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A new protodidelphid (Mammalia, Marsupialia, Didelphimorphia) from the Itaboraí Basin and its implications for the evolution of the Protodidelphidae

LEONARDO M. CARNEIRO[1,2,3]

[1]Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva, Prédio das Pós-graduações do Instituto de Biologia, Interbloco B/C, Centro de Ciências da Saúde (CCS), Campus Ilha do Fundão, Universidade Federal do Rio de Janeiro/UFRJ, Avenida Carlos Chagas Filho, 373, Cidade Universitária, 21941-590 Rio de Janeiro, RJ, Brazil
[2]Laboratório de Mastozoologia/LAMAS, Departamento de Zoologia, Universidade Federal do Estado do Rio de Janeiro, Avenida Pasteur, 458, Sala 501, Urca, 22290-240 Rio de Janeiro, RJ, Brazil
[3]Laboratório de Paleontologia e Paleoecologia da Sociedade de História Natural, Travessa Florêncio Augusto Chagas, nº 8B, 2560-230, Torres Vedras, Portugal

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Abstract: The Protodidelphidae was a group of marsupials that lived in Gondwana from the early to middle Eocene. Among South American faunas, the Itaboraí Basin calls attention by the presence of four genera and six species. Herein is described Bergqvistherium primigenia gen. et sp. nov., a new protodidelphid from the Itaboraí Basin - lower Eocene. This taxon differs from other protodidelphids in the smaller size, developed entocristid, less brachyo-bunoid adaptations, and entoconid more mesial than the hypoconid. These characters are recovered as plesiomorphies of the Protodidelphidae, supporting Bergqvistherium as an early-divergent lineage of this group. The Protodidelphidae fauna of the Itaboraí Basin is represented by less specialized "basal" taxa, such as Bergqvistherium and Periprotodidelphis; and more specialized apical taxa, such as Guggenheimia, Protodidelphis, and Carolocoutoia. This result indicates that the diversification of apical protodidelphids probably was a result of a relatively short-time event, occurring during the early Eocene. This evolutionary event can be directly correlated to the increase in the temperatures and the extension of tropical forests resulted by the Paleocene-Eocene Thermal Maximum during the Itaboraiense time span. The study supported a Late Cretaceous origin for the Protodidelphidae, which agrees with molecular studies for the Didelphimorphia.

Key words: Metatheria, Paleogene, systematics, teeth.

E-mail: leonardo.carneiro8@gmail.com
ORCid: https://orcid.org/0000-0001-9385-431X
* Contribution to the centenary of the Brazilian Academy of Sciences.

INTRODUCTION

The Protodidelphidae Marshall, 1987, is an extinct marsupial lineage that existed during the early and middle Eocene in South America and Antarctic Peninsula (Paula Couto 1952, 1962, 1970, Marshall 1987, Goin et al. 1999, Tejedor et al. 2009, Oliveira and Goin 2011, 2012) and (Oliveira É.V., unpublished data). This taxon is represented by *Protodidelphis* Paula Couto 1952; *Guggenheimia* Paula Couto, 1952; *Carolocoutoia* Goin et al. 1998; and *Periprotodidelphis* Oliveira and Goin, 2011.

The oldest occurrences of this lineage are known for the Itaboraí Basin, Rio de Janeiro, Brazil, and Las Flores, Argentina; both considered as lower Eocene (Itaboraian SALMA – around 55-52 Ma – Woodburne et al. 2014a) in age. All members of the Protodidelphidae are known to have existed during this time span. The youngest fossil records are known for the La Meseta Formation, Antarctica, and Paso del Sapo, Argentina; both date from the lower-middle Eocene ("Sapoan" SALMA) (Goin et al. 1999, Tejedor et al. 2009), which identifies the Protodidelphidae as a short time span surviving lineage during the Paleogene of South America. Notwithstanding, the evolution of other metatherian lineages can be traced back to the Paleocene of South America or even to the Late Cretaceous of North America (Case et al. 2005, Forasiepi et al. 2009, Goin et al. 2012, 2016, Oliveira and Goin 2012, Carneiro and Oliveira 2017a, b, Carneiro 2018), which is also expected for the Protodidelphidae.

The Paleocene metatherian fossil bearing localities in South America are restricted to Tiupampa, Bolivia (lower Paleocene – Tiupampian SALMA – Muizon 1992); Laguna Umayo, Peru (upper Paleocene or Itaboraian SALMA – Sigé et al. 2004, Gelfo and Sigé 2011); Grenier section of the Lefipán Formation, Argentina (lower Paleocene – Goin et al. 2006), and Punta Peligro, Argentina (lower Paleocene – Peligran SALMA – Woodburne et al. 2014b); however, none of these localities have a protodidelphid among the identified metatherians. The Paleocene diversification of the Protodidelphidae can be inferred based on the great diversity of this group during the Itaboraian SALMA (early Eocene), as four genera are recorded, as commented. Among them, *Guggenheimia* is considered by Oliveira and Goin (2011) as an early-divergent lineage of the Protodidelphidae based on the relatively smaller size and less bunoid molars. Nevertheless, this genus shows several morphological traits that support an earlier evolutionary history for the Protodidelphidae.

