Wilson, 1988), proving that mid-Tertiary diversity for some groups was greater than (or at least different from) their Quaternary diversity.

Despite arguments to the contrary, hypotheses of vicariance in the strict sense proposed by Rosen (1975, 1985) are probably no more readily falsifiable than ones invoking dispersal as historical explanations for biotic distributions. At this stage of knowledge it is possibly more productive to ask whether there was any sort of "common cause" that could have made Antillean colonization (however accomplished) easier for land vertebrates at one time rather than another. Various lines of evidence indicate that a possible optimum for colonization occurred between the end of the Middle Eocene and the beginning of the Late Oligocene (fig. 4). During this interval there was diachronous compression along the northern and southern Caribbean Plate boundaries (Pindell and Barrett, 1990), substantial terminal Palaeogene uplift along the axes of the Greater Antillean and Aves Ridg-

es (Holcombe et al., 1990; Maurrasse, 1990), and a drop in eustatic sea-level of 160 m, ca. 30 mya (Haq et al., 1987; but see Hallam, 1992). According to Algar and Erikson (1992), progressive Palaeogene overthrusting by the eastward-moving Caribbean Plate created a forebulge in northern South America close to the southernmost part of the Aves Ridge arc (future Venezuelan Antillas Menores). This is consistent with the evidence discussed by Speed et al. (1993) for an Oligocene collision between the South American continental slope and the Paleogene magmatic arc of the southern Lesser Antilles, followed by uplift in Early Miocene. This event may have produced the continental terminus of a connector (realized as closely spaced islands, long peninsula, or actual landbridge) involving the Aves Ridge and thence the Greater Antilles (cf. Holcombe and Edgar, 1990), especially during times of low sea level. How long conditions favorable for the movement of land vertebrates might have persisted is of course unknown, but it was surely not very long.

By contrast, vergence between Cuba and Florida never closed the Straits of Florida, and the Yucatan Channel has existed in some form since the Cretaceous. Long persistence of these marine barriers offers an explanation for the low number of apparently North American elements in the mammalian fauna—just two taxa, the insectivores *Solenodon* and *Nesophontes* (MacFadden, 1980). (Significant presence of Central American elements in the herpetofauna [Guyer and Savage, 1986] may imply a different temporal optimum for this group.) Immunological distance (ID) measurements for a number of reptile and amphibian groups display wide scattering when calibrated against a molecular clock model (Hedges et al., 1992). Scattering, with estimated divergences as late as the Pleistocene in some cases, is said to falsify Rosen's (1975) Caribbean vicariance hypothesis while favoring dispersal as the overall method of faunal formation in the West Indies. However, these results do not preclude the scenario offered here, because we infer that faunal emplacement was a mid-Tertiary event, not terminal Cretaceous as envisaged by Rosen. (For a discussion of the inappropriateness of ID measurements for correlat-

ing events in earth history and phylogeny, see Page and Lydeard, in press.)

Congruence among Quaternary faunal suites of the major islands suggests the impact of another common cause. We assume that ancestors of the known Quaternary rodents, primates, sloths, and insectivores were in place on landmasses in the Caribbean by the mid-Tertiary. It was at this time that reorganization of stress fields within the Caribbean Plate began to progressively disrupt the originally more compact Greater Antilles Ridges by horizontally displacing large blocks (islands) along left lateral faults (Mann and Burke, 1984; Pindell and Barrett, 1990; Holcombe et al., 1990; Ross and Scotese, 1988;

Iturralde-Vinent, 1988). Concomitant creation of deep water gaps between islands (e.g., Windward Passage between Cuba and Hispaniola) could have produced true vicariant separation of populations that were formerly continuous. Any compositional differences between individual island faunas (e.g., apparent absence of heptaxodontid rodents in Cuba, platyrrhine monkeys in Puerto Rico) may thus be evidence of postvicariance local extinction, not failed dispersal. Losses, if they occurred, are potentially demonstrable with fossil evidence, illustrating how paleontology may play yet another role in resolving leading problems in Caribbean biogeography.

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