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Origin of the Greater Antillean Land Mammal Fauna, 1: New Tertiary Fossils from Cuba and Puerto Rico

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ABSTRACT

A new isolobodontine capromyid rodent (*Zazamys veronicae*, new genus and species) and a new platyrrhine primate (unnamed genus and species A) are described from material recovered at Domo de Zaza, an important late Early Miocene locality in south-central Cuba near the town of Sancti Spiritus. Also described is a femur believed to represent a small megalonychid sloth (unnamed genus and species B), from a well-dated Early Oligocene site near the town of Yauco in southwestern Puerto Rico.

These and other discoveries in the Greater Antilles establish that these islands supported a diverse land mammal fauna from the Oligocene onward. Pertinent geological evidence is consistent with the proposition that the initiators of all or practically all founder clades of Antillean land mammals were emplaced there near the Eocene-

Oligocene boundary. Under the terms of this model it is not expected that any land mammal faunal elements of greater than Late Eocene age will be found in these islands. It is reasonable to infer that Tertiary Antillean mammal groups were widely distributed throughout this terrain, and the discovery of a biogeographical "ghost" (*Zazamys*) supports this.

Emergent parts of the present-day Greater Antilles were in a close-packed array until the commencement of the Neogene. They formed part of a long-lasting positive topographic feature of the Caribbean Basin, here dubbed GAARlandia. During the Late Eocene-Oligocene, this feature included Cuba, northern Hispaniola, Puerto Rico, Virgin Islands, Aves Rise, and the Venezuelan Antillas Menores. Since latest Oligocene, GAARlandia has undergone disruption and fragmentation

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into its modern insular components, a process that forced vicariance of the original fauna. Extinction has also shaped the distribution of Antillean land

mammals throughout the later Cenozoic, and this has important implications for interpreting their historical biogeography.

RESUMEN

Un nuevo roedor capromydo isolobodóntido (*Zazamys veronicae*, nuevo género y especie) y un nuevo primate platyrrhino (género y especie A, sin denominar) se describen a partir del material recuperado en Domo de Zaza, una importante localidad fosilífera del Mioceno Inferior tardío situada en la región sur-central de Cuba, cercana a la ciudad de Sancti Spiritus. También se describe un fémur que se cree representa un pequeño pezoso megalonychido (género y especie B, sin denominar), de un sitio paleontológico bien datado de edad Oligoceno Inferior, localizado cerca de la ciudad de Yaucu, en el suroeste de Puerto Rico.

Estos descubrimientos, unido a otros recientes realizados en las Antillas Mayores, permiten establecer que estas islas ya soportaban una variada fauna de mamíferos terrestres a partir del Oligoceno. Las evidencias geológicas son consistentes con la proposición de que los iniciadores de todos, o prácticamente de todos los clados fundadores de la fauna de mamíferos terrestres antillanos, se emplazaron en estas tierras cerca del límite Eoceno-Oligoceno. Bajo los términos de este modelo, es de esperar que ningún mamífero terrestre más antiguo que Eoceno Superior sea encontrado en

estas islas. Es razonable, asimismo, inferir que los grupos de mamíferos terrestres estaban ampliamente distribuidos en las tierras antillanas, y el descubrimiento de un "fantasma" biogeográfico (*Zazamys*) en el Mioceno Inferior de Cuba, sustenta esta afirmación.

Las partes emergidas de las actuales Antillas Mayores formaban entonces un conjunto más compacto hasta el comienzo del Neógeno. Ellas formaban parte de un elemento topográfico positivo muy duradero en la cuenca del Caribe, el cual aquí se denomina GAARlandia. Durante el Eoceno Superior-Oligoceno, este elemento incluía a Cuba, La Española septentrional, Puerto Rico, Islas Vírgenes, Cresta de Aves y las Antillas Menores Venezolanas. A partir del Oligoceno tardío, comenzó la fracturación y dispersión de GAARlandia hasta formar sus componentes insulares actuales, un proceso que forzó la vicariancia de la fauna original. Las extinciones que han ocurrido a través del Cenozoico tardío, también es probable que hayan contribuido a conformar la distribución actual de los mamíferos terrestres Antillanos, y estos tiene importantes implicaciones para la interpretación de su biogeografía histórica.

INTRODUCTION

How and when the ancestors of the land vertebrate fauna of the Greater Antilles managed to reach those islands are topics perennially debated in biogeography (for recent examples, see Hedges et al. [1992, 1994] and Page and Lydeard [1994]). Although agreement concerning the method(s) of colonization is evidently not in sight, there is a growing fossil tally (table 1) which provides undeniable evidence that founder clades were already well represented in the islands by the mid-Cenozoic. As noted elsewhere (MacPhee and Wyss, 1990), fossils are empirical documents with temporal as well as phylogenetic implications, and as such are critically important to the reconstruction of biogeographical history.

In this report we announce the discovery of the second and third land mammals of Tertiary age from Cuba, and bring attention to the first such discovery made in Puerto

Rico. We also extend and modify our model of the land-mammal colonization of the Greater Antilles (MacPhee and Iturralde-Vinent, 1994). In the text, the age of stage and epoch boundaries cited in millions of years (Ma) follows the framework of Harland et al. (1990).

ABBREVIATIONS

AMNH	American Museum of Natural History
AMNH M	American Museum of Natural History, Department of Mammalogy
AMNH VP	American Museum of Natural History, Department of Vertebrate Paleontology
e	estimate (in measurement, due to breakage)
Fm	formation
JD	Juana Díaz Fm (sensu Frost et al.,

	1983), not including "upper carbonate member"
Ma	millions of years (ago)
MNHNH	Museo Nacional de Historia Natural (La Habana)
MNHNH P	Museo Nacional de Historia Natural (La Habana), paleontological collections of Departamento de Colecciones
MNHNH V	Museo Nacional de Historia Natural (La Habana), vertebrate collections of Departamento de Colecciones
rev.	reversed (as applied to figures, to facilitate comparison)
UC	"upper carbonate member," in older definitions of Juana Díaz Fm

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EARLY MIOCENE RODENT AND PRIMATE FROM CUBA

A new capromyid rodent, referable to subfamily Isolobodontinae, is named here on the basis of dental material from the important Early Miocene locality of Domo de Zaza in the province of Sancti Spiritus. A platyrrhine monkey is also represented in the Zaza material by a single, well-preserved astragalus. Although the astragalus appears to represent a species new to science, it makes a poor holotype. Accordingly, until specimens capable of providing a secure diagnosis are discovered, we shall simply refer to the new Zaza anthropoid as "unnamed genus and species A (primate)." Locality information is kept purposely brief, since this site and its context is fully described in another paper (MacPhee et al., in prep.).

RODENTIA

CAPROMYIDAE: ISOLOBODONTINAE

Zazamys veronicae, new genus and species

HOLOTYPE: Left mandibular ?M3 (MNHNH P 3072; fig. 1A, F–G), found in lag deposit near south end of Domo de Zaza section by O. Jiménez in February 1994.

ETYMOLOGY: *Zaza* (locality name) + $\mu\upsilon\sigma$ (mouse). Species name for Veronica Mahanger MacPhee, in gratitude for her unflinching help and sharp editing pencil.

TYPE LOCALITY AND AGE: Domo de Zaza, a locality in late Early Miocene Lagunitas Fm of south-central Cuba. For detailed locality information and age assessment, see MacPhee and Iturralde-Vinent (1994) and MacPhee et al. (in prep.).

REFERRED MATERIAL: Right mandibular M1 or M2 (MNHNH P 3058, fig. 1B, rev.) and left mandibular M1 or M2 (MNHNH P 3071, fig. 1C), found in lag by (respectively) P. Valdés in November 1993 and R. MacPhee in February 1994.

DIAGNOSIS: The type and only species of *Zazamys* is *Z. veronicae*, genus and species

TABLE 1
Reported Tertiary Freshwater and Terrestrial Vertebrates of the Greater Antilles^a

Island	Age/Formation/Locality	Reference
Cuba^b		
<i>Imagocnus zaza</i> (Megalonychidae, Xenarthra)	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spiritus	MacPhee & Iturralde-Vinent, 1994
<i>Zazamys veronicae</i> (Capromyidae, Rodentia)	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spiritus	This paper
Unnamed genus and species A (Platyrrhini, Primates)	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spiritus	This paper
Unidentified bird	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spiritus	MacPhee et al., in prep.
Unidentified pelomedusid turtle	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spiritus	MacPhee et al., in prep.
Hispaniola^{c,d,e}		
<i>Cichlasoma woodringi</i> (Cichlidae, Perciformes)	?M. Miocene; Las Cahobas Fm; Mirebalais, Haiti	Cockerell, 1924
<i>Anolis dominicanus</i> (Iguanidae, Sauria)	?Miocene; amber deposits; Dominican Republic	Rieppel, 1980
<i>Sphaerodactylus</i> sp. (Gekkonidae, Sauria)	?Oligo-Miocene; amber deposits; Dominican Republic	Kluge, 1995
<i>Eleutherodactylus</i> sp. (Leptodactylidae, Anura)	?Late Eocene; amber deposits; Dominican Republic	Poinar & Cannatella, 1987
cf. <i>Nesocittes</i> (Picidae, Aves)	?U. Eocene-E. Miocene; amber deposits; Dominican Republic	Laybourne et al., 1994
Unidentified mammal (?rodent)	?Miocene; amber deposits; Dominican Republic	Poinar, 1988
Puerto Rico		
Boid (Ophidia)	E. Miocene; Cibao Fm; Aguadilla	MacPhee & Wyss, 1990
?Iguanid (Sauria)	E. Miocene; Cibao Fm; Aguadilla	MacPhee & Wyss, 1990
Unnamed genus and species B (Tardigrada)	E. Oligocene; Juana Diaz Fm; Yauco	This paper
Unidentified pelomedusid turtle	E. Miocene; Cibao Fm; Aguadilla	MacPhee & Wyss, 1990

^a This table updates table 2 of MacPhee and Iturralde-Vinent (1994), which should be consulted for additional remarks.

^b Intact carapaces and plastrons of pelomedusid turtles have been recovered in situ from lagoonal deposits in Lagunitas Fm. This strongly implies that they were freshwater-adapted (cf. MacPhee and Iturralde-Vinent, 1994, table 2); the habitat of Puerto Rico pelomedusids is still ambiguous, but we include them in this paper.

^c See Grimaldi (in press) for discussion of the general problem of dating some ambers; listed ages follow authors' reports, with question marks expressing level of doubt.

^d *Cichlasoma woodringi* may not be distinguishable from extant species (M. L. Smith, personal commun.).

^e "*Sphaerodactylus*" *dommeli* (Böhme, 1984) may be an anole rather than a sphaerodactyl according to Kluge (1995, citing D. Frost, personal commun.).

diagnoses are therefore the same. Among known Antillean taxa, *Zazamys veronicae* most closely resembles the Quaternary Antillean genus *Isolobodon*, representatives of which are known from Hispaniola, Puerto Rico, Mona Island, and several of the Virgin Islands, but not from Cuba (Anthony, 1926; Reynolds et al., 1953; Varona, 1974; Woods,

1989b). Whether this multi-island range is original or the result of human introductions has long been debated (cf. Allen, 1942; Morgan and Woods, 1986), but for the purposes of this paper we accept the occurrence of *Isolobodon* on both Hispaniola and Puerto Rico as natural. Also, in agreement with Woods (1989b) we accept *Isolobodon portoricensis*

and *I. montanus* as good species, but follow Reynolds et al. (1953) in considering *I. levir* as synonymous with *I. portoricensis*.