During a survey of the paleontological collection in the Departamento Nacional de Produção Mineral (DNPM), an isolated m3 of a 'protodidelphid-like' taxon was identified in the fossils collected in 1968, which differs in several ways from other genera from the Itaboraí Basin. Interestingly, this material is similar in some morphological traces to *Guggenheimia*; however, it bears some plesiomorphic characters for a brachyo-bunoid taxon, supporting a probable earlier divergence.

Here, it is described a new genus of protodidelphid from the Itaboraí Basin, discussing its implications for the evolution of the Protodidelphidae and for the fauna of the Itaboraí Basin.

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York, New York, USA; **MCN-PV**, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **DNPM**, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; **MCT** (ex **DGM**, Divisão de Geologia e Mineralogia), Museu de Ciências da Terra, Rio de Janeiro, Brazil; **MLP**, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; **MN**, Museu Nacional, Rio de Janeiro, Brazil.

Other abbreviations: **m**, lower molars with the numbers corresponding to its positioning; **EECO**, Early Eocene Climatic Optimum; **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age; **SEM**, Scanning Electron Microscope.

MATERIALS AND METHODS

The type specimen of the new taxon (*i.e.* MCT 4387-M – see below) is deposited at the Departamento de Produção Mineral (DNPM), Rio de Janeiro, Brazil. The type specimen is from the Itaboraí Basin, São José de Itaboraí, Rio de Janeiro, Brazil (22º45'9.9144''S, 42º51'53.5536''W) (Fig. 1).

The Brazilian taxa were directly analyzed (*i.e.* fossil specimens and casts), in addition, literature descriptions, casts, digital and SEM pictures were also analyzed. The North American taxa were studied based on literature descriptions, casts, digital and SEM pictures. The casts of Naturita Formation taxa and several specimens of *Varalphadon* were sent by Richard L. Cifelli and Joshua E. Cohen from the Sam Noble Oklahoma Museum of Natural History, USA. A list of casts is given in the supplementary material, that can be accessed here https://www.researchgate.net/publication/327248822_Supplementary_Material.

Figure 1 - Location map showing the region and coordinates of the Itaboraí Basin, São José de Itaboraí, Rio de Janeiro, Brazil (22º45'9.9144''S, 42º51'53.5536''W). Figure adapted from the figure 1 (p. 106) from Oliveira and Goin (2011).

The SEM pictures of the new taxon were made with the scanning electron microscope JEOL JSM-6390LV at the Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional, Rio de Janeiro, Brazil.

The data matrix is based on the characters published in Ladevèze and Muizon (2010), Luo et al. (2011), Abello (2013), Forasiepi et al. (2015), Muizon et al. (2015), Wilson et al. (2016), Beck (2017), Carneiro and Oliveira (2017a, b), and Carneiro (2018). The matrix is based mainly on dental characters from upper and lower dentition of fossil and living metatherians.

The morphological matrix was submitted to a new technology search with TNT 1.5 (Goloboff and Catalano 2016) using the sectorial, ratchet, drift and tree fusing strategies with 500 replications. The morphological matrix is available as supplementary material, also at https://www.researchgate.net/publication/327248822_Supplementary_Material. Bremer supports and tree scores were calculated with TNT 1.5. The phylogeny presents 642 unordered characters, including cranial, dentary, dental and postcranial characters, and 184 therian taxa, including more than 170 metatherians and closely related taxa, from the Cretaceous and Cenozoic of North America, Asia, South America, Antarctic, Europe and Australia.

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

Marsupialiformes Vullo et al. 2009

Notometatheria Kirsch et al. 1997

Marsupialia Illiger, 1811 (McKenna and Bell 1997)

Order Didelphimorphia Gill, 1872

†Family Protodidelphidae Marshall 1987

†Genus *Bergqvistherium* gen. nov.

(Fig. 2)

ZooBank Life Science Identifier (LSID) - urn:lsid:zoobank.org:act:0DDF46FB-B2DF-467C-A8D5-96F03CB989E6

Etymology: 'Bergqvist', in honor of Lílian Paglarelli Bergqvist for her contributions for the knowledge of the Itaboraí Basin; '*therium*', from the Greek, beast; a common designation of fossil mammals. Gender is feminine.

Type species: *Bergqvistherium primigenia* sp. nov.

Included species: The type only.

Diagnosis: Differs from other protodidelphids in the smaller size, less brachyo-bunoid lower molars, greater labiolingual compression and lesser mesiodistal compression of the trigonid, paraconid

