Early Oligocene chinchilloid caviomorphs from Puerto Rico and the initial rodent colonization of the West Indies

Laurent Marivaux, Jorge Vélez-Juarbe, Gilles Merzeraud, Francois Pujos, Lázaro W Viñola López, Myriam Boivin, Hernán Santos-Mercado, Eduardo Cruz, Alexandra Grajales, James Padilla, et al.

▶ To cite this version:

Laurent Marivaux, Jorge Vélez-Juarbe, Gilles Merzeraud, Francois Pujos, Lázaro W Viñola López, et al.. Early Oligocene chinchilloid caviomorphs from Puerto Rico and the initial rodent colonization of the West Indies. Proceedings of the Royal Society B: Biological Sciences, 2020, 287, pp.20192806. 10.1098/rspb.2019.2806 . hal-02477415

HAL Id: hal-02477415
https://hal.umontpellier.fr/hal-02477415

Submitted on 17 Jun 2020

Early Oligocene chinchilloid caviomorphs from Puerto Rico and the initial rodent colonisation of the West Indies

Laurent Marivaux[1], Jorge Vélez-Juarbe[2], Gilles Merzeraud[3], François Pujos[4], Lázaro W. Viñola López[5], Myriam Boivin[6], Hernán Santos-Mercado[7], Eduardo J. Cruz[7], Alexandra Grajales[7], James Padilla[7], Kevin I. Vélez-Rosado[8], Mélody Philippon[9], Jean-Len Léticée[9], Philippe Münch[3] and Pierre-Olivier Antoine[1]

[1]Laboratoire de Paléontologie, Institut des Sciences de l'Évolution de Montpellier (ISE-M, UMR 5554, CNRS/UM/IRD/EPHE), c.c. 064, Université de Montpellier (UM), Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France

[2]Department of Mammalogy, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA

[3]Géosciences Montpellier (UMR 5243, CNRS/UM/Université des Antilles), c.c. 060, Université de Montpellier (UM), Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France

[4]Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT–CONICET–Mendoza, Avda. Ruiz Leal s/n, Parque Gral. San Martín, 5500 Mendoza, Argentina

[5]Florida Museum of Natural History, University of Florida, Gainesville, FL 32611-7800, USA

[6]Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy, CONICET, IdGyM, Av. Bolivia 1661, San Salvador de Jujuy 4600, Jujuy, Argentina

[7]Department of Geology, University of Puerto Rico, Mayagüez Campus, PO Box 9017, Mayagüez, Puerto Rico 00681, USA

[8]Museum of Paleontology and Department of Earth and Environmental Sciences, University of Michigan, 1109 Geddes Ave., Ann Arbor, MI 48109, USA

[9]Géosciences Montpellier (UMR 5243, Université des Antilles/CNRS/UM), Université des Antilles, Campus de Fouillole, F-97159 Pointe-à-Pitre Cedex, Guadeloupe, France (French West Indies)

*** Corresponding author:**
Laurent Marivaux
Laboratoire de Paléontologie, c.c. 064
Institut des Sciences de l'Évolution de Montpellier
(ISE-M, UMR 5554 CNRS/UM/IRD/EPHE)
Université de Montpellier
Place Eugène Bataillon
F-34095 MONTPELLIER Cedex 05
Phone: +33 467 144 911
E-Mail: Laurent.Marivaux@UMontpellier.fr
ORCID identifier: https://orcid.org/0000-0002-2882-0874

Abstract

By their past and present diversity, rodents are among the richest components of Caribbean land mammals. Many of these became extinct recently. Causes of their extirpation, their phylogenetic affinities, the timing of their arrival in the West Indies, and their biogeographical history are all ongoing debated issues. Here we report the discovery of dental remains from lower Oligocene deposits (~29.5 Ma) of Puerto Rico. Their morphology attests to the presence of two distinct species of chinchilloid caviomorphs, closely related to dinomyids in a phylogenetic analysis, and thus of undisputable South American origin. These fossils represent the earliest Caribbean rodents known thus far. They could extend back to 30 Ma the lineages of some recently-extinct Caribbean giant rodents (*Elasmodontomys* and *Amblyrhiza*), which are also retrieved here as chinchilloids. This new find has substantial biogeographical implications since it demonstrates an early dispersal of land mammals from South America to the West Indies, perhaps via the emergence of the Aves Ridge that occurred *ca.* 35–33 Ma (GAARlandia hypothesis). Considering both this new palaeontological evidence and recent molecular divergence estimates, the natural colonisation of the West Indies by rodents likely occurred through multiple and time-staggered dispersal events (chinchilloids, then echimyid octodontoids [spiny rats/hutias], caviids, and lastly oryzomyin muroids [rice rats]).

Keywords: Caribbean, Rodentia, Chinchilloidea, Palaeogene, Palaeobiogeography, GAARlandia

1. Introduction

Due to their geological history and tropical insularity, West Indies display a rich and highly endemic diversity of vertebrates, resulting from a series of adaptive radiations over time [1,2], associated with a complex historical biogeography among lineages (dispersal *vs* vicariance [3-7]). Caribbean rodents are one of the most speciose and remarkable land mammal components of the West Indies. They comprise diverse members of a muroid tribe (Oryzomyini, Sigmodontinae [8]), several representatives of caviomorph hystricognaths (Caviomorpha, Hystricognathi), and other rodent groups recently introduced by humans [9,10]. Among endemic hystricognaths are the extinct and extant hutias (Capromyinae) and the extinct heteropsomyines (Heteropsomyinae), both being echimyid octodontoids (spiny rats [5,11-15]), and lastly the extinct "giant hutias" ("Heptaxodontidae"). The content and high-level systematics of the "Heptaxodontidae" have been widely disputed over the last decades (chinchilloids *vs* cavioids *vs* octodontoids; for a historical review see [16], pp. 4-6). When and how the ancestors of these distinctive groups of rodents and other land organisms dispersed into the Caribbean islands are widely-debated issues [5,6,11,17-28]. The rodent fossil record in the West Indies was long restricted to Pleistocene–Holocene and, to a lesser extent, Miocene epochs (for a review see [10]). However, two rodent incisors distinct in size were recently unearthed in shallow marine Oligocene deposits from two remote localities of northwestern Puerto Rico [29]. These findings evidence a much older evolutionary history of rodents on the Caribbean islands, at least in the Greater Antilles [5,7,10,19]. Based on their enamel microstructure, both specimens were assigned to non-octodontoid caviomorphs, i.e. cavioids, chinchilloids, or erethizontoids [29-32].

Rodent fossils described here derive from the LACM locality 8060, documenting the lower part of the San Sebastian Formation (early–early late Oligocene) in the Río Guatemala section, northwestern Puerto Rico (figure 1). ^{87}Sr/^{86}Sr mean ages-dates calculated on low-Mg calcite *Kuphus incrassatus* shells allow for bracketing the age of LACM Loc. 8060 between 29.78 and 29.17 Ma (late Rupelian [33]). LACM Loc. 8060 is the type locality of the halitheriine dugongid sirenian, *Priscosiren atlantica* [34], in the ribcage of which the oldest rodent incisor was previously unearthed by one of us (J.V.-J. [29]). During a joint field campaign in February 2019 (GAARAnti project), our team excavated the LACM Loc. 8060 fossil-bearing layer and performed wet-screening operations of the concerned sediments, which allowed us for recovering three rodent molariform teeth, documenting at least two distinct species. Two specimens (a complete molar and a half molar), compatible in size with the lower incisor formerly discovered in the same locus, permit to describe a new small-bodied chinchilloid caviomorph (*Borikenomys praecursor* gen. et sp. nov.). Although fragmentary, the third dental specimen testifies to the presence of a distinctively larger species, also referred to as a chinchilloid. Here we describe these new fossils documenting the earliest Caribbean caviomorph rodents known thus far. We discuss their affinities with potential South American relatives and consider palaeobiogeographical inferences, particularly with regard to the timing and pattern of West Indies colonisation(s) by rodents. From a macroevolutionary perspective, we also address the potential ties of these Oligocene Caribbean chinchilloids with recently-extinct large rodent species ("giant hutias") from the

Anguilla bank (*Amblyrhiza* Cope, 1886; middle–late Pleistocene of Anguilla–St-Martin–St-Bartholomew islands) and Puerto Rico (*Elasmodontomys* Anthony, 1916; Pleistocene–Holocene), for which a chinchilloid status has long and iteratively been advocated.

2. Results

(a) Systematic Palaeontology

The fossil specimens described in this paper are permanently stored in the paleontological collections of the Natural History Museum of Los Angeles County (LACM), Los Angeles, USA.

Class Mammalia Linnaeus, 1758; Order Rodentia Bowdich, 1821; Infraorder Hystricognathi Tullberg, 1899; Parvorder Caviomorpha Wood, 1955; Superfamily Chinchilloidea Bennett, 1833; Family ?Dinomyidae Alston, 1876

***Borikenomys praecursor* gen. et sp. nov.**

Etymology. Generic name refers to "*Borikén*", the Native Amerindian *Taíno* name of the Puerto Rico Island (*Borinquén*) in the Caribbean, with the Greek suffix *μυς* (mys), mouse. Epithet in reference to the pioneer status of this rodent in the Caribbean islands.

Holotype. LACM 162447, right lower m3 (figure 2*a-f*).

