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Authors: MacPHEE, R.D.E., ITURRALDE-VINENT, M.A., and GAFFNEY, EUGENE S.

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Domo de Zaza, an Early Miocene Vertebrate Locality in South-Central Cuba, with Notes on the Tectonic Evolution of Puerto Rico and the Mona Passage[1]

R.D.E. MACPHEE,[2] M.A. ITURRALDE-VINENT,[3] AND EUGENE S. GAFFNEY[4]

ABSTRACT

This report summarizes the results of paleontological and geological investigations carried out during the 1990s at Domo de Zaza, a late Early Miocene vertebrate locality in south-central Cuba. Paleontologically, the most important result of fieldwork at Zaza was the first discovery of terrestrial mammals of Tertiary age in Cuba. Three terrestrial mammal taxa are now known from this locality—a megalonychid sloth (*Imagocnus zazae*), an isolobodontine capromyid rodent (*Zazamys veronicae*), and a platyrrhine primate (***Paralouatta marianae,*** new species). In addition to these finds, a number of selachian, chelonian, crocodylian, cetacean, and sirenian remains have been recovered.

Domo de Zaza is a low hill transected by a large artificial channel, the Canal de Zaza, whose walls provide an extensive exposure of Miocene sediments attributable to the Lagunitas Formation (Fm). This formation is laterally and vertically complex, showing evidence of at least four different depositional regimes. However, the sedimentary sequence indicates that all depositional phases took place within a broader episode of transgression. Estimated Burdigalian age (16.1–21.5 Ma) for Lagunitas Fm is based on the presence of marine invertebrate taxa corresponding to the late Early Miocene *Miogypsina*–Soritiidae zone. The overall transgressive

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[2] Curator, Division of Vetebrate Zoology (Mammalogy), American Museum of Natural History. e-mail: macphee@amnh.org

[3] Curator, Museo Nacional de Historia Natural, Obispo 61, Plaza de Armas, La Habana 10100, Cuba; Research Associate, Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History. e-mail: iturralde@mnhnc.inf.cu

[4] Curator, Division of Paleontology, American Museum of Natural History. e-mail: esg@amnh.org

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aspect of Lagunitas suggests rising sea level, possibly in correlation with a global onlap event. Within Burdigalian time, the most likely correlate is the eustatic rise centered on 17.5–18.5 Ma.

Most of the vertebrate fossils were recovered from lagoonal and alluvial beds; those from lagoonal beds are exceptionally well preserved. The terrestrial facies displays evidence of paleosol formation, subaerial erosion, and plant life in the form of grass and palm pollen. Other evidence indicates that most of the present-day highlands of Cuba, including the Cordillera del Escambray near Zaza, have been continuously subaerial since the latter part of the Late Eocene. Although no land vertebrate fossils of this age are known from Cuba, recent discoveries elsewhere in the Greater Antilles indicate that land vertebrates could have colonized landmasses in the Caribbean Basin as early as 33–36 Ma.

Recently, marine geological data have been interpreted as showing that (1) the Mona Passage began to form in the Early Oligocene, and (2) the Puerto Rico/Virgin Island block was entirely transgressed by shallow marine environments during the period between the Late Oligocene and the Early Pliocene. However, the seismic reflection profile evidence for an Early Oligocene opening of the Passage is ambiguous. Even if the separation of Puerto Rico and eastern Hispaniola occurred relatively early, it remains more probable than not that this happened in the medial Oligocene or even somewhat later (i.e., ≤30 Ma). On the other hand, the evidence is not at all ambiguous concerning the hypothesized mid-Cenozoic inundation of Puerto Rico: it did not happen. When available land and marine indicators are adequately compared, apparent contradictions in datasets can be evaluated and resolved. When examined in this way, the preponderance of evidence supports the contention that Puerto Rico has been an emergent landmass and has supported terrestrial environments continuously since the latest Eocene.

RESUMEN

Este reporte resume los resultados de las investigaciones geológicas y paleontológicas llevadas a cabo durante la década de los noventa en Domo de Zaza, una importante localidad paleontológica para vertebrados del Mioceno Inferior tardío, situada en Cuba sur central. Domo de Zaza es una localidad significativa pues en ella aparecieron los primeros mamíferos terrestres del Terciario de Cuba. En ella se han encontrado restos fósiles de tres mamíferos terrestres identificables—un perezoso megaloníchido (*Imagocnus zazae*), un roedor capromido isolobontino (*Zazamys veronicae*), y un primate platyrrínido (que aquí se nombra ***Paralouatta marianae,*** new species). Adicionalmente a estos hallazgos, se ha recuperado numerosos restos fósiles de seláchidos, tortugas, cocodrilos, cetáceos, y sirénidos.

Domo de Zaza es una pequeña colina que fue cortada por un canal artificial, el Canal de Zaza, en cuyas paredes afloran por más de 1.5 km sedimentos del Mioceno que se atribuyen a la Formación Lagunitas. Esta formación es lateral y verticalmente compleja, mostrando evidencias de al menos cuatro diferentes ambientes deposicionales. No obstante, la secuencia sedimentaria es característica de un evento general de transgresión, de edad Burdigaliano (16.1–21.5 Ma) según los taxones de invertebrados marinos que corresponden a la zona *Miogypsina*–Soritiidae. El caracter transgresivo general de la Formación Lagunitas parece corresponder con una elevación del nivel del mar, que pudiera correlacionarse tentativamente con el evento de onlap datado en 17.5–18.5 Ma de antiguedad.

La mayoría de los fósiles de vertebrados recuperados provienen de capas lagunales y aluviales; los de las capas lagunales extremadamente bien preservados. Las facies terrestres muestran evidencias de formación de paleosuelos, erosión subaérea y vida vegetal en forma de granos de polen de grama y palmáceas. Otras evidencias indican que la mayoría de las zonas altas de Cuba, incluyendo la Cordillera del Escambray cercana a Zaza, se han mantenido continuamente subaéreas desde el Eoceno Superior. Aunque no se conocen fósiles de vertebrados terrestres de esta antigüedad en Cuba, los descubrimientos recientes en otras partes de las Antillas Mayores indican que los vertebrados terrestres pudieron colonizar las tierras de la cuenca del Caribe tan temprano como hace 33–36 Ma.

Recientemente algunos datos de geología marina han sido interpretados en el sentido de que (1) el Paso de Mona se comenzó a formar en el Oligoceno Inferior, y (2) que el bloque Puerto Rico/Islas Vírgenes fue completamente cubierto por mares poco profundos a causa de una transgresión que abarcó entre el Oligoceno Superior y el Plioceno Inferior. Ambos eventos tendrían importantes consecuencias para la biología. Las evidencias que aportan los perfiles de reflección sísmica en cuanto a la edad Oligoceno Inferior de apertura del Paso son ambíguas. Incluso si Puerto Rico y La Española se separaron en el Oligoceno, es más probable que este evento haya ocurrido en el Oligoceno medio o algo después (≤30 Ma). Por otra parte, la evidencia no es ambigua en cuanto a la inundación de Puerto Rico en el Terciario superior: esto nunca ocurrió. Cuando los datos geológicos y paleontológicos de mar y tierra se comparan por completo, las contradicciones aparentes son resueltas con facilidad. La evidencia es completamente consistente con el criterio de que Puerto Rico ha estado emergido desde el Eoceno Superior, y no ha sufrido posteriormente ninguna transgresión total.

INTRODUCTION

> Tropical soils and climate are not conducive to the long-term preservation of bone, and all but the largest islands lack sufficient deposits in which bones of terrestrial vertebrates have their best chance of being preserved over millions of years. Historical biogeography of the Caribbean is thus disadvantaged by the lack of hard evidence from early periods in the Cenozoic.
>
> —Gregory K. Pregill and Brian I. Crother (1999: 341)

As the epigraph notes, the fossil record of land vertebrates in the West Indies is lamentably incomplete. However, there are a few places at which a combination of good preservation and good exposure combine to give us a brief glimpse into the islands' distant past. Among these rare places is the locality of Domo de Zaza. Since 1990, crews from the Museo Nacional de Historia Natural in La Habana and the American Museum of Natural History in New York City have undertaken quasi-annual expeditions to this Early Miocene locality situated in central Sancti Spíritus province (see fig. 1). During the past decade, a small but interesting trickle of fossil vertebrates has come out of Zaza, including the first terrestrial mammals of confirmed Tertiary age found in the Greater Antilles (MacPhee and Iturralde-Vinent, 1994, 1995a, 1995b). Now, with the recent discovery of a number of new Tertiary vertebrate localities in the Greater and Lesser Antilles (Donovan et al., 1990; MacPhee and Wyss, 1990; MacPhee and Iturralde-Vinent, 1995b; MacPhee and Grimaldi, 1996; Domning et al., 1997; Pregill, 1999; Iturralde-Vinent and MacPhee, 1999; MacPhee et al., 2000a, 2000b; table 1), it is to be hoped that paleontological sources for unravelling the biogeographical history of the Caribbean region will continue to increase. To this end, the present paper summarizes information relating to the geological context of Domo de Zaza and provides an annotated catalog of the most significant fossil vertebrates recovered to date.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History
AMNH–M	Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History
AMNH–VP	Division of Paleontology (Vertebrate Paleontology), American Museum of Natural History
MNHNCu	Museo Nacional de Historia Natural, La Habana
MNHNCu–P	Paleontological collection, Museo Nacional de Historia Natural, La Habana

OTHER ABBREVIATIONS

Fm	formation
Ma	millions of years (ago)
Sr	Strontium (^{87}Sr/^{86}Sr dating method)

DOMO DE ZAZA: PHYSICAL SETTING AND STRATIGRAPHY

DOMO DE ZAZA AND ITS ENVIRONS

Because Cuba still lacks a significant Tertiary vertebrate record (in sharp contrast to its very rich Quaternary record), there are no ‘‘proven’’ collecting areas in which prospecting efforts might usefully be concentrated (Acevedo-Gonzalez and Arredondo, 1982; Iturralde-Vinent and MacPhee, 1999). On the assumption that land vertebrates have had a long, but as yet largely unknown, history in this part of the Caribbean Basin, in our prospecting activities we have concentrated on areas around heights-of-land that would have been subaerial at least through

TABLE 1

Tertiary Vertebrates Reported from the Greater Antilles (to 2002)[a]

Species and group[b]	Age, formation, locality, civil division	First report or name bestowed by:
Cuba		
Imagocnus zazae (Megalonychidae, Xenarthra)	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	MacPhee and Iturralde-Vinent, 1994
Zazamys veronicae (Capromyidae, Rodentia)	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	MacPhee and Iturralde-Vinent, 1995b
Paralouatta marianae (Platyrrhini, Primates)	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	MacPhee and Iturralde-Vinent, 1995a; this paper
Metaxytherium riveroi (Dugongidae, Sirenia)	M. Miocene; Güines Fm; Matanzas	Varona, 1972
Metaxytherium sp. (Dugongidae, Sirenia)	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	MacPhee and Iturralde-Vinent, this paper
Unident. dugongid	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	MacPhee and Iturralde-Vinent, this paper
Unident. physeterid	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	MacPhee and Iturralde-Vinent, this paper
Unident. crocodilians	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	MacPhee and Iturralde-Vinent, this paper
Unident. pelomedusoid turtle	E. Miocene; Lagunitas Fm; Domo de Zaza, S. Spíritus	Gaffney, this paper
Hispaniola[c]		
Anolis dominicanus (Iguanidae, Sauria)	E.-M. Miocene; La Toca Fm; Dominican Republic	Rieppel, 1980
cf. *Anolis chlorocyanus* species-group (Iguanidae, Sauria)	E.-M. Miocene; La Toca Fm; Dominican Republic	De Queiroz et al., 1998
"*Sphaerodactylus dommeli*" (Gekkonidae, Sauria)[d]	E.-M. Miocene; La Toca Fm; Dominican Republic	Böhme, 1984
Eleutherodactylus sp. (Leptodactylidae, Anura)	E.-M. Miocene; La Toca Fm; Dominican Republic	Poinar and Cannatella, 1987
cf. *Nesoctites* (Picidae, Aves)	E.-M. Miocene; La Toca Fm; Dominican Republic	Laybourne et al., 1994
Unident. ?rodent	E.-M. Miocene; La Toca Fm; Dominican Republic	Poinar, 1988
Unident. insectivore	E.-M. Miocene; La Toca Fm; Dominican Republic	MacPhee and Grimaldi, 1996
Unident. crocodilians, turtles, sirenians	E.-M. Miocene; La Toca Fm; Dominican Republic	MacPhee and Iturralde-Vinent, unpubl. obs.
Puerto Rico		
Halitherium antillense (Dugongidae, Sirenia)	E. Oligocene; ?Juana Diaz Fm; Rio Jacaguas	Matthew, 1916
Caribosiren turneri (Dugongidae, Sirenia)	L. Oligocene; San Sebastian Fm; San Sebastián	Reinhart, 1959
Metaxytherium calvertense (Dugongidae, Sirenia)	E. Miocene; Cibao Fm; Toa Alta	MacPhee and Wyss, 1990
Puertoricomys corozalus (Echimyidae, Rodentia)	?late Tertiary; unident. Fm; Corozal	Woods, 1989
Bairdemys hartsteini (Testudines, Pelomedusoides)	E. Miocene; Cibao Fm; Bayamon	Wood, 1972; Gaffney and Wood, 2002
Unident. boid	E. Miocene; Cibao Fm; Aguadilla	MacPhee and Wyss, 1990
Unident. ?iguanid	E. Miocene; Cibao Fm; Aguadilla	MacPhee and Wyss, 1990
Unident. sloth	E. Oligocene; Juana Diaz Fm; Yauco	MacPhee and Iturralde-Vinent, 1995b
Unident. crocodilians, turtles, sirenians	E. Oligocene; Juana Diaz Fm; Yauco	MacPhee and Iturralde-Vinent, 1995b

TABLE 1
(Continued)

Species and group[b]	Age, formation, locality, civil division	First report or name bestowed by:
Jamaica[e]		
Prorastomus sirenoides (Prorastomidae, Sirenia)	E.-M. Eocene, ?Guy's Hill Fm; Trelawny	Owen, 1855; see also Domning and Clark, 1993
Pezosiren portelli (Prorastomidae, Sirenia)	M. Eocene; Guy's Hill Fm; St. James	Domning, 2001
Hyrachyus sp. (Hyracodontidae, Perissodactyla)	M. Eocene; Guy's Hill Fm; St. James	Domning et al., 1997
Charactosuchus kugleri (Thoracosauridae, Crocodylia)	M. Eocene; Guy's Hill Fm; Manchester	Berg, 1969; Domning and Clark, 1993
Unident. sirenian	M. Eocene; Guy's Hill Fm; St. James	Domning, in prep.
Unident. mammal[f]	M. Eocene; Guy's Hill Fm; St. James	MacPhee et al., 2000a
Unident. ?iguanid	M. Eocene; Guy's Hill Fm; St. James	Pregill, 1999
Unident. crocodilians, turtles, sirenians	M. Eocene; Stettin Fm; Clarendon	MacPhee and Iturralde-Vinent, unpubl. obs.

[a] This table updates table 1 of MacPhee and Ituralde-Vinent (1995b). Although this list excludes fishes, it may be noted that *Cichlasoma* (*Parapetenia) woodringi* (Cichlidae, Perciformes; Cockerell, 1924), from the ?M. Miocene Las Cahobas Fm (Mirebalais, Haiti), is essentially indistiguishable from the living species *Cichlasoma haitiensis* (Burgess and Franz, 1989) and is the only fossil fish from the West Indies currently regarded as an obligatory freshwater species. As to the Lesser Antilles, not listed here, sloth and capybara remains of latest Pliocene or early Pleistocene age from Grenada (MacPhee et al., 2000b) are the only known Tertiary land-vertebrate fossils from these islands. Sirenian remains have been reported from many sites in the Greater Antilles (e.g., MacPhee and Wyss, 1990; Domning, 2001). Fossil pelomedusoid turtles from the Greater Antilles could be marine or freshwater, but most Miocene Caribbean pelomedusoids have been reported from near-shore marine sediments (Sánchez-Villagra et al., 2000; Gaffney and Wood, 2002). Elements referrable to crocodilians, sirenians, and turtles are occasionally seen in tailings from amber mining operations in Yanigua Fm localities in the Dominican Republic (Iturralde-Vinent and MacPhee, 1996; Iturralde-Vinent, 2001). Since the fossils are in the same beds as the amber, it is reasonable to think that they are coeval (thus Early Miocene; for full discussion of the age of amber-bearing deposits in Hispaniola, see Iturralde-Vinent and MacPhee, 1996]). The holotype and only known specimen of *Metaxytherium riveroi* is from an immature animal (MacPhee, unpubl. obs.); species validity uncertain.

[b] "Unident." in this table means that fossils have not been assigned to a given genus/species.

[c] Age of Dominican amber follows assessment of Iturralde-Vinent and MacPhee (1996), not original authors' assignments. Additional vertebrate inclusions in Dominican amber have been discovered in recent years (including embedded hair, feathers, lizards) and are in the process of being described by various workers.

[d] Identification challenged by Kluge (1995); specimen is probably an anole.

