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On: 27 January 2014, At: 07:47

Publisher: Taylor & Francis

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Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

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Published online: 07 Jan 2014.

To cite this article: Jorge Vélez-Juarbe, Thomas Martin, Ross D. E. Macphee & Diana Ortega-Ariza (2014) The earliest Caribbean rodents: Oligocene caviomorphs from Puerto Rico, *Journal of Vertebrate Paleontology*, 34:1, 157-163, DOI: [10.1080/02724634.2013.789039](https://doi.org/10.1080/02724634.2013.789039)

To link to this article: <http://dx.doi.org/10.1080/02724634.2013.789039>

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THE EARLIEST CARIBBEAN RODENTS: OLIGOCENE CAVIOMORPHS FROM PUERTO RICO

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ABSTRACT—The Greater Antilles was once home to a diverse array of endemic groups of caviomorph rodents. Many of these became extinct, together with endemic insectivores, sloths, and primates, in what is widely considered an archetypical example of Quaternary extinction on oceanic islands. When and how the ancestors of these land mammals arrived on these islands is debated. Here we report on the discovery, for the first time, of undoubted rodent incisors in Oligocene contexts in Puerto Rico. The enamel microstructure of the Puerto Rican fossils is consistent with caviomorph affinities, particularly with extinct Pleistocene species from Puerto Rico and Anguilla (Lesser Antilles). These fossils represent the oldest rodents now known from the West Indies, as well as the oldest record of caviomorphs north of the Equator. Their presence in the Greater Antilles by the early Oligocene suggests that caviomorph rodents must have begun to disperse throughout South America, and beyond, very soon after their initial radiation (currently pegged to middle or late Eocene). This, together with other lines of evidence, is consistent with the landspan hypothesis for the origin of the Greater Antillean land mammal fauna, although other mechanisms, including overwater transport, cannot be ruled out.

INTRODUCTION

The origin of the land mammal fauna of the Greater Antilles has long been regarded as a biogeographical conundrum. One contentious issue is whether the progenitors of some or all of the major Antillean lineages of rodents, sloths, primates, and eulipotyphlans made the crossing to these islands via a series of apparently uncoordinated overwater dispersal events at various times during the Cenozoic (Hedges et al., 1992; Hedges, 1996, 2006), or as a result of a single arrival event involving a hypothesized landspan (GAARlandia hypothesis; MacPhee and Iturralde-Vinent, 1995; Iturralde-Vinent and MacPhee, 1999), predicted to have briefly existed around the time of the Eocene–Oligocene transition. The facts may, however, point to a more complex biogeographical picture than these rather stark alternatives, as is surely the case for bats (Dávalos, 2004). The Antillean eulipotyphlan lineage (Solenodontidae + *Nesophontes*) is possibly the oldest: a recent divergence date estimate places the split between *Solenodon* and other eulipotyphlan taxa in the latest Mesozoic, and might have arrived to the Caribbean islands at a point in the late Cretaceous when they were closer to the North American landmass (Roca et al., 2004). Limited paleontological evidence indicates that sloths were evidently present by early Oligocene (Yauco locality, Puerto Rico; MacPhee and Iturralde-Vinent, 1995), whereas primates and caviomorph rodents are not known to occur until early Miocene (Domo de Zaza locality, Cuba; MacPhee, 2009). So far, most of the dated primate evidence is no older than Quaternary; genetic evidence on extant platyrrhines does not support a first appearance date for the taxa represented on the islands earlier than about 20 Ma

(Dávalos, 2004; Cooke et al., 2011), which, if correct, indicates that the Antillean primates could not have arrived much earlier than early Miocene. All of the groups considered so far, except the eulipotyphlans, have South American sister taxa. One group of oryziomyine muroid rodents managed to reach a number of the Lesser Antilles as well as Jamaica; they, too, are later arrivals, presumably from South America (Turvey et al., 2010). More detailed accounts of the history of each of these taxa can be found in Woods et al. (2001) and MacPhee (2005).