Occlusal pattern, root shape, and arc of curvature of the teeth in the *Zazamys* hypodigm indicate that all are lower molars. Lower molars of *Zazamys* have two lingual reentrant folds (mesoflexid and metaflexid) and one buccal fold (hypoflexid), as is generally characteristic of capromyids (Woods, 1989b). *Zazamys* differs from all capromyines and hexolobodontines sensu Woods (1989b, 1992) in that the *thick* continuous shell of cementum encircling the molariforms of taxa in these two subfamilies is absent. *Zazamys* resembles the plagiodontines *Plagiodontia* and *Rhizoplagiodontia* in that cementum is limited to reentrant folds, but differs in that the folds themselves are not obliquely oriented (see below). *Zazamys* resembles the isolobodontines *Isolobodon portoricensis* and *I. montanus* in the patterning of occlusal surfaces. However, there are differences which indicate that separation at the generic level is warranted. The lower molars of *Zazamys* differ from those of *I. portoricensis* in the following respects: (1) Reentering metaflexid and hypoflexid meet at the center of the occlusal surface, enclosing roughly equal areas of dentine between their arms; in *Isolobodon*, metaflexid-hypoflexid juncture is lingually displaced, so that metaflexid arms are considerably shorter than hypoflexid arms and area of dentine enclosure is considerably smaller. (2) Ridged cementum is essentially restricted to reentrant folds and is barely discernible on tooth columns (see fig. 1); in *Isolobodon*, ridged cementum is easily distinguishable outside of reentrant folds. (3) Reentrants are much more compressed (also more compressed than in *I. montanus*, which is intermediate in this regard).

DESCRIPTION: Because these teeth are isolated finds, their orientation in the jaw during life is not certain. However, judging from the location of intraproximal wear facets and other features, they were probably seated in such a way that the reentrants were more or less normal to the axis of the jaw.

The teeth are judged to be hypselodont (evergrowing, with open roots) and probably hypsodont, although ontogenetic data and

complete jaws would be needed to confirm these points. Cementum forms noticeable ridges only within reentrant folds (fig. 1F, F'), but in MNHNH P 3072 there are barely discernible, quasiparallel lineaments detectable on external surfaces (fig. 1F, arrows). As far as may be determined without a histological examination, these lineaments are not separately composed of cementum but seem to lie within the enamel. It is unclear whether this condition in *Zazamys* can be validly regarded as antecedent to the highly pronounced version of cementum ridging seen in *Isolobodon* (fig. 1E). In capromyines, cementum within reentrant folds has a much less organized, frothy texture.

Because cementum layers on capromyid teeth are applied to smooth enamel surfaces, they can and do scale off. However, small "islands" of cementum usually remain, except in specimens that have been severely abraded. The teeth from Zaza are not significantly abraded and we therefore conclude that complete sleeves of cementum were never present.

PHYLOGENETIC RELATIONSHIPS: Isolobodontines and plagiodontines are closely related and are often included in the same subfamily (e.g., by Varona, 1974). Woods (1989a) defined 14 character state differences between *Isolobodon* and *Plagiodontia*, but of these only one (ridged cementum on external surfaces of tooth) can be evaluated on the basis of the existing *Zazamys* hypodigm. Within Cavimorpha, loss or modification of external cementum on molars is not distributed in a way that is consistent with the likeliest phylogenetic reconstructions of the group; multiple convergences across the suborder have therefore occurred. Ridging, however, appears to be a unique synapomorphy of isolobodontine capromyids, occurring (as far as is now known) in no other caviomorph clade. Possession of a version of this character decisively places *Zazamys* next to known isolobodontines, a fact which can be suitably underlined by including the Zaza rodent in subfamily Isolobodontinae.

It is widely agreed that capromyids and echimyids are closely related, although there is rather less agreement concerning within-group relationships and the closeness of their affiliation with other caviomorphs (cf. Corbet

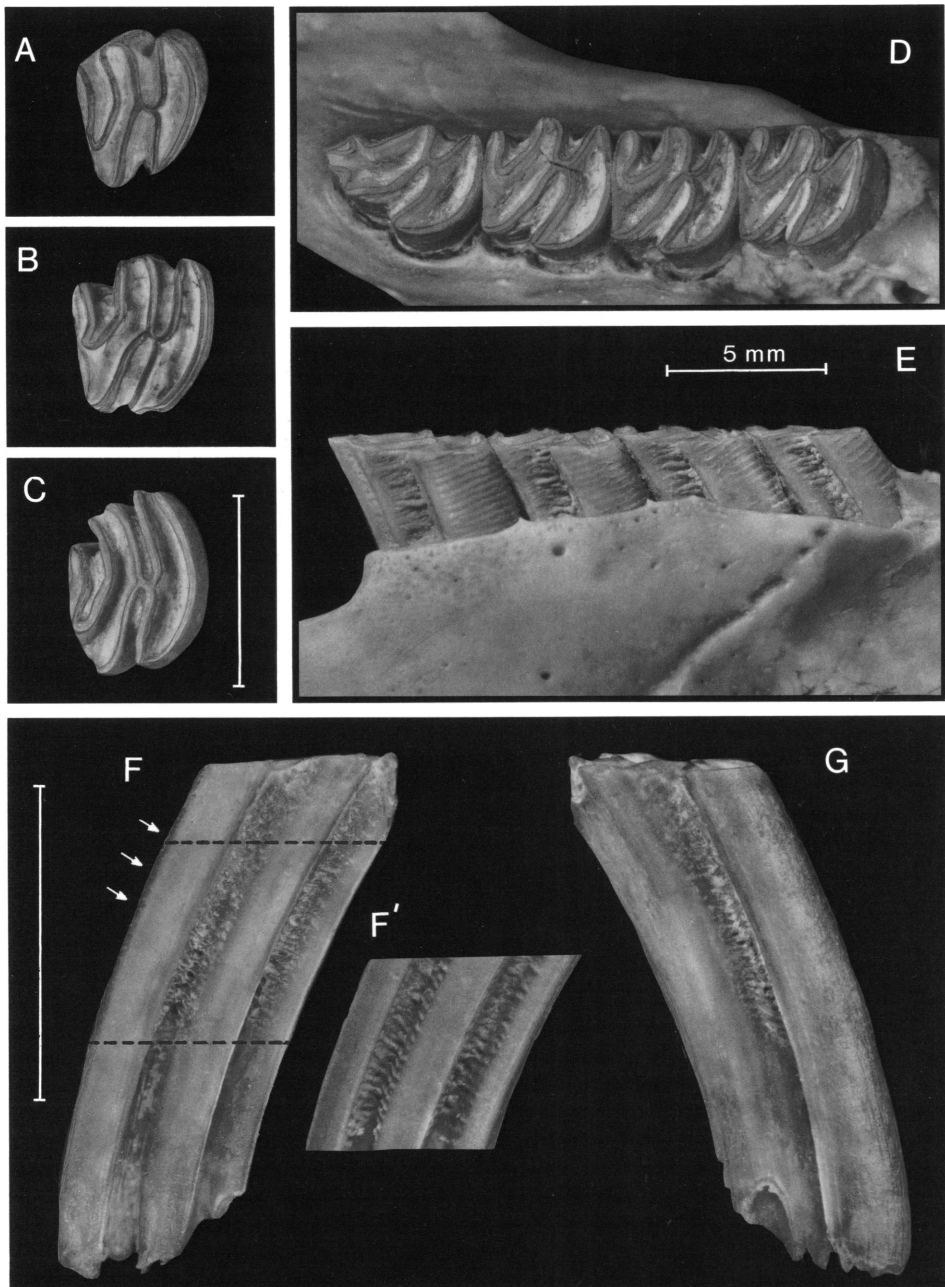


Fig. 1. Holotype of *Zazamys veronicae* (MNHNH P 3072), a left mandibular M3, is seen in occlusal (A), lingual (F), lingual detail (F'), and buccal (G) views, from Early Miocene locality of Domo de Zaza in south-central Cuba. Referred specimens seen in occlusal view are (B), a right (rev.) lower M1 or M2 (MNHNH P 3058); and (C), a left lower M1 or M2 (MNHNH P 3071). Compare to left mandibular dentition of *Isolobodon portoricensis* (AMNH M 38409), in occlusal (D) and buccal (E) aspects (anterior is to the left). Note, in F, presence of periodic banding on enamel (arrows), mimicking lines of ridged cementum in *Isolobodon*; note also, in F' (cast), the organization of interflexid cementum. All scales are 5 mm.

and Hill, 1980; Reig, 1981; Patterson and Wood, 1982; Woods, 1989a, 1989b). Woods (1989b) has recently considered these issues in some detail, and has concluded that capromyids are derived from echimyids (or a common ancestor of echimyids, myocastorids, and octodontids). Since capromyids have not been identified paleontologically or neontologically in surrounding mainlands, this argument carries the implication that capromyids must have evolved wholly within the Greater Antilles. If Capromyidae as usually defined is a holophyletic group restricted to the Greater Antilles and some nearby islands, then based on our reconstruction of Antillean faunal history this clade could not have originated earlier than about 42 Ma—i.e., the beginning of the Late Eocene, the earliest time at which it would have been feasible for land mammals to take up permanent residency (see Discussion).

PRIMATES

ANTHROPOIDEA: PLATYRRHINI

Unnamed Genus and Species A (Primate)

MATERIAL: Right astragalus (MNHNH P 3059; table 2, fig. 2), found in lag deposit near south end of Domo de Zaza section by O. Jiménez in November 1993.

PRELIMINARY EVALUATION: At the time of its discovery in 1993, MNHNH P 3059 was thought to be morphologically distinct from astragali of all known mainland New World primates, including near-coevals from Patagonia like *Carlocebus* and *Soriacebus* (MacPhee and Iturralde-Vinent, 1995). More recently, a partial astragalus (MNHNH V 205) attributable to the Cuban monkey *Paralouatta varonai* (fig. 3) has turned up in a faunal collection from Cueva Alta (for site description, see Jaimez Salgado et al., 1992). The two elements are extraordinarily similar in size and details of shape, which suggests (un-surprisingly) that they represent the same narrow monophyletic group.

The following morphological description uses the terminology and measurement methods of Meldrum (1990); table 2 should be consulted for measurement values and acronyms. In astragalus length, the Zaza specimen places near the upper end of the size

distribution in extant platyrrhines as presented by Meldrum (1990), being exceeded in this regard only by *Ateles*, *Alouatta*, and *Lagothrix* (*Brachyteles* was not included). Comparable dimensions of the astragalus from Cueva Alta are slightly larger. The head of the Zaza specimen is slightly damaged medially, but the navicular facet was clearly ovoid in shape with its long axis (as measured by HDW) somewhat obliquely set. The head is missing from the Cueva Alta specimen. The necks of both specimens are comparatively short but robust. The angle described by the neck on astragalus body is approximately 30° in each specimen (Meldrum's method). The anterior calcaneal facet of the Zaza anthropoid is extensive proximally, showing no tendency to taper in the direction of the deep astragalus sinus. Distally, it meets the navicular facet along a raised margin; a nonarticular strip between facets is not present. The anterior calcaneal facet on the astragalus assigned to *P. varonai* is damaged, but there is no doubt that the facet was just as extensive proximally. The posterior calcaneal facet is very large in both specimens. "Waisting" in the medial third of the facet is slight, especially in the *Paralouatta* astragalus. Indeed, the ratios of facet length to width (PCL/PCW) in these specimens are considerably higher than in any of the taxa or fossils sampled by Meldrum (1990). The astragalus sinus is much deeper in the Zaza specimen than in the one from Cueva Alta. By contrast, trochlear height (TH) is somewhat higher in *P. varonai*.

