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PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS

OS METATÉRIOS DA BACIA DE ITABORAÍ: SISTEMÁTICA E DIVERSIDADE

LEONARDO DE MELO CARNEIRO

RECIFE

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OS METATÉRIOS DA BACIA DE ITABORAÍ: SISTEMÁTICA E DIVERSIDADE

Tese de Doutorado apresentada à coordenação do Programa de Pós-graduação em Geociências (PPGEOC), da Universidade Federal de Pernambuco (UFPE), como parte dos requisitos da qualificação para a obtenção do grau de Doutor em Geociências

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“The Itaboraí fauna is not only the largest, but also the most diverse yet discussed (...)”

(Michael O. Woodburne et al. 2014a, p. 40).

RESUMO

Metatheria representou o grupo de mamíferos paleogenos de maior diversidade da América do Sul. Dentre as faunas paleogenas, a fauna de metatérios do Eoceno inicial (idade mamífero Itaboraiense SALMA) da Bacia de Itaboraí, município de Itaboraí, RJ, Brasil, é uma das mais importantes. Essa localidade preservou a maior diversidade de metatérios insetívoros, frugívoros e táxons com especializações durófagas (*Didelphopsis*, *Eobrasilia*, *Gaylordia* e *Periprotodidelphis*) em uma única associação faunística do Paleogeno-Neogeno das Américas. Os metatérios foram representados por, pelo menos, 29 gêneros e 44 espécies cujas massas corporais variavam entre 2-3 gramas (*Minusculodelphis minimus*) a 10 kg (*Eobrasilia coutoi*), abrangendo diversos nichos tróficos: Frugivoria, folivoria, faunivoria, insetivoria, durofagia, carnivoria e onivoria. Durante a presente tese, a descoberta de novos espécimes (dentição, dentários e maxilas) elevou para mais de 1000 o número de espécimes desse clado em coleções brasileiras. Esses espécimes permitiram conhecer a dentição superior (exceto *Procaroloameghinia*, *Silvenator* e *Thylacopygmaeus*), inferior (exceto *Periprotodidelphis*) e dentários (exceto *Eobrasilia*) de quase todos os metatérios de Itaboraí. A fauna metateriana de Itaboraí compreendeu os mais antigos representantes conhecidos dos Didelphimorphia (Monodelphopsiidae rank nov.: *Monodelphopsis*; e Protodidelphidae: *Guggenheimia*, *Protodidelphis*, *Robertbutleria* e *Carolocoutoia*), e um possível Australidelphia-“Woodburnodontidae” (*Austropedimys*), a linhagem-irmã aos Microbiotheria e Diprotodontia. *Robertbutleria* foi resgatado com base em inúmeras características compartilhadas exclusivamente com *Carolocoutoia* em comparação a *Protodidelphis*. A presença de Paucituberculata não foi confirmada na fauna, visto que “*Riolestes*” representa um dente decíduo de *Robertbutleria*. Sparassodonta foi representado na fauna por *Patene*, *Silvenator* e *Xenocynus*, que ocuparam o nicho trófico dos principais mamíferos predadores. Polydolopimorphia foi representado por *Epidolops*, o metatério mais abundante dessa fauna; *Gashternia*, de dieta folívoro-frugívora; e os enigmáticos Eobrasiliidae (*Periprotodidelphis* e *Eobrasilia*). “*Zeusdelphys complicatus*” é reconhecido como um sinônimo júnior de *E. coutoi*. A grande variedade de “ameridélfos” Itaboraienses incluiu, entre outros, Bergqvistheriidae fam. nov. (Peradectoidea gen. nov., *Bergqvistherium*), Bobbschaefferiidae fam. nov. (*Bobbschaefferia*), Mirandatheriidae rank nov. (Pucadelphyoidea gen. nov. e *Mirandatherium*), Caroloameghiniidae (*Procaroloameghinia*), Jaskhadelphyoidea superfam. nov.-Gaylordiidae fam. nov. (*Gaylordia*), Jaskhadelphyoidea superfam. nov.-Jaskhadelphyidae (*Minusculodelphis*), Jaskhadelphyoidea superfam. nov.-Jaskhadelphyidae-Marmosopsiidae subfam. nov. (*Marmosopsis*), Sternbergiidae-Sternbergiinae (*Carolopaulacoutoia*),

Sternbergiidae-Didelphopsiinae subfam. nov. (*Didelphopsis* e *Itaboraidelphys*), Herpetotheriidae-Rumiodontinae (*Thylacopygmaeus*), Derorhynchidae (*Diogenesia*, *Derorhynchus*) e Derorhynchidae-Cooniinae subfam. nov. (Derorhynchidae gen. nov.). “Clados cretáceos norte-americanos” (Hatcheriformes, Pediomyidae, Stagodontidae) não são mais identificados para o Eoceno inicial em Itaboraí. Anatoliadelphidae e Peratheriinae são potenciais clados irmãos dos “Glasbiidae” e Sternbergiidae/Herpetotheriidae-Rumiodontinae sul-americanos, suportando preliminarmente a hipótese da Atlantogea. Dimorfismo sexual (e.g., *Gaylordia macrocynodonta*) é identificado, principalmente, pela altura/robustez do dentário e diferença de tamanho nos sexos. Os oito morfótipos de petrosos identificados em Itaboraí (PtI a PtVIII) pertencem a um stem-Marsupialia (*Epidolops* [PtI]), Pucadelphyda (Pucadelphyoidea gen. nov. [PtII]), Jaskhadelphyoidea (*Marmosopsis*, *Gaylordia* e *Minusculodelphis* [PtIII, PtIV, PtVIII]), Sternbergiinae (*Carolopaulacoutoia* [PtV]), Derorhynchidae (PtVI) e Rumiodontinae (*Thylacopygmaeus* [PtVII]). Para os metatérios, a exploração de diferentes nichos tróficos entre táxons aparentados pode ser constatada principalmente pela morfologia mandibular, especialmente em táxons frugívoros e carnívoros.

PALAVRAS-CHAVE: Didelphimorphia. Eoceno inicial. Itaboraiense. Marsupialia. Paleoecologia. Sistemática.

ABSTRACT

Metatheria represented the most diverse group of Paleogene mammals in South America. Among the Paleogene faunas, the early Eocene metatherian fauna (Itaboraiense SALMA) from the Itaboraí Basin, municipality of Itaboraí, RJ, Brazil, is one of the most prominent. This locality preserved the greatest diversity of insectivorous, frugivorous, and durophagous metatherians (*Didelphopsis*, *Eobrasilia*, *Gaylordia*, and *Periprotodidelphis*) in a single faunal association from the Paleogene-Neogene of the Americas. The metatherians were represented by at least 29 genera and 44 species whose body masses ranged from 2-3 g (*Minusculodelphis minimus*) to 10 kg (*Eobrasilia coutoi*), covering various trophic niches: frugivory, folivory, faunivory, insectivory, durophagy, carnivory and omnivory. During this thesis, the discovery of new specimens (dentition, teeth and jaws) brought the number of specimens of this clade in Brazilian collections to over 1000. These specimens made it possible to learn about the upper dentition (except *Procaroloameghinia*, *Silvenator*, and *Thylacopygmaeus*), lower dentition (except *Periprotodidelphis*) and jaw (except *Eobrasilia*) of almost all the metatherians from Itaboraí. The metatherian fauna of Itaboraí included the oldest known representatives of the Didelphimorphia (Monodelphopsiidae rank nov.: *Monodelphopsis*; and Protodidelphidae: *Guggenheimia*, *Protodidelphis*, *Robertbutleria*, and *Carolocoutoia*), and an Australidelphia-“Woodburnodontidae” (*Austropedionomys*), the sister lineage to Microbiotheria and Diprotodontia. *Robertbutleria* was rescued based on numerous characteristics shared exclusively with *Carolocoutoia* compared to *Protodidelphis*. The presence of Paucituberculata was not confirmed in the fauna, as “*Riolestes*” represents a deciduous tooth of *Robertbutleria*. Sparassodonta was represented in the fauna by *Patene*, *Silvenator*, and *Xenocynus*, which occupied the trophic niche of the main mammalian predators. Polydolopimorphia was represented by *Epidolops*, the most abundant metatherian in this fauna; *Gashternia*, with a folivorous-frugivorous diet; and the enigmatic Eobrasiliidae (*Periprotodidelphis* and *Eobrasilia*). “*Zeusdelphys complicatus*” is recognized as a junior synonym of *E. coutoi*. The wide variety of Itaboraiense “ameridelphians” included, among others, Bergqvistheriidae fam. nov. (Peradectoidea gen. nov., *Bergqvistherium*), Bobbschaefferiidae fam. nov. (*Bobbschaefferia*), Mirandatheriidae rank nov. (Pucadelphyoidea gen. nov. and *Mirandatherium*), Caroloameghiniidae (*Procaroloameghinia*), Jaskhadelphyoidea superfam. nov.-Gaylordiidae fam. nov. (*Gaylordia*), Jaskhadelphyoidea superfam. nov.-Jaskhadelphyidae (*Minusculodelphis*), Jaskhadelphyoidea superfam. nov.-Jaskhadelphyidae-Marmosopsiidae subfam. nov. (*Marmosopsis*), Sternbergiidae-Sternbergiinae (*Carolopaulacoutoia*), Sternbergiidae-Didelphopsiinae subfam. nov. (*Didelphopsis* and *Itaboraidelphys*),

Herpetotheriidae-Rumiodontinae (*Thylacopygmaeus*), Derorhynchidae (*Diogenesia*, *Derorhynchus*), and Derorhynchidae-Cooniinae subfam. nov. (Derorhynchidae gen. nov.). “North American Cretaceous clades” (Hatcheriformes, Pediomyidae, Stagodontidae) are no longer identified for the early Eocene in Itaboraí. Anatoliadelphidae and Peratheriinae are potential sister clades of the South American “Glasbiidae” and Sternbergiidae/Herpetotheriidae-Rumiodontinae, preliminarily supporting the Atlantogea hypothesis. Sexual dimorphism (e.g., *Gaylordia macrocynodonta*) is identified mainly by the height/robustness of the dentary and size difference between the sexes. The eight petrosal morphotypes identified in Itaboraí (PtI to PtVIII) belong to a stem-Marsupialia (*Epidolops* [PtI]), Pucadelphyda (Pucadelphyoidea gen. nov. [PtII]), Jaskhadelphyoidea (*Marmosopsis*, *Gaylordia*, and *Minusculodelphis* [PtIII, PtIV, PtVIII]), Sternbergiinae (*Carolopaulacoutoia* [PtV]), Derorhynchidae (PtVI) and Rumiodontinae (*Thylacopygmaeus* [PtVII]). For metatherians, the exploitation of different trophic niches between related taxa can be identified mainly by mandibular morphology, especially in frugivorous and carnivorous taxa.

KEY-WORDS: Didelphimorphia. Early Eocene. Itaboraiense. Marsupialia. Petrosal. Systematics.

LISTA DE ABREVIATURAS E SIGLAS

- AMNH - American Museum of Natural History, New York, NY, EUA
- MCN-PV - Seção de Paleontologia, Museu de Ciências Naturais, Secretaria do Meio Ambiente e Infraestrutura (SEMA; [ex. Fundação Zoobotânica do Rio Grande do Sul, FZBRGS]), Porto Alegre, RS, Brasil
- MCT (ex DGM – Divisão de Geologia e Mineralogia), coleção de mamíferos (mamíferos de Itaboraí), Museu de Ciências da Terra (MCTer), Rio de Janeiro, RJ, Brasil
- MLP - Museo de La Plata, La Plata, Argentina
- MN- Museu Nacional do Rio de Janeiro, Rio de Janeiro, RJ, Brasil
- UERJ - Universidade do Estado do Rio de Janeiro, Rio de Janeiro, RJ, Brasil
- UFPE - Universidade Federal de Pernambuco, Recife, PE, Brasil
- UFRGS - Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brasil
- UFRJ-DG- Coleção de paleontologia do Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brasil
- YPFB Pal - Colecciones de Paleontología del Centro de Tecnología Petrolera de Yacimientos Petrolíferos Fiscales de Bolivia, Santa Cruz, Bolivia
- Acc - crista supranumerária (sensu GOIN, 2007)
- c - canino inferior
- C - canino superior
- CaCu - faceta calcâneo-cuboide do calcâneo (sensu SZALAY, 1994)
- CaCud - sub-faceta calcâneo-cuboide distal do calcâneo (homóloga a sub-faceta calcâneo-cuboide auxiliar – CaCua) (sensu SZALAY, 1994)
- CaCum - sub-faceta calcâneo-cuboide medial do calcâneo (sensu SZALAY, 1994)
- CaCup - sub-faceta calcâneo-cuboide proximal do calcâneo (homóloga a sub-faceta calcâneo-cuboide lateral – CaCul) (sensu SZALAY, 1994)
- Dh - altura do dentário
- dp3 - terceiro pré-molar inferior decíduo
- DP3 - terceiro pré-molar superior decíduo
- Dt - diastema
- Dw - largura do dentário
- i - incisivo inferior (números indicam seu *locus* correspondente) (sensu HERSHKOVITZ, 1995)
- I - incisivo superior (números indicam seu *locus* correspondente) (sensu HERSHKOVITZ, 1995)

IMG - Itaboraí metatherian group (referente a elementos tarsais – i.e., calcâneo e astrágalo) (sensu SZALAY, 1994)

IMGF - Itaboraí metatherian group femur (sensu SZALAY e SARGIS, 2001)

L - comprimento (obs. para os dentes compreende a dimensão mesio-distal)

LM2e - comprimento estimado para o segundo molar superior em função do comprimento do petroso

m - molar inferior (números indicam seu *locus* correspondente)

M - molar superior (números indicam seu *locus* correspondente);

Me - área estimada para um molar superior em função das dimensões do *promontorium* de um petroso;

mA - área de molar inferior (obs. a área corresponde a L x W)

MA - área de molar superior (obs. a área corresponde a L x W)

Me - área de molar inferior estimada em função da regressão da área do *promontorium*

p, Pré-molar inferior (números indicam seu *locus* correspondente)

P, Pré-molar superior (números indicam seu *locus* correspondente)

PtApromol - área do *promontorium* do petroso

PtL - comprimento do petroso

PtLpromol - comprimento do *promontorium* do petroso

Pt - morfótipo de petroso isolado

Rt - espaço retro-molar

StA - cúspide estilar A

StB - cúspide estilar B

StB1 - cúspide estilar supernumerária posicionada disto-labialmente a StB

StC - cúspide estilar C

StD - cúspide estilar D

StE - cúspide estilar E

Tb - “trabécula óssea” (i.e., reduzido espaço ósseo entre os alvéolos dos elementos de dentição inferior)

Tri - trigônido

Tal - talônido

W - largura (obs. para os dentes compreende a dimensão labio-lingual)

MC - massa corporal

OCEI - Ótimo Climático do Eoceno Inicial (EECO, Early Eocene Climatic Optimum)

FABI - First American Biotic Interchange (tradução: Primeiro Intercâmbio Biótico das Américas) (sensu GOIN et al, 2012, 2016)

MEV - microscopia eletrônica de varredura

NMI - número mínimo de indivíduos;

AMP - árvores mais parcimoniosas (MPTs, most parsimonious trees)

MA - milhões de anos atrás

NALMA - North American Land Mammal Age (tradução: Idade Mamífero Terrestre Norte-americanas)

MTPE - Máximo Termal do Paleoceno-Eoceno (PETM, Paleocene-Eocene Thermal Maximum)

RW/L - razão largura pelo comprimento

SALMA - South American Land Mammal Age (tradução: Idade Mamífero Terrestre Sul-americanas)

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1 INTRODUÇÃO

Metatheria Huxley, 1880 compreende o clado de Mammalia Linnaeus, 1758 que inclui todos os Marsupialia Illiger, 1811 atuais, os extintos e todos os táxons mais próximos a esse grupo do que aos Eutheria Gill, 1872 (GOIN et al., 2016; BECK, 2017). No Hemisfério Sul, os metatérios representaram o clado de mamíferos de maior diversidade taxonômica para o Paleogeno, o que atesta a sua grande importância para a Paleomastozoologia sul-americana (GOIN e OLIVEIRA, 2007; GOIN et al., 1998a, 2009, 2016; OLIVEIRA e GOIN, 1999, 2011, 2012, 2015; OLIVEIRA et al., 2016, 2021; BECK, 2017; CARNEIRO e OLIVEIRA, 2017a, 2017b, 2023; CARNEIRO et al., 2018; CARNEIRO, 2018, 2019; RANGEL et al., 2019, 2023a, 2023b).

Durante o isolamento geográfico da América do Sul em grande parte do Paleogeno, os metatérios experimentaram uma diversificação evolutiva ocupando zonas adaptativas extremamente diversas, e que em outras partes do mundo eram ocupadas por outros grupos de mamíferos (OLIVEIRA e GOIN, 2012). Atualmente, neste continente, os Metatheria restringem-se aos Didelphidae, Caenolestidae e Microbiotheridae (GOIN et al., 2016), todos pertencentes a Marsupialia (BECK, 2017; CARNEIRO, 2019).

Dentre as localidades fossilíferas com metatérios paleogenos da América do Sul, a fauna da Bacia de Itaboraí destaca-se por apresentar a maior diversidade fóssil conhecida para o grupo (com quase 30 gêneros e mais de 40 espécies). A localidade de Itaboraí também corresponde a fauna temporalmente “mais próxima” a registrar os efeitos paleoambientais e faunísticos resultantes do Máximo Termal do Paleoceno-Eoceno (MTPE) (GOIN et al., 2016), evento que resultou no aumento de 5-8 °C na temperatura média do planeta por liberação massiva e “rápida” de dióxido de carbono na atmosfera terrestre entre 55.5-55.3 Ma (BOWEN et al., 2015). Essas erupções vulcânicas resultaram na expansão das florestas e climas tropicais na América do Sul durante o Eoceno inicial, especialmente durante o Ótimo Climático do Eoceno Inicial (OCEI), condições paleoambientais associadas à diversificação dos metatérios na América do Sul.

Por conta disso, o MTPE + OCEI são considerados como os eventos paleoambientais “mais significativos” para a evolução dos metatérios durante o Paleogeno (WOODBURNE et al., 2014; GOIN et al., 2016; CARNEIRO, 2019; TARQUINI et al., 2022; CARNEIRO e OLIVEIRA, 2023), o que confere a fauna de Itaboraí uma posição de destaque no que se refere a compreensão da evolução dos metatérios no Hemisfério Sul.

Com relação a essa fauna, estudos envolvendo os metatérios são conhecidos desde o final da década de 40. Os fósseis de vertebrados preservados em fissuras no calcáreo que constitui essa bacia foram coletados e estudados pela equipe de Carlos de Paula Couto (Museu Nacional [MN]), American Museum of Natural History (AMNH) (PAULA COUTO, 1952, 1962, 1970) e Júlio da Silva Carvalho, diretor da Divisão de Geologia e Mineralogia (DGM) do Departamento Nacional de Produção Mineral (DNPM). Ao final da década de 60, novas fendas foram encontradas e exploradas pelos pesquisadores Ignácio Muniz da UFRJ, e Lillewyn Ivor Price e Diógenes de Almeida Campos, ambos do Museu de Ciências da Terra (MCT, [ex DGM]). Posteriormente, os espécimes associados aos metatérios foram revisados por Marshall (1987). Uma década depois, Oliveira (1998) apresentou uma nova revisão desses espécimes, sendo os seus resultados utilizados como base pelas coleções brasileiras para identificação taxonômica dos metatérios nelas presentes.

A grande diversidade de táxons já descrita para a localidade de Itaboraí em associação com a idade geologicamente “próxima” ao Máximo Termal do Paleoceno-Eoceno (MTPE) fazem dessa fauna uma das mais importantes e completas assembleias de vertebrados para o estudo da evolução e adaptação das paleomastofaunas sul-americanas após o grande evento paleoclimático ocorrido por volta de 55.5-55.3 milhões de anos atrás.

Apesar do grande volume de trabalhos relacionados aos metatérios de Itaboraí e de sua importância a nível global para a compreensão da evolução das faunas sul-americanas, os metatérios de Itaboraí ainda carecem de análises mais detalhadas. No âmbito desta tese, muitos espécimes inéditos foram estudados, no que novos dados sobre as relações oclusivas entre molares superiores e inferiores, morfologia dentária e mandibular, reassociação de petrosos isolados com táxons da fauna, afinidades filogenéticas, relações paleobiogeográficas e inferências ecomorfológicas são apresentadas para os metatérios de Itaboraí.

Em adição, apresenta-se a maior e mais diversa matriz morfológica para o clado dos metatérios já produzida na literatura científica, o que permitiu um grande avanço na compreensão da evolução desses animais durante o Paleogeno. Nesse contexto, apresenta-se nesta tese uma revisão taxonômico-sistemática para o clado dos metatérios com o intuito de redefinir o que se conhece sobre o clado de mamíferos mais diversos do Paleogeno da América do Sul.

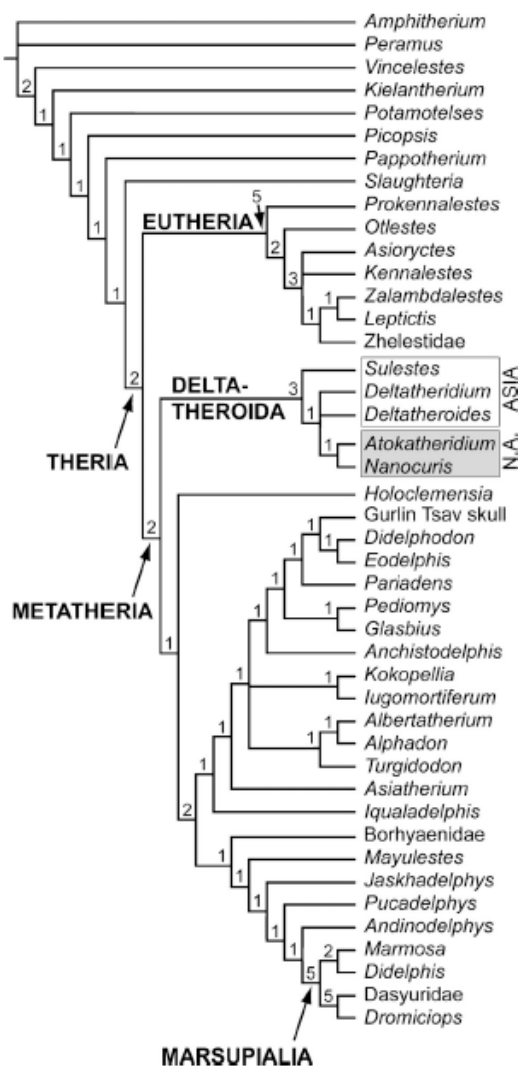
2 REVISÃO BIBLIOGRÁFICA

2.1 METATHERIA: DEFINIÇÃO, ORIGEM E PALEOBIOGEOGRAFIA

2.1.1 América do Norte e Ásia

Segundo Kielan-Jaworowska, Cifelli e Luo (2004), Metatheria é definido como a linhagem que compreende todos os animais mais próximos dos marsupiais do que dos placentários. Metatheria é representado pelo clado dos Deltatheroida Kielan-Jaworowska, 1982, que compreende os Deltatheridiidae Gregory e Simpson, 1926, e táxons afins; e pelo seu clado-irmão, Marsupialiformes Vullo et al., 2009 (VULLO et al., 2009), que inclui os Marsupialia. A relação de grupo-irmão entre Deltatheroida + Marsupialiformes foi suportada por diversos estudos e análises filogenéticas, que remontam desde a década de 90 (KIELAN-JAWOROWSKA e NESSOV, 1990; AVERIANOV, ARCHIBALD e EKDALE, 2010; ROUGIER, WIBLE e NOVACEK, 2004; ROUGIER, DAVIS e NOVACEK, 2015; WILSON e RIEDEL, 2010) (fig. 2.1), modificando a ideia inicial de que os Deltatheroida poderiam ser um grupo mais antigo ao clado Eutheria + Metatheria (BUTLER e KIELAN-JAWOROWSKA, 1973).

Figura 1 - Filogenia entre Metatheria e Deltatheroida (WILSON e RIDLE, 2010). É possível notar a relação de grupo irmão entre Deltatheroida + Metatheria.



Fonte: Wilson e Ridle (2010).

Originalmente, considerava-se que os Metatheria (i.e., Deltatheroidea + Marsupialiformes) tiveram sua origem e irradiação “basal” durante o Cretáceo Inicial da Ásia (LUO et al., 2003). Entretanto, os mais antigos metatérios são conhecidos para o Grupo Trinity (Cretáceo Inferior), USA, América do Norte (ver, e.g., KIELAN-JAWOROWSKA e CIFELLI, 2001; DAVIS, CIFELLI e KIELAN-JAWOROWSKA, 2008; DAVIS e CIFELLI, 2011; AVERIANOV, 2015), indicando que a origem desse clado remonta há, pelo menos, 110 milhões de anos no continente norte-americano. Os dois metatérios conhecidos para essa fauna são *Oklatheridium szalai* Davis, Cifelli, Kielan-Jaworowska, 2008, e *Atokatheridium boreni* Kielan-Jaworowska e Cifelli, 2001. A presença desses táxons demonstra que os Metatheria já haviam se diversificado durante o Cretáceo Inicial (LUO et al., 2003). Curiosamente, apesar de *Oklatheridium* e *Atokatheridium* serem considerados como representantes dos Deltatheroidea (ver e.g., AVERIANOV, ARCHIBALD e EKDALE, 2010), muitas de suas características indicam que eles podem representar linhagens mais antigas que os Deltatheroidea +

Marsupialiformes. Isso resgataria uma origem mais recente para a dicotomia entre Deltatheroidea e Marsupialiformes.

Os mais antigos Marsupialiformes são conhecidos para o início do Cenomaniano (entre 100-98 Ma, Cretáceo Tardio) da América do Norte (EUA) e Europa (França). Dentre os representantes conhecidos para a América do Norte estão *Kokopellia juddi* Cifelli, 1993, *Sinbadelphys schmidtii* Cifelli, 2009, *Pariadens mckennai* Cifelli, 2009 e *Adelodelphys muizoni* Cifelli, 2009 (CIFELLI, 1993; CIFELLI e MUIZON, 1997; CIFELLI, 2009). Por sua vez, dentre os táxons europeus, destacam-se *Arcantiodelphys marchandi* Vullo, Gheerbrant, Muizon et al, 2009, que é considerado como filogeneticamente mais próximo dos Marsupialiformes do que dos Deltatheroidea (VULLO, GREERBRANT, MUIZON et al., 2009), e *Pariadens?* Cifelli e Eaton, 1987 (VULLO, GREERBRANT, BEUREL et al., 2020). A nível de curiosidade, Vullo et al. (2020) considerou os espécimes de *Pariadens?* franceses como pertencendo a um Stagodontidae Marsh, 1889, que é um posicionamento similar ao considerado por outros autores (EATON, 1993; CIFELLI, 2004; WILLIAMSON, BRUSATTE, CARR et al., 2012; WILLIAMSON, BRUSATTE e WILSON, 2014). Entretanto, essa hipótese foi contestada por Fox e Naylor (2006). Considerando *Pariadens*, suas características morfológicas não permitem tal classificação, visto que o p3 recuperado na França não é hipertrofiado e bulboso, e os molares inferiores não apresentam um paracônido subigual em altura ao protocônido, uma sinapomorfia dos Stagodontidae (ver e.g., CLEMENS, 1966; COHEN, 2017).

Dentre os táxons conhecidos para o Cenomaniano inicial, *Kokopellia*, *Sinbadelphys* e *Adelodelphys* não possuem posição taxonômica definida, sendo considerados como linhagens “basais” dos Marsupialiformes (CIFELLI, 1993; CIFELLI e MUIZON, 1997; CIFELLI, 2004; WILLIAMSON, BRUSATTE, CARR et al., 2012; WILLIAMSON, BRUSATTE e WILSON, 2014). Por sua vez, *Archantiodelphys*, *Dakotadens* e *Pariadens* representam membros do clado Archimetatheria Szalay, 1994 (sensu CARNEIRO e OLIVEIRA, 2017a), que compreende Stagodontioidea Marshall e Kielan-Jaworowska, 1992 (*Pariadens* + Stagodontidae; sensu CARNEIRO e OLIVEIRA, 2017a) + Pediomyoidea *latu sensu* (*Arcantiodelphys?*, *Dakotadens?* Eaton, 1993; *Scalaridelphys* Cohen, Davis e Cifelli, 2021; + Pediomyoidea (Simpson, 1927) [*Aquiladelphys* Fox, 1971, *Iqualadelphys* Fox, 1897, *Pedimys* Marsh, 1889, *Unnuakomys* Eberli, Clemens, McCarthy et al, 2019, *Leptalestes* Davis, 2007, e *Protolambda* Osborn, 1898]; sensu CARNEIRO e OLIVEIRA, 2017a; CARNEIRO, OLIVEIRA e GOIN, 2018). Isso indica que Metatheria, Deltatheroidea, Marsupialiformes e Archimetatheria (Stagodontioidea e Pediomyoidea *latu sensu*) já haviam se diversificado durante o Cretáceo Inicial (proavelmente, no limite Aptiano-Albiano ou durante o Albiano).

Considerando a biogeografia dos Metatheria, a presença de uma maior diversidade de táxons restritos à América do Norte pode ser considerada como um indicativo de que a irradiação "basal" desse clado ocorreu, de fato, na América do Norte durante o Cretáceo Inicial (ver CIFELLI, 2004). A presença de alguns Marsupialiformes na Europa indica que esse clado já havia se diversificado durante o Cretáceo Inicial na América do Norte preteritamente a sua dispersão para a Europa, como originalmente proposto por Vullo et al. (2009, 2020). Entretanto, as faunas do Cretáceo Inicial e Cenomaniano inicial não apresentam (até o presente momento) representantes reconhecidos dos Alphadontia Archer, 1984 (sensu CARNEIRO e OLIVEIRA, 2017b), Peradectia Marshall, Case e Woodburne, 1990, Sudameridelphia Szalay, 1994 (sensu CARNEIRO e OLIVEIRA, 2023) e táxons mais aparentados a esses do que aos Archimetatheria. Isso pode indicar que esses clados se diversificaram durante o Cretáceo Tardio.

Por sua vez, o Cretáceo da Ásia apresenta uma grande diversidade de Deltatheroidea, com cinco gêneros reconhecidos (*Deltatheridium* Gregory e Simpson, 1926, *Deltatheroides* Gregory e Simpson, 1926, *Sulestes* Nessel, 1985, *Tsagandelta* Rougier, Davis e Novacek, 2015, e *Lotharidium* Bi, Jin, Li et al., 2015), todos atualmente considerados como pertencentes a Deltatheridiidae (ver ROUGIER, WIBLE e NOVACEK, 1998; 2004; AVERIANOV, ARCHIBALD e EKDALE, 2010; BI, JIN, LI et al., 2015; ROUGIER, DAVIS e NOVACEK, 2015), e um Marsupialiformes, *Asiatherium reshetovi* Trofimov e Szalay, 1994 (TROFIMOV e SZALAY, 1994; SZALAY e TROFIMOV, 1996). Dentre esses, o mais antigo é *Sulestes* do Turoniano (Cretáceo Tardio) do Uzbequistão (AVERIANOV e KIELAN-JAWOROWSKA, 1999; AVERIANOV, ARCHIBALD e EKDALE, 2010). É possível considerar que Deltatheroidea apresenta como área ancestral o continente asiático (caso *Oklatheridium* e *Atokatheridium* não representem membros desse clado), Deltatheridiidae teria se originado na Ásia e Marsupialiformes na América do Norte.

Durante o Cenomaniano tardio, os Marsupialiformes apresentam uma maior diversidade, sendo os principais taxa conhecidos para a Formação Naturita, Utah, EUA: *Alphadon* sp., *Dakotadens morrowi* Eaton, 1993, *Dakotadens* sp., *Eoalphadon clemensi* (Eaton, 1993), *Eoalphadon lillegraveni* (Eaton, 1993), *Eoalphadon woodburnei* Eaton, 2009, *Varalphadon janetae* Carneiro, 2018, *Pariadens kirklandi* Cifelli e Eaton, 1987 e *Protalphadon* sp. (CIFELLI e EATON, 1987; EATON, 1993, 2009). A Formação Cedar Mountain, Utah, EUA, também apresenta alguns Marsupialiformes, como *Dakotadens pertritus* Cifelli, Cohen e Davis, 2016, e o enigmático *Culicolestes kielanae* Cifelli, Cohen e Davis, 2016; sendo esta fauna datada em aproximadamente 97 Ma (CIFELLI, COHEN e DAVIS, 2016). *Eoalphadon*, inicialmente considerado como uma espécie de *Alphadon* por Eaton (1993), mantém a sua

posição como um Alphasodontidae (EATON et al., 1999; EATON, 1993, 2009). *Varalphadon* sp. foi descrito como *Varalphadon janetae* (CARNEIRO, 2018). Por sua vez, *Culicolestes* e *Protalphadon* sp. não foram propriamente revisados até o presente momento.

A fauna do Turoniano e Coniaciano é pouco conhecida no registro fóssil. A principal fauna conhecida é a do Membro Smoky Hollow da Formação Straight Cliffs, Utah, EUA, provisoriamente atribuída ao Turoniano médio ou superior. Durante esse período os mamíferos são pouco preservados a nível mundial (CIFELLI, 1990a; COHEN, 2017; COHEN, DAVIS e CIFELLI, 2020, 2021), ainda assim, alguns metatérios são conhecidos. Dentre os metatérios conhecidos destacam-se *Anchistodelphys delicatus* Cifelli, 1990a (*Varalphadon delicatus*, segundo EATON e CIFELLI, 2013); *Fumodelphodon pulveris* Cohen, 2017 e *Hoodotherium praeceps* Cohen, 2017, ambos Stagodontidae; *Scalaridelphys martini* (Cohen, Davis e Cifelli, 2020), *S. aquilana* (Cohen, Davis e Cifelli, 2020) e *Pediomyoidea?* indet. (ver Cohen, Davis e Cifelli, 2020), e alguns espécimes não atribuídos a um gênero ou espécie específicos (CIFELLI, 1990a). Por sua vez, *Varalphadon* sp. foi identificado para o final do Coniaciano, sendo representado por um único molar inferior isolado (EATON, 2006a), que foi associado a *V. janetae* por Carneiro (2018).

Os metatérios do Santoniano-Campaniano inicial (Aquilan NALMA) são muito mais abundantes e mais diversos do que os conhecidos para o Cenomaniano, Turoniano e Coniaciano (CIFELLI, 1990b, 1990c; EATON, 2006a, 2006b, 2013; DAVIS, CIFELLI e COHEN, 2016; COHEN, 2017; COHEN, DAVIS e CIFELLI, 2020, 2021). Dentre os taxa do Aquilan NALMA destacam-se *Albertatherium* Fox, 1971, *Alphadon* Simpson, 1927, *Anchistodelphys* Cifelli, 1990c, *Apistodon* (Davis, 2007), *Aquiladelphis* (Fox, 1971), *Eodelphis* Matthew, 1916, *Iqualadelphis* Fox, 1987, *Iugomortiferum* Cifelli, 1990c, *Protalphadon* Cifelli, 1990b, *Turgidodon* Cifelli, 1990b, *Varalphadon* (Johanson, 1996a) e outros espécimes com identificação incerta (CIFELLI, 1990c; DAVIS, CIFELLI e COHEN, 2016; EATON et al., 1999; EATON, 2006a, 2006b, 2013; JOHANSON, 1995, 1996a). Durante esse período temporal é conhecido para a América do Norte um grande Tribosphenida, em comparação com outros metatérios da época; *Zygiocuspis goldingi* Cifelli, 1990d, é tido como um dos maiores mamíferos do Aquilan NALMA (CIFELLI, 1990d). Entretanto, mesmo sendo considerado como um Tribosphenida não-Theria, esse táxon apresenta inúmeras características compatíveis com a linhagem dos Stagodontidae. As principais faunas dessa idade estão localizadas nas Formações Eagle, Wahweap e Straight Cliffs, Utah, EUA.

O Campaniano superior (Judithian NALMA) é representado pelas Formações “Mesaverde”, Wyoming; Marshalltown, New Jersey; Kaiparowits, Utah; Two Medicine Formation, Montana; Fruitland, New Mexico; Aguja, Texas; e Judith River, Montana, EUA;

Oldman, Alberta; Dinosaur Park, Alberta; and Milk River, Alberta, Canada. Durante esse estágio os Metatheria são tão diversos quanto os do Aquilan NALMA, e, de fato, muitos gêneros sobrevivem do Santoniano até o final do Campaniano. Dentre os taxa representados durante o Judithian NALMA destacam-se: *Alphadon*, *Turgidodon*, *Protalphadon*, *Varalphadon*, *Bistius* Clemens e Lillegraven, 1986; *Aenigmadelphys* Cifelli e Johanson, 1994; *Leptalestes* Davis, 2007; *Protolambda* (Osborn, 1898), *Pedimys* Marsh, 1889; *Eodelphis*, *Didelphodon* Marsh, 1889; e *Ectocentrocrustus* Case, Goin e Woodburne, 2005 (CASE, GOIN e WOODBURNE, 2005; CIFELLI, 1990b, 1994; CIFELLI e JOHANSON, 1994; DAVIS, 2007; EATON, CIFELLI, HUTCHISON et al., 1999; CLEMENS, 1991; CLEMENS e LILLEGRAVEN, 1986; FOX, 1979a, 1979b, 1981; FOX e NAYLOR, 2006; GRANDSTAFF et al., 1992; LILLEGRAVEN, 1969; LILLEGRAVEN e MCKENNA, 1986; MONTELLANO, 1988; RIGBY e WOLBERG, 1987; SAHNI, 1972; SCOTT e FOX, 2015; WOODWARD, 1916).

O Maastrichtiano (“Edmontonian” e Lancian NALMAs; CIFELLI, EBERLE, LOFGREN et al., 2012) apresentou uma alta diversidade para a linhagem dos Metatheria. Muitas linhagens presentes durante o Judithian NALMA são consideradas extintas, baseado no registro fóssil atual, após o limite Campaniano-Maastrichtiano (e.g. *Aenigmadelphys*, *Varalphadon*, *Ectocentrocrustus* e *Bistius*), enquanto outras espécies sobrevivem após esse período (e.g. *Eodelphis*, *Didelphodon*, *Aquiladelphis*, *Leptalestes*, *Pedimys*, *Protolambda*, *Protalphadon*, e *Alphadon*) (CASE GOIN e WOODBURNE, 2005; CLEMENS, 1966; DAVIS, 2007; FLYNN, 1986; LILLEGRAVEN, 1969; RIGBY e WOLBERG, 1987; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014). É durante o Maastrichtiano que ocorrem as primeiras ocorrências de *Nortedelphys* Case, Goin e Woodburne, 2005; *Hatcheritherium* Case, Goin e Woodburne, 2005; e *Nanocuris* Fox, Scott e Bryant, 2007 (CASE, GOIN e WOODBURNE, 2005; DAVIS, 2007; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014). As principais Formações do Maastrichtiano na América do Norte são: Lancian, Wyoming; Hell Creek, Montana e South Dakota; Kirtland, New Mexico; North Horn, Utah; St. Mary River, Montana, EUA; Edmonton, Canada (BREITHAUPT, 1982; CIFELLI e MUIZON, 1998; CLEMENS, 2002; FOX e NAYLOR, 1986; FOX, 1989; FLYNN, 1986; HUNTER, HARTMAN e KRAUSE, 1997; HUNTER e ARCHIBALD, 2002; HUNTER, HEINRICH e WEISHAMPEL, 2010; OSBORN, 1893; SIMPSON, 1927; WILLIAMSON e WEIL, 2008; WILSON e RIEDEL, 2010).

O Cretáceo da América do Norte apresenta muitas linhagens consideradas endêmicas, dentre as quais se destacam os “Alphadontidae” (Marshall, Case e Woodburne, 1990), os Pedimyioidea (Simpson, 1927) e os Stagodontidae Marsh, 1889 (WILLIAMSON et al., 2014). Os metatérios norte-americanos sofreram uma grande redução em sua diversidade durante o

limite Cretáceo–Paleoceno (KPg), com a extinção de quase todas as linhagens conhecidas para o Cretáceo, à exceção dos Peradectia (WILLIAMSON et al., 2014) e Sudameridelphia.

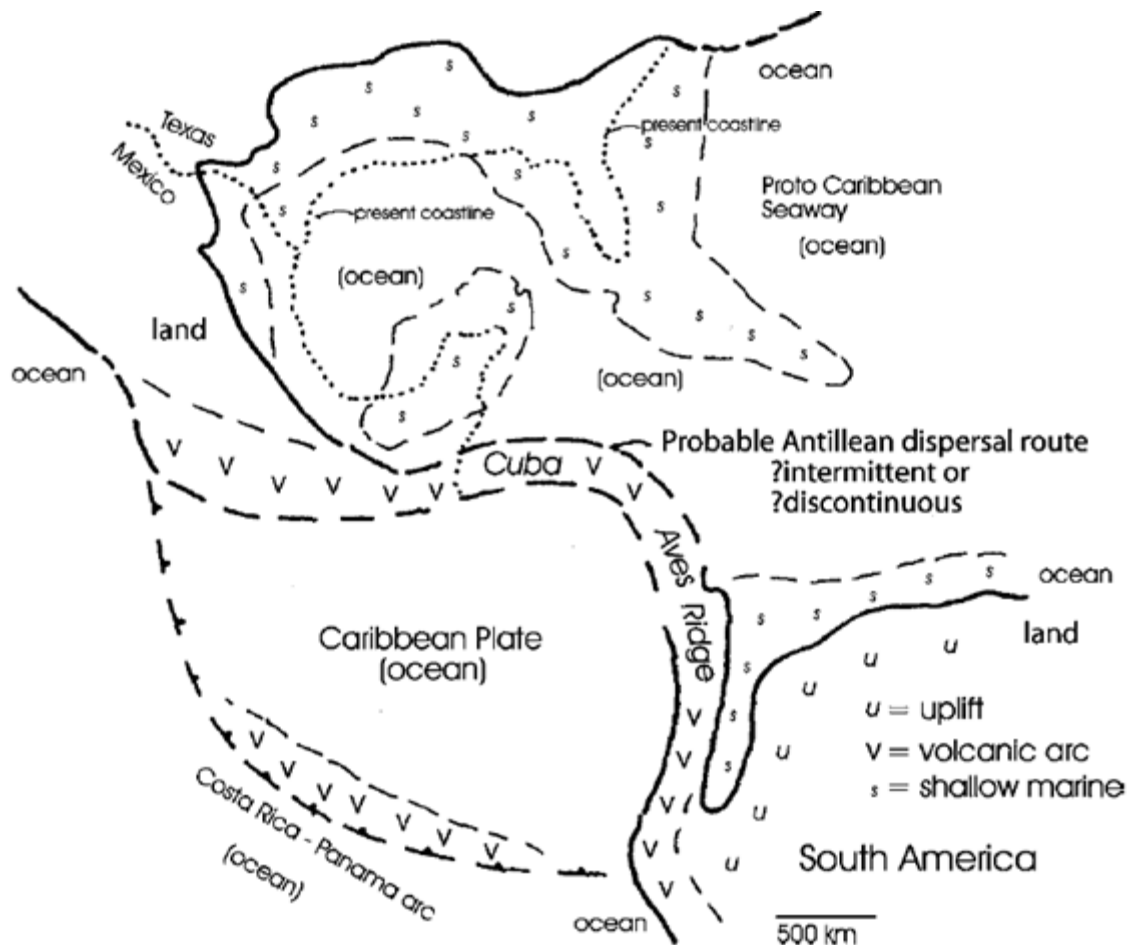
2.1.2 A origem dos metatérios sul-americanos

Com relação a chegada dos metatérios a América do Sul, muitos estudos debateram esse assunto: Clemens (1968) defendeu a hipótese de que “didelfídeos” basais, como *Alphadon*, colonizaram a América do Sul e Austrália durante o Cretáceo Tardio e Cenozoico inicial, enquanto os metatérios europeus corresponderiam a uma linhagem a parte, representando uma dispersão independente da que originou os metatérios do Hemisfério Sul. Paula Couto (1974) concluiu que uma origem norte ou sul-americana eram igualmente parcimoniosas (baseando-se no registro fóssil da época) e que a linhagem dos Australidelphia seria a última a ter surgido na evolução dos Metatheria. Ele seguiu as ideias propostas por Clemens (1968) de que os metatérios europeus seriam descendentes de linhagens norte-americanas. A ideia de que os táxons africanos e europeus são mais próximos dos norte-americanos do que dos sul-americanos nunca foi devidamente elucidada e alguns estudos propõem que os metatérios africanos e europeus são aparentemente mais próximos dos sul-americanos do que dos norte-americanos (MABESOONE e STINNESBECK, 1993). Atualmente, as relações filogenéticas entre os metatérios do Cenozoico norte-americano, sul-americano e euro-afro-asiático nunca foi elucidada ou discutida em detalhes.

Szalay (1994) analisou os elementos pós-cranianos de muitos metatérios e propôs que todas as linhagens sul-americanas teriam derivado de um único ancestral norte-americano, pertencendo esse ancestral a um “stock peradectoideo”. Entretanto, estudos recentes indicam que muitas linhagens de metatérios sul-americanos já existiam durante o Cretáceo da América do Norte (e.g. Hatcheriformes, Polydolopiformes, “Eobrasilinae” e Pediomyoidea), o que indicariam uma dispersão do Hemisfério Norte para o Hemisfério Sul ou mesmo um intercâmbio faunístico durante o Cretáceo Final (i.e. FABI) (CASE e WOODBURNE, 1986; CASE, GOIN e WOODBURNE, 2005; PASCUAL, 2006; ORTIZ-JAUREGUIZAR, 2009; GOIN et al., 2016). Segundo esses estudos, a fauna sul-americana é representada por linhagens “invasoras” norte-americanas que se irradiaram durante o Paleoceno no Hemisfério Sul. Essas faunas chegaram à América do Sul através da Placa do Caribe; durante o Cretáceo Final o mar do caribe era mais estreito e raso do que é hoje, sendo formado por diversos arcos de ilhas por conta do vulcanismo intenso (‘Aves Ridge’) (fig. 2.2). As faunas da América do Sul, Antártica e Austrália estão claramente relacionadas, indicando que um grande evento de dispersão

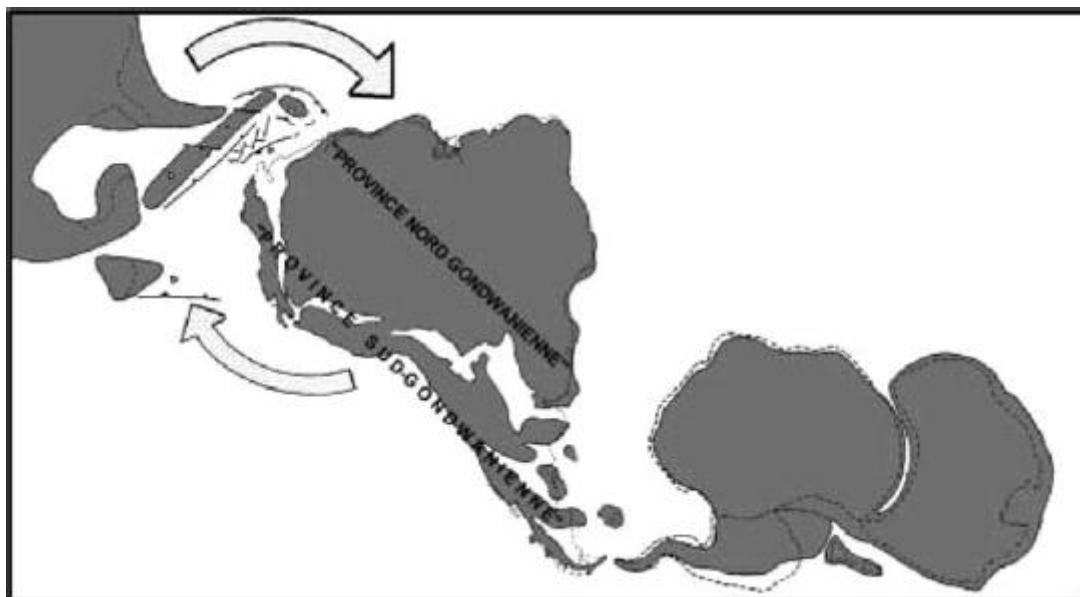
ocorreu entre esses três continentes (ORTIZ-JAUREGUIZAR, 1996, 2009; PASCUAL, 2006; PASCUAL e ORTIZ-JAUREGUIZAR, 2007; REGUERO, GELFO, LÓPEZ et al., 2014; WOODBURN e CASE, 1996) (fig. 2.3).

Figura 2 - Reconstrução da Placa do Caribe apresentando as prováveis rotas paleobiogeográficas do grupo.



Fonte: Pindell (1994).

Figura 3 - Reconstrução do posicionamento da América do Norte e de Gondwana durante o Cretáceo Final.



Fonte: Pascual e Ortiz-Jaureguizar (2007).

Dentre os Metatheria, a linhagem dos Marsupialia Gill, 1872 não havia se diversificado até 82,5 milhões de anos atrás (maa), com quatro linhagens cruzando o limite KPg (i.e., Didelphimorphia, Paucituberculata, Peramelemorphia e demais linhagens). Dentre as linhagens atuais, a primeira a diversificar-se foi a dos Didelphimorphia (82,5 maa), seguida pelos Paucituberculata (73,8 maa), Peramelemorphia (66,8 maa), Diprotodontia + Microbiotheria (63,6 maa) e por último as linhagens dos Dasyuromorphia + Notoryctemorphia (58,5 maa) (BININDA-EMONDS, CARDILLO, JONES et al., 2007).

Segundo Archer, Horovitz e Sánchez-Villagra (2004), o clado "Ameridelphia" Szalay, 1982 (i.e., Didelphimorphia + Paucituberculata) seria parafilético, visto que os Paucituberculata seriam mais próximos dos Australidelphia Szalay, 1982 (Microbiotheria, Peramelemorphia, Notoryctemorphia, Dasyuromorphia e Diprotodontia) do que propriamente dos Didelphimorphia. O clado Australidelphia seria monofilético, estando os Microbiotheria e os Peramelemorphia como os táxons mais basais dessa linhagem, entretanto Bininda-Emonds, Cardillo, Jones et al. (2007) classifica os Peramelemorphia como a linhagem mais basal dentre os Australidelphia e Microbiotheria como uma linhagem aparentada a linhagem dos Diprotodontia (Fig. 2.5). Beck (2008), por sua vez, classifica os Microbiotheria como a linhagem mais basal dos Australidelphia e Peramelemorphia como grupo irmão dos Dasyuromorphia + Notoryctemorphia.

2.3 PALEOBIOGEOGRAFIA: HEMISFÉRIO SUL

O registro mais antigo confirmado de um Metatheria na América do Sul é o ?Polydolopimorphia basal *Cocatherium lefipantum* Goin et al., 2006; encontrado na Formação Lefipán, Província de Chubut, Argentina, datada para o Paleoceno inferior (GOIN, PASCUAL, TEJEDOR et al., 2006). A Formação Umayo, Peru, tem a sua idade geológica discutida atualmente: inicialmente, essa formação foi datada para o Limite KPg (Cretáceo Final–Maastrichtiano superior/Paleoceno inferior–Daniano) (SIGÉ, 1971, 1972; CROCHET e SIGÉ, 1993, 1996), entretanto, ela é atualmente considerada como sendo Paleoceno superior–Eoceno inferior (SIGÉ, SEMPERE, BUTLER et al, 2004). Outra fauna antiga da América do Sul é a da Formação Molino, Tiupampa, Bolívia, considerada como Paleoceno inferior em idade (MARSHALL, MUIZON e SIGÉ, 1983; MUIZON, MARSHALL e SIGÉ, 1984; MUIZON, 1992); antes da descoberta de *Cocatherium*, a fauna de Tiupampa era considerada como a mais antiga fauna com metatérios na América do Sul. Um dentário muito fragmentado encontrado na Formação Río Colorado, Argentina, pode representar o mais antigo Metatheria da América do Sul (GOIN, CARLINI e PASCUAL, 1986), visto que a formação é datada para o Cretáceo Final (Maastrichtiano); entretanto, como não foram atribuídas afinidades conclusivas para esse espécime, a fauna da Formação Río Colorado não é considerada como a mais antiga com metatérios da América do Sul.

A fauna de Tiupampa (Paleoceno inferior; Tiupampense SALMA), Bolívia, é conhecida por possuir pelo menos 12 táxons atribuídos aos Metatheria: *Allqokirus australis* Marshall e Muizon, 1988; “*Peradectes*” *austrinum* (Sigé, 1971); *Roberthoffstetteria nationalgeographica* Marshall, Muizon e Sigé, 1983 (MARSHALL, MUIZON e SIGÉ, 1983; MUIZON, MARSHALL e SIGÉ, 1984); *Khasia cordillerensis* Marshall e Muizon, 1988; *Pucadelphys andinus* Marshall e Muizon, 1988; *Mizquedelphys pilpinensis* Marshall e Muizon, 1988; *Incadelphys antiquus* Marshall e Muizon, 1988; *Andinodelphys cochabambensis* Marshall e Muizon, 1988; *Tiulordia floresi* Marshall e Muizon, 1988; *Jaskhadelphys minutus* Marshall e Muizon, 1988 (MUIZON, 1992); *Mayulestes ferox* Muizon, 1994 (MUIZON, 1994, 1998); e *Szalinia gracilis* Muizon e Cifelli, 2001 (MUIZON e CIFELLI, 2001). Há 63,2 Ma (atualmente 64 Ma; ver WOODBURNE, GOIN, RAIGEMBORN et al., 2014), Tiupampa era uma região quente, pantanosa e de clima subtropical, apresentando estações do ano definidas (MUIZON, 1998).

A fauna de Laguna Umayo e Chulpas, Peru, apresentam pelo menos três táxons formalmente atribuídos a Metatheria: “*Peradectes*” *austrinum*, *Chulpasia mattaui* Crochet e Sigé, 1993; e *Sillustania quechuense* Crochet e Sigé, 1996 (SIGÉ, 1971; CROCHET e SIGÉ,

1993, 1996). Sigé (1972) descreve vários espécimes associados à linhagem dos Metatheria, mas, infelizmente, esses espécimes não foram confidentemente atribuídos a nenhum táxon até o momento. Atualmente, a fauna de Laguna Umayo e Chulpas foi considerada como contemporânea a fauna de Itaboraí (i.e. Eoceno inicial; Itaboraiense SALMA) (ver e.g., SIGÉ, SEMPERE, BUTLER et al., 2004); mas recentemente foi considerada como Paleoceno inicial em idade (ver CHORNOGUBSKY e GOIN, 2015).

A fauna de Santa Rosa, Peru, é tentativamente associada à Formação Yahuarango (Oligoceno inferior; ver e.g., CAMPBELL et al., 2021) e apresenta pelo menos 11 táxons descritos: *Rumiodon inti* Goin e Candela, 2004; *Patene campbelli* Goin e Candela, 2004; *Incadolops ucayali* Goin e Candela, 2004; *Wamradolops tsullodon* Goin e Candela, 2004; *Hondonadia pittmanae* Goin e Candela, 2004; *Perulestes cardich* Goin e Candela, 2004; *Perulestes fraileyi* Goin e Candela, 2004; *Sasawatsu mahaynaq* Goin e Candela, 2004; *Kirutherium paititiensis* Goin e Candela, 2004; *Wirunodon chanku* Goin e Candela, 2004; e *Kiruwamaq chisu* Goin e Candela, 2004 (GOIN e CANDELA, 2004).

A fauna de Tinguiririca (Eoceno tardio–Oligoceno inicial; Tinguiririquense SALMA), Chile, é conhecida principalmente pela presença de *Kramadolops abanicoi* Flynn e Wyss, 1999; *Klohnia charrieri* Flynn e Wyss, 1999; e *Pascualdelphys fierrorensis* Flynn e Wyss, 1999 (FLYNN e WYSS, 1999). A fauna de Tinguiririca representa os primeiros sinais de adaptação da fauna para ambientes mais abertos ricos em plantas mais abrasivas, sendo nesse período que se registram as mais antigas evidências de hypsodontia em ungulados e metatérios sul-americanos. A diversidade de ungulados é majoritariamente folívora, enquanto os metatérios são considerados como frugívoros (*Kramadolops* e *Klohnia*) ou insetívoros (*Pascualdelphys*) (CROFT, FLYNN e WYSS, 2008); entretanto, estudos recentes indicam certo índice de folivoria para os dois Polydolopimorphia da formação (ZIMICZ, 2011; 2012).

Outra fauna do Chile de idade Satacruciense SALMA (Mioceno inicial, aproximadamente 17,5–16 Ma) é representada por quatro espécies de *Palaeothentes* (Paucituberculata–Palaeothentidae) e *Cladosicts* (Sparassodonta). Essa idade é coincidente com início do soerguimento da Cordilheira dos Andes. Interessantemente, a fauna de roedores é muito mais diversa, com pelo menos 20 espécies (FLYNN, NOVACEK, DODSON et al., 2002), o que indica um maior domínio faunístico desses animais em comparação com os ecossistemas do final do Paleogeno e início do Neogeno, talvez uma resposta adaptativa aos ambientes mais abertos do Oligoceno–Neogeno.

Uma das mais famosas faunas da América do Sul é a de São José de Itaboraí (BERGQVIST et al., 2009). A bacia de Itaboraí é uma das menores bacias sedimentares do Brasil (cerca de 1 Km²), mas, em contraste ao tamanho, ela é muito fossilífera. Ela foi

preenchida por uma série de calcários clásticos e químicos (travertinos), cortados verticalmente por canais de dissolução, onde a maioria dos fósseis foi encontrada (BERGQVIST et al., 2009). Atualmente, a Bacia de Itaboraí é considerada como Eoceno inferior (Itaboraiense SALMA; WOODBURN et al., 2014). Itaboraí possui mais de 27 gêneros conhecidos: *Patene* Paula Couto, 1961; *Nemolestes* Ameghino, 1902; *Carolocoutoia* Goin, Oliveira e Candela, 1998; *Guggenheimia* Paula Couto, 1952a; *Protodidelphis* Paula Couto, 1952a; *Periprotodidelphis* Oliveira e Goin, 2011; *Zeusdelphys* Marshall, 1987; *Derorhynchus* Paula Couto, 1952a; *Derorhynchidae* gen. nov. 1; *Derorhynchidae* gen. nov. 2; *Minusculodelphis* Paula Couto, 1962; *Marmosopsis* Paula Couto, 1962; *Monodelphopsis* Paula Couto, 1952a; *Eobrasilia* Simpson, 1947; *Gaylordia* Paula Couto, 1952a; *Carolopaulacoutoia* (Paula Couto, 1970); *Didelphopsis* Paula Couto, 1952a; *Itaboraidelphys* Marshall e Muizon, 1984; *Procaroloameghinia* Marshall, 1982a; *Peradectidae* gen. nov. 1; *Pediomyoidea* gen. nov. 1; *Riolestes* Goin et al., 2009; *Bardalestes* Goin et al., 2009; *Bobbschaefferia* Paula Couto, 1970; *Mirandatherium* (Paula Couto, 1952a); *Epidolops* Paula Couto, 1952b; *Gashternia* Simpson, 1935 (BECK, 2016; GOIN, OLIVEIRA e CANDELA, 1998; GOIN e OLIVEIRA, 2007; MARSHALL, 1982a; 1984; 1987; PAULA COUTO, 1952a; 1952b; 1961, 1962, 1970, 1979; OLIVEIRA, 1998; OLIVEIRA e GOIN, 2011; 2015; OLIVEIRA, ZIMICZ e GOIN, 2016; SIMPSON, 1947; WOODBURN et al., 2014). É possível destacar ainda a presença de um provável *Pucadelphyidae* em Itaboraí (LADEVÈZE e MUIZON, 2010).

Recentemente descoberta, a fauna da Formação Guabirota, localizada em Curitiba, Estado do Paraná, Brasil, é datada como pertencendo à idade Barranquense SALMA (Eoceno médio tardio). A paleocomunidade de metatérios é representada por um *Paleothentoidea* (*Paucituberculata*) não formalmente descrito (gen. et sp. indet.), *Nemolestes* (*Sparassodonta*) e um *Argyrolagoidea* (*Polydolopimorphia*) não formalmente descrito (gen. et sp. indet.) (SEDOR et al., 2016).

Dentre os países do Hemisfério Sul, a Argentina concentra o maior número de bacias fossilíferas com registros de *Metatheria*. Tendo em vista o grande número de formações, elas serão citadas e comentadas brevemente. As duas faunas mais antigas com *Metatheria*: Formações Río Colorado (GOIN, CARLINI e PASCUAL, 1986) e Lefipán (GOIN et al., 2006), comentadas anteriormente, apresentam um único espécime cada. Durante o Eoceno muitas faunas destacam-se, mas dentre elas destaco a fauna de Paso del Sapo (TEJEDOR, GOIN, GELFO et al., 2009), com pelo menos 12 gêneros conhecidos. Na fauna de Antofagasta de La Sierra foram encontrados os metatérios *Bonapartherium* sp. nov., atualmente, *Bonapartherium serrensis*; *?Prepidolops alonsoi*, atualmente, *Punadolops alonsoi* (Pascual, 1980a); e cf. *Arminiheringia* Ameghino, 1902; atualmente, *Arminiheringia* sp. (GOIN, CANDELA e

LÓPEZ, 1998; LOPEZ, 1997). Durante o Oligoceno, a mais famosa fauna é de Gran Barranca, Formação Sarmiento, Tinguiririquense SALMA (Oligoceno inicial; ver GOIN, ABELLO e CHORNOGUBSKY, 2010), com pelo menos 18 gêneros conhecidos. O Mioceno Argentino é conhecido, por exemplo, pelas faunas do Valle de Santa María e Río Corral Quemado, Mioceno Inferior (MARSHALL e PATTERSON, 1981); níveis Colhuehuapienses de Gran Barranca, Mioceno inicial (GOIN, ABELLO, BELLOSI et al., 2007); Formación Pinturas (CHORNOGUBSKY e KRAMAZ, 2012; GOIN, TEJEDOR, ABELLO et al., 2010), com gêneros diversos da família Microbiotheriidae, como *Pachybiotherium* e *Microbiotherium*; do Cerro Azul, Mioceno superior (ABELLO, MONTALVO e GOIN, 2002; GOIN, MONTALVO e VISCONTI, 2000), com representantes dos Argyrolagidae (*Argyrolagus* e *Microtragulus*), Caenolestoidea (*Pliodolops*), Sparassodonta (*Achlysictis*), Didelphidae (*Thylamys*, *Zygolestes*, *Thylatheridium*, *Hyperdidelphys*, *Lutreolina*) e Sparassocynidae (*Sparassocynus*). Um trabalho de grande importância para a paleontologia Argentina foram os trabalhos de Simpson (SIMPSON, 1932; 1948; 1970a). Marshall, Muizon e Hoffstetter (1894) revisam vários espécimes coletados na Patagonia por André Tournouër, incluindo metatérios das idades Casamayorenses, Deseadenses, Colhuehuapienses e Santacrucenses SALMAS, representando 23 espécies, 17 gêneros, cinco famílias e quatro superfamílias.

As SALMAS (South American Land Mammal Ages) são idades baseadas na diversidade de mamíferos terrestres encontradas nesses locais. As SALMAS foram inicialmente revisadas por Marshall, Hoffstetter e Pascual (1983). Recentemente, Woodborne, Goin, Raigemborn et al. (2014) apresentaram a mais atualizada revisão das faunas sul-americanas.

No continente Antártico, a única fauna conhecida é a da Formação La Meseta, Eoceno inicial (Riochiquense SALMA). Essa fauna é representada por pelo menos oito gêneros: *Derorhynchus*, *Pauladelphys* Goin et al., 1999; *Marambiotherium* Goin et al., 1999; *Woodburnodon* Goin et al., 2007; *Perrodelphys* Goin et al., 1999; *Xenostylus* Goin et al., 1999; *Protodidelphis* e *Antarctodolops* Woodburne e Zinsmeister, 1984 (CASE, 2006; CHORNOGUBSKY, GOIN e REGUERO, 2009; GOIN, CASE, WOODBURNE et al., 1999; GOIN, ZIMICZ, REGUERO et al., 2007). Essa fauna registra os mais antigos membros conhecidos da ordem Microbiotheria Ameghino, 1889 (GOIN, CASE, WOODBURNE et al., 1999; GOIN, ZIMICZ, REGUERO et al., 2007).

A mais antiga fauna australiana com metatérios é a fauna de Tingamarra, Murgon, Austrália (GODTHELP, ARCHER, CIFELLI et al., 2002). Essa fauna é representada por pelo menos quatro táxons seguramente pertencentes à linhagem dos metatérios já descritos: *Chulpasia jimthorselli* Sigé et al., 2009; *Thylacotinga bartholomaii* Archer, Godthelp e Hand, 1993; *Archaeonothos henkgodthelpi* Beck, 2015; *Djarthia murgonensis* Godthelp, Wroe e

Archer, 1999 (ARCHER, GODTHELP e HAND, 1993; GODTHELP, WROE e ARCHER, 1999; SIGÉ, ARCHER, CROCHET et al., 2009; BECK, 2015). Beck (2008; 2012) apresenta os dois mais antigos e basais táxons atribuídos à linhagem dos Australidelphia: *Djathia* e um gênero ainda não descrito. Beck (2008) descreve espécimes cranianos e pós-cranianos e os associa com *Djathia murgonensis*, recuperando este táxon como um Marsupialia-Australidelphia basal. O gênero ainda não descrito foi identificado por um calcâneo, que representa um mosaico entre um “Ameridelphia” e um Australidelphia (BECK, 2012).

No Hemisfério Sul, em especial na América do Sul, a irradiação dos Metatheria parece estar diretamente relacionada com o Máximo Termal do Paleoceno-Eoceno (MTPE) (ver e.g., WOODBURN, GOIN, BOND et al., 2013; GOIN et al., 2016), que ocorreu entre de 55,5 e 55,3 Ma (BOWEN, MAIBAUER, KRAUS et al., 2015). Esse período é compatível com a expansão de florestas tropicais, que ocuparam quase toda a América do Sul, e a diversificação de árvores frutíferas (WOODBURN, GOIN, BOND et al., 2013; GOIN et al., 2016), o que levou ao surgimento de diversas linhagens frugívoras e folívoras (OLIVEIRA e GOIN, 2011; ZIMICZ, 2011; 2012; 2014a; GOIN et al., 2016). A idade Itaboraiense (*Itaboraian* SALMA) foi datada entre 53-50 Ma, coincidindo com o Ótimo Climático do Eoceno Inicial (EECO, sigla em inglês) (WOODBURN, GOIN, REIGEMBORN et al., 2014).

A extinção de muitas linhagens sul-americanas parece estar diretamente relacionada com o resfriamento global que ocorreu de forma gradual durante o Eoceno médio a superior, resultando na glaciação do Oligoceno inferior. Os ambientes ficaram gradualmente mais secos e com vegetação mais aberta, o que levou a extinção de diversas linhagens frugívoros comuns durante o Eoceno inferior na América do Sul (GOIN et al., 2016). Entretanto, estudos recentes apontam que a variação na sazonalidade das Planícies Argentinas (Gran Barranca) não foi tão evidente como aceito atualmente (KOHN, JOSEF, MADDEN et al., 2004). Dentre os grupos extintos durante esse evento na América do Sul estão os Polydolopimorphia, Herpetotheriidae, Peradectoidea e Protodidelphidae (GOIN et al., 2016). Uma das últimas faunas antes da glaciação oligocênica é a fauna da Formação Sarmiento (Tinguiririquense SALMA) na Argentina (GOIN, ABELLO e CHORNOGUBSKY, 2010), que registra os últimos Caroloameghiniidae, Glasbiidae, Rosendolopidae, alguns Argyrolagoidea (*Klohnia* Flynn e Wyss, 1999, e *Epiklohnia* Goin, Abello e Chornogubsky, 2010). Após esse evento climático, os Didelphidae, Sparassocynidae, Paucituberculata, Argyrolagidae e Borhyaenoidea apresentam um evento de irradiação (ABELLO, 2013; GOIN, MONTALVO, VISCONTI, 2000; GOIN, ABELLO, BELLOSI et al., 2007; GOIN et al., 2016; ZIMICZ, 2011).

Atualmente, os Metatheria sul-americanos estão restritos a um pequeno número de Didelphidae, Caenolestidae e Microbiotheriidae (FLYNN e WYSS, 2004; FORASIEPI e CARLINI, 2010).

2.4 SISTEMÁTICA

2.4.1 Sparassodonta ameghino, 1894

Os Sparassodonta compreendem um grupo de metatérios sul-americanos, cuja tendência evolutiva se deu em direção à dieta carnívora especializada, verificada em seus dentes através da paulatina e gradual perda do metacônido, redução do tamanho do protocone, da plataforma estilar ampliada e redução do talonido, dentre outros caracteres (OLIVEIRA e GOIN, 2012).

Dentre os Sparassodonta, os Borhyaenoidea foram metatérios carnívoros que viveram do Paleoceno inicial ao Plioceno final da América do Sul (BABOT, POWELL e MUIZON, 2002; FORASIEPI, GOIN e MARTINELLI, 2009; MUIZON, 1998; SIMPSON, 1970a), evoluindo na América do Sul por 55 milhões de anos (FORASIEPI e CARLINI, 2010); atualmente, é um clado extinto. O grupo incluía formas variando entre espécies com tamanhos semelhantes a doninhas até espécies predadoras do tamanho de ursos (BABOT, POWELL e MUIZON, 2002). A superfamília Borhyaenoidea incluía marsupiais predadores que habitaram a América do Sul durante o Paleogeno quando o continente estava isolado (ARGOT, 2004a), sendo os principais mamíferos terrestres carnívoros durante esse período (ARGOT, 2004b).

Os Borhyaenoidea mantiveram uma posição de topo na cadeia alimentar na América do Sul durante a maior parte do Cenozoico, apresentando um complexo funcional dentário relacionado a uma dieta hipercarnívora (ARGOT, 2004a; MUIZON, 1999); eles apresentavam um forte desenvolvimento da musculatura nugal, uma adaptação também relacionada com seus hábitos carnívoros (ARGOT, 2003a). Todos os Borhyaenoidea do Mioceno, a exceção de *Borhyanea*, foram caracterizados com membros anteriores relativamente poderosos e mãos com capacidades de manuseio, o que indica que os membros anteriores apresentavam adaptações voltadas para um hábito manipulador, sendo úteis para escalar e capturar presas (ARGOT, 2004c). Dentre os Borhyaenoidea, *Callistoe vincei*, *Lycopsis* e *Borhyaena* apresentavam membros anteriores que indicavam hábitos mais terrestres para esses animais (ARGOT e BABOT, 2011).

Dentre os Metatheria, a hipercarnivoria evoluiu em pelo menos três clados distintos: os australianos Diprotodontia, família Thylacoleonidae; e Dasyuromorpha; e os sul-americanos Sparassodonta (GOSWAMI, MILNE e WROE, 2011).

Acredita-se que a combinação de fatores biológicos (sucessão biológica dos Metatheria por Placentários) e fatores físicos estocásticos podem ter sido os principais fatores relacionados com a extinção desses animais (ARGOT, 2004a; PREVOSTI, FORASIEPI e ZIMICZ, 2011); entretanto, um estudo recente associa a extinção dos Sparassodonta como um fenômeno gradual, não estando diretamente relacionado com fatores climáticos ou competitivos (LÓPEZ-AGUIRRE, ARCHER, HAND et al., 2016). Tal conclusão também foi proposta em uma revisão de *Parahyaenodon argentinus*, considerado como o último Sparassodonta de grande porte da América do Sul; na revisão, os espécimes são atribuídos a um Procyonidae (i.e. Eutheria), fazendo com que o último Sparassodonta tenha se extinguido pelo menos quatro milhões de anos antes da chegada do primeiro Carnivora (i.e. Procyonidae) na América do Sul; o que exclui a idade de uma exclusão competitiva entre o grupo e os Carnivora (FORASIEPI, MARTINELLI e GOIN, 2007).

Hondadelphys fieldsi Marshall, 1976, família Hondadelphidae, é considerado um Sparassodonta basal e generalista (MARSHALL, CASE e WOODBURNE, 1990), embora as características dentárias desse referido táxon sejam muito estranhas para os padrões dos Borhyaenoidea (GOIN, 2003). Inicialmente, *Hondadelphys* foi considerado como um Didelphidae (MARSHALL, 1976), mas atualmente, filogenias recentes o posicionam como um Sparassodonta basal (FORASIEPI, BABOT e ZIMICZ, 2014).

Os Thylacosmilidae representaram uma das mais bizarras morfologias dentre os predadores do Neogeno nativos da América do Sul, apresentando a sua morfologia craniana semelhanças com a de felino dente de sabre, como os Machairodontinae, ambos apresentando caninos superiores hipertrofiados. Acredita-se que seus caninos eram capazes de perfurar e cortar o alimento, assim como seus pré-molares e molares eram capazes de furar e esmagar o alimento consumido; esses animais deveriam nocautear suas presas com golpes frontais com o crânio, visto que o mesmo possuía ossos reforçados para resistir ao impacto (suportar força de mordida?); ao contrário do que se pensava, esses animais devem ter sido predadores ativos, representando uma versão “exagerada” de um Borhyaenidae e Proborhyaenidae (GOIN e PASCUAL, 1987). Eles foram os últimos representantes de grande porte dos Borhyaenoidea e, também, os últimos Metatheria de grande porte a habitar a América do Sul (FORASIEPI e CARLINI, 2010). Esses animais assumiram um nicho ecológico similar aos felinos dente-de-sabre (TURNBULL e SEGALL, 1984); entretanto, é possível que a família já estivesse extinta quando os primeiros Carnivora chegaram à América do Sul (GOIN e PASCUAL, 1987).

Segundo Forasiepi, Sanchez-Villagra, Goin et al. (2006); Forasiepi, Babot e Zimicz (2014), os Sparassodonta seriam classificados em dois grandes grupos: “Hathliacynidae” + Borhyaenoidea. A principal revisão da família Hathliacynidae foi realizada por Marshall

(1981), sendo a subfamília representada por 12 gêneros. Hoje, a linhagem foi elevada a categoria de família (FORASIEPI, BABOT e ZIMICZ, 2014).

A superfamília Borhyaenoidea é classicamente representada pelos Borhyaenidae (Prothylacininae + Borhyaeninae), Proborhyaenidae e Thylacosmilidae, embora a monofilia de muitas dessas linhagens ainda está sujeita a debate (GOIN, 2003). A subfamília Prothylacininae foi inicialmente revisada por Marshall (1979), sendo hoje considerada como uma linhagem para- ou polifilética (FORASIEPI, BABOT e ZIMICZ, 2014). A filogenia dos Sparassodonta ainda é muito debatida entre os pesquisadores, como mencionado, estando tanto a composição taxonômica como as relações filogenéticas longe de serem resolvidas (FORASIEPI, GOIN e TAUBER, 2004), principalmente pelo grande número de espécimes fósseis incompletos (BABOT, POWELL e MUIZON, 2002).

2.4.2 *Pediomyoidea* Simpson, 1927

Os *Pediomyoidea* são atualmente representados por quatro gêneros: *Aquiladelphis*, *Pediomys*, *Protolambda*, *Leptalestes* e *Iqualadelphis* (DAVIS, 2007; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014). A linhagem é atualmente considerada como um grupo endêmico do Cretáceo Superior da América do Norte, embora estudos defendam a presença dessa linhagem na América do Sul (MARSHALL, 1987; MARSHALL, CASE e WOODBURN, 1990; MUIZON, MARSHALL e SIGÉ, 1984; MUIZON, 1992; OLIVEIRA, 1999; OLIVEIRA e GOIN, 2012; SIGÉ, 1972).

Os primeiros registros confirmados para a linhagem são conhecidos para o Santoniano-Campaniano inferior (EATON, 2006a; 200b; 2013). *Aquiladelphis* é o táxon mais bem representado nessas faunas, enquanto os *Pediomyidae* são representados em sua maioria por dentes decíduos superiores (DP3) isolados e um molar muito desgastado provisoriamente associado com o gênero *Leptalestes*. Esse clado apresentou a sua maior diversidade e abundância durante o Campaniano superior e o Maastrichtiano (CLEMENS, 1961, 1966; DAVIS, 2007; LILLEGRAVEN, 1969). O grupo é considerado extinto durante o KPg, não sobrevivendo durante o Paleogeno na América do Norte (DAVIS, 2007; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014). Caso sejam confirmadas, a presença de um *Pediomyoidea* em Itaboraí (MARSHALL, 1987; MUIZON, 1992) poderia representar o último registro dessa linhagem, comprovando uma sobrevivência durante o Paleogeno na América do Sul.

Os *Pediomyoidea* são caracterizados por possuírem uma evidente redução da parte anterior da plataforma estilar; cuspe estilar B (StB) reduzida, vestigial ou ausente; paracone

convexo e metacone comprimido (i.e., arredondado e piramidal, respectivamente); paracônido desenvolvido, e entocônido comprimido ou levemente inflado (DAVIS, 2007).

2.4.3 Stagodontidae Marsh, 1889

A família Stagodontidae é considerada atualmente como uma linhagem endêmica do Cretáceo da América do Norte (FOX e NAYLOR, 2006; SCOTT e FOX, 2015; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014). Os primeiros registros dessa linhagem são conhecidos para o Turoniano por um pré-molar isolado levemente desgastado (CIFELLI, 1990c). A família também é registrada durante o Santoniano-Campaniano inferior (Aquilan NALMA) através de talonidos isolados atribuídos a *Eodelphis* (EATON, 2013). A maior diversidade do grupo é atingida durante o Campaniano superior-Maastrichtiano (Judithian, “Edmontonian” e Lancian NALMAs) com três espécies de *Didelphodon* e duas de *Eodelphis* ocorrendo nos EUA e Canadá (CLEMENS, 1966; FOX, 1981; FOX e NAYLOR, 1986, 2006; HUNTER e PEARSON, 1996; HUNTER e ARCHIBALD, 2002; MATTHEW, 1916; SAHNI, 1972; SCOTT e FOX, 2015; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014; WOODWARD, 1916).

A posição filogenética de *Pariadens* é considerada como enigmática, mas alguns estudos consideram esse táxon como o membro mais basal da família Stagodontidae (CIFELLI, 2004; EATON, 1993; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014), enquanto outros o consideram como não pertencendo a linhagem dos Metatheria (FOX e NAYLOR, 2006).

Os Stagodontidae são elementos faunísticos raros em todas as idades e formações da América do Norte (SCOTT e FOX, 2015). Atualmente, a paleoecologia do grupo é bastante discutida na literatura, especialmente relacionada aos hábitos alimentares do grupo. Os hábitos alimentares durófagos são amplamente aceitos na literatura, sendo a evidente hipertrofia dos pré-molares uma das principais características associadas ao grupo (FOX e NAYLOR, 1986, 2006; LOFGREN, 1992; WILSON et al., 2016); entretanto, os hábitos semiaquáticos propostos por Szalay (1994) foram contestados por Fox e Naylor (2006). Os Stagodontidae são considerados como um dos maiores metatérios do Campaniano superior e Maastrichtiano da América do Norte (CLEMENS, 1966; FOX e NAYLOR, 2006; WILLIAMSON et al., 2014).

Ladevèze e Muizon (2010) recuperaram *Eobrasilia* como grupo-irmão de *Didelphodon*, o que indicaria uma dispersão norte-americana para a América do Sul durante o Cretáceo Superior dos ancestrais de *Eobrasilia*. Infelizmente, essa proposta nunca foi propriamente testada. *Eobrasilia*, *Gaylordia*, *Tiulordia* e *Didelphopsis* foram agrupados na subfamília

“Eobrasilinae” Marshall, 1987, baseado na presença de adaptações durófagas presentes nos pré-molares (i.e. pré-molares inflados, em especial o terceiro pré-molar). A validade dos “Eobrasilinae” é contestada por diversos estudos (LADEVÉZE e MUIZON, 2010; OLIVEIRA e GOIN, 2012; OLIVEIRA e GOIN, 2011; OLIVEIRA, ZIMICZ e GOIN, 2016).

2.4.4 “Alphadontidae” Marshall, Case e Woodburne, 1990

Os “Alphadontidae” são atualmente considerados como um grupo para- (KIELAN-JAWOROWSKA, CIFELLI e LUO, 2004) ou polifilético (WILLIAMSON et al., 2012; WILLIAMSON et al., 2014). O gênero *Alphadon* foi separado em diversos gêneros: *Protalphadon*, *Turgidodon*, *Varalphadon* e *Nortedelphys* (CASE, GOIN e WOODBURNE, 2005; CIFELLI, 1990b; JOHANSON, 1996a). A subfamília Alphadontinae foi proposta por Marshall, Case e Woodburne (1990) para incluir as espécies de *Alphadon* e *Albertatherium*. A subfamília foi incluída na família Peradectidae Crochet, 1979.

Filogenias recentes envolvendo o grupo proporcionaram pouca evidência substancial para as reais afinidades dos táxons dessa linhagem (JOHANSON, 1996a; KIELAN-JAWOROWSKA, CIFELLI e LUO, 2004; MARSHALL, CASE e WILLIAMSON et al., 2012; WILLIAMSON et al., 2014; WOODBURNE, 1990), além disso, muitos taxa considerados como linhagens basais (e.g. *Aenigmadelphys* e *Bistius*; ver e.g., CIFELLI e JOHANSON, 1994; DAVIS, 2007; KIELAN-JAWOROWSKA, CIFELLI e LUO, 2004; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014) poderiam ser incluídos na linhagem dos “Alphadontidae”.

Eaton (1993) indica que muitos dos espécimes atribuídos a *Pariadens kirklandi* poderiam representar outra espécie de grande porte, o que representaria uma quimera; de forma interessante, alguns espécimes do hipodigma de *Pariadens kirklandi* se assemelham bastante a um “Alphadontidae”. *Nortedelphys* foi descrito a partir de parte do hipodigma de “*Alphadon*” *rhaister* Clemens, 1966; sendo inicialmente agrupado com os Herpetotheriidae Trouessart, 1879, devido à presença de uma centrocrista dilambdodonte invasiva (CASE, GOIN e WOODBURNE, 2005); entretanto, Williamson et al. (2012) e Williamson et al. (2014) recuperaram uma posição independente para esse táxon e os Herpetotheriidae. Assim como os demais táxons mencionados, *Nortedelphys* também apresenta todas as características de um “Alphadontidae”.

Os primeiros registros dos “Alphadontidae” ocorrem durante o Cenomaniano, Formação Dakota, Utah, EUA (EATON, 1993, 2006a; WILLIAMSON et al., 2012; WILLIAMSON et al., 2014), como os primeiros registros de *Eoalphadon*. Durante o Santoniano-Campaniano inferior (Aquilana NALMA), a fauna dos “Alphadontidae” é muito

mais diversa, com os primeiros registros de *Protalphadon*, *Aenigmadelphys*, *Albertatherium* e *Alphadon* (DAVIS, CIFELLI e COHEN, 2016; EATON, 2006b, 2006c, 2013; EATON et al., 1999; JOHANSON, 1995, 1996a). A fauna do Campaniano superior (Judithian NALMA) é muito similar à do Santoniano-Campaniano inferior, diferindo pela ausência de *Albertatherium* (WILLIAMSON et al., 2012; WILLIAMSON et al., 2014). A fauna do Maastrichtiano difere das faunas do Campaniano pela ausência de *Aenigmadelphys* e pelos primeiros registros de *Nortedelphys* e de novas espécies de *Alphadon* e *Protalphadon*. A extinção do grupo está diretamente relacionada à extinção em massa ocorrida durante o Limite Cretáceo-Paleogeno (Limite KPg; ver WILLIAMSON et al., 2014). *Turgidodon petiminis* Storer, 1991, é considerado como a última espécie sobrevivente do gênero (Maastrichtiano superior) (STORER, 1991), entretanto, muitas das características desse táxon são similares as de *Alphadon rhaister*.

2.4.5 Polydolopimorphia (Ameghino, 1897); Archer, 1984

Os Polydolopimorphia representam um grupo conhecido para o Cretáceo Tardio da América do Norte (CASE, GOIN e WOODBUNE, 2005), Anatólia (MAGA e BECK, 2017; MÉTAIS et al, 2018) e para o Paleogeno do Hemisfério Sul (BECK, 2016; CARLINI, PASCUAL e GOIN, 2007; CHIMENTO, AGNOLIN e NOVAS, 2014; CHORNOGUBSKY e GOIN, 2015; FLYNN e WYSS, 1999, 2004; GARCÍA-LÓPEZ e BABOT, 2015; GOIN, CANDELA e LÓPEZ, 1998; GOIN e CANDELA, 1998, 2004, 2010; GOIN, MONTALVO e VISCONTI, 2000; GOIN, CANDELA e MUIZON, 2003; GOIN, PASCUAL, TEJEDOR et al., 2006; GOIN e OLIVEIRA, 2007; GOIN, CANDELA, ABELLO et al., 2009; GOIN e ABELLO, 2013; MARSHALL, 1982b; PASCUAL, 1980a, 1980b; PASCUAL e CARLINI, 1987; PASCUAL, GOIN e CARLINI, 1994; PAULA COUTO, 1952b, 1979; ORTIZ, LÓPEZ, BABOT et al., 2012; SÁNCHEZ-VILLAGRA e KAY, 1997; SÁNCHEZ-VILLAGRA, KAY e ANAYA-DAZA, 2000; SÁNCHEZ-VILLAGRA, 2001; SIMPSON, 1928, 1970b, 1970c; TEJEDOR et al., 2009; VILLARROEL e MARSHALL, 1988; WOLFF, 1984; WOODBURNE e ZINSMEISTER, 1984).

A provável existência desses animais em depósitos da América do Norte indica que o grupo já existia há pelo menos 75 milhões de anos (CASE, GOIN e WOODBURNE, 2005; GOIN et al., 2006; GOIN et al., 2016) com *Ectocentrocrustus foxi* Case, Goin e Woodburne, 2005, um provável Polydolopiformes Kinman, 1994 (CASE, GOIN e WOODBURNE, 2005). Os últimos representantes do grupo são os Argyrolagidae, 1904, *Microtragulus* Ameghino, 1904, e *Argyrolagus* Ameghino, 1904, que sobreviveram até o Plioceno superior (WOLFF,

1984; ORTIZ, LÓPEZ e BABOT et al., 2012) e Plioceno inferior (WOLFF, 1984; ZIMICZ, 2011) da Argentina, respectivamente.

Dentre os membros dessa ordem, os Polydolopidae estão entre os primeiros fósseis de marsupiais a serem descritos para a América do Sul (FLYNN e WYSS, 2004). Os Polydolopimorphia representam o grupo, em geral, mais abundante nas faunas com metatérios durante o Paleogeno sul-americano, embora sejam bem mais raros durante o final do Paleogeno (Oligoceno superior) e Neogeno (Mioceno e Plioceno) (GOIN et al., 2016). *Epidolops ameghinoi* é o mais abundante metatério de Itaboraí, Brasil (PAULA COUTO, 1952a; 1952b; 1970; 1979; SZALAY, 1994), *Wamradolops tsullodon* é o mais abundante metatério de Santa Rosa, Peru (GOIN e CANDELA, 2004), *Pliodolops unicus* é o mais abundante metatério de Paso del Sapo (TEJEDOR et al., 2009); e *Antarctodolops* é o mais abundante metatério da Formação La Meseta, Antártica (CHORNOGUBSKY, GOIN e REGUERO, 2009), por exemplo.

Os Polydolopimorphia apresentam um grau variado de "Pseudodiprotodontismo" (*sensu* RIDE, 1964), que representa a hipertrofia dos últimos pré-molares (principalmente os inferiores); o termo 'pseudodiprotodonte' é usualmente empregado tanto como designação formal e informal para diversos grupos (a maioria extintos) de marsupiais da América do Sul possuindo os primeiros incisivos hipertrofiados e procumbentes, como os Paucituberculata e os Polydolopimorphia (GOIN, CANDELA, ABELLO et al., 2009a).

De especial interesse é o padrão apresentado pelos molares superiores de cada grupo (GOIN e CANDELA, 1996), que no geral, apresentam molares braquiodontes com cristas pouco desenvolvidas e cúspides baixas e arredondadas. A morfologia dentária desses animais, especialmente os molares bunodontes, é compatível com hábitos onívoros do tipo insetívoros/frugívoros ou folívoros (GOIN e CANDELA, 1996; PASCUAL, 1980a, 1980b; ZIMICZ, 2011, 2012, 2014a). O padrão generalizado dos molares dos Polydolopimorphia é quadrangular, como nos Paucituberculata, entretanto, as duas linhagens seguiram processos evolutivos distintos (i.e., convergência evolutiva), representando, portanto, linhagens não aparentadas (GOIN et al., 2016). Entretanto, nenhum estudo atualmente publicado na literatura buscou comprovar a origem única do padrão quadrangular para os Polydolopimorphia, ou seja, ainda hoje não é possível comprovar se os molares quadrangulares representam uma homologia para a ordem ou se foram adquiridos diversas vezes na evolução do grupo (i.e., caráter homoplástico).

O padrão dos molares dos Polydolopidae é um dos mais aberrantemente derivados dentre os Metatheria extintos e viventes, apresentando molares bunodontes (OLIVEIRA e GOIN, 2011). Dentre as características mais marcantes dos molares desses animais estão à

presença de pelo menos duas fileiras de cúspides orientadas mesio-distalmente (algumas vezes apresentam três fileiras no primeiro molar superior) e a existência de três cúspides principais no limite da porção lingual dos molares superiores (CHORNOGUBSKY, GOIN e REGUERO, 2009; TEJEDOR, GOIN, GELFO et al., 2009), semelhantes aos dos Multituberculata e alguns Rodentia (GOIN, CANDELA e MUIZON, 2003).

Atualmente, os táxons da ordem Polydolopimorphia são classificados em diversas famílias: Polydolopidae Ameghino, 1987; Prepidolopidae Pascual, 1981; Bonapartheriidae Pascual, 1980b; Argyrolagoidea Ameghino, 1904; Gashterniidae Marshall, 1984; Rosendolopidae Goin, Abello e Chornogubsky, 2010; e Sillustaniidae Crochet e Sigé, 1996 (CHORNOGUBSKY e GOIN, 2015; GOIN et al., 2016; OLIVEIRA e GOIN, 2012). Os Rosendolopidae, Prepidolopidae, Gashterniidae, Bonapartheriidae e Argyrolagoidea representam os Bonapartheriiformes Pascual, 1980b (GOIN, CANDELA, ABELLO et al., 2009a; GOIN et al., 2016). Os Polydolopidae e Sillustaniidae representam os Polydolopiformes (CHORNOGUBSKY e GOIN, 2015; GOIN et al., 2016). Os Argyrolagoidea são representados pelas famílias Patagoniidae Pascual e Carlini, 1984; Argyrolagidae e Groeberiidae Patterson, 1952 (GOIN et al., 2016).

Os Groeberiidae já foram classificados em uma ordem e superfamília a parte dos Polydolopimorphia (Groeberida Pascual, Goin e Carlini, 1994 – Groeberioidea [Patterson, 1952] Clemens e Marshall, 1976) (PASCUAL, GOIN e CARLINI, 1994). *Patagonia peregrina* Pascual e Carlini, 1987, única espécie do gênero *Patagonia* e da família Patagoniidae já foi classificada na superfamília Patagonioidea Pascual e Carlini, 1987, a parte dos Argyrolagoidea (PASCUAL e CARLINI, 1987). Entretanto, todas as linhagens citadas são hoje interpretadas como pertencendo à linhagem dos Polydolopimorphia, subordem Bonapartheriiformes, superfamília Argyrolagoidea (GOIN, CANDELA, ABELLO et al., 2009a; GOIN e ABELLO, 2013; GOIN et al., 2016). Um estudo recente apresentou evidências para o agrupamento de *Groeberia* e *Patagonia* como Mammaliformes basais (Gondwanatheria?) (CHIMENTO, AGNOLIN e NOVAS, 2014), entretanto, os dois táxons apresentam várias características que os posicionam como metatérios (GOIN et al., 2016). *Wamradolops tsullodon* de Santa Rosa, Peru (Oligoceno inferior; ver e.g., CAMPBELL et al., 2021) é considerado como um Polydolopimorphia *incertae sedis* (i.e. sem posição definida para a linhagem especificada) (GOIN e CANDELA, 2004).

Os Argyrolagidae são caracterizados pela hypsodontia dos molares, característica compatível com dietas mais abrasivas, como a herbivoria e granivoria. Tal adaptação pode ter sido uma resposta às mudanças climáticas ocorridas durante o Oligoceno inferior (ZIMICZ, 2011). *Proargyrolagus bolivianus* Wolff, 1984, um Argyrolagidae, apresenta muitos detalhes

em sua dentição que sugere uma dieta extremamente abrasiva, principalmente pela presença das altas coroas de seus molares; essa característica está presente em insetívoros modernos; entretanto, o grande desenvolvimento das mesmas pode indicar uma dieta composta, pelo menos em parte, de espécimes vegetais, a exemplo de sementes capturadas no solo (SÁNCHEZ-VILLAGRA e KAY, 1997; ZIMICZ, 2011). O reduzido tamanho corporal dos *Argyrolagoidea* não é compatível com a folivoria estrita, o que poderia indicar dietas mais ou menos variadas, com o consumo de folhas e sementes, ou mesmo com períodos associados de hibernação para poupar energia (ZIMICZ, 2011).

Os *Prepidolopidae* são considerados como os *Bonapartheriiformes* mais generalizados (GOIN, CANDELA e LÓPEZ, 1998) e são representados por *Prepidolops* Pascual, 1980a; *Punadolops* Pascual, 1983; *Incadolops* e *Perrodelphys*. O grupo é tido como uma linhagem onívora em sentido amplo (*Prepidolops* e *Punadolops*) ou frugívora (*Incadolops* e *Perrodelphys*) (ZIMICZ, 2014a). A família é conhecida para a Argentina (GOIN, CANDELA e LÓPEZ, 1998; PASCUAL, 1980a, 1980b), Peru (GOIN e CANDELA, 2004) e Antártica (GOIN, CASE, WOODBURNE et al., 1999).

Os *Rosendolopidae* são considerados como os mais basais *Bonapartheriiformes*, sendo a família representada por dois gêneros: *Rosendolops* e *Hondonadia* (GOIN, ABELLO e CHORNOGUBSKY, 2010). A família apresenta hábitos granívoros (*Hondonadia*) e insetívoros (*Rosendolops*) (GOIN, ABELLO e CHORNOGUBSKY, 2010; ZIMICZ, 2012; 2014a).

A superfamília *Bonapartheriioidea* é representada pelos *Gashterniidae* e *Bonapartheriidae* (GOIN, CANDELA, ABELLO et al., 2009a; ZIMICZ, 2012; 2014a). A família *Bonapartheriidae* é representada por *Epidolops* e *Bonapartherium*, sendo restrita ao Eoceno da América do Sul (Goin et al., 2016). A família apresenta hábitos alimentares granívoros/insetívoros (*Bonapartherium*) ou frugívoros (*Epidolops*) (ZIMICZ, 2014a). Os primeiros registros confirmados para a família ocorrem durante a idade Itaboraiense SALMA (Eoceno inferior); os últimos registros datam da idade Vaquense (PASCUAL, 1980b). A família *Gashterniidae*, restrita ao gênero *Gashternia* Simpson, 1935, com duas espécies: *Gashternia ctalehor* Simpson, 1935, e *Gashternia carioca*; ambas registradas para o Eoceno inferior (GOIN e OLIVEIRA, 2007; SIMPSON, 1948; TEJEDOR, GOIN, GELFO et al., 2009). Inicialmente descrito como um táxon frugívoro/insetívoro (GOIN e OLIVEIRA, 2007), hoje, o gênero é caracterizado como folívoro (ZIMICZ, 2012; 2014a).

2.4.6 Glasbiidae clemens, 1966; Protodidelphidae Marshal, Case e Woodburne, 1990; Chulpasiinae Sigé et al., 2009; Hatcheriformes Case, Goin e Woodburne, 2005; e táxons afins

Os Glasbiidae são uma linhagem representada na América do Norte unicamente pelo gênero *Glasbius*. *Glasbius* é representado por duas espécies: *Glasbius intricatus* Clemens, 1966, e *Glasbius twitchelli* Archibald (1982), ambas restritas ao Lancian NALMA (Maastrichtiano superior) (ARCHIBALD, 1982; CLEMENS, 1966, 1973; WILLIAMSON e WEIL, 2008). *Glasbius* é considerado um raro membro das Formações Lancian e Hell Creek, Wyoming, EUA (ARCHIBALD, 1982; CLEMENS, 1966, 1973), mas é relativamente mais abundante no Membro Naashoibito da Formação Kirtland, New Mexico, EUA.

As afinidades filogenéticas de *Glasbius* são bastante discutidas na literatura: Clemens (1966, 1973) e Paula Couto (1979) consideraram *Glasbius* como uma subfamília dos Didelphidae; Archer (1984) elevou o táxon para a categoria de família; Reig, Kirsch e Marshall (1987) agruparam *Glasbius* com os Microbiotheriidae; Case, Goin e Woodburne (2005) e Goin et al. (2016) consideraram os Glasbiidae como membros da subordem Hatcheriformes Case, Goin e Woodburne, 2005, a linhagem mais basal dos Polydolopimorphia; Davis (2007) considerou os Glasbiidae como uma linhagem dos Pediomyoidea; Williamson et al. (2012) e Williamson et al. (2014) consideraram *Glasbius* como grupo-irmão de *Roberthoffstetteria* Muizon, Marshall e Sigé, 1984 (i.e. intimamente relacionado com os Polydolopimorphia).

O paradigma envolvendo *Glasbius* é amplamente discutido, visto que esse táxon é considerado como um ‘ET’ na América do Norte, devido ao seu aparecimento “repentino” e sua raridade durante o Maastrichtiano (CIFELLI, EBERLE, LOFGREN et al., 2012; CLEMENS, 2002; DAVIS, 2007). Clemens (1968) discute as prováveis afinidades de *Glasbius* com outros taxa norte-americanos, mas o identifica apenas como uma linhagem independente. A diversidade dos Glasbiidae é maior na América do Sul, com os gêneros *Palangania* Goin et al., 1998, e *Periakros* Goin, Abello e Chornogubsky, 2010, o que poderia explicar a problemática envolvendo *Glasbius* (GOIN e CANDELA, 1998; GOIN, ABELLO e CHORNOGUBSKY, 2010). Ainda assim, nenhum estudo atual analisou formalmente as afinidades de *Glasbius* com outros Metatheria Norte e sul-americanos.

A linhagem dos Hatcheriformes Case, Goin e Woodburne, 2005, é considerada como a mais basal subordem dos Polydolopimorphia, sendo representada pelos Glasbiidae e *Hatcheritherium alpha* Case, Goin e Woodburne, 2005. A linhagem é representada principalmente por táxons norte-americanos que apresentam uma morfologia braquiodonte, com coroas baixas, cuspes com certo grau de arredondamento, cristas baixas, e protocone

desenvolvido (CASE, GOIN e WOODBURNE, 2005). Filogenias recentes agruparam *Glasbius* como uma linhagem basal próxima aos Polydolopimorphia e Microbiotheria (CHORNOGUBSKY e GOIN, 2015; GOIN, CANDELA, ABELLO et al., 2009a). *Hatcheritherium* indica uma origem norte-americana para os Polydolopimorphia (CASE, GOIN e WOODBURNE, 2005). *Glasbius*, por sua vez, pode representar um táxon invasor sul-americano na América do Norte, o que explicaria a “ausência” de táxons ancestrais ou intimamente relacionados a ele na América do Norte.

Reigia punae Pascual, 1983, é um táxon enigmático da América do Sul, condição que resultou em diversas interpretações para as suas afinidades filogenéticas desde o seu descobrimento: Pascual (1983) agrupou esse táxon com os Glasbiinae-Didelphidae; Reig, Kirsch e Marshall (1987) agruparam esse táxon com os Glasbiinae-Microbiotheriidae, conjuntamente com *Protodidelphis* e *Glasbius*; Marshall (1987) agrupou *Reigia* com *Bobbschaefferia*, *Guggenheimia*, *Protodidelphis* e *Zeusdelphys*, sendo incluídos na subfamília Protodidelphinae-Caroloameghiniidae-Polydolopimorphia; Marshall, Case e Woodburne (1990) consideraram *Reigia* como o único membro da subfamília Reigiinae-Prepidolopidae-Polydolopimorphia. Entretanto, Goin e Candela (2010) descartaram a inclusão de *Reigia* e Protodidelphidae com os Polydolopimorphia, considerando *Reigia* como um representante da ordem Didelphimorphia.

Os Protodidelphidae são um grupo de metatérios que viveram exclusivamente durante o Paleogeno no Hemisfério Sul (OLIVEIRA e GOIN, 2011), sendo classificados como uma linhagem basal da ordem Polydolopimorphia (MARSHALL CASE e WOODBURNE, 1990); como uma linhagem independente deste grupo e basal a maioria dos taxa de Itaboraí (OLIVEIRA e GOIN, 2011); ou como um grupo próximo aos Didelphidae (LADEVÈZE e MUIZON, 2010). Atualmente, as afinidades dos Protodidelphidae com os Polydolopimorphia não é mais aceita (GOIN e CANDELA, 2010).

Essa família é caracterizada por possuir molares bunodontes, com cristas cortantes pouco desenvolvidas (GOIN OLIVEIRA e CANDELA, 1998; MARSHALL, CASE e WOODBURNE, 1990; OLIVEIRA e GOIN, 2011, 2012). Segundo Zimicz (2012), os táxons bunodontes possuíam dentes com cúspides baixas e infladas, provavelmente relacionadas com uma dieta onívora ou, em alguns casos, a frugivoria.

Bobbschaefferia foi originalmente classificado como um Didelphidae (PAULA COUTO, 1970), entretanto, estudos e filogenias recentes indicam maiores afinidades desse táxon com os Protodidelphidae ou Glasbiidae como um Polydolopimorphia basal (GOIN et al., 2016; OLIVEIRA e GOIN, 2011, 2016); entretanto, estudos recentes excluem os Protodidelphidae dos Polydolopimorphia (GOIN e CANDELA, 2010), o que indica uma

posição enigmática para esse táxon. *Mirandatherium* foi classificado como um Didelphidae (MARSHALL, CASE e WOODBURN, 1990; PAULA COUTO, 1952a, 1970) ou como um Microbiotheria basal (CASE, GOIN e WOODBURN, 2005; MARSHALL, 1987; OLIVEIRA e GOIN, 2011), entretanto, suas foram contestadas por outros estudos (GOIN e ABELLO, 2013; OLIVEIRA e GOIN, 2012; OLIVEIRA, ZIMICZ e GOIN, 2016). Atualmente, *Mirandatherium* é considerado como um Polydolopimorphia basal (OLIVEIRA e GOIN, 2012; OLIVEIRA ZIMICZ e GOIN, 2016).

A subfamília Chulpasiinae Sigé, Archer, Crochet et al, 2009, é atualmente representada por três espécies: *Chulpasia mattaui* de Chulpas, Peru (CROCHET e SIGÉ, 1993); *Chulpasia jimthorselli* e *Thylacotinga bartholomaii* de Tingamarra, Austrália; sendo a distribuição temporal da família conhecida para o Paleoceno inferior–Eoceno inferior. A subfamília apresenta adaptações bunodontes, o que é indicativo de hábitos alimentares frugívoros (SIGÉ ARCHER, CROCHET et al., 2009). A subfamília foi inicialmente considerada como uma linhagem dos Bonapartheriiformes-Polydolopimorphia (CASE GOIN e WOODBURN, 2005), entretanto, estudos recentes indicam que essa linhagem seria basal aos Polydolopimorphia ou nem pertenceriam a esse grande grupo (CHORNOGUBSKY e GOIN, 2015).

2.4.7 Peradectoidea Marshall, Case e Woodburne, 1990

A linhagem dos Peradectoidea Marshall, Case e Woodburne, 1990, é conhecida para a América do Norte (BOWN, 1979; DAHLBERG et al., 2016; FOX, 1983; HOROVITZ et al., 2009; HOUGH, 1961; KORTH, 1994, 2009; MCGREW, 1937; ROTHECKER e STORER, 1996; SLAUGHTER, 1978; WILLIAMSON e TAYLOR, 2011; WILLIAMSON et al., 2012; WILLIAMSON e LOFGREN, 2014), América do Sul (GOIN, 2006; OLIVEIRA e GOIN, 2012; MUIZON, 1992; SIGÉ, 1971, 1972), Europa (CROCHET, 1979; RUSSELL, GALOYER, LOUIS et al., 1988), África (CROCHET, THOMAS, SEM et al., 1992) e Austrália (BECK, 2015), sendo portanto um grupo cosmopolita durante o Paleogeno. A superfamília é atualmente representada pelo Peradectidae e Caroloameghiniidae Ameghino, 1901 (GOIN, 2006; GOIN et al., 2016).

Os primeiros registros confirmados do grupo foram recuperados durante o Paleoceno inferior da América do Norte (DAHLBERG, EBERLE, SERTICH et al., 2016; WILLIAMSON e TAYLOR, 2011; WILLIAMSON et al., 2012; WILLIAMSON e LOFGREN, 2014) e do Sul (MUIZON, 1992; SIGÉ 1971, 1972). Um provável Peradectidae foi registrado no Campaniano superior (Judithian NALMA) na Formação Terlingua, Texas, EUA (CIFELLI, 1994);

infelizmente, suas afinidades com o grupo ainda não foram propriamente estudadas. Os Peradectoidea sobreviveram até o Oligoceno superior–Mioceno inferior na América do Norte (HOUGH, 1961; KORTH, 1994, 2009; MCGREW, 1937; SLAUGHTER, 1978). Um provável Peradectinae, *Siamoperadectes minutus* Ducrocq et al., 1992, foi encontrado em depósitos do Mioceno médio na Tailândia (DUCROCQ et al., 1992); caso sejam comprovadas suas afinidades com o grupo, esse táxon representaria o mais recente Peradectoidea conhecido (i.e., o último membro do grupo).

Estudos realizados em esqueletos preservados de um provável Peradectidae na fauna de Messel, Alemanha (KOENIGSWALD e STORCH, 1992), e em um crânio preservado de *Mimoperadectes houdei* Horovitz, Martin, Bloch et al., 2009, demonstraram que os Peradectidae apresentavam hábitos escansoriais/arborícolas. Essa família já foi classificada como pertencendo à ordem Didelphimorphia, sendo a linhagem mais basal desse grupo (HOROVITZ, MARTIN, BLOCH et al., 2009); entretanto, estudos recentes recuperaram uma posição mais basal para esse grupo (BECK, 2012, 2016; OLIVEIRA e GOIN, 2015). Essa problemática ainda não foi propriamente elucidada, visto que outros estudos recentes consideram os Peradectoidea (i.e., Peradectidae e Caroloameghiniidae) como pertencentes à linhagem dos Didelphimorphia (GOIN et al., 2016).

A família Caroloameghiniidae, endêmica da América do Sul (GOIN, 2006), corresponde a uma linhagem aparentada aos Peradectidae, constituindo com estes a linhagem dos Peradectoidea (GOIN, 2006). Esses animais apresentavam molares bunodontes, o que poderia indicar uma precoce tendência a hábitos alimentares frugívoros; a dentição e morfologia do dentário desses animais convergem com a dos Primates, o que poderia indicar hábitos alimentares e papéis ecológicos similares entre ambos (GOIN, OLIVEIRA e CANDELA, 1998; GOIN, 2006; MARSHALL, 1982a; OLIVEIRA e GOIN, 2011). Os espécimes fósseis associados a essa família são raros na América do Sul, o que dificulta um posicionamento mais preciso de suas reais afinidades filogenéticas (GOIN, 2006; OLIVEIRA e GOIN, 2012). O mais antigo Caroloameghiniidae é *Procaroloameghinia* da Bacia de São José de Itaboraí (Itaboraiense SALMA, Eoceno inferior), inicialmente considerado como o “ancestral ideal” de *Caroloameghinia* Ameghino, 1901 (GOIN, 2006; MARSHALL, 1982a; OLIVEIRA e GOIN, 2011), devido as suas características menos especializadas em comparação com *Caroloameghinia*. O último Caroloameghiniidae conhecido é *Canchadelphys cristata* Goin, Abello e Chornogubsky, 2010, da Formação Sarmiento (Tinguiririquense SALMA, Oligoceno inicial), Argentina.

2.4.8 Pucadelphyidae Muizon, 1998; e Mayulestidae Muizon, 1994

Os Pucadelphyidae, como *Pucadelphys andinus* e *Andinodelphys cochabambensis*, estão entre os Metatheria mais basais conhecidos para a América do Sul (BECK, GODTHLP, WEISBECKER et al., 2008; BECK, 2012, 2016; HOROVITZ, MARTIN, BLOCH et al., 2009; LADEVÈZE, 2007; OLIVEIRA e GOIN, 2015), embora alguns autores considerem certas similaridades entre *Andinodelphys* e os Peradectidae (OLIVEIRA e GOIN, 2015).

Pucadelphys andinus mensurava 135 mm da ponta do focinho à base da cauda e cerca de 270 mm da ponta do focinho à ponta da cauda (MARSHALL, MUIZON e SIGOGNEAU-RUSSELL, 1995). Essa espécie apresentava hábitos generalistas, semelhantes aos do gênero vivente *Monodelphis*, e terrestres, embora pudesse escalar arbustos, possivelmente para fugir de predadores. Apresentava um padrão de locomoção quadrúpede, podendo locomover-se velozmente (ARGOT, 2001, 2002, 2003b), possuindo hábitos semelhantes aos do atual *Metachirus*, ambos possuindo agilidade e capacidade para saltar em solo, embora *Metachirus* apresente adaptações mais claras à vida terrestre (ARGOT, 2001). É conhecido que *P. andinus* também possuía habilidades limitadas de escavação (MARSHALL, MUIZON e SIGOGNEAU-RUSSELL, 1995), embora análises de Argot (2001) contrariem essa hipótese. Uma característica interessante dessa espécie reside no fato deles apresentarem um forte dimorfismo sexual entre machos e fêmeas, com os machos possuindo um crânio mais largo e robusto, além de caninos muito maiores do que as fêmeas. Os machos eram em média 35% maiores do que as fêmeas, característica essa que pode estar relacionada com a poliginia (LADEVÈZE, MUIZON, BECK et al., 2011).

Ladevèze (2007) e Ladevèze e Muizon (2010) indicam a presença de um Pucadelphyda ainda não descrito para Itaboraí, sendo representado por petrosos isolados. Essa hipótese foi confirmada no âmbito desta tese

A família Mayulestidae foi criada por Muizon (1994) para incluir os táxons *Mayulestes ferox* e *Allqokirus australis*, ambos endêmicos de Tiupampa. Os Mayulestidae foram inicialmente classificados como uma família basal da superfamília Borhyaenoidea (MUIZON, 1994, 1998), porém hoje, sua afinidade com os Borhyaenoidae é questionada (FORASIEPI, SANCHEZ-VILLAGRA, GOIN et al., 2006). *Mayulestes* é atualmente classificado como grupo-irmão dos Pucadelphyidae e dentre os Metatheria mais basais da América do Sul (BECK, GODTHELP, WEISBECKER et al., 2008; BECK, 2012, 2016; HOROVITZ, MARTIN, BLOCH et al., 2009; LADEVÈZE, 2007; OLIVEIRA e GOIN, 2015). A posição de *Mayulestes* por vezes é encontrada como grupo-irmão de *Andinodelphys* + *Pucadelphys*, enquanto em

outras ele é considerado como grupo-irmão de *Pucadelphys*. Goin (2003) discute as similaridades da dentição de *Mayulestes* com os Peradectidae.

Mayulestes ferox foi considerado como um Borhyaenoidea basal devido às semelhanças de sua dentição com a desses animais, que apresentavam claras adaptações para uma dieta majoritariamente carnívora (MUIZON, 1994, 1998). Goin (2003) caracteriza a dentição dos “Mayulestidae” como a de uma linhagem que parecia estar evoluindo para desenvolver hábitos mais carnívoros; a dentição desses táxons apresentava algumas adaptações voltadas para dietas mais carnívoras, a exemplo de um paracone um pouco menor que o metacone, que é sempre maior e mais alto; o protocone apresenta uma notável tendência à redução, embora em *Mayulestes* ele seja relativamente grande. *Allqokirus australis* apresenta um protocone um pouco menor (MUIZON e LANGE-BADRÉ, 1997), cúspides estilares moderadamente desenvolvidas, talônido levemente reduzido, a pré-paracrista e a pós-metacrista não é reduzida em comprimento etc. (GOIN, 2003).

Mayulestes ferox possuía claras habilidades arborícolas, mas como um mamífero predador, também poderia caçar em solo. Seu esqueleto demonstrava que este animal era bastante ágil, o que era bastante compatível com seus hábitos predadores (MUIZON, 1998; ARGOT, 2001; 2002; 2003b); ele também apresentava uma cauda preênsil, auxiliando na movimentação arbórea, além das suas mãos e pés também serem preênsil, sendo o seu padrão de locomoção semelhante ao de esquilos e musaranhos (MUIZON, 1998). O índice de arborealidade é menor em *Pucadelphys*, mais desenvolvido em *Andinodelphys* e ainda mais evidente em *Mayulestes* (MUIZON e BABOT, 2003), indicando uma pequena sobreposição de nicho entre esses taxa.

2.4.9 Jaskhadelphyidae Muizon, 1992; e táxons afins

A família Jaskhadelphyidae Muizon, 1992, é representada atualmente por quatro táxons: *Jaskhadelphys minutus*, *Minusculodelphis minimus* Paula Couto, 1962; *Minusculodelphis modicum* Oliveira, Zimicz e Goin, 2016; e *Kiruwamaq chisu* (GOIN e CANDELA, 2004; MUIZON, 1992; OLIVEIRA, ZIMICZ e GOIN, 2016). Os membros dessa família são conhecidos principalmente pelo seu tamanho minúsculo (MUIZON, 1992; MUIZON e CIFELLI, 2001; PAULA COUTO, 1962), visto que estes animais deveriam ter pesado menos que 10 g (OLIVEIRA, ZIMICZ e GOIN, 2016). O provável habitat desses animais deveria ser a serapilheira nos solos dos ecossistemas em que foram encontrados, compatível com a presença de minúsculos invertebrados, os quais esses animais deveriam ser especializados no consumo (OLIVEIRA, ZIMICZ e GOIN, 2016).

Jaskhadelphys é endêmico de Tiupampa (MUIZON, 1992), *Minusculodelphis* de Itaboraí (MARSHALL, 1987; PAULA COUTO, 1962, 1970) e *Kiruwamaq* de Santa Rosa (GOIN e ABELLO, 2004). A família é restrita ao Paleogeno da América do Sul, nas idades Tiupampense (Paleoceno inferior), Itaboraiense (Eoceno inferior) e Mustersense (Eoceno superior), como exemplificado acima. As afinidades da família ainda são discutidas: Filogenias recentes recuperaram a família como uma linhagem próxima de *Gaylordia*, *Tiulordia*, *Szalinia* e *Monodelphopsis* (OLIVEIRA e GOIN, 2011; OLIVEIRA, ZIMICZ e GOIN, 2016), entretanto, nenhum agrupamento formal foi proposto até agora.

Gaylordia e *Tiulordia* representam uma linhagem de metatérios restrita ao Paleoceno inferior da Bolívia (Tiupampa) e Eoceno inferior de Itaboraí (Brasil). O grupo é caracterizado pela presença de molares bulbosos; além de um forte padrão de desgaste, um indicativo de adaptações durófagas (OLIVEIRA e GOIN, 2015). O grupo, ainda não nominado formalmente, é representado por três espécies: *Gaylordia macrocynodonta*, *Gaylordia mater* Oliveira e Goin, 2015; e *Tiulordia floresi* (MUIZON, 1992; OLIVEIRA e GOIN, 2011; OLIVEIRA, ZIMICZ e GOIN, 2016). A primeira espécie é caracterizada por apresentar o maior grau de hipertrofia dos pré-molares, enquanto as outras duas possuem pré-molares com algum grau de hipertrofia. A maior espécie da linhagem é *Gaylordia mater*. As três espécies representam metatérios de pequeno porte (OLIVEIRA e GOIN, 2015). Estudos prévios suportam as afinidades desses animais com os Jaskhadelphyidae (OLIVEIRA e GOIN, 2011; OLIVEIRA, ZIMICZ e GOIN, 2016) e com os Pucadelphyidae (OLIVEIRA e GOIN, 2015).

Marshall (1987) agrupou *Gaylordia*, *Tiulordia*, *Eobrasilia* e *Didelphopsis* na subfamília “Eobrasilinae”, um agrupamento polifilético. A principal característica usada pelo autor para validar essa linhagem foi à presença de pré-molares hipertrofiados. Atualmente, a validade da subfamília é contestada (LADEVÈZE e MUIZON, 2010; OLIVEIRA e GOIN, 2011, 2012; OLIVEIRA, ZIMICZ e GOIN, 2016).

Marmosopsis, *Szalinia*, *Incadelphys* e *Mizquedelphys* são táxons enigmáticos e pouco conhecidos, sendo considerados como táxons próximos as Jaskhadelphyidae em filogenias e estudos recentes (MUIZON e CIFELLI, 2001; OLIVEIRA e GOIN, 2011; OLIVEIRA, ZIMICZ e GOIN, 2016). Muizon e Cifelli (2001) descreveram *Szalinia* como um dos menores metatérios de Tiupampa, superando em tamanho apenas *Jaskhadelphys*. Os autores do referido estudo descrevem *Szalinia* como apresentando um encurtamento do rostró, uma característica também presente em *Gaylordia macrocynodonta*. As afinidades diretas desse táxon com linhagens norte-americanas também foram descartadas no estudo.

Mizquedelphys e *Incadelphys* são táxons endêmicos de Tiupampa (MUIZON, 1992). Atualmente, esses animais são considerados com afinidades próximas ou pertencendo à família

Pucadelphyidae (GOIN, 2003; OLIVEIRA e GOIN, 2015). *Incadelphys* apresenta várias similaridades com *Marmosopsis*, o que poderia indicar afinidades filogenéticas entre esses dois táxons (MUIZON, 1992), entretanto, nenhum estudo publicado até o momento conseguiu suportar essa hipótese.