[e] Stettin and Guy's Hill Fms, previously classified as members of the Chapelton Fm, are now separately designated as formations (Robinson and Mitchell, 1999) and assigned M. Eocene age.

[f] Possibly but doubtfully primate.

most of the Tertiary, whatever the ambient sea level. The most productive locality discovered using this strategy is Domo de Zaza, a roughly circular structural uplift located approximately 18 km SE of the city of Sancti Spíritus, on the southern coastal plain bordering the central Cuba highlands (Alturas de Santa Clara, del Nordeste de Las Villas, and Cordillera del Escambray). Río Zaza (fig. 1) is one of several rivers draining the eastern and southern flanks of the largest of these massifs, the Cordillera del Escambray (max. elev., 1754 m). In the 1970s, the lower Zaza basin was substantially modified by construction of a dam and diversion of river water through an artificial channel, the Canal de Zaza (figs. 1, 2B), to serve irrigation works on the south coast. To create the canal it was necessary to cut through Domo de Zaza approximately 1 km S of the dam site. The resulting transect provides one of the very few glimpses of the underlying stratigraphy of this region, which is otherwise almost devoid of relief. The paleontologically productive area consists of approximately 1.5 km of horizontal exposure on both sides of the canal; maximum vertical exposure is 10–15 m (fig. 2B–D). Easting and northing coordinates are $x = 670{,}500$, $y = 216{,}000$ on Map 4381-III (Guasimal quadrangle) of the 1:50,000 map of Cuba issued by the Instituto de Geodesia y Cartografía in La Habana, Cuba.

Additional domelike structures occur on either side of the La Trocha fault zone (fig. 2A), near the towns of Violeta and Baraguá. The most impressive of these are the Lomas de Judas de la Cunagua, a brachyanticline feature exhibiting dips up to 60°. Unfortunately, the stratigraphy of these uplifts is not well exposed, which limits their paleontological interest. Limited exposures of Lagunitas Fm are also encountered along road cuts (e.g., roads between Zaza Dam and the villages of San Carlos, Cayo Yero, Alevinaje, and La Sierpe; road from Sancti Spíritus to Trinidad). One of them, Zaza Dug-Out, located immediately south of the main dam (fig. 1), has yielded fossils of sirenians, crocodiles, rays, sharks, and turtles, showing that even small exposures repay exploration.

DESCRIPTION OF LAGUNITAS FORMATION

The gravel, sand, clay, and rare limestone intercalations exposed on channel sidewalls at Domo de Zaza are referable to the Lagunitas Fm, an Early Miocene unit defined by E. Popov in 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). Because no published description of the Lagunitas Fm is available, and because we have used this formational name (MacPhee and Iturralde-Vinent, 1994, 1995a; Iturralde-Vinent and MacPhee, 1999), we take this opportunity to provide a brief characterization of the unit.

NAME: Lagunitas Formation.

ORIGINAL DESCRIPTION: E. Popov in Kantchev et al. (MS).

TYPE LOCALITY: The type locality designated by Popov is a small outcrop located 1.2–3.0 km E of Trinidad, on highway linking Trinidad and Banao, in the province of Sancti Spíritus (fig. 1). The section is poor and is now extensively weathered. By contrast, excellent Lagunitas exposures exist along Canal de Zaza, especially at Domo de Zaza (fig. 2B–D), which we formally designate here as a cotype locality.

DESCRIPTION OF TYPE SECTION: The unit covers various complexes of older rocks, including metamorphic rocks south of Banao. The youngest lithostratigraphic unit overlain by Lagunitas is Oligocene Las Cuevas Fm, in the type area. Lagunitas is in turn overlain by Middle Miocene Güines Fm and younger sediments.

As described by Popov in Kantchev et al. (MS), the type section includes two subunits (beginning with base): (1) 10-m polymictic conglomerates with detrital quartz, metamorphic rocks, and limestones derived from Las Cuevas Fm. Matrix is soft silty clay, yellow in color. (2) 55–60-m silty clays, siltites with sandstone intercalations and lenses, and some conglomerates and sandy limestones. In highest part of the exposed section, sandstone and conglomerates are massive and indurated with calcareous cement. This subunit is capped by massive coralline limestones of Güines Fm. Fossils include *Miogypsina antillea*, *Heterostegina antillea*, and *Sorites* sp.

EXTENT: Best developed in the southeast part of Sancti Spíritus province; laterally associated with Arabos Fm, in the form of a wide belt stretching from Río Jatibonico to eastern side of Bahía de Cienfuegos and

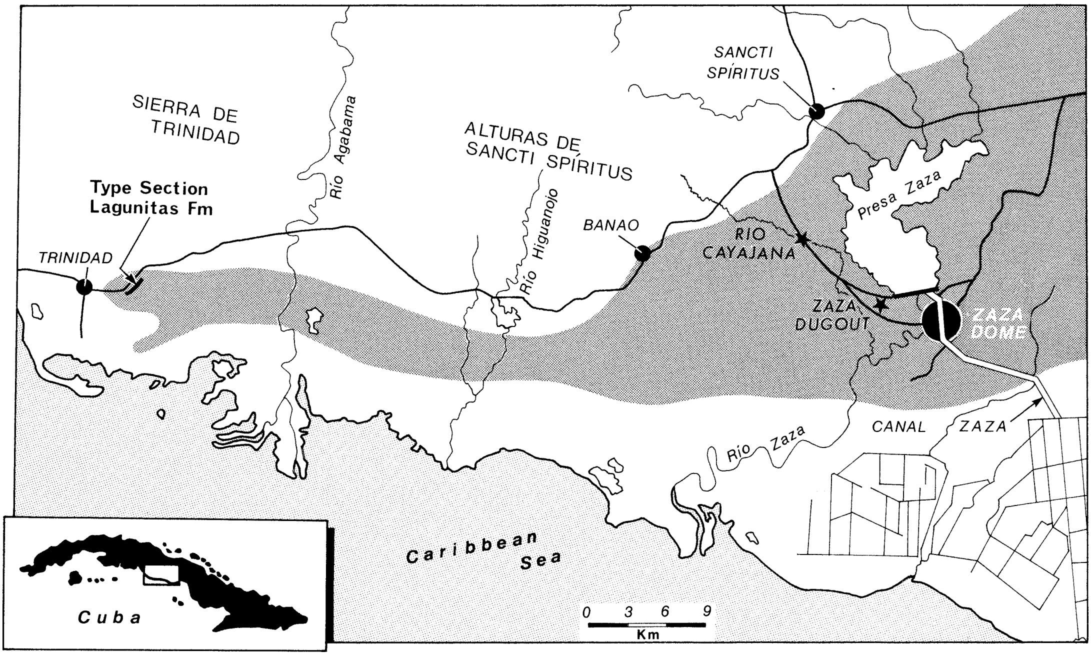


Fig. 1. Sketch map of south-central Cuba, showing pertinent localities discussed in text. Alturas de Sancti Spíritus and Sierra de Trinidad constitute together the Cordillera del Escambray. Shaded area, surficial extent of Lagunitas Fm.

skirting south and east flanks of Cordillera del Escambray (fig. 1). Partial temporal and lithological equivalents of Lagunitas Fm situated elsewhere in Cuba include the Arabos, Paso Real, Rosario, and Magantilla Fms (Iturralde-Vinent, 1969; Iturralde-Vinent et al., 1987). In Hispaniola, Lagunitas Fm can be roughly correlated in age and lithology with the Maissade and Yanigua Fms (Iturralde-Vinent and MacPhee, 1999). In Puerto Rico the most similar unit is the Cibao Fm (MacPhee and Iturralde-Vinent, 1995b).

Fossil Content and Age: Invertebrate fossils reported by Popov from various outcrops of Lagunitas Fm and from samples collected by the authors from Domo de Zaza are typical of late Early Miocene age. The complete faunal list (table 2) confirms the absence of any fossil assemblage indicative of basal Early Miocene (*Lepidocyclina–Miogypsina* zone), which seems to be missing throughout central Cuba (Iturralde-Vinent, 1969). The joint presence of *Miogypsina antillea*, *Heterostegina antillea*, and *Sorites marginalis* is characteristic of the *Miogypsina*–Soritiidae zone, which is in turn equivalent to the *Catapsydrax stainforthi–Globigerinatheka insueta* zones of Iturralde-Vinent (1969, 1970). The presence of *Procythereis* cf. *deformis* indicates that the Lagunitas Fm is younger than the *Catapsydrax dissimilis* zone (van den Bold, 1988). Chronostratigraphically, this faunal interval should correspond to Burdigalian zones M3–4 (16.3–18.8 Ma) as interpreted by Berggren et al. (1995).

The Lagunitas section probably contains a major sequence boundary. Although it would be necessary to have detailed evidence to demonstrate the point conclusively, in all likelihood the Calcarenite Bed, described in detail below, marks the main transgression (onlap) event. Accepting this inference, the age of the uppermost part of the section exposed at Domo de Zaza can be further constrained to 17.5–18.5 Ma, coincident with the isochronous onlap event identified by Haq et al. (1987) in their global eustatic chronology. The Calcarenite Bed cuts across all older layers exposed at Domo de Zaza and also outcrops elsewhere in the region, making it a valuable marker horizon.

Fig. 2. (**A**) Paleogeography of Cuba as a series of archipelagos, late Early Miocene; Domo de Zaza is located in the central archipelago, near La Trocha fault. (**B**) Northwest wall of Canal de Zaza trench (canal seen in foreground; surface of water to uppermost sandy gravel bed is approximately 10 m). (**C**) Detail, showing one of the larger channel cuts (geology hammer below lettering provides scale). (**D**) Detail, showing main lithofacies present in Lagunitas Fm (geology hammer provides scale). Key: *CL,* marine carbonate layer; *CB,* marine Calcarenite Bed; *GC,* lagoonal clay; *PS,* paleosol; *SG,* alluvial sandy gravel. In part A, numbered features indicate areal distribution of the following formations: 1, Paso Real; 2, Rosario; 3, Los Arabos; 4, Lagunitas; 5, Magantilla.

TABLE 2
Inventory of Invertebrate Taxa Recovered at Domo de Zaza (Lagunitas Fm)[a]

Taxa	Marine limestone	Lagoonal clay	Alluvium
Foraminifera			
Ammonia beccarii		x	
Amphistegina, aff. *A. taberana*	x		
Amphistegina angulata	x		
Archaias aduncus	x		
Archais angulatus	x		
Discorbis sp.		x	
Elphidium discoidale		x	
Elphidium nautiloideum		x	
Elphidium sagrei		x	
Heterostegina antillea	x		
Myogypsina antillea	x		
Pyrgo sp.		x	
Sorites marginalis	x		
Ostracoda			
Aurila, aff. *A. cicatricosa*		x	
Bairdia antillea		x	
Bairdia bradyi		x	
Caudites sp.		x	
Costa (Rectotrachileberis) sp.		x	
Cytheropteron sp.		x	
Haplocytheridea cubensis		x	
Haplocytheridea sp.		x	
Loxoconcha antillea nodosa		x	
Loxoconcha cubensis		x	
?*Procythereis*, cf. *deformis*		x	
Quadricythereis antillea		x	
Mollusca			
Crassostrea vaughani insularis			x
Glycymeris acuticostatus, aff. *G. a. guaica*	x		
Glycymeris jamaicanus	x		
Chlamys spp.	x		

[a] Compiled from Popov (in Kantshev et al., MS), with additional identifications by Silvia Blanco and Consuelo Díaz using authors' samples; for biochronological significance, see text.

We have provisional evidence of a second onlap event that occurred in early Middle Miocene, represented by the transition between the Lagunitas and the overlying Guines Fm. The transitional beds—outcropping in a small quarry north-northeast of Domo de Zaza—consist of strongly weathered, whitish to yellowish limestones, containing abundant molds of shallow water marine taxa and overlain by coquinal limestones.

STRONTIUM ISOTOPIC AGE: In order to verify the age of the cotype locality, shell samples were collected for $^{87}Sr/^{86}Sr$ analysis from four horizons along the canal transect (lowest marine bed to youngest coquinal horizon). Calculated ages (table 3) were determined by Paul A. Mueller (University of Florida). Unfortunately, the results are inconsistent with other data. The oldest samples (1 and 2) in terms of stratigraphic position yielded the youngest dates, and none of the dates agree with the age obtained by conventional time-stratigraphic methods (>16.5 Ma). We conclude that the samples submitted for dating underwent some form of diagenesis, and that the oldest Sr age obtained (14.68 Ma) should be considered to represent no more than a minimum age.

TABLE 3
Lagunitas Formation: $^{87}Sr/^{86}Sr$ Dating Results, Domo de Zaza

Sample	Material	Position in section	$^{87}Sr/^{86}Sr$	Calculated age (Ma)[a]
1	*Crassostrea vaughani*	bottom	0.70892	5.47
2	*Crassostrea vaughani*	middle	0.70895	5.24
3A	*Crassostrea vaughani, Glycymeris* spp.	top	0.70882	11.71
3B	*Crassostrea vaughani, Glycymeris* spp.	top	0.70875	14.68

[a] Ages calculated using segmented curve following SRM-987 normalization to 0.710235 (see Geyh and Schleicher, 1990).

DESCRIPTION OF THE DOMO DE ZAZA SECTION, LAGUNITAS FM

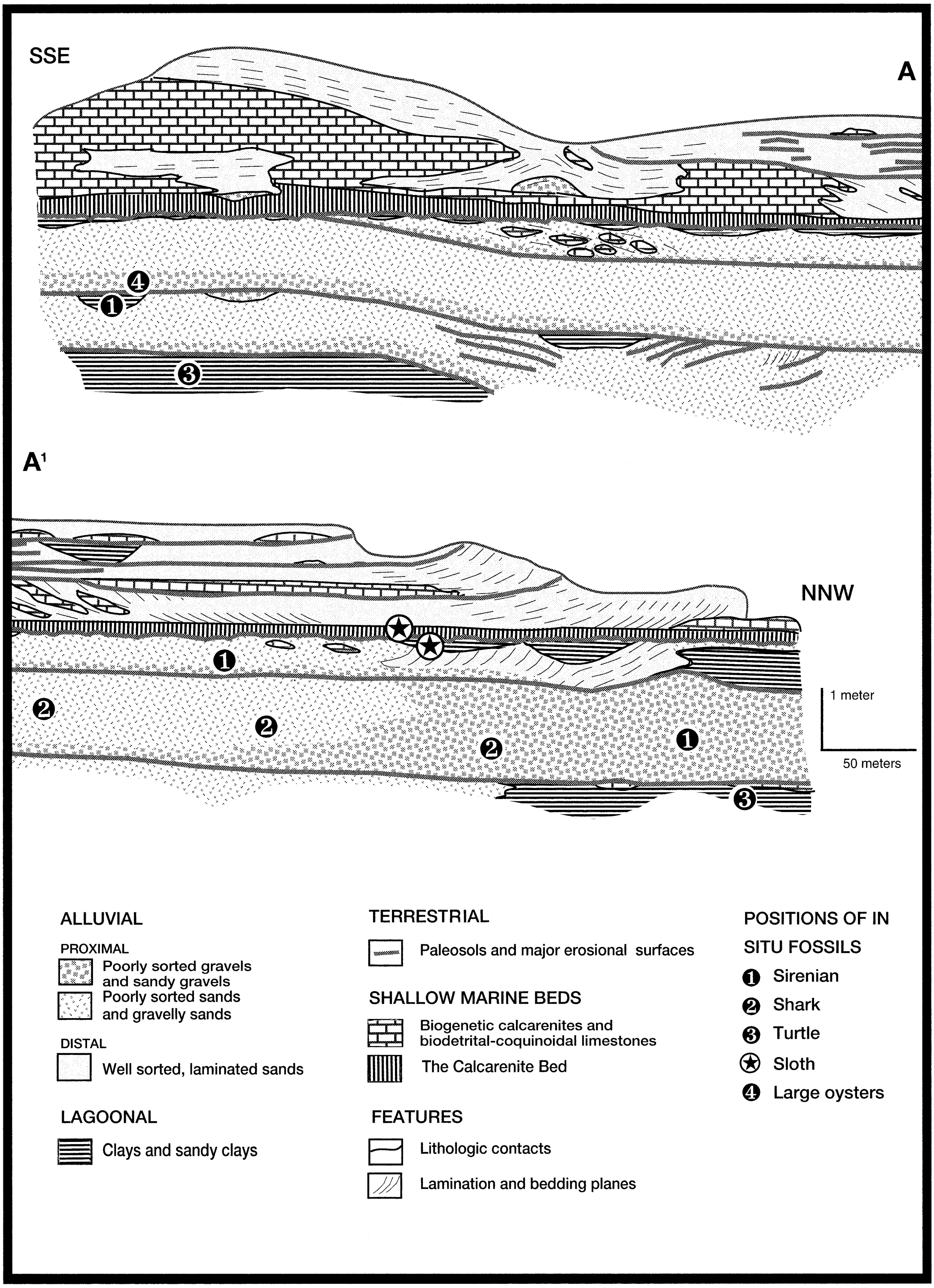
The section exposed at Domo de Zaza is laterally and vertically complex, showing evidence of at least four different depositional regimes within the limited area of exposure, from fully terrestrial to shallow marine. The exposed part of the section shows evidence of several short-term coastal onlap events; the main one began with thick alluvial (sand and gravel) deposition, followed by a short period of lagoonal development (clay), and ended with a ubiquitous shallow marine phase (Calcarenite Bed). However, within this cycle there were clearly shorter phases of uplift and subsequent submersion marked by alluvial channelling, paleosol development, animal bioturbation, and other features (fig. 3).