In both specimens, the trochlear articular surface is high, parallel-sided (not "wedged"), and extensive from front to back. The trochlear spool is moderately deep, and in proximal aspect the medial rim is slightly higher than the lateral. The tibial articular surface terminates proximally in a long, fluted shelf that would have guided the tibial and fibular flexors. In *P. varonai* this area is broken and abraded. Distally, the tibial articular surface ends more or less abruptly in both specimens. Medially, a shallow stop for the tibial medial malleolus encroaches on the neck. The distal margin of the lateral trochlear rim projects beyond the level of the astragalus body in both specimens, but especially so in the Cueva Alta astragalus. The articular surface for the

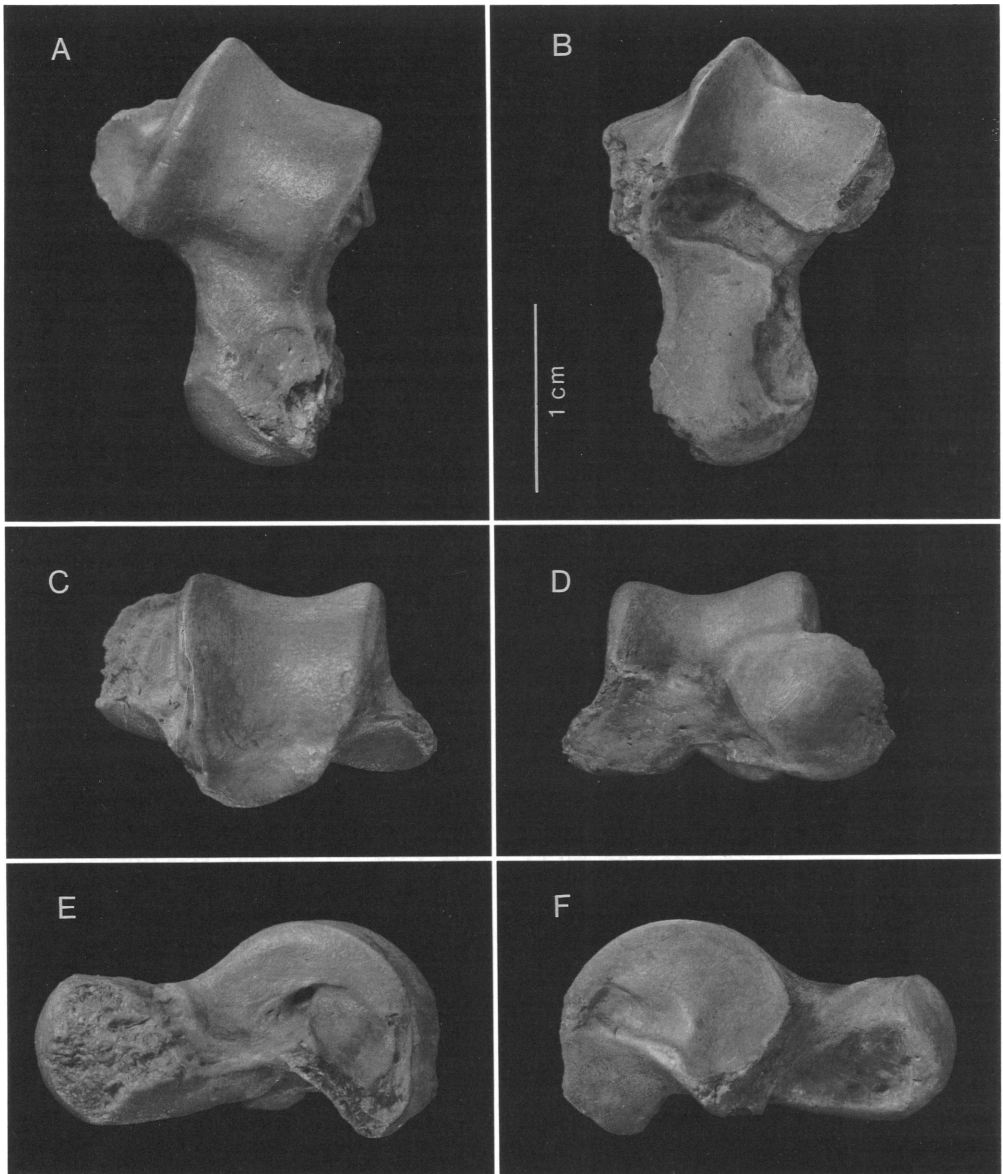


Fig. 2. Astragalus (MNHNH P 3059) of an anthropoid (unnamed genus and species A), from Early Miocene locality of Domo de Zaza, south-central Cuba. Views are A, dorsal; B, ventral; C, proximal; D, distal; E, medial; and F, lateral.

fibula is flat, but ventrad it spreads out laterally to a marked degree. The posterolateral process of Meldrum (1990) seems to have been absent in both specimens, unless the tiny eminence in the Cueva Alta specimen can be so regarded.

The fact that there are only minor differences between these two astragali (e.g., slight-

ly higher trochlea, wider posterior calcaneal facet, shallower astragalar sinus in *P. varonai*) underlines the high probability that the species which they represent are closely related. In fact, this degree of similarity begs a question: if Zaza is confirmably late Early Miocene in age (MacPhee et al., in prep.), are the fossils from Cueva Alta truly as young as

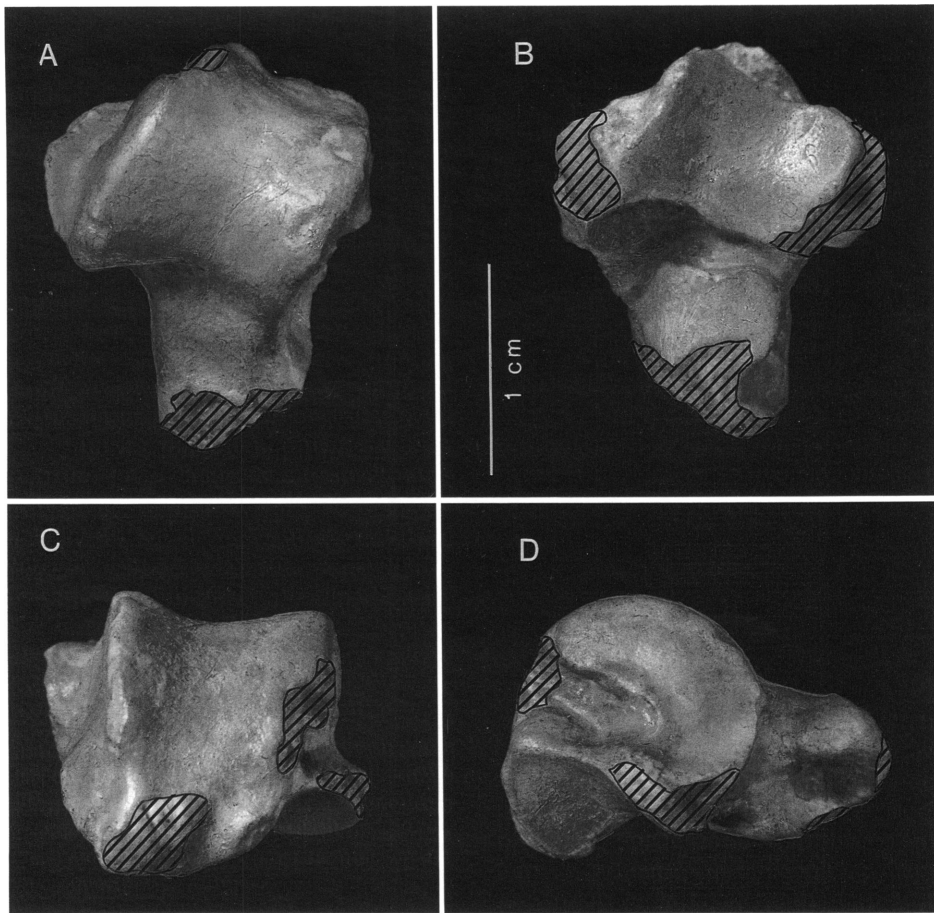


Fig. 3. Astragalus (MNHNH V 205) attributed to *Paralouatta varonai*, from Cueva Alta, Sierra de los Organos, western Cuba. Views are A, dorsal; B, ventral; C, proximal; and D, lateral. Shading denotes abraded areas.

Quaternary? Sloth bones from Cueva Alta (and Cueva del Mono Fósil, to which it is connected by a fossiliferous fissure) were found to be beyond the effective range of ^{14}C dating (M. Tamers, personal commun.), and no usable calcite-bone associations have been

found in these caves to make U/Th dating worthwhile. Accordingly, the Quaternary age assessment for the monkey caves has to be based on the character of the recovered faunule, which largely consists of taxa known from localities of proven or suspected Qua-

TABLE 2
Measurements (in mm) of Zaza and Cueva Alta Astragali^a

Specimen	L	HDW	HDH	ACF	PCL	PCW	TW	TH	ATW	PTW	W
MNHNH P 3059	20.0	9.7e	7.3e	12.7	9.5	5.5	11.7	10.8	9.2	9.1	16.5
MNHNH V 205	—	—	—	—	10.0e	6.9	12.0e	11.9	10.5	10.5e	16.9e

^a For landmarks used in measurement, see Meldrum (1990). Key: ACF anterior calcaneal facet; ATW anterior trochlear width; HDH head height; HDW head width; L length; PCL posterior calcaneal facet length; PCW posterior calcaneal facet width; PTW posterior trochlear width; TH trochlear height; TW trochlear width; W width. The letter e indicates that the measurement is estimated (due to breakage).