Hypodigm. LACM 162446 (figure 2*g-j*), fragment of a left lower molar (mesiolingual part); MA 316, left lower incisor [29].

Horizon locality. Late early Oligocene LACM Loc. 8060 fossil site in the Río Guatemala, San Sebastian Formation, San Sebastián, Puerto Rico [29,33-35].

Diagnosis (based on the holotype). Small-sized chinchilloid with high-crowned and rooted teeth, likely taeniodont to non-taeniodont with wear. Cuspids and stylids not visible, being subsumed within thick lophids forming laminar cristids that are inclined, oblique, parallel, nearly contiguous (very narrow inter-laminar spaces – flexids/fossettids – filled with cement), and characterised by a marked heterogeneous thickness of the enamel layer. Tetralaminar pattern including a metalophulid I complex, a second cristid formed by a neomesolophid possibly associated with a branch of the posterior arm of the protoconid, a hypolophid in continuity with the ectolophid, and a posterolophid.

Description. See electronic supplementary material.

Gen et sp. indet.

Specimen. LACM 162448 (figure 2*k-n*), fragment of an upper (mesial laminae) or of a lower cheek tooth (distal laminae).

Horizon locality. Late early Oligocene LACM Loc. 8060 fossil site in the Río Guatemala, San Sebastian Formation, San Sebastián, Puerto Rico [30,34-36].

Description. See electronic supplementary material.

(b) Comparisons

Although worn, damaged and/or fragmentary, these three dental specimens (figure 2) reveal a suite of anatomical details unusual among rodents in general, but otherwise found only in some advanced chinchilloid caviomorphs from South America. This is particularly shown in the development of a multi-crested occlusal pattern characterised by large and oblique cristids, without apparent cuspids (subsumed within cristids), thereby forming laminae almost in contact to each other but remaining separate by very narrow and deep furrow-like flexids or fossettids, filled with cement. Among chinchilloids, regardless of the differences of crown elevation among taxa (protohypsodonty *vs* euhypsodonty), this laminar dental pattern with adjacent, almost contiguous laminae (elasmodonty) is characteristic of *i)* dinomyids (i.e., extant *Dinomys* plus extinct Neogene taxa: *Potamarchus*, *Pseudopotamarchus*, *Isostylomys*, *Drytomomys*, *Tetrastylus*, *Gyriabrus*, *Eumegamys*, etc. [36-39]; and to some extent "*Scleromys*" [40]) and *ii)* chinchillids (extant chinchillines [*Chinchilla* and *Lagidium*] and extinct and extant lagostomines [*Lagostomus* and fossil kin] [41]). In contrast, this pattern differs from the condition observed in extinct Neogene neoepiblemid chinchilloids (e.g., *Neoepiblema*, *Phoberomys*, etc. [42-44]), in which the laminae remain well separated due to the presence of wide flexids (wide inter-laminar space, filled with cement). Another key character observed on the three Puerto Rican specimens is the enamel layer configuration of each lamina, which displays a marked heterogeneous thickness (thin leading edge and thick trailing edge; figure 2*b, i, n*). In chinchilloids, this peculiar dental trait is characteristic of *i)* all stem and crown chinchillids and *ii)* hypsodont dinomyids [45]. Some advanced basal chinchilloids (stem chinchillids?) such as the Oligocene–early Miocene *Eoviscaccia* and the early Miocene *Garridomys,* also show such a pattern [45-46]. In lower-crowned alleged dinomyids, such as *Scleromys*, this trait is only insinuated [45], whereas it is absent in basal chinchilloids (e.g., Oligocene *Incamys*, *Eoincamys* and *Chambiramys*, and Miocene

Microscleromys [40,47-50]) and neoepiblemids [42-44]. This peculiar dental trait is also retrieved in some unrelated rodent groups having convergently developed high-crowned teeth with slightly inclined, arcuate and compressed crests and cristids (e.g., in highly derived archaeomyin theridomorphs, or in some taxa among rhizomyine, tachyoryctine, nesomyine and otomyine muroids; for illustrations, see [51]). Nevertheless, their dental Bauplan is distinct from what is observed in the Río Guatemala teeth, which discards any assignment to such rodent lineages. As for high-crowned elasmodontous chinchillids [62] and dinomyids, the heterogeneous enamel layer in these distant rodents likely results from analogous physical developmental constraints linked to hypsodonty and inclined laminar-like structure achievements.

Interestingly, on the LACM 162448 dental fragment (including a complete lamina), the thin leading edge of the enamel layer is slightly undulating and includes punctually some irregularities (figure 2*k-m*). These small undulations could be homolog, in a much lesser extent, to the crenulation observed on the thin leading edges of laminae of upper and lower teeth of some Neotropical potamarchine dinomyids (such as in *Potamarchus* [38]). The two teeth documenting *Borikenomys* (LACM 162446 and LACM 162447) do not display this kind of irregularities on the thin enamel layers corresponding to the leading edges of the laminae. For the latter taxon, the best-preserved tooth (LACM 162447; figure 2*a-f*) is tetralophodont (= tetralaminar), including a posterolophid, a hypolophid (+ ectolophid), a neomesolophid (+ possibly a branch of the posterior arm of the protoconid [Papd]), and a metalophulid I complex (figure 3*a-b*). A tetralophodont pattern including a neomesolophid or its variants (or a combination of other structures) as a second cristid is widespread among caviomorphs [53]. In dinomyid chinchilloids, in addition to the unusual marked heterogeneous thickness of the enamel layer of the laminae (to the exception of *Scleromys*), lower molars display a well-defined laminar neomesolophid (combined or not with a Papd [44]). However, several dinomyids (such as *Potamarchus*, *Gyriabrus*, *Isostylomys*, and *Eumegamys*) can also develop a pentalophodont (= pentalaminar) pattern by the addition of a neolophid between the neomesolophid and the metalophulid I complex. In lacking this neolophid, *Borikenomys* displays a tetralaminar pattern consistent with that observed on lower molars (at least m3) characterizing certain other dinomyids, such as "*Scleromys*", *Drytomomys* and *Tetrastylus* [37,40,54]. However, unlike in the three latter genera, the neomesolophid in *Borikenomys* is not connected to the median or buccal part of the metalophulid I, but to the protoconid or possibly to a short posterior arm of the protoconid (figure 3*a-b*). A pseudo-tetralophodont pattern is also observed in several basal chinchilloids (such as *Eoincamys*, *Incamys*, *Chambiramys*, and *Microscleromys* [50]) and in more advanced basal chinchilloids (*Garridomys* and possibly *Eoviscaccia* [45,46,50]), which show a neomesolophid variably developed in length and variably connected to the metalophulid I or remaining buccally free. Modern chinchillids exhibit a trilaminar pattern (*Chinchilla* and *Lagidium*; electronic supplementary material, figure S1*f*) or even a bilaminar pattern (*Lagostomus*) on lower molars, which would be primarily due to the absence of the laminar neomesolophid (non-development, loss or fusion with the metalophulid I; in *Chinchilla* and *Lagidium* [44]), and to the loss and/or fusion of some other cristids (in *Lagostomus* [45]). The same seems to be true for neoepiblemids (*Phoberomys* and *Neoepiblema vs Perimys* and *Doryperimys* [42-44,55]), which show a simplified trilaminar to bilaminar pattern on lower molars (often linked to wear during ontogenetic growth), whereas their upper molars, notably the M3, may display in some taxa a much more complex pattern, secondarily pluri-laminated [56,57].

Borikenomys differs from most basal chinchilloids (except *Chambiramys*, which has pseudo-taeniodont or taeniodont lower molars; see [49]) and from all dinomyids, chinchillids and neoepiblemids, in displaying an apparent non-taeniodont pattern (hypofossettid not confluent with the metafossettid). This pattern results from the presence of an anterior arm of the hypoconid-like cristid (figure 3*a-b*). However, this dental feature could be linked to the advanced stage of wear of the specimen available (LACM 162447), as observed in heavily worn lower molars of *Garridomys* or "*Scleromys*" [40,45], which have taeniodont pristine teeth (i.e., without arm).

3. Discussion

The fossil material at LACM Loc. 8060 documents two distinct rodent taxa from the early Oligocene of Puerto Rico. These dental remains display a suite of anatomical details entirely consistent with caviomorph affinities. The laminar pattern (as specifically described above) and the heterogeneous thickness of the lamina enamel layer clearly set these two species apart from octodontoids, cavioids, erethizontoids and stem caviomorphs *sensu* Boivin et al. [50], but in turn underscore their unequivocal chinchilloid affinities. Such an assignment is further consistent with the enamel microstructure condition depicted on the isolated lower incisor (MA 316) previously found in the same locality (LACM Loc. 8060). This incisor, compatible in size with the two *Borikenomys* cheek teeth, is here tentatively assigned to the same taxon. Its enamel crystallite arrangement (figure 3*d-e*) typifies a subtype 2 of multiserial Hunter-Schreger bands (HSBs) [29]. Among caviomorph hystricognaths, such a microstructural pattern is evolutionarily intermediary and primarily found in several extinct and extant chinchilloids (notably dinomyids), but also in some extinct and extant cavioids and erethizontoids (other members of the latter superfamilies also have primitive subtype 1 or transitional subtype 1-2 of multiserial HSBs [30,31]). This enamel condition differs substantially from that found in extinct and extant octodontoids analysed, which display more derived and crack-resistant enamel crystallite arrangements from an early stage in their evolutionary history (i.e., subtype 2-3 and chiefly subtype 3 of multiserial HSBs [30-32,58]).