For the purpose of this description, observations on the section exposed at Domo de Zaza are organized according to environment of deposition. The four distinct depositional regimes that can be recognized (marine, lagoonal, alluvial, and terrestrial) are described in detail. The longitudinal section (fig. 3) of the northwestern face of the canal schematically illustrates the relationships of these environments to one another. As would be expected, land and freshwater facies predominate on the north-northwestern side of the section, nearest the ancient land area (fig. 2A), while marine facies cluster on the south-southeastern side, facing the Caribbean Sea.

Marine Facies: Shallow-water marine conditions in the Zaza section are indicated by several calcareous horizons, light yellow to cream in color, that locally attain thicknesses up to 1–2 m. However, with only one exception, these beds pinch out laterally. The exception is the Calcarenite Bed mentioned above, which runs through the entire exposure (figs. 2B–D, 3). This strongly bioturbated deposit contains small amounts of sand, gravel, and clay, mostly at base. Marine fossils occur sporadically, except at top, where the calcarenite transitionally becomes biocalcarenite and coquinite (i.e., a limestone largely composed of shells). Ichnofossils of

→

Fig. 3. Diagrammatic longitudinal section, west wall of Canal de Zaza (vertical scale highly exaggerated). A and A^1 are coincident points. Lithofacies are organized according to environment of deposition (shallow marine, lagoonal, alluvial, terrestrial). Marine sediments are more common to south-southeast, while nonmarine facies dominate the north-northwestern half of the section. Upsection, marine facies progressively onlap to the north-northwest, indicating general marine transgression. Most of the fossils described in this report were recovered from the float and are therefore of uncertain stratigraphic placement. Positions of certain fossils found in situ are noted on the section. Among in situ land-mammal fossils, the ?mold of the sloth caniniform (MNHNCu–P 3015) was found in the Calcarenite Bed at the position marked by the upper star. The sloth partial pelvis (MNHNCu–P 3021) was recovered in a context stratigraphically below this bed (lower star). All other sloth elements, as well as all material referred to the pitheciine platyrrhine *Paralouatta marianae* and the isolobodontine capromyid *Zazamys veronicae*, were found in the float and therefore could have come from levels stratigraphically above or below the Calcarenite Bed.


SSE
A
❹
❶
❸
A¹
NNW
❶
❷
❷
❷
❶
❸
1 meter
50 meters
ALLUVIAL
PROXIMAL
Poorly sorted gravels and sandy gravels
Poorly sorted sands and gravelly sands
DISTAL
Well sorted, laminated sands
LAGOONAL
Clays and sandy clays
TERRESTRIAL
Paleosols and major erosional surfaces
SHALLOW MARINE BEDS
Biogenetic calcarenites and biodetrital-coquinoidal limestones
The Calcarenite Bed
FEATURES
Lithologic contacts
Lamination and bedding planes
POSITIONS OF IN SITU FOSSILS
❶ Sirenian
❷ Shark
❸ Turtle
✪ Sloth
❹ Large oysters

various invertebrates are evident on the upper surface of the Calcarenite Bed, as is evidence of emergence in the form of desiccation cracks. Highly irregular erosion features are seen on its lower surface.

Throughout this bed, and projecting deep into the underlying clay and sand, are large numbers of quasicylindrical pipes. These pipes, which are filled with the overlaying deposit of calcarenite, are assumed to be tunnels excavated by invertebrates. In agreement with sedimentary features and faunal content (table 2), we interpret the environment of deposition of the calcarenite as a very shallow tidal shelf on which isolated sandy keys were exposed.

Coquinal limestones, also occurring at Zaza, are largely composed of bivalves (especially small oyster species and pectinids), gastropods, and occasional isolated corals, crustaceans, echinoderms, large forams, coralline algae, and small invertebrates associated with the biocalcarenites (table 2). The small oyster beds probably represent nearshore deposits surrounding small keys. These deposits are found either on top of the Calcarenite Bed as massive layers ranging from a few centimeters to 1–2 m in thickness, or as isolated lenses in a similar range of thicknesses within lagoonal clay, sandy clay, or alluvial sandy gravel. Deposition in a backreef shelf environment is strongly indicated for all of these marine sediments. Vertebrate fossils in these limestones include crocodile remains and elasmobranch teeth in associated lag deposits. Among the latter are shallow-water shark species such as *Negaprion brevirostris* (Iturralde-Vinent et al., 1996).

Lagoonal Facies: These predominantly light green clays, with brown and red spotting and minor amounts of sand, occur in beds up to 1 m thick. At the base of the calcarenites and on top of alluvial channel deposits they occur as lenses (<20 cm). There is evidence of horizontal lamination as well as weathering and soil development at several levels within these clays (see below). Bioturbation is indicated by thin calcareous sand pipes, some of which appear to represent root casts. Casts are encountered more frequently in the weathered horizon than elsewhere, as are irregularly shaped calcareous nodular concretions that are probably due to weathering processes. Small amounts of ligneous material have also been recovered, including poorly preserved stems and leaves probably attributable to mangrove associations.

Thin, laminated clays suggest quiet water conditions, as might occur in evanescent cutoff lagoons. The occurrence of brackish and freshwater ostracods and certain forams (e.g., *Ammonia beccari*) suggests that these lagoons were no more than moderately saline. The best preserved vertebrate remains recovered at Domo de Zaza come from lagoonal beds (figs. 2D, 3). For example, the partial pelvis attributed to *Imagocnus zazae* (MNHNCu–P 3021) was found in situ in a sand lens within the lagoonal clay (fig. 3, lower star; fig. 8).

Alluvial Facies: At Domo de Zaza this depositional environment is well represented by extensive beds of different types of siliciclastic sediments. Compositional features establish beyond doubt that the source area of these sediments was the Alturas del Escambray. As the outcrop at Domo de Zaza is oriented north-northwest–south-southeast, the observed section is roughly parallel to the source area.

The alluvial deposits are of several types. The most extensive unit represented in the middle of the Zaza exposure is a thick (1.5–2 m) bed of poorly sorted, sandy, angular to subangular gravel, moderately cemented by carbonates and low in clay content (fig. 2B, *SG*). The gravel fraction varies in its compositional characters, but in general it fines upward and toward the south-southeast. The main sandy gravel unit is usually overlain by calcarenite, although in places it is covered by lagoonal clay. The main sandy gravel unit is represented throughout the Domo de Zaza exposure; two other gravel units, above and below the main one, also occur. These sediments were probably deposited during short-term turbulent sheet flow events in a coastal plain setting.

True river channel deposits can also be found at Zaza, from 1–2 m to 10–15 m in width and varying somewhat in content (fig. 2C, *channel*). These occur as distinct channels dissecting the previously described gravels, marine calcareous units, and lagoonal clays. Grey to yellowish-green interbedded sands and gravels are the most frequent, followed by well-laminated beds of pure sand, fine to medium grain. In many cases the channel deposit is succeeded by lagoonal clay. Cross or inclined bedding planes in these sands achieve values of as much as 30–45° and usually trend east, east-northeast, or east-southeast, indicating that in general the direction of progradation was easterly (away from source area). Several layers of thin paleosols or weathered sands occur within the channel deposits (and even within the sandy gravel dissected by these channels).

Some channels appear to have originated via tidal action. These features can be 1–2 m to as much as 5–7 m in width and 0.5–1.0 m in thickness. Typically, they are filled with clay or sandy clay and contain stacks of very large oysters in life position (valves up to 54 mm in length, referred by Popov [in Kantchev et al., MS] to *Crassostrea vaughani insularis*). In some north–south trending channels, oyster shells are consistently oriented, no doubt reflecting the predominant direction of water flow (fig. 3).

Vertebrate fossils, mostly poorly preserved, are fairly common in the sandy gravel unit and channel deposits. Collected specimens include sirenian rib fragments and vertebrae, turtle shell pieces, and shark teeth. A few fish vertebrae and crocodile long bones and teeth (not noted in fig. 3) have also been recovered.

Terrestrial Facies: Although clastic materials derived from terrestrial sources are frequently seen in Tertiary facies in Cuba, it is much rarer to find direct evidence of terrestrial conditions (Iturralde-Vinent, 1969, 1988). However, at Domo de Zaza there are several indicators of the transient presence of terrestrial conditions during the deposition of Lagunitas sediments. Particularly striking is paleosol development in the lagoonal clay (fig. 2D, *PS*). In the section, paleosol development is typically marked by (1) a violet to dark red clay horizon ~15 cm in thickness which (2) changes downsection through a distance of 10–15 cm to brown or yellow clay and finally (3) to less weathered green clay. The contact between horizons is transitional and irregular. Paleosol clay tends to wedge out laterally through distances of 2 m or less. This kind of paleosol development is sometimes repeated three or more times within a single meter of section in the lagoonal clay. In some areas the top part of the paleosol had been eroded away and is unconformably overlain by sandy gravel or limestone. Other weathered horizons are found within and at the top of the alluvial sandy gravel deposits. Here, red hardpan several centimeters thick overlies light- to dark-brown horizons. We infer that soil was washed away by later river flows in these places, except for small patches which are locally preserved.

Additional evidence of emergence is encountered on the top of the Calcarenite Bed, in which indications of soil-forming processes are seen in the form of calcretes and calcareous reniform concretions and nodules of various sizes in the sandy clays.

Long (>10 cm), vertically oriented tubes infilled with reddish sand are common in the paleosol clays. We interpret these structures as casts of terrestrial plant roots because of the form and branching of the tubes. This interpretation is supported by the presence, in the violet clays, of palynomorphs referable to Arecaceae (the palm *Sabal* sp. indet.) and Graminaceae (A. Areces-Mallea, personal commun.). The presence of palm and grass pollen is consistent with a savanna or swamp environment. (Here it may be mentioned that several late Paleogene and early Neogene contexts in Cuba, Hispaniola, and Puerto Rico have produced ample evidence of complex terrestrial plant communities on these islands in mid-Tertiary time [Borhidi and Muñiz, 1980; Borhidi, 1985; Graham and Jarzen, 1969; Graham, 1990; see also Selmeier, 1990; Iturralde-Vinent and MacPhee, 1999].)

As noted, the source of most of the clastic load in the alluvial deposits at Domo de Zaza is the metamorphic rocks of the Cordillera del Escambray, the closest peaks of which comprise the Alturas de Sancti Spíritus, 20 km to the west. This is the only highland in the vicinity in which such rocks outcrop. Farther to the north and east, potential source rocks include volcanics, ophiolites, and sedimentary rocks, but clastic materials derived from these rocks are not abundant in the Zaza section.

The rivers transporting clastic material to the then-existing seashore at Zaza would have been comparatively short, which partly explains the angularity and poor sortation of the gravel fraction. A careful inspection of the Domo de Zaza section clearly establishes that there is a series of alluvial beds which pinch out to the south-southeast and increase in thickness to the north-northwest (fig. 3). Several alluvial flood events, in the form of massive sandy gravel horizons a few meters in thickness, are recorded in this part of the section. Flood events were clearly retreating toward the north-northwest through time; as one passes upward in the section, the edge of each successive sandy gravel bed ends next to the previous one in that direction (fig. 3). Marine deposits display the opposite pattern, being more abundant upsection and extending progressively to the north-northwest (i.e., landward). Both features are normal for a transgression. Here it is important to note that the well-bedded laminated sand on the top of the section is medium-grained, very well sorted, predominantly laminar and thin-layered compared to other clastic units, and interfingered with marine facies. This indicates that the sand was deposited in a marine or deltaic environment (see Iturralde-Vinent and MacPhee, 1999).

Paleogeographical Inferences

The paleogeography of Cuba during the late Early Miocene, the stage of deposition of the Lagunitas Fm, is depicted in figure 2A. This map is intended to portray maximum land areas, as determined from isochronous sediments in contiguous basins and indicated paleoenvironments of deposition. Nonterrestrial areas are identified on the basis of known coastal environments and sediment source (Iturralde-Vinent, 1969, 1978, 1982, 1988). For additional details on the Tertiary paleogeography of Cuba and other parts of the Caribbean region, consult Iturralde-Vinent and MacPhee (1999).

For much of middle to late Cenozoic time, Cuba consisted of three separate archipelagos (here dubbed the western, central, and eastern) distributed along the north-nothwest–south-southeast trend of the present island. The islands forming these archipelagos were situated on a shallow shelf subdivided by somewhat deeper channels (Iturralde-Vinent, 1988). During major regressions (Eocene–Oligocene boundary, Oligocene–Miocene boundary, Late Miocene–Pliocene), the archipelagos were temporarily united and finally became permanently so at the end of the Pliocene regression (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 in different archipelagoes.

We envisage south-central Cuba during the Early Miocene to have been a small but high island ringed by periodically inundated keys and shallow seas (fig. 2A). Cordillera del Escambray, positive since the Late Paleogene or earlier (Iturralde-Vinent, 1969, 1982, 1988, 1996), was drained by ancient rivers that would have formed extensive deltaic deposits along their lower courses, like the one exposed at Domo de Zaza. The only terrestrial taxa known from this period are from Domo de Zaza, which would have been part of the central Cuban archipelago (fig. 2A). In whole or in part, the ancestors of these taxa may have reached this part of future Cuba during the brief existence of the GAARlandia landspan at the Eocene–Oligocene boundary (MacPhee and Iturralde-Vinent, 1995b; Iturralde-Vinent and MacPhee, 1999). Thus, by the Early Miocene, when the sediments forming the Domo de Zaza locality were being laid down, terrestrial vertebrate colonization may have already been underway in this part of the Greater Antilles for 15 Ma or more (see also Notes on the Tectonic Evolution of Puerto Rico and Mona Passage).

SYSTEMATIC PALEONTOLOGY

This section summarizes, by major taxon, the chief paleontological discoveries made at Domo de Zaza through the most recent field season (February 1998), including remains of previously undocumented mammalian and nonmammalian vertebrates (bony fishes, elasmobranchs, crocodylians, and chelonians) and additions made to hypodigms of species described by MacPhee and Iturralde (1994, 1995a). Other than our work, the only published reference to vertebrate fossils in the Lagunitas Fm occurs in a paper by Trelles Duelo (1936). He briefly mentioned having collected sirenian bones in what is now known to be a Lagunitas outcrop along the Río Cayajaná. This river was revisited in 1992, but no bone-bearing outcrops were identified.

Collection technique at Zaza consisted mainly of close inspection of outcrop and float. As noted, few vertebrate fossils were recovered in situ. Screen washing of matrix, conducted as a test in 1992 and 1994 and on a large scale in 1998, produced only a few vertebrate fossils (exclusively fish) and forams. In view of the poor results from screen washing, this technique is not recommended for vertebrate collection at Domo de Zaza unless the available labor pool is large.

It was our original intention to publish our account of the mammalian fauna together with several short treatments of nonmammalian taxa by other specialists. This has turned out to be impractical, as to date only the reports on the chelonians (by Eugene Gaffney) and sharks and rays (by M. Iturralde-Vinent and coworkers) have been finished. It is hoped that the other groups will eventually be published by the workers to whom the material has been entrusted.

PRIMATES

The endemic platyrrhine monkeys of the Greater Antilles remain an enigmatic and poorly known group (MacPhee, 1996; MacPhee et al., 1996; Horovitz, 1997, 1999; Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2002). During the latter part of the Quaternary, each of these islands possessed at least one endemic platyrrhine, with the apparent exception of Puerto Rico. Jamaica may have had as many as three monkey species in the late Pleistocene (Ford, 1990), although only *Xenothrix mcgregori* is known from more than one or two specimens (MacPhee and Fleagle, 1991). Recent cladistic studies aimed at placing West Indian monkeys within the larger phylogenetic framework of platyrrhine evolution indicate that the Antillean taxa comprise a monophyletic group closely related to the extant (and exclusively continental) titi monkey, *Callicebus* (Horovitz and MacPhee, 1999; MacPhee and Horovitz, 2002).

The only direct evidence for the time of platyrrhine arrival in the Greater Antilles consists of a single astragalus recovered at Domo de Zaza (MacPhee and Iturralde-Vinent, 1995a, 1995b). This provides a minimum age of Early Miocene for the arrival of monkeys in the northern Greater Antilles, although for other reasons we suspect that the original influx occurred significantly earlier (MacPhee and Iturralde-Vinent, 1995b; Iturralde-Vinent and MacPhee, 1999). Here we make the Zaza astragalus the holotype of the new species described in subsequent paragraphs. In the interests of space we limit descriptions to necessary differentiae and basic measurements; additional comparisons and illustrations can be found in our earlier paper (MacPhee and Iturralde-Vinent, 1995b).