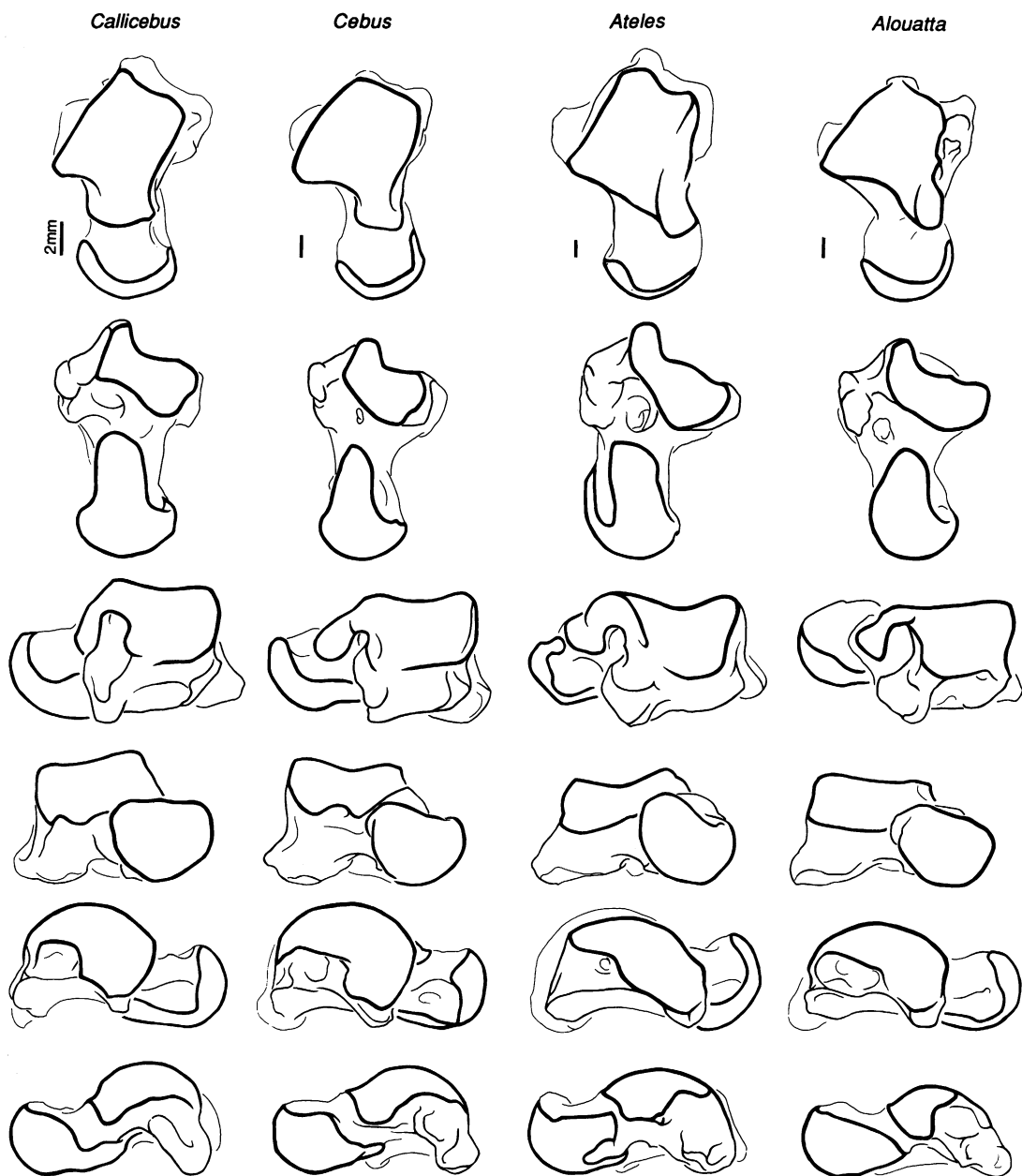


Fig. 4. Astragali of representative extant platyrrhines. Sequence of views (top to bottom of page) is dorsal, ventral, proximal, distal, lateral, and medial. Note individual scales.

ternary age elsewhere in Cuba (see Jaimez Salgado et al., 1992). However, there are some unique occurrences: in addition to *Paralouatta*, a previously unknown owl and sloth have also been recovered, from localities

within these caves (Oscar Arredondo, personal commun.). Since the fissures from which the faunule was collected are not connected with the present sedimentary floors of the caves, and since the cave entrances are sit-

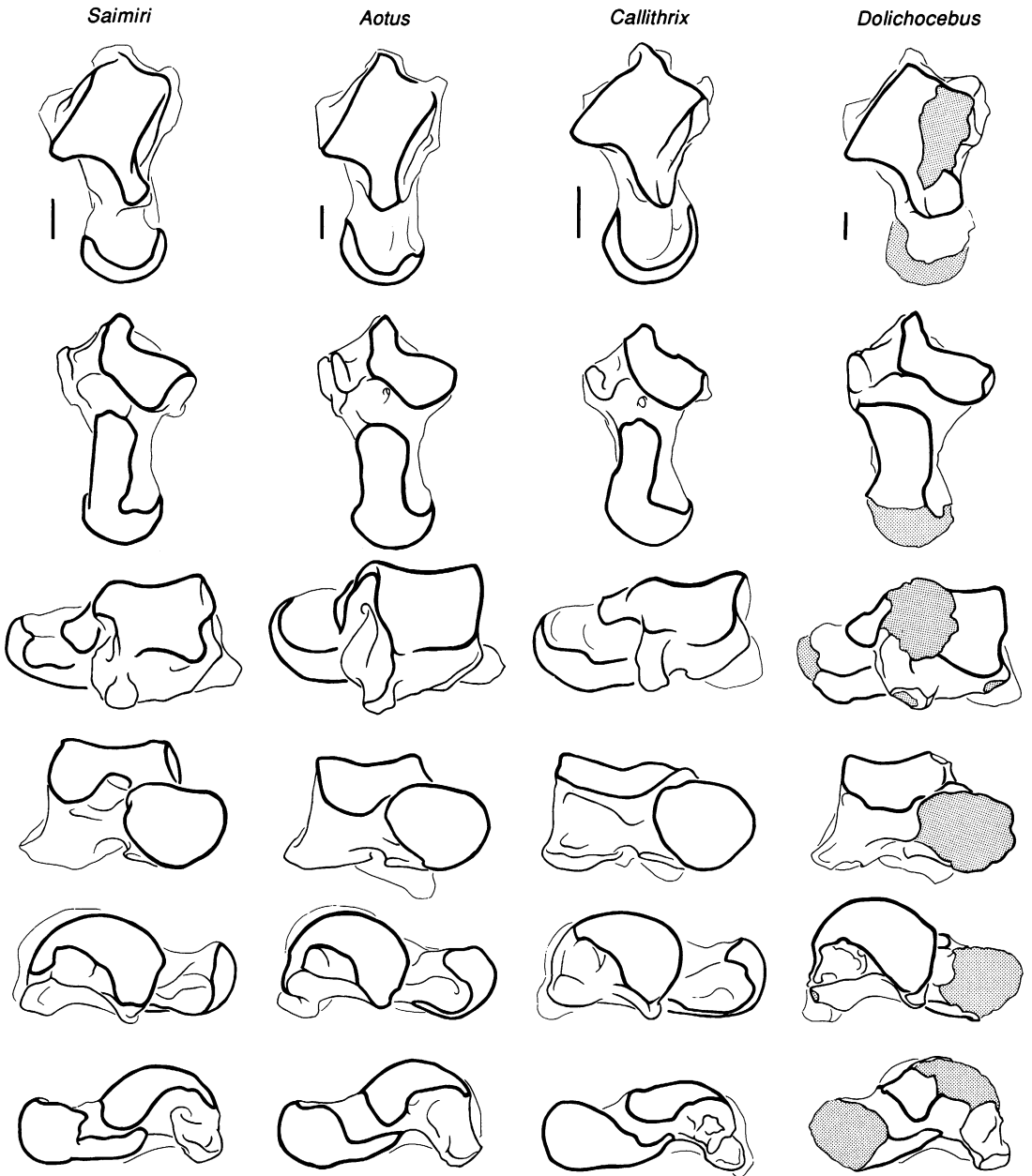


Fig. 4. Continued.

uated high above the present valley floor, it is distinctly possible that the fissure fillings sample a much earlier fauna.

Figure 4 provides schematic views of the astragali of some extant platyrrhines and a specimen usually referred to *Dolichocebus gaimanensis*, an extinct Patagonian species

(cf. Meldrum, 1990). Several points emerge from a comparison of these astragali with the Zaza and Cueva Alta specimens. First, the Cuban monkeys are not especially similar to any of the species illustrated (but see below). This applies in particular to *Alouatta*, the genus originally thought to be the closest living

relative of *Paralouatta* (Rivero and Arredondo, 1991). Among other distinctive features, the astragalus of *Alouatta* exhibits a "wedged" trochlea, low trochlear relief, indistinct margins, vertical medial articular surface for the tibia, and a large posteromedial process. The Cueva Alta specimen lacks these features, as does the better-preserved astragalus from Zaza. What, then, is the proper sister group of the Cuban monkeys?

In a cladistic analysis of a selection of craniodental characters, MacPhee et al. (1995) found that, among sampled Quaternary platyrrhines, the extinct Hispaniolan anthropoid *Antillothrix* (= "*Saimiri*") *bernensis* grouped most closely with *Paralouatta varonai*. These Antillean taxa joined *Callicebus* at the next node. By contrast, no close relationship between the Antillean monkeys and atelines (including *Alouatta*) was indicated. Consistent with the trend of the craniodental evidence, *Callicebus* shows more astragalar resemblances to the Cuban fossils than atelines do. In extant titi monkeys, the trochlea is high and only slightly "wedged," trochlear walls are subvertical, and calcaneal facet shape is substantially similar to the Zaza and Cueva Alta specimens. However, correspondences to *Dolichocebus* and other extant platyrrhines such as *Saimiri* (fig. 4) also exist, raising the distinct possibility that much of this morphology is simply primitive (see also MacPhee and Iturralde-Vinent, 1995).

We find that the Zaza and Cueva Alta astragali fail to support an affiliation of the Cuban monkeys with either *Alouatta* or atelines in general (cf. *Ateles*, fig. 4).³ The hypothesis that the closest living relative of the Cuban and Hispaniolan monkeys is *Callicebus*, as suggested by craniodental characters (MacPhee et al., 1995), is plausible but requires additional evidence and testing.

³ The only biogeographical reason for considering atelines in the context of platyrrhine evolution in Cuba has disappeared. The holotype and only known specimen of *Ateles* (= *Montaneia anthropomorphus*—the supposedly endemic "Cuban spider monkey"—is less than three centuries old. It probably represents an imported *A. fusciceps*, as has long been suspected on morphological grounds (see MacPhee and Rivero de la Calle, 1995).

AN EARLY OLIGOCENE SLOTH FROM PUERTO RICO

While engaged in a preliminary survey in southern Puerto Rico in March 1994, our field party discovered a fossiliferous site near the town of Yauco, in the southwestern part of the island. Among the vertebrate fossils we recovered was the proximal part of a mammalian femur, here referred to the xenarthran clade Tardigrada. This discovery offers the hope that Puerto Rico can be tied into the paleobiogeographical picture being developed for the other Greater Antilles (MacPhee and Wyss, 1990; MacPhee and Iturralde-Vinent, 1994). Of equal interest is the apparent age of the Yauco sediments. As we note in greater detail below, fossil evidence indicates that these sediments are Early Oligocene (*Globigerina ampliapertura* zone, or about 33–34 Ma according to the time zonation utilized by Berggren et al. [1992]). Yauco may therefore be older than the Zaza locality by 15 Ma or more, making it by far the oldest land vertebrate site with a well-constrained age in the West Indies. Oddly enough, if the femur is that of a megalonychid, as we think is highly probable, it becomes the oldest specimen so far referred to that family (cf. Pascual et al., 1990). This means very little by itself, other than to underline the fact that tardigrades had to have been well diversified and widely distributed in the Neotropics before the Oligocene.

XENARTHRA

TARDIGRADA: ?MEGALONYCHIDAE

Unnamed Genus and Species B (Tardigrade)

MATERIAL: Left proximal femur (AMNH VP 129883, fig. 5), preserving head, neck, and trochanters. Found by C. Flemming in March 1994.

PRELIMINARY EVALUATION: Our criteria for assigning this specimen to Mammalia are as follows: (1) greater and lesser trochanters large, projecting, and situated on a marked oblique; (2) medullary cavity not densely filled with cancellous bone; (3) proximal articular end ovoid, with well-defined border marking attachment of joint capsule; and (4) large fovea in the center of the femoral head. Corporately, these features indicate that AMNH

VP 129883 represents a mammal, and distinguish it from conditions encountered in chelonians, crocodylians, and squamates.

Referral to Tardigrada (i.e., the monophyletic taxon containing all sloths, living and extinct) is considered reasonable because of strong resemblances to Quaternary and Recent sloths and because there is no other plausible candidate among other land mammal taxa having Antillean representation (i.e., Lipotyphla, Primates, Rodentia). On biogeographical grounds it is reasonable to believe that the Yauco sloth will prove to represent a member of Megalonychidae, the only sloth family that provably managed to colonize West Indian islands (for recent treatments of Antillean and mainland members of this family, see White [1993]). Consistent with this is the fact that the specimen bears a particularly close resemblance to the proximal femora of certain living and extinct megalonychids (fig. 6). These resemblances include (1) markedly open angle formed by femoral neck and diaphysis, (2) position and orientation of the trochanters, (3) cross-sectional shape of the shaft, and (4) spherical proximal articular surface. A minor difference from extant *Choloepus* (and *Bradypus*) is the presence of a fovea for ligamentum teres; Quaternary Antillean megalonychids are usually foveate (Fischer, 1971). The chief difference is size: the Yauco femur represents an animal as small as or smaller than living *Bradypus*, while *Neocnus*, *Acratocnus*, and *Choloepus* are considerably larger. Indeed, the Yauco sloth would appear to be one of the smallest fossil tardigradans on record (see White [1993] for evidence of very small sloths in the Santacrucian of Argentina). In this regard it stands in marked contrast to Early Miocene *Imagocnus*, which appears to have been nearly the size of *Megalocnus* (~200 kg according to Paula Couto [1979]).