(a) Macroevolutionary implications

Based on our preferred dental homology hypotheses (figure 3*a-c*; electronic supplementary material, figures S1 and S2), a cladistic assessment of the dental evidence (513 characters scored in 110 rodent taxa; see electronic supplementary material) unambiguously supports the placement of *Borikenomys* within the Chinchilloidea clade among caviomorphs, close to the Dinomyidae (figure 4). It also allows for supporting the chinchilloid status of the larger unnamed tooth from LACM Loc. 8060 and of the large Pleistocene caviomorph rodent species (“giant hutias” or “heptaxodontids”) from Puerto Rico (*Elasmodontomys* Anthony, 1916) and from the Anguilla Bank (*Amblyrhiza* Cope, 1868) in the West Indies: *Amblyrhiza* and *Elasmodontomys* are retrieved as an advanced stem chinchilloid and a dinomyid, respectively (figure 4). Interestingly, the enamel microstructure of the MA 316 incisor from LACM Loc. 8060 (as well as that of the MA 308 incisor found in the early late Oligocene Lares Limestone of Puerto Rico [29]) is similar with that characterising the incisors of *Elasmodontomys* and *Amblyrhiza* (i.e., subtype 2 of multiserial HSBs [30]). Because of their “multi-lamellar” cheek tooth organisation, the systematics of these two Caribbean taxa (as well as that of *Quemisia* from Hispaniola, *Clidomys* and *Xaymaca* from Jamaica, and *Tainotherium* from Puerto Rico, all from Pleistocene–Holocene contexts [59-63]) has long been the subject of controversy (chinchilloids *vs* cavioids *vs* octodontoids [16]). Based on characters of the ear region anatomy, MacPhee [16] underlined that *Amblyrhiza* shares several derived features with chinchilloids (close to chinchillids and dinomyids), whereas *Elasmodontomys* displays a primitive basicranial morphology, which does not allow for a precise supra-familial assignment (? Octodontoidea). As highlighted by Martin in Vélez-Juarbe et al. [29], the enamel microstructure of the incisors of *Amblyrhiza* and *Elasmodontomys* also precludes octodontoid affinities, notably with capromyine echimyids (hutias), the most abundant group of West Indian caviomorphs (at least in the Greater

Antilles, excluding Puerto Rico). Following the criteria exposed in Boivin and Marivaux [53], a detailed comparative analysis of dental morphology among “giant hutias” and other caviomorphs can be undertaken. Considering here the lower dentition only (as part of our comparative study with the m3 of *Borikenomys*), *Amblyrhiza* and *Elasmodontomys* have taeniodont lower teeth, exhibiting a multi-laminar pattern with inclined, oblique, parallel, arcuate and nearly contiguous laminar cristids, a marked heterogeneous thickness of the lamina enamel layer (thin leading edges and thick trailing edges), and very narrow inter-laminar spaces (flexids) filled with cement (electronic supplementary material, figure S1*d-e*). Their dental pattern is unambiguously of chinchilloid affinities, and highly divergent from that of octodontoids (notably Caribbean capromyine and heteropsomyine echimyids), cavioids, and erethizontoids among caviomorphs. As for *Borikenomys*, topological identification of the laminar cristids, cuspid regions and flexids (figure 3*a-c*), can be proposed for *Elasmodontomys* and *Amblyrhiza* on the basis of the cristid orientation, position and connections. Lower teeth of *Elasmodontomys* are tetralaminar (electronic supplementary material, figure S1*d*), including a posterolophid, a hypolophid in continuity with an ectolophid, a neomesolophid, and a metalophulid I complex. The neomesolophid would be connected to the buccal extremity of the metalophulid I. Lower teeth of *Amblyrhiza* are trilaminar (electronic supplementary material, figure S1*e*), differing from those of *Elasmodontomys* in the loss of the neomesolophid or fusion of that laminar cristid with the metalophulid I complex. The lower dental pattern of *Amblyrhiza* is quite reminiscent of that of modern South American chinchillids *Chinchilla* and *Lagidium* (electronic supplementary material, figure S1*f*), whereas that of *Elasmodontomys* is similarly recalling that of the extinct dinomyid *Tetrastylus* and, to some extent, of modern *Dinomys*, which may explain their inferred close relationships (figure 4).

The dental pattern of *Borikenomys*, although primitive in some aspects (e.g., mesodonty or protohypsodonty, presence of an anterior arm of the hypoconid and of a well-defined neomesolophid, not connected to the metalophulid I but to the protoconid or its posterior arm), fully matches that of the large-bodied Pleistocene *Elasmodontomys* and *Amblyrhiza*. In contrast, it clearly differs from that of Caribbean echimyid octodontoids, both extinct and extant (i.e., *Zazamys*, *Puertoricomys*, *Heteropsomys*, *Boromys*, *Brotomys*, *Isolobodon*, *Hexolobodon*, *Rhizoplagiodontia*, *Macrocapromys*, and modern capromyines such as *Plagiodontia*, *Capromys*, *Mesocapromys*, *Geocapromys*, and *Mysateles* [5,11,64-67]). The same is true for the fragment of tooth (LACM 162448; figure 2*k-n*) also recovered at LACM Loc. 8060, which documents a larger chinchilloid species, the dental structure of which is even more strikingly similar with that of *Amblyrhiza* and *Elasmodontomys* (electronic supplementary material, figures S1*d-e* and S2*a-d*). Given the unequivocal chinchilloid dental affinities of these Oligocene and Pleistocene taxa, the question remains as to whether *Borikenomys* and the associated larger species from LACM Loc. 8060 could have a potential link with these two emblematic "giant hutias" from the West Indies in the total absence of Caribbean Neogene fossil record for that group. What and where is the origin of *Amblyrhiza*, *Elasmodontomys* and their hypothetical kin on other islands? As chinchilloids, should we consider *Borikenomys* and the associated larger species recorded in lower Oligocene deposits of Puerto Rico as tightly related to the *Elasmodontomys* and *Amblyrhiza* lineages? Shedding light on this critical issue would require additional specimens documenting these earliest Caribbean chinchilloid rodents, hypothetical Neogene remains, and enhancing the morphological evidence available for *Amblyrhiza* and *Elasmodontomys*, assembled in a more comprehensive morpho-anatomical and taxonomical phylogenetic analysis.

(b) Palaeobiogeographic implications

Regardless of the supra-familial assignment of *Borikenomys* and the associated larger species recorded at the Río Guatemala locality, their presence in lower Oligocene deposits of Puerto Rico testifies to a Palaeogene dispersal of caviomorph rodents from South America to the West Indies. However, it cannot be asserted whether it was widely or only shortly before their appearance in the Puerto Rican fossil record [29]. Given the presence of two distinct chinchilloid species, we wonder if this record results from an *in-situ* radiation of a chinchilloid branch after its arrival on the islands, a single dispersal event involving two or more associated chinchilloid species, or the result of two distinct chinchilloid dispersals from South America to the islands. A northern South America land connection with the West Indies island complex, or an over-water transport between these lands might have been at the origin of such chinchilloid rodent dispersal(-s) from northern South America to the West Indies. This rodent example would support the GAARlandia hypothesis advocating that such a land connection occurred around the Eocene-Oligocene transition (EOT [11,18,19]). This subaerial connection between South America and the West Indies complex, corresponding to the emerged Aves Ridge, is also advocated for explaining the origin of other terrestrial organisms on the Caribbean islands [7,22,24-28] or the dispersal from the islands to main land [35]. Moreover, once phylogenetically constrained (figure 4), the South American fossil record is compatible with chinchilloid dispersal(s) from northern areas of South America around the

EOT, i.e. during GAARlandia times (35–33 Ma). The only caveat consists in considering a ghost lineage among Dinomyidae (figure 4).

The dispersals of chinchilloids and echimyid octodontoids toward the West Indies were probably fully disconnected events: the first dispersal(s) likely occurred by the EOT whereas the event(s) at the origin of the hutias and other spiny rats on the islands (capromyines and heteropsomyines, respectively) were most probably Miocene in age. Indeed, recent gene-based phylogenies of extant Neotropical echimyids (including Caribbean capromyines and main land echimyines and euryzygomatomyines) support an early–middle Miocene divergence of hutias from their sister taxon *Carterodon*, thereby suggesting a Neogene West Indian colonisation by octodontoids [12,14]. The presence of capromyine echimyids in the Greater Antilles is besides attested in lower Miocene deposits of Cuba with *Zazamys* [5,11]. However, the mode (over-water transport or land connection so far unidentified) and pathway of this expected Miocene dispersal remain unknown.