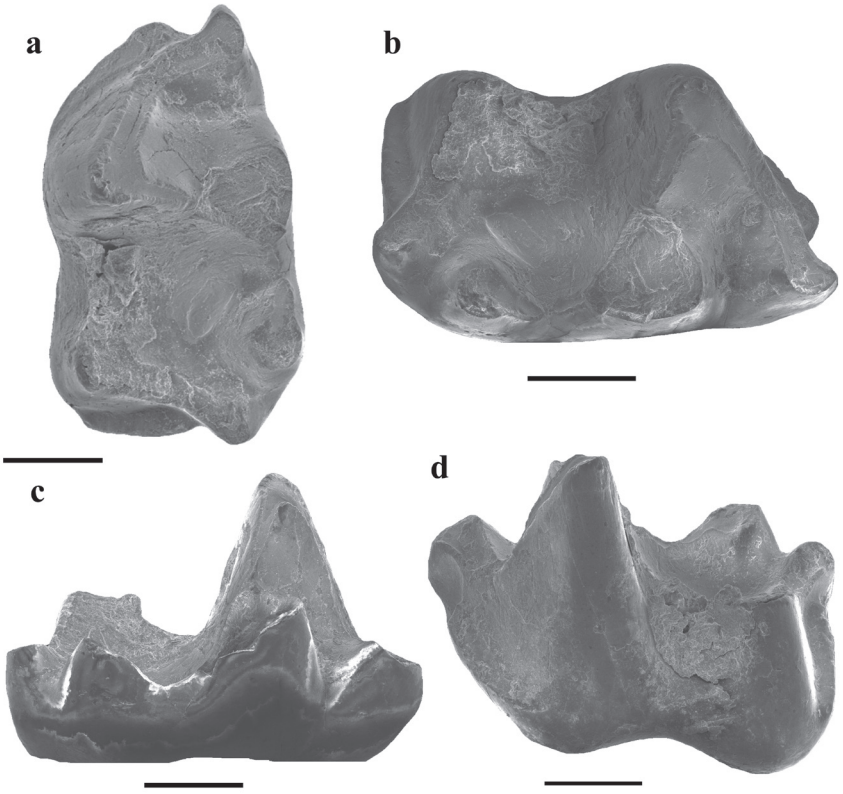

Figure 2 - Type specimen of *Bergqvistherium primigenia*. SEM pictures of the type specimen of *Bergqvistherium primigenia* (MCT 4387-M), a left m3: **a**, occluso-labial; **b**, occlusal; **c**, lingual; **d**, labial views. Scale bar: 0,5 mm.

less lingually shifted and more mesiodistally developed, paraconid apex mesially oriented, paracristid with a straight shape in occlusal view, greater development of the entocristid, and greater development of the posterobasal cingulid. Differs from *Guggenheimia brasiliensis* and *G. crocheti* in the following combination of characters: entoconid mesial to hypoconid, more developed paraconid, less brachyo-bunoid lower molars; greater development of the distolabial crest of the metaconid and developed entocristid. Differs from *Guggenheimia* sp. from Las Flores, Argentina (e.g. MLP 90-II-5-79, a left m3; and MLP 90-II-5-72, a right m3), in the presence of a much less inflated entoconid, paracristid not "curved", paraconid less lingually positioned than metaconid, greater development of the entocristid, distolabial crest of the metaconid, anterobasal cingulids; and trigonid not so mesiodistally compressed. Differs from *Periprotodidelphis* and *Carolocoutoia* in the much smaller size and less inflated molar. Differs from *Protodidelphis* in the markedly smaller size, less bunoid molar, less inflated and conical entoconid, entoconid mesial to hypoconid and paraconid more developed (Fig. 3).

Type locality: Fresh water travertine deposits of the fissure explored in 1968 at São José de Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al. 2009). Itaboraí Formation, lower Eocene in age Woodburne et al. (2014a).

Locality and horizon: Fissure discovered and worked in 1968, of the Itaboraí Formation, Itaboraí Basin, municipality of Itaboraí, State of Rio de Janeiro, Brazil (Bergqvist et al. 2009). Lower Eocene, Itaboraian SALMA (ca 53-50 Ma; sensu Woodburne et al. 2014a).

†*Bergqvistherium primigenia* sp. nov.

(Fig. 2)

Etymology: 'primigenia' from the Greek '*primigenius*' ('*primus*' = first; '*genus*' = origin, birth) in reference of its earlier divergent condition to other protodidelphids.

Diagnosis: As for the genus.

Holotype: MCT 4387-M, a left m3 (Fig. 2).

Hypodigm: The type only.

Locality and horizon: As for the genus.

Description: The m3 is 2,16 mm in mesiodistal length, 1,29 mm in the labiolingual width of the trigonid, and 1,26 mm in the labiolingual width of the talonid. The paraconid is moderately developed and slightly more labially positioned than the metaconid, and its apex is mesially projected. The paracristid is short and does not show a "curved" shape. The trigonid is mesiodistally and labiolingually compressed. The metaconid is slightly distal (i.e. nearly aligned) to the protoconid. The entoconid is conical, and well-developed, but not massive (i.e. does not occupy most of or the entire lingual half of the talonid basin). The entocristid and the distolabial crest of the metaconid are developed. The hypoconid is distal to the entoconid. The cristid obliqua contacts the distal wall of the trigonid somewhat more labial than the carnassial notch. The hypoconulid is moderately developed and is twinned to the entoconid, but is not distolingual in position. The anterobasal cingulid is moderately developed and the posterobasal cingulid is well-developed.

Measurements: See Table I.

Remarks: Bergqvistherium primigenia is considered to be a protodidelphid based on the presence of a conical and well-developed entoconid, brachyodont molar, developed cingulids, metaconid distal to protoconid, paraconid slightly more lingual than the metaconid, and paraconid with some degree of mesiodistal compression.