The Yauco femur is morphologically closer to *Neocnus* and *Choloepus* than it is to *Acratocnus*, the only Quaternary sloth known from Puerto Rico. The phylogenetic significance of this (if any) is hard to assess in the absence of adequate material. There are several different and mutually exclusive views concerning the interrelationships of the Antillean sloths (e.g., Varona, 1974; Paula Couto, 1979; Arredondo, 1988), although we believe that

there is some support for brigading Puerto Rican *Acratocnus*, Hispaniolan *Synocnus*, and Cuban *Neocnus* and *Miocnus* in one unit (equivalent to tribe Acratocnini, Varona [1974]). If this grouping is monophyletic, acratocnins, like some other assemblages of closely related Antillean taxa, had a multi-island distribution; this regularity requires explanation (see Discussion).

LOCALITY AND AGE: The sloth femur was recovered at Locality AMNH PR 1994/1, situated just south of Yauco on Highway 3133 (figs. 7, 8). Sediments in this region are apportioned to Early Oligocene Juana Díaz Fm and an overlying but unnamed carbonate unit, as described in more detail below.

The Yauco locality is situated within the former "lower clastic member" of the Juana Díaz Fm (Monroe, 1980). The Juana Díaz Fm has long been informally divided into two members, an upper carbonate (UC) unit and a lower clastic unit (Moussa and Seiglie, 1970, 1975; Monroe, 1980). Frost et al. (1983) have proposed that the Juana Díaz Fm (hereafter abbreviated as JD) be restricted to the lower clastic member, a proposal that we follow in this paper. The UC, allocated to a new formation as yet unnamed, correlates with the *Globorotalia opima opima*-*Globigerina angulituralis* zone and is presumed to be of Late Oligocene age. The JD correlates with the *Globigerina ampliapertura* zone and is therefore older (Pessagno, 1963; Seiglie and Bermúdez, 1969; Moussa and Seiglie, 1970, 1975; van den Bold, 1971; Todd and Low, 1979; Frost et al., 1983). Abundant planktonic forams reported from the JD include *Globigerina ampliapertura*, *G. haoi*, *G. angustiumbilitata*, *G. ciperoensis*, *G. rohri*, *G. venezuelana*, and *Cassigerinella chipolensis* (Seiglie and Bermúdez, 1969). Facies sampling very shallow water and terrestrial environments have no planktonic forams, but do yield *Amphistegina floridana*, *Angulogerina vicksburgensis*, *Baggina cojimarensis*, *Pararotalia mexicana* and *Lepidocyclus undosa*, all of which are typical Oligocene markers (Todd and Low, 1979).

The Yauco section exposes both JD and UC (figs. 8, 9). The JD belongs to the "inshore shelf sandstones and conglomerates" facies of Frost et al. (1983, their fig. 2). This latter unit, 60–70 m thick, is composed of clays,



Fig. 5. Proximal part of a left femur (AMNH VP 129883) of a megalonychid sloth (unnamed genus and species B), from Early Oligocene Locality AMNH 1994/1, near Yauco, SW Puerto Rico. Views are A, anterior; B, posterior; C, lateral; and D, medial. Scale is 1 cm.

sands and gravels with some marly coquina intercalations. The top of the unit is an erosional horizon where conglomeratic limestones of a few centimeters thickness merge into corallgal reef limestones of the UC. The base of the section was not observed.

Fine-grain sands and sandy clays, with abundant oxidized plant remains, comprise the most common lithology. These beds form units tens of centimeters thick, distinctly fining upward and incorporating caliche and other indications of soil-forming processes. Small concentrations of gypsum, apparently epidiagenetic, occur as fracture fillings in some of the clays and sandy clays. Such features are consistent with terrestrial conditions and an oscillating freshwater table, as might occur in relation to swamps and lagoons close to a shoreline. Alluvial beds (figs. 8, 9) occur as

small, laterally overlapping river channels of a few meters thickness, and are more frequent in the lower half of the exposed section.

Near the base of the outcrop, poorly sorted coarse-grained conglomerates occur as intercalations, two to three meters in thickness, with clasts up to 15 cm in diameter. These conglomerates were probably deposited during flood events. In localities near Yauco, and also to the east of the locality, conglomerates at the base of the JD reach thicknesses greater than 50 m and are intercalated with red paleosols. It is possible that the basal parts of these conglomerates are as old as latest Eocene (cf. figs. 9, 10).

Three marly coquinite horizons, two to three meters thick and located near the base, middle, and top of the section, are formed mainly by fragmentary or complete tests of

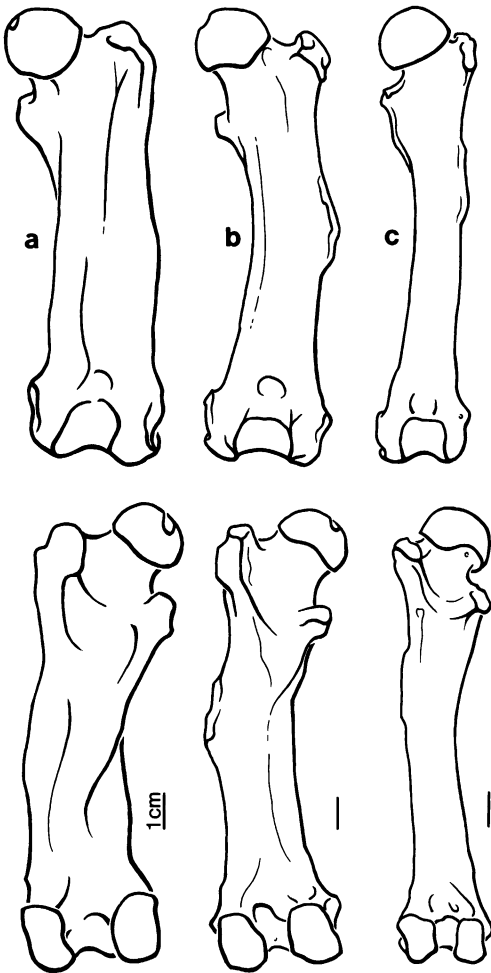


Fig. 6. Left femora of (a) *Neocnus* sp. (Arredondo coll.), (b) *Acratocnus ondontrigonus* (AMNH VP 17716.-1), and (c) *Choloepus hoffmanni* (AMNH M 139772), in anterior (top) and posterior (bottom) views.

Lepidocyclus undosa. Occurring in smaller numbers are shells of gastropods (turritelids), bivalves (pectinids, ostreids, etc.), echinoderms, and crustaceans, with occasional shark teeth and isolated coral fragments. These *Lepidocyclus* coquinites have been interpreted as forereef deep-shelf facies by Frost et al. (1983), but at Yauco the coquinite beds are embedded in sediments deposited in a near-shore environment, with an invertebrate faunal assemblage characteristic of very shallow water. Consistent with this interpretation is the discovery of freshwater/brackish

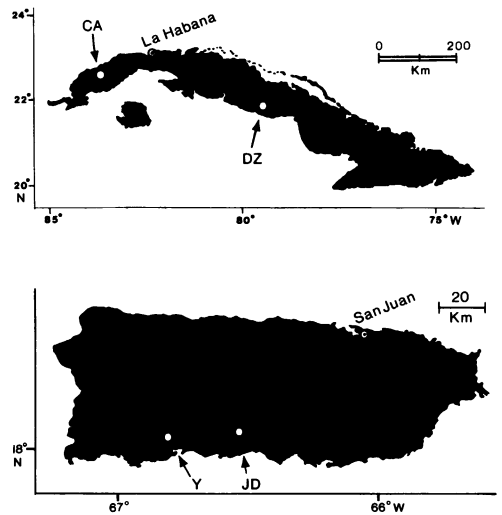


Fig. 7. Location of referenced localities in Cuba (top) and Puerto Rico (bottom). Key: CA, Cueva Alta; DZ, Domo de Zaza; Y, Yauco; and JD, Juana Díaz.

water vertebrates (sirenians, crocodiles, and turtles) in the same sediments. The coquinite beds probably represent short-lived, shallow-water marine invasions of the coastal plain. Further east, similar beds intercalated with sandy lenses outcrop along the Río Jacaguas, from which sirenian fossils have been recovered (Matthew, 1916).

It is not yet possible to determine whether some horizons at Yauco are more productive of vertebrate remains than others. The sloth femur was discovered in the upper half of the section, within a lag developed from a clay/sandy clay/caliche sequence. A number of articulated sirenian bones, found in the middle of the measured section, were associated with sandy clays evidently deposited in brackish conditions. A few well-preserved crocodile skull elements and fragments of turtle shell were found in alluvial channel deposits near the base of the section.

In order to test age determinations of the JD in the Yauco section, four samples were collected and analyzed for microfossil content. Sampling horizons are indicated in figure 8 as 94/16D (coquinite near base of JD), 94/16C (clays 10 m above), 94/16B (middle portion of JD), and 94/16A (base of UC). The samples yield benthic forams, rare planktonic forams, fish teeth, echinoderm spines, and

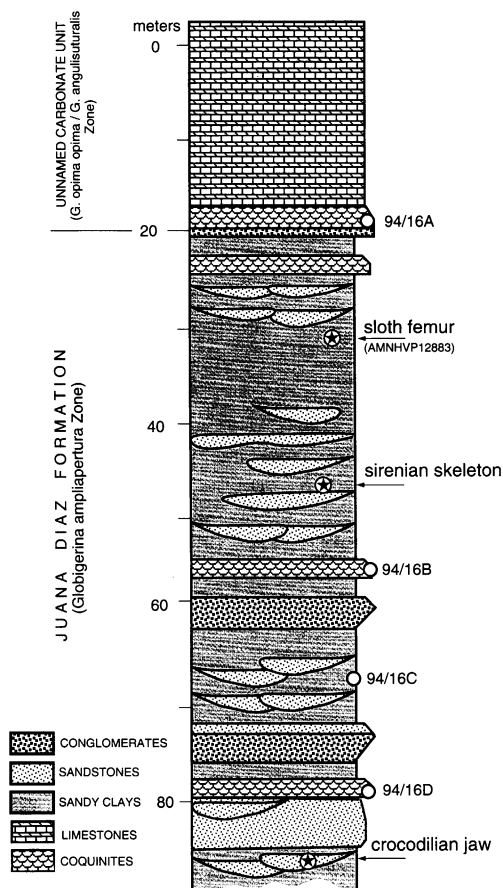


Fig. 8. Columnar section of Locality AMNH 1994/1, near Yauco, SW Puerto Rico. Lenslike features are alluvial channels (see also fig. 9). Also indicated are approximate positions of facies yielding vertebrate fossils (⊗) and invertebrate sapling horizons (○). Tardigradan femur was recovered from float.

ostracods (this last very abundant in sample 94/16C).

In each horizon the assemblage of forams (table 3) is typical Lower Oligocene, because the Upper Oligocene markers *Miogypsina* and *Miogypsinoidea* are absent. The absence of these marker taxa is consistent with the interpretation that these beds were deposited in the Early Oligocene, as indicated by the planktonic foram data referenced above. No large depositional hiatus is evident between the JD and the UC units, because foraminiferal assemblages are similar (table 3, samples 94/16A and B), although they are sep-

arated by an erosional surface associated with a thin conglomeratic bed (figs. 8, 9).