The EOT is characterised by a global glaciation event, which has deeply reshaped landscapes and biodiversity at the world scale [68-69]. At tropical-equatorial latitudes, this global cooling mostly provoked sustainable precipitation drops and increased seasonality. In the Neotropics, the aridification of climate resulted in the decrease of plant morpho-diversity and in the opening of terrestrial environments, hitherto dominated by evergreen rainforest (70). Unquestionably, these changes have drastically affected small mammal guilds and promoted geographical range shifts, eventually leading to extinction, but also favouring dispersals for some “pre-adapted” species [50,71]. Among caviomorph rodents, extant chinchilloids (and cavioids) span a wide range of terrestrial habitats. Chinchilloids are well adapted to dry and open environments, which can also be hypothesised in some way for their extinct kin. In other words, early chinchilloids (or cavioids) from northern South America would have dispersed through open land corridors more easily than obligate forest- or tree-dwellers such as co-occurring erethizontoids or octodontoids [72]. This differential dispersive capacity would likely explain the sole presence of chinchilloids in lower Oligocene deposits of Puerto Rico. Earlier records of terrestrial vertebrates in the Greater Antilles come from the Eocene of Jamaica, but those represent lineages of North American affinities which left no descendants in the region, owing in great part to the unique geologic history of that island [6,73]. Therefore, the fossils from Río Guatemala and other early Oligocene localities in Puerto Rico [11] represent the earliest direct evidence of colonisation of the Greater Antilles by South American lineages of terrestrial vertebrates that are either currently present (e.g., coquí frogs [J.V.-J., work in progress]) or became extinct during the Pleistocene–Holocene.

4. Summary and conclusions

Palaeontological dental evidence, gathering occlusal morphology and enamel microstructure, attest to the presence of two distinct species of chinchilloid caviomorph rodents in lower Oligocene deposits of Puerto Rico. *Borikenomys* and the associated larger species recorded are closely related to South American dinomyid chinchilloids. The Palaeogene fossil record of chinchilloids at low latitudes in South America remains so far poorly documented, which prevents any identification of coeval mainland close relatives of these Puerto Rican chinchilloids. Nevertheless, this discovery testifies to the presence of chinchilloids in the West Indies during the Palaeogene, with an arrival on the islands around the Eocene–Oligocene transition, via the GAARlandia land bridge or by an over-water dispersal (rafting). In addition, given the estimated age of the origin of the Caribbean hutias deriving from molecular analyses (capromyine octodontoids: early–middle Miocene), the natural colonisation of the West Indies by rodents likely occurred through multiple and time-staggered dispersal events (chinchilloids then subsequently echimyid octodontoids (+ caviid, but in southern lesser Antilles only [74]), and lastly oryzomyin muroids).

Finally, from a macroevolutionary perspective, the current discovery raises the critical question of a possible link between these Oligocene Puerto Rican chinchilloids and some of the Pleistocene–Holocene West Indian “giant hutias” (*Elasmodontomys* and *Amblyrhiza*), for which a chinchilloid status is also supported here. Our phylogenetic results, while emphasising proximity, do not formally establish such a link. However, these results are preliminary inasmuch as the proposed position of *Borikenomys* is likely to evolve with additional morphological data. If this phylogenetic link is confirmed, these endemic giant Caribbean rodents could have a remarkable antiquity on the islands (as for Caribbean sloths [27,28] and coquí frogs [J.V.-J., work in progress]), and thus could represent a unique case of long-lived insular rodent lineage. Alternatively, these Oligocene Puerto Rican chinchilloids could have become extinct without descendants. Accordingly, the fore comers of Pleistocene “giant chinchilloid hutias” would have dispersed much more recently (perhaps as part of the dispersal wave that was at the origin of the Caribbean echimyid octodontoids). In any event, the pre-Pleistocene evolutionary history of these “giant hutias” remains so far entirely undocumented on the islands. These emblematic large rodents were only recently extirpated from the West Indies, in which they possibly evolved during more than 30 million years in these tropical islands. An improved palaeontological documentation of their evolutionary history would be therefore of critical importance for a better understanding of the island evolution of mammals over a long period of time.

Authors' contributions. P.-O.A., L.M., J.V.-J. and P.M. designed research; L.M., J.V.-J., G.M., F.P., L.W.V.L., H.S.-M., E.J.C., A.G., J.P., K.I.V.-R., M.P., J.-L.L., P.M. and P.-O.A. performed research and collected field data; M.B. and L.M. analysed data and performed phylogenetic analyses; L.M. and P.-O.A. wrote the paper; M.B., L.W.V.L., F.P., P.M. and J.V.-J. critically revised the manuscript.

Competing interests. We declare we have no competing interests.

Funding. This research was supported by the French "Agence Nationale de la Recherche" (ANR) in the framework of the GAARAnti program (ANR-17-CE31-0009) and of the LabEx CEBA (ANR-10-LABX-0025-01).

Acknowledgements. We are indebted to Anne-Lise Charruault and Renaud Lebrun (ISE-M) for µ-CT scan acquisitions and treatments, and to Thomas Martin (Universität Bonn, Germany) for sharing enamel microstructure SEM photographs of Puerto Rican rodent incisors. We thank Ross D. E. MacPhee and Lorrain J. Meeker (AMNH, New York, USA), Alexandra van der Geer (Naturalis, Leiden, Netherlands) and her brother Bartholomeus for providing us photographs of *Elasmodontomys* specimens and of *Amblyrhiza* specimens from the AMNH and the Leiden Naturalis collections (courtesy of John de Vos and Reinier van Zelst). Many thanks to Odile and Gilles Maincent for their help during the field mission at St-Bartholomew, in search of new *Amblyrhiza* fossils. We are grateful to Céline Robinet (Museo de La Plata, Argentina) for her well-appreciated discussion regarding the ecology of living chinchilloids, to Pierre-Henri Fabre, Fabien Condamine, Frédéric Delsuc and François Catzeflis (ISE-M) for discussions regarding Caribbean mammals. Finally, we thank the Montpellier RIO Imaging (MRI) and the LabEx CeMEB for access to the µCT-scanning station EasyTom 150 / Rx Solutions (ISE-M, Montpellier, France). This is ISE-M publication 2020-013 Sud.

References

1. Ricklefs R, Bermingham E. 2008 The West Indies as a laboratory of biogeography and evolution. *Phil. Trans. Roy. Soc. B* **363**, 2393-2413. (doi:10.1098/rstb.2007.2068)

2. Losos J, Ricklefs R. 2009 Adaptation and diversification on islands. *Nature* **457**, 830-836. (doi:10.1038/nature07893)
3. Hedges SB. 1996 Historical biogeography of West Indian vertebrates. *Annu. Rev. Ecol. Syst.* **27**, 163-196.
4. Hedges SB. 2001 Caribbean biogeography: an outline. In *Biogeography of the West Indies: patterns and perspectives* (eds CA Woods, FE Sergile), pp. 15-33. Boca Raton, FL: CRC Press.
5. Woods CA, Borroto Paéz R, Kilpatrick CW. 2001 Insular patterns and radiations of West Indian rodents. In *Biogeography of the West Indies: patterns and perspectives* (eds CA Woods, FE Sergile), pp. 335-353. Boca Raton, FL: CRC Press.
6. Dávalos LM. 2004 Phylogeny and biogeography of Caribbean mammals. *Biol. J. Linn. Soc.* **81**, 373-394.
7. MacPhee RDE. 2005 'First' appearances in the Cenozoic land-mammal record of the Greater Antilles: significance and comparison with South American and Antarctic records. *J. Biogeogr.* **32**, 551-564. (doi:10.1111/j.1365-2699.2004.01231.x)
8. Brace S., Turvey ST, Weksler M, Hoogland MLP, Barnes I. 2015 Unexpected evolutionary diversity in a recently extinct Caribbean mammal radiation. *Proc. Roy. Soc. B* **282**, 20142371. (doi:10.1098/rspb.2014.2371)
9. Cooper RG. 2008 A synopsis of rodent species in the Caribbean Islands, endemic and invasive. *Living World,* 1-7.
10. MacPhee RDE. 2009 *Insulae infortunatae*: establishing a chronology for Late Quaternary mammal extinctions in the West Indies. In *American Megafaunal Extinctions at the End of the Pleistocene* (ed G Haynes), pp. 169-193. Springer Netherlands. (doi:10.1007/978-1-4020-8793-6)
11. MacPhee RDE, Iturralde-Vinent MA. 1995 Origin of the Greater Antillean land mammal fauna, 1: New Tertiary fossils from Cuba and Puerto Rico. *Am. Mus. Novit.* **3141**, 1-30.
12. Fabre P-H, Vilstrup JT, Raghavan M, Der Sarkissian C, Willerslev E, Douzery EJP, Orlando L. 2014 Rodents of the Caribbean: origin and diversification of hutias unravelled by next-generation museomics. *Biol. Lett.* **10**, 20140266. (doi:10.1098/rsbl.2014.0266)
13. Fabre P-H, Upham NS, Emmons LH, Justy F, Leite YLR, Loss AC, Orlando L, Tilak M-K, Patterson BD, Douzery EJP. 2017 Mitogenomic phylogeny, diversification, and biogeography of South American spiny rats. *Mol. Phylogenet. Evol.* **34**, 613-633. (doi:10.1093/molbev/msw261)
14. Courcelle M, Tilak M-K, Leite YLR, Douzery EJP, Fabre P-H. 2019 Digging for the spiny rat and hutia phylogeny using a gene capture approach, with the description of a new mammal subfamily. *Mol. Phylogenet. Evol.* **136,** 241-253. (doi:10.1016/j.ympev.2019.03.007)
15. MacPhee RDE, Iturralde-Vinent MA, Gaffney ES. 2003 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. *Am. Mus. Novit.* **3394**, 1-42.
16. MacPhee RDE. 2011 Basicranial morphology and relationships of Antillean Heptaxodontidae (Rodentia, Ctenohystrica, Caviomorpha). *Bull. Am. Mus. Nat. Hist.* **363**, 1-70.