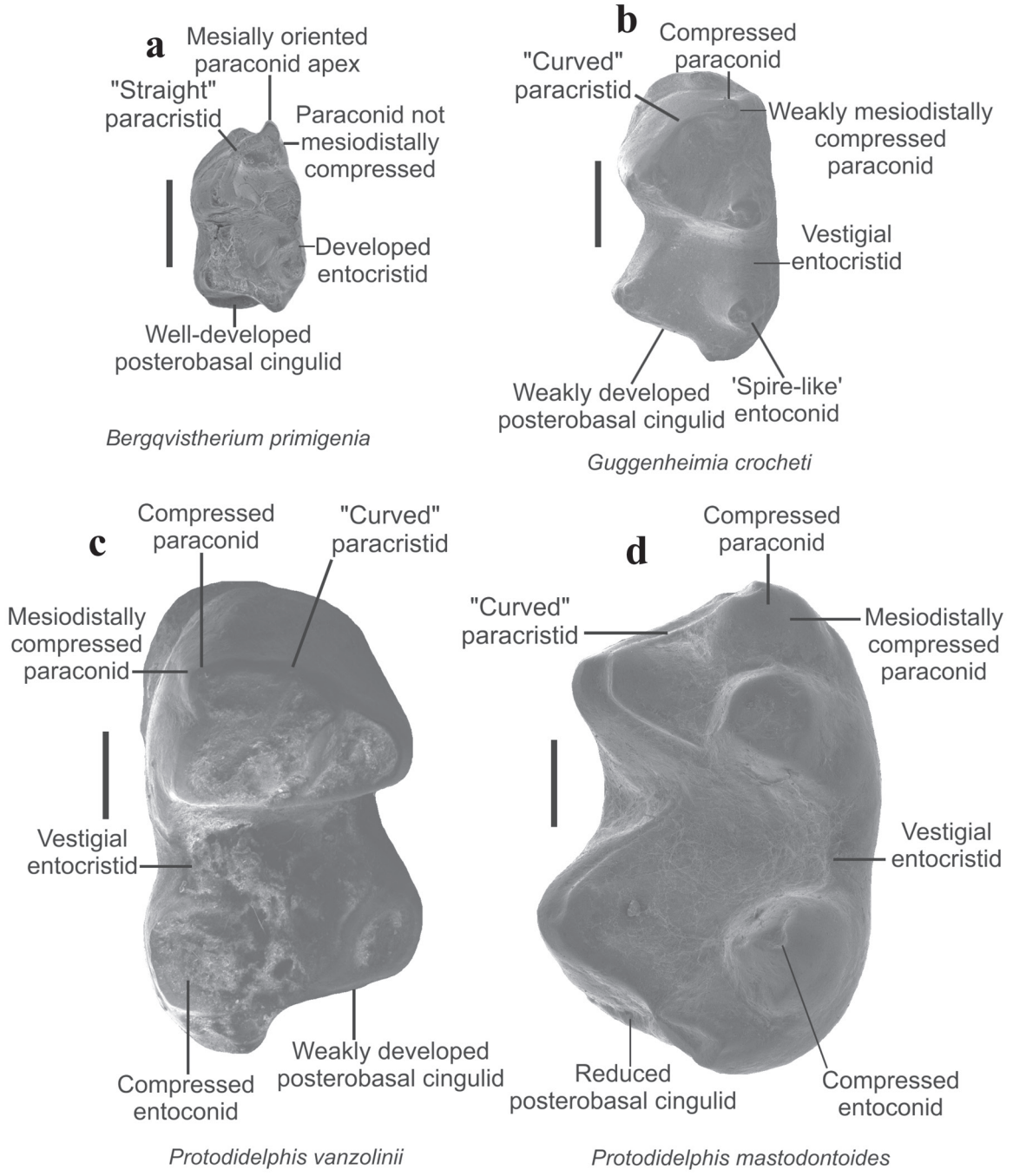

Figure 3 - Comparative morphology of the lower molars of the Brazilian protodidelphids. Differential morphology between *Bergqvistherium*, *Guggenheimia* and *Protodidelphis*: **a**, *Bergqvistherium primigenia*: MCT 4387-M, a left m3 (type specimen), in occlusal view; **b**, *Guggenheimia crocheti*: DGM 314-M, an incomplete left dentary with m2-4 and alveoli of i1-m1 (type specimen), showing the m3 in occlusal view; **c**, *Protodidelphis vanzolinii*: DGM 250-M, nearly complete right dentary, showing the m3 in occlusal view; **d**, *Protodidelphis mastodontoidea*: MCT 2819-M, left m2 in occlusal view. The proportional size difference between these taxa is preserved. Scale bars: 1mm.

TABLE I
Measurements (mm) of the third lower molars (m3) of *Bergqvistherium primigenia* gen. et sp. nov and other protodidelphids. The size range of known specimens is indicated and based on the specimens from the Museu Nacional (MN), Rio de Janeiro; Museu de Ciências da Terra (MCT), Rio de Janeiro; Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN-PV), Porto Alegre, Brazil; and American Museum of Natural History (AMNH), New York, USA. Length: mesiodistal axis; width: labiolingual axis.

Taxa	m3 length	m3 width
Bergqvistherium primigenia	2,16 mm	1,29 mm
Guggenheimia brasiliensis	2,86 mm	2,04 mm
Guggenheimia crocheti	3,16-3,2 mm	1,77-2,02 mm
Protodidelphis vanzolinii	4,6-5,5 mm	3,4-3,67 mm
Protodidelphis mastodontoides	5,81-6,19 mm	3,63-4,18 mm

It should not be considered as belonging to the Chulpasiinae as it lacks a talonid somewhat wider than trigonid, the entoconid is relatively less developed (i.e. not massive developed), the hypoconulid is relatively smaller, and the paraconid is relatively narrower and more mesiodistally compressed.