Here we describe two rodent incisors from Oligocene localities in Puerto Rico. The morphology of these incisors indicates that their affinities unequivocally lie within Caviomorpha. Importantly, these finds push back the fossil record of this taxon in the Greater Antilles approximately 9–10 million years, coeval with the earliest presence of megalonychid sloths in the region (MacPhee and Iturralde-Vinent, 1995; MacPhee, 2005). These Puerto Rican Oligocene caviomorphs are the oldest known members of this infraorder north of the Equator, as well as the oldest outside South America (Fig. 1A). Dispersal of caviomorphs thus occurred early in their evolutionary history, not only within South America (Antoine et al., 2012), but also northward, beyond the current margin of that continent.

Abbreviations—**HSB**, Hunter-Schreger band; **IPM**, interprismatic matrix; **MA**, enamel sample acronym at Steinmann-Institut für Geologie, Mineralogie und Paläontologie of Universität Bonn, Germany; **PE**, portio externa; **PI**, portio interna; **PLEX**, prismless external layer; **SALMA**, South American Land Mammal Age.

MATERIALS AND METHODS

Enamel Microstructure

Pieces a few millimeters long were cut off the incisors using a minidrill diamond-coated disk and were embedded in polyester resin for easier handling. After hardening of resin, specimens

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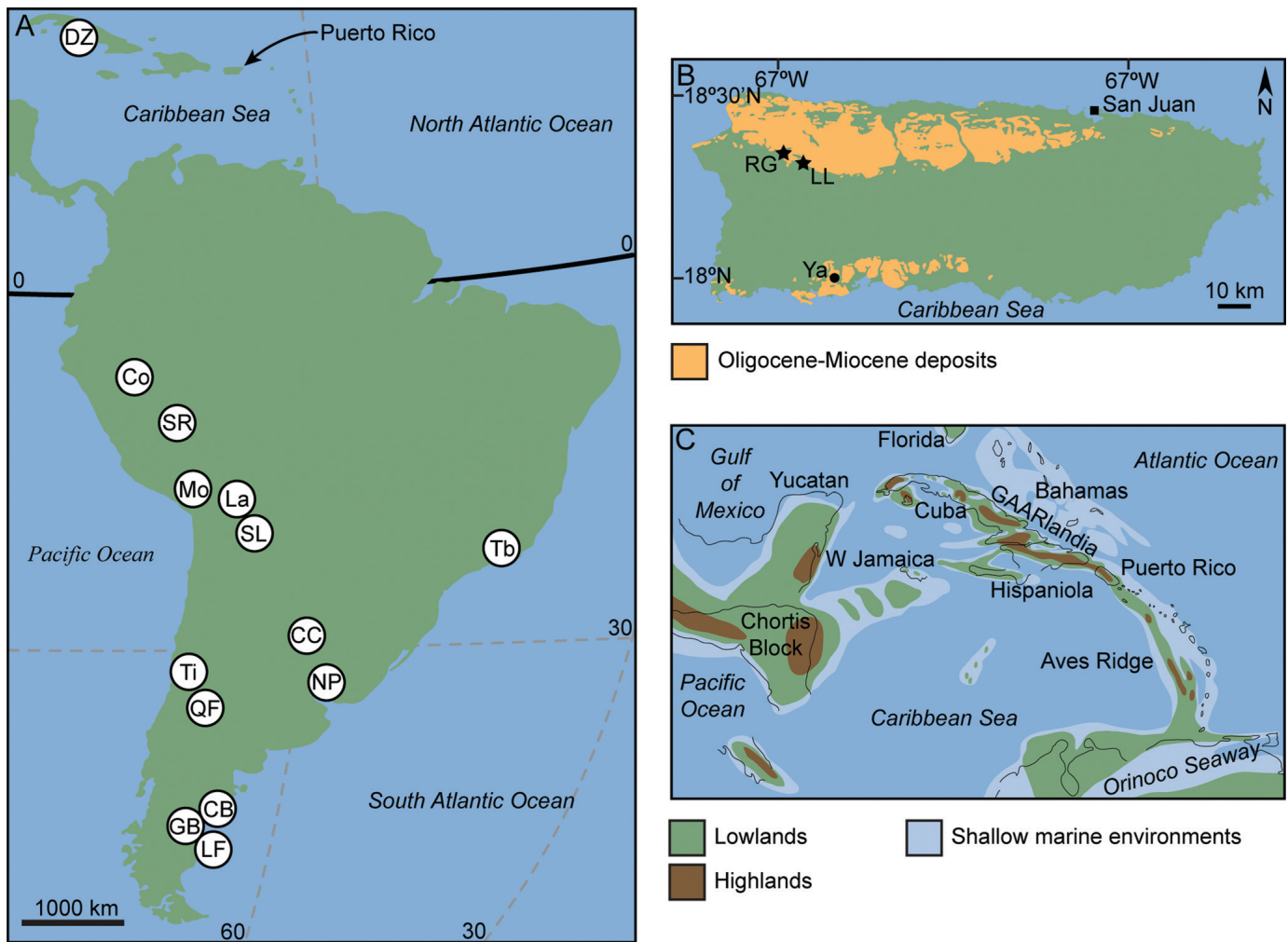