Although there is a prejudice in paleontology against using remains other than teeth as holotype specimens, in this case the decision to use a postcranial element is warranted. First, astragali of major clades of platyrrhines tend to exhibit morphological patterns that provide some rational basis for assessing phylogenetic relationships (Meldrum, 1990). Secondly, because of their conformation and strength properties, astragali tend to survive a wide range of taphonomic processes and are therefore among the postcranial bones most likely to be recovered in paleontological contexts (Behrensmeyer and Hill, 1980). Thirdly, expeditions to Domo de Zaza mounted in recent years specifically to find additional primate fossils have been unsuccessful in this objective, and it will probably be some years before this locality is intensively searched again. There are no other localities known in this time range other than the ones described in this paper. In view of these considerations, it is appropriate to provide a formal name for this monkey at this time.

Paralouatta marianae, new species
(Platyrrhini, Pitheciidae)

HOLOTYPE: Right astragalus (MNHNCu–P 3059; fig. 4; Unnamed Genus and Species A of MacPhee and Iturralde-Vinent, 1995b).

TYPE LOCALITY AND AGE: Domo de Zaza,

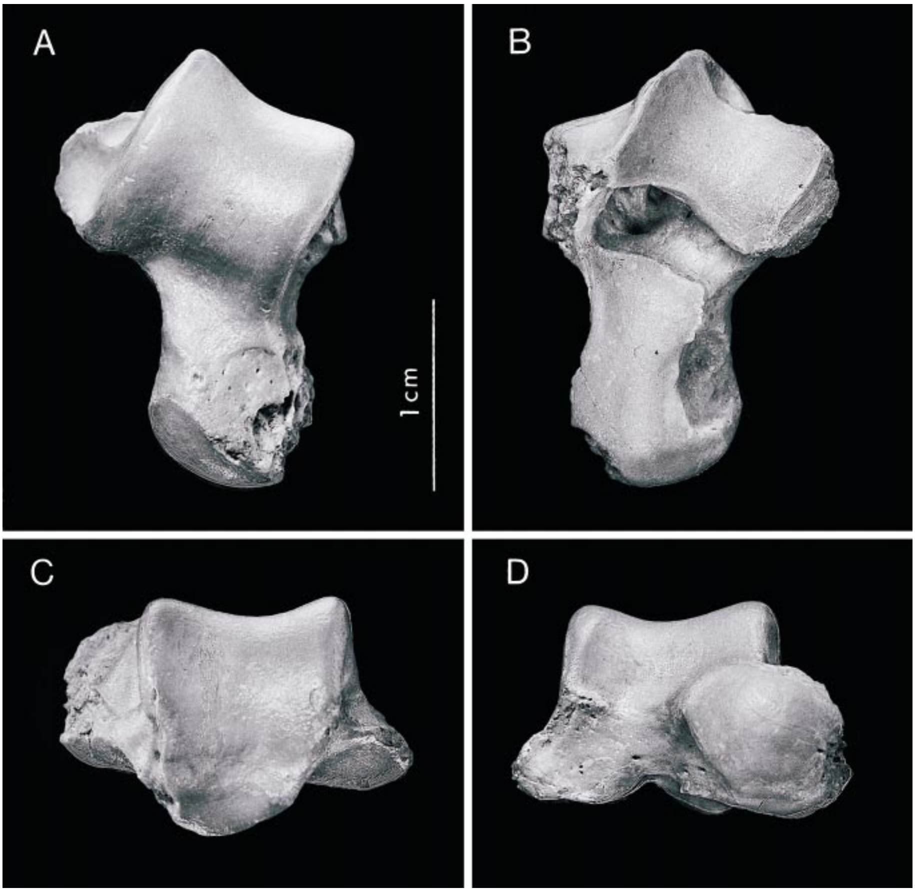


Fig. 4. Astragalus of *Paralouatta marianae*, holotype (MNHNCu–P 3059), from Domo de Zaza: (**A**) dorsal, (**B)** ventral, (**C)** proximal (posterior), and (**D**) distal (anterior) views. For description, see text.

in lag deposit near south end of section, south-central Cuba.

DISCOVERER AND DATE OF DISCOVERY: Osvaldo Jiménez Vásquez in November 1993.

REFERRED MATERIAL: None.

ETYMOLOGY: Species named for Mariana Saker Labrada, director of MNHNCu and beloved wife of M.A. Iturralde-Vinent.

DIAGNOSIS: MNHNCu–P 3059 differs most notably from astragali of extant large-bodied platyrrhine monkeys (*Alouatta*, *Brachyteles*, *Lagothrix*) in possessing a relatively parallel-sided rather than wedge-shaped trochlear surface and a tall astragalar body. For measurements of holotype, see table 5.

Descriptions and measurements (see table 4) are distilled from the lengthier presentation in MacPhee and Iturralde-Vinent (1995b: 7–12). Of immediate interest is the very large size of MNHNCu–P 3059: in astragalar length, for example, it places near the upper end of the size distribution seen in extant platyrrhines, adjacent to the largest atelines (see data of Meldrum, 1990). The head bears an ovoid navicular facet on a short neck which is oriented at about 30° (Meldrum's method). The very large posterior calcaneal facet exhibits the highest facet length : width ratio found among platyrrhines, living or extinct.

The Zaza specimen is similar in these and many other features to the Cueva Alta astragalus (MNHNCu–P 2565 [formerly accessioned as MNHNCu–V 205]) referred to *P. varonai* by MacPhee and Iturralde-Vinent

TABLE 4

Measurements of Primate Astragalus from Domo de Zaza, in mm

(MNHNCu-P 3059, Holotype of *Paralouatta marianae*)

L[a]	HDW	HDH	ACF	PCL	PCW	TW	TH	ATW	PTW	W
20.0	9.7[b]	7.3[b]	12.7	9.5	5.5	11.7	10.8	9.2	9.1	16.5

[a] Abbreviations: **L**, length (maximum); **HDW**, head width; **HDH**, head height; **ACF**, anterior calcaneal facet length; **PCL**, posterior calcaneal facet length; **PCW**, posterior calcaneal facet width; **TW**, trochlear width; **TH**, trochlear height; **ATW**, anterior trochlear width; **PTW** , posterior trochlear width; **W**, width (maximum).

[b] Measurement not reflecting true value because of loss or breakage of bone. For landmarks used in taking measurements, see Meldrum (1990).

(1995b). The *marianae* holotype differs in being somewhat smaller, with a slightly lower trochlea, narrower posterior calcaneal facet, and deeper astragalar sinus.

By contrast, differences from most other platyrrhines are considerable (MacPhee and Iturralde-Vinent, 1995a, 1995b). This point applies a fortiori to *Alouatta*, the genus originally claimed to be the closest living relative of *Paralouatta* (cf. Rivero and Arredondo, 1991). For example, the distinctive astragalus of *Alouatta* exhibits a ‘‘wedged’’ trochlea, low trochlear relief, indistinct margins, vertical medial articular surface for the tibia, and a large posteromedial process. All of these features are missing or quite differently constructed in the *marianae* holotype (as well as the less well-preserved *varonai* astragalus from Cueva Alta). Given the marked difference in size, it is to be expected that derived correspondences to *Callicebus* (which we regard as a much closer relative) will be few. There is certainly a general resemblance in the form and degree of trochlear relief, presence of subvertical trochlear walls, and shape of calcaneal facet, but these features occur in other taxa (e.g., *Saimiri*) and are probably best interpreted as primitive.

Whatever the broader meaning of the characters just detailed, at the alpha level there can be no serious doubt that MNHNCu–P 3059 represents a species closely allied with and perhaps even ancestral to Quaternary *P. varonai*. (Astragalar features were not part of the original generic diagnosis of *Paralouatta* made by Rivero and Arredondo [1991].)

Discussion: Placement of the new species in *Paralouatta* may seem unwarranted, since this appears to give this genus a temporal extent of 17–18 million years or more. However, in making this allocation we were guided by two considerations. First, astragalar morphology is sufficient to establish that the two taxa are closely related, but not to determine whether a generic distinction could be sustained. More material will be required before this point can be settled; for the present, we prefer to be conservative. Secondly, the age of the two nearby sites which have yielded *Paralouatta varonai* is undetermined. The presumption is that they are late Quaternary, but for reasons reviewed by MacPhee and Iturralde-Vinent (1995b) they may be significantly older. Until age and distinctiveness can be better clarified, the reasonable course is to provisionally place the Zaza specimen in the existing and well-characterized genus *Paralouatta*. Placement of *Paralouatta* in Pitheciinae (Callicebini) follows Horovitz (1997, 1999) and MacPhee and Horovitz (2002); for another opinion, see Rosenberger (2002).

The large body size of *Paralouatta* has functional implications. Although island gigantism is a well-known phenomenon and is seen in other primate clades (most notably among Malagasy ‘‘subfossil’’ lemurs), the other named taxa in the Antillean clade (Jamaican *Xenothrix* and Hispaniolan *Antillothrix*) are considerably smaller. *Paralouatta marianae* is by far the largest platyrrhine known from the Neotropical Miocene (cf. size estimates of various extinct taxa by Meldrum and Kay, 1997). MacPhee and Iturralde-Vinent (1995a) suggested that the Zaza primate may have been an above-branch walker/runner according to Meldrum’s (1990) criteria, but perhaps was not an energetic leaper given its large body size. However, it should be emphasized that limb bones referred to *P. varonai* are highly distinctive and show convergences on certain extant Old World monkeys, such as *Semnopithecus entellus*, that spend significant time on the ground (MacPhee, in prep.). Although nothing is known of postcranial adaptations of *P. marianae* other than those implied by the astragalus, features of its later and probably slightly larger relative may indicate that some amount of terrestriality occurred in species of this genus. Further insights will require better and more informative fossils.

RODENTIA

The West Indian rodent fauna is of great interest because it was notably diversified and derived from several monophyletic groups within Caviomorpha (as well as one muroid group, the oryzomyin sigmodontines). Sadly, today almost nothing is left of this fauna, most of which became extinct after the arrival of humans (Morgan and Woods, 1986; Woods, 1993; MacPhee and Flemming, 1999).

Although abundant remains of extinct rodents occur in Quaternary cave sites on many West Indian islands, only two taxa have been described as specifically being Tertiary in age: *Puertoricomys corozalus* (Woods, 1989), an echimyid from Puerto Rico; and *Zazamys veronicae*, an isolobodontine capromyid from Domo de Zaza. The type locality of *Puertoricomys* has not been relocated (MacPhee and Wyss, 1990), and for the present its age is best regarded as indeterminant. However, its distinctiveness from other heteropsomyine taxa (Woods, 1989), all of which are plausibly late Quaternary, suggests that it may be older (?Pliocene; MacPhee and Wyss, 1990).

Zazamys veronicae is known from only three teeth (see below), but these are sufficient to establish its credentials as an isolobodontine capromyid. The subfamilial modifier is important, because all other Cuban capromyids (living or extinct) are members of Capromyinae. Isolobodontines are known (as endemics) from Hispaniola and, in the case of one species, also from Puerto Rico and some of the Virgin Islands (as an Amerindian introduction) (Flemming and MacPhee, 1999). However, the view that isolobodontines were always absent from Cuba is no longer tenable (e.g., Simpson, 1956). The biogeographical implications of *Zazamys*, especially in light of the concept of GAARlandia and ‘‘island–island’’ vicariance, are explored by Iturralde-Vinent and MacPhee (1999).

It would be of great interest to know if other ‘‘ghost’’ taxa like *Zazamys* existed in Cuba during the Tertiary. Among the obvious candidates are the heptaxodontids: this possibly paraphyletic group of large to extremely large caviomorphs is known from the islands of Jamaica, Hispaniola, Puerto Rico, and Anguilla/St. Martin (cf. Pascual et al., 1990; MacPhee et al. 1989), but, strangely, nothing even remotely heptaxodontidlike has ever been reported from Cuba. Were they simply never there, or did they die out early (i.e., prior to the Quaternary)?

Zazamys veronicae
(Capromyidae, Isolobodontinae)

ORIGINAL DESCRIPTION: MacPhee and Iturralde-Vinent, 1995b.

Material: Holotype is a left lower M1 or M2 (MNHNCu–P 3071; fig. 5), found in lag deposit near south end of Domo de Zaza in 1994. Referred material includes a right (MNHNCu–P 3058) and a left lower M1 or M2 (MNHNCu–P 3072), also found in lag.

Discussion: No additional specimens referable to this species have been recovered since 1994.

Xenarthra

Until the middle Holocene or perhaps somewhat later, megalonychid sloths formed a significant component of the land mammal fauna of the insular Neotropics. All of these ‘‘Antillean sloths’’, as they may be informally called, are now extinct. Although there is no doubt that Antillean sloths are proximally related to both the extant two-toed sloth *Choloepus* (Webb, 1985; White, 1993; White and MacPhee, 2001) and the Neogene megalonychids of Argentina (Kraglievich, 1923; Scillato-Yané, 1979; Pascual et al., 1985), the history of this family in northern South America and the Caribbean region is exceedingly obscure.

Phyllophagans first arrived on land masses related to the Greater Antilles at least as early as 32 Ma, possibly by crossing the GAARlandia landspan (MacPhee and Iturralde-Vinent, 1995b; Iturralde-Vinent and MacPhee, 1999). The earliest empirical evidence for their presence in Cuba comes from Domo de Zaza, which has produced a number of remains attributable to *Imagocnus zazae*, the first fully diagnosable Tertiary land mammal to be discovered anywhere in the Greater Antilles. In naming this species, MacPhee and Iturralde-Vinent (1994) limited their specimen descriptions to the holotype palate and an isolated molariform. We take this opportunity to amplify the original descriptions and to characterize other sloth remains recovered from this site. These other elements probably belong to the same species (and are therefore placed in its hypodigm), although we are aware that the evident size disparities among specimens hint that a second, even larger Zaza sloth may be represented in this material.

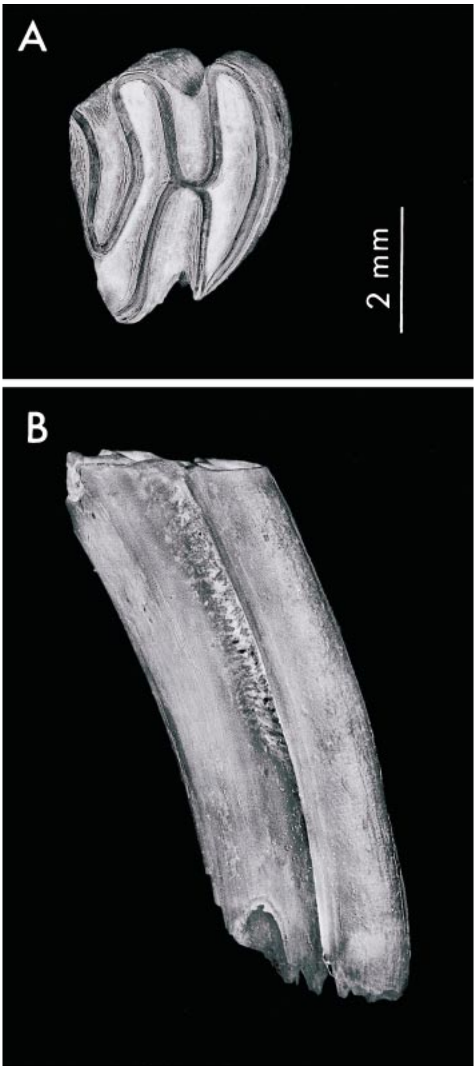


Fig. 5. Left mandibular M3 of *Zazamys veronicae* (MacPhee and Iturralde-Vinent, 1995b), holotype (MNHNCu–P 3071), from Domo de Zaza: (**A**) occlusal and (**B**) buccal views. For description, see text.

Imagocnus zazae
(Tardigrada, Megalonychidae, Megalocninae)

Original Description: MacPhee and Iturralde-Vinent, 1994.

Material: Holotype is an edentulous palate (MNHNCu–P 3014; fig. 6) with partial alveoli for posterior molariforms, but lacking rostral end.

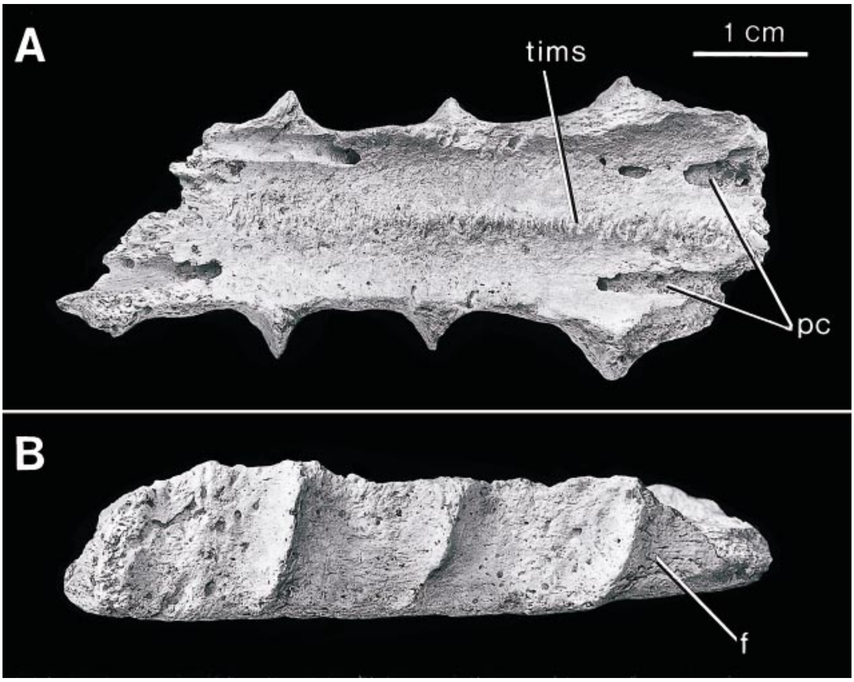


Fig. 6. Palate of *Imagocnus zazae* (MacPhee and Iturralde-Vinent, 1994), holotype (MNHNCu–P 3014), from Domo de Zaza: (**A**) dorsal and (**B**) lateral views. Key: **tims,** torus on intermaxillary suture; **pc,** palatine canal; **f,** fossa in advance of alveolus of first molariform. For description, see text.