DISCUSSION

GEOLOGICAL CONSTRAINTS AND LAND MAMMAL BIOGEOGRAPHY OF THE GREATER ANTILLES

In an earlier paper (MacPhee and Iturralde-Vinent 1994), we proposed that both dispersal and vicariance have occurred in the formation of the Antillean mammal fauna, and that this point might be tested by an appropriate program of paleontological investigations. It was inferred that the dispersal phase occurred first and involved the movement of species *en bloc* out of northern South America (whence all known major taxa except Antillean lipotyphlans derive) and onto subaerial landmasses in the central Caribbean. How this was accomplished in detail is of course uncertain. However, unlike most other proponents of dispersal, we assume that some critical event occurred in the early Cenozoic which briefly altered the configuration of lands and the amount of open water that had to be crossed. That is, dispersals were not spread out over a long time span, but instead occurred within a very narrow interval. The later, vicariant phase involved subdivision of founder clades⁴ by the erection of water barriers produced by tectonic dismemberment and reconfiguration of the existing chain of islands. This phase is elsewhere described as "island-island" vicariance (MacPhee and Wyss, 1990); it differs from

⁴ Optimally, the number of "founder clades" recognized for Antillean land mammals ought to be equal to the number of initiators (propagules) that were phylogenetically separate from one another (i.e., separate species) at the time of original colonization. Our present view is that a minimum of eight initiators has to be inferred to explain the existing land mammal evidence for the Greater Antilles, distributed as follows: Primates (two initiators), Rodentia (three), Insectivora (two), Xenarthra (one). There could, of course, have been more than one initiator per lower-level monophyletic group, as some authors have inferred (e.g., Morgan and Woods, 1986). For the Greater Antilles as geographically defined, accounting for late-evolving oryzomyins (Rodentia) requires a ninth initiator—but only for Jamaica, which is not considered part of GAARlandia as defined in this paper.

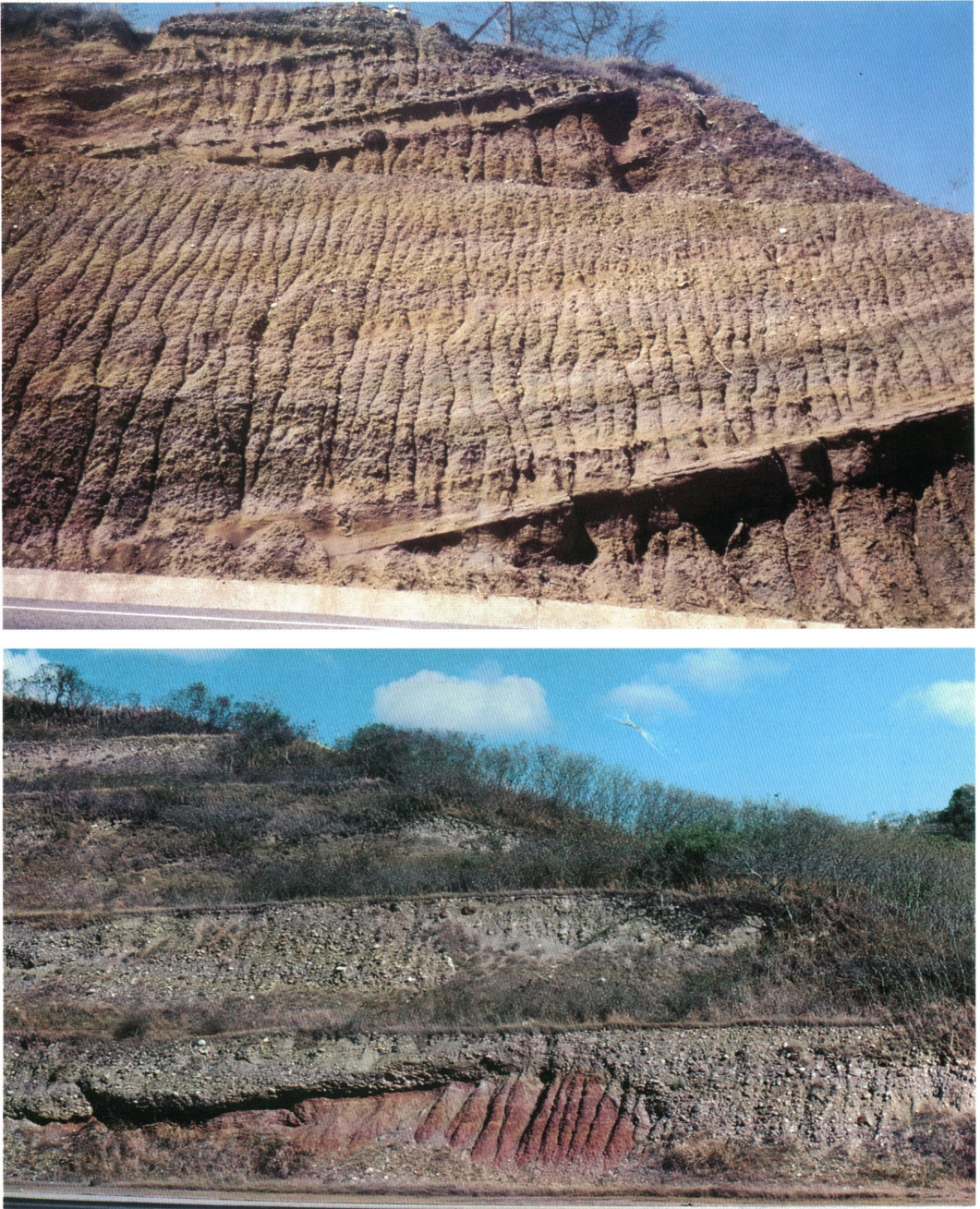


Fig. 9. Top, View of Locality AMNH PR 94/1, near Yauco, southwestern Puerto Rico; section exposing Early Oligocene coastal plain environment of Juana Díaz Fm (sensu Frost et al., 1983). **Bottom,** View of ?latest Eocene–Early Oligocene poorly sorted alluvial conglomerates at base of Juana Díaz Fm, Highway 52 near town of Juana Díaz, southern Puerto Rico; red sandy clays exposed beneath unconformity represent a paleosol. Coeval conglomerates onlapping older deposits are found in Puerto Rico, Cuba, and Hispaniola, where they represent subaerial erosion products formed during the phase of active late Paleogene uplift discussed in text.

TABLE 3
 Locality AMNH PR 1994/1 (Yauco): Identified Foraminifera

Taxa	Samples ^a			
	94/16A (UC)	94/16B (JD)	94/16C (JD)	94/16D (JD)
<i>Baggina</i> , aff. <i>B. xenoula</i> ^b				X
<i>Lepidocyclina undosa</i> ^c	X	X		X
<i>Lepidocyclina gigas</i> ^c		X		
<i>Lepidocyclina</i> , cf. <i>L. canellei</i> ^c		X		
<i>Lepidocyclina</i> , cf. <i>L. giraudia</i> ^c	X			
<i>Lepidocyclina</i> , cf. <i>L. vaughani</i> (?) ^c				X
<i>Lepidocyclina</i> , cf. <i>L. canellei</i> or <i>L. vaughani</i> ^c		X		
<i>Pararotalia mexicana</i> ^b			X	X
<i>Pararotalia</i> , cf. <i>P. guantanamoensis</i> ^b				X
<i>Gypsina</i> sp. ^c	X			
<i>Palaeonummulites dius</i> ^c	X	cf.		X
<i>Amphistegina</i> sp. ^c		X		
<i>Globigerina</i> , cf. <i>G. angustiumbilicata</i> ^b			X	

^a For location of sampling horizons, see fig. 8.

^b Identified by Lic. Gena Fernández (CIDP-Cupet, Cuba).

^c Identified by Prof. Edward Robinson (University of the West Indies, Mona, Jamaica).

Rosen's (1975, 1985) concept, which assumes that most of the critical vicariantly-controlled events in Caribbean biogeographical history were "continent-island." New paleontological discoveries and reconsideration of pertinent geological evidence permit some additional elaborations, presented below.

In our model we specifically proposed that land mammal dispersal to the Greater Antilles could have occurred across portions of the Aves Rise, if (as is often assumed) parts of this feature were subaerial for a limited time in the mid-Tertiary. Other possibilities, such as movements across the Yucatan Channel, Nicaragua Rise, or Lesser Antilles, cannot be completely excluded but are much less plausible for land mammals for one reason or another (briefly summarized below).

Holcombe and Edgar (1990) considered fairly elaborate scenarios in which islands of various sizes and interconnectivities were reconstructed for the spine of the Aves Rise, assuming differing subsidence regimes. They noted in particular that the thin sedimentary deposits covering large parts of the Aves Rise (<500 m of Late Cretaceous and Cenozoic sediment combined) imply that the Rise was positive with respect to the sea floor during most of the Cenozoic. Other facts also support the contention that a major part of the Aves Rise must have once been emergent.

The simultaneous and extensive development of coarse-grained clastic deposits in the Greater Antilles and northern South America during the latest Eocene–Early Oligocene (fig. 10) indicates that active uplift took place throughout the positive portions of the Caribbean, including the Aves Rise, at essentially the same time. Likewise, recovery of Late Eocene and Early Miocene shallow water limestones from the walls of the Aves Rise (Fox et al., 1971) confirms the positive character of the Aves during the early and middle Tertiary. An intriguing feature of the dredge samples described by Fox et al. (1971) is that no Oligocene rocks were identified in any of them. Although the evidence is of a negative quality, the absence of Oligocene rocks in these samples correlates with the presence of same-age hiatuses and subaerially deposited conglomerates elsewhere in the Greater Antilles (fig. 10). Taken together, this evidence tends to confirm the view that the Aves Rise was uplifted around the time of the Eocene–Oligocene boundary, although it is to be hoped that some day this inference will be confirmed by a coring program.

The late Paleogene uplift event in the Caribbean region, which was coincidental with the worldwide Pyrenean phase of tectogenesis (Leonov and Khain, 1987; Brezsnýánszky and Iturralde-Vinent, 1978, 1987), resulted