FIGURE 1. **A**, map of South America and the Caribbean showing localities mentioned in the text; **B**, map of Puerto Rico showing the distribution of Oligocene and Neogene deposits and the localities mentioned in the text; **C**, paleogeographical reconstruction of the Caribbean region during the late Eocene/early Oligocene (modified from Iturralde-Vinent and MacPhee, 1999). **Abbreviations:** **CB**, Cabeza Blanca; **CC**, Curuzú Cuaita; **Co**, Contamaná; **DZ**, Domo de Zaza; **GB**, Gran Barranca; **La**, Lacayani; **LF**, La Flecha; **LL**, Lares Limestone; **Mo**, Moquegua; **NP**, Nueva Palmira; **QF**, Quebrada Fiera; **RG**, Rio Guatemala; **SL**, Salla-Luribay; **SR**, Santa Rosa; **Tb**, Taubaté; **Ti**, Tinguiririca; **Ya**, Yauco.

were cut transversely and longitudinally with a low speed saw. Subsequently, specimens were ground smooth with 1200 corundum slurry on a glass plate, rinsed, dried, and etched for 2–4 seconds with 7% (2 N) HCl to make morphological details visible. After ultrasonic cleansing and rinsing with distilled water, the specimens were dried, mounted on scanning electron microscope (SEM) stubs and sputter-coated with gold (3 minutes). The specimens were studied under a CamScan MV 2300 scanning electron microscope.

Localities

The north coast Tertiary basin of Puerto Rico encompasses several lithologic units ranging from ?latest Eocene to late Miocene or Pliocene, and representing a variety of marine and near shore environments (Monroe, 1980; Seiglie and Moussa, 1984; MacPhee and Wyss, 1990; Ward et al., 2002). The fossils described here come from two localities within this sedimentary basin, the Rio Guatemala (RG) and Lares Limestone (LL) localities (Fig. 1A, B). At the RG locality, beds of the San Sebastian Formation are exposed, discontinuously, along the banks

of the river. The overall lithology of the San Sebastian Formation along this section consists of conglomerates and paleosols interbedded with marine mudstones and siltstones and occasional cross-bedded coarse sand units (Vélez-Juarbe et al., 2007). This lithology is characteristic of the basal San Sebastian Formation (Monroe, 1980; Ward et al., 2002). The San Sebastian incisor (MA 316) was collected from a ~30-cm-thick, siliciclastic mudstone unit exposed over an area of about 6 m². Other fossils collected from this unit include associated cranial and postcranial elements of halitheriine dugongids, crocodylian teeth, postcranial elements of a pelomedusoid turtle, and ginglymostomatid shark teeth. This unit likely represented a shallow marine or brackish nearshore lagoon. Prior collecting efforts along this section, north of where our fossil was collected, yielded the remains of a gryposuchine gavialoid and echinoderms (Vélez-Juarbe et al., 2007; Vélez-Juarbe and Santos, 2008).

Locality LL consists of 760-m-long roadcut, where three different formations are exposed. These are, in stratigraphic order, the upper part of the San Sebastian Formation (~7 m in thickness), Lares Limestone (~35 m thick), and the base of the Montebello Limestone (~7 m thick) (Ortega-Ariza, 2009). The

TABLE 1. Stable isotope data from *Kuphus incrassatus* samples from the middle and top of the Lares Limestone as exposed along road PR-111.