2.4.10 Herpetotheriidae Trouessart, 1879; Sternbergiidae (Szalay, 1994) McKenna e Bell, 1997; e Derorhynchidae Goin, Case, Woodburne et al., 1999

Os Herpetotheriidae, Sternbergiidae e Derorhynchidae são um grupo registrado para a América do Norte (EBERLE e STORER, 1995; FOX, 1983; GABBERT, 1998; HOROVITZ, MARTIN, BLOCH et al., 2008; HOUGH, 1961; JOHANSON 1996b; KORTH, 1994; KORTH e EATON, 2004; MCGREW, 1937; ROTHECKER e STORER, 1996; SÁNCHEZ-VILLAGRA, LADEVÈZE, HOROVITZ et al., 2007; WILLIAMSON e TAYLOR, 2011), América do Sul (GOIN e CANDELA, 2004; OLIVEIRA e GOIN, 2012; PAULA COUTO, 1952a, 1962, 1970; TEJEDOR, GOIN, GELFO et al., 2009), Antártica (GOIN, CASE, WOODBURN e al., 1999), Austrália (GODTHELP, WROE e ARCHER, 1999), Europa e África (BADIOLA e CUESTA, 2006; BOWN e SIMONS, 1984; FERNANDÉZ, 1992; FURIÓ et al., 2012; HOOKER, SANCHEZ-VILLAGRA, GOIN et al., 2008; LADEVÈZE, SMITH e SMITH, 2012; MARTIN, CASE, JAGT et al., 2005; PEREDA-SUBERBIOLA, 2009; PIETRO e RUMMEL, 2015; RUSSELL, GALOYER, LOUIS et al., 1988; SIMONS e BOWN, 1984; STORCH e HAUBOLD, 1989), e Ásia (CROCHET, ANTOINE, BENAMMI et al., 2007; EMRY, LUCAS, SZALAY et al., 1995; GABUNIA, SHEVYREVA e GABUNIA, 1990; STORCH e QIU, 2002) apresentaram uma distribuição do Cretáceo Final (MARTIN, CASE, JAGT et al., 2005) ao Mioceno na Ásia (STORCH e QIU, 2002), Europa (FURIÓ, RUIZ-SÁNCHEZ, CRESPO et al., 2012); Austrália (ARCHER, 1976) e América do Norte (EBERLE e STORER, 1995; KORTH 1994; MCGREW, 1937), sendo inicialmente considerados como Didelphidae basais e, de fato, preenchem essa lacuna no registro fóssil.

Os Herpetotheriidae são atualmente posicionados como grupo irmão dos Marsupialia, sendo essa posição suportada por sete inequívocas sinapomorfias do crânio, dentição e pós-crânio (BECK, 2012; HOROVITZ, MARTIN, BLOCH et al., 2009; SÁNCHEZ-VILLAGRA, LADEVÈZE, HOROVITZ et al., 2007). Os Herpetotheriidae, Derorhynchidae e “Sternbergiidae” são considerados como um grupo monofilético devido à presença de uma centrocrista dilambdodonte (i.e. em formato de ‘V’) invasiva na plataforma estilar como principal característica (OLIVEIRA e GOIN, 2012), entretanto, outros metatérios também possuem essa morfologia: Peramelemorphia (GUROVICH, TRAVOUILLON, BECK et al.,

2014; MUIRHEAD e FILAN, 1995; MUIRHEAD, 2000; TRAVOUILLO, GUROVICH, BECK et al., 2010; TRAVOUILLO, BECK, HAND et al., 2013) e *Nortedelphys* (CASE, GOIN e WOODBURNE, 2005). Segundo Beck (2012), a centrocrista dilambdodonte surgiu pelo menos cinco vezes na história evolutiva do grupo. Ainda assim, muitos estudos atestam as relações filogenéticas próximas entre Herpetotheriidae, Derorhynchidae e “Sternbergiidae” (OLIVEIRA e GOIN, 2011; OLIVEIRA, ZIMICZ e GOIN, 2016).

A família “Sternbergiidae” foi proposta para agrupar *Carolopaulacoutoia*, *Itaboraidelphys* e *Didelphopsis*. Atualmente, a validade dos “Sternbergiidae” é contestada por muitos estudos, visto que *Carolopaulacoutoia* parece ser filogeneticamente mais próximo dos Herpetotheriidae, e *Itaboraidelphys* + *Didelphopsis* parecem formar uma linhagem-irmã basal aos Herpetotheriidae e Derorhynchidae (OLIVEIRA e GOIN, 2011, 2012; OLIVEIRA, ZIMICZ e GOIN, 2016).

Análises do esqueleto pós-craniano de *Herpetotherium* demonstram que esse táxon apresentava os processos das vértebras lombares longos, delgados antero-posteriormente e com uma inclinação anterior, sendo mais semelhantes às de *Mayulestes* e *Pucadelphys*, e em contraste com muitos didelídeos atuais, em que os processos espinhosos são baixos e largos antero-posteriormente; essa morfologia sugere que a parte inferior das costas permite mais movimentos de flexão e extensão, o que é típico de animais terrestres (SÁNCHEZ-VILLAGRA, LADEVÈZE, HOROVITZ et al., 2007; HOROVITZ, MARTIN, BLOCH et al., 2009). Resultados similares foram recuperados para *Amphiperatherium* na fauna de Messel, Alemanha (Eoceno inferior) (KOENIGSWALD e STORCH, 1992).

2.4.11 Marsupialia: Didelphimorphia Gill, 1872; e “Didelphoidea” Gray, 1821

A ordem Didelphimorphia é representada pelas famílias Didelphidae (GARDNER, 2008; VOSS e JANSÁ, 2009) e Sparassocynidae (REIG e SIMPSON, 1972). A ordem Didelphimorphia compreende atualmente 18 gêneros com 91 espécies classificadas em uma única família, Didelphidae (GARDNER, 2008).

O clado “Didelphoidea” é atualmente considerado um clado polifilético, incluindo uma variedade de metatérios do Cretáceo Superior da América do Norte ao Neogeno da América do Sul (KIELAN-JAWOROWSKA, CIFELLI e LUO, 2004; FORASIEPI, GOIN, MARTINELLI et al., 2009). Os “Didelphoidea” foram representados por pelo menos 10 famílias distintas, incluindo entre eles os Didelphidae, os Sparassocynidae, atualmente agrupados na ordem Didelphimorphia, os Pucadelphyidae, Mayulestidae, Herpetotheriidae, Peradectidae,

Protodidelphidae e etc. Atualmente, essa linhagem é representada pelos Didelphidae e Sparassocynidae (GOIN, 1991, 1995).

Os Didelphidae são mamíferos de pequeno a médio porte; a maioria alcançando da ponta do focinho a base da cauda cerca de 100 a 300 mm e um peso entre 20 e 500 gramas (VOSS e JANSÁ, 2009). Dentre os táxons atuais, *Didelphis virginiana* (Kerr, 1972) é considerado o maior didelfídeo vivente, apresentando um peso médio de 2,52 kg, sendo os machos um pouco mais pesados que as fêmeas (GARDNER, 1982 apud GOIN et al., 2009), em contra partida, *Chacodelphys formosa* (Shamel, 1930) é considerada a menor espécie de Didelphidae vivente, atingindo o holótipo (representando por um indivíduo jovem-adulto) 68 mm da ponta do focinho a base da cauda e pesando, provavelmente cerca de 10 g (VOSS, GARDNER e JANSÁ, 2004).

A maioria dos Didelphidae apresentam focinhos pontiagudos, grande *rhinaria*, vibrissas bem desenvolvidas, olhos proeminentes, orelhas membranosas, pelagem não espinhosa, pés pentadáctilos, caudas nuas e membros com tamanhos semelhantes (*subequal*) (VOSS e JANSÁ, 2009). Todas as espécies viventes de didelfídeos neotropicais apresentam uma semelhança geral relacionada às formas do corpo e do crânio, sendo classicamente considerados como um grupo morfologicamente conservado, entretanto, estudos com morfometria geométrica tenham demonstrado diferenças marcantes entre os membros dessa família (ASTÚA, HINGST-ZAHER, MARCUS et al., 2000).

Os Didelphidae compreendem uma ampla radiação ecológica, com espécies apresentando hábitos locomotores tão diversos como terrestres (ambos cursorial e escansorial), arborícolas e semiaquático (MARSHALL, 1978), e hábitos alimentares que variam desde os altamente frugívoros até os quase estritamente carnívoros; existindo também espécies generalistas (ASTÚA, HINGST-ZAHER, MARCUS et al., 2000; CASELLA e CÁCERES, 2006; FERNANDES, ANDRADE e SILVA JÚNIOR, 2006; SANTORI e ASTÚA, 2012; VIEIRA e ASTÚA, 2003). Dentre os gêneros de Didelphidae fósseis destacam-se: *Zygolestes* (GOIN, 1997), *Thylophorops* (REIG, KIRSCH e MARSHALL, 1987; GOIN, ZIMICZ, REYES et al., 2009), *Sairadelphys* (OLIVEIRA, NOVA, AVILLA et al., 2011) e *Hyperdidelphys* (GOIN e PARDIÑAS, 1996). Espécies extintas de gêneros ainda viventes são, por exemplo: *Didelphis solimoensis* (COZZUOL, GOIN, REYES et al., 2006), *Lutreolina* sp., *Thylamys pinei* (GOIN, MONTALVO e VISCONTI, 2000) e *Marmosa laventica* (MARSHALL, 1976). Os mais antigos Didelphidae são conhecidos para o Mioceno inferior da Argentina (GOIN, ABELLO, BELLOSI et al., 2007; GOIN e ABELLO, 2013), embora ainda não formalmente descritos.

Os Sparassocynidae Archer, 1984 representaram uma família de marsupiais carnívoros de pequeno porte, com tamanhos semelhantes aos de uma doninha, que viveram na América do Sul durante o lapso temporal incluído entre o Mioceno tardio e o Plioceno tardio (ABELLO, REYES, CANDELA et al., 2015). A família Sparassocynidae é representada por diferentes espécies do gênero *Sparassocynus*, a exemplo de *S. bahiai* Mercerat, 1898 e *S. derivatus*; e *Hesperocynus dolgopola* (ABELLO, REYES, CANDELA et al., 2015). Eles são classicamente considerados como os parentes mais próximos dos Didelphidae (REIG e SIMPSON, 1972; ABELLO, REYES, CANDELA et al., 2015).

Esses animais apresentavam características morfológicas e dentárias associadas a uma dieta mais carnívora em comparação com os Didelphidae (FORASIEPI, GOIN e MARTINELLI, 2009; REIG e SIMPSON, 1972), representando um grupo mais adaptado a uma dieta mais carnívora. A característica mais marcante do grupo está relacionada com uma morfologia singular e derivada da cavidade auditiva (FORASIEPI, GOIN e MARTINELLI, 2009), o que poderia indicar hábitos predadores para essas espécies, pois as adaptações da cavidade auditiva estão relacionadas a uma maior acuidade auditiva (REIG e SIMPSON, 1972). A família também apresentava outras adaptações para hábitos carnívoros: fortalecimento estrutural do rosto e dos arcos zigomáticos, robustez da mandíbula, maior altura dos trigonidos, redução do talonido e etc. (GOIN e MONTALVO, 1988).

O último táxon vivente dessa família foi *Sparassocynus derivatus*. Ele viveu durante o Plioceno, chegando ao Pleistoceno da Argentina, entre 4-1,5 milhões de anos atrás, sendo sua provável extinção decorrente da substituição ecológica por mamíferos placentários que cruzaram o Istmo do Panamá durante o Plioceno. As marcantes características na morfologia craniana desse táxon demonstram que ele apresentava hábitos um pouco, mas não muito, mais carnívoro ou predador do que em outros didelfídeos. O gênero *Lutreolina* é o táxon atual com hábitos carnívoros mais semelhantes aos de *Sparassocynus*, embora *Lutreolina* seja moderadamente menos carniceiro. *Sparassocynus* apresentava um desenvolvimento dos seios epi e hipotimpânicos relativamente grande, sendo essa uma característica peculiar para o gênero. Os autores sugerem que o desenvolvimento dessa região estaria relacionado ao hábito predador da espécie, auxiliando-o a encontrar presas. As adaptações no ouvido também sugerem que esse animal viveu em regiões abertas com umidade moderada, semelhante a estepes temperadas (REIG e SIMPSON, 1972). Adaptações similares também são conhecidas para *Hesperocynus*, embora menos desenvolvidas que em *Sparassocynus* (FORASIEPI, GOIN, MARTINELLI, 2009). *Lutreolina*, *Hyperdidelphys* e *Sparassocynus* coexistiram durante o Plioceno da América do Sul (SIMPSON, 1902).

Alguns táxons da família Didelphidae apresentaram características que apontam para a evolução em direção a uma dieta mais carnívora, a exemplo das espécies do gênero *Hyperdidelphys* (GOIN e PARDIÑAS, 1996). A evolução dessas espécies exemplifica claramente o processo de adaptação para dietas carnívoras, em grande parte suportada pelos didelphóideos sul-americanos durante o Cenozoico Tardio, principalmente nas adaptações evidenciadas na morfologia dentária desses animais. O desenvolvimento dos seios epitimpânicos é visualizado em algumas espécies desse gênero, como *Hyperdidelphys dimartinoi*, sendo também visualizada nos Sparassocynidae, como citado anteriormente (GOIN e PARDIÑAS, 1996; REIG e SIMPSON, 1972; REIG, KIRSCH e MARSHALL, 1987).

O desenvolvimento de adaptações carnívoras em várias linhagens distintas de Didelphoidea durante o Cenozoico Tardio não parece ser algo casual. Os Sparassodonta desapareceram nesse mesmo lapso temporal, o que poderia representar uma sucessão faunística na América do Sul durante esse período; entretanto, essa suposta sucessão faunística dentre os Didelphoidea ocorreu de forma parcial, com a extinção de diversos metatérios carnívoros de pequenos e grandes portes mais especializados durante o Plioceno, e a persistência de alguns táxons carnívoros até recentemente, a exemplo de *Lutreolina* (GOIN e PARDIÑAS, 1996).

2.4.12 Marsupialia: Paucituberculata Ameghino, 1894

A linhagem dos Paucituberculata constitui um clado de marsupiais endêmico da América do Sul (ABELLO, 2013; FORASIEPI, SÁNCHEZ-VILLAGRA, SCHMELZLE et al., 2014; MARSHALL, 1980). Os extintos Paucituberculata apresentavam uma distribuição mais ampla do que os atuais representantes dessa ordem, e o registro fóssil demonstra que eles alcançaram sua maior diversidade taxonômica durante o Mioceno inicial e médio (ABELLO e CANDELA, 2010). Tradicionalmente, três grupos principais de Paucituberculata são conhecidos: os Caenolestidae e os extintos Abderitidae e Palaeothentidae (GOIN, CANDELA, ABELLO et al., 2009). Eles são considerados como marsupiais 'pseudodiprotodontes', um grupo sem validade taxonômica (OLIVEIRA e GOIN, 2012). Uma das primeiras revisões feitas para o grupo foi proposta por Marshall (1980).

Os mais antigos Paucituberculata datam do Eoceno inferior de Itaboraí e de Las Flores, sendo *Bardalestes* Goin, Candela, Abello et al., 2009; e *Riolestes* Goin, Candela, Abello et al., 2009, os dois táxons mais basais atribuídos a essa ordem (GOIN, CANDELA, ABELLO et al., 2009). *Bardalestes* é considerado como endêmico de Las Flores, enquanto *Riolestes* é endêmico de Itaboraí. A principal característica desses animais está na presença de dentição heterocronal, ou seja, retenção de caracteres juvenis em indivíduos adultos. Outro táxon com afinidades

incertas em relação às outras linhagens da ordem Paucituberculata é *Fieratherium sorex* Forasiepi, Goin, Abello et al., 2013, do Oligoceno superior da Argentina (Deseadense SALMA). Atualmente, esse táxon é considerado como o grupo irmão de Bardalestes, Caenolestoida + Palaeothentoidea, não sendo incluído na ordem Paucituberculata (FORASIEPI, GOIN, ABELLO et al., 2013); entretanto, uma filogenia mais recente já o posiciona como um Paucituberculata basal (ABELLO, 2013). *Evolestes* é outro Paucituberculata basal da América do Sul, sendo conhecido para o Oligoceno inferior da Argentina (Tinguiririquense SALMA; ver GOIN, ABELLO e CHORNOGUBSKY, 2010) e para o Oligoceno inicial-tardio da Bolívia (GOIN, SANCHEZ-VILALGRA, ABELLO et al., 2007). Esse táxon, também de afinidades incertas, é considerado como uma linhagem basal sobrevivente durante o Paleogeno da América do Sul. De forma interessante, *Bardalestes*, *Riolestes* e *Fieratherium* são extremamente similares em dentição, enquanto *Evolestes* é muito similar aos Caenolestidae.

Os Palaeothentoidea compreenderam uma linhagem extinta de paucituberculatos que viveu desde o Eoceno inicial (e.g. *Quirogalestes almagaucha* Goin e Candela, 1998; Casamayorense SALMA; GOIN e CANDELA, 1998) até o limite Mioceno médio-Mioceno superior (ABELLO, 2013; RINCÓN, SHOCKEY, ANAYA et al., 2015). A superfamília incluiu as famílias Pichipilidae (*Quirogalestes*, *Pichipilus* e *Phonocdromus*), Abderitidae (*Abderites*, *Parabderites* e *Pithecullites*), Palaeothentidae (*Palaeothentes*, *Carlothentes*, *Acdestodon*, *Antawallathentes*, *Titanothentes*, *Trelewthentes* e *Acdestes*), além de táxons basais como *Perulestes*, *Sasawatsu* e *Pilchenia*.

Os Pichipilidae são conhecidos do Eoceno inicial até Mioceno inicial, entretanto, o grupo apresenta um lapso temporal durante o Eoceno médio-tardio e Oligoceno. A família é considerada atualmente a linhagem mais basal dos Palaeothentoidea (ABELLO, 2013).

Sasawatsu e *Perulestes* são conhecidos para o Eoceno tardio? do Peru (GOIN e CANDELA, 2004), enquanto *Pilchenia* é conhecida para o Oligoceno inicial e tardio da Argentina (GOIN, ABELLO e CHORNOGUBSKY, 2010). A exceção dos Pichipilidae, as demais linhagens da ordem Paucituberculata não sobreviveram após o Oligoceno tardio (ABELLO, 2013). *Pilchenia* é considerado um frugívoro/insetívoro, *Perulestes* um frugívoro e *Sasawatsu* um frugívoro estrito (ZIMICZ, 2012).

Os Abderitidae são representados por metatérios com hábitos alimentares granívoros/insetívoros (ZIMICZ, 2012). Essa família apresenta como principais características terceiros pré-molares hipertrofiados plagiaulacoideos com trigônido laminar com cristas oblíquas bem desenvolvidas por quase toda a extensão do mesmo, e talônido desenvolvido; outra característica da família está na presença de cristas transversais nos molares, que simulam

aparentemente lofos de animais herbívoros (ABELLO e RUBILAR-ROGERS, 2012; ABELLO, 2013; DUMONT, STRAIT e FRISCIA, 2000; ORTIZ-JAUREGUIZAR, 2003). A linhagem é conhecida do Oligoceno superior ao Mioceno médio-tardio (ABELLO, 2013).

Palaeothentidae representou o clado com maior diversidade dos Paucituberculata com pelo menos sete gêneros conhecidos e duas subfamílias descritas, sendo importantes componentes das faunas do Oligoceno-Mioceno médio (Deseadense-Santacruciense SALMAs) da América do Sul (RAE, BOWN e FLEAGLE, 1996). Dentre os gêneros conhecidos, *Palaeothentes* representa o gênero com maior diversidade para o clado, com pelo menos oito espécies descritas. A principal característica do grupo é a presença de uma paracristida cortante e bem desenvolvida no m1 (i.e. primeiro molar inferior) (ABELLO, 2013; BOWN e FLEAGUE, 1993; RINCÓN, SHOCKEY, ANAYA et al., 2015). O último membro conhecido para a linhagem foi *Acdestes? maddeni* do Mioceno médio-tardio da Bolívia (GOIN, SÁNCHEZ-VILLAGRA, KAY et al., 2003).

O mais basal Caenolestidae, segundo filogenias atuais, foi *Stilotherium* Ameghino, 1887, sendo conhecido para o Mioceno inicial (Santacruciense SALMA). A presença desse animal durante o Mioceno indica que os Paucituberculata se diversificaram após a extinção dos Polydolopidae e dos Bonaparteriiformes (PASCUAL e HERRERA, 1975; RINCÓN, SHOCKEY, ANAYA et al., 2015). Outro Caenolestidae fóssil é *Pliolestes* do Mioceno tardio-Plioceno inicial (ABELLO, 2013; GOIN, MONTALVO e VISCONTI, 2000). Os Paucituberculata atuais são representados por seis espécies nos gêneros *Caenolestes*, *Lestoros* e *Rhyncholestes*, sendo os dois últimos monotípicos, e todos eles pertencendo à família Caenolestidae (GOIN, CANDELA, ABELLO et al., 2009). Uma característica marcante da família é o desenvolvimento excessivo do primeiro par de incisivos inferior, que são projetados frontalmente, enquanto o restante é reduzido (VIEIRA e ASTÚA, 2003). Esses animais são vulgarmente conhecidos como 'musaranhos-marsupiais' devido ao seu pequeno tamanho e aos hábitos insetívoros-faunívoros (GOIN, SÁNCHEZ-VILLAGRA, ABELLO et al., 2007).

Dentre as espécies atuais, *Caenolestes* Thomas, 1895 é encontrado nas regiões mais ocidentais da Venezuela, Colômbia, Equador, e no extremo norte do Peru (LUND e PACHECO, 2003); *Lestoros inca* (Thomas, 1917) é encontrado no sul do Peru; e *Rhyncholestes raphanurus* Osgood, 1924 no sul do Chile e Argentina (ALBUJA e PATTERSON, 1996).

2.4.13 Microbiotheria Ameghino, 1889

A ordem Microbiotheria é atualmente representada por um único gênero, *Dromiciops* Thomas, 1894, conhecido vulgarmente como monito del monte (GOIN et al., 2007).

Dromiciops representa atualmente o único táxon vivente no continente sul-americano pertencente à linhagem dos Australidelphia (BECK, 2008). Estudos recentes propõem a presença de três espécies associadas ao gênero (D'ELÍA, HURADO e D'ANATRO, 2016). A distribuição desse táxon está restrita as florestas temperadas do extremo sul da Cordilheira dos Andes, de 36° a 43° de Latitude Sul (GOIN et al, 2007).

Os mais antigos fósseis da linhagem dos Microbiotheria são conhecidos para o Eoceno inferior da Formação Meseta, Antártica: *Woodburnodon casei* (GOIN et al., 2007) e *Marambiotherium glacialis* (GOIN e CARLINI, 1995; GOIN et al., 1999). Microbiotheriídeos fósseis também são conhecidos para a Argentina: *Eomicrobiotherium*, *Oligobiotherium*, *Clenia*, *Microbiotherium* (GOIN, ABELLO e CHORNOGUBSKY, 2010; CHORNOGUBSKY e KRAMAZ, 2012; GOIN e ABELLO, 2013), *Pachybiotherium* (GOIN, TEJEDOR, ABELLO et al., 2010). O táxon peruano *Kirutherium paititiensis* (GOIN e CANDELA, 2004) é tido como o único Microbiotheria fora do Reino Austral (i.e. Argentina, Chile, Antártica e Austrália). Archer et al. (1999) *apud* Beck (2012) descreve um provável Microbiotheria para a Fauna de Tingamarra, Austrália, entretanto, as afinidades desse espécime com os Microbiotheria nunca foram confirmadas.

A primeira revisão realizada com a linhagem foi realizada por Marshall (1982c), em que ele revisa não apenas microbiotheriídeos, como também alguns Paucituberculata e *Coona*. Outra revisão recente foi proposta por Goin e Abello (2013), em que *Eomicrobiotherium*, *Oligobiotherium*, *Clenia*, *Microbiotherium* e *Pachybiotherium* foram agrupados em uma linhagem monofilética independente de *Microbiotherium* e *Dromiciops*, mas, a filogenia conta apenas com essas duas linhagens, o que não garante por si só que ambas sejam filogeneticamente relacionadas.

3 OBJETIVOS

3.1 OBJETIVO GERAL

Estudo taxonômico e sistemático dos metatérios da Bacia de Itaboraí (Eoceno inicial, idade mamífero Itaboraiense [Itaboraiense SALMA]) com enfoque nas relações filogenéticas dos representantes dessa localidade com táxons de outras faunas do Paleogeno do Hemisfério Sul (i.e. América do Sul, Antártida e Austrália) e Cretáceo-Paleogeno da América do Norte e Europa.

3.2 OBJETIVOS ESPECÍFICOS

- a) Realizar a revisão taxonômica dos espécimes associados aos metatérios da Bacia de Itaboraí, buscando reavaliar o *status* taxonômico desses táxons como registrado nas coleções dos museus brasileiros, propor novas associações entre elementos de dentição superior e inferior para os táxons que são conhecidos apenas por uma destas séries e descrever possíveis novos táxons para a fauna de Itaboraí;
- b) Revisar as hipóteses de associações dos oito morfótipos de petrosos isolados (PtI a PtVIII) recuperados na Bacia de Itaboraí;
- c) Formalizar uma matriz morfológica padrão a ser utilizada para estudos futuros com o clado dos Metatheria, buscando elucidar as afinidades sistemáticas dos metatérios dessa fauna, confirmar a presença de supostos clados norte-americanos na América do Sul (e.g., Alphadontia, Pediomyoidea e Stagodontidae) e elucidar as relações dos táxons de Itaboraí com táxons do Paleogeno Europeu (e.g., Anatoliadelphidae, “Peradectidae”, Peratheriinae).

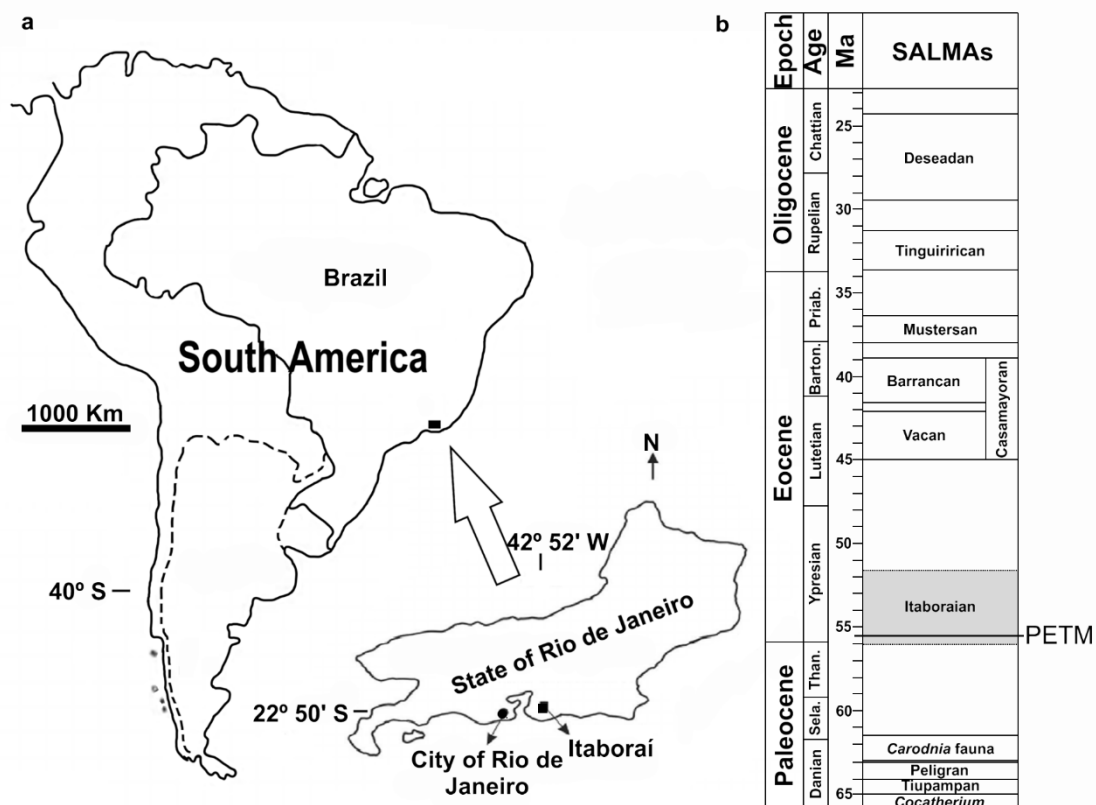
4 METODOLOGIA

4.1 MATERIAIS ESTUDADOS

4.1.1 Espécimes estudados

Todos os espécimes estudados no âmbito desta tese são provenientes da Bacia de Itaboraí, localizada no município de Itaboraí, Rio de Janeiro (RJ), Brasil (22° 45' 9.91" S, 42° 51' 53.55" W) (ver, e.g., RICCOMINI et al., 2004; BERGQVIST et al., 2009). Essa fauna é considerada como sendo do Eoceno inicial, idade Itaboraiense [Itaboraiense SALMA] (53-50 Ma, com base em datações feitas em sedimentos da Formação Las Flores; ver WOODBURN et al., 2014a), ainda que estudos prévios considerem uma abrangência temporal abrangendo desde o Eoceno inicial (ver e.g., BERGQVIST et al., 2009; CHORNOGUBSKY, 2021; entre 56-51 Ma) (Figura 4):

Figura 4 - Localização da Bacia de Itaboraí (A) e cronologia comparativa da assembleia dessa Bacia (B), destacando as SALMAs. O Itaboraiense está marcado em cinza e indicado por um desenho esquemático de um dente de metatério. A data considerada para a ocorrência do Máximo Termal do Paleoceno-Eoceno está indicada.



Fonte: O mapa de localização foi adaptado de Oliveira et al. (2021) e a coluna geocronológica foi adaptada de Chornogubsky (2021).

Foram estudados cerca de 1000 elementos de dentição, maxilas e dentários de metatérios pertencentes a, pelo menos, 29 gêneros e 44 espécies da Bacia de Itaboraí depositados no MCN-PV (Coleção de paleontologia de vertebrados do Museu de Ciências Naturais), MCTer (Museu de Ciências da Terra; ex. DGM), MN (Museu Nacional) e UFRJ-DG (Coleção de paleontologia do Departamento de Geologia da Universidade Federal do Rio de Janeiro). Os espécimes do AMNH (American Museum of Natural History) foram estudados a partir de moldes pertencentes ao Laboratório de Paleontologia da UFPE sob curadoria do Prof. Dr. Édison Vicente Oliveira e imagens enviadas por Russell K. Engelman (Case Western Reserve University [CWRU]) com autorização de Jin Meng (AMNH) e Judy Galkin (AMNH).

Em 02 de setembro de 2018, um incêndio destruiu a coleção de metatérios do MN. Felizmente, moldes produzidos durante o doutorado do Prof. Dr. Édison Vicente Oliveira preservaram diversos espécimes dessa coleção, incluindo os holótipos (a exceção de *Bobbschaefferia fluminensis* [MN 1360-V]). Esses moldes estão atualmente no Laboratório de Paleontologia da UFPE. Em adição, fotografias em estereomicroscópio de parte dos espécimes dessa coleção feitas na própria coleção do MN por Leonardo de Melo Carneiro em 2017-2018

e pelo Prof. Dr. Édison Vicente Oliveira entre 2010-2012 permitiram um estudo mais detalhado de parte dos espécimes dessa coleção.

Os petrosos de Itaboraí foram estudados por Ladevèze (2004, 2007) e Ladevèze e Muizon (2010). Infelizmente, acredita-se que esses espécimes também foram destruídos com o incêndio do museu. Portanto, as informações aqui apresentadas seguem quase que exclusivamente as descrições, classificações e dados desses autores. O incremento desta tese está na revisão taxonômica da fauna de metatérios, aumento do número de espécimes (N) e número mínimo de indivíduos (MNI) para cada táxon, revisão das dimensões dos espécimes estudados (e.g., dentes, dentários), inclusão dos caracteres propostos por Ladevèze e Muizon (2010) na matriz construída no âmbito deste doutorado e consideração da regressão de Beck et al. (2008) como um segundo elemento para sugestão das associações.

O número total de espécimes por táxon (i.e., dentes, dentários e maxilas) e a completude de cada táxon da fauna metateriana da Bacia de Itaboraí estão apresentados em ‘5 Resultados, 5.2 Taxonomia e Sistemática, 5.2.1 Diversidade, *status* taxonômico e identificação dos metatérios da Bacia de Itaboraí, Tabelas 5.1 e 5.2’. A lista completa dos espécimes estudados com diversos dados relacionados (e.g., número de coleção, táxon, descrição do espécime, se já foi fotografado, se possui imagens em MEV e observações gerais) está apresentada no **Apêndice A**.

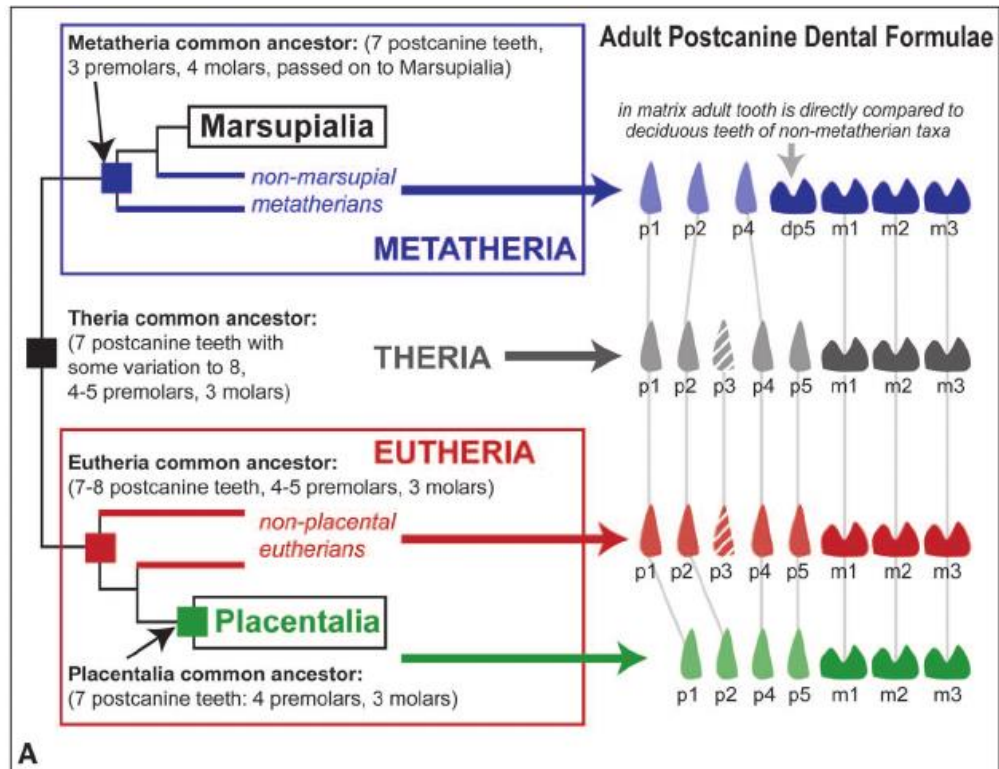
4.1.2 Nomenclatura e terminologia morfo-anatômica

A nomenclatura utilizada para os componentes de dentição superiores e inferiores dos metatérios de Itaboraí foram baseados em Oliveira e Goin (2011). Os elementos de dentição superior são identificados por letras em maiúsculo (I, C, P, DP, M) e os inferiores por letras minúsculas (i, c, p, dp e m).

Os *loci* dos pré-molares foram denominados como P1-3/p1-3, sendo os *loci* P3/p3 dos metatérios homólogos aos *loci* P4/p4 dos Eutheria e outros Theria (O’LEARY et al., 2013). Os *loci* P1/p1 e P2/p2 são homólogos aos P1/p1 e P2/p2 dos Eutheria (figura 4.2).

Os *loci* dos molares foram denominados como M1-4/m1-4, sendo os *loci* M2/m2 dos metatérios homólogos aos *loci* M1/m1 dos Eutheria e outros Theria, os *loci* M3/m3 homólogos aos *loci* M2/m2 e os *loci* M4/m4 homólogos aos *loci* M3/m3 (O’LEARY et al., 2013). O *loci* M1/m1 é possivelmente homólogo ao DP5/dp5 dos Eutheria e outros Theria (O’LEARY et al., 2013) (figura 5).

Figura 5 - Relações de homologias dentárias entre metatérios e eutérios.

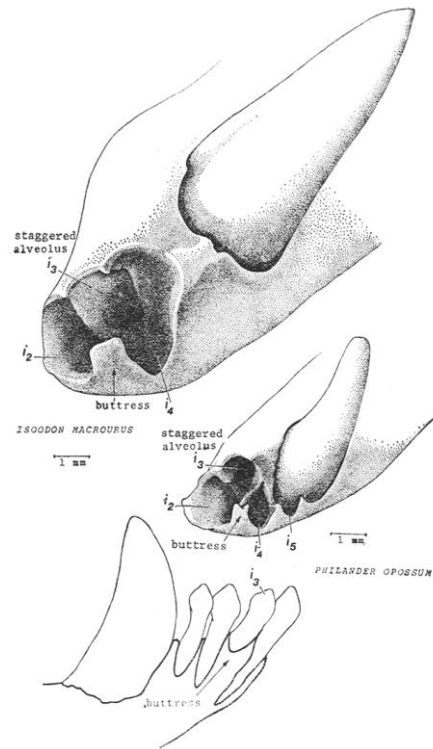


Fonte: O'LEARY et al. (2013, p. 666, fig. 3A).

Com relação a nomenclatura dos molares, outras propostas foram apresentadas na literatura. Marshall (1987), Marshall e Muizon (1988), Muizon (1992) consideraram os decíduos dos metatérios (DP/dp3) como M/m1, o primeiro molar (M/m1) como M/m2, o segundo/antepenúltimo como M/m3, o terceiro/penúltimo como M/m4, e o quarto/último como M/m5. No âmbito desta tese, a dentição decídua dos metatérios recebeu a nomenclatura padrão de publicações recentes (DP/dp3) (ver e.g., OLIVEIRA e GOIN, 2011; CARNEIRO et al., 2018). Com relação a série molar, eles foram reconhecidos em função de sua posição em sentido antero-posterior: M/m1, M/m2, M/m3 e M/m4.

A nomenclatura dos incisivos baseou-se em Hershkovitz (1982), que considerou os incisivos dos metatérios como I1-5 e i2-5. A definição de um i3 sobremontado (*staggered*) é baseada no estudo supracitado (ver esquema abaixo, Figura 6). A nomenclatura pós-craniana seguiu Szalay (1994), e Szalay e Sargis (2001). A nomenclatura considerada para os petrosos seguiu Ladevèze (2004, 2007), Ladevèze e Muizon (2007, 2010) e Muizon et al. (2018).

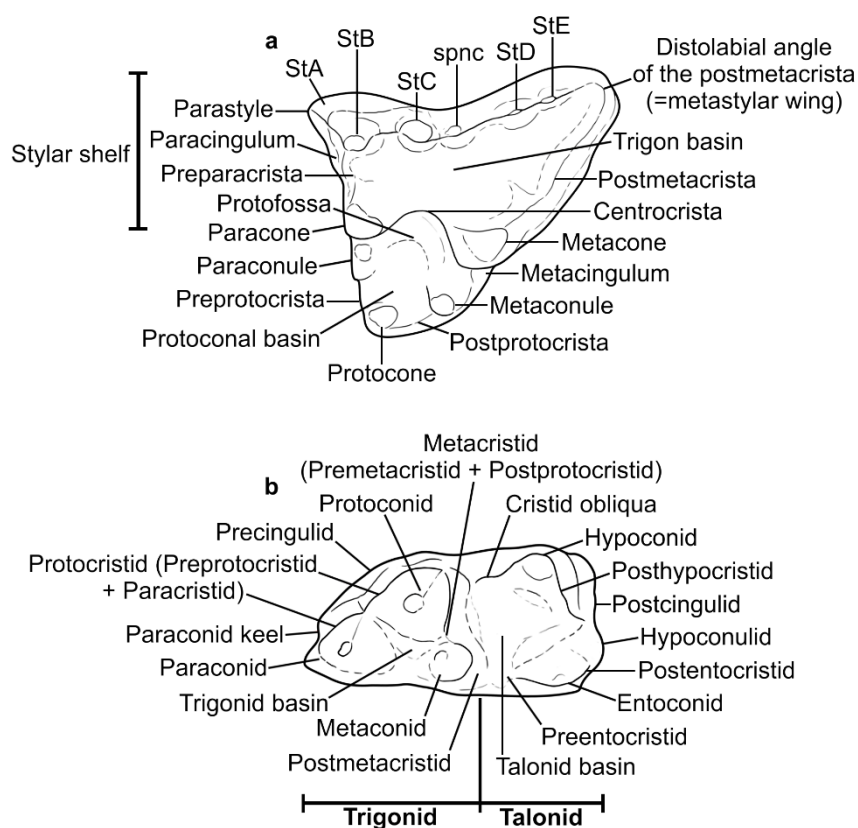
Figura 6 - Terceiros incisivos inferiores sobremontados (*staggered*) em *Isoodon macrourus* (acima) e *Philander opossum* (centro, em vista cranial; abaixo, em vista labial).



Fonte: Hershkovitz (1982, p. 13, fig. 2).

A nomenclatura considerada para as estruturas dos pré-molares e molares (e.g., cúspide, crista, bacia, cingulo/cingulido) baseou-se em diversos artigos da literatura (GOIN et al., 2010; ZIMICZ, 2012, 2014; OLIVEIRA e GOIN, 2012; WILLIAMSON et al., 2012; FORASIEPI et al., 2015; ENGELMAN et al., 2018, 2020a, 2020b; MUIZON et al., 2018; BABOT et al., 2020, 2022; MUIZON e LADEVÈZE, 2020, 2022; CHORNOGUBSKY, 2021). Abaixo estão ilustradas as principais estruturas dos molares superiores e inferiores dos metatérios estudados nesta tese (Figura 7):

Figura 7 - Desenho esquemático dos molares superiores e inferiores de um metatério apresentando uma lista geral das principais estruturas da dentição de um metatério utilizadas na construção da matriz morfológica. O esquema utilizou como base os molares superiores e inferiores de *Xenocynus crypticus* Carneiro et al., 2024a.



Fonte: Uso autorizado por Sérgio Lages (2024) adaptado de Carneiro et al. (2024a).

4.2.3 Imagens e outras ilustrações

As imagens dos espécimes do Museu de Ciências da Terra (MCTer) e coleção de paleontologia da Universidade Federal do Rio de Janeiro (UFRJ-DG) foram feitas com câmera digital modelo Câmera Canon Rebel T100 com lente 50 mm e anéis de extensão para macrofotografia e estereomicroscópios modelos Zeiss Stemi 508 Greenough Stereo Microscope com câmera Axiocam 208 e Zeiss Stemi 2000. A medição dos espécimes foi realizada com o *software* de medição digital ImageJ (FERREIRA e RASBAND, 2012).

As imagens em microscopia eletrônica de varredura (MEV) foram produzidas com os modelos: JEOL JSM-6390LV do Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional (MN), Rio de Janeiro, RJ, Brasil; modelo Quanta FEI 250 da Unidade de Microscopia Avançada, Centro Nacional de Biologia Estrutural e Bioimagem (CENABIO), Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, RJ, Brasil; modelo Tescan Vega 3 do Núcleo de Microscopia Eletrônica da COPPE, Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, RJ, Brasil; modelo JEOL 6060 do Centro de Microscopia e Microanálise da Universidade Federal do Rio Grande do Sul (CMM, UFRGS), Porto Alegre, RS, Brasil; modelo JEOL JSM-5200 do Museu de

Ciências Naturais da antiga Fundação Zoobotânica do Rio Grande do Sul (MCN-PV, FZBRGS/RS), Porto Alegre, RS, Brasil; modelo Phenon XL do Laboratório de Micropaleontologia Aplicada (LMA), Instituto de Pesquisa em Petróleo e Energia (LITPEG), Universidade Federal de Pernambuco (UFPE), Recife, PE, Brasil; e modelo JEOL JSM-6510LV do Instituto de Química, Universidade do Estado do Rio de Janeiro (UERJ).

4.2.4 Taxonomia

A diversidade de metatérios de Itaboraí baseou-se inicialmente nas propostas taxonômicas e sistemáticas de Marshall (1987), Goin et al. (1998a, 2009), Oliveira (1998), Goin e Oliveira (2007), Oliveira e Goin (1999, 2011, 2012, 2015), Oliveira et al. (2016, 2021), Beck (2017), Carneiro e Oliveira (2017a, b), Carneiro et al. (2018), Carneiro (2019) e Rangel et al. (2019). Em adição, os resultados seguiram estudos publicados durante o âmbito desta tese (como resultado dela ou não), como Oliveira et al. (2021), Carneiro e Oliveira (2023), Rangel et al. (2023a, 2023b) e Carneiro et al. (2024a, 2024b, 2024c, 2024d).

Essas hipóteses foram reavaliadas mediante à revisão taxonômica dos espécimes de Itaboraí, revisão das associações dos petrosos com diferentes táxons da fauna e dos resultados das análises filogenéticas. A listagem dos elementos de dentição conhecidos para os metatérios de Itaboraí está apresentada em ‘5 Resultados, 5.2 Taxonomia e Sistemática, 5.2.3 Classificação sistemática dos metatérios da Bacia de Itaboraí, Tabela 5.3’.

A identificação taxonômica dos metatérios de Itaboraí baseou-se, inicialmente, nos resultados de Oliveira (1998), sendo essas identificações revisadas. Em adição aos espécimes estudados por Oliveira (1998), os espécimes do MN classificados como *incertae sedis* foram identificados e descritos; os espécimes depositados na coleção da UFRJ-DG foram estudados e suas fotografias e imagens em MEV são apresentadas pela primeira vez; dezenas de novos dentes isolados e centenas de dentários de metatérios encontrados na coleção do MCTer foram identificados, descritos, fotografados e tombados (i.e., adicionados à coleção), e os espécimes do MCN-PV foram reestudados, espécimes nunca antes estudados dessa coleção foram formalmente estudados (ver e.g., CARNEIRO et al., 2024a) e novos espécimes descobertos foram tombados na coleção (ver listagem completa no **Apêndice A**).

Para identificação e associação entre molares superiores e inferiores, os mesmos parâmetros considerados por Oliveira (1998, p. 18) foram seguidos (com algumas adições a sua linha de evidências):

a) Comprimento relativo dos pré-molares e molares (LPx/Lpx; LMx/Lmx, em que ‘x’ representa um dos *loci* dentário, e.g., P/p2, M/m3) (em geral, o comprimento dos molares

superiores e inferiores são similares para os segundo e terceiro molares, o que permite uma associação indireta – obs. pes.);

b) Abundância relativa das espécies, baseada no NMI (o NMI é um indicativo da abundância de um táxon com base nos espécimes conhecidos);

c) Morfologia dos pré-molares, molares e dentários (e.g., bunodontia, presença de estruturas acessórias [e.g., cúspulas supranumerárias]);

d) Ocorrência de espécies apenas com molares inferiores ou apenas com molares superiores (limitação amostral taxonômica; sensu MARSHALL, 1984; ver e.g., “*Zeusdelphys*” e “*Riolestes*”);

e) Afinidades sistemáticas previamente consideradas (e.g., Caroloameghiniidae já foi considerado como pertencendo aos “Peradectoidea” ou Didelphimorphia);

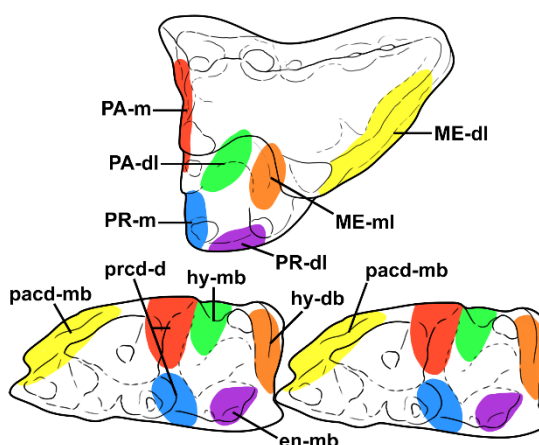
f) Plasticidade fenotípica (i.e., variações morfológicas) com enfoque principal na variação natural de tamanho e morfologia das estruturas molares, e morfologia dos alvéolos em maxilas e dentários;

g) Padrões morfométricos e morfofuncionais (i.e., índices calculados com base nos diferentes elementos de dentição e na morfologia dos dentários; e.g., PS, forma do pré-molar);

h) Relações de oclusão entre os molares (e.g., marca de desgaste no M3 de *Carolocoutoia ferigoloi* e cúspide supranumerária no talônido do m3).

As associações propostas para molares superiores e inferiores foram baseadas na morfologia, tamanho e relações oclusivas entre as estruturas, como indicado na figura abaixo (Figura 8):

Figura 8 - Oclusão dentária entre os molares superiores e inferiores de um metatério. As cores similares demarcadas nos molares superiores e inferiores indicam relações oclusais entre as estruturas/facetas marcadas. A nomenclatura seguiu Schultz et al. (2020). O esquema utilizou como base os molares superiores e inferiores de *Xenocynus crypticus* Carneiro et al., 2024a.



Fonte: Uso autorizado por Sérgio Lages (2024) adaptado de Carneiro et al. (2024a).

A classificação de tamanho dos metatérios de Itaboraí foi baseada no comprimento da série molar inferior (Lm1-4) (CARNEIRO e OLIVEIRA, 2023, p. 273). Para tal, foram considerados, na classificação, dentários com série molar/série alveolar completas para os metatérios de Itaboraí. O comprimento da série molar inferior foi preferido ao da série molar superior devido ao maior número de séries inferiores preservadas para diferentes espécies (quase a totalidade da fauna de metatérios de Itaboraí apresenta a série molar ou alveolar inferior conhecida) em comparação as séries superiores. Para táxons que não possuem séries molares ou alveolares preservadas (e.g., *Eobrasilia coutoi*), as dimensões dos molares isolados (comprimento [L]; e largura [W]) foram consideradas para sua classificação de tamanho por meio de comparação relativa com outros táxons da fauna. Com relação a classificação de Carneiro e Oliveira (2023), algumas modificações foram feitas nos limites de cada categoria com base na descoberta dos novos espécimes no âmbito desta tese.

A classificação de tamanho para cada espécie de metatério de Itaboraí está apresentada em ‘5 Resultados, 5.2 Taxonomia e Sistemática, 5.2.3. Classificação de tamanho e estimativa de massa corporal, Tabela 5.4’. Os limites considerados para as categorias de tamanho estão listados na tabela abaixo (Tabela 4.1):

Tabela 4.1 - Categorias de tamanho definidas com base no comprimento total da série molar inferior (Lm1-4), em milímetros (mm), e os seus respectivos limites (mínimo e máximo) de massa corporal estimadas (MC), em gramas (g) e quilogramas (kg), considerados para os metatérios de Itaboraí (sensu CARNEIRO et al., 2024b). MC, massa corporal estimada; Lm1-4, comprimento da série molar inferior.

Categoria de tamanho	Lm1-4 (mm)	MC (g e Kg)

Minúsculo	Lm1-4 < 5.00 mm	MC < 15 g
Muito pequeno	5.00 mm < Lm1-4 < 6.20 mm	15 g < MC < 40 g
Pequeno	6.20 mm < Lm1-4 < 9.40 mm	40 g < MC < 150 g
Médio	9.40 mm < Lm1-4 < 15.50 mm	150 g < MC < 1 kg
Grande	15.50 mm < Lm1-4 < 22.00 mm	1 kg < MC < 3.3 kg
Muito grande	22.00 mm < Lm1-4	3.3 kg < MC < 10 kg

Fonte: Carneiro et al. (2024a).

Existem outras duas classificações de tamanho apresentadas na literatura para os metatérios de Itaboraí:

a) Marshall (1987): agrupou os metatérios não-Sparassodonta nas seguintes categorias de tamanho: 1) muito pequeno (*Minusculodelphis*), 2) pequeno (*Carolopaulacoutoia*, *Derorhynchus*, *Gaylordia*, *Marmosopsis*, *Mirandatherium* e *Monodelphopsis*), 3) médio (*Bobbschaefferia*, *Guggenheimia*, *Itaboraaidelphys* e *Procaroloameghinia*), 4) grande (*Didelphopsis* e *Protodidelphis*), e 5) muito grande (*Eobrasilia* e “*Zeusdelphys*”).

b) Zimicz (2012): agrupou os metatérios não-Sparassodonta (i.e., “*Ameridelphia*”/“*Poliprotodontes*” e *Polydolopimorphia*) nas seguintes categorias em função de sua massa corporal estimada (MC): 1) muito pequeno (<10 g), 2) pequeno (10-100 g), 3) médio (100-1000 g), e 4) grande (>1000 g). Para os Sparassodonta, Zimicz (2012) considerou três categorias de tamanho baseadas na massa corporal: 1) pequeno (<2 kg), 2) médio (2-10 kg), e 3) grande (>10 kg).

A categoria de tamanho minúsculo aqui utilizada é equivalente a categoria de tamanho muito pequeno de Marshall (1987); as categorias muito pequeno e pequeno são equivalentes à categoria pequeno de Marshall (1987) e Zimicz (2012); a categoria dos médios é equivalente as de Marshall (1987) e Zimicz (2012); e as categorias grande e muito grande são similares as de Marshall (1987) e equivalentes a categoria grande de Zimicz (2012).

Em adição, Rangel et al. (2023b) classificou os Sparassodonta com menos de 10 kg como pertencendo a categoria de tamanho dos pequenos. Para esta presente tese, os Sparassodonta de Itaboraí foram agrupados com base na classificação de tamanho apresentada por Carneiro e Oliveira (2023), visto que o maior deles (*Silvenator brasiliensis*) apresentou uma massa corporal estimada (MC) menor que 10 kg (ver ‘5 Resultados, 5.2 Taxonomia e Sistemática, 5.2.3. Classificação de tamanho e estimativa de massa corporal, Tabela 5.4’).

A presente tese não seguiu uma classificação com base exclusivamente na massa corporal estimada (MC), como proposta por Zimicz (2012), pelo fato dessa medida ser diretamente dependente das dimensões dos molares (ver metodologias abaixo). Nesse contexto, a MC compreende uma variável dependente das dimensões dos molares (L, W ou área [A]). Baseado nisso, utilizou-se uma classificação baseada no comprimento da série molar inferior (Lm1-4), indicando as massas corporais estimadas correspondentes a cada categoria (limites mínimo e máximo, ver Tabela 4.1).

Salienta-se que o autor desta tese subdividiu a categoria dos pequenos de Marshall (1987) e Zimicz (2012) nas categorias muito pequeno e pequeno devido à presença (na Bacia de Itaboraí) de espécies cogenéricas simpátricas em que uma apresenta maiores dimensões (categoria dos pequenos) e outra menores dimensões (categoria dos muito pequenos). Essa observação permite inferir que durante o Eoceno inicial (Itaboraiense SALMA) existiam nichos tróficos distintos para ambas as espécies. A consideração dessas duas categorias de tamanho como válidas parece resgatar um padrão ecomorfológico (e, consequentemente, evolutivo e funcional) mais “natural” para os metatérios de Itaboraí. Curiosamente, esse padrão é observado apenas para metatérios da categoria trófica dos insetívoros. Portanto, nesta tese, as categorias de tamanho muito pequeno e pequeno seguiram a proposta de Carneiro e Oliveira (2023, p. 273).

As categorias de tamanho grande e muito grande foram consideradas devido aos táxons da categoria dos grandes apresentarem dietas mais generalizadas do que os da categoria dos muito grandes, que, por sua vez, são mais especializados (ver e.g., ZIMICZ, 2012; RANGEL et al., 2023b; CARNEIRO et al., 2024d). Apesar do maior tamanho, os três metatérios muito grandes da fauna de Itaboraí (*Carolocoutoia ferigoloi*, *Silvenator brasiliensis* e *Eobrasilia coutoi*) apresentam dentições evidentemente transformadas e comparativamente mais especializadas que seus respectivos táxons irmãos (*Robertbutleria*, *Patene* e *Periprotodidelphis*, respectivamente). Dessa forma, a categorização dos metatérios em duas categorias de tamanho distintas aparenta resgatar nichos ecomorfológicos distintos, considerando os metatérios frugívoros e faunívoros (pelo menos, para a Bacia de Itaboraí). Portanto, nesta tese, as categorias de tamanho muito pequeno e pequeno seguiram a proposta de Carneiro e Oliveira (2023, p. 273).

4.2.5 Estimativa de massa corporal (MC)

As estimativas de massa corporal para cada táxon de Itaboraí seguiram métodos baseados em regressões, cujas fórmulas base são:

$$\ln Y = a + b(\ln X)$$

$$\log Y = a + b(\log X)$$

lnY ou **logY** é o logaritmo natural/logaritmo da massa corporal (**lnMC/logMC**); **a** é a intercepção; **b** é a inclinação, e **lnX** ou **logX** é o logaritmo natural/logaritmo da medida do molar (comprimento, largura ou área [no âmbito desta tese, lnX representa o comprimento/dimensão mesio-distal]).

As regressões foram baseadas no modelo de Myers (2001), que considerou o comprimento das séries molares superiores (LM1-4) e inferiores (Lm1-4), assim como o comprimento das séries alveolares superiores e inferiores. O modelo de Gordon (2003) utilizou medidas de comprimento, largura e área para cada *locus* de molar superior e inferior. Devido ao fato de muito metatérios possuírem séries molares com diferenças de tamanho entre os molares (e.g., *Epidolops ameghinoi* $m1 > m2 > m3 > m4$; *Patene simpsoni* $m1 < m2 < m3 < m4$) e séries molares inferiores serem conhecidas para praticamente todos as espécies de metatérios de Itaboraí, a regressão de Myers (2001) foi preferencialmente escolhida.

Com relação ao modelo de Myers (2001), considerou-se as regressões obtidas para o comprimento da série molar superior (**UMORL**), comprimento da série alveolar superior (**UMRL**), comprimento da série molar inferior (**LMORL**) e comprimento da série alveolar inferior (**LMRL**). **LMORL** e **UMORL** são medidas desde o limite mesial da coroa do primeiro molar até o limite distal da coroa do quarto molar (i.e., do parástilo ao limite disto-labial da pós-metacrista). **LMRL** e **UMRL** são medidas obtidas a partir dos alvéolos em vez dos molares, correspondendo a distância do limite mesial do alvéolo anterior do primeiro molar até o limite distal do alvéolo posterior do quarto molar (para descrições mais detalhadas, ver MYERS, 2001). As regressões citadas são baseadas no ‘*all species data-set*’ de Myers (2001, p. 103) possuem as seguintes fórmulas:

$$\log_{10} y = -0.914 + 3.320(\log_{10} x) \text{ UMORL (Eq. 1) } [r^2: 0.967]$$

$$\log_{10} y = -0.944 + 3.372(\log_{10} x) \text{ UMRL (Eq. 2) } [r^2: 0.970]$$

$$\log_{10} y = -1.253 + 3.540(\log_{10} x) \text{ LMORL (Eq. 3) } [r^2: 0.962]$$

$$\log_{10} y = -1.302 + 3.602(\log_{10} x) \text{ LMRL (Eq. 4) } [r^2: 0.962]$$

‘y’ corresponde a massa corporal (MC); ‘x’ corresponde o comprimento das séries molar superior (Eq. 1 – UMORL), alveolar superior (Eq. 2 – UMRL), molar inferior (Eq. 3 – LMORL) e alveolar inferior (Eq. 4 – LMRL).

A maioria das massas corporais estimadas (MC) calculadas nesta tese foram baseadas, principalmente, nas séries molares e alveolares inferiores, visto que dentários com essas séries preservadas são conhecidos para a grande maioria dos metatérios de Itaboraí. Considerando as séries molares superiores, ainda que elas apresentem índices de erro menores que os calculados para as séries molares inferiores (ver MYERS, 2001), elas são menos conhecidas em comparação com as séries inferiores. Dessa forma, as MCs de um determinado táxon estão apresentadas indicando se os valores foram obtidos com base nas séries inferior (inf.) e/ou superior (sup.), quando ambas são conhecidas para um determinado táxon.

Todas as estimativas de massa corporal são apresentadas em gramas (g) e/ou quilogramas (Kg). A MC das espécies de metatérios de Itaboraí está apresentada em ‘5 Resultados, 5.2 Taxonomia e Sistemática, 5.2.4 Classificação de tamanho e estimativa de massa corporal, Tabela 5.5’. A MC específica para cada um dos espécimes mais completos (i.e., aqueles que possuem série molares e/ou série alveolares superiores e/ou inferiores completas ou praticamente completas) considerados para uso nas equações está disponível como **Apêndice B**.

4.2.6 Estrutura faunística dos metatérios da fauna de Itaboraí

A abundância relativa (**AR**) das diferentes espécies, gêneros, subfamílias e famílias foram calculados com base no NMI. Essa metodologia permitiu avaliar quais táxons foram mais abundantes na fauna de Itaboraí.

O cálculo da abundância relativa de cada táxon foi obtido com base na seguinte equação:

$$AR = (NMI_{tx}/NMI_t) * 100 \text{ (Eq. 5)}$$

AR, abundância relativa; NMI_{tx} , número mínimo de indivíduos de um táxon; NMI_t , número mínimo de indivíduos total para a fauna de Itaboraí.

A abundância relativa para as espécies de metatérios de Itaboraí em relação a toda a fauna metateriana dessa localidade, a abundância relativa para cada espécie em relação ao seu clado (e.g., família, subfamília) e categoria de tamanho estão apresentadas em ‘5 Resultados, 5.3 Estrutura faunística, Tabelas 5.6, 5.7 e 5.8’.

4.3 REAVALIAÇÃO DOS PETROSOS DE ITABORAÍ

Os petrosos isolados de Itaboraí foram descritos, mensurados e estudados por Ladevèze (2004, 2007) e Ladevèze e Muizon (2010), com informações adicionais apresentadas por Beck (2017), Muizon et al. (2018) e Ladevèze et al. (2020). Para realizar as associações com os táxons conhecidos a partir de dentes, o estudo de Ladevèze e Muizon (2010, p. 764) utilizou a regressão da área do *promontorium* (PtApromol) contra a regressão da área molar (M/me). Dessa forma, eles estimaram as áreas dos molares (M/me) dos metatérios compatíveis com o tamanho dos petrosos com base nas seguintes equações:

$$y = 0,174x^{1.3287} \text{ (Eq. 6) } [r^2: 0.894]$$

$$y = 0,1107x^{1.327} \text{ (Eq. 7) } [r^2: 0.887]$$

$$y = 0,1282x^{1.4474} \text{ (Eq. 8) } [r^2: 0.8559]$$

$$y = 0,0804x^{1.4426} \text{ (Eq. 9) } [r^2: 0.8738]$$

‘y’ corresponde às áreas do M2, m2, M3 e m3, respectivamente (Eq. 6-9); ‘x’ corresponde a área do *promontorium* (PtApromol). Os valores de r^2 de cada equação está apresentado entre [].

De forma similar, Beck et al. (2008) tentaram associar petrosos e calcâneos isolados da fauna de Tingamarra, Murgon, Austrália (Eoceno inicial, ~54.6 Ma; ver BECK, 2012) com os metatérios conhecidos para a fauna. Para tal, eles estimaram o comprimento do M2 com base no tamanho do petroso com base na seguinte fórmula:

$$y = 0,629x - 1,602 \text{ (Eq. 10) } [r^2: 0.883]$$

‘y’ é o comprimento do M2 e ‘x’ é o comprimento do petroso. O valor de r^2 da equação está apresentado entre [].

Com o intuito de revisar as associações propostas para os petrosos com os táxons da fauna de Itaboraí, as duas referidas metodologias foram seguidas (ver e.g., LADEVÈZE, 2004, 2007; BECK et al., 2008; LADEVÈZE e MUIZON, 2010; MUIZON et al., 2018), mas com algumas contribuições diferenciais. Em relação a metodologia de Ladevèze e Muizon (2010), os cálculos das áreas por eles estimados foram considerados, em primeiro lugar, como um indicativo da categoria de tamanho para um determinado morfótipo de petroso (e.g., muito pequeno, pequeno etc.), a fim de avaliar a diversidade total de metatérios compatível em tamanho com as estimativas.

Em seguida, as áreas dos molares estimadas em função dos petrosos (**Me/me**) foram comparadas com as áreas dos molares calculadas para os metatérios de Itaboraí (**Ma/ma**) para avaliação das maiores probabilidades de associação dentro de uma categoria de tamanho (e.g., o PtIII pertenceu a um metatério da categoria de tamanho dos muito pequenos, apresentando

dimensões estimadas congruentes com o Peradectoidea gen. et sp. nov. 2, *Marmosopsis juradoi* e *Gaylordia doelloi*). Para a metodologia de Beck et al. (2008), o comprimento do m2 (Lm2), além do comprimento do M2 (LM2), foi também considerado, uma vez que os segundos molares superiores e inferiores são frequentemente semelhantes em comprimento (obs. pes.); isso permitiu a consideração nessa regressão de táxons com M2 desconhecidos.

Baseado nessas mudanças, a metodologia empregada nessa tese apresentou as seguintes etapas: Primeiro, a revisão taxonômica dos metatérios de Itaboraí identificou, no mínimo, 29 gêneros e 44 espécies (ver GOIN et al., 1998a; OLIVEIRA, 1998; GOIN e OLIVEIRA, 2007; GOIN et al., 2009; OLIVEIRA e GOIN, 2011, 2015; OLIVEIRA et al., 2016, 2021; BECK, 2017; CARNEIRO e OLIVEIRA, 2017a, 2017b, 2023; CARNEIRO et al., 2018; CARNEIRO, 2019; RANGEL et al., 2019, 2023a, 2023b; MUIZON e LADEVÈZE, 2020), um aumento notável na diversidade quando comparado com Ladevèze e Muizon (2010), que consideraram apenas 17 gêneros e 19 espécies. A revisão taxonômica resultou na identificação mais confiável dos espécimes, o que resultou em áreas dos molares (**Ma/ma**) mais precisas para cada táxon dos metatérios de Itaboraí.

Em segundo, os oito morfótipos de petrosos propostos por Ladevèze (2004, 2007) e Ladevèze e Muizon (2010) (i.e., PtI a PtVIII) foram agrupados dentro das categorias de tamanho consideradas no âmbito desta tese (i.e., categorias de tamanho: minúsculo, muito pequeno, pequeno, médio, grande e muito grande) com base em suas áreas molares estimadas (**Me/me**) como obtido por Ladevèze e Muizon (2010). Isso foi seguido devido à observação de que alguns táxons possuem áreas dos molares superiores (**Ma**) congruentes com as áreas estimadas (**Me**) para um determinado morfótipo de petroso; entretanto, as áreas calculadas para os molares inferiores (**ma**) do mesmo táxon podem ser incongruentes com as áreas estimadas (**me**) para o mesmo morfótipo de petroso (e.g., PtVI é congruente com as áreas calculadas para os molares superiores de *Austropedimys marshalli*, mas maiores que as áreas calculadas para os molares inferiores dessa espécie).

Essas diferenças de congruência entre molares superiores e inferiores podem estar relacionadas a morfologia da coroa dos táxons de Itaboraí (e.g., braquiodontia, bunodontia, molares subquadrangulares, molares superiores mesio-distalmente comprimidos). Observou-se que táxons frugívoros apresentam áreas relativamente maiores que as de outros táxons de mesma categoria de tamanho com dietas mais carnívoro-insetívoras. Consequentemente, as áreas estimadas dos molares (**Me/me**) calculadas por Ladevèze e Muizon (2010) foram consideradas como um indicativo da categoria de tamanho congruente ao morfótipo do petroso e não necessariamente a um referido táxon.

Além disso, a abundância relativa (baseada no número mínimo de indivíduos [NMI])

foi também considerada, visto que alguns táxons são, aparentemente, mais abundantes do que outros, o que “aumentaria” a probabilidade de associação com um dos morfótipos de petroso (ver metodologia base como proposta por BECK, 2017). Entretanto, essa variável não deve ser considerada “por si só”, visto que a abundância relativa de um táxon depende muito do esforço amostral no momento da coleta e triagem e da natureza diagenética da Bacia.

Finalmente, os resultados da análise filogenética que compreendeu apenas metatérios com petrosos preservados ou associados e os oito morfótipos de petrosos de Itaboraí (*‘petrosal-based’* taxa) foram considerados para uma atribuição mais confiável desses elementos, uma vez que algumas categorias de tamanho possuem um número de táxons muito maior em comparação com a diversidade de morfótipos compatíveis com ela (e.g., categoria dos pequenos). As afinidades dos táxons de uma mesma categoria são, em geral, muito variadas (categoria dos pequenos possui, dentre outras, Bonapartheriidae, Caroloameghinioidea, Derorhynchidae, Didelphimorphia, Peradectoidea e etc.), no que as afinidades recuperadas pela análise filogenética podem proporcionar hipóteses de associação mais confiáveis para os morfótipos de petrosos.

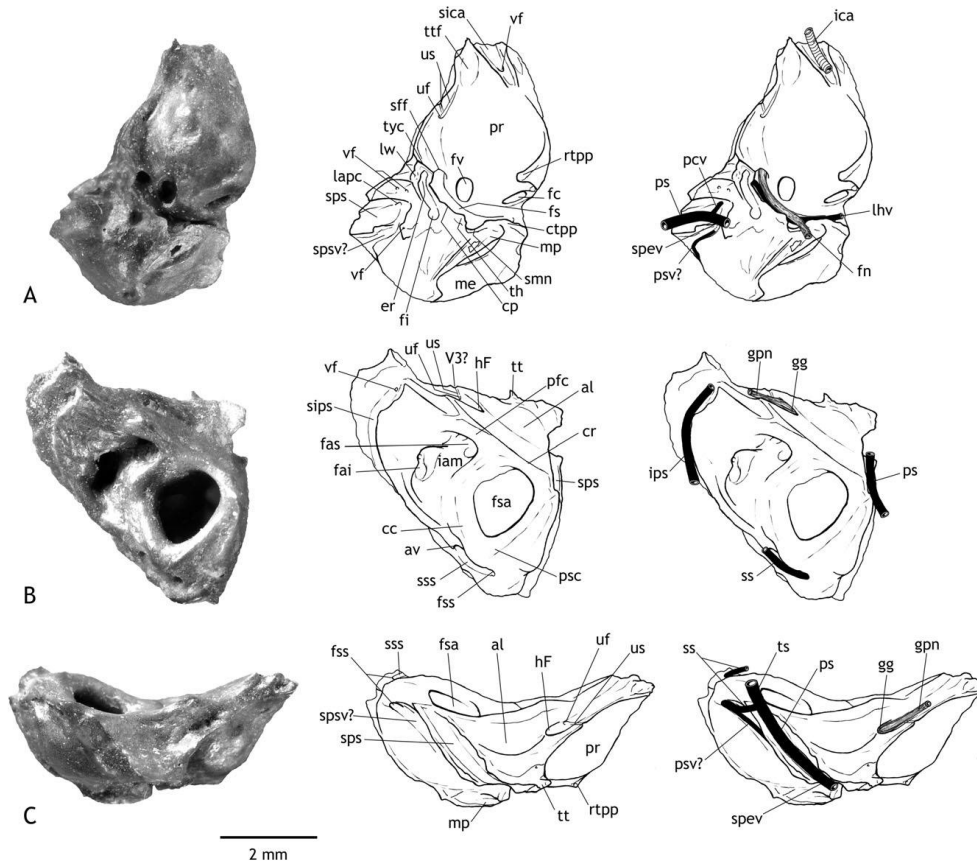
Em adição, salienta-se que crânios com petrosos *in locu* ou a eles associados são conhecidos para diversos grupos fósseis sul-americanos e norte-americanos (e.g., WIBLE, 1990; MENG e FOX, 1995; LADEVÈZE e MUIZON, 2007; BECK et al., 2008; HOROVITZ et al., 2009; AVERIANOV et al., 2010; FORASIEPI et al., 2015; WILSON et al., 2016; MUIZON e LADEVÈZE, 2020; MUIZON et al., 2018; ENGELMAN et al., 2020b; LADEVÈZE et al., 2020). Estes grupos (listados abaixo) suportam a identificação desses elementos cranianos para diversos grupos fósseis conhecidos até o presente momento, o que aumenta a confiabilidade das afinidades recuperadas pela análise filogenética para os petrosos isolados de Itaboraí. Deve-se observar que os seguintes clados sul-americanos não possuem petrosos associados: a) Jaskhadelphyidae e táxons aparentados, b) “Peradectoidea” sul-americanos, c) Sternbergiidae, d) Derorhynchidae, e) Polydolopimorphia *strictu sensu* (i.e., Polydolopiformes e Bonapartheriiformes), f) “Glasbiidae” sul-americanos, e g) Caroloameghinioidea.

Entretanto, Sternbergiidae e Derorhynchidae são frequentemente recuperados como mais aparentados aos Peratheriinae e Herpetotheriidae; e em menor grau aos Marsupialia (e.g., HOOKER et al., 2008; OLIVEIRA e GOIN, 2011, 2012; CARNEIRO et al., 2018; CARNEIRO, 2019; OLIVEIRA et al., 2021). Por sua vez, o clado dos Jaskhadelphyidae foi recuperado como próximo aos Pucadelphyda ou como o grupo-irmão dos Notometatheria (e.g., OLIVEIRA e GOIN, 2011; OLIVEIRA et al., 2016; WILSON et al., 2016; CARNEIRO et al., 2018; CARNEIRO, 2019; RANGEL et al., 2019, 2023a, 2023b; OLIVEIRA et al., 2021,

CARNEIRO e OLIVEIRA, 2023). Essas hipóteses sistemáticas foram consideradas com o objetivo de embasar as associações sugeridas nesta tese.

A matriz de dados da análise filogenética dos petrosos incluiu 52 táxons, em que 49 são metatérios, sendo nove ‘táxons baseados apenas em caracteres de petrosos’ (i.e., ‘*petrosal-based*’ taxa), e 648 caracteres (ver exemplo de caracteres dos petrosos incluídos na matriz morfológica na figura 9). Para essa matriz, foram incluídos apenas táxons com petrosos associados: Marsupialia (Didelphimorphia, Paucituberculata e Australidelphia), *Djarthia* (Marsupialia, Australidelphia; seguindo a combinação proposta por BECK et al., 2008; mas ver resultados desta tese), *Herpetotherium* (Notometatheria, Herpetotheriidae), *Peratherium* e *Amphiperatherium* (Notometatheria, Peratheriinae), *Pucadelphys* e *Andinodelphys* (Pucadelphyda, Pucadelphyidae), Sparassodonta (Pucadelphyda), *Mimoperadectes* (Peradectia, Peradectoidea, Peradectidae), *Didelphodon* (Archimetatheria, Stagodontoidea, Stagodontidae), *Pediomys* (Archimetatheria, Pediomyoidea, Pediomysidae), *Turgidodon* (Alphadontia, Alphadontidae), *Sulestes* e *Deltatheridium* (Deltatheroidea, Deltatheriidae) e os ‘*petrosal-based* taxa’, sendo os oito morfótipos de petrosos de Itaboraí (PtI, PtII, PtIII, PtIV, PtV, PtVI, PtVII e PtVIII) e um morfótipo de petroso isolado de Tiupampa, Bolívia (MHNC 8369; LADEVÈZE e MUIZON, 2007).

Figura 9 - Morfótipo de petroso isolado de Itaboraí VI (PtVI), um petroso direito (MN 6734-V) em suas diferentes vistas (A, ventral; B, dorsal; C, lateral) e com as estruturas consideradas na análise filogenética destacadas em desenhos esquemáticos.



Fonte: Ladevèze e Muizon (2010, p. 753, fig. 1).

A matriz de dados foi analisada com o modelo de busca *New Technology Search* do TNT 1.5 (GOLOBOFF e CATALANO, 2016) utilizando as estratégias *sectorial*, *ratchet*, *drift*, and *tree-fusing* com 100 replicações. Esse modelo de busca foi baseado em Wilson et al. (2016) e baseia-se no fato de que a matriz morfológica possui mais de 100 táxons e/ou caracteres. Esse número é considerado como um valor limite para um ‘*Traditional Search*’ pelo TNT 1.5, visto que não explora todas as nuvens de possibilidades possíveis (GOLOBOFF et al., 2008). Os valores de suporte de Bremer e as pontuações das árvores foram também calculados com o TNT 1.5. Os caracteres da matriz não apresentam ‘pesagem’ (*implied weight*) ou a ferramenta ‘*constraint*’ (que pré-agrupa os clados e táxons antes da análise ser realizada). O intuito dessas escolhas metodológicas foi o de interferir o mínimo quanto possível na análise. Em adição, o ‘ordenamento’ (*ordered characters*) de alguns caracteres não influenciou na topologia da filogenia, visto que as árvores mais parcimoniosas (AMPs) recuperadas com base em caracteres não ordenados e ordenados diferiram apenas no valor do suporte de Bremer como apresentado no artigo 1 (ver CARNEIRO e OLIVEIRA, 2023).

Em resumo, foram utilizados três critérios principais para a atribuição dos petrosos a um dos táxons de Itaboraí:

a) tamanho compatível, com base nos resultados dos modelos de Ladevèze e Muizon (2010),

nos resultados obtidos pela equação de Beck et al. (2008), nas dimensões e áreas recalculadas após a revisão taxonômica da fauna, e nas novas categorias de tamanho propostas;

b) abundância relativa na fauna com base no número mínimo de indivíduos (MNI) calculado para cada táxon após revisão taxonômica;

c) afinidades filogenéticas, tal como recuperadas pela análise filogenética.

Posteriormente as associações dos oito morfótipos dos petrosos com algum dos táxons de Itaboraí, uma segunda análise filogenética foi realizada com a mesma matriz base de caracteres e com a mesma metodologia considerada para a filogenia dos petrosos isolados. O diferencial dessa segunda análise foi a codificação de caracteres de dentição, mandibulares, cranianos e pós-cranianos (quando aplicáveis) aos oito ‘*petrosal-based*’ taxa devido a associação deles com algum dos táxons de Itaboraí.

Essa abordagem serviu para estudar as implicações de uma amostragem “completa” (i.e., incluindo diversos elementos distintos para um táxon) para os táxons de Itaboraí quando os caracteres dos petrosos são adicionados a eles (em sua grande maioria, os táxons de Itaboraí possuem caracteres codificados de dentição e dentário). Além disso, a mesma análise possibilita a tentativa preliminar de reconstrução do morfótipo ancestral dos petrosos dos diferentes clados sul-americanos e pode ajudar a resgatar a provável morfologia ancestral dos Sudameridelphia.

4.4 MATRIZ MORFOLÓGICA E ANÁLISE FILOGENÉTICA

A matriz morfológica utilizada no âmbito desta tese baseou-se nas filogenias prévias de Carneiro e Oliveira (2017a, b), Carneiro (2018, 2019), Carneiro et al. (2018), Rangel et al. (2019, 2023a, 2023b), Oliveira et al. (2021), Carneiro et al. (2024a, 2024b, 2024c, 2024d) e Guimarães et al. (2024). Essas matrizes compreenderam caracteres de inúmeras filogenias publicadas na literatura (e.g., LADEVÈZE, 2004, 2007; LADEVÈZE e MUIZON, 2007, 2010; DAVIS, 2007; GOIN et al., 2009, 2018; OLIVEIRA e GOIN, 2011, 2015; ABELLO, 2013; CHORNOGUBSKY e GOIN, 2015; ABELLO et al., 2018, 2021; OLIVEIRA et al., 2016; WILSON et al., 2016; BECK, 2017; MAGA e BECK, 2018; MÉTAIS et al., 2018; MUIZON et al., 2018; BECK et al., 2020; CHORNOGUBSKY, 2020; ENGELMAN et al., 2020; LADEVÈZE et al., 2020; MUIZON e LADEVÈZE 2020, 2022; BEARD et al., 2023; GILLESPIE et al., 2023).

A matriz morfológica utilizada para a análise filogenética provém de uma matriz base iniciada no âmbito da dissertação de Leonardo M. Carneiro sob orientação do Prof. Dr. Édison V. Oliveira, que apresentava como objetivo congregar diversas matrizes morfológicas

consideradas para o grupo dos metatérios em uma única matriz morfológica. A mesma matriz de dados já foi publicada e revisada por diversas fontes (e.g., CARNEIRO e OLIVEIRA, 2017a, b; CARNEIRO, 2018, 2019; CARNEIRO et al., 2018; RANGEL et al., 2019, 2023a, 2023b; OLIVEIRA et al., 2021).

As diferentes correções publicadas na literatura (e.g., MUIZON et al., 2018; MUIZON e LADEVÈZE, 2020) foram consideradas e já estão incluídas na matriz morfológica aqui apresentada. Desse modo, para construção dessa matriz, os caracteres e estados de caracteres das matrizes supracitadas são frequentemente revisados, corrigidos e/ou excluídos.

Com relação aos táxons não-metatérios incluídos na análise filogenética (e.g., Eutheria), a codificação para os seus caracteres de dentição seguiu as homologias apresentadas por O’Leary et al. (2013) (ver figura 4.2). Nesse caso, os caracteres considerados para os primeiros molares (M/m1) dos metatérios são equivalentes aos caracteres dos quintos pré-molares decíduos (DP/dp5) dos Theria não-Metatheria; os caracteres dos segundos molares (M/m2) dos metatérios são equivalentes aos dos primeiros molares (M/m1) dos Theria não-Metatheria; os dos terceiros/penúltimos molares (M/m3) dos metatérios com os dos segundos/penúltimos molares (M/m2) dos Theria não-Metatheria; e os dos quartos/últimos molares (M/m4) dos metatérios com os dos terceiros/últimos molares (M/m3) dos Theria não-Metatheria (os termos penúltimo e último são aqui considerados visto que alguns artigos da literatura [e.g., MUIZON et al., 2018] identificam os pré-molares e molares com essa terminologia e não como ‘1’, ‘2’, ‘3’ etc.). No caso dos pré-molares, os caracteres considerados para o terceiros pré-molares (P/p3) dos metatérios são equivalentes aos dos quartos pré-molares (P/p4) dos Theria não-Metatheria. Para os primeiros (P/p1) e segundos (P/p2) pré-molares, as codificações são equivalentes, visto que são considerados como homólogos (ver O’LEARY et al., 2013).

A matriz morfológica utilizada no âmbito desta tese para as análises filogenéticas apresenta 233 táxons, sendo 225 metatérios, e 729 caracteres de dentição, dentário, crânio e pós-crânio, tornando essa matriz morfológica a maior em número de caracteres e diversidade de gêneros e clados considerados até o presente momento.

A matriz de dados foi analisada com o modelo de busca *New Technology Search* do TNT 1.5 (GOLOBOFF e CATALANO, 2016) utilizando as estratégias *sectorial*, *ratchet*, *drift*, and *tree-fusing* com 100 replicações como apresentado por Wilson et al. (2016). Esse modelo de busca foi similar ao anteriormente apresentado (ver ‘4. Materiais e métodos, 4.3 Reavaliação dos petrosos de Itaboraí’). Em adição, a presença de caracteres ‘dependentes’ não alterou a topologia da filogenia em comparação com análises feitas com o mínimo de caracteres dependentes quanto possível (ver resultados em CARNEIRO et al., 2024d).

Em resumo, as análises filogenéticas supracitadas compreenderam uma ampla

diversidade de táxons a fim de avaliar as relações filogenéticas entre táxons parcialmente completos ou quase completos em sua evidência morfológica (i.e., com caracteres de dentição, mandibulares, cranianos e pós-cranianos) e táxons restritos em termos de evidências morfológicas (e.g., táxons baseados unicamente em caracteres de dentição e/ou mandibulares). A listagem de todos os caracteres, caracteres codificados por táxon e as árvores mais parcimoniosas considerados nas análises filogenéticas estão apresentadas no artigo 5 (ver CARNEIRO et al., 2024d).

5 RESULTADOS

5.1 APRESENTAÇÃO DOS RESULTADOS

Os resultados dessa tese estão apresentados como quatro artigos publicados (CARNEIRO et al., 2024a, 2024b, 2024c, 2024d), um capítulo de livro (CARNEIRO e OLIVEIRA, 2023) e um artigo em fase de revisão (ver apresentação dos mesmos no **Apêndice C**).

Artigo 1 - CARNEIRO, L. M.; OLIVEIRA, É. V. Paleogene metatherians from the Itaboraí Basin: Diversity and affinities. p. 269-324. In: CÁCERES, N. C.; Dickman, C. R. (Eds.) American and Australasian Marsupials. **Springer Nature Switzerland AG**, Cham, 2023. DOI: https://doi.org/10.1007/978-3-030-88800-8_5-1.

Artigo 2 - CARNEIRO, L. M.; BAMPI, H.; RANGEL, C. C.; GUIMARÃES, B. M. G.; SILVA, R. C.; OLIVEIRA, É. V. A new metatherian (Mammalia) from the Itaboraí Basin (Early Eocene), Brazil: implications to trophic niche partitioning between large-sized “didelphoid-like” metatherians. **Journal of South American Earth Sciences**, v. 139, 104895, 2024a. DOI: <https://doi.org/10.1016/j.jsames.2024.104895>

Artigo 3 - CARNEIRO, L. M.; ZANESCO, T.; BERGQVIST, L. P.; GOIN, F. J.; GUEDES, F. R.; AGNES, A.; OLIVEIRA, É. V. New material of *Carolocoutoia* (Mammalia, Marsupialia, Didelphimorphia): systematic affinities and dietary inferences. **Journal of South American Earth Sciences**, v. 134, 104777, 2024b. DOI: <https://doi.org/10.1016/j.jsames.2023.104777>.

Artigo 4 - CARNEIRO, L. M.; GOIN, F. J.; BAMPI, H.; SILVA, R. C.; RANGEL, C. C.; GUIMARÃES, B. M. G.; ARÊAS, M. R. A tiny-sized Herpetotheriidae (Mammalia, Metatheria) from the Itaboraí basin (early Eocene), Brazil: Paleobiogeographic and systematic implications for Herpetotheriidae. **Journal of South American Earth Sciences**, v. 144, 105016, 2024d. DOI: <https://doi.org/10.1016/j.jsames.2024.105016>.

Artigo 5 - CARNEIRO, L. M.; OLIVEIRA, E. V.; SILVA, R. C.; BAMPI, H.; ARÊAS, M. R. Systematic and trophic diversity of protodidelphines (Mammalia, Marsupialia, Protodidelphidae): Evidence of a short time diversification during the onset of the Eocene.

Journal of South American Earth Sciences, v. 148, 105140, 2024c. DOI: <https://doi.org/10.1016/j.jsames.2024.105104>.

Artigo 6 – CARNEIRO, L. M.; GOIN, F. J.; OLIVEIRA, É. V.; SILVA, R. C.; BAMPI, H. A new derorhynchid (Mammalia, Metatheria) from the Itaboraí Basin (early Eocene), Brazil, and the trophic diversity of derorhynchids during the onset of the Eocene. **Journal of Mammalian Evolution**.

5.2 TAXONOMIA E SISTEMÁTICA

5.2.1 Diversidade, status taxonômico e identificação dos metatérios da Bacia de Itaboraí

No âmbito desta tese, a fauna metateriana da Bacia de Itaboraí foi representada por, pelo menos, 29 gêneros e 44 espécies: *Austropedimys marshalli* Carneiro, Oliveira e Goin, 2018; *Bergqvistherium primigenia* Carneiro, 2019; *Bobbschaefferia fluminensis* (Paula Couto, 1952b), *Bobbschaefferia* sp. nov., *Carolocoutoia ferigoloi* Goin, Oliveira e Candela, 1998; *Carolopaulacoutoia itaboraiensis* (Paula Couto, 1970); *Carolopaulacoutoia* sp. nov. (ver OLIVEIRA, 1998); Derorhynchidae gen. et sp. nov. (ver CARNEIRO et al., 2024e, em revisão - ARTIGO 6); *Derorhynchus singularis* Paula Couto, 1952a; *Derorhynchus* sp. nov. 1; *Derorhynchus* sp. nov. 2; *Didelphopsis cabrerai* Paula Couto, 1952b; *Didelphopsis* sp. nov. (ver OLIVEIRA, 1998); *Diogenesia brevirostris* Oliveira, Carneiro e Goin, 2021; *Diogenesia* sp. nov. (ver OLIVEIRA, 1998); *Eobrasilia coutoi* Simpson, 1947; *Epidolops ameghinoi* Paula Couto, 1952b; *Gashternia carioca* Goin e Oliveira, 2007; *Gaylordia doelloi* (Paula Couto, 1970); *Gaylordia macrocynodonta* Paula Couto, 1952a; *Gaylordia mater* Oliveira e Goin, 2015; *Guggenheimia brasiliensis* Paula Couto, 1952a; *Guggenheimia crocheti* Oliveira e Goin, 2011; *Itaboraidelphys camposi* Marshall e Muizon, 1984; *Itaboraidelphys* sp. nov.; *Marmosopsis juradoi* Paula Couto, 1962; *Marmosopsis* sp. nov. (ver OLIVEIRA, 1998); *Minusculodelphis minimus* Paula Couto, 1962; *Minusculodelphis modicum* Oliveira, Zimicz e Goin, 2016; *Mirandatherium alipioi* (Paula Couto, 1952a); *Monodelphopsis travassosi* Paula Couto, 1952a; *Monodelphopsis* sp. nov.; *Patene simpsoni* Paula Couto, 1952b; Peradectoidea gen. et sp. nov. 1 (ver OLIVEIRA, 1998); Peradectoidea gen. et sp. nov. 2 (ver OLIVEIRA, 1998); *Periprotodidelphis bergqvistae* Oliveira e Goin, 2011; *Procaroloameghinia pricei* Marshall, 1982a; *Protodidelphis vanzolinii* Paula Couto, 1952a; Pucadelphyoidea gen. et sp. nov. 1; Pucadelphyoidea gen. et sp. nov. 2; *Robertbutleria mastodontoidea* Marshall, 1987;

Silvenator brasiliensis (Rangel et al., 2023a); *Thylacopygmaeus oliveirai* Carneiro et al., 2024c; e *Xenocynus crypticus* Carneiro et al., 2024a.

Dentre os táxons de metatérios considerados para essa localidade, os seguintes são identificados como sinonímias no âmbito desta tese: 1) “*Zeusdelphys complicatus*” (Marshall, 1987) (considerado como sinônimo júnior de *Eobrasilia coutoi* [ver CARNEIRO, 2024b, dados não publicados]), e 2) “*Riolestes capricornicus*” Goin., 2009 (considerado como sinônimo júnior de *Robertbutleria mastodontoidea*; ver CARNEIRO, 2024a [dados não publicados]).

Dentre os metatérios propostos para essa localidade, os seguintes táxons foram considerados como sinonímias ou apresentaram mudanças de nomenclatura por autores prévios: *Epidolops* “*gracilis*” (Paula Couto, 1961; sinonimizado como *Epidolops ameghinoi* por MARSHALL, 1982b); *Gaylordia* “*mendesi*” (Paula Couto, 1970; sinonimizado como *Gaylordia doelloi* por MARSHALL, 1987); “*Ischyrodidelphis castellanosi*” (Paula Couto, 1962; sinonimizado como *Patene simpsoni* por MARSHALL, 1981; ver RANGEL et al., 2019); “*Mirandaia ribeiroi*” (Paula Couto, 1952b; nome corrigido para *Mirandatherium alipioi* por PAULA COUTO, 1952c, visto que *Mirandaia* já havia sido previamente atribuído a um Nematodea); *Schaefferia* (Paula Couto, 1952b; nome corrigido para *Bobbschaefferia* por PAULA COUTO, 1970, visto que *Schaefferia* já havia sido previamente atribuído a um Arthropoda); *Sternbergia* (Paula Couto, 1970; nome corrigido para *Carolopaulacoutoia* por MCKENNA e BELL, 1997, visto que *Sternbergia* já havia sido previamente atribuído a uma planta); “*Xenodelphys*” (Paula Couto, 1962; sinonimizado como *Gaylordia* por MARSHALL, 1987). Todas as sinonímias e mudanças de nomenclatura supracitadas foram seguidas no âmbito desta tese.

Dentre os espécimes estudados, o lote MN 2896-V compreendia 94 dentários edentados provenientes da fenda de 1949 (ver catálogo do MN). Devido ao incêndio do MN, esses espécimes não puderam ser formalmente incluídos nesta tese. Entretanto, o presente autor desta tese (LM Carneiro) observou esses espécimes durante suas visitas à coleção entre 2017-2018. Dentre os dentários desse lote, pelo menos, 28 espécimes pertenciam a *Marmosopsis juradoi*. Por conta da provável destruição desses espécimes, eles não foram incluídos nos cálculos do número mínimo de indivíduos (MNI) e abundâncias relativas (AR) desta tese. Ainda assim, vale a pena salientar que *M. juradoi* é mais abundante do que o apresentado nesta tese. Diversos dentários edentados apresentam identificações preliminares (cf), não sendo incluído nos hipodigmas das espécies (ver **Apêndice A**).

A lista das espécies de metatérios de Itaboraí com o seu referido número de espécimes associados por instituição museológica está apresentada abaixo (Tabela 5.1):

Tabela 5.1 - Lista do total de espécimes (i.e., dentição, dentário e maxila) atribuídos às espécies de metatérios de Itaboraí por instituições (AMNH, MCN-PV, MN, MCTer, UFRJ-DG). Na listagem abaixo, não estão listados petrosos e elementos pós-cranianos. A listagem abaixo inclui os 94 dentários sem dentes preservados do lote MN 2895-V do Museu Nacional (identificados entre parêntesis) e alguns espécimes indeterminados do MCTer. As células destacadas em cinza indicam que o holótipo da espécie se encontra entre os espécimes. As células em laranja indicam que o espécime escolhido como futuro holótipo de um novo táxon encontra-se entre os espécimes. AMNH, American Museum of Natural History; MCN-PV, Coleção de paleovertebrados do Museu de Ciências Naturais da antiga Fundação Zoobotânica do Rio Grande do Sul; MCTer, Museu de Ciências da Terra; MN, Museu Nacional; UFRJ-DG, Coleção de paleontologia da Universidade Federal do Rio de Janeiro. N, número de espécimes.

	MN	MCTer	MCN-PV	UFRJ-DG	AMNH	N
<i>Austropedimys marshalli</i>	1	16		2		19
<i>Bergqvistherium primigenia</i>	2	18	2	2	1	25
<i>Bobbschaefferia fluminensis</i>	2	1				3
<i>Bobbschaefferia</i> sp. nov.	2	4				6
<i>Carolocoutoia ferigoloi</i>		2	1	1		4
<i>Carolopaulacoutoia itaboraiensis</i>	5	56	3	1		65
<i>Carolopaulacoutoia</i> sp. nov.	3		1			4
<i>Derorhynchidae</i> gen. et sp. nov.	6	12	2			20
<i>Derorhynchus singularis</i>	2	5			1	8
<i>Derorhynchus</i> sp. nov. 1		11	1	6		18
<i>Derorhynchus</i> sp. nov. 2		1				
<i>Didelphopsis cabrerai</i>	10	19	2	1		32
<i>Didelphopsis</i> sp. nov.	4	12	2			18
<i>Diogenesia brevirostris</i>		1				1
<i>Diogenesia</i> sp. nov.	1	42		1		44
<i>Eobrasilia coutoi</i>		1	1		1	3
<i>Epidolops ameghinoi</i>	49	113		9	10	181
<i>Gashternia carioca</i>		1	1			2
<i>Gaylordia doelloi</i>	3	1				4
<i>Gaylordia macrocynodonta</i>	4	20		1	1	26
<i>Gaylordia mater</i>		31				31
<i>Guggenheimia brasiliensis</i>		1				1

<i>Guggenheimia crocheti</i>	1	6				7
<i>Itaboraaidelphys camposi</i>	1	13	6			20
<i>Itaboraaidelphys</i> sp. nov.		22	1			23
<i>Marmosopsis juradoi</i>	36	37		1		74
<i>Marmosopsis</i> sp. nov.		26	1	4		31
<i>Minusculodelphis minimus</i>	3	1				4
<i>Minusculodelphis modicum</i>		5	1			6
<i>Mirandatherium alipioi</i>	4	9	1	1	1	16
<i>Monodelphopsis</i> sp. nov.		5	1	3		9
<i>Monodelphopsis travassosi</i>	3	1				4
<i>Patene simpsoni</i>	17	28	1	5	2	53
Peradectoidea gen. et sp. nov. 1		35	2			37
Peradectoidea gen. et sp. nov. 2		1				1
<i>Periprotodidelphis bergqvistae</i>		4				4
<i>Procaroloameghinia pricei</i>		1				1
<i>Protodidelphis vanzolinii</i>	4	6	4		2	16
Pucadelphyoidea gen. et sp. nov. 1		15				15
Pucadelphyoidea gen. et sp. nov. 2		3				3
<i>Robertbutleria mastodontoidea</i>	3	6	7	1	1	18
<i>Silvenator brasiliensis</i>	1	7				8
<i>Thylacopygmaeus oliveirai</i>		1				1
<i>Xenocynus crypticus</i>		4	3	2		9
Indet.	94	23				117
Total	261	626	44	41	20	992

Fonte: O autor (2023).

Considerando-se os metatérios reconhecidos nesta tese e os resultados da revisão de seus respectivos espécimes associados, a maioria dos gêneros passou a apresentar molares superiores (exceto *Procaroloameghinia*, *Silvenator* e *Thylacopygmaeus*) e inferiores (exceto *Periprotodidelphis*), região dos pré-molares inferiores preservada nos dentários (exceto *Eobrasilia* e *Thylacopygmaeus*) e dentários quase completos com série molar ou alveolar dos molares inferiores preservada (exceto *Eobrasilia*, *Periprotodidelphis* e *Silvenator brasiliensis*).

A completude dentária e mandibular para cada espécie de metatério de Itaboraí está indicada abaixo (Tabela 5.2):

Tabela 5.2 - Elementos de dentição e mandibulares conhecidos para os metatérios de Itaboraí. O ‘x’ indica que o elemento é conhecido. As células marcadas em cinza indicam que os elementos são conhecidos (dente ou dentário) ou que a série alveolar dos pré-molares e molares está preservada em associação. As células brancas com um ‘x’ indicam que apenas os alvéolos dos dentes são conhecidos, que as séries alveolares dos pré-molares e molares estão parcialmente preservadas ou que o dentário é parcialmente conhecido (fragmento de dentário ou dentário incompleto).

Taxa	I	C	P1	P2	DP 3	P3	M 1	M 2	M 3	M 4	P1 -3	M 1-4	i	c	p1	p2	dp 3	p3	m1	m2	m3	m4	p1-m1 3 -4	Dd
<i>Austropeidomys marshalli</i>					x		x	x	x	x		x		x	x	x		x	x	x	x	x	x	x
<i>Bergqvistherium primigenia</i>								x	x				x	x	x	x		x	x	x	x	x	x	x
<i>Bobbschaefferia fluminensis</i>													x	x	x	x		x	x	x		x	x	x
<i>Bobbschaefferia</i> sp. nov.													x	x	x	x		x	x	x	x	x	x	x
<i>Carolocoutoia ferigoloi</i>								x	x						x	x		x	x	x	x	x	x	x
<i>Carolopaulacoutoia itaboraiensis</i>					x		x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x
<i>Carolopaulacoutoia</i> sp. nov.													x	x	x	x		x	x	x	x	x	x	x
<i>Derorhynchidae</i> gen. et sp. nov.						x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x
<i>Derorhynchus singularis</i>						x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x
<i>Derorhynchus</i> sp. nov. 1							x	x	x						x	x		x	x	x	x	x	x	x
<i>Derorhynchus</i> sp. nov. 2													x	x	x	x		x	x	x			x	x
<i>Didelphopsis cabrerai</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Didelphopsis</i> sp. nov.						x	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x	x
<i>Diogenesia brevirostris</i>															x	x		x	x	x	x	x	x	x
<i>Diogenesia</i> sp. nov.					x		x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x
<i>Eobrasilia coutoi</i>	x	x	x			x	x		x		x	x									x			

MAMMALIA Linnaeus, 1758

METATHERIA Huxley, 1880

MARSUPIALIFORMES Vullo, Geerbrandt, Muizon et al., 2009

SUDAMERIDELPHIA (Szalay, 1994) comb. nov.

Definição. Clado único e exclusivo a incluir todos os táxons mais próximos a *Didelphis* do que a *Alphadon*, *Didelphodon*, *Pedionomys* e *Peradectes*.

Clados incluídos. Bergqvistheriidae nov.; Jaskhadelphyoidea nov.; Pucadelphyda Muizon et al., 2018; Polydolopimorphia Archer, 1984; Sternbergiidae (Szalay, 1994) Goin, 2003; Herpetotheriidae Trouessart, 1879; Derorhynchidae Goin, Case, Woodburne et al., 1999; Marsupialia Illiger, 1811, e todos os táxons mais próximos a esses do que a “Peradectia” Marshall, Case e Woodburne, 1990.

†JASKHADELPHYOIDEA superfam. nov.

Diagnose. Diferem dos demais Sudameridelphia na seguinte combinação de caracteres: molares superiores comprimidos mesio-distalmente (exceto M1-2 dos Marmosopsiinae subfam. nov.), plataforma estilar moderada a ampla (i.e., próxima a 50% da largura do molar no M3; sensu LADEVÈZE et al., 2020), parástilo bem estendido mesialmente no M3, paracone e metacone aproximados, mas não fusionados em suas bases; protocones mesio-distalmente comprimidos, trigônido bem mais alto que o talônido (entre 2.5-3.0x; sensu LADEVÈZE et al., 2020), talônido mais curto que o trigônido, hipocônido comprimido mesio-distalmente, p1 alinhado ao eixo da série pré-molar/molar ou incipientemente oblíquo em relação a esse último, e terceiro trocânter distalmente posicionado na diáfise femoral, estando bem afastado do trocânter menor.

Clados incluídos. Jaskhadelphyidae Muizon, 1992; Gaylordiidae fam. nov.; e *Szalinia* Muizon e Cifelli, 2001.

†GAYLORDIIDAE fam. nov.

Diagnose. Diferem dos demais Jaskhadelphyoidea na presença de molares com forma relativamente mais subquadrangular (i.e., mais equivalente em sua razão largura/comprimento) (mais alongados nos demais Jaskhadelphyidae; i.e., relativamente mais estreitos em relação ao comprimento), trigônido comprimido mesio-distalmente nos m2-3, cristida oblíqua curta a reduzida, pré-molares inflados, especialmente o p3; e dentário relativamente mais robusto.

Gêneros incluídos. *Gaylordia* Paula Couto, 1952a; *Tiulordia* Marshall e Muizon, 1988.

Comentários. Gaylordiidae representou uma linhagem dos Jaskhadelphyoidea mais especializada na predação de invertebrados de exoesqueleto rígido (ver OLIVEIRA e GOIN, 2015). A presença de molares relativamente mais equivalentes em largura x comprimento (RW/L), pré-molares inflados, especialmente o p3, e dentários robustos indicam a exploração de recursos alimentares de maior dureza que os demais membros do clado.

†JASKHADELPHYIDAE Muizon, 1992

†MARMOSOPSIIDAE subfam. nov.

Diagnose. Diferem dos demais Jaskhadelphyidae na presença de M1-2 não comprimidos mesio-distalmente, e paracone e metacone relativamente mais separados nos M1-2.

Gêneros incluídos. *Marmosopsis* Paula Couto, 1962; *Incadelphys* Marshall e Muizon, 1988.

Comentários. Marmosopsiinae representou a linhagem mais generalizada dentre os Jaskhadelphyoidea. Os representantes desse clado apresentam os M1-2 não comprimidos mesio-distalmente, e paracone e metacone mais separados nos M1-2. Esses animais devem ter apresentado hábitos alimentares similares aos de alguns Didelphidae vivos, como *Gracilinanus*, *Cryptonanus* e *Marmosa*, em que invertebrados representam os principais recursos alimentares explorados, mas sem descartar frutos como um possível alimento.

†Ordem PUCADELPHYDA Muizon, Ladevèze, Selva et al., 2018

†BOBBSCHAEFFERIIDAE fam. nov.

Diagnose. Diferem dos Caroloameghinioidea na seguinte combinação de caracteres: StC e StD pouco desenvolvidas a reduzidas (StC e StD presentes e relativamente desenvolvidas nos mais antigos Caroloameghinioidea), StC mais próxima da StB, StC1 presente (ausente nos Caroloameghinioidea), metacone com borda labial plana (i.e., forma piramidal; sensu CASE et al., 2005) (metacone com borda convexa [i.e., forma cônica; sensu CASE et al., 2005] nos Caroloameghinioidea), protocone moderado (i.e., subigual em comprimento ao metacone; sensu ENGELMAN et al., 2020a) (protocone amplo [i.e., mais longo que o metacone; sensu ENGELMAN et al., 2020a]), p2-3 mais altos que os protocônidos dos m1-4 e algo comprimidos labio-lingualmente (p2-3 ligeiramente mais altos que os protocônidos dos m1-4 e inflados, especialmente o p3), i2 marcadamente hipertrofiado aos i3-4 (condição ausente nos Caroloameghinioidea), i3 não sobremontado ao i2 (i3 sobremontado ao i2 nos Caroloameghinioidea). Difere dos Pucadelphyidae na presença de plataforma estilar estreita (plataforma estilar moderada nos Pucadelphyidae), ectoflexus raso nos M2-3 (ectoflexus moderado a profundo nos M2-3 dos Pucadelphyidae), centrocrista reta (centrocrista ligeiramente dilambdodonte nos Pucadelphyidae), expansão distal do protocone pouco

desenvolvida (expansão distal do protocone bem desenvolvida nos M1-2 dos Pucadelphyidae), i2 marcadamente hipertrofiado aos i3-4 (condição ausente nos Caroloameghinioidea), i3 não sobremontado ao i2 (i3 sobremontado ao i2 nos Caroloameghinioidea). Difere dos “Peradectoidea” na presença de plataforma estilar estreita no M3 (plataforma estilar ampla nos “Peradectoidea”), entocônido comprimido labio-lingualmente (entocônido cônico a relativamente cônico nos “Peradectoidea”), hipoconulido labialmente posicionado ao entocônido (hipoconulido disto-lingual ou disto-labial ao entocônido nos “Peradectoidea”).

Gêneros incluídos. *Bobbschaefferia* (Paula Couto, 1970) e *Estelestes* Novacek et al., 1991.

Comentários. A dentição de *Bobbschaefferia* representa um mosaico entre a dentição dos “Peradectoidea” sul-americanos e a dos Pucadelphyda. Esse táxon apresenta cúspides estilares pouco desenvolvidas, a exceção da StB, StC próxima a StB, StC1 presente, centrocrista reta, paracone em posição ligeiramente lingual a do metacone (o que é mais similar a um “Peradectoidea”); entretanto, apresenta entocônidos muito comprimido labio-lingualmente e hipoconulidos labialmente posicionados aos entocônidos. Nesse contexto, *Bobbschaefferia* compartilha um maior número de caracteres apomórficos com os Pucadelphyda do que com os “Peradectoidea” sul-americanos, no que é mais seguro considerá-lo como mais aparentado aos Pucadelphyda do que as “Peradectoidea”, ainda que ele retenha diversas simplesiomorfias em sua dentição (especialmente nos molares superiores). As características únicas de *Bobbschaefferia* parecem representar apomorfias dessa linhagem evolutivamente convergentes com a dos Microbiotheria (e.g., plataforma estilar estreita, centrocrista reta, i3 não sobremontado ao i2).

†CAROLOAMEGHINIOIDEA (Marshall, 1987) comb. nov.

Diagnose. Diferem dos demais Sudameridelphia na seguinte combinação de caracteres: StC mais próxima da StD (podendo essas duas cúspides estarem fusionadas), paracone com borda labial plana e metacone com borda distal convexa, paracone orientado em um eixo mesio-labial/disto-lingual no M2, protocone amplo. Difere dos Polydolopimorphia na ausência de hipsodontia unilateral. Difere dos Pucadelphyidae na presença de coroas dos pré-molares e molares mais braquio-bunodontes (coroas tribosfênicas nos Pucadelphyidae; sensu MARSHALL, 1987), M3 não comprimido mesio-distalmente (M3 comprimido nos Pucadelphyidae), plataforma estilar rasa (profunda nos Pucadelphyidae), protocone amplo no M3 e expansão distal do protocone bem desenvolvida (protocone comprimido mesio-distalmente e moderado nos Pucadelphyidae) e entocônido bem desenvolvido (entocônido pouco desenvolvido nos Pucadelphyidae). É possível que os Pucadelphyidae representasse uma linhagem insetívora ou carnívora generalizada (=insetívoro-carnívora), enquanto os

Caroloameghinioidea provavelmente compreenderam uma linhagem insetívoro-frugívora ou frugívora.

Clados incluídos. Caroloameghiniidae; Mirandatheriidae (Szalay, 1994) rank nov.

Comentários. A dentição dos Caroloameghinioidea é indubitavelmente similar a dos Pucadelphyidae em diversos aspectos: cúspides estilares StA, StB, StC, StD e StE presentes, protocone amplo, expansão distal do protocone bem desenvolvida, paracônido algo comprimido mesio-distalmente, entocônido comprimido labio-lingualmente e p1 claramente menor que o p2. As principais diferenças entre os dois grupos estão relacionadas principalmente a coroa mais braquiodonte dos Caroloameghinioidea, em que a plataforma estilar é relativamente mais rasa e o entocônido relativamente mais desenvolvido. O Pucadelphyoidea gen. nov. de Itaboraí representa um mosaico entre um Pucadelphyidae e *Mirandatherium*, visto que apesar das suas similaridades com o primeiro, ele compartilha um maior número de apomorfias com o segundo (i.e., apresenta afinidades sistemáticas mais próximas de *Mirandatherium*).

†MIRANDATHERIIDAE (Szalay, 1994) rank. nov.

Diagnose. Diferem dos Caroloameghiniidae na seguinte combinação de caracteres: molares braquiodontes (bunodontes nos Caroloameghiniidae, exceto *Canchadelphys cristata* Goin et al., 2010), molares superiores com forma subtriangular (trapezoide ou ovoide nos Caroloameghiniidae), trigônido não comprimido mesio-distalmente (trigônido comprimido mesio-distalmente nos Caroloameghiniidae), entocônido comprimido labio-lingualmente (entocônido piramidal ou algo piramidal nos Caroloameghiniidae), hipoconulido labialmente posicionado ao entocônido (entocônido disto-labial ao entocônido).

Gêneros incluídos. *Mirandatherium* Paula Couto, 1952c; Pucadelphyoidea gen. nov.; *Apeirodon* Babot, Rougier, Garcia-López et al., 2020; *Reigia* Pascual, 1983.

Comentários. Mirandatheriidae apresenta diversos caracteres em comum aos Caroloameghiniidae, diferenciando-se principalmente na dentição menos bunodonte. É possível que os Mirandatheriidae representassem uma linhagem mais generalizada, enquanto os Caroloameghiniidae representaram uma linhagem frugívora mais especializada. As diferenças entre esses dois grupos estão de acordo com as mudanças paleoambientais resultantes do Máximo Termal do Paleoceno-Eoceno (MTPE) e Ótimo Climático do Eoceno Inicial (OCEI), em que linhagens mais generalizadas coexistem com linhagens irmãs com dentição bunodonte mais especializada (ver e.g., OLIVEIRA e GOIN, 2011; ZIMICZ, 2012; GOIN et al., 2016; CARNEIRO, 2019; CARNEIRO e OLIVEIRA, 2023; CARNEIRO, ZANESCO, BERGQVIST et al., 2024b).

Supercohort NOTOMETATHERIA (Kirsch et al., 1997) comb. nov.

Definição. Clado único e exclusivo dos Sudameridelphia a incluir todos os táxons mais próximos a *Didelphis* do que a *Jaskhadelphys minutus*, *Borhyaena tuberosa* e *Pucadelphys andinus*.

†STERNBERGIIDAE (Szalay, 1994) McKenna e Bell, 1997

†DIDELPHOSIINAE Subfam. nov.

Diagnose. Diferem de *Carolopaulacoutoia* (=Sternbergiinae) e dos demais metatérios sul-americanos na seguinte combinação de caracteres: tamanho médio a grande, plataforma estilar moderada a ampla no M3, cúspides estilares supranumerárias frequentemente presentes, especialmente associadas as StC e StD; metacônulo frequentemente cônico e não cristado, p3 hipertrofiado (i.e., p3 mais longo que o m1).

Genotipia. *Didelphopsis* Paula Couto, 1952a.

Gêneros incluídos. *Didelphopsis*; *Itaboraidelphys* Marshall e Muizon, 1984.

Comentários. As relações de parentesco próximas entre *Didelphopsis* e *Itaboraidelphys* foram discutidas em Goin (2003), Oliveira e Goin (2011), Carneiro e Oliveira (2023) e Rangel et al. (2023a). De fato, esses dois táxons diferem principalmente em suas características morfofuncionais: *Didelphopsis* é um durófago especializado, com p2 inflado e p3 bulboso; e coroas braquio-bunodonte. Por sua vez, *Itaboraidelphys* é mais generalizado, visto que apresenta um maior conjunto de simplesiomorfias para os Notometatheria (e.g., coroa tribosfênica [sensu MARSHALL, 1987], p2-3 subiguais em tamanho, ausência de diastema entre os p1-2).

†DERORHYNCHIDAE Goin, Case, Woodburne et al., 1999

†COONINAE Subfam. nov.

Diagnose. Diferem dos demais Derorhynchidae na seguinte combinação de caracteres: molares com coroas relativamente mais braquiodontes, talônido mais largo que o trigônido no m3 e entocônido hipertrofiado e piramidal em forma.

Genotipia. *Coona* Simpson, 1938.

Gêneros incluídos. *Coona*; *Pauladelphys* Goin, Case, Woodburne et al., 1999; Derorhynchidae gen. nov. (ver GOIN e FORASIEPI, 1997 [dados não publicados]; OLIVEIRA, 1998 [dados não publicados]; OLIVEIRA, CARNEIRO e GOIN, 2021; CARNEIRO e OLIVEIRA, 2023).

Comentários. Os representantes da subfamília Cooninae apresentam entocônidos hipertrofiados e piramidais em forma, bacias do talônido amplas no m3 e coroas relativamente

mais infladas que os demais membros dos Derorhynchidae. Os primeiros a observarem essas diferenças foram Goin e Forasiepi (1997, p. 8 [dados não publicados]), quem sugeriram que o Derorhynchidae gen. nov. deveria apresentar uma dieta com uma maior componente frugívora que os outros Derorhynchidae Itaboraienses. Essa morfologia é observada em metatérios com dietas frugívoras (e.g., *Procaroloameghinia*, *Protodidelphis*). É possível que esse clado dos Derorhynchidae tenha se especializado em dietas mais frugívoras em relação a *Diogenesia* e *Derorhynchus*. Essa observação está relacionada às mudanças paleoambientais resultantes do Máximo Termal do Paleoceno-Eoceno (MTPE) e Ótimo Climático do Eoceno Inicial (OCEI), em que diversas linhagens de metatérios desenvolveram dentições braquiodontes e bunodontes. Essas morfologias são indicativas de dietas onívoras ou frugívoras (ver e.g., GOIN e FORASIEPI, 1997 [dados não publicados]; ZIMICZ, 2012; CARNEIRO e OLIVEIRA, 2023).

†Ordem POLYDOLOPIMORPHIA Archer, 1984

†Subordem BONAPARTHERIIFORMES Pascual, 1980a

†EOBRASILIIDAE (Marshall, 1987) rank nov.

Diagnose. Diferem dos demais Bonaparteriiformes na presença de M3 comprimido mesio-distalmente, centrocrista baixa, reta e não aberta; e p2-3 hipertrofiados e bulbosos. Diferem dos Gashterniidae Marshall, 1987, Bonaparteriidae Pascual, 1980a e Argyrolagoidea Ameghino, 1904 na presença de centrocrista reta (centrocrista aberta nos táxons supracitados), metacônulo pouco desenvolvido e não hipertrofiado (metacônulo ‘tipo-hipocone’ nos táxons supracitados), p1 birradiculado (p1 unirradiculado ou ausente nos táxons supracitados). Diferem dos Prepidolopidae na centrocrista reta (centrocrista aberta e invasiva na plataforma estilar nos Prepidolopidae), protocone moderado (protocone amplo nos Prepidolopidae), paracônido bem desenvolvido (paracônido reduzido a ausente nos Prepidolopidae). Diferem dos Rosendolopidae na presença de centrocrista reta (centrocrista aberta e invasiva na plataforma estilar nos Rosendolopidae), p2-3 bulbosos e hipertrofiados (p2-3 não hipertrofiados nos Rosendolopidae), p3 marcadamente maior que o p2 (p2 subigual a mais longo que o p3 nos Rosendolopidae).

Genotípia. *Eobrasilia* Simpson, 1927.

Gêneros incluídos. *Eobrasilia*; *Periprotodidelphis* Oliveira e Goin, 2011.

Comentários. Eobrasiliidae foi originalmente proposto como uma subfamília de Didelphidae (i.e., Eobrasiliinae) por Marshall, 1987. Esse clado foi proposto para incluir todos os metatérios com dentição indicativa de dieta durófaga especializada da fauna de Itaboraí, como *Didelphopsis*, *Eobrasilia* e *Gaylordia* devido a presença de p2-3 hipertrofiados e bulbosos (ver MARSHALL, 1987). Entretanto, Carneiro e Oliveira (2017a) concluíram que “Eobrasiliinae”

representava um clado polifilético e que para recuperar a sua monofilia, ele deveria incluir apenas *Eobrasilia*. Esse clado dos Polydolopimorphia apresenta uma convergência com os Anatoliadelphidae do Eoceno médio da Turquia (ver, e.g., MAGA e BECK, 2017; MÉTAIS et al., 2018; CARNEIRO, 2019; BEARD et al., 2023), mas representam clados distintos, visto que a dentição inferior de *Eobrasilia* é similar a dos Rosendolopidae Goin, e *Gashternia* (e.g., paracônido e metacônido praticamente fusionados, entocônido hipertrofiado).

MARSUPIALIA Illiger, 1814

DIDELPHIMORPHIA Gill, 1872

†PROTODIDELPHIDAE Marshall, Case e Woodburne, 1990

†PROTODIDELPHINAE (Marshall, 1987) comb. nov.