PHYLOGENETIC ANALYSIS AND SYSTEMATIC IMPLICATIONS

The analysis found 24 most parsimonious trees (trees score = 2944; CI = 0.296; HI = 0.704; RI = 0.669) (Fig. 4). Following the results, *Bergqvistherium* is recovered as the sister taxon of *Periprotodidelphis* + *Anatoliadelphys* and *Guggenheimia*, *Protodidelphis* + *Carolocoutoia*, as an early-divergent lineage of the Protodidelphidae.

The Protodidelphidae is the sister taxon of the Glasbiidae Clemens, 1966; which is represented by *Palangania*, *Periakros* and *Glasbius*. Protodidelphidae and Glasbiidae are the sister taxa of *Reigia*. The Protodidelphidae, Glasbiidae and *Reigia* are recovered as the sister taxon of the Didelphoidea, which is represented by the Didelphidae, Sparassocynidae and *Monodelphopsis*. These lineages represent the Didelphimorphia and can be considered as belonging to the Marsupialia (Fig. 4). The inclusion of the Protodidelphidae among the Didelphimorphia was supported by the analyses of Ladevèze and Muizon (2010), Carneiro and Oliveira (2017a, b) and Carneiro (2018).

The pylogenetic analysis support the sister relation between *Periprotodidelphis* and *Anatoliadelphys*, recovering a South American ancestral area for the lineage of the last taxon. This result differs from the one of Maga and Beck (2017), who proposed a North American ancestor area for *Anatoliadelphys*. This result can be considered as preliminary evidence supporting the hypothesis of the Atlantogea, as proposed by Ezcurra and Agnolín (2012).

DISCUSSION

THE LATE CRETACEOUS-EARLY PALEOGENE ORIGIN OF THE PROTODIDELPHIDAE

The PETM (Paleocene-Eocene Thermal Maximum) probably occurred around 55,2 Ma, with the increase of the global temperatures and the extension of tropical forests (Bowen et al. 2015). This event is correlated with the increase in abundance and diversity of metatherians in South America, especially bachyo-bunoid taxa, such as the Protodidelphidae and the Polydolopimorphia, as recorded in the localities dating back to the Itaboraian SALMA (Woodburne et al. 2014a, b, Goin et al. 2016).

The presence of five different genera with seven species among the metatherian assemblage of the Itaboraí Basin (i.e. *Bergqvistherium primigenia*, *Guggenheimia brasiliensis*, *G. crocheti*, *Periprotodidelphis bergqvistae*, *Protodidelphis vanzolinii*, *P. mastodontoides* and *Carolocoutoia ferigoloi*) supports the diversification of the Protodidelphidae beginning earlier than the