Sample	Stratigraphic location within section	$\delta^{13}\text{C}$			$\delta^{18}\text{O}$		
		Corrected run 1	Corrected run 2	Average runs 1–2	Corrected run 1	Corrected run 2	Average runs 1–2
PR-111 GPS	Top	1.57	1.83	1.70	-1.76	-1.43	-1.60
PR-111 T1	Top	1.92	1.97	1.95	-0.88	-0.53	-0.71
PR-111 M2	Mid	-1.14	-1.08	-1.11	-2.29	-2.01	-2.15
PR-111 M8	Mid	-0.92	-1.19	-1.06	-1.85	-2.25	-2.05

δ values are in ‰ on the PDB scale.

Lares Limestone at this locality is known for the abundance of corals and other invertebrates (Johnson et al., 2006; Vélez-Juarbe and Santos, 2008; Ortega-Ariza, 2009) and represents back-reef complexes and coral bioherm environments (Seiglie and Moussa, 1984). The unit where the Lares incisor (MA 308) was collected is part of the third parasequence of Ortega-Ariza (2009). This unit consists of mudstone to wackestone, with skeletal grains and coal fragments towards the top, facies change towards the south to coral boundstone. Other vertebrate remains collected from this unit include osteichthyan and chondrichthyan teeth, pelomedusoid shell fragments, and dugongid ribs and vertebrae. This unit is interpreted as a back-reef lagoon environment.

Dating of Localities

Kuphus incrassatus bivalve samples composed of low-magnesium calcite were used to obtain strontium isotope data for age determination of the Lares Limestone. Samples were taken from middle and top of the section exposed along road PR-111. Each sample was analyzed for stable carbon and oxygen isotopic ratios, using a ThermoFinnigan MAT 253 continuous-flow system at the KPESIL Laboratory, University of Kansas, and cathodoluminescence microscope with generally operating conditions of 50 mTorr, 10 kV, and 0.5 mA at the Kansas Geological Survey. Both procedures assess whether post-depositional diagenesis had affected the mineralogy of the original shell material. All samples showed very little post-depositional diagenesis (Table 1). Samples determined to be unaltered by diagenesis were selected for strontium isotope data (Table 2). The analyses were performed in the Isotope Geochemistry Laboratories, University of Kansas, and normalized to standard reference material NBS-987 of 0.710248. Strontium isotope ratios were produced using a signal strength of $\text{Sr}88 = 4 \text{ V}$ on a VG Sector 54 mass spectrometer operating in dynamic mode. Uncertainty was assigned as the largest value between instrumental error and uncertainties associated with the Sr-seawater curve of McArthur et al. (2001). Strontium isotope ratios were then converted to numerical ages using McArthur et al. (2001).

Strontium isotopic values for *Kuphus* tubes from the base of the Lares Limestone at this same locality range from 0.708087 (27.17) to 0.708105 (26.58) (Johnson et al., 2006; Ramirez et al., 2006). This suggests an age of $27.17 \pm 0.73 \text{ Ma}$ to $26.58 \pm 0.74 \text{ Ma}$ for the deposition of the base of the Lares Limestone. Our results (Table 2) combined with previously published values gives an age

of deposition between 27.17 ± 0.73 and $24.70 \pm 0.40 \text{ Ma}$ for the Lares Limestone at this locality. The San Sebastian Formation lies stratigraphically below the Lares Limestone, which suggests an age greater than $\sim 27 \text{ Ma}$. The lithology of the San Sebastian locality is consistent with what is considered basal San Sebastian Formation (Monroe, 1980; Ward et al., 2002), suggesting that it is relatively older than $\sim 27 \text{ Ma}$, which in turn is consistent with the correlative stratigraphic evidence presented by Iturralde-Vinent and MacPhee (1999).