17. Hedges SB, Hass CA, Maxson LR. 1992 Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proc. Natl. Acad. Sci. U.S.A.* **89**, 1909-1913.
18. MacPhee RDE, Iturralde-Vinent MA. 2005 The interpretation of Caribbean paleogeography: reply to Hedges. In *Proceedings of the International Symposium on Insular Vertebrate Evolution: the Palaeontological Approach* (eds JA Alcover, P Bover), pp. 175-184. Monografies de la Societat d'Historia Natural de les Balears.
19. Iturralde-Vinent MA, MacPhee RDE. 1999 Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bull. Am. Mus. Nat. Hist.* **238**, 1–95.
20. Hedges SB. 2006 Paleogeography of the Antilles and origin of West Indian terrestrial vertebrates. *Ann. Missouri Bot. Gard.* **93**, 231-244.
21. Heinicke MP, Duellman WE, Hedges SB. 2007 Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 10092-10097. (doi:10.1073/pnas.0611051104)
22. Alonso R, Crawford AJ, Bermingham E. 2012 Molecular phylogeny of an endemic radiation of Cuban toads (Bufonidae: *Peltophryne*) based on mitochondrial and nuclear genes. *J. Biogeogr.* **39**, 434-451. (doi:10.1111/j.1365-2699.2011.02594.x)
23. Ali JR. 2012 Colonizing the Caribbean: is the GAARLandia land-bridge hypothesis gaining a foothold? *J. Biogeogr.* **39**, 431-433. (doi:10.1111/j.1365-2699.2011.02674.x)
24. Matos-Maraví P, Aguila RN, Peña C, Miller JY, Sourakov A, Wahlberg N. 2014 Causes of endemic radiation in the Caribbean: evidence from the historical biogeography and diversification of the butterfly genus Calisto (Nymphalidae: Satyrinae: Satyrini). *BMC Evol. Biol.* **14**, 199. (doi:10.1186/s12862-014-0199-7)
25. Chamberland L, McHugh A, Kechejian S, Binford GJ, Bond JE, Coddington J, Dolman G, Hamilton CA, Harvey MS, Kuntner M, Agnarsson I. 2018 From Gondwana to GAARlandia: evolutionary history and biogeography of ogre-faced spiders (*Deinopis*). *J. Biogeogr.* **45**, 2442-2457. (doi:10.1111/jbi.13431)
26. Čandek K, Agnarsson I, Binford GJ, Kuntner M. 2019 Biogeography of the Caribbean *Cyrtognatha* spiders. *Sci. Rep.* **9**, 397. (doi:10.1038/s41598-018-36590-y)
27. Delsuc F, Kuch M, Gibb GC, Karpinski E, Hackenberger D, Szpak P, Martinez JG, Mead JL, McDonald HG, MacPhee RDE, et al. 2019 Ancient mitogenomes reveal the evolutionary history and biogeography of sloths. *Curr. Biol.* **29**, 1-12. (doi:10.1016/j.cub.2019.05.043)
28. Presslee S, Slater GJ, Pujos F, Forasiepi AM, Fischer R, Molloy K, Mackie M, Olsen JV, Kramarz AG, Taglioretti M, et al. 2019 Palaeoproteomics resolves sloth relationships. *Nat. Ecol. Evol.* **3**, 1121–1130. (doi:10.1038/s41559-019-0909-z)
29. Vélez-Juarbe J, Martin T, MacPhee RDE, Ortega-Ariza D. 2014 The earliest Caribbean rodents: Oligocene caviomorphs from Puerto Rico. *J. Vertebr. Paleontol.* **34**, 157-163. (doi:10.1080/02724634.2013.789039)
30. Martin T. 1992 Schmelzmikrostruktur in den inzisiven alt-und neuweltlicher hystricognather nagetiere. *Palaeovertebrata* **Mém. extra.**, 1-168.
31. Martin T. 1994 African origin of caviomorph rodents is indicated by incisor enamel microstructure. *Paleobiology* **20**, 5-13.

32. Boivin M, Marivaux L, Salas-Gismondi R, Vieytes EC, Antoine P-O. 2019 Incisor enamel microstructure of Paleogene caviomorph rodents from Contamana and Shapaja (Peruvian Amazonia). *J. Mammal. Evol.* **26**, 389-406. (doi:10.1007/s10914-018-9430-4)
33. Ortega-Ariza D, Franseen EK, Santos-Mercado H, Ramirez WR, Core-Suarez EE. 2015 Strontium isotope stratigraphy for Oligocene-Miocene carbonate systems in Puerto Rico and the Dominican Republic: implications for Caribbean processes affecting depositional history. *J. Geol.* **123**, 539-560. (doi:10.1086/683335)
34. Vélez-Juarbe J, Domning DP. 2014 Fossil Sirenia of the West Atlantic and Caribbean region: X. *Priscosiren atlantica*, gen. et sp. nov. *J. Vertebr. Paleontol.* **34**, 951-964. (doi:10.1080/02724634.2013.815192)
35. Vélez-Juarbe J, Brochu CA, Santos H. 2007 A gharial from the Oligocene of Puerto Rico: transoceanic dispersal in the history of a non-marine reptile. *Proc. Roy. Soc. B* **274**, 1245-1254. (doi:10.1098/rspb.2006.0455)
36. Kramarz AG. 2006 *Neoreomys* and *Scleromys* (Rodentia, Hystricognathi) from the Pinturas Formation, late Early Miocene of Patagonia, Argentina. *Rev. Mus. Arg. Cie. Nat., Nueva Ser.* **8**, 53-62.
37. Kerber L, Bissaro Junior MC, Negri FR, Pereira de Souza-Filho J, Guilherme E, Schmaltz Hsiou A. 2018 A new rodent (Caviomorpha: Dinomyidae) from the upper Miocene of southwestern Brazilian Amazonia. *Hist. Biol.* **30**, 985-993. (doi:10.1080/08912963.2017.1327529)
38. Kerber L, Negri FR, Ribeiro AM, Vucetich MG, Pereira de Souza-Filho J. 2016 Late Miocene potamarchine rodents from southwestern Amazonia, Brazil - with description of new taxa. *Acta Palaeontol. Pol.* **61**, 191-203. (doi:10.4202/app.00091.2014)
39. Rinderknecht A, Bostelmann E, Ubilla M. 2018 Making a giant rodent: cranial anatomy and ontogenetic development in the genus *Isostylomys* (Mammalia, Hystricognathi, Dinomyidae). *J. Syst. Palaeontol.* **16**, 245-261. (doi:10.1080/14772019.2017.1285360)
40. Walton AH. 1997 24. Rodents. In *Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia* (eds RF Kay, RH Madden, RL Cifelli, JJ Flynn), pp. 392-409. Washington: Smithsonian Institution Press.
41. Rasia L, Candela AM. 2017 Systematic revision of the vizcachas (Rodentia, Caviomorpha, Chinchillidae) from the Chapadmalal Formation, Late Pliocene of Buenos Aires province. *Ameghiniana* **57**, 50-69.
42. Rasia L, Candela AM. 2018 Reappraisal of the giant caviomorph rodent *Phoberomys burmeisteri* (Ameghino, 1886) from the late Miocene of northeastern Argentina, and the phylogeny and diversity of Neoepiblemidae. *Hist. Biol.* **30**, 486-495. (doi:10.1080/08912963.2017.1294168)
43. Kerber L, Negri FR, Sanfelice D. 2019 Morphology of cheek teeth and dental replacement in the extinct rodent *Neoepiblema* Ameghino, 1889 (Caviomorpha, Chinchilloidea, Neoepiblemidae). *J. Vertebr. Paleontol.* e1549061. (doi:10.1080/02724634.2018.1549061)
44. Boivin M, Antoine P-O, Benites-Palomino A, Marivaux L, Salas-Gismondi R. 2019 A new record of a giant neoepiblemid rodent from Peruvian Amazonia and an overview of lower tooth dental homologies among chinchilloids. *Acta Palaeontol. Pol.* **64**, 627-642. (doi:10.4202/app.00609.2019)