Diagnose. Diferem de *Guggenheimia* nas seguintes características: porte grande e muito grande, coroa bunodonte, molares superiores não comprimidos mesio-distalmente, ausência de StC, pós-metacrista curta, bacia do protocone estreita a reduzida, protocone moderado e excêntrico, trigônido comprimido mesio-distalmente, e entocônido piramidal a comprimido labio-lingualmente.

Genotípia. *Protodidelphis* Paula Couto, 1952a.

Gêneros incluídos. *Protodidelphis*; *Robertbutleria* Marshall, 1987; *Carolocoutoia* Goin, Oliveira e Candela, 1998a.

Comentários. Os Protodidelphinae estavam entre os maiores metatérios da idade Itaboraense sul-americana, perdendo em tamanho apenas para os Eobrasiliinae (*Eobrasilia coutoi*) e Sparassodonta (*Silvenator brasiliensis*). Esses animais apresentam dentições indicativas de dietas frugívoras mais especializadas em comparação com *Guggenheimia*. Oliveira e Goin (2011) e Carneiro (2019) consideraram que os Protodidelphidae se diversificaram “rapidamente”, tornando-se elementos faunísticos comuns em faunas do Ótimo Climático do Eoceno Inicial (OCEI) (ver e.g., OLIVEIRA e GOIN, 2011; CARNEIRO, 2019; CARNEIRO e OLIVEIRA, 2023). A evolução desse grupo parece estar diretamente relacionada aos eventos termiais resultantes do Máximo Termal do Paleoceno-Eoceno (MTPE), que aumentaram as temperaturas e pluviosidade médias globais (ver e.g., GOIN et al., 2012, 2016; ZIMICZ, 2012; WOODBURN et al., 2014a, 2014b; TARQUINI et al., 2022), permitindo as expansões de florestas tropicais por quase toda a América do Sul (WOODBURN et al., 2014b), especialmente durante o Ótimo Climático do Eoceno Inicial (ver e.g., GOIN et al., 2012, 2016; ZIMICZ, 2012; WOODBURN et al., 2014a, 2014b).

†MONODELPHOPSIIDAE (Szalay, 1994) rank nov.

(=†MONODELPHOSIINAE Szalay, 1994)

Diagnose. Definido por monotipia.

Genotipia. *Monodelphopsis* Paula Couto, 1952a.

Gêneros incluídos. O gênero tipo apenas.

Comentários. Em sua descrição original, Szalay (1994) não apresentou uma descrição clara desse táxon. Carneiro e Oliveira (2023, p. 309-311) discutiram a morfologia similar entre *Monodelphopsis*, *Guggenheimia* e Didelphidae: presença de StB e StD infladas e cônicas, StC reduzida, pós-metacrista longa, centrocrista dilambdodonte, cênulos reduzidos, protocone moderado e pouco deslocado mesialmente, presença de expansões basais do protocone e cingulidos marginais estendidos nos p2-3. Em adição, a presença de entocônido comprimido labio-lingualmente é uma característica compartilhada entre *Monodelphopsis* e os Didelphidae. Nesse contexto, *Monodelphopsis* é o mais antigo representante dos Didelphoidea (i.e., o clado que compreende *Monodelphopsis*, Didelphidae + Sparassocynidae [mas ver Sparassocyninae sensu BECK e TAGLIORETTI, 2019]) conhecido até o presente momento.

Dessa forma, a classificação adotada no âmbito desta tese está resumida abaixo (Tabela 5.3):

Tabela 5.3 - Classificação sistemática dos metatérios da Bacia de Itaboraí. Os táxons dessa fauna estão destacados em negrito. Clados não descritos ou formalizados na literatura (nov.) estão destacados em negrito. “ ”, indica que a validade do táxon não está definida (i.e., possivelmente parafilético ou polifilético – requer revisão); ?, indica incerteza a respeito da existência de um referido clado. 5.2.4 Classificação de tamanho (Lm1-4) e massa corporal estimada (MC).

Magnacohort Sudameridelphia (Szalay, 1994) sensu Carneiro e Oliveira, 2023

†Bergqvistheriidae Fam. **nov.**

†**Peradectoidea** gen. et sp. **nov.** 1

†**Peradectoidea** gen. et sp. **nov.** 2

†**Bergqvistherium** *primigenia* Carneiro, 2019

†Jaskhadelphyoidea Superfam. **nov.**

†Gaylordiidae Fam. **nov.**

†**Gaylordia** *macrocynodonta* Paula Couto, 1952a

†**Gaylordia** *doelloi* (Paula Couto, 1962) Marshall, 1987

†**Gaylordia** *mater* Oliveira e Goin, 2015

†Família Jaskhadelphyidae Muizon, 1992

†Subfamília Jaskhadelphyinae Muizon, 1992

†**Minusculodelphis** *minimus* Paula Couto, 1962

†**Minusculodelphis** *modicum* Oliveira, Zimicz e Goin, 2016

†Marmosopsiinae Subfam. **nov.**

- †*Marmosopsis juradoi* Paula Couto, 1962
- †*Marmosopsis* sp. nov.
- †Superordem Pucadelphyda Muizon et al., 2018
 - †Bobbschaefferiidae Fam. nov.?
 - †*Bobbschaefferia fluminensis* (Paula Couto, 1952a) Paula Couto, 1970
 - †*Bobbschaefferia* sp. nov.
 - †Superfamília Caroloameghinioidea (Marshall, 1987) sensu Carneiro e Oliveira, 2023
 - †Família Mirandatheriidae (Szalay, 1994) rank nov.
 - †Pucadelphyoidea gen. et sp. nov. 1
 - †Pucadelphyoidea gen. et sp. nov. 2
 - †*Mirandatherium alipioi* (Paula Couto, 1952a) Paula Couto, 1952c
 - †Família Caroloameghiniidae (Ameghino, 1901) Goin, 2007
 - †*Procaroloameghinia pricei* Marshall, 1982a
- †Ordem Sparassodonta Ameghino, 1894
 - †*Xenocynus crypticus* Carneiro et al., 2024a
 - †*Patene simpsoni* Paula Couto, 1952b
 - †*Silvenator brasiliensis* (Rangel et al., 2023a) Rangel, Carneiro e Oliveira, 2023b
- Supercohort Notometatheria (Kirsch et al., 1997) Carneiro e Oliveira, 2023
 - †Família Sternbergiidae (Szalay, 1994) McKenna e Bell, 1997
 - †Subfamília Sternbergiinae Szalay, 1994
 - †*Carolopaulacoutoia itaboraiensis* (Paula Couto, 1970)
 - †*Carolopaulacoutoia* sp. nov.
 - †Didelphopsiinae Subfam. nov.
 - †*Didelphopsis cabrerai* Paula Couto, 1952a
 - †*Didelphopsis* sp. nov.
 - †*Itaboraidelphys camposi* Marshall e Muizon, 1984
 - †*Itaboraidelphys* sp. nov.
 - †Família Herpetotheriidae Trouessart, 1879
 - †Subfamília Rumiodontinae Carneiro et al., 2024c
 - †*Thylacopygmaeus oliveirai* Carneiro et al., 2024c
 - †Família Derorhynchidae Goin et al., 1999
 - †*Diogenesia brevirostris* Oliveira, Carneiro e Goin, 2021
 - †*Diogenesia* sp. nov.
 - †*Derorhynchus singularis* Paula Couto, 1952a
 - †*Derorhynchus* sp. nov. 1
 - †*Derorhynchus* sp. nov. 2
 - †Cooninae subfam. nov.
 - †*Derorhynchidae* gen. et sp. nov.
- †Ordem Polydolopimorphia Archer, 1984
 - †Família Eobrasiliidae (Marshall, 1987) rank. nov.
 - †*Eobrasilia coutoi* Simpson, 1947
 - †*Periprotodidelphis bergqvistae* Oliveira e Goin, 2011

- †Subordem Bonapartheriiformes Pascual, 1980a
 - †Família Gashterniidae Marshall, 1987
 - †*Gashternia carioca* Goin e Oliveira, 2007
 - †Superfamília Bonapartherioidea Pascual, 1980a
 - †Família Bonapartheriidae Pascual, 1980a
 - †Subfamília Epidolopinae Pascual e Bond, 1981
 - †*Epidolops ameghinoi* Paula Couto, 1952b
- Cohort Marsupialia Illiger, 1811
 - Ordem Didelphimorphia Gill, 1872
 - †Família Protodidelphidae Marshall, Case e Woodburne, 1990 sensu Carneiro et al., 2024d
 - †*Guggenheimia brasiliensis* Paula Couto, 1952a
 - †*Guggenheimia crocheti* Oliveira e Goin, 2011
 - †Subfamília Protodidelphinae (Marshall, 1987) sensu Carneiro et al., 2024d
 - †*Protodidelphis vanzolinii* Paula Couto, 1952a
 - †*Robertbutleria mastodontoidea* Marshall, 1987
 - †*Carolocoutoia ferigoloi* Goin, Oliveira e Candela, 1998
 - Superfamília Didelphoidea (Gray, 1821) sensu Carneiro e Oliveira, 2023
 - †Família Monodelphopsiidae Szalay, 1994 **rank nov.**
 - †*Monodelphopsis travassosi* Paula Couto, 1952a
 - †*Monodelphopsis sp. nov.*
 - Superordem Australidelphia (Szalay, 1982) sensu Beck et al., 2014
 - †Família Woodburnodontidae? Goin et al., 2007
 - †*Austropedimys marshalli* Carneiro, Oliveira e Goin, 2018

Fonte: O autor (2023).

A fauna metateriana de Itaboraí foi representada por táxons que pesavam entre 2-3 g (*Minusculodelphis minimus*) até 10 kg (*Eobrasilia coutoi*). *Minusculodelphis minimus* compreendeu um dos menores metatérios conhecidos até o presente momento (e um dos menores mamíferos conhecidos). *Eobrasilia coutoi* representou o maior metatério não-Sparassodonta conhecido para a América do Sul e Antártica, sendo esse último ainda maior que *Thylophorops lorenzini* Goin et al., 2009.

Considerando as categorias de tamanho consideradas nesta tese (ver Tabela 4.1), a classificação por tamanho dos metatérios de Itaboraí está resumida abaixo (Tabela 5.4):

Tabela 5.4 - Classificação de tamanho das diferentes espécies da fauna de Itaboraí com base no comprimento da série molar inferior (Lm1-4) ou das dimensões dos molares (LM/m2; LM/m3). ?,

molares superiores ou inferiores desconhecidos; ~, comprimento aproximado; (), medidas com bases em alvéolos; >, valor mínimo para uma das determinadas variáveis.

	Lm1-4	LM/m2	LM/m3	Categoria
<i>Minusculodelphis minimus</i>	3.00-3.13	?/0.76-0.79	?/0.80-0.84	Minúsculo
<i>Minusculodelphis modicum</i>	3.90-4.00	1.18/1.03	1.18/1.04-1.09	Minúsculo
<i>Thylacopygmaeus oliveirai</i>	4.72	?/?	?/~1.24	Minúsculo
Peradectoidea gen. et sp. nov. 2	5.35	?/1.37	?/1.34	Muito pequeno
<i>Marmosopsis juradoi</i>	4.90-5.99	1.24-1.29/1.24-1.54	1.18-1.35/1.29-1.51	Muito pequeno
<i>Gaylordia doelloi</i>	5.35-5.74	?/1.36-1.47	?/1.39-1.49	Muito pequeno
<i>Diogenesia brevirostris</i>	5.73	?/1.50	?/1.53	Muito pequeno
<i>Derorhynchus</i> sp. nov. 2	5.76	?/1.51	?/?	Muito pequeno
<i>Carolopaulacoutoia</i> sp. nov.	5.92-6.15	?/1.53-1.58	?/1.52-1.60	Muito pequeno
<i>Marmosopsis</i> sp. nov.	6.87	?/1.63-1.75	1.70/1.63-1.77	Pequeno
<i>Carolopaulacoutoia itaboraiensis</i>	6.67-7.27	1.82-1.95/1.78-1.87	1.66-1.73/1.79-1.82	Pequeno
Derorhynchidae gen. et sp. nov.	7.41-7.59	1.97-2.21/1.88-1.92	1.92-2.16/1.92-1.99	Pequeno
<i>Derorhynchus singularis</i>	7.33-7.35	1.94/1.86-1.90	?/1.86-1.93	Pequeno
<i>Diogenesia</i> sp. nov.	6.75	1.84-1.98/1.70-1.99	1.71-1.87/1.86-1.98	Pequeno
<i>Austropedimys marshalli</i>	7.47-7.51	2.00/1.96-2.01	1.91-1.94/1.93-1.98	Pequeno
Peradectoidea gen. et sp. nov. 1	7.68	1.95-2.18/1.87-1.88	1.89-2.14/2.06-2.07	Pequeno
<i>Derorhynchus</i> sp. nov. 1	6.85-7.79	1.86/1.75-2.00	1.86/1.75-1.98	Pequeno
<i>Gaylordia macrocynodonta</i>	6.35-7.73 (F)_7.07-8.02 (M)	1.65 (F)_? (M)/1.63-1.93 (F)_1.79-2.00 (M)	1.64 (F)_? (M)/1.65-2.03 (F)_1.82-2.18 (M)	Pequeno
<i>Monodelphopsis</i> sp. nov.	7.83	1.96/2.00	1.82/?	Pequeno
<i>Gaylordia mater</i>	7.33-8.15	2.10-2.19/1.89-2.10	1.96-1.97/1.91-2.15	Pequeno

<i>Monodelphopsis travassosi</i>	8.06-9.13	?/2.19-2.41	?/2.05-2.32	Pequeno
<i>Bergqvistherium primigenia</i>	8.48-9.17	2.48/2.19-2.33	2.33/2.17-2.41	Pequeno
Pucadelphyoidea gen. et sp. nov. 1	~9.63	?/2.25	2.55/2.29	Médio
<i>Epidolops ameghinoi</i>	7.79-9.74	1.66-2.45/2.31-3.21	1.21-1.75/1.72-2.56	Médio
Pucadelphyoidea gen. et sp. nov. 2	~10.26	?/2.71	2.65/?	Médio
<i>Bobbschaefferia</i> sp. nov.	~9.67~10.24	?/2.53-2.66	?/2.33	Médio
<i>Mirandatherium alipioi</i>	9.43-10.46	2.61/2.43-2.64	2.66-3.00/2.57-2.87	Médio
<i>Guggenheimia brasiliensis</i>	10.72	?/2.52-2.66	?/2.81	Médio
<i>Procaroloameghinia pricei</i>	11.14	?/2.83	?/2.87	Médio
<i>Guggenheimia crocheti</i>	12.43-12.89	?/3.06-3.27	?/3.13-3.44	Médio
<i>Bobbschaefferia fluminensis</i>	12.88	?/3.33	?/3.19	Médio
<i>Periprotodidelphis bergqvistae</i>	~13.70	?/3.40	3.62/?	Médio
<i>Gashternia carioca</i>	14.79	?/4.22	?/4.35	Médio
<i>Itaboraidelphys</i> sp. nov.	14.84	4.12/3.67-3.94	4.14/3.87-4.07	Médio
<i>Itaboraidelphys camposi</i>	14.11-15.07	3.92-4.18/3.67-3.94	3.77-3.94/3.87-4.07	Médio
<i>Didelphopsis cabrerai</i>	16.57	4.32-4.83/4.30	4.54-4.79/4.42-4.66	Grande
<i>Xenocynus crypticus</i>	16.80-16.98	4.04-4.53/3.96-4.19	4.73-4.80/3.78-4.38	Grande
<i>Didelphopsis</i> sp. nov.	17.61-18.14	5.60/4.54-4.82	5.60/4.57-5.19	Grande
<i>Protodidelphis vanzolinii</i>	19.25-19.75	4.85-5.03/4.76-4.94	5.15-5.55/5.01-5.13	Grande
<i>Robertbutleria mastodontoidea</i>	20.38	4.76-5.40/5.32-5.66	5.50-5.78/5.73-6.00	Grande
<i>Patene simpsoni</i>	19.17-19.71	4.93-5.45/4.85-5.40	4.76-6.14/5.04-5.84	Grande
<i>Carolocoutoia ferigoloi</i>	24.24	5.74/6.02	6.86/6.91	Muito grande

<i>Silvenator brasiliensis</i>	~27.31	?/7.23	?/?	Muito grande
<i>Eobrasilia coutoi</i>	~30.21	?/6.00	8.18/?	Muito grande

Fonte: O autor (2023).

Abaixo segue a listagem das massas corporais (MC) calculadas para cada uma das espécies de metatérios dessa localidade e o modelo empregado na estimativa da MC (ver Tabela 5.5):

Tabela 5.5 - Estimativas de massa corporal (MC) calculadas em gramas (g) e quilogramas (Kg) para os metatérios da fauna de Itaboraí. inf, baseado na série molar inferior; x, máximo; MC, massa corporal estimada; MCG, massa corporal estimada com base no modelo de Gordon (2003); m, mínimo; sup, baseado na série molar superior. Para as medidas em gramas, ‘.’ indica decimal e centesimal (i.e., 1.25 g) e ‘,’ indica milhar (i.e., 1,2 g = 1.200 g). As MCs de *Eobrasilia coutoi* foram calculadas considerando uma estimativa do provável LM1-4.

Taxa	MCmin (g)	MCmin (Kg)	MCmax (g)	MCmax (Kg)
<i>Austropediomys marshalli</i>	56	0.056	100	0.100
<i>Bergqvistherium primigenia</i>	109	0.109	162	0.162
<i>Bobbschaefferia fluminensis</i>	257	0.257	467	0.467
<i>Bobbschaefferia</i> sp. nov.	234	0.234		
<i>Carolocoutoia ferigoloi</i>	4,46	4.46		
<i>Carolopaulacoutoia itaboraiensis</i>	53	0.053	61	0.061
<i>Carolopaulacoutoia</i> sp. nov.	30	0.030	34	0.346
Derorhynchidae gen. nov. sp. nov.	52	0.052	120	0.120
<i>Derorhynchus singularis</i>	38	0.038	85	0.085
<i>Derorhynchus</i> sp. nov. 1	52	0.052	79	0.079
<i>Derorhynchus</i> sp. nov. 2	27	0.027		
<i>Didelphopsis cabrerai</i>	1,15	1.15	1,7	1.700
<i>Didelphopsis</i> sp. nov.	1,78	1.78	2,04	2.040
<i>Diogenesia brevirostris</i>	21	0.021		
<i>Diogenesia</i> sp. nov.	47	0.047	100	0.100
<i>Eobrasilia coutoi</i>	6,78	6.78	10,0	10
<i>Epidolops ameghinoi</i>	79	0.079	173	0.173

<i>Gashternia carioca</i>	1,12	1.12		
<i>Gaylordia doelloi</i>	20	0.021	27	0.027
<i>Gaylordia macrocynodonta</i> (F)	37	0.037	79	0.079
<i>Gaylordia macrocynodonta</i> (M)	56	0.056	91	0.091
<i>Gaylordia mater</i>	61	0.061	93	0.093
<i>Guggenheimia brasiliensis</i>	245	0.245		
<i>Guggenheimia crocheti</i>	338	0.338	478	0.478
<i>Itaboraidelphys camposi</i>	708	0.708	912	0.912
<i>Itaboraidelphys</i> sp. nov.	891	0.891	1,00	1
<i>Marmosopsis juradoi</i>	15	0.015	27	0.027
<i>Marmosopsis</i> sp. nov.	40	0.040	51	0.051
<i>Minusculodelphis minimus</i>	2	0.002	3	0.003
<i>Minusculodelphis modicum</i>	5	0.005	7	0.007
<i>Mirandatherium alipioi</i>	162	0.162	209	0.209
<i>Monodelphopsis</i> sp. nov.	87	0.087		
<i>Monodelphopsis travassosi</i>	87	0.087	129	0.129
<i>Patene simpsoni</i>	2,13	2.13	2,75	2.75
<i>Peradectoidea</i> gen. nov. sp. nov. 1	76	0.076	131	0.131
<i>Peradectoidea</i> gen. nov. sp. nov. 2	20	0.021		
<i>Periprotodidelphis bergqvistae</i>	616	0.616		
<i>Procaroloameghinia pricei</i>	245	0.245		
<i>Protodidelphis vanzolinii</i>	1,95	1.950	2,51	2.51
<i>Pucadelphyoidea</i> gen. nov. sp. nov. 1	79	0.079	151	0.151
<i>Pucadelphyoidea</i> gen. nov. sp. nov. 2	112	0.112	162	0.162
<i>Robertbutleria mastodontoidea</i>	2,57	2.57	2,82	2.82
<i>Silvenator brasiliensis</i>	5,49	5.49	6,02	6.025
<i>Thylacopygmaeus oliveirai</i>	12	0.012		
<i>Xenocynus crypticus</i>	1,09	1.09	1,48	1.48

Fonte: O autor (2023).

5.3 ESTRUTURA FAUNÍSTICA

Com relação à composição faunística dos metatérios de Itaboraí (com base nos espécimes estudados no âmbito desta tese), *Epidolops ameghinoi* foi o representante mais abundante com um número mínimo de indivíduos (MNI) de 63 e apresentando uma abundância relativa para a fauna (ARfau) de 19.63%. *Epidolops ameghinoi* foi seguido por *Marmosopsis juradoi* (MNI: 37; ARfau: 11.53%), *Carolopaulacoutoia itaboraiensis* (MNI: 21; ARfau: 6.54%) e etc. (ver Tabela 5.6). Os três táxons mais abundantes de Itaboraí (*Epidolops ameghinoi*, *Marmosopsis juradoi* e *Carolopaulacoutoia itaboraiensis*) representam 37.70% de todos os indivíduos associados aos metatérios dessa localidade. Portanto, esses três táxons compreenderam mais de um terço de todos os metatérios de Itaboraí.

Deve-se salientar que dentre os 94 dentários edentados de Itaboraí depositados no Museu Nacional (MN), pelo menos 28 deles pertenciam a *Marmosopsis juradoi*, no que esse táxon apresenta um mínimo de 14 indivíduos (MNI: 37 + 14 = 51). Entretanto, como essa identificação foi realizada de forma preliminar antes do incêndio do MN, os espécimes desse lote do MN (MN 2896-V) não foram considerados nas análises de AR.

O NMI, a AR para cada uma das espécies de metatérios em proporção a fauna metateriana de Itaboraí (ARfau) e a sua AR para os clados em que são classificados (ARcl) estão indicados abaixo. A ARfau de cada subfamília/família reconhecida para a Bacia de Itaboraí também estão indicadas (ver Tabela 5.6):

Tabela 5.6 - Composição faunística dos metatérios de Itaboraí. Os valores de abundância relativa (AR) foram obtidos com base no número mínimo de indivíduos (MNI). ARfau, abundância relativa na fauna; ARcl, abundância relativa para o clado; N, número total de espécimes associados a um determinado táxon; Ngn, número de gêneros; Nsp, número de espécies; NMI, número mínimo de indivíduos.

Clado	Taxa	Ngn	Nsp	N	NMI	ARfau	ARcl
Bobbschaefferiidae		1	3	12	8	2,49%	
	<i>Bobbschaefferia fluminensis</i>			3	2	0,62%	25,00%
	<i>Bobbschaefferia</i> sp. nov.			6	4	1,25%	50,00%
Bonapartheriidae		1	1	181	63	19,63%	
	<i>Epidolops ameghinoi</i>			181	63	19,63%	100,00%
Caroloameghiniidae		1	1	1	1	0,31%	
	<i>Procaroloameghinia pricei</i>			1	1	0,31%	100,00%
Derorhynchidae		3	5	91	33	10,28%	
	<i>Derorhynchus singularis</i>			8	6	1,87%	18,18%

<i>Derorhynchus</i> sp. nov. 1	18	6	1,87%	18,18%		
<i>Derorhynchus</i> sp. nov. 2	1	1	0,31%	3,03%		
<i>Diogenesia brevirostris</i>	1	1	0,31%	3,03%		
<i>Diogenesia</i> sp. nov.	44	10	3,12%	30,30%		
Cooninae	1	1	20	10	3,12%	30,30%
Derorhynchidae gen. et sp. nov.	20	10	3,12%	30,30%		
Eobrasiliidae	2	2	7	4	1,25%	
<i>Eobrasilia coutoi</i>	3	3	0,93%	75,00%		
<i>Periprotodidelphis bergqvistae</i>	4	1	0,31%	25,00%		
Gashterniidae	1	1	2	1	0,31%	
<i>Gashternia carioca</i>	2	1	0,31%	100,00%		
Gaylordiidae	1	3	61	30	9,35%	
<i>Gaylordia doelloi</i>	4	4	1,25%	13,33%		
<i>Gaylordia macrocynodonta</i>	26	13	4,05%	43,33%		
<i>Gaylordia mater</i>	31	13	4,05%	43,33%		
Jaskhadelphyidae	1	2	10	6	1,87%	
<i>Minusculodelphis minimus</i>	4	3	0,93%	50,00%		
<i>Minusculodelphis modicum</i>	6	3	0,93%	50,00%		
Herpetotheriidae	1	1	1	1	0,31%	
<i>Thylacopygmaeus oliveirai</i>	1	1	0,31%	100,00%		
Marmosopsiidae	1	2	106	48	14,95%	
<i>Marmosopsis juradoi</i>	74	37	11,53%	77,08%		
<i>Marmosopsis</i> sp. nov.	32	11	3,43%	22,92%		
Mirandatheriidae	2	2	31	11	3,43%	
<i>Mirandatherium alipioi</i>	16	8	2,49%	72,73%		
Peradectoidea gen. et sp. nov. 1	15	4	0,93%	27,27%		
Pucadelphyoidea gen. et sp. nov. 2	3	2	0,62%	25,00%		
Monodelphopsiidae	1	2	13	6	1,87%	
<i>Monodelphopsis</i> sp. nov.	9	3	0,93%	50,00%		
<i>Monodelphopsis travassosi</i>	4	3	0,93%	50,00%		

Peradectoidea	2	3	63	25	7,79%	
<i>Bergqvistherium primigenia</i>			25	13	4,05%	52,00%
Peradectoidea gen. nov. sp. 1			37	11	3,43%	44,00%
Peradectoidea gen. nov. sp. 2			1	1	0,31%	4,00%
Protodidelphidae	4	5	46	12	3,74%	
<i>Guggenheimia brasiliensis</i>			1	1	0,31%	8,33%
<i>Guggenheimia crocheti</i>			7	3	0,93%	25,00%
Protodidelphinae	3	3	38	8	2,49%	66,67%
<i>Carolocoutoia ferigoloi</i>			4	1	0,31%	8,33%
<i>Protodidelphis vanzolinii</i>			16	4	1,25%	33,33%
<i>Robertbutleria mastodontoidea</i>			18	3	0,93%	25,00%
Sparassodonta	3	3	70	18	5,59%	
<i>Patene simpsoni</i>			53	10	3,11%	55,56%
<i>Silvenator brasiliensis</i>			8	4	1,24%	22,22%
<i>Xenocynus crypticus</i>			9	4	1,24%	22,22%
Sternbergiidae	3	6	162	49	15,26%	
Sternbergiinae	1	2	69	24	7,48%	48,98%
<i>Carolopaulacoutoia itaboraiensis</i>			65	21	6,52%	42,86%
<i>Carolopaulacoutoia</i> sp. nov.			4	3	0,93%	6,12%
Didelphopsiinae	2	4	93	25	7,79%	51,02%
<i>Didelphopsis cabrerai</i>			32	11	3,42%	22,45%
<i>Didelphopsis</i> sp. nov.			18	6	1,86%	12,24%
<i>Itaboraidelphys camposi</i>			19	3	0,93%	6,12%
<i>Itaboraidelphys</i> sp. nov.			24	5	1,55%	10,20%
Woodburnodontidae	1	1	19	5	1,55%	
<i>Austropedimys marshalli</i>			19	5	1,55%	100,00%
Total	-	29	43	876	321	1 -

Fonte: O autor (2023).

Dentre os clados suprafamiliares (i.e., infra-ordem, subordem, ordem e superordem) de metatérios identificados para Itaboraí, Jaskhadelphyoidea foi o mais abundante (MNI: 84; ARfau: 26.17%; em que *Marmosopsis juradoi* representa 44.05% dos indivíduos reconhecidos para esse grupo), seguido pelos Polydolopimorphia (MNI: 68; ARfau: 21.18%; em que *Epidolops ameghinoi* representa 92.65% dos indivíduos reconhecidos para esse grupo). Considerando apenas os dois clados supracitados, eles representaram quase 47.35% de todos os indivíduos do clado Metatheria reconhecidos na Bacia de Itaboraí.

Pelo contrário, Marsupialia representou o clado menos abundante (7.17%) em número de indivíduos reconhecidos para a Bacia de Itaboraí. Dentre eles, os Protodidelphidae representaram 52.17% de todos os indivíduos desse clado reconhecidos na Bacia de Itaboraí.

O NMI e a AR para cada os clados suprafamiliares estão indicados abaixo (ver Tabela 5.7):

Tabela 5.7 - Composição faunística dos clados suprafamiliares de Metatheria reconhecidos para a Bacia de Itaboraí. A Abundância relativa (AR) de cada clado em relação a fauna de metatérios (ARfau) e a AR de cada família considerando a sua ordem (ARcl) foram calculados com base no número mínimo de indivíduos (MNI) correspondentes. ARfau, abundância relativa na fauna; ARcl, abundância relativa para o clado; N, número total de espécimes associados a um determinado táxon; Nfam, número de famílias para cada ordem; Ngn, número de gêneros; Nsp, número de espécies; NMI, número mínimo de indivíduos.

Clade	Taxa	Nfam	Ngn	Nsp	N	NMI	ARfau	ARcl
Bergqvistheriidae		1	2	3	63	25	7,79%	
	<i>Bergqvistherium primigenia</i>				25	13	4,05%	52,00%
	Peradectoidea gen. nov. sp. 1				37	11	3,43%	44,00%
	Peradectoidea gen. nov. sp. 2				1	1	0,31%	4,00%
Jaskhadelphyoidea		3	3	7	177	84	26,17%	
Gaylordiidae			1	3	61	30	9,35%	35,71%
	<i>Gaylordia doelloi</i>				4	4	1,25%	4,76%
	<i>Gaylordia macrocynodonta</i>				26	13	4,05%	15,48%
	<i>Gaylordia mater</i>				31	13	4,05%	15,48%
Jaskhadelphyidae			1	2	10	6	1,87%	7,14%

	<i>Minusculodelphis minimus</i>	4	3	0,93%	3,57%
	<i>Minusculodelphis modicum</i>	6	3	0,93%	3,57%
Marmosopsiidae		1	2	106	48 14,95% 57,14%
	<i>Marmosopsis juradoi</i>	74	37	11,53%	44,05%
	<i>Marmosopsis</i> sp. nov.	32	11	3,43%	13,10%
Pucadelphyda		4	7	9	114 38 11,84%
Bobbschaefferiidae		1	3	12	8 2,49% 21,05%
	<i>Bobbschaefferia fluminensis</i>	3	2	0,62%	5,26%
	<i>Bobbschaefferia</i> sp. nov.	6	4	1,25%	10,53%
Caroloameghiniidae		1	1	1	1 0,31% 2,63%
	<i>Procaroloameghinia pricei</i>	1	1	0,31%	2,63%
Mirandatheriidae		2	2	31	11 3,43% 28,95%
	<i>Mirandatherium alipioi</i>	16	8	2,49%	21,05%
	Peradectoidea gen. et sp. nov. 1	15	3	0,93%	7,89%
	Pucadelphyoidea gen. et sp. nov. 2	3	2	0,62%	5,26%
Sparassodonta		3	3	70	18 5,61% 47,37%
	<i>Patene simpsoni</i>	53	10	3,12%	26,32%
	<i>Silvenator brasiliensis</i>	8	4	1,25%	10,53%
	<i>Xenocynus crypticus</i>	9	4	1,25%	10,53%
Polydolopimorphia		3	4	4	190 68 21,18%
Bonapartheriidae		1	1	181	63 19,63% 92,65%
	<i>Epidolops ameghinoi</i>	181	63	19,63%	92,65%
Eobrasiliidae		2	2	7	4 1,25% 5,88%
	<i>Eobrasilia coutoi</i>	3	3	0,93%	4,41%
	<i>Periprotodidelphis bergqvistae</i>	4	1	0,31%	1,47%
Gashterniidae		1	1	2	1 0,31% 1,47%
	<i>Gashternia carioca</i>	2	1	0,31%	1,47%
Sternbergiidae		1	3	6	162 49 15,26%

<i>Carolopaulacoutoia itaboraiensis</i>	65	21	6,54%	42,86%			
<i>Carolopaulacoutoia</i> sp. nov.	4	3	0,93%	6,12%			
<i>Didelphopsis cabrerai</i>	32	11	3,43%	22,45%			
<i>Didelphopsis</i> sp. nov.	18	6	1,87%	12,24%			
<i>Itaboraidelphys camposi</i>	19	3	0,93%	6,12%			
<i>Itaboraidelphys</i> sp. nov.	24	5	1,56%	10,20%			
Notometatheria	5	10	14	170	57	17,76%	
Notometatheria (n Marsupialia)	2	4	6	92	34	10,59%	59,65%
Herpetotheriidae		1	1	1	1	0,31%	2,94%
<i>Thylacopygmaeus oliveirai</i>				1	1	0,31%	2,94%
Derorhynchidae		3	5	91	33	10,28%	97,06%
Derorhynchidae gen. et sp. nov.				20	10	3,12%	29,41%
<i>Derorhynchus singularis</i>				8	6	1,87%	17,65%
<i>Derorhynchus</i> sp. nov. 1				18	6	1,87%	17,65%
<i>Derorhynchus</i> sp. nov. 2				1	1	0,31%	2,94%
<i>Diogenesia brevirostris</i>				1	1	0,31%	2,94%
<i>Diogenesia</i> sp. nov.				44	10	3,12%	29,41%
Notometatheria (Marsupialia)	3	6	8	78	23	7,17%	40,35%
Monodelphopsiidae		1	2	13	6	1,87%	26,09%
<i>Monodelphopsis</i> sp. nov.				9	3	0,93%	13,04%
<i>Monodelphopsis travassosi</i>				4	3	0,93%	13,04%
Protodidelphidae		4	5	46	12	3,74%	52,17%
<i>Carolocoutoia ferigoloi</i>				4	1	0,31%	4,35%
<i>Guggenheimia brasiliensis</i>				1	1	0,31%	4,35%
<i>Guggenheimia crocheti</i>				7	3	0,93%	13,04%
<i>Protodidelphis vanzolinii</i>				16	4	1,25%	17,39%
<i>Robertbutleria mastodontoidea</i>				18	3	0,93%	13,04%

Woodburnodontidae		1	1	19	5	1,56%	21,74%
	<i>Austropedimys marshalli</i>			19	5	1,56%	21,74%
Total	-	17	29	43	876	321	

Fonte: O autor (2023).

Seguindo os resultados apresentados para a estrutura faunística dos metatérios da Bacia de Itaboraí, é possível observar uma dominância faunística de *Epidolops ameghinoi*. Salienta-se que Polydolopimorphia é considerado como o clado de Metatheria mais abundante da América do Sul e Antártica em praticamente todas (senão em todas) as faunas desses continentes após os eventos do Máximo Termal do Paleoceno-Eoceno e Ótimo Climático do Eoceno inicial (ver PAULA COUTO, 1961; WOODBURNE e ZEINMESTER, 1986; GOIN e CANDELA, 2004; TEJEDOR et al., 2009; GOIN et al., 2010, 2016). Dessa forma, a abundância relativa de *Epidolops ameghinoi* argumenta em favor de uma idade eocênica inicial para a assembleia faunística de Itaboraí (ver WOODBURNE et al., 2014a; GOIN et al., 2016).

Considerando as categorias de tamanho, os Jaskhadelphyoidea representaram o clado mais abundante dentre os metatérios minúsculos (ARcs: 85.71%; *Minusculodelphis*) e muito pequenos (ARcs: 89.13%; *Marmosopsis juradoi* e *Gaylordia doelloi*, 80.43% e 8.70%, respectivamente). Pelo contrário, os Marsupialia são os metatérios menos abundantes dentre a categoria dos pequenos, compreendendo menos de 10% dos indivíduos reconhecidos para essa categoria de tamanho (ARcs: 8.80%; *Monodelphopsis* e *Austropedimys*, 4.80% e 4.00%, respectivamente).

Dentre a categoria dos médios, *Epidolops ameghinoi* é de longe o mais abundante dentre os metatérios (ARcs: 64.95%), sendo seguido pelos Pucadelphyda (ARcs: 20.62%). Os demais Polydolopimorphia (*Periprotodidelphis bergqvistae* e *Gashternia carioca*) dessa categoria de tamanho são absolutamente mais raros que *E. ameghinoi*, representando ambos apenas 0.62% (ARcs) dos metatérios de médio porte da Bacia de Itaboraí.

Ao contrário do que foi apresentado por Muizon et al (2018), *Itaboraidelphys* não é um táxon muito abundante, visto que ele representa apenas 2.49% de todos os indivíduos de metatérios reconhecidos na fauna (ARfau) e 8.25% dos indivíduos de metatérios de médio porte (ARcs), sendo a sua abundância relativa similar à de *Bobbschaefferia* dentre os médios (ARfau e ARcs: 2.49% e 8.25%, respectivamente). Dessa forma, o argumento de que o PtII não poderia pertencer a *Bobbschaefferia* por causa de sua reduzida abundância não é suportado pelos resultados da presente tese.

Dentre os metatérios de porte grande e muito grande, os Sparassodonta representam 36.84% e 50% de todos os indivíduos de metatérios reconhecidos para essas duas categorias (ARcs), respectivamente. Dentre os metatérios de grande porte, os Sternbergiidae-Didelphopsiinae (*Didelphopsis* spp.) são os mais abundantes, representando 44.74% de todos os indivíduos de metatérios reconhecidos para essa categoria de tamanho (ARcs). Por sua vez, os Protodidelphidae (Marsupialia) são menos abundantes nas duas categorias (ARcs: 18.42% e 12.50%, respectivamente) que os Sternbergiidae e Sparassodonta, sendo na categoria dos muito grandes ainda menos abundante que *Eobrasilia* (ARcs: 37.50%).

Para os valores de abundância dos metatérios com base nas categorias de tamanho, ver abaixo (Tabela 5.8):

Tabela 5.8 - Composição faunística das categorias de tamanho reconhecidas nesta tese para os Metatheria da Bacia de Itaboraí. A Abundância relativa (AR) de cada espécie em relação a fauna de metatérios (ARfau) e a AR de cada espécie e clado considerando a sua respectiva categoria de tamanho (ARcs) foram calculados com base no número mínimo de indivíduos (MNI) correspondentes. As células destacadas em cinza indicam a categoria de tamanho; as células em laranja compreendem os dados das famílias. ARfau, abundância relativa na fauna; ARcs, abundância relativa para a categoria de tamanho; N, número total de espécimes associados a um determinado táxon; Ngn, número de gêneros; Nsp, número de espécies; NMI, número mínimo de indivíduos.

Categoria de tamanho	Taxa	Ngn	Nsp	NMI	ARfau	ARcs
Minúsculo		2	3	7	2,18%	
Jaskhadelphyidae		1	2	6		85,71%
	<i>Minusculodelphis minimus</i>			3	0,93%	
	<i>Minusculodelphis modicum</i>			3	0,93%	
Herpetotheriidae		1	1	1		14,29%
	<i>Thylacopygmaeus oliveirai</i>			1	0,31%	
Muito pequeno		5	5	46	14,33%	
Derorhynchidae		1	1	1	0,31%	2,17%
	<i>Diogenesia brevirostris</i>			1	0,31%	
Gaylordiidae		1	1	4	1,25%	8,70%
	<i>Gaylordia doelloi</i>			4	1,25%	
Marmosopsiidae		1	1	37	11,53%	80,43%
	<i>Marmosopsis juradoi</i>			37	11,53%	

Peradectoidea	1	1	1	0,31%	2,17%
Peradectoidea gen. nov. sp. 2			1	0,31%	
Sternbergiidae-Sternbergiinae	1	1	3	0,93%	6,52%
<i>Carolopaulacoutoia</i> sp. nov.			3	0,93%	
Pequeno	10	13	125	38,94%	
Derorhynchidae	3	4	32	9,97%	25,60%
<i>Derorhynchus singularis</i>			6	1,87%	
<i>Derorhynchus</i> sp. nov.			6	1,87%	
<i>Diogenesia</i> sp. nov.			10	3,12%	
Derorhynchidae gen. et sp. nov.			10	3,12%	
Gaylordiidae	1	2	26	8,10%	20,80%
<i>Gaylordia macrocynodonta</i>			13	4,05%	
<i>Gaylordia mater</i>			13	4,05%	
Marmosopsiidae	1	1	11	3,43%	8,80%
<i>Marmosopsis</i> sp. nov.			11	3,43%	
Monodelphopsiidae	1	2	6	1,87%	4,80%
<i>Monodelphopsis travassosi</i>			3	0,93%	
<i>Monodelphopsis</i> sp. nov.			3	0,93%	
Bergqvistheriidae	2	2	24	7,48%	19,20%
<i>Bergqvistherium primigenia</i>			13	4,05%	
Peradectoidea gen. nov. sp. 1			11	3,43%	
Sternbergiidae-Sternbergiinae	1	1	21	6,54%	16,80%
<i>Carolopaulacoutoia itaboraiensis</i>			21	6,54%	
Woodburnodontidae	1	1	5	1,56%	4,00%
<i>Austropedimys marshalli</i>			5	1,56%	
Médio	9	13	97	30,22%	
Bobbschaefferiidae	1	3	8	2,49%	8,25%
<i>Bobbschaefferia fluminensis</i>			2	0,62%	
<i>Bobbschaefferia</i> sp. nov.			4	1,25%	

Bonapartheriidae	1	1	63	19,63%	64,95%
<i>Epidolops ameghinoi</i>			63	19,63%	
Caroloameghiniidae	1	1	1	0,31%	1,03%
<i>Procaroloameghinia pricei</i>			1	0,31%	
Eobrasiliidae	1	1	1	0,31%	1,03%
<i>Periprotodidelphis bergqvistae</i>			1	0,31%	
Gashterniidae	1	1	1	0,31%	1,03%
<i>Gashternia carioca</i>			1	0,31%	
Mirandatheriidae	2	2	11	3,43%	11,34%
<i>Mirandatherium alipioi</i>			8	2,49%	
Peradectoidea gen. et sp. nov. 1			3	0,93%	
Pucadelphyoidea gen. et sp. nov. 2			2	0,62%	
Protodidelphidae	1	2	4	1,25%	4,12%
<i>Guggenheimia brasiliensis</i>			1	0,31%	
<i>Guggenheimia crocheti</i>			3	0,93%	
Sternbergiidae- Didelphopsiinae	1	2	8	2,49%	8,25%
<i>Itaboraidelphys camposi</i>			3	0,93%	
<i>Itaboraidelphys</i> sp. nov.			5	1,56%	
Grande	5	6	38	11,84%	
Protodidelphidae- Protodidelphinae	2	2	7	2,18%	18,42%
<i>Protodidelphis vanzolinii</i>			4	1,25%	
<i>Robertbutleria mastodontoidea</i>			3	0,93%	
Sparassodonta	2	2	14	4,36%	36,84%
<i>Patene simpsoni</i>			10	3,12%	
<i>Xenocynus crypticus</i>			4	1,25%	
Sternbergiidae- Didelphopsiinae	1	2	17	5,30%	44,74%
<i>Didelphopsis cabrerai</i>			11	3,43%	

<i>Didelphopsis</i> sp. nov.	6	1,87%			
Muito grande	3	3	8	2,49%	
Eobrasiliidae	1	1	3	0,93%	37,50%
<i>Eobrasilia coutoi</i>			3	0,93%	
Protodidelphidae- Protodidelphinae	1	1	1	0,31%	12,50%
<i>Carolocoutoia ferigoloi</i>			1	0,31%	
Sparassodonta	1	1	4	1,25%	50,00%
<i>Silvenator brasiliensis</i>			4	1,25%	
Total			321		-

Fonte: O autor (2023).

5.4 REASSOCIAÇÃO DOS PETROSOS DE ITABORAÍ

Ladevèze (2004, 2007) e Ladevèze e Muizon (2010) descreveram oito morfótipos de petrosos (PtI a PtVIII). Utilizando-se de regressões, número de materiais por táxon e tamanho dos materiais, esses autores recuperaram as seguintes possíveis associações para os petrosos de Itaboraí: PtI e PtVI com *Gaylordia macrocynodonta* e *Mirandatherium alipioi*, PtII com *Bobbschaefferia fluminensis*, PtIII, PtV e PtVII com *Marmosopsis juradoi* e *Gaylordia doelloi*, PtIV com *Carolopaulacoutoia itaboraiensis* e PtVIII com *Minusculodelphis*. Entretanto, esses autores não formalizaram essas associações. Posteriormente, Beck (2017) associou o PtII a *Epidolops ameghinoi* e Muizon et al (2018) associou o mesmo petroso a *Itaboraidelphys camposi*.

Um resumo das diferentes hipóteses de associação dos petrosos de Itaboraí estão indicadas abaixo (Tabela 5.9):

Tabela 5.9 - Morfótipos de petrosos de metatérios recuperados em Itaboraí (ver LADEVÈZE, 2004, 2007; LADEVÈZE e MUIZON, 2010) com suas referidas associações com metatérios dessa fauna sugeridas em estudos prévios e na presente tese. Pt, Morfótipo de petroso.

Pt	Ladevèze e Muizon (2010)	Beck (2017)	Muizon et al. (2018)	Tese	Clado

	<i>Gaylordia</i>			Stem-Marsupialia
PtI	<i>macrocynodonta</i> ou <i>Mirandatherium alipioi</i>		<i>Epidolops ameghinoi</i>	
PtII	<i>Bobbschaefferia fluminensis</i> ou <i>Procaroloameghinia pricei</i>	<i>Epidolops ameghinoi</i>	<i>Bobbschaefferia</i> spp., <i>Mirandatherium alipioi</i> ou <i>Pucadelphyoidea</i> gen. nov. spp.	Pucadelphyda- Bobbschaefferia + Caroloameghinioidea
PtIII	<i>Gaylordia doelloi</i> ou <i>Marmosopsis juradoi</i>		<i>Marmosopsis</i> spp.	Jaskhadelphyoidea
PtIV	<i>Carolopaulacoutoia itaboraiensis</i>		<i>Gaylordia</i> spp. (<i>Gaylordia macrocynodonta</i> ou <i>G. mater</i>)	Jaskhadelphyoidea
PtV	<i>Gaylordia doelloi</i> ou <i>Marmosopsis juradoi</i>		<i>Carolopaulacoutoia</i> spp.	Sternbergiidae
PtVI	<i>Gaylordia macrocynodonta</i> ou <i>Mirandatherium alipioi</i>		Derorhynchidae (Derorhynchidae gen. et sp. nov., <i>Derorhynchus</i> spp. ou <i>Diogenesia</i> sp. nov.)	Derorhynchidae
PtVII	<i>Gaylordia doelloi</i> ou <i>Marmosopsis juradoi</i>		<i>Thylacopygmaeus oliveirai</i>	Herpetotheriidae- Rumiodontinae
PtVIII	<i>Minusculodelphis minimus</i>		<i>Minusculodelphis</i> spp.	Jaskhadelphyoidea- Jaskhadelphyidae

Fonte: O autor (2023).

Considerando os resultados das aplicações das regressões de Ladevèze e Muizon (2010) e Beck et al. (2008), da revisão taxonômica e do MNI, diversos táxons poderiam ser associados aos morfótipos de petrosos, com exceção dos morfótipos PtVIII, que é unicamente congruente com *Minusculodelphis*, e PtVII, unicamente congruente com *Thylacopygmaeus oliveirai*. Portanto, a consideração de tamanho estimado com base nos dois modelos de regressão supracitados e a abundância relativa com base no MNI não representaram variáveis definitivas para justificar a associação desses elementos cranianos isolados com alguma das espécies da Bacia de Itaboraí. Isso ocorre pelo fato dessa localidade apresentar uma grande diversidade de metatérios, especialmente para a categoria dos pequenos.

De forma contrária, considerando-se a abundância relativa dos diferentes clados em função das categorias de tamanho (ARcs) pode-se chegar a conclusões mais precisas sobre as afinidades dos petrosos e os possíveis táxons que podem ser a eles associados (ver Tabela 5.10).

Tabela 5.10 - Composição faunística das categorias de tamanho reconhecidas nesta tese para os Metatheria da Bacia de Itaboraí. A Abundância relativa (AR) de cada família para cada uma das categorias de tamanho foram calculados com base no número mínimo de indivíduos (MNI) correspondentes. Os clados estão ordenados em suas respectivas categorias de tamanho com base em suas abundâncias relativas, sendo os mais abundantes listados primeiro e os menos abundantes listados por último. AR, abundância relativa.

	AR
Minúsculo	2.18%
Jaskhadelphyidae	85.71%
Herpetotheriidae	14.29%
Muito pequeno	14.33%
Marmosopsiidae	80.43%
Gaylordiidae	8.70%
Sternbergiidae	6.52%
Derorhynchidae	2.17%
Peradectoidea	2.17%
Pequeno	38.94%
Derorhynchidae	25.60%
Gaylordiidae	20.80%
Peradectoidea	19.20%
Sternbergiidae	16.80%
Marmosopsiidae	8.80%
Monodelphopsiidae	4.80%
Woodburnodontidae	4.00%
Médio	30.22%
Bonapartheriidae	64.95%
Mirandatheriidae	11.34%
Bobbschaefferiidae	8.25%
Sternbergiidae	8.25%

Protodidelphidae	4.12%
Caroloameghiniidae	1.03%
Eobrasiliidae	1.03%
Gashterniidae	1.03%
Grande	11.84%
Sternbergiidae	44.74%
Sparassodonta	36.84%
Protodidelphidae	18.42%
Muito grande	2.49%
Sparassodonta	50.00%
Eobrasiliidae	37.50%
Protodidelphidae	12.50%

Fonte: O autor (2023).

Dentre a categoria dos muito pequenos, os Jaskhadelphyoidea representam por volta de 90% dos indivíduos identificados, sendo *Marmosopsis juradoi* responsável por mais de 80% deles. Portanto, um dos três petrosos pertencentes a essa categoria de tamanho (PtIII, PIV e PtV) deve, obrigatoriamente, pertencer a *M. juradoi*. Baseado nisso, a hipótese de Muizon e Ladevèze (2022), que considerou *Marmosopsis* como pertencendo a um clado irmão ao dos Pucadelphyidae (i.e., “Pucadelphyoidea” sensu MUIZON e LADEVÈZE, 2022) não foi suportada nesta tese. Nenhum dos três morfótipos compatíveis em tamanho com essa espécie pode ser recuperado como um Pucadelphyda.

Para as categorias dos médios, grandes e muito grandes, a diversidade supragenérica (i.e., família) é menor e, na categoria dos médios, as abundâncias relativas são muito distintas entre os clados. Dessa forma é possível associar com relativa segurança os petrosos a nível supragenérico, pelo menos, para essa categoria.

Como já mencionado, *Epidolops ameghinoi* representa sozinho quase 20% de todos os espécimes recuperados na Bacia de Itaboraí, no que é improvável que os PI ou PII não pertençam a esse táxon. A julgar pelas afinidades recuperadas para os Argyrolagidae (ver e.g., BECK, 2017; ABELLO e CANDELA, 2020) e *Anatoliadelphys* (ver e.g., MAGA e BECK, 2017; MÉTAIS et al., 2018; CARNEIRO, 2019; BEARD et al., 2023) é improvável que os Polydolopimorphia não representem um clado próximo aos Marsupialia (ainda que não possam ser considerados como Marsupialia). Nesse contexto, o PtI é o morfótipo mais plausível a ser associado a *E. ameghinoi*.

Desconsiderando *Epidolops ameghinoi* como um candidato para a associação do PtII, Pucadelphyda é o segundo grupo mais abundante para a categoria dos médios e com táxons próximos em tamanho as dimensões estimadas para esse morfótipo. Nesta tese, Caroloameghiniidae e Mirandatheriidae (i.e., Caroloameghinioidea) são considerados como membros desse clado. Portanto, *Mirandatherium alipioi*, *Procaroloameghinia pricei*, o Pucadelphyoidea gen. et sp. nov. 1 e o Pucadelphyoidea gen. et sp. nov. 2 são os táxons mais prováveis de serem associados ao PtII. *Guggenheimia* é desconsiderado devido às suas maiores afinidades aos Didelphimorphia (ver CARNEIRO e OLIVEIRA, 2023). A julgar pela abundância relativa e tamanho, o PtII deveria pertencer a mais de um táxon desse grupo, como *Mirandatherium alipioi* ou o Pucadelphyoidea gen. nov. spp., visto que *P. pricei* é representado por apenas um único espécime.

Os resultados comparativos das regressões com as áreas e dimensões estimadas cada espécie de metatério da Bacia de Itaboraí estão apresentados abaixo (Tabela 5.11):

Tabela 5.11 - Resultado das hipóteses de associação dos morfótipos de petrosos da fauna de Itaboraí com base nas regressões de Ladevèze e Muizon (2010) e Beck et al. (2008). As áreas calculadas para os molares dos metatérios de Itaboraí estão indicadas, assim como as áreas estimadas em função da área do *promontorium* dos petrosos. PIIa compreende as medidas originais apresentadas em Ladevèze e Muizon (2010); enquanto PIIb compreende as medidas revisadas em Muizon et al. (2018), sendo essa última a considerada no âmbito desta tese. e, área estimada em função do *promontorium*; LM/m, comprimento do molar, com o número especificando o *locus* correspondente; Lm1-4, comprimento da série molar inferior; Pt, morfótipo de petroso; ra, área dos molares; ~, valor estimado com base em espécies incompletos e/ou isolados.

	Lm1-4	LM2/Lm2	LM3/Lm3	M2 ra	m2 ra	M3 ra	m3 ra	M2e	m2e	M3e	m3e	LM 2e	Pt
<i>Minusculodelphis minimus</i>	3.00- 3.13	?	0.76-0.79	?	0.80-0.84	0.38- 0.42	0.46- 0.52	0.77- 1.57	0.49- 0.99	0.65- 1.41	0.40- 0.87	?	PV III
<i>Minusculodelphis modicum</i>	3.90- 4.00	1.18/1.03	1.18/1.04- 1.09	1.27	0.65	1.27	0.67- 0.72	0.77- 1.57	0.49- 0.99	0.65- 1.41	0.40- 0.87	?	PV III
<i>Thylacopygmaeus oliveirai</i>	4.72	~/?	~/~1.24				0.85	1.21- 1.62	0.77- 1.03	1.06- 1.46	0.66- 0.91	?	PV II
Peradectoidea gen. et sp. nov. 2	5.35	~/1.37	~/1.34		1.12		1.07						

<i>Marmosopsis juradoi</i>	4.90-5.99	1.24-1.29/1.24-1.54	1.18-1.35/1.29-1.51	1.81-2.00	0.96-1.38	1.77	1.08-1.36	1.98-2.66	1.25-1.69	1.81-2.50	1.12-1.55	1.29	PV
<i>Gaylordia doelloi</i>	5.35-5.74	?/1.36-1.47	?/1.39-1.49		1.21-1.49		1.48-1.58	2.56-2.74	1.62-1.73	2.40-2.58	1.49-1.60	1.39	PII I
<i>Diogenesia brevirostris</i>	5.73	?/1.50	?/1.53		1.41		1.48						
<i>Derorhynchus</i> sp. nov. 2	5.76	?/1.51	?/?		1.43								
<i>Carolopaulacoutoia</i> sp. nov.	5.92-6.15	?/1.53-1.58	?/1.52-1.60	2.49	1.46-1.55		1.48	2.97	1.88	2.82	1.75	1.54	PI V
<i>Marmosopsis</i> sp. nov.	6.87	?/1.63-1.75	1.70/1.63-1.77		1.82	3.26	1.68-1.74						
<i>Carolopaulacoutoia itaboraiensis</i>	6.67-7.27	1.82-1.95/1.78-1.87	1.66-1.73/1.79-1.82	3.44-3.83	1.47-1.71	3.25-3.66	1.60-1.92						
<i>Derorhynchidae</i> gen. et sp. nov.	7.41-7.59	1.97-2.21/1.88-1.92	1.92-2.16/1.92-1.99	4.83	2.21-2.30	4.36-4.96	2.28	4.53	2.87	4.46	2.77	1.95	PV I
<i>Derorhynchus singularis</i>	7.33-7.35	1.94/1.86-1.90	?/1.86-1.93	3.99	2.06-2.11		2.04-2.14						
<i>Diogenesia</i> sp. nov.	6.75	1.84-1.98/1.70-1.99	1.71-1.87/1.86-1.98	3.86-4.33	1.97-2.72	3.85-4.02	2.14-2.37						
<i>Austropeidiomys marshalli</i>	7.47-7.51	2.00/1.96-2.01	1.91-1.94/1.93-1.98	4.91		5.16-5.17	2.05						
<i>Peradectoidea</i> gen. et sp. nov. 1	7.68	1.95-2.18/1.87-1.88	1.89-2.14/2.06-2.07	4.15-5.10	1.76-1.99	4.63-4.86	2.21	4.53	2.87	4.46	2.77	1.95	PV I
<i>Derorhynchus</i> sp. nov.	6.85-7.79	1.86/1.75-2.00	1.86/1.75-1.98	3.17	1.98-2.41	4.03	1.99						
<i>Gaylordia macrocynodonta</i>	6.35-8.02	1.65/1.63-2.00	1.64/1.65-2.18	3.04	2.02-2.96		2.17-2.72						
<i>Monodelphopsis</i> sp. nov.	7.83	1.96/2.00	1.82/?	3.96	2.39	3.81							

<i>Gaylordia mater</i>	7.33-8.15	2.10-2.19/1.89-2.10	1.96-1.97/1.91-2.15	5.29-5.60	2.77-3.02	5.41-5.51	2.48-3.23		
<i>Monodelphopsis travassosi</i>	8.06-9.13	?/2.19-2.41	?/2.05-2.32		2.93				
<i>Bergqvistherium primigenia</i>	8.48-9.17	2.48/2.19-2.33	2.33/2.17-2.41	6.44	3.05-3.47	6.01	3.20-3.36		
Pucadelphyoidea gen. et. sp. nov.	~9.63	?/2.25	2.55/2.29		2.83	7.14	2.31	4.26-5.77	2.69-3.65
								4.17-5.82	2.58-3.60
									2.64
									PII
<i>Epidolops ameghinoi</i>	7.79-9.74	1.66-2.45/2.31-3.21	1.21-1.75/1.72-2.56	4.78-8.29	3.27-6.73	2.78-4.05	2.41-4.83	4.37-4.67	2.77-2.96
								4.29-4.61	2.66-2.86
									2.85
									PI
Pucadelphyoidea gen. et sp. nov. 2	~9.67-~10.24	?/2.53-2.66	?/2.33		3.44		3.28	4.26-5.77	2.69-3.65
								4.17-5.82	2.58-3.60
									2.64
									PII
<i>Bobbschaefferia</i> sp. nov.	~10.26	?/2.71	2.65/?		3.93	8.56		4.26-5.77	2.69-3.65
								4.17-5.82	2.58-3.60
									2.64
									PII
<i>Mirandatherium alipioi</i>	9.43-10.46	2.61/2.43-2.64	2.66-3.00/2.57-2.87	7.10	3.57-4.17	10.17	3.60-4.50	4.26-5.77	2.69-3.65
								4.17-5.82	2.58-3.60
									2.64
									PII
<i>Guggenheimia brasiliensis</i>	10.72	?/2.52-2.66	?/2.81		5.18		5.55		
<i>Procaroloameghinia pricei</i>	11.14	?/2.83	?/2.87		4.86		4.66		
<i>Guggenheimia crocheti</i>	12.43-12.89	?/3.06-3.27	?/3.13-3.44		6.23		6.53-7.51		
<i>Bobbschaefferia fluminensis</i>	12.88	?/3.33	?/3.19				7.80		
<i>Periprotodidelphis bergqvistae</i>	~13.70	?/3.40	3.62/?			17.84			
<i>Gashternia carioca</i>	14.79	?/4.22	?/4.35	15.05*					
<i>Itaboraidelphys</i> sp. nov.	14.84	4.12/3.67-3.94	4.14/3.87-4.07	15.96-17.51	7.32-9.36	16.66-17.88	7.38-9.97		

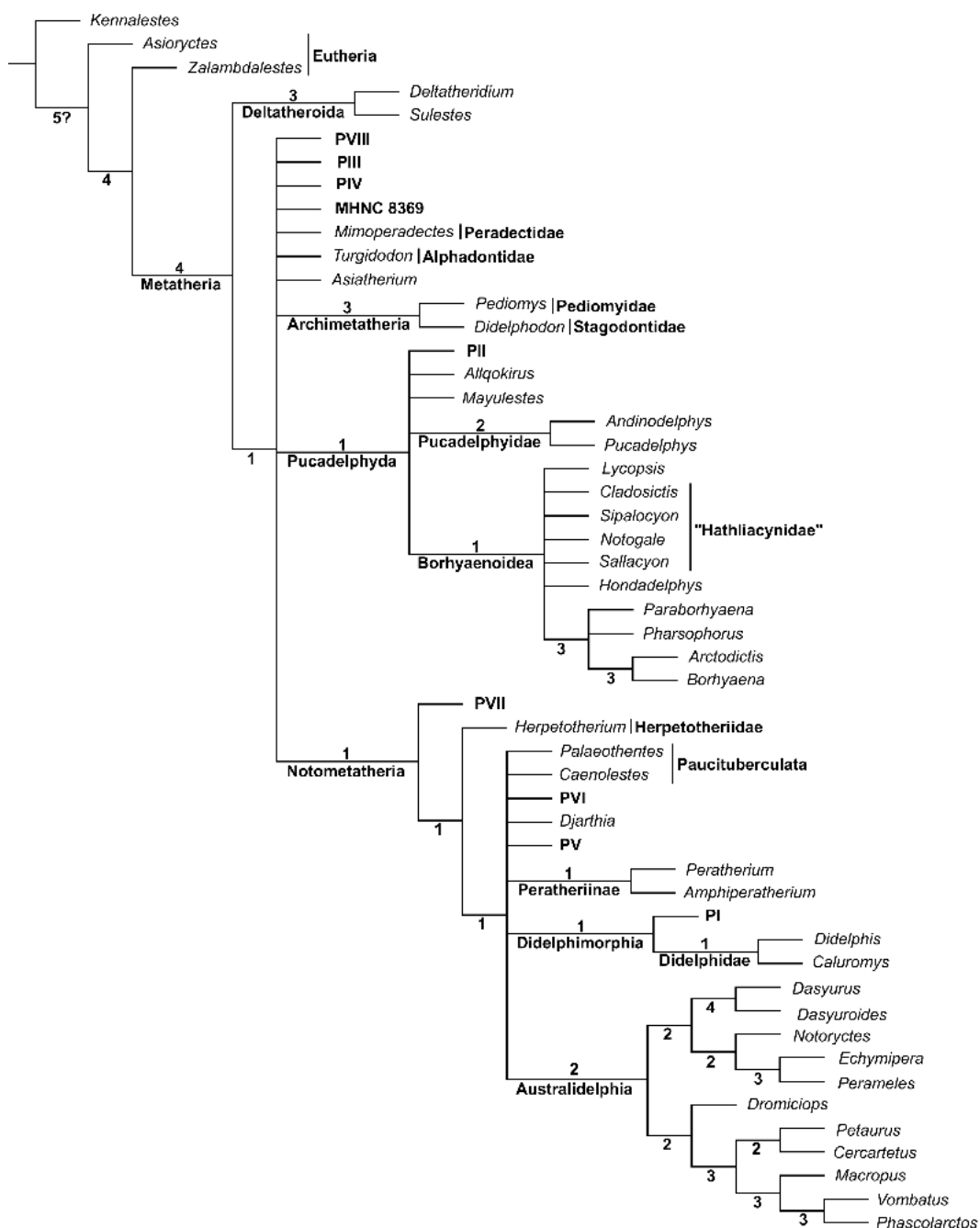
<i>Itaboraidelphys camposi</i>	14.11-15.07	3.92-4.18/3.67-3.94	3.77-3.94/3.87-4.07	15.96-17.51	7.32-9.36	16.66-17.88	7.38-9.97		
<i>Didelphopsis cabrerai</i>	16.57	4.32-4.83/4.30	4.54-4.79/4.42-4.66	18.96-23.26	12.85	24.05	11.93-		
<i>Xenocynus crypticus</i>	16.80-16.98	4.04-4.53/3.96-4.19	4.73-4.80/3.78-4.38	19.16	8.07		6.99		
<i>Didelphopsis</i> sp. nov.	17.61-18.14	5.60/4.54-4.82	5.60/4.57-5.19	33.04	15.13	31.86	17.93		
<i>Protodidelphis vanzolinii</i>	19.25-19.75	4.85-5.03/4.76-4.94	5.15-5.55/5.01-5.13	24.95-25.70	14.62-	16.23-30.50	-		
<i>Robertbutleria mastodontoidea</i>	20.38	4.76-5.40/5.32-5.66	5.50-5.78/5.73-6.00	23.04-28.73	17.68-	30.57-			
<i>Patene simpsoni</i>	19.17-19.71	4.93-5.45/4.85-5.40	4.76-6.14/5.04-5.84	17.87-25.00	12.75-	38.92-40.24	15.12-		
<i>Carolocoutoia ferigoloi</i>	24.24	5.74/6.02	6.86/6.91	24.05		30.15	47.66		
<i>Silvenator brasiliensis</i>	~27.31	?/7.23	?/?		27.33				
<i>Eobrasilia coutoi</i>	~30.21	?/6.00	8.18/?			77.22			

Fonte: O autor (2023).

Por sua vez, com relação aos resultados da análise filogenética, os petrosos apresentaram as seguintes afinidades sistemáticas: PtI (stem-Marsupialia [Polydolopimorphia?]), PtII (Pucadelphyda), PtIII, PtIV, PtV e PtVIII (Sudameridelphia não-Pucadelphyda e não-Notometatheria; i.e., “Peradectoidea” sul-americanos, Jaskhadelphyoidea e/ou Sternbergiidae), e PtVI e PtVII (Notometatheria não-Marsupialia; i.e., Peratheriinae, Herpetotheriidae ou Derorhynchidae).

As afinidades sistemáticas consideradas nesta tese para os metatérios de Itaboraí podem ser conferidas na Tabela 5.3, e as afinidades sistemáticas recuperadas para os petrosos de Itaboraí podem ser conferidas abaixo (Figura 5.3):

Figura 5.3 - Árvore de consenso estrito das 68 árvores mais parcimoniosas (Score/Steps = 1735; CI = 0.383; RI = 0.622) encontradas na análise. Os morfótipos de petrosos de Itaboraí estão destacados em negrito. Os números abaixo e acima dos ramos representam os valores do suporte de Bremer.



Fonte: O autor (2023).

Finalmente, com base no conjunto de evidências apresentados nesta tese, as seguintes associações são sugeridas para os oito morfótipos de petrosos de metatérios de Itaboraí: PtI com *Epidolops ameghinoi*, PtII com um *Pucadelphyda* (*Mirandatherium alipioi*, *Pucadelphyoidea*

gen. et sp. nov. 1 e/ou Pucadelphyoidea gen. et sp. nov. 2), PtIII com *Marmosopsis* spp., PtIV com *Gaylordia* spp., PtV com *Carolopaulacoutoia* spp., PtVI com um Derorhynchidae (*Diogenesia* sp. nov., Derorhynchidae gen. et sp. nov., *Derorhynchus singularis* ou *Derorhynchus* sp. nov. 1), PtVII com *Thylacopygmaeus oliveirai*, e PtVIII com *Minusculodelphis* spp.

6 CONCLUSÕES

A Bacia de Itaboraí, Itaboraí, RJ, sudeste do Brasil, representa a localidade com a maior diversidade Paleógena para o clado dos Metatheria, compreendendo um mínimo de 29 gêneros e 44 espécies agrupados em 16 famílias de praticamente todos os clados suprafamiliares conhecidos até o presente momento (exceto Polydolopimorphia-Polydolopiformes e Marsupialia-Paucituberculata e Agreodonta). A diversidade morfológica e paleoecológica observada em Itaboraí é comparável apenas com a de faunas australianas miocênicas e quaternárias.

Os metatérios dessa localidade variaram entre 2-3 g (*Minusculodelphis minimus*) e 10 kg (*Eobrasilia coutoi*), representando um dos menores metatérios (e mamíferos) conhecidos até o presente momento e o maior metatério não-Sparassodonta da América do Sul, respectivamente. Os metatérios de Itaboraí compreenderam todas as subcategorias (minúsculo, muito pequeno, pequeno, médio, grande e muito grande) consideradas para mamíferos de pequeno porte (i.e., menos de 10 kg).

Os metatérios de Itaboraí ocuparam diversos nichos tróficos: faunivoria/carnivoria preferencial (*Silvenator brasiliensis*), carnivoria/carnivoria generalizada (*Patene simpsoni*, Pucadelphyoidea gen. et spp. nov., *Xenocynus crypticus*), insetivoria especializada (*Derorhynchus* spp., *Diogenesia brevirostris*, *Gaylordia* spp., *Marmosopsis juradoi*, *Minusculodelphis* spp.), insetivoria generalizada (*Austropeidiomys marshalli*, *Bergqvistherium primigenia*, *Carolopaulacoutoia* spp., Derorhynchidae gen. et sp. nov., *Diogenesia* sp. nov., *Marmosopsis* sp. nov., *Monodelphopsis* spp., Peradectoidea gen. et spp. nov., *Thylacopygmaeus oliveirai*), onivoria (*Bobbschaefferia* spp., *Didelphopsis cabrerai*, *Itaboraidelphys* spp., *Mirandatherium alipioi*), frugivoria generalizada (*Didelphopsis* sp. nov., *Guggenheimia* spp., *Procaroloameghinia pricei*, *Protodidelphis vanzolinii*), frugivoria especializada (*Carolocoutoia ferigoloi*, *Robertbutleria mastodontoidea*), frugívoro-granivoria/esclerocarpia (*Eobrasilia coutoi*, *Periprotodidelphis bergqvistae*), folivoria (*Gashternia carioca*) e mista (*Epidolops ameghinoi*).

A Bacia de Itaboraí apresenta a maior diversidade de metatérios com dietas durófagas conhecidas até o presente momento, com quatro gêneros e cinco espécies (*Didelphopsis cabrerai*, *Eobrasilia coutoi*, *Gaylordia doelloi*, *G. macrocynodonta*, *Periprotodidelphis bergqvistae*). Metatérios com dieta graminívora/pastadora, granívora especializada, hipercarnívora/carnivoria especializada ou malacófaga não são reconhecidos para essa localidade.

A Bacia de Itaboraí apresentou diversos táxons metaterianos endêmicos, como *Eobrasilia*, *Gaylordia*, *Minusculodelphis*, *Periprotodidelphis*, *Thylacopygmaeus* e *Xenocynus*. É possível que esses clados apresentassem uma distribuição paleobiogeográfica Tropical (Brasil), não ocorrendo em zonas Austrais (e.g., Patagônia). Entretanto, Itaboraí e Las Flores, Argentina, compartilham uma similaridade faunística de metatérios de 59%, que compreende 19 gêneros (*Austropedimys*, *Bergqvistherium*, *Bobbschaefferia*, *Carolopaulacoutoia*, *Derorhynchidae* gen. nov., *Derorhynchus*, *Didelphopsis*, *Diogenesia*, *Epidolops*, *Gashternia*, *Guggenheimia*, *Itaboraidelphys*, *Marmosopsis*, *Mirandatherium*, *Monodelphopsis*, *Procaroloameghinia*, *Protodidelphis*, *Peradectoidea* gen. nov., *Pucadelphyoidea* gen. nov.). Essas diferenças estão potencialmente relacionadas a zoneamento biogeográfico.

Os elementos petrosais dos Polydolopimorphia (*Epidolops ameghinoi* – PtI), Caroloameghinioidea-Pucadelphyda (*Bobbschaefferia* spp. ou *Pucadelphyoidea* gen. et sp. nov. 1 – PtII), Jaskhadelphyoidea-Jaskhadelphyidae (*Minusculodelphis* spp. – PtVIII), Jaskhadelphyoidea-Jaskhadelphyidae? (*Marmosopsis* spp. – PtIII), Jaskhadelphyoidea-Gaylordiidae (*Gaylordia* spp. – PtIV), Notometatheria-Sternbergiidae (*Carolopaulacoutoia* spp. – PtV), Notometheria-Derorhynchidae (*Derorhynchidae* gen. et sp. nov., *Derorhynchus* spp., *Diogenesia* spp. –PtVI) e Notometatheria-Herpetotheriidae-Rumiodontinae (*Thylacopygmaeus* – PtVII) são reconhecidos. Em adição, o primeiro elemento petrosal de um Marsupialia (MCN-PV 1402) foi reconhecido para a Bacia de Itaboraí (*Monodelphopsis travassosi* ou *Guggenheimia* spp.).

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**APÊNDICE A – LISTA DOS MATERIAIS ESTUDADOS NAS DIFERENTES
COLEÇÕES BRASILEIRAS (MCN-PV, MCT.M., MN e UFRJ-DG) E MOLDES DO
AMERICAN MUSEUM OF NATURAL HISTORY (AMNH)**

Lista dos materiais estudados nas diferentes coleções brasileiras e moldes do American Museum of Natural History (AMNH). **AMNH**, American Museum of Natural History, New York, NY, USA; **MCN-PV**, Seção de Paleontologia, Museu de Ciências Naturais da antiga Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, RS, Brasil; **MCT.M (ex DGM** – Divisão de Geologia e Mineralogia), coleção de mamíferos de Itaboraí, Museu de Ciências da Terra, Rio de Janeiro, RJ, Brasil; **MN**, Museu Nacional do Rio de Janeiro, Rio de Janeiro, RJ, Brasil. (^), holótipo; (!), holótipo ou parátipo de sinonímia (= *nomen nudum*; *nomen vanum*; táxon inválido); (*), extraviado ou emprestado (previamente observado, fotografado e estudado na coleção); (?), extraviado (não estudado, figurado ou observado há muito tempo - i.e., antes de 2010); (s/n), material figurado por Leonardo M. Carneiro, mas perdido antes de receber número de tombo.

Número de Coleção	Táxon	Descrição do material
DGM 170-M	<i>Epidolops ameghinoi</i>	dentário direito com m2-3, e alvéolos do c-m1 e m4
DGM 171-M	<i>Epidolops ameghinoi</i>	dentário esquerdo com p2-m3, e alvéolos i1-2, c e m4
DGM 172-M	<i>Epidolops ameghinoi</i>	dentário direito sem dentes preservados
DGM 173-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com m2, e alvéolos dos p3-m1 e m3-4
DGM 174-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p3-m3 e alvéolos do m4
DGM 175-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p3-m2 e alvéolos dos m3-4
DGM 176-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p3-m3 e raízes do p2

DGM 177-M	<i>Epidolops ameghinoi</i>	dentário direito com p3-m3, e raízes do p2 e m4; quebrado em duas partes: p3 e molares
DGM 178-M	<i>Epidolops ameghinoi</i>	dentário esquerdo com p2-m2, e raízes do i1-c e m3-4
DGM 179-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p2-m3 e alvéolos do m4
DGM 180-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m1-2 e alvéolos dos m3-4; processos angular e coronoide preservados (processo coronoide separado do resto do material)
DGM 181-M	<i>Epidolops ameghinoi</i>	dentário direito com p2-m2, e alvéolos dos i1-c e m3-4
DGM 182-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p3, e raízes do p2 e m1-4
DGM 183-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p2-m2 e alvéolos dos m3-4
DGM 184-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p2-m2 e alvéolos dos m3-4
DGM 185-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com raízes do m1-4
DGM 186-M	<i>Gaylordia macrocynodonta</i>	dentário esquerdo com p3-m1 e alvéolos dos p2, m2-4
DGM 187-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m1-2 e alvéolos dos c-p3 e m3-4
DGM 188-M (!)	<i>Epidolops ameghinoi</i>	dentário direito incompleto com p2-m3 presentes e alvéolos do m4
DGM 189-M	<i>Epidolops ameghinoi</i>	dentário direito sem dentes preservados
DGM 190-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p3-m2, e raízes do i1-p2 e m3-4

DGM 191-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p2-m1 e raízes do m2-4
DGM 192-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com alvéolos dos m1-4
DGM 193-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com m1-2 e alvéolos dos m3-4
DGM 194-M	<i>Epidolops ameghinoi</i>	dentário direito sem dentes preservados
DGM 195-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com alvéolos dos m1-4
DGM 196-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p3-m2 e alvéolos dos m3-4
DGM 197-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m2-3 e alvéolos do m4
DGM 198-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P3-M3
DGM 199-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3-M3
DGM 200-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3, e alvéolos dos P2 e M1-2
DGM 201-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3
DGM 202-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com parte do P3
DGM 203-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P2-M3
DGM 204-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P3-M3
DGM 205-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P3-M1 e alvéolos do M2

DGM 206-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com M1-3 e alvéolos do M4
DGM 207-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p2, parte do p3, e alvéolos dos i1-p1 e m1-2
DGM 208-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com m1 e m3, e alvéolos dos p2-3, m2 e m4
DGM 209-M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado sem dentes e com os alvéolos do p2-m4
DGM 219-M	<i>Didelphopsi s sp. nov.</i>	dentário esquerdo edentado com alvéolos dos i2-4, c, p1-3, m1-4
DGM 243-M	<i>Didelphopsi s cabrerai</i>	dentário direito incompleto com raízes do i4, C, com p1-m4 presentes
DGM 250-M	<i>Protodidelp his vanzolinii</i>	dentário direito incompleto com p3 (solto), m1, m3, m4 incompleto (lado lingual não preservado), alvéolo do canino, alvéolo posterior do p1, alvéolos dos p2 e m2; processo angular presente e base do processo coronoide
DGM 253-M	<i>Didelphopsi s sp. nov.</i>	fragmento de dentário esquerdo com m4 incompleto ainda em erupção (sem o paracônido?)
DGM 271-M (^)	<i>Protodidelp his vanzolinii</i>	fragmento de crânio com porções rostral e palatal esquerdas com P3-M1 e M4, raízes dos P1-2, alvéolo do C, e alvéolos dos M2-3; limite do forâmen maxilo-palatino preservado
DGM 277-M	<i>Didelphopsi s sp. nov.</i>	dentário esquerdo edentado com alvéolos dos p1-3, m1-4; dividido em duas partes: p1-3 e m1-4
DGM 297-M (^)	<i>Guggenhei mia brasiliensis</i>	dentário esquerdo incompleto com p1-m4 presentes
DGM 301-M	<i>Itaboraaidelp hys camposi</i>	fragmento de dentário direito com m2-3 e alvéolo posterior do m1; m3 rachado entre o trigônido e o talônido
DGM 303-M	<i>Protodidelp his vanzolinii</i>	maxilar direito incompleto com M1-4
DGM 314-M	<i>Guggenhei mia crocheti</i>	dentário esquerdo incompleto com m2-4 presentes e alvéolos dos i1-m1

DGM 315-M	<i>Guggenheimia crocheta</i>	dentário esquerdo incompleto com m3 completo e alvéolos dos C-m2 e alvéolo anterior do m4
DGM 319-M	<i>Protodidelphis vanzolinii</i>	dentário esquerdo com p3 (solto), alvéolos desgastados dos m1-4, alvéolo do i5, c, alvéolos dos p1-2; dentário quebrado em duas partes: parte dos incisivos e canino; e resto do dentário
DGM 321-M (= AMN H 49851 (^)	<i>Epidolops ameghinoides</i>	crânio quase completo (faltando parte da caixa craniana, basiesfenoide e anterior parte da pré-maxila), mas com claras evidências de compressão e achatamento. Apresenta P3-M2 direitos, P2-M2 esquerdos, e alvéolos dos caninos, M3-4 e P2 direito. Mandíbula associada faltando a parte anterior da borda dos incisivos, com i1-2 direitos, c esquerdo, p2-m3 direitos e esquerdos e alvéolos dos m4
DGM 324-M	<i>Patene simpsoni</i>	dentário direito com m3 e alvéolos dos p2-3, m1-2 e m4
DGM 329-M (^)	<i>Gaylordia macrocynodontia</i>	crânio com porção rostral e frontal preservados com C, P2-M3 direitos, M1-2 esquerdos, raízes do P1 direito, raiz antero-labial do M4 direito e C esquerdo. Dentário esquerdo com p3-m1, raízes dos p1-2, e m2-3
DGM 331-M	<i>Patene simpsoni</i>	maxila esquerda edentada com alvéolos dos P3 e M1-4 (quebrada em duas partes: i) M2-4 e parte do M1; e ii) parte do M1 e P3
DGM 361-M	<i>Mirandatherium alipioi</i>	dentário direito incompleto com m2-4 presentes e alvéolos do m1
DGM 362-M	<i>Bergqvistherium primigenia</i>	dentário direito incompleto com m2-3 presentes, talônido do p3, e raízes do m1 e m4
DGM 363-M	<i>Mirandatherium alipioi</i>	fragmento de dentário esquerdo edentado com alvéolos dos m3-4
DGM 364-M	<i>Carolopaula acoutoia itaboraiensis</i>	dentário direito edentado com alvéolo posterior do p1, e alvéolos dos p2-3 e m1-4
DGM 642-M	<i>Didelphopsis</i> sp. nov.	M3 esquerdo

DGM 649-M	<i>Peradectoid</i> <i>ea</i> gen. nov. sp. 2	dentário esquerdo incompleto com alvéolo posterior do p1, alvéolos do p2, raízes do p3 e com m1-4 presentes
DGM 650-M (^)	<i>Diogenesia</i> <i>brevirostris</i>	dentário direito incompleto com alvéolos dos p1-2, raízes do p3 e do m1, e m2-4 presentes
DGM 651-M	<i>Derorhynch</i> <i>us</i> sp. nov.	dentário esquerdo incompleto com m1-4
DGM 652-M	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	dentário esquerdo incompleto com m4 e talônido do m3 "folgado" no alvéolo
DGM 654-M (*)	<i>Patene</i> <i>simpsoni</i>	m3 direito
DGM 655-M (*)	<i>Patene</i> <i>simpsoni</i>	m4 direito
DGM 656-M	<i>Patene</i> <i>simpsoni</i>	m4 direito com raízes preservadas e quebrado em duas partes: trigônido e talônido
DGM 657-M	cf. <i>Nemolestes</i> sp.	m2 direito com raízes preservadas, sendo a anterior menos preservada que a posterior
DGM 659-M	<i>Patene</i> <i>simpsoni</i>	m1 esquerdo com raiz posterior
DGM 660-M	<i>Guggenhei</i> <i>mia crocheti</i>	fragmento de dentário direito com m4
DGM 797-M	<i>Patene</i> <i>simpsoni</i>	M3 direito
DGM 798-M	<i>Patene</i> <i>simpsoni</i>	m3 esquerdo com raízes preservadas

DGM 799-M (*)	<i>Patene simpsoni / Itaboraaidelp hys camposi</i>	fragmento de maxila com M3 e raízes do M4
DGM 800-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P2-M3
DGM 801-M	<i>Patene simpsoni</i>	m2 direito com raízes preservadas, sendo a anterior menos preservada que a posterior
DGM 802-M	<i>Didelphopsis s cabrerai</i>	M4 direito
DGM 803-M	<i>Derorhynch us singularis</i>	maxilar esquerdo incompleto com alvéolos do M3, e M1-2 e M4 completos
DGM 804-M	<i>Itaboraaidelp hys camposi</i>	dentário direito incompleto com m2-3 presentes e alvéolos do m1 e m4
DGM 805-M + DGM 924-M (^)	<i>Procaroloa meghinia pricei</i>	dentário direito fraturado em duas partes com alvéolos dos C-p2, e p3-m4
DGM 806-M (^)(!)	<i>Eobrasilia bergqvistae</i>	M3 esquerdo
DGM 807-M	<i>Carolopaul acoutoia itaboraiensis</i>	maxilar esquerdo incompleto com M2-4 presentes
DGM 808-M (^)	<i>Austropedio mys marshalli</i>	maxilar esquerdo incompleto M2-4
DGM 810-M (^)	<i>Gaylordia mater</i>	dentário direito incompleto com m2-4

DGM 811-M	<i>Marmosops</i> s sp. nov.	fragmento de dentário direito com m3-4
DGM 812-M	<i>Diogenesia</i> sp. nov.	dentário esquerdo incompleto com p3, m3-4 presentes, alvéolos dos i, c, p1-2, e m1-2; m3 com entocônido danificado (localizado sobre o talônido) e m4 solto do dentário)
DGM 813-M	<i>Diogenesia</i> sp. nov.	maxila esquerda incompleta com M1-2, alvéolos do M3 e um alvéolo do M4
DGM 814-M	<i>Itaboraidelp</i> <i>hys camposi</i>	dentário direito incompleto com m1-4 presentes
DGM 815-M	<i>Didelphopsi</i> s <i>cabrerai</i>	m4 direito com raízes parcialmente preservadas
DGM 816-M	<i>Epidolops</i> <i>ameghinoi</i>	dp3 esquerdo
DGM 817-M (^)	<i>Itaboraidelp</i> <i>hys camposi</i>	dentário direito incompleto com p3-m4 presentes
DGM 892-M	<i>Epidolops</i> <i>ameghinoi</i>	dentário direito com p2-3, m1 e alvéolos dos i2-5, c, p1 e m2-4; processo coronoide parcialmente preservado
DGM 893-M	<i>Epidolops</i> <i>ameghinoi</i>	fragmento de maxila esquerda com P2-M2
DGM 894-M (*)	<i>Patene</i> <i>simpsoni</i>	m2 direito
DGM 895-M	<i>Itaboraidelp</i> <i>hys camposi</i>	m3 direito com raízes parcialmente preservadas
DGM 896-M (^) (!)	<i>Protodidelp</i> <i>his</i> <i>mastodontoi</i> <i>des</i>	M1 esquerdo
DGM 897-M	<i>Epidolops</i> <i>ameghinoi</i>	fragmento de dentário direito com m2-4, alvéolos do m1 (quebrados); processos coronoide, angular e côndilo mandibular presentes

DGM 898-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P2, e alvéolos dos C, P1, P3-M4
DGM 899-M	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m2, e alvéolos dos c-m1 e m3-4
DGM 900-M	<i>Epidolops ameghinoi</i>	dentário esquerdo pouco preservado (separado em três partes) com p3, m1-2 (separados do material); alvéolos dos i2-4, c, p1-2 e m1-4
DGM 901-M	<i>Epidolops ameghinoi</i>	dentário direito com p3-m2, e alvéolos dos p1-2 e m3-4
DGM 902-M	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com p3 (quebrado em sua face lingual e sem talônido), e alvéolos (muito pouco preservados) dos p2 e m1-4
DGM 903-M	<i>Epidolops ameghinoi</i>	dentário direito com p3-m1, e alvéolos dos i2-5, c, p2 e m2-4
DGM 904-M	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com m1-2 e alvéolos dos i2-4, c, p1-p3; parte da porção ventral do dentário não preservada
DGM 905-M	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com p2-m2
DGM 906-M	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com p2-m2; porção ventral muito danificada ou perdida
DGM 907-M	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com m1-3 e alvéolo do m4
DGM 908-M	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com p3; alvéolo do i2, c, e alvéolos do p2
DGM 909-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com M1 (solto), M2 e alvéolos do M3-4
DGM 910-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3-M1 e alvéolos dos M2-4
DGM 911-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3-M2 e alvéolos do M3
DGM 912-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P2-M3 e alvéolo do M4

DGM 913-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P2-M2
DGM 914-M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3-M3 e alvéolos do P2
DGM 915-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P3-M1 e alvéolos do M2
DGM 916-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com M2-3 e alvéolo do M4
DGM 917-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda edentada com alvéolo do I4?, C, P1?, P2-3 e M1- 2
DGM 918-M	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P2, P3 (muito danificado, sobrando apenas a parede mesial), M1-2 e parte dos alvéolos do M3
DGM 919-M	<i>Eobrasilia bergqvistae</i>	dentário direito incompleto com p1-3, alvéolos dos i, c, m1 e alvéolo anterior do m2
DGM 920-M	Peradectoid ea gen. nov. sp. 1	dentário esquerdo incompleto com raízes dos p1-2 e m1, e p3 e m2-4 presentes
DGM 921a- M (^)	<i>Minusculod elphis modicum</i>	dentário direito incompleto com m1-4 presentes
DGM 921b- M	<i>Minusculod elphis modicum</i>	dentário direito incompleto com alvéolos dos m1-2 e m4, e m3 completo
DGM 922-M	<i>Bergqvisthe rium primigenia</i>	dentário direito incompleto com m1-4; côndilo mandibular presente
DGM 923-M	<i>Itaboraaidelp hys camposi</i>	dentário direito incompleto com p2-m1 presentes e alvéolos do m2
DGM 925-M	<i>Gaylordia macrocynod onta</i>	fragmento de dentário direito com p1-m1

DGM 926-M	<i>Itaboraaidelp hys camposi</i>	maxilar esquerdo incompleto com M2-3 e alvéolos anteriores do M4
DGM 927-M	<i>Carolopaul acoutoia itaboraiensi s</i>	dentário direito incompleto com p2-m3 presentes, e p3 irrompendo
DGM 928-M	<i>Austropedio mys marshalli</i>	dentário direito incompleto, com m3-4 presentes, raíz posterior do p1, raíz anterior e alvéolos posteriores do p2-3, e alvéolos dos m1-2
DGM 929-M	<i>Bobbschaeff eria sp. nov.</i>	fragmento de dentário esquerdo com p2 e p3; alvéolos do p1 e m1-2, raiz do c e alvéolo dos i2-5
DGM 930-M	<i>Diogenesia sp. nov.</i>	fragmento de dentário com p3 e alvéolos dos p1-2, m1-2 e alvéolo anterior do m3
DGM 931-M	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com raízes dos p1-2 e m2-4, e com p3-m1 presentes
DGM 932-M (*)	<i>Carolopaul acoutoia itaboraiensi s</i>	dentário direito incompleto com m1-3 presentes e alvéolos do m4
DGM 933-M	cf. <i>Armintodelp hys sp.</i>	dentário direito incompleto com m3-4 presentes
DGM 966-M	<i>Carocoutoia ferigoloi</i>	Dentário direito quase completo com m2 (muito desgastado), m3-4, alvéolos dos p1-3 e m1; e parte da fossa massetérica
DGM 970-M	cf. <i>Nemolestes sp.</i>	fragmento de dentário esquerdo com m1, alvéolos do p3 e alvéolo posterior do p2
DGM 1033-M	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com m2
MCT 2374-M (=	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P2-3 e alvéolos do M1

DGM 635-M)		
MCT 2375- M (=	<i>Epidolops ameghinoi</i>	dentário esquerdo com p2-3, m1; alvéolos dos m2-4; processo angular
DGM 636-M)		
MCT 2376- M (=	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com p3, m1-3; alvéolo do p2 e alvéolos do m4
DGM 637-M)		
MCT 2377- M (=	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com p3, m1-2; alvéolos dos m3-4
DGM 638-M)		
MCT 2378- M (=	<i>Epidolops ameghinoi</i>	dentário esquerdo com m1-3 e alvéolos do m4; processo angular presente
DGM 639-M)		
MCT 2379- M (=	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com m2 e alvéolos dos p2-3, m1 e m3-4
DGM 640-M)		
MCT 2380- M (=	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com m1-2 e alvéolos dos m3-4
DGM 641-M)		
MCT 2382- M (=	<i>Patene simpsoni</i>	fragmento de maxila esquerda com M2, alvéolos dos M1 e M3-4; arco zigomático com parte anterior preservada

DGM 643-M)		
MCT 2383- M (=	<i>Gaylordia</i>	dentário direito com m1-2, m4 e alvéolos do m3; côndilo mandibular e processo
DGM 644-M)	<i>mater</i>	angular presentes
MCT 2384- M (=	<i>Gaylordia</i>	dentário esquerdo com p3, m1 (desgastado), m2 (parcialmente desgastado), m4,
DGM 645-M)	<i>mater</i>	raízes e fragmento do m3
MCT 2385- M (=	<i>Gaylordia</i>	dentário esquerdo com m1-2 (desgastados), e alvéolos dos m3-4; parte do
DGM 646-M)	<i>macrocyndonta</i>	processo coronoide
MCT 2386- M (=	<i>Gaylordia</i>	dentário direito incompleto com m3 e alvéolos dos m2 e m4
DGM 647-M)	<i>mater</i>	
MCT 2387- M (=	<i>Gaylordia</i>	dentário direito com p3-m1
DGM 648-M)	<i>mater</i>	
MCT 2764- M	<i>Diogenesia</i> sp. nov.	M1 direito
MCT 2765- M	<i>Diogenesia</i> sp. nov.	M2 esquerdo
MCT 2766- M	<i>Diogenesia</i> sp. nov.	M2 direito, quebrado em duas partes (paracone, metacone e plataforma estilar) e protocone

MCT 2767- M	<i>Diogenesia</i> sp. nov.	M3 direito
MCT 2768- M	<i>Didelphopsi</i> <i>s cabrerai</i>	M1 direito
MCT 2769- M	<i>Protodidelp</i> <i>his</i> <i>mastodontoi</i> <i>des</i>	M2 esquerdo
MCT 2770- M	<i>Didelphopsi</i> <i>s sp. nov.</i>	m1 esquerdo com raiz anterior preservada
MCT 2771- M	<i>Didelphopsi</i> <i>s sp. nov.</i>	m2 direito com parte da raiz posterior preservada
MCT 2772- M	<i>Didelphopsi</i> <i>s cabrerai</i>	m4 esquerdo
MCT 2773- M	<i>Didelphopsi</i> <i>s sp. nov.</i>	m4 esquerdo
MCT 2774- M	<i>Gaylordia</i> <i>mater</i>	m3 direito
MCT 2775- M	<i>Gaylordia</i> <i>mater</i>	m3 direito
MCT 2776- M	<i>Gaylordia</i> <i>mater</i>	m3 direito
MCT 2777- M	<i>Gaylordia</i> <i>mater</i>	M1 direito

MCT 2778- M	<i>Gaylordia mater</i>	M2 esquerdo
MCT 2779- M	<i>Gaylordia mater</i>	M2 esquerdo
MCT 2780- M	<i>Gaylordia mater</i>	M3 esquerdo
MCT 2781- M	<i>Gaylordia mater</i>	M1 direito incompleto
MCT 2782- M	<i>Guggenhei mia crocheti</i>	m3 esquerdo
MCT 2783- M	<i>Guggenhei mia crocheti</i>	M1 esquerdo
MCT 2784- M	<i>Itaboraidelp hys camposi</i>	m3 esquerdo com raiz posterior
MCT 2785- M	<i>Itaboraidelp hys camposi</i>	m4 direito
MCT 2786- M	<i>Didelphopsi s cabrerai</i>	M1 direito
MCT 2787- M	<i>Itaboraidelp hys camposi</i>	M1 direito
MCT 2788- M	<i>Itaboraidelp hys camposi</i>	M2 esquerdo

MCT 2789- M	<i>Itaboraidelp hys camposi</i>	M2 esquerdo
MCT 2790- M	<i>Itaboraidelp hys camposi</i>	M3 esquerdo
MCT 2791- M	Peradectoid ea gen. nov. sp. 1	M1 direito
MCT 2792- M	Peradectoid ea gen. nov. sp. 1	M1 esquerdo
MCT 2793- M	Peradectoid ea gen. nov. sp. 1	M1 direito
MCT 2794- M	Peradectoid ea gen. nov. sp. 1	M2 direito
MCT 2795- M	Peradectoid ea gen. nov. sp. 1	M2 direito
MCT 2796- M	Peradectoid ea gen. nov. sp. 1	M2 direito
MCT 2797- M	Peradectoid ea gen. nov. sp. 1	M3 direito
MCT 2798- M	<i>Austropedio mys marshalli</i>	M1 esquerdo
MCT 2799- M	<i>Austropedio mys marshalli</i>	M3 esquerdo

MCT 2800- M	<i>Austropedio mys marshalli</i>	M4 direito
MCT 2801- M	<i>Itaboraidelp hys camposi</i>	m2 direito
MCT 2802- M	<i>Itaboraidelp hys camposi</i>	m1 direito
MCT 2803- M	<i>Didelphopsi s cabrerai</i>	m2 direito
MCT 2804- M	<i>Itaboraidelp hys camposi</i>	m2 direito
MCT 2805- M	<i>Itaboraidelp hys camposi</i>	m2 direito
MCT 2806- M	<i>Itaboraidelp hys camposi</i>	m2 direito
MCT 2807- M	<i>Itaboraidelp hys camposi</i>	m3 esquerdo
MCT 2808- M	<i>Itaboraidelp hys camposi</i>	m3 direito
MCT 2809- M	<i>Itaboraidelp hys camposi</i>	m3 direito
MCT 2810- M	Peradectoid ea gen. nov. sp. 1	M3 direito quebrado (plataforma estilar, paracone e metacone)

MCT 2811- M	<i>Didelphopsis cabrerai</i>	m4 direito com raízes preservadas
MCT 2812- M	<i>Itaboraidelp hys camposi</i>	M2 esquerdo
MCT 2813- M	<i>Itaboraidelp hys camposi</i>	M3 direito com raízes parcialmente preservadas
MCT 2814- M	<i>Itaboraidelp hys camposi</i>	M4 direito com raízes parcialmente preservadas
MCT 2815- M	<i>Minusculod elphis modicum</i>	M3 direito
MCT 2816- M	<i>Mirandathe rium sp. nov.</i>	M3 direito
MCT 2817- M	<i>Protodidelp his mastodontoi des</i>	m2 esquerdo com raiz posterior
MCT 2818- M	<i>Protodidelp his mastodontoi des</i>	m1 esquerdo
MCT 2819- M	<i>Protodidelp his mastodontoi des</i>	m2 esquerdo
MCT 2820- M	<i>Carolopaul acoutoia itaboraiensi s</i>	DP3 direito completo

MCT 2821- M	<i>Carolopaul acoutoia itaboraiensi s</i>	M2 esquerdo (quebrado em duas partes)
MCT 2822- M	<i>Carolopaul acoutoia itaboraiensi s</i>	M2 esquerdo
MCT 2823- M	<i>Carolopaul acoutoia itaboraiensi s</i>	M3 direito
MCT 2824- M	<i>Carolopaul acoutoia itaboraiensi s</i>	M3 direito
MCT 2825- M	<i>Carolopaul acoutoia itaboraiensi s</i>	M3 direito
MCT 2826- M	<i>Carolopaul acoutoia itaboraiensi s</i>	M3 direito
MCT 2827- M	<i>Protodidelp his vanzolinii</i>	m2 direito
MCT 2828- M	<i>Protodidelp his vanzolinii</i>	m3 direito
MCT 2829- M	<i>Diogenesia sp. nov. / Derorhynch us sp. nov.</i>	M2 esquerdo

MCT 2830- M (!)	<i>Eobrasilia coutoi</i>	M2 direito
MCT 4386- M	<i>Austropedio mys marshalli</i>	DP3 esquerdo
MCT 4387- M (^)	<i>Bergqvisthe rium primigenia</i>	m1 esquerdo
MCT. M.4425	<i>Diogenesia sp. nov.</i>	m3 esquerdo
MCT. M.4429	<i>Mirandathe rium sp. nov.</i>	talônido de m1 direito com raiz
MCT. M.4432	<i>Peradectoid ea gen. nov. sp. 1</i>	m2 esquerdo
MCT. M.4433	<i>Monodelpho psis sp. nov.</i>	m2 direito incompleto, faltando o paracônido
MCT. M.4434	<i>Diogenesia sp. nov.</i>	M2 esquerdo
MCT. M.4435	<i>Carolopaul acoutoia itaboraiensi s</i>	Fragmento de maxila direita com M3 e alvéolo posterior do M2 (dente está solto)
MCT. M4436	<i>Peradectoid ea gen. nov. sp. 1</i>	Fragmento de maxila direita com M3, alvéolos do M2 e parte do arco zigomático
MCT. M.4438	<i>Itaboraidelp hys camposi</i>	DP3 esquerdo
MCT. M.4439	<i>Epidolops ameghinoi</i>	DP3 direito

<i>Carolopaul</i>		
MCT.	<i>acoutoia</i>	M3 direito
M.4440	<i>itaboraiensi</i> s	
<i>Carolopaul</i>		
MCT.	<i>acoutoia</i>	M2 direito
M.4441	<i>itaboraiensi</i> s	
MCT.	<i>Marmosopsi</i>	m2 direito
M.4442	<i>s juradoi</i>	
MCT.	<i>Diogenesia</i>	M1 direito
M.4443	sp. nov.	
MCT.	<i>Diogenesia</i>	M1 direito
M.4444	sp. nov.	
MCT.	<i>Marmosopsi</i>	fragmento de dentário direito com m4 e alvéolos do m3
M.4448	<i>s juradoi</i>	
MCT.	<i>Eobrasilia</i>	p3 esquerdo com coroa completamente desgastada
M.4449	<i>bergqvistae</i>	
MCT.	<i>Diogenesia</i>	maxila esquerda com M2-3 e alvéolo anterior do M4
M.4455	sp. nov.	
MCT.	<i>Didelphopsi</i>	m4 esquerdo faltando a porção lingual do talônido
M.4456	s sp. nov.	
MCT.	<i>Epidolops</i>	fragmento de maxila direita com M1-2 e porção anterior do arco zigomático
M.4457	<i>ameghinoi</i>	
MCT.	<i>Epidolops</i>	m2 direito
M.4458	<i>ameghinoi</i>	
MCT.	<i>Epidolops</i>	M1 direito com um raiz preservada
M.4459	<i>ameghinoi</i>	
MCT.	<i>Diogenesia</i>	dentário esquerdo com alvéolos dos m2-4 (porção lingual danificada)
M.4460	sp. nov.	
MCT.	<i>Diogenesia</i>	talônido de m2 direito
M.4461	sp. nov.	

MCT. M.4463	<i>Epidolops ameghinoi</i>	dentário esquerdo edentado com alvéolo posterior do p3 (anterior parcialmente preservado) e alvéolos dos m1-4
MCT. M.4466	<i>Eobrasilia bergqvistae</i>	coroa de M2 esquerdo com plataforma estilar, paracone, metacone e paracônulo preservados
MCT. M.4467	<i>Carolopaul acoutoia itaboraiensi</i> s	M3 esquerdo
MCT. M.4468	<i>Diogenesia</i> sp. nov.	M3 esquerdo
MCT. M.4469	<i>Peradectoid</i> ea gen. nov. sp. 1	M1 direito
MCT. M.4470	<i>Peradectoid</i> ea gen. nov. sp. 1	m4 esquerdo com raízes parcialmente preservadas
MCT. M.4471	<i>Carolopaul acoutoia itaboraiensi</i> s	m4 esquerdo com raiz anterior preservada
MCT. M.4472	<i>Diogenesia</i> sp. nov.	M1 direito
MCT. M.4473	<i>Bergqvisthe rium primigenia</i>	m4 esquerdo raízes preservadas
MCT. M.4474	<i>Marmosopsi</i> s sp. nov.	m4 esquerdo com raízes preservadas
MCT. M.4475	<i>Diogenesia</i> sp. nov.	coroa de M2 direito sem o parástilo
MCT. M.4476	<i>Bergqvisthe rium primigenia</i>	coroa de m1 direito

	<i>Minusculod</i>	
	<i>elphis</i>	
MCT.	<i>modicum</i> /	M1 ou M2 direito com plataforma estilar, paracone e metacone
M.4477	cf.	
	<i>Armintodelp</i>	
	<i>hys</i> sp.	
	<i>Bergqvisthe</i>	
MCT.	<i>rium</i>	m3 direito com raízes preservadas
M.4478	<i>primigenia</i>	
	<i>Indet.</i>	
MCT.		talônido de m3 direito com raiz posterior
M.4479		
	<i>Carolopaul</i>	
MCT.	<i>acoutoia</i>	M2 esquerdo com raízes preservadas
M.4480	<i>itaboraiensi</i>	
	<i>s</i>	
	<i>Diogenesia</i>	
MCT.	sp. nov.	talônido de m2 esquerdo com raiz posterior
M.4481		
	<i>Carolopaul</i>	
MCT.	<i>acoutoia</i>	coroa de m1 direito
M.4482	<i>itaboraiensi</i>	
	<i>s</i>	
	<i>Marmosopsi</i>	
MCT.	s sp. nov.	m1 direito com raiz posterior
M.4483		
	<i>Indet.</i>	
MCT.		trigônido de m1 direito
M.4484		
	<i>Peradectoid</i>	
MCT.	ea gen. nov.	m3 esquerdo
M.4485	sp. 1	
	<i>Marmosopsi</i>	
MCT.	s sp. nov.	m2 direito
M.4486		
	<i>Carolopaul</i>	
MCT.	<i>acoutoia</i>	M2 esquerdo
M.4487	<i>itaboraiensi</i>	
	<i>s</i>	

MCT. M.4488	Peradectoid ea gen. nov. sp. 1	m2 direito
MCT. M.4489	<i>Diogenesia</i> sp. nov.	M1 direito
MCT. M.4490	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	M2 direito
MCT. M.4491	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	M4 direito
MCT. M.4492	<i>Diogenesia</i> sp. nov.	M3 esquerdo sem plataforma estilar anterior
MCT. M.4493	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	M3 esquerdo
MCT. M.4494	<i>Gaylordia</i> <i>mater</i>	m3 esquerdo
MCT. M.4495	<i>Diogenesia</i> sp. nov.	M3 esquerdo
MCT. M.4496	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	M1 direito
MCT. M.4497	<i>Gaylordia</i> <i>mater</i>	m2 direito
MCT. M.4498	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	M1 direito

MCT. M.4499	<i>Gaylordia</i> <i>mater</i>	m3 direito
MCT. M.4500	<i>Diogenesia</i> sp. nov.	M2 direito
MCT. M.4501	<i>Diogenesia</i> sp. nov.	M1 esquerdo
MCT. M.4502	Indet.	trigônido de m3 esquerdo
MCT. M.4503	<i>Diogenesia</i> sp. nov.	M1 direito
MCT. M.4504	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	M1 direito (quebrado em duas partes)
MCT. M.4505	<i>Diogenesia</i> sp. nov.	M2 esquerdo
MCT. M.4506	Peradectoid ea gen. nov. sp. 1	m1 esquerdo
MCT. M.4507	Indet.	trigônido de m1 esquerdo
MCT. M.4508	<i>Diogenesia</i> sp. nov.	M2 direito
MCT. M.4509	<i>Diogenesia</i> sp. nov.	M3 esquerdo
MCT. M.4510	<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> s	m2 direito
MCT. M.4511	<i>Marmosopsi</i> s sp. nov.	m3 esquerdo

	<i>Carolopaul</i>	
MCT.	<i>acoutoia</i>	m3 direito
M.4512	<i>itaboraiensi</i>	
	s	
	<i>Carolopaul</i>	
MCT.	<i>acoutoia</i>	M3 esquerdo
M.4513	<i>itaboraiensi</i>	
	s	
	<i>Austropedio</i>	
MCT.	<i>mys</i>	M1 esquerdo
M.4514	<i>marshalli</i>	
MCT.	<i>Diogenesia</i>	M2 esquerdo
M.4515	sp. nov.	
	<i>Carolopaul</i>	
MCT.	<i>acoutoia</i>	M2 esquerdo
M.4516	<i>itaboraiensi</i>	
	s	
MCT.	<i>Eobrasilia</i>	m3 direito com raiz posterior preservada
M.4519	<i>bergqvistae</i>	
MCT.	Indet.	p2 ou p3 direito
M.4520		
MCT.	Indet.	P2 direito
M.4522		
	<i>Carolopaul</i>	
MCT.	<i>acoutoia</i>	Fragmento de maxila esquerda com M1-2 e alvéolos parcialmente preservados do M3
M.4523	<i>itaboraiensi</i>	
	s	
MCT.	cf.	coroa de M3 esquerdo com protocone danificado (deslocado de sua posição original)
M.4524	<i>Guggenheimia</i> sp.	
MCT.	Indet.	fragmento de dentário com alvéolo posterior do m3, alvéolos do m4 e parte do processo coronoide
M.4525		

MCT. M.4526	Indet.	trigônido de um m2 esquerdo sem o paracônido
MCT. M.4527	Peradectoid ea gen. nov. sp. 1	M3 direito parcialmente preservado com plataforma estilar, paracone e metacone
MCT. M.4528	Indet.	trigônido de m1 esquerdo
MCT. M.4529	Peradectoid ea gen. nov. sp. 1	fragmento de dentário esquerdo com m4 e alvéolos parcialmente preservados do m3
MCT. M.4530	<i>Bergqvisthe rium primigenia</i>	m2 direito
MCT. M.4533	<i>Itaboraaidelp hys camposi</i>	talônido de m2 direito com parte distal do trigônido e raíz posterior
MCT. M.4534	<i>Epidolops ameghinoi</i>	P3 direito
MCT. M.4535	<i>Epidolops ameghinoi</i>	P3 esquerdo
MCT. M.4536	Indet.	trigônido de m2 direito
MCT. M.4537	<i>Gashternia carioca</i>	dentário direito quase completo (processo coronoide danificado) com m3 e alvéolos dos i2-4, c, p1-3, m1-2 e m4
MCT. M.4538	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com m1-3 e alvéolos do p3 e m4; base do processo coronoide quebrada
MCT. M.4539	<i>Epidolops ameghinoi</i>	dentário quase completo (processo coronoide quebrado) deformado por sedimento, mostrando apenas a parte mesial do p3 fraturado
MCT. M.4541	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com m2, alvéolos do m1 e m3
MCT. M.4542	<i>Patene simpsoni</i>	fragmento de maxila direita edentada com alvéolos dos M1 (parcialmente preservados), M2-4

MCT. M.4543	<i>Didelphopsis s cabrerai</i>	M4 esquerdo incompleto com plataforma estilar, paracone e metacone
MCT. M.4544	<i>Patene simpsoni</i>	trigônido de m4 esquerdo com raiz
MCT. M.4545	<i>Patene simpsoni</i>	trigônido de m2 esquerdo com raiz
MCT. M.4546	<i>Epidolops ameghinoi</i>	dentário esquerdo com alvéolos parciais dos m1-2 e alvéolos dos m3-4
MCT. M.4547	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com i2-4, c, p2-3 e m1
MCT. M.4548	<i>Epidolops ameghinoi</i>	p3 direito com raiz anterior
MCT. M.4549	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com M1 e alvéolo mesio-labial do M2
MCT. M.4550	<i>Epidolops ameghinoi</i>	P3 direito com raízes quebradas
MCT. M.4551	<i>Epidolops ameghinoi</i>	p3 esquerdo com raiz anterior
MCT. M.4552	<i>Epidolops ameghinoi</i>	P3 esquerdo com raiz anterior e posteriores quebradas
MCT. M.4553	<i>Epidolops ameghinoi</i>	m3 esquerdo
MCT. M.4554	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com alvéolos dos m2-4
MCT. M.4555	<i>Epidolops ameghinoi</i>	m1 direito com hipocônido quebrado
MCT. M.4556	<i>Epidolops ameghinoi</i>	fragmento parcial de dentário direito
MCT. M.4557	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com alvéolos do P3 e M1-2

MCT. M.4558	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com alvéolos dos m1-4
MCT. M.4559	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com alvéolos parcialmente preservados do m3 e alvéolo do m4
MCT. M.4560	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com alvéolos dos P3 e M1-3
MCT. M.4561	<i>Epidolops ameghinoi</i>	dentário esquerdo incompleto com alvéolos parciais do m1 e alvéolos dos m2-4; processo coronoide parcialmente preservado
MCT. M.4562	<i>Epidolops ameghinoi</i>	dentário esquerdo incompleto com alvéolos dos p3 e m1-4
MCT. M.4563	<i>Epidolops ameghinoi</i>	dentário direito com alvéolos dos i2-4, c, p2-3, m1-4 e processo coronoide incompleto
MCT. M.4564	<i>Epidolops ameghinoi</i>	dentário direito com alvéolos parciais do p3, e alvéolos dos m1-4
MCT. M.4565	<i>Epidolops ameghinoi</i>	dentário esquerdo incompleto com alvéolos do p3 e m1-4; processo coronoide parcialmente preservado
MCT. M.4566	<i>Epidolops ameghinoi</i>	dentário direito incompleto com raízes dos m1-4 e resquícios dos alvéolos do p3
MCT. M.4567	<i>Epidolops ameghinoi</i>	dentário direito com alvéolos dos i2-4, c, p2-3, m1-4 e processo coronoide incompleto
MCT. M.4568	<i>Epidolops ameghinoi</i>	fragmento de dentário direito com p3 e alvéolo do p2
MCT. M.4569	<i>Epidolops ameghinoi</i>	dentário esquerdo quase completo com sedimentos, p3, m1
MCT. M.4570	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com alvéolos dos P3, M1-2 e alvéolo lingual do M3
MCT. M.4571	cf. <i>Guggenheimia</i> sp.	trigônido esquerdo de m1
MCT. M.4574	<i>Marmosopsi</i> s sp. nov.	m3 esquerdo

MCT. M.4576	cf. <i>Nemolestes</i> sp.	canino inferior esquerdo
MCT. M. (s/n) 1	<i>Marmosops</i> <i>s juradoi</i>	M3 esquerdo
MCT. M. (s/n) 2	<i>Epidolops</i> <i>ameghinoi</i>	m3 esquerdo com raízes preservadas
MCT. M. (s/n) 3	Indet.	dp3 direito com parte das raízes preservadas

**Númer
o de
Coleção
o
(petros
o)**

Táxon

Descrição do material

MCT. M.4462	cf. <i>Armintodelphys</i> sp.	Petroso de metatério (PtVII)
MCT. M.4521	cf. <i>Armintodelphys</i> sp.	Petroso de metatério (PtVII)
MCT. M.4531	<i>Epidolops</i> <i>ameghinoi</i>	Petroso de metatério (PtII)
MCT. M.4540	Derorhynchi dae ou Peradectoid ea	Petroso de metatério (PtVI ou PtNovo)

**Númer
o de
Coleção**

Táxon

Descrição do material

o (pós-crânio)		
DGM 921(c)-M	<i>Minusculod elphis modicum</i>	Fêmur esquerdo completo
MCT. M.4532	?	Fêmur direito completo
Número de Coleção o (n identificado)	Táxon	Descrição do material
MCT. M.326 (?)	<i>Patene simpsoni</i>	osso occipital
MCT. M.365 (?)	?	?
MCT. M.658 (?)	<i>Patene simpsoni</i>	dp3 ou m1 danificado em sua parte disto-lingual (faltando parte do entocônido e hipoconulido)
Ungula dos (in Metath eria)	Táxon	Descrição do material
MCT. M.653	<i>Asmithwood wardia scotti</i>	fragmento de dentário esquerdo com dp3? ou dp4?
MCT. M.797	<i>Miguelsoria parayirunho r? e Protoliptern a</i>	x4 pré-molares decíduos (DP1 ou DP2?) (x2 taxa - x1 maior [amarelo] e x3 menores [pretos])

	<i>ellipsodonto</i>	
	<i>ides?</i>	
MCT.	<i>Ricardocifel</i>	
M.2866	<i>lia</i>	fragmento de dentário com p4 em erupção
-M	<i>protocenica</i>	
	Ungulado	
	(<i>Tetragonos</i>	
MCT.	<i>tylops</i>	dp3 ou dp4 com coroa, mas sem raízes (espaço interno "oco") de um ungulado
M.2826	<i>apsthomasi</i>	muito grande
	ou	
	Pyrotheria?)	