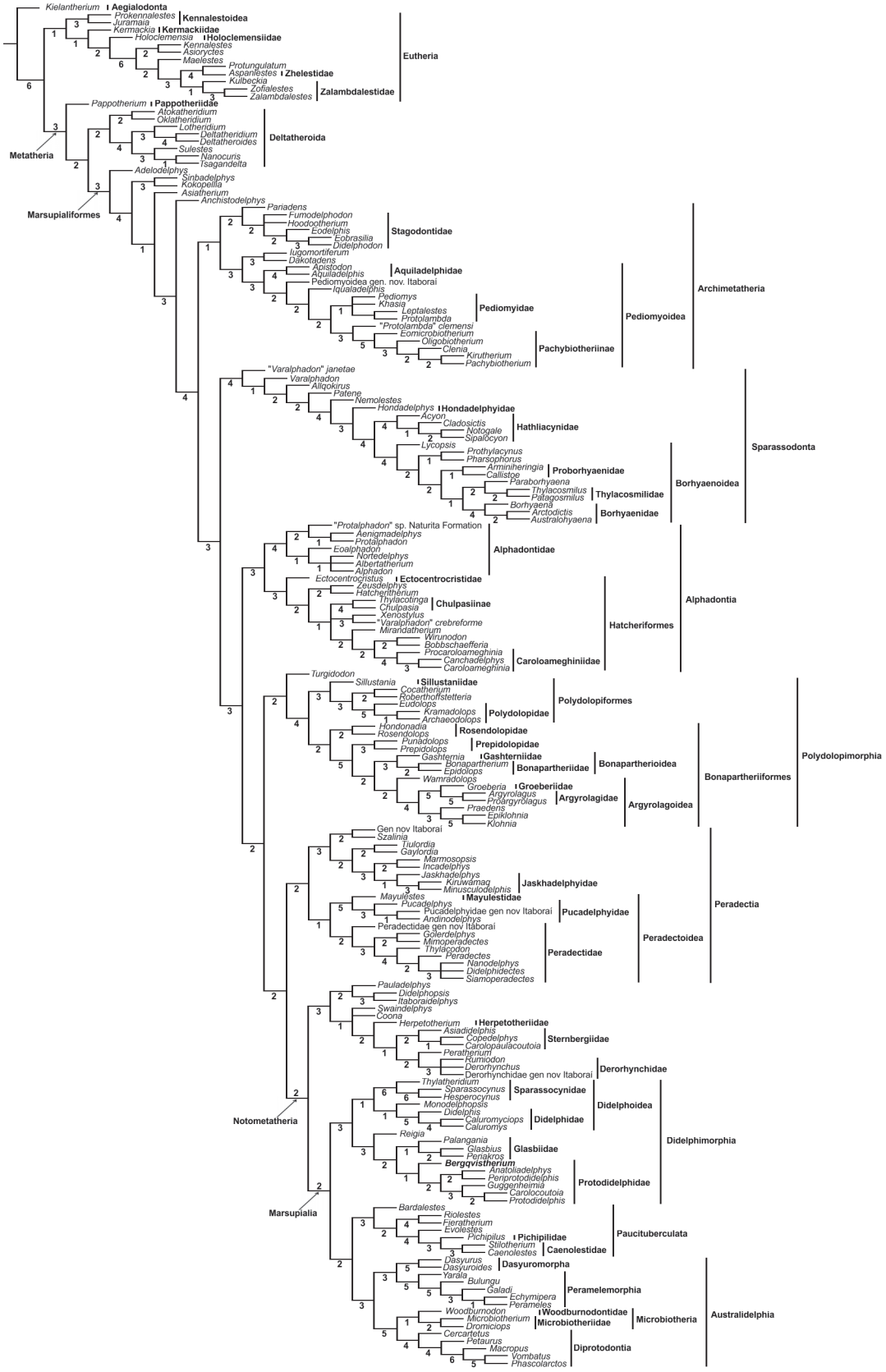
Kielantherium
Aegialodonta
Prokennalestes
Juramaia
Kennalestoidea
Kermackia
Kermackiidae
Holoclemensia
Holoclemensiidae
Kennalestes
Asioryctes
Maelestes
Protungulatum
Aspanlestes
Zhelestidae
Kulbeckia
Zofialestes
Zalambdalestes
Zalambdalestidae
Eutheria
Pappotherium
Pappotheriidae
Atokatheridium
Oklatheridium
Lotheridium
Deltatheridium
Deltatheroides
Sulestes
Nanocuris
Tsagandelta
Deltatheroida
Metatheria
Adelodelphys
Sinbadelphys
Kokopellia
Asiatherium
Marsupialiformes
Anchistodelphys
Pariadens
Fumodelphodon
Hoodootherium
Eodelphis
Ectobrasilia
Didelphodon
Stagodontidae
Iugomortiferum
Dakotadens
Apistodon
Aquiladelphis
Aquiladelphidae
Pediomyoidea gen. nov. Itaborai
Iqualadelphis
Pediomys
Khasia
Leptalestes
Protolambda
Pediomyidae
"Protolambda" clemensi
Eomicrobiotherium
Oligobiotherium
Clenia
Kirutherium
Pachybiotherium
Pachybiotheriinae
Pediomyoidea
Archimetatheria
"Varalphadon" janetae
Varalphadon
Allqokirus
Patene
Nemolestes
Hondadelphys
Hondadelphyidae
Acyon
Cladosictis
Notogale
Sipalocyon
Hathliacynidae
Lycopsis
Prothylacynus
Pharsophorus
Arminiheringia
Callistoe
Proborhyaenidae
Paraborhyaena
Thylacosmilus
Patagosmilus
Thylacosmilidae
Borhyaenoidea
Borhyaena
Arctodictis
Australohyaena
Borhyaenidae
Sparassodonta
"Protalphadon" sp. Natarita Formation
Aenigmadelphys
Protalphadon
Eoalphadon
Nortedelphys
Albertatherium
Alphadon
Alphadontidae
Ectocentrocristus
Ectocentrocristidae
Zeusdelphys
Hatcheritherium
Thylacotinga
Chulpasiinae
Chulpasia
Xenostylus
"Varalphadon" crebreforme
Mirandatherium
Wirunodon
Bobbschaefferia
Procaroloameghinia
Canchadelphys
Caroloameghiniidae
Caroloameghinia
Hatcheriformes
Alphadontia
Turgidodon
Sillustania
Sillustaniidae
Cocatherium
Roberthoffstetteria
Eudolops
Kramadolops
Polydolopidae
Archaeodolops
Polydolopiformes
Hondonadia
Rosendolops
Rosendolopidae
Punadolops
Prepidolopidae
Prepidolops
Gashternia
Gashterniidae
Bonapartherium
Epidolops
Bonapartheriidae
Bonapartherioidea
Wamradolops
Groeberia
Groeberiidae
Argyrolagus
Argyrolagidae
Prodargyrolagus
Argyrolagoidea
Bonapartheriiformes
Polydolopimorphia
Praedens
Epiklohnia
Klohnia
Gen nov Itaborai
Szalinia
Tiulordia
Gaylordia
Marmosopsis
Incadelphys
Jaskhadelphys
Kiruwamag
Jaskhadelphyidae
Minusculodelphis
Mayulestes
Mayulestidae
Pucadelphys
Pucadelphyidae gen nov Itaborai
Pucadelphyidae
Andinodelphys
Peradectidae gen nov Itaborai
Peradectoidea
Peradectia
Golerdelphys
Mirmoperadectes
Thylacodon
Peradectes
Peradectidae
Nanodelphys
Didelphidectes
Siamoperadectes
Pauladelphys
Didelphopsis
Itaboraidelphys
Swaindelphys
Coona
Herpetotherium
Herpetotheriidae
Asiadidelphis
Copedelphys
Carolopaulacoutoia
Sternbergiidae
Peratherium
Kumiodon
Derorhynchus
Derorhynchidae
Derorhynchidae gen nov Itaborai
Thylatheridium
Sparassocynus
Sparassocynidae
Hesperocynus
Monodelphopsis
Didelphoidea
Didelphis
Caluromyciops
Didelphidae
Caluromys
Notometatheria
Reigia
Palangania
Glasbius
Glasbiidae
Peniakros
Didelphimorphia
Bergqvistherium
Anatoliadelphys
Periprotodidelphis
Guggenheimia
Protodidelphidae
Carolocoutoia
Protodidelphis
Marsupialia
Bardalestes
Riolestes
Fieratherium
Evolestes
Pichipilus
Pichipilidae
Stilotherium
Caenolestidae
Caenolestes
Paucituberculata
Dasyurus
Dasyuroides
Dasyuromorpha
Yalalla
Bulungu
Galadi
Peramelemorphia
Echymipera
Perameles
Woodburnodon
Woodburnodontidae
Microbiotherium
Microbiotheriidae
Microbiotheria
Australidelphia
Dromiciops
Cercartetus
Petaurus
Macropus
Vombatus
Phascolarctos
Diprotodontia