Referred material (figs. 7–10) now comprises two fragmentary molariforms (MNHNCu–P 3100, 3013); a right maxillary fragment (MNHNCu–P 3165), preserving parts of two alveoli; a partial pelvis (MNHNCu–P 3021), comprising most of the centra of sacrals 2 and 3, part of the sacral portion of the vertebral canal, and (on the left side only) part of the ilium; another sacral fragment, consisting only of the bodies of sacral ?2 and ?3 (MNHNCu–P 3017); an anterior caudal vertebra (MNHNCu–P 3050), lacking a portion of the centrum, parts of the transverse processes, and the spinous process; and a left distal humerus (MNHNCu–P 3027), diaphysis only.

The palate (fig. 6) is distinctively slothlike in having a thick cross-section, a narrow interalveolar space, large numbers of palatal nutrient foramina, and subparallel rows of tooth sockets. It preserves three half-alveoli on each side, the alveolar rows being separated by a very narrow interalveolar distance. The toothrows are very slightly divergent caudally. Ventrally, there is a pronounced mesial ridge bordering the alveolar rows, and also a midsagittal torus along the intermaxillary suture. A small portion of the right maxillopalatine suture is preserved; it joins the intermaxillary suture at the transverse level of the alveolus of the third molariform. In the Quaternary Puerto Rican megalonychid *Acratocnus*, the mesial ridges are better developed and the midsagittal torus is less developed. In the extant megalonychid *Choloepus*, both kinds of ridges are negligible even in large specimens, and the toothrows are divergent rostrally rather than caudally.

Degrees of toothrow convergence/divergence vary within extinct families, and it may be that row conformation is a poor character. Weber (1928) stated that the toothrows in megatheriids are parallel, while in mylodontids they can be parallel (*Scelidotherium*) or divergent (*Mylodon*). Englemann (1985) regarded anterior divergence of toothrows as probably primitive for sloths, but all three families have representatives in which they are subparallel. It may be that he was counting anterior, caniniform teeth as part of the toothrow, in which case anterior divergence is probably primitive. However, restricting attention to the molariform teeth indicates that the subparallel condition is more likely to be plesiomorphous.

The channels for the palatine vasculature and nerves can be seen in section in figure 6A. In the primitive case, sensory branches from the palate travel within palatal soft tissues and leave through foramina located in the rear of the mouth, to the pterygopalatine ganglion. The greater palatine artery or its equivalent, ultimately a branch of the maxillary artery, also travels unenclosed and supplies the palatal mucous membrane, glands, and gums. In tardigradans, by contrast, the bone of the palate tends to partly enclose the pathways of the palatine nerves and arteries, so that fibers and distributaries have to travel through individual small foramina to gain or leave their trunks. In some taxa, such as *Imagocnus*, the nerve and arterial trunks are completely isolated within long tubes. In others, channels are less deeply buried or take the form of simple grooves on the palatal surface (as in *Choloepus*).

In addition to small, rather randomly arranged emissary foramina, in tardigradans there is normally a pair of larger, vaguely symmetrical foramina (anterior palatine foramina) in the rostral part of the palate. In most megalonychid taxa, the anterior palatine foramina are situated at the transverse level of the first molariforms. In a few taxa, *Acratocnus* and *Parocnus* included, they are regularly situated much farther forward. There is probably individual variation in this feature. The situation in *Imagocnus* is not completely certain because the portion of the palate anterior to the first molariforms was not preserved, although it is clear that no large paired foramina are represented on the part that is left. We accordingly infer that the anterior palatine foramina were situated well in advance of the first molariforms, as in *Acratocnus* and *Parocnus*. When they are distinguishable in *Choloepus* they are also rostrally situated.

The dorsal surface of the palate, which would have functioned as the floor of the nasal cavity, also bears a midsagittal ridge, on which the cartilaginous nasal septum presumably rested. Laterally, there is a well-marked fossa, typical of megalonychids, in advance of the first molariform.

The two recovered teeth (MNHNCu–P 3013 and MNHNCu–P 3100; fig. 7) are clearly megalonychid. In morphology the teeth closely resemble mandibular molariforms of the Quaternary Cuban species *Parocnus browni*, but metrically they are intermediate between this species and the larger *Megalocnus rodens* (for additional systematic commentary, see White and MacPhee, 2001).

The referred maxillary fragment (MNHNCu–P 3165, not illustrated) consists only of the external surface of the bone covering two molariform alveoli. It clearly accommodated teeth within the size range of known molariforms of *Imagocnus*, but its condition does not warrant detailed description.

The partial pelvis (MNHNCu–P 3021; fig. 8C, D) was found in situ, exposed on a manmade terrace cut into the canal wall (fig. 3, lower star). The specimen is in poor condition, perhaps because it was weathered before it was originally buried. The ventral surface of MNHNCu–P 3021 is dominated by the fragmentary centra of upper sacral vertebrae, whose lateral masses are solidly fused with the contiguous portions of the ilia. The Zaza pelvis is actually slightly larger and more robust than AMNH–VP 49976, a nearly complete (although partly reconstructed) pelvis of Quaternary *Megalocnus rodens* (fig. 8A, B). Sacral vertebral bodies are flanked by ventral sacral foramina of extraordinary size and the sacral canal is enormous, again larger than in Quaternary *Megalocnus* (table 5).

Extreme ventral projection of sacral centra is characteristic of Antillean sloths and is not seen to so marked an extent in *Hapalops* and other South American megalonychids. Well-developed ridges on the ventral surfaces of the centra (presumably for iliacus m. attachment) are present, as in Quaternary Antillean sloths. Foramina for basivertebral veins, seen perforating lumbar and sacral vertebrae in members of all major tardigradan taxa (de Burlet, 1922), can also be seen in MNHNCu–P 3021 (but rather indistinctly because of damage).

On the left side, the dorsal aspect of the pelvis (not illustrated) bears remnants of two major longitudinal crests (crista sacralis la-

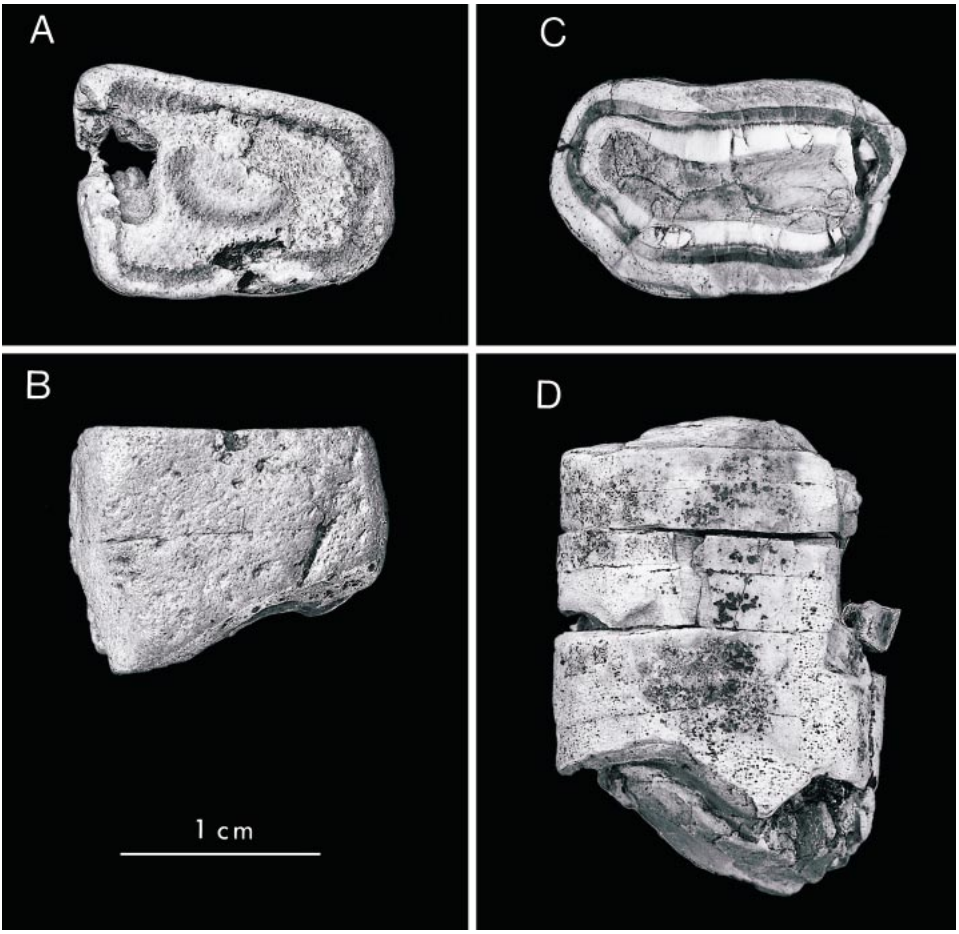


Fig. 7. Sloth molariforms attributed to *Imagocnus zazae*, from Domo de Zaza: (**A**) actual occlusal and (**B**) lateral aspects of presumed mandibular molariform (MNHNCu–P 3013); (**C**) broken cross-sectional and (**D**) lateral aspects of presumed maxillary molariform (MNHNCu–P 3100). For description, see text.

teralis and crista sacralis medialis, for attachment of epaxial musculature), in the gutter between which are stacked the dorsal apertures of the sacral foramina. In Quaternary Antillean megalonychids, these cristae are positioned fairly close together, and the gutter defined between them is a deep groove. In the Lagunitas fossil, the cristae are much farther apart (40% more separation than in *Megalocnus rodens*; table 5), and the gutter is relatively less deep. Whether these features mean that the complete Lagunitas pelvis was considerably larger than that of *M. rodens* cannot be settled, but they certainly show that proportions were different.

The anterior caudal vertebra (MNHNCu–P 3050; fig. 9) is imperfect, but it resembles anterior caudals of large Quaternary Antillean sloths in detail and there can be no question about its allocation. The four hemal facets on the ventral aspect of the centrum and the associated bridges enclosing large vascular foramina are diagnostic, occurring in much the same way in *Parocnus* and other Quaternary Cuban sloths (Fischer, 1971). The precise position of this vertebra within the skeleton of the tail cannot be fixed, but from the marked separation of its pre- and postzygapophyses it is probably one of the anteriormost. The extremely robust tail skel-

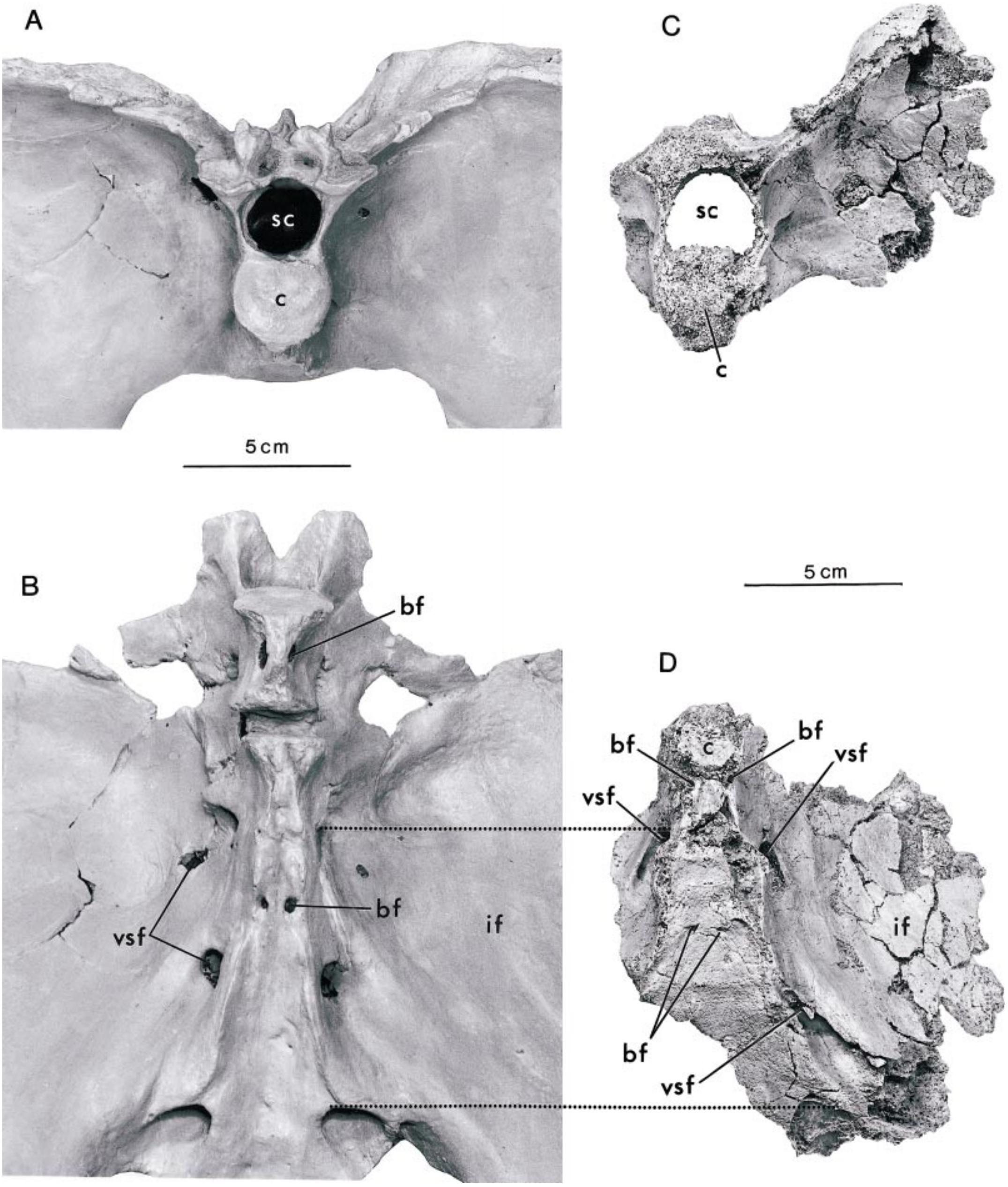


Fig. 8. Pelvis of large-bodied Quaternary megalonychid *Megalocnus rodens* (AMNH–VP 49976) from Ciego Montero (**A, B**), compared to poorly preserved pelvis attributed to Early Miocene *Imagocnus zazae* (MNHNCu–P 3021) from Domo de Zaza (**C, D**). A and C, superior aspect; B and D, ventral aspect. Key: **bf,** basivertebral foramina; **c,** centrum of first sacral/last lumbar; **if,** iliac fossa; **sc,** spinal canal; **vsf,** ventral sacral foramina. Note that the two pelves are approximately the same size, as judged by distances between homologous points (e.g., dotted lines between homologous canals for sacral spinal nerves). This evidence confirms that megalonychids of very large body size existed in the Cuban Miocene. AMNH–VP 49976 is depicted as a complete specimen by Matthew and Paula Couto (1959: pls. 17–19).

TABLE 5
Measurements of Megalonychid Posteranials from Domo de Zaza, in mm

	SCTD	CW	CH	CLCM	DSFW
Sacrum[a]					
MNHNCu–P 3021 (?*Imagocnus zazae*)	29.2	28.8	16.8	50.0	57.5
AMNH-VP 49976 (*Megalocnus rodens*)	23.2	35.0	11.4	30.0	39.0
	CAP	CVD	TPW	GH	IZM
Anterior Caudal Vertebra[b]					
MNHNH P 3050 (?*Imagocnus zazae*)	34.5	27.7	>100[c]	>70	46[c]
Megalocnus rodens (Fischer, 1971)[d]	—	—	94.4	50.5	—

[a] Abbreviations: **SCTD,** sacral canal, transverse diameter; **CW**, centrum, transverse width, at level of second ventral sacral foramen; **CH**, centrum, anteroposterior height, at level of second ventral sacral foramen; **CLCM**, crista sacralis lateralis to crista sacralis medialis (midsagittal plane), transverse distance; **DSFW**, second dorsal sacral foramina, transverse distance between.

[b] Abbreviations: **CAP**, centrum, anteroposterior height; **CVD**, centrum, ventrodorsal width (in midsagittal plane); **TPW**, transverse processes, greatest distance (2 X distance between intact transverse process and midsagittal plane); **GH,** vertebra, ventral surface of centrum to tip of spinous process (as preserved); **IZM**, interzygapophyseal distance, maximum.