Ungula dos (n Metath eria)	Táxon	Descrição do material
MCT. M.4464		
MCT. M.4465		
	<i>Protoliptern</i>	
MCT. M.4517	<i>a</i> <i>ellipsodonto</i>	
	<i>ides</i>	
	<i>Protoliptern</i>	
MCT. M.4518	<i>a</i> <i>ellipsodonto</i>	
	<i>ides</i>	
MCT. M.4573		
MCT. M.4575		
Metath eria (n	Táxon	

Itaborai)		
MCT. M.432	<i>Thylamys?</i>	fragmento de dentário com m1-3 e alvéolos do m4
Número de Coleção	Táxon	Descrição do material
MN 1331-V (^)	<i>Patene simpsoni</i>	fragmento de maxila direita com P3-M4
MN 1332-V	<i>Patene simpsoni</i>	M4 esquerdo
MN 1335-V	<i>Patene simpsoni</i>	M2 direito incompleto
MN 1336-V	<i>Patene simpsoni</i>	trigônido de m3 direito
MN 1337-V	<i>Patene simpsoni</i>	trigônido de m4 esquerdo
MN 1338-V	<i>Patene simpsoni</i>	trigônido de m4 direito
MN 1339-V	<i>Patene simpsoni</i>	trigônido de m4 direito
MN 1340-V	<i>Patene simpsoni</i>	trigônido de m3 direito
MN 1341-V	<i>Patene simpsoni</i>	trigônido de m3 direito
MN 1342-V	<i>Patene simpsoni</i>	trigônido de m1 direito
MN 1343-V	<i>Patene simpsoni</i>	trigônido de m2 direito, sem metacônido

MN 1344-V	cf. <i>Nemolestes</i> sp.	m4 direito
MN 1345-V	<i>Didelphopsi</i> s sp. nov.	M4 esquerdo
MN 1346-V	<i>Didelphopsi</i> s sp. nov.	m3 esquerdo
MN 1347-V	<i>Didelphopsi</i> s sp. nov.	m4 direito
MN 1348-V (^)	<i>Derorhynch</i> <i>us</i> <i>singularis</i>	dentário direito quase completo, com raízes dos i1-2, alvéolos dos i3-4 e c, raízes dos p1-m1, e m2-4 completos
MN 1350-V (^)	<i>Bobbschaeff</i> <i>eria</i> <i>fluminensis</i>	dentário esquerdo incompleto com p2-3 e m3-4 completos, raízes do p1, m2, e alvéolos dos i1-3, c e m1
MN 1351-V (!)	<i>Patene</i> <i>simpsoni</i>	dentário direito fragmentado com p3-m2, trigônido de m3, alvéolos do m4 e p2
MN 1352-V	<i>Patene</i> <i>simpsoni</i>	trigônido de m2 direito
MN 1353-V	<i>Patene</i> <i>simpsoni</i>	m2 esquerdo com raízes preservadas
MN 1354-V	<i>Patene</i> <i>simpsoni</i>	m3 esquerdo
MN 1355-V	<i>Gaylordia</i> <i>macrocynod</i> <i>onta</i>	dentário direito quase completo com alvéolos do p1 e p2-m4 completos
MN 1357-V	<i>Gaylordia</i> <i>macrocynod</i> <i>onta</i>	dentário esquerdo com p3 e m3, e alvéolos dos p1-2, m1-2 e m4

MN 1358-V	<i>Gaylordia macrocynodonta</i>	dentário direito com p3, alvéolos dos p1-2 e do m1-4
MN 1359-V (^)	<i>Mirandatherium alipioi</i>	dentário direito incompleto com p2-m2, alvéolos do p1, m3, e parte do alvéolo anterior do m4
MN 1360-V	<i>Bobbschaefferia sp. nov.</i>	m2 esquerdo com protocônido pouco preservado
MN 1362-V	<i>Bergqvistherium primigenia</i>	dentário direito incompleto com m2-3
MN 1363-V	<i>Bobbschaefferia sp. nov.</i>	dentário direito incompleto com m3 e raiz anterior e talônido do m2
MN 1364-V	<i>Mirandatherium alipioi</i>	m2 direito
MN 1365-V (^)	<i>Monodelphopsis travassosi</i>	fragmento de dentário esquerdo com p3-m1
MN 1366-V	<i>Gaylordia macrocynodonta</i>	dentário esquerdo com m1, alvéolos dos p2-3 e m2-4
MN 1367-V	<i>Marmosopsis juradoi</i>	fragmento de dentário direito com m4
MN 1368-V	<i>Carolopaulacoutoia itaboraiensis</i>	fragmento de dentário direito com m4
MN 1371-V	<i>Protodidelphis vanzolinii</i>	m1 esquerdo
MN 1372-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto

MN 1373-V	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com m1-3, e alvéolo do m4
MN 1374-V	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com m1-2, e alvéolos dos m3-4
MN 1376-V	<i>Epidolops ameghinoi</i>	dentário direito fragmentado sem dentes preservados com alvéolos do m1-4
MN 1377-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1378-V	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com m1-3
MN 1381-V	<i>Epidolops ameghinoi</i>	dentário direito com p2-m2 e raízes do m3-4
MN 1382-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1383-V	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m1-3 e alvéolo do m4
MN 1384-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1385-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1386-V	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado e sem dentes preservados com alvéolos do m1-4
MN 1387-V	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m1-2 e raízes do c-p3
MN 1388-V	<i>Epidolops ameghinoi</i>	dentário direito com alvéolos do c-m4

MN 1389-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1390-V	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p3 e alvéolos do i1-c e p2
MN 1392-V	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m1-2 e alvéolos do m3-4
MN 1394-V	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com m1-3 e alvéolos do m4
MN 1395-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1397-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1398-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1399-V (*)	<i>Epidolops ameghinoi</i>	dentário incompleto
MN 1400-V (!)	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p2-m2
MN 1401-V	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p2-3
MN 1402-V	<i>Epidolops ameghinoi</i>	Fragmento de dentário esquerdo sem dentes e com alvéolos dos m1-4
MN 1403-V	<i>Epidolops ameghinoi</i>	Fragmento de dentário esquerdo sem dentes e com alvéolos dos m1-4
MN 1405-V	<i>Epidolops ameghinoi</i>	Fragmento de dentário esquerdo sem dentes e com alvéolos dos m1-4 e raízes do p3

MN 1407-V	<i>Epidolops ameghinoi</i>	fragmento de maxilar direito com P3-M2
MN 1408-V (*)	<i>Epidolops ameghinoi</i>	maxila
MN 1409-V	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com P2 e M1-2, e raízes do P3
MN 1410-V	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3-M1
MN 1411-V	<i>Epidolops ameghinoi</i>	fragmento com maxila direita com P3 e alvéolos dos M1-2
MN 1413-V (*)	<i>Epidolops ameghinoi</i>	maxila
MN 1414-V (*)	<i>Epidolops ameghinoi</i>	maxila
MN 1415-V	<i>Epidolops ameghinoi</i>	fragmento de maxila esquerda com M2
MN 1416-V	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com M1-2
MN 1417-V	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3 e M2 muito danificado
MN 1418-V	<i>Epidolops ameghinoi</i>	P3 direito incompleto
MN 1419-V	<i>Epidolops ameghinoi</i>	P3 direito incompleto
MN 1420-V	<i>Epidolops ameghinoi</i>	P3 direito incompleto
MN 1421-V	<i>Epidolops ameghinoi</i>	M2 esquerdo

MN	<i>Epidolops</i>	
1422-V	<i>ameghinoi</i>	M1 direito
MN	<i>Epidolops</i>	
1423-V	<i>ameghinoi</i>	parte anterior de M1 esquerdo
MN	<i>Epidolops</i>	
1424-V	<i>ameghinoi</i>	incisivo inferior (i2)
MN	<i>Patene</i>	
1425-V	<i>simpsoni</i>	p3 direito
MN	<i>Didelphopsi</i>	
1426-V	<i>s sp. nov.</i>	M1 esquerdo
MN	<i>Protodidelp</i>	
1427-V	<i>his</i> <i>vanzolinii</i>	M4 direito
MN	<i>Patene</i>	
1428-V	<i>simpsoni</i>	trigônido de m4 direito
MN 1429-V (^)	<i>Didelphopsi</i> <i>s cabrerai</i>	maxilar esquerdo quase completo, com parte dos alvéolos do C e P3, raízes dos P1-2, e M1-4 presentes
MN	<i>Monodelpho</i>	
2340-V	<i>psis</i>	dentário direito quase completo, mas fragmentado em duas partes, estando a anterior com p1-m2 e alvéolos dos i2-c; e parte posterior com alvéolos do m3 e
+ MN	<i>travassosi</i>	m4 completo
2351-V		
MN	<i>Itaboraaidelp</i>	
2341-V	<i>hys camposi</i>	m3 esquerdo
MN	<i>Minusculod</i>	
2342-V (^)	<i>elphis</i> <i>minimus</i>	dentário esquerdo com p1-2 e m2-4 completos, raízes do p3, e talônido do m1
MN	<i>Marmosopsi</i>	
2343-V (^)	<i>s juradoi</i>	dentário direito quase completo com p2-m4
MN	<i>Marmosopsi</i>	
2344-V	<i>s juradoi</i>	dentário esquerdo incompleto com p2-m3 completos e talônido do m4

MN 2345-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com m1-2, m4 e raízes do m3
MN 2346-V	<i>Marmosopsi s juradoi</i>	dentário direito com m2-3, alvéolo do c, e alvéolos do p1-m1 e m4
MN 2347-V	<i>Derorhynch idae gen. nov.</i>	parte posterior de dentário esquerdo com m4, alvéolos do m3, e processo coronoide e côndilo mandibular presente
MN 2348-V	<i>Marmosopsi s juradoi</i>	dentário esquerdo incompleto com m3-4
MN 2349-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com c-p3, e raízes do m1
MN 2350-V	<i>Marmosopsi s juradoi</i>	dentário direito quase completo com p3-m4, e alvéolos do c e p1
MN 2352-V	<i>Derorhynch idae gen. nov.</i>	maxilar esquerdo com M1 e alvéolos dos M2-3
MN 2353-V	<i>Carolopaul acoutoia itaboraiensi s</i>	dentário direito fragmentado com m3 e alvéolos dos m2 e m4
MN 2354-V	<i>Derorhynch idae gen. nov.</i>	dentário esquerdo incompleto com m1-4 e p3 sem a coroa preservada (apenas a base da mesma e as raízes)
MN 2355-V	<i>Mirandathe rium alipioi</i>	dentário esquerdo incompleto com p3 não irrompido e com m1 completo, alvéolos dos i, c, m2, e alvéolo anterior do m3
MN 2356-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com m1-4
MN 2357-V	<i>Carolopaul acoutoia sp. nov.</i>	dentário direito incompleto com p2-3 e m4, limite posterior do alvéolo do c, alvéolo posterior do p1 e alvéolos dos m1-3

MN 2359-V (*)	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com p3-m3
MN 2360-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com trigonido do m2 e m3 completo
MN 2470-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com p2-m3
MN 2471-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com p1-2 e m1
MN 2472-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com p2 e m1
MN 2473-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com m2
MN 2474-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com m1
MN 2475-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com raízes do m3 e m4 presente
MN 2476-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com m4
MN 2477-V	<i>Marmosopsi s juradoi</i>	dentário direito incompleto com m1
MN 2478-V	<i>Marmosopsi s juradoi</i>	maxila direita incompleta com M1-2
MN 2479-V	<i>Marmosopsi s juradoi</i>	M3 direito
MN 2480-V (*)	<i>Marmosopsi s juradoi</i>	fragmento de maxila esquerda com M1-3
MN 2481-V	<i>Carolopaul acoutoia sp. nov.</i>	maxila esquerda incompleta com M1-2 e alvéolos do P3 e M3

MN	<i>Marmosopsi</i>	
2482-V	<i>s juradoi</i>	maxila direita incompleta com M1-2
MN	<i>Marmosopsi</i>	
2483-V	<i>s juradoi</i>	maxila direita incompleta com M1-2, alvéolos do M3 e M4
MN	<i>Marmosopsi</i>	
2484-V	<i>s juradoi</i>	dentário esquerdo incompleto com m1-3
MN	<i>Marmosopsi</i>	
2485-V	<i>s juradoi</i>	dentário esquerdo incompleto com p2-m3
MN	<i>Marmosopsi</i>	
2486-V	<i>s juradoi</i>	dentário esquerdo incompleto com p2 e m2
MN	<i>Gaylordia</i>	
2487-V	<i>doelloi</i>	dentário esquerdo quase completo com m3-4 e alvéolos do p1-m2
MN	<i>Epidolops</i>	
2492-V	<i>ameghinoi</i>	dentário direito quase completo com p2-m4 completos
MN	<i>Marmosopsi</i>	
2495-V	<i>s juradoi</i>	dentário esquerdo incompleto com m2-3
MN	<i>Marmosopsi</i>	
2496-V	<i>s juradoi</i>	dentário esquerdo incompleto com m1-2 e trigônido do m3
MN	<i>Marmosopsi</i>	
2497-V	<i>s juradoi</i>	dentário esquerdo incompleto com m1-2
MN	<i>Marmosopsi</i>	
2498-V	<i>s juradoi</i>	dentário esquerdo incompleto com p2-m2
MN	<i>Marmosopsi</i>	
2499-V	<i>s juradoi</i>	dentário esquerdo incompleto com p3 e m3 presentes, alvéolos dos i, c, p1-2, m1-2 e m4
MN	<i>Marmosopsi</i>	
2500-V	<i>s juradoi</i>	dentário esquerdo incompleto com talônido do m2 e com m3-4 presentes
MN	<i>Marmosopsi</i>	
2501-V	<i>s juradoi</i>	dentário esquerdo incompleto com m3 e alvéolos do m4
MN	<i>Marmosopsi</i>	
2502-V	<i>s juradoi</i>	dentário esquerdo incompleto com o talônido do p1 e com p2-3 completos

MN 2503-V	<i>Minusculod elphis minimus</i>	dentário direito com alvéolos dos i2-c e m2, e com p1-3 e m2-4
MN 2504-V (!)	<i>Gaylordia doelloi</i>	dentário esquerdo incompleto com m2, e alvéolos do m1 e m3-4
MN 2506-V	<i>Derorhynch idae gen. nov.</i>	maxilar esquerdo incompleto com M1-3 e alvéolos do P3
MN 2878(a) -V	<i>Itaboraidelp hys camposi</i>	M3 direito
MN 2878(b))-V	<i>Didelphopsi s cabrerai</i>	M2 direito
MN 2878(c) -V	<i>Didelphopsi s cabrerai</i>	p3 esquerdo muito desgastado
MN 2879-V	<i>Epidolops ameghinoi</i>	maxilar direito com P3 e alvéolos C-P2 e M1-2. Pré-orbital forâmen pode ser identificado
MN 2880-V	<i>Epidolops ameghinoi</i>	dentário direito com p3-m3 completo, alvéolos dos i1-p1, p2 e m4
MN 2881-V	<i>Epidolops ameghinoi</i>	dentário esquerdo com p3-m3, e alvéolos dos c-p1, p2 e m4
MN 2882-V (!)	<i>Gaylordia doelloi</i>	dentário direito quase completo com p2-m4
MN 2883a- V	<i>Didelphopsi s cabrerai</i>	m3 direito
MN 2883b- V	<i>Didelphopsi s cabrerai</i>	m1 direito incompleto

MN 2884-V	<i>Didelphopsis cabrerai</i>	maxilar direito incompleto com P1-2, M4, e alvéolos do C e dos P3-M3
MN 2885-V	<i>Didelphopsis cabrerai</i>	porção proximal de dentário direito com alvéolos do m4 e raiz posterior do m3
MN 2886-V	<i>Derorhynchidae gen. nov.</i>	dentário direito incompleto com p2 e m2-3, raiz anterior do m1, alvéolo do c, p1, p3, alvéolo posterior do m1, e alvéolo anterior do m4
MN 2887-V	<i>Diogenesia sp. nov.</i>	dentário direito incompleto com p3 e m2, raiz anterior do e talônido do m1, raiz anterior e alvéolo posterior do m3, alvéolos do p1-2
MN 2888-V	<i>Bergqvistherium primigenia</i>	m3 esquerdo
MN 2889-V	<i>Monodelphopsis travassosi</i>	fragmento de dentário esquerdo com m3, alvéolos do m2 e raiz anterior e alvéolo posterior do m4
MN 2890-V	<i>Carolopaulacoutoia sp. nov.</i>	dentário esquerdo incompleto com parte do alvéolo do i3, c, alvéolos do p1, p3-m1, e com p2 e m2-4 presentes
MN 2892-V (^)	<i>Carolopaulacoutoia itaboraiensis</i>	dentário direito muito incompleto com raízes do m2, talônido do m3 e com m4 completo
MN 2893-V	<i>Didelphopsis cabrerai</i>	dp3 direito (coroa)
MN 2894(a 1)-V	<i>Mirandatherium alipioi</i>	M3 direito
MN 2894(a 2)-V	<i>Derorhynchidae gen. nov.</i>	M3 direito
MN 2894(b)-V	<i>Didelphopsis cabrerai</i>	DP3 direito

MN 2894(c 1)-V	<i>Carolopaul acoutoia sp. nov.</i>	m3 direito
MN 2894(c 2)-V	<i>Carolopaul acoutoia itaboraiensi s</i>	m4 direito
MN 2896(a) -V	<i>Carolopaul acoutoia itaboraiensi s</i>	fragmento de dentário direito com p3 e alvéolos do p2, posterior do p1 e anterior do m1
MN 2896(b) -V	<i>Monodelpho psis travassosi</i>	fragmento de dentário esquerdo com p2 e alvéolos do p3
MN 2896(c) -V	<i>Derorhynch us singularis</i>	fragmento de dentário esquerdo com p2 e alvéolo posterior do p1
MN 2897(a) -V	<i>Protodidelp his vanzolinii</i>	M2 esquerdo
MN 2897(b) -V	<i>Protodidelp his mastodontoi des</i>	M2 direito
MN 2897(c) -V	<i>Protodidelp his mastodontoi des</i>	M3 direito
MN 2897(d) -V	<i>Protodidelp his vanzolinii</i>	M2 esquerdo
MN 2898-V	<i>Protodidelp his</i>	m2 esquerdo

<i>mastodontoides</i>		
MN 2899(a)-V	<i>Guggenheimia crocheta</i>	m1 direito
MN 2899(b)-V	<i>Bobbschaefferia fluminensis</i>	m2 direito
MN 2900-V	<i>Epidolops ameghinoi</i>	dp3 direito
MN 2901-V	<i>Minusculodelphis minimus</i>	dentário esquerdo incompleto com m2-4
Número de Coleção (Lotes)		
Táxon		Descrição do material
MN 2891-V	Lote com vários dentes isolados	1 pré-molar, 1 molar direito e 2 molares esquerdos
MN 2895-V	Lote com dentários sem dentes preservados	x94 dentários de pequeno tamanho sem dentes
Número de Coleção (petrosos)		
Táxon		Descrição do material
MN 6726-V	<i>Monodelphopsis travassosi</i>	Petroso morfótipo I

MN 6727-V	<i>Monodelpho</i> <i>psis</i> <i>travassosi</i>	Petroso morfótipo I
MN 6728-V	<i>Epidolops</i> <i>ameghinoi</i>	Petroso morfótipo II
MN 6729-V	<i>Epidolops</i> <i>ameghinoi</i>	Petroso morfótipo II
MN 6730-V	<i>Gaylordia</i> <i>doelloi</i>	Petroso morfótipo III
MN 6731-V	<i>Gaylordia</i> <i>doelloi</i>	Petroso morfótipo III
MN 6732-V	<i>Carolopaul</i> <i>acoutoia</i> sp. nov.	Petroso morfótipo IV
MN 6733-V	<i>Marmosopsi</i> <i>s juradoi</i>	Petroso morfótipo V
MN 6734-V	<i>Derorhynch</i> <i>idae</i> gen. nov.	Petroso morfótipo VI
MN 6735-V	<i>Minusculod</i> <i>elphis</i> <i>minimus</i>	Petroso morfótipo VIII
MN 6736-V	<i>Marmosopsi</i> <i>s juradoi</i>	Petroso morfótipo V
MN 6737-V	cf. <i>Armintodelp</i> <i>his</i> sp.	Petroso morfótipo VII
MN 6738-V	cf. <i>Armintodelp</i> <i>his</i> sp.	Petroso morfótipo VII

MN 6739-V	cf. <i>Armintodelph</i> <i>his sp.</i>	Petroso morfótipo VII
MN 6740-V	<i>Minusculod</i> <i>elphis</i> <i>minimus</i>	Petroso morfótipo VIII
Número de Coleção (n identificado)	Táxon	Descrição do material
MN 1369-V (?)	<i>Gaylordia</i> <i>macrocynd</i> <i>onta</i>	?
MN 2358-V (?)	<i>Marmosopsi</i> <i>s juradoi</i>	?
Ungulados (in Metathesia)	Táxon	Descrição do material
MN 2505-V	<i>Miguelsoria</i> <i>parayirunho</i> <i>r?</i>	p4?
MN 2671-V (!)	? (="Paleocla <i>dosictis</i> <i>mosesi</i> ")	P2?
Número de Coleção	Táxon	Descrição do material

MCN- PV 1785	<i>Itaboraidelp hys camposi</i>	m3 esquerdo quase completo
MCN- PV 1786	<i>Didelphopsi s cabrerai</i>	m1 direito quase completo
MCN- PV 1789	<i>Itaboraidelp hys camposi</i>	m3 direito quase completo
MCN- PV 1790 (!) (*)	<i>Protodidelp his mastodontoi des</i>	dp3 esquerdo
MCN- PV 1791	<i>Itaboraidelp hys camposi</i>	m1 direito quase completo
MCN- PV 1792	<i>Minusculod elphis modicum</i>	M2 direito completo
MCN- PV 1794	<i>Didelphopsi s sp. nov.</i>	M2 direito quase completo
MCN- PV 1795	<i>Derorhynch idae gen. nov.</i>	dentário esquerdo incompleto com m2, raízes do p1-2, alvéolos do c, p3, m1 e m3, e alvéolo anterior do m4
MCN- PV 1796	<i>Carolopaul acoutoia itaboraiensi s</i>	dentário direito muito incompleto com o alvéolo posterior do m3 e com m4 presente
MCN- PV 1797	<i>Mirandathe rium alipioi</i>	fragmento de maxila direita com M2, alvéolos do M3 e parte dos alvéolos do M4
MCN- PV	<i>Diogenesia sp. nov. /</i>	m1 direito completo

1798	<i>Derorhynch</i>	
(*)	<i>us sp. nov.</i>	
MCN-	<i>Protodidelp</i>	
PV	<i>his</i>	DP3 esquerdo completo
1799	<i>mastodontoi</i>	
	<i>des</i>	
MCN-		
PV	<i>Gashternia</i>	P3-M1 esquerdos
1801	<i>carioca</i>	
(^) (*)		
MCN-		
PV	<i>Carolocouto</i>	M3 esquerdo
1802	<i>ia ferigoloi</i>	
(^)		
MCN-	<i>Bergqvisthe</i>	
PV	<i>rium</i>	M2 direito
1803	<i>primigenia</i>	
MCN-		
PV	<i>Didelphopsi</i>	m2 esquerdo quase completo
1804	<i>s cabrerai</i>	
MCN-	<i>Protodidelp</i>	
PV	<i>his</i>	m1 esquerdo quase completo
1805	<i>vanzolinii</i>	
MCN-	<i>Protodidelp</i>	
PV	<i>his</i>	M3 esquerdo quase completo
1806	<i>mastodontoi</i>	
	<i>des</i>	
MCN-	<i>Carolopaul</i>	
PV	<i>acoutoia</i>	dentário direito incompleto com raízes dos p1-3, alvéolos do m1 e com m2-3
1807	<i>itaboraiensi</i>	presentes
	<i>s</i>	
MCN-		
PV	<i>Didelphopsi</i>	M2 esquerdo incompleto
1814	<i>s sp. nov.</i>	

MCN- PV 1816	<i>Protodidelp his mastodontoi des</i>	m3 esquerdo
MCN- PV 1817	<i>Protodidelp his mastodontoi des</i>	m3 esquerdo, entocônido não preservado
MCN- PV 1818	<i>Protodidelp his vanzolinii</i>	m1 direito quase completo
MCN- PV 1819	<i>Protodidelp his mastodontoi des</i>	m3 esquerdo
MCN- PV 1820	<i>Protodidelp his mastodontoi des</i>	m4 esquerdo
MCN- PV 1821	<i>Protodidelp his vanzolinii</i>	m4 esquerdo quase completo
	<i>Patene simpsoni</i>	m1 direito
	<i>Monodelpho psis travassosi</i>	dentário com p2-3
	<i>Mirandathe rium alipioi</i>	dentário
	<i>Gashternia carioca</i>	m1 esquerdo
	<i>Derorhynch idae gen. nov.</i>	M3 direito

<i>Itaboraidelp</i> <i>hys camposi</i>	talônido e parte de trigônido de m4 direito
<i>Carolopaul</i> <i>acoutoia</i> <i>itaboraiensi</i> <i>s</i>	m4 esquerdo
<i>Bergqvisthe</i> <i>rium</i> <i>primigenia</i>	m4 direito com paracônido quebrado
<i>Peradectoid</i> <i>ea gen. nov.</i> <i>sp. 1</i>	M2 direito
<i>Itaboraidelp</i> <i>hys camposi</i>	dp3 direito

Número de Coleção	Táxon	Descrição do material
UFRJ-DG 14(a)-M	<i>Itaboraidelp</i> <i>hys camposi</i>	fragmento anterior de dentário esquerdo edentado com alvéolos dos p2-3 e m1-2
UFRJ-DG 14(b+c)-M	<i>Itaboraidelp</i> <i>hys camposi</i>	dentário esquerdo edentado com alvéolos dos p1-3, m1 e m3-4 (quebrado na parte do m2)
UFRJ-DG 14(d)-M	<i>Gaylordia</i> <i>macrocyodontia</i>	Dentário direito edentado incompleto com alvéolo posterior do p3 e alvéolos dos m1-4
UFRJ-DG 14(e)-M	<i>Epidolops</i> <i>ameghinoi</i>	Fragmento de dentário direito edentado com alvéolos dos m2-3

UFRJ-		
DG	<i>Derorhynch</i>	
15(a)-	<i>us sp. nov.</i>	dentário direito edentado com alvéolos dos p2-3 e m1-4
M		
UFRJ-		
DG	<i>Marmosopsi</i>	
15(b)-	<i>s sp. nov.</i>	Dentário edentado direito com alvéolos dos p3, m1-2 e alvéolo anterior do m3
M		
UFRJ-		
DG	<i>Epidolops</i>	
16(a)-	<i>ameghinoi</i>	Maxila edentada esquerda com alvéolos do P2-3 e M1-M2
M		
UFRJ-		
DG	<i>Didelphopsi</i>	
16(b)-	<i>s cabrerai</i>	maxila edentada direita com alvéolos do M2-3 e alvéolos dos M1 e M4
M		parcialmente preservados
UFRJ-		
DG	<i>Bergqvisthe</i>	
17(a)-	<i>rium</i>	Dentário edentado esquerdo com alvéolos dos i2-4, c, p1-3 e m1-4, e raiz do i5
M	<i>primigenia</i>	
UFRJ-		
DG	<i>Austropedio</i>	
17(b)-	<i>mys</i>	Dentário edentado esquerdo com alvéolos dos p1-3 e m1-4
M	<i>marshalli</i>	
UFRJ-		
DG	<i>Monodelpho</i>	fragmento de dentário esquerdo com alvéolo posterior do m3 e alvéolos do m4.
17(c)-	<i>psis sp. nov.</i>	Processo coronoide, processo angular e parte do côndilo mandibular
M		
UFRJ-		
DG	<i>Guggenhei</i>	
17(d)-	<i>mia</i>	Fragmento de dentário esquerdo edentado com alvéolos dos p2-3, m1-2 e
M	<i>brasiliensis</i>	alvéolo anterior do m3
UFRJ-		
DG 18-	<i>Patene</i>	Maxila direita edentada com alvéolos do M2 (parcialmente preservados) e
M	<i>simpsoni</i>	alvéolos dos M3-4

UFRJ- DG 23- M	<i>Epidolops ameghinoi</i>	dentário esquerdo quebrado em duas partes: i) com m2 e alvéolos dos p3-m1 e m3-4; e ii) com alvéolos dos i2-4, c e p2
UFRJ- DG 24- M + UFRJ- DG 29- M	<i>Epidolops ameghinoi</i>	dentário direito fragmentado em duas partes: i) fragmento com m1-2 (UFRJ 24-M); e ii) fragmento com p2 e alvéolos dos p1, c e i2-4
UFRJ- DG 26- M	<i>Epidolops ameghinoi</i>	dentário esquerdo com m1-2 e alvéolos dos m3-4. Parte ventral danificada
UFRJ- DG 28- M	<i>Marmosopsi s sp. nov.</i>	dentário esquerdo completo com p2-3 e m1-3, alvéolos do i2-5, c, p1 e m4
UFRJ- DG 32- M	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3 (parte mesial levemente danificada), M1 e parte dos alvéolos dos M2; porção anterior do arco zigomático preservada
UFRJ- DG 55- M	<i>Epidolops ameghinoi</i>	fragmento de dentário esquerdo com p3 e m1-m3, alvéolos dos p1-2 e m4
UFRJ- DG 57(a)- M	<i>Patene simpsoni</i>	trigônido de m4 direito
UFRJ- DG 57(b)- M	<i>Patene simpsoni</i>	m2 esquerdo
UFRJ- DG 145-M	<i>Derorhynch us sp. nov.</i>	M2 esquerdo

UFRJ- DG 146-M	<i>Marmosopsi s juradoi</i>	m4 esquerdo
UFRJ- DG 147-M	<i>Marmosopsi s sp. nov.</i>	M1 esquerdo
UFRJ- DG 148-M	<i>Derorhynch us sp. nov.</i>	m2 direito
UFRJ- DG 149-M	<i>Marmosopsi s sp. nov.</i>	M3 direito
UFRJ- DG 150-M	<i>Epidolops ameghinoi</i>	m1 esquerdo
UFRJ- DG 151-M	<i>Bergqvisthe rium primigenia</i>	M3 direito
UFRJ- DG 153-M	<i>Monodelpho psis sp. nov.</i>	M3 esquerdo
UFRJ- DG 154-M	<i>Derorhynch us sp. nov.</i>	M3 esquerdo
UFRJ- DG 155-M	<i>Carolopaul acoutoia itaboraiensi s</i>	m4 direito sem metacônido
UFRJ- DG 189-M	<i>Patene simpsoni</i>	m1 direito sem raízes
UFRJ- DG 218-M	<i>Diogenesia sp. nov.</i>	M4 esquerdo

UFRJ- DG 222-M	<i>Patene simpsoni</i>	M1 esquerdo parcialmente preservado (plataforma estilar, paracone e metacone)
UFRJ- DG 223-M	<i>Carolocouto ia ferigoloi</i>	Coroa de M2 direito
UFRJ- DG 232-M	<i>Epidolops ameghinoi</i>	M3 esquerdo com duas das três raízes preservadas
UFRJ- DG 318-M	<i>Derorhynch us sp. nov.</i>	M1 esquerdo faltando o parástilo (StA)
UFRJ- DG 319-M	<i>Austropedio mys marshalli</i>	m1 esquerdo incompleto, faltando o paracônido
UFRJ- DG 320-M	<i>Derorhynch us sp. nov.</i>	m1 direito
UFRJ- DG 353-M	<i>Monodelpho psis sp. nov.</i>	M2 esquerdo
Númer o de Coleçã o (pós- crânio)	Táxon	Descrição do material
UFRJ- DG 128-M	Metatheria indet.	Calcâneo esquerdo
Númer o de Coleçã o (n	Táxon	Descrição do material

identificado)		
UFRJ-DG	Metatheria	
325-M	indet.	Falange ungueal
(?)		
Número de Coleção	Táxon	Descrição do material
AMNH 39424	<i>Eobrasilia coutoi</i>	fragmento rostral do crânio com P1-3 direitos e P3 esquerdo muito desgastados, alvéolos dos C, P1-3 esquerdos, M1-2 e M4, M3 direito e M3 esquerdo muito danificado
AMNH 49801 (ex MN 1356-V)	<i>Gaylordia macrocynodonta</i>	dentário direito incompleto com alvéolos do m3 e com p2-m2 presentes
AMNH 49802 (ex MN 1361-V)	<i>Mirandatherium alipioi</i>	dentário direito incompleto com m2 e raiz anterior e talonido do m1, e raízes do m3
AMNH 49803 (ex MN 1370-V)	<i>Protodidelphis vanzolinii</i>	m2 direito
AMNH 49804 (ex MN 1333-V)	<i>Patene simpsoni</i>	M1 esquerdo
AMNH 49805 (ex MN	<i>Patene simpsoni</i>	M2 direito

1334- V)		
AMNH 49806 (ex MN 1396- V)	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p1 e raízes do p2
AMNH 49807 (ex MN 1375- V)	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com m2 e alvéolos dos m3-4
AMNH 49808 (ex MN 1379- V)	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p2-m2, raiz do c e alvéolos do m3-4
AMNH 49809 (ex MN 1380- V)	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p2-m2 e alvéolos do c e m3-4
AMNH 49810 (ex MN 1391- V)	<i>Epidolops ameghinoi</i>	dentário esquerdo fragmentado com p2-3 e alvéolos do c
AMNH 49811 (ex MN 1393- V)	<i>Epidolops ameghinoi</i>	dentário direito fragmentado com p2 e m1-2, e p3 danificado
AMNH 49812 (ex MN	<i>Epidolops ameghinoi</i>	fragmento de maxila direita com P3-M2

1412-			
V)			
AMNH			
49813	<i>Epidolops</i>		
(ex MN	<i>ameghinoi</i>	fragmento de maxilar esquerdo com P3-M1	
1406-			
V)			
AMNH			
49814	<i>Epidolops</i>		
(ex MN	<i>ameghinoi</i>	dentário esquerdo fragmentado com m1-2 e alvéolos do m3	
1404-			
V)			
AMNH			
49826	<i>Derorhynch</i>		
(ex MN	<i>us</i>	dentário direito incompleto com alvéolos do p1-m1, e com m2-4 presentes	
1349-	<i>singularis</i>		
V)			
AMNH			
49857	<i>Protodidelp</i>		
(ex	<i>his</i>	dentário direito quase completo com p1-m1, alvéolo do c, raízes dos m2-3, raiz	
DGM	<i>vanzolinii</i>	anterior e talônido do m4	
320-M)			
	<i>Protodidelp</i>		
AMNH	<i>his</i>		
49858	<i>mastodontoi</i>	dentário esquerdo incompleto com p2-m2	
	<i>des</i>		
AMNH			
49859	<i>Bergqvisthe</i>		
(ex	<i>rium</i>	dentário direito incompleto com m2-4 presentes, alvéolos do m1 e alvéolo	
DGM	<i>primigenia</i>	posterior do p3	
360-M)			
AMNH	<i>Epidolops</i>		
49860	<i>ameghinoi</i>	dentário direito com m2, e alvéolos dos c-p1 and m3-m4	

Fonte: O autor (2023).

APÊNDICE B – ESTIMATIVA DE MASSA CORPORAL CALCULADA PARA OS METATÉRIOS DA BACIA DE ITABORAÍ

Estimativa de massa corporal calculada para diferentes espécimes de metatérios da fauna de Itaboraí. A massa corporal é baseada em Meyers (2001). Os holótipos estão destacados em negrito. **BM**, massa corporal; **Lm1-4**, comprimento da série molar inferior

Specimen	Taxa	Lm1-4	BM (g)	BM (Kg)	Series
MCT.M.928	<i>Austropedimys marshalli</i>	7.51	70.79	0.070	lower
UFRJ-DG 17(b)-M	<i>Austropedimys marshalli</i>	7.47*	69.18	0.069	lower
MCT.M.808	<i>Austropedimys marshalli</i>	~7.50	97.72	0.097	upper
AMNH 49859	<i>Bergqvistherium primigenia</i>	9.04	135.00	0.135	lower
MCT.M.362	<i>Bergqvistherium primigenia</i>	8.77	120.23	0.120	lower
MCT.M.922	<i>Bergqvistherium primigenia</i>	9.17	141.25	0.141	lower
MN 1362-V	<i>Bergqvistherium primigenia</i>	~9.01	131.83	0.132	lower
UFRJ-DG 17(a)-M	<i>Bergqvistherium primigenia</i>	8.48*	109.65	0.109	lower
MN 1350-V	<i>Bobbschaefferia fluminensis</i>	12.88	467.74	0.467	lower
MCT.M.929	<i>Bobbschaefferia fluminensis</i>	~10.80	263.03	0.263	lower
MCT.M.966	<i>Carolocoutoia ferigoloi</i>	24.24	4,466.84	4.466	lower
MN 2892-V	<i>Carolopaulacoutoia itaboraiensis</i>	~6.96	53.70	0.053	lower
MCT.M.927	<i>Carolopaulacoutoia itaboraiensis</i>	~7.05	56.23	0.056	lower
MCT.M.932	<i>Carolopaulacoutoia itaboraiensis</i>	7.27	61.66	0.061	lower
MCT.M.807	<i>Carolopaulacoutoia itaboraiensis</i>				upper
MN 2890-V	<i>Carolopaulacoutoia</i> sp. nov.	5.92	30.20	0.030	lower
MN 2357-V	<i>Carolopaulacoutoia</i> sp. nov.	~6.15	34.67	0.034	lower
MN 2354-V	<i>Derorhynchidae</i> gen. nov. sp. nov.	7.41	64.57	0.064	lower
MN 2886-V	<i>Derorhynchidae</i> gen. nov. sp. nov.	~7.51	66.07	0.066	lower
MN 1348-V	<i>Derorhynchus singularis</i>	7.33	64.57	0.064	lower
AMNH 49826	<i>Derorhynchus singularis</i>	7.35	66.07	0.066	lower
MCT.M.803	<i>Derorhynchus singularis</i>	6.93	75.86	0.076	upper

MCT.M.651	<i>Derorhynchus</i> sp. nov.	6.85	50.12	0.050	lower
UFRJ-DG 15(a)-M	<i>Derorhynchus</i> sp. nov.	7.79*	81.28	0.081	lower
MCT.M.243	<i>Didelphopsis cabrerai</i>	16.57	1,148.15	1.148	lower
MN 1429-V	<i>Didelphopsis cabrerai</i>	17.52	1,584.89	1.585	upper
MN 2894(b)-V	<i>Didelphopsis cabrerai</i>	16.76*	1,479.11	1.479	upper
UFRJ-DG 16(b)-M	<i>Didelphopsis cabrerai</i>	~16.19*	1,348.96	1.349	upper
MCT.M.219	<i>Didelphopsis</i> sp. nov.	18.14*	1,995.26	1.995	lower
MCT.M.277	<i>Didelphopsis</i> sp. nov.	17.61*	1,778.28	1.778	lower
MCT.M.650	<i>Diogenesia brevirostris</i>	5.73	26.92	0.027	lower
MCT.M.812	<i>Diogenesia</i> sp. nov.	6.75	47.86	0.048	lower
MN 1887-M	<i>Diogenesia</i> sp. nov.	~7.50	66.07	0.066	lower
MCT.M.930	<i>Diogenesia</i> sp. nov.	~7.50*	67.61	0.067	lower
AMNH 39424	<i>Eobrasilia coutoi</i>	[24.03]	[4,677.3 5]	[4.677]	upper
MCT.M.4537	<i>Gashternia carioca</i>	14.79	812.83	0.812	lower
DGM 329-M	<i>Gaylordia macrocynodonta</i>	~6.35	38.02	0.038	lower
AMNH 49801 (ex MN 1356-V)	<i>Gaylordia macrocynodonta</i>	~7.07	56.23	0.056	lower
DGM 186-M	<i>Gaylordia macrocynodonta</i>	7.77	79.43	0.079	lower
MCT 2385-M (= DGM 646-M)	<i>Gaylordia macrocynodonta</i>	7.71	77.62	0.077	lower
DGM 925-M	<i>Gaylordia macrocynodonta</i>	~6.30	37.15	0.037	lower
MN 1355-V	<i>Gaylordia macrocynodonta</i>	7.18	56.23	0.056	lower
MN 1357-V	<i>Gaylordia macrocynodonta</i>	8.07	91.20	0.091	lower
MN 1358-V	<i>Gaylordia macrocynodonta</i>	7.70	77.62	0.077	lower
MN 1366-V	<i>Gaylordia macrocynodonta</i>	7.06	56.23	0.056	lower
UFRJ-DG 14(d)-M	<i>Gaylordia macrocynodonta</i>	7.73*	79.43	0.079	lower
MN 2504-V	<i>Gaylordia doelloi</i>	~5.35	20.89	0.021	lower
MN 2487-V	<i>Gaylordia doelloi</i>	5.54	22.91	0.023	lower
MN 2882-V	<i>Gaylordia doelloi</i>	5.78	26.92	0.027	lower
DGM 810-M	<i>Gaylordia mater</i>	~7.98	85.11	0.085	lower
MCT 2383-M (= DGM 644-M)	<i>Gaylordia mater</i>	7.65	72.44	0.072	lower
MCT 2384-M (= DGM 645-M)	<i>Gaylordia mater</i>	8.15	93.33	0.093	lower
MCT 2386-M (= DGM 647-M)	<i>Gaylordia mater</i>	7.33*	61.66	0.061	lower
MCT 2387-M (= DGM 648-M)	<i>Gaylordia mater</i>	~7.85*	79.43	0.079	lower

MCT.M.314	<i>Guggenheimia crocheti</i>	12.43	407.38	0.407	lower
MCT.M.315	<i>Guggenheimia crocheti</i>	12.89	478.63	0.478	lower
MCT.M.297	<i>Guggenheimia brasiliensis</i>	10.72	245.47	0.245	lower
MCT.M.817	<i>Itaboraidelphys camposi</i>	15.07	831.76	0.831	lower
MCT.M.804	<i>Itaboraidelphys camposi</i>	14.84	776.25	0.776	lower
MCT.M.814	<i>Itaboraidelphys camposi</i>	14.11	645.65	0.645	lower
MN 2343-V	<i>Marmosopsis juradoi</i>	5.31	20.42	0.020	lower
MN 2344-V	<i>Marmosopsis juradoi</i>	5.51	22.91	0.023	lower
MN 2345-V	<i>Marmosopsis juradoi</i>	5.63	25.12	0.025	lower
MN 2346-V	<i>Marmosopsis juradoi</i>	~5.11	18.20	0.018	lower
MN 2350-V	<i>Marmosopsis juradoi</i>	5.53	22.91	0.023	lower
MN 2356-V	<i>Marmosopsis juradoi</i>	~5.48	21.38	0.021	lower
MN 2470-V	<i>Marmosopsis juradoi</i>	~5.63	25.12	0.025	lower
MN 2485-V	<i>Marmosopsis juradoi</i>	~4.90	15.49	0.015	lower
MN 2497-V	<i>Marmosopsis juradoi</i>	5.57	22.91	0.023	lower
MN 2498-V	<i>Marmosopsis juradoi</i>	~5.74	26.92	0.027	lower
UFRJ-DG 28-M	<i>Marmosopsis</i> sp. nov.	6.87	51.29	0.051	lower
UFRJ-DG 15(b)-M	<i>Marmosopsis</i> sp. nov.	~6.50	40.74	0.040	lower
MN 2342-V	<i>Minusculodelphis minimus</i>	3.13	3.16	0.003	lower
MN 2503-V	<i>Minusculodelphis minimus</i>	3.00	2.69	0.002	lower
DGM 921(a)-M	<i>Minusculodelphis modicum</i>	4.00	7.59	0.007	lower
DGM 921(b)-M	<i>Minusculodelphis modicum</i>	~3.90	6.92	0.006	lower
MN 1359-V	<i>Mirandatherium alipioi</i>	~10.46	223.87	0.223	lower
MCT.M.361	<i>Mirandatherium alipioi</i>	9.43	151.36	0.151	lower
MN 2355-V	<i>Mirandatherium alipioi</i>	~9.57	162.18	0.162	lower
MN 1365-V	<i>Monodelphopsis travassosi</i>	~8.28	100.00	0.100	lower
MN 2889-V	<i>Monodelphopsis travassosi</i>	~8.20	97.72	0.097	lower
MN 2340-V + MN 2351-V	<i>Monodelphopsis travassosi</i>	~9.13	138.04	0.138	lower
UFRJ-DG 17(c)-M	<i>Monodelphopsis</i> sp. nov.	~7.61	72.44	0.072	lower
MCT.M.324	<i>Patene simpsoni</i>	19.71	2,137.96	2.138	lower
MN 1351-V	<i>Patene simpsoni</i>	19.17	1,905.46	1.905	lower
MN 1331-V	<i>Patene simpsoni</i>	21.66	3,162.28	3.162	upper
MCT.M.331	<i>Patene simpsoni</i>	19.45*	2,511.89	2.512	upper

MCT.M.2382 (= MCT.M.643)	<i>Patene simpsoni</i>	16.98*	1,584.89	1.585	upper
UFRJ-DG 14(b+c)-M	<i>Patene simpsoni</i>	16.80*	1,288.25	1.288	lower
MCT.M.920	Peradectoidea gen. nov. sp. nov. 1	7.68	75.86	0.076	lower
MCT.M.649	Peradectoidea gen. nov. sp. nov. 2	5.35	20.89	0.021	lower
[MCT.M.919, 806]	<i>Periprotodidelphis bergqvistae</i>	~14.53	758.58	0.759	lower
MCT.M.805 + MCT.M.924	<i>Procaroloameghinia pricei</i>	11.14	281.84	0.281	lower
MCT.M.250	<i>Protodidelphis vanzolinii</i>	19.75	2,137.96	2.138	lower
MCT.M.319	<i>Protodidelphis vanzolinii</i>	19.25	1,949.84	1.95	lower
MCT.M.271	<i>Protodidelphis vanzolinii</i>	19.69	2,398.83	2.399	upper
MCT.M.303	<i>Protodidelphis vanzolinii</i>	20.28	2,630.27	2.630	upper
UFRJ-DG 1195-M	<i>Robertbutleria mastodontoidea</i>	20.38	2,570.40	2.570	lower
MCT.M.933	<i>Thylacopygmaeus oliveirai</i>	~4.74	12.88	0.013	lower
[MCT.M.657, 970 + MN 1344-V]	<i>Silvenator brasiliensis</i>	~27.31	7,413.10	7.413	lower
UFRJ-DG 14(b+c)-M	<i>Xenocynus crypticus</i>	16.71*	1,380.38	1.380	lower
MCT.M.2382 (=MCT.M.643)	<i>Xenocynus crypticus</i>	16.65*	1,479.11	1.479	upper
MCT.M.4590	<i>Xenocynus crypticus</i>	16.49*	1,445.44	1.445	upper

Fonte: O autor (2023).

APÊNDICE C – ARTIGOS PRODUZIDOS NO ÂMBITO DA TESE**ARTIGO 1****Chapter 5****Paleogene Metatherians from the Itaboraí Basin:
Diversity and Affinities**

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Abstract

Metatherians represented the most diverse group of Paleogene mammals of South America. The early Eocene metatherian fauna of Itaboraí, Brazil, was one of the most prominent. This fauna preserved a great diversity of tiny and very small insectivore assemblages, specialized durophagous, and brachydont-bunodont metatherians and is represented by 29 genera and 39 species, which are tooth-based taxa. The fauna preserved the oldest confirmed representatives of Didelphimorphia, as well as possible stem-Paucituberculata, but with no Australidelphia.

Furthermore, the probable presence of the North American Late Cretaceous groups in the fauna, such as *Pediomyoidea*, *Hatcheriformes*, and *Stagodontidae* is also discussed. Sparassodonts, such as *Patene*, represented the top mammalian predators of the fauna. The large variety of Itaboraíense “ameridelphians” includes, amongst others, “peradectoids”, caroloameghinioids, jaskhadelphyids, and sternbergiids, which represented earlier metatherian clades than the marsupials. Polydolopimorphians were represented by *Epidolops*, the most abundant metatherian of this fauna, and *Gashternia*. Caroloameghinioids should not be assigned to Didelphimorphia, and is here regarded as “peradectoids”. Derorhynchidae was the sister taxon of Herpetotheriidae. The reassessment of the eight petrosal morphotypes recovered in Itaboraí supports the common origin for the majority of South American clades and has enabled their reassessment to representatives of this fauna.

Keywords: Didelphimorphia. Early Eocene. Itaboraíense. Marsupialia. Petrosal. South America.

5.1 Introduction and Historical Background

“The Itaboraí fauna is not only the largest, but also the most diverse yet discussed (...)” (Woodburne et al. 2014: 40).

Metatherians represented one of the most important mammalian faunal elements of the Cenozoic in South America (Goin et al. 2016). The notable diversity achieved by the representatives of this group during the early Eocene in this continent has been considered as an important base for multiple hypotheses, suggesting they were essential elements of the First American Biotic Interchange (FABI) (Goin et al. 2012), which occurred around the Late Cretaceous-earliest Paleocene. Two important South American land mammal ages (SALMAs), which enable the reconstruction of metatherian diversity in South America during the Paleocene and early Eocene, are located in Tiupampa, Bolivia (early Paleocene – Tiupampan SALMA – 65.1-64.8 MYA sensu Muizon et al. 2018), and the faunal localities of the Itaboraí Basin, Brazil, and Las Flores, Argentina, both of which represent the early Eocene time span (Itaboraíense SALMA – 53-50 MYA sensu Woodburne et al. 2014). Within this context, the Itaboraí Basin, located in the Brazilian state of Rio de Janeiro, is one of the most significant localities for the evolutionary context of Metatheria from the early Paleogene of Western Gondwana (Fig. 5.1A). In addition to metatherians, this fauna features several other mammals and its relevance may

be assessed in aspects such as: (1) its great antiquity (early Eocene in age), (2) its northernmost geographical position in relation to other faunas of a similar time span, and (3) its great mammalian diversity.

FIGURE 5.1

The Itaboraí Basin is filled by limestone deposits that has preserved a rich fauna of Paleogene mammals currently dated as lower Eocene in age (Itaboraiense SALMA – sensu Woodburne et al. 2014; but see e.g., Bergqvist et al. 2009 in which a late Paleocene-early Eocene age was proposed for this locality) (Fig. 5.1B). It is located in the municipality of São José de Itaboraí (22°50'20"S and 42°52'30"W), in the metropolitan region of Rio de Janeiro, in the state of Rio de Janeiro (RJ), Brazil (Bergqvist et al. 2009; Oliveira and Goin 2011). The exploration of this basin has resulted in a rich paleontological contribution to the evolution of South American mammals, with the most diverse fauna of Paleogene mammals in Brazil (Bergqvist et al. 2009). Amongst the mammals recorded in the basin, the metatherians represent the most diverse group, with 23 genera and 27 species formally described in the literature (Marshall 1987; Oliveira and Goin 2011, 2012; Carneiro 2019; Carneiro et al. 2018), although new as yet undescribed taxa have also been recognized (see e.g., Oliveira 1998 and this present chapter – i.e. ‘gen nov’ and other assigned taxa to a genus but as yet not formally described, e.g., *Carolopaulacoutoia* sp.).

The first metatherian to be described from this fauna was *Eobrasilia coutoi* Simpson, 1947, for which the type specimen (AMNH 39424) is a badly damaged skull, which was discovered by engineers in charge of the local limestone quarry. Due to the damaged condition of the specimen, it was sent to the American Museum of Natural History (AMNH), New York, US, to be prepared (Simpson 1947). In the subsequent year, an exploration team led by Carlos de Paula Couto was sent to explore the locality in pursuit of new fossil findings (Paula Couto 1949). The expedition explored some limestone dissolution fissures discovered in the locality, and recovered several vertebrate remains, including metatherians, “ungulates”, crocodiles, etc. (Paula Couto 1949; Bergqvist et al. 2009). Over the following years, other fossil specimens were also collected, thereby expanding the diversity of metatherians from this locality (see e.g., Paula Couto, 1952a, b, c, 1961, 1962, 1970; Marshall 1982a, b, 1984, 1987; Oliveira 1998).

The majority of metatherian fauna discovered in the Itaboraí Basin was described by Paula Couto in a series of publications (Paula Couto 1952a, b, c, 1961, 1962, 1970). Later, Marshall (1982a, b, 1984, 1987) described new taxa, such as *Procaroloameghinia pricei* Marshall, 1982a, and provided a review of the affinities of the described taxa by Paula Couto,

including several new undescribed specimens. Marshall's results (1987) were used as a basis for the doctorate thesis of Édison V. Oliveira and his advisers Jorge Ferigolo and Francisco J. Goin (Oliveira 1998), who provided the most current taxonomic study of the fauna, which was soon followed by the Brazilian collections and recent studies (Goin et al. 1998, 2009; Goin and Oliveira 2007; Oliveira et al. 2016, 2021; Oliveira and Goin 1999, 2011, 2012, 2015; Beck 2017; Carneiro and Oliveira 2017a, b; Carneiro et al. 2018; Carneiro 2019; Rangel et al. 2019). These studies have attested to the richness of this fauna 70 years after the first representative of this group was originally described.

In this chapter, the current knowledge regarding the taxonomic significance of the Itaboraí metatherians is summarized, highlighting the importance of these taxa within the context of the evolutionary history of this group. This compilation of data is herein presented as a summary of both classic and recent data for senior and aspirant researchers, as well as for metatherian enthusiasts, in order to provide an updated compilation of data to support future studies and to highlight the importance of Itaboraiense metatherians to paleontology, both in Brazil and worldwide.

5.2 Methodological Approach

5.2.1 Taxonomy and specimens

The chapter discussion is based on the analysis of more than 460 teeth of metatherian specimens held in Brazilian collections (i.e., MCT (ex DGM), MN, MCN-PV, and UFRJ), casts from AMNH specimens, isolated petrosals from MN, and postcranial elements from MCT. The number of dental specimens for each taxon is indicated (Fig. 5.2). The complete list of studied taxa is presented as supplementary material in appendix 5.1.

FIGURE 5.2

The size classification for the Itaboraiense metatherians used in this chapter is based on the lower molar series length (Lm1-4) (see supplementary material in appendix 5.2). The size categories are tiny (<5.00 mm), very small (5.00-6.80 mm), small (6.80-9.50 mm), medium (9.50-15.00 mm), large (15.00-25.00 mm), and very large (>25.00 mm). Taxa with no preserved lower molars series (i.e., dentaries with alveoli of m1-4 or with preserved m1-4) were grouped based on the relative size of their upper and lower molars (see supplementary material appendix 5.2).

5.2.2 Dietary inferences

The variety of possible food resources explored by the Itaboraíense taxa is discussed throughout the chapter based on relative size and the general morphology of upper and lower molars and premolars. The dietary inferences have been based on

Zimicz's (2012), who proposed the following trophic categories: carnivory, omnivory, insectivory-frugivory, strict insectivory (for this chapter, insectivory and strict insectivory), strict frugivory, folivory, and granivory. Zimicz (2012:20) grouped the carnivorous metatherians following Van Valkenburgh's classification (1991), which proposed hypercarnivory (i.e., a diet consisting entirely of vertebrates), mesocarnivory/faunivory (i.e., a diet consisting firstly of vertebrates, although insects and other invertebrates are also explored) and hypocarnivory/omnivory (i.e., a diet consisting mostly of non-vertebrate food resources, such as invertebrates, fruit etc.).

5.2.3 Image acquisition

The scanning electron microscope (SEM) images presented in this chapter were produced with the JEOL JSM-6390LV SEM at the Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional, Rio de Janeiro, RJ, Brazil (MN/RJ); Núcleo de Microscopia Eletrônica da COPPE, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil (UFRJ/RJ), and Centro de Microscopia e Microanálise da Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil (CMM –UFRGS/RS).

5.2.4 Applied terminology

The teeth nomenclature used for the dental components of the upper and lower dentition of the Itaboraí metatherians were those established by Oliveira (1998) and Oliveira and Goin (2011) (Fig. 5.3). The postcanine dentition nomenclature considered the premolar loci as P1-3/p1-3 and the molar loci as M1-4/m1-4. The incisor nomenclature followed that of Oliveira and Goin (2011) (i.e., i2-5), and the postcranial nomenclature that of Szalay (1994), and Szalay and Sargis (2001).

FIGURE 5.3

5.2.5 Petrosal reassessment analysis

The isolated petrosals recovered from the Itaboraí Basin were described, measured, and studied by Ladevèze (2004, 2007) and Ladevèze and Muizon (2010), with additional data provided by Beck (2017), Muizon et al. (2018), and Muizon and Ladevèze (2020). The current re-analysis

was based on the results obtained by the methodology conducted by Ladevèze (2007), and Ladevèze and Muizon (2010), who provided the most comprehensive attempts to associate the isolated petrosals with the taxa from the Itaboraí fauna. They used the regressed promontorium area against the regression of the molar area in order to assign the petrosals to one taxon of this fauna. In addition, these authors also provided phylogenetic analyses, which resulted in some incongruence regarding the expected size assignment of the petrosals and the systematic affinities recovered for the same taxa.

The same methodology was followed in this chapter, with some differential contributions. Firstly, the taxonomic review of Itaboraí's metatherians identified 29 genera and 39 species (see e.g., Oliveira 1998), a remarkable increase in diversity when compared with Ladevèze and Muizon (2010), who considered only 17 genera and 19 species. This revision resulted in a more reliable identification of the specimens and a more accurate size range and area for each taxon, resulting in the re-calculation of the second and third molar areas for all Itaboraí's taxa.

Secondly, the eight petrosal morphotypes were grouped within the size categories considered for this chapter (i.e., tiny, very small, small, medium, large, and very large) based on the estimated molar areas of Ladevèze and Muizon (2010). This was followed due to the observation that some taxa have congruent upper molar areas but incongruent lower molar areas with the estimate for some of the petrosal morphotypes (see supplementary materials appendix 5.3 Table 5.2). These differences in congruence between upper and lower molars should be related to ecomorphological adaptations of Itaboraí's taxa. Therefore, it was considered the estimated molar areas calculated by Ladevèze and Muizon (2010) as an indicative of the size category congruent with the petrosal morphotype. In addition, the relative abundance (based on the minimum number of individuals – MNI) was also considered as some taxa are more abundant than others, which increases the probability of association with a petrosal morphotype (see similar methodology in Beck 2017).

Thirdly, the results of the phylogenetic analysis were considered for a more reliable assignment of the eight petrosal's morphotypes, as some size categories have a greater number of taxa in comparison with petrosal morphotypes. The data matrix of the petrosal phylogenetic analysis (see 5.13) included 52 taxa, in which 49 were metatherians and nine were 'petrosal-based taxa' (i.e., "taxa" represented only by petrosal characters), and 572 characters (see supplementary material appendix 5.4). For petrosal matrix, taxa with associated petrosals (extant marsupials, pucadelphyids, sparassodonts, deltatheroids, *Mimoperadectes*, *Didelphodon*, *Pedimys*, *Turgidodon*, *Herpetotherium*, and peratheriines), *Djarthia* (following the combination proposed by Beck 2008), the eight isolated petrosals from Itaboraí (PI, PII, PIII, PIV, PV, PVI, PVII and PVIII), and one isolated petrosal from Tiupampa, Bolivia (MHNC 8369 – Ladevèze

and Muizon 2007) were considered. The results of this analysis are discussed in detail later in the chapter (5.13). The data matrix was analyzed with a new technology search with TNT 1.5 (Goloboff and Catalano 2016) using the sectorial, ratchet, drift, and tree-fusing strategies with 100 replications. Bremer support values and tree scores were calculated with TNT 1.5.

Therefore, three major criteria for assigning the petrosals were used: (i) a compatible size, as estimated by Ladevèze and Muizon (2010), the results considering the equation of Beck et al. (2008), and the revised measurements and size categories provided by the authors of this chapter; (ii) the phylogenetic affinities, as recovered by the phylogenetic analysis; and (iii) the relative abundance in the fauna based on the minimum number of individuals (MNI) calculated for each taxon.

5.3 Taxonomic concept

The diversity mentioned in this chapter primarily followed the taxonomic proposals of Goin and Oliveira (2007), Goin et al. (1998, 2009), Oliveira and Goin (2011, 2012, 2015), Oliveira et al. (2016), Carneiro and Oliveira (2017a, b), Carneiro et al. (2018), Carneiro (2019), Rangel et al. (2019) and Oliveira et al. (2021); in addition to the new data resulting from this re-analysis of the specimens. The results of the petrosal phylogenetic analysis (see 5.2.5 and 5.13) were used also as base evidence for the taxonomic concept presented in this chapter. The conclusions followed in this chapter are indicated in Table 5.1.

TABLE 5.1

5.4 “North American” Metatherian Groups in the Itaboraí Fauna

The origin of South American metatherians is linked to the FAB I (First American Biotic Interchange), a late Maastrichtian (around 69-66 MYA) biotic interchange between North and South America (see e.g., Goin et al. 2012, 2016). Amongst the representatives of the Itaboraí fauna, some of them have been considered as representatives of North American clades, such as *Austropedimys*, *Eobrasilia* and *Zeusdelphys*. In the following topics, their systematic affinities and dietary inferences will be discussed.

5.4.1 *Austropedimys*: a pediomyoid in South America?

Classically, *Pediomyoidea* was a Late Cretaceous North American endemic group, which disappeared after the Cretaceous-Paleogene boundary (K-Pg boundary) (Wilson 2014). Notwithstanding, several authors have claimed that this group survived in South America during the Paleogene period, and was recorded in Tiupampa, Bolivia (Carneiro et al. 2018),

Laguna Umayo, Peru (Sigé 1972), Itaboraí, Brazil (Szalay 1994; Oliveira 1998; Oliveira and Goin 2012; Goin et al. 2016; Carneiro et al. 2018), and Las Flores, Argentina (Woodburne et al. 2014).

Amongst the South American fossil records, the Itaboraí fauna draws particular attention due to the fossil record of *Austropediomys*, the possible youngest and first-described representative of this group in South America (Fig. 5.4). Initially, *Austropediomys* was considered to represent the upper dentition of *Monodelphopsis travassosi* (DGM 808-M) by Marshall (1987), Marshall et al. (1990), and Muizon (1992). However, Oliveira (1998), and Oliveira and Goin (2012) considered that this specimen represented another taxon, a hypothesis confirmed by Carneiro et al. (2018), who described it as *Austropediomys marshalli*.

FIGURE 5.4

Davis (2007) defined Pedomyidae based on the following synapomorphies: an evident reduction of the parastylar lobe, a rounded labial wall of paracone and flattened labial wall of metacone, and an absence of StB. Furthermore, Carneiro et al. (2018) identified the presence of lingual accessory conular structures to the conules (i.e., conuloids) on the upper dentition of *Austropediomys*, which was also identifiable on the upper dentition of Aquiladelphidae and Pedomyidae, although less developed than that of *Austropediomys*.

Austropediomys presents a combination of unique morphological traits (i.e., autapomorphies) in comparison to other pediomyoids, such as reduced para- and metacingula, a convex labial wall of the metacone, and the presence of a moderately robust StB (see e.g., Oliveira 1998; Oliveira and Goin 2012; Carneiro et al. 2018). This combination of features led Muizon and Ladevèze (2020) to reject closely affinities between *Austropediomys* and pediomyoids, suggesting stem-microbiotherian affinities instead. Moreover, a nearly complete jaw (DGM 928-M) did not support the inclusion of *Austropediomys* as a microbiotheriid, as its hypoconid is not well-labially salient on m3, m4 is not reduced in comparison with m3, the anterobasal cingulid is not reduced, hypoconulid is not labially shifted and the talonid of m4 is not shortened.

The upper molars of *Austropediomys* present some degree of mesiodistal compression, small stylar cusps on M2-3, closely spaced paracone and metacone, an elongated protoconal basin, the presence of inflated conuloids, and a moderately expanded protocone (Carneiro et al. 2018). The mesiodistal compression of its molars indicates a short rostrum, and the inflation of its conuloids seems to resemble, by homoplasy, the rounded and inflated metaconules of other taxa, such as *Itaboraidelphys* and *Didelphopsis*. These features indicate that *Austropediomys*

was probably adapted to the ingestion of hard food resources, such as hard exoskeleton insects and/or seeds.

5.4.2 *Eobrasilia*: a probable Brazilian stagodontid and the diversity of durophagous metatherians from Itaboraí

Stagodontidae Marsh, 1889b represented another important group of metatherians from the Late Cretaceous period of North America (Clemens 1966; Brannick and Wilson 2018). Stagodontidae is characterized by the presence of inflated premolars, a stout dentary; large, lower molars with enlarged paraconids similarly sized to the protoconids (Clemens 1966; Wilson et al. 2016).

The possible presence of stagodontids in South America was briefly suggested by Simpson (1947) and Marshall (1984), who commented on the similarities between *Eobrasilia* and *Didelphodon* Marsh 1889a; nonetheless, they did not formalize *Eobrasilia* as a representative of this group. On a similar concept, Ladevèze and Muizon (2010) recovered *Eobrasilia* as the sister taxon of *Didelphodon* in their phylogenetic analysis.

Eobrasilia coutoi is represented by a badly broken, incomplete skull with heavily worn teeth (Simpson 1947), and by a fragmentary dentary also with heavily worn teeth (Marshall 1984) (Fig. 5.5). Unfortunately, the absence of preserved dental elements resulted in little attention being paid to this taxon in the literature since its formal description was traditionally identified as a potential “missing-link” between the Borhyaenoidea and “Didelphoidea” metatherians (sensu Simpson 1947) or as a Didelphidae (sensu Paula Couto 1962). The presence of large, inflated premolars, especially the p3, led *Eobrasilia* to be grouped with *Didelphopsis*, *Tiulordia*, and *Gaylordia* into the polyphyletic “Eobrasiliinae”, within Didelphidae by Marshall (1987) and Didelphimorphia by Oliveira (1998).

FIGURE 5.5

Carneiro and Oliveira (2017b) discussed the great number of similarities between *Eobrasilia* and stagodontids, particularly *Didelphodon* (but see e.g., Brannick and Wilson 2018; Eldridge et al. 2019). These taxa are very large for ‘didelphoid standards’ (see Methodological approach – 5.2) and share the presence of inflated premolars, p3 with bulbous roots, a robust jaw, a reinforced palate, a reduced, mesiodistally compressed m1; an obliquely oriented p1, and three semi-procumbent lower incisors (i2-4), in which i4 is markedly smaller than i2-3. All of these are considered as synapomorphies of Stagodontidae and supposed autapomorphies of *Eobrasilia* amongst South American metatherians (Marshall 1987; Carneiro and Oliveira

2017b). Furthermore, *Eobrasilia* and *Didelphodon* are the only metatherians that share an evident mesiodistal development of the third lower premolars (p3), an adaptation, which was recovered by Carneiro and Oliviera (2017b) as a synapomorphy for them.

Within the Itaboraí metatherians, *Eobrasilia coutoi* differs from *Didelphopsis cabrerai*, another durophagous taxon, in the presence of enlarged, semi-procumbent lower incisors, a narrow anteriorly, foreshortened anterior ramus of the dentary; a semi-procumbent lower canine, an incipiently three-rooted p3, p3 with bulbous roots, and an extremely bulbous dentary below p3 (Marshall 1987).

Didelphopsis cabrerai presents a large, rounded and bulbous p3, in which two roots are easily identified. The specialized durophagous adaptations of this taxon are evidenced by an isolated heavily worn down p3 (MN 2878(c)-V), its type specimen (MN 1429-V) plus some other specimens (e.g., MN 2883(a)-V). Oliveira (1998) identified a second morphotype for *Didelphopsis* (i.e., *Didelphopsis* sp.). This taxon is around 40% larger in its overall dimensions than *D. cabrerai*; even so, it is too small to be considered compatible with the missing dentition of *Eobrasilia coutoi*.

Gaylordia is another metatherian in which durophagous adaptations have been identified. Originally, Paula Couto (1952b) described *G. macrocynodonta*; later, Paula Couto (1962) proposed “*Xenodelphis doelloi*” and Paula Couto (1970) proposed *G. “mendesii*”. Marshall (1987) synonymized “*X. doelloi*” and *G. “mendesii*” as *G. doelloi*. More recently, Oliveira and Goin (2015) described *Gaylordia mater*. *Gaylordia mater* presents a less derived dentition in comparison to *G. macrocynodonta* and *G. doelloi*, since the former has a longer retromolar space (larger than 50% of m4’s length), and an inflated, although non bulbous, p3 in comparison with the other two (Oliveira and Goin 2015).

Based on this, Carneiro and Oliveira (2017b) revised the “eobrasiliines”; a proposed group based on the synapomorphic presence of a bulbous, inflated p3, and concluded that the specialized durophagous adaptations shared between *Eobrasilia*, *Didelphopsis* and *Gaylordia* were a result of convergent evolution. Thus, Carneiro and Oliveira (2017b) proposed the polyphyly of “Eobrasiliinae”, a similar result to previous studies (see e.g., Oliveira and Goin 2011). Moreover, a recently found damaged, isolated right p3 with preserved roots (MCT.M.4430) assigned to *Didelphopsis* sp. indicates that this taxon had proportionally smaller p3 than *D. cabrerai*. These studies concluded that a bulbous, large p3 should be considered as an autapomorphy of some species (e.g., *G. macrocynodonta* and *D. cabrerai*) and not as a symplesiomorphy for “Eobrasiliinae”.

The discussed features (e.g., robust jaws, bulbous and large p3) for stagodontids, *Gaylordia* and *Didelphopsis* represent specializations for ingesting hard food resources, such

as mollusk shells, hard seeds, hard exoskeleton arthropods, dry fruits or bones (Wilson et al. 2016; Carneiro and Oliveira 2017b), as these represent specializations for crushing (Clemens 1966; Marshall 1984; Wilson et al. 2016). The presence of three specialized taxa adapted to durophagy is uniquely found in the Itaboraí fauna in comparison with other global faunas, since *Eobrasilia* and *Gaylordia* are endemic to this locality. Carneiro and Oliveira (2017b) discussed the possibility that these taxa were specialized to ingest snails, which requires a strong bite and a resistant dentition in order to break the shell of these invertebrates. A similar pattern of adaptation is also recognizable in *Malleodectes* Arena et al., 2011, which was specialized to ingest gastropods (Arena et al. 2011; Archer et al. 2016).

Carneiro and Oliveira (2017b) proposed that such a diversity of durophagous metatherians in a single fauna may be related to the great diversity and abundance of snails found in this locality (Carneiro and Oliveira 2017b). However, snails from the Itaboraí Basin were not found in association with metatherians in the dissolution fissures from which most of the fossils were retrieved (Paula Couto 1949; Bergqvist et al. 2009). One explanation for this apparent absence was provided by Paula Couto (1949: 9)¹: “We believe, however, that this almost total absence of fossil shells is simply due to the fact that shells are much more fragile than bones and teeth, especially those of gastropods, and thus have much less resilience to blows than teeth and bones”. If confirmed, the apparent absence of gastropods in association with the metatherians is a consequence of the preservation bias.

The dentition of *Gaylordia* indicates some adaptations to insectivory (e.g., mesiodistally compressed upper molars and protocone, broad stylar shelf, reduced conules), with evident durophagous adaptations in *G. macrocynodonta* and *G. doelloi* (e.g., large, bulbous p3). *Didelphopsis* presents some omnivorous adaptations (e.g., a broad protocone, brachydonty, an inflated metaconule, poorly inflated StB and StD, a labial cusp to the ectoloph of the centrocrista and a relatively flattened entoconid), which may support insects, fruits and gastropods as possibly explored food resources (i.e., insectivory-frugivory of Zimicz 2012). The larger *Didelphopsis* sp. could be considered as being more adapted to insectivory-frugivory (see e.g., Zimicz 2012) based on its larger size, inflated, but not bulbous p3, and an m4's talonid longer than the trigonid. *Didelphopsis cabrerai* had more evident durophagous adaptations (e.g., large, bulbous P3/p3), which might support an omnivorous-durophagous diet for it, with hard exoskeleton insects, seeds and fruits as potentially explored food resources.

Eobrasilia seems to be the most specialized of these three genera and the most probable to be adapted to the ingestion of gastropods (see e.g., Carneiro and Oliveira 2017b). Unfortunately, as no molar has been assigned to this taxon, a diet specification could not be properly proposed. Nonetheless, the very large size and evident durophagous adaptations of this

taxon are indicative of a more specialized diet in comparison to *Gaylordia* and *Didelphopsis*.

5.4.3 *Zeusdelphys*: a very large, enigmatic metatherian from the Itaboraí fauna

The enigmatic *Zeusdelphys complicatus* represented one of the largest known metatherians of the Itaboraí fauna, rivaling in size with *Eobrasilia* and cf. *Nemolestes* (Oliveira 1998; Oliveira and Goin 2011; Carneiro and Oliveira 2017a). Its very large size, wrinkled enamel, bunodont molars, and large StB and StD are indicative of a specialized diet (Carneiro and Oliveira 2017a), such as strict frugivory (Zimicz 2012). Unfortunately, *Zeusdelphys* has been identified only by a single upper molar, which contributes for its enigmatic nature (Fig. 5.6). One curious fact is that the epithet ‘*complicatus*’ proposed by Marshall (1987) for the species *Z. complicatus* was based on the wrinkled condition of its molar enamel, rather than its “complicated” affinities.

FIGURE 5.6

Zeusdelphys was initially considered a M3 (and less likely, M2) of *Eobrasilia coutoi* by Marshall (1984). Later, Marshall (1987:125-126) presented a review of Itaboraí’s metatherians, in which he described *Zeusdelphys complicatus* emphasizing that “(...) based on additional knowledge of the complementary structure of upper and lower dentitions of Itaboraí taxa, it became apparent that this tooth and the lower dentition of *Eobrasilia* are not structurally compatible”. However, Marshall’s (1987) conclusion about the validity of *Zeusdelphys* as an independent taxon from *Eobrasilia* was based on its definition of “Eobrasiliinae”, which is a polyphyletic taxon.

More recently, Goin et al. (1998), Oliveira (1998), Oliveira and Goin (2011), Oliveira et al. (2016), and Carneiro and Oliveira (2017a) considered the type specimen of *Zeusdelphys* (MCT 2830-M/ex DGM 896a-M) as a M1? based on the presence of a shallow ectoflexus, a short postmetacrista, a mesially shifted protocone and a StB partially fused with the paracone. Nevertheless, the also very large and bunodont *Carolocoutoia ferigoloi* shows similar upper molar features on its M2 or M3 (MCN-PV 1802). This observation supports the previously referred combination of features as plausible for M2-3 of specialized bunodont taxa.

If a M1, *Zeusdelphys* would be twice as large as the expected size of first upper and lower molars of *Eobrasilia* (based on preserved alveoli of the specimens AMNH 39424 and DGM 919-M); however, if a M3, then *Zeusdelphys* would be similar to the expected size of a M3 of *Eobrasilia*. Based on this, the authors of this chapter do not discard Marshall’s (1984) original hypothesis that *Zeusdelphys* represents a M3 of *Eobrasilia* (i.e., *Zeusdelphys* could

represent a junior synonymous of *Eobrasilia*).

After Marshall (1987), *Zeusdelphys* became considered as a Protodidelphinae – Caroloameghiniidae – Polydolopimorphia based on the presence of wrinkled enamel, a bunodont molar, a very large size, a metacone larger than the paracone, a large protocone, and large StB and StD. Oliveira (1998) and Oliveira and Goin (2011) discussed the similarities between this taxon with Chulpasiinae Sigé et al., 2009, and *Hatcheritherium alpha* Case et al., 2005 but considered these similarities to have resulted from convergent evolution, concluding that *Zeusdelphys* should be considered as a protodidelphid.

Later, Carneiro and Oliveira (2017a) re-discussed the affinities of *Zeusdelphys* with Protodidelphidae, and included *Glasbuis*, *Hatcheritherium alpha*, and “Alphadontidae” Marshall et al., 1990 in the discussion. Based on their results, *Zeusdelphys* differs from protodidelphids due to the presence of a large and lingually shifted StC?, pyramidal styler cusps, three cusps on the postmetacrista and well-developed accessory crests on StD. To the contrary, *Zeusdelphys complicatus* shared several features with *Hatcheritherium alpha* (see e.g., Carneiro and Oliveira 2017a): the presence of three cusps associated with the postmetacrista, discontinuous centrocrista (sensu Carneiro and Oliveira 2017a – i.e., postparacrista is straight, whereas the premetacrista is obliquely oriented and invasive on the styler shelf), a bifurcated medium accessory crest on StD, concave medial borders on StB and StD and the evident pyramidal shape of these two styler cusps. This combination of characters led Carneiro and Oliveira (2017a) to assign *Zeusdelphys* as a representative of Hatcheriformes, within Alphadontia (i.e., the group that includes “Alphadontidae” + Hatcheriformes).

The presence of three cusps associated with the postmetacrista is only present in some Late Cretaceous metatherians and *Zeusdelphys* in South America, which would be an indicative of “North American” affinities for it (Carneiro and Oliveira 2017a). However, the absence of other preserved elements of *Zeusdelphys* does not allow further conclusions.

5.5 The Itaboraí Fauna Confirms the Occurrence of North American “Peradectoids” During the Early Eocene in South America

“Peradectia” Marshall et al., 1990 is an enigmatic group of Late Cretaceous and Paleogene metatherians. The oldest known representative of “Peradectia” is from the Judithian NALMA (late Campanian; Late Cretaceous – around 72 MYA) of the Aguja Formation, Terlingua local fauna, West Texas, USA (Cifelli 1994), which supports a late Campanian oldest occurrence for Sudameridelphia and a late Campanian beginning of the FABI. “Peradectia” reached its greatest diversity during the Cenozoic of North America, with six genera and more than 10 species. Nevertheless, some possible “peradectoids” have been identified in South America: Santa Lucía

Formation, Bolivia; Laguna Umayo Formation, southern Peru (late Paleocene-early Eocene – Sigé et al. 2009; or Peligran SALMA – early Paleocene – Chornogubsky and Goin 2015), Itaboraí Basin, Brazil; Las Flores, southern Argentina, and Paso del Sapo local faunas, southern Argentina (early middle Eocene – Tejedor et al. 2009). Amongst these, the Itaboraí fauna is highlighted based on the presence of the ‘gen nov 1’ and *Bergqvistherium*.

There are two identifiable species of the ‘gen nov 1’ (Fig. 5.7) in the Itaboraí fauna, which mainly differ in size and the degree of compression of the entoconid (see e.g., Oliveira 1998). The ‘gen nov 1 et sp nov 1’ is one of the smallest taxa of the fauna (Fig. 5.7E). This species is smaller in size, with a more labiolingually compressed entoconid and lacks the evident labiolingual compression and trigonid of m2 presented in ‘gen nov 1 et sp nov 2’. The very small size of this species would support an insectivorous diet.

The ‘gen nov 1 et sp nov 2’ (Fig. 5.7A-D) from the Itaboraí fauna is identified by the presence of a broad styler shelf, which covers 50% of the total width of M3; a paracone and metacone almost subequal in height on M3 (a slightly broader metacone) and a larger metacone on M1-2, a ‘spire-like’, inflated entoconid, and hypoconulid somewhat centrally shifted on m4. This species presents substantially labiolingually compressed premolars with sharp mesial and distal walls (autapomorphy), which are almost symmetric on the lateral view (DGM 920-M).

The presence of labiolingually expanded paraconids, with a very labiolingually compressed trigonid on m2, a labiolingually compressed m2, and sharp, symmetric p3 represent adaptations to carnivory and insectivory. However, the presence of a ‘spire-like’ entoconid, a talonid and trigonid almost subequal in length, a broad styler shelf and a moderately robust protocone supports a more hypocarnivorous diet (omnivory-carnivory as suggested by Oliveira 1998). Through evidence-based sources, the ‘gen nov 1 et sp nov 2’ was probably an insectivorous taxon (see e.g., Zimicz 2012).

FIGURE 5.7

Oliveira (1998) identified a second “peradectoid” from Itaboraí, considering it to be similar to *Andinodelphys*. However, the pucadelphydan affinities of *Andinodelphys* have been extensively discussed by Muizon et al. (2018). Later, this ‘second peradectoid’ was described as *Bergqvistherium primigenia* by Carneiro (2019) (Fig. 5.7F-H). Carneiro (2019) initially grouped *Bergqvistherium* within Protodidelphidae, but the assignment of some isolated upper molars to this taxon (MCN-PV 1803 and UFRJ 151-M) support its “peradectoid” affinities.

Bergqvistherium presents a broad, developed styler shelf on M3 (covering 50% or more of the transverse width) (Fig. 5.7F), a small to reduced StD, two twinned StCs on M2-3, a

twisted paracone on M2 (Fig. 5.7G), a moderately expanded protocone, a somewhat rounded, expanded distal wall of the protocone and a metaconid distal to the protoconid (Fig. 5.7H). *Bergqvistherium* differs from the ‘gen nov 1’ due to the presence of more brachydonty adaptations, two StCs (twinned StC) on upper molars, a twisted paracone on M2, lower molars are relatively less “elongated”, especially m3, and lower molars trigonids are more mesiodistally compressed. The dental adaptations, such as brachydont molars, a sharp entocristid, a moderately expanded protocone and a broad styler shelf, support an omnivorous diet.

5.6 The Diversification of Bunodont Metatherians in South America and the Paleocene-Eocene Thermal Maximum (PETM)

5.6.1 Early Eocene faunas from South America after the PETM

As previously mentioned, the Itaboraí Basin is currently considered to have preserved an early Eocene fauna (Itaboraiense SALMA), following the conclusions of Goin et al. (1998, 2009, 2010, 2012, 2016), Oliveira (1998), Goin and Oliveira (2007), Oliveira and Goin (2011, 2012, 2015), Woodburne et al. (2014), Oliveira et al. (2016), Beck (2017), Carneiro and Oliveira (2017a, b), Carneiro (2018, 2019), Carneiro et al. (2018), and Rangel et al. (2019).

The early Eocene epoch assigned to this fauna has been inferred on the basis of correlations with the fauna recovered from Las Flores Formation, Chubut, in Argentina (Fig. 5.1A). Indeed, the local faunas of Itaboraí and Las Flores are extremely similar, as presented by Oliveira (1998), Oliveira and Goin (2012), Zimicz (2012), and Woodburne et al. (2014), with, at least, 17 metatherian genera shared between them.

Bowen et al. (2015) concluded that during the Paleocene-Eocene transition (around 55.5 MYA), two massive, rapid releases of carbon into the atmosphere, due to volcanic activities, resulted in the abrupt warming of the earth’s climate by 5° C to 8° C. This paleoclimatic event resulted in the expansion of tropical forests and fruit plants worldwide (Woodburne et al. 2014). After this event, polydolopimorphians, which are rare or, at least, less abundant than other metatherian groups (see Tiupampa faunal diversity presented in Marshall and Muizon 1988; Muizon 1992), became by far the most abundant group of metatherians from the Eocene to the early Oligocene of South America. In addition, an increase in the diversity of several brachydont and bunodont taxa is identified as an evolutionary response to these events.

The recorded fauna of Itaboraí, following Zimicz’s (2012) categories, preserved two strict frugivorous taxa (i.e., *Carolocoutoia* and *Zeusdelphys*), two frugivorous/folivorous polydolopimorphians (i.e., *Epidolops* and *Gashternia*), several insectivorous-frugivorous bunodont taxa (e.g., *Bobbschaefferia*, *Guggenheimia*, *Periprotodidelphis*,

Procaroloameghinia, and *Protodidelphis*) and some omnivorous brachydont taxa (e.g., *Bergqvistherium* and *Mirandatherium*), which also presented some degree of frugivorous adaptations. With the exception of the Las Flores fauna, no other fauna in the world has demonstrated a similar number of brachydont-bunodont metatherians (Oliveira and Goin 2011, 2012).

Goin (2012, 2016), Woodburne et al. (2014), and Carneiro (2019) considered the PETM as the most important Paleogene diversification event in the evolution of South American metatherians. This hypothesis has been discussed by Carneiro (2019), who suggested a short-time diversification of protodidelphids based on the great diversity of this group in the Itaboraí fauna, with four genera and six species. These results could also be extended for polydolopimorphians (see e.g., Goin et al. 2016) and caroloameghinioids, as discussed below.

5.6.2 A reassessment of bunodont metatherians from the Itaboraí Basin

The bunodont metatherians of the Itaboraí fauna have been studied since the 1990s. Amongst these studies, Oliveira and Goin (2011) provided a focused systematic study for most of the taxa from this locality, which was later reviewed by Carneiro and Oliveira (2017a) and Carneiro (2019). The presence of a moderate to reduced stylar shelf, brachydonty-bunodonty adaptations (e.g., low crests, rounded cusps), an inflated metaconule and entoconid, a broad protocone and talonid basin, a developed protoconal and labial cingula, a mesiodistally compressed trigonid, and a reduced paraconid, represented compatible adaptations with omnivory, insectivory-frugivory and strict frugivory (Oliveira 1998; Oliveira and Goin 2011, 2012; Carneiro and Oliveira 2017a; Carneiro 2019).

Amongst these groups, Caroloameghiniidae is a Paleogene group of frugivorous metatherians, which is represented by *Procaroloameghinia* (Fig. 5.8), *Caroloameghinia* and *Canchadephys* (Marshall 1982a; Goin et al. 1998, 2010; Goin 2007; Oliveira and Goin 2011, 2012). Marshall (1982a) and Goin (2007) defined this group as presenting two accessory crests on StB (acc1 and acc2 – sensu Goin 2007), very broad (i.e., well mesio-distally expanded), straight centrocrista, narrow stylar shelf, conical and large entoconids, mesiodistally compressed trigonids, inflated premolars and reduced p1.

The systematic affinities of caroloameghinioids have always been a constant point of discussion: Marshall (1987) included amongst the caroloameghiniids, several brachydont-bunodont metatherians from Itaboraí, such as *Procaroloameghinia*, *Protodidelphis*, *Bobbschaefferia*, *Guggenheimia*, *Zeusdelphys* and other taxa, such as *Glasbius* Clemens, 1966, *Roberthoffstetteria* Marshall et al., 1983 and *Reigia* Pascual, 1983. Later, Marshall et al. (1990) considered Caroloameghiniinae as “peradectids”, along with “Peradectinae” and

“Alphadontinae”, mostly based on the presence of a straight centrocrista. The “peradectoid” affinities of this group were also suggested by Goin et al. (1998) and Goin (2007).

FIGURE 5.8

This confused concept of Caroloameghiniidae was chiefly based on the presence of bunodont adaptations in the dentition of these taxa (Oliveira 1998; Oliveira and Goin 2011), in which several taxa were grouped in a polyphyletic clade. The phylogenetic analyses provided by Oliveira and Goin (2011), Oliveira et al. (2016), Carneiro and Oliveira (2017b), Carneiro (2018, 2019), and Carneiro et al. (2018) recovered a polyphyletic state of these “generalized” bunodont taxa, with three major groups of frugivorous metatherians: Caroloameghinoidea, Polydolopimorphia and Protodidelphidae.

Other taxa from Itaboraí that should also be considered as more closely related to caroloameghinoids or glasbiids are *Bobbschaefferia* (originally, *Schaefferia* (Paula Couto, 1952b)), *Mirandatherium* (originally, “*Mirandaia ribeiroi*” (Paula Couto, 1952c)) and the ‘gen nov 2’ (Fig. 5.9A-B). Oliveira (1998) recovered *Bobbschaefferia*, *Glasbius*, *Procaroloameghinia*, and *Caroloameghinia* as the sister group of the ‘gen nov 2’. A similar result was suggested by Babot et al. (2020), who considered the ‘gen nov 2’ (for them, aff. *Bobbschaefferia* sp. as proposed by Oliveira and Goin (2011) – MCT 2816-M), *Reigia* and *Apeirodon* Babot et al., 2020, as possible polydolopimorphians, along with *Glasbius*. The affinities of *Reigia*, *Apeirodon* and *Bobbschaefferia* (Fig. 5.9E) with *Glasbius* were based on the presence of a slightly inflated metaconule, a bulky protocone, a moderately developed or narrow styler shelf, an inflated StB and StD, brachydonty-bunodonty adaptations, a broad talonid basin, and a mesiodistally compressed trigonid. Notwithstanding, the bunodont adaptations of caroloameghinoids are less derived than those of *Glasbius* and other “glasbiids” (see e.g., Oliveira 1998; Babot et al. 2020).

Mirandatherium (Fig. 5.9C-D) was considered as a representative of its own group (i.e., Mirandatheriidae) by Szalay (1994), as a microbiotheriid by Marshall (1987) and Oliveira and Goin (2011) mostly based on its well-labially salient hypoconid and labially placed hypoconulid; and as a caroloameghinoid by Carneiro and Oliveira (2017b), Carneiro (2018, 2019), and Carneiro et al. (2018). Two upper molars assigned as aff. *Bobbschaefferia* sp. by Oliveira and Goin (2011) (MN 2894(a1)-V and MCN PV 1797) should be assigned to *Mirandatherium* due to its features (e.g., relatively lower crests, a more ‘u-shaped’ protocone, StB with reduced accessory crests, brachydonty) and compatible size. This association excludes the hypothesis of close affinities between *Mirandatherium* and microbiotherians; a result

previously proposed by Goin and Abello (2013) but supports close affinities with glasbiids and caroloameghiniids.

In line with this proposal, the ‘gen nov 2’, *Mirandatherium* and *Bobbschaefferia* share a great number of features: a flattened, relatively large entoconid, and a broad and labially projected hypoconid. *Bobbschaefferia* differs from *Mirandatherium* due to its relatively larger paraconid and more robust jaw (Fig. 5.9E). *Mirandatherium* presents a more “opened” trigonid, a p3 with the posterior root located slightly lingual to m1 and a short metacingulum (Fig. 5.9C-D). The ‘gen nov 2’ was firstly assigned to *Mirandatherium* by Marshall (1987) but it differs from other taxa in the presence of an entoconid clearly distal to hypoconid on m1 and a developed basal posterior projection of the protocone on M3 (see e.g., Babot et al. 2020). Furthermore, it differs from *Mirandatherium* also in the presence of a relatively longer talonid on m4 and p3 not lingually oriented (see Oliveira 1998:233).

The dentition of *Mirandatherium* supports an omnivorous diet for this taxon, since there is evidence of adaptations to ingest invertebrates and also, to a lesser degree, possibly fruits (e.g., shorter talonids than the trigonid on m4 and nearly subequal on m1-3, an “opened” trigonid, a small paraconid, a ‘u-shaped’ protocone, a moderately developed styler shelf, sharp crests, a postprotocrista distolingual expansion with a short metacingulum). The inflated metaconule and broad hypoconid may support the ingestion of hard food resources, such as hard exoskeleton insects and seeds. A similar conclusion could also be inferred for the ‘gen nov 2’.

Bobbschaefferia presents frugivorous adaptations, although not as specialized as *Procaroloameghinia* or *Protodidelphis*. Moreover, its robust jaw, mesiodistally compressed trigonid with a similarly sized paraconid and metaconid seems to represent some adaptations for ingesting hard food resources, such as seeds, hard exoskeleton insects or dry fruits. Based on this, *Bobbschaefferia* should be considered as an insectivorous-frugivorous taxon.

The adaptations of *Bobbschaefferia* resemble the molar and premolar adaptations of protodidelphids, such as inflated, somewhat rounded premolars, a slightly labially salient hypoconid, robust jaws and short trigonids. However, *Bobbschaefferia* differs from protodidelphids (Didelphimorphia) in the relatively greater difference in height between the trigonid and the talonid, and the absence of ‘spire-like’ entoconids. It also differs from protodidelphids in that it has no large, inflated StD, except for *Periprotodidelphis*; and the m4 talonid is not longer than the trigonid.

Procaroloameghinia was probably more adapted to ingesting fruits (e.g., more inflated ‘pyramidal’ entoconids, a more advanced bunodonty, a more compressed trigonid, an inflated, rounded p3). Goin et al. (1998) and Zimicz (2012) referred to an upper molar assigned to

Procaroloameghinia (MLP 90-II-5-138, an M2), this specimen presents a bulky protocone and an inflated, large StB and StD, which support its frugivorous adaptations.

Furthermore, glasbiids and caroloameghinioids lack the dental synapomorphies of didelphimorphians (see discussion later in this chapter on 5.11), and should therefore not be considered as ‘true’ marsupials. The possibility that these taxa were grouped as hatcheriforms is also unlikely, since they present an incipient dilambdodont centrocrista, lack three cusps on the postmetacrista and an “ornamented” StD with several accessory crests.

Based on current discussion, the presence of several lineages of metatherians in the Itaboraí fauna with brachydonty-bunodonty adaptations (i.e., polydolopimorphians, protodidelphids and caroloameghinioids) supports the hypothesis of convergent evolution between these groups as a possible evolutionary response to PETM events.

5.7 Sparassodonts from the Itaboraí Fauna Support an Early Occupation of the Hypercarnivorous Mammalian Ecological Niche in South America

Sparassodonta was an endemic South American group of derived carnivorous metatherians (Prevosti and Forasiepi 2018; Rangel et al. 2019; contra Carneiro 2018). This group was represented by medium to very large carnivorous taxa that evolved to occupy the role of the main mammalian predators during most of the Paleogene and Neogene, which included saber-tooth, bone-cracker, weasel-like, and bear-sized taxa (Prevosti and Forasiepi 2018).

The Paleocene representatives of Sparassodonta are *Mayulestes ferox* Muizon, 1994 and *Allqokirus australis* Marshall and Muizon, 1988 from the lower Paleocene period of the Santa Lucía Formation, Bolivia (Tiupampa fauna – see e.g., Muizon 1992, 1994; Muizon et al. 2018; Rangel et al. 2019). After Tiupampa, the oldest confirmed occurrences of this group are from the Itaboraí fauna, represented by *Patene simpsoni* (Fig. 5.10A-D) and cf. *Nemolestes* (Fig. 5.10E). This fauna stands out as an important assemblage, since it represents the most ancient fossil record presently known of sparassodonts after the PETM.

FIGURE 5.10

During the early Eocene, sparassodonts were amongst the largest metatherians of the Itaboraí fauna, with *Patene simpsoni* reaching the size of a domestic cat and weighing around 1.35 kg, and cf. *Nemolestes* with a body mass of around 5.72 kg (Zimicz 2012; Prevosti and Forasiepi 2018). *Patene simpsoni* differs from cf. *Nemolestes* in the smaller size, presence of a relatively larger metaconid on m4 and a longer talonid on m4. This combination of features

indicates that *P. simpsoni* probably represented a faunivorous predator (i.e., a mesocarnivorous taxon – sensu Zimicz 2012), whereas cf. *Nemolestes* represented a top mammalian predator of the fauna, with a suggested hypercarnivorous diet (see e.g., Zimicz 2012; Prevosti and Forasiepi 2018; Rangel et al. 2019). These results support the previous conclusions of Zimicz (2012), Prevosti and Forasiepi (2018), and Rangel et al. (2019) regarding a low niche overlapping between *Patene* and cf. *Nemolestes* amongst the mammalian assemblage of Itaboraí.

The specialized carnivorous adaptations of sparassodonts are recognizable by their modified dentition, which differs from every other metatherian group in South America in the evident reduction and absence of a metaconid and talonid on the lower molars. These metatherians also show an enlargement of the paraconid on the lower molars and, in more specialized taxa, an evident reduction of the stylar shelf, paracone and protocone on the upper molars (Zimicz 2012; Carneiro 2018; Rangel et al. 2019).

Most of sparassodonts should be considered as hypercarnivorous taxa (Zimicz 2012; Prevosti and Forasiepi 2018); however, the consideration of mesocarnivorous adaptations for the oldest representatives of this group, such as *Patene* indicates that this group “gradually” evolved to hypercarnivory during the Cenozoic (Zimicz 2012; Rangel et al. 2019). The presence of the relatively large and specialized cf. *Nemolestes* indicates that during the early Eocene sparassodonts had already occupied the ecological niche of mammalian predators in South America (Zimicz 2012; Rangel et al. 2019). Based on this, the Itaboraí fauna has preserved the oldest hypercarnivorous sparassodont currently known (i.e., cf. *Nemolestes* – see e.g., Rangel et al. 2019).

5.8 The Itaboraí Fauna Has Preserved the Most Diverse Fauna of Tiny Insectivorous Metatherians of South America

The recognition of tiny and very small-sized metatherians in the fossil record of Gondwana is known for the Paleogene of Antarctic (e.g., *Derorhynchus minutus* Goin et al., 1999) and Bolivia (e.g., *Szalinia gracilis* Muizon and Cifelli, 2001, *Jaskhadelphys minutus* Marshall and Muizon, 1988). However, it is in the Itaboraí fauna that the number of tiny and very small metatherians reached their greatest diversity in a single preserved locality, with at least seven genera and nine species, including *Minusculodelphis minimus*, *M. modicum* – Jaskhadelphyidae; *Marmosopsis juradoi*, *Marmosopsis* sp. and *Gaylordia doelloi* – these taxa are more closely related to jaskhadelphyids than to any other metatherian group; *Diogenesia brevirostris* – Derorhynchidae; *Armintodelphys* sp. – Herpetotheriidae?; *Carolopaulacoutoia* sp. – Sternbergiidae; and the ‘gen nov 1 et sp nov 1’ – “Peradectoidea”.

Jaskhadelphyids and closely related taxa comprise the most diverse group of tiny/very small-sized metatherians from the Itaboraí fauna, with the largest described representatives of this clade being *Gaylordia macrocynodonta* (Fig. 5.11A) and *G. mater* (Fig. 5.11B-D). The smallest representative, *Minusculodelphis minimus*, is the smallest Late Cretaceous, Paleogene and Neogene non-marsupial metatherian currently known, in which the largest known specimen has lower molars smaller than 0.90 mm in length and 0.65 mm in width. The jaskhadelphyids *M. minimus*, along with *M. modicum* (Fig. 5.11E-G), *Jaskhadelphys minutus* and *Kiruwamaq chisu* are considered to have weighed around 5g to 15g (see e.g., Zimicz 2012; Oliveira et al. 2016). The tiny size of *Minusculodelphis* and other jaskhadelphyids supports a strict insectivorous diet for them (see e.g., Zimicz 2012; Oliveira et al. 2016).

FIGURE 5.11

Zimicz (2012) and Oliveira et al. (2016) considered the representatives of this group as insectivorous or strict insectivorous taxa. As adaptations to insectivory, Oliveira et al. (2016) and Carneiro (2018) considered the presence of small, well mesially shifted paraconid, “open” trigonid (i.e., not mesiodistally compressed), tall and pinched trigonid cuspids, talonid shorter and narrower than the trigonid, reduced entoconid, mesiodistally compressed hypoconid, hypoconulid at the distolingual corner of the talonid, mesiodistally compressed upper molars, reduced conules, broad styler shelf, closely spaced paracone and metacone, and metacone much larger than the paracone. All these features are present in *Szalinia*, *Gaylordia*, *Marmosopsis* and jaskhadelphyids, which indicate that these taxa represented an insectivory adapted group, with *Tiulordia* + *Gaylordia* secondarily adapting to durophagy (see e.g., Marshall 1987; Oliveira 1998; Oliveira and Goin 2011, 2012, 2015; Zimicz 2012; Oliveira et al. 2016; Carneiro and Oliveira 2017b).

Marmosopsis juradoi (Fig. 5.11H-K) represented the second most abundant metatherian of the fauna, with at least 42 identified specimens, and were relatively much more abundant than other very small-sized insectivorous metatherians, such as the ‘gen nov 1 et sp nov 1’ (one specimen), *Diogenesia brevirostris* (one specimen), *Armintodelphys* sp. (one specimen), *Carolopaulacoutoia* sp. (two specimens) and *Marmosopsis* sp. (two specimens) (see Fig. 5.2). *Marmosopsis* was probably adapted to insectivory, similarly to *Minusculodelphis*, but perhaps not so specialized (see e.g., Zimicz 2012).

A second species of *Marmosopsis* is identified by its larger size, more robust dentary and more developed hypoconid on m4 (Oliveira 1998:138-141). Here, this taxon is identified as *Marmosopsis* sp. (Fig. 5.11L). This species represented another insectivorous taxon from the

Itaboraí's fauna, judging by its dental features; however, it was probably more adapted to consume harder food resources than *M. juradoi* due to its more labially positioned paraconid, robust dentary and more mesiodistally compressed trigonid (see e.g., Oliveira 1998:141).

The preserved partial skulls of *Gaylordia macrocynodonta* (DGM 329-M) and *Szalinia gracilis* Muizon and Cifelli, 2001 (see Muizon and Cifelli 2001) share some similar features: a short, broad rostrum, and a large, single lacrimal foramen. This unique combination of features may support their close affinities. Moreover, the dental features shared between these two taxa, *Tiulordia*, *Mizquedelphys*, *Incadelphys*, *Marmosopsis* and jaskhadelphyids (e.g., small entoconid, talonid shorter than trigonids, mesiodistally compressed upper molars, closely spaced paracone and metacone) have supported a closely relation for them in recent phylogenies (see e.g., Oliveira and Goin 2011; Oliveira et al. 2016; Carneiro et al. 2018; Rangel et al. 2019).

Oliveira et al. (2016) described the femur of *Minusculodelphis modicum* (DGM 921c-M) (Fig 5.11M). The presence of a developed third trochanter indicates terrestrial adaptations, and a possible understorey microhabitat for this taxon (Szalay and Sargis 2001). The understorey stratum registers the greatest abundance of soft-bodied Arthropoda, Gastropoda (i.e., snails and slugs), Annelida, and Onychophora (Oliveira et al. 2016).

Furthermore, the femur of *Minusculodelphis modicum* presents a third trochanter located about one third the distance down the shaft from the proximal end. This pattern is very similar to that of the femur morphotype 4 (see Szalay and Sargis 2001), which is the most abundant morphotype recovered in the fauna (with, at least, 11 specimens – *Marmosopsis juradoi*?). If confirmed, this feature could be interpreted as a synapomorphy of jaskhadelphyids and other more closely related taxa, such as *Marmosopsis*.

5.9 Polydolopimorphians from Itaboraí Fauna Help to Elucidate the Evolution and Affinities of These Eocene Faunal Dominant Metatherians

Polydolopimorphia represented the most abundant, diverse group of Paleogene metatherians and have been found in Western Gondwana in South America (Paula Couto 1952a, 1961, 1970; Marshall et al. 1983; Marshall and Muizon 1988; Muizon 1992; Goin and Candela 1996, 2004; Goin et al. 1998, 2010, 2012, 2016; Tejedor et al. 2009; Zimicz 2014; Chornogubsky and Goin 2015), Antarctic (Goin et al. 1999, 2018) and Australia (Sigé et al. 2009). This group probably also occurred in North America (*Glasbius* – Clemens 1966; Davis 2007) and Anatolia (Maga and Beck 2017; Métais et al. 2018). Amongst the occurrences in South America, the Itaboraí fauna recorded two taxa related to this group: *Epidolops ameghinoi* and *Gashternia carioca*, both belonging to Bonaparthieriiformes.

The importance of *Epidolops ameghinoi* (Fig. 5.12) is based on the fact that this taxon presents, in the words of Paula Couto (1952a:4): “An almost complete, although flattened skull, with premolars and molars present, and an associated complete mandible, with a well preserved dentition, were collected there”; “these are the most complete skull, mandible, and dentitions of marsupials of this family (at that time, *Epidolops* belonged to Polydolopidae) ever found, and because of them we have reached a better understanding of the morphology, structure, and affinities of the Polydolopidae”; and “the polydolopids are, aside from the didelphids (at that time, “didephids” included almost all “polyprotodonts” from the Itaboraí fauna, in exception of the time conception of Borhyaenidae), the most representative element in the Paleocene fauna of São José de Itaboraí, not in the number of forms but in the number of specimens (...)”.

FIGURE 5.12

Indeed, *Epidolops ameghinoi* is represented by more than 147 dental and jaw elements (MNI: 45) in the collections with Itaboraí fauna (see Fig. 5.2). This taxon encompasses more than three times more elements than the second most abundant metatherian in the fauna, *Marmosopsis juradoi*, which is represented by 42 dental and jaw elements (MNI: 20). This “absolute” abundance of *Epidolops* regarding other metatherians is evidence in favor of the hypothesis of Goin et al. (2012, 2016) and Woodburne et al. (2014) regarding the importance of the PETM for the evolution and increase in the abundance of polydolopimorphians in South America.

On the contrary, *Gashternia carioca* is only represented by a single specimen (MCN PV 1801). The more diagnostic features of this taxon are the presence of large serrations and a lingual ‘protocone’ on its plagiaulacoid P3 (Goin and Oliveira 2007). Its upper molar differs from the one of *Epidolops* in the presence of several symplesiomorphies for Polydolopimorphia, such as presence of StE, short postmetacrista and preparacrista, paracone more labial than the metacone, and metacone larger than the paracone. On this combination of features, *Gashternia* seems to represent an early clade of specialized bonapartherioid polydolopimorphians, as discussed by Goin and Oliveira (2007).

More recently, Beck (2017) extended the understanding of the systematic affinities of Polydolopimorphia, as he included in the concept of his data matrix, cranial and some associated postcranial elements to *Epidolops*, such as the calcaneus morphotype IMG (Itaboraí Metatherian Group) VII, also described and assigned to this taxon by Szalay (1994); and the petrosal morphotype II (PII). The PII was recovered as more closely related to pucadephydans by Ladevèze and Muizon (2010).

Furthermore, Beck (2017) rejected the marsupial affinities of *Epidolops* based on the assigned petrosal morphotype (PII), which is compatible with Pucadelphyda; and the assigned tarsal element (IMG VII), as this tarsal morphotype shows only a single calcaneocuboid facet. The calcanei of Marsupialia have a subdivided calcaneocuboid facet, in which didelphimorphians have the calcaneocuboid facet subdivided into two subfacets (CaCud – distal calcaneocuboid facet; and CaCup – proximal calcaneocuboid facet – see discussion on 5.11) and paucituberculatans and australidelphians present three subfacets: the auxiliary calcaneocuboid facet (CaCua – homologous with the distal calcaneocuboid facet of didelphids), the lateral calcaneocuboid facet (CaCul – homologous with the proximal calcaneocuboid facet of didelphids), and the medial calcaneocuboid facet (CaCum – not present on didelphimorphians) (Szalay 1994; Beck 2017).

Bonapartherioids polydolopimorphians are identified by the presence of plagiaulacoid premolars (Fig. 5.12C), subquadrangular molars (Fig. 5.12A), robust protocones, ‘hypocone-like’ metaconules, developed and paired StB + paracone and StD + metacone, “open” centrocrista, brachydonty-bunodonty, modified short jaws, and mandibular condyle aligned with the tooth series. This combination of features enabled bonapartherioids to explore a wide range of food resources, representing a unique degree of adaptation in comparison with other metatherians during most of the Paleogene (Zimicz 2012, 2014; Goin et al. 2016).

Zimicz (2012, 2014) concluded that *Epidolops* should be considered as a mixed-feeder or generalist taxon, with seeds, dry fruits, invertebrates, and leaves amongst the possible explored food resources (i.e., folivory, frugivory, insectivory, and granivory - generalist). The wide variety of possible explored food resources could explain the greater abundance of this taxon with regard to other metatherians. *Gashternia* was considered to be a frugivorous/folivorous taxon (see e.g., Goin and Oliveira 2007) or a strict folivorous taxon (see e.g., Zimicz 2012, 2014). The folivorous adaptations of *Gashternia* represent a unique diet specialization in comparison to other metatherians of the Itaboraí fauna.

5.10 ‘Herpetotheriid-like’ Taxa from the Itaboraí Fauna

Herpetotheriidae is classically considered to be a North American and European lineage (Ladevèze et al. 2020). The oldest occurrences of this group are from the Maastricht Formation, the Netherlands, Europe (latest Maastrichtian – Late Cretaceous – around 66 MYA) (Martin et al. 2005). The oldest North American herpetotheriids are from the early Paleocene of US (Torrejonian NALMA – 64-63 MYA – Williamson and Taylor 2011), with *Swaindelphys* Johanson, 1996 (Johanson 1996; Williamson and Taylor 2011). The group reached its apex of

diversity during the Eocene and Oligocene in the northern continents (i.e., North America and Europe) (e.g., Korth 1994; Ladevèze et al. 2020).

Curiously, several taxa from South America have also been associated with herpetotheriids (see e.g., Oliveira 1998), which includes *Carolopaulacoutoia* (Fig. 5.13A-E), *Itaboraidelphys camposi* (Fig. 5.13F-G), *Didelphopsis cabrerai* (Fig. 5.13H-I), *Didelphopsis* sp. (Fig. 5.13J-K), Derorhynchinae Marshall, 1987 (Oliveira 1998; Oliveira and Goin 2012), and *Rumiodon* Goin and Candela, 2004 from the late Eocene of Peru (see e.g., Goin and Candela 2004).

Herpetotheriidae has been considered to represent the sister taxon of Marsupialia (Beck 2017; Maga and Beck 2017) or as ‘true’ marsupials (Wilson et al. 2016). Furthermore, Muizon et al. (2018) and Ladevèze et al. (2020) recovered a paraphyletic “Herpetotheriidae”, as *Herpetotherium* Cope, 1873 was recovered as being more closely related to Marsupialia than to *Peratherium* + *Amphiperatherium* (i.e., Peratheriinae Ladevèze et al., 2020). In addition, Goin and Candela (2004), and Oliveira and Goin (2012) considered *Rumiodon* and *Carolopaulacoutoia*, respectively, as South American herpetotheriids.

FIGURE 5.13

In a systematic context, Szalay (1994) proposed Sternbergiinae in order to include *Carolopaulacoutoia* (= *Sternbergia*, as a representative of Paucituberculata). Later, McKenna and Bell (1997) modified this taxon from a subfamily to a family rank (i.e., Sternbergiidae). Oliveira (1998) and Goin (2003) suggested the inclusion of *Carolopaulacoutoia*, *Itaboraidelphys*, *Marmosopsis*, *Didelphopsis*, *Djarthia* Godthelp et al., 1999, *Ankotarinja* Archer, 1976, and *Keeuna* Archer, 1976 as representatives of this group. However, Oliveira and Goin (2011), Carneiro and Oliveira (2017b), and Rangel et al. (2019) did not recover a monophyletic Sternbergiidae with the inclusion of these taxa (but see discussion below).

Oliveira (1998) observed that sternbergiids present a diagnostic trait, the presence of a cusp at the labial edge of the centrocrista (see e.g., Archer 1976; Oliveira 1998). This central cuspule/ridge is identified on *Carolopaulacoutoia*, *Itaboraidelphys*, *Didelphopsis*, *Maastrichtidelphys* and *Peratherium*. No derorhynchid or herpetotheriid described so far presented this cusp. The central cuspule/ridge has been considered as evidence in support of closer affinities of European “herpetotheriids” and South American sternbergiids, as previously discussed by other studies (see e.g., Oliveira 1998; Goin and Candela 2004; Hooker et al. 2008; Oliveira and Goin 2011, 2012).

Oliveira (1998), Oliveira and Goin (2011), Oliveira et al. (2016), Carneiro and Oliveira (2017b), Carneiro (2019), Carneiro et al. (2018), and Rangel et al. (2019) supported the sister relation of *Itaboraidelphys* + *Didelphopsis* based on the presence of moderately inflated metaconules, two supernumerary cusps associated to StC (i.e. three central cusps), moderately inflated entoconid, large size, and somewhat mesiodistally compressed trigonid. The main differences of these two taxa are based on their dental adaptations: *Itaboraidelphys* presents some mesocarnivorous or hypocarnivorous adaptations, such as broad styler shelf, slightly inflated metaconule, ‘v-shaped’ protocone, small paraconid, slightly distally shifted metaconid and p3 larger than the m1. These features support the exploration of insects and vertebrates as part of its diet. *Didelphopsis* presents omnivorous-durophagous adaptations, as discussed (see e.g., Oliveira 1998; Zimicz 2012; Carneiro and Oliveira 2018). In fact, both taxa are so similar that some specimens were interchangeably identified (e.g., MN 2878(b)-V) identified as *Itaboraidelphys camposi* by Marshall (1987) and, later, reassigned to *Didelphopsis cabrerai* by Oliveira (1998:82) based on the presence of a shallow ectoflexus, ‘u-shaped’ centrocrista, short paracingulum, and relatively more inflated and greater number of styler cusps.

Marshall and Muizon (1988), Muizon (1992), and Muizon et al. (2018) highlighted some dental similarities between *Itaboraidelphys* and *Andinodelphys*. Such hypothesis led Muizon et al. (2018) and Muizon and Ladevèze (2020) to suggest a possible association of the petrosal type II to *Itaboraidelphys* based on a compatible size and possible pucadelphyid affinities. However, *Didelphopsis* and *Itaboraidelphys* differ from *Andinodelphys* in the more invasive centrocrista, the presence of a central cusp on the apex of centrocrista, presence of supernumerary styler cusps, a more inflated and more linguallly shifted metaconule (see specimens MCT 2788-M and MN 2878(a)-V of *I. camposi*, MN 2878(b)-V of *Didelphopsis cabrerai*, and DGM 642-M of *Didelphopsis* sp.), and m4 hypoconulid not as the tallest talonid cuspid. This combination of features resembles more *Carolopaulacoutoia* and peratheriines than pucadelphyids. Thus, pucadelphydan affinities for *Itaboraidelphys* and *Didelphopsis* were not considered in this chapter.

Carolopaulacoutoia was a small taxon easily identified by its large, conical StC closely positioned to StB. This condition is similar to the ‘gen nov 1’, a “peradectoid” from Itaboraí fauna. These two taxa show some similarities, in addition to the position of StC: conical entoconid, mesiodistally developed trigonids, “pinched” hypoconids, not shortened talonids, especially on m4. This great number of shared features led Marshall (1987) to include the ‘gen nov 1’ as part of the hypodigma of *Carolopaulacoutoia*. Later, Oliveira (1998:146-151) separated both taxa and considered that *Carolopaulacoutoia* differs from the ‘gen nov 1’ on the

presence of an invasive centrocrista, absence of a ‘spire-like’ entoconid and more ‘premolariform’ p3 (i.e., the mesial wall of p3 is more convex than the distal one).

The dental adaptations of *Carolopaulacoutoia*, such as the invasive centrocrista, acute protocone, mesially expanded trigonid, small entoconid and ‘pinched’ hypoconid support an insectivorous diet.

Another ‘herpetotheriid-like’ group found in Itaboraí is Derorhynchidae, which was first proposed as a subfamily rank by Marshall (1987) but was later elevated to the category of family by Goin et al. (1999). Currently, Derorhynchidae included *Derorhynchus*, *Pauladelphys* Goin et al., 1999, *Coona* and, more recently, Oliveira et al. (2021) assigned *Diogenesia* and the ‘gen nov 3’ from the Itaboraí and Las Flores faunas to this group.

Oliveira et al. (2021) identified Derorhynchidae as a group of Paleogene metatherians with a labial contact of the cristid obliqua with the distal wall of the trigonid, a somewhat labially salient hypoconid, a moderately developed styler shelf and a developed, non-subdivided StC (Fig. 5.14). This group of Paleogene metatherians shares with herpetotheriids (e.g., *Herpetotherium* and *Copedelphys* Korth, 1994) the presence of enlarged, semi-procumbent lower incisors i2 and i3 (see Fig. 5.14D), which was considered as synapomorphies for them by Oliveira et al. (2021). This condition separates these two groups from sternbergiids, which present less enlarged, semi-procumbent lower incisors (see DGM 243-M, type specimen of *Didelphopsis cabrerai*, and comparisons with peratheriines as provided by Korth 1994: 385).

Amongst the Itaboraí derorhynchids, *Derorhynchus singularis* (Fig. 5.14H-K) is easily identified by its elongated jaw (Paula Couto 1952b, 1962). This taxon presents a long diastema between p1 and p2, evidently semi-procumbent canines and an abrupt elevation of the jaw at the p3 level, at which the anterior root of p3 is at a lower level than the posterior one. The upper dentition of *D. singularis* presents a shallow ectoflexus; mesiodistally expanded protocone, moderately developed styler shelf and developed styler cusps, especially StB and StC. A diagnostic trait (i.e., autapomorphy) of this taxon is the presence of a supernumerary and tiny cusp located at the distolabial wall of StB on M2 (Fig. 5.14H), a condition found in the two M2 currently assigned to this species (DGM 803-M and UFRJ 145-M).

With regard to the other two derorhynchids of the fauna, *Diogenesia* (Fig. 5.15C-G) is identified by the presence of a relatively more acute protocone, twisted paracone on M1, moderately developed styler shelf, very invasive centrocrista on the styler shelf, shallow and relatively short dentary, mesiodistally compressed paraconid and hypoconid subequal or slightly narrower than the trigonid on m1-3. *Diogenesia* has two identifiable species: *Diogenesia brevirostris* is smaller, presents a relatively larger paraconid and subequal trigonids

and talonids in width; whereas *Diogenesia* sp. is larger, has a hypoconid more labially salient on m1-2 and reduced posterobasal cingulids.

Following Oliveira et al. (2021), *Diogenesia* was recovered as the sister taxon of other derorhynchids (e.g., *Derorhynchus*, *Coona*, *Pauladelphys* and the ‘gen nov 3’) based on the presence of a relatively shorter and shallower dentary, supernumerary stylar cusps on the posterior stylar shelf on M1 and a more ‘v-shaped’ protocone.

The last derorhynchid of the fauna, the ‘gen nov 3’ (Fig. 5.14A-B) differs from the other two in the presence of a deeper ectoflexus on the upper molars, moderately robust dentary with no abrupt elevation of the jaw; ‘pyramidal’ entoconid that is somewhat twisted when compared with the paraconid and metaconid, and slightly labially salient hypoconid on m1-3. The morphology of its entoconid is similar to that of *Pauladelphys* and *Coona* Simpson, 1938, which supported their close affinities, following Oliveira et al. (2021).

The ‘gen nov 3’ differs from *Pauladelphys* in the relatively less developed entoconid, less mesiodistally compressed trigonid, more labially salient hypoconid and upper molars with deeper ectoflexus. This taxon differs from *Coona pattersoni* Simpson, 1938 in the entoconid more mesially placed than the hypoconid, relatively larger hypoconulid on m4, and relatively longer retromolar space.

Derorhynchids were probably an insectivorous adapted group, although not as specialized as jaskhadelphyids and *Marmosopsis*. *Diogenesia* is probably more adapted to insectivory as indicated by its very invasive centrocrista and ‘v-shaped’ protocone; the ‘gen nov 3’ was probably an omnivorous taxon based on its large, pyramidal entoconid, broad protocones on M1-2, which may indicate the ingestion of fruits; and its deep ectoflexus, mesially shifted paraconid, and slightly reduced stylar shelf indicate the consumption of invertebrates. *Derorhynchus* was probably an insectivorous or hypocarnivorous taxon based on its evidently mesiodistally compressed premolars, slightly shorter talonids than trigonids, conical entoconids, moderately robust dentary, abrupt increase in the height of dentary at the level of p3-m1, elongated jaw and semi-procumbent, enlarged lower incisors. For this taxon, invertebrates were probably an important food resource (see e.g., Zimicz 2012).

FIGURE 5.14

Another curious taxon from Itaboraí’s fauna is *Armintodelphys* sp. (Fig. 5.15). This taxon is only larger than *Minusculodelphis* and differs from the remaining taxa of the fauna due to the presence of a metaconid distally positioned to the protoconid on m3-4, slightly labiolingually compressed entoconid, labially salient hypoconid, low height difference between

the trigonid and talonid, and labial contact of the cristid obliqua. This combination of features suggests affinities with derorhynchids, herpetotheriids or stem paucituberculatans.

The overall features of this taxon also resemble *Armintodelphys*, a Paleogene North American and European taxon. Within this concept, *Armintodelphys* sp. is more similar to *A. duffraingi* Smith and Smith, 2013 regarding the short talonid on m4, distolingually positioned hypoconulid, metaconid distal to protoconid on m3, and “open” trigonid. However, the Itaboraí’s taxon differs from *A. duffraingi* in the relatively larger entoconid, more labially salient hypoconid and more labially shifted contact of the cristid obliqua.

FIGURE 5.15

5.11 Didelphimorphians from the Itaboraí Fauna, a Response to the Paleoclimatic Events of the PETM

“Two calcanea that attest to the existence of this group (Didelphimorphia), along with a single calcaneus making up IMG XII (and IMG V), represent the only unquestionable tarsal remains that share the synapomorphous calcaneal attributes of the living family Didelphidae”
(Szalay 1994:171).

Marsupialia is a group currently represented by Didelphimorphia, Paucituberculata, and Australidelphia (sensu Beck 2017; Carneiro and Oliveira 2017a, b; Carneiro 2018, 2019; Carneiro et al. 2018; Maga and Beck 2017; Rangel et al. 2019). However, several extinct groups have been claimed as extinct representatives of Marsupialia, such as Protodidelphidae (Goin and Candela 1996; Goin et al. 1998, 2016; Oliveira 1998), Polydolopimorphia (Oliveira 1998; Goin et al. 2009, 2010, 2016, 2018; Ladevèze and Muizon 2010; Chornogubsky and Goin 2015; Métais et al. 2018), some fossil taxa from the Itaboraí fauna (see e.g., Ladevèze and Muizon 2010), “Peradectidae” (Wilson et al. 2016), Herpetotheriidae (Wilson et al. 2016), and Caroloameghiniidae (Eldridge et al. 2019). Based on direct observations, Protodidelphidae and *Monodelphopsis* should be recognized as the oldest known ‘true’ representatives of Didelphimorphia.