MID-TERTIARY SEDIMENTARY ENVIRONMENTS AND STRATIGRAPHIC UNITS OF THE GREATER ANTILLES AND SOUTH AMERICA

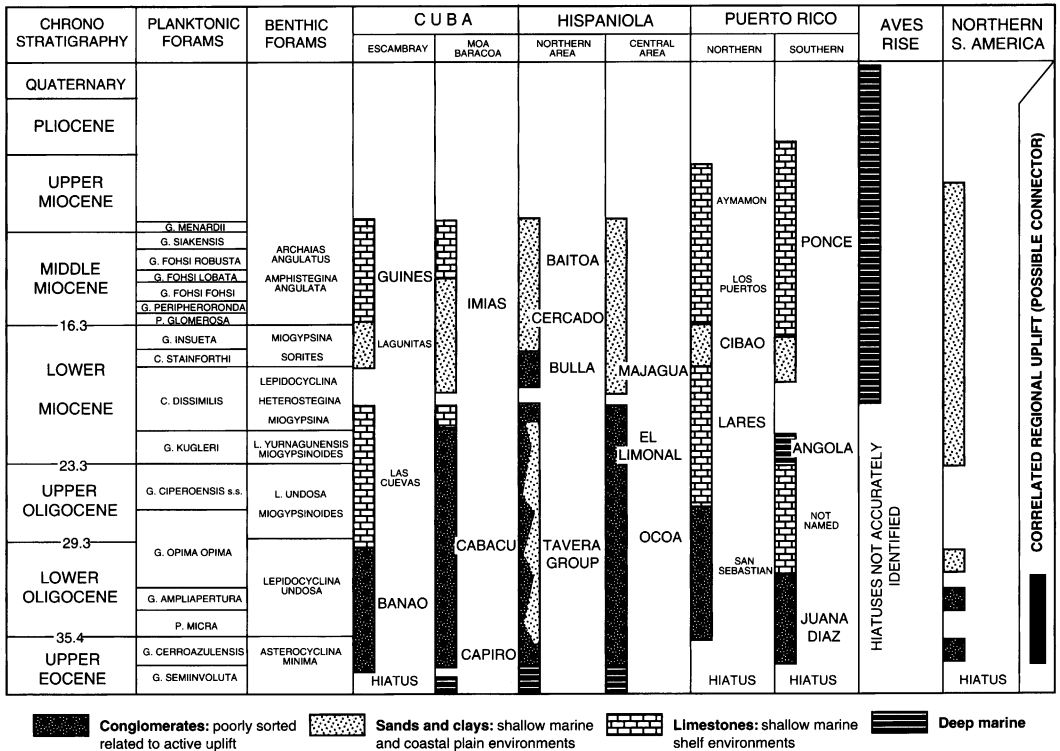


Fig. 10. Mid-Tertiary sedimentary environments and stratigraphic units for selected areas in the Greater Antilles, Aves Rise, and northern South America (Venezuela). Note (a) correlated deposition of coarse conglomerates in the latest Eocene–Early Oligocene throughout the area, suggesting regional uplift, followed by (b) marine sedimentation from mid-Oligocene through Middle Miocene, indicating regional transgression. Under the dispersal hypothesis favored in this paper, the optimal period for land mammal colonization of the Greater Antilles was at or near the Eocene–Oligocene boundary; by the Early Miocene transgression, the window was closed. Sources: Cuba—Iturralde-Vinent (1969, 1972), Nagy et al. (1983), Brezsnayánszky and Iturralde-Vinent (1978), Cobiella et al. (1977); Hispaniola—Lewis et al. (1990), Mann et al. (1992); Puerto Rico—Monroe (1980), Frost et al. (1983); Aves Rise—Fox et al. (1971), Holcombe et al. (1990); northern South America (Venezuela)—Anonymous (1970), Dallmus and Graves (1972).

in the creation of a large positive feature on the Caribbean sea floor—GAARlandia, formed by the Greater Antilles Ridge and the Aves Rise. Ridge and Rise are also related as members of the original “Great Arc of the Caribbean” formed in the Cretaceous (Burke, 1988). At present the chief subaerial components of GAARlandia are Cuba, Hispaniola, Puerto Rico, Virgin Islands, Aves Island, and some islands on the northern fringe of South America (e.g., parts of the Venezuelan Antillas Menores). Prior to the Late Eocene, Cuba, northern Hispaniola, Puerto Rico and the Virgin Islands were not linearly

distributed as they are today, but instead formed a much more compact array, with the eastern islands being situated considerably to the west of their present locations (Malfait and Dinkelman, 1972; Ross and Scotese, 1988; Van Fossen and Channell, 1988; Pindell and Barrett, 1990).

In addition to general uplift, we originally posited that dispersals could be more precisely correlated with the dramatic lowering of global sea level ca. 29 Ma identified by Haq et al. (1987), since a major regression would have increased the total land area over which animals might have dispersed. A nec-

essary corollary of this proposition is that mammal fossils much older than mid-Oligocene time would not be expected to occur in Antillean localities. However, the Yauco sloth demonstrates that tardigradans were already in GAARlandia by the Early Oligocene. Evidently, the mid-Oligocene sea level drop of -160 m did not initiate dispersal, at least in the case of sloths. Either the sea level drop under discussion is not accurately dated, or was not global, or for some other reason did not affect GAARlandia in the way originally imagined.

By contrast, the evidence for the widespread effect of uplift correlated with the Pyrenean tectogenetic phase is consistent throughout the sampled region (fig. 10). In Cuba, there is considerable evidence for depositional hiatuses and extensive development of coarse-grained, poorly sorted conglomerates during the Late Eocene–Early Oligocene (Iturralde-Vinent, 1972; Nagy et al., 1983; Brezsnýánszky and Iturralde-Vinent, 1978, 1985). The same is true for Hispaniola, where coeval uplift produced most of the present Cordillera Central and Cordillera Oriental. At this time, northern Hispaniola and the eastern end of Cuba were physically connected as subaerial landmasses (Calais et al., 1992; Lewis et al. 1990; Mann et al., 1992; Iturralde-Vinent, 1994b). Coarse-grained conglomerates and coastal depositional environments certainly appear in Early Oligocene facies in Puerto Rico (fig. 9; Monroe, 1980), and, as noted above, it is possible that the basal conglomerates of the Juana Díaz Fm are even older (latest Eocene). These observations demonstrate that correlated uplift also occurred in the eastern Greater Antilles, creating subaerial connections between these islands as Meyerhoff (1933) originally suggested. One implication of this is that GAARlandia might have acted as a barrier between Atlantic and Caribbean circulations, which would in turn help to explain such apparent anomalies as the striking difference between Oligocene faunal assemblages on the north and south sides of Puerto Rico (Bold, 1971; Kaye, 1959). These observations are consistent with Donnelly's (1989, 1990) inference, from analysis of biological silica content of pelagic sediments, that the Aves Ridge (and the nascent Lesser Antilles) acted as a

barrier to the circulation of intermediate and deep water at ~ 40 Ma. Donnelly noted that nothing more than a discontinuous island arc was implied by this evidence. Whether or not surface water circulation was broadly interrupted at this time has not been investigated.

If terrestrial colonizations could have occurred in the latest Eocene or Early Oligocene, why could they not have occurred earlier, such as in the Middle Eocene? Earlier colonizations cannot be ruled out, but even if they occurred, it seems unlikely that any colonizing clades of that age could have persisted into the later Cenozoic. Although subaerial landmasses of some sort existed within the Caribbean Sea from time to time from the Cretaceous onward, they would have been subjected repeatedly to episodes of subsidence and transgression (most notably in Maastrichtian, Late Paleocene/Early Eocene, and Middle Eocene [Khudoley and Meyerhoff, 1971; Iturralde-Vinent, 1982; Maurasse 1990]). Our conclusion is that mammals, at least, could not have successfully colonized and survived on the nascent islands of the Greater Antilles until these bodies became *permanently* subaerial subsequent to the beginning of the Late Eocene, when the whole belt was tectonically deformed (Khudoley and Meyerhoff, 1971; Lewis et al., 1990; Iturralde-Vinent, 1982, 1994a).

The last or NeoCaribbean tectonic phase of Greater Antillean evolution, from Miocene to Recent, has been described in several papers (Mann and Burke, 1984; Larue et al., 1990; Mann et al., 1990). During this phase, uplift was followed by a general transgression (fig. 9). In addition, several pull-apart basins and related features opened or expanded along the northern Caribbean plate boundary, among them the Cayman Trough southeast of Cuba (Iturralde-Vinent, 1988, 1991; Calais and Lepinay, 1991), Mona Canyon (Larue et al., 1990; Masson and Scanlon, 1991), and the Sombrero Basin–Anegada Passage system east of the Virgin Islands (Mann et al., 1990; Jany et al., 1990). As a result, deep-water channels and basins now divide the blocks comprising the Greater Antilles Ridge into several isolated tectonic units, some of which have large subaerial portions. The marked subsidence of the Aves Rise (by 400–1400 m from Miocene onward) would have



Fig. 11. Section of slightly deformed Early–Middle Miocene clastic carbonate deposits, SE Cuba; viewpoint is from east. Sandwiched between subhorizontal beds, a thick horizon composed of large clinoforms dips south (i.e., in direction of the Cayman Trough) at an angle of $\sim 50^\circ$.

prevented this structure from acting as a connector at any time in the Neogene (Holcombe and Edgar, 1990; Holcombe et al., 1990).

Evidence for the factors that produced the NeoCaribbean tectonic event is well represented in southeastern Cuba. Along the island's southern flank (=north wall of the Cayman Trench), various compressional features are recorded in the rock record, including overthrusting, reverse faulting, tight folding, and strong fracturing of latest Eocene and older rocks (Lewis and Straczek, 1955; Cobiella et al., 1977). By contrast, Miocene and younger deposits are undeformed, showing only a few degrees of tilting and deepening toward the south (Lewis and Straczek, 1955; Cobiella et al., 1977), probably in relation to a transtensional tectonic environment. Lower–Middle Miocene clastic rocks outcropping in fault-bounded grabens in southeastern Cuba display very large south-dipping clinoforms, indicating the existence nearby of a steeply walled deep (fig. 11). The only possible candidate is the Cayman Trough, which must therefore have come into existence about this time (Iturralde-Vinent 1991, 1994b). The change in tectonic regime from transpressional (pre-Miocene) to transtensional (Miocene and thereafter) recorded in southeastern

Cuba probably represents a rotation of the direction of stresses throughout the Caribbean, from ENE–WSW to more or less directly E–W. The changeover correlates well with the Savic tectogenetic event at the Oligocene–Miocene boundary recorded elsewhere in the world (Schwan, 1980; Leonov and Khain, 1987). A significant consequence of Caribbean stress-field rotation was disruption and dispersion of the terranes that formed Hispaniola–Puerto Rico–Virgin Islands (Lewis et al., 1990; Mann et al. 1990; Larue and Ryan, 1990; Larue et al., 1990) along the northern boundary of the Caribbean Plate. Equivalent disruptions occurred along the southern boundary of the Caribbean Plate, affecting Curaçao, Aruba, and Venezuelan Antillas Menores (Dallmus and Graves, 1972; Pindell and Barrett, 1990; Mann et al., 1990).

Finally, note must be made of the severe constraints operating on other apparently plausible routings for biotic immigration:

Central America (Nicaragua Rise–Cayman Ridge)

The Nicaragua Rise and Cayman Ridge were evidently a single geological entity before the opening of the Cayman Trough; both have vulcano-plutonic arc rocks of latest Cre-

taceous–Paleogene age as partial basement (Holcombe et al., 1990; Holcombe and Edgar, 1990). The Nicaragua Rise is sometimes cited as a possible avenue for mammals into the Greater Antilles via Jamaica (see discussion by Buskirk, 1985), often in connection with an assumed North American origin for Antillean lipotyphlans. However, emergence of the entire Nicaragua Rise–Cayman Ridge complex seems unlikely because each component is draped by later Cenozoic marine deposits, implying submergence during the period of interest. These sediments are Eocene and younger in the case of the Cayman Ridge, Eocene through Quaternary on the Nicaragua Rise near the Central American mainland, and Eocene through Miocene in Jamaica (Holcombe et al., 1990; Maurasse, 1990). Although there are certain faunal similarities between Jamaica and the rest of the Greater Antilles, there are also substantial differences (e.g., absence of insectivores) which imply that its contacts with other islands have been limited (Buskirk, 1985; Morgan, 1993).

Yucatan Channel

Offshore seismic and sonar research in the western Caribbean Sea (see especially Case et al., 1990; Holcombe et al., 1990) conclusively demonstrates that a land connection did not exist between western Cuba and the Yucatan Peninsula during the Tertiary. The topography of the basin between westernmost Cuba and Cozumel consists of a series of unconnected ridges separated by deep trenches, some of them >2 km below sea level. Therefore, sea-level drops, even of great magnitude, would not have appreciably affected the paleogeography of this area. In any case, latest Eocene and Oligocene sinistral strike-slip motion along the Pinar Fault would have acted to widen, not shorten, the separation between Cuba and the Yucatan Peninsula (Iturralde-Vincent, 1994a). It is possible that a much older connection (?late in the Middle Cretaceous) between Central America and westernmost Cuba once existed, since metamorphic rocks recovered from ridges in the Yucatan Channel are similar to those outcropping in the Maya Mountains of Belize and in western Cuba (Pindell and Dewey, 1982). However, even if this connection involved subaerial exposure of lands, it was far too early to

have influenced the dispersal of the land mammal groups known from the Greater Antilles.