[c] Measurement not reflecting true value because of loss or breakage of bone.

[d] Fischer (1971: 671, table 30), measurements of anterior caudals of specimens 170 and 171, Pío Domingo Cave.

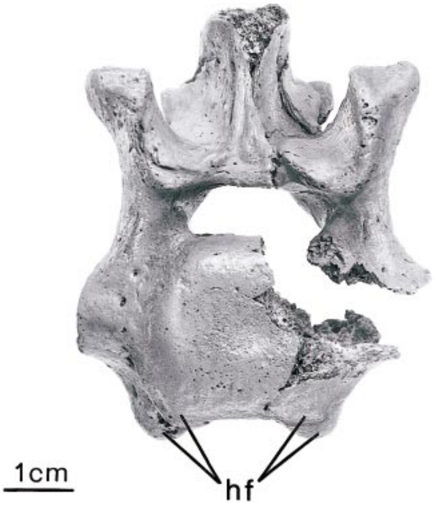


Fig. 9. Anterior caudal vertebra (MNHNCu–P 3050) from Domo de Zaza, attributed to *Imagocnus zazae*; cranial view. Key: **hf,** location of hemal facets on ventral surface of centrum. For description, see text.

etons of Quaternary sloths consisted of approximately 20 elements (Fischer, 1971). Representative measurements (table 5) indicate that the Zaza specimen is in the size range of *Megalocnus rodens*.

A fragmentary distal humerus found in 1994 (MNHNCu–P 3027; fig. 10) is here referred to Megalonychidae, although the specimen consists of the diaphysis only. In general conformation, the specimen agrees in detail with humeri of Quaternary *Parocnus* and *Acratocnus* (cf. White and MacPhee, 2001). It differs from the humeri of *P. browni* and *P. serus* in possessing an entepicondylar foramen (the aperture of the foramen is gone, but the diaphyseal sulcus is recognizable). It additionally differs from *Parocnus* in that the deltopectoral eminence is situated low (= distally) on the bone and lacks any lateral ‘‘flare’’. *Acratocnus* is similar in these regards, but all Quaternary *Acratocnus* species are smaller than MNHNCu–P 3027. *Megalocnus* is much larger, and *Neocnus* is much smaller. Assuming it was fully maturated at the time of death (the distal break occurred above the position of the epiphysis), the humerus suggests a smaller animal than does the pelvis.

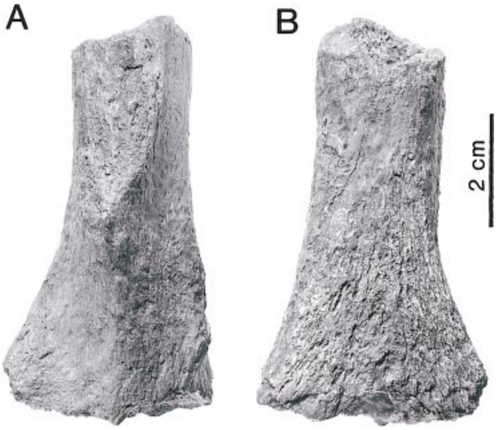


Fig. 10. Poorly preserved distal portion of humeral diaphysis (MNHNCu–P 3027) from Domo de Zaza, attributed to *Imagocnus zazae*: (**A**) anterior and (**B**) posterior aspects. For description, see text.

DISCUSSION: Although significant differences in the body masses of individual sloths are implied by some of the Zaza specimens (e.g., *Parocnus*-sized molariforms vs. *Megalocnus*-sized or larger pelvis), the systematic significance of this is hard to evaluate. It may be that more than one species of large sloths existed in Cuba during the Early Miocene. Alternatively, body sizes and proportions may have varied substantially within *Imagocnus zazae*, as they are known to have done in many Quaternary Antillean sloth species (MacPhee et al., 2000c; White and MacPhee, 2001). Until sample sizes improve, this issue cannot be usefully addressed. For the same reason, it is equally difficult to fix the phylogenetic position of *Imagocnus*. Although it displays no exclusive resemblance to any single Quaternary sloth, on the whole it seems closer to Megalocninae than Choleopodinae as organized by White and MacPhee (2001). We therefore tentatively assign *Imagocnus* to the former subfamily without, however, deciding whether it is closer to *Megalocnus* or *Parocnus* (or is the sister taxon to both, which is probably more likely).

CETACEA (ODONTOCETI)

Remarkably, Domo de Zaza has yielded evidence of toothed whales, although the material is too unsatisfactory to yield much in-

Fig. 11. Odontocete (?anterior) tooth, cetacean Species A (MNHNCu–P 3090), from Domo de Zaza: (**A**) distal and (**B**) side views. Note large ‘‘wear’’ facet. Specimen probably represents a physeterid, although no specific allocation is proposed at this time. For description, see text.

sight into the taxa represented. However, as a completely new group to the West Indian fossil record, their presence is worth recording.

Cetacean Species A

MATERIAL: Isolated tooth (MNHNCu–P 3090) recovered in 1994 by M. Iturralde-Vinent in lag deposit (fig. 11).

ATTRIBUTION: The tooth’s size (76.7 mm, greatest length; 19.7 mm, greatest width) and other distinctive features immediately preclude attribution of this specimen to Sirenia or, indeed, any mammalian group other than Odontoceti. The likeliest allocation is Physeteridae, although no exact match could be found in the literature.

The tooth is moderately curved, entirely free of enamel, with no waisting or other feature marking the transition from root to crown. A thick (>1 mm) coating of cementum, broken off in places, covers the root. The crown end bears numerous, very distinct ‘‘anular’’ growth lines, and terminates as a smooth-surfaced conus with a well-marked wear facet. The apical end of the root, ovoid in section, rapidly narrows near the terminus; the pulp cavity is open but mostly filled in, so that it extends as a vacuity only a few millimeters into the substance of the tooth. This may indicate that the tooth came from an aged animal (E. Fordyce, personal commun.).

Except for this last feature, all of these characters occur in *Orycterocetus* (L. Miocene Calvert Fm; cf. Kellogg, 1965) and its close relatives in Physeteridae. *Orycterocetus* fossils display long, open pulp cavities (?age related), and at least some teeth are longitudinally fluted (Kellogg, 1965). Fluting is very slightly indicated in the Zaza specimen. The wear facet on the posterior surface may indicate the presence of opposing teeth, although this condition can be found in mandibular teeth of modern *Physeter* (which lacks erupted maxillary teeth) as the result of contact with abrasive food (Boschma, 1938).

Although the specimen probably represents a species distinct from those currently recognized for *Orycterocetus*, the similarities are strong enough to support the idea that a closely related sperm whale lived in the Caribbean region in the Early Miocene. Physeterids are known from the Middle Miocene in North America and Early Miocene in South America (Fordyce and Barnes, 1994); the Zaza specimen is apparently the first sperm whale of significant antiquity to be reported from the West Indies (and one of the few reports of a fossil cetacean of any sort from this area; cf. Ray, 1964).

This specimen was compared to the tusk of the rytiodontine dugongid *Dioplotherium manigaulti* as illustrated and described by Domning (1989a). MNHNCu–P 3090 resembles ‘‘typical’’ *Dioplotherium* tusks in having moderate curvature, cementum covering, prominent growth lines, shallow pulp cavity, and no or very little enamel. However, *Dioplotherium* tusks are typically thicker, longer, and lozenge-shaped (‘‘bladelike’’) in cross-section, among other distinguishing features. However, according to Domning (1989b) rytiodontines differ among themselves as to whether there is an apical wear facet and ''self-sharpening edge'' on tusks, and there is some shape similarity between MNHNCu–P 3090 and Domning's so-called ''variant'' specimen, YPM 21334. While some degree of morphological convergence between rytiodontine tusks and sperm whale teeth is apparent—unsurprisingly, given the simple geometrical shapes involved—we feel confident that MNHNCu–P 3090 is better referred to the latter than to the former.

Cetacean Species B

Material: Isolated tooth (MNHNCu–P 3086) recovered by the 1994 field party (fig. 12).

Attribution: We offer this specimen as a cetacean with some hesitancy, as it is far from complete and there is certainly room for disagreement until better material comes to hand. However, it is critical to note that there is a definite crown-root junction, and the crown itself is composed of enamel. In our opinion, this combination of features indicates that the specimen is mammalian rather than crocodylomorph, the only other reasonable possibility.

The enamel is black and densely wrinkled. The preserved part of the specimen is essentially acorn-shaped and is very slightly compressed (maximum width at base of crown, 14.5 mm; maximum width at right angle to previous measurement, 13.6 mm; height of crown as preserved, 15.0 mm). There is a slight keel or carina, and the apex of the crown is slightly abraded. There is no cingulum or suggestion of accessory cusps. Presumably, the crown capped a long root, now broken off, of the sort seen in many odontocetes.

The relationships of this fossil are quite unclear, although its size and some details of its construction make odontocetes the likeliest candidate. Ewan Fordyce (Univ. Otago), who has kindly examined photographs of this specimen, noted that the keel could have supported tiny denticles, now worn away—a rather ancient feature (cf. better-developed ''cusps'' or denticles of archaic odontocetes, e.g., Squalodontidae, Kentriodontidae), archaic mysticetes (e.g., Aetiocetidae), and archaeocetes (e.g., Basilosauridae). Wrinkled enamel has been reported for archaic physeterids (e.g., *Scaldicetus*) and some other archaic cetaceans (basal mysticetes, later archaeocetes), although in other respects the Zaza tooth is sui generis. However, Fordyce doubts that any fine allocation of the tooth is possible at this point, although he rules out any described group of delphinoids, platanistoids, and ziphiids. It is just possible that it is a physeterid.

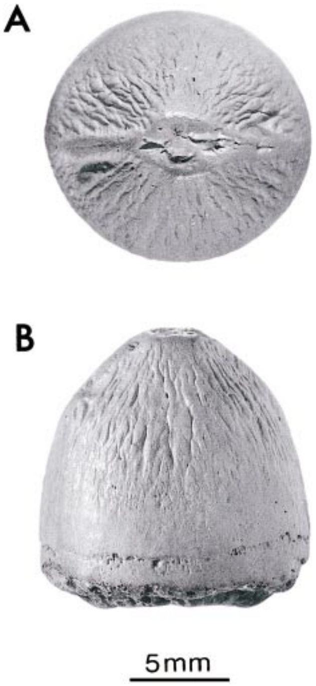


Fig. 12. Apparent odontocete tooth-crown, cetacean Species B (MNHNCu–P 3086), from Domo de Zaza: (**A**) crown and (**B**) side views. Allocation as to major taxon within odontocetes is uncertain. For description, see text.

SIRENIA

Material: Skull cap (MNHNCu–P 3124; fig. 13); squamosal with zygomatic process (MNHNCu–P 3316; fig. 14); proximal epiphysis of humerus (MNHNCu–P 3091); caudal vertebra (MNHNCu–P 3024); numerous ribs and rib fragments (accessioned as MNHNCu–P 3010); and a large number of unaccessioned vertebral fragments and other osteosclerotic/pachyostotic fragments not securely identified as to element. Only the first two elements not-

Fig. 13. Dugongid skullcap (MNHNCu–P 3124) from Domo de Zaza, allocation otherwise uncertain; dorsal view. For description, see text.

ed above are illustrated here. Recovered by various field parties between 1990 and 1998.

ATTRIBUTION: The sirenians of Zaza seem to have been exclusively dugongid, as would be expected given that trichechids did not invade the Caribbean area until later in the Miocene (Domning, 1989a). Two dugongids are possibly represented in the fossil material, one of which may be *Metaxytherium* (or some other hydrodamaline). However, as the material is quite poor we have refrained from making taxonomic allocations at this time.

The Atlantic–Caribbean area was the site of significant dugongid diversity during the early and middle Neogene (Domning, 1988, 1989a, 1989b, 1990, 2001; MacPhee and Wyss, 1990). Although sirenian fossils are known from a number of localities in Cuba (Iturralde-Vinent, personal obs.), virtually none of this material has been described. At present, the only named Tertiary sirenian from Cuba is the hydrodamaline *Metaxytherium riveroi* (Varona, 1972, 1974), based on the jaw of an immature animal recovered from E.–M. Miocene Güines Fm near Matanzas. Few characters distinguish this species from *M. calvertense* as described by Kellogg (1966); indeed, it may not be distinguishable at all if dental homologies were misinterpreted by Varona, as seems likely (D. Domning, personal commun., cited by MacPhee and Wyss, 1990).

DESCRIPTION: In view of their generally poor condition, the Zaza sirenian fossils do not merit extensive description.

The skullcap (fig. 13) consists, as is usual in sirenians, of the co-ossified parietals and supraoccipital. The temporal ridges are low, widely separated, and nearly parallel (as opposed to rostrally convergent as in *Halitherium*, or divergent as in *Metaxytherium* and many other taxa). At their closest approach, the ridges are separated by a gap of ~40 mm (vs. 15 mm in *M. calvertense*). Skullcap length (external occipital protuberance to anterior border of parietals, in midsagittal plane) is 70.3 mm (cf. >100 mm in *M. calvertense*), while minimum biparietal width (at right angle to foregoing measurement, immediately anterior to position of lambdoidal suture) is 60.0 mm (cf. 65 mm in *M. calvertense*). This suggests that the Zaza skullcap is proportioned differently from that of *Metaxytherium*. Measurements are closer to those of the ?*Caribosiren* skullcap from the Miocene of Puerto Rico figured by MacPhee and Wyss (1990), although here also temporal line curvature differs from that of the Zaza specimen. Recently described rytiodontines from the Caribbean–Atlantic area (Domning, 1989a, 1989b, 1990) also differ notably from the Zaza specimen for the few characters that can be compared.

The partial temporal (fig. 14) consists of most of the zygomatic process of the squamosal, glenoid area, and squama. The petrous portion is not preserved. In this case, correspondence to *Metaxytherium* is actually quite close, especially in the conformation of the glenoid and postglenoid regions (cf. illustrations presented by Kellogg, 1966; Domning, 1989a).

The humeral head (MNHNCu–P 3091), not illustrated, is very poorly preserved and is noteworthy only for its size: maximum dimensions of the head are 83.5 mm by 75.0+ mm, which correspond well with measure-

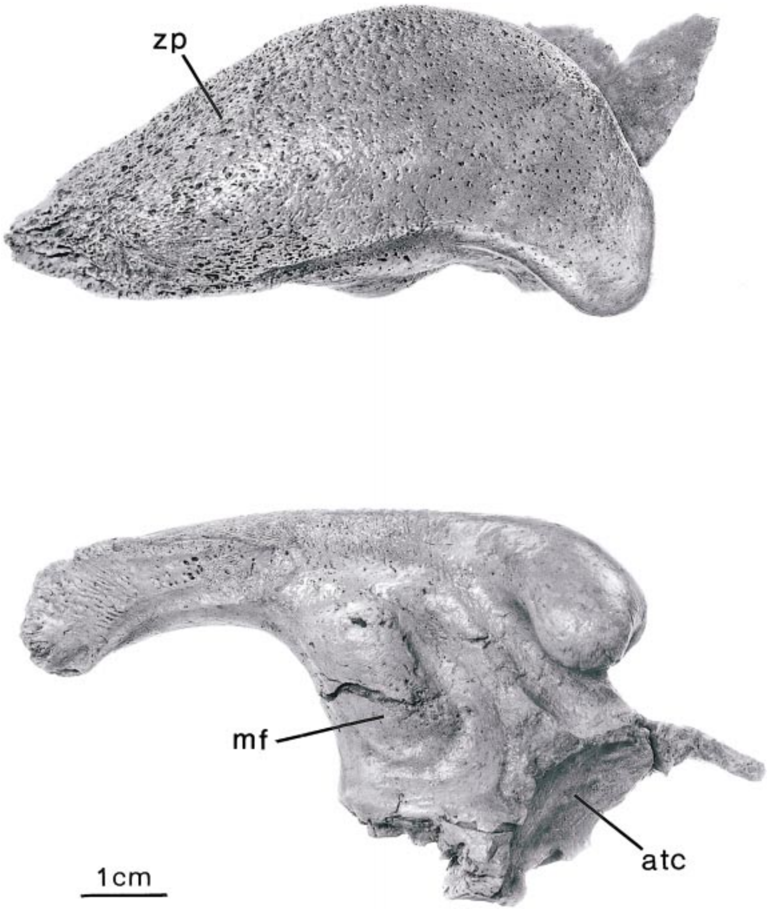


Fig. 14. Dugongid temporal (MNHNCu–P 3316) from Domo de Zaza, possibly attributable to *Metaxytherium* sp.: (**top**) lateral and (**bottom**) ventral views. Key: **atc,** anterior wall of tympanic cavity; **mf,** mandibular fossa; **zp,** zygomatic process of temporal. For description, see text.

ments reported by Kellogg (1966) for *M. calvertense* but are somewhat larger than those for *M. floridanum* provided by Domning (1989a). Morphologically all that can be said is that the head is highly rounded, as is typical for sirenians. The caudal vertebra (MNHNCu–P 3024), also not illustrated, is quite small (centrum height, 24.4 mm), but otherwise corresponds closely to Kellogg's (1966) description of caudal vertebra morphology in *M. calvertense* (which had at least 20 caudals).