Figure 4 - The result of the phylogenetic analysis. Consensus tree of the 24 most parsimonious trees found in the analysis. *Bergqvistherium* is highlighted in bold. Numbers below the branches indicate the Bremer Support.

Itaboraian SALMA time span (i.e. early Eocene – sensu Woodburne et al. 2014a).

The phylogenetic analysis recovered *Glasbius* as an apical glasbiid, which indicates that the lineages of the other glasbiid (*i.e. Palangania* and *Periakros*), *Reigia* and the Protodidelphidae existed by the time of the oldest fossil records of the former taxon in the USA (i.e. around 66 Ma, latest Maastrichtian – Clemens 1966, Davis 2007, Williamson et al. 2012, 2014, Boyd et al. 2017). If correct, these results support a Late Cretaceous origin of the Protodidelphidae, with this group surviving as a rare lineage in the faunas of South America before the PETM.

This evidence should not be treated as surprising, as molecular studies date the origin of the Didelphimorphia to the Santonian-early Campanian time span during the Late Cretaceous, around 80-79 Ma (Kirsch et al. 1997, Bininda-Emonds et al. 2007), which is a compatible time span for the results recovered by the phylogenetic analysis.

The apical position of *Glasbius* among the glasbiid and the early Campanian (Late Cretaceous) origin of the Didelphimorphia indicate that Marsupialia did not evolve in North America during the Late Cretaceous. This result supports an 'Aves Ridge' or Gondwanan origin for the Didelphimorphia and Marsupialia.

THE PROTODIDELPHIDAE FAUNA OF THE ITABORAI BASIN: EVIDENCE OF A SHORT-TIME DIVERSIFICATION DURING THE ITABORAIENSE

Among the protodidelphids found in the Itaboraí Basin, *Periprotodidelphis* and *Bergqvistherium* are represented just by a single tooth; while a far more abundant *Protodidelphis* (30 teeth for both species) and a moderately more abundant *Guggenheimia* (seven teeth) are also recorded (Oliveira and Goin