Other Possibilities

Although the Lesser Antilles seem to be well situated to act as a discontinuous corridor across which mammals might have migrated from South America, the evidence is against any taxa having done so at a point early enough to comport with the fossil evidence now coming out of the Greater Antilles. Most of the evolutionary development of this arc occurred subsequent to the latest Eocene–Oligocene (Maury et al., 1990). Nevertheless, a very limited suite of mammalian taxa got partway up the chain by some mechanism. This suite includes a sloth and a capybara in Grenada during the Pliocene (R. Singer, personal commun.) and sigmodontines in the northernmost Lesser Antilles during the Quaternary (Morgan and Woods, 1986). Sloths, of course, occurred in the Greater Antilles, but sigmodontines did not, except in Jamaica where one species is known from Recent deposits (Morgan, 1993). Another imponderable is that Anguilla and St. Martin, but no other Lesser Antillean islands, bore a heptaxodontid rodent (*Amblyrhiza*) related to *Elasmodontomys* from Puerto Rico. Each of these cases represents an interpretative problem, but it needs to be noted also that several of these “anomalous” taxa are very poorly described (or even undescribed) and additional information on their phylogenetic relationships is sorely needed.

The Beata Rise, south of Hispaniola, does not physically extend as far as South America (Case et al., 1990). Its age is uncertain, although Santonian and younger sediments occur on the structure (Holcombe et al., 1990). Furthermore, its aspect as a submarine promontory of Hispaniola may be a relatively recent phenomenon (Mann and Burke, 1984; Mann et al., 1990). The Rise has subsided ~1000 m since the Middle Eocene; but since most of the Ridge lies at –2500 to –3000 m, its opportunity for subaerial exposure must have been limited (Holcombe et al., 1990).

SIGNIFICANCE OF FOSSIL LAND-MAMMAL DISCOVERIES

Three of the four major clades of Antillean mammals known from the Quaternary—Tar-

digrada, Caviomorpha, and Platyrrhini—are now known, for certain, to have existed on landmasses in the central Caribbean Basin during the mid-Tertiary (table 1). The only major taxon now missing from the Tertiary picture is Lipotyphla, and its absence is surely due to the vagaries of fossil discovery, not actual absence. It is equally important to note that, by contrast, nothing of an unexpected nature has yet shown up—no marsupials, no carnivores, no condylarths, and so on (cf. Perfit and Williams, 1989). In short, to the degree that the few fossil discoveries made to date can be considered representative of mid-Tertiary diversity, the Antillean land mammal fauna was essentially the same then as now in terms of major taxa. A similar pattern appears to be emerging for other vertebrate groups, in the sense that specimens complete enough to permit confident assignment to named lower-level groups have all turned out to be referable to extant clades having Antillean representation (table 1). The Tertiary arthropod fauna conflicts with this neat picture to some degree, for it includes several “unexpected” taxa that are not part of the modern Neotropical fauna (Wilson, 1988; D. Grimaldi, personal commun.). In addition, according to Graham (1990), the Tertiary flora of the islands has a distinctly North American aspect, quite unlike the modern flora which is overwhelmingly South American in affinity. However, as Borhidi (1985) notes, in addition to North and South American components there are also elements of African, Pacific, and Tethyan origin. It is to be hoped that additional discoveries will add to the database needed to resolve the complex botanical history of these islands.

ZAZAMYS FROM CUBA

Zazamys veronicae is a true biogeographical “ghost”—that is, an extinct member of a clade that lived outside the clade’s supposed distribution area (and whose existence was unsuspected prior to the discovery of fossil material). Quaternary representatives of *Isolobodontinae* are known from Hispaniola, Puerto Rico, and some of the Virgin Islands, but because no members of this clade survived into Pleistocene/Recent time in Cuba, they were assumed never to have occupied that island (e.g., Simpson, 1956).

How did *isolobodontines* reach Cuba? One possibility is that *Zazamys veronicae* represents a unique occurrence of *isolobodontines* in Cuba, its proximate ancestor having been rafted in from Hispaniola, the alleged center of *isolobodontine* diversity (Woods, 1989a). A difficulty with this interpretation is that *Zazamys* is morphologically more primitive than *Isolobodon*, its apparent sister taxon, which—reversing the logic implicit in center-of-diversity argumentation—indicates that Hispaniolan *isolobodontines* are derived from a Cuban source.

A more interesting possibility is that the complementary distribution of *Zazamys* and *Isolobodon* is strictly due to vicariance, i.e., the subdivision of populations through the erection of a barrier, in this instance the subdivision of land. Island-island vicariance is robust in that it provides a common-cause explanation for a number of distributional features and potential sister-group pairings. As noted above, there is solid geological support for the contention that the Windward and Mona Passages did not exist as such prior to the Miocene. Thus, during the critical period when land mammals were most likely to have entered the Greater Antilles—latest Eocene through Early Oligocene (fig. 10)—Cuba, northern Hispaniola, and Puerto Rico probably constituted a single landmass (MacPhee and Iturralde-Vinent, 1994). However, this situation could not have prevailed for a lengthy period: Cuba was already separated into three large archipelagos by the beginning of the Early Miocene (Iturralde-Vinent, 1969), and eastern Cuba and northern Hispaniola would no longer have been in contact by this time (Calais et al., 1992). This information suggests that the “orderly” distribution of many Quaternary Antillean taxa may not have been due to dozens of individual rafting events among the various islands, creating a superficial, ahistorical faunal similarity, but instead to the dissociation of the islands themselves as they progressively parted company with their resident biotas already in place. Some sister-group pairings already recognized or commented upon in the literature that may be a result of vicariant events affecting Cuba and Hispaniola include *Miocnus* + *Synocnus* in *Megalonychidae* (cf. Varona, 1974), *Nesophontes micrus* + *N. paramicrus* in *Nesophontidae* (cf. Patterson, 1962), and *Par-*

alouatta varona + *Antillothrix bernensis* in Platyrrhini (MacPhee et al., 1995). For the reasons cited above, island-island vicariance also accounts for the existence of *Zazamys* in Cuba. It can be predicted that other "ghosts" having closest relatives on adjacent islands will be found, as the Antillean fossil record continues to improve.

Zazamys has a direct bearing on another problem, which is the estimation of the antiquity of certain clades of Antillean rodents. Previously, Woods (1982, 1989a) inferred that the rodent colonization(s) took place in the medial to later Oligocene, which is in reasonable agreement with the evidence presented here. However, in his most detailed analysis of the problem, Woods (1989b: 83) concluded that Antillean capromyids and echimyids are derived from an echimyid ancestor that

... invaded the Greater Antilles from South America either via island-hopping through the Lesser Antilles or by rafting directly to Puerto Rico or eastern Hispaniola, which has served as the center of evolution for capromyids. The time of this invasion is unknown but all available data suggest it was after the Oligocene and probably as recently as the late Miocene. The first radiation gave rise to plagiodontine, hexolobodontine, and isolobodontine lineages on Hispaniola, and later (Pliocene and Pleistocene) to the capromyine lineage that inhabits Cuba, Jamaica, and the Bahamas.

I propose that spiny rats (Heteropsomyinae tentatively retained in the Echimyidae), hutias (Capromyidae sensu stricto), and giant hutias (Heptaxodontidae sensu lato) all invaded the Greater Antilles sometime after the middle Miocene.

Zazamys proves that the minimum age for the start of the invasion, however it may have occurred, could have been no later than Early Miocene, not Middle or Late Miocene, and for geological reasons was assuredly earlier still. Furthermore, because it is identifiably isolobodontine, the morphology of *Zazamys* demonstrates that the cladistic split between isolobodontines and their sister taxon within Capromyidae must also have occurred before the late Early Miocene. Since there are no Tertiary fossils for other groups of Antillean rodents, it might still be maintained in a dis-

persalist hypothesis that they arrived later. However, this introduces new complications, since in the case of Capromyidae, the non-isolobodontine subfamilies as defined by Woods must have originated as early as or earlier than Isolobodontinae. Where were they, if not in the Antilles? Similarly, with the discovery of an Early Oligocene sloth in Puerto Rico, Woods' (1989a: 771) speculation that sloths may not have entered the Greater Antilles until the Late Miocene can also be rejected.

ZAZA ANTHROPOID

Too little is known of the Zaza primate to build a picture of its phylogenetic relationships, but its similarity to *Paralouatta* (and the latter's distinctiveness within Platyrrhini) raises one issue that needs brief treatment. In the systematic literature concerning endemic West Indian monkeys, it is frequently assumed that these monkeys have to be the little-differentiated, insular representatives of Recent mainland clades. Thus although Williams and Koopman (1952) recognized the morphological distinctiveness of the holotype of *Xenothrix mcgregori* and were ultimately unable to fit it within the confines of any existing subfamily, they still concluded that it could be comfortably regarded as "cebid." In a similar vein, Rosenberger (1977) and Rosenberger et al. (1990) argued that *Xenothrix* is a kind of pitheciine because of similarities in jaw shape, despite the absence of detailed resemblances in molar morphology. Likewise, Rímoli (1977) preferred to deposit the unusual monkey maxilla from Cueva Berne within *Saimiri* (as *S. bernensis*) rather than consider the more radical alternative that it represented a distinct clade. In a rather different way Ford and Morgan (1986) and Ford (1990) have also perpetuated this approach, although they have emphasized morphology over systematic affiliations.

The assumption that—if we just look long and hard enough—every Antillean fossil monkey can be shoehorned into one or another extant clade of mainland platyrrhines at a low categorical level is no longer defensible in either theory or practice. Discovery of the Zaza anthropoid demonstrates that

platyrrhines were certainly present in the Greater Antilles at the start of the Neogene, and probably considerably earlier. If the Zaza anthropoid is a member of the same monophyletic group as the one recently recognized for *Paralouatta* and *Antillothrix* by MacPhee et al. (1995), the implication is that the cladistic event separating this group from its closest mainland relatives must have been at least as early—making it one of the oldest nodes yet recovered within Platyrrhini.

SUMMARY

Recent discoveries in Cuba and Puerto Rico establish that the initiators of most (and perhaps all) founder clades of Antillean land mammals were emplaced on subaerial portions of GAARlandia by the mid-Tertiary. Evidence for a specific horizon in the mid-Tertiary is still thin, but in our opinion the immigration event(s) occurred at or near the Eocene–Oligocene boundary, probably within a very narrow interval. We consider it unlikely that successful emplacements could have occurred much earlier than Late Eocene

because of the lack of permanent landmasses within the Caribbean Sea. Since the emergent parts of the Greater Antilles Ridge were in a close-packed array until the commencement of the Neogene, it is reasonable to believe that initiator populations could have been well distributed across GAARlandia. With the fragmentation of GAARlandia, progressive divergence of vicariated lineages would have begun; also, some island lineages would later become extinct (e.g., isolobodontines in Cuba). It is possible that fossil members of founder clades will eventually be discovered in each of the modern Greater Antilles, with the possible exception of Jamaica, whose paleoposition during the Eocene–Oligocene needs to be better constrained in our opinion. Other mammalian clades may have dispersed at the same time as the familiar Antillean clades that survived into the Quaternary, but if so they must have died out soon after arrival. No such clades have yet been identified. Our model may or may not be generalizable to other Antillean vertebrate taxa; this will have to be settled by the appropriate specialists in these groups.

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