The first protodidelphids were discovered in the Itaboraí Basin by Paula Couto (1952b), with the description of *Protodidelphis* (Fig. 5.16A-D) and *Guggenheimia* (Fig. 5.16F-I), although at that time they were considered as didelphids (Protodidelphidae was proposed by Marshall 1987). Later, other findings increased the knowledge and diversity of this group (see e.g., Paula Couto 1962, 1970; Marshall 1987; Oliveira 1998; Goin et al. 1999, 2016; Tejedor et al. 2009;

Oliveira and Goin 2011, 2012; Carneiro 2019). Currently, Protodidelphidae is confidently represented by *Guggenheimia*, *Protodidelphis*, and *Carolocoutoia* (Fig. 5.16E). For *Periprotodidelphis* (Fig. 5.16J), its affinities are better discussed below.

FIGURE 5.16

Protodidelphidae is recorded during the Eocene in Itaboraí, Brazil, Las Flores, La Borda (Woodburne et al. 2014), and Laguna Fría, Argentina (Tejedor et al. 2009), which supports a short biochron for their fossil record in comparison with other metatherian clades (see e.g., Carneiro 2019), such as those for Jaskhadelphyidae, Caroloameghiniidae, Pediomyidae and “Peradectidae”. This condition recovers Protodidelphidae as an important group for the biostratigraphy of South American land mammal faunas (SALMA), since its occurrences range from the early Eocene to the middle Eocene of South America (Itaboraiense to “Sapoan” SALMAs). The youngest representative of Protodidelphidae is a *Protodidelphis* from La Borda and Laguna Fría localities, southern Argentina (Tejedor et al. 2009).

Protodidelphidae is defined by the contact of the postprotocrista with the medial wall of the metacone (synapomorphy). The upper molars of these didelphimorphians show inflated StB and StD, reduced or absent StC, dilambdodont centrocrista and an eccentric protocone. *Guggenheimia* and *Protodidelphis* are the only protodidelphids with associated lower molars and both show almost subequal trigonid and talonid in height, enlarged ‘spire-like’ entoconids, vestigial or absent entocristid, slightly labial contact of the cristid obliqua with the distal trigonid wall, and mesiodistally compressed paraconids. *Guggenheimia* and *Protodidelphis* present robust dentaries; moderately inflated third lower premolars (p3), and lack semi-procumbent lower incisors. The general shape of the dentary and premolars indicates some adaptations to durophagy, similarly to *Bobbschaefferia*; nevertheless, these taxa could not be considered as specialized as *Gaylordia*, *Didelphopsis* and *Eobrasilia*.

This combination of features is also considered to be adaptations to frugivory, with the most extreme represented by *Carolocoutoia* (Goin et al. 1998; Oliveira 1998; Oliveira and Goin 2011; Carneiro 2019). Protodidelphids are considered to be adapted to insectivory-frugivory (*Periprotodidelphis*, *Protodidelphis*, *Guggenheimia* – see e.g., Goin et al. 1998, 2016; Oliveira and Goin 2011, 2012; Zimicz 2012; Carneiro 2019) or strict frugivory (*Carolocoutoia* – see e.g., Zimicz 2012) based on their dental adaptations.

Within Protodidelphidae, *Carolocoutoia* is the largest taxon of this group (see e.g., Goin et al. 1998; Oliveira 1998; Oliveira and Goin 2011), with a mesiodistal length of 6.78 mm and a labiolingual width of 7.03 mm. Amongst the Itaboraí metatherians, *Carolocoutoia* is only

smaller than *Eobrasilia coutoi*, *Zeusdelphys complicatus* and cf. *Nemolestes* (see e.g., Goin et al. 1998; Oliveira and Goin 2011).

Periprotodidelphis is an enigmatic “protodidelphid” originally identified as a possible M4 of *Protodidelphis mastodontoides* (this last taxon was originally described as “*Robertbutleria*” *mastodontoidea* by Marshall 1987, and later considered as *Protodidelphis* by Oliveira and Goin 1999). *Periprotodidelphis* resembles protodidelphids in the bunodont upper molars, and labially salient StB, although much more salient in *Periprotodidelphis*; robust protocone and metacone much larger than the paracone. Notwithstanding, it differs from other representatives of the family due to the presence of a large StC, a relatively more mesiodistally compressed M3, a preprotocrista much longer than the postprotocrista and a postprotocrista that does not contact the medial wall of the metacone.

Periprotodidelphis presents a narrower metastylar lobe than the parastylar lobe, a premetacrista that merges with a parallel crest that descends from StD and a slightly inflated metaconule. Curiously, these features are identified on “glasbiids” and chulpasiids + anatoliadelphyids (sensu Métais et al. 2018). Carneiro (2019) recovered *Periprotodidelphis* as the sister taxon of *Anatoliadelphys* Maga and Beck, 2017. Unfortunately, *Periprotodidelphis* has been identified just by a single upper molar, which thereby restricts comparisons with other groups. Nonetheless, the overall features of this taxon present more similarities with “glasbiids” than to protodidelphids. On its overall features, *Periprotodidelphis* would represent a compatible upper molar morphotype for *Bobbschaefferia*, which is only known by lower molars.

Protodidelphids have been considered as representatives of Didelphimorphia since Goin and Candela (1996), based on the presence of a metacone much larger than the paracone, dilambdodont centrocrista, eccentric, robust protocone; reduced conules, broad talonid basin, and moderately developed stylar shelf. In the lower molars protodidelphids has the posterobasal cingulid very poor developed (Oliveira and Goin 2011). Protodidelphidae differs mainly from “glasbiids”, anatoliadelphyids and chulpasiids (i.e. early representatives of Polydolopimorphia) due to the absence of inflated metaconule on upper molars.

The presence of two calcanea morphotypes with two subfacets on the calcaneocuboid facet of the calcaneus (IMG V and IMG XII) supports the occurrence of didelphimorphians in the Itaboraí fauna (see e.g., Szalay 1994). The subfacets are not as developed as those of didelphids, but are nonetheless identifiable (see e.g., Szalay’s 1994 schematic drawings and the Fig. 5.17). These two calcanei morphotypes represent the oldest confirmed tarsal elements of didelphimorphians currently known.

The IMG XII represents one of the largest morphotypes (very likely, *Protodidelphis*), and is only smaller than the IMG XIII (probably *Patene simpsoni*), whereas the IMG V (Fig. 5.17) is compatible in size with a small metatherian (*Monodelphopsis travassosi*?). The size of these two calcanei is compatible with the diversity of didelphimorphians of the Itaboraí fauna, which is the only group of metatherians with small to very large representatives in the fauna.

FIGURE 5.17

Monodelphopsis is another enigmatic taxon from Itaboraí (Fig. 5.18). Described by Paula Couto (1952b), the hypodigma of this species have been substantially reduced by Oliveira (1998), who assigned part of it to *Austropedimys* as well as to other taxa. *Monodelphopsis* is characterized by the presence of a labiolingually expanded and mesially positioned paraconid, flattened, reduced entoconid, short talonid (especially on m4), hypoconulid near the distolingual corner of the talonid, and p2 larger than p3 (Fig. 5.18C2).

The presence of a taller and longer p2 than p3 is considered to be a synapomorphy of Didelphidae (see e.g., Voss and Jansa 2009). Furthermore, this character has also been identified on some sparassocynids, such as *Hesperocynus dolgopola* (Reig, 1958) (see e.g., Abello et al. 2015), and on the Itaboraiense *Monodelphopsis*, as commented. Another important feature that supports the assignment of *Monodelphopsis* to Didelphimorphia is the full development of the marginal cingulids of the lower premolars (see Figs. 5.16I and 5.18C1-2).

These marginal cingulids are shared features between *Monodelphopsis*, didelphids, sparassocynids (*Hesperocynus*, *Sparassocynus*), and protodidelphids (*Guggenheimia*, *Protodidelphis*). The presence of these cingulids on lower premolars, especially on p3, has not been identified amongst other Itaboraiense metatherians with the exception of the representatives of Didelphimorphia. The marginal cingulids of *Monodelphopsis*, *Guggenheimia* and *Protodidelphis* are so easily observable that Paula Couto (1962: figs. 6B and 10B-C, p. 149, 156) and Marshall (1987: figs. 19C; 30A, C; 34C and 35C, p. 109, 118 and 121) included these features in their schematic drawings regarding the premolars of these three taxa. Based on these observations, these cingulids represent a synapomorphy of Didelphimorphia.

The upper molars of *Monodelphopsis* (Fig. 5.18A-B) present protoconal basal expansions, reduced paracingulum that contacts the talon at a lower level than the protoconal basin, and preprotocrista merging with the lingual wall of the metacone. All these features are also found in other didelphimorphians, thereby supporting the inclusion of *Monodelphopsis* within Didelphimorphia. The upper dentition of *Monodelphopsis* presents moderately developed, but inflated, StB and StD, and a vestigial StC (one specimen lacks StC – UFRJ 153-

M). This morphological pattern is also present amongst protodidelphids, didelphids and sparassocynids, and could represent the symplesiomorphic upper molar pattern of this clade.

The dental adaptations of *Monodelphopsis* support an insectivorous or faunivorous diet for this taxon, such as the presence of a labiolingually expanded and mesially positioned paraconid, short talonid, reduced entoconid, distolingually positioned hypoconulid, and moderately robust dentary. *Monodelphopsis* resembles sparassocynid didelphoids in the presence of short talonids, mesiodistally expanded trigonid, and small labiolingually expanded paraconids, but differ in the more robust protocone on M3, narrower styler shelf, an inflated, small StD; flattened, reduced entoconid, distolingual position of the hypoconulid, non-mesially merged metaconid and protoconid, and mesially positioned paraconid. The m4 of *M. travassosi* presents an evidently longer trigonid than talonid, which supports insectivorous or faunivorous adaptations.

FIGURE 5.18

The Itaboraí fauna represented the most diverse known assemblage of didelphimorphian marsupials during the Paleogene (five genera and seven species, considering *Periprotodidelphis* as a representative of this group), which supports the importance of the PETM and Itaboraí fauna in understanding the evolution of didelphimorphian marsupials (see e.g., Goin et al. 2012, 2016; Woodburne et al. 2014; Carneiro 2019). The assignment of protodidelphids and *Monodelphopsis* to Didelphimorphia completed a ‘ghost-lineage gap’ for this group of marsupials in the fossil record. The oldest confirmed paucituberculatans and australidelphians are dated from the early Eocene of Las Flores local fauna, Argentina (Las Flores – see e.g., Goin et al. 2009) and Tingamarra local fauna, Australia (see e.g., Beck 2012), respectively. These data are compatible with the fossil record of Paucituberculata and Australidelphia, and in this respect, Itaboraí provides more evidence for the evolutionary history of these two groups, as discussed below.

5.12 Did Paucituberculatans and Australidelphians Exist in the Itaboraí Fauna? A Brief Review

The presence of paucituberculatans and australidelphians in the Itaboraí fauna has been under discussion since Marshall (1987) and Szalay (1994), who proposed the presence of stem-paucituberculatans amongst the taxa recovered from this locality but no australidelphians. More recently, Goin et al. (2009) described *Riolestes capricornicus* (Fig. 5.19), which has been considered as one of the oldest paucituberculatans currently known (see also e.g., Oliveira and

Goin 2012; Abello 2013). Later, Carneiro (2019) recovered *Riolestes* as the sister group of *Fieratherium sorex* Forasiepi et al., 2014, a stem-Paucituberculata, supporting an early divergent condition for *Riolestes* compared to other representatives of this group.

FIGURE 5.19

Contrary to these studies, some authors have suggested that *Riolestes* would represent a deciduous third lower premolar (dp3) of a large metatherian from the Itaboraí fauna (see e.g., Eldridge et al. 2019). If confirmed, there would be no representative of Paucituberculata in Itaboraí. However, new data has indicated that *Riolestes* could be represented by two lower molars?: MCN-PV 1790 (type specimen), considered as a left m1?, and MN 2900-V, a right m3?. These two teeth present some differences: (i) firstly, MCN-PV 1790 is 0.70 mm larger than MN 2900-V; (ii) the entoconid of the type specimen is more flattened and relatively more developed than that of MN 2900-V; and (iii) the hypoconulid of the type specimen is more lingually positioned than that of MN 2900-V. These few morphological differences could be indicative of different molar loci or dp3 features of different species (one larger and one smaller – *Protodidelphis* and *Itaboraidelphys*?).

Following the original proposal of Goin et al. (2009) (i.e., *Riolestes* is represented by molars), it is then plausible to consider that *Riolestes* had already acquired a reduction in the size of the third molar when compared to the first and second molars, similarly for *Fieratherium* and other paucituberculatans. Furthermore, MN 2900-V completely preserved the anterior and posterior roots; a contrary condition to the majority of dp3s of the Itaboraí metatherians, which are represented by a thin crown preserving their structures, although no roots have been preserved with them.

The studies of Szalay (1994) on isolated tarsal elements from Itaboraí rejected the presence of australidelphians in the fauna but suggested that some of the small taxa could be related to Paucituberculata (i.e., Sternbergiinae, as previously discussed). The presence of earlier representatives of Paucituberculata in the Itaboraí fauna was also proposed by Ladevèze and Muizon (2010) based on the study of isolated petrosals recovered in this locality. These authors recovered the petrosal type V as belonging to a clade that includes Paucituberculata + *Epidolops* (i.e. Paucituberculata + Polydolopimorphia). However, *Riolestes* is much larger than the expected size of the petrosal type V, a condition which would support a second taxon of Paucituberculata in Itaboraí. With regard to this debate, the isolated petrosals recovered in Itaboraí have provided significant data, as discussed below.

5.13 A Reassessment of the Isolated Petrosals from Itaboraí: New Data for the Evolutionary History of South American Metatherians

The presence of isolated petrosals in the Itaboraí fauna was firstly discussed by Ladevèze (2004), who described two morphotypes (petrosal type I and II – PI and PII). Later, Ladevèze (2007) and Ladevèze and Muizon (2004, 2010) described six more petrosal morphotypes of this fauna (i.e., PIII, PIV, PV, PVI, PVII and PVIII). Based on Ladevèze and Muizon (2010), PVIII is congruent in size to *Minusculodelphis minimus*, PVII, PV and PIII to *Marmosopsis juradoi* or *Gaylordia doelloi*, PIV to *Carolopaulacoutoia itaboraiensis*, PVI to *G. macrocynodonta*, PI to *Mirandatherium alipioi*, and PII to *Bobbschaefferia fluminensis*. Later, Beck (2017) considered PII as compatible in size with *Epidolops ameghinoi* and Muizon et al. (2018) with *Itaboraidelphys camposi*.

Following the methodology considered for this chapter, the size compatibility of Itaboraí's petrosals resulted on the following classification for them: PVIII and PVII belonged to tiny taxa, a curious result as only two taxa (*Minusculodelphis* and *Armintodelphys* sp.) are grouped within this size category; PIII, PIV and PV should be assigned to very small taxa; and PI and PVI are compatible with small taxa. PII has two different measurements published in the literature: (i) the one of Ladevèze and Muizon (2010) (i.e., PII(a)), which is compatible with a medium-sized taxon; and (ii) the one of Muizon et al. (2018) (i.e., PII(b)), which is compatible with a small to medium-sized taxon (see supplementary materials appendix 5.3).

Based on the newly calculated molar areas, PVIII is assigned to *Minusculodelphis*, which is the only taxon with compatible dimensions. The assignment of this petrosal morphotype to *Minusculodelphis* was previously suggested by Ladevèze and Muizon (2010) and Oliveira et al. (2016).

PVII is only compatible with the tiny *Armintodelphys* sp. This taxon is larger than *Minusculodelphis* and about the size of the smallest known specimen of *Marmosopsis juradoi* (see supplementary materials appendix 5.2). These dimensions are compatible with the estimated molar areas calculated by Ladevèze and Muizon (2010). Thus, the association of this petrosal morphotype with *Armintodelphys* sp. is here suggested. Despite its apparently lower abundance (MNI: 1), this is the only taxon with a compatible size range for PVII. Furthermore, this data indicates that the apparent greater abundance of a taxon should not be considered a trustworthy result on itself.

PVI and PI are within the size range of small-sized metatherians, a size category represented by 11 taxa. Ladevèze and Muizon (2010) recovered PI and PVI as being compatible in size to *Mirandatherium alipioi* and *Gaylordia macrocynodonta*, respectively. However, the taxonomic revision presented in this chapter concluded that the dimensions of *M. alipioi* are larger for

these two petrosals morphotypes. Amongst the representatives of this size category, any of the 11 taxa could be considered as plausible associations for these two petrosals based only on the estimated size (supplementary material appendix 5.3).

Moreover, the phylogenetic analysis recovered PVI and PVII within Notometatheria (Fig. 5.20). These two morphotypes should be excluded from Marsupialia based on the absence of a well-developed, anterolaterally directed wing formed by the rostral tympanic process of petrosal (character 282²) (see e.g., Ladevèze 2004). PVI and PVII should be assigned to derorhynchids and/or herpetotheriids based on the following evidences: (i) rostral tympanic process of petrosal developed as a low crest (ch. 282¹), and (ii) presence of an expanded caudal tympanic process of petrosal (ch. 289¹). This second feature is recorded only for *Peratherium*, *Herpetotherium* and Paucituberculata + Australidelphia, in addition to these two petrosal morphotypes (see supplementary materials appendix 5.3). The close affinities between herpetotheriids and derorhynchids were discussed by Oliveira et al. (2021) and it is supported by this review. Therefore, PVI should be assigned to a small-sized derorhynchid, such as *Derorhynchus singularis*, *Diogenesia* sp. and the ‘gen nov 3’.

PV, PIII and PIV are within the size range of *Marmosopsis juradoi*, *Gaylordia doelloi*, *Diogenesia brevirostris*, ‘gen nov 1 et sp nov 1’, *Carolopaulacoutoia* sp. and *Marmosopsis* sp. Following the relative abundance and compatible size, *Marmosopsis juradoi* should be considered as the most plausible taxon for the assignment of one of these petrosals morphotypes (MNI: 20), followed by *Gaylordia doelloi* (MNI: 2). Amongst these three morphotypes, PIV is slightly larger than the other two, which should indicate a relatively larger taxon of this size category, which may support its assignment to *Carolopaulacoutoia* sp. or *Marmosopsis* sp.

The phylogenetic analysis recovered PIII, PIV and PVIII as sudameridelphian metatherians other than pucadelphydians (i.e., Pucadelphyidae, Sparassodonta) and notometatherians (i.e., Derorhynchidae, Herpetotheriidae and Marsupialia), which excludes associations with *Diogenesia brevirostris*, a derorhynchid (Fig. 5.20). Considering the size dimensions, relative abundance and systematic affinities, PIII would be more plausibly assigned to *G. doelloi*. This consideration is based on the size range of PV, which is compatible in size only with *M. juradoi*. Despite the proposed affinities of *Marmosopsis* with jaskhadelphyids (Oliveira and Goin 2011; Oliveira et al. 2016) and sternbergiids (Goin et al. 1998), both hypotheses do not exclude the assignment of PV to this taxon, as the features recovered by the phylogenetic analysis for its placement as a notometatherian are highly homoplastic (e.g., vestigial to absent mastoid tympanic process (ch. 288²) – see supplementary materials appendix 5.3). These results agree with Ladevèze (2007) and Ladevèze and Muizon (2010), who also considered PIII and PV congruent in size with *G. doelloi* and *M. juradoi*.

Based on the same evidence, PIV should be assigned to *Carolopaulacoutoia* sp. Originally, Ladevèze (2007) and Ladevèze and Muizon (2010) assigned this taxon to *C. itaboraiensis*; however, the analysis results support the assignment to *Carolopaulacoutoia* sp. instead of *C. itaboraiensis*. If confirmed, the consideration of sternbergiids as notometatherians is here not supported.

PII was recovered in a polytomy with pucadelphyids and sparassodonts, as a Pucadelphyda (Fig. 5.20). Both pucadelphydians known for Itaboraí (i.e., *Patene* and cf. *Nemolestes*) are larger than expected for this morphotype. Following the estimations of Ladevèze and Muizon (2010 – i.e., PII(a)), PII would be compatible in size with a medium-sized metatherian; nevertheless, larger specimens of *Epidolops ameghinoi* are compatible in the estimated m2 area (see supplementary material appendix 5.3). When the measurements of Muizon et al. (2018 – i.e. PII(b)) are considered, PII is compatible with a large small-sized metatherian, such as *Bergqvistherium primigenia* and *Epidolops ameghinoi*.

Beck (2017) suggested assigning PII to *Epidolops* using the regressed promontorium area against the total cranial length (based on DGM 321-M), and not the regression of the molar area against the promontorium area, since the molars of *Epidolops* are reduced in size from the first to the last molar (see e.g., Szalay 1994). This condition of *Epidolops* should therefore result in an association of petrosals smaller than those expected for this taxon, as the first molar is the largest. Beck (2017) also considered the relative abundance, in which *Epidolops* is by far the most abundant metatherian of this fauna (MNI: minimum 45).

Moreover, the equation of Beck et al. (2008) also supported *Epidolops ameghinoi* as the most plausible taxon for the assignment of PII. Based on the measurements of Muizon et al. (2018) (i.e., PII(b)), the estimated M2/m2 length for this petrosal morphotype is about 2.73 mm, which is congruent with the size range of *E. ameghinoi*. Thus, based on present discussion, PII would be better assigned to *E. ameghinoi*, supporting Beck's (2017) conclusions.

Furthermore, no definitive polydolopimorphian petrosal have been recovered so far, which enables *Epidolops* as a plausible candidate. If confirmed, polydolopimorphians should be considered as closely related to or as representatives of Pucadelphyda.

PI should be assigned to *Monodelphopsis* based on the following evidences: (i) PI falls in the expected size estimated for a small-sized metatherian, such as *Monodelphopsis* (see supplementary materials appendix 5.3), (ii) PI was recovered as more closely related to didelphids in the phylogentic analysis based on a well-developed, anterolaterally directed wing formed by the rostral tympanic process of petrosal (ch. 288¹) and a caudal tympanic process of petrosal forms a small crest that does not wholly floor the postpromontorial sinus (ch. 289⁰) (see Fig. 5.20), and (iii) *Monodelphopsis* shares several dental features with didelphimorphians

(see discussion 5.11) (the authors do not discard the possibility that the didelphimorphian IMG V also belongs to this taxon).

These preliminary results have provided new hypotheses that should support more detailed studies regarding the isolated petrosals of the Itaboraí fauna and the systematic affinities of South American metatherians, such as the pucadelphydan affinities for polydolopimorphians and the oldest didelphimorphian petrosal currently found.

FIGURE 5.20

5.14 Conclusions and Future Perspectives

The Itaboraí fauna has preserved one of the most diverse assemblages currently known for the metatherian clade. The fauna has recorded 29 genera and 39 species (considering *Riolestes* as a valid taxon) (Fig. 5.21), with representatives of the Alphadontia-Hatcheriformes (*Zeusdelphys*), Archimetatheria-Stagodontidae (*Eobrasilia*), Archimetatheria-Pediomyoidea (*Austropediomys*), “Peradectia”-“Peradectoidea” (‘gen nov 1’, *Bergqvistherium*), “Peradectia”-“Peradectoidea”-Caroloameghinioidea (‘gen nov 2’, *Mirandatherium*), “Peradectia”-“Peradectoidea”-Caroloameghinioidea-Caroloameghiniidae (*Procaroloameghinia*), Jaskhadelphyidae and closely related taxa (*Gaylordia*, *Marmosopsis*, *Minusculodelphis*), Pucadelphyda-Sparassodonta (*Patene*, cf. *Nemolestes*), Polydolopimorphia-Glasbiidae (*Bobbschaefferia*), Polydolopimorphia-Bonaparteriiformes (*Epidolops*, *Gashternia*), Sternbergiidae (*Carolopaulacoutoia*, *Didelphopsis*, *Itaboraidelphys*), Notometatheria-Derorhynchidae (*Armintodelphys* sp., *Derorhynchus*, *Diogenesis*, ‘gen nov 3’), Marsupialia-Didelphimorphia-Protodidelphidae (*Periprotodidelphis*, *Guggenheimia*, *Protodidelphis*, *Carolocoutoia*), Marsupialia-Didelphimorphia (*Monodelphopsis*) and Marsupialia-Paucituberculata (*Riolestes*). Within this concept, the systematic diversity of the Itaboraí fauna, as presented in this chapter, highlights its importance for the evolution of metatherians on a global level.

FIGURE 5.21

The Itaboraí fauna has preserved the most diverse fauna of tiny and very small insectivorous, specialized durophagous and brachydont-bunodont metatherians for the global Paleogene fossil record. The Itaboraí fauna represents the “temporarily closest” fauna currently known to be preserved after the PETM event in South America. The independent adaptations of several groups to frugivory resulted in a polyphyletic state for most of these groups, such as

Caroloameghinioidea, Protodidelphidae and Polydolopimorphia. It seems that the increase in global temperatures, humidity and rainfall, and the extension of tropical biomas represented important paleoenvironmental and paleoclimatic variables for the “short-time” increase in the diversity of frugivorous taxa. Based on this, these data support the importance of the PETM for the evolution of South American metatherians.

The Itaboraí fauna has preserved the oldest confirmed representatives of Didelphimorphia, and a possible Paucituberculata, but has not confirmed Australidelphia. The evidence at hand does not support the inclusion of Polydolopimorphia within Marsupialia. Caroloameghinioidea should also not be included within Didelphimorphia and should be considered as a group of “peradectoids” or “glasbiids”.

Furthermore, it should be noted that some specimens recovered from the Itaboraí Basin are still preserved in the original sediment, and are gradually being recovered and studied. In addition, undergoing studies regarding the isolated post-cranial elements, especially the 13 tarsal morphotypes identified by Szalay (1994) and the 10 femur morphotypes by Szalay and Sargis (2001) would also increase the knowledge on the systematic and evolutionary history of Gondwanan metatherians. This fauna still has much to contribute to the evolutionary history of metatherians and subsequent years will lead to further knowledge on this important faunal assemblage.

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Cross-References

- 1) Paleogene Metatherians from the Itaboraí Basin: Systematics, Paleobiogeography and Evolutionary Context (by Carneiro and Oliveira)
- 2) Cenozoic Metatherian Evolution in the Americas (by Francisco Goin)
- 3) Oligocene-Miocene Marsupials from Riversleigh: Diversity, Affinities, and Paleobiogeographic Context (by Michael Archer)

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Table 5.1. Systematic classification of Itaboraí's metatherians followed in this chapter. The suprageneric rank classification is indicated.

†Order Alphadontia (Archer, 1984) Carneiro and Oliveira, 2017a

†Suborder Hatcheriformes Case et al., 2005

†Family indet.

†***Zeusdelphys complicatus*** Marshall, 1987

†Order Archimetatheria Szalay, 1994

†Superfamily Stagodontioidea Marshall and Kiealan-Jaworowska, 1992

†Family Stagodontidae Marsh, 1889

†***Eobrasilia coutoi*** Simpson, 1947

†Superfamily Pediomyoidea (Simpson, 1927) Davis, 2007

†Family indet.

†***Austropedionomys marshalli*** Carneiro et al., 2018

Magnacohort Sudameridelphia Szalay, 1994

†Order “Peradectia” Marshall et al., 1990

†Superfamily “Peradectoidea” Marshall et al., 1990

†Family “Peradectidae” Crochet, 1979

†**Gen nov 1 et sp nov 1**

†**Gen nov 1 et sp nov 2**

†***Bergqvistherium primigenia*** Carneiro, 2018b

†Superfamily Caroloameghinioidea Marshall, 1987

†Family Mirandatheriidae Szalay, 1994

†***Mirandatherium alipoi*** (Paula Couto, 1952b)

†**Gen nov 2**

†Family Caroloameghiniidae Clemens, 1966

†***Procaroloameghinia pricei*** Marshall, 1982a

†Superorder Pucadelphyda Muizon et al., 2018

†Order Sparassodonta Ameghino, 1894

†**Cf. *Nemolestes* sp.**

†***Patene simpsoni*** Paula Couto, 1952a

†Order Polydolopimorphia Archer, 1984

†Family Glasbiidae Clemens, 1966

†***Bobbschaefferia fluminensis*** (Paula Couto, 1952b)

†Suborder Bonapartheriiformes Pascual, 1980a

- †Superfamily Bonapartherioidea Pascual, 1980a
- †Family Gashterniidae Marshall, 1987
 - †*Gashternia carioca* Goin and Oliveira, 2007
- †Family Bonapartheriidae Pascual, 1980a
- †Subfamily Epidolopinae Pascual and Bond, 1981
 - †*Epidolops ameghinoi* Paula Couto, 1952a
- †Order indet.
 - †Family indet.
 - †*Gaylordia doelloi* (Paula Couto, 1962)
 - †*Gaylordia macrocynodonta* Paula Couto, 1952b
 - †*Gaylordia mater* Oliveira and Goin, 2015
- †Superfamily indet.
 - †Family indet.
 - †*Marmosopsis juradoi* Paula Couto, 1962
 - †*Marmosopsis* sp.
- †Family Jaskhadelphyidae Muizon, 1992
 - †*Minusculodelphis minimus* Paula Couto, 1962
 - †*Minusculodelphis modicum* Oliveira et al., 2016
- Supercohort Notometatheria Kirsch et al., 1997
 - †Family Sternbergiidae (Szalay, 1994) McKenna and Bell, 1997
 - †*Carolopaulacoutoia itaboraiensis* (Paula Couto, 1970)
 - †*Carolopaulacoutoia* sp.
 - †*Didelphopsis cabrerai* Paula Couto, 1952b
 - †*Didelphopsis* sp.
 - †*Itaboraidelphys camposi* Marshall and Muizon, 1984
 - †Family Derorhynchidae Goin et al., 1999
 - †*Armintodelphys* sp.
 - †*Derorhynchus singularis* Paula Couto, 1952b
 - †*Diogenesia brevirostris* Oliveira et al. 2021
 - †*Diogenesia* sp.
 - †Gen nov 3
- Cohort Marsupialia Illiger, 1811
- Order Didelphimorphia Gill, 1872
 - †Family Protodidelphidae Marshall, 1987
 - †*Carolocoutoia ferigoloi* Goin et al., 1998

†*Guggenheimia brasiliensis* Paula Couto, 1952b

†*Guggenheimia crocheti* Oliveira and Goin, 2011

†*Periprotodidelphis bergqvistae* Oliveira and Goin, 2011

†*Protodidelphis vanzolinii* Paula Couto, 1952b

†*Protodidelphis mastodontoides* (Marshall, 1987)

Superfamily Didelphoidea Gray, 1821

†Family Monodelphopsiidae Szalay, 1994

†*Monodelphopsis travassosi* Paula Couto, 1952b

Order Paucituberculata Ameghino, 1894

†*Riolestes capricornicus* Goin et al., 2009

Figure Captions

Fig. 5.1. The Itaboraí fauna: locality and biochron. **A.** Location map showing the region and coordinates of the Itaboraí Basin, São José de Itaboraí, Rio de Janeiro, Brazil (22° 45' 9.9144'' S, 42° 51' 53.5536'' W). **B.** Stratigraphic relationships of the Itaboraiense SALMA with other Paleogene SALMAs. The followed age for the Itaboraí's fauna is indicated by a white arrow in the figure (i.e., Itaboraiense – 56.1-51.4 MYA – sensu Chornogubsky 2020). **EECO**, Early Eocene Climatic Optimum; **PETM**, Paleocene-Eocene Thermal Maximum. The Itaboraiense SALMA is highlighted in gray.

Fig. 5.2. Number of studied elements for each metatherian species from the Itaboraí fauna used for the concept of this chapter. The amount of studied taxa is based on teeth, jaw and skull specimens. The isolated petrosals, fragments of skulls, and post-cranial remains were not included. **N**, number of specimens; **MNI**, minimum number of individuals.

Fig. 5.3. Dental terminology utilized as exemplified by an upper (**A**) and lower molar (**B**).

Fig. 5.4. SEM pictures of the possible pediomyoid *Austropedimys marshalli*. SEM pictures of DGM 808-M (type specimen), a left maxilla fragment with M2-4: **A.** occlusal view; SEM picture of MCT 2798-M, a left M1: **B.** occlusal view; SEM picture of DGM 928-M, incomplete right dentary with m3-4 and alveoli of p1-m2: **C.** occlusal view of the dentary. Scale bars: 1mm.

Fig. 5.5. SEM photographs of the possible stagodontid *Eobrasilia coutoi*. DGM 919-M, fragmented right dentary: **A1.** p3 in antero-lingual view; **A2.** alveoli of m1 roots, with partially preserved paraconid of the right m1, and alveoli of m2 anterior root; **A3,** p2 in antero-lingual view showing the lingual flexid; **A4,** incisors and canine alveoli. **i** , lower incisor; **c**, lower canine. Scale bars: 1 mm.

Fig. 5.6. SEM picture of the possible hatcheriform *Zeusdelphys complicatus*. MCT 2830-M (type specimen), a right M1? in occlusal view. Scale bar: 1 mm.

Fig. 5.7. SEM pictures of the peradectoids from the Itaboraí fauna. SEM picture of MCT 2797-M, a right M3 of 'gen nov 1 et sp nov 2': **A.** occlusal view; SEM picture of MCT 2795-M, a right M2 of 'gen nov 1 et sp nov 2': **B.** occlusal view; SEM picture of DGM 920-M, an incomplete left dentary with p3 and m2-4 of 'gen nov 1 et sp nov 2': **C.** occlusal view of m2-

4; SEM picture of MCT.M.4432, a left m2 of 'gen nov 1 et sp nov 2': **D.** lingual view; SEM picture of DGM 649-M, incomplete left dentary, showing preserved m1-4 of 'gen nov 1 et sp nov 1': **E.** occlusal view; SEM picture of UFRJ 151-M, a right M3 of *Bergqvistherium primigenia*: **F.** occlusal view; SEM picture of MCN-PV 1803, a right M2 of *B. primigenia*: **G.** occlusal view; SEM picture of MCT 4387-M (type specimen), a left m1 of *Bergqvistherium primigenia*: **H.** occlusal view. Scale bars: 1 mm.

Fig. 5.8. Stereo and SEM pictures of the caroloameghiniid *Procaroloameghinia pricei*. DGM 805 + 924 M (type specimen), right dentary with alveoli of canine and p1, and complete p3-m4: **A1.** lingual view; **A2.** labial view; **A3.** occlusal view; **A4.** detail of the canine and lower incisors; **A5,** p3-m4 in occlusal view. **i.** lower incisor. Scale bars: A1-3 = 3 mm; A5 = 1 mm.

Fig. 5.9. SEM pictures of the caroloameghinoids gen nov 2 and *Mirandatherium alipioi* and the possible glasbiid or caroloameghinoid *Bobbschaefferia fluminensis*. SEM picture of MCT 2816-M, a right M3 of the gen nov 2: **A.** occlusal view; SEM picture of MN 1363-V, an incomplete right dentary with talonid of m2 and m3 of the gen nov 2: **B.** occluso-labial view; SEM picture of DGM 361-M, an incomplete right dentary with m2-4 of *Mirandatherium alipioi*: **C.** occlusal view; SEM picture of MN 2894-V(a1), a right M3 of *M. alipioi*: **D.** occlusal view; stereo picture of a cast of MN 1350-V (type specimen), an incomplete left dentary with p2-3, m3-4 and alveoli of i-p1 and m1-2 of *Bobbschaefferia fluminensis*: **E.** occlusal view. Scale bars = 1 mm.

Fig. 5.10. SEM pictures of the sparassodonts *Patene simpsoni* and cf. *Nemolestes* from the Itaboraí fauna. Combined SEM pictures of MN 1331-V (type specimen), a fragment of right maxilla with P3-M4 of *P. simpsoni*: **A1.** occlusal view; **A2.** labial view; SEM pictures of UFRJ 189-M, a right m1 of *P. simpsoni*: **B1.** occlusal view; **B2.** lingual view; **B3.** labial view; SEM pictures of DGM 654-M, a right m3 of *P. simpsoni*: **C1.** occlusal view; **C2.** distal view; **C3.** labial view; **C4.** lingual view; SEM picture of MN 1344-V, a left m4 of cf. *Nemolestes*: **D.** lingual view. Scale bars = 1 mm.

Fig. 5.11. Stereo and SEM pictures of *Gaylordia*, *Marmosopsis* and the jaskhadelphyid *Minusculodelphis* from the Itaboraí fauna. Stereo pictures of DGM 329-M (type specimen), anterior portion of a fragmented skull and anterior portion of the left hemimandible of *Gaylordia macrocynodonta*: **A1.** ventral view of the skull; **A2.** lingual view of the jaw; SEM pictures of MCT 2778-M, a left M2 of *G. mater*: **B1.** lingual view; **B2.** occlusal view; SEM

picture of MCT 2780-M, a left M3 of *G. mater*: **C.** occlusal view; SEM picture of MCT 810-M (type specimen), an incomplete right dentary with m2-4 of *G. mater*: **D.** occlusal view; SEM picture of DGM 921a-M (type specimen), an incomplete right dentary with m1-4 of *Minusculodelphis modicum*: **E.** occlusal view; SEM pictures of DGM 921b-M, an incomplete dentary with m3, showing the m3 of *M. modicum*: **F1.** occlusal view; **F2.** lingual view; SEM picture of MCT 2815-M, a right M3 of *M. modicum*: **G.** occlusal view; stereo picture of MN 2470-V, a right dentary with p2-m3 and alveoli of p1 and m4 of *Marmosopsis juradoi*: **H.** labial view; stereo picture of MN 2498-V, incomplete left dentary with p2-m3 of *M. juradoi*: **I.** anterior part of the jaw, showing the incisors alveoli, canine alveolus and p1-2 alveoli; SEM picture of MCT.M.4442, a right m2 of *M. juradoi*: **J.** occluso-labial view; SEM picture of MCT 1333-LE, a left M3 of *M. juradoi*: **K.** occluso-mesial view; SEM picture of DGM 811-M, a fragment of right dentary with m3-4, showing m3-4 of *Marmosopsis* sp.: **L.** occlusal view; stereo pictures of DGM 921c-M, a left femur of *M. modicum*: **M1.** anterior view; **M2.** posterior view. **i.** lower incisor; **Gt.** great trochanter; **Lt.** lesser trochanter; **Tf.** trochanteric fossa; **Tt.** third trochanter. Scale bars = **A-G, I-L:** 1 mm; **H:** 5 mm; **M:** 2 mm.

Fig. 5.12. SEM pictures of the polydolopimorphian *Epidolops ameghinoi*. SEM pictures of DGM 897-M, a fragment of right dentary with m2-4: **A1.** occlusal view; **A2.** occlusal view of the molars and anterior part of the coronoid process, showing the retro-molar space; **A3.** lingual view of the jaw fragment; **A4.** occluso-lingual view; SEM pictures of MCT 1348-LE, an incomplete dp3: **B1.** labial view; **B2.** occlusal view; SEM pictures of DGM 177-M, a right dentary with p3-m3 broken in two parts: **C1.** labial view of the plagiaulacoid p3; **C2.** mesial view of the plagiaulacoid p3. Scale bars = 1 mm.

Fig. 5.13. SEM pictures of the sternbergiids from the Itaboraí fauna. SEM picture of MCT.M4441, a right M2 of *Carolopaulacoutoia itaboraiensis*: **A.** occlusal view; SEM picture of MCT.M.4440, a right M3 of *C. itaboraiensis*: **B.** occlusal view; SEM picture of MCT.M.4435, a fragment of right maxilla with M2 and posterior alveolus of M1 of *C. itaboraiensis*: **C.** occlusal view; SEM picture of DGM 932-M, a incomplete right dentary with m1-3 and alveoli of m4 of *C. itaboraiensis*: **D.** occlusal view of m1-3; SEM picture of UFRJ 155-V, a right m4 of *C. itaboraiensis*: **E.** occlusal view; SEM picture of DGM 926-M, a fragment of left maxilla with M2-3, showing the M2 of *Itaboraidelphys camposi*: **F.** occlusal view; SEM picture of DGM 804-M, a right m2 of *I. camposi*: **G.** occlusal view; SEM picture of MCT 2768-M, a right M1 of *Didelphopsis cabrerai*: **H.** occlusal view; SEM picture of MCN-PV 1786, a right m1 of *D. cabrerai*: **I.** occlusal view; SEM picture of DGM 642-M, a left M3

of *Didelphopsis* sp.: **J.** occlusal view; SEM picture of MCT 2773-M, a left m4 of *Didelphopsis* sp.: **K.** occlusal view. Scale bars = 1 mm.

Fig. 5.14. SEM pictures of the derorhynchids from the Itaboraí fauna. MN 2886-V, an incomplete right dentary with m2-3 of gen nov 3: **A1.** lingual view of m2-3; **A2.** occlusal view of m2-3; SEM picture of MN 2894a2-V, a right M3 of gen nov 3: **B.** occlusal view; SEM picture of DGM 812-M, an incomplete left dentary with p3 and m3-4 of *Diogenesia* sp.: **C.** occlusal view of m3-4; Stereo picture of the anterior portion of DGM 812-M, showing the alveoli of i2-5, c and p1-2: **D.** antero-labial view; SEM picture of MCT.M.4425, a left m3 of *Diogenesia* sp.: **E.** occlusal view; SEM picture of MCT.M.4434, a left M2 of *Diogenesia* sp.: **F.** occlusal view; SEM picture of MCT 2766-M, a right M3 of *Diogenesia* sp.: **G.** occlusal view; SEM picture of UFRJ 145-M, a left M2 of *Derorhynchus singularis*: **H.** occlusal view; SEM picture of UFRJ 154-M, a left M3 of *D. singularis*: **I.** occlusal view; SEM picture of UFRJ 320-M, a right m1 of *D. singularis*: **J.** occlusal view; SEM picture of UFRJ 148-M, a right m2 of *D. singularis*: **K.** occlusal view. Scale bars = 1 mm.

Fig. 5.15. SEM picture of the occlusal view of the specimen DGM 933-M, an incomplete right dentary with m3-4, assigned to *Armintodelphys* sp. Scale bar = 1 mm.

Fig. 5.16. SEM pictures of the protodidelphids from the Itaboraí fauna. Combined SEM pictures of *Protodidelphis vanzolinii*: DGM 303-M, a fragment of right maxilla with M1-4: **A.** occlusal view; SEM picture of DGM 250-M, incomplete right dentary with p3-m1, m3 and m4 lacking the lingual side of *P. vanzolinii*: **B.** occlusal view of m3; SEM picture of DGM 896-M (type specimen), a left M1 of *P. mastodontoides*: **C.** occlusal view; SEM picture of MCT 2819-M, a left m2 of *P. mastodontoides*: **D.** occlusal view; SEM picture of MCN-PV 1802 (type specimen), a left M3 of *Carolocoutoia ferigoloi*: **E.** occlusal view; SEM picture of MCT 2782-M, a left M1 of *G. crocheti*: **F.** occlusal view; SEM picture of DGM 314-M (type specimen), an incomplete left dentary with m2-4 and alveoli of i1-m1 of *G. crocheti*: **G.** occlusal view of preserved m3; SEM pictures of DGM 297-M (type specimen), an incomplete left dentary with p1-m4 of *Guggenheimia brasiliensis*: **H.** occlusal view of the lower molar series; **I.** lingual view of p1-3 and m1; SEM picture of DGM 806-M (type specimen), a left M3 of *Periprotodidelphis bergqvistae*: **J.** occlusal view. Scale bars = 1 mm.

Fig. 5.17. SEM picture of DGM 1180-M (IMG V from Szalay 1994), a right calcaneus possibly belonging to *Monodelphopsis travassosi* in distal view. The calcaneus structures are identified.

CaCud. distal calcaneocuboid facet; **CaCup.** proximal calcaneocuboid facet; **CoA.** Calcaneoastragalar facet; **gtpl.** groove for tendon of peroneus longus **pp.** peroneal process; **sc.** sulcus calcanei; **Su.** sustentacular facet. Scale bars = 1 mm.

Fig. 5.18. SEM pictures of the didelphoid *Monodelphopsis travassosi*. SEM picture of UFRJ 357-M, a left M2: **A.** occlusal view; SEM picture of UFRJ 153-M, a left M3: **B.** occlusal view; SEM pictures of MN 1365-V (type specimen), a fragment of left dentary with p2-m1: **C1.** occlusal view; **C2.** labial view. Scale bars = 1 mm.

Fig. 5.19. SEM pictures of the specimen MN 2900-V, a possible third lower molar (or deciduous third lower premolar) of *Riolestes capricornicus*: **A1.** occlusal view; **A2.** lingual view. Scale bar = 1 mm.

Fig. 5.20. Result of the petrosal's phylogenetic analysis. Consensus tree of the 68MPTs (Score = 1735; CI = 0.383; RI = 0.622) found in the analysis. The Itaboraí's petrosal morphotypes are highlighted in bold. Numbers below the branches indicate the Bremer Support.

Fig. 5.21. Comparative diversity of the metatherians from the Itaboraí fauna. The size difference between the illustrated taxa is proportional and based on their real size difference. **A.** *Zeusdelphys complicatus*; **B.** *Eobrasilia coutoi*; **C.** cf. *Nemolestes*; **D.** *Carolocoutoia ferigoloi*; **E.** *Patene simpsoni*; **F.** *Protodidelphis vanzolinii*; **G.** *Protodidelphis mastodontoides*; **H.** *Didelphopsis* sp.; **I.** *Didelphopsis cabrerai*; **J.** *Itaboraidelphys camposi*; **K.** *Periprotodidelphis bergqvistae*; **L.** *Epidolops ameghinoi*; **M.** *Gashternia carioca*; **N.** *Mirandatherium alipioi*; **O.** *Guggenheimia crocheti*; **P.** gen nov 2; **Q.** *Procaroloameghinia pricei*; **R.** *Guggenheimia brasiliensis*; **S.** *Bergqvistherium primigenia*; **T.** *Gaylordia mater*; **U.** *Monodelphopsis travassosi*; **V.** gen nov 1 et sp nov 2; **W.** *Austropedimys marshalli*; **X.** *Derorhynchus singularis*; **Y.** gen nov 3; **Z.** *Carolopaulacoutoia itaboraiensis*; **AA.** *Diogenesia* sp.; **AB.** *Marmosopsis* sp.; **AC.** gen nov 1 et sp nov 1; **AD.** *Marmosopsis juradoi*; **AE.** *Armintodelphys* sp.; **AF.** *Minusculodelphis modicum*; **AG.** *Diogenesia brevirostris*; **AH.** *Riolestes capricornicus*; **AI.** *Bobbschaefferia fluminensis*. Scale bars = 1 mm.

ARTIGO 2

**A new metatherian (Mammalia) from the Itaboraí Basin (Early Eocene),
Brazil: implications to trophic niche partitioning between large-sized
“didelphoid-like” metatherians**

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Abstract. The Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro state, Brazil, preserved an Early Eocene vertebrate assemblage. Among its representatives, Metatheria comprises its most diverse clade, with a minimum of 29 genera and 43 species. Considering this diversity, large-sized taxa (based on didelphid standards, i.e., between 1 kg and 3.3 kg) are represented by *Didelphopsis*, *Protodidelphis* and *Patene*, each considered to have explored different trophic niches. However, the discovery of a new large-sized metatherian from this locality, here named *Xenocynus crypticus* gen. et sp. nov., indicates that the trophic complexity of Itaboraí's metatherians could not be so well-defined. *Xenocynus crypticus* gen. et sp. nov. is identified by the presence of its reduced StD, long postmetacrista, short protocone, talonid's area much smaller than the one of trigonid, spaced paraconid and metaconid (bases are not in contact), molar series increasing in size from m1 to m4, deep maxillary pits between upper molars, and robust symphysis. We included *Itaboraidelphys camposi*, *X. crypticus* gen. et sp. nov. and other large-sized taxa in two PCA analyses, the first considering morphometric measurements and the second considering some morphofunctional indexes, to test their placement in morphospace. Our analyses indicated that these taxa exhibit distinctive morphometric and morphofunctional patterns, suggesting low trophic niches overlapping between them. The results indicate that *X. crypticus* gen. et sp. nov. was a generalized carnivore (insectivory-carnivory), more specialized than the insectivorous/omnivorous *Itaboraidelphys camposi*, but less specialized than the larger *Patene simpsoni*, a carnivorous taxon.

Keywords: Itaboraiense SALMA; Paleoecology; Paleogene; Protodidelphidae; South America; Sternbergiidae

1. Introduction

The Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro state, Brazil (22° 50' 20" S; 42° 52' 30" W) dated as Early Eocene in age (53-50 Ma, Itaboraiense SALMA; see Woodburne et al., 2014) is one of the smallest sedimentary basins from Brazil (Bergqvist et al., 2009). However, despite its small dimensions, this locality has preserved the most diverse fauna of metatherians from the Cretaceous, Paleogene, and Neogene so far known, with almost a thousand specimens (considering teeth, dentaries, and maxillae) that represent a minimum of 29 genera and 43 species, as presented by Carneiro (2023).

These metatherian taxa from Itaboraí weighted from 2-3 g (*Minusculodelphis minimus*; see Oliveira et al., 2016) up to 10 kg (*Eobrasilia coutoi*; see Carneiro, 2023), and explored different trophic niches (faunivory, carnivory, insectivory, omnivory, mixed, frugivory, folivory; see Paula Couto, 1952a, 1952b, 1961, 1962, 1970; Marshall, 1987; Goin et al., 1998; Goin and Oliveira, 2007; Zimicz, 2012, 2014; Oliveira and Goin, 2011, 2016; Carneiro and Oliveira, 2017a, 2017b; Carneiro, 2019; 2023; Rangel et al., 2019, 2023a, 2023b; Carneiro and Oliveira, 2023).

Among these, large-sized taxa (between 1 kg and 3.3 kg; sensu Carneiro, 2023; Carneiro and Oliveira, 2023) are represented by *Didelphopsis cabrerai* Paula Couto, 1952a; *Didelphopsis* sp. nov. (Oliveira, 1998 – unpublished data; see Carneiro and Oliveira, 2023), *Protodidelphis vanzolinii* Paula Couto, 1952a; *Protodidelphis mastodontoides* (Marshall, 1987), and *Patene simpsoni* Paula Couto, 1952b. These taxa have been considered omnivores (*Didelphopsis*; see Zimicz, 2012), frugivores (*Protodidelphis*; see Goin et al., 1998; Oliveira and Goin, 2011, 2012; Zimicz, 2012; Carneiro, 2019, 2023; Carneiro and Oliveira, 2023), and generalized carnivores (*Patene*; see Rangel et al., 2019, 2023a, 2023b). Therefore, it can be suggested that their co-existence could result from the exploitation of differential trophic niches. However, this hypothesis has never been formally tested.

A survey of Brazilian collections containing metatherian specimens from Itaboraí

(MCN-PV, MCTer, MN, and UFRJ-DG; see institutional abbreviations below) resulted in the identification of some maxillae, dentaries, upper and lower molars specimens that deviate from the observed features of large-sized metatherians of this fauna (see Carneiro, 2023). One of these specimens (MCT.M.2382; ex. MCT.M.643) was initially mentioned by Paula Couto (1970:32) as: “undetermined didelphid of medium size”. This specimen had never undergone a detailed examination in any of the three major taxonomic/systematic revisions of the metatherians of the Itaboraí fauna (Paula Couto, 1952a, 1952b, 1961, 1962, 1970; Marshall, 1987; Oliveira, 1998 – unpublished data), prior to the one of Carneiro (2023).

The specimen MCT.M.2382 resembles the smaller *Itaboraidelphys camposi* Marshall and Muizon, 1984, differing on some features (e.g., larger size, absence of supernumerary cuspules on the styler shelf, and M2 longer than wider). Moreover, several features of this morphotype indicate a generalized carnivorous diet for it (very long postmetacrista in comparison with preparacrista, short protocone), whereas *I. camposi* has been considered an insectivorous-omnivorous taxon (see Zimicz, 2012). Therefore, this morphotype differs from *I. camposi* based on morphological, morphometric and morphofunctional features, indicating that this and other specimens represent a new taxon (gen. et sp. nov.) from the Itaboraí Basin.

In summary, a new metatherian from the Itaboraí Basin is described, discussing its morphological and morphofunctional differences from *Itaboraidelphys* and other large-sized metatherians from the Itaboraí Basin and its implications for the “large-sized” metatherian trophic niche structure of this locality.

Institutional Abbreviations. **MCN-PV**, Coleção de Paleovertebrados do Museu de Ciências Naturais da Secretaria de Meio Ambiente (SEMA; ex. Fundação Zoobotânica do Rio Grande do Sul), Porto Alegre, Brazil; **MCT**, Museu de Ciências da Terra, Serviço Geológico do Brasil (MCTer-SGB), Rio de Janeiro, Brazil; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **UFRJ-DG**, Coleção de Macrofósseis do Departamento de

Geologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Other Abbreviations. **A**, area; **BM**, body mass; **DH**, dentary height; **Dt**, diastema; **H**, height; **L**, length; **Lm**, lower molar series length; **M**, postmetacrista; **M**, upper molars with the numbers corresponding to its positioning (M1-4); **m**, lower molars with the numbers corresponding to its positioning (m1-4); **MPT**, most parsimonious tree; **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **PPA**, preparacrista; **R**, ratio; **RDS**, relative dentary shape ($DH/Lm1-4$); **RPS**, relative premolar size ($Wp3/3\sqrt{BM}$); **SALMA**, South American Land Mammal Age; **SEM**, scanning electron microscope; **tal**, talonid; **tri**, trigonid; **W**, width.

2. Materials and methods

2.1 Study site

The Itaboraí Basin is in the municipality of Itaboraí, state of Rio de Janeiro, in southeastern Brazil, with geographical coordinates 22° 45' 9.9144" S, 42° 51' 53.5536" W (Fig. 1a). For more data about the Itaboraí Basin, see Bergqvist et al. (2009), and Rangel et al. (2023b).

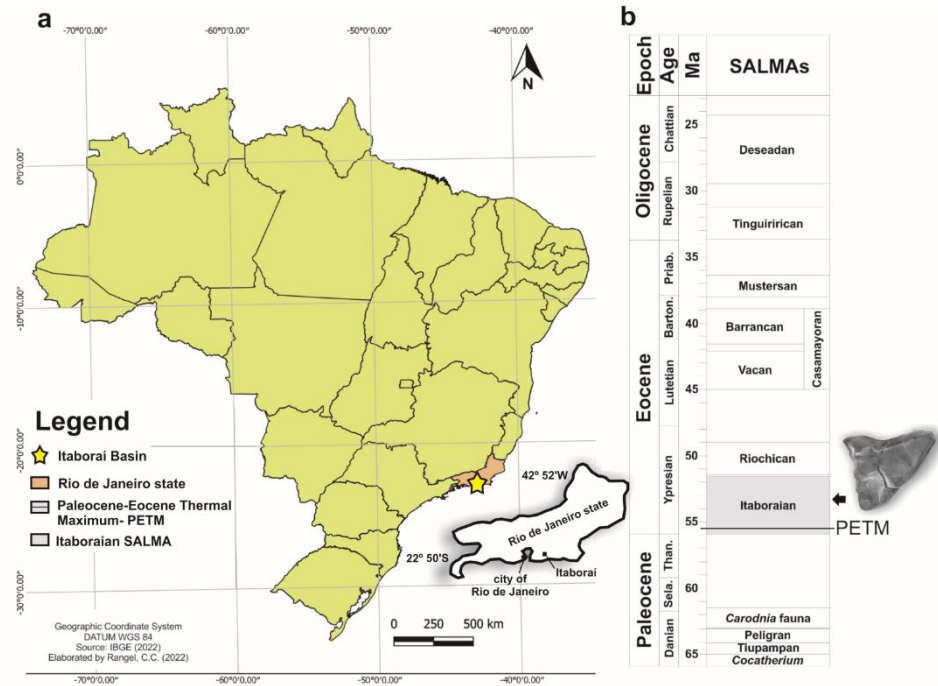


Fig. 1 The Itaboraí fauna: locality and biochron. **a**, Map showing the region and the coordinates of the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (22° 45' 9" S; 42° 51' 53" W). **b**, The stratigraphic relationships of the Itaboraiense SALMA with other Paleogene SALMAs. A plausible age range for the Itaboraí SALMA is highlighted in grey. The occurrence of *Xenocynus crypticus* gen. et sp. nov. is suggested by a black arrow and a digital image of the MCT.M.2382 (holotype), a left maxilla with M2 and alveoli of M1 and M3-4. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 500 Km.

2.2 Studied specimens

All studied specimens are from the Itaboraí Basin, Municipality of Itaboraí (Rangel et al., 2019; Carneiro, 2023; Carneiro and Oliveira, 2023) (Fig. 1). The studied specimens are housed in the collections of MCN-PV, Porto Alegre, state of Rio Grande do Sul, Brazil; MCT.M (ex DGM) and UFRJ-DG, Rio de Janeiro, state of Rio de Janeiro, Brazil. A list of studied specimens is presented as supplementary material (Appendix 1).

The metatherian fauna from the Itaboraí Basin is represented by at least 29 genera and 43 species, with almost 1000 specimens (considering only specimens represented by teeth, jaws

and maxillae; see Carneiro, 2023). This elevated number of specimens allows a “more secure” recognition of taxa’s dental and jaw patterns, intraspecific phenotypic plasticity, size span, and systematic affinities (Carneiro, 2023).

The SEM images were performed with JEOL JSM-6390LV at the Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional (MN), Rio de Janeiro, RJ, Brazil; JEOL JSM-6510LV at the Instituto de Química, Universidade Estadual do Rio de Janeiro (UERJ), Rio de Janeiro, RJ, Brazil; and JEOL 6060 at the Centro de Microscopia e Microanálise da Universidade Federal do Rio Grande do Sul (CMM, UFRGS), Porto Alegre, RS, Brazil.

The estimated body mass of the studied taxa was based on the regression equations of Myers (2001), which considers the length of the lower molar series ($\log_{10}BM = -1.253 + 3.540[\log_{10}Lm1-4]$) and the length of the upper molar series ($\log_{10}BM = -0.914 + 3.320[\log_{10}LM1-4]$). All body masses are presented in kilograms (see supplementary material, appendix 2).

The size classification for Itaboraí’s metatherians was taken from Carneiro and Oliveira (2023), following some adjustments presented by Carneiro (2023), who based their classification on the length of the lower molar series (Lm1-4) and body masses (BM; see Table 1). All measurements of studied specimens are presented as supplementary material (Appendix 3).

Table 1. Size categories considered for Early Eocene Itaboraí’s metatherians (sensu Carneiro 2023) based on their lower molar series length (in mm) and maximum and minimum limits of estimated body masses (BM) in grams (g) and kilograms (kg). BM, estimated body mass; Lm1-4, lower molar series length

Size category	Lm1-4 (mm)	BM (g and Kg)
Tiny	Lm1-4 < 5.00 mm	BM < 15 g

Very small	5.00 mm < Lm1-4 < 6.20 mm	15 g < BM < 40 g
Small	6.20 mm < Lm1-4 < 9.40 mm	40 g < BM < 150 g
Medium	9.40 mm < Lm1-4 < 15.50 mm	150 g < BM < 1 kg
Large	15.50 mm < Lm1-4 < 22.00 mm	1 kg < BM < 3.3 kg
Very large	22.00 mm < Lm1-4	3.3 kg < BM < 10 kg

2.3 Principal Component Analyses

To discriminate the new taxon from *Itaboraidelphys* and other large-sized metatherians (*Didelphopsis* spp., *Patene simpsoni*, and *Protodidelphis* spp.), a principal component analysis (PCA) was conducted based on five morphometric parameters (**L** = lower molar length; **Ltal** = talonid length; **Ltri** = trigonid length; **Wtal** = talonid width; and **Wtri** = trigonid width) measured from lower molar specimens of studied taxa. The included specimens were identified by their molar locus (m1, m2 or m3). The analysis used the variance-covariance matrix. This PCA technique was performed on the R environment (R core team, 2013). These data have been included as supplementary material (Appendix 3).

Moreover, we performed a second PCA analysis based on eight morphofunctional indices (see Table 3), including the new taxon, *Itaboraidelphys* and other large-sized metatherians from Itaboraí. This analysis included *Didelphopsis cabrerai*, *Didelphopsis* sp. nov., *Itaboraidelphys camposi*, *Patene simpsoni*, *Protodidelphis mastodontoides*, *Protodidelphis vanzolinii*, and the new taxon (see below). The analysis used the variance-covariance matrix. This PCA technique was performed on the R environment (R core team, 2013). These data have been included as supplementary material (Appendix 4). The R script of PCA analyses is presented as supplementary material (Appendix 5).

3. Systematic Paleontology

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

Marsupialiformes Vullo et al., 2009

Sudameridelphia (Szalay, 1994) sensu Carneiro and Oliveira, 2023; Carneiro, 2023

Incertae sedis

†*Xenocynus* gen. nov.

Zoobank: urn:lsid:zoobank.org:act:40DF7A51-4686-4BEA-92B4-8118F9E635A8

Derivation of the genus name. From the Greek “*xénos*” (strange, foreigner), in reference to its “mosaic and strange” morphology in comparison with other Paleogene generalized carnivorous metatherians, and ‘*cynus*’, from the Greek “*kyon*” (dog), a common terminology for faunivorous-carnivorous metatherians, such as *Hesperocynus* and *Sparassocynus*. Gender is masculine.

Diagnosis. Large (sensu Carneiro, 2023; Carneiro and Oliveira, 2023) South American Eocene metatherian with estimated body mass between 1.38 kg and 1.48 kg. Differs from other Itaboraense SALMA metatherians in the following combination of features: M2 longer than wider, StC closely spaced to StB on M2, flattened and reduced StD, metacone with a distally oriented apex; tall, pyramidal and crested paraconule, protocone with a distolingual expansion (i.e., protoconal bulge; sensu Muizon and Ladevèze, 2020), spaced paraconid and metaconid bases (i.e., not in contact; sensu Muizon and Ladevèze, 2020), paraconid larger than metaconid on m2, evident labial contact of the cristid obliqua with the distal border of the trigonid on m2, flattened and low entoconid (shorter than hypoconulid), maxillae with deep pits between upper molars, and strong mandibular symphysis (but not ankylosed; sensu Marshall, 1979).

Type species. *Xenocynus crypticus* sp. nov.

Included species. The type only.

Type Locality and Horizon. Itaboraí Basin, Municipality of Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al., 2009). Early Eocene, Itaboraense SALMA (53–50 Ma; sensu Woodburne et

al., 2014).

Comparisons. *Xenocynus* gen. nov. differs from *Didelphopsis* (Fig. 2) in having a vestigial StD (always present and well-developed in *Didelphopsis*), absence of supernumerary cuspsules on the stylar shelf (frequently present in *Didelphopsis*), absence of a central supernumerary cusp at the center of the stylar shelf (variably present in *Didelphopsis*), centrocrista not more labially shifted than the labial borders of paracone and metacone (centrocrista more labially shifted in *Didelphopsis* [i.e., the apex of the centrocrista is more labially placed than the labial border of paracone and metacone; see Fig. 2), well-developed paraconule (small to vestigial paraconule in *Didelphopsis*), paraconid with mesial keel (absent in *Didelphopsis*), paraconid larger than metaconid on m2 (paraconid always smaller in length and height than the metaconid on m1-3 in *Didelphopsis*), convex labial border of the protoconid (flat labial border of the protoconid in *Didelphopsis*), p2 slightly smaller than p3 (RLp2/Lp3: 0.90-0.91; see Table 3) (p2 evidently smaller than p3 in *Didelphopsis* [RLp2/Lp3: 0.72-84]; see Table 3), and anterior mental foramen of the dentary much larger than the posterior one (mental foramina subequal in *Didelphopsis*).

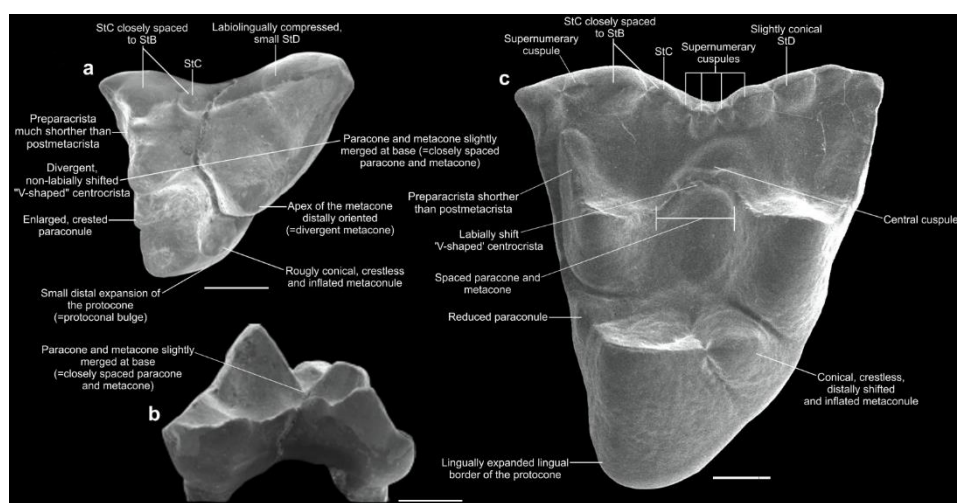


Fig. 2 Comparative upper molar differences between *Xenocynus* gen. nov. and *Didelphopsis* Paula Couto, 1952a. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal; **b**, labial views. *Didelphopsis* sp. nov. Oliveira, 1998 (unpublished data; see Carneiro and Oliveira, 2023): **c**, MCT.M.642, a left M3 in occlusal

view. Scale bars = 1 mm.

Differs from *Itaboraidelphys* (Fig. 3) in having a larger size (10-15% larger than *Itaboraidelphys camposi* based on Lm1-4; see Table 3), a vestigial StD (always present and moderately to well-developed in *Itaboraidelphys*), absence of supernumerary cuspsules on the stylar shelf (present in *Itaboraidelphys*), absence of a central supernumerary cusp at the center of the stylar shelf (variable in *Itaboraidelphys*), centrocrista not more labially shifted than the labial borders of paracone and metacone (centrocrista more labially shifted in *Itaboraidelphys*), well-developed paraconule (small to vestigial paraconule in *Itaboraidelphys*), paraconid with mesial keel (absent in *Itaboraidelphys*), paraconid larger than metaconid on m2 (paraconid always smaller in length and height than the metaconid on m1-3 in *Itaboraidelphys*), convex labial border of the protoconid (flat labial border of the protoconid in *Itaboraidelphys*), p2 smaller than p3 (RLp2/Lp3: 0.90-0.91; see Table 3) (p2 subequal to p3 in *Itaboraidelphys* [RLp2/Lp3: 0.96-1.14]; see Table 3), and anterior mental foramen of the dentary much larger than the posterior one (mental foramina subequal in *Itaboraidelphys*).

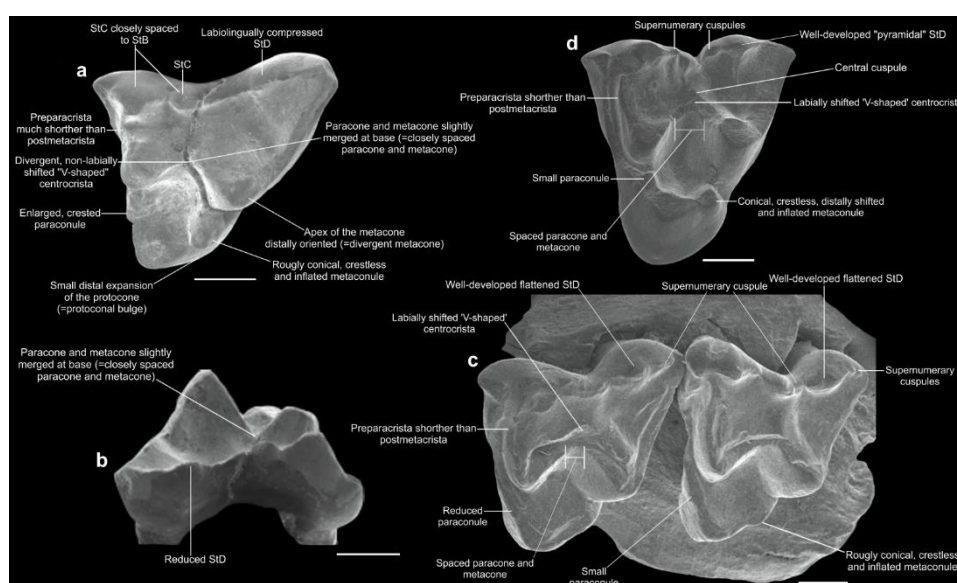


Fig. 3 Comparative upper molar differences between *Xenocynus* gen. nov. and *Itaboraidelphys* Marshall and Muizon, 1984. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal; **b**, labial views.

Itaboraidelphys camposi Marshall and Muizon, 1984: **c**, MCT.M.926, a fragment of a left maxilla with M2-3 in occluso-mesial view; **d**, MCT.M.2789, a left M2 in occlusal view. Scale bars = 1 mm.

Differs from *Patene* (see Fig. 4) by its smaller size (13-24% smaller than *Patene simpsoni* based on Lm1-4; see Table 3), presence of a ‘V-shaped’ centrocrista (straight centrocrista in *Patene*), presence of flat labial border of the paracone and metacone (conical in *Patene*), spaced paracone and metacone (paracone and metacone merged at 50% of their height; sensu Muizon et al., 2018); a roughly conical, slightly inflated and weakly crested metaconule on M2 (subtriangular and crested in *Patene*), talonid wider than the trigonid on m2 (m2 with a talonid narrower than the trigonid in *Patene*), cristid obliqua with a labial contact on m2 (ventral to the carnassial notch on m2 in *Patene*), shallower condition of the dentary (RDS: 0.52; *P. simpsoni* RDS: 0.61; see Table 3), and more curved posterior border of the dentary ventral to the coronoid process (straight in *P. simpsoni*).

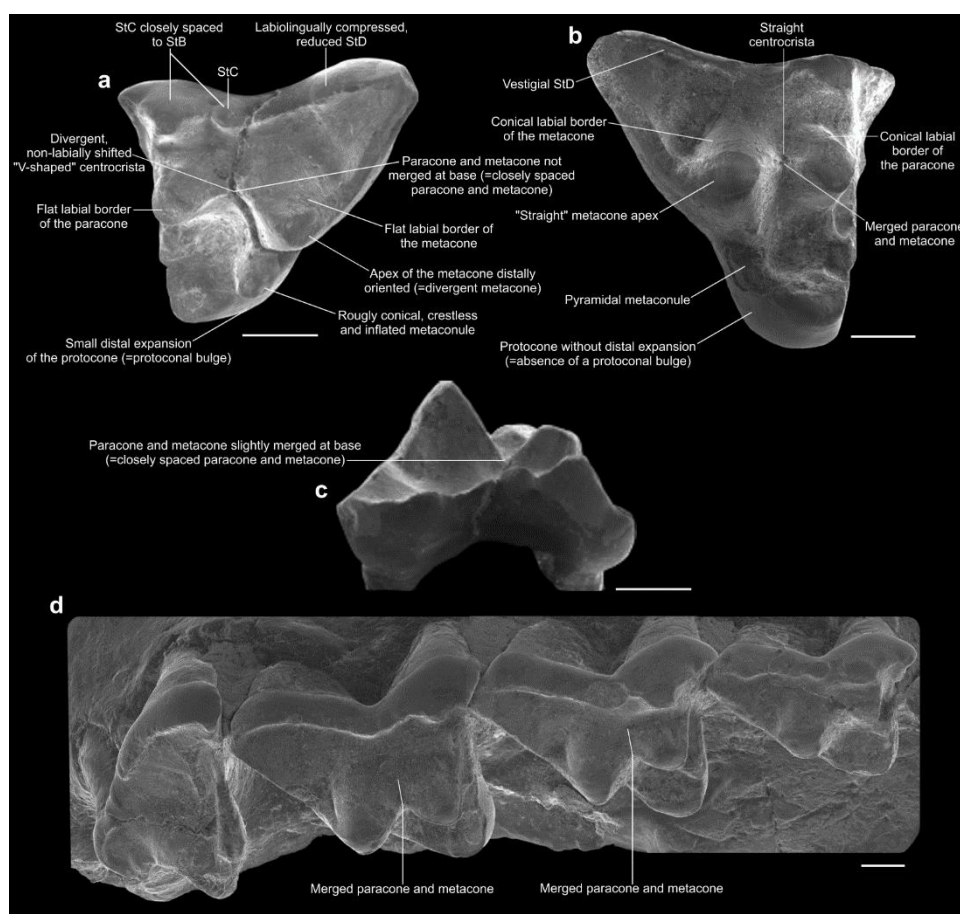


Fig. 4 Comparative upper molar differences between *Xenocynus* gen. nov. and *Patene* Simpson, 1935. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal, **c**, labial views. *Patene simpsoni* Paula Couto, 1952a: M2 of MN 1331-V, holotype, in **b**, occlusal, **d**, labial views. Scale bars = 1 mm.

Differs from *Protodidelphis* (see Fig. 5) by its smaller size (15-18% and 18-19% smaller than *Protodidelphis vanzolinii* and *P. mastodontoides*, respectively, based on Lm1-4; see Table 3), tribosphenic crown (sensu Marshall, 1987) (bunodont crown in *Protodidelphis*), asymmetric stylar shelf, in which the distal lobe is broader than the mesial one (symmetric stylar shelf [=mesial and distal lobes subequal in width] in *Protodidelphis*), developed StC (StC absent in *Protodidelphis*), reduced and labiolingually compressed StD (conical and hypertrophied StD in *Protodidelphis*), centrocrista not more labially shifted than the labial borders of paracone and metacone (centrocrista more labially shifted in *Protodidelphis*), closely spaced paracone and metacone (spaced paracone and metacone); a roughly conical, slightly inflated and weakly crested metaconule on M2 (reduced to absent in *Protodidelphis*), trigonid taller (ca. 2-2.5x)

than the talonid (trigonid only slightly taller than the talonid in *Protodidelphis*), talonid shorter than the trigonid on m2 (m2 with a talonid longer than the trigonid in *Protodidelphis*), cristid obliqua with a labial contact on m2 (slightly labial to the carnassial notch on m2 in *Protodidelphis*), small and labiolingually compressed entoconid (conical and hypertrophied entoconid in *Protodidelphis*), shallower condition of the dentary (RDS: 0.52; *Protodidelphis* spp. RDS: 0.60-0.61; see Table 3).

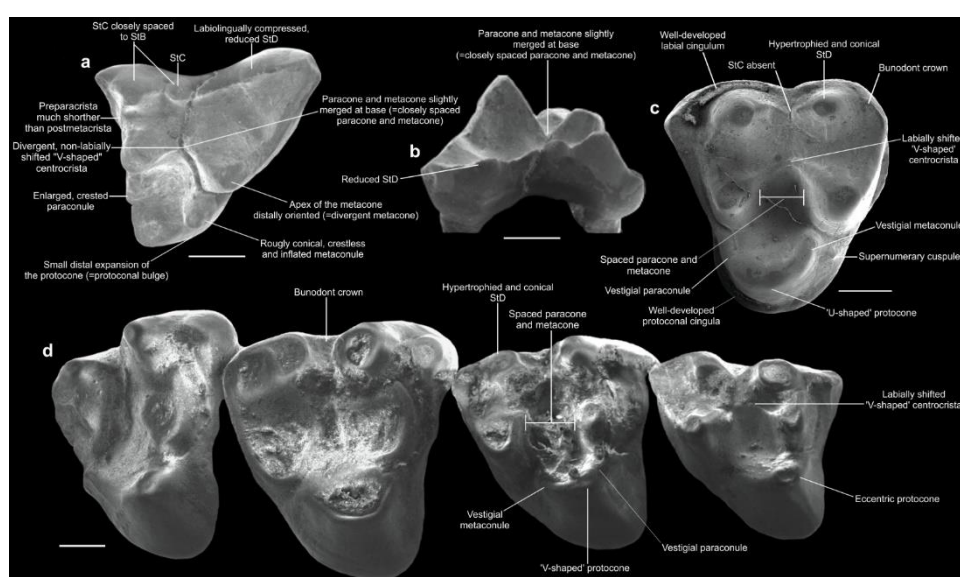


Fig. 5 Comparative upper molar differences between *Xenocynus* gen. nov. and *Protodidelphis* Paula Couto, 1952a. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal, **c**, labial views. *Protodidelphis mastodontoides* (Marshall, 1987): **c**, MCT.M.806, a left M1, holotype, in occlusal view; **d**, MCT.M.303, a right maxilla with M1-4 in occlusal view. Scale bars = 1 mm.

Remarks. *Xenocynus* gen. nov. was one of the last metatherians identified in the Itaboraí Basin, along with an undescribed pucadelphyid (see Carneiro, 2023). The first specimen of *Xenocynus* gen. nov. to be mentioned in the literature (MCT.M.2382, holotype) had not been studied for the last 53 years. The identification of *Xenocynus* gen. nov. was possible due to direct comparisons between its specimens with other metatherians from the Itaboraí Basin (see Carneiro, 2023). The morphological features and morphofunctional indices identify *Xenocynus*

gen. nov. as a distinct taxon of the Itaboraí Basin (see PCA analyses below).

†*Xenocynus crypticus* sp. nov.

(Figs. 5-7)

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Derivation of specific name. From the Latin “*crypticus*” (hidden) in reference to its unnoticed presence among Itaboraí’s metatherians.

Diagnosis. As for the genus.

Holotype. MCT.M.2382 (=MCT.M.643, a left maxilla with M2 and alveoli of M1 and M3-4) (Fig. 6).

Hypodigm. The holotype; MCN-PV 1788, a right m2 (Fig. 7i-l); MCN-PV1793, a left m1 (Fig. 7a-d); MCN-PV 1813, a right m1, lacking the hypoconulid (Fig. 7e-h); MCT.M.4590, a left maxilla with alveoli of M1, with incomplete mesiolabial alveolus, M2-3, and M4, with an incomplete distolabial alveolus; MCT.M.4606, a fragment of a right maxilla with alveoli of M3-4; UFRJ-DG 14(a)-M, an anterior fragment of a left dentary with alveoli of p2-3, m1-2 and part of the posterior alveolus of p1 (Fig. 8a-c); and UFRJ-DG 14(b+c)-M, an incomplete left dentary with alveoli of p1-3, m1, m3 and m4 (damaged at the level of m2 alveoli) (Fig. 8d-f).

Locality and age. All specimens were collected in the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al., 2009). The specimens MCT.M.2382 (holotype), UFRJ-DG 14(b+c)-M and UFRJ-DG 14(a)-M were collected in 1967, and specimens MCN-PV 1793, MCN-PV 1788, MCN-PV 1813, MCT.M.4590 and MCT.M.4606 have no date. Early Eocene, Itaboraiense SALMA (see Woodburne et al., 2014).

Description. The maxillae (MCT.M.2382, MCT.M.4590, and MCT.M.4606) display deep pits between upper molars. Based on preserved alveoli and tooth, the M1 is evidently smaller than M2, which is smaller than M3 (see Fig. 6a). The M4 is slightly smaller than M3 (i.e., $M1 < M2 < M3 > M4$). The lingual alveolus of the upper molars is mesiodistally compressed.

The M2 (MCT.M.2382, holotype; Fig. 6b-c) is longer than wider. It has a moderately developed styler shelf (i.e., represents 33% to 50% of the molar width; sensu Ladevèze et al., 2020), with a distal lobe of the styler shelf wider than the mesial one. The ectoflexus is centrally placed and is moderately deep. The StA is small and is slightly more labially placed than StB. The StB is the largest styler cusp and is placed slightly mesially to the paracone's apex. This cusp displays three crests: the mesiolabial crest, which reaches StA; the mesiolingual crest, which merges with the preparacrista; and the distolabial crest, which merges with StC. A moderately developed StC is nearly twinned with the distal border of StB. StD is weakly developed, labiolingually compressed and twinned with a reduced styler cuspule (StE?). The preparacrista is short, vertically oriented, reaching StB. The postmetacrista is obliquely oriented and clearly longer than the preparacrista (about 3x longer). The distolabial angle of this crest is not preserved. The centrocrista is slightly "V-shaped". The specimen is damaged at the metacone's medial border, resulting in a craniolabial displacement of the metacone. The paracone is much smaller than the metacone, and both have flat labial borders (i.e., pyramidal shape; sensu Case et al., 2005). These two structures are labially aligned and have their bases incipiently merged (=closely spaced paracone and metacone; short protofossa). The protoconal basin is developed. The conules are well-developed. The metaconule is larger than the paraconule. The paraconule displays a sharp and tall internal conular crest, whereas the metaconule shows a weakly developed internal crest. The metaconule is moderately inflated and roughly conical in shape. The protocone is small (i.e., shorter than the metacone; sensu Muizon et al., 2018; Engelman et al., 2020), mesially oriented (but not eccentric, i.e., not aligned with StB and the paracone; sensu Oliveira and Goin, 2011) and bears a distolingual expansion (i.e., protoconal bulge; sensu Muizon and Ladevèze, 2020). The paracingulum is long (i.e., it reaches the protoconal basin; sensu Carneiro et al., 2018). A metacingulum is absent.

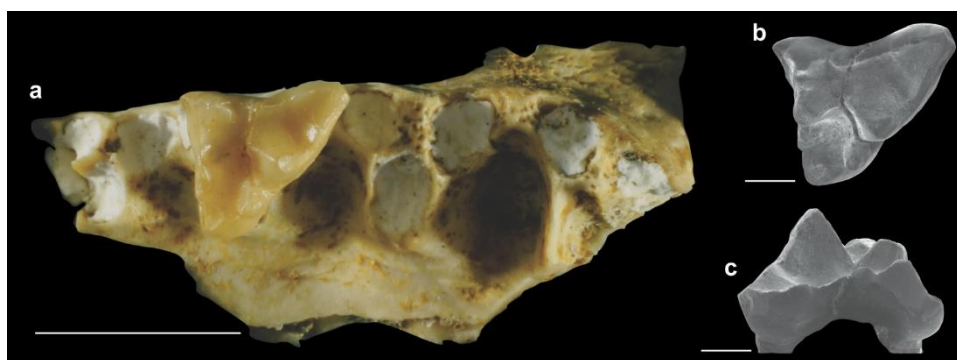


Fig. 6 *Xenocynus crypticus* gen. et sp. nov. Digital image of MCT.M.2382, a left maxilla with M2, and alveoli of M1 and M3-4: **a**, ventral view; SEM image of the preserved M2: **b**, occlusal; **c**, labial views. Scale bars: **a** = 5 mm; **b-c** = 1 mm.

The m1 (MCN-PV 1793, MCN-PV 1813; Fig. 7a-h) has a trigonid that is larger than the talonid (the talonid represents 70-71% of the trigonid area); it is almost as twice as tall as the talonid (ca. 2x) and as broad as the talonid (i.e., subequal in width). The paraconid is subequal in length (=as robust as) although shorter in height than the metaconid in both studied specimens. A paraconid mesial keel is easily observable. The metaconid is well-developed and distal to the protoconid. The bases of paraconid and metaconid are separated (i.e., their bases are not in contact; sensu Muizon and Ladevèze, 2020), “opening” the trigonid basin in the lingual view. The protoconid is the largest cusp of the trigonid and is labially placed. The labial side of the protoconid is convex in the distal view (i.e., broader at its mid-height). The postprotocristid and the metacristid are obliquely oriented concerning the mesiodistal axis of the tooth. The talonid cusps are nearly subequal in height (the entoconid seems slightly smaller than the hypoconulid and the hypoconid). The cristid obliqua is long and has a labial contact with the trigonid’s distal border at the protoconid apex’s level, resulting in a small hipoflexid. The hypoconid is transversely aligned with the entoconid. The entoconid is flattened at its labial face and is subequal in height to the hypoconulid. The entocristid is sharp and lacks a carnassial notch. The hypoconulid is more labial than the entoconid but is not centrally placed (distolabially placed to the entoconid). The precingulid is

developed (i.e., present on both the paraconid and protoconid; sensu Muizon et al., 2018). The postcingulid is short (MCN-PV 1793) or well-developed, although it is not connected to the labial cingulid (MCN-PV 1813). The labial cingulid is short and does not extend beyond the levels of the distal border of the protoconid and the apex of the hypoconid. The labial cingulid is not developed. These teeth are considered m1 based on the presence of a paraconid shorter (in height) than the metaconid.

The m2 (MCN-PV 1788; Fig. 7i-l) differs from m1 and is identified by the following features: its trigonid is larger than the talonid (the talonid represents 69% of the trigonid area), and it is much taller than the talonid (based on the preserved part of the protoconid, it seems that the trigonid is ca. 2.5x taller than the talonid; sensu Ladevèze et al., 2020) and the talonid is slightly wider than the trigonid. The paraconid is slightly larger than the metaconid. A paraconid mesial keel is weakly developed, resulting in a straight paraconid without mesial expansion at the tooth's base. The cristid obliqua is long and has a labial contact with the distal wall of the trigonid, nearly at the distolabial border of the protoconid. The entocristid is sharp and shows a carnassial notch. This tooth is considered an m2 based on its paraconid being larger than the metaconid and the presence of a relatively larger protoconid in comparison with m1.

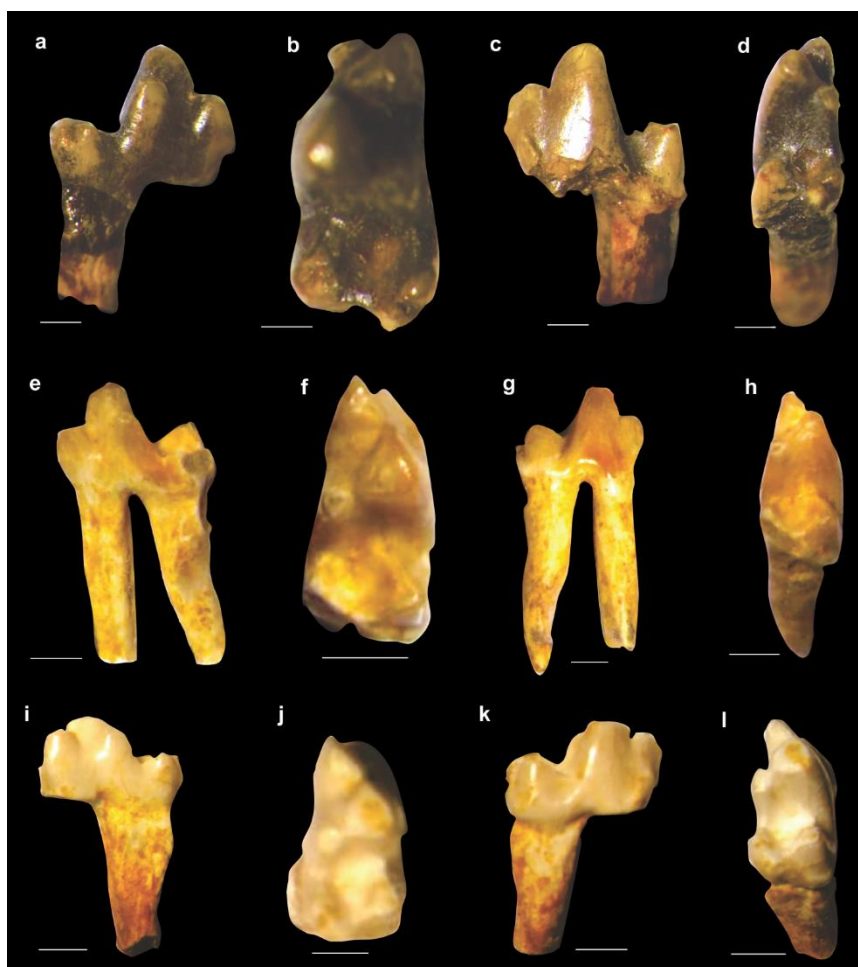


Fig. 7 Lower molars of *Xenocynus crypticus* gen. et sp. nov. Digital images of the specimens MCN-PV 1793, left m1: a, lingual; b, occlusal; c, labial; d, distal views; MCN-PV 1813, right m1: e, lingual; f, occlusal; g, labial; h, distal views; MCN-PV 1788, right m2: i, lingual; j, occlusal; k, labial; l, distal views. Scale bars = 1 mm.

The dentaries (UFRJ-DG 14(a)-M and UFRJ-DG 14(b+c)-M; Fig. 8) are shallow, judging by their height (UFRJ-DG 14(b+c)-M DH_{m3-4} : 8.69 mm; RDS: 0.52; UFRJ-DG 14(a)-M DH_{m2-3} : 7.78 mm). The mandibular symphysis is well-developed and extends posteriorly to the level of the posterior root of p2. Two mental foramina are observable in UFRJ-DG 14(b+c)-M; the anterior one is the largest and is placed below the point of p1 (the anterior mental foramen is not preserved in UFRJ-DG 14(a)-M). In contrast, the posterior one is smaller, cranio-ventrally compressed, and placed below the level of p3-m1 embrasure in both dentaries. There is a short diastema between p1 and p2 in both dentaries (UFRJ-DG 14(a)-M dt_{p1-2} : 0.76 mm; UFRJ-DG 14(b+c)-M dt_{p1-2} : 1.17 mm). There is an increase in the height of the dentary at the

level of m1 (i.e., the anterior alveolus of m1 is more cranially placed than the posterior alveolus of p3), with the condition of the specimen UFRJ-DG 14(a)-M more developed than the one of the specimen UFRJ-DG 14(b+c)-M.

The alveoli of p1 are obliquely oriented and moderately smaller than those of p2, and the posterior alveolus is much larger than the anterior one. Based on preserved alveoli, the p2 is slightly smaller than p3. The alveoli of p2-3 are longer than the alveoli of m1 (see Table 2). The m2 is larger than m1 but smaller than m3, and m4 is the largest lower molar, based on preserved alveoli (see Table 2).

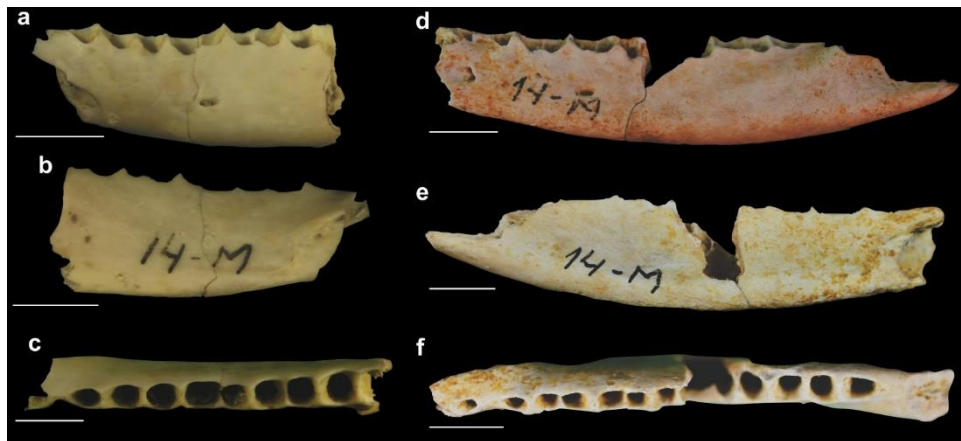


Fig. 8 Dentaries of *Xenocynus crypticus* gen. et sp. nov. Digital images of UFRJ-DG 14(a)-M, an anterior fragment of a left dentary with alveoli of p2-3, m1-2 and part of the posterior alveolus of p1: **a**, labial; **b**, lingual; **c**, occlusal views; UFRJ-DG 14(b+c)-M, an incomplete left dentary with alveoli for p1-3 and m1-4 (damaged at the level of m2 alveoli): **d**, labial; **e**, lingual; **f** occlusal views. Scale bars = 4 mm. Credits of the images: T. Z. Ferreira (UFRJ).

Measurements. See Table 2.

Table 2 Dental measurements (in mm) of *Xenocynus crypticus* gen. et sp. nov. The holotype is highlighted in bold. **Dt**, diastema; **L**, length; **M/m**, molar; **P/p**, premolar; **W**, width; **()**, talonid dimensions; ~, incomplete tooth or alveoli; *, based on alveoli dimensions

LP1	LP2	LP3	LM1	WM1	LM2	WM2	LM3	WM3	LM4	WM4	LM

1-4											
MCT.M.											
2382 (=											
MCT.M.				3.44*		4.33	4.11	4.66		4.22	16.6
643)								*		*	5*
MCT.M.				~3.6				4.78		4.02	16.4
4590				5*		4.04*		*		*	9*
MCT.M.								4.81		~2.8	
4606								*		2*	
Lm											
Lp1	Lp2	Lp3	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3	Lm4	Wm4	1-4
					2.19						
MCN-					(1.44	1.70					
PV 1788					) -	(1.80)					
					3.63						
					2.10						
MCN-					(1.45	1.67					
PV 1793					) -	(1.72)					
					3.55						
					2.13						
MCN-					(1.43	1.65					
PV 1813					) -	(1.74)					
					3.56						
UFRJ-											
DG	~0.7	3.89	4.00					~1.4			
14(a)-M	8*	*	*	3.57*		3.93*		2*			
UFRJ-											
DG	2.02	3.83	4.21					4.38		4.66	16.7
14(b+c)-	*	*	*	3.48*		4.19*		*		*	1*
M											

Remarks. The holotype of *Xenocynus crypticus* gen. et sp. nov. (MCT.M.2382; ex. MCT.M.643) was initially described by Paula Couto (1970:32), who stated: “comes from an undetermined didelphid of medium size”. Paula Couto described *Didelphopsis cabrerai* Paula

Couto, 1952a, *Patene simpsoni* Paula Couto, 1952b, and *Protodidelphis vanzolinii* Paula Couto, 1952a; then, he considered the specimen MCT.M.2382 as a different taxon from these three.

Later, Marshall (1987:127) stated that Paula Couto “did not compare any of these with named taxa”, including the specimen MCT.M.2382. It is unclear if Marshall compared the specimen MCT.M.2382 with other Itaboraí’s metatherians, as he has not directly commented about it. Marshall and Muizon (1984) described *Itaboraidelphys camposi*; however, these authors have never compared this species with the specimen MCT.M.2382.

Furthermore, other specimens assigned to *Xenocynus crypticus* gen. et sp. nov. have never been examined before this study. These specimens have been collected in the Itaboraí fauna and deposited without a formal identification (e.g., *Patene?*; marsupial, tooth, mammal) and registration, i.e., they had not yet received a collection number before Carneiro (2023). This author associated the maxillae, dentaries and teeth to this taxon based on the combination of several morphological and morphometric parameters (e.g., size, presence of maxillae pits between upper molars, the shape of the lingual alveolus of upper molars, molar series size relations, relative size between p2 and p3, and p3 and m1, presence of a diastema between p1 and p2, symphysis development, number of lower incisors; see also Table 3), which differentiate these elements from every other metatherian from the Itaboraí Basin (see e.g., comparisons, and Carneiro, 2023). After Carneiro (2023), almost all metatherian taxa from the Itaboraí Basin have now been assigned maxillae and dentaries.

5. Results of PCA analyses

The first PCA analysis recovered the Ltri (=length of the trigonid) as the principal component (PC1) (‘X’ axis), which represents 77.4% of the variation identified by the analysis. The Wtal (=width of the talonid) was the second principal component (PC2) (‘Y’ axis), representing 19.8% of the variation identified by the analysis (Fig. 9).

The PCA1 results reveal that *Xenocynus crypticus* gen. et sp. nov., *Itaboraidelphys camposi*, and *Patene simpsoni* are discriminated by their lower molar measurements (Fig. 9), indicating that they are independent taxa.

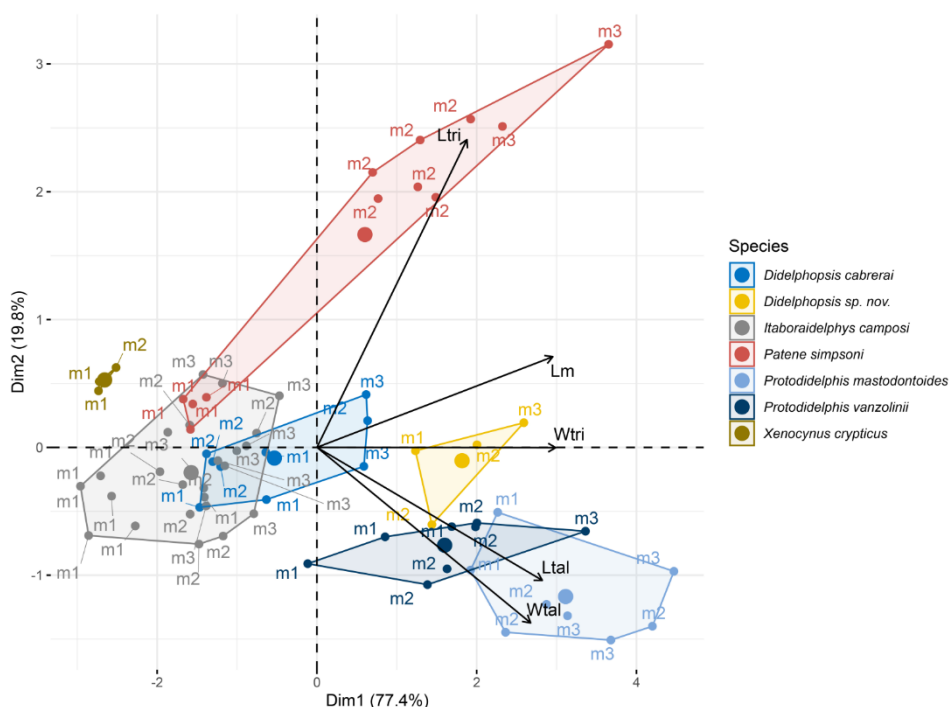


Fig. 9 Principal component analysis (PCA) of five morphometric indices based on lower molar measurements for *Xenocynus crypticus* gen. et sp. nov., *Itaboraidelphys camposi*, *Didelphopsis* spp., *Protodidelphis* spp., and *Patene simpsoni*. **L** = lower molar length; **Ltal** = talonid length; **Ltri** = trigonid length; **Wtal** = talonid width; **Wtri** = trigonid width.

The second PCA analysis recovered the RDS (Relative dentary shape = $DH/Lm1-4$) as the principal component (PC1) ('X' axis), which represents 60% of the variation identified by the analysis. The relative area of the talonid ($=Atal/Atri$) was the second principal component (PC2) ('Y' axis), representing 23.5% of the variation identified by the analysis (Fig. 10).

The results of the PCA2 reveal that *Xenocynus crypticus* gen. et sp. nov. is morphofunctionally more similar to *Patene simpsoni* than to *Itaboraidelphys camposi*. *Xenocynus crypticus* gen. et sp. nov. and *P. simpsoni* are discriminated from other considered

taxa in the M2 longer than wider, p3 labiolingually compressed (low values of RPS, relative premolar size), preparacrista much shorter than postmetacrista (low values of LPPA/PM), and talonid proportionally reduced and much lower than the trigonid (Atal/Atri and Htal/Htri, respectively). *Patene simpsoni* is discriminated by its lower value of Lp1-3/Lm1-4, as this taxon lacks diastemata and the lower molar series increases in length from m1 to m4 (*Xenocynus crypticus* gen. et sp. nov. has a long diastema between p1 and p2).

Protodidelphis spp. are discriminated by their moderately robust dentaries (RDS about 0.6), talonids more developed than trigonids (higher values of Atal/Atri), and nearly subequal talonid and trigonid in height (higher values of Htal/Htri). *Didelphopsis* spp. are discriminated by their enlarged and bulbous p3s (higher values of RPS and Lp1-3/Lm1-4 [relative anterior length of the dentary by the lower molar series length]). *Itaboraidelphys camposi* is discriminated from *Didelphopsis* spp. by its proportionally longer p2 in comparison with p3 (Lp2/Lp3) and by *X. crypticus* gen. et sp. nov. and *P. simpsoni* by its proportionally larger talonid (Atal/Atri), more inflated (=less labiolingually compressed) p3 (RPS), and relatively longer preparacrista (LPPA/LPM).

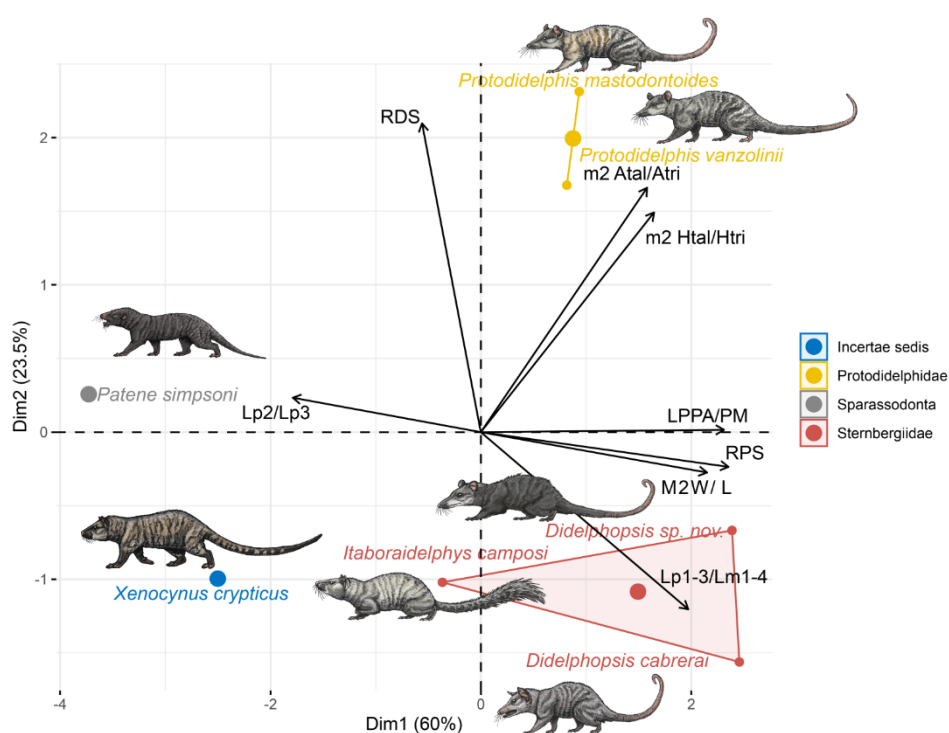


Fig. 10 Principal component analysis (PCA) based on eight morphometric and morphofunctional indices for *Xenocynus crypticus* gen. et sp. nov., *Itaboraidelphys camposi*, *Didelphopsis* spp., *Protodidelphis* spp., and *Patene simpsoni*. **A**, area; **H**, height; **L**, length; **Lm1-4**, lower molar series length; **M/m**, upper/lower molar with the numbers corresponding to its positioning (M/m1-4); **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **PM**, postmetacrista; **PPA**, preparamacrista; **RDS**, relative dentary shape; **RPS**, relative premolar size; **tal**, talonid; **tri**, trigonid; **W**, width. Schematic drawings are not at scale. Credits: The artistic drawings of Itaboraí's metatherians were made by Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com).

6. Discussion

6.1 Dietary inferences for *Xenocynus*

Xenocynus gen. nov. displays a combination of dental and dentary features indicative of an insectivorous-carnivorous diet (i.e., generalized carnivory; sensu Rangel et al., 2023b). The most significant morphofunctional indexes that support this conclusion are the RPS (1.30) and m2 relative area (i.e., Atal/Atri: 0.69). Van Valkenburgh (1991), Zimicz (2012), and Maga and Beck (2017) considered higher values of RPS as indicative of a durophagous specialization, whereas low values are observed on non-durophagous insectivorous and carnivorous taxa. Therefore, the RPS index indicates that *X. crypticus* gen. et sp. nov. was not a durophage. In addition, the low value of the relative area of m2 suggests an insectivorous to carnivorous diet, as the talonid is reduced compared to the trigonid. If an omnivorous or frugivorous taxon, *Xenocynus crypticus* gen. et sp. nov. should have a talonid slightly less developed or as developed (see *Didelphopsis cabrerai* and *Itaboraidelphys camposi*; see Table 3) or a talonid more developed to more developed than the trigonid (see *Didelphopsis* sp. nov. and *Protodidelphis* spp.; see Table 3), respectively.

The presence in *Xenocynus crypticus* gen. et sp. nov. of an asymmetric styler shelf (i.e., the mesial and distal lobes of the styler shelf have different widths; sensu Carneiro, 2023) with a distal lobe broader than the mesial one, closely spaced paracone and metacone, mesiodistally

compressed protocone, trigonid more developed than talonid (see $m2Atal/Atri$ ratio), trigonid much taller than talonid (see $Htal/Htri$ ratio), mesially shifted paraconid (i.e., low contact or no contact between the bases of paraconid and metaconid), and flattened and short entoconid are indicative of insectivorous and carnivorous diets, as several metatherians with inferred insectivorous diets have similar features (e.g., *Gaylordia*, *Minusculodelphis*; see, e.g., Oliveira and Goin, 2015; Oliveira et al., 2016; Carneiro and Oliveira, 2023). Moreover, the presence of deep maxillary pits between upper molars (sensu Suárez et al., 2023), a progressive increase in size of molar series from M/m1 to M/m4, a labiolingually compressed and reduced StD, an obliquely oriented and long postmetacrista (3x longer than preparacrista) on M2, and an enlarged paraconid on m2 are indicative of a carnivorous diet (sensu Rangel et al., 2019, 2023a, 2023b).

On the contrary, the presence of a moderate styler shelf (i.e., between 33% and 50% of the tooth width; sensu Ladevèze et al., 2020), roughly conical and inflated metaconule, protocone with a distolingual expansion (i.e., protoconal bulge; sensu Muizon and Ladevèze, 2020), talonid broader than trigonid, and cristid obliqua with an evident labial contact with the distal border of the trigonid is indicative of an insectivorous to omnivorous diet (see dietary inferences of Itaboraí's metatherians in Zimicz, 2012; Carneiro, 2023; Carneiro and Oliveira, 2023).

In addition, *Xenocynus crypticus* gen. et sp. nov. displays a long diastema (i.e., subequal to longer than the anterior root of p2; see Engelman et al., 2018) between p1 and p2, a shallow dentary (i.e., $RDS < 0.6$), and convex posterior border of the dentary, which are indicative of insectivorous to omnivorous diets, as faunivores and hypercarnivores have moderate to robust dentaries ($RDS > 0.6$), straighter posterior border of the dentary, and, frequently, lack diastemata between lower canine and premolars (see Engelman et al., 2018).

Following the results of PCA2, *Xenocynus crypticus* gen. et sp. nov. is morphofunctionally more similar to *Patene simpsoni* than to *Itaboraidelphys camposi*. Its “left”

placement in the morphospace suggests a carnivorous diet, although less specialized than that of *Patene simpsoni*.

Furthermore, *Xenocynus crypticus* gen. et sp. nov. has a combination of morphological and morphofunctional features indicative of an insectivorous-carnivorous diet (i.e., it was a generalized carnivore). *Xenocynus crypticus* gen. et sp. nov. probably had a “more carnivorous diet” in comparison with the extant *Lutreolina crassicaudata*, which has a generalized carnivorous diet, preying primarily on vertebrates and invertebrates (including worms, snails, and crabs) but also ingesting fruits and seeds (see e.g., Pessano et al., 2004; Facure and Ramos, 2010). The morphological pattern between these two taxa is very similar, with both sharing maxillae with deep pits between upper molars, asymmetric styler shelf (the distal lobe is broader than the mesial one), mesiodistally compressed protocone on M2, lower molar series increasing in size from m1 to m4, trigonids more developed than talonids, labial contact of the cristid obliqua with the distal border of the trigonid, low dentary (i.e., RDS < 0.6), and presence of a short diastema between p1 and p2. However, *Xenocynus crypticus* gen. et sp. nov. seems to be “a relatively more specialized carnivore” based on the presence of an enlarged paraconid on m2. In short, *Xenocynus crypticus* gen. et sp. nov. may have occupied a similar trophic niche to the extant *L. crassicaudata*.

6.2 Evidence of low niche partitioning between large-sized metatherians: *protodidelphids*, *sparassodonts*, and *sternbergiids* in the Itaboraí Basin

The results of a PCA analysis focused on some morphofunctional indexes (Fig. 10) recovered *Didelphopsis*, *Itaboraidelphys*, *Patene*, *Protodidelphis*, and *Xenocynus* gen. nov. in different morphospaces. This result is indicative of differential patterns of morphofunctional features for each of them, suggesting that these taxa had probably explored different trophic niches.

A list of some morphological and morphometric features of *Itaboraidelphys* and large-sized metatherians (*Didelphopsis*, *Protodidelphis*, *Patene*, and *Xenocynus* gen. nov.) is presented below (Table 3):

Table 3 Some morphological and morphometrical data of *Xenocynus crypticus* gen. et sp. nov., *Itaboraidelphys camposi*, *Didelphopsis* spp., *Protodidelphis* spp., and *Patene simpsoni* from the Itaboraí Basin. **A**, area; **BM**, body mass (in kg); **DH**, dentary height; **H**, height; **L**, length (in mm); **M/m**, molar; **p**, lower premolar; **PM**, postmetacrista; **PPA**, preparacrista; **tal**, talonid; **tri**, trigonid; **W**, width; *, measurement made from an incomplete specimen. **RDS**: $DH/Lm1-4$; **RPS**: $Wp3/3\sqrt{BM}$.

		LM/ m1- 4	m2 Atal/ Atri	m2 Htal/ Htri	LPP A/L PM	M2 W/ L	Lp1- 3/Lm1-4	Lp2/Lp 3	RDS	RPS
<i>Itaboraidelphys camposi</i>		14.1								
	0.64	1-	0.83-							
	-			0.73	0.58	1,06	0.67	0.96-	0.44-	1.87
	0.83	15.0	1.04					1.14	0.53	
<i>Xenocynus crypticus</i> gen. et sp. nov.		7								
	1.38	16.4								
	-	9-	0.69	0.66*	0.29	0,95	0.68	0.90-	0.52	1.30
	1.48	16.7						0.91		
<i>Didelphopsis cabrerai</i>		1								
	1.15	16.1								
	-	9-	0.86-							
	1.59	17.5	0.91	0.70	0.61	1,06	0.81	0.72-	0.52	2.94
<i>Didelphopsis</i> sp. nov.		2								
	1.78	17.6								
	-	1-	0.98-							
	1.99	18.1	1.05	0.91	0.54	1,05	0.78	0.68-	0.47-	2.83
		4						0.80	0.55	

<i>Protodidelph</i>										
<i>is</i>										
	2.57	20.3	1.38-							
<i>mastodontoid</i>		8	1.63	0.99	0.61	1,03	0.63	0.75	0.62	2.21
<i>es</i>										
		19.2								
<i>Protodidelph</i>	1.95	5-	1.18-					0.95-		
<i>is vanzolinii</i>	-	20.2	1.33	0.95	0.62	1,02	0.67	0.96	0.60	2.19
	2.63	8								
		19.1								
<i>Patene</i>	1.90	7-	0.45-					0.90-		
<i>simpsoni</i>	-	21.6	0.65	0.56	0.38	0,94	0.51	0.94	0.61	1.28
	3.16	6								

Itaboraidelphys camposi has several features indicative of an insectivorous-omnivorous diet: moderate to sharp crests, moderate to broad styler shelf (i.e., between 33% and 50% or nearly 50% of the tooth length on M3; sensu Ladevèze et al., 2020), mesial lobe of the styler shelf narrower than the distal one, moderate StD, preparacrista only slightly shorter than postmetacrista on M3, presence of a central cuspule on the styler shelf (see, e.g., Oliveira, 1998 – unpublished data; Goin, 2003; Carneiro, 2023; Carneiro and Oliveira, 2023), centrocrista dilambdodont and invasive on the styler shelf, conical and inflated metaconule, moderately developed protocone, protocone with a distolingual expansion (protoconal bulge; sensu Muizon and Ladevèze, 2020), paraconid lower than metaconid on m1-3, conical and moderate entoconid, roughly subequal and slightly inflated p2-3, absence of diastemata, shallow dentary (i.e., RDS < 0.6), straight to gently convex posterior border of the dentary. *Itaboraidelphys camposi* might have explored invertebrates as its principal food resource, but fruits could also represent an important component of its diet (see, e.g., Zimicz, 2012).

Didelphopsis cabrerai has a similar combination of features to *Itaboraidelphys camposi* (see the results of the PCA 1 about a significant overlapping between m1-2 of *Didelphopsis*

cabrerai with m2-3 of *Itaboraidelphys camposi*; Fig. 9), differing mainly on the presence of more inflated crowns (i.e., bunodonty), symmetric styler shelf (i.e., the mesial and distal lobes are nearly to subequal in width), more ‘U-shaped’ dilambdodont centrocrista, paracone and metacone relatively more spaced, relatively broader protocone, and hypertrophied and bulbous P/p3. These features are indicative of an omnivorous-durophagous diet. Zimicz (2012) considered *Didelphopsis* as an omnivorous taxon, with *Didelphopsis cabrerai* as a more insectivorous-omnivorous taxon, and *Didelphopsis* sp. nov. as a frugivorous taxon. This last taxon has, in comparison with *D. cabrerai*, more inflated crowns, a more lingually expanded lingual border of the protocone, a lower height difference between trigonid and talonid, relatively shorter (i.e., more mesiodistally compressed) trigonids, and longer and broader talonids (see morphofunctional indexes in Table 3), which are indicative of a frugivorous diet.

Therefore, *Didelphopsis* could have explored invertebrates, fruits, seeds, and snails as food resources, with *Didelphopsis cabrerai* as a specialized omnivorous-durophagous taxon, whereas *Didelphopsis* sp. nov. was a frugivorous-durophagous taxon (see e.g., Zimicz, 2012; Carneiro and Oliveira, 2017a; Carneiro, 2023; Carneiro and Oliveira, 2023). *Didelphopsis cabrerai* might have explored hard food resources, like exoskeleton invertebrates, seeds, and dry fruits, due to the identification of some of its dental specimens with moderate to advanced wear stages (e.g., MCT.M.243, MCT.M.4833, MCT.M.4840, MCT.M.4898, MN 1429-V [holotype], MN 2878(c)-V, MN 2883(b)-V; see Carneiro, 2023). On the contrary, none of the specimens assigned to *Didelphopsis* sp. nov. displays moderate to advanced wear (its specimens show only initial apical wear), suggesting a diet based on “softer” food resources, like turgent fruits (sensu Zimicz, 2012). It cannot be ruled out that *Didelphopsis* sp. nov. used its hypertrophied P/p3 to crush food with high initial resistance but with internal soft tissues.

Protodidelphis spp. have several features indicative of frugivorous diets: inflated crowns, blunt crests, rounded and low cusps (i.e., bunodonty), inflated and hypertrophied StB and StD, absence of StC, short and “rounded” postmetacrista, labiolingually compressed

protoconal basin, reduced to absent conules, mesiodistally compressed trigonids, well-developed talonids, “curved” protocristid (i.e., paracristid + preprotocristid), hypertrophied, conical and inflated entoconids, and moderately robust dentaries (i.e., RDS = 0.6).

Among its two recognized species from Itaboraí, *Protodidelphis vanzolinii* has a combination of features indicative of a more generalized diet than *Protodidelphis mastodontoides*. The former taxon has a relatively less inflated crown, relatively more developed crests, ‘V-shaped’ protocone, entoconid more closely placed to the distal border of the metaconid (suggesting a relatively more mesiodistally compressed protocone in antagonistic upper molars; see Oliveira and Goin, 2011), short diastema between p1 and p2, straightly oriented premolars (i.e., premolars have their longer axis [length] at the same orientation to the lower molar series axis), and presence of a retro-molar space. On the contrary, *Protodidelphis mastodontoides* lacks diastemata and retro-molar space on its dentary and has more inflated crowns, wrinkled enamel on lower molars talonid basin, ‘U-shaped’ and more mesiodistally developed protocones, and obliquely oriented lower premolars.

Following our PCA results, *Protodidelphis mastodontoides* was more specialized than *P. vanzolinii*. The former taxon has a combination of features indicative of a more specialized frugivorous diet than *P. vanzolinii*, which displays some features indicative of an insectivorous component on its diet (e.g., the presence of a ‘V-shaped’ protocone, a diastema between p1 and p2, and a retro-molar space).

Moreover, the presence in *P. mastodontoides* of wrinkled (crenulated/rugose) enamel in talonid basins of lower molars is a shared feature with other extant and extinct mammals, such as Polydolopidae (see Chornogubsky, 2021), and Plesiadapidae (see Jehle et al., 2018). Zimicz (2012:292) commented that these enamel structures probably worked as multiple small crests, increasing the cutting of food, like vegetable fibres, by molars. Considering Zimicz’s (2012) conclusions, *Protodidelphis mastodontoides* may have explored more fibrous fruits than *Protodidelphis vanzolinii*, as its talonid basin wrinkles probably increased the processing of

fibres by the increase in the surface of contact between teeth and fibrous food, and teeth resistance during the masticatory movements as well. Nevertheless, we did not recover evidence that *P. mastodontoides* was a durophagous taxon.

Ledogar et al. (2012) observed that pitheciines explore unripe fruits as food (i.e., sclerocarpic harvesting). However, these taxa have more robust jaws, hypertrophied and convex angular process of the dentary, and a straighter posterior border of the dentary compared with protodidelphids. Consequently, these extant taxa display a greater combination of features that are more similar to *Eobrasilia coutoi* than to protodidelphids. Therefore, we rule out unripe fruits (sclerocarpic harvesting) as a possible food resource for *Protodidelphis mastodontoides*.

Furthermore, *Patene simpsoni* was a generalized carnivore (see Rangel et al., 2019, 2023a, 2023b). This taxon displays several features indicative of a carnivorous diet: asymmetric stylar shelf, with the distal lobe broader than the mesial one; flattened and reduced StD, postmetacrista much longer than preparacrista, paracone and metacone merged at more than 50% of their height (sensu Muizon et al., 2018), small protocone (i.e., protocone is shorter than the metacone; sensu Engelman et al., 2018), reduced to absent distolingual expansion of the protocone, trigonid more developed than talonid (talonid is shorter and narrower than the trigonid), enlarged paraconid, which is larger than the metaconid, deep hypoflexid, entoconid lower than the hypoconulid, molar series increasing in length from M/m1 to M/m4, maxillae with deep palatal pits between upper molars, labiolingually compressed premolars, reduced to absent diastemata, and moderately robust dentary ($0.6 < \text{RDS} < 0.8$; sensu Muizon et al., 2018).