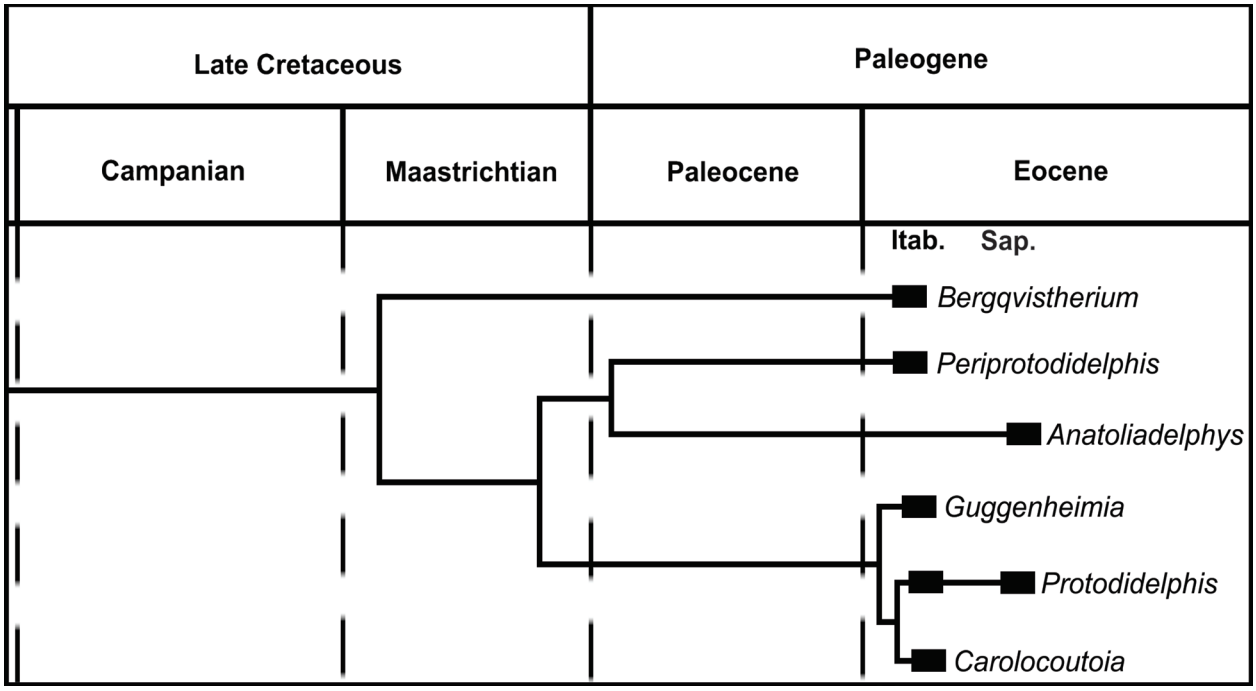

Figure 5 - Temporal cladogram of the Protodidelphidae. Phylogeny of the Protodidelphidae calibrated in time, based on the phylogeny present in the figure 4. The wide bars indicate the recorded temporal range of the Protodidelphidae genera. The SALMAs that present protodidelphids are identified. **SALMAs**: Itaboraian; "Sapoan".

2011). The protodidelphids recovered in most of the collections at this locality show a greater number of apomorphies than *Bergqvistherium* and *Periprotodidelphis* (e.g. more brachyo-bunoid molars, larger size, relatively smaller paraconids and more inflated entoconids), which supports a more specialized frugivorous diet for them (Goin et al. 1998, Oliveira and Goin 2011, 2012, Zimicz A.N., unpublished data).

Woodburne et al. (2014a) placed the Itaboraí Basin during the lower Eocene (Itaboraian SALMA), being correlated with the Early Eocene Thermal Optimum (EETO); and Woodburne et al. (2014b) discussed the increase in extension of the tropical forests in South America after the PETM, which can be associated to the increase in the abundance and diversity of more bunoid mammals, like the protodidelphids *Guggenheimia*, *Protodidelphis*, and *Carolocoutoia*.

The phylogenetic analysis recovered *Bergqvistherium* and *Periprotodidelphis* as earlier divergent lineages of the Protodidelphidae, which supports an older origin for these two taxa than *Guggenheimia*, *Protodidelphis*, and *Carolocoutoia*. The existence of "basal" and apical faunal components in the Itaboraí Basin indicates that the diversification and increase in abundance of more apical and specialized frugivorous protodidelphids probably took place during the Itaboraian SALMA. The lower Eocene age dated for the Itaboraí Basin indicates that the diversification of *Guggenheimia, Protodidelphis*, and *Carolocoutoia* occurred in a relatively short time span, with the increase in the temperatures as the main environmental event correlated to the increase in size, brachyo-bunodonty and other frugivorous adaptations for these three genera.

The dental adaptations of *Guggenheimia* indicate the ingestion of hard food items, judging by the robust dentary and greater mesiodistal compression of the upper molars; *Protodidelphis* was more likely to be a frugivorous-generalist, and *Carolocoutoia* a strict frugivorous (Zimicz A.N., unpublished data). This indicates an apparently lower niche overlapping between these three genera and a wide range of occupied trophic levels for this group, as *Bergqvistherium* is more likely to be a small frugivorous-generalist taxon.

The great taxonomical and ecological diversity of the Protodidelphidae from the Itaboraí Basin support the PETM as the main environmental event responsible for the evolution of the group. Some previous studies have proposed the hypothesis that the fossil bearing deposits of the Itaboraí Basin span a considerable age range (i.e. from the late Paleocene to early Eocene) (Gayet et al. 1991, Marshall et al. 1997, Rage 1998, Bergqvist et al. 2009, Pinheiro et al. 2012). This could be tentatively followed, as the protodidelphids of the Itaboraí Basin show a relative degree of morphological and ecological specialization, with "basal" and apical taxa in the same locality; however, the lower Eocene time span of the Itaboraí Basin, as proposed by Woodburne et al. (2014a, b), is here followed based on the bunoid adaptations present in the apical protodidelphids of this fauna, which are compatible with the increase of the extension of the tropical forests, as proposed by Woodburne et al. (2014b).

These evidences follow the results of Goin et al. (2012, 2016) and Woodburne et al. (2014a, b), who considered the Itaboraí Basin as lower Eocene in age, and attested the importance of the PETM as one of the most important environmental events during the Paleogene for the evolution of the South American metatherians.

The extinction of the Protodidelphidae could be related to the global cooling that happened during the Eocene, as no member of this lineage is known to have lived after the middle Eocene of South America and Antarctic (i.e. "Sapoan" SALMA – Woodburne et al. 2014a) (Fig. 5).

CONCLUSIONS

The description of *Bergqvistherium primigenia* from the Itaboraí Basin increases the diversity of the Protodidelphidae in this locality. The presence of several plesiomorphic traits in this taxon supported its recovering in the phylogenetic analysis as an early-divergent protodidelphid.

The phylogenetic analysis supported a Late Cretaceous origin for the Protodidelphidae. Following the results, the increase in the abundance, trophic diversity and diversification of apical taxa of this group can be directly correlated to the environmental changes that occurred after the PETM.

The presence of "basal" and apical genera of the Protodidelphidae in the Itaboraí Basin indicates that the diversification of more apical taxa was probably a result of a relatively short-time evolutionary event during the time span of the Itaboraiense (early Eocene), as a response to the increase in temperatures and extension of the tropical forests in South America.

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