45. Kramarz AG, Vucetich MG, Arnal M. 2013 A new Early Miocene chinchilloid hystricognath rodent. An approach to the understanding of the early chinchillid dental evolution. *J. Mammal. Evol.* **20**, 249-261. (doi:10.1007/s10914-012-9215-0)
46. Kramarz AG. 2001 Registro de *Eoviscaccia* (Rodentia, Chinchillidae) en estratos colhuehuapenses de Patagonia, Argentina. *Ameghiniana* **38**, 237-242.
47. Lavocat R. 1976 Rongeurs Caviomorphes de l'Oligocène de Bolivie; II Rongeurs du bassin Déseadien de Salla-Luribay. *Palaeovertebrata* **7**, 15-90.
48. Boivin M, Marivaux L, Candela AM, Orliac MJ, Pujos F, Salas-Gismondi R, Tejada-Lara JV, Antoine P-O. 2017 Late Oligocene caviomorph rodents from Contamana, Peruvian Amazonia. *Pap. Palaeontol.* **3**, 69-109. (doi:10.1002/spp2.1068)
49. Boivin M, Marivaux L, Pujos F, Salas-Gismondi R, Tejada-Lara JV, Varas-Malca RM, Antoine P-O. 2018 Early Oligocene caviomorph rodents from Shapaja, Peruvian Amazonia. *Palaeontographica Abt. A* **311**, 87-156. (doi:10.1127/pala/2018/0075)
50. Boivin M, Marivaux L, Antoine P-O. 2019 L’apport du registre paléogène d’Amazonie sur la diversification initiale des Caviomorpha (Hystricognathi, Rodentia): implications phylogénétiques, macroévolutives et paléobiogéographiques. *Geodiversitas* **41**, 143-245. (doi: 10.5252/geodiversitas2019v41a4)
51. Stehlin HG, Schaub S. 1951 Die trigonodontie der simplicidentaten Nager. *Schweiz. Palaeontol. Abh.* **67**, 1-385.
52. Koenigswald v W, Sander PM. 1997 Schmelzmuster differentiation in leading and trailing edges, a specific biomechanical adaptation in rodents. In *Tooth enamel microstructure* (eds W Koenigswald v, PM Sander), pp. 259-266. Rotterdam: Balkema.
53. Boivin M, Marivaux L. 2018 Dental homologies and evolutionary transformations in Caviomorpha (Hystricognathi, Rodentia): new data from the Paleogene of Peruvian Amazonia. *Hist. Biol.* in press. (doi:10.1080/08912963.2018.1506778)
54. Candela AM, Nasif NL. 2006 Systematics and biogeographic significance of *Drytomomys typicus* (Scalabrini in Ameghino, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystricognathi) from Northeast of Argentina. *N. Jahrb. Geol. Palaont. Mh.* **3**, 165-181.
55. Kramarz AG, Bond M, Arnal M. 2015 Systematic description of three new mammals (Notoungulata and Rodentia) from the early Miocene Cerro Bandera Formation, Northern Patagonia, Argentina. *Ameghiniana* **52**, 585-597. (doi:10.5710/AMGH.27.06.2015.2906)
56. Carrillo JD, Sanchez-Villagra MR. 2015 Giant rodents from the Neotropics: diversity and dental variation of late Miocene neoepiblemid remains from Urumaco, Venezuela. *Paläontol. Zeitsch.* **89**, 1057-1071. (doi:10.1007/s12542-015-0267-3)
57. Rasia L, Candela AM. 2018 Upper molar morphology, homologies and evolutionary patterns of chinchilloid rodents (Mammalia, Caviomorpha). *J. Anat.* **234**, 50-65. (doi:10.1111/joa.12895)
58. Martin T. 2004 Incisor enamel microstructure of South America's earliest rodents: implications for caviomorph origin and diversification. In *The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru* (ed KE Campbell), pp. 131-140. Los Angeles, CA: Natural History Museum of Los Angeles County.
59. Anthony HE. 1920 New mammals from Jamaica. *Bull. Am. Mus. Nat. Hist.* **42**, 469-475.

60. Miller GS. 1929 Mammals eaten by Indians, owls, and spaniards in the coast region of the Dominican Republic. *Smithson. Misc. Collect.* **82**, 1-16.
61. MacPhee RDE, Flemming C. 2003 A possible heptaxodontine and other caviidan rodents from the Quaternary of Jamaica. *Am. Mus. Novit.* **3422**, 1-42.
62. Morgan GS, Wilkins L. 2003 The extinct rodent *Clidomys* (Heptaxodontidae) from a late Quaternary cave deposit in Jamaica. *Caribbean J. Earth Sci.* **39**, 34-41.
63. Turvey ST, Grady FV, Rye P. 2006 A new genus and species of 'giant hutia' (*Tainotherium valei*) from the Quaternary of Puerto Rico: an extinct arboreal quadruped? *J. Zool.* **270**, 585-594. (doi:10.1111/j.1469-7998.2006.00170.x)
64. Anthony HE. 1916 Preliminary report of fossil mammals from Porto Rico, with descriptions of a new genus of ground sloth and two new genera of hystricomorph rodents. *Ann. New York Acad. Sci.* **27**, 193-203.
65. Anthony HE. 1927 Mammals of Porto Rico, living and extinct - Rodentia and Edentata. *Scientific Survey of Porto Rico and the Virgin Islands* **9**, 97-155.
66. Miller GS. 1916 Bones of mammals from Indian sites in Cuna and Santo Domingo. *Smithson. Misc. Collect.* **66**, 1-11.
67. Williams EE, Koopman KF. 1951 A new fossil rodent from Puerto Rico. *Am. Mus. Novit.* **1515**, 1-9.
68. Berggren WA, Prothero DR. 1992 *Eocene-Oligocene climatic and biotic evolution: an overview*. Princeton, NJ: Princeton University Press.
69. Zachos JC, Dickens GR, Zeebe RE. 2008 An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–283. (doi:10.1038/nature06588)
70. Jaramillo C, Rueda MJ, Mora G. 2006 Cenozoic plant diversity in the Neotropics. *Science* **311**, 1893-1896. (doi:10.1126/science.1121380)
71. Blois JL, Hadly EA. 2009 Mammalian response to Cenozoic climatic change. *Annu. Rev. Earth Pl. Sc.* **37**, 8.1-8.28. (doi:10.1146/annurev.earth.031208.100055)
72. Wilson DE, Lacher TE, Mittermeier RA. 2016 *Handbook of the mammals of the world. Vol. 6. Lagomorphs and Rodents*. Barcelona: Lynx Edicions.
73. Robinson E. 1994 Jamaica. In *Caribbean geology: an introduction* (eds SK Donovan, TA Jackson), pp. 111-127. Kingston: University of the West Indies Publishers Association.
74. MacPhee RDE, Singer R, Diamond M. 2000 Late Cenozoic Land Mammals from Grenada, Lesser Antilles Island-Arc. *Am. Mus. Novit.* **3302**, 1-20.
75. Upham NS, Patterson BD. 2015 Evolution of caviomorph rodents: a complete phylogeny and timetree for living genera. In *Biology of caviomorph rodents: diversity and evolution* (eds AI Vassallo, D Antenucci), pp. 63-120. Buenos Aires: SAREM Series A.

Figure captions

Figure 1. Location, geological maps, and stratigraphical context of the fossil-bearing locality (LACM Loc. 8060; yellow asterisk), situated in the Río Guatemala of Puerto Rico (West Indies). This locality was found in the lower part of the San Sebastian Formation in the Río Guatemala section. $^{87}Sr/^{86}Sr$ mean ages-dates calculated on low-Mg calcite shells of *Kuphus incrassatus* bivalves allow for bracketing the age of the LACM Loc. 8060 (fossil symbol + rodent silhouette) between 29.78 and 29.17 Ma (late Rupelian [33]).

Figure 2. Dental remains of chinchilloid rodents from the late early Oligocene of Puerto Rico. *Borikenomys praecursor* gen. et sp. nov. (*a-j*): (*a-f*) LACM 162447, right lower m3 in occlusal (*a*), cross-sectional (*b*), ventral (*c*), buccal (*d*), mesial (*e*) and lingual (*f*) views; (*g-j*) LACM 162446, fragment of a left lower molar (mesiolingual part) in occlusal (*g-h*), cross-sectional (*i*) and lingual (*j*) views. Chinchilloid gen. et sp. indet.: (*k-n*) LACM 162448, fragment of an upper tooth (mesial laminae) or of a left lower tooth (distal laminae) in mesial (*k*), buccal or lingual (*l*), occlusal (*m*) and cross-sectional views. The cross-section (yellow segments) for each tooth (*b*, *i*, and *n*) shows the heterogeneous thickness of the enamel layer (red lines), which is thicker on the trailing edges than on the leading edges. The images are 3D digital models of the fossil specimens, obtained by X-ray µCT surface reconstruction.

Figure 3. Dental structures and hypotheses of homologies for the LACM 162447 right lower m3, and enamel microstructure of the MA 316 lower incisor attributed to *Borikenomys praecursor* gen. et sp. nov. (*a-c*), dental nomenclature of the occlusal surface of LACM 162447: identification of cuspids and cristids (*a*), reported on an interpretative schematic drawings (*b*), and identification of the fossettids (*c*); (*d-e*), incisor enamel microstructure of MA 316: enamel longitudinal section (*d*) and detail of that section (*e*) showing the crystallite arrangement typifying a subtype 2 of multiserial Hunter-Schreger bands (modified from [29]; Scanning electron photomicrographs courtesy of T. Martin). Number denominations of the dental structures: **1**, protoconid region; **2**, posterior arm of the protoconid; **3**, metalophulid I; **4**, metaconid region; **5**, posterior arm of the metaconid; **6**, neomesolophid; **7**, mesostylid region; **8**, entoconid region; **9**, hypolophid; **10**, posterolophid; **11**, anterior arm of the hypoconid; **12**, hypoconid region; **13**, ectolophid; **14**, hypoflexid (hypofossettid); **15**, anteroflexid (anterofossettid); **16**, mesoflexid (mesofossettid); **17**, metaflexid (metafossettid); **Tr**, trailing edge; **Ld**, leading edge.