Following our second PCA analysis, we infer that *Patene simpsoni* had a unique trophic niche compared to other large-sized Itaboraí's metatherians. This taxon has a combination of morphological and morphometric features indicative of a more specialized carnivorous diet than *Xenocynus crypticus* gen. et sp. nov. Considering extant marsupials, *Patene simpsoni* resembles *Dasyurus* spp. in the presence of an asymmetric stylar shelf (the

distal lobe is broader than the mesial one), increase in the size of molar series from m1 to m4, talonids smaller than trigonids, presence of enlarged paraconids, spaced paraconid and metaconid, especially on m3-4, well-developed labial cingulids, developed entoconids, and straighter posterior border of the dentary. *Dasyurus* is a generalized carnivore that preys on vertebrates and invertebrates but also ingests seeds and fruit as possible food resources (Rayner et al., 2011). *Patene simpsoni* may have had feeding habits similar to *Dasyurus*, as a generalized carnivore preying mostly on vertebrates, but invertebrates represent important food resources in its diet.

6.3 The Paleocene-Eocene Thermal Maximum (PETM) + the Early Eocene Climatic Optimum (EECO) and the trophic structure of *Itaboraidelphys*, *Xenocynus* gen. nov., and other large-sized metatherians

Our results indicate that the co-existence of similarly sized metatherians from different clades can be partially explained by the exploitation of different trophic niches. Protodidelphids represented specialized frugivores, sternbergiids were insectivorous to omnivorous taxa, with different species having different levels of trophic specializations (from insectivory to frugivory), and sparassodonts represented the main mammalian predators of this locality (this last conclusion has been discussed in more details by Rangel et al., 2023b).

During the Early Eocene, the Paleocene-Eocene Thermal Maximum (PETM) + Early Eocene Climatic Optimum (EECO) represented the warmest period of the Paleogene (see, e.g., Ortiz-Jaureguizar and Cladera, 2006; Goin et al., 2012, 2016; Zimicz, 2012; Woodburne et al., 2014). The PETM happened around 55.5 and 55.3 M.y.a., increasing average global temperatures between 5°C and 8°C due to two massive CO₂ liberations in the atmosphere (see Bowen et al., 2015). Zimicz (2012) and Goin et al. (2016) proposed that the increase in global temperatures and humidity during the early Eocene allowed the diversification of several

clades, with many taxa displaying brachyo-bunodont crowns, which is indicative of omnivorous to frugivorous diets. Considering sparassodonts, Tarquini et al. (2022) and Rangel et al. (2023b) linked these thermic events to the increase in the taxonomic/systematic diversity and trophic specializations of sparassodonts during the early Eocene.

Considering large-sized metatherians from the Itaboraí Basin, it is possible to observe a similar evolutionary pattern presented by the above-mentioned studies. Among the six known species (*Xenocynus crypticus* gen. et sp. nov., *Didelphopsis cabrerai*, *Didelphopsis* sp. nov., *Protodidelphis vanzolinii*, *Protodidelphis mastodontoides*, and *Patene simpsoni*), four of them had omnivorous to frugivorous diets (i.e., about 67% of this diversity). Moreover, the presence of two carnivorous metatherians also suggests a taxonomic/systematic diversification regarding this trophic niche during the Early Eocene.

In summary, the metatherians from the Itaboraí Basin represent a good model for paleoecological studies regarding early Eocene mammal-bearing faunas. The completeness of metatherian taxa from Itaboraí after Carneiro (2023) strongly supports previous paleoecological studies presented in the literature (e.g., Zimicz, 2012).

7. Conclusions

Xenocynus crypticus gen. et sp. nov. is an early Eocene (Itaboraiense SALMA) large-sized metatherian from the Itaboraí Basin. This taxon probably had a generalized carnivorous diet (insectivory-carnivory). This taxon displays a greater combination of features indicative of a more specialized carnivorous diet than *Itaboraidelphys* but less so than *Patene*. The co-existence of large-sized metatherians can be partially explained by the exploitation of different trophic niches.

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L.M.C. (coordinated the study, wrote the main manuscript text, prepared the tables and figures, and made the database of performed PCA analyses), H.B. (wrote the main manuscript text, performed PCA analyses, and prepared its figures), C.C.R. (wrote the main manuscript text, prepared the figures), B.M.G.G. (wrote the main manuscript text), R.C.S. (wrote the main manuscript text and prepared its figures), É.V.O. (wrote the main manuscript text). All authors reviewed the manuscript.

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FIGURE CAPTIONS

Fig. 1 The Itaboraí fauna: locality and biochron. **a**, Map showing the region and the coordinates of the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (22° 45' 9'' S; 42° 51' 53'' W). **b**, The stratigraphic relationships of the Itaboraiense SALMA with other Paleogene SALMAs. A plausible age range for the Itaboraí SALMA is highlighted in grey. The occurrence of *Xenocynus crypticus* gen. et sp. nov. is suggested by a black arrow and a digital image of the MCT.M.2382 (holotype), a left maxilla with M2 and alveoli of M1 and M3-4. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 500 Km.

Fig. 2 Comparative upper molar differences between *Xenocynus* gen. nov. and *Didelphopsis* Paula Couto, 1952a. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal; **b**, labial views. *Didelphopsis* sp. nov. Oliveira, 1998 (unpublished data; see Carneiro and Oliveira, 2023): **c**, MCT.M.642, a left M3 in occlusal view. Scale bars = 1 mm.

Fig. 3 Comparative upper molar differences between *Xenocynus* gen. nov. and *Itaboraidelphys* Marshall and Muizon, 1984. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal; **b**, labial views. *Itaboraidelphys camposi* Marshall and Muizon, 1984: **c**, MCT.M.926, a fragment of a left maxilla with M2-3 in occluso-mesial view; **d**, MCT.M.2789, a left M2 in occlusal view. Scale bars = 1 mm.

Fig. 4 Comparative upper molar differences between *Xenocynus* gen. nov. and *Patene* Simpson, 1935. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal, **c**, labial views. *Patene simpsoni* Paula Couto, 1952a: M2 of MN 1331-V, holotype, in **b**, occlusal, **d**, labial views. Scale bars = 1 mm.

Fig. 5 Comparative upper molar differences between *Xenocynus* gen. nov. and *Protodidelphis* Paula Couto, 1952a. *Xenocynus crypticus* gen. et sp. nov.: M2 of MCT.M.2382, holotype, in **a**, occlusal, **c**, labial views. *Protodidelphis mastodontoides* (Marshall, 1987): **c**, MCT.M.806, a left M1, holotype, in occlusal view; **d**, MCT.M.303, a right maxilla with M1-4 in occlusal view. Scale bars = 1 mm.

Fig. 6 *Xenocynus crypticus* gen. et sp. nov. Digital image of MCT.M.2382, a left maxilla with M2, and alveoli of M1 and M3-4: **a**, ventral view; SEM image of the preserved M2: **b**, occlusal; **c**, labial views. Scale bars: **a** = 5 mm; **b-c** = 1 mm.

Fig. 7 *Xenocynus crypticus* gen. et sp. nov. Digital images of the referred specimens: MCN-PV 1793, left m1: **a**, lingual; **b**, occlusal; **c**, labial; **d**, distal views; MCN-PV 1813, right m1: **e**, lingual; **f**, occlusal; **g**, labial; **h**, distal views; MCN-PV 1788, right m2: **i**, lingual; **j**, occlusal; **k**, labial; **l**, distal views. Scale bars = 1 mm.

Fig. 8 Dentaries of *Xenocynus crypticus* gen. et sp. nov. Digital images of UFRJ-DG 14(a)-M, an anterior fragment of a left dentary with alveoli of p2-3, m1-2 and part of the posterior alveolus of p1: **a**, labial; **b**, lingual; **c**, occlusal views; UFRJ-DG 14(b+c)-M, an incomplete left dentary with alveoli for p1-3 and m1-4 (damaged at the level of m2 alveoli): **d**, labial; **e**, lingual; **f** occlusal views. Scale bars = 4 mm. Credits: T. Z. Ferreira (UFRJ).

Fig. 9 Principal component analysis (PCA) of five morphometric indices based on lower molar measurements for *Xenocynus crypticus* gen. et sp. nov., *Itaboraidelphys camposi*, *Didelphopsis* spp., *Protodidelphis* spp., and *Patene simpsoni*. **L** = lower molar length; **Ltal** = talonid length; **Ltri** = trigonid length; **Wtal** = talonid width; **Wtri** = trigonid width.

Fig. 10 Principal component analysis (PCA) based on eight morphometric and morphofunctional indices for *Xenocynus crypticus* gen. et sp. nov., *Itaboraidelphys camposi*, *Didelphopsis* spp., *Protodidelphis* spp., and *Patene simpsoni*. **A**, area; **H**, height; **L**, length; **Lm1-4**, lower molar series length; **M/m**, upper/lower molar with the numbers corresponding to its positioning (M/m1-4); **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **PM**, postmetacrista; **PPA**, preparacrista; **RDS**, relative dentary shape; **RPS**, relative premolar size; **tal**, talonid; **tri**, trigonid; **W**, width. Schematic drawings are not at scale. Credits: The artistic drawings of Itaboraí's metatherians were made by Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com).

TABLE TITLES

Table 1 Size categories considered for Early Eocene Itaboraí's metatherians (sensu Carneiro 2023) based on their lower molar series length (in mm) and maximum and minimum limits of estimated body masses (BM) in grams (g) and kilograms (kg). BM, estimated body mass; Lm1-4, lower molar series length

Table 2 Dental measurements (in mm) of *Xenocynus crypticus* gen. et sp. nov. The holotype is highlighted in bold. **Dt**, diastema; **L**, length; **M/m**, molar; **P/p**, premolar; **W**, width; **()**, talonid dimensions; ~, incomplete tooth or alveoli; *, based on alveoli dimensions

Table 3 Some morphological and morphometrical data of *Xenocynus crypticus*, *Itaboraidelphys camposi*, *Didelphopsis* spp., *Protodidelphis* spp., and *Patene simpsoni* from the Itaboraí Basin. **A**, area; **BM**, body mass (in kg); **DH**, dentary height; **H**, height; **L**, length (in mm); **M/m**, molar; **p**, lower premolar; **PM**, postmetacrista; **PPA**, preparacrista; **tal**, talonid; **tri**, trigonid; **W**, width; *, measurement made from an incomplete specimen. **RDS**: $DH/Lm1-4$; **RPS**: $Wp3/3\sqrt{BM}$.

ARTIGO 3

**New material of *Carolocoutoia ferigoloi* (Mammalia, Marsupialia, Didelphimorphia):
systematic affinities and dietary inferences**

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Key words: Brazil, Didelphimorphia, Early Eocene, Itaboraí, Metatheria, Paleogene, Protodidelphidae, Systematics.

Abstract. *Carolocoutoia ferigoloi* Goin *et al.*, 1998, is one of the largest metatherians of the Itaboraí fauna (Early Eocene, Southeastern Brazil). It was originally identified from a single upper molar with a markedly bunodont crown, wrinkled enamel, and a robust protocone. Here, we describe a nearly complete right dentary of *C. ferigoloi* with the alveoli of the premolars and first lower molar, a very worn second lower molar, complete third and fourth lower molars, and a right second upper molar. *Carolocoutoia* differs from other protodidelphids in having inflated, conical trigonid cusps, a more flattened entoconid, a developed entocristid, and a supernumerary cusp labial to the entoconid. *Carolocoutoia* was recovered in our phylogenetic analysis as the sister taxon of *Protodidelphis* Paula Couto, 1952a, since both share the presence of an anteriorly recurved dentary, wrinkled enamel, and a sinuous crest between styler cusps B and D. The inflated, conical trigonid cusps of *Carolocoutoia* represent an evolutionary convergence with other South American Paleogene mammals, such as some ungulates, and the polydolopimorphian *Roberthoffstetteria* Marshall *et al.*, 1983. We also present the second record of a pathology (molar extrusion) in a metatherian from Itaboraí. Based on its molar crown morphology, *Carolocoutoia ferigoloi* was a specialized frugivorous metatherian. The occurrence of a specialized frugivorous protodidelphid in the Itaboraí fauna is in line with the well-established increase in global temperatures and the expansion of tropical forests after the Paleocene-Eocene Thermal Maximum (around 55.5-55.3 million years ago).

1. Introduction

Carolocoutoia ferigoloi Goin *et al.*, 1998, is one of the largest identified metatherians from the Itaboraí fauna (São José de Itaboraí, Rio de Janeiro, Southeastern Brazil; early Eocene, Itaboraiense SALMA; see Bergqvist *et al.* 2009), with a similar size to that of the extant *Didelphis virginiana* Kerr, 1792 (see Goin *et al.* 1998; Zimicz 2012). This taxon, identified initially from a single upper molar, was assigned to Protodidelphidae (Mammalia, Metatheria, Didelphimorphia) due to its large size, a highly bunodont dentition, wrinkled enamel, inflated, and hypertrophied stylar cusps B (StB) and D (StD), an absence of stylar cusp C (StC), a dilambdodont ‘V-shaped’ centrocrista, a much larger metacone than the paracone, reduced or absent conules, a robust protocone, and a small protoconal cingulum (Oliveira and Goin 2011).

Outstanding among the specimens recovered from the Itaboraí Basin was a relatively large right lower jaw (MCT.M.966) with bunodont and unique lower molar features, which was initially informally assigned to the small litoptern *Miguelsoria parayirunhor* (Paula Couto, 1952b). However, several of its features preclud its referral to this taxon or to any other South American native ungulate. These include the presence of an unfused, non-ossified symphysis, obliquely oriented first and second lower premolars (p1 and p2, respectively), a slightly arched lower molar series, a labial contact of the cristid obliqua, an accentuated distally placed hypoconulid, a smaller last lower molar (m4) than the penultimate lower molar (m3), a lack of Hunter-Schreger bands (which are present in *M. parayirunhor* and all Itaboraí ungulates; Line and Bergqvist 2005), an evidently convex edge of the dentary ventral to the coronoid process, as well as a deep masseteric fossa. In contrast, all these features favour its referral to the Metatheria.

When considering the largest bunodont metatherians of the Itaboraí fauna (*Carolocoutoia ferigoloi*, *Eobrasilia coutoi* Simpson, 1947, *Protodidelphis* Paula Couto, 1952a and *Zeusdelphys complicatus* Marshall, 1987), it becomes evident that the specimen MCT.M.966 is only consistent in size with *C. ferigoloi*. Both *E. coutoi* and *Z. complicatus*

exhibit larger proportions, especially noticeable in the upper molars, which exceed 8.00 mm in length (see Marshall 1984, 1987; Carneiro and Oliveira 2017a, 2017b). Furthermore, the third upper and lower premolars (P/p3) of *Eobrasilia* are substantially larger than those observed in MCT.M.966. Additionally, the lower dentition of *Protodidelphis* is known (see Paula Couto 1952b; Marshall 1984, 1987; Oliveira and Goin 2011). We find that the specimen MCT.M.966 closely matches the expected size and morphology (the bunodont aspect of its molars and inflated cusps) of a lower dentition of *C. ferigoloi*. In addition, the dimension and spatial orientation of the occlusal surface of the upper and lower third molars support the association herein proposed. Other features consistent with its classification within Protodidelphidae include an increase in the size of lower molars from the first (m1) to the third (m3), obliquely oriented p1 and p2, a slightly reduced m4 compared to m3, and an m4 exhibiting an enlarged, conical entoconid (Goin *et al.* 1998; Oliveira and Goin 2011, 2012; Carneiro 2019; Carneiro and Oliveira 2023).

In this study, we describe the first known lower jaw elements and second upper molar (M2) of *Carolocoutoia ferigoloi*. We also infer its body mass and potential diet and discuss the systematic affinities of the genus.

Institutional abbreviations. **MCT.M** (ex **DGM**, Divisão de Geologia e Mineralogia): Museu de Ciências da Terra, Rio de Janeiro, Rio de Janeiro, Brazil; **MCN-PV**: Museu de Ciências Naturais, the paleontology collection of the Fundação Zoobotânica do Rio Grande do Sul, Rio Grande do Sul, Brazil; **UFRJ-DG**: Museu da Geodiversidade, the paleontology collection of the Departamento de Geologia at the Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Other abbreviations. **A**: area; **BM**: body mass; **c**: lower canine; **DH**: dentary height; **EECO**: Early Eocene Climatic Optimum; **L**: length; **ln**: natural logarithm; **m**: lower molars (numbers indicate their corresponding locus); **M**: upper molars (numbers indicate their corresponding

locus); **Ma**: millions of years ago; **p**: lower premolars (numbers indicate their corresponding locus); **P**: upper premolars (numbers indicate their corresponding locus); **RDS**, relative dentary shape; **RW/L**: ratio between the width by the length; **StA**: stylar cusp A; **StB**: stylar cusp B; **StC**: stylar cusp C; **StD**: stylar cusp D; **PETM**: Paleocene-Eocene Thermal Maximum; **SALMA**: South American Land Mammal Age; **SEM**: Scanning Electron Microscope; **W**: width.

2. Materials and methods

2.1 Studied specimens

All specimens assigned to *Carolocoutoia ferigoloi* are from the Itaboraí Basin, São José de Itaboraí, Rio de Janeiro, Brazil (22° 45' 9.91" S, 42° 51' 53.55" W) (Bergqvist *et al.* 2019) (Fig. 1). The Itaboraí faunal association has been attributed to the early Eocene (53-50 Ma; Ypresian Stage; see Woodburne *et al.* 2014a).

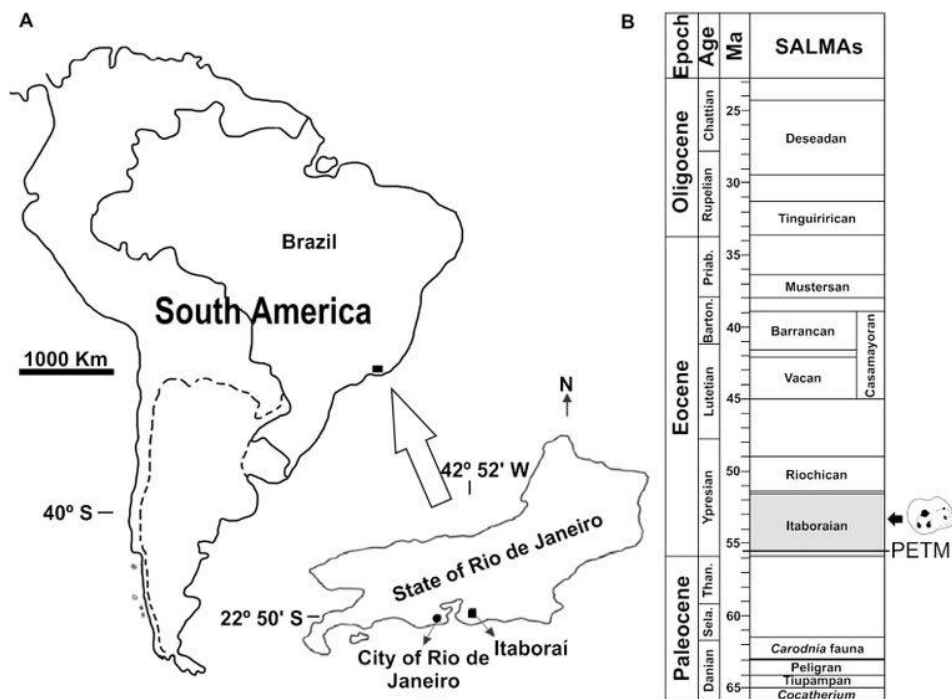


Fig. 1. The Itaboraí fauna: locality and biochron. **A**, Location map showing the region and coordinates of the Itaboraí Basin, São José de Itaboraí, Rio de Janeiro, Brazil (22° 45' 9.91" S; 42°

51° 53' W); **B**, Chronological relationships of the Itaboraense SALMA with other Paleogene SALMAs. The considered age for Itaboraí fauna is highlighted in grey (*i.e.*, Itaboraense SALMA, 56.1-51.4 Ma; see Chornogubsky 2021; but see also Woodburne *et al.* 2014). The chronological occurrence of *Carolocoutoia*, in B, is indicated by a black arrow and a schematic drawing of MCN-PV 1802. **Barton.**, Bartonian; **PETM**, Paleocene-Eocene Thermal Maximum; **Priab.**, Priaborian; **SALMA**, South American Land Mammal Age; **Sel.**, Seladian; **Than.**, Thanetian. Scale bar equals 1000 Km.

2.2 Phylogenetic analysis

The species discussed here was included in a data matrix, which follows Rangel *et al.* 2023 and references therein (see Muizon *et al.* 2018; Beck *et al.* 2020; Engelman *et al.* 2020; Abello *et al.* 2020; Chornogubsky 2021), which is composed of 636 unordered characters (256 dental, 21 jaw, 167 cranial, 192 post-cranial) and 56 metatherians from the Cretaceous and Cenozoic era of North America, Asia, South America, Antarctica, Europe, and Australia. Additionally, four non-metatherian therians were included as outgroups. The phylogenetic analysis was performed with a new technology search on TNT 1.5 (Goloboff and Catalano 2016) using the sectorial, ratchet, drift, and tree-fusing strategies with 100 replications. Bremer support values and tree steps were also calculated with TNT 1.5. The list of included characters, matrix, and the list of synapomorphies are presented as supplementary materials (Appendix 1).

2.3 Estimation of body mass

The body mass of *Carolocoutoia ferigoloi* was estimated using one of the regression models from Myers (2001), which considers the length of the lower molar series ($\log_{10}BM = -1.253 + 3.540 * [\log_{10}Lm1-4]$). All body masses are shown in kilograms. Size classifications for 'didelphoid-standard' metatherians (*i.e.*, all metatherians, excluding Sparassodonta and

Diprotodontia) were taken from Carneiro and Oliveira (2023), who based their classification on the length of the lower molar series (Lm1-4): tiny (<5.00 mm), very small (5.00-6.80 mm), small (6.80-9.40 mm), medium (9.40-15.50 mm), large (15.50-22.00 mm), and very large (>22.00 mm).

3. Systematic paleontology

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

Marsupialiformes Vullo *et al.*, 2009

Sudameridelphia Szalay, 1994 (sensu Carneiro and Oliveira 2023)

Notometatheria Kirsch *et al.*, 1997 (sensu Carneiro and Oliveira 2023)

Marsupialia Illiger, 1811 (sensu Beck *et al.* 2014)

Didelphimorphia Gill, 1872

†Protodidelphidae Marshall *et al.*, 1990

Emended diagnosis from Marshall (1987), Marshall *et al.* (1990), Goin *et al.* (1998), Oliveira and Goin (2011). Differs from other metatherians in the following combination of features: medium to very large size (Carneiro and Oliveira 2023), rapid increase in the size of the molars from M/m1 to M/m3 (see Oliveira and Goin 2011), M2-3 with inflated, conical StB, reduced to absent StC, inflated StD; small to absent conules, presence of a postprotocrista reaching the mesio-lingual wall of the metacone (Fig. 2A), trigonid and talonid almost subequal in height or trigonid only slightly higher than the talonid; inflated and hypertrophied entoconid on m1-4; sharp increase in size from p1 to p2-3.

Included taxa. *Protodidelphis* Paula Couto, 1952a; *Guggenheimia* Paula Couto, 1952a; *Carolocoutoia* Goin *et al.*, 1998.

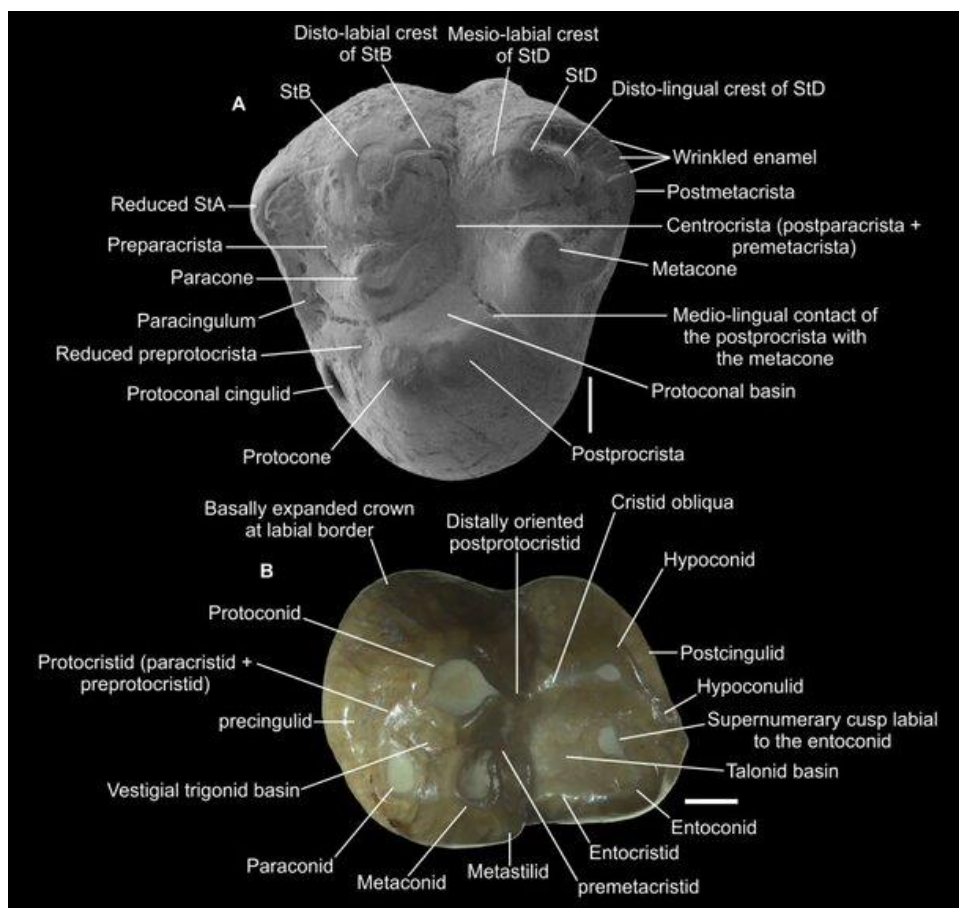


Fig. 2. *Carolocoutoia ferigoloi* Goin *et al.*, 1998 upper and lower molars dental features. Scanning electron microscope (SEM) image of MCN-PV 1802, holotype, a left M3, in occlusal view (**A**); MCT.M.966, showing its m3 in occlusal view (**B**). Scale bars: 1 mm.

†*Carolocoutoia* Goin *et al.*, 1998

Emended diagnosis from Goin *et al.* (1998), Oliveira and Goin (2011). A very large (Lm1-4 > 22.00 mm) Paleogene South American didelphimorphian marsupial with a body mass estimated at around 4.46 kg (Myers 2001). Differs from other Itaboraiense metatherians in the presence of a very narrow protoconal basin in the upper molars, in having inflated and rounded trigonid cusps, an almost vestigial trigonid basin in m3-4, metaconid with an expanded disto-lingual border, forming a ‘crest-like’ metastylid (*sensu* Beck *et al.* 2020), and in the presence of an ‘enamel cusp-like structure’ disto-labial to the entoconid in the lower molars.

Comparisons. *Carolocoutoia* differs from *Protodidelphis* in the following features: absence of diastemata between c, p1-3 and p3-m1 (a diastema is present between p1-2 in *Protodidelphis vanzolinii*, but absent in *P. mastodontoides*), posterior border of the dentary ventral to the coronoid process clearly convex (less convex in *Protodidelphis vanzolinii*, but as convex as in *P. mastodontoides*); in the upper molars, thicker enamel, increased bunodonty, and very low, blunt crests; labial edge of M2-3 basally expanded (not expanded in *Protodidelphis vanzolinii* and with a labial cingulum in *P. mastodontoides*), more mesially shifted StA than StB on M3 (StA and StB are aligned or StA is slightly lingually shifted in *Protodidelphis*), absence of a mesio-lingual crest of StB (present in *Protodidelphis*), well-developed disto-lingual crest of the StD (reduced or absent in *Protodidelphis*), very short preparacrista (more developed in *Protodidelphis*), evidently curved/convex postmetacrista (postmetacrista slightly convex in *Protodidelphis*), paracone smaller than the StD, metacone and StB (a smaller paracone than the StB and metacone, but similar to StD in *Protodidelphis*), mesiodistally expanded protocone with basal edge lingually expanded and inflated (less expanded protocone and more conical in *Protodidelphis*); in the lower molars, slightly taller trigonid, that is wider than the talonid on m3 (trigonid and talonid nearly similar in height and width in *Protodidelphis*), postprotocristid merged with the cristid obliqua (i.e., distally ‘opened’ trigonid) (postprotocristid and metacristid in contact in *Protodidelphis*; i.e., distally ‘closed’ trigonid basin), cristid obliqua labially contacting the distal border of the trigonid (very slightly labial in *Protodidelphis*), the presence of a very low entocristid (entocristid absent in *Protodidelphis*), more labiolingually compressed entoconid (conical and inflated [=‘spire-like’] in *Protodidelphis*), hypoconulid labially placed to the entoconid (hypoconulid slightly labial to the entoconid in *Protodidelphis*), short precingulid (i.e., restricted to the paraconid and mesio-lingual border of the trigonid; sensu Muizon *et al.* 2018) (long precingulid in *Protodidelphis*; i.e., reaches the labial border of the protoconid), precingulid and “trigonid basin” almost at the same level (a more basally placed precingulid than the

trigonid basin in *Protodidelphis*); in the lower premolars, obliquely oriented p1-3 (p1-3 nearly aligned to the premolar/molar axis in *Protodidelphis vanzolinii*, but oblique in *P. mastodontoides*).

Differs from *Guggenheimia* in the following features: its much larger size, with more robust and more wrinkled enamel, its increased bunodonty, non mesiodistally compressed M3 (i.e., more ‘ovoid’ or rounded in shape) (mesiodistally compressed in *Guggenheimia*), the upper molars have a narrower styler shelf, more mesially shifted StA on M3 (StA aligned with StB in *Guggenheimia*), presence of a sinuous crest between StB and StD (formed by the contact between the disto-labial crest of StB and the mesio-labial crest of StD; see Oliveira and Goin 2011) (a condition absent in *Guggenheimia*), more rounded, shorter postmetacrista (longer and obliquely oriented in *Guggenheimia*), lower centrocrista, and mesiodistally expanded and eccentric protocone (mesiodistally compressed and not eccentric in *Guggenheimia*); in the lower molars, developed entocristid (absent in *Guggenheimia*), more flattened entoconid (conical in *Guggenheimia*), and longer p3 alveoli than those of m1 (implying a hypertrophied p3).

Type species. *Carolocoutoia ferigoloi* Goin *et al.*, 1998.

Included species. The type only.

Geographic and stratigraphic occurrence. Itaboraí Formation, Itaboraí Basin, Municipality of São José de Itaboraí, State of Rio de Janeiro, Brazil (Bergqvist *et al.* 2009). 22° 50' 26.46''S, 42° 52' 43.89'' W. Early Eocene, Itaboraiense SALMA Ypresian Stage; see Woodburne *et al.* 2014a.

†*Carolocoutoia ferigoloi* Goin *et al.*, 1998

(Figs. 3-7)

Diagnosis. As for the genus by monotypy.

Type material. MCN-PV 1802, left M3 (Fig. 3).

Referred material. MCT.M.966, incomplete right dentary with the alveoli of p1-3 and m1, plus a very worn m2 and complete m3-4 (Figs. 5-7; 7E-H, 8B); UFRJ-DG 223-M, right M2 (Fig. 4).

Geographic and stratigraphic occurrence. From the fissure discovered in 1949 in the Itaboraí Formation, Itaboraí Basin, municipality of São José de Itaboraí, State of Rio de Janeiro, Brazil (Bergqvist *et al.* 2009). Early Eocene, Itaboraiense SALMA (53-50 Ma; Ypresian Stage; see Woodburne *et al.* 2014a).

Description. The M3 (MCN-PV 1802, holotype; Fig. 3) is slightly wider than long (RW/L: 1.03). The crown enamel is thick and heavily wrinkled. The styler shelf is moderately developed (i.e., it represents between 33% and 50% of the width of the tooth; sensu Ladevèze *et al.* 2020). The mesial lobe of the styler shelf is slightly larger and broader than the distal lobe. The StA is very low (although signs of wear or breakage may be observed), and it is slightly more lingually placed than the apex of the StB. The StB is enlarged, conical, and much larger than the paracone and StD and is the largest of the styler cusps. The StB presents no parallel, lingually oriented crest or mesiolingual crest (sensu Carneiro 2019). The StC is absent, and the StD is enlarged, as developed as the paracone, although less voluminous and lower than the metacone. This styler cusp presents a short, low disto-lingual crest that forms a ridge on the disto-labial border of the StD. The StB and StD are in contact with one another (i.e., the distal wall of the StB is in contact with the mesial wall of the StD), forming a vertical ridge between them. A sinuous crest connecting the apices of the StB and StD (sensu Oliveira and Goin 2011). The preparacrista is very short and oriented towards StA but does not reach this cusp. The postmetacrista is short, although longer than the preparacrista, and is somewhat rounded with wrinkled enamel (similar to small crenulations). The paracone is lower than the StB, metacone and StD, and the labial wall is flat. The metacone is as voluminous as the StB but is lower than this cusp, and the labial wall is flat. The centrocrista is dilambdodont and very low. There are no conules. The protocone is labiolingually robust, moderately

mesio-mesiodistally developed (i.e., the protocone is as broad as the metacone; sensu Engelman *et al.* 2020), and eccentric (i.e., aligned with the apices of the StB and paracone; sensu Oliveira and Goin 2011). The trigon basin is less deep and lingual to the paracone, since the labial edge of the protocone is close to the lingual edge of the paracone and is very narrow, lingual to the metacone. A wear facet located on the mesial-most part of the postprotocrista, distal to, but in contact with, the protocone apex. There is a small, short preprotoconal cingulum. The paracingulum is complete (i.e., it reaches the level of the protoconal basin and merges with it; sensu Muizon *et al.* 2018). The metacingulum is absent. This tooth may be inferred as an M3, due to the mesial lobe of the stylar shelf, which is slightly more developed than the distal lobe, a postprotocrista wear mark (see discussion below), and the width/length ratio.

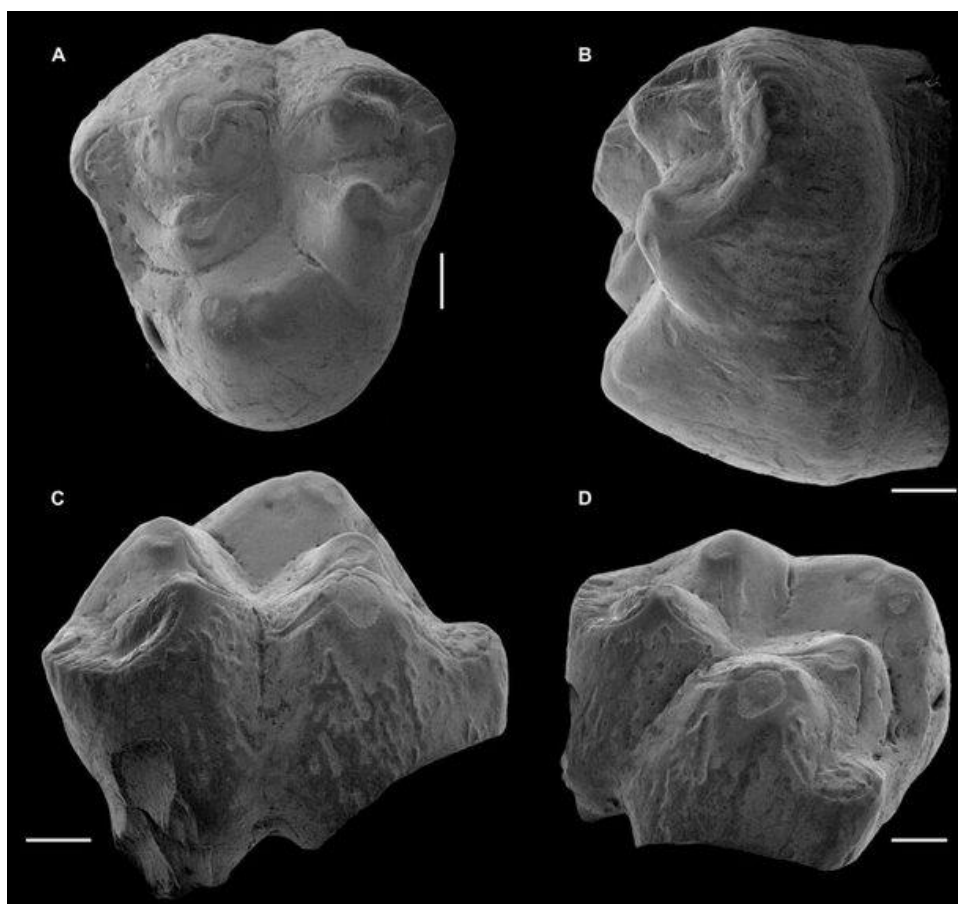


Fig. 3. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; MCN-PV 1802, holotype, a left M3. Scanning electron microscope (SEM) images in occlusal (**A**), distal (**B**), labial (**C**), and mesio-labial (**D**) views. Scale bars: 1 mm.

The M2 (UFRJ-DG 223-M; Fig. 4) is similar to the M3, except for the following remarks: it is as wide as long (RW/L: 1.01). The distal lobe of the stylar shelf is slightly broader and more voluminous than the mesial. The StB has a very short, low parallel lingually oriented crest (*sensu* Carneiro 2019) that descends from its apex but lacks a mesio-lingual crest (*sensu* Carneiro 2019). The StD has a short, low, parallel, lingually oriented crest (*sensu* Carneiro 2019) that reaches the trigon basin. The vertical ridge between StB and StD is deeper than the one on M3. A slightly crested metaconule is observed. Unlike the M3, no wear facet is observed on the mesial-most part of the postprotocrista, although the postprotocrista is lingually concave with a somewhat sinuous shape. There are traces of a mesial protoconal cingulum. The paracingulum is complete (i.e., it reaches and merges with the protoconal basin level; *sensu* Muizon *et al.* 2018), although a metacingulum is absent. This tooth is referred to as an M2 based on the distal lobe of the stylar shelf, which is slightly wider than the mesial lobe due to the presence of a small metaconule and the width/length ratio.

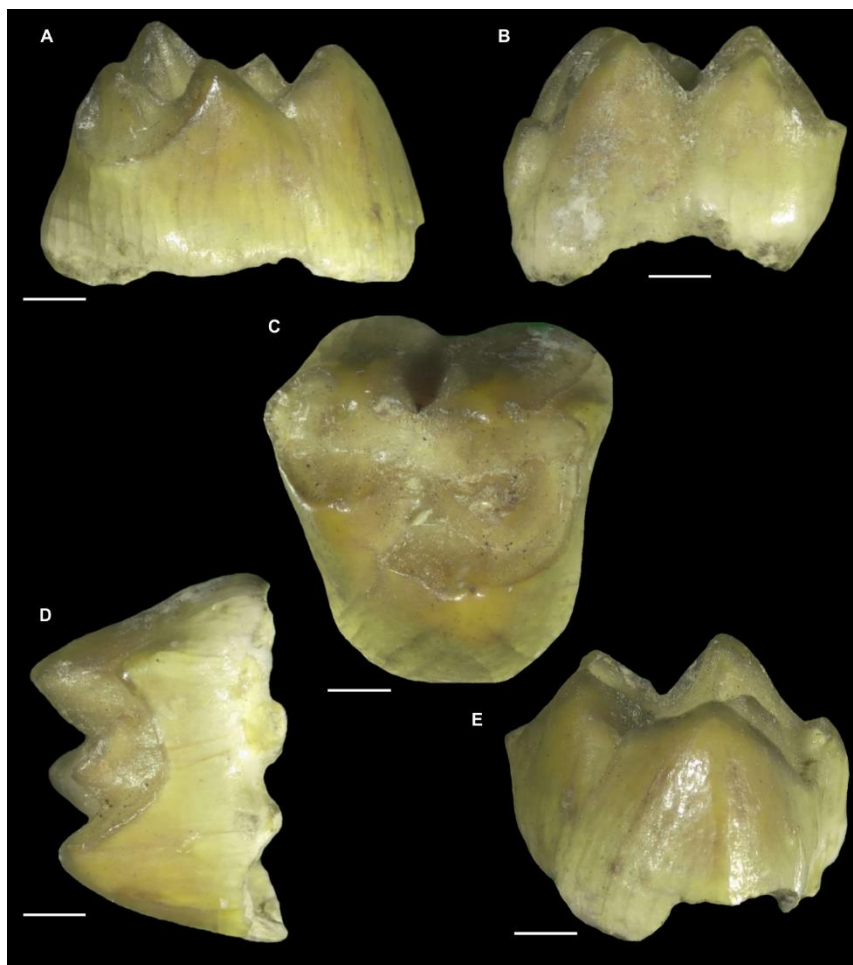


Fig. 4. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; UFRJ-DG 223-M, a right M2. **A**, disto-labial; **B**, labial; **C**, occlusal; **D**, mesial; **E**, lingual views. Scale bars: 1 mm.

The dentary (specimen MCT.M.966; Fig. 5) has a relative dentary shape (i.e., a dentary height [DH]/lower molar series length [Lm1-4] ratio - RDS) of about 0.6 (i.e., the dentary is moderately high – between 0.6 and 0.8; sensu Engelman *et al.* 2020). The symphysis is not fused (i.e., not ankylosed or ossified; see Marshall 1981) and reaches the level of the anterior root of p3. Three mental foramina are located below p1-p2, p2-p3, and m1, a condition also observed in one specimen of *Guggenheimia crocheti* (MCT.M.315). The anterior and posterior foramina are larger than those in the middle. There is a short retromolar space between m4 and the base of the ascending ramus (which is not preserved in the specimen). The mandibular condyle and the angular process are not preserved, whereas the coronoid process is restricted

to its base. The masseteric fossa is very deep. The ventral edge of the dentary ventral to the coronoid process is strongly convex. The deepest point of the dentary is below m3-4.

The alveoli of p1 are obliquely oriented regarding the premolar-molar axis (i.e., the mesial half is more lingual than the distal). There are no diastemata between c-p1, p1-2 or p2-3. The alveoli of p2 are clearly larger than those of p1 but smaller than those of p3. The alveoli of p2 are obliquely oriented, although less than those of p1. The largest premolar is p3, inferred by the dimensions of the alveoli. In the lower premolars, there is an evident increase in the size between p1-2 and p3. The p3 is longer than the m1, based on the dimensions of the alveoli.

The posterior root of p3 extends to the lingual border of the anterior root of m1. The alveoli of m1 indicate that this tooth is smaller than the p3 and m2 and is the smallest of the molars.

There is a marked increase in the size of the lower molars from m1 to m3. The lower molar series is slightly 'arched' in occlusal view (sensu Goin and Carlini 1995), being medially concave at the level of p3/m1.

Fig. 5. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; MCT.M.966, incomplete right dentary with alveoli of p1-3 and m1, a very worn m2, and preserved m3-4. **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bars: 5 mm.

The X-ray image enabled us to observe the morphology of the roots of the teeth in loci. The anterior roots of p3 and m1-4 extend more ventrally than posterior ones (i.e., anterior roots are longer than posterior ones). The roots of p3 are more ventrally developed than those of m1. The m1 roots are the shortest compared to p3 and the lower molars. The m1 roots are not in contact, similar to the m3 and m4 roots, although unlike the p3 and m2 roots, which are in contact. The distal third of the posterior root of the m2 is anteriorly recurved. The roots of m3 and m4 are roughly straight. The m3 has the largest roots, which are dorsally displaced in

their alveoli, a pathological condition known as molar extrusion (Tiago *et al.* 2016) (see discussion below). This condition resulted in m3 above the other lower molars (see discussion below). The roots of m4 are not aligned on the same axis, contrary to those of m1-3 and p3, due to the placement of the distal root on the anterior border of the ascending ramus of the coronoid process (Fig. 6).

Fig. 6. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; X-ray image of MCT.M.966 in labial view.

The m2 is completely worn, and its crown traces are barely identifiable (Fig. 7.A-C). The dimensions of the width and length of the talonid and trigonid are similar. Judging by the preserved parts of the trigonid, the protoconid would have been the largest of the trigonid cusps. The metaconid would have been aligned or just slightly distal to the protoconid. The paraconid is lingually aligned with the metaconid based on the preserved bases of both cusps. The hypoconid is a robust cusp closely placed to the distal wall of the trigonid, resulting in a short hypoflexid. The cristid obliqua is also heavily worn and runs from the hypoconid to the disto-labial border of the trigonid. The entoconid may be identified by the elevated crown lingual to the hypoconulid. There is no observable trace of a supernumerary cusp labial to the entoconid (see m3 description). A centrally placed hypoconulid is identified by its preserved base more labial than the entoconid.

Interestingly, the wear on this tooth forms a deep basin on the lingual half of the talonid, a feature previously unobserved on other metatherians. This basin extends from the lingual border of the talonid to its centre and is likely a consequence of the occlusion between the protocone of M2 and the talonid basin. The presence of a precingulid cannot be evaluated due to wear, but a postcingulid is absent.

The m3 is the largest of the lower molars (Fig. 7.D-F). The trigonid is higher and broader but is similar in length. The trigonid cusps are inflated and rounded in shape. The trigonid basin is absent due to the appressed placement of the trigonid cusps. The paraconid is the smallest of the trigonid cusps and is positioned at the mesio-lingual corner of the trigonid and does not connate with the metaconid. The paracristid is very short and anterolingual-posterolabially oriented (sensu Abello *et al.* 2020). The metaconid is lower and clearly less robust than the protoconid. The metacristid is labio-distally oriented and has no contact with the postprotocristid (i.e., there is an opening on the distal border of the trigonid). There is a crest-like metastylid disto-lingual to the metaconid. The protoconid is the most prominent cusp and is labiolingually aligned with the metaconid. The labial wall of the protoconid is markedly inflated, with some labial expansion of its base. A short, low postprotocristid runs distally from the apex of the protoconid, merging with the cristid obliqua. The cristid obliqua is short, labially concave, and contacts the distal border of the trigonid on the level of the apex of the protoconid. The hypoconid is the largest of the talonid cusps, slightly taller but evidently more voluminous than the entoconid. The posthypocristid of the hypoconid is short and low and reaches the hypoconulid. The hypoconid is also inflated, as is the protoconid but more disto-mesially expanded. A labial cingulid is not observed. The entoconid is somewhat labiolingually compressed and labiolingually aligned to the hypoconid. The entocristid is a low, relatively long crest that extends mesially, closing the lingual border of the talonid basin. The hypoconulid is the smallest of the talonid cusps and is very low and mesiodistally compressed. It is located disto-labial to the entoconid. A ‘cusp-like’ structure is placed at the center of the talonid basin, labial to the entoconid, lingual to the hypoconid, and mesial to the hypoconulid. A wear structure similar to a low crest connects the entoconid and the supernumerary cusp. A small precingulid is present. A postcingulid is absent.

While the m4 trigonid and talonid have almost the same length and height, the talonid is narrower than the trigonid (Fig. 7.G-I). The trigonid basin is absent due to the appressed

placement of the trigonid cusps. The paraconid is evidently mesiodistally compressed and is much more reduced compared to m3. The paraconid is by far the smallest of the trigonid cusps. The paracristid is much longer than m3 and is mesiolingual-distolabially oriented (sensu Abello *et al.* 2020). The metaconid is larger than the paraconid but smaller than the protoconid. The metacristid is vestigial or absent (the advanced worn condition of the metaconid allows no further conclusions). A slightly developed metastylid forms a small crest distolingual to the metaconid (sensu Beck *et al.* 2020). The protoconid is the largest cusp and is labiolingually aligned with the metaconid. The talonid cusps are well-developed, except for the hypoconulid. The entoconid is a large, rounded cusp that occupies a large portion of the lingual half of the talonid basin. The entocristid is low and straight. The hypoconid is also a large, rounded cusp that occupies a large portion of the labial half of the talonid basin. The cristid obliqua reaches the trigonid distal border slightly labial to the carnassial notch. The hypoconulid is a low, rounded cusp located at the centre of the distal edge of the tooth (i.e., at the median axis of m4; sensu Rangel *et al.* 2019). The presence of a supernumerary cusp cannot be evaluated due to the advanced condition of wear on this tooth. A transversal wear structure similar to a crest, like that on m3, is also observable. The wear pattern forms a ‘cloverleaf-like’ pattern. The precingulid is reduced, and a postcingulid is absent.

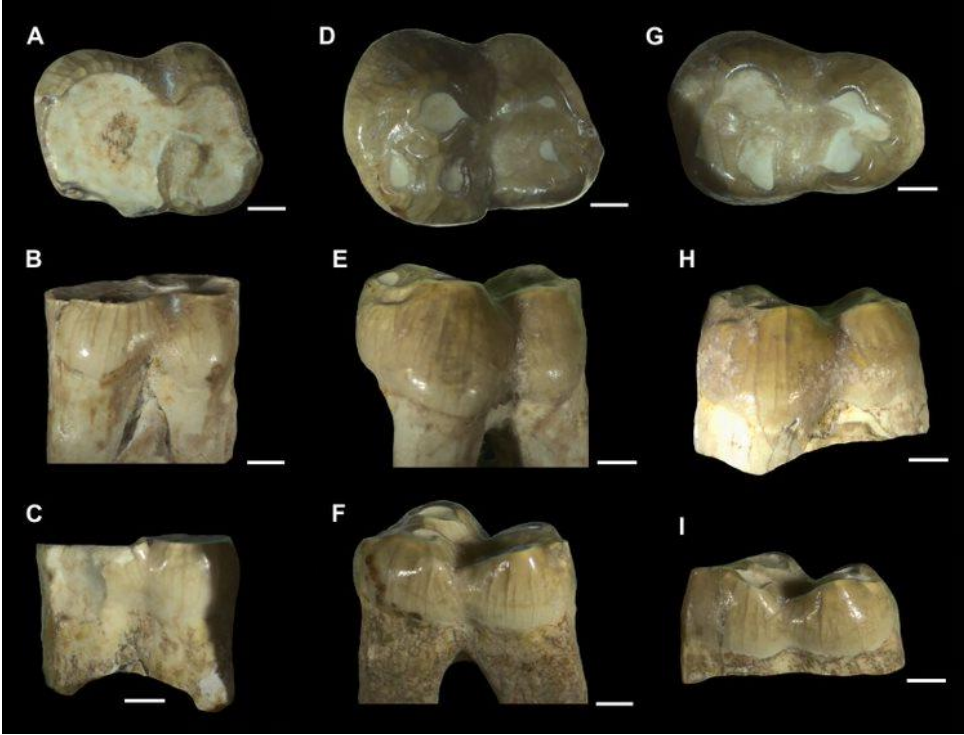


Fig. 7. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; MCT.M.966, details of m2, m3 and m4. **A-C**, m2 in occlusal (A), reversed labial (B), and lingual (C) views; **D-F**, m3 in occlusal (D), reversed labial (E), and lingual (F) views; **G-I**, m4 in occlusal (G), reversed labial (H), and lingual (I) views. Scale bars: 1 mm.

Measurements. See Table 1.

Table 1. Measurements (mm) of *Carolocoutoia ferigoloi* Goin *et al.* 1998. The holotype is highlighted in bold. **DH**, dentary height; **L**, length (mesiodistal axis); **M/m**, molar; **P/p**, premolar; **W**, width (labiolingual axis). *, based on alveoli dimensions; [], trigonid measurements; (), talonid measurements.

	L	W	L	W	L	W	L	L	W							L
	P	P	P	P	P	P	P1	M	M	LM2	WM	LM3	WM3	LM4	WM4	M
	1	1	2	2	3	3	-3	1	1		2					1-4

all Itaboraí ungulates of comparable size), (8) hypoconulid placed markedly more distal than the entoconid (still distal, but less pronounced), (9) m4 hypoconulid reduced in size, being the smallest of the talonid cusps (enlarged and the largest talonid cusp of the m3), (10) m4 smaller than the m3 (m3 similar to m2 or longer, considering that the m2-3 of ungulates/eutherians are homologous to the m3-4 of metatherians; sensu O’leary *et al.* 2013), (11) lack of Hunter-Schreger bands (present in almost all Itaboraí ungulates; unknown for *Asmithwoodwardia*, see Line and Bergqvist 2005, and *Nanolophodon*, see Castro *et al.* 2021), (12) a clearly convex edge of the mandibular ramus ventral to the coronoid process (straighter or slightly curved), and (13) deep masseteric fossa (shallow) (Fig. 8). This set of features in specimen MCT.M.966 thereby make it clearly distinct from most Itaboraí ungulates and, in turn, more similar to metatherians.

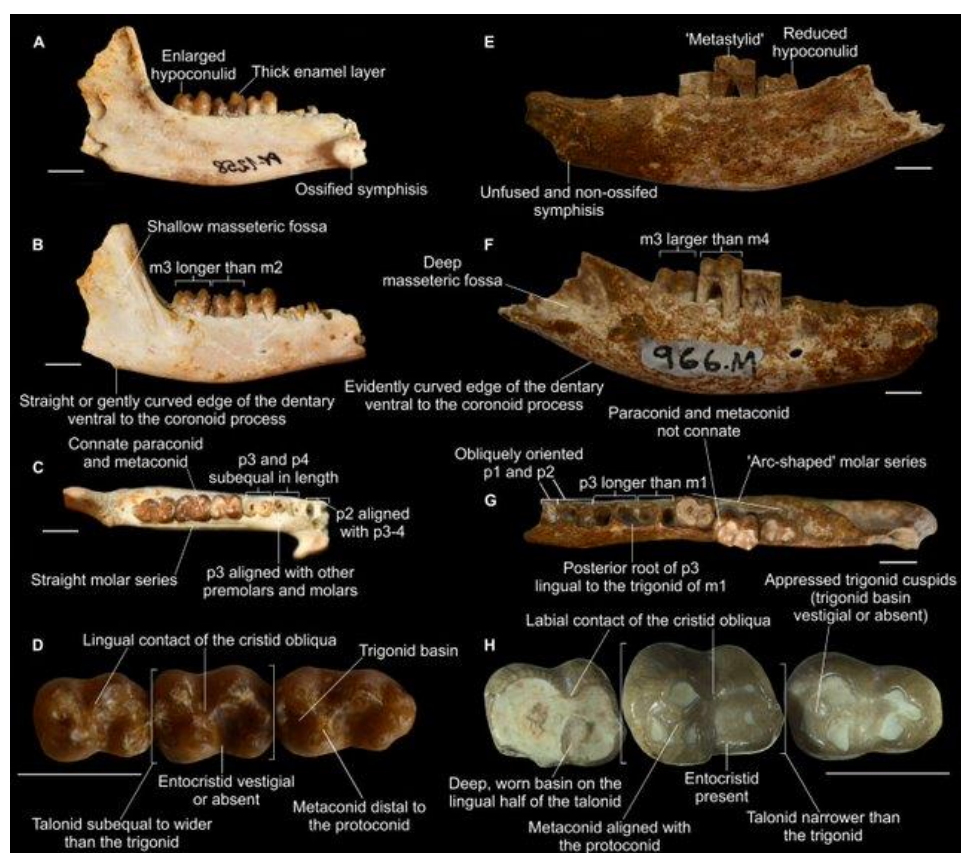


Fig. 8. Differential jaw and lower dental features between *Carolocoutoia ferigoloi* (MCT.M.966) and the Itaboraí ungulate *Miguelsoria parayirunhur* (MCN-PV 1258, an

incomplete left dentary with the alveoli of p2-4 and with m1-3) taken as a model. **A-D**, MCN-PV 1258; **E-H**, MCT.M.966. **A**, MCN-PV 1258, lingual view; **B**, MCN-PV 1258, labial view (reversed); **C**, MCN-PV 1258, dorsal view; **D**, MCN-PV 1258, occlusal view of the lower molar series (m1-3); **E**, MCT.M.966, lingual view; **F**, MCT.M.966, labial view; **G**, MCT.M.966, dorsal view; **H**, MCT.M.966, occlusal view of the lower molar series (m2-4). Scale bars: 5 mm.

4. Results

4.1 Body mass and size category

The estimated body mass of *Carolocoutoia ferigoloi* is around 4.46 kg. According to the size categories of Carneiro and Oliveira (2023) for ‘didelphoid-standard’ metatherians, *Carolocoutoia* was a very large metatherian (i.e., Lm1-4: > 22.00 mm).

4.2 Occlusal relationships in *Carolocoutoia ferigoloi*

The analysis of the occlusal morphology of the holotype of *Carolocoutoia ferigoloi* (MCN-PV 1802), which correlates rather well with the morphology of MCT.M.966, together with the similarities in the enamel morphology (wrinkled and thick on both specimens), and the lack of any other compatible known taxa, both in size and morphology, allows us, with reasonable certainty, to assign MCT.M.966 as the lower dentition of *C. ferigoloi*.

The type specimen of *Carolocoutoia ferigoloi* (MCN-PV 1802) bears a second wear mark immediately distal to the apex of the protocone (on the mesial-most part of the postprotocrista), which is a unique wear pattern in comparison with that of other metatherians of the Itaboraí fauna (Fig. 9.A). This wear mark suggests that a complementary occlusal structure must be present in the lower dentition of this species.

Accordingly, the m3 of the specimen MCT.M.966 displays a supernumerary cusp labial to the entoconid (Fig. 9.B). This feature is, most likely, the occlusal antagonist structure that caused the wear mark distal to the apex of the protocone (Fig. 9.B).

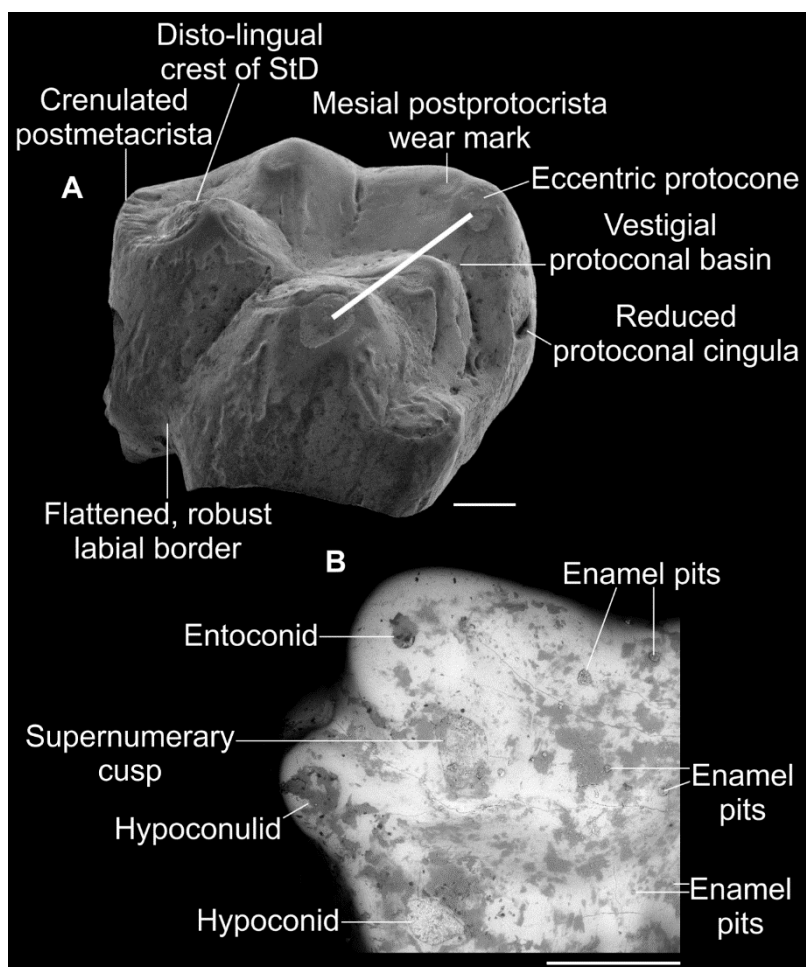


Fig. 9. Detail of the upper and lower molar features of the *Carolocoutoia ferigoloi* Goin *et al.* 1998. **A**, MCN-PV 1802 (holotype), left M3 in mesio-labial view; **B**, talonid of the m3 of MCT.M.966, an incomplete dentary with alveoli of p1-3, m1 and with m2-4, in occlusal view. The thick line in figure **A** indicates the mesial alignment between StB, the paracone and the protocone (i.e., eccentric protocone). Scale bars: 1 mm.

The protocone occludes with the talonid basin between the metaconid's distal border and the entoconid's mesial border (see Zimicz 2012). Hence, the wear mark distal to the apex of the protocone should be related to the supernumerary cusp labial to the entoconid (Fig. 10). There is a good match in the occlusal relations between the cusps and the wear structures of the

upper and lower molars when superimposed. This observation also argues in favour of assigning specimen MCT.M.966 to *Carolocoutoia ferigoloi*.

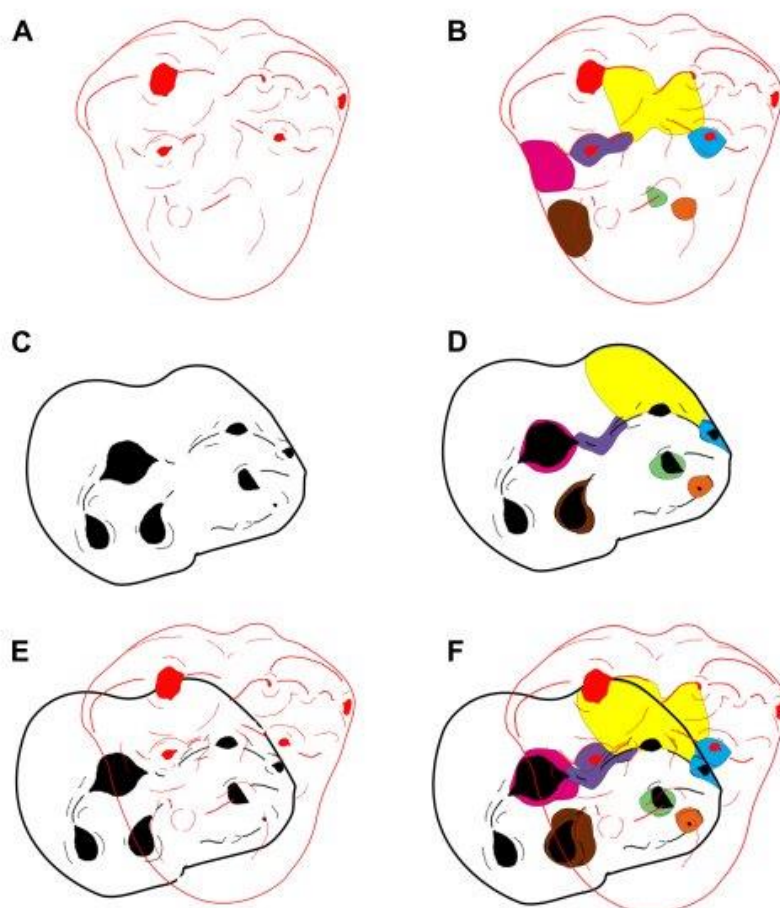


Fig. 10. Occlusal relations of *Carolocoutoia ferigoloi* Goin *et al.* 1998. The schematic drawings are based on MCN-PV 1802 (holotype), a left M3 (**A-B**), and the m3 of MCT.M.966 (**C-D**), an incomplete right dentary with m2-4. The color marks indicate correspondent occlusal surfaces between upper and lower molars (**E-F**).

4.3 Phylogenetic analysis

The phylogenetic analysis recovered two of the most parsimonious trees. Following the results of the phylogenetic analysis, *Carolocoutoia* was recovered as a member of Protodidelphidae (Fig. 11), which is represented by *Guggenheimia*, *Protodidelphis*, and

Carolocoutoia. The features that support this clade are: the presence of protoconal cingula (character 54[1]), contact of the postprotocrista with the medio-lingual wall of the metacone (ch. 57[1]), a very small difference in height between the trigonid and talonid (ch. 134[2]), hypoconid placed mesially to the entoconid (ch. 139[0]), slightly labial contact of the cristid obliqua with the distal wall of the trigonid (ch. 141[3]), m4 with hypertrophied entoconid (ch. 170[1]), p2 obliquely oriented in comparison with the premolar and molar axis (ch. 216[1]), and moderately high dentary (i.e., the ratio between the dentary height and the length of the lower molar series is similar to or larger than 0.60 but less than 0.80; sensu Muizon *et al.* 2018).

Protodidelphis and *Carolocoutoia* were recovered as sister taxa based on the following features: the presence of a short postmetacrista (ch. 36[1]), wrinkled enamel on the disto-labial wall of the posterior lobe of the styler shelf (ch. 81[1]), and transverse orientation of the paracristid (ch. 114[1]).

Bergqvistherium Carneiro, 2019 was originally considered an early protodidelphid (see Carneiro 2019). However, the discovery of two upper molars of this taxon (UFRJ-DG 151-M, a right M3, and MCN-PV 1803, a right M2; see Carneiro and Oliveira 2023) identified it as a “peradectoid” based on its broad styler shelf (i.e., about 50% of the molar width; sensu Muizon *et al.* 2018), straight centrocrista, and reduced styler cusps. Therefore, *Bergqvistherium* is not regarded as a protodidelphid.

Carneiro (2019) recovered *Anatoliadelphys* Maga and Beck, 2017, and *Periprotodidelphis* Oliveira and Goin, 2011 as sister taxa. These two taxa were recovered by his phylogenetic analysis within Protodidelphidae. However, in the phylogenetic analysis herein performed (Fig. 11), *Anatoliadelphys* and *Orhaniyeia* Métais *et al.* 2018 (=Anatoliadelphyidae Métais *et al.* 2018) fall within Polydolopimorphia, based on the presence of unilateral hypsodonty (sensu Goin and Candela 2004; Goin *et al.* 2010, 2022; i.e., exodaenodonty; sensu Sigé *et al.* 2009) on the lower molars (ch.83[1]), a synapomorphy of

Polydolopimorphia (see Goin *et al.* 2022). The absence of unilateral hypsodonty on the lower molars excludes protodidelphids from the Polydolopimorphia.

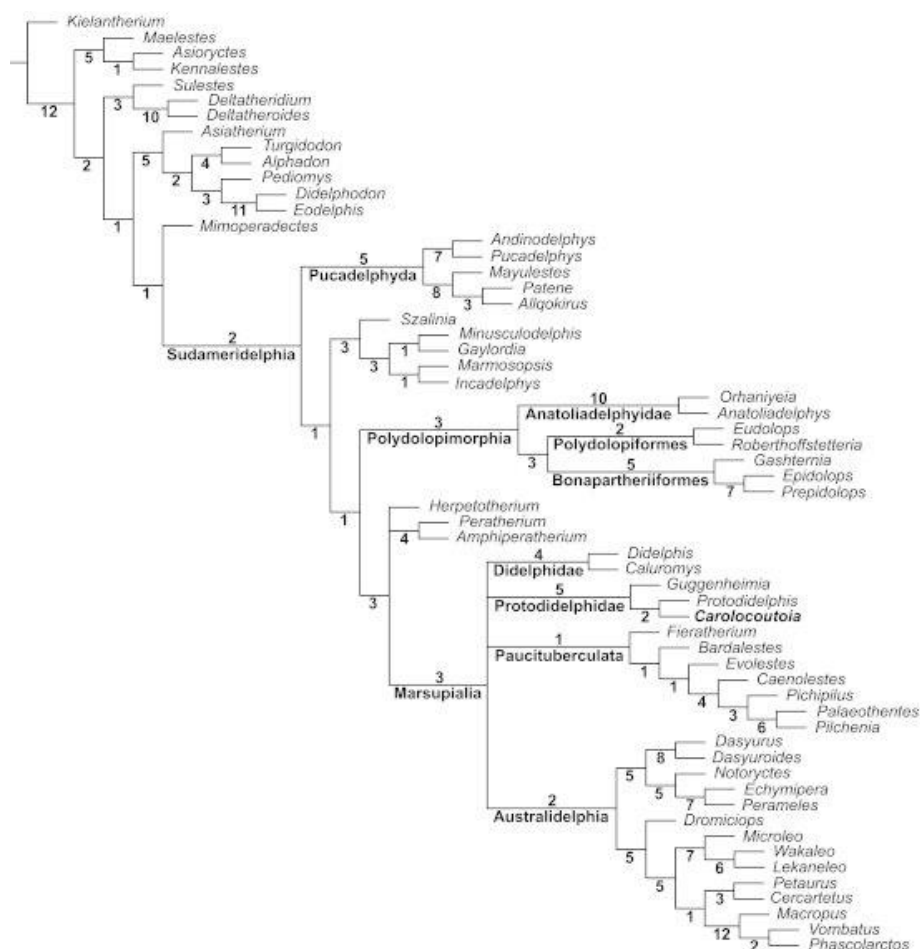


Fig. 11. Strict consensus tree of the two most parsimonious trees (steps: 1831; CI: 0.381; RI: 0.563) recovered in the phylogenetic analysis. *Carolocoutoia* is highlighted in bold. Numbers below and above the branches indicate Bremer Support.

5. Discussion

Carolocoutoia ferigoloi is the largest protodidelphid (Goin *et al.* 1998; Oliveira and Goin 2011; Zimicz 2012; Carneiro and Oliveira 2023), and the second largest didelphimorphian so far known, being only smaller than *Thylophorops* (see Goin *et al.* 2009).

The discovery of a dentary of this species (MCT.M.966) provided further data supporting a specialized frugivorous diet for this taxon (Goin *et al.* 1998; Zimicz 2012). The dentary shows an anteroposterior compression of the anterior part (i.e., the part that held incisors, canine, and premolars), in which the p1 is nearly transversal to the premolar/molar axis; the p3 is enlarged but not bulbous (based on its preserved alveoli), there is no retro-molar space, the posterior border of the dentary ventral to the coronoid process is evidently convex/curved (Fig. 8). This combination of features is also observed on other Itaboraiense metatherians with inferred frugivorous diets (e.g., *Procaroloameghinia*, *Protodidelphis*).

Moreover, this dentary does not have features indicative of a durophagous diet (e.g., granivore), as it lacks a strong anteroposterior compression of its anterior part (e.g., *Didelphodon vorax*, *Didelphopsis cabrerai*, *Gaylordia macrocynodonta*, *Eobrasilia coutoi*; see Carneiro and Oliveira 2017a), an abrupt or evident increase in the height at the level of p3/m1 (e.g., *Arminiheringia*, *Eomakharia*, *Pachybiotherium*; see Goin *et al.* 2010; Zimicz 2012; Engelman *et al.* 2020), straight or slightly angled/curved posterior border (see, e.g., Oliveira and Goin 2015; Carneiro and Oliveira 2017a; Engelman *et al.* 2020), and the dentary is not stout (RDS is about 0.60; i.e., moderately robust sensu Carneiro and Oliveira 2023). In metatherians with robust dentaries (indicative of durophagy), the RDS is higher than 0.60 (sensu Carneiro and Oliveira 2023).

The lower dentition has brachydont and bunodont teeth, trigonid and talonid similar in height, a mesiodistally compressed trigonid, a reduced trigonid basin, voluminous, rounded trigonid cusps, an open distal edge of the trigonid (i.e., the metacristid and postprotocristid do not merge), a ‘crested’ metastylid, a supernumerary cusp mesiolabial to the entoconid, a relatively narrow talonid in comparison with the trigonid, low, variably present cristids, and an enlarged entoconid (Fig. 2.B; 7). This combination of features suggests that the dentition of *C. ferigoloi* was more suitable for crushing soft foods rather than shearing fibrous fruits/hard exoskeleton invertebrates or breaking hard foods, as observed in, for example, *Protodidelphis*

and *Eobrasilia*, respectively (Goin *et al.* 1998; Oliveira and Goin 2011; Zimicz 2012; Carneiro and Oliveira 2023). Therefore, it is likely that the diet of *C. ferigoloi* was based on processing food resources with low initial resistance, such as fruits (see also Oliveira and Goin 2011; Zimicz 2012).

The crown morphology of *Carolocoutoia ferigoloi* suggests that it had little or no mediolateral movement while chewing food (i.e., jaw movements were mostly orthal/vertical). Accordingly, from the wear signs in the lower dentition, no medio-lateral or mesio-distal movement component may be inferred, conditions indicative of folivory and granivory (Walker *et al.* 1978; Teaford and Walker 1984). Conversely, several enamel pits on the talonid basin of the m3 of MCT.M.966 may be observed (Fig. 9.B). Green and Resar (2012:291) stated, “enamel-covered molars in frugivorous mammals tend to have enlarged crushing surfaces on teeth that have a higher pit density”. The observation of enamel pits on the lower dentition of *C. ferigoloi* is in accordance with the consideration of a specialized frugivorous diet for this taxon.

Among other protodidelphids, *Carolocoutoia* differs from *Guggenheimia* spp. and *Protodidelphis vanzolinii* by having a slightly narrower talonid than the trigonid on m3 (Fig.2.B). The m3 of *P. mastodontoides* (Marshall 1987) also presents a slightly narrower talonid than the trigonid (see MCN-PV 1816, a left m3), although it differs in the proportionally much larger hypoconid and entoconid. The narrower talonid than the trigonid in *C. ferigoloi* is related to the labiolingually narrow protoconal basin (Fig. 2.A), in which the labial border of the protocone and the lingual border of the paracone are placed very close to one another. The narrow condition of the protoconal basin on M3 suggests little mediolateral movement while chewing food since the protocone has little space to “move” during occlusion with the talonid. This condition differs from that of *Guggenheimia* spp. and *P. vanzolinii*, in which the talonid is as wide as or even wider than the trigonid, indicating a relatively larger lateral component (for a detailed discussion on occlusal and masticatory movements, see Zimicz 2012).

Among South American metatherians, the molar crown morphology of *Carolocoutoia ferigoloi* reveals several resemblances to that of *Roberthoffstetteria nationalgeographica* from the early Paleocene of Bolivia (65.1-64.8 Ma, Tiupampan SALMA; see Muizon *et al.* 2018). Zimicz (2012) considered *R. nationalgeographica* as an insectivorous-granivorous taxon, although the ingestion of fruits was not ruled out. It should be noted, however, that *Carolocoutoia* is much larger than *Roberthoffstetteria* (i.e., it is outside of the average body mass range for granivores; see Zimicz 2012), and the enamel on M3 is more robust and wrinkled, a condition similar to other suggested frugivorous metatherian taxa, such as *Caroloameghinia* Ameghino, 1901, *Protodidelphis* and *Eobrasilia*; see Goin 2007; Oliveira and Goin 2011; Carneiro and Oliveira 2017a). Therefore, it is plausible that *C. ferigoloi* had a higher frugivorous component in its diet than *R. nationalgeographica*.

The presence of wrinkled enamel is also observed on some Pitheciinae, a clade of New World Primates with durophagous diets (frugivory-granivory, sclerocarp) (Ledogar *et al.* 2012), which may suggest a similar condition for *Carolocoutoia ferigoloi*. However, aside from minor similarities, pitheciine's lower molars are notably different from that of *C. ferigoloi*: 1) absence of unilateral hypsodonty in *Carolocoutoia* (present, with metaconid taller than the protoconid, in pitheciines), 2) trigonid and talonid similar in length or talonid slightly shorter (talonid clearly longer than the trigonid in pitheciines), 3), conical and individualized trigonid cuspids (low-shaped and poorly differentiated trigonid cuspids), 4) trigonid basin vestigial to absent (trigonid basin well labiolingually developed), 5) hypoconid less labially salient than the protoconid (hypoconid as salient as the protoconid), 6) talonid basin relatively small (talonid basin markedly developed), and 7) absent of talonid basin wrinkled enamel (present) (see Fig. 2.A-B). Considering other metatherians, pitheciine's dental morphology is remarkably similar to the one of *Epidolops ameghinoi* (see Beck 2017) and polydolopids (see Chornogubsky 2021), which have been considered as mixed feeders

(i.e., can explore a broad range of food resources: invertebrates, seeds, leaves, fruits).

Therefore, we do not consider a frugivorous-granivorous or sclerocarpic diet for *C. ferigoloi*.

Another interesting feature observed on the MCT.M.966 is that the m3 has suffered molar extrusion and is less worn than m2 and m4 (Fig. 5, 6, 8). In metatherians, the m4 is the least worn molar since it is the last one to erupt (Forasiepi and Sánchez-Villagra 2014).

Therefore, this condition is relatively unexpected.

Molar extrusion occurs when a molar loses its occlusal antagonist due to malformation, breakage, disease, or advanced age (see Tiago *et al.* 2016). The teeth are held in the alveolus by a system of collagen fibrils that attach themselves to the cementum on one side and to the alveolar bone on the other. These fibrils and the alveolar bone have an active metabolism and are constantly remodeling (resorption and synthesis). Thus, the teeth are kept in position by forces from the neighboring teeth, the antagonists, the cheek, and the tongue. In case of imbalance, the teeth tend to move to the side with the least resistance (Tiago *et al.* 2016). Since the m3 presents a certain degree of wear, the extrusion may have resulted from the antagonist breaking during adulthood. The fully erupted, moderately worn m4 confirms that the MCT.M.966 represents an adult individual.

The lack of an antagonist changes the mastication pattern, which may have been responsible for the excessive wear of m2 and the greater level of wear of m4 compared to m3, given that the tooth wear gradient of protodidelphids seems to be low (for a tooth wear gradient definition, see Koenigswald 2014). In metatherians, most wear on premolars and molars occurs on p3 and m1, followed by p2 and m2, p1 and m3, and m4 (see the above-mentioned differential degree of wear in the lower molars of *Gaylordia* in Oliveira and Goin 2015). Moreover, the loss of the antagonist may have also been responsible for the lingual displacement of the m3 about the other molars (Fig. 5) in searching for a better adjustment during occlusion.

Other pathological features, probably related to one another, are also observed in the mandible of *Carolocoutoia*, such as a marked alveolar bone loss around the labial side of the mesial root of m3 (Fig. 5) and a possible inflammatory lesion (radiolucent) in the apical region of the roots (Fig 5). Both may (or may not) have been a consequence of the extrusion of m3 and its unnatural position, which led to trauma during jaw occlusion.

A survey of fossil metatherian literature undertaken by Costa *et al.* (2021) has shown that few pathological conditions have been recorded in fossil Metatheria, and the ones described here are the first associated with teeth.

Furthermore, Oliveira and Goin (2011) and Carneiro (2019) linked the apparently “short-time” evolutionary history of protodidelphids with the paleoenvironmental changes that resulted from the events of the PETM (around 55.50 Ma; Bowen *et al.* 2015), which increased global temperatures and tropical biomes throughout South America during the early Eocene (Woodburne *et al.* 2014a; Goin *et al.* 2016), primarily due to the increase in global temperatures (see Tarquini *et al.* 2022). Carneiro (2019) commented that the occurrence of several protodidelphids with different degrees of bunodonty in a single locality (the Itaboraí Basin) would support a “rapid” evolutionary diversification for this clade after the PETM.

This paleoclimatic event may be directly linked to an increase in the abundance and diversity of frugivorous metatherians from the early Eocene until the early middle Eocene (Itaboraiense to “Sapuan” SALMAS). The Itaboraí fauna is remarkable due to the presence of the greatest number of taxa with a frugivorous or omnivorous-frugivorous diet in a single locality: *Guggenheimia brasiliensis* Paula Couto, 1952a, *G. crocheti* Oliveira and Goin, 2011, *Protodidelphis vanzolinii*, *P. mastodontoides*, *Carolocoutoia ferigoloi*, *Bobbschaefferia fluminensis* Paula Couto, 1952a, *Eobrasilia coutoi*, *Bergqvistherium primigenia*, *Didelphosis* sp. nov., *Procaroloameghinia pricei* Marshall, 1982, *Derorhynchidae* gen. et sp. nov., *Carolopaulacoutoia* sp. nov., *Gashternia carioca* Goin and Oliveira, 2007, and *Epidolops ameghinoi* Paula Couto, 1952b (see Marshall 1987; Goin *et al.* 1998; Goin and Oliveira 2007;

Oliveira and Goin 2011, 2012; Zimicz 2012; Goin *et al.* 2016; Carneiro 2019; Carneiro and Oliveira 2023).

Amongst these taxa, protodidelphids are known to have occurred in faunas after the PETM (Goin *et al.* 1998; Oliveira and Goin 2011, 2012; Carneiro 2019; Carneiro and Oliveira 2023); nevertheless, the result of our phylogenetic analysis supports a Paleocene origin for Protodidelphidae. It is plausible that the paleoenvironmental changes after the PETM increased in the diversity and abundance of protodidelphids in South America.

The last (and most recent) occurrence of this group is recorded for the middle Eocene of Argentina (*Protodidelphis*; see Tejedor *et al.* 2009), an observation that could be linked with a reduction in the global temperatures after the Early Eocene Climatic Optimum (EECO). During the middle Eocene, the extensive tropical forests that covered most of the South American continent were replaced by “savanna-like” environments (Woodburne *et al.* 2014a, b; Goin *et al.* 2016), with an increase in the diversity of terrestrial mammals, hypsodont metatherians and several taxa with granivorous or herbivorous diets (Goin *et al.* 2010). Therefore, this environmental turnover could be related to the disappearance of the protodidelphids in the fossil record after the early middle Eocene. This observation led Oliveira and Goin (2011), Carneiro (2019), and Carneiro and Oliveira (2023) to consider protodidelphids as fossil guides of early to middle Eocene (i.e., Itaboraense to Riochican SALMAs) faunas.

6. Conclusions

Carolocoutoia ferigoloi is one of the largest metatherians from the Itaboraí fauna. Its large size, advanced bunodonty, reduced crests, blunt cusps, the presence of enamel pits, enlarged StB and StD, a narrow to vestigial protoconal basin, and the evidently convex edge of the dentary ventral to the coronoid process provide support for its specialized frugivorous diet.

The identification of a lower molar extrusion in the assigned dentary of *C. ferigoloi* (MCT.M.966) represents the second record of pathology in a metatherian from the Itaboraí basin, and the first record of this condition registered in the literature for an extinct metatherian.

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Declaration of competing interest

We have no conflicts of interest to disclose.

Declaration of generative AI in scientific writing

We have not used generative AI in scientific writing.

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FIGURE CAPTIONS

Fig. 1. The Itaboraí fauna: locality and biochron. **A**, Location map showing the region and coordinates of the Itaboraí Basin, São José de Itaboraí, Rio de Janeiro, Brazil (22° 45' 9'' S; 42° 51' 53'' W); **B**, Chronological relationships of the Itaboraiense SALMA with other Paleogene SALMAs. The considered age for Itaboraí fauna is highlighted in gray (*i.e.*, Itaboraiense SALMA, 56.1-51.4 Ma; see Chornogubsky 2021; but see also Woodburne *et al.* 2014). The chronological occurrence of *Carolocoutoia*, in B, is indicated by a black arrow and a schematic drawing of MCN-PV 1802. **Barton.**, Bartonian; **PETM**, Paleocene-Eocene Thermal Maximum; **Priab.**, Priaborian; **SALMA**, South American Land Mammal Age; **Sel.**, Seladian; **Than.**, Thanetian. Scale bar equals 1000 Km.

Fig. 2. *Carolocoutoia ferigoloi* Goin *et al.*, 1998 upper and lower molars dental features. Scanning electron microscope (SEM) image of MCN-PV 1802, holotype, a left M3, in occlusal view (**A**); MCT.M.966, showing its m3 in occlusal view (**B**). Scale bars: 1 mm.

Fig. 3. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; MCN-PV 1802, holotype, a left M3. Scanning electron microscope (SEM) images in occlusal (**A**), distal (**B**), labial (**C**), and mesio-labial (**D**) views. Scale bars: 1 mm.

Fig. 4. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; UFRJ-DG 223-M, a right M2. **A**, disto-labial; **B**, labial; **C**, occlusal; **D**, mesial; **E**, lingual views. Scale bars: 1 mm.

Fig. 5. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; MCT.M.966, incomplete right dentary with alveoli of p1-3 and m1, a very worn m2, and preserved m3-4. **A**, labial view; **B**, lingual view; **C**, occlusal view. Scale bars: 5 mm.

Fig. 6. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; X-ray image of MCT.M.966 in labial view.

Fig. 7. *Carolocoutoia ferigoloi* Goin *et al.*, 1998; MCT.M.966, details of m2, m3 and m4. **A-C**, m2 in occlusal (A), reversed labial (B), and lingual (C) views; **D-F**, m3 in occlusal (D), reversed labial (E), and lingual (F) views; **G-I**, m4 in occlusal (G), reversed labial (H), and lingual (I) views. Scale bars: 1 mm.

Fig. 8. Differential jaw and lower dental features between *Carolocoutoia ferigoloi* (MCT.M.966) and the Itaboraí ungulate *Miguelsoria parayironhur* (MCN-PV 1258, an incomplete left dentary with the alveoli of p2-4 and with m1-3) taken as a model. **A-D**, MCN-PV 1258; **E-H**, MCT.M.966. **A**, MCN-PV 1258, lingual view; **B**, MCN-PV 1258, labial view (reversed); **C**, MCN-PV 1258, dorsal view; **D**, MCN-PV 1258, occlusal view of the lower molar series (m1-3); **E**, MCT.M.966, lingual view; **F**, MCT.M.966, labial view; **G**, MCT.M.966, dorsal view; **H**, MCT.M.966, occlusal view of the lower molar series (m2-4). Scale bars: 5 mm.

Fig. 9. Detail of the upper and lower molar features of the *Carolocoutoia ferigoloi* Goin *et al.* 1998. **A**, MCN-PV 1802 (holotype), left M3 in mesio-labial view; **B**, talonid of the m3 of MCT.M.966, an incomplete dentary with alveoli of p1-3, m1 and with m2-4, in occlusal view. The thick line in figure **A** indicates the mesial alignment between StB, the paracone and the protocone (i.e., eccentric protocone). Scale bars: 1 mm.

Fig. 10. Occlusal relations of *Carolocoutoia ferigoloi* Goin *et al.* 1998. The schematic drawings are based on MCN-PV 1802 (holotype), a left M3 (**A-B**), and the m3 of MCT.M.966 (**C-D**), an incomplete right dentary with m2-4. The color marks indicate correspondent occlusal surfaces between upper and lower molars (**E-F**).

Fig. 11. Strict consensus tree of the two most parsimonious trees (steps: 1831; CI: 0.381; RI: 0.563) recovered in the phylogenetic analysis. *Carolocoutoia* is highlighted in bold. Numbers below and above the branches indicate Bremer Support.

TABLE LEGEND

Table 1. Measurements (mm) of *Carolocoutoia ferigoloi*. The holotype is highlighted in bold. **DH**, dentary height; **L**, length (mesio-distal axis); **M/m**, molar; **P/p**, premolar; **W**, width (labiolingual axis). *, based on alveoli dimensions; [], trigonid measurements; (), talonid measurements.

ARTIGO 4

A tiny-sized Herpetotheriidae (Mammalia, Metatheria) from the Itaboraí Basin (early Eocene), Brazil: Paleobiogeographic and systematic implications for Herpetotheriidae

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Abstract. The Itaboraí Basin, located in Itaboraí, Rio de Janeiro, Brazil, has preserved one of the most important early Eocene vertebrate assemblages of the Southern Hemisphere. Among its representatives, Metatheria comprises its most diverse group, with a minimum of 29 genera and 43 species. Considering this diversity, tiny and very small taxa are represented by Jaskhadelphyidae and closely related taxa, “Peradectoidea”, Sternbergiidae, Derorhynchidae, and an undescribed taxon with uncertain affinities, previously referred to as “cf. *Armintodelphys*”. Here, this last taxon is named *Thylacopygmaeus oliveirai* gen. et sp. nov.; it is distinguished by its extremely small size (inferred body mass less than 15 g) and in that its lower molars show the metaconid placed distally to the protoconid and a developed postentocristid. Two PCA analyses of *T. oliveirai* and other tiny-sized taxa from Itaboraí indicate that the new taxon exhibits distinctive morphometric and morphofunctional patterns compared to other sympatric tiny-sized taxa. The inclusion of *T. oliveirai* gen. et sp. nov. in a phylogenetic analysis recovered it as the sister taxon of *Rumiodon*, an early Oligocene herpetotheriid from Peru, based on the presence of a labiolingually compressed metaconid on m3 and a labiolingually compressed protoconid on m4. We group these two taxa within the Herpetotheriidae in a new clade, the Rumiodontinae nov. Contrary to a previous hypothesis, *Thylacopygmaeus* is not closely related to *Armintodelphys*. The results confirm the Paleogene occurrence of Herpetotheriidae in South America.

Keywords: Itaboraí Basin; Itaboraiense SALMA; Notometatheria; Paleogene; Peratheriinae; Rumiodontinae nov.

1. Introduction

The Itaboraí Basin, Municipality of Itaboraí, Rio de Janeiro state, Brazil (22° 50' 20" S; 42° 52' 30" W) dated as early Eocene in age (Ypresian Stage, Itaboraiense SALMA; see Woodburne et al., 2014) is one of the smallest sedimentary basins from Brazil (Bergqvist et al., 2009). Despite its small dimensions, this basin has preserved one of the world's most diverse metatherian faunas from the Cretaceous-Paleogene so far known, with almost a thousand recovered specimens, representing at least 29 genera and 43 species, as shown by Carneiro (2023 [unpublished data]).

Estimated body masses of the metatherians from this locality show that they weighted from 2-3 g (*Minusculodelphis minimus* Paula Couto, 1962; see Oliveira et al., 2016) up to 10 kg (*Eobrasilia coutoi* Simpson, 1947; see Carneiro, 2023 [unpublished data]). There is a diverse assemblage of tiny and very small-sized taxa, with at least seven genera and eight species (*Minusculodelphis minimus*, *M. modicum* Oliveira et al., 2016, cf. *Armintodelphys*, *Marmosopsis juradoi* Paula Couto, 1962, Peradectoidea gen. nov. sp.2 [sensu Carneiro and Oliveira, 2023], *Gaylordia doelloi* (Paula Couto, 1962), *Diogenesia brevirostris* Oliveira et al., 2021, and *Carolopaulacoutoia* sp. [sensu Carneiro and Oliveira, 2023]) recognized so far (Carneiro and Oliveira, 2023). Among their representative materials, specimen MCT.M.933, a posterior fragment of a right dentary with m3-4, calls attention. This tiny specimen was previously considered to belong to a taxon closely related to *Mirandatherium* Paula Couto, 1952b, *Marambiotherium* Goin et al., 1999 (see Oliveira, 1998 [unpublished data]), Herpetotheriidae, Derorhynchidae, Paucituberculata, or *Armintodelphys* Krishtalka and Stuck, 1983a (see Carneiro and Oliveira, 2023). However, a detailed study has yet to be done considering this specimen.

Previous studies have proposed biogeographic connections between South and North America (First American Biotic Interchange [FABI]; see, e.g., Goin et al., 2012, 2016) and

between South America and Africa-Europe (Atlantogea; see, e.g., Ezcurra and Agnolín, 2012; Carneiro, 2019; Crespo and Goin, 2021) during the Late Cretaceous (Campanian to Maastrichtian) to the Paleocene, respectively. These hypotheses indicate that the shared metatherian fauna between North America, South America and Europe should be a result of dispersal events that probably happened during the Late Cretaceous (Maastrichtian) throughout the Paleocene (see, e.g., Case et al., 2005; Goin et al., 2012, 2016; Smith and Smith, 2013; Martin et al., 2005; Carneiro and Oliveira, 2017a, 2017b; Carneiro, 2018; Carneiro et al., 2018; Ladevèze et al., 2020; Muizon and Ladevèze, 2022).

Among metatherian clades related to these biogeographic events, “Peradectidae” and Herpetotheriidae have the utmost significance for understanding these biogeographic events (see Crespo and Goin, 2021). The Paleogene occurrences of herpetotheriids and “peradectids” in South America have been tentatively considered in the literature (see, e.g., Sigé, 1972; Marshall and Muizon, 1988; Goin and Candela, 2004; Oliveira and Goin, 2006, 2012; Carneiro and Oliveira, 2023), although never confirmed.

Rumiodon Goin and Candela, 2004, from the early Oligocene of Peru, is a putative herpetotheriid from South America (this taxon was tentatively included within Herpetotheriidae [cf. Herpetotheriidae] by Goin and Candela, 2004). This taxon has been considered a herpetotheriid, but no study has discussed its proper affinities. This taxon shares several features with specimen MCT.M.933 from the Itaboraí Basin, thus suggesting that herpetotheriid, or herpetotheriid-like taxa, could be more diverse than previously thought in South America.

Here, a new “herpetotheriid-like” metatherian from the Itaboraí Basin is identified, and its systematic affinities and biogeographic implications for the Herpetotheriidae are discussed.

Institutional Abbreviations. **MCN-PV**, Coleção de Paleovertebrados do Museu de Ciências Naturais da Secretaria de Meio Ambiente (SEMA; ex. Fundação Zoobotânica do Rio Grande do Sul), Porto Alegre, Brazil; **MCT**, Museu de Ciências da Terra, Serviço Geológico do Brasil

(MCTer-SGB), Rio de Janeiro, Brazil; **MHNC**, Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia; **MN**, Museu Nacional (MN/UFRJ), Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **QM F**, Paleontological collection of the Queensland Museum, South Brisbane, Queensland, Australia; **UFRJ-DG**, Coleção de Macrofósseis do Departamento de Geologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Other Abbreviations. **A**, area; **BM**, body mass; **ch.**, character; **DHm3-4**, dentary height below m3-4; **e**, estimated; **H**, height; **L**, length; **Lm1-4**, length of the lower molar series; **M**, upper molars with the numbers corresponding to its positioning (M1-4); **m**, lower molars with the numbers corresponding to its positioning (m1-4); **MPT**, most parsimonious tree; **NALMA**, North American Land Mammal Age; **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **PETM**, Paleocene-Eocene Thermal Maximum; **prom**, promontorium; **R**, ratio; **ra**, relative area (A_{tal}/A_{tri}); **RDS**, relative dentary shape (DH_{m3-4}/L_{m1-4}); **RGA**, relative grinding area ($\sqrt{A_{tal}/L_{tri}}$); **rh**, relative height (H_{tal}/H_{tri}); **Retro**, length of the retro-molar space; **RTPP**, rostral tympanic process of the petrosal; **SALMA**, South American Land Mammal Age; **SEM**, scanning electron microscope; **subfam**, subfamily; **tal**, talonid; **tri**, trigonid; **W**, width.

2. Materials and methods

2.1 Study site

The Itaboraí Basin is located in the municipality of Itaboraí, Rio de Janeiro, in southeastern Brazil; its geographical coordinates are 22° 45' 9.9144" S, 42° 51' 53.5536" W (Fig. 1a). For more data about the Itaboraí Basin and its stratigraphic context, see Bergqvist et al. (2009), and Rangel et al. (2023a).

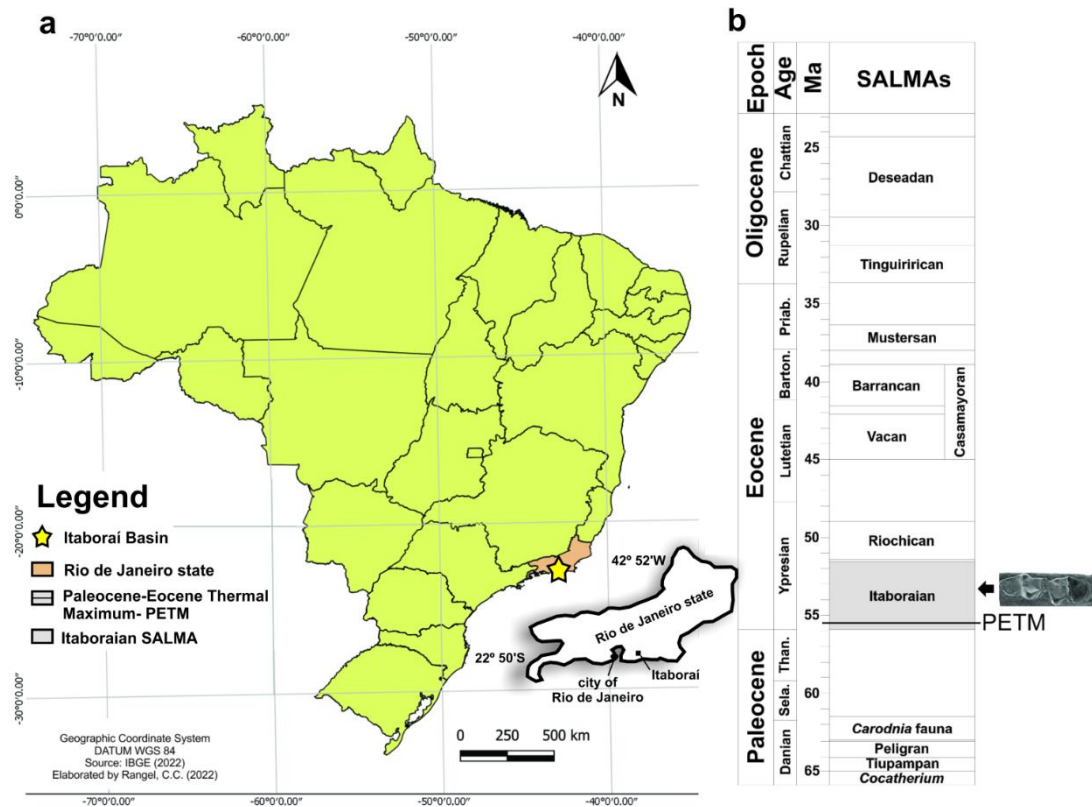


Fig. 1. Locality and age of the Itaboraí fauna. **a**, Map of Brazil showing the region and the coordinates of the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro (22° 45' 9" S; 42° 51' 53" W). **b**, Biochronological relationships of the Itaboraíense SALMA with other Paleogene SALMAs. The age range for the Itaboraí SALMA follows Carneiro and Oliveira (2023; see Woodburne et al., 2014 for an alternative chronology). The occurrence of *Thylacopygmaeus oliveirai* gen. et sp. nov. is suggested by a black arrow and a digital image of the MCT.M.933 (holotype), a posterior fragment of a right dentary with m3-4. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 500 Km.

2.2 Studied specimens

All studied specimens come from the Itaboraí Basin, municipality of Itaboraí (Fig. 1). The holotype of the studied specimen is deposited in the MCT. Other studied specimens are housed in the collections of MCN-PV, municipality of Porto Alegre, Rio Grande do Sul, Brazil; MCT (formally known as DGM), MN; and UFRJ-DG, municipality of Rio de Janeiro, Rio de Janeiro, Brazil. A list of studied specimens is presented as supplementary material (Appendix 1).

The metatherian fauna from the Itaboraí Basin is represented by almost 1,000 recovered specimens (considering only specimens represented by teeth, jaws, and maxillae; see, e.g., Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023). This elevated number of specimens allows a “more secure” recognition of taxa’s dental and jaw patterns, intraspecific phenotypic plasticity, size span, and systematic affinities (Carneiro et al., 2024a).

Digital images of MCT’s specimens were made with a Zeiss Stemi 508 Greenough Stereo Microscope with an Axiocam 208 camera. SEM images were performed with a JEOL JSM-6390LV scanner at the Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional (MN), Rio de Janeiro, RJ, Brazil; Quanta FEI 250 at the Unidade de Microscopia Avançada, Centro Nacional de Biologia Estrutural e Bioimagem (CENABIO), Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, RJ, Brazil; Tescan Vega 3 at the Núcleo de Microscopia Eletrônica da COPPE, Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, RJ, Brazil; Phenon XL at the Laboratório de Micropaleontologia Aplicada (LMA), Instituto de Pesquisa em Petróleo e Energia (LITPEG), Universidade Federal de Pernambuco (UFPE), Recife, PE, Brazil; and JEOL JSM-6510LV at the Instituto de Química, Universidade Estadual do Rio de Janeiro (UERJ), Rio de Janeiro, RJ, Brazil.

The estimated body mass of the studied taxon was based on the regression equations of Myers (2001), which considers the length of the lower molar series ($\log_{10}BM = -1.253 + 3.540[\log_{10}Lm1-4]$). The size classification for Itaboraí’s metatherians was taken from Carneiro and Oliveira (2023), who based their classification on the length of the lower molar series (Lm1-4) and body masses (BM; see Table 1). All measurements of studied specimens are presented as supplementary material (Appendix 2).

Table 1. Size categories considered for early Eocene Itaboraí’s metatherians (sensu Carneiro et al., 2024a) based on their lower molar series length (in mm) and maximum and minimum limits

of estimated body masses (BM) in grams (g) and kilograms (kg). **BM**, estimated body mass; **Lm1-4**, lower molar series length.

Size category	Lm1-4 (mm)	BM (g and Kg)
Tiny	Lm1-4 < 5.00 mm	BM < 15 g
Very small	5.00 mm < Lm1-4 < 6.20 mm	15 g < BM < 40 g
Small	6.20 mm < Lm1-4 < 9.40 mm	40 g < BM < 150 g
Medium	9.40 mm < Lm1-4 < 15.50 mm	150 g < BM < 1 kg
Large	15.50 mm < Lm1-4 < 22.00 mm	1 kg < BM < 3.3 kg
Very large	22.00 mm < Lm1-4	3.3 kg < BM < 10 kg

2.3 Principal Component Analyses

To discriminate the new taxon from other tiny and very small-sized metatherians from Itaboraí, a principal component analysis (PCA1) was conducted based on two variables: the lower molar length (**Lm**) and the relative area of the lower molars (**ra** = **Atal/Atri**) measured from lower molar specimens of studied taxa. The included specimens were identified by their molar locus (m1, m2, m3, and m4). The analysis used the variance-covariance matrix. This PCA technique was performed on the R statistical computing program (R core team, 2013). These data have been included as supplementary material (Appendix 2).

A second PCA analysis (PCA2) was performed, considering only the average value of Lm and ra for the m3 of each taxon. We chose m3's locus because all studied specimens have preserved m3. This simplified analysis allows better comparisons between the m3 of the new taxon and those from other tiny- and very small-sized metatherians from Itaboraí. The analysis used the variance-covariance matrix. This PCA technique was performed on the R statistical computing program (R core team, 2013). These data have been included as supplementary material (Appendix 2), and the R script (Appendix 6) is presented as supplementary material.

2.4 Phylogenetic analysis

A phylogenetic analysis (PA) was based on a morphological data matrix that comprises 728 characters and 80 therian taxa, including 72 metatherian taxa, from the Cretaceous and Cenozoic of North America, Asia, South America, Antarctic, Europe, and Australia (see Carneiro et al., 2024b and references therein). The matrix was run to a new technology search with TNT 1.5 (Goloboff and Catalano, 2016) using the sectorial, ratchet, drift, and tree-fusing strategies with 100 replications. Bremer supports and tree scores were calculated with TNT 1.5. The list of characters, characters by taxon, and synapomorphies are presented as supplementary material (Appendices 3-5).

3. Systematic Paleontology

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

Marsupialiformes Vullo et al., 2009

Sudameridelphia (Szalay, 1994) sensu Carneiro and Oliveira, 2023

Notometatheria (Kirsch et al., 1997) sensu Oliveira et al., 2021

†Herpetotheriidae Trouessart, 1879

†Rumiodontinae subfam. nov.

Diagnosis. Differs from *Herpetotherium* Trouessart, 1879 and *Copedelphys* Korth, 1994 in the presence of a labiolingually compressed metaconid on m3 and a labiolingually compressed protoconid on m4.

Genotype. *Rumiodon* Goin and Candela, 2004.

Included taxa. *Rumiodon* and *Thylacopygmaeus* gen. nov.

Remarks. Rumiodontinae nov. represent a South American subclade of herpetotheriids. The occurrence of rumiodontines nov. in Brazil (Itaboraí Basin, early Eocene; sensu Woodburne

et al., 2014) and Peru (Santa Rosa fauna, early Oligocene; see Campbell et al., 2021) suggests a Paleogene Neotropical geographic distribution of Herpetotheriidae in South America.

†*Thylacopygmaeus* gen. nov.

cf. *Armintodelphys* Carneiro and Oliveira, 2023: 305, fig. 15.

(Fig. 2)

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Derivation of the genus name. From the Greek *thylakos* (“sack”, “pouch”), implying its metatherian condition, and from the Latin *pygmaeus* (“dwarf”, “pygmy”), in reference to its minute size. The gender is masculine.

Diagnosis. Differs from other Itaboraiense SALMA metatherians in the following features: tiny size (sensu Carneiro and Oliveira, 2023); estimated body mass of about 12 g. Dentary bone with a proportionally long retromolar space (see Fig. 5). Lower molars (m3-4; see Fig. 2) with a metaconid distally placed to the protoconid (i.e., metaconid and protoconid are not transversally/labiolingually aligned), presence of developed postmetacristid, which is merged with the preentocristid; talonid broader than the trigonid on m3, developed postentocristid, hypoconulid smaller than the entoconid on m3; m4 with spaced bases of the paraconid and metaconid (i.e., their bases are not in contact), a labiolingually compressed protoconid, and an obliquely oriented posthypocristid.

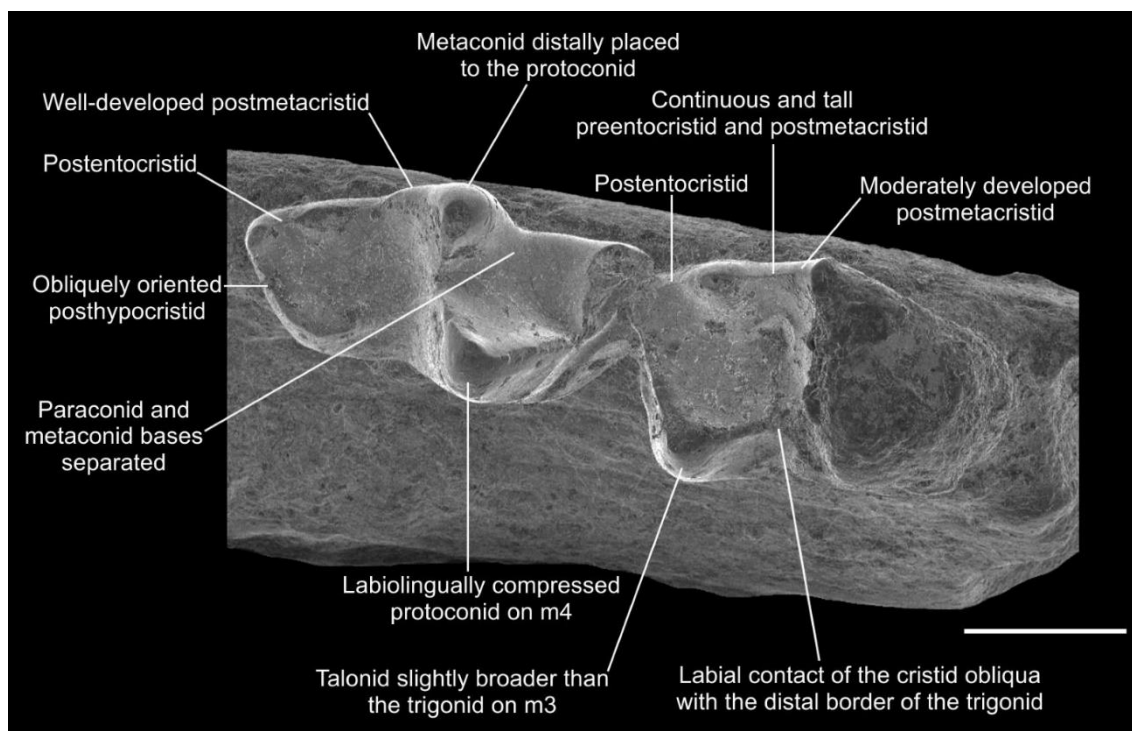


Fig. 2 Diagnostic combination of features of *Thylacopygmaeus* gen. nov. SEM image of the specimen MCT.M.933, holotype of *Thylacopygmaeus oliveirai* gen. et sp. nov., a posterior fragment of a right dentary with m3-4 in occlusal view. Scale bars = 0.5 mm.

Type species. *Thylacopygmaeus oliveirai* sp. nov.

Included species. The type only.

Type Locality and Horizon. Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al., 2009). Early Eocene, Ypresian Stage, Itaboraiense SALMA (53-50 Ma; sensu Woodburne et al., 2014).

Comparisons. *Thylacopygmaeus* gen. nov. differs from *Rumiodon* Goin and Candela, 2004 (Fig. 3b) in having a smaller size (~50% smaller based on known m3-4; see *Rumiodon* sp. measurements in Goin and Candela, 2004), metaconid distally placed to the protoconid on m3-4 (metaconid and protoconid transversally aligned in *Rumiodon*), continuous preentocristid with the postmetacristid (notched preentocristid in *Rumiodon*), obliquely oriented posthypocristid (posthypocristid transversally oriented in *Rumiodon*), and hypoconulid distolabially/distomedially placed to the entoconid (hypoconulid distal to the entoconid in

Rumiodon).

Thylacopygmaeus gen. nov. differs from *Carolopaulacoutoia* McKenna and Bell, 1997 (Fig. 3c-d) in having a metaconid distally placed to the protoconid on m3-4 (metaconid slightly distal or transversally aligned to the protoconid on m3-4 in *Carolopaulacoutoia*); cristid obliqua of m3 contacts more labially the distal wall of the trigonid (cristid obliqua contacting only slightly labial to the metacristid notch in *Carolopaulacoutoia*); postmetacristid and preentocristid continuous, lacking a notch (notched preentocristid in *Carolopaulacoutoia*); m4 with the talonid shorter than the trigonid (m4 with the talonid as long as the trigonid in *Carolopaulacoutoia*).

Differs from *Diogenesia* (Fig. 3e) in having a more mesially extended trigonid (more mesiodistally compressed in *Diogenesia*); metaconid distally placed to the protoconid (metaconid and protoconid transversally aligned in *Diogenesia*); moderately to well-developed postmetacristid (reduced to weakly developed in *Diogenesia*), tall preentocristid (low preentocristid in *Diogenesia*); developed postentocristid (absent in *Diogenesia*); m4 subequal to larger than the m3 (m4 smaller than m3 in *Diogenesia*).

Differs from *Gaylordia* (Fig. 3f) in having molars with a less inflated crown; metaconid distally placed to the protoconid (transversally aligned in *Gaylordia*); continuous and high postmetacristid and preentocristid (reduced postmetacristid and low preentocristid in *Gaylordia*); m3 talonid slightly broader than the trigonid; (talonid narrower than the trigonid in *Gaylordia*); long cristid obliqua (very short to reduced cristid obliqua in *Gaylordia*); cristid obliqua of m3 contacts more labially the distal wall of the trigonid (cristid obliqua contacting only slightly labial to the metacristid notch in *Gaylordia*); hypoconid spaced from the distal wall of the protoconid (hypoconid closely spaced to nearly in contact with the distal wall of the protoconid in *Gaylordia*); m4 with spaced paraconid and metaconid (m4 with the bases of paraconid and metaconid in closer contact in *Gaylordia*).

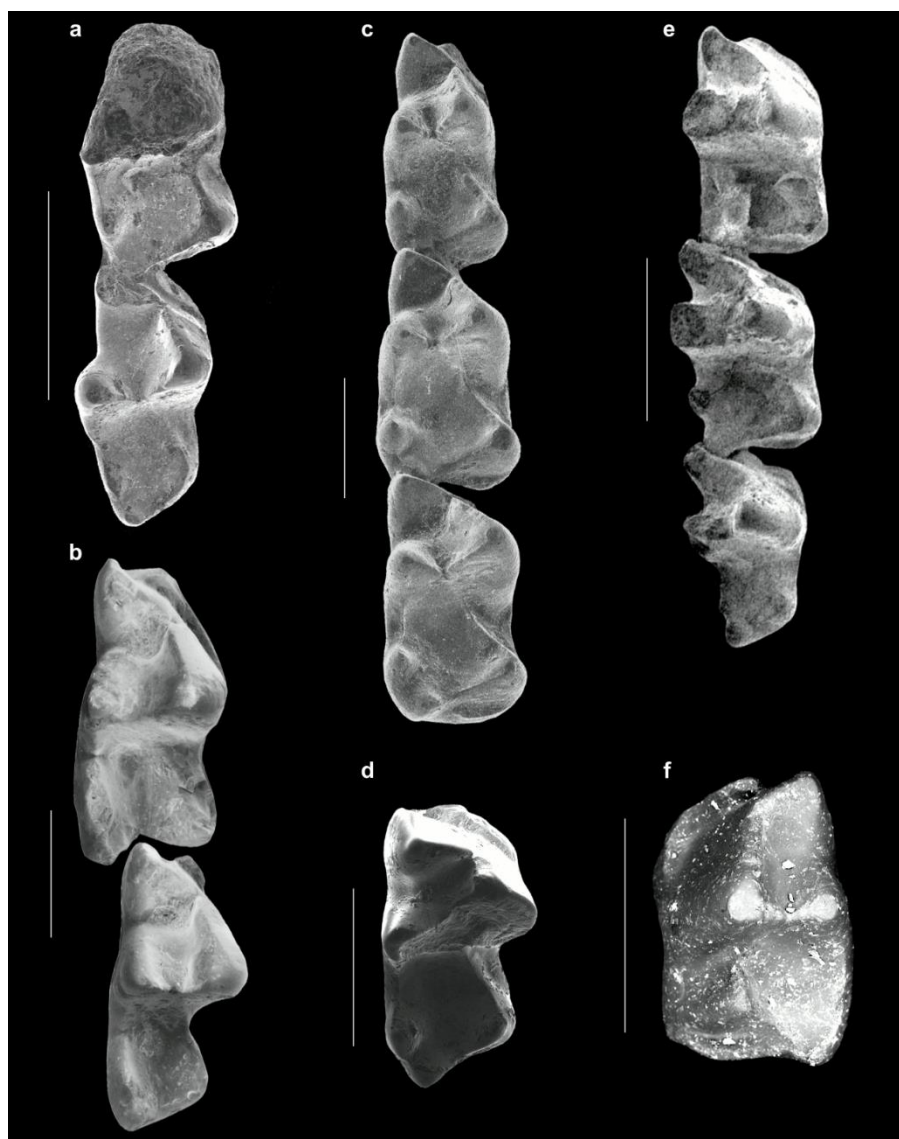


Fig. 3 Comparative SEM images of rumiodontines nov. and Itaboraí's very small- and small-sized metatherians.

a, *Thylacopygmaeus oliveirai* gen et sp. nov.: MCT.M.933 (holotype), a posterior fragment of a right dentary with m3-4, in occlusal view. **b**, *Rumiodon* sp.: LACM 140583, left m3 and m4 in occlusal view (after Goin and Candela, 2004: fig. 3; images inverted to facilitate comparisons). **c**, *Diogenesia brevirostris* Oliveira et al., 2021: MCT.M.650 (holotype), incomplete right dentary with m2-4, and alveoli of p1-3 and m1, in occluso-labial view. **d-e**, *Carolopaulacoutoia itaboraiensis* (Paula Couto, 1970): **d**, MCT.M.927, incomplete right dentary with p2, p3 (erupting), m1-3, and alveoli of i2-5 and c, and alveoli of p1, in occlusal view; **e**, UFRJ-DG 155-M, right m4 in occlusal view. **f**, *Gaylordia doelloi* (Paula Couto, 1962): MN 2504-V (holotype, cast), incomplete left dentary with m2, and alveoli of m1 and m3-4 of a juvenile specimen, in occlusal view. Scale bars = 1 mm.

Differs from *Marmosopsis* (Fig. 4b-e) in having the metaconid distally placed to the

protoconid (metaconid and protoconid transversally aligned in *Marmosopsis*); talonid wider than the trigonid on m3 (talonid narrower than the trigonid in *Marmosopsis*); cristid obliqua of m3 contacts more labially the distal wall of the trigonid (cristid obliqua contacting only slightly labial to the metacristid notch in *Marmosopsis*); taller preentocristid (low preentocristid in *Marmosopsis*), m4 with a tricuspid (hypoconid, hypoconulid, and entoconid) talonid (m4 with a bicuspid [hypoconid and hypoconulid] or unicuspid [hypoconulid] talonid in *Marmosopsis*).

Differs from *Minusculodelphis* (Fig. 4f) in having a larger size (~31% larger than *Minusculodelphis minimus* and ~16% larger than *M. modicum*); metaconid distally placed to the protoconid (metaconid and protoconid transversally aligned in *Minusculodelphis*); well-developed postmetacristid (reduced postmetacristid in *Minusculodelphis*); moderately developed entoconid (reduced entoconid in *Minusculodelphis*); m4 with a tricuspid (hypoconid, hypoconulid, and entoconid) talonid (m4 with a bicuspid [hypoconid and hypoconulid] or unicuspid [hypoconulid] talonid in *Minusculodelphis*).

Differs from *Peradectoidea* gen. nov. (*sensu* Carneiro and Oliveira, 2023; Fig. 4g) in having a more mesially expanded trigonid (more mesiodistally compressed in *Peradectoidea* gen. nov.); metaconid distally placed to the protoconid (metaconid and protoconid transversally aligned in *Peradectoidea* gen. nov.); cristid obliqua of m3 contacts more labially the distal wall of the trigonid (cristid obliqua contacting only slightly labial to the metacristid notch in *Peradectoidea* gen. nov.); continuous and tall postmetacristid and preentocristid (low and notched preentocristid in *Peradectoidea* gen. nov.); m4 with the talonid shorter than the trigonid (almost subequal talonid and trigonid in *Peradectoidea* gen. nov.).