Emergence of Puerto Rico

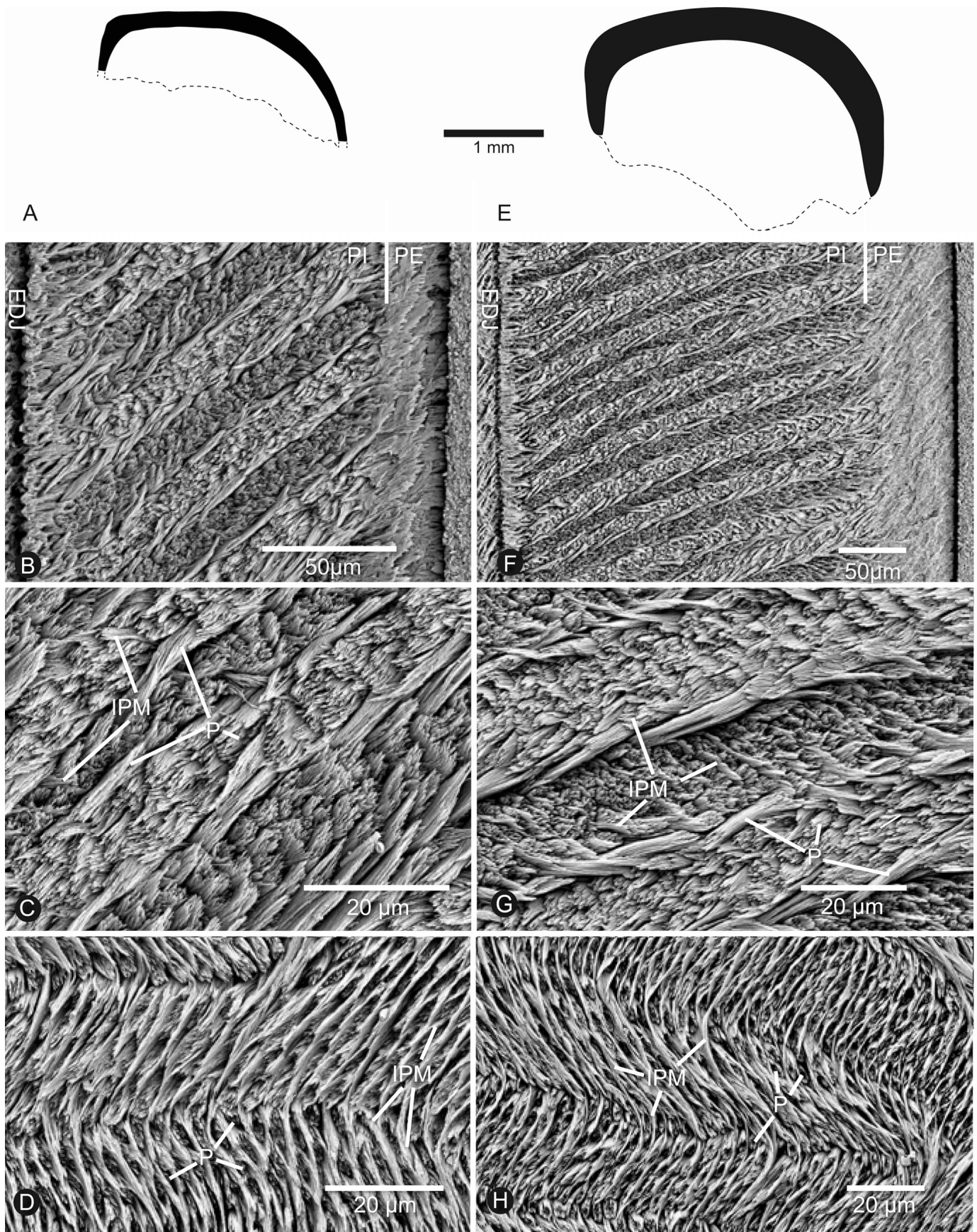
It has long been accepted that some portion of Puerto Rico must have been subaerial exposed during the late Paleogene and later (e.g., Meyerhoff, 1933; Monroe, 1980; Donnelly, 1992; Iturralde-Vinent and MacPhee, 1999); however, van Gestel et al. (1999) have recently argued on the basis of offshore seismic reflection profiles that the Puerto Rico/Virgin Islands block (PRVIB) was submerged between the mid Oligocene to early Pliocene. As detailed by MacPhee et al. (2003), this conclusion is significantly contradicted by available geological and fossil evidence, none of which is considered by van Gestel et al. (1999). In particular, evidence that the PRVIB has been emergent since the latest Eocene includes (1) an angular unconformity between the late Tertiary section and older rocks, indicating a long period of emergence and subsequent subaerial erosion; (2) absence of late Eocene marine rocks or reworked fossils in younger rocks, such as Lares Limestone, within the PRVIB; and (3) the occurrence of ?latest Eocene/early Oligocene conglomerates at the base of the San Sebastian Formation and coeval units. The marine limestones making up the Lares Limestone occur locally only, and overlay the San Sebastian Formation and interfinger with terrestrially derived sediments of the Mucarabones Sand (Monroe, 1980; Ward et al., 2002). In sum, there is no evidence that the interior of Puerto Rico was ever transgressed during the Neogene, although there was surely variation in its areal extent and relief.