Figure 4. Phylogenetic position of *Borikenomys praecursor* gen. et sp. nov. in a high-level hystricognathous rodent phylogeny. This colour-coded and simplified phylogenetic tree derives from the strict consensus topology of a cladistic assessment of the dental evidence available. Heuristic searches yielded 12 equally most parsimonious trees of 3336.89 steps each (CI = 0.564; RI = 0.602). This simplified strict consensus tree is transposed here onto a chronostratigraphical context. The solid bars of different lengths indicate the stratigraphical occurrences/ranges of the rodents sampled. Note the phylogenetic positions of the Caribbean *Borikenomys*, *Elasmodontomys* and *Amblyrhiza*, nested within the Chinchilloidea clade. Light grey bars within Chinchillidae correspond to the credibility interval (95%) of the molecular divergence age estimates, as provided in Upham and Patterson [75]. Selected characters and character states, as well as the taxon/character matrix [50] plus the assumptions (Nexus format) are provided online as electronic supplementary material. The full strict consensus tree topology is provided in electronic supplementary material, figure S3. The time interval suggested for the chinchilloid dispersal to the Caribbean (~35–33 Ma) is compatible with the GAARlandia hypothesis (light grey strip [11]). Pictures of lower toothrows: *Elasmodontomys obliquus* (AMNH-17137, right p4-m2; photograph courtesy of R. D. E. MacPhee via L. J. Meeker) and of *Amblyrhiza inundata* (AMNH-11837, right p4-m3; photograph courtesy of A. van der Geer); Scale bars = 1 cm.

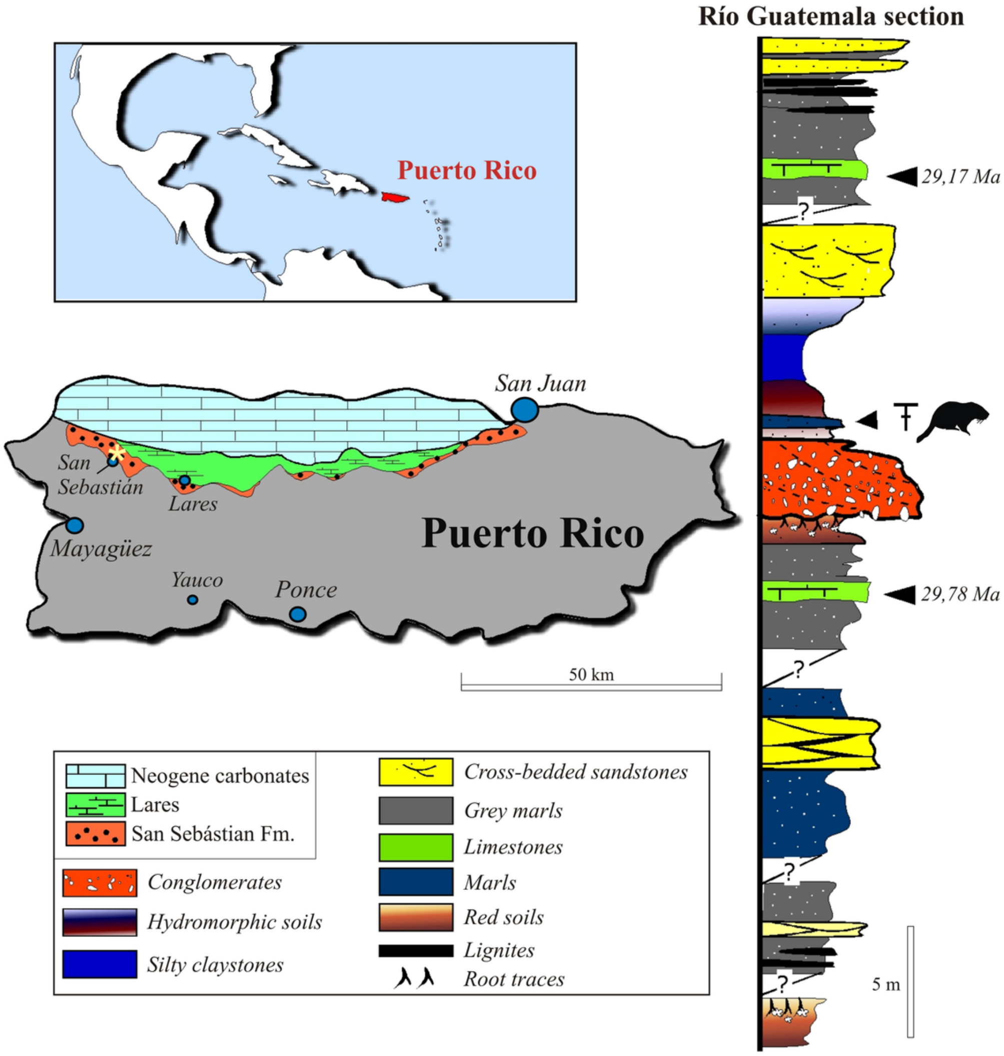

Figure 1. Location, geological maps, and stratigraphical context of the fossil-bearing locality (LACM Loc. 8060; yellow asterisk), situated in the Río Guatemala of Puerto Rico (West Indies). This locality was found in the lower part of the San Sebastian Formation in the Río Guatemala section. 87Sr/86Sr mean ages-dates calculated on low-Mg calcite shells of Kuphus incrassatus bivalves allow for bracketing the age of the LACM Loc. 8060 (fossil symbol + rodent silhouette) between 29.78 and 29.17 Ma (late Rupelian [33]).

95x101mm (300 x 300 DPI)

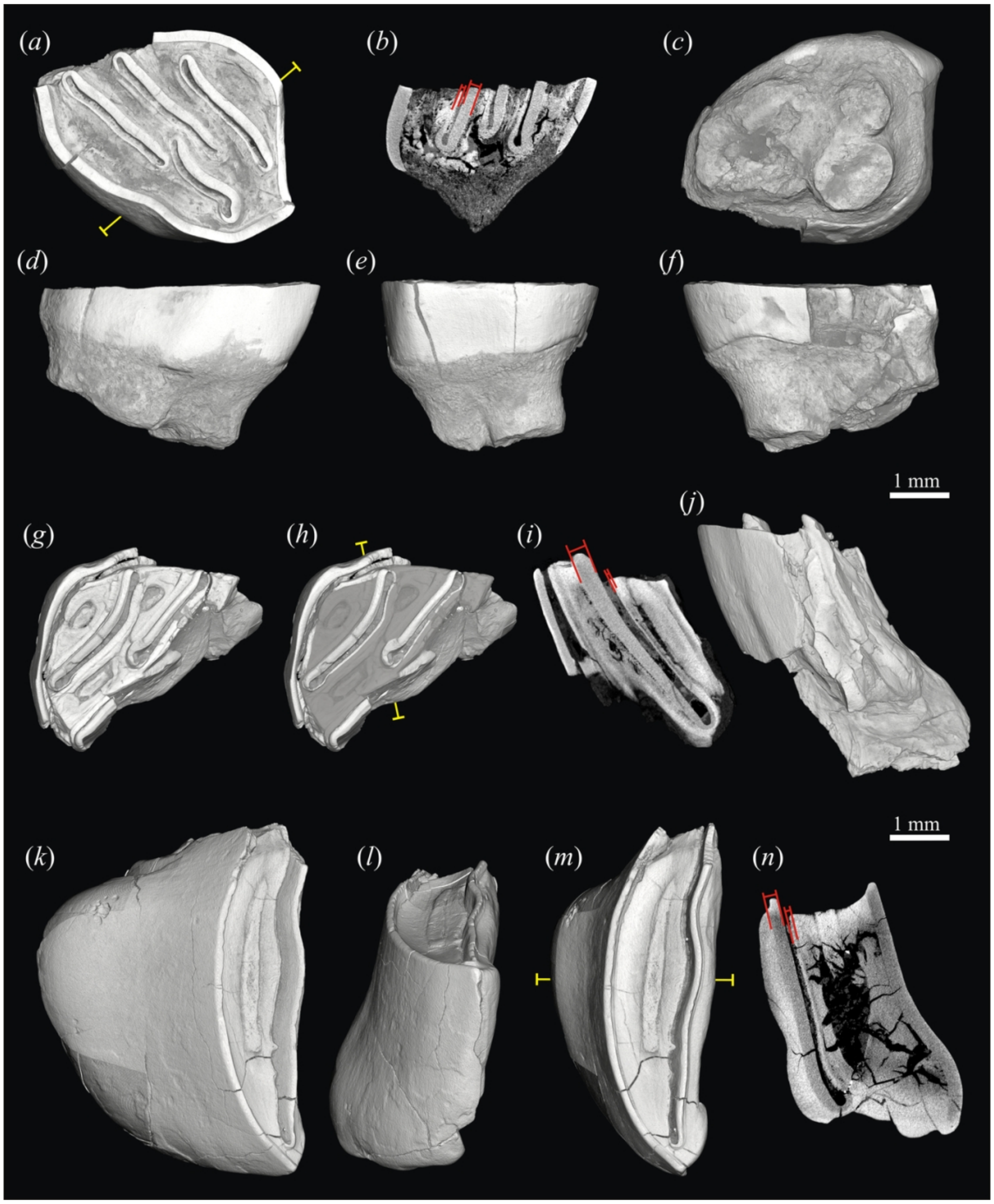

Figure 2. Dental remains of chinchilloid rodents from the late early Oligocene of Puerto Rico. Borikenomys praecursor gen. et sp. nov. (a-j): (a-f) LACM 162447, right lower m3 in occlusal (a), cross-sectional (b), ventral (c), buccal (d), mesial (e) and lingual (f) views; (g-j) LACM 162446, fragment of a left lower molar (mesiolingual part) in occlusal (g-h), cross-sectional (i) and lingual (j) views. Chinchilloid gen. et sp. indet.: (k-n) LACM 162448, fragment of an upper tooth (mesial laminae) or of a left lower tooth (distal laminae) in mesial (k), buccal or lingual (l), occlusal (m) and cross-sectional views. The cross-section (yellow segments) for each tooth (b, i, and n) shows the heterogeneous thickness of the enamel layer (red lines), which is thicker on the trailing edges than on the leading edges. The images are 3D digital models of the fossil specimens, obtained by X-ray µCT surface reconstruction.