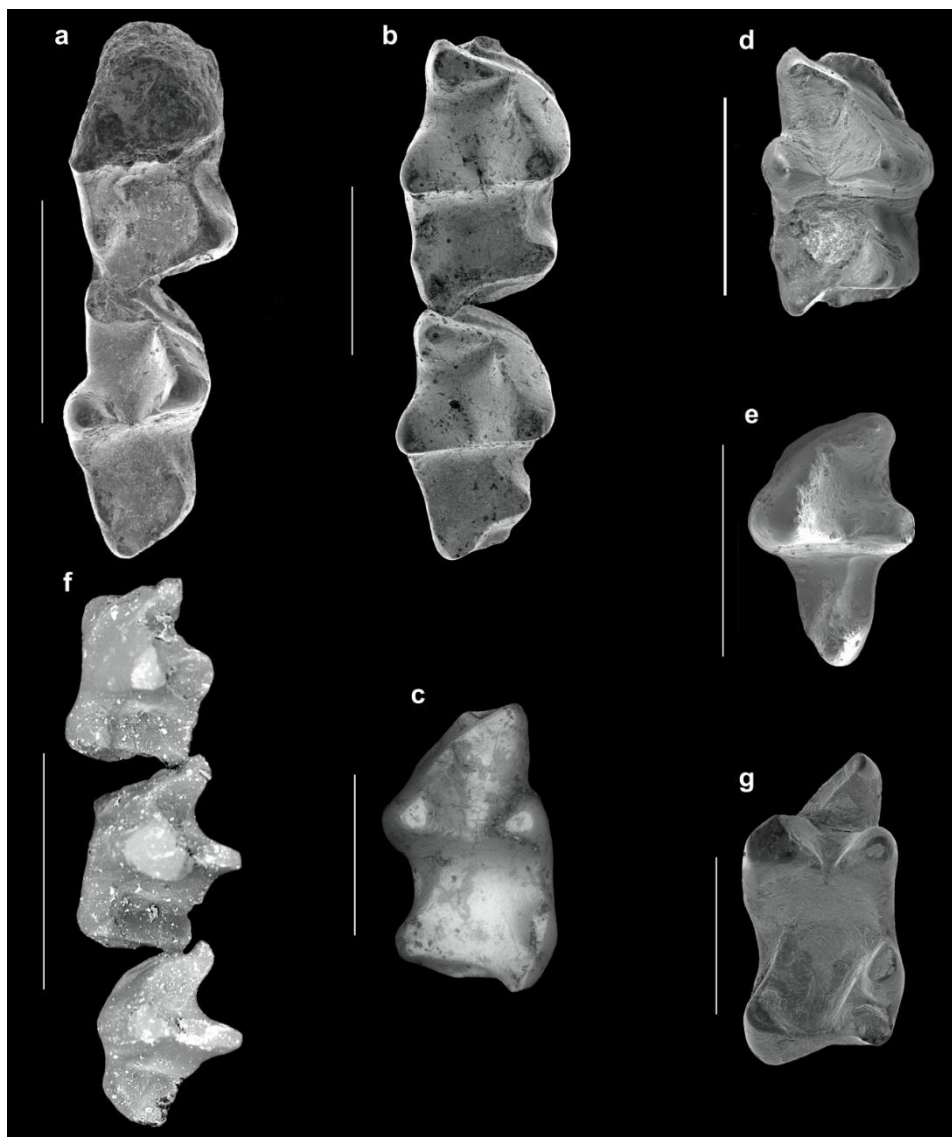


Fig. 4 Comparative SEM images of *Thylacopygmaeus* gen. nov. and Itaboraí's very small- and small-sized metatherians. **a**, *Thylacopygmaeus oliveirai* gen et sp. nov.: MCT.M.933 (holotype), a posterior fragment of a right dentary with m3-4, in occlusal view. **b-c**, *Marmosopsis* sp. (sensu Carneiro and Oliveira, 2023): **b**, MCT.M.811, a fragment of a right dentary with m3-4, in occlusal view; **c**, *Marmosopsis* sp.: partial view of specimen UFRJ-DG 28-M showing the m3 in occlusal view. *Marmosopsis juradoi* Paula Couto, 1962: **d**, MCT.M.4442, right m3 in occluso-labial view; **e**, UFRJ-DG 146-M, left m4 in occlusal view. **f**, *Minusculodelphis minimus* Paula Couto, 1962: MN 2348-V (holotype, cast), left dentary with p1-2, m1-4, and alveoli of p3 (the p1 and m1 were posteriorly damaged in the specimen; see Marshall, 1987) in occluso-labial view. **g**, “*Peradectoidea* gen. nov. sp.1” (sensu Carneiro and Oliveira, 2023): MCT.M.4432, left m2 in occluso-distal view. Scale = 1 mm.

Differs from *Mirandatherium* in its much smaller size (about 0.51-0.56% of the Lm1-4

of *Mirandatherium alipioi*), teeth not bunodont (bunodont in *Mirandatherium*), presence of well-developed postmetacristid (reduced postmetacristid in *Mirandatherium*), mesiodistally compressed and “V-shaped” hypoconid on m3 (hypoconid not compressed and more “U-shaped” on m3 in *Mirandatherium*), m4 subequal to slightly longer than the m3 (m4 smaller than the m3 in *Mirandatherium*), very long retro-molar space (retro-molar space reduced to absent in *Mirandatherium*), and a low dentary (comparatively higher in *Mirandatherium*).

Remarks. *Thylacopygmaeus* gen. nov. was initially considered a closely related taxon to *Mirandatherium* from the early Eocene of Brazil and Argentina (see, e.g., Paula Couto, 1952a, 1962, 1970; Woodburne et al., 2014), and *Marambiotherium* from the early Eocene of Antarctica (Goin and Carlini, 1995; Goin et al., 1999), by Oliveira (1998: 182-184 [unpublished data]). This last author observed that *Thylacopygmaeus* gen. nov. (for him, aff. *Mirandatherium* sp.) shares with *Mirandatherium* a metaconid distally placed to the protoconid, a moderate entoconid, and a low hypoconulid that is separated from the entoconid. He also stated that this taxon shares with *Marambiotherium* (at the time, this taxon had not yet been described) a low hypoconid on m4. However, the holotype of *Thylacopygmaeus oliveirai* differs from that of *Marambiotherium glacialis* in having the m4 longer than the m3 (m4 moderately smaller than the m3 in *Marambiotherium*).

Later, Carneiro and Oliveira (2023) observed that *Thylacopygmaeus* gen. nov. (for these authors, cf. *Armintodelphys*) differs from other Itaboraí’s metatherians in having a distally placed metaconid to the protoconid, a slightly labiolingually compressed entoconid, a labially salient hypoconid, a lower height difference between the trigonid and talonid, and a more labial contact of the cristid obliqua. These authors also mentioned that this combination of features indicates affinities with the Derorhynchidae, Herpetotheriidae, and Paucituberculata. Furthermore, they placed this taxon within the Derorhynchidae (see Carneiro and Oliveira, 2023: table 1).

Carneiro and Oliveira (2023) observed that *Thylacopygmaeus* gen. nov. resembles

Armintodelphys, an Eocene North American and European peradectid, especially *A. duffraingi* Smith and Smith, 2013, from the early Eocene of Belgium (see Smith and Smith, 2013), based on an “open” trigonid (in lingual view), a metaconid distally placed to the protoconid, a talonid shorter (in mesiodistal length) than the trigonid on m4, and a hypoconulid at the lingual half of the talonid (i.e., not centrally placed/at midline of the talonid). However, *Armintodelphys* has a talonid narrower than the trigonid on m3, an entoconid smaller than the hypoconid and hypoconulid, and a slightly more labial contact of the cristid obliqua with the trigonid (see, e.g., Krishtalka and Stuck, 1983a, 1983b, 1984; Smith and Smith, 2013). Consequently, the morphological dental pattern of *Thylacopygmaeus* gen. nov. differs from the one of *Armintodelphys*, ruling out possible close affinities between them (see also the results of the phylogenetic analysis).

†*Thylacopygmaeus oliveirai* sp. nov.

aff. *Mirandatherium* sp. Oliveira, 1998 [unpublished data]: 182, fig. 79.

cf. *Armintodelphys* Carneiro and Oliveira, 2023: 305, fig. 15.

(Fig. 5)

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Derivation of specific name. “*oliveirai*” in honor of the Prof. Dr. Édison Vicente Oliveira (UFPE) for his contributions to the knowledge of Itaboraí’s metatherians.

Diagnosis. As for the genus.

Holotype. MCT.M.933, an incomplete posterior fragment of a right dentary with m3-4, and posterior alveolus of m2 (Fig. 5).

Hypodigm. The holotype only.

Locality and age. The holotype and only known specimen was collected in the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al., 2009). Early Eocene, Ypresian stage, Itaboraiense SALMA (sensu Woodburne et al., 2014).

Description. Dentary (MCT.M.933 [holotype]; Fig. 5). The dentary is very shallow (DHm3-

4: 1.74 mm), with its height slightly greater than the length of m4. The anterior part of the dentary (i.e., the part comprising the incisors, canine, and premolars, and m1) was not preserved. It is impossible to assess whether the premolar/molar series is arched/sinuuous (*sensu* Goin and Carlini, 1995). The dentary is slightly damaged on its ventral wall (at the level of m4 and retro-molar space). The retro-molar space is long (i.e., longer than 50% of the length of m4; *sensu* Oliveira and Goin, 2015). The posterior wall of the dentary ventral to the coronoid process is slightly angled. Only the anterior part of the masseteric fossa is preserved, including the base of the coronoid process. The mandibular foramen is poorly developed and is positioned posterior to the cranioventral axis of the coronoid process. The angular process is poorly developed and medially oriented. The coronoid process and mandibular condyle are not preserved.

m2 (MCT.M.933; holotype). The m2 is unknown for the species, being known only from its partially preserved alveoli. Judging by their dimensions, this tooth was similar in size to m3.

m3 (MCT.M.933; holotype; Fig. 5). The trigonid is longer than the talonid but slightly narrower than the latter. The height of the trigonid compared to that of the talonid cannot be assessed due to the lack of preservation of the protoconid; however, based on the preserved part, the former was at least 2x taller than the talonid (probably 2.5x). The paraconid is not preserved; however, its base can be identified, so its relative height cannot be inferred. Judging by its preserved base, the paraconid is positioned slightly labial to the metaconid, is mesially extended, and is labiolingually robust. The metaconid is preserved only by its base, and its relative height is impossible to assess. The metaconid is positioned distally to the protoconid, presenting a transversely oriented premetacristid and a moderately developed postmetacristid (this crest is somewhat damaged). The protoconid can be identified by its base, as the cusp is badly damaged. Judging by its dimensions, it was the largest cusp of the molar. The protoconid is labiolingually compressed and has an angled preprotocristid (i.e.,

mesiolingually oriented) and a transversely oriented postprotocristid. The postprotocristid and premetacristid (i.e., the metacristid) are in contact, forming the distal wall of the trigonid. The hypoflexid is not lingually invasive in the talonid basin (a consequence of the labial contact of the cristid obliqua). The cristid obliqua is relatively long and has a labial contact with the distal wall of the trigonid (i.e., it is only slightly lingual to the apex of the protoconid). A developed labial cingulid is almost continuous with the postcingulid. The hypoconid is slightly mesiodistally compressed (but not robust) and slightly labially salient than the protoconid. The posthypocristid is obliquely oriented. The preentocristid is moderately developed and fused with the postmetacristid. The entoconid is slightly labiolingually compressed, somewhat conical, equal in height to the hypoconid, and higher than the hypoconulid. The entoconid and hypoconid are transversely aligned. The postentocristid is low. The hypoconulid is damaged, but judging by its preserved part, it would be the smallest of the talonid cusps. This cusp is positioned distolabial to the entoconid. The precingulid is very damaged, but judging from its preserved part, it extended to the mesiolabial wall of the protoconid (i.e., long precingulid; *sensu* Muizon et al., 2018). The postcingulid is present and is thin.

m4 (MCT.M.933; holotype; Fig. 5). The m4 differs from the m3 in the following features: it is subequal in length to the m3. Its talonid is clearly narrower, lower (more than 3x) and shorter than the trigonid. The paraconid is extended mesially and is placed away from the metaconid (i.e., their bases have minimal contact or are not in contact). The paraconid is damaged, but judging by its preserved part, this cusp was probably smaller than the metaconid. The metaconid is relatively shorter and more conical than the one of m3. The postmetacristid is well-developed. The protoconid is labiolingually compressed. The cristid obliqua contacts the distal wall of the trigonid slightly labial to the metacristid notch. The labial cingulid is short (i.e., it does not extend distally beyond the apex of the hypoconid; *sensu* Abello et al., 2013). The talonid cusps are clearly lower than trigonid ones. The

hypoconid is the largest of the talonid cusps and is transversely aligned with the entoconid. The entoconid is labiolingually compressed and is the smallest of the talonid cusps, being slightly lower than the others and clearly smaller. The preentocristid is fused with the postmetacristid, forming a continuous crest with the entoconid and postentocristid. The hypoconulid is relatively further away from the entoconid, is subequal in height to the hypoconid, and is at the lingual half of the talonid (i.e., it is not centrally/midline placed). The precingulid is long and well-developed, reaching the mesiolabial wall of the protoconid. The postcingulid is absent.

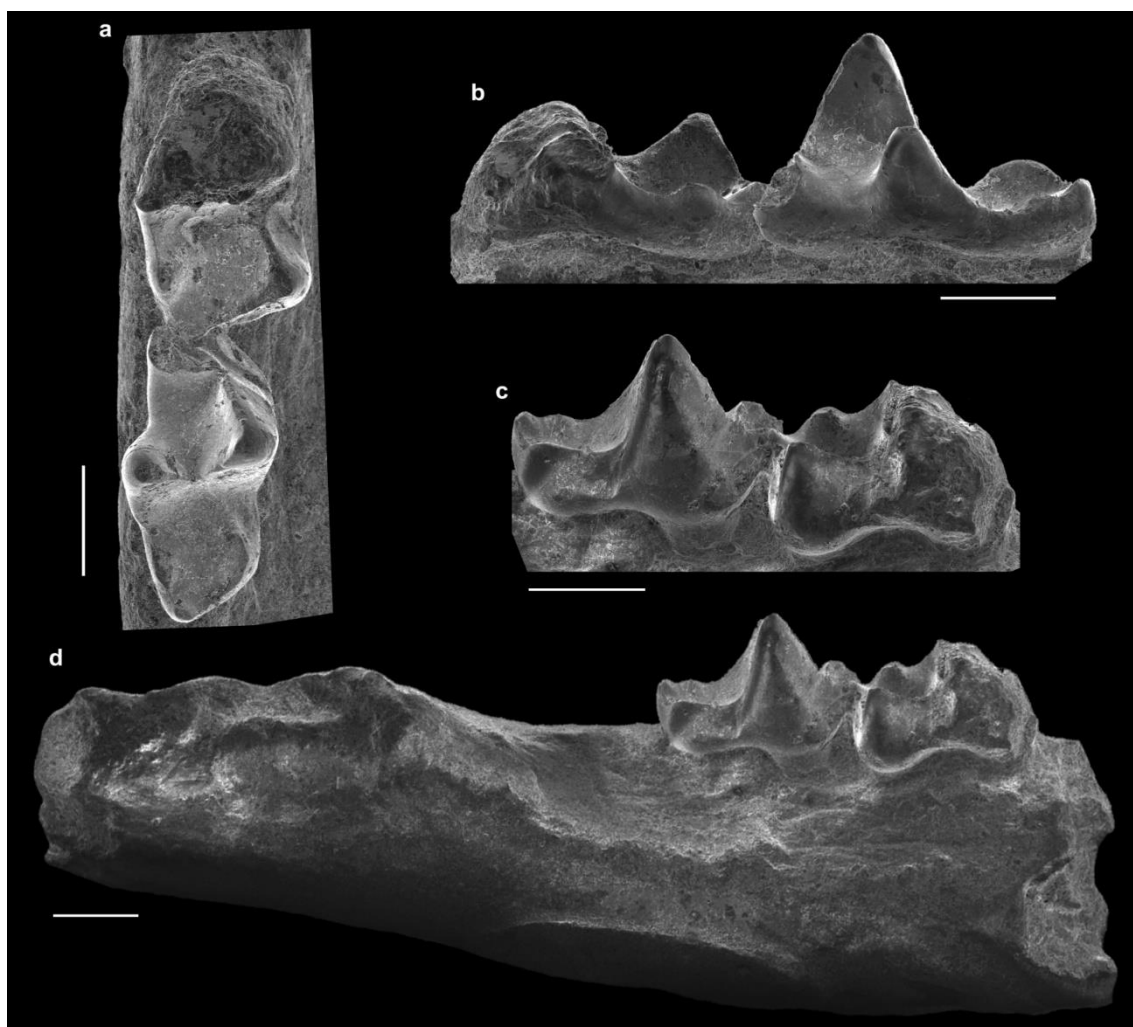


Fig. 5 *Thylacopygmaeus oliveirai* gen. et sp. nov. SEM images of the holotype (MCT.M.933), a posterior fragment of a right dentary with m3-4: **a-c**, details of the molars in occlusal (**a**), lingual (**b**), and labial (**c**) views; **d**, the dentary in lateral view. Scale bars = 0.5 mm.

Measurements. See Table 2.

Table 2 Dental measurements (in mm) and some morphometric and morphofunctional variables of the holotype of *Thylacopygmaeus oliveirai* gen. et sp. nov. **A**, area; **DHm3-4**, dentary height below m3-4; **H**, height; **L**, length; **Lm1-4**, length of the lower molar series; **m**, lower molar; **ra**, relative area (A_{tal}/A_{tri}); **RDS**, relative dentary shape (DH_{m3-4}/L_{m1-4}); **RGA**, relative grinding area ($\sqrt{A_{tal}/L_{tri}}$); **rh**, relative height (H_{tal}/H_{tri}); **Retro**, length of the retro-molar space; **W**, width; (), talonid dimensions; [], estimated length; ~, incomplete specimen; *, based on alveoli dimensions.

	Lm2	Lm3	Wm 3	Lm4	Wm 4	Lm1 -4	DH m3-4	Retr o	RDS	RGA	ra	rh
											m3:	m3:
											0.45	~0.4
											(0.38	2
		~0.6		0.71							) -	(0.34
MC		4	0.71	(0.48	0.70	[~4.6	1.74	1.10	~0.3	0.66	0.84/	) - ?/
T.M.	~0.7	(0.52	(0.73	) -	(0.46	7]			8		m4:	m4:
933	1*	) -	)	1.19	)						0.50	0.72
		1.16									(0.22	(0.27
											) -	) -
											0.44	0.34

Estimated body mass. 12 g.

Remarks. The holotype of *Thylacopygmaeus oliveirai* gen. et sp. nov. (MCT.M.933) was initially described and figured by Oliveira (1998: 182-184), who did not provide additional comments; the specimen was never mentioned in any further study dealing with the metatherian fauna from Itaboraí (see, e.g., Oliveira and Goin, 2006, 2011, 2012, 2015; Oliveira et al., 2016, 2021). Curiously, specimen MCT.M.933 was not formally studied by Marshall (see Marshall, 1987). The last material cited in his study with Itaboraí's metatherians (Marshall, 1987) is specimen MCT.M.932 (*Carolopaulacoutoia itaboraiensis*).

Carneiro and Oliveira (2023) provided the first formal mention in the literature of specimen MCT.M.933. These authors figured it (their fig. 15) and provided the first systematic hypotheses regarding the affinities of this taxon. Nevertheless, these authors did not study this specimen in detail.

Known materials of *Thylacopygmaeus oliveirai* gen. et sp. nov. are currently restricted to its holotype (MCT.M.933). However, more than 10,000 vertebrate specimens recovered in the Itaboraí Basin held in the MCT are currently under study (specimens preserved in original sediments are not included). These huge number of specimens are held in more than 600 entrance lots, in which the screening of only 12 of these provided more than 400 new metatherian specimens (considering only teeth, jaws, and maxillae) for the Itaboraí fauna (see Carneiro, 2023 [unpublished data]). These entrance lots are currently under study, which may result in more complete specimens for *Thylacopygmaeus oliveirai* gen. et sp. nov. In these lots, new specimens of *Marmosopsis juradoi* (about 37 specimens), *Minusculodelphis minimus* (a single specimen), and *Minusculodelphis modicum* (two specimens) have been recovered.

5. Results of PCA analyses

The two PCA analyses recovered the ra (=relative talonid per trigonid area) as the principal component (PC1) ('X' axis), representing 62.28% and 60.60% of the variation identified by the analyses. The Lm (=lower molar length) was the second principal component (PC2) ('Y' axis), representing 37.72% and 39.40% of the variation identified by the analyses (Fig. 6).

The PCAs results reveal that *Thylacopygmaeus oliveirai* gen. et sp. nov. is identified by its slightly smaller measurements, except for *Minusculodelphis*. *Thylacopygmaeus oliveirai* gen. et sp. nov., the Peradectoidea gen. nov. sp.2, and *Carolopaulacoutoia* sp. are identified by their m3's, which display relatively larger talonids compared to the trigonids, resulting in their placement at the upper right quadrant of the analysis (Fig. 6). In contrast, *Diogenesia*

brevirostris, *Gaylordia doelloi*, and *Marmosopsis juradoi* are identified by their m3's relatively smaller talonids compared to the trigonids, resulting in their placement at the lower quadrants of the analysis (Fig. 6).

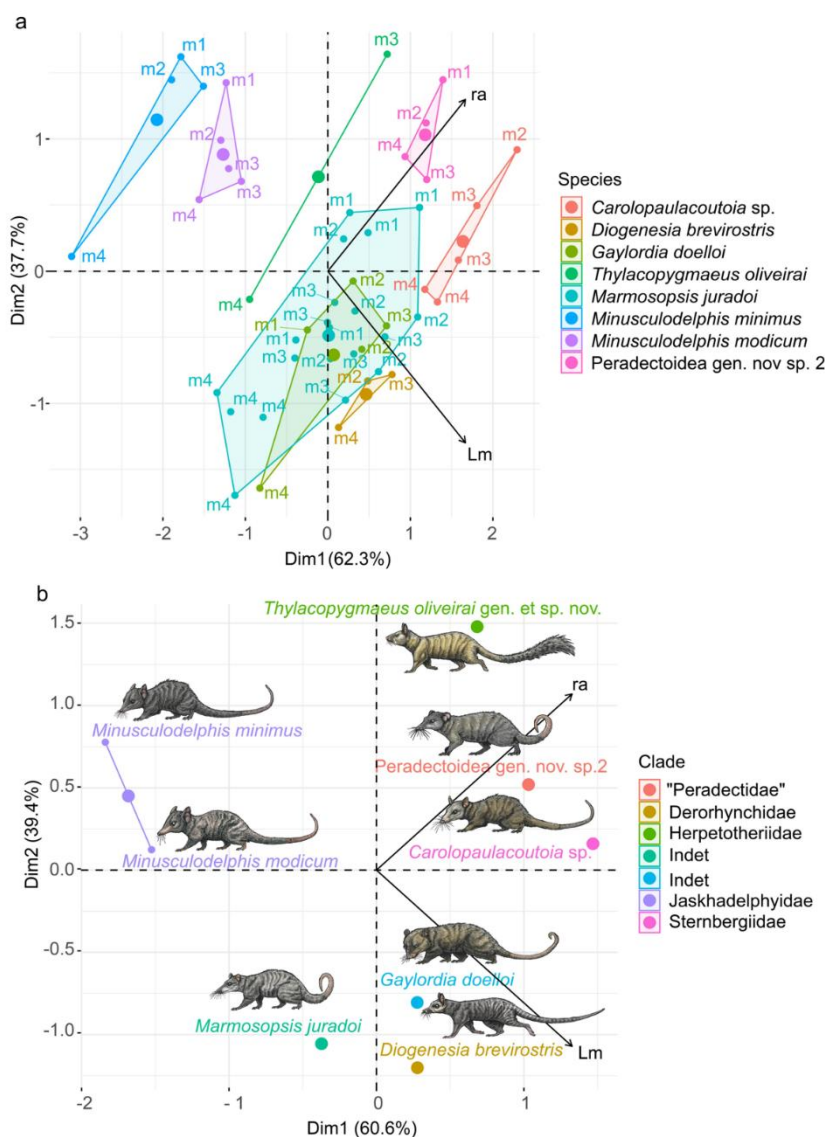


Fig. 6 Principal component analyses (PCA) of two morphometric indices based on lower molar measurements for *Carolopaulacoutoia* sp., *Diogenesia brevirostris* Oliveira et al., 2021; *Gaylordia doelloi* (Paula Couto, 1962); *Thylacopygmaeus oliveirai* gen. et sp. nov.; *Marmosopsis juradoi* Paula Couto, 1962; *Minusculodelphis minimus* Paula Couto, 1962; *Minusculodelphis modicum* Oliveira et al., 2016; and *Peradectoidea* gen. nov. sp.2. **a**, PCA analysis with lower molar's loci (m1, m2, m3, and m3); **b**, PCA analysis with the m3 locus average indexes' values. **Lm** = lower molar length; **ra** = Atal/Atri. **A**, area; **tal**, talonid; **tri**, trigonid. Credits: The artistic drawings of Itaboraí's metatherians were made by Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com).

6. Results of the phylogenetic analysis

Our phylogenetic analysis PA recovered 81 MPTs (Score: 1935; CI: 0.373; RI: 0.599) (Fig. 7). Following the results of the phylogenetic analysis, *Thylacopygmaeus* gen. nov. is autapomorphic based on the presence of a metaconid distally placed to the protoconid (character 147, state 0 – reversion). *Thylacopygmaeus* gen. nov. was recovered as the sister taxon of *Rumiodon* based on the presence of a labiolingually compressed metaconid (ch. 146, state 1), a developed postentocristid (ch. 187, state 1) and a labiolingually compressed protoconid on m4 (ch. 205, state 1). These two taxa are grouped within Rumiodontinae nov. (node 114).

Rumiodontinae nov., *Herpetotherium* and *Copedelphys* are sister taxa (Herpetotheriidae; node 113) based on the presence of a paracone labially placed than the metacone (ch. 49, state 1). Moreover, *Djathia* Godthelp et al., 1999 was recovered as the sister taxon of Herpetotheriidae (node 111) based on a distolabially oriented postmetacrista on M3 (ch. 40, state 1) and p2 and p3 subequal in size (ch. 265, state 1).

Peratherium and *Amphiperatherium* (Peratheriinae; node 112) were recovered as sister taxa based on the presence of an M1 with an extreme posterolabial extension of the metastylar angle (ch. 36, state 1). *Didelphopsis* and *Itaboraidelphys* (node 109) were sister taxa based on the presence of P/p3 longer than M/m1 (chs. 231 and 268, state 1). These two clades (node 110) were recovered as sister taxa based on the presence of a distolabially oriented postmetacrista on M3 (ch. 40, state 1). Moreover, they are recovered as the sister taxa of *Carolopaulacoutoia* (Sternbergiidae; node 108) based on the presence of a StC closely spaced to StB (ch. 18, state 1).

Nortedelphys was recovered as the sister taxon of *Alphadon* (i.e., Alphadontia-Alphadontidae; node 89) based on the following features: presence of a supernumerary

cuspsule distolabial to the StB (StB1; ch. 10, state 1), StB with a concave medial/distal border (ch. 11, state 1), StC lingually placed to StB and StD (ch. 17, state 1), metacone with flat labial wall (ch. 50, state 1), m1 and m2-3 cristid obliqua reaching the distal wall of the trigonid at metacristid's notch (ch. 131 and 174, states 1 and 2, respectively), and entoconid larger than the hypoconulid (ch. 178, state 2). Therefore, *Nortedelphys* is not recovered within Herpetheriidae.

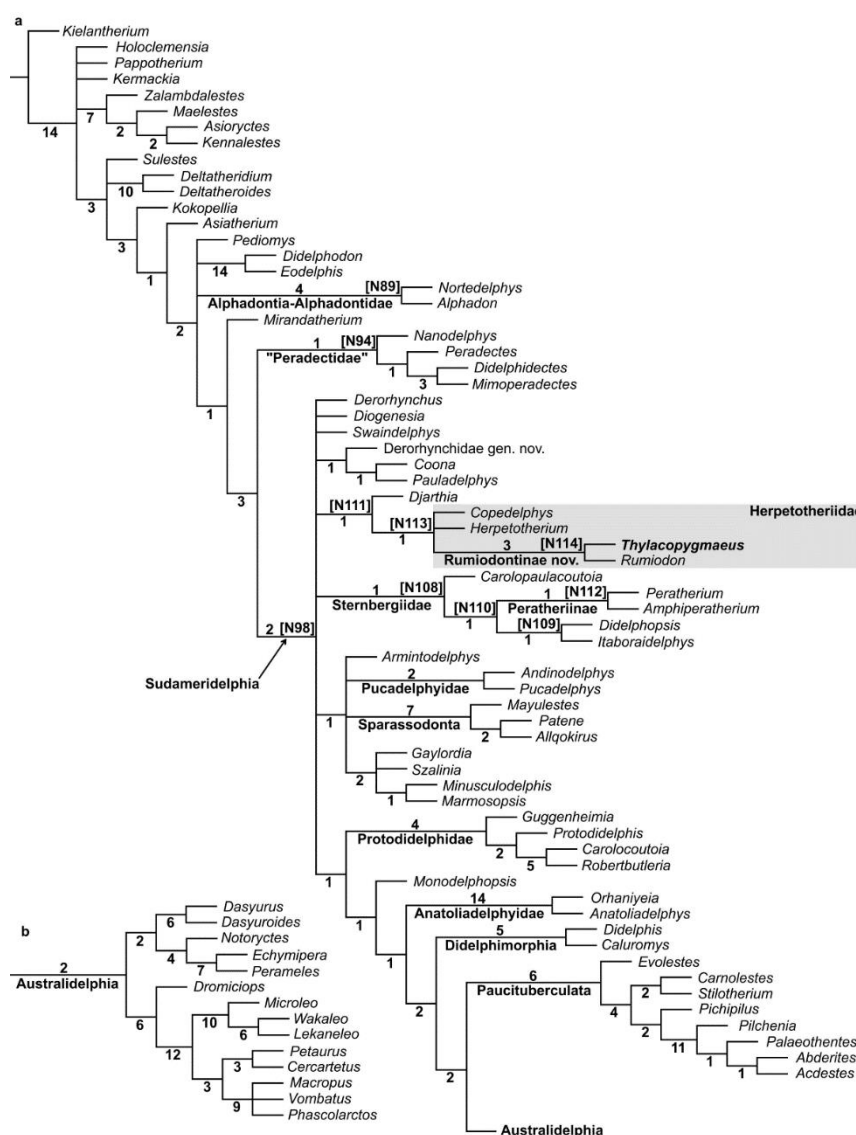


Fig. 7 Strict consensus tree of the 81 MPTs (Score: 1935; CI: 0.373; RI: 0.599) recovered in the phylogenetic analysis. **a**, results of the phylogenetic analysis without Australidelphia's taxa; **b**, result of the phylogenetic analysis, showing Australidelphia taxa only. Numbers above and below the branches indicate Bremer Support

values. The number of the nodes of Alphadontia-Alphadontidae (node 89), the clade of *Didelphopsis* and *Itaboraidelphys* (node 109), the clade of *Djarthia* and Herpetotheriidae (node 111), Herpetotheriidae (113), Peratheriinae (node 112), Rumiodontinae nov. (114), Sternbergiidae (node 108), and the clade of Peratheriinae, *Didelphopsis* and *Itaboraidelphys* (node 110) are presented with [N_number of the node]. *Thylacopygmaeus* gen. nov. is highlighted in bold. Herpetotheriidae is highlighted in grey. **N**, node.

7. Discussion

7.1 Systematic affinities of *Rumiodontinae* nov. and other “herpetotheriid-like” taxa

Herpetotheriidae have been considered a North American and Euro-Afro-Asian clade of Paleogene and Neogene metatherians (see, e.g., Williamson et al., 2012, 2014; Ladevèze et al., 2020; Wessels et al., 2024). Classically, several taxa with dilambdodont “V-shaped” centrocrista have been included within this clade (e.g., *Nortedelphys* Case et al., 2005; *Swaindelphys* Johanson, 1996). However, the diagnosis of Herpetotheriidae is not well defined, as it is based on symplesiomorphic dental features for Sudameridelphia (node 98), like the presence of a dilambdodont “V-shaped” centrocrista (ch. 54, state 1).

Several studies have defined Herpetotheriidae based on comparisons with “Peradectidae” (see, e.g., Johanson, 1996). In this concept, “Peradectidae” is usually determined by the presence of a well-developed stylar shelf, straight centrocrista, presence of postentocristid, and subequal (at height) talonid cuspids (see, e.g., Korth, 1994; Johanson, 1996; Williamson et al., 2014). In contrast, Herpetotheriidae have opposing features, like a comparatively narrower stylar shelf, “V-shaped” centrocrista, absence of postentocristid, and entoconid larger than hypoconulid (see, e.g., see, e.g., Korth, 1994; Johanson, 1996; Williamson et al., 2014). However, most of these features display evident phenotypic plasticity within the Herpetotheriidae and “Peradectidae” taxa, except for the shape of the centrocrista (dilambdodont in Herpetotheriidae and straight in “Peradectidae”).

In summary, all North American and European Paleogene taxa with dilambdodont centrocrista were grouped within Herpetotheriidae. In contrast, taxa with a straight centrocrista were grouped within “Peradectidae” (see, e.g., Williamson et al., 2014). Nevertheless, a straight centrocrista is a plesiomorphy for Metatheria (see character 54, state 0), restricting its validity for the definition of some clades (e.g., “Peradectidae”), as it can represent a retained symplesiomorphy instead of a synapomorphy.

Consequently, some studies have recovered a “polyphyletic” Herpetotheriidae, excluding some taxa as members of this clade. Carneiro and Oliveira (2017) recovered *Nortedelphys* Case et al., 2005 within Alphadontia (i.e., the clade that includes Alphadontidae and closely related taxa; sensu Carneiro and Oliveira, 2017a; see node 89). Ladevèze et al. (2020) recovered the Paleogene-Neogene peratheriines as an earlier divergent clade than Herpetotheriidae, which was recovered by them as more closely related to Marsupialia (the phylogenetic analysis recovered Peratheriinae within Sternbergiidae; see node 108). Moreover, our results did not confidently recover *Swaindelphys* Johanson, 1996 as a herpetotheriid (see Fig. 7).

The grouping of *Thylacopygmaeus* gen. nov. and *Rumiodon* within Herpetotheriidae (node 113) extends this discussion. Herpetotheriids have been tentatively identified in South America (see Goin and Candela, 2004). However, no previous study has tested this hypothesis in the context of a phylogenetic analysis. Our data suggest that this group occurred in South America during the Paleogene.

Following the results of the phylogenetic analysis, Rumiodontinae nov. was recovered within Herpetotheriidae. However, the latter lacks a well-defined diagnosis. Consequently, the low Bremer supports recovered by the analysis (see Fig. 7) are low (Bremer Support: 1). Moreover, the monophyly of “Herpetotheriinae” (i.e., the clade that includes *Herpetotherium* and *Copedelphys*) was not recovered (see node 113). In contrast, Rumiodontinae nov. is well-supported (Bremer Support: 3), allowing their description as a new subclade of

Herpetotheriidae.

The analysis recovered Peratheriinae as the sister taxon of *Didelphopsis* and *Itaboraidelphys* (node 110) within Sternbergiidae (i.e., the clade that includes *Carolopaulacoutoia*, *Didelphopsis*, *Itaboraidelphys*, and Peratheriinae; see node 108). Peratheriines have been classically regarded as closer to North American “herpetotheriines”; however, no study has ever confidently confirmed this sister relation (see Ladevèze et al., 2020). These uncertain affinities led to the hypothesis that peratheriines dispersed from South America instead of North America (Crespo and Goin, 2021). The results of the phylogenetic analysis suggest that Euro-Afro-Asian peratheriines might represent a subclade of Sternbergiidae (node 108), a South American clade of Paleogene “herpetotheriid-like” taxa (see Carneiro and Oliveira, 2023). Furthermore, this should be treated as tentative, as the Bremer Supports are low (see Fig. 7).

Similarly, the inconclusive affinities of *Swaindelphys* considered the oldest known herpetotheriid (see, e.g., Johanson, 1996; Williamson and Taylor, 2011), do not allow further conclusions regarding its herpetotheriid affinities. Following Johanson (1996), *Swaindelphys* differs from herpetotheriids (among other features) in the presence of a vertically/labially oriented (=posterolabially of Johanson, 1996) postmetacrista. On the contrary, herpetotheriids have a more distally oriented postmetacrista (Johanson, 1996).

A vertically oriented postmetacrista on M3 is a shared condition between *Swaindelphys* and some South American sudameridelphians, such as *Bergqvistherium primigenia* Carneiro, 2019; *Carolopaulacoutoia itaboraiensis* (Paula Couto, 1970), derorhynchids, *Gaylordia mater* Oliveira and Goin, 2015; *Mayulestes ferox* Muizon, 1994; *Minusculodelphis modicum*, the Peradectoidea gen. nov. (see, e.g., Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023), pucadelphyids etc.

Considering Notometatheria, *Carolopaulacoutoia* and derorhynchids display a labially oriented postmetacrista on M3. In contrast, herpetotheriids, peratheriines, *Didelphopsis*,

Itaboraidelphys, and marsupials display a comparatively more distally oriented postmetacrista on M3 (see, e.g., Carneiro et al., 2018; Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023). However, this feature is recovered as independently acquired between the clade that comprehends *Didelphopsis*, *Itaboraidelphys*, and Peratheriinae (node 110) and the one that includes *Djarthia* and Herpetotheriidae (node 111).

Moreover, *Swaindelphys* differs from *Diogenesia* (considered the most generalized derorhynchid by Oliveira et al., 2021; Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023), herpetotheriids (except for *Rumiodon*), and sternbergiids in the presence of well-developed and non-subdivided StC and StD, whereas the other taxa frequently have supernumerary cuspules on the styler shelf (see, e.g., Korth, 1994; Carneiro and Oliveira, 2023).

Considering South American metatherians, several taxa display fully developed StA, StB, StC, and StD (e.g., derorhynchids, early Paleocene sparassodonts, *Gaylordia*, “glasbiids”, polydolopiformes, pucadelphyids, and sternbergiids; see, e.g., Carneiro and Oliveira, 2023; Muizon, 1992; Muizon et al., 2018), indicating that this pattern seems to represent the ancestral condition for Sudameridelphia. Accordingly, the presence of supernumerary cuspules seems to be independently acquired by several clades, including notometatherians (e.g., *Carolopaulacoutoia*, *Didelphopsis*, *Diogenesia*, *Herpetotherium*, *Itaboraidelphys*, *Peratherium*; see, e.g., Carneiro and Oliveira, 2023; Ladevèze et al., 2020) and Sparassodonta (e.g., *Patene simpsoni*, *Procladosictis anomala*, *Xenocynus crypticus*; see, e.g., Carneiro et al., 2024a; Rangel et al., 2019, 2023b).

Moreover, Carneiro and Oliveira (2023) suggested that Marsupialia’s ancestral dental pattern very likely displayed a reduced StC, as the earliest members of this clade lack this cusp or have a reduced one (see, e.g., *Austropedimys*, *Bardalestes*, protodidelphids, and *Monodelphopsis*). Therefore, the presence of well-developed non-subdivided styler cusps (StB, StC, and StD) in *Swaindelphys* seems to represent an ancestral pattern within

Notometatheria.

Furthermore, Herpetotheriidae is pending a proper diagnosis in the literature. This confused taxonomic concept resulted in the inclusion of several dilambdodont taxa within this clade. The unresolved affinities of Herpetotheriidae with other non-Marsupialia notometatherian clades (see Fig. 7) do not allow further biogeographic conclusions regarding its ancestral area to the early Paleocene. For Peratheriinae, the result of the phylogenetic analysis suggests a maximum early Paleocene origin for this clade in South America (see the hypothesis of Crespo and Goin, 2021).

Summarizing, following the PA results, we regard *Thylacopygmaeus* gen. nov. and *Rumiodon* as belonging to the Herpetotheriidae, supporting the occurrence of this clade in South America from the early Eocene (53-50 Ma; sensu Woodburne et al., 2014) up until the early Oligocene (maximum 29.6 ± 0.08 Ma; see a discussion about the age of Santa Rosa in Campbell et al., 2021). *Thylacopygmaeus* gen. nov. (Fig. 8) represents the oldest record of a herpetotheriid in South America and the first record of a herpetotheriid during the Eocene in this subcontinent. This result increases the number of metatherian clades in the Itaboraí Basin.

Furthermore, our results confirm the hypotheses of Goin and Candela (2004), who proposed herpetotheriid affinities for *Rumiodon*, and Carneiro and Oliveira (2023), who mentioned possible herpetotheriid affinities for *Thylacopygmaeus* gen. nov. (by then regarded as cf. *Armintodelphys*).

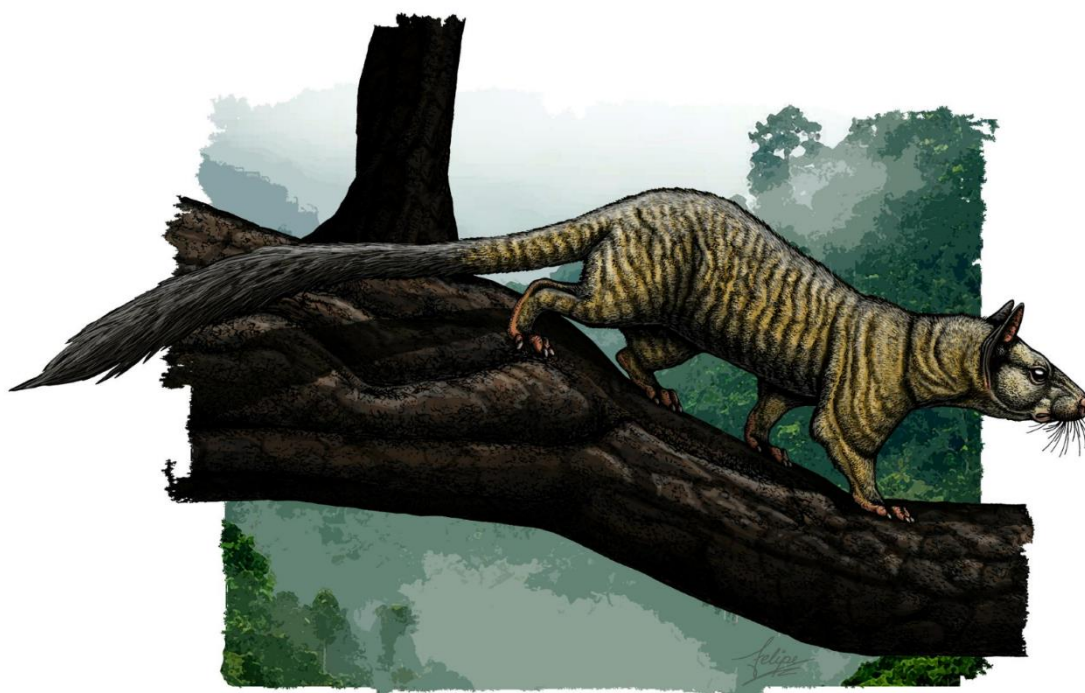


Fig. 8 Artistic drawing of *Thylacopygmaeus oliveirai* gen. et sp. nov. Credits: Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com).

7.2 Dietary inferences for *Thylacopygmaeus oliveirai* gen. et sp. nov.

The onset of the Eocene is marked by two massive releases of CO₂ in the Atmosphere due to volcanic events that increased average global temperatures from about 5° C to 8° C (Bowen et al., 2015). These events resulted in the Paleocene-Eocene Thermal Maximum (PETM). The PETM + the Early Eocene Climatic Optimum (EECO) is considered the most relevant paleoenvironmental event correlated with the increase in diversity of metatherians in South America (see, e.g., Oliveira and Goin, 2011; Goin et al., 2012, 2016; Zimicz, 2012 [unpublished data]; Carneiro, 2019; Tarquini et al., 2022; Carneiro and Oliveira, 2023).

The Itaboraí Basin has preserved one of the most diverse faunas with tiny- and very small-sized metatherians, with seven genera and eight species (see Carneiro and Oliveira, 2023). The co-existence of these taxa could result from differential trophic niches and the use of habitat strata, as similarly inferred for large-sized metatherian taxa from Itaboraí (see Carneiro et al., 2024a). Accordingly, the results of PCA analyses (Fig.12) suggest that these

taxa explored three differential trophic niches: 1) generalized insectivory (*Carolopaulacoutoia* sp., *Thylacopygmaeus oliveirai* gen. et sp. nov., and the material referred as *Peradectoidea* gen. nov. sp.2), 2) strict/specialized insectivory (*Diogenesia brevirostris*, *Gaylordia doelloi*, and *Marmosopsis juradoi*), and 3) “minimalized” specialized insectivory (*Minusculodelphis* spp.).

Considering *Minusculodelphis*, Oliveira et al. (2016) suggested that this taxon survived in a tropical/equatorial forest’s understory or leaf litter microhabitat. The PCA analyses placed *Minusculodelphis* in an extreme left placement, “very far” from *Thylacopygmaeus oliveirai* gen. et sp. nov. and very small-sized metatherians. This result suggests that the diminutive dimensions of *Minusculodelphis* may indicate that this taxon occupied a singular niche compared to other metatherians during the early Eocene.

Thylacopygmaeus oliveirai gen. et sp. nov., *Carolopaulacoutoia* sp., and the *Peradectoidea* gen. nov. sp.2 (sensu Carneiro and Oliveira, 2023) occupied a differential trophic niche than that of *Diogenesia brevirostris*, *Gaylordia doelloi*, and *Marmosopsis juradoi*. Despite their similar dimensions, these two groups differ mainly in the relative areas between the talonid and the trigonid (ra). The first taxa display larger talonids, suggesting a less specialized insectivorous diet than the second group.

Insectivorous metatherians are generally characterized by the presence of mesially oriented trigonids, talonids shorter and much lower than trigonids, mesiodistally compressed and distolabially oriented hypoconids, small to vestigial entoconids, labiolingually compressed premolars, slender dentaries, and long retro-molar space (see Carneiro and Oliveira, 2023). It is also observable that specialized insectivores display diastemata between lower canines and p1 and between premolars (i.e., relatively long anterior part of the dentary [i.e., the part represented by lower incisors, canine, and premolars; RPM; sensu Carneiro et al., 2024a]), such as *Derorhynchus singularis* and *Marmosopsis* spp. (see, e.g., Paula Couto, 1952a, 1962; Carneiro, 2023 [unpublished data]).

The two above-mentioned morphogroups were insectivores (i.e., invertebrates represented essential food items in their diet). However, the presence of relatively larger talonids in the first group suggests that these taxa may have had a more generalized/less specialized diet than the second group's taxa. The extant didelphids are considered insectivores-omnivores (see, e.g., Cáceres and Monteiro-Filho, 2001; Lessa and Geise, 2010, 2014; Camargo et al., 2013; Castilheiro and Santos Filho, 2013; Astúa and Guilhon, 2023), with very small-sized taxa (e.g., *Gracilinanus agilis*) preying mainly on invertebrates but fruits and small vertebrates can also be explored as food (see, e.g., Camargo et al., 2013). *Thylacopygmaeus oliveirai* gen. et sp. nov., *Carolopaulacoutoia* sp., and the Peradectoidea gen. nov. sp.2 (sensu Carneiro and Oliveira, 2023) probably had similar diets to extant didelphids, preying mainly invertebrates but fruits representing important food (i.e., insectivory-omnivory). Nevertheless, smaller vertebrates cannot be ruled out as occasional food.

The second group has two trophic niches: 1) *Gaylordia doelloi*, an insectivorous-durophagous taxon, and 2) *Diogenesia brevirostris* and *Marmosopsis juradoi*. *Gaylordia doelloi* has hypertrophied and bulbous p2-3, subquadrangular and somewhat inflated crowns, and reduced retro-molar space (see, e.g., Paula Couto, 1962, 1970; Marshall, 1987; Oliveira and Goin, 2015; Carneiro and Oliveira, 2023). These features indicate a durophagous diet (see, e.g., Marshall, 1987; Oliveira and Goin, 2015; Carneiro and Oliveira, 2017b, 2023). In contrast, *Diogenesia brevirostris* and *M. juradoi* have dental features indicative of a specialized insectivorous diet. Therefore, *Gaylordia doelloi* probably explored a differential trophic niche compared to *D. brevirostris* and *M. juradoi*. Furthermore, tiny- and very small-sized metatherians explored differential trophic niches, which may explain the great diversity recorded in the Itaboraí Basin.

8. Conclusions

Thylacopygmaeus oliveirai gen. et sp. nov. is an early Eocene (Itaboraiense SALMA)

tiny-sized herpetotheriid from the Itaboraí Basin. *Thylacopygmaeus* gen. nov. and *Rumiodon* are sister taxa grouped in a new clade, Rumiodontinae nov., within the Herpetotheriidae. This clade is identified by the presence of a labiolingually compressed metaconid on m3, a developed postentocristid, and a labiolingually compressed protoconid on m4.

The fossil record indicates that herpetotheriids lived in South America during the Paleogene from the early Eocene (Itaboraí Basin, Brazil) up to the early Oligocene (Santa Rosa local fauna, Peru). In contrast, the occurrence of this group during the Paleocene in North America and South America is still under debate, as our results did not confidently recover *Swaindelphys* as a member of Herpetotheriidae, and no member of this clade has been reported for the Paleocene of South America.

Finally, based on the results of the phylogenetic analysis, the geographical origin of Herpetotheriidae is still an open question. However, our results indicate that European Peratheriinae, traditionally regarded as a result of dispersal(s) from North America, is a subclade of Sternbergiidae. This conclusion suggests a South American ancestral area for this clade (see hypothesis of Crespo and Goin, 2021), with Euro-Afro-Asian taxa dispersing from South America via Africa to Europe (Atlantogea hypothesis; see Ezcurra and Agnolín, 2012), as similarly hypothesized for other metatherian taxa (Anatoliadelphidae; see Carneiro, 2019).

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Declaration of competing interest

We have no conflicts of interest to disclose.

Declaration of generative AI in scientific writing

We have not used generative AI in scientific writing.

Declaration of author contributions

L.M.C. (coordinated the study, wrote the main manuscript text, prepared the tables and figures, made the database of performed phylogenetic and PCA analyses, and related supplementary files), F.J.G. (wrote the main manuscript text, provided detailed comparisons between studied taxa, prepared its figures, and wrote the supplementary material, appendix 8), H.B. (wrote the main manuscript text, performed PCA analysis, and prepared related figures), R.C.S. (wrote the main manuscript text and prepared its figures), C.C.R. (wrote the main manuscript text, prepared the geographic and stratigraphic figure, and contributed to the database of the first phylogenetic analysis), B.M.G.G. (wrote the main manuscript text), M.R.A. (wrote the main manuscript text). All authors reviewed the manuscript.

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FIGURE CAPTIONS

Fig. 1. Locality and age of the Itaboraí fauna. **a**, Map of Brazil showing the region and the coordinates of the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro (22° 45' 9'' S; 42° 51' 53'' W). **b**, Biochronological relationships of the Itaboraiense SALMA with other Paleogene SALMAs. The age range for the Itaboraí SALMA follows Carneiro and Oliveira (2023; see Woodburne et al., 2014 for an alternative chronology). The occurrence of *Thylacopygmaeus oliveirai* gen. et sp. nov. is suggested by a black arrow and a digital image of the MCT.M.933 (holotype), a posterior fragment of a right dentary with m3-4. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 500 Km.

Fig. 2 Diagnostic combination of features of *Thylacopygmaeus* gen. nov. SEM image of the specimen MCT.M.933, holotype of *Thylacopygmaeus oliveirai* gen. et sp. nov., a posterior fragment of a right dentary with m3-4 in occlusal view. Scale bar = 0.5 mm.

Fig. 3 Comparative SEM imagens of rumiodontines nov. and Itaboraí's very small-sized metatherians. **a**, *Thylacopygmaeus oliveirai* gen et sp. nov.: MCT.M.933 (holotype), a fragment of right dentary with m3-4, in occlusal view. **b**, *Rumiodon* sp.: LACM 140583, left m3 and m4 in occlusal view (after Goin and Candela, 2004: fig. 3; images inverted to facilitate comparisons). **c**, *Diogenesia brevirostris* Oliveira et al., 2021: MCT.M.650 (holotype), incomplete right dentary with m2-4, and alveoli of p1-3 and m1, in occluso-labial view. **d-e**, *Carolopaulacoutoia itaboraiensis* (Paula Couto, 1970): **d**, MCT.M.927, incomplete right dentary with p2, p3 (erupting), m1-3, and alveolus of i2-5 and c, and alveoli of p1, in occlusal view; **e**, UFRJ-DG 155-M, right m4 in occlusal view. **f**, *Gaylordia doelloi* (Paula Couto, 1962): MN 2504-V (holotype), incomplete left dentary with m2, and alveoli of m1 and m3-4 of a juvenile specimen, in occlusal view. Scale bars = 1 mm.

Fig. 4 Comparative SEM imagens of *Thylacopygmaeus* gen. nov. and Itaboraí's very small- and small-sized metatherians. **a**, *Thylacopygmaeus oliveirai* gen et sp. nov.: MCT.M.933 (holotype), a fragment of right dentary with m3-4, in occlusal view. **b-c**, *Marmosopsis* sp. (sensu Carneiro and Oliveira, 2023): **b**, MCT.M.811, fragment of a right dentary with m3-4, in occlusal view; **c**, *Marmosopsis* sp.: partial view of specimen UFRJ-DG 28-M showing the m3 in occlusal view. *Marmosopsis juradoi* Paula Couto, 1962: **d**, MCT.M.4442, right m3 in occluso-labial view; **e**, UFRJ-DG 146-M, left m4 in occlusal view. **f**, *Minusculodelphis minimus* Paula Couto, 1962: MN 2348-V (holotype, cast), left dentary with p1-2, m1-4, and alveoli of p3 (the p1 and m1 were posteriorly damaged in the specimen; see Marshall, 1987) in occluso-labial view. **g**, "Peradectoidea gen. nov. sp. l" (sensu Carneiro and

Oliveira, 2023): MCT.M.4432, left m2 in occluso-distal view. Scale bars = 1 mm.

Fig. 5 *Thylacopygmaeus oliveirai* gen. et sp. nov. SEM images of the holotype (MCT.M.933), a posterior fragment of a right dentary with m3-4: **a-c**, details of the molars in occlusal (**a**), lingual (**b**), and labial (**c**) views; **d**, the dentary in lateral view. Scale bars = 0.5 mm.

Fig. 6 Principal component analyses (PCA) of two morphometric indices based on lower molar measurements for *Carolopaulacoutoia* sp., *Diogenesia brevirostris* Oliveira et al., 2021; *Gaylordia doelloi* (Paula Couto, 1962); *Thylacopygmaeus oliveirai* gen. et sp. nov.; *Marmosopsis juradoi* Paula Couto, 1962; *Minusculodelphis minimus* Paula Couto, 1962; *Minusculodelphis modicum* Oliveira et al., 2016; and *Peradectoidea* gen. nov. sp.2. **a**, PCA analysis with lower molar's *loci* (m1, m2, m3, and m3); **b**, PCA analysis with the m3 *locus* average indexes' values. **Lm** = lower molar length; **ra** = Atal/Atri. **A**, area; **tal**, talonid; **tri**, trigonid. Credits: The artistic drawings of Itaboraí's metatherians were made by Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com).

Fig. 7 Strict consensus tree of the 81 MPTs (Score: 1935; CI: 0.373; RI: 0.599) recovered in the phylogenetic analysis. **a**, results of the phylogenetic analysis without Australidelphia's taxa; **b**, result of the phylogenetic analysis, showing Australidelphia taxa only. Numbers above and below the branches indicate Bremer Support values. The number of the nodes of Alphadontia-Alphadontidae (node 89), the clade of *Didelphopsis* and *Itaboraidelphys* (node 109), the clade of *Djarthia* and Herpetotheriidae (node 111), Herpetotheriidae (113), Peratheriinae (node 112), Rumiodontinae nov. (114), Sternbergiidae (node 108), and the clade of Peratheriinae, *Didelphopsis* and *Itaboraidelphys* (node 110) are presented with [N_number of the node]. *Thylacopygmaeus* gen. nov. is highlighted in bold. Herpetotheriidae is highlighted in grey. **N**, node.

Fig. 8 Artistic drawing of *Thylacopygmaeus oliveirai* gen. et sp. nov. Credits: Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com).

TABLE TITLES

Table 1. Size categories considered for early Eocene Itaboraí's metatherians (sensu Carneiro et al., 2024) based on their lower molar series length (in mm) and maximum and minimum limits of estimated body masses (BM) in grams (g) and kilograms (kg). **BM**, estimated body mass; **Lm1-4**, lower molar series length.

Table 2 Dental measurements (in mm) and some morphometric and morphofunctional variables of the holotype of *Thylacopygmaeus oliveirai* gen. et sp. nov. **A**, area; **DHm3-4**, dentary height below m3-4; **H**, height; **L**, length; **Lm1-4**, length of the lower molar series; **m**, lower molar; **ra**, relative area (A_{tal}/A_{tri}); **RDS**, relative dentary shape ($DHm3-4/Lm1-4$); **RGA**, relative grinding area ($\sqrt{A_{tal}/L_{tri}}$); **rh**, relative height (H_{tal}/H_{tri}); **Retro**, length of the retro-molar space; **W**, width; (), talonid dimensions; [], estimated length; ~, incomplete specimen; *, based on alveoli dimensions.

ARTIGO 5

Systematic and trophic diversity of protodidelphines (Mammalia, Marsupialia, Protodidelphidae): evidence of a short time diversification during the onset of the Eocene

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Abstract. The Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil, preserved an early Eocene vertebrate assemblage. Among its representatives, Metatheria comprises its most diverse clade, with at least 29 genera and 43 species. Among large- to very large-sized taxa, protodidelphids are represented by *Protodidelphis vanzolinii*, *P. mastodontoides*, and *Carolocoutoia ferigoloi*. *Protodidelphis mastodontoides* was initially considered a different genus, *Robertbutleria*; however, the synonymy of *Robertbutleria* with *Protodidelphis* has never been tested. A phylogenetic analysis recovered *Robertbutleria* as the sister taxon of *Carolocoutoia* and not *Protodidelphis*. *Robertbutleria* and *Carolocoutoia* share the presence of rounded upper molars, evident bunodonty, rounded postmetacrista, U-shaped protocone, asymmetric placement of m4, obliquely oriented p1-3, and absence of diastemata. The analysis recovered that the dental features considered for the synonymy of *Robertbutleria* with *Protodidelphis* represented plesiomorphies for Protodidelphidae (e.g., sinuous crest between StB and StD, marked increase in the size of the molars from M/m1 to M/m3). Based on the results, an emended diagnosis of Protodidelphinae (the clade that includes *Protodidelphis*, *Robertbutleria*, and *Carolocoutoia*) is presented. Two principal component analyses (PCAs) recognized protodidelphine taxa in different morphospaces, indicating differential allometric and morphofunctional patterns. *Protodidelphis* was a generalized frugivore, *Robertbutleria* was a fibrous frugivore, and *Carolocoutoia* was a turgent frugivore. Moreover, the similar morphological and morphofunctional indexes of protodidelphines suggest a “short time” evolutionary diversification for this clade, and that trophic specializations do not necessarily require great morphological changes, allowing the sympatric co-existence of morphologically similar ingroup genera.

Keywords: Didelphimorphia; Itaboraí Basin; Itaboraiense SALMA; Marsupialia; Paleocene-Eocene Thermal Maximum; Paleoecology

1. Introduction

The Itaboraí Basin, Municipality of Itaboraí, Rio de Janeiro state, Brazil (22° 50' 20" S; 42° 52' 30" W) dated as early Eocene in age (Ypresian Stage, Itaboraiense SALMA; see Woodburne et al., 2014) is one of the smallest sedimentary basins from Brazil (Bergqvist et al., 2009). However, despite its small dimensions, this locality has preserved one of the most diverse faunas with metatherians known so far, with at least 29 genera and 43 species (Carneiro et al., 2024a).

Among them, large- to very-large taxa (large-sized: between 1 kg and 3.3 kg; very large-sized: between 3.3 kg and 10 kg; sensu Carneiro et al., 2024a) were represented by four major clades: Polydolopimorphia, Protodidelphidae, Sternbergiidae, and Sparassodonta (see, e.g., Carneiro and Oliveira, 2023; Carneiro et al., 2024a). Protodidelphids represented the most abundant frugivorous metatherians from the Itaboraí Basin (see, e.g., Oliveira and Goin, 2011; Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023), with three taxa identified for these size categories: *Protodidelphis vanzolinii* Paula Couto, 1952; *Protodidelphis mastodontoides* (Marshall, 1987), and *Carolocoutoia ferigoloi* Goin et al., 1998. Considering these three taxa, *Protodidelphis mastodontoides* was initially assigned to another genus, *Robertbutleria* (Marshall, 1987).

Marshall (1987) described *Robertbutleria* based on two isolated upper molars (MCT.M.896(a), a left M1, and MCT.M.896(b), a left M2). He initially recognized this taxon as a member of Caroloameghiniinae based on the presence of a bunodont crown and upper molars with a rounded shape. Nevertheless, years later, Marshall et al. (1990) regrouped *Robertbutleria* within Protodidelphidae. Goin et al. (1998) considered *Robertbutleria* as the sister taxon of *Carolocoutoia* based on sharing inflated and wrinkled upper molars. Later, Oliveira and Goin (2011) considered *Robertbutleria* a junior synonym of *Protodidelphis* based on their abrupt increase in the size of upper/lower molar series, presence of a zigzag

crest between StB and StD, and protodidelphid (and not caroloameghiniid) affinities. These authors observed that the abrupt increase in the size of the upper/lower molar series is a synapomorphy of Protodidelphidae and that the presence of a zigzag crest between StB and StD is observable in *Protodidelphis*, *Robertbutleria* (for them, *Protodidelphis mastodontoides*), and *Carolocoutoia*.

Marshall (1987) and Goin et al. (1998) identified some dental features (e.g., rounded upper molars shape, comparatively more bunodont crown) that differ *Robertbutleria* from *Protodidelphis*. However, Oliveira and Goin (2011) have not considered or discussed these features in the concept of synonymizing *Robertbutleria* with *Protodidelphis*. Similarly, Carneiro (2023 [unpublished data]) identified other dental and jaw features shared between *Robertbutleria* and *Carolocoutoia* but not *Protodidelphis*. Consequently, Carneiro (2023 [unpublished data]) concluded that the synonymizing of *Robertbutleria* with *Protodidelphis* has yet to be discussed in detail, as it was never tested in phylogenetic analyses.

In summary, the taxonomic validity of *Robertbutleria* and its systematic affinities are reviewed. In addition, the systematic and trophic evolutionary contexts of Itaboraí's protodidelphids are also discussed.

Institutional Abbreviations. **AMNH**, American Museum of Natural History, New York, NY, USA; **MCN-PV**, Coleção de Paleovertebrados do Museu de Ciências Naturais da Secretaria de Meio Ambiente (SEMA; former Fundação Zoobotânica do Rio Grande do Sul), Porto Alegre, RS, Brazil; **MCT**, Museu de Ciências da Terra, Serviço Geológico do Brasil (MCTer-SGB), Rio de Janeiro, RJ, Brazil; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil; **UFRJ-DG**, Coleção de Macrofósseis do Departamento de Geologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil.

Other Abbreviations. **A**, area; **Ang**, angle; **BM**, body mass; **ch**, character; **DHm3-4**, dentary height below m3-4; **dt**, diastema(ta); **EECO**, Early Eocene Climatic Optimum; **ent**, entoconid;

H, height; **L**, length; **Lm1-4**, length of the lower molar series; **M/m**, upper/lower molars with the numbers corresponding to its positioning (M/m1-4); **MEL**, relative distance between metaconid's and entoconid's apices by the lower molar length ($L_{met-ent}/L_{mx}$); **met**, metaconid; **MPT**, most parsimonious tree; **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **PCA**, Principal Component Analysis; **PETM**, Paleocene-Eocene Thermal Maximum; **R**, ratio; **ra**, relative area (A_{tal}/A_{tri}); **RDS**, relative dentary shape (DH_{m3-4}/L_{m1-4}); **RGA**, relative grinding area ($\sqrt{A_{tal}/L_{tri}}$); **rh**, relative height (H_{tal}/H_{tri}); **RPM**, relative length of the anterior part of the dentary ($L_{p1-3+dt}/L_{m1-4}$); **SALMA**, South American Land Mammal Age; **SEM**, scanning electron microscope; **tal**, talonid; **tri**, trigonid; **W**, width.

2. Materials and methods

2.1 Study site

The Itaboraí Basin is in the Municipality of Itaboraí, Rio de Janeiro, in southeastern Brazil, with geographical coordinates 22° 45' 9.9144" S, 42° 51' 53.5536" W (Fig. 1a). For more data about the Itaboraí Basin, see Bergqvist et al. (2009), and Rangel et al. (2023a).

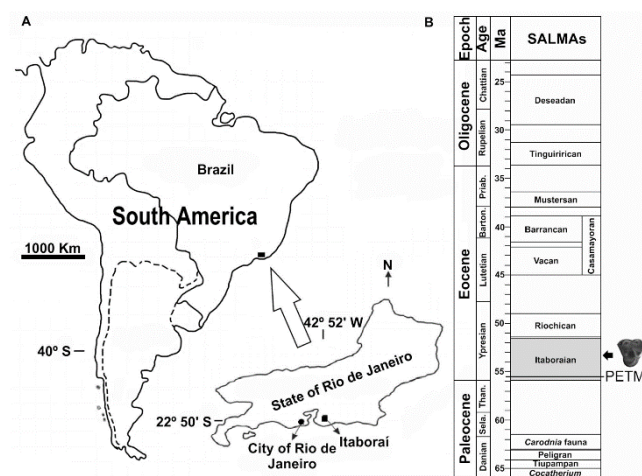


Fig. 1 The Itaboraí fauna: locality and biochron. **a**, Map showing the region and the coordinates of the Itaboraí

Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (22° 45' 9'' S; 42° 51' 53'' W). **b**, The stratigraphic relationships of the Itaboraiense SALMA with other Paleogene SALMAs. A plausible age range for the Itaboraí SALMA is highlighted in grey (see Carneiro and Oliveira, 2023). The occurrence of *Robertbutleria mastodontoidea* Marshall, 1987 is suggested by a black arrow and the SEM image of specimen MCT.M.896 (holotype), a left M1. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 1000 Km.

2.2 Studied specimens

All studied specimens are from the Itaboraí Basin, Municipality of Itaboraí (Fig. 1). The studied specimens are housed in MCN-PV, MCT (former DGM), MN, and UFRJ-DG collections. A list of studied specimens is presented as supplementary material (Appendix 1).

The metatherian fauna from the Itaboraí Basin is represented by almost 1000 specimens (considering only specimens represented by teeth, jaws, and maxillae; see, e.g., Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023; Carneiro et al., 2024a). This elevated number of specimens allows the recognition of taxa's dental and jaw patterns, intraspecific phenotypic plasticity, size span, and systematic affinities (Carneiro et al., 2024a). However, more than 10000 vertebrate specimens from this locality have never been studied at any level (Carneiro et al., 2024a, 2024b).

The digital images of MCT's specimens were made with a Zeiss Stemi 508 Greenough Stereo Microscope with an Axiocam 208 camera. The SEM images were performed with JEOL JSM-6390LV at the Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional (MN), Rio de Janeiro, RJ, Brazil; JEOL 6060 SEM at the Centro de Microscopia Eletrônica, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil; and JEOL JSM-6510LV at the Instituto de Química, Universidade Estadual do Rio de Janeiro (UERJ), Rio de Janeiro, RJ, Brazil.

The estimated body masses of studied taxa and the size classification considered for

Itaboraí's metatherians were taken from Carneiro et al. (2024a). All measurements of studied specimens are presented as supplementary material (Appendix 2).

2.3 Principal Component Analyses

To recognize different allometric/morphometric patterns between the species of protodidelphines from Itaboraí (*Carolocoutoia ferigoloi* Goin et al., 1998; *Protodidelphis vanzolinii* Paula Couto, 1952; *Robertbutleria mastodontoidea* Marshall, 1987), we performed a Principal Component Analysis (PCA) based on five parameters (**L** = lower molar length; **Ltal** = talonid length; **Ltri** = trigonid length; **Wtal** = talonid width; and **Wtri** = trigonid width) measured from the lower molars of these taxa. The included teeth were identified by their type of molar locus (m1, m2, m3, or m4; see scores in Appendix 2). A second PCA was performed based on eight morphofunctional indexes, plotting the mean per variable in the biplot. These PCA analyses were performed on the R environment (R core team, 2013), and the datasets and the R script are presented as supplementary material (Appendices 2 and 7, respectively).

2.4 Phylogenetic analysis

The phylogenetic analysis was based on a morphological data matrix that comprises 729 characters (318 dental, 24 jaw, 183 cranial, 201 postcranial) and 72 therian taxa, including 64 metatherians (represented by genera), from the Cretaceous and Cenozoic of North America, Asia, South America, Antarctic, Europe, and Australia. The 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 100 replications. Absolute Bremer supports and tree scores

were calculated with TNT 1.5. The list of characters, characters by taxon, and synapomorphies are presented as supplementary material (Appendices 3-5).

3. Systematic Paleontology

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

Marsupialiformes Vullo et al., 2009

Sudameridelphia (Szalay, 1994) sensu Carneiro and Oliveira, 2023

Notometatheria (Kirsch et al., 1997) sensu Oliveira et al., 2021

Marsupialia Illiger, 1811

Didelphimorphia Gill, 1872 sensu Carneiro et al., 2024c

†Protodidelphidae Marshall, Case, and Woodburne, 1990 sensu Goin et al., 1998

†Protodidelphinae Marshall, 1987

Emended diagnosis. Differs from *Guggenheimia* in having larger dimensions, more evident bunodont crown, upper molars (M2-3) not mesiodistally compressed (M2-3 mesiodistally compressed in *Guggenheimia*), absence of StC (StC variably present in *Guggenheimia*; see Oliveira and Goin, 2011), more labiolingually compressed and mesiodistally expanded protoconal basin (broader and narrower in *Guggenheimia*), more mesiodistally compressed trigonid on m2-3 (more mesially extended in *Guggenheimia*), and pyramidal-shaped entoconids (conical entoconids in *Guggenheimia*).

Genotype. *Protodidelphis* Paula Couto, 1952.

Included taxa. *Carolocoutoia* Goin et al, 1998; *Protodidelphis*; *Robertbutleria* Marshall, 1987.

Remarks. Protodidelphines were among the largest and most abundant frugivorous metatherians during the early Eocene and early middle Eocene (Itaboraiense to Riochican SALMAs; see, e.g., Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023),

representing guide fossils from the early Eocene (Itaboraiense SALMA) to early middle Eocene South American faunas (see Zimicz, 2012 [unpublished data]). These taxa are known as the oldest didelphimorphians (Goin et al., 1998; Carneiro, 2019; Carneiro and Oliveira, 2023; Carneiro et al., 2024c).

†*Robertbutleria* Marshall, 1987

†*Robertbutleria* MARSHALL, 1987: p. 122.

†*Protodidelphis* OLIVEIRA e GOIN, 2011: p. 114.

(Fig. 2)

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Emended diagnosis. Large (sensu Carneiro et al., 2024a) South American Eocene protodidelphid with estimated body mass between 2.57 kg and 2.82 kg. Differs from other protodidelphines in having rounded/ovoid-like upper molars, marked bunodont crown, well-developed labial and protoconal cingula (mesial and distal protoconal cingula) on M1-3, presence of enamel supernumerary cuspules (i.e., crenulations or thickened enamel structures similar to cuspules in different parts of the molars [e.g., on labial cingulum, distal to the metaconule, mesio basal to the hypoconid]), U-shaped protocone, talonids more developed than trigonids, and talonid basin with wrinkled/crenulated enamel.

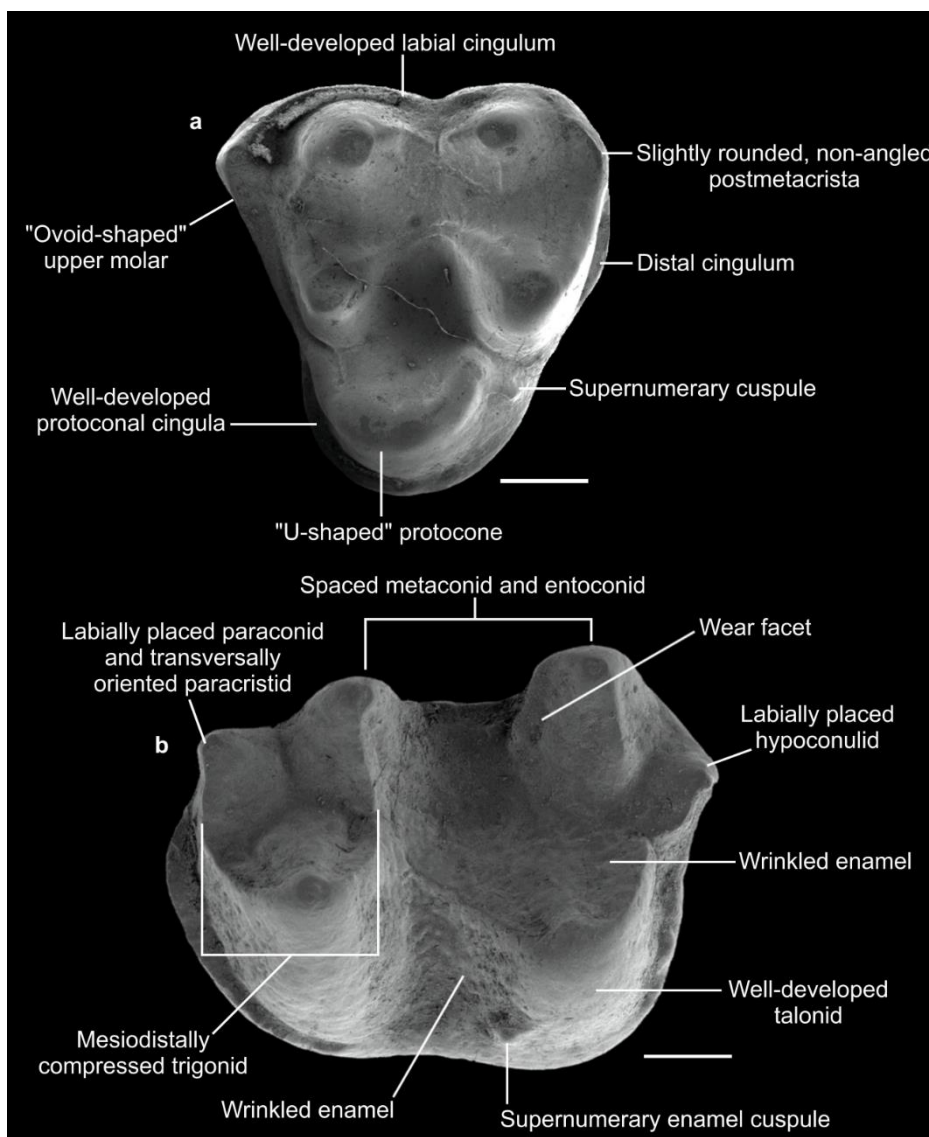


Fig. 2 Diagnostic combination of features of *Robertbutleria* Marshall, 1987. SEM images of specimens: **a**, MCT.M.896, holotype, left M1 in occlusal view; **b**, MCN-PV 1819, left m3 in occluso-labial view. Scale bars = 1 mm.

Type species. *Robertbutleria mastodontoidea* Marshall, 1987.

Included species. The type only.

Type Locality and Horizon. Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al., 2009). Early Eocene, Ypresian Stage, Itaboraiense SALMA (sensu Woodburne et al., 2014); Cerro Pan de Azúcar, Chubut, Argentina (Chornogubsky et al., 2023). Early-middle Eocene, Ypresian to Lutetian Stages, Riochican SALMA (sensu Chornogubsky

et al., 2023).

Comparisons. *Robertbutleria* differs from *Protodidelphis* (Fig. 3) in having more inflated crown (i.e., bunodont), thicker and more wrinkled enamel layer, rounded/ovoid upper molars (subtriangular in *Protodidelphis*), rounded postmetacrista with no distolabial angle/metastylar wing (metastylar wing/distolabial angle of the postmetacrista present in *Protodidelphis*, especially on M1), U-shaped and non-recumbent protocone (V-shaped and recumbent protocone in *Protodidelphis*), wrinkled enamel on the talonid basin and labial cingulum (condition absent in *Protodidelphis*), talonids more developed, entoconid more spaced/separated from the metaconid (average MEL value: 0.46; *Protodidelphis vanzolinii*: average MEL value: 0.49), hypoconulid labially placed to the entoconid (hypoconulid distolingual to the entoconid in *Protodidelphis*), m4 asymmetrically placed (i.e., the posterior alveolus/root is in a more cranial placement than the anterior alveolus/root; condition absent or reduced in *Protodidelphis*), obliquely oriented premolars (premolars aligned to the premolar/molar axis in *Protodidelphis*), and absence of diastemata (presence of a diastema between p1 and p2 in *Protodidelphis*).

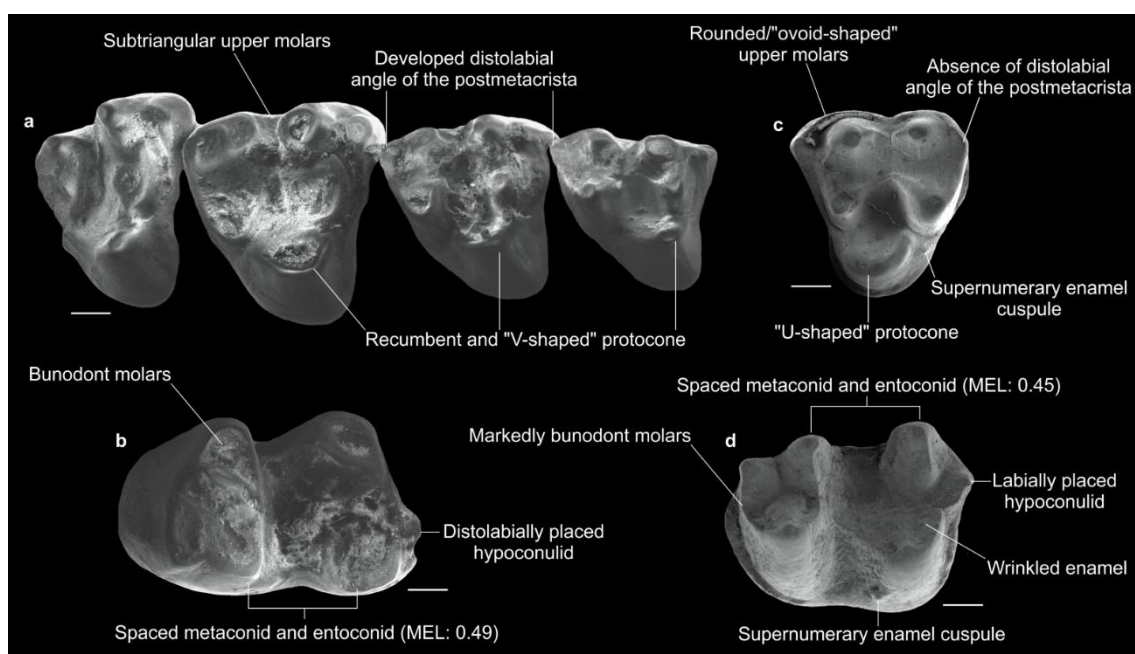


Fig. 3

Comparative upper molar differences between *Robertbutleria* Marshall, 1987 and *Protodidelphis* Paula Couto,

1952. *Protodidelphis vanzolinii* Paula Couto, 1952: **a**, MCT.M.303, right maxilla with M1-4 in occluso-lingual view; **b**, MCT.M.250, a right dentary with p3, m1, m3-4, and alveoli of m2, showing the m3 in occlusal view; *Robertbutleria mastodontoidea* Marshall, 1987: **c**, MCT.M.896 (holotype), left M1 in occlusal view; **d**, MCN-PV 1819, left m3 in occluso-labial view. Scale bars = 1 mm.

Differs from *Carolocoutoia* (Fig. 4) in having a smaller size, less bunodont and wrinkled crown, less ovoid-shaped upper molars, presence of labial cingulum (condition absent in *Carolocoutoia*; in this taxon, the labial border is basally expanded), reduced distolingual crest of StD (well-developed distolingual of StD in *Carolocoutoia*), developed preparacrista and mesiolingual crest of StB (reduced preparacrista and mesiolingual crest of StB absent in *Carolocoutoia*), longer and slightly curved postmetacrista (shorter and markedly curved postmetacrista in *Carolocoutoia*), developed protoconal basin (reduced protoconal basin in *Carolocoutoia*), presence of supernumerary enamel cusps (condition absent in *Carolocoutoia*), precingulid basally placed than the trigonid basin (precingulid almost at the same level as the reduced trigonid basin in *Carolocoutoia*), trigonid cusps not rounded in shape (trigonid cusps rounded/spire-like in shape in *Carolocoutoia*), talonid longer and broader than the trigonid on m2-3 (talonid shorter and slightly narrower than the trigonid in *Carolocoutoia*), presence of wrinkled enamel in the talonid basin and hypoflexid (condition absent in *Carolocoutoia*), pyramidal entoconid (labiolingually compressed entoconid in *Carolocoutoia*), absence of supernumerary cups in the talonid basin (condition present in *Carolocoutoia*).

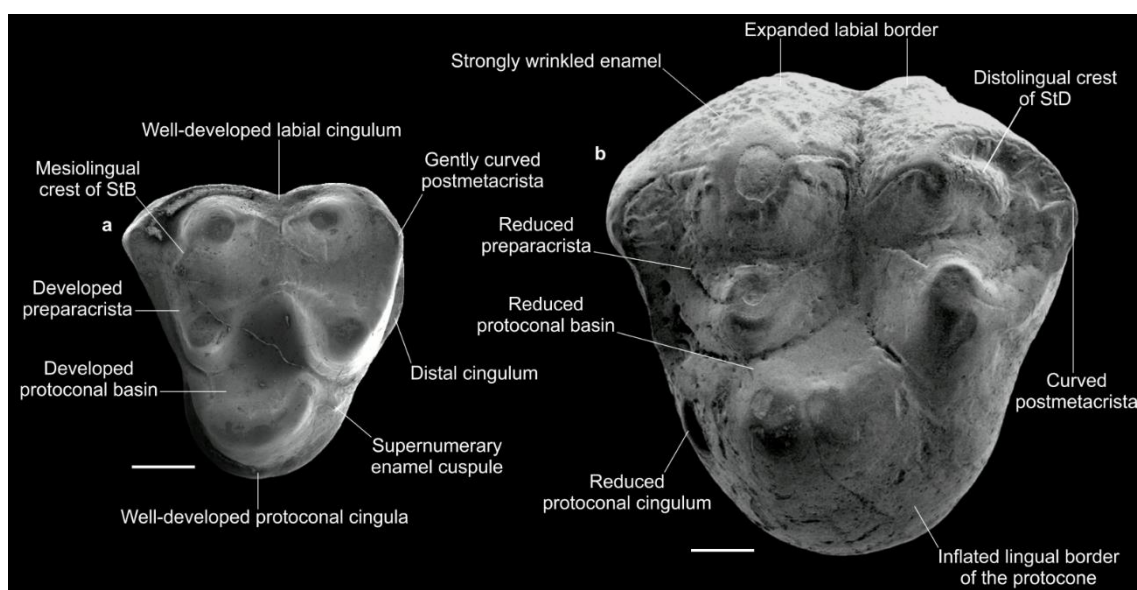


Fig. 4

Comparative upper molar differences between *Robertbutleria* Marshall, 1987 and *Carolocoutoia* Goin et al., 1998. *Robertbutleria mastodontoidea* Marshall, 1987: **a**, MCT.M.896 (holotype), left M1 in occlusal view; *Carolocoutoia ferigoloi* Goin et al., 1998: **b**, MCN-PV 1802 (holotype), a left M3 in occlusal view. Scale bars = 1 mm.

Remarks. Marshall (1987) initially identified *Robertbutleria* as a member of Caroloameghiniidae, sharing close affinities with *Glasbius*. Marshall mentioned that these two taxa are quite similar, differing only on a few features (e.g., larger size, more inflated crown, absence of StC, and less developed crests and conules in *Robertbutleria*). In this way, Marshall concluded that the differences observed represent different degrees of development or relative expression of these features between these two taxa. Ultimately, these numerous similarities led him to consider *Glasbius* as an ideal ancestor of *Robertbutleria*.

Later, Marshall et al. (1990) included *Robertbutleria* within Protodidelphidae with *Bobbschaefferia*, *Guggenheimia*, and *Protodidelphis*. Goin et al. (1998) agreed with the protodidelphid affinities for *Robertbutleria* and considered it the sister taxon of *Carolocoutoia*. Furthermore, Oliveira and Goin (2011) considered *Robertbutleria* a junior synonym of *Protodidelphis* (see discussion below).

†*Robertbutleria mastodontoidea* Marshall, 1987

†*Robertbutleria mastodontoidea* MARSHALL, 1987: 123, figs. 39.

†*Robertbutleria mastodontoidea* GOIN et al, 1998: p. 155, plate 1b.

†*Protodidelphis mastodontoides* OLIVEIRA, 1998: p. 209, figs. 88a-d.

†*Protodidelphis mastodontoides* OLIVEIRA e GOIN, 2011: p. 114, figs. 9A-E.

†*Protodidelphis mastodontoides* CARNEIRO, 2019: p. 6, fig. 3d.

†*Protodidelphis mastodontoides* CARNEIRO e OLIVEIRA, 2023: p. 307, fig. 16c-d.

(Figs. 5-6)

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Emended diagnosis. As for the genus (defined by monotypy).

Holotype. MCT.M.896 (ex-MCT.M.896(a)), left M1 (Fig. 5a-c).

Hypodigm. The holotype; AMNH 49858, fragment of a left dentary with p2-3, m1-2, and alveoli of p1 (partially preserved); MCN-PV 1799, left DP3; MCN-PV 1806, left M3 (Fig. 5d); MCN-PV 1816, left m3 (Fig. 5i); MCN-PV 1817, left m3 without entoconid (Fig. 5j); MCN-PV 1819, left m3 (Fig. 5k); MCN-PV 1820, left m4 (Fig. 5l); MCT.M.215, posterior fragment of an edentulous left dentary with alveoli of m2-4, damaged alveoli of m1, and base of the coronoid process with preserved mandibular foramen (Fig. 6a-c); MCT.M.2769 (ex-DGM 896(b)-M), left M2; MCT.M.2817, left m1 with posterior root; MCT.M.2818, left m2; MCT.M.2819, left m2 (Fig. 5e-h); MN 2897(b)-V, right M2; MN 2897(c)-V, right M3; MN 2898-V, left m2; UFRJ-DG 1195-M, left edentulous dentary with alveoli of p2-m4, posterior alveolus of p1 (anterior alveolus partially preserved), and anterior part of the coronoid process (Fig. 6d-f).

Locality and age. Most studied specimens were collected in the fissure explored in 1949 (see Bergqvist et al., 2009); and specimen UFRJ-DG 1195-M has no stratigraphic context (no date). Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al., 2009). Early Eocene, Ypresian Stage, Itaboraiense SALMA (sensu Woodburne et al., 2014).

Description. DP3 (MCN-PV 1799). The crown is very inflated. This tooth is much longer

than wide. The stylar shelf is reduced on its mesial lobe and narrow (i.e., less than 33% of the molar labiolingual width; sensu Ladevèze et al., 2020) on its distal lobe (i.e., asymmetrical stylar shelf). The labial edge of the crown is basally expanded, forming a slender labial cingulum, which has small crenulations labially positioned to the mesiolingual crest of StD. The parastyle is moderately developed and is in a slightly lingual position to StB, being much more labial than the apex of the paracone. StA is reduced. StB is extremely compressed labiolingually, reduced in height, and slightly oriented on a mesiolingual/distolabial axis. StB displays two crests: the mesiolabial and the mesiolingual, lacking the distolingual crest. StC is absent. StD is well developed and is the largest stylar cusp. This cusp is conical and hypertrophied, with its lingual base in contact with the labial edge of the metacone. StD has a marked apical wear facet. The StD has a well-developed mesiolabial crest, which runs mesiolingually, contacting the apex of the paracone. Labially to the paracone, this crest has two reduced enamel elevations similar to cusps, which display apical wear facet. The preparacrista is labially directed, being in contact with the mesiolingual crest of the StB (the point of contact between these two shows slight inflation with signs of apical wear), and is relatively long, being much smaller than the postmetacrista (ca. 2x). The postmetacrista is slightly oblique and ends in a marked distolabial angle. The centrocrista is low, open (i.e., the postparacrista and premetacrista have no point of contact; sensu Goin and Candela, 2004) and invasive (sensu Carneiro and Oliveira, 2023) on the stylar shelf. The postparacrista reaches, at its most labial point, the mesial crest of StD, and the preparacrista reaches the mesiolingual border of StD. The paracone is smaller (ca. 2x) and more labially positioned than the metacone. The paracone and metacone have flat labial edges (i.e. pyramidal shape; sensu Case et al., 2005) and are separated (i.e. protofossa present). The protofossa is relatively broad. The protocone basin is longer than it is wide. The paraconule is vestigial, and the metaconule is slightly developed and pyramidal, with a low internal crest (i.e., premetaconular crest). The protocone is moderate in length (i.e., similar to the metacone;

sensu Engelman et al., 2020) and eccentric (i.e., aligned with the apices of the paracone and StB; sensu Oliveira and Goin, 2011). The postprotocrista is slightly longer than the preprotocrista. The protocone has an apical wear facet, and the protocristae have wear facets, especially the preprotocrista. The protoconal cingulids are well developed but not merged. The paracingulum is long (i.e., it reaches the protoconal basin; sensu Carneiro et al., 2018), and the metacingulum is absent. The most pronounced wear facets of the molar are observed on the preprotocrista as well as the apices of StD and the protocone.

M1 (MCT.M.896 [holotype]; Fig. 5a-c). This tooth is wider than long. The styler shelf is moderate (i.e., between 33% and 50% of the width of the molar; sensu Ladevèze et al., 2020), with the mesial and distal lobes being subequal in width. The labial cingulum is markedly developed, with an enamel cusp-like elevation labially positioned to the mesial edge of StD. The ectoflexus is shallow and central. The parastyle is moderate, and StA is slightly lingual compared to StB. StA is moderately developed. StB is conical and hypertrophied, being the largest of the styler cusps. This cusp lacks a mesiolabial crest but displays mesiolingual and distolabial crests. The latter is more inflated in its mesialmost part (i.e., immediately distal to the apex of StB). StB is nearly labially aligned with the apex of the paracone, which is subequal in size but shorter than StB. StC is absent. StD is relatively conical, with a slightly flat labial edge, and is well developed. This cusp is nearly subequal in size to the paracone. The StD has a relatively low middle crest. The distolabial crest of StB and the mesiolabial crest of StD have a straight trajectory but are not in contact, resulting in a notch between them. StE is poorly developed, markedly mesiodistally compressed, and is lingually positioned compared to the other styler cusps. The following pattern is observed in order of size: StB > StD > StA > StE. The preparacrista is short and labially oriented towards StB, contacting the mesiolingual crest of the latter. The postmetacrista is much longer than the preparacrista (ca. 3x). The distolabial angle of the postmetacrista is absent (i.e., this crest has a rounded shape/trajectory). The centrocrista is slightly dilambdodont, relatively low, and

practically non-invasive on the stylar shelf. The premetacrista has a more labial position than the postparacrista due to the larger size and more labial position of the metacone than the paracone. The paracone is smaller than the metacone (ca. 2x) and is in a slightly lingual position to the latter. The bases of the paracone and metacone are practically aligned lingually, their labial edges are labiolingually compressed, and they are separated (i.e., protofossa present). The paraconule is absent, and the metaconule is recognized by a small enamel crestless elevation, which is lingually positioned at the base of the metacone. A fissure separates the metaconule from the lingual edge of the metacone. The protocone is moderate in length (sensu Engelman et al., 2020), U-shaped (i.e., slightly bulged), and mesially oriented but not eccentric. The postprotocrista is slightly more curved than the preprotocrista and slightly longer than the latter. The postprotocrista is oriented towards the mediolingual edge of the metacone (i.e., internal contact of the postprotocrista; sensu Carneiro, 2019). A well-developed protoconal cingulum is present on the mesial and distal edges of the protocone. An elevation of enamel is identified distal to the metaconule (i.e., enamel supernumerary cuspule). The paracingulum is long, and the metacingulum is absent. A distal cingulum (i.e., basal cingular expansion of the crown distal to the metacone and not continuous with the postprotocrista/postmetaconular crests) is developed. The specimen MCT.M.896 (holotype) displays evidence of an initial apical wear stage, with observable wear facets more evident on its lingual edge (i.e., protocone and protocristae).

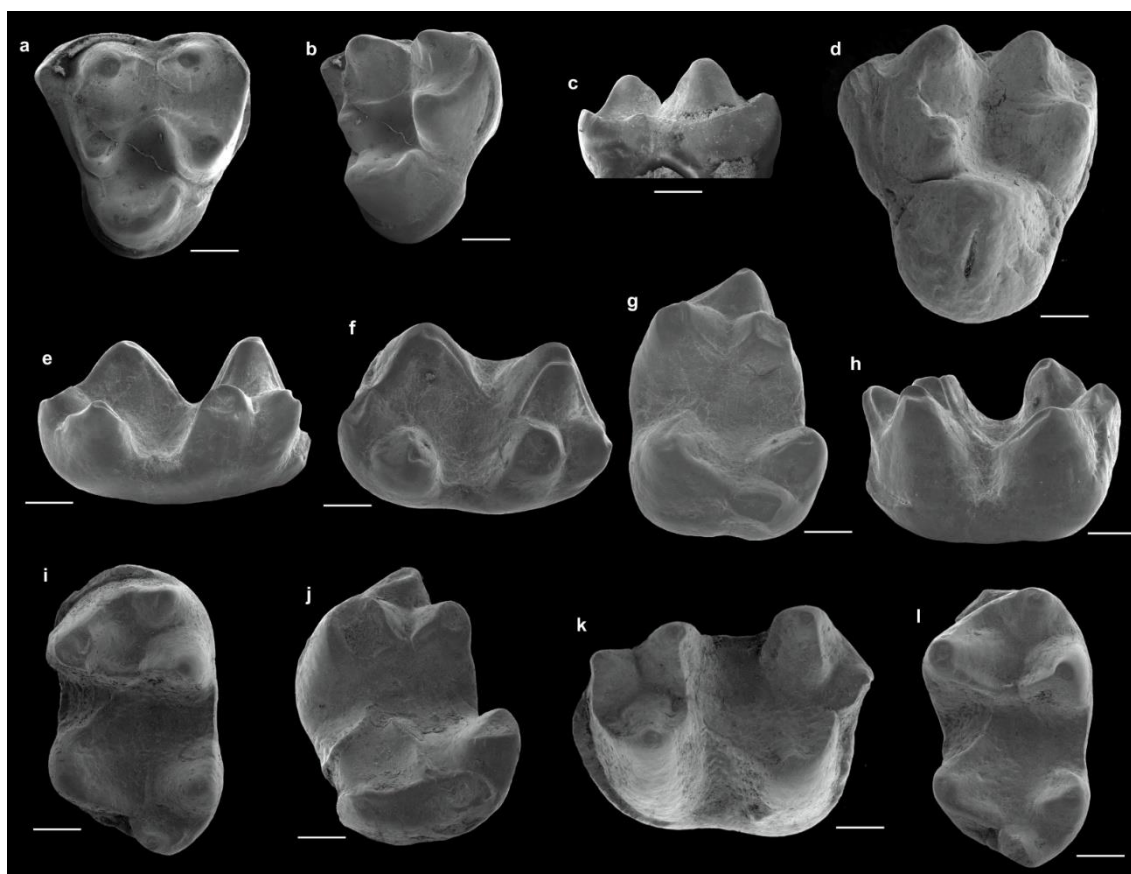


Fig. 5

Isolated molars of *Robertbutleria mastodontoidea* Marshall, 1987. MCT.M.896, holotype, left M1 in (a) occlusal, (b) distal, and (c) labial views; d, MCN-PV 1806, left M3 in occluso-lingual view; MCT.M.2819, left m2 in (e) lingual, (f) occlusal, (g) occluso-distal, and (h) labial views; i, MCN-PV 1816, left m3 in occlusal view; j, MCN-PV 1817, left m3 in occluso-distal view; k, MCN-PV 1819, left m3 in occluso-labial view; l, MCN-PV 1820, left m4 in occlusal view. Scale bars = 1 mm.

M2 (MCT.M.2769 [ex-MCT.M.896(b)], MN 2897(b)-V). M2 differs from M1 and is identified by the following features: this molar is slightly longer than wide. The styler shelf is moderate, and the distal lobe is slightly broader than the mesial one. The labial cingulum presents slight crenulations, especially between the StB and StD. The notch between StB and StD is relatively deeper. StB is relatively more hypertrophied and has a slightly flatter labial border. StB has a more developed mesiolabial crest. The distolabial and mesiolabial crests have a slightly sinuous trajectory (a condition more evident in specimen MN 2897(b)-V). The middle crest of StD is developed in both specimens, being more developed in specimen MN

2897(b)-V. StE is relatively less developed. The postmetacrista is relatively shorter. The centrocrista is arch-shaped (=invasive U shape). The paracone is positioned labially to the metacone (MCT.M.2769 [ex-MCT.M.896(b)]) or transversely aligned to the latter (MN 2897(b)-V). The mesial portion of the protoconal basin (i.e., the portion lingual to the paracone) is relatively narrower than in M1; this condition is more marked in specimen MN 2897(b)-V. The metaconule is vestigial (MN 2897(b)-V) or reduced (MCT.M.2769 [ex-MCT.M.896(b)]). The protocone is more domed, presenting a more evident U shape. The postprotocrista is slightly longer than the preprotocrista. The postprotocrista is in contact with the mid-labial edge of the metacone (MN 2897(b)-V) or separated from it by a shallow fissure (MCT.M.2769 [ex-MCT.M.896(b)]). The protoconal cingulum is markedly developed (MN 2897(b)-V) or somewhat developed (MCT.M.2769 [ex-MCT.M.896(b)]), with the mesial and distal cingulum separated (i.e., protoconal cingulum not continuous/merged). The distal protoconal cingulum may be subequal (MN 2897(b)-V) or more developed (MCT.M.2769 [ex-MCT.M.896(b)]) than the mesial cingulum. Known M2s display a similar wear pattern to M1. The specimen MN 2897(b)-V presents a slightly more advanced wear stage than specimen MCT.M.2769 (ex-MCT.M.896(b)).

M3 (MCN-PV 1806 [Fig. 5d], MN 2897(c)-V). M3 differs from M1-2 and is identified by the following features: this molar is wider than long. The parastyle is relatively more reduced, being more developed in specimen MCN-PV 1806. StA is labially aligned with StB (MCN-PV 1806) or only slightly more lingual than the latter (MN 2897(c)-V). The StB is more markedly hypertrophied, especially in specimen MCN-PV 1806, which is massively developed. StD has a slightly more concave mesial edge than anterior molars. The middle crest of StD is relatively more developed. The distolabial crest of StB and the mesiolabial crest of StD have a straighter trajectory (i.e., lack a 'zigzag' shape). The preparacrista is relatively longer, especially in specimen MN 2897(c)-V, where it practically reaches StA and presents a more oblique trajectory. The postmetacrista is slightly longer than the preparacrista

(between 1.2-1.5x, with the smallest difference observed in specimen MN 2897(c)-V). The postmetacrista is more convex, especially in specimen MCN-PV 1806. The enamel is relatively more wrinkled in specimen MCN-PV 1806 than in specimen MN 2897(c)-V. The centrocrista is very low (a condition less evident in specimen MN 2897(c)-V) and practically open since the postparacrista and premetacrista are thinner and lower in their labial-most edges (especially in specimen MN 2897(c)-V). The paracone is in a position slightly more lingual (MCN-PV 1806) or slightly more labial (MN 2897(c)-V) than that of the metacone. The protofossa is comparatively longer than the anterior molars (i.e., comparatively more spaced paracone and metacone). The protocone is relatively more eccentric in specimen MCN-PV 1806. The postprotocrista is much longer than the preprotocrista, with this condition more evident in specimen MCN-PV 1806. The postprotocrista is in contact with the mediolingual edge of the metacone. The protoconal cinguli are well developed (more developed in specimen MCN-PV 1806) and not fused. The distal protoconal cingulum is slightly broader than the mesial one. The paracingulum is relatively thinner. The most marked wear facets of the molar are observed on the centrocrista and the lingual edge of the tooth (i.e., protocone and protoconal crests). However, the molars studied display a low level of wear, especially specimen MCN-PV 1806.

Dentary (AMNH 49858, MCT.M.215, UFRJ-DG 1195-M; Fig. 6). The dentary is moderately robust (RDS: 0.61). The mandibular symphysis is not fused and extends to the limit between the alveoli of p2-3. The portion of the dentary anterior to the p1 is unknown. The ventral edge of the dentary is convex, with its deepest point at the level of the m3. Two mental foramina are present: the anterior one, positioned ventrally to the anterior alveolus of p2 (UFRJ-DG 1195-M), and the posterior one, positioned ventrally to the posterior alveolus of m1 (UFRJ-DG 1195-M). The anterior foramen is not hypertrophied and is similar in size to the posterior one (UFRJ-DG 1195-M). No diastemata are observed between c-p1, p1-2, p2-3 and p3-m1. The premolar/molar series is practically straight (*sensu* Goin and Carlini, 1995) in

specimen UFRJ-DG 1195-M. The dentary displays a slight abrupt difference in height at the level of p3 (AMNH 49858) and m1 (UFRJ-DG 1195-M). The retro-molar space is reduced, as the dentary displays a gradual growth in height from m4 to the ascending branch of the coronoid process, in which the m4 is asymmetrically positioned in the dentary (i.e., the anterior alveolus is in a more ventral position than the posterior alveolus; see MCT.M.215, UFRJ-DG 1195-M). The increase in height of the dentary posterior to m4 is relatively longer and more oblique in specimen UFRJ-DG 1195-M. The posterior edge of the dentary ventral to the coronoid process is angled (*sensu* Muizon et al., 2018), with this condition more evident in specimen UFRJ-DG 1195-M). The coronoid process is partially preserved. The masseteric fossa is deep, and the ascending ramus of the coronoid process is almost vertical. The mandibular foramen appears to be positioned distal to the cranioventral axis of the coronoid process (MCT.M.215). The angular process is medially oriented (MCT.M.215). The mandibular condyle is unknown for the species.



Fig. 6

Dentaries of *Robertbutleria mastodontoidea* Marshall, 1987. MCT.M.215, posterior fragment of an edentulous left dentary with alveoli of m2-4, damaged alveoli of m1, and base of the coronoid process with preserved

mandibular foramen, in (a) labial, (b) occlusal, and (c) lingual views; UFRJ-DG 1195, left edentulous dentary with alveoli of p2-m4, posterior alveolus of p1 (anterior alveolus partially preserved), and anterior part of the coronoid process, in (d) labial, (e) occlusal, and (f) lingual views. Scale bars = 5 mm.

Lower premolars (AMNH 49858, UFRJ-DG 1195-M). p1 is known only from its alveoli. The p1 is the smallest of the premolars, much smaller than the p2. This tooth has a markedly oblique orientation concerning to the premolar/molar axis. The posterior alveolus of p1 is slightly smaller than the anterior alveolus of p2, but the anterior alveolus of p1 is much smaller than the posterior one (AMNH 49858). In specimen UFRJ-DG 1195-M, the posterior alveolus of p1 is much smaller than p2's anterior alveolus. p2 is known from specimen AMNH 49858. This tooth is obliquely oriented concerning the premolar/molar axis. The p2 is moderately smaller than the p3 and has an inflated crown, a small precingulid, and a distal cusp that is poorly developed and centrally placed. The main cusp is asymmetrical, as the mesial edge is more convex, and the distal edge is more obliquely oriented. The distobasal heel of p2 is short and broad (i.e., labiolingually well developed). The p3 is the largest of the premolars, being taller than the protoconid of the molars but shorter (in length) than the m1 (i.e., p3 is not hypertrophied). The p3 is obliquely oriented to the premolar/molar axis. The crown is markedly inflated. The p3 displays a precingulid, which forms a mesial expansion. This last feature is less developed than the p2 (in lingual view). The p3 displays a reduced labial cusp and a distolingually placed distal cusp, the latter being relatively more developed than that of p2. Known premolars do not present mesially extended marginal cingulids (i.e., precingulid and talonid basin are not fused/merged; sensu Carneiro and Oliveira, 2023). The premolar series shows a marked increase in size from p1 to p2-3.

m1 (AMNH 49858, MCT.M.2817). The trigonid is slightly taller, narrower, and shorter than the talonid. The trigonid is mesiodistally compressed. The talonid is wider than the trigonid due to a lingual inflation of the entoconid. The paraconid is the smallest cusp of the trigonid. This cusp is mesiodistally compressed and is in a slightly labial position to the

metaconid. The bases of the paraconid and metaconid are in contact. The metaconid is smaller than the protoconid and is slightly distal to the latter. The metaconid has a reduced postmetacristid. The protoconid is the largest cusp of the molar, displaying a mesiolingually oriented (i.e., angled) preprotocristid. The metacristid (i.e., postprotocristid + premetacristid) is transversely oriented, distally closing the trigonid. The cristid obliqua has a slightly labial contact (i.e., at the level of the protoconid's lingual base) with the trigonid's distal border. The hypoflexus is shallow (i.e., very little invasive in the talonid basin), and the labial cingulid is poorly developed. A mesiodistally oriented wear facet is observed between the metaconid and entoconid at the lingual edge of the talonid (this facet is more marked in specimen MCT.M.2817). The hypoconid is robust and does not protrude labially to the protoconid (in specimen MCT.M.2817, the hypoconid is slightly more labially salient than the protoconid). The posthypocristid is slightly obliquely oriented. The preentocristid is absent. The entoconid is pyramidal, transversely aligned with the hypoconid, and taller than the latter. The entoconid is inflated and expands lingually beyond the edge of the talonid. The postentocristid is absent (a distolabially oriented wear facet is present but should not be confused with a postentocristid). The hypoconulid is poorly developed, much lower than the entoconid, and slightly extended distally. This cusp is positioned distolabial to the entoconid. The precingulid is long (i.e., it reaches the protoconid; sensu Muizon et al., 2018), and the postcingulid is reduced. A poorly developed wear facet is present between the metaconid's distal edge and the entoconid's mesial edge. Apical wear facets can be observed, mainly at the apex of the molar cusps, being more evident in specimen AMNH 49858.

m2 (AMNH 49858, MCT.M.2818, MCT.M.2819 [Fig. 5e-h]; MN 2898-V). The m2 differs from the m1 and is identified by the following features: the trigonid is slightly taller (ca. 0.5x), much narrower, and shorter than the talonid. The trigonid is comparatively more mesiodistally compressed. The paraconid is mesiodistally compressed, and the paracristid is practically transverse. The metaconid is distally positioned to the protoconid. The

postmetacristid is practically absent. The preprotocristid is more angled, presenting a comparatively more convex trajectory than the paracristid. The talonid basin and hypoflexus enamel are wrinkled (easily seen in specimen MCT.M.2818 due to its metallization). The hypoflexus is more invasive in the talonid basin, and the labial cingulid is tenuous, long, and fused to the postcingulid. A supernumerary cusp at the mesiolabial base of the hypoconid may be absent (MCT.M.2818) or reduced (MCT.M.2819). The entoconid is relatively well away from the distal edge of the protoconid and in a more distal position to the hypoconid. The hypoconulid is labially positioned to the entoconid. The postcingulid is well developed. The oblique ridge and posthypocristid are the most worn ridges, while all cusps display early apical wear. All cusps display apical wear, but specimen AMNH 49858 is the most worn.

m3 (MCN-PV 1816, MCN-PV 1817, MCN-PV 1819; Fig. 5j-k). The m3 differs from the m1-2 and is identified by the following features: the m3 has a somewhat more elongated morphology than the m1-2. The trigonid is much shorter than the talonid. The hypoconid may be less labially salient (MCN-PV 1816), as broad as (MCN-PV 1817), or broader (MCN-PV 1819) than the trigonid. The trigonid is relatively more compressed mesiodistally, resulting in greater contact between the bases of the paraconid and metaconid. The paraconid is very compressed mesiodistally, well developed labiolingually, and very short mesiodistally (in occlusal view), presenting a semi-lunar shape. The paraconid is more labially positioned than the metaconid. The metaconid is almost transversely aligned (MCN-PV 1816) or slightly distal to the protoconid (MCN-PV 1817, MCN-PV 1819). The postmetacristid is reduced. The enamel of the talonid basin is wrinkled (MCN-PV 1816, MCN-PV 1819). The oblique crest presents little labial contact with the distal edge of the trigonid (at the level of the lingual base of the protoconid), so the hypoflexid is invasive in the talonid basin. A basal cusp at the mesiolabial angle of the hypoconid may be absent (MCN-PV 1817), reduced (MCN-PV 1816), or developed (MCN-PV 1819). The posthypocristid displays a practically transversal (MCN-PV 1817) or slightly oblique trajectory (MCN-PV 1816, MCN-PV 1819). The

entoconid is slightly distal to the hypoconid (MCN-PV 1817) or distal (MCN-PV 1816, MCN-PV 1819) to the hypoconid. A marked wear facet between the metaconid and entoconid on the lingual edge can be observed in MCN-PV 1816 and MCN-PV 1819. The postcingulid is poorly developed (MCN-PV 1817) or well-developed (MCN-PV 1816, MCN-PV 1819).

m4 (MCN-PV 1820; Fig. 5l). The m4 differs from the m1-3 and is identified by the following features: the trigonid is relatively taller (ca. 0.5x), slightly wider, and shorter than the talonid. The trigonid is relatively less compressed mesiodistally. The paraconid is relatively more developed, slightly smaller than the metaconid, and more mesially oriented. The metaconid is slightly distal to the protoconid. The protoconid is relatively more labially salient. The enamel of the talonid basin and hypoflexus is wrinkled. The cristid obliqua displays a contact with the distal edge of the trigonid slightly labial to the fissure of the metacristid. The labial cingulid is long and fused to the postcingulid. The posthypocristid is relatively shorter and is slightly oblique. The wear facet between the metaconid and the entoconid is well-developed. The entoconid has a markedly inflated lingual edge and is well-spaced from the metaconid's distal edge. The hypoconulid is more labiolingually developed, distally oriented, and taller. The hypoconulid is lingually positioned. The postcingulid is short. The metacristid (in particular, the postprotocristid) and the lingual wear mark between the metaconid and entoconid represent the main wear facets of the molar.

Measurements. See Table 1.

Table 1 Dental measurements (in mm) of *Robertbutleria mastodontoidea* Marshall, 1987. The holotype is highlighted in bold. Measurements of specimen MN 2898-V are based on Paula Couto (1970). For lower molars, the measurements are expressed in the following order: [precingulid length], trigonid length, (talonid dimensions – length or width), and – total length. **DP**, deciduous third premolar; **L**, length; **M/m**, upper/lower molar; **P/p**, upper/lower premolar;

W, width; ~, incomplete specimen; *, based on alveoli dimensions.

	L	W	L	W	L	W	L	W	LM1	W	LM2	W	LM3	W	LM4	W	M
	P	P	P	P	D	D	P	P		M1		M2		M3		M	1
	1	1	2	2	P3	P	3	3								4	-
						3											4
M																	
CT																	
.M									4.13	4.2							
.89										1							
6																	
M																	
CN							3										
-					3.	.											
PV					94	3											
17						6											
99																	
M																	
CN																	
-													5.63	5.6			
PV														3			
18																	
06																	
M																	
CT																	
.M.										4.64		4.6					
27												6					
69																	
M																	
N																	
28												5.3					
97(										5.40		9					
b)-																	
V																	
M																	
N																	
28													5.78	5.9			
97(														6			

									.
									1
									7
									)
									~
M									2
CT									1
.M.				~4.47*	5.43*	5.69*	~5.57*		.
21									1
5									6
									*
M									
CT				[0.11]	2.8				
.M.				2.23	4				
28				(2.58)	(3.				
17				- 4.92	23)				
M									
CT						[0.19]	3.1		
.M.						2.03	1		
28						(2.69)	(3.		
18						- 4.91	53)		
M									
CT						[0.16]	3.0		
.M.						1.97	7		
28						(2.89)	(3.		
19						- 5.02	39)		
M									
N									
28						4.6	3.4		
98-									
V									
UF	~								2
RJ-	1	4	4						1
D	.	.	.						.
G	9	2	6	4.84*	5.17*	5.67*	5.50*		1
11	5	5	7						8
95	*	*	*						*

Estimated body masses. 2.57 kg (see Carneiro et al., 2024a) to 2.82 kg.

Remarks. *Robertbutleria mastodontoidea* was initially identified by Marshall (1987) based on two upper molars (MCT.M.896 [holotype; ex-DGM 896(a)-M]; MCT.M.2769 [ex-DGM 896(b)-M]). Later, Oliveira and Goin (2011) increased the hypodigm of this species, including specimen AMNH 49858, and some specimens from MN (MN 2897(b)-V and MN 2897(c)-V), MCN-PV (MCN-PV 1799, MCN-PV 1806, MCN-PV 1816, MCN-PV 1817, MCN-PV 1819, MCN-PV 1820), and MCT (MCT.M.2817, MCT.M.2818, and MCT.M.2819). Furthermore, the present study identified a new specimen from MCT (MCT.M.215) and UFRJ-DG (UFRJ-DG 1195-M).

The dentaries (MCT.M.215 and UFRJ-DG 1195-M) are assigned to *Robertbutleria mastodontoidea* based on the compatible size, moderately high dentary, obliquely oriented premolars, and asymmetric alveoli of m4. The last two are distinctive features of *R. mastodontoidea* among large-sized metatherians from the Itaboraí Basin. Moreover, the presence of obliquely oriented premolars, deep masseteric fossa, and convex posterior border of the dentary identify specimens MCT.M.215 and UFRJ-DG 1195-M as belonging to a metatherian (see Carneiro et al., 2024c).

The specimen MN 2898-V is recognized as a m2 of *Robertbutleria mastodontoidea* based on its size and width by length ratio (RW/L: 0.74; *R. mastodontoidea* [m2 range: 0.69-0.75]; RW/L *Protodidelphis vanzolinii* [m2 range: 0.66-0.71]), whereas specimen MN 1371-V is assigned to *P. vanzolinii* based on the same evidence (RW/L: 0.65; RW/L *P. vanzolinii* [m1 range: 0.65-0.68]; RW/L *R. mastodontoidea* [m1 range: 0.67-0.69]). Based on the observations of Carneiro (2023 [unpublished data]), the m1-3 of *R. mastodontoidea* have greater RW/L ratios than homologous ones of *Protodidelphis vanzolinii* (see also PCA1's results and the supplementary material [Appendix 2]).

5. Results of PCA analyses

The first PCA revealed that PC1 explains 75.7% of the data variation, whereas PC2 explains 17.6% (Fig. 7a). The PCA1 also highlights that *Robertbutleria mastodontoidea* (blue convex hull) is more associated with high Ltal (positive values of PC2) and low Lttri values (negative values of PC2), which indicates larger talonids and shorter trigonids. Conversely, *Carolocoutoia ferigoloi* (red convex hull) presents the inverse, with low Ltal and high Lttri values, suggesting shorter talonids and longer trigonids for this species. Finally, *Protodidelphis vanzolinii* (green convex hull) is more associated negatively with the Lm, Wtal, and Wtri in the left region of PC1, indicating smaller allometric dimensions (i.e., small lower molars and shorter talonids and trigonids) for such species (Fig. 7a).

The second PCA revealed that PC1 explains 63.7% of the data variation, while PC2 explains 36.3% of the data variation (Fig. 7b). The PCA2 also highlights that *Robertbutleria mastodontoidea* is more associated with RGA, RDS, and m3ra in the left upper quadrant of the morphospace, indicating shorter and more robust dentaries, larger talonids, and shorter trigonids. In contrast, *Protodidelphis vanzolinii* is more associated with RPM, Lp2/Lp3, and m3MEL in the upper right region of the morphospace, suggesting longer dentaries, more spaced metaconid and entoconid, and less reduced p2s than p3s. *Carolocoutoia ferigoloi* was placed in the right lower region of the morphospace and is more explained by negative values for the PC2, suggesting less robust dentaries and smaller talonids (Fig. 7b).

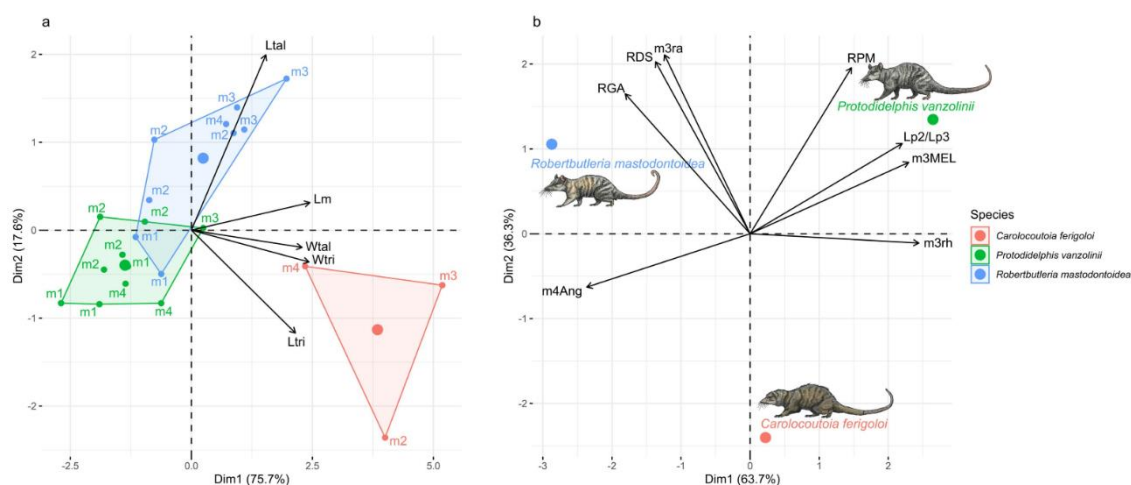


Fig. 7

Principal component analyses (PCA) of some morphometric and morphofunctional indexes based on lower molar measurements for *Protodidelphis vanzolinii* Paula Couto, 1952; *Robertbutleria mastodontoidea* Marshall, 1987; *Carolocoutoia ferigoloi* Goin et al., 1998. **a**, PCA analysis with lower molar's *loci* (m1, m2, m3, and m4) morphometric indexes (Lm, Ltri, Ltal, Wtri, and Wtal). Convex hulls are colored according to different species. **b**, PCA analysis with eight morphofunctional indexes (Lp2/Lp3, m3ra, m3rh, m3MEL, m4Ang, RGA, RDS, and RPM). **A**, area; **DHm3-4**, dentary height below m3-4; **dt**, diastema(ta); **ent**, entoconid; **H**, height; **L**, length; **Lm1-4**, length of the lower molar series; **m**, lower molar; **m4Ang**, angle of m4 (=asymmetric m4) in degrees; **MEL**, relative distance between metaconid's and entoconid's apices by the lower molar length (Lmet-ent/Lmx), measured based on m3; **met**, metaconid; **p**, lower premolar; **R**, ratio; **ra**, relative area (Atal/Atri); **RDS**, relative dentary shape (DHm3-4/Lm1-4); **RGA**, relative griding area ($\sqrt{\text{Atal/Ltri}}$); **rh**, relative height (Htal/Htri); **RPM**, relative length of the anterior part of the dentary (Lp1-3+dt/Lm1-4); **tal**, talonid; **tri**, trigonid; **W**, width. Credits: The artistic drawings of Itaboraí's protodidelphines were made by Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com).