SYSTEMATIC PALAEOONTOLOGY

MAMMALIA Linnaeus, 1758
 RODENTIA Bowdich, 1821
 HYSTRICOGNATHI Tullberg, 1899
 CAVIOMORPHA Wood, 1955
 Gen. et sp. indet. A
 (Fig. 2A–D)

TABLE 2. Strontium isotope age determination from *Kuphus incrassatus* tubes from the middle and top of the Lares Limestone section exposed on road PR-111.

Sample	Stratigraphic location within section	$^{87}\text{Sr}/^{86}\text{Sr}$	Absolute age (Ma)	Instrumental error (Ma)	Curve error (Ma)	Best age (Ma)
PR-111 GPS	Top	0.708167	24.70	0.14	0.22	24.70 ± 0.40
PR-111 T1	Top	0.708162	24.81	0.15	0.22	24.81 ± 0.22
PR-111 M2	Mid	0.708130	25.70	0.18	0.27	25.70 ± 0.27
PR-111 M8	Mid	0.708121	25.97	0.24	0.32	25.97 ± 0.32



Specimen—Left lower incisor (MA 316).

Locality—West bank of Río Guatemala, about 170 m southwest of junction between roads 446 and Camino Sector Lechuza, San Sebastián, Puerto Rico; collected by J.V.J., April 30, 2006 (Fig. 1B).

Formation and Age—San Sebastian Formation, early Oligocene, Rupelian (33.9–28.4 Ma). Other fossils found in the same horizon include shark and crocodylian teeth, dugongid sirenians, and pelomedusoid turtles.

Description—The enamel is double-layered with multiseriate Hunter-Schreger bands (HSB) in the inner enamel layer (portio interna, PI) and radial enamel in the outer enamel layer (portio externa, PE). HSB comprise three to five prisms and are 40° inclined apically. Prism cross-sections are oval in the PI and lancet-shaped (strongly laterally compressed) in the PE. Crystallites of interprismatic matrix (IPM) run at an acute angle to the prism long axes. In the PE and PI, IPM anastomoses regularly between prisms (best seen in cross-section; Fig. 2D). Transition zones, where prisms switch from one HSB to the next higher HSB, are present (visible in longitudinal section; Fig. 2B). The enamel thickness is 150 μm and the PE constitutes 25% of the total enamel thickness. In the PE, prisms are inclined 60° apically. A very thin prismless external layer (PLEX) is present.

Gen. et sp. indet. B
(Fig. 2E–H)

Specimen—Right lower incisor (MA 308).

Locality—West-facing roadcut along road PR-111, km. 27.2, San Sebastián, Puerto Rico (18°19'47"N, 66°56'50"W); collected by J.V.J. July 25, 2005 (Fig. 1B).

Formation and Age—Mudstone unit within the Lares Limestone, late Oligocene, Chattian (27.17 ± 0.73 to 24.70 ± 0.40 Ma). This unit has yielded invertebrates, fish, dugongid sirenian, and podocnemid turtle remains and coal fragments.