114x138mm (300 x 300 DPI)

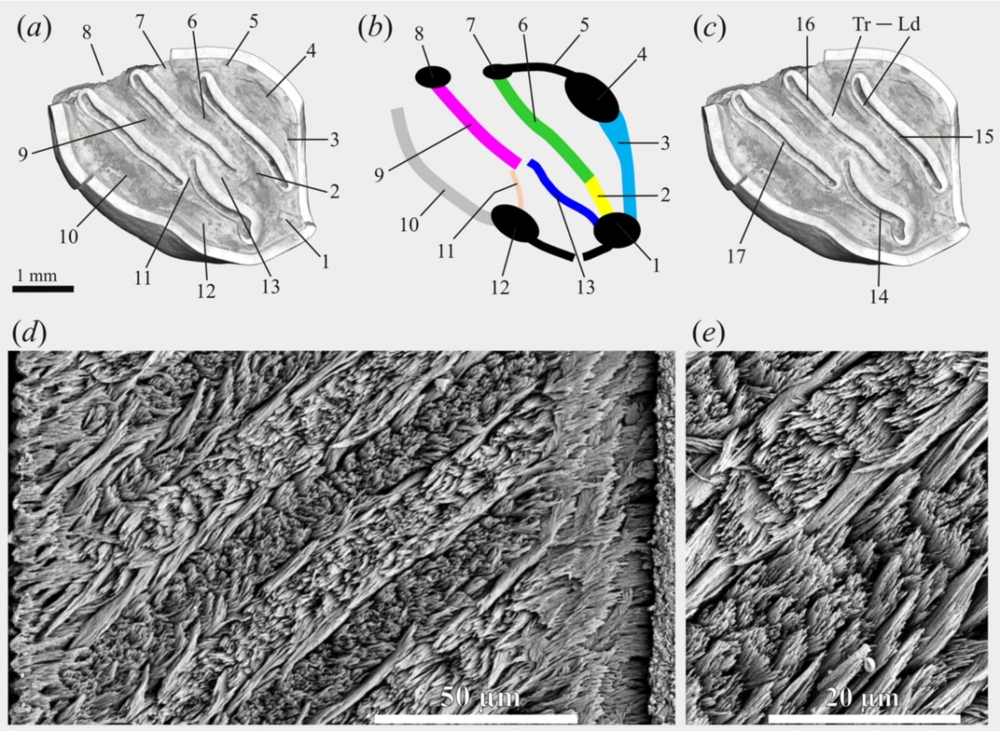

Figure 3. Dental structures and hypotheses of homologies for the LACM 162447 right lower m3, and enamel microstructure of the MA 316 lower incisor attributed to Borikenomys praecursor gen. et sp. nov. (a-c), dental nomenclature of the occlusal surface of LACM 162447: identification of cuspids and cristids (a), reported on an interpretative schematic drawings (b), and identification of the fossettids (c); (d-e), incisor enamel microstructure of MA 316: enamel longitudinal section (d) and detail of that section (e) showing the crystallite arrangement typifying a subtype 2 of multiserial Hunter-Schreger bands (modified from [29]; Scanning electron photomicrographs courtesy of T. Martin). Number denominations of the dental structures: 1, protoconid region; 2, posterior arm of the protoconid; 3, metalophulid I; 4, metaconid region; 5, posterior arm of the metaconid; 6, neomesolophid; 7, mesostylid region; 8, entoconid region; 9, hypolophid; 10, posterolophid; 11, anterior arm of the hypoconid; 12, hypoconid region; 13, ectolophid; 14, hypoflexid (hypofossettid); 15, anteroflexid (anterofossettid); 16, mesoflexid (mesofossettid); 17, metaflexid (metafossettid); Tr, trailing edge; Ld, leading edge.

103x75mm (300 x 300 DPI)

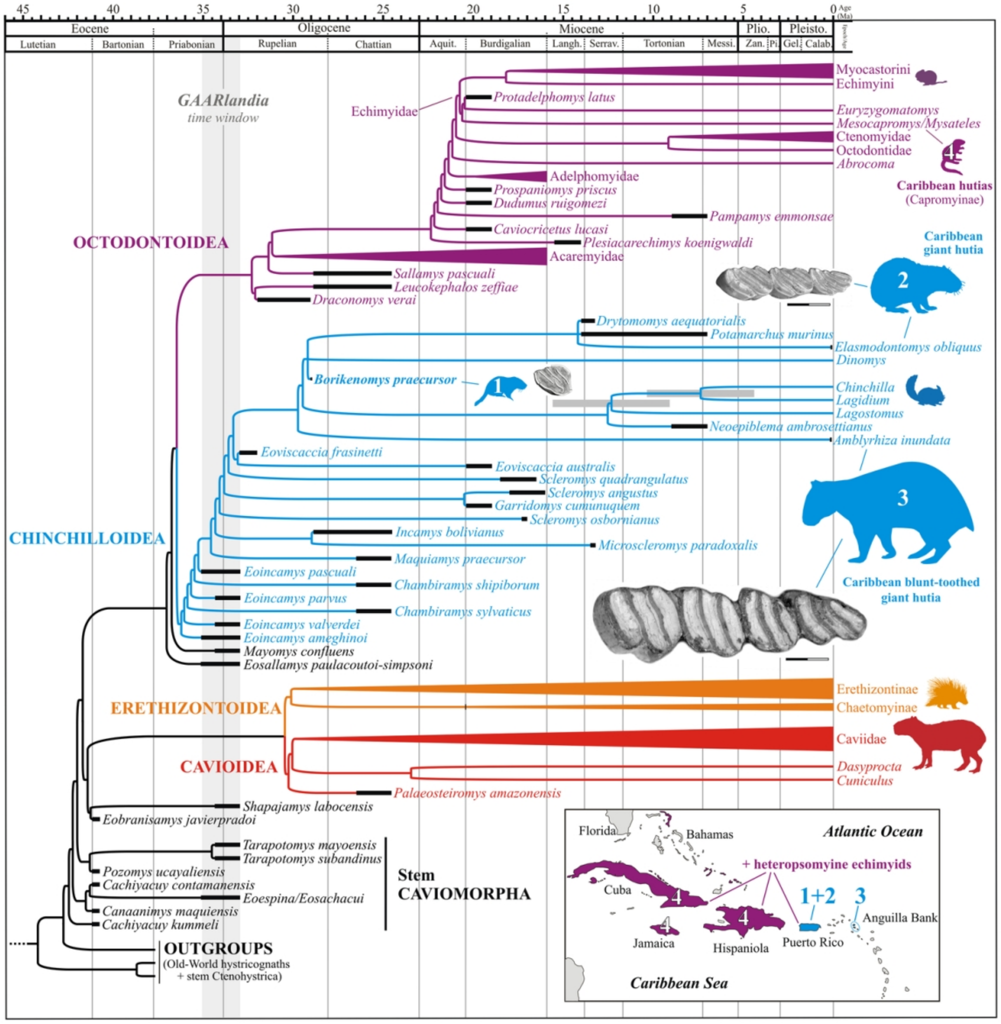

Figure 4. Phylogenetic position of Borikenomys praecursor gen. et sp. nov. in a high-level hystricognathous rodent phylogeny. This colour-coded and simplified phylogenetic tree derives from the strict consensus topology of a cladistic assessment of the dental evidence available. Heuristic searches yielded 12 equally most parsimonious trees of 3336.89 steps each (CI = 0.564; RI = 0.602). This simplified strict consensus tree is transposed here onto a chronostratigraphical context. The solid bars of different lengths indicate the stratigraphical occurrences/ranges of the rodents sampled. Note the phylogenetic positions of the Caribbean Borikenomys, Elasmodontomys and Amblyrhiza, nested within the Chinchilloidea clade. Light grey bars within Chinchillidae correspond to the credibility interval (95%) of the molecular divergence age estimates, as provided in Upham and Patterson [75]. Selected characters and character states, as well as the taxon/character matrix [50] plus the assumptions (Nexus format) are provided online as electronic supplementary material. The full strict consensus tree topology is provided in electronic supplementary material, figure S3. The time interval suggested for the chinchilloid dispersal to the Caribbean (~35–33 Ma) is compatible with the GAARlandia hypothesis (light grey strip [11]). Pictures of lower toothrows: Elasmodontomys obliquus (AMNH-17137, right p4-m2; photograph courtesy of R. D. E. MacPhee via L. J. Meeker) and of Amblyrhiza inundata (AMNH-11837, right p4-m3; photograph courtesy of A. van der Geer); Scale bars = 1 cm.

123x126mm (300 x 300 DPI)