In conclusion, although there are some indications that a dugong closely allied with if not identical to *Metaxytherium* sp. is represented in the Domo de Zaza collections, decisive evidence (e.g., strongly downturned snout, dental features listed by Domning [1989a]) will be required before any systematic allocation can be confidently made. Presence of seagrass feeders in the Zaza area 17 Ma would certainly be expected, given the wide expanse of shallow waters framing the Cuban archipelago at that time.

TESTUDINES (PLEURODIRA, PELOMEDUSOIDES)

MATERIAL: Carapace (MNHNCu–P 3012) lacking nuchal, pygal, and anterior peripherals; plastron lacking right mesoplastron, most of right hypoplastron and xiphiplastron, and posterior margin of left xiphiplastron.

Left half of carapace (AMNH–VP 27465; fig. 15A) with seven neurals and adjacent

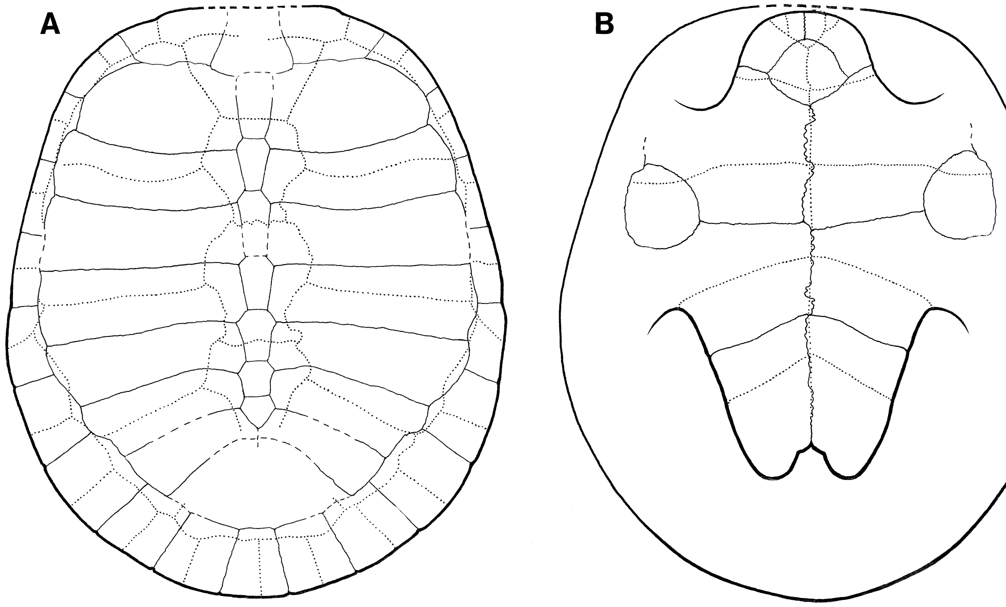


Fig. 15. (**A**) Turtle carapace (AMNH–VP 27465) and (**B**) plastron (AMNH–VP 27466) from Domo de Zaza, Pelomedusidae incertae sedis. For description, see text.

proximal parts of right costals; peripherals 1–9 and left edge of nuchal present; plastron lacking anterior margin, right epiplastron, right half of entoplastron, anterior portion of right hyoplastron, most of right bridge, posterior edges of both xiphiplastra; right and left pelves present.

Plastron (AMNH–VP 27466; fig. 15B) badly fractured but lacking only anterior margin; left bridge and parts of left xiphiplastron; carapace fragments.

Portion of plastron (AMNH–VP 27467).

ATTRIBUTION: The four listed specimens are very similar to one another and we conclude that they almost certainly belong to the same species. The species in question is clearly a pleurodire, because the pelvis is fused to the carapace and plastron—a diagnostic synapomorphy of Pleurodira (Gaffney and Meylan, 1988). Small, laterally placed mesoplastra are characteristic of the Pelomedusoides, and this may be provisionally considered a shell synapomorphy of the group. This attribution could be placed beyond doubt if it could be established that the cervical scale is absent (a pelomedusoid synapomorphy; Gaffney and Meylan, 1988), but unfortunately none of the specimens preserves a complete nuchal bone. Overall, the strong similarity of the shell of the Cuban species to known podocnemidids, such as *Podocnemis*, supports the identification offered here. The higher taxonomy of pleurodires follows Gaffney and Wood (2002) in recognizing the Hyperfamily Pelomedusoides, which contains the families Podocnemididae, Bothremydidae, and Pelomedusidae sensu stricto (containing only *Pelusios* and *Pelomedusa*).

Despite the fact that the shell of the Cuban species is almost completely known, there are serious problems in assigning it to a more specific taxonomic level. This is partly due to the disarray of pelomedusoid systematics occasioned by the traditional emphasis on shell characters as a basis for diagnosing chelonian taxa. For some turtle groups in which shell characters have been adequately surveyed and analyzed, and complete (or nearly complete) specimens are available for study, the traditional emphasis is perhaps not misplaced. Most pelomedusoids, however, are strikingly conservative in shell morphology (Wood and Diaz de Gamero, 1971; Gaffney and Zangerl, 1968), and therefore the exclusive use of shell characters practically invites the creation of paraphyletic groups. An outstanding example of this is the systematic history of the genus *Podocnemis*, which retains a generalized pelomedusoid shell type. A large number of fossil species, mostly defined on the basis of shell characters, have been assigned to this genus; these taxa range in age from Cretaceous through Tertiary, and in area from North and South America to Africa and Asia. When cranial material is available, however, in most cases the basis for assignment to *Podocnemis* sensu stricto collapses (e.g., Gaffney and Zangerl, 1968; Wood, 1970; Pritchard and Trebbau, 1984; Gaffney and Wood, 2002). *Podocnemis* (sensu Gaffney, 1979, excluding *Erymnochelys* and *Peltocephalus*) has a distinctive skull and cervical morphology, and all validly ascribed living and extinct species are restricted to South America.

Having said this, it is necessary to observe that although the Cuban species has a shell that closely resembles that of *Podocnemis* (*P. expansa* in particular; see Description), there is no assurance or even a high likelihood that the Cuban form possessed the cranial and vertebral synapomorphies currently used to define this genus. No pelomedusoids have been described from Cuba heretofore, although there are records from the Tertiary of Puerto Rico (Wood, 1972; Wood and Gaffney, 1989; Gaffney and Wood, 2002). The latter consist of a fragmentary shell (AMNH–VP 1836), identifiable only to Pelomedusoides, from the late Oligocene San Sebastian Fm (Wood, 1972; see also MacPhee and Wyss, 1990), and a series of well-preserved skulls and shells (Gaffney and Wood, 2002) attributed to the new podocnemidid genus, *Bairdemys*. The Puerto Rican record is *Bairdemys hartsteini*, a form most closely related to *Stereogenys* (Eocene–Oligocene of Egypt) and *Shweboemys* (Miocene–Pliocene of Pakistan and Burma), equivalent to the unnamed taxon B9 of Gaffney and Meylan (1988). It is probably from near-shore marine sediments. The other Puerto Rican record, AMNH–VP 1836, is thought to have been deposited ''partly under brackish and partly under nearshore marine conditions'' (Wood, 1972: 2). Much the same thing could be said of the Cuban pelomedusoid. *Bairdemys* is also found in presumed near-shore sediments in Venezuela (Sánchez-Villagra et al., 2000; Gaffney and Wood, 2002). The living *Podocnemis* itself is restricted to freshwater, but fossil evidence indicates that marine-adapted Podocnemididae were common in the past. The Cuban form is therefore ambiguous as an environmental indicator.

Description: Carapace (fig. 15A) similar in size and shape to *Podocnemis expansa*; oval, peripherals flaring posteriorly, approximately 68–70 cm minimum length (restored length, based on AMNH VP 27465). Nuchal, suprapygal, and pygal not known, remaining carapace bones similar to *Podocnemis*. Seven neurals present: neural 1 four-sided, neurals 2–5 six-sided and coffin-shaped, neural 6 six-sided and equidimensional, and neural 7 five-sided and smaller than others. Eighth costals meeting at midline, seventh costals separated by neural 7. *Bairdemys venezuelensis* (Wood and Diaz de Gamero, 1971; Gaffney and Wood, 2002) is unusual among Pelomedusoides in lacking neural bones in the carapace. The fragmentary Puerto Rican shell material, possibly associated with *Bairdemys*, does have at least some neurals. The presence of neurals in the Cuban species does not preclude it from belonging to *Bairdemys* or a near relative, as this feature can vary between species of turtles in the same genus.

Carapacial sulci similar to *Podocnemis* except that vertebral scales 2–4 narrow posteriorly, producing thereby a distinct but somewhat irregularly curved edge (similar to *P. erythrocephala* as figured by Pritchard and Trebbau, 1984: fig. 8). Little of vertebral 5 preserved.

Plastron completely known (fig. 15B) and similar in size and shape to *Podocnemis expansa*. Anterior lobe curved, not truncated as in *Kenyaemys*; anterior lobe shorter than posterior lobe, as in *Podocnemis*. Intergular scale single, distinctly larger than gular scales; completely separates gulars and partly separates humerals. Gulars are slightly smaller than their equivalents in most *P. expansa* and are entirely situated on epiplastra. Intergular extends onto entoplastron only for a short distance, as in *P. erythrocephala* as figured by Pritchard and Trebbau (1984: fig. 8). Humeral–pectoral sulcus lies entirely on hyoplastron, just posterior and parallel to epiplastron–hyoplastron suture. Mesoplastra longer than wide, with pectoral–abdominal sulcus lying across anterior portion as in *Bothremys,* in contrast to many (but not all) *Podocnemis* specimens. Axillary buttress strong, reaching peripheral 3 and extending nearly halfway across costal 1. Inguinal buttress distinctly weaker than axillary, as in *P. expansa*, only slightly attached to costal 5. Margins of posterior lobe straight but tapering. Xiphiplastron and xiphiplastral (anal) notch best seen in AMNH–VP 27466. Posterior margin of xiphiplastron rounded as in *Podocnemis* and *Bothremys*, in contrast to the acute margin found in *Taphrosphys*. On dorsal surface of xiphiplastron, pubic scar oval, not as elongate as in *Podocnemis*. Ischiac scar triangular, near edge of xiphiplastron, as in *Podocnemis*. Xiphiplastral notch acute rather than rounded. Known portions of pelvis indistinguishable from *Podocnemis expansa*.

DISCUSSION: The close similarities of the Zaza turtle with *Podocnemis* and other podocnemidids suggest identifying it with this group. Although it is likely that the Zaza pelomedusoid is a podocnemidid, until better material is found, it should be treated as Pelomedusoides incertae sedis (Testudines, Pleurodira, Pelomedusoides).

ELASMOBRANCHIA

MATERIAL: Isolated elements such as teeth, vertebrae, and spines of various fish groups have been recovered from Canal de Zaza and other places where Lagunitas Fm outcrops. The elasmobranchs have been worked up systematically by Iturralde-Vinent and coworkers (1996, 1998), and the reader is referred to these papers for further details. The elasmobranchs found at Zaza are essentially cosmopolitan species and therefore shed little light on the specific nature of the marine biota living around central Cuba in the Early Miocene. However, the species assemblage suggests the existence of warm, shallow, nearshore marine environments at this time (Iturralde-Vinent et al., 1996), which is consistent with the presence of extensive marine limestone and marl facies in the Lagunitas Fm.

Shark teeth were collected from marine rocks and lag deposits derived from marine beds in various parts of the Domo de Zaza exposure. Four shark and two ray species have been identified in the collection so far.

ATTRIBUTION: All material consists of isolated teeth. Except where indicated, galeomorph material was recovered from lag deposits at Domo de Zaza in August 1990 by a team composed of R. MacPhee, M. Smith, R. Rojas, and M. Iturralde-Vinent. Myliobatid material was collected from the same place and also (in the case of MNHNCu–P 3121 and 3122) from nearby Zaza Dug-Out.

Galeomorpha: Carcharhinidae

Carcharhinus obscurus (MNHNCu–P 2219, 3033)

Hemipristis serra (MNHNCu–P 2221, 3034 and 3036; plus fragmentary tooth MNHN 2268 collected by M. Iturralde-Vinent and R. MacPhee in 1996).

Negaprion brevirostris (MNHNCu–P 3037).

Galeomorpha: Sphyrnidae

Sphyrna mokarran (MNHNCu–P 3032).

Batomorphii: Myliobatidae

Myliobatis sp. (MNHNCu–P 3102, fragmentary tooth with eroded occlusal surface, collected by M. Iturralde-Vinent, R. Rojas, and R. MacPhee, February 1994; MNHNCu–P 3120, collected by R. MacPhee and M. Itrurralde-Vinent, June 1996).

Aetobatus arcuatus (MNHNCu–P 3119, collected by M. Iturralde-Vinent, R. Rojas, and R. MacPhee, February 1994; MNHNCu–P 3121 and 3122, collected at Zaza Dug-Out by M. Iturralde-Vinent, R. MacPhee, C. Flemming, and S. Díaz, June 1996).

NOTES ON THE TECTONIC EVOLUTION OF PUERTO RICO AND MONA PASSAGE

The GAARlandia hypothesis (Iturralde-Vinent and MacPhee, 1999; MacPhee and Iturralde-Vinent, 2000) proposes that, at approximately the time of the Eocene–Oligocene transition (~35–32 Ma), general uplift of the blocks comprising the northern Greater Antilles and the spine of the Aves Rise created a structure, the Greater Antilles–Aves Rise (or ''GAARlandia'') landspan that was briefly (≤1 Ma?) connected to northwestern South America. Shortly thereafter, tectonic movements began to subdivide this structure in various complex ways. Biogeographically, the single most important implication of the GAARlandia hypothesis is that certain South American mammals, and possibly other terrestrial animals, may have been able to disperse up the landspan into the future Greater Antilles before subsidence and tectonic dismemberment occurred. The central importance of the idea of GAARlandia is that it provides a common-cause explanation for many aspects of faunal formation in the Greater Antilles. Naturally, the explanatory power of this hypothesis is dependent on whether these events have been correctly chronicled, and it is therefore important to test it against the results of other investigations, whether biological or geological, whenever opportunity offers.

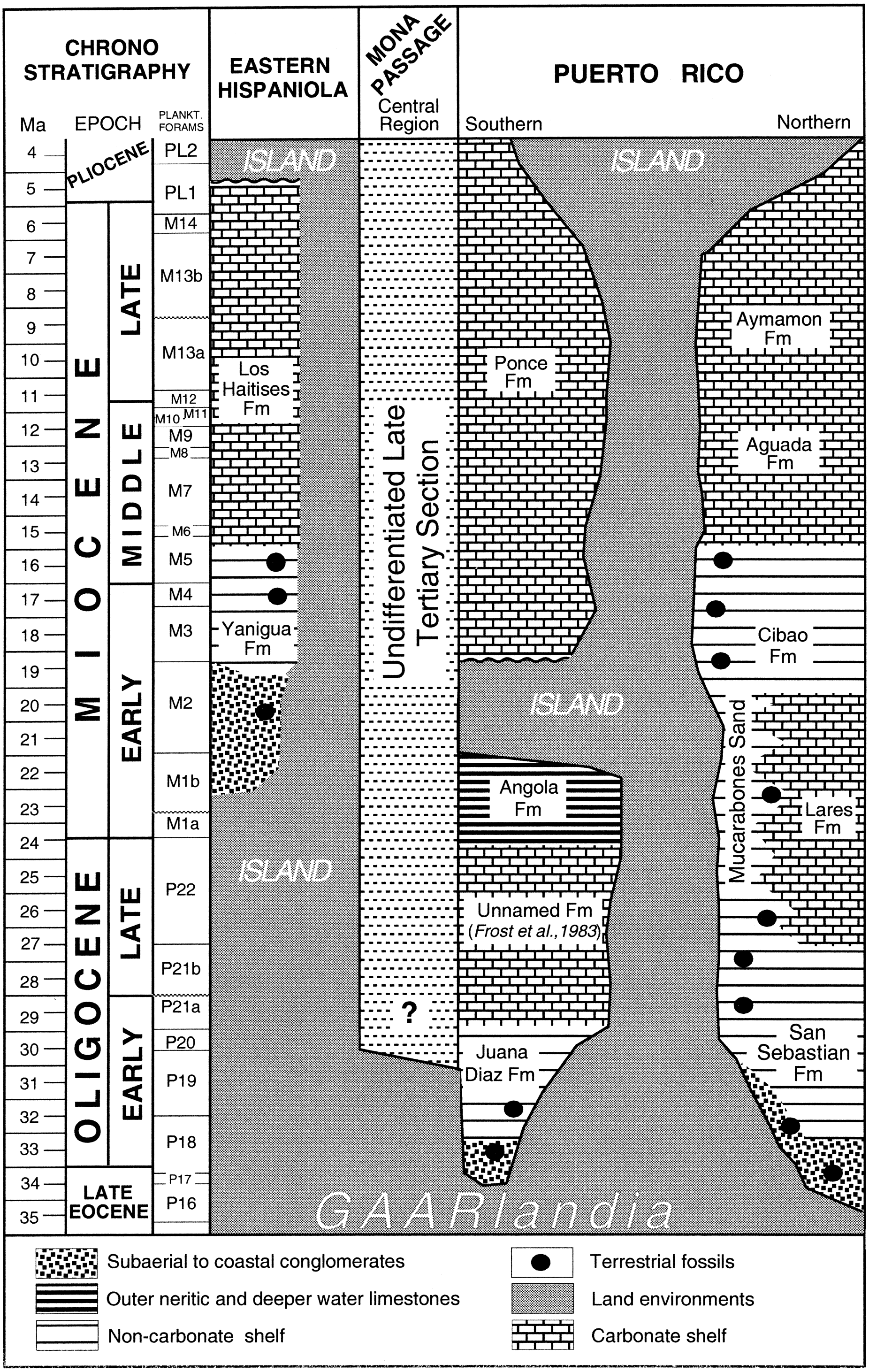
Two recent studies (van Gestel et al., 1998, 1999) offer interpretations of the tectonic evolution of Puerto Rico and the Mona Passage that contradict critical aspects of the GAARlandia hypothesis. The relevant issues may be conveniently bundled into two related series of topics: (1) The Mona Passage, which separates eastern Hispaniola and the Puerto Rico/Virgin Islands block, originated in the Early Oligocene. If this is correct, then subdivision of GAARlandia began almost immediately after the landspan's emergence. (2) The Puerto Rico/Virgin Islands block (PRVIB) was completely submerged between the Late Oligocene and the Early Pliocene. If this is correct, no terrestrial biotic elements in Puerto Rico or the Virgin Islands could be older than 5.2 Ma (start of the Early Pliocene).