Description—Differs from the San Sebastian incisor in that the outer surface of the enamel is smooth and also thinner. As in MA 316, the enamel is double-layered with multiseriate HSB in the PI and radial enamel in the PE. HSB comprise three to five prisms and are 20° inclined apically. Prism cross-sections are oval in the PI and lancet-shaped in the PE. Crystallites of IPM run at a very acute angle (angle is actually slightly lower than in MA 316) to the prism long axes. In the PE and PI, IPM anastomoses regularly between prisms (best seen in cross-section; Fig. 2H). Transition zones, where prisms switch from one band to the next higher band are present (visible in longitudinal section; Fig. 2F). The enamel thickness is 330 μm and the PE constitutes 20% of the total enamel thickness. In the PE, prisms are 55° inclined apically. A very thin PLEX is present.

DISCUSSION

Comparison with other Caviomorphs and Relationships among Heptaxodontids

Among caviomorph rodents three subtypes of multiseriate HSB occur, differing mainly in the angle between IPM and prism long axes. In the most plesiomorphic subtype, IPM runs parallel or at a very low angle to prism long axes, whereas it runs at an acute angle (about 45°) or even a right angle (90°) in more derived subtypes. In the most derived subtype (90°), IPM forms plates between the prisms (so-called interrow sheets) and does not anas-

tomose. This subtype is confined to octodontoids (Martin, 1992, 1994). The incisor enamel microstructure of both Puerto Rican rodent incisors is characterized by multiseriate HSB with an IPM that runs parallel at a very low angle to prism long axes and is thus plesiomorphic. This subtype is observed in chinchilloids and cavioids (Martin, 1994). The presence of this kind of enamel microstructure rules out a relationship with octodontoids because the latter display, from an early stage in their evolutionary history, the more derived subtype of microstructure (e.g., *Platyptitamyx*; Martin, 1992, 1994, 2004).

As one of our reviewers noted, the fact that enamel microstructure is primitive could mean that some caviomorph lineage not otherwise known from the Antillean fossil record might be represented by the new discoveries from Puerto Rico (cf. 'unexpected' rodent finds in a continental context; Vucetich et al., 2005). This is an intriguing speculation, although the present material is too limited to support further analysis. At least as far as the existing West Indian caviomorph record is concerned, the Puerto Rican material shows most similarities to *Elasmodontomys obliquus* Anthony, 1916 (Puerto Rico), and *Amblyrhiza inundata* Cope, 1868 (Anguilla/St. Martin). Martin (1992:fig. 98–100) observed the plesiomorphic condition (i.e., multiseriate HSB with acute angular and anastomosing IPM) in the incisors of both of these taxa. These two species have long been included in Heptaxodontidae, a poorly characterized group that (depending on author) also includes species from Jamaica and Hispaniola as well as South America (for a recent review of the confused systematic history of this taxon, see MacPhee, 2009, 2011). The octodontoid family Echimyidae (including *Capromys* and its allies, formerly placed in their own family; see Woods et al., 2001; Leite and Patton, 2002; Galewski et al., 2005) constitute the other generally recognized group of West Indian caviomorphs. Echimyids present the most derived subtype of multiseriate HSB seen in caviomorphs, with rectangular, plate-like IPM (Martin, 1992:fig. 175).

The higher relationships of heptaxodontids have long been debated, as have its within-group organization. MacPhee (2011) considered the grouping to be paraphyletic on the basis of the morphology of the ear region. Several derived characters indicate that *Amblyrhiza* belongs in Chinchilloidea, close to Chinchillidae and Dinomyidae. By contrast, *Elasmodontomys* is basiscranially primitive and therefore difficult to place, although some authors have pointed to dental and other features as possible evidence of octodontoid affinities (e.g., Woods, 1982; but see Martin, 1992:138). The plesiomorphic state of its enamel microstructure rules out octodontoid affinities for *Elasmodontomys*, but does not establish in which other recognized grouping of caviomorphs this genus should be seated. Because the amount of useful evidence is slim, the best procedure at present is to regard Heptaxodontidae as an artificial assemblage, supported by primitive characters only. (*Clidomys* from Jamaica, also nominally a heptaxodontid, is also better placed elsewhere according to Pascual et al. [1990], whereas other taxa that have been placed in the group [i.e., *Quemisia* and *Xaymaca*] might actually not belong to it or are not known from enough material [MacPhee, 2011].)