6. Results of phylogenetic analysis

The phylogenetic analysis recovered two MPTs (Score: 1962; CI: 0.368; RI: 0.609) (Fig. 8). Following the results of the phylogenetic analysis, *Robertbutleria* is recovered as the sister taxon of *Carolocoutoia* based on the presence of hypertrophied StB (character 12, state 1), hypoconulid labially placed than the entoconid (ch. 192, state 1), m4 in a more cranial placement than the m3/molar series horizontal ramus increasing in height from m1 to m4 (ch. 221, state 1), p1 transversally oriented (ch. 257, state 2), and p2 obliquely oriented (ch. 265, state 1).

Protodidelphinae is recovered based on the presence of a thicker enamel layer (ch. 97, state 1), paraconid labial to the metaconid on m2-3 (ch. 140, state 1), and pyramidal entoconid (ch. 180, state 2). Protodidelphidae is supported by the following features: presence of protoconal cingulum/cinguli (ch. 62, state 1), postprotocrista reaching the mesiolingual border of the metacone (ch. 65, state 1), m1 preentocristid reduced to absent (ch. 129, state 1), hypoconid mesial to the entoconid on m2-3 (ch. 172, state 0; reversion), and moderately robust

dentary (ch. 319, state 1).

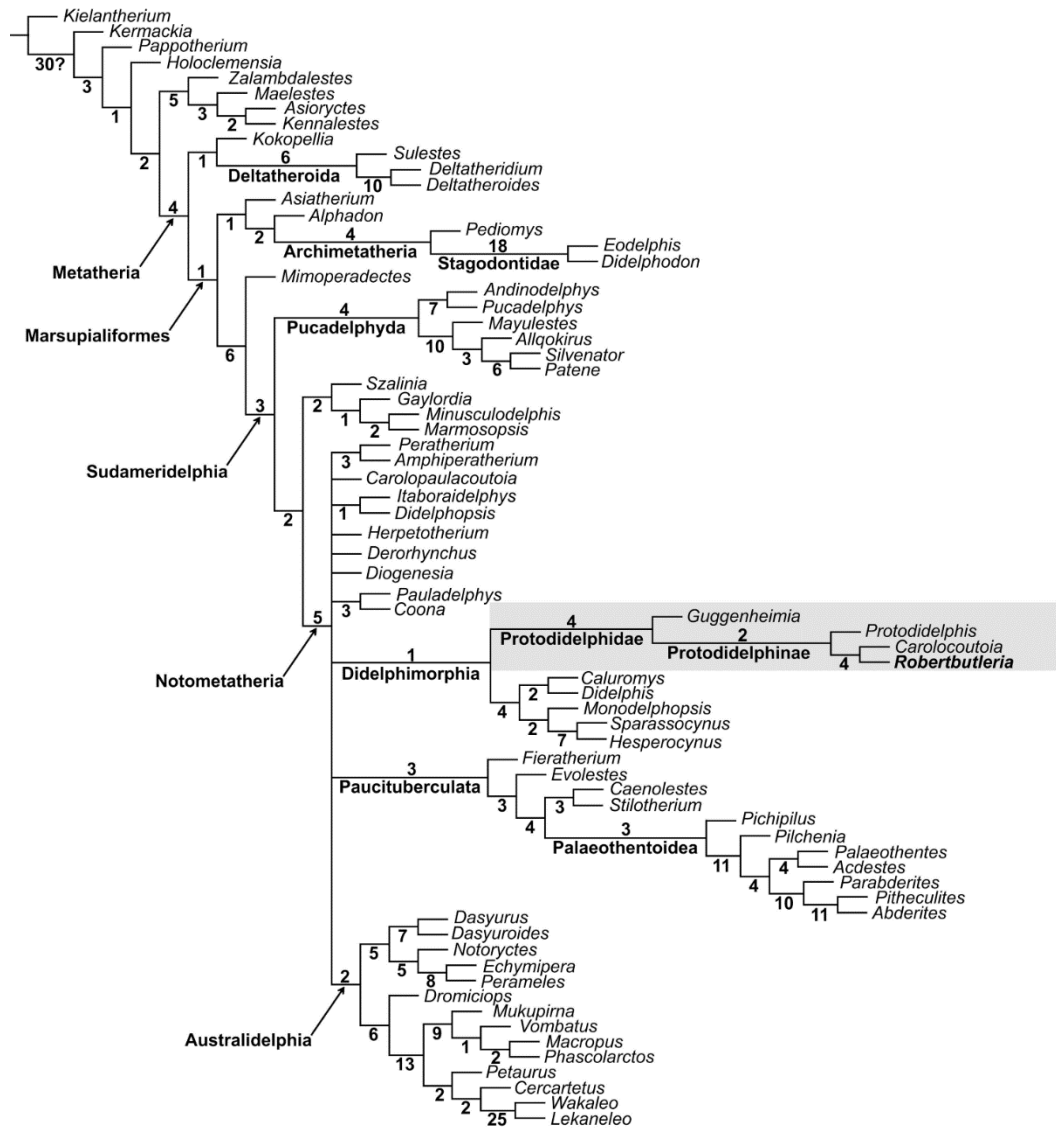


Fig. 8 Strict consensus tree of the two most parsimonious trees (Score: 1962; CI: 0.368; RI: 0.609) recovered in the phylogenetic analysis. Numbers above and below the branches indicate Absolute Bremer Support values. *Robertbutleria* Marshall, 1987 is highlighted in bold. Protodidelphidae is highlighted in grey.

8. Discussion

8.1 Systematic affinities of *Robertbutleria*

In the description of *Robertbutleria*, Marshall (1987: 123) observed that this taxon is similar in size and general structure to *Protodidelphis* but differs in having 1) more ovoid upper molars, 2) more bunodont cusps, 3) shorter postmetacrista (actually, this observation is not accurate, as the M3 of specimen MCT.M.303 [*Protodidelphis vanzolinii*] has a very short postmetacrista), 4) protocone apex placed in a more midlingual position (the protocone of *Robertbutleria mastodontoidea* is U-shaped and not eccentric, a contrary condition to the V-shaped and procumbent protocone of *Protodidelphis*), and 5) presence of well-developed labial and lingual cinguli (this observation is not accurate, as the holotype of *Protodidelphis vanzolinii* [MCT.M.271] displays a developed labial cingulum on M1 and specimen MN 2897(d)-V, left M3, displays well-developed protoconal and labial cinguli).

Goin et al. (1998: 152) considered *Robertbutleria* as the sister taxon of *Carolocoutoia* (a result recovered by the phylogenetic analysis). According to these authors, *Robertbutleria* shares with *Carolocoutoia*, but not with *Protodidelphis*, several features: 1) marked bunodonty, 2) poorly developed ridges, 3) enamel crenulations on the postmetacrista, and 4) presence of a distolabial crest of StD (however, *Protodidelphis vanzolinii* also displays this crest in some specimens [e.g., MCT.M.303]). Consequently, these authors observed that *Carolocoutoia* represents a more inflated, wrinkled, and larger version of *Robertbutleria*.

We identified new shared features between *Robertbutleria* and *Carolocoutoia* were identified (it is noteworthy that all of these features are more marked in *Carolocoutoia* than in *Robertbutleria*): 1) rounded/curved postmetacrista (i.e., without a distolabial angle of the postmetacrista) in M1-3, 2) bulging and U-shaped protocone (this implies an entoconid somewhat labiolingually compressed and distolingually placed in the talonid; see explanation in Oliveira, 1998: 215 [unpublished data]), 3) higher RW/L (i.e., lower molars proportionally wide in relation to length [which may represent a consequence of the more ovoid shape of the upper molars]), 4) labially positioned hypoconulid to the entoconid, 5) m4 in an asymmetrical position in relation to the molar series (i.e., the posterior alveolus/root is in a more cranial

position than the anterior alveolus/root), 6) p1 evidently oblique and p2-3 slightly oblique in relation to the premolar/molar series' axis, and 7) absence of retromolar space. Consequently, *Robertbutleria* and *Carolocoutoia* are more similar to each other than to *Protodidelphis* in all these features.

In contrast, *Protodidelphis* has an obliquely oriented postmetacrista with a distolabial angle (i.e., metastylar wing), especially on M1, and a V-shaped protocone. These two features are also observed in *Guggenheimia*, a non-protodidelphine protodidelphid, recovering both states as plesiomorphic for Protodidelphidae. Therefore, *Robertbutleria* and *Carolocoutoia* shared derived states for these two characters. This conclusion agrees with Goin et al. (1998), who considered that *Protodidelphis* displayed the most dental plesiomorphic pattern among protodidelphines.

Several dental features shared between *Robertbutleria* and *Protodidelphis* are highly plastic in the latter. *Protodidelphis* have specimens with developed labial and protoconal cingula (especially the species of Yacimiento Las Flores; see Zimicz, 2012 [unpublished data]) or specimens that practically lack these features (e.g., the species from Paso del Sapo and some *P. vanzolinii* from the Itaboraí Basin; see, e.g., Tejedor et al., 2009; Oliveira and Goin, 2011), whereas *Robertbutleria* has well-developed labial and protoconal cingula in all known specimens. Moreover, a labial cingulum and a mesial protoconal cingulum are also observable (although less developed) in *Guggenheimia* (MCT.M.2782), and a mesial protoconal cingulum is also observed on the M3 of *Carolocoutoia ferigoloi* (MCN-PV 1802, holotype). Consequently, these features should be better considered as retained plesiomorphies for Protodidelphidae and not autapomorphies of *Protodidelphis* (see the results of the phylogenetic analysis).

Accordingly, the presence of a sinuous 'zigzag' crest formed by the distolabial crest of StB and the mesiolabial crest of StD is also highly plastic among *Protodidelphis*, with some species having a straighter (i.e., less sinuous) pattern (see Tejedor et al., 2009). In addition, a

zigzag pattern can also be identified on the upper molars of *Robertbutleria* and *Carolocoutoia*. Consequently, a zigzag pattern has no taxonomic or systematic validity supporting synonymizing between *Protodidelphis* and *Robertbutleria*, representing an ancestral state for Protodidelphinae.

Furthermore, Marshall (1987: 150) explained that the assignment of a taxon to a clade should be made not by the appearance of primitive/plesiomorphic characters but by the first appearance of derived/apomorphic characters. Protodidelphines are a good model to explain Marshall's statement: Despite the overall similarities between *Robertbutleria* and *Protodidelphis*, the presence of several apomorphic features (e.g., markedly inflated and thick enamel crown, ovoid-like shape of upper molars, absence of a distolabial angle of the postmetacrista, 'U-shaped' protocone, asymmetrically placed m4, obliquely oriented lower premolars, and absence of diastemata) shared between *Robertbutleria* and *Carolocoutoia* but not *Protodidelphis* supports the sister relation of the first two.

In summary, the suggested co-generic nature of *Protodidelphis* and *Robertbutleria* (i.e., that *Robertbutleria* is a junior synonymy of *Protodidelphis*) was based on retention plesiomorphic dental features. Consequently, *Robertbutleria* is not a junior synonym of *Protodidelphis*. Therefore, the initial concept (that *Robertbutleria* is a valid taxon), as proposed by Marshall (1987) and Goin et al. (1998), should be followed.

8.2 Dietary inferences for Itaborai's protodidelphines: evidence of low trophic niche partitioning between *Protodidelphis*, *Robertbutleria*, and *Carolocoutoia*

The Paleocene-Eocene Thermal Maximum (PETM) + the Early Eocene Climatic Optimum (EECO) are considered the most relevant paleoenvironmental event correlated with the increase in diversity of metatherians in South America (see, e.g., Oliveira and Goin, 2011; Goin et al., 2012, 2016; Zimicz, 2012 [unpublished data]; Carneiro, 2019; Tarquini et al., 2022;

Carneiro and Oliveira, 2023). These two events happened during the onset of the Eocene as a consequence of two massive releases of CO₂ in the Atmosphere due to volcanic eruptions (Bowen et al., 2015). These volcanic events resulted in the increase in average global temperatures to about 5° C to 8° C (Bowen et al., 2015), the expansion of tropical forests, and the increase in abundance of fruit-bearing trees (see, e.g., Woodburne et al., 2014a, 2014b; Goin et al., 2012, 2016; Zimicz, 2012 [unpublished data]).

Carneiro et al. (2024a) concluded that large-sized metatherians from the Itaboraí Basin explored different preferential food, with *Protodidelphis vanzolinii* and *Robertbutleria mastodontoidea* (at the time, *Protodidelphis mastodontoides*) exploring frugivorous trophic niches. In addition, the very large-sized *Carolocoutoia ferigoloi* was one of the largest known didelphimorphians and the most specialized frugivorous taxon of this clade (see, e.g., Goin et al., 1998; Oliveira and Goin, 2011; Carneiro and Oliveira, 2023; Carneiro et al., 2024b).

Robertbutleria mastodontoidea displays marked bunodont teeth, rounded upper molars, mesiodistally developed and low protocone, talonid basins of lower molars with wrinkled enamel, well-developed talonids, asymmetric m4 (i.e., the posterior alveolus/root of m4 is more cranially placed than the anterior one, resulting on an angle with the lower molar series level), hypertrophied and bulbous p3, obliquely oriented lower premolars compared to the premolar/molar dental axis, shorter anterior part of the dentary, reduced retro-molar space, moderately robust dentary (RDS: 0.61), and convex posterior border of the dentary. This combination of features indicates a frugivorous diet for this taxon (see discussion in Carneiro and Oliveira, 2023; Carneiro et al., 2024a, 2024c).

Moreover, the wrinkled enamel layer observed on the talonids of *Robertbutleria mastodontoidea* may have increased in the occlusal surface area of its lower molars (see, e.g., Zimicz, 2012 [unpublished data]; Carneiro et al., 2024a). These talonid wrinkles function as reduced enamel crests/concavities, increasing the surface of contact between the tooth and the food and allowing the processing of more resistant fibers (Zimicz, 2012 [unpublished data]).

Accordingly, the thick enamel layer could offer further protection for the tooth during the mastication of fibrous fruits with soft, pliable seeds (Kinzey, 1992; Vogel et al., 2008). Kinzey (1992) commented that pitheciids premolar and molar crenulations associated with reduced cusp relief probably facilitate the secondary breakdown of seeds during grinding. Consequently, Kinzey (1992) considered grinding rather than crushing. In summary, the enamel wrinkles observed on *R. mastodontoidea* may have increased the processing of fibrous fruits with soft, pliable seeds.

Zimicz (2012 [unpublished data]) and Solé and Ladevèze (2017) have observed that larger protocones and talonids are indicative of a more important dietary masticatory component, as the protocone/talonid is related to food maceration and crushing. This morphofunctional pattern also indicates frugivorous, fibrous, and omnivorous diets (see Carneiro and Oliveira, 2023; Carneiro et al., 2024a, 2024b, 2024c). Thomason (1991) observed that shorter dentaries are related to stronger bite forces. Similarly, Carneiro and Oliveira (2017a, 2023), Rangel et al. (2019, 2023a), and Carneiro et al. (2024a, 2024c) observed that higher values of RDS and dentaries with straighter posterior edges are observed on durophagous and carnivorous metatherians.

These observations suggest that *Robertbutleria mastodontoidea* could have explored a more important resistant food component than sympatric protodidelphines. However, the absence of crushing P/p3s (sensu Carneiro and Olivera, 2017a) rules out a specialized durophagous diet. Furthermore, this taxon differs from other sympatric protodidelphids in the possible exploration of more fibrous fruits, which demands a more important masticatory component (evidenced by the longer protocones and well-developed talonids).

Table 2 Some morphological and morphometrical data of *Carolocoutoia ferigoloi*, *Protodidelphis vanzolinii*, and *Robertbutleria mastodontoidea* from the Itaboraí Basin. **A**, area (L x W); **DHm3-4**, dentary height below m3-4; **dt**, diastema(ta); **H**, height; **L**, length;

Lm1-4, length of the lower molar series; **m**, upper/lower molars with the numbers corresponding to its positioning (M/m1-4); **m4Ang**, angle of m4 (=asymmetric m4) in degrees; **MEL**, relative distance between metaconid's and entoconid's apices by the lower molar length ($L_{met-ent}/L_{mx}$), measured based on m3; **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **ra**, relative area (A_{tal}/A_{tri}); **RDS**, relative dentary shape (DH_{m3-4}/L_{m1-4}); **RGA**, relative grinding area ($\sqrt{A_{tal}/L_{tri}}$); **rh**, relative height (H_{tal}/H_{tri}); **RPM**, relative length of the anterior part of the dentary ($L_{p1-3+dt}/L_{m1-4}$); **tal**, talonid; **tri**, trigonid; **W**, width.

Taxon	Lp2/L p3	m3rh	m3ra	m3ME L	m4Ang	RPM	RGA	RD S
<i>Carolocoutoia ferigoloi</i>	0,74	0,87	0,84	0,46	16	0,61	1,07	0,59
<i>Robertbutleria mastodontoidea</i>	0,72	0,84	1,58	0,45	24	0,63	1,38	0,61
<i>Protodidelphis vanzolinii</i>	0,85	0,89	1,25	0,49	0	0,67	1,16	0,6

On the contrary, *Carolocoutoia ferigoloi* has index values (m3ra, RGA) compatible with exploiting soft food resources that do not require extensive masticatory movements, as its talonids are comparatively reduced (Carneiro et al., 2024c).

Carolocoutoia ferigoloi has a greater combination of dental features indicative of a specialized frugivorous diet among Itaboraí's metatherians (see, e.g., Zimicz, 2012 [unpublished data]; Carneiro and Oliveira, 2023; Carneiro et al., 2024b). The presence of a markedly bunodont crown, evidently thick enamel layer, rounded shape of upper molars, reduced protoconal basin, low and mesiodistally expanded protocone, conical trigonid cuspids (=spire-like), reduced to vestigial trigonid basin, small talonid basin, well-developed and cranially shifted precingulid (i.e., the precingulid is almost at the same level as the trigonid basin) is indicative of a specialized frugivorous diet (Carneiro et al., 2024b). The reduction of the protoconal basin and the low protocone indicate a reduction in masticatory movements,

suggesting an oral movement that presses turgent/soft fruits (sensu Zimicz, 2012 [unpublished data]). The thick enamel layer of *Carolocoutoia*'s molars protect against seeds in these ingested fruits (Kinzey, 1992; Vogel et al., 2008).

Finally, *Protodidelphis vanzolinii* has the most generalized dental features observed among protodidelphines: developed talonids (m3ra and RGA), moderately robust dentary (RDS), shorter distance between the metaconid and the entoconid (a consequence of its more 'V-shaped' and less mesiodistally expanded protocones; MEL), p2 less reduced than p3 (an ancestral state for Sudameridelphia; see, e.g., Carneiro and Oliveira, 2023; Carneiro et al., 2024a), and presence of a diastema between p1 and p2 (a shared condition with some specimens of *Guggenheimia crocheti* from Itaboraí; e.g., MCT.M.315).

Protodidelphis vanzolinii has a more generalized dentition compared to *R. mastodontoidea*. The former displays less bunodont crown, more subtriangular upper molars, less labiolingually compressed entoconids, more spaced entoconids and metaconids, absence of wrinkled enamel on the talonid basin of lower molars and supernumerary cusps, 'V-shaped' and comparatively taller protocones, presence of a diastema between p1 and p2, premolars aligned to the premolar/molar dental axis, m4 not asymmetrically placed, and presence of a retro-molar space (see, e.g., Paula Couto, 1952, 1962, 1970; Carneiro and Oliveira, 2023; Carneiro et al., 2024c). This combination of features indicates a frugivorous diet but not as specialized as the one of *R. mastodontoidea*.

Thomason (1991) concluded that longer dentaries are correlated with weaker bite forces due to greater distances between the temporomandibular joint and the point of the force application. Zimicz (2012 [unpublished data]) and Carneiro et al. (2024b) observed that specialized insectivorous metatherians could display diastemata between the lower canine and p1 and between premolars, resulting in long dentaries. In contrast, hypercanivorous, durophagous, and frugivorous metatherians frequently have shorter dentaries, as previously explained. Consequently, *Protodidelphis vanzolinii* probably had a less specialized

frugivorous diet than other sympatric protodidelphines. This species probably had a more important insectivorous or omnivorous component in its diet, resembling extant didelphids (Lessa and Geise, 2010).

Moreover, considering extant non-marsupial South American mammals, like small Primates, *Robertbutleria*, and callitrichid monkeys share the presence of bunodont molars, low, moderate in length, and U-shaped protocone, well-developed protoconal cingula, talonid larger than the trigonid, low height difference between the trigonid and talonid, absence of diastemata between the lower canine and premolars, and asymmetric m4 (for callitrichid, see Swindler, 2002). However, these taxa differ in the more angled posterior edge of the dentary in *Robertbutleria* (straighter in callitrichids) and less developed angular process in *Robertbutleria* (evidently more developed in callitrichids). These differences may be related to a more important folivorous and exudated component for callitrichids (e.g., Rylands, 1989; Passos, 1999; Jackson and Reichard, 2020) than *R. mastodontoidea*.

Robertbutleria mastodontoidea probably had a similar diet to extant *Leontopithecus chrysopygus*, which is a mainly frugivorous callitrichid primate that also ingests invertebrates and small vertebrates as food (Passos, 1999). For this primate species, turgent fruits are the most important food component of its diet, representing about 68% of explored items (Passos, 1999). Accordingly, for *Leontopithecus chrysomelas* and *Callithrix kuhli*, fruits may represent 74% to 89% and 63% to 70% of their diets, respectively (Rylands 1989). It can be hypothesized that *R. mastodontoidea* occupied an analogous frugivorous trophic niche to extant callitrichids.

In summary, the three protodidelphines from the Itaboraí Basin very likely explored differential frugivorous trophic niches: *Protodidelphis vanzolinii* was a generalized frugivore; *Robertbutleria mastodontoidea* was a frugivore that potentially explored fibrous fruits (fibrous frugivore), and *Carolocoutoia ferigoloi* was a specialized frugivore, exploring soft and turgent fruits that do not require repetitive or strong masticatory movements to be

ingested. The possible low niche overlapping between these three taxa can partially explain their co-existence in the Itaboraí Basin.

Furthermore, our results demonstrate a case in which different trophic niches are explored while little morphological change is visible. It is also noticeable that few modifications from an ancestral pattern can allow diversification to differential trophic niches, such as a slightly more robust and shorter dentary, asymmetrical positioning of the m4, and increase in molar occlusal surface area (marked bunodonty, acquisition of wrinkled enamel). Similarly, the results here presented support the previous observations of Oliveira and Goin (2011) and Carneiro (2019), who proposed that protodidelphids experienced a short time increase in diversity during the early Eocene, probably because of the paleoenvironmental modifications resulting from the PETM + EECO (see, e.g., Goin et al., 2016).

9. Conclusions

Robertbutleria is a valid genus of Protodidelphidae. This taxon shares exclusively with *Carolocoutoia* rounded/ovoid upper molars, markedly inflated crowns, rounded postmetacrista, U-shaped protocone, asymmetric m4, obliquely oriented lower premolars, especially p1-2, and lack diastemata. *Protodidelphis* displays more symplesiomorphies among protodidelphines, justifying its earlier divergence than *Robertbutleria* and *Carolocoutoia*.

Among protodidelphids, protodidelphines (*Protodidelphis*, *Robertbutleria*, and *Carolocoutoia*) have larger dimensions, more inflated, thick, and wrinkled crowns, and pyramidal entoconids than *Guggenheimia*. Protodidelphines apparently had a short time of diversification, probably due to the paleoenvironmental changes resulting from the PETM + EECO. The representatives of this clade had different trophic niches (generalized frugivory, fibrous frugivory, and specialized soft frugivory), indicating that trophic diversification does not require evident morphological modifications to happen.

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Declaration of competing interest

We have no conflicts of interest to disclose.

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We have not used generative AI in scientific writing.

Declaration of author contributions

L.M.C. (coordinated the study, wrote the main manuscript text, prepared the tables and figures, and made the database of performed PA analysis, and PCA analyses), E.V.O. (wrote the main manuscript text), R.C.S. (wrote the main manuscript text, and prepared its images and figures), H.B. (wrote the main manuscript text, performed PCA analyses, and prepared related figures), and M.R.A. (wrote the main manuscript text). All authors reviewed the manuscript.

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FIGURE CAPTIONS

Fig. 1 The Itaboraí fauna: locality and biochron. **a**, Map showing the region and the coordinates of the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (22° 45' 9'' S; 42° 51' 53'' W). **b**, The stratigraphic relationships of the Itaboraiense SALMA with other Paleogene SALMAs (see Carneiro and Oliveira, 2023). A plausible age range for the Itaboraiense SALMA is highlighted in grey. The occurrence of *Robertbutleria mastodontoidea* Marshall, 1987 is suggested by a black arrow and a SEM image of the MCT.M.896 (holotype), a left M1. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 1000 Km.

Fig. 2 Diagnostic combination of features of *Robertbutleria* Marshall, 1987. SEM images of specimens: **a**, MCT.M.896, holotype, left M1 in occlusal view; **b**, MCN-PV 1819, left m3 in occluso-labial view. Scale bars = 1 mm.

Fig. 3 Comparative upper molar differences between *Robertbutleria* Marshall, 1987 and *Protodidelphis* Paula Couto, 1952. *Protodidelphis vanzolinii* Paula Couto, 1952: **a**, MCT.M.303, right maxilla with M1-4 in occluso-lingual view; **b**, MCT.M.250, a right dentary with p3, m1, m3-4, and alveoli of m2, showing the m3 in occlusal view; *Robertbutleria mastodontoidea* Marshall, 1987: **c**, MCT.M.896 (holotype), left M1 in occlusal view; **d**, MCN-PV 1819, left m3 in occluso-labial view. Scale bars = 1 mm.

Fig. 4 Comparative upper molar differences between *Robertbutleria* Marshall, 1987 and *Carolocoutoia* Goin et al., 1998. *Robertbutleria mastodontoidea* Marshall, 1987: **a**, MCT.M.896 (holotype), left M1 in occlusal view; *Carolocoutoia ferigoloi* Goin et al., 1998: **b**, MCN-PV 1802 (holotype), a left M3 in occlusal view. Scale bars = 1 mm.

Fig. 5 Isolated molars of *Robertbutleria mastodontoidea* Marshall, 1987. MCT.M.896, holotype, left M1 in **(a)** occlusal, **(b)** distal, and **(c)** labial views; **d**, MCN-PV 1806, left M3 in occluso-lingual view; MCT.M.2819, left m2 in **(e)** lingual, **(f)** occlusal, **(g)** occluso-distal, and **(h)** labial views; **i**, MCN-PV 1816, left m3 in occlusal view; **j**, MCN-PV 1817, left m3 in occluso-distal view; **k**, MCN-PV 1819, left m3 in occluso-labial view; **l**, MCN-PV 1820, left m4 in occlusal view. Scale bars = 1 mm.

Fig. 6 Dentaries of *Robertbutleria mastodontoidea* Marshall, 1987. MCT.M.215, posterior fragment of an edentulous left dentary with alveoli of m2-4, damaged alveoli of m1, and base of the coronoid process with preserved mandibular foramen, in (a) labial, (b) occlusal, and (c) lingual views; UFRJ-DG 1195, left edentulous dentary with alveoli of p2-m4, posterior alveolus of p1 (anterior alveolus partially preserved), and anterior part of the coronoid process, in (d) labial, (e) occlusal, and (f) lingual views. Scale bars = 5 mm.

Fig. 7 Principal component analyses (PCA) of some morphometric and morphofunctional indexes based on lower molar measurements for *Protodidelphis vanzolinii* Paula Couto, 1952; *Robertbutleria mastodontoidea* Marshall, 1987; *Carolocoutoia ferigoloi* Goin et al., 1998. **a**, PCA analysis with lower molar's *loci* (m1, m2, m3, and m4) morphometric indexes (Lm, Ltri, Ltal, Wtri, and Wtal). Convex hulls are colored according to different species. **b**, PCA analysis with eight morphofunctional indexes (Lp2/Lp3, m3ra, m3rh, m3MEL, m4Ang, RGA, RDS, and RPM). **A**, area; **DHm3-4**, dentary height below m3-4; **dt**, diastema(ta); **ent**, entoconid; **H**, height; **L**, length; **Lm1-4**, length of the lower molar series; **m**, lower molar; **m4Ang**, angle of m4 (=asymmetric m4) in degrees; **MEL**, relative distance between metaconid's and entoconid's apices by the lower molar length (Lmet-ent/Lmx), measured based on m3; **met**, metaconid; **p**, lower premolar; **R**, ratio; **ra**, relative area (Atal/Atri); **RDS**, relative dentary shape (DHm3-4/Lm1-4); **RGA**, relative grinding area ($\sqrt{\text{Atal/Ltri}}$); **rh**, relative height (Htal/Htri); **RPM**, relative length of the anterior part of the dentary (Lp1-3+dt/Lm1-4); **tal**, talonid; **tri**, trigonid; **W**, width. Credits: The artistic drawings of Itaboraí's metatherians were made by Felipe A. Elias from the PaleoZOOBR (www.paleozooobr.com).

Fig. 8 Strict consensus tree of the two most parsimonious trees (Score: 1962; CI: 0.368; RI: 0.609) recovered in the phylogenetic analysis. Numbers above and below the branches indicate Absolute Bremer Support values. *Robertbutleria* Marshall, 1987 is highlighted in bold. Protodidelphidae is highlighted in grey.

TABLE TITLES

Table 1 Dental measurements (in mm) of *Robertbutleria mastodontoidea* Marshall, 1987. The holotype is highlighted in bold. Measurements of specimen MN 2898-V are based on Paula Couto (1970). For lower molars, the measurements are expressed in the following order: [precingulid length], trigonid length. (talonid dimensions – length or width), and – total length. **DP**, deciduous third premolar; **L**, length; **M/m**, upper/lower molar; **P/p**, upper/lower premolar; **W**, width; ~, incomplete specimen; *, based on alveoli dimensions.

Table 2 Some morphological and morphometrical data of *Carolocoutoia ferigoloi*, *Protodidelphis vanzolinii*, and *Robertbutleria mastodontoidea* from the Itaboraí Basin. **A**, area (L x W); **DHm3-4**, dentary height below m3-4; **dt**, diastema(ta); **H**, height; **L**, length; **Lm1-4**, length of the lower molar series; **m**, upper/lower molars with the numbers corresponding to its positioning (M/m1-4); **m4Ang**, angle of m4 (=asymmetric m4) in degrees; **MEL**, relative distance between metaconid's and entoconid's apices by the lower molar length (Lmet-ent/Lmx), measured based on m3; **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **ra**, relative area (Atal/Atri); **RDS**, relative dentary shape (DH m3-4/Lm1-4); **RGA**, relative grinding area ($\sqrt{\text{Atal/Ltri}}$); **rh**, relative height (Htal/Htri); **RPM**, relative length of the anterior part of the dentary (Lp1-3+dt/Lm1-4); **tal**, talonid; **tri**, trigonid; **W**, width.

ARTIGO 6

PERIÓDICO: JOURNAL OF MAMMALIAN EVOLUTION

A new derorhynchid (Mammalia, Metatheria) from the Itaboraí Basin (early Eocene), Brazil, and the trophic diversity of derorhynchids during the onset of the EoceneLEONARDO M. CARNEIRO^{1,2,*}

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Statements and declarations

Declaration of competing interest EVO is a member of the JME Editorial Board but was not involved in evaluating this manuscript.

Declaration of generative AI in scientific writing We have not used generative AI in scientific writing.

Declaration of author contributions L.M.C. (coordinated the study, wrote the main manuscript text, made images [digital and SEM] of the specimens, prepared the tables [Table(s) 1-3] and figures [Fig. 2-4, 6-8, 10], made the morphological database of the phylogenetic analysis, performed the phylogenetic analysis, and made the database of PCAs analyses), F.J.G. (wrote the main manuscript text and presented detailed comparisons of included taxa), E.V.O. (wrote the main manuscript text, made the map image [Fig. 1], and made images of the specimens [Fig. 9]), R.C.S. (wrote the main manuscript text, made images of MCTer's specimens, and prepare its figures [Fig. 5]), and H.B. (wrote the main manuscript text, performed PCA analyses, and prepare its figures [Fig. 11]). All authors reviewed the manuscript.

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Abstract. Derorhynchidae is a Paleogene clade of South American and Antarctic metatherians. Among the localities with representatives of this clade, the Itaboraí Basin outstands by the presence of three genera and at least five species (one genus and three species still undescribed). Herein, we presented a new derorhynchid from this locality, *Streptorhynchus tropicalis* gen. et sp. nov., discussing its affinities and dietary inferences. *Streptorhynchus* is identified by the presence of a mesially placed ectoflexus, StC close to StD, pyramidal entoconid, and m4 with a labial contact of the cristid obliqua with the distal border of the trigonid. Phylogenetic analysis recovered *Streptorhynchus*, *Pauladelphys*, and *Coona* as sister groups (Cooninae new subfamily) based on the presence of a pyramidal entoconid and m4 with a labial contact of the cristid obliqua with the distal wall of the trigonid. *Pauladelphys* and *Coona* are sister taxa based on the presence of a reduced hypoconulid. Moreover, two PCA analyses were performed based on morphometric and morphofunctional indexes of Itaboraí's derorhynchids. The results indicate that lower molars of derorhynchids are morphometrically similar, except those of *Diogenesia brevirostris*, which are smaller than other Itaboraí's derorhynchids. Nevertheless, their morphofunctional indexes are very different, especially those related to dentary shape, suggesting the exploitation of differential trophic niches. *Streptorhynchus* was an omnivore, *Derorhynchus* was a “durophagous” insectivore, and *Diogenesia* was an insectivore. *Derorhynchus singularis* has a longer and more robust jaw than *Derorhynchus* sp. and *Diogenesia brevirostris* has taller trigonids, smaller talonids, and a shallower dentary than *Diogenesia* sp.

Keywords: Early Eocene Climatic Optimum; Derorhynchidae; Itaboraiense SALMA; Paleocene-Eocene Thermal Maximum; Paleoecology; South America

Introduction

Derorhynchidae (Marshall, 1987) Goin, Case, Woodburne et al., 1999 was a Paleogene (early Paleocene to middle Eocene) clade of very-small to medium-sized (see Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023) notometatherians (i.e., the clade that includes Sternbergiidae, Peratheriinae, Herpetotheriidae, Derorhynchidae, Marsupialia and taxa more closely related to one of these groups; sensu Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023) that occurred in South America (Brazil and Argentina) and Antarctica (see Simpson 1938; Paula Couto 1952, 1962, 1970; Marshall 1982, 1987; Goin et al. 1999, 2022; Goin 2003; Goin and Abello 2013; Oliveira et al. 2021; Carneiro and Oliveira 2023). This clade is represented by four genera and at least six species described so far: *Derorhynchus singularis* Paula Couto, 1952; *Derorhynchus minutus* Goin, Case, Woodburne et al., 1999; *Pauladelphys juanjoi* Goin, Case, Woodburne et al., 1999; *Coona pattersoni* Simpson, 1938; *C. gutierrezii* (Del Corro, 1977), and *Diogenesia brevirostris* Oliveira, Carneiro and Goin, 2021. However, several derorhynchid specimens (representing several putative new taxa) known in some South American and Antarctic mammal-bearing localities, such as Punta Peligro, Itaboraí, Las Flores, La Meseta/Marambio, Cabeza Blanca, La Barda and Laguna Fría local faunas (see e.g., Oliveira 1998 [unpublished data]; Goin 2003; Goin et al. 1999, 2022; Tejedor et al. 2009; Zimicz 2012 [unpublished data]; Woodburne et al. 2014a; Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023) have yet to be formally described in the literature.

Among South American localities with derorhynchids, the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro state, Brazil (22° 50' 20" S; 42° 52' 30" W; Fig. 1a) dated as early Eocene in age (53-50 Ma, Itaboraiense SALMA; see Woodburne et al. 2014a; Fig. 1b) outstands in relevance. This locality has preserved the most diverse fauna of metatherians from the Paleogene so far known, with a minimum of 29 genera and 43 species, as presented by Carneiro et al. (2024a). In this locality, derorhynchids are important members of Metatheria, comprising about 10% of the recovered metatherian specimens (see Carneiro 2023 [unpublished data]).

Considering this diversity, several studies (Oliveira 1998 [unpublished data]; Oliveira and Goin 2006, 2012; Zimicz 2012; Woodburne et al. 2014a; Oliveira et al. 2021; Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023) have identified up to three genera and five species of Derorhynchidae from this locality: *Derorhynchus singularis*, *Diogenesia brevirostris*, and three putative new taxa described in these studies as *Derorhynchus* sp., *Diogenesia* sp., and genus et sp. nov. (the latter is formally presented below).

Gen. et sp. nov. from the Itaboraí Basin (previously identified as “*Chaishullenia*” nomem nudum, Derorhynchidae gen nov, new taxon, gen nov 3; see, e.g., Goin and Forasiepi 1997 [unpublished data] Oliveira 1998 [unpublished data]; Bergqvist et al. 2005; Oliveira and Goin 2006, 2012; Woodburne et al. 2014a; Oliveira et al. 2021; Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023) is identified by the presence of enlarged, pyramidal-like (i.e., with a flat labial border and a conical lingual border; sensu Carneiro 2023 [unpublished data]) entoconid in its lower molars (see Oliveira 1998 [unpublished data], Carneiro 2023 [unpublished data], Carneiro and Oliveira 2023). This feature (as others as well) led to inferences about a “more frugivorous diet for this taxon” in comparison with other derorhynchids from the Itaboraí Basin and Las Flores local faunas (see, e.g., Goin and Forasiepi 1997 [unpublished data]; Oliveira 1998 [unpublished data]; Zimicz 2012; Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023). However, this hypothesis has never been tested in the literature.

Here, we present this new derorhynchid from the Itaboraí Basin, discussing its affinities and dietary inferences. We also tested the hypothesis that Itaboraí’s derorhynchids had explored different trophic niches.

Institutional Abbreviations. **AMNH**, American Museum of Natural History, New York, NY, USA; **MCN-PV**, Coleção de Paleovertebrados do Museu de Ciências Naturais da Secretaria de Meio Ambiente (SEMA; ex. Fundação Zoobotânica do Rio Grande do Sul), Porto Alegre, Brazil; **MCT**, Museu de Ciências da Terra (MCTer), Serviço Geológico do Brasil (MCTer-SGB), Rio de Janeiro, Brazil; **MN**, Museu Nacional (MN/UFRJ), Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **UFRJ-DG**, Coleção de Macrofósseis do Departamento de Geologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Other Abbreviations. **A**, area; **BM**, estimated body mass; **ch.**, character; **DH**, dentary height; **dt**, diastema/diastemata; **EECO**, Early Eocene Climatic Optimum; **H**, height; **hp**, hypertrophied; **L**, length; **Lm**, lower molar series length; **M**, upper molars with the numbers corresponding to its positioning (M1-4); **m**, lower molars with the numbers corresponding to its positioning (m1-4); **MPT**, most parsimonious tree; **p**, lower premolars with the numbers corresponding to its positioning (p1-3); **PA**, phylogenetic analysis; **PC**, principal component; **PCA**, principal component analysis; **PETM**, Paleocene-Eocene Thermal Maximum; **R/r**, ratio; **ra**, relative area of the talonid by the trigonid (Atal/Atri); **RDS**, relative dentary shape ($\text{DH}/\text{Lm1-4}$); **RGa**, relative grinding area ($\sqrt[2]{\text{Atal}/\text{Lm4tri}}$); **rh**, relative height of the talonid by the trigonid (Htal/Htri); **RPM**, relative length of the anterior part of the dentary ($\text{Lp1-3} + \text{dt}/\text{Lm1-4}$); **RPS**, relative premolar size ($\text{Wp}^{3/3}/\sqrt{\text{BM}}$); **rt**, retro-molar space; **SALMA**, South American Land Mammal Age; **SEM**, scanning electron microscope; **tal**, talonid; **tri**, trigonid; **W**, width.

Materials and methods

Study site

The Itaboraí Basin is in the municipality of Itaboraí, Rio de Janeiro, in southeastern Brazil, with geographical coordinates 22° 45' 9.9144" S, 42° 51' 53.5536" W (Fig. 1a). For more data about the Itaboraí Basin, see Bergqvist et al. (2009), and Rangel et al. (2023).

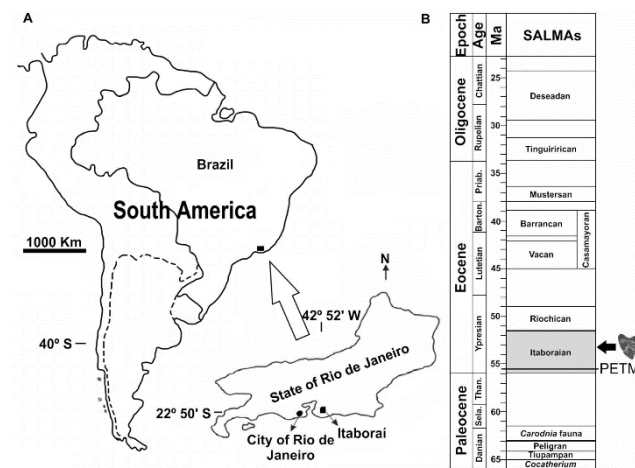


Fig. 1 The Itaboraí fauna: locality and biochron. **a**, Map showing the region and the coordinates of the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (22° 45' 9" S; 42° 51' 53" W). **b**, The stratigraphic relationships of the Itaboraiense SALMA with other Paleogene SALMAs. A plausible age range for the Itaboraí SALMA is highlighted in grey. The occurrence of the gen. et sp. nov. is suggested by a black arrow and a digital image of the MN 2894(a2)-V, a right M3. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 1000 Km

Studied specimens

All studied specimens are from the Itaboraí Basin, municipality of Itaboraí (Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023) (Fig. 1). The studied specimens are housed in the collections of AMNH, MCN-PV, MCTer (ex DGM), MN/UFRJ, and UFRJ-DG.

The gen. et sp. nov. and specimens identified as *Derorhynchus* sp. and *Diogenesia* sp. have been

previously presented and discussed in Oliveira (1998 [unpublished data]), Oliveira et al. (2021), Carneiro (2023 [unpublished data]), and Carneiro and Oliveira (2023). A list of studied derorhynchid specimens is presented as Online Resource (Appendix 1).

The digital images of specimens from MCTer were made with a Zeiss Stemi 508 Greenough Stereo Microscope with an Axiocam 208 camera. The SEM images were made with a JEOL JSM-6390LV at the Centro de Microscopia Eletrônica de Varredura do Departamento de Invertebrados do Museu Nacional, Museu Nacional (MN/UFRJ); and JEOL JSM-6510LV at the Instituto de Química, Universidade do Estado do Rio de Janeiro (UERJ), municipality of Rio de Janeiro, RJ, Brazil.

Estimated body masses of studied taxa were based on the dental regressions of Myers (2001), which considers the length of the lower molar series (LMORL: $\log_{10}BM = -1.253 + 3.540 \cdot [\log_{10}Lm1-4]$) and the length of the upper molar series (UMORL: $\log_{10}BM = -0.914 + 3.320 \cdot [\log_{10}LM1-4]$). All body masses are shown in grams (see Online Resource, appendix 2).

The size classification for Itaboraí’s metatherians was taken from Carneiro et al. (2024a), who based their classification on the length of the lower molar series (Lm1-4) and estimated body masses (BM; see Table 1). All measurements of studied specimens are presented as Online Resource (Appendix 3).

Table 1. Size categories considered for early Eocene Itaboraí’s metatherians (sensu Carneiro et al. 2024a) based on their lower molar series length (in mm) and maximum and minimum limits of estimated body masses (BM) in grams (g) and kilograms (kg). BM, estimated body mass; Lm1-4, lower molar series length

Size category	Lm1-4 (mm)	BM (g and Kg)
Tiny	Lm1-4 < 5.00 mm	BM < 15 g
Very small	5.00 mm < Lm1-4 < 6.20 mm	15 g < BM < 40 g
Small	6.20 mm < Lm1-4 < 9.40 mm	40 g < BM < 150 g
Medium	9.40 mm < Lm1-4 < 15.50 mm	150 g < BM < 1 kg
Large	15.50 mm < Lm1-4 < 22.00 mm	1 kg < BM < 3.3 kg
Very large	22.00 mm < Lm1-4	3.3 kg < BM < 10 kg

Phylogenetic Analysis

The morphological data matrix is based on Guimarães et al. (2024) and is included as supplementary material. It comprises 729 characters (318 dental, 24 jaw, 183 cranial, 201 postcranial) and 73 therian taxa,

including 65 metatherians (represented by genera), from the Cretaceous and Cenozoic of North America, Asia, South America, Antarctic, Europe, and Australia; and eight extinct non-metatherian mammals as outgroups.

The 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 100 replications. Some characters are treated as ordered (see Appendix 4). Absolute Bremer supports and tree scores were calculated with TNT 1.5. The list of characters, characters by taxon, and synapomorphies are presented as Online Resource (Appendices 4-6).

Principal Component Analyses (PCAs)

To discriminate the new taxon (see below) from other derorhynchids from Itaboraí (*Derorhynchus singularis*, *Derorhynchus* sp., *Diogenesia brevirostris*, and *Diogenesia* sp.), a principal component analysis (PCA) was conducted based on five morphometric parameters (**L** = lower molar length; **Ltal** = talonid length; **Ltri** = trigonid length; **Wtal** = talonid width; and **Wtri** = trigonid width) measured from lower molar specimens of studied taxa. The included specimens were identified by their molar locus (m1, m2, m3, and m4).

We performed a second PCA analysis based on six morphofunctional indices (ra, RDS, RGA, rh, RPM, and RPS), including the new taxon (gen. et sp. nov.), *Derorhynchus singularis*, *Derorhynchus* sp., *Diogenesia brevirostris*, and *Diogenesia* sp. These variables have been considered for setting dietary inferences in extinct metatherians (see, e.g., Zimicz 2012 [unpublished data], Rangel et al. 2023; Churchill et al. 2023; Carneiro et al. 2024a, 2024b, 2024c, 2024d), which can indicate different morphofunctional patterns for Itaboraí's derorhynchids.

These analyses used variance-covariance matrixes and were performed with the R software (R core team 2013). The dataset and the load of PCAs have been included as Online Resource (Appendices 7-8). The R scripts of PCAs are presented as Online Resource (Appendix 9).

Systematic Paleontology

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

Marsupialiformes Vullo et al., 2009

Sudameridelphia Szalay, 1994 (sensu Carneiro, 2023 [unpublished data]; Carneiro and Oliveira, 2023)

Notometatheria Kirsch et al., 1997 (sensu Oliveira et al., 2021; Carneiro and Oliveira, 2023)

†Derorhynchidae Marshall, 1987 (sensu Goin, Case, Woodburne et al., 1999)

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†Cooninae new

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Diagnosis. Members of Cooninae differs from other derorhynchids in the presence of enlarged, pyramidal entoconids (conical or slightly labiolingually compressed in *Derorhynchus* and *Diogenesia*) and m4 with a labial contact of the cristid obliqua with the distal border of the trigonid, resulting in a reduced to nearly absent labial cingulid (m4 with a cristid obliqua contacting the distal border of the trigonid ventral the carnassial notch/at the midline of the tooth in *Derorhynchus* and *Diogenesia*; i.e., developed labial cingulid).

Genotype. *Coona* Simpson, 1938.

Included genera. *Coona*, *Pauladelphys* Goin, Case, Woodburne et al., 1999, and *Streptorhynchus* gen. nov.

Remarks. This clade of derorhynchids is represented by taxa with dental features indicative of “more insectivorous-frugivorous diets” (=omnivory) in comparison with *Derorhynchus* and *Diogenesia* (see discussion below), which are regarded as insectivores (see, e.g., Zimicz 2012; Carneiro and Oliveira 2023).

†*Streptorhynchus* gen. nov.

(Fig. 2)

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Etymology. From the Greek “*streptos*” (twisted, in the form of a chain), in reference to its arc-shaped (“S-shaped”; sensu Goin and Carlini 1995; Carneiro et al. 2024b) lower teeth series in the dentary, and “*rhynchus*” (snout), a common terminology for derorhynchids (twisted snout). Gender is masculine.

Diagnosis. Differs from other metatherians in the following combination of features (Fig. 2): Upper molars with mesially positioned ectoflexus (i.e., the deepest part of the ectoflexus is labial to the postparacrista), well-developed parastyle on M3, preparastyle (i.e., cusplular structure resulting from the thickening of the lingual crest of StA) variably present on M1-3, StC distal to the ectoflexus on M1-2 and centrodistally placed on M3, and conules pyramidal in shape, often high and crested. Lower molars with the talonid more labially salient than the trigonid on m1-3, hypoconid not mesiodistally compressed, entoconid pyramidal in shape (i.e., the labial edge is flat and the lingual edge is convex, being slightly twisted on a mesiolabial/distolingual axis, and showing an obliquely oriented wear facet or postentocristid), m4 with a talonid slightly narrower than the trigonid and with a cristid obliqua that has a labial contact with the distal edge of the trigonid.

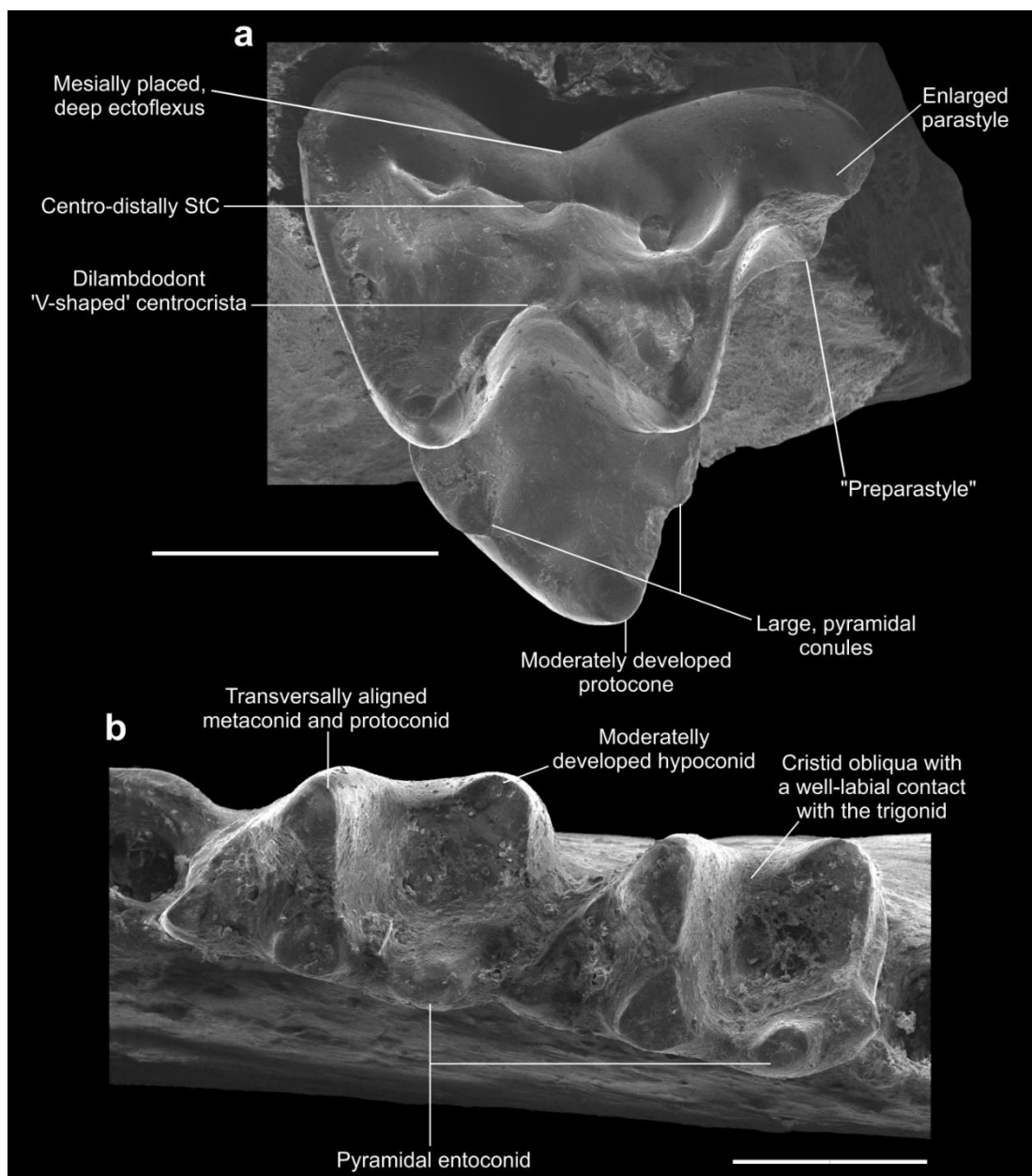


Fig. 2 Diagnostic combination of features of *Streptorhynchus* gen. nov.: **a**, MN 2894(a2)-V, a right M3 in occlusal view; **b**, MN 2886-V, an incomplete right dentary with m2-3 and partially preserved p2 in occlusal view. Scale bars = 1 mm

Type species. *Streptorhynchus tropicalis* sp. nov.

Included species. The type only.

Type Locality and age. Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (Bergqvist et al. 2009).

Early Eocene, Ypresian Stage, Itaboraiense SALMA (sensu Woodburne et al. 2014a).

Comparisons. Species of *Streptorhynchus* differ from those of *Coona* in having a more developed hypoconulid (reduced in *Coona*) and a mandibular symphysis that reaches the level of p1-2 embrasure or the anterior root of

p2 (reaches the anterior root of p3 in species of *Coona*). They differ from species of *Pauladelphys* in having a smaller size, less inflated molars, metaconid shorter (in height) than the protoconid (metaconid and protoconid subequal [in height] in species of *Pauladelphys*), and more developed hypoconulid (reduced in species of *Pauladelphys*).

Streptorhynchus tropicalis differs from species of *Derorhynchus* (Fig. 3) in having relatively deeper and mesially placed ectoflexus on M2-3 (ectoflexus shallow in species of *Derorhynchus*; ectoflexus distally placed in *Derorhynchus* sp.), M3 with an enlarged parastyle (M3 with small parastyle in species of *Derorhynchus*), preparastyle variably present (preparastyle absent in species of *Derorhynchus*), conules relatively more developed (small to reduce in species of *Derorhynchus*), metaconid not labiolingually compressed on m1-2 (metaconid commonly labiolingually compressed on m1-2 in species of *Derorhynchus*), cristid obliqua on m2-3 with a well-labial to fully labial/lateral contact (i.e., at the level of the protoconid apex or at the distolabial border of the protoconid) with the distal border of the trigonid (cristid obliqua on m2-3 with a labial contact [i.e., labial to the metacristid notch and more lingual than the apex of the protoconid] with the distal border of the protoconid in species of *Derorhynchus*), hypoconid not mesiodistally compressed and not distolingually oriented (hypoconid mesiodistally compressed and distolingually oriented in species of *Derorhynchus*), pyramidal entoconid (conical entoconid in species of *Derorhynchus*), m4 with a labial contact of the cristid obliqua with the distal border of the trigonid (m4 with a midline to slightly labial contact of the cristid obliqua with the distal border of the trigonid in species of *Derorhynchus*), m4 with a talonid only slightly narrower than the trigonid (m4 with a talonid clearly smaller than the trigonid in species of *Derorhynchus*), and relatively short (RPM: 0.62-0.67) anterior part of the dentary (relatively long [RPM: 0.80-1.21] anterior part of the dentary in species of *Derorhynchus*).

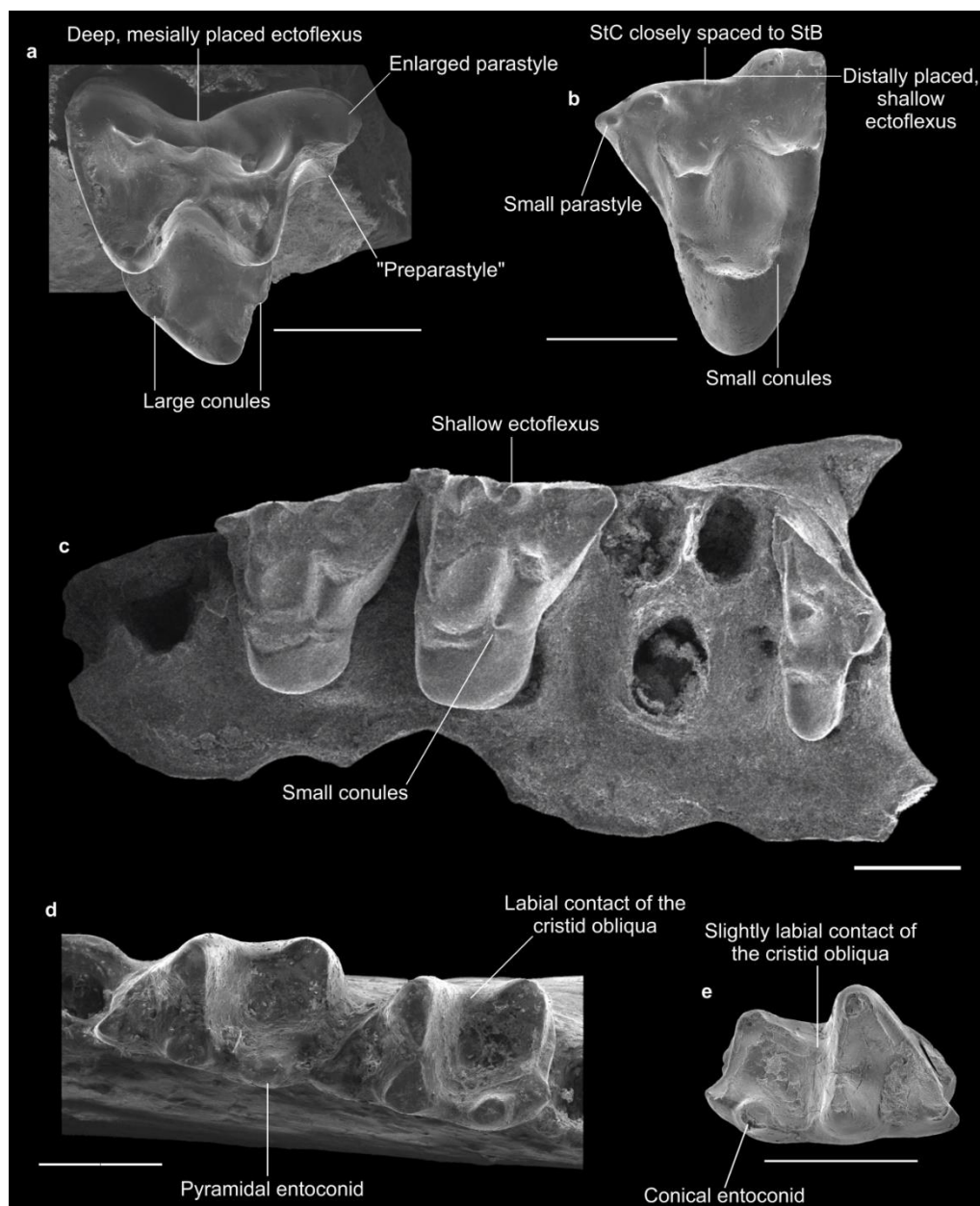


Fig. 3 Comparative upper molar differences between *Streptorhynchus* gen. nov. and *Derorhynchus* Paula Couto, 1952. *Streptorhynchus tropicalis* gen. et sp. nov.: **a**, MN 2894(a2)-V, a right M3 in occlusal view; **d**, MN 2886-V, an incomplete right dentary with m2-3 and partially preserved p2; *Derorhynchus* sp.: **b**, UFRJ-DG 154-M, a left M3 in occlusal view; **e**, MCT.M.4425, a left m3 in occlusal view; *Derorhynchus singularis* Paula Couto, 1952: **c**, MCT.M.803, a left maxilla with M1-2, M4, and alveoli of M3 in occlusolingual view. Scale bars = 1 mm

Streptorhynchus tropicalis differs from species of *Diogenesia* (Fig. 4) in having a symmetrical styler shelf (i.e., mesial and distal lobes of the styler shelf are subequal in width) on M2-3 (asymmetric styler shelf [i.e., mesial and distal lobes are not subequal in width; in the case of *Diogenesia*, the distal lobe is broader than the mesial one] in species of *Diogenesia*), mesially placed ectoflexus on M2-3 (distally placed ectoflexus on M2-

3 in species of *Diogenesia*), StC closely spaced to StD on M1-2 (StC closely spaced to StB on M1-3 in species of *Diogenesia*), conules relatively more developed (small to reduce in species of *Diogenesia*), moderately developed (i.e., protocone and metacone subequal in length; sensu Engelman et al. 2018) protocone (protocone mesio-distally compressed [i.e., protocone shorter [in length] than the metacone; sensu Engelman et al. 2018] in species of *Diogenesia*), cristid obliqua on m3 with a well-labial to fully labial/lateral contact with the distal border of the trigonid (cristid obliqua on m3 with a slightly labial [i.e., only slightly labial to the ‘carnassial notch’/midline of the tooth] to labial contact with the distal border of the trigonid in species of *Diogenesia*), hypoconid not mesiodistally compressed and not distolingually oriented (hypoconid mesiodistally compressed and distolingually oriented on m2-3 [specially on m3] in species of *Diogenesia*), pyramidal entoconid (conical to slightly labiolingually compressed entoconid in species of *Diogenesia*), m4 with a labial contact of the cristid obliqua with the distal border of the trigonid (m4 with a midline to slightly labial contact of the cristid obliqua with the distal border of the trigonid in species of *Diogenesia*), procumbent lower canine (not procumbent in species of *Diogenesia*), and relatively more robust dentary (RDS: 0.45-0.48) (lower and less robust dentary [RDS: 0.34-0.40] in species of *Diogenesia*) (Fig. 4).

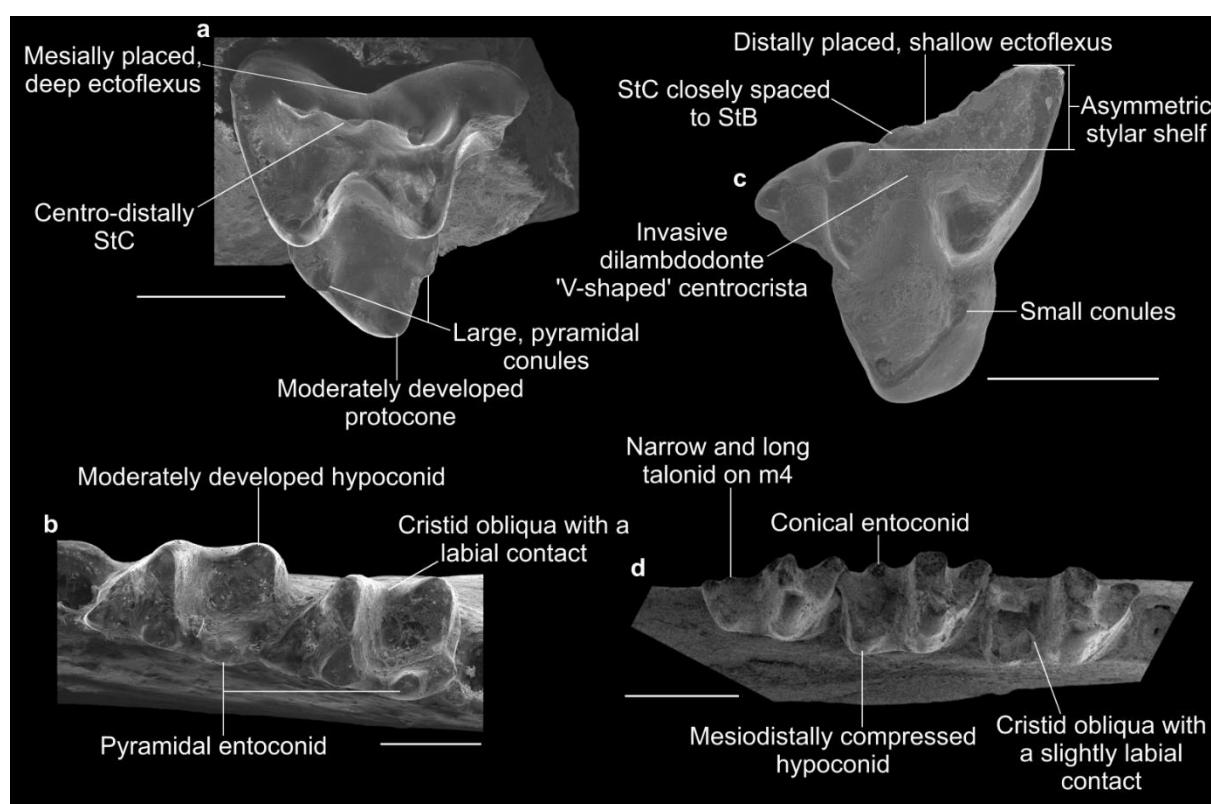


Fig. 4 Comparative upper molar differences between *Streptorhynchus* gen. nov. and *Diogenesia* Oliveira, Carneiro and Goin, 2021. *Streptorhynchus tropicalis* gen. et sp. nov.: **a**, MN 2894(a2)-V, a right M3 in occlusal view; **b**, MN 2886-V, an incomplete right dentary with m2-3 in occlusal view; *Diogenesia* sp.: **c**, MCT.M.4434, a left M2

in occlusal view; *Diogenesia brevirostris* Oliveira, Carneiro and Goin, 2021: **d**, MCT.M.650, holotype, an incomplete right dentary with m2-4 in occlusolabial view. Scale bars = 1 mm

Remarks. *Streptorhynchus* was recovered in the phylogenetic analysis of Oliveira et al. (2021) as the sister taxon of *Coona* and *Pauladelphys* due to the presence of a labiolingually compressed entoconid (in this case, pyramidal in shape) and m4 with a labial contact of the cristid obliqua with the distal border of the trigonid. *Streptorhynchus* differs from *Coona* and *Pauladelphys* mainly by the presence of a larger hypoconulid, which was recovered as a symplesiomorphic state for derorhynchids.

†*Streptorhynchus tropicalis* sp. nov.

(Figs. 5-9)

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Etymology. From the Latin “*tropicalis*” (from the tropics) in reference to its occurrence in Brazilian territory.

Diagnosis. As for the genus.

Holotype. MCT.M.4875, incomplete left maxilla with M1-3, alveoli of M4 and zygomatic arch partially preserved (Fig. 5).

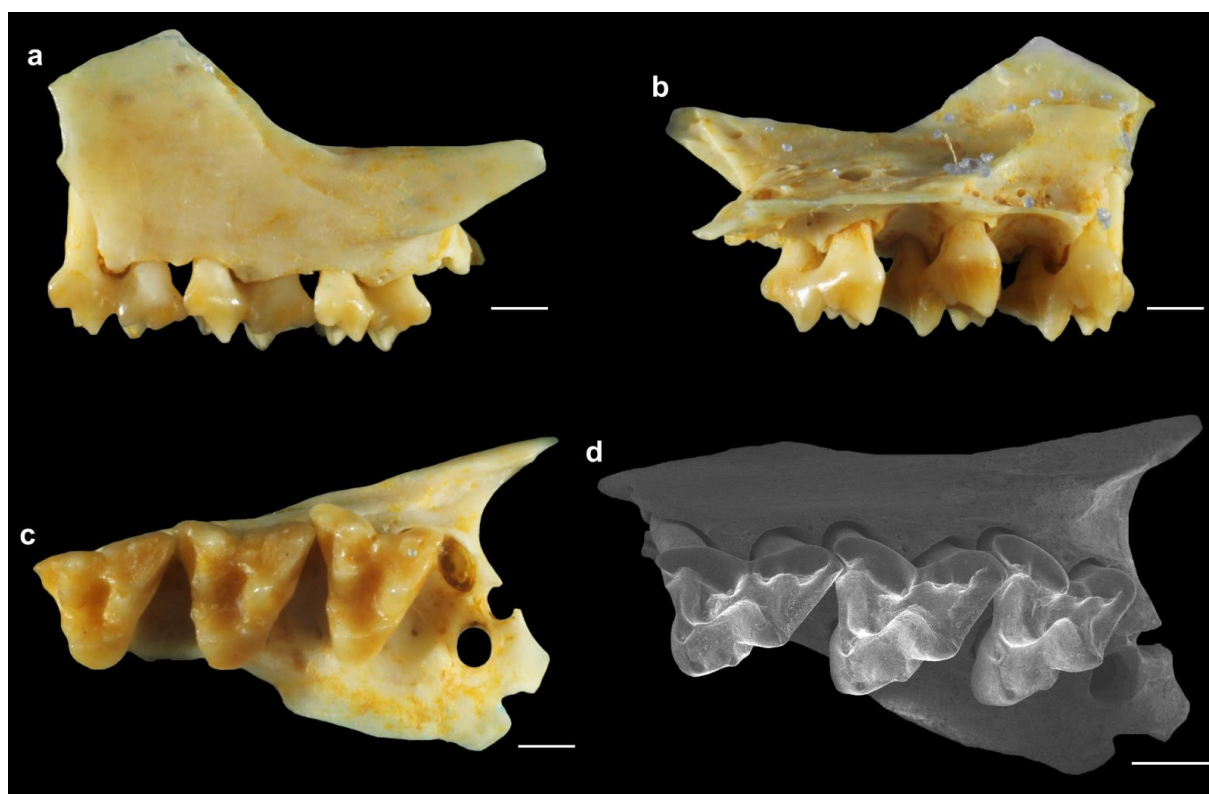


Fig. 5 Specimen MCT.M.4875 (holotype), incomplete left maxilla with M1-3, alveoli of M4, and partially

preserved zygomatic arch, of *Streptorhynchus tropicalis* gen. et sp. nov. shown in (a) labial; (b) occlusal; (c) lingual views; (d) SEM image of this specimen in occlusolabial view. Scale bars = 1 mm

Hypodigm. The holotype; MCN-PV s/n, a right M3; MCN-PV 1795, incomplete left dentary with m2, and alveoli of i2-5, c, p1-3, m1, m3, and anterior alveolus of m4 (Fig. 5); MCT.M.4641, talonid of a left m3; MN 2347-V, posterior fragment of a left dentary with m4, alveoli of m2-3, coronoid process and mandibular condyle; MN 2352-V, left maxilla with M1 and alveoli of M2-3 (Fig. 6b-c); MN 2354-V, incomplete left dentary with p3 (base of the crown) and m1-4 (Fig. 9); MN 2506-V, incomplete left maxilla with M1-3 and alveoli of P3 (Fig. 6a); MN 2886-V, incomplete right dentary with p2, m2-3, anterior root and posterior alveolus of m1, alveolus of c, alveoli of p1, p3, and anterior alveolus of m1 (Fig. 7c-e); MN 2894(a2)-V, right M3 (Fig. 7a-b).

Locality and age. All specimens were collected in the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil. Specimen MCT.M.4641 was collected in the fissure explored in 1949; MN 2347-V, MN 2352-V, MN 2354-V, and MN 2506-V were collected in the fissure explored in 1948-49; MN 2894(a2)-V was donated by Dr. Hilgard O'Reilly Sternberg in 1962 (Paula Couto 1970); MN 2886-V was collected in 1964; MCT.M.4875 was collected in 1967; other specimens have no date and lack stratigraphic data. Early Eocene, Ypresian Stage, Itaboraiense SALMA (Woodburne et al. 2014a).

Description. Maxilla (MCT.M.4875, MN 2506-V; Figs. 6a, 7). The maxilla has very shallow to shallow pits between the upper molars. Based on preserved alveoli and teeth, the M1 is smaller than M2, and M2 is subequal or slightly larger than M3. Based on the alveoli dimensions, the M4 is smaller than M3 (i.e., $M1 < M2 \mid M3 > M4$). The medial alveolus of the upper molars is anteroposteriorly compressed but mediolaterally elongated.

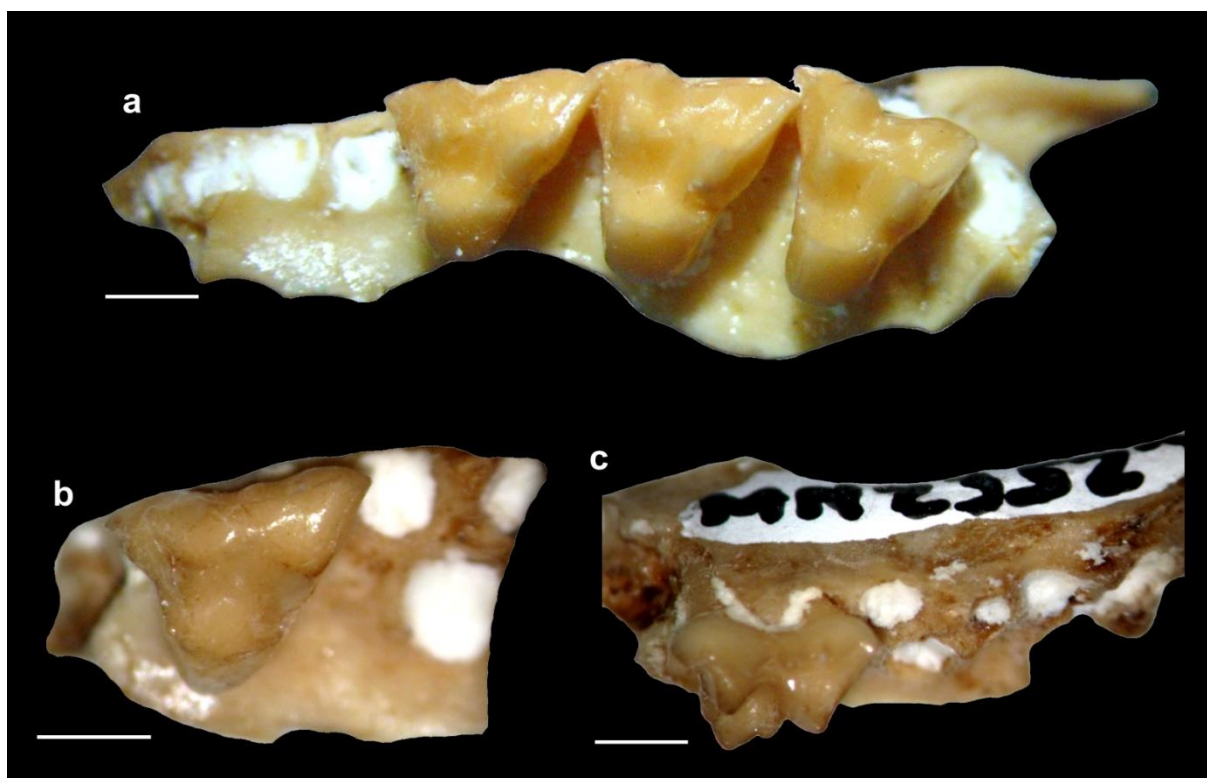


Fig. 6 Upper molars and maxillae of *Streptorhynchus tropicalis* gen. et sp. nov. from the Museu Nacional (MN/UFRJ), Rio de Janeiro, Brazil: **a**, MN 2506-V, an incomplete left maxilla with M1-3, alveoli of P2-3, and partially preserved alveoli of M4 in occlusolingual view; **b-c**, MN 2352-V, a very fragmentary left maxilla with M1 in **(b)** occlusal; **(c)** occlusolabial views. Scale bars = 1 mm. Credits: The image of the specimen MN 2506-V (image **a**) is a property of L.P. Bergqvist (UFRJ)

P2 (MN 2506-V; Fig. 6a). The P2 is known only from its posterior alveolus. Based on the dimensions of its alveoli, P2 is probably narrower (the posterior alveolus of P2 is almost subequal in width with the anterior alveolus of P3) and slightly shorter than P3 ($RLP2/LP3$: ~ 0.80).

P3 (MN 2506-V; Fig. 6a). The P3 is known only from its alveoli. The alveoli of P3 are shorter than M1 (i.e., P3 is not hypertrophied; $RLP3/LM1$: ~ 0.71) and approximately half the width of M1.

M1 (MCT.M.4875, MN 2352-V, MN 2506-V; Figs. 5-6). This molar is longer than wide. The stylar shelf is narrow (i.e., less than 33% of the molar width; sensu Ladevèze et al. 2020), with the distal lobe broader than the mesial one. The ectoflexus is shallow and mesially positioned (i.e., labially situated relative to the postparacrista). There is no evidence of a labial cingulum. The parastyle is slightly lingual to StB (MCT.M.4875, MN 2352-V, MN 2506-V). StA is smaller than StB. A preparastyle (i.e., a “cusp-like” structure resultant from the thickening of the lingual crest of StA) is present in the specimens MCT.M.4875 and MN 2352-V. StB is the largest of the stylar cusps, somewhat labiolingually compressed and labially aligned with the apex of the

paracone. This cusp is subequal to, or slightly taller than the paracone but less voluminous. The StB has a mesiolabial crest that contacts StA and a distolabial crest that contacts StD. StC is distally positioned relative to the ectoflexus, and is small (MN 2506-V) to moderate (MCT.M.4875, MN 2352-V) compared to StB. The StD is subequal in size (MN 2352-V, MN 2506-V) or slightly smaller (MCT.M.4875) than StC and is slightly conical (MCT.M.4875, MN 2506-V) or labiolingually compressed (MN 2352-V). StE is absent (MN 2352-V) or present (MCT.M.4875, MN 2506-V). In order of size, StB > StC | StD > StA > StE. The preparacrista is very short (comparatively longer in specimen MN 2506-V) compared to the postmetacrista and obliquely oriented towards StA. The postmetacrista is approximately 3x longer and is distolabially oriented, having a marked distolabial angle. The centrocrista is dilambdodont, “U-shaped”, and non-invasive on the styler shelf. The centrocrista in specimens MN 2352-V and MN 2506-V is labially at the same level as the labial borders of the paracone and metacone, whereas the one of specimen MCT.M.4875 reaches a slightly more labial position than the labial borders of the paracone and metacone. The paracone is smaller than the metacone (ca 2x; sensu Muizon et al. 2018), slightly oriented on the mesiolabial/distolingual axis (i.e., slightly “twisted”; sensu Goin and Candela 2004; Carneiro and Oliveira 2023), and in a slightly more labial position than the metacone. The paracone and metacone are separated (i.e., protofossa present) and have flat labial edges (i.e., pyramidal shape; sensu Case et al. 2005). The protoconal basin is developed but somewhat labiolingually compressed. The conules are pyramidal in shape, crested, and small (MN 2352-V, MN 2506-V) to moderately developed (MCT.M.4875). The conules are labially aligned, and the metaconule is slightly larger than the paraconule. The protocone is moderate (i.e., subequal in length to the metacone; sensu Engelman et al. 2018) and slightly mesially shifted (less shifted in MN 2352-V and more mesially shifted in MN 2506-V). The postprotocrista is slightly longer than the preprotocrista. The preprotocrista extends to the lingual edge of the paracingulum but is not continuous with it. The protocone has a slight distal expansion (=protoconal bulge; sensu Muizon and Ladevèze 2020; see the specimen MN 2506-V) and lacks protoconal cingula. The paracingulum is short (i.e., it does not reach the level of the protoconal basin; sensu Carneiro et al. 2018), and the metacingulum is also short (i.e., it does not extend beyond the apex of the metacone, being restricted to its distolingual base; sensu Muizon and Ladevèze 2020).

M2 (MCT.M.4875, MN 2506-V; Figs. 5-6a). The M2 differs from M1 in the following features: This tooth is slightly wider than long. The mesial lobe of the styler shelf is wider. The ectoflexus is deeper. The parastyle is more mesially extended. StB has a small mesiolingual crest that contacts the preparacrista in specimen MCT.M.4875. The preparacrista is relatively longer (ca. 2x the length of the postmetacrista) but does not contact StA (its mesiolabial limit coincides with the mesiolabial crest of StB). The postmetacrista is less obliquely oriented. The centrocrista is relatively more invasive on the styler shelf (although not “truly” invasive) and is “V-shaped”. The paracone and metacone are labially aligned. The paracone is slightly oriented on a

mesiolabial/distolingual axis (MCT.M.4875), but this condition is absent in specimen MN 2506-V. The lingual border of the protocone is relatively less robust than the one of M1. The paracingulum is long and continuous with the preprotocrista.

M3 (MCN-PV s/n, MCT.M.4875, MN 2506-V, MN 2894(a2)-V; Figs. 5, 6a, 7a-b). The M3 differs from M1-2 and is identified by the following features: This tooth is wider than long. The mesial lobe is broader, being slightly narrower than the distal lobe (MN 2506-V) or subequal to the latter (MCN-PV s/n, MCT.M.4875, MN 2894(a2)-V). The ectoflexus is deeper. The parastyle is moderately mesially extended (MN 2894(a2)-V) to well extended mesially (MCN-PV s/n, MCT.M.4875, MN 2506-V). The “preparastyle” is present in specimens MCT.M.4875 and MN 2894(a2)-V, with this feature relatively more developed in the latter. StB is smaller than the paracone. StC is relatively closer to StD. The preparacrista is relatively longer (about 1.8x the length of the postmetacrista), vertically oriented, and reaches StB (this crest contacts the mesiolingual crest of StB). The postmetacrista is slightly obliquely oriented (MCN-PV s/n) or vertically oriented (MCT.M.4875, MN 2506-V, MN 2894(a2)-V), and its distolabial angle can be developed (MCN-PV s/n) or practically absent (i.e., rounded distolabial edge of the postmetacrista; see MCT.M.4875, MN 2506-V, MN 2894(a2)-V). The paracone is relatively more developed than on M1-2 but is still smaller than the metacone (the specimen MN 2894(a2)-V displays a paracone that is only slightly shorter than the metacone). The centrocrista is dilambdodont and non-invasive on the stylar shelf. The conules are relatively more developed than on M1-2 (the specimen MCN-PV s/n displays a relatively more advanced wear of the protocone, protocristae and conules, not allowing a confident identification of these structures). The protocone is relatively more mesiodistally compressed in comparison with those of M1-2. The paracingulum has a well-developed crest lingual to StA, similar to a cusp (preparastyle) in some specimens (MN 2506-V and MN 2894(a2)-V). The metacingulum is reduced to absent.

M4 (MCT.M.4875, MN 2506-V; Figs. 5 and 6a). The M4 is known only by its alveoli. Based on the alveoli, this tooth should be slightly smaller than the M3. The specimen MN 2506-V shows only the anterolateral alveolus of M4, whereas the specimen MCT.M.4875 preserves all M4 alveoli (anterolateral, posterolateral, and medial).

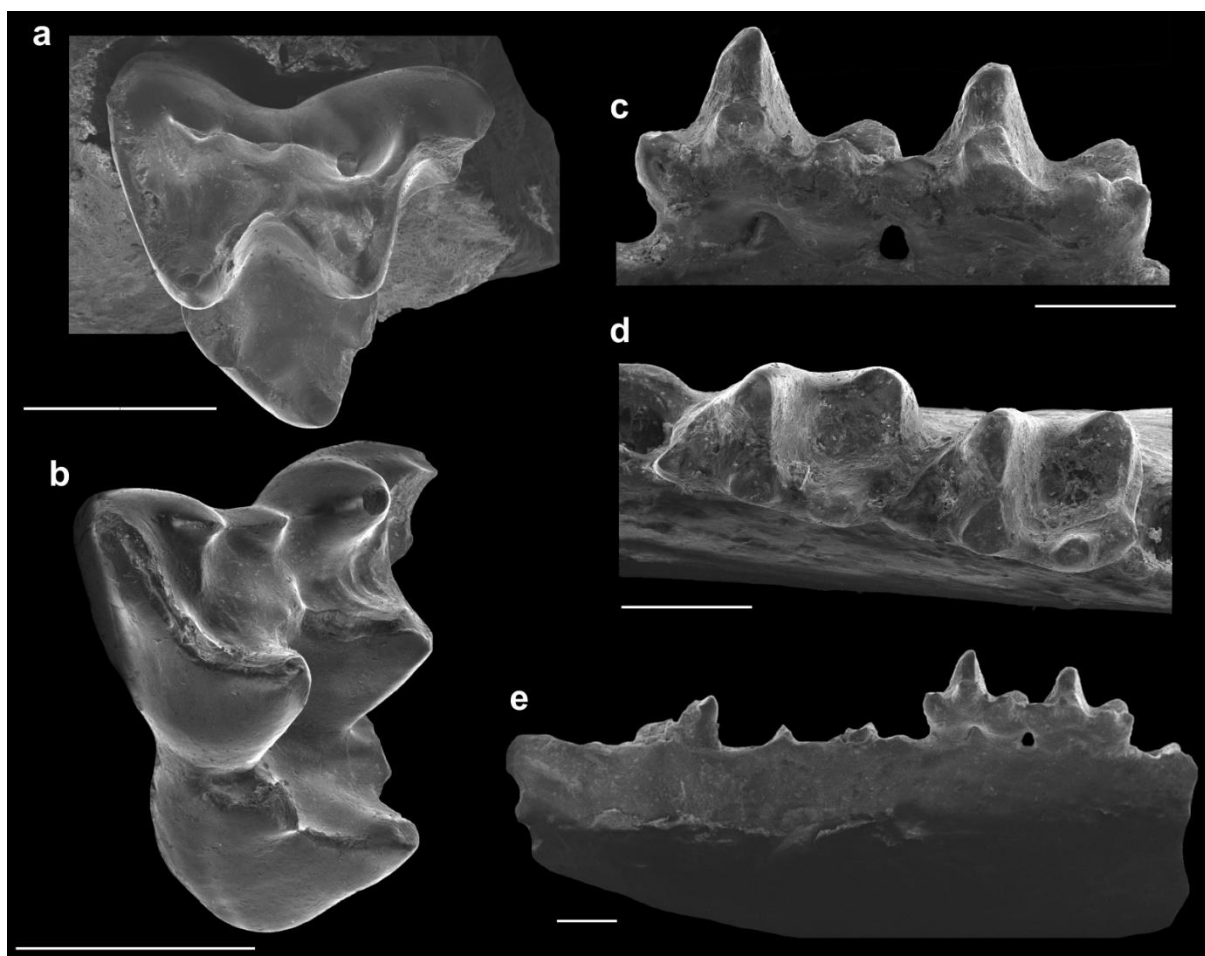


Fig. 7 SEM images of some specimens of *Streptorhynchus tropicalis* gen. et sp. nov. of the Museu Nacional (MN/UFRJ): **a-b**, MN 2894(a2)-V, a right M3, shown in **(a)** occlusal; **(b)** occlusodistal views; **c-e**, MN 2886-V, an incomplete right dentary with m2-3 and partially preserved p2, shown in **(c)** lingual; **(d)** occlusal; **(e)** labial views. Scale bars = 1 mm

Dentary (MCN-PV 1795, MN 2347-V, MN 2354-V, MN 2886-V; Figs. 7e, 8-9). The dentary is not robust (DHm3-4: 3.31-3.52 mm; RDS: 0.45-0.48; i.e., RDS lower than 0.60; sensu Carneiro and Oliveira 2023). The mandibular symphysis is not fused and extends ventrally below the anterior alveolus of the p2 (MCN-PV 1795 and MN 2886-V). The anterior part of the dentary is angled (i.e., anterocranially oriented; MCN-PV 1795 and MN 2886-V). Two mental foramina are identified: the anterior one, ventrally positioned below the diastema of p1-2 (MN 2886-V) or below p2 (MCN-PV 1795), and the posterior one, ventrally positioned below the anterior alveolus of m1. These foramina are subequal in size. A diastema between p1-2 is present in specimen MN 2886-V (Ldt: 0.32 mm) but is reduced to absent in specimen MCN-PV 1795. The premolar/molar series is well-arched/sinuuous (sensu Goin and Carlini 1995; Carneiro et al. 2024b) in most specimens (except in specimen MN 2354-V, in which it is relatively less arched/sinuuous). The dentary is uneven in height at the level of the p3-

m1, in which one of these teeth is asymmetrically positioned (i.e., the alveoli are not positioned at the same height in the dentary, one being in a more ventral position and the other in a more cranial position). This increase in the height is weakly developed (MN 2354-V, MN 2886-V) or well developed (MCN-PV 1795). In some specimens, the p3 is asymmetrically positioned (i.e., the anterior alveolus is more ventrally positioned than the posterior one, e.g., MN 2886-V) or both p3 and m1 are asymmetrically placed (MCN-PV 1795). The retro-molar space is long (i.e., 50% or more of the length of the m4; sensu Oliveira and Goin 2015; see MN 2347-V and MN 2354-V; Lrt: 1.00-1.25 mm). The posterior edge of the dentary ventral to the coronoid process is angled (MN 2347-V, MN 2354-V; sensu Muizon et al. 2018). The mandibular foramen is well-developed and positioned anterior to the cranioventral axis of the coronoid process (MN 2347-V). The angular process is medially oriented and weakly developed (MN 2347-V). The coronoid process is complete in specimen MN 2347-V. The mandibular condyle is cylindrical and positioned well above the molar series (MN 2347-V).



Fig. 8 Specimen MCN-PV 1795, incomplete left dentary with m2, and alveoli of i2-5, c, p1-3, m1, m3, and anterior

alveolus of m4 of *Streptorhynchus tropicalis* gen. et sp. nov. shown in (a) occlusal; (b) lingual; (c) labial views.

Scale bars = 1 mm

Lower incisors (MCN-PV 1795; Fig. 8). The lower incisors are known only by their alveoli. The i2-3 are hypertrophied and subequal in size. The i3 is staggered to the i2. The i4 is smaller than the i2-3. The i5 is reduced, being much smaller than the i2-4, and is separated from the lower canine by a bony trabecula.

Lower canine (MCN-PV 1795; Fig. 8). The lower canine is known only by its alveolus. This tooth is well-developed and apparently procumbent (based on its alveolus shape).

Lower premolars (MCN-PV 1795, MN 2354-V, MN 2886-V; Figs. 8-9). The p1 is known only from its alveoli. The p1 is moderately smaller than the p2 and is obliquely oriented. The p2 is slightly smaller than p3 and is aligned with the premolar series axis. The p2 is partially preserved in specimen MN 2886-V, showing a small distal cusp. The p3 (MN 2354-V) is slightly inflated and has a somewhat oval shape. The only known p3 of this species is preserved only by its crown base and is smaller (i.e., not hypertrophied) than the m1 in specimen MN 2354-V. However, its alveoli are longer than m1 (except in specimen MN 2354-V, in which the alveoli of p3 are shorter than m1). The premolar series shows a moderate growth in size ($p1 < p2 < p3$).

m1 (MN 2354-V; Fig. 9). The m1 is smaller than m2-3, but larger than m4. The trigonid is moderately taller (ca. 1.5x; sensu Ladevèze et al. 2020), subequal in length, and narrower than the talonid. The paraconid is the smallest cusp of the trigonid and is lingually aligned with the metaconid. The bases of the paraconid and metaconid are in slight contact. The metaconid is slightly distal and smaller than the protoconid and has a moderately developed postmetacristid. The protoconid is the largest cusp and has a mesiolingually oriented (=angled) preprotocristid. The metacristid (i.e., postprotocristid + premetacristid) is transversely oriented, closing the trigonid distally. The cristid obliqua has a completely labial/lateral contact with the distal edge of the trigonid. The hypoflexid is reduced, and a labial cingulid is absent. The hypoconid is more labially salient than the trigonid and is not mesiodistally compressed. The posthypocristid is slightly obliquely oriented. The preentocristid is short and poorly developed. The entoconid is well developed, practically occupying the entire lingual margin of the talonid, is pyramidal shape (i.e., the lingual edge is somewhat convex, and the labial edge is flat), and is transversely aligned and taller than the hypoconid. The postentocristid is absent. The hypoconulid is small, much shorter (in height) than the entoconid, and distolabially to the entoconid. The precingulid is long (i.e., it reaches the labial base of the protoconid; sensu Muizon et al. 2018), and the postcingulid is poorly developed.

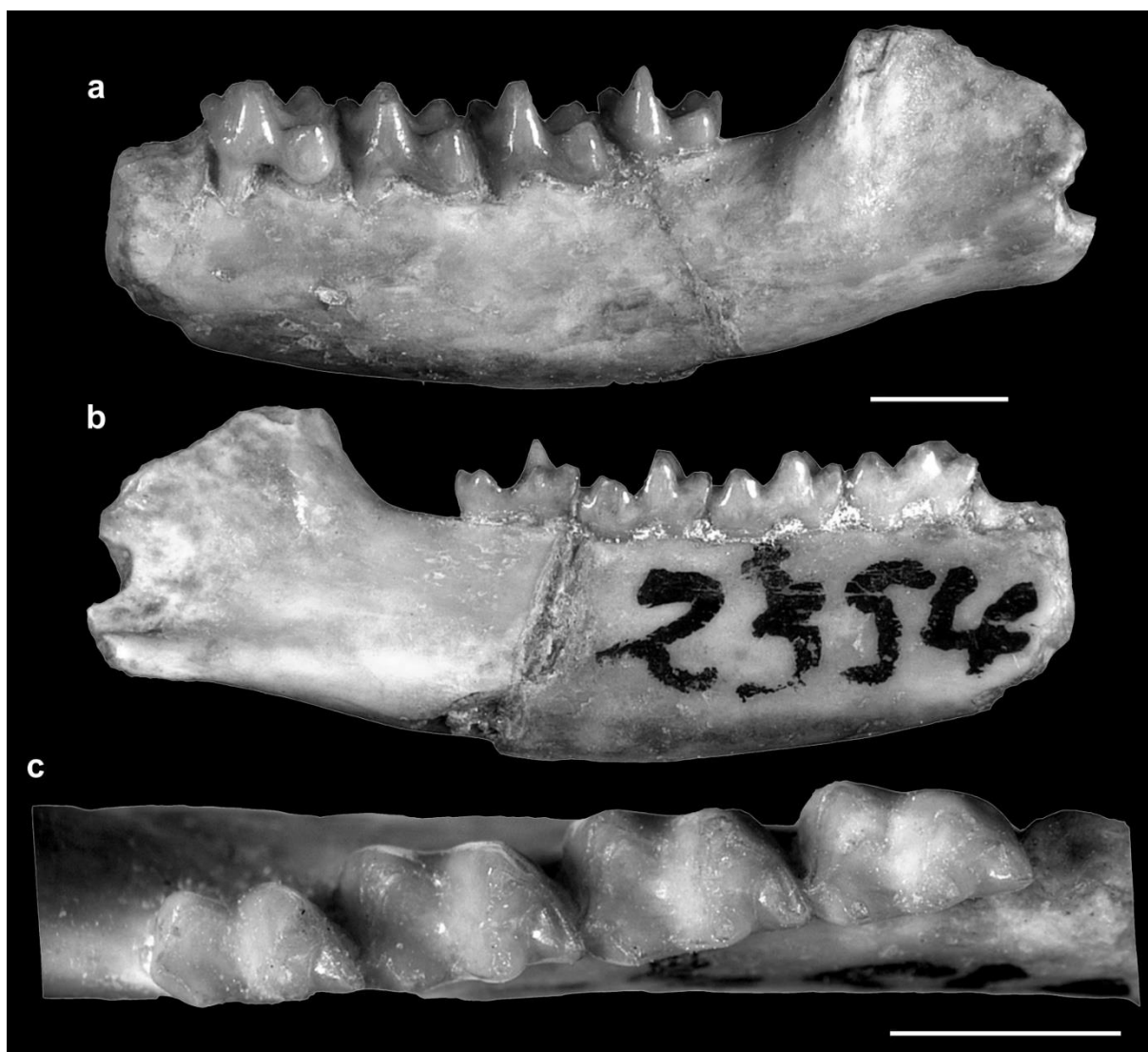


Fig. 9 Specimen MN 2354-V, an incomplete left dentary with m1-4 and damaged p3, of *Streptorhynchus tropicalis* gen. et sp. nov. shown in (a) labial; (b) lingual; (c) occlusal views. Scale bars = 2 mm

m2 (MCN-PV 1795, MN 2354-V, MN 2886-V; Figs. 7c-e, 8-9). The m2 differs from m1 and is identified by the following features: The trigonid is comparatively more mesiodistally compressed. The trigonid is mesially extended (MN 2886-V) or somewhat mesiodistally compressed (MCN-PV 1795, MN 2354-V). The paraconid is less mesially oriented. The metaconid is transversely aligned with the protoconid. The cristid obliqua has a very labial (MN 2354-V) or complete labial/lateral contact (MCN-PV 1795, MN 2886-V). The hypoconid is more robust. The posthypocristid is more transversely oriented. The postcingulid is poorly developed (MN 2354-V, MN 2886-V) to reduced (MCN-PV 1795).

m3 (MCT.M.4641, MN 2354-V, MN 2886-V; Figs. 7c-e, 9). The m3 differs from m1-2 and is identified by the following features: The trigonid is relatively more developed mesially and taller. The trigonid is mesially

developed (MN 2886-V) or somewhat mesiodistally compressed (MN 2354-V). The cristida obliqua has a very labial contact with the distal edge of the trigonid. The hypoconid is relatively more mesio-distally compressed than that of m2 (MN 2354-V, MN 2886-V), although it remains relatively robust. The entoconid occupies the entire lingual edge of the talonid (MN 2354-V) or only part of it (MN 2886-V). The entoconid is relatively less developed than those of m2. The hypoconulid is smaller than the entoconid (a more evident reduction is observed in specimen MN 2886-V). In specimens MN 2354-V and MN 2886-V, the hypoconulid shows a moderate to advanced state of wear. Nevertheless, specimen MCT.M.4641 displays an unworn hypoconulid that is lower crowned than the entoconid but is not reduced. The postcingulid is relatively more developed.

m4 (MN 2347-V, MN 2354-V; Fig. 9). The m4 differs from m1-3 and is identified by the following features: The m4 is slightly shorter and narrower than the m3. The trigonid is relatively taller. The talonid is slightly narrower than the trigonid (MN 2347-V) or almost subequal in width (MN 2354-V). The cristid obliqua has a labial contact with the distal edge of the trigonid (i.e., below the protoconid apex). The entoconid is well developed, being higher than the hypoconid and slightly lower (MN 2347-V) or subequal in height to the hypoconulid (MN 2354-V). The hypoconulid is lingually positioned, although in a relatively more labial position relative to the entoconid.

Measurements. See Table 2.

Table 2 Dental measurements (in mm) of *Streptorhynchus tropicalis* gen. et sp. nov. The holotype is highlighted in bold. For lower molars, the measurements are expressed in the following order: trigonid length, (taloid dimensions – length or width), and – total length. **L**, length; **M/m**, molar; **P/p**, premolar; **W**, width; **()**, taloid dimensions; **[]**, length of premolar alveoli; **~**, incomplete tooth, alveoli or molar series; *****, based on alveoli dimensions

[illegible]

MN														
235					2.2	2.0								
2-V					5	2								
MN														
250					2.2	2.0	2.2	2.2	2.0	2.3				~7.
6-V					9	9	1	7	8	3				90
MN														
289														
4(a									1.9	2.2				
2)-									5	7				
V														

	Lp1	Lp2	Wp 2	Lp3	Wp 3	Lm 1	W m1	Lm 2	W m2	Lm 3	W m3	Lm 4	W m4	Lm 1-4
MC								1.0						
N-								6	1.1					
PV								(0.8	4					~7.
179								1) -	(1.3					22
5								1.8	5)					
								7						
MC											1.1			
T.										(0.8	6			
M.4										3)	(1.2			
641											1)			
												1.0		
												4	1.0	
MN												(0.6	6	
234												9) -	(0.8	
7-V												1.7	7)	
												3		
						1.0		0.9		1.0		1.0		
						5	1.0	9	1.2	4	1.2	0	1.0	
MN			~1.	~0.		(0.8	8	(0.8	5	(0.8	4	(0.7	4	7.3
235			33	63		1) -	(1.2	9) -	(1.3	9) -	(1.2	2) -	(0.9	9
4-V						1.8	9)	1.8	9)	1.9	9)	1.7	8)	
						6		8		3		2		

			1.0	1.1		
	~1.		7	1.1	3	1.1
MN	45	0.5	(0.8	3	(0.8	6
288	[1.7	6	2) -	(1.2	6) -	(1.2
6-V	5*]		1.8	7)	1.9	2)
			9		9	

Estimated body masses. Body masses range from 52 g to 120 g.

Remarks. The specimens of *Streptorhynchus tropicalis* gen. et sp. nov. (MN 2347-V, MN 2354-V, MN 2886-V) were initially identified as *Monodelphopsis travassosi* by Paula Couto (1962, 1970) and Marshall (1987) or as ‘Didelphidae incertae sedis’ (MN 2352-V, MN 2506-V and MN 2894(a2)-V) by Paula Couto (1962, 1970) and Marshall (1987). In addition, Marshall (1987) considered the specimen MN 2506-V as the upper dentition of *Mirandatherium alipioi*.

Oliveira (1998 [unpublished data]) also identified the specimens MN 2352-V and MN 2894(a2)-V as the upper dentition of *Mirandatherium alipioi*. In the same study, Oliveira (EVO) identified the specimens MCN-PV 1795 and MN 2886-V as *Streptorhynchus tropicalis* gen. et sp. nov. (“*Chaishullenia* sp.” nomem nudum); the specimen MN 2354-V as *Austropedionomys marshalli*; and the specimen MN 2347-V was tentatively identified as *Monodelphopsis travassosi*. Bergqvist et al. (2005), following the taxonomic concept of Oliveira (1998 [unpublished data]), presented the first images of *S. tropicalis* (specimens MN 2886-V and MN 2506-V) in the literature. Later, Goin et al. (2009) were the first to formally consider the specimen MN 2506-V as a derorhynchid, identifying it as *Derorhynchus* sp.

The specimens of *Streptorhynchus tropicalis* gen. et sp. nov. from the MN comprised most of the hypodigm of this species. Unfortunately, the fire that hit the institution in September 2018 may have destroyed most of the specimens of this taxon. The specimen MN 2347-V survived the fire (but very burned), as it was visualized (from an image) and identified by the first author of this study (LMC).

Moreover, *Streptorhynchus tropicalis* displays some degree of phenotypic plasticity, especially related to the shape of its dentary. The increase in the height of the dentary ventral to p3-m1 is remarkably different between the studied specimens: the dentary in specimen MN 2354-V does not display an evident uneven in height below p3-m1, whereas specimen MCN-PV 1795 exhibits an evident uneven in height. In addition, the crown of the specimens can be relatively more inflated (MCN-PV 1795, MN 2354-V) or less inflated (MN 2886-V). Specimens MCN-PV 1795 and MN 2354-V display relatively more mesiodistally compressed trigonids, and more robust hypoconids and entoconids compared to specimen MN 2886-V.

The upper molars (MCT.M.4875, MN 2352-V, MN 2506-V, and MN 2894(a2)-V) are assigned to this taxon based on their compatible size and presence of a “preparastyle” (a condition observed in derorhynchids’ upper molars). Therefore, these upper molars are assigned to a derorhynchid (*Streptorhynchus tropicalis*).

The great distance between the apex of the protocone and the apex of the centrocrista (i.e., broad protoconal basin) observed in the above-mentioned specimens suggests a broad talonid on lower molars (see occlusal relations in, e.g., Zimicz 2012). Species of *Derorhynchus* have labiolingually compressed protoconal basins, suggesting comparatively narrower talonids than those of *Streptorhynchus* and *Diogenesia*. The more “U-shaped” centrocrista of the assigned upper molars are compatible with the relatively more robust (i.e., not mesiodistally compressed) hypoconids of *S. tropicalis*. The centrocrista of *Derorhynchus* sp. and *Diogenesia* sp. are clearly more “V-shaped”, as their hypoconids are more mesiodistally compressed, having a narrow and pinched apex. The mesiodistally compressed and distolabially oriented hypoconids of *Derorhynchus* and *Diogenesia* suggest a mesiodistally compressed metacone, an observed condition on the upper molars assigned to these taxa (see Figs. 3-4). These conditions are not observed in the upper molars assigned to *S. tropicalis*. The comparatively less mesiodistally compressed metacone is compatible with the comparatively more robust and less distally oriented hypoconids of *S. tropicalis*.

Moreover, the enlarged entoconids of *S. tropicalis* indicate comparatively longer postprotocristae than preprotocristae, especially on M1-2. In M3, this difference is less evident. The m3 of *S. tropicalis* has comparatively less developed entoconids than m1-2, a compatible morphological pattern observed on the assigned upper molars. Furthermore, the specimens MCT.M.4875, MN 2352-V, MN 2506-V, and MN 2894(a2)-V are morphologically compatible with the lower molars of *S. tropicalis*.

The upper molars (MN 2352-V, MN 2506-V and MN 2894(a2)-V) of *Streptorhynchus tropicalis* were previously assigned as *Mirandatherium alipioi* (this hypothesis was previously proposed by Marshall 1987 based on the specimen MN 2506-V); however, this assignment cannot be made due to their smaller size (LM1-4: 7.83 mm to 7.90 mm; *Mirandatherium alipioi* Lm1-4: 9.40 mm to 10.00 mm) and contrary molar series pattern. In *M. alipioi*, the lower molars increase in size from m1 to m3, which indicates a similar pattern for upper molars. In derorhynchids, the M1 is the longest tooth, whereas the M3 is the shortest. In addition, the hypoconids of *M. alipioi* have a rounded apex, suggesting a comparatively less “V-shaped” centrocrista, and are clearly more robust and longer, indicating well-spaced paracone and metacone.

The specimen MN 2347-V, a posterior fragment of a left dentary with the m4, the coronoid process, and the mandibular condyle, was assigned to *Monodelphopsis travassosi* (see Paula Couto 1962). However, this specimen has a labial contact of the cristid obliqua and a talonid slightly shorter than the trigonid (see Table 1). In contrast, the m4 of *M. travassosi* (MN 2351-V; see Paula Couto 1962; and Carneiro 2023 [unpublished data])

has a mesially oriented preprotocristid (this condition is observed on m1-4 of *Monodelphopsis*, representing an “autapomorphy” of this taxon; see Carneiro 2023 [unpublished data]), much lower and shorter talonid than the trigonid, and reduced talonid cuspids. The specimen MN 2354-V was identified as a *Monodelphopsis travassosi* by Marshall (1987). Still, this specimen also differs from specimen MN 2351-V by the absence of a mesially oriented preprotocristid and the presence of enlarged, pyramidal-like entoconids. In resume, these specimens should be assigned to *Streptorhynchus tropicalis*.

Results of the phylogenetic analysis

The phylogenetic analyses recovered a single most parsimonious tree (Score: 1967; CI: 0.367; RI: 0.610) (Fig. 10). *Streptorhynchus* gen. nov. was recovered as the sister taxon of *Pauladelphys* and *Coona* (i.e., Cooninae new subfamily) based on the presence of a pyramidal entoconid (character 180, state 2) and a labial contact of the cristid obliqua with the distal border of the protoconid on m4 (ch. 210, state 1). *Pauladelphys* and *Coona* were recovered as sister taxa based on the presence of an entoconid much taller than the hypoconid (ch. 178, state 2) and a reduced hypoconulid (ch. 191, state 1).

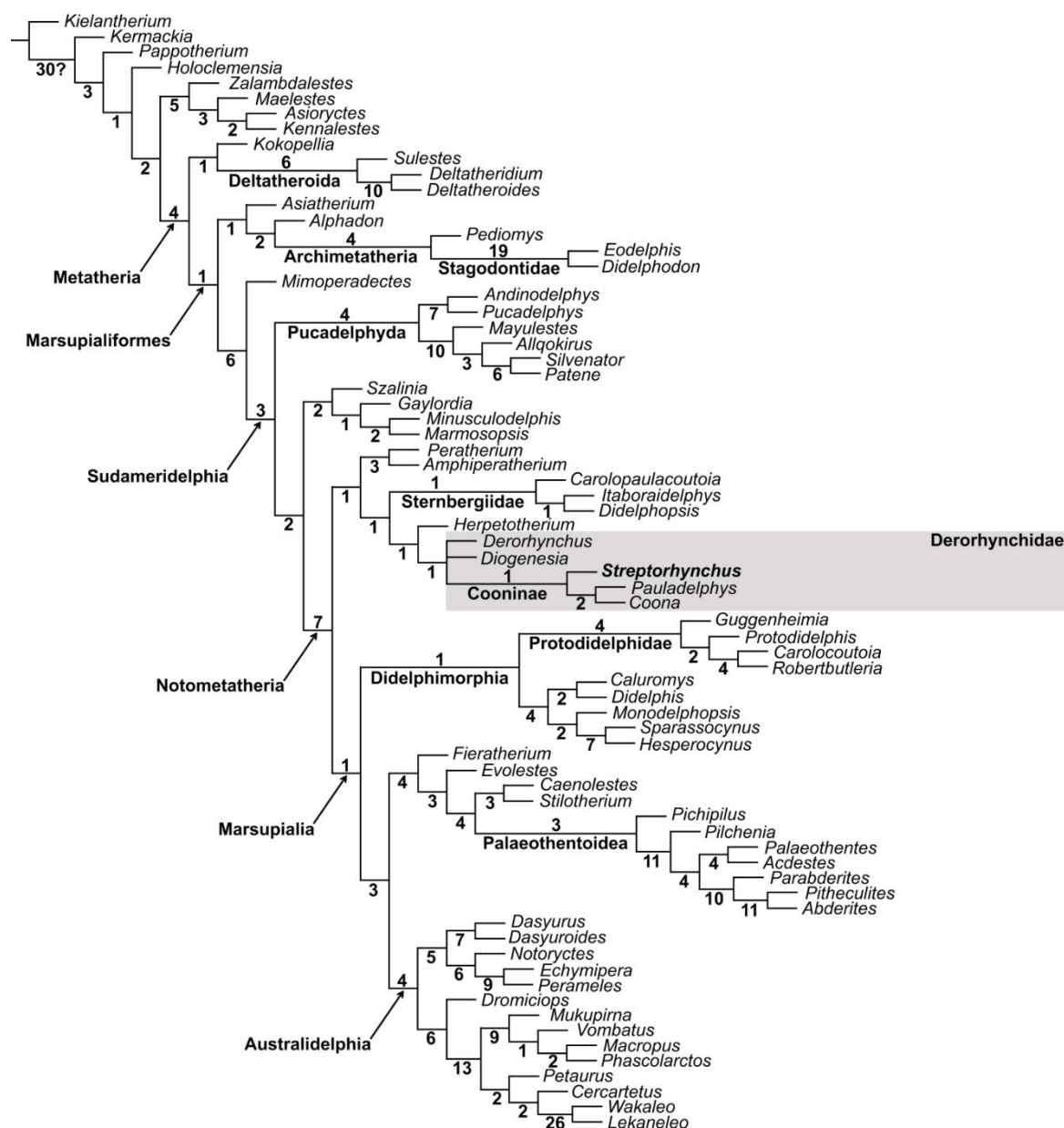


Fig. 10 Consensus tree of the single most parsimonious trees found in the phylogenetic analyses (Score: 1967; CI: 0.367; RI: 0.610). Numbers below and above the branches indicate Bremer support values. *Streptorhynchus* gen. nov. is highlighted in bold. Derorhynchidae is highlighted in grey

Results of PCA analyses

The first PCA shows a total of about 88% of data explanation based on PC1 (72%) and PC2 (17.9%; Fig.11a), with the Lm and Wtri the variables that better explain the data variation of PC1 (about 25% and 22%, respectively) and Ltri and Ltal variables better explaining the data variation of the PC2 (about 63% and 28%).

These results highlight that the lower molars of derorhynchids are similar in their measurements and morphometric patterns, except for *Diogenesia brevirostris*, which is clearly smaller (allometry) compared to other Itaboraí's derorhynchids (Fig. 11a).

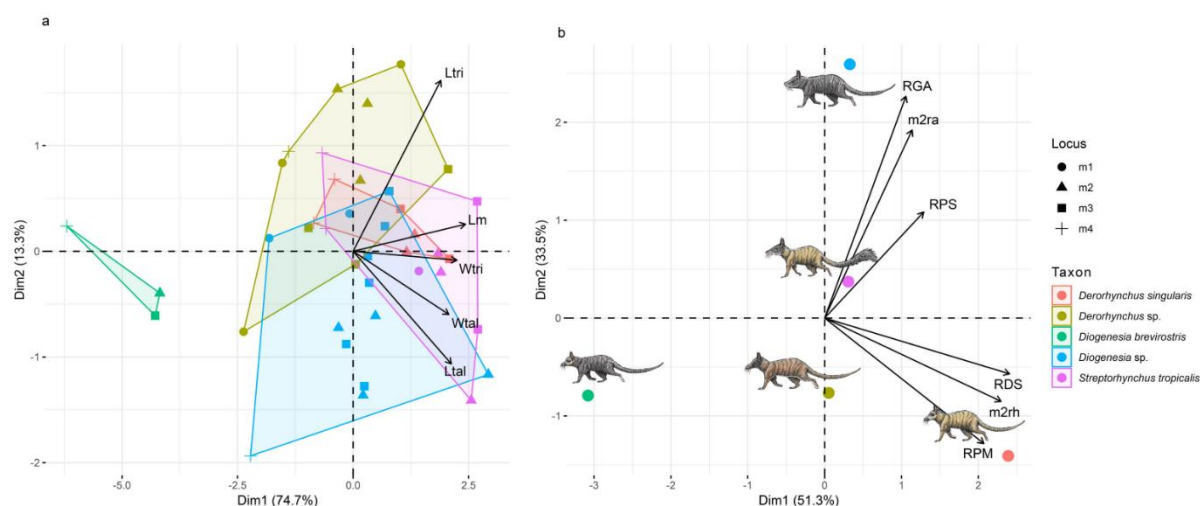


Fig. 11 Principal component analyses (PCA) of some morphometric and morphofunctional indexes based on lower molar measurements for *Streptorhynchus tropicalis* gen. et sp. nov., *Derorhynchus singularis* Paula Couto, 1952, *Derorhynchus* sp., *Diogenesia brevirostris* Oliveira et al., 2021; and *Diogenesia* sp. **a**, First PCA with lower molar's loci (m1, m2, m3, and m4) morphometric indexes (Lm, Ltri, Ltal, Wtri, and Wtal); **b**, second PCA with six morphofunctional indexes (m2ra, m2rh, RGA, RDS, RPM, and RPS). **A**, area; **BM**, body mass; **dt**, diastema/diastemata; **H**, height; **L**, length; **m1-4**, lower molar series length; **m**, lower molar with the numbers corresponding to its positioning (m1-4); **p**, lower premolars with the numbers corresponding to its positioning; **p1-3**, lower premolar series length (p1-3); **PC**, principal component; **R/r**, ratio; **RDS**, relative dentary shape ($\text{DH}/\text{Lm1-4}$); **RGA**, relative grinding area ($2\sqrt{\text{Atal}/\text{Lm4tri}}$); **RPM**, length of the anterior part of the dentary ($\text{Lp1-3} + \text{dt}$) by the length of the lower molar series (Lm1-4); **RPS**, relative premolar shape ($\text{Wp3}/3\sqrt{\text{BM}}$); **tri**, trigonid; **W**, width. Schematic drawings are not at scale. Credits: The artistic drawings of Itaboraí's metatherians were made by Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com)

The PCA2 shows a total of 84.8% of data explanation based on PC1 (51.3%) and PC2 (33.5%; Fig.11b), with RDS (about 30%), m2rh (about 28%), and RPM (about 22.5%) representing the variables that better explain the data variation of PC1, and RGA (about 40%) and m2ra (about 29%) representing the variables that better explain the data variation of PC2.

The results of the PCA2 reveal that *Streptorhynchus tropicalis* and *Diogenesia* sp. are morphofunctionally

more similar in comparison with other derorhynchids from the Itaboraí Basin. These two taxa are discriminated from other sympatric derorhynchids by the relatively more developed talonids on m2 and m4 (m2ra: 0.86-0.95 [Average: 0.90] and 1.05, respectively; RGA: 0.74-0.84 [Average: 0.79] and 1.02, respectively; see Table 3). Nevertheless, *Streptorhynchus tropicalis* is discriminated from other derorhynchids (except for *Derorhynchus singularis*) on its relatively higher dentary (RDS: 0.45-0.48 [Average: 0.47]), and *Diogenesia* sp. is discriminated by its relatively more developed talonid on m2 and m4 (m2ra: 1.05; RGA: 1.02). *Streptorhynchus tropicalis* is also discriminated from *Diogenesia* sp. by its longer anterior part of the dentary (RPM: 0.62-0.67 [Average: 0.64]; RPM *Diogenesia* sp.: 0.58-0.64 [Average: 0.61]) and relatively higher talonid on m2 (m2rh: 0.64-0.80 [Average: 0.73]; m2 rh *Diogenesia* sp.: 0.67). These differences resulted in the righter and lower placement of *S. tropicalis* compared with *Diogenesia* sp. in morphospace (see Fig. 11b).

Moreover, *Diogenesia* is also discriminated from other derorhynchids by its relatively higher trigonids (m2rh: 0.56 and 0.67 for *D. brevirostris* and *Diogenesia* sp., respectively). *Diogenesia brevirostris* is discriminated by its relatively smaller talonid on m2 (m2ra: 0.53; RGA: 0.62), higher trigonid on m2 (m2rh: 0.56), and short anterior part of the dentary (RPM: 0.52), resulting on its extreme left and lower placement in the morphospace.

Derorhynchus singularis is discriminated by its longer anterior part of the dentary (i.e., the part that comprehends lower incisors, canine, and premolars, including diastema(ta); RPM: 1.21) and more robust dentary (RDS: 0.58), resulting on its rightest and lowest placement in the morphospace. The RPM of *Derorhynchus singularis* is about twice higher than those of other derorhynchids (see Table 3). *Derorhynchus singularis* is also discriminated from *Derorhynchus* sp. by its more labiolingually compressed premolars (RPS: 1.65; RPS *Derorhynchus* sp.: 1.92; see Table 3).

Derorhynchus sp. is discriminated from other derorhynchids by its relatively longer anterior part of the dentary (RPM: 0.80), smaller talonid on m4 (RGA: 0.57), and relatively higher trigonid on m2 (m2rh: 0.70-0.71 [average: 0.70]), resulting on its left and lower placement in the morphospace. This taxon is morphofunctionally more similar to *Diogenesia brevirostris* than to any other derorhynchid from the Itaboraí Basin; nevertheless, *D. brevirostris* is morphofunctionally more specialized than *Derorhynchus