TIME OF ORIGIN OF THE MONA PASSAGE

On the basis of information available at the time, we (Iturralde-Vinent and MacPhee, 1999) inferred that the Mona Passage first appeared as a marine basin in the Middle Miocene (~11–16 Ma). Our grounds for this inference were that (1) on both the Hispaniolan and Puerto Rican sides of the Mona Passage, deformed Cretaceous/Paleogene arc sections outcrop below Quaternary limestones, suggesting that there had been a barrier to marine deposition (i.e., a land connection) until late in the Cenozoic; and (2) regional tectonic reconstructions implied that the Passage was of late or neotectonic origin (more specifically, that the Passage was formed as a consequence of Miocene–Pliocene extensional stress due to rotation of Puerto Rico [Larue and Ryan, 1998]). We also noted, however, that ''additional data from the floor of the Mona Passage would help to clarify the history of this connection'' (Iturralde-Vinent and MacPhee, 1999: 35).

Van Gestel et al. (1998) have developed a different interpretation of the probable time of opening of the Mona Passage, based on their interpretation of a variety of newly collected as well as previously archived offshore seismic reflection profiles. Two profiles, based on lines shot along different tracks through the Passage (their figures 14 and 15), do indeed show a rather thick section of sedimentary rocks, the basal beds of which thin toward the latitude of Mona Island. On this basis the authors assume that the sediments flooring the Passage are probably the same age as those in the better-studied Puerto Rico North Coast Basin, where well-dated Early Oligocene–Early Pliocene carbonates drape arc-related basement rocks (middle column, fig. 16).

Although this is an interesting possibility, some cautionary notes have to be sounded. The absence of well corings or accessible outcrops and the lack of uniform thickness in the lower part of the seismostratigraphic section mean, in effect, that there is no direct evidence of the section's actual age, nor any way currently to verify the proposed age for the sedimentary section filling the Passage. The oldest rocks exposed on Isla Mona and Isla Monito are relatively pure limestones generally regarded as Middle or Early Miocene in age (Kaye, 1959), although recently an Early Miocene or Late Oligocene age has been suggested on the basis of dolomitization studies (W. Ramírez, personal commun.). By contrast, the oldest Oligocene marine sediments exposed on land in Puerto Rico are of Early Oligocene age, and consist of thin beds


CHRONO STRATIGRAPHY
Ma
EPOCH
PLANKT. FORAMS
EASTERN HISPANIOLA
MONA PASSAGE
Central Region
PUERTO RICO
Southern
Northern
4
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33
34
35
PLIOCENE
MIOCENE
LATE
MIDDLE
EARLY
OLIGOCENE
LATE
EARLY
LATE EOCENE
PL2
PL1
M14
M13b
M13a
M12
M10
M11
M9
M8
M7
M6
M5
M4
M3
M2
M1b
M1a
P22
P21b
P21a
P20
P19
P18
P17
P16
ISLAND
Los Haitises Fm
Yanigua Fm
ISLAND
Undifferentiated Late Tertiary Section
?
ISLAND
Ponce Fm
Aymamon Fm
Aguada Fm
Cibao Fm
ISLAND
Angola Fm
Mucarabones Sand
Lares Fm
Unnamed Fm (Frost et al.,1983)
Juana Diaz Fm
San Sebastian Fm
GAARlandia
Subaerial to coastal conglomerates
Outer neritic and deeper water limestones
Non-carbonate shelf
Terrestrial fossils
Land environments
Carbonate shelf

intercalated within what is otherwise an essentially terrestrial section. Fully marine conditions are not encountered until the medial Oligocene (fig. 16; see also MacPhee and Iturralde-Vinent, 1999). This evidence indicates that Oligocene transgression occurred in parts of the PRVIB and probably the Mona Passage area, but after rather than before ~30 Ma (fig. 16). While we look forward to seeing further substantiation of the correlations suggested by van Gestel et al. (1998), we would prefer to see that come from something other than seismic data (e.g., seafloor drilling).

Notwithstanding the need for additional evidence, if indeed the Mona Passage opened in the Oligocene, we propose the earliest empirically defensible date should be approximately 30 Ma or slightly earlier (i.e., in the medial rather than the Early Oligocene), coincident with extensive development of marine rocks in the northern and southern late Tertiary basins of Puerto Rico (see Iturralde-Vinent and MacPhee [1999: fig. 20] and the following section). It is also of interest that the seismic reflection profile data indicate that other marine basins in the area are much younger: thus St. Croix has been isolated from the Saba Bank only since the Middle Miocene, and the Virgin Passage (between the Puerto Rico bank and the Virgin Islands) has existed as a marine channel only since the Pliocene (van Gestel et al., 1998). As to western GAARlandia—essentially composed of the units making up Cuba and eastern Hispaniola—the tectonic and stratigraphic evidence continues to favor later (Miocene) subdivision (Iturralde-Vinent and MacPhee, 1999).

An earlier opening of the Mona Passage (by 10 Ma or more compared to our original estimate) has some interesting implications. With regard to Antillean paleogeography, redating the opening strongly reinforces our suspicion that the period of maximum continuity and emergence of GAARlandia (see above) had to have been extremely short (Iturralde-Vinent and MacPhee, 1999: 59). With regard to Antillean biogeography, redating also limits the period available for island–island vicariance. For example, species of the endemic choloepodine sloth genus *Acratocnus* are currently known from Cuba, Hispaniola, and Puerto Rico (Quaternary localities only). If they achieved this distribution via island–island vicariance rather than through several distinct episodes of overwater transport, as we think (see also White and MacPhee, 2001), then their last common ancestor must have lived in GAARlandia prior to 30 Ma. The partial sloth femur from the locality of Yauco (Puerto Rico), dated to the Early Oligocene (MacPhee and Iturralde-Vinent, 1995b), is consistent with the early presence of sloths on that island, even if the specimen itself cannot be definitively allocated to Choloepodinae. The same logic applies to the history of nesophontid insectivores and heptaxodontid and heteropsomyine

←

Fig. 16. An ‘‘emergence history’’ of part of eastern GAARlandia (eastern Hispaniola, Mona Passage, and Puerto Rico), from Late Eocene to mid-Pliocene. Diagram indicates that the eastern Hispaniola block and the Puerto Rico/Virgin Islands block were connected and subaerial during the brief GAARlandia landspan phase. Since Early Oligocene, parts of GAARlandia began to founder and subdivide, as is suggested by the presence of thin marine intercalations in the dominantly terrestrial section of San Sebastian Fm and Juana Diaz Fm (above the basal conglomerates). Mona Passage began to open as a consequence of movements along major faults and rotation of the PRVIB, but probably did not become a *permanent* marine barrier until 30 Ma or somewhat later. Opening was doubtless progressive, although this is not depicted here. Terrestrial environments are distinguished from shelf and marine environments by shading conventions (see key). Vertical/horizontal extent of shading indicates continuity of the environment in question over time/area. Thus, the panels representing eastern Hispaniola and Puerto Rico indicate that, while subaerial land has been continuously present since the Late Eocene, the amount has clearly varied (scale is suggestive only). In the panels, symbols for terrestrial fossils are positioned within named formations if there is paleontological evidence for the presence of land plants or animals in relevant sediments. However, placement and number of symbols should not be interpreted to mean precise times or frequencies.

rodents, although for these groups there is as yet no fossil evidence from critical periods.

EMERGENCE OF PUERTO RICO

Another controversial interpretation proposed by van Gestel et al. (1999) in a second recent paper concerns the emergence of Puerto Rico (i.e., the appearance of terrestrial environments on the PRVIB). These authors present a tectonic history of the PRVIB during the Cenozoic that differs substantially from traditional interpretations (e.g., Meyerhoff, 1933; Monroe, 1980; Donnelly, 1992; Larue, 1994) and considerably conflicts with the GAARlandia hypothesis (Iturralde-Vinent and MacPhee, 1999). In particular, van Gestel et al. (1999) do not accept that portions of this block have been continuously emergent since the latest Eocene, preferring instead a three-phase tectonic evolution that allows for considerable periods of nonemergence. The three phases, largely based on their interpretations of offshore seismic reflection data from the North Coast Basin, are as follows: phase 1, Cretaceous to Middle Eocene, active vulcanism, uplift, emergent land along axis of island arc; phase 2, medial Oligocene to Early Pliocene, ‘‘period of tectonic quiescence’’, complete subsidence of the PRVIB, carbonates deposited across latter’s entire width; and phase 3, Early Pliocene to Holocene, uplift, re-emergence, and acquisition of present coastlines. Importantly, the very short interval stipulated for Neogene emergence (Pliocene and later) is plainly inconsistent with a lengthy history of vertebrate colonization of the PRVIB, whether this was accomplished by overwater or landspan dispersal.

In our view this scenario of complete submergence from the medial Oligocene to Early Pliocene is contradicted by available geological, vertebrate paleontological, and paleobotanical information—most of which is not discussed or referenced by van Gestel et al. (1999). The reader is referred to our summary paper (Iturralde-Vinent and MacPhee, 1999) for background information and to figure 16 for the position and relationship of various formations named in the following paragraphs.

Geological Evidence: Phase 1 of the model developed by van Gestel et al. (1999) conflates two quite different tectonic regimes experienced by the PRVIB—the Paleocene–Middle Eocene volcanic arc phase, and the Late Eocene to medial Oligocene uplift phase. This is recognized, for example, by Larue et al. (1998: fig. 16) in their recent reconstruction, which divides the Tertiary tectonic history of Puerto Rico into four rather than three phases. Separate recognition of the Late Eocene/Early Oligocene phase of uplift is critical, because it covers the ‘‘post arc’’ orogenic deformation which had wide effects along the whole Greater Antilles/Aves Rise (and, not incidentally, led to the formation of GAARlandia). Supporting evidence for this uplift event as it affected the PRVIB is diverse (Monroe, 1980; MacPhee and Iturralde-Vinent, 1995b; Larue et al., 1998; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2001): (1) the angular unconformity between the late Tertiary section and the oldest arc section, marking a long period of emergence and subsequent subaerial erosion; (2) the absence of Late Eocene marine rocks (or even reworked Late Eocene marine fossils) in younger rocks within the Puerto Rico/Virgin Island block; (3) the occurrence of ?latest Eocene/Early Oligocene conglomerates of terrestrial origin at the base of both the San Sebastian (north basin) and Juana Díaz Fms (south basin). These facts cannot be explained unless the block was continuously emergent through the Eocene–Oligocene transition.

Equally problematic is the characterization of phase 2 by van Gestel et al. (1999) as a ‘‘period of tectonic quiescence’’ and complete subsidence from the mid-Oligocene to Early Pliocene. Long-established facts lead to just the opposite conclusion. Although the northern and southern flanks of Puerto Rico differ stratigraphically in many ways, in both areas sections dating from the beginning of the Oligocene to the end of the early Middle Miocene (33–14 Ma) typically contain terrigenous clastic material eroded from the igneous-sedimentary Cretaceous–Eocene core (Monroe, 1980; Iturralde Vinent and Hartstein, 1998), which means that emergent land had to have been present through this entire interval. The following points lend further support to this contention (see fig. 16; Frost et al., 1983; MacPhee and Wyss, 1990; Iturralde-Vinent and MacPhee, 1999; Iturralde-Vinent, 2001): (1) the main San Sebastian Fm in the northern half of Puerto Rico and the upper Juana Diaz Fm and unnamed formation of Frost et al. (1983) in the south contain nonmarine sediments and fossils; (2) the marine limestones making up Lares Fm (Late Oligocene–Early Miocene) occur locally only, and interfinger with terrestrially derived sediments of the San Sebastian Fm and Mucarabones Sands (eastern lateral equivalent of Lares and lower Cibao Fms); (3) in several localities the Cibao Fm (Early Miocene) directly overlies structural highs in the Cretaceous and Paleogene volcanic arc sections, indicating that the latter were uplifted and emergent until the Early–Middle Miocene; (4) the Cibao Fm contains abundant nonmarine intercalations and other sedimentological indications of the occurrence of land; (5) the Aguada Fm (Middle Miocene) represents a carbonate shelf and fringing reef, but contains some terrigenous clastic quartz and very rare beds of lignite as well as desiccation cracks; and (6) later Miocene and Pliocene formations (Aymamon, Camuy, Angola, and Ponce Fms; ‘‘unnamed formation’’ of Frost et al., [1983]) are typical marine-shelf facies, similar to those which today surround places in the Cuban archipelago characterized by low relief or low sediment output (or both) (Pushcharovsky et al., 1988). Mere presence of such sediments is not dispositive of the absence of land, and, as always, should be evaluated in relation to all other relevant evidence.

Monroe (1980: 57) stated that, notwithstanding the absence of clastics in Aymamon rocks, land of ‘‘very low relief that probably stood not far above sea level’’ was still present in the Middle Miocene. Perhaps most importantly, he also noted that there is no positive evidence that the interior of Puerto Rico was transgressed in the Neogene. In other words, no vestige of Neogene sedimentary units have ever been identified in Puerto Rico outside the carbonate units framing the coasts, despite very active programs of outcrop exploration in the last century (Monroe, 1980). Absent an unprecedented rate of erosion in central Puerto Rico, or the complete failure of carbonate rocks to form except along the coasts, this evidence by itself strongly indicates that no mid-Tertiary or later transgression of this island could have been complete.

In summary, the preponderance of geological facts establish, *contra* van Gestel et al. (1999), and in line with Meyerhoff (1933) and Iturralde-Vinent and MacPhee (1999: figs. 6–8), that significant portions of the Puerto Rico/Virgin Island block have been emergent since the latest Eocene, although doubtless there was variation in its areal extent and relief.

VERTEBRATE PALEONTOLOGICAL AND PALEOBOTANICAL EVIDENCE: San Sebastian and Juana Diaz Fms present abundant evidence of terrestrial plant remains, including petrified wood (Graham and Jarzen, 1969; Graham, 1996), as well as good examples of paleosol development (MacPhee and Wyss, 1990; MacPhee and Iturralde-Vinent, 1995b). These are unambiguous indicators that land was present during the latter part of the Oligocene, perhaps land of high relief (Graham and Jarzen, 1969). Furthermore, in Early Miocene sediments in both areas terrestrial plant and animal fossils have been recovered (Graham, 1996; MacPhee and Wyss, 1990; MacPhee and Iturralde-Vinent, 1995b; Iturralde-Vinent and Hartstein, 1998; Iturralde-Vinent, 2001), including specimens that indisputably indicate terrestrial conditions (boid and ?iguanid fossils from locality AMNH PR 88-1, Cibao Fm; MacPhee and Wyss, 1990). In fact, van Gestel et al. (1999: 279) agree that in Late Oligocene/Early Miocene Lares Fm, ‘‘siliclastic sedimentation . . . may have represented the final stages of the erosional event that produced the underlying San Sebastian Formation’’, but they failed to include this point in their characterization of phase 2 paleogeography.

In closing, we emphasize that van Gestel et al. (1999) did not misinterpret their basic paleogeographical data, which concern many other topics of no direct relevance here. Rather, the problem is that, in making their specific inductions about emergence vs. nonemergence of Puerto Rico, they failed to consider sources of contrary evidence (e.g., vertebrate paleontology). This underscores how important it is to consider carefully all relevant information when making paleogeographical investigations, and to pay particular attention to apparent contradictions in datasets before reaching settled conclusions (Crother and Guyer, 1996).

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