Implications for Caviomorph Biogeography and Origin of the Greater Antillean Land Mammal Fauna

The recent description of middle Eocene (Barrancan SALMA) caviomorphs from the Peruvian Amazon (Fig. 1A) (Antoine

← FIGURE 2. Incisor cross-sections and incisor enamel microstructure of studied specimens. Left column: MA 316, right column: MA 308. **A** and **E**, incisor cross-sections with enamel cover (black); **B** and **F**, enamel longitudinal sections; **C** and **G**, detail of PI in enamel longitudinal sections; **D** and **H**, detail of PI in enamel cross-sections. In the longitudinal section, tip of the incisor is towards the top. **Abbreviations:** **EDJ**, enamel dentine junction; **IPM**, interprismatic matrix; **P**, prism; **PE**, portio externa; **PI**, portio interna.

et al., 2012) has pushed back their fossil record ~9 million years earlier than previously thought, a timing that is more consistent with molecular divergence estimates (Poux et al., 2006). The next oldest records are from the early Oligocene (Tinguirirican SALMA) deposits of Santa Rosa (Perú; Martin, 2004; Frailey and Campbell, 2004), Tinguiririca (Chile; Wyss et al., 1993, 1994; Flynn et al., 2003; Croft et al., 2008; Bertrand et al., 2012), and Gran Barranca (Argentina; Vucetich et al., 2010) (Fig. 1A). The rodents from Puerto Rico are contemporaneous with these and with late Oligocene (Deseadan SALMA) deposits of Salla-Luribay (Bolivia; Hoffstetter and Lavocat, 1970; Lavocat, 1976; Patterson and Wood, 1982), Taubaté (Brazil; Vucetich and Ribeiro, 2003), and Moquegua (Perú; Shockey et al., 2009) among others (Fig. 1A). The Puerto Rican rodents are thus the oldest known occurrence of caviomorphs north of the Equator as well the oldest outside South America (Fig. 1A); evidently, dispersal of early caviomorphs occurred both south (Antoine et al., 2012) and north from a very early period.

Arrival of these rodents to the Greater Antilles would have been facilitated by the presence of a land connection with northern South America (whether or not over-water transport was important as well for some groups; Hedges, 2006). One of the contending arguments for the origin of the Greater Antillean land mammal fauna, the GAARlandia hypothesis, calls for the presence of such a connection (Fig. 1C; MacPhee and Iturralde-Vinent, 1995; Iturralde-Vinent and MacPhee, 1999). This landspan (i.e., a dead-end connector between a continent and one or more oceanic islands) is estimated to have been briefly subaerial during the late Eocene–early Oligocene. Although numerous lines of geological evidence favor the existence of such a connector (Iturralde-Vinent and MacPhee, 1999), deep-sea drilling conducted at appropriate localities along its submerged spine (present-day Aves Rise) is required to establish whether subaerial conditions once existed there, and for how long (cf. Ali, 2012). In addition to the sloth evidence from Yauco already mentioned, molecular estimates of divergence between the endemic Greater Antillean toad *Peltophrone* spp. and its sister taxon point to a late Eocene–early Oligocene split (Alonso et al., 2012), which is consistent with the paleogeographical model proposed by the GAARlandia hypothesis. A landspan could have also facilitated dispersal of gryposuchine gavialoids from the Caribbean (Velez-Juarbe et al., 2007) to the South American landmass. The finds reported here underline the importance of further field work, on Puerto Rico and elsewhere in the Caribbean, to unearth additional clues relevant to interpreting the origins and antiquity of the Greater Antillean land mammal fauna in general, and caviomorph biogeography and evolution in particular.

ACKNOWLEDGMENTS

J.V.J. was partially supported by the WBHR-LSAMP Bridge to the Doctorate Program at Howard University and a predoctoral fellowship from the National Museum of Natural History, Smithsonian Institution. D. Kranz provided the artwork of Figure 2 and G. Oleschinski (both Universität Bonn) assisted with SEM. This work benefited from the comments of three anonymous reviewers. This is contribution 15 to the series “Origins of the Antillean Land Mammal Fauna.”

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Submitted December 10, 2012; revisions received March 11, 2013; accepted March 18, 2013.

Handling editor: Guillermo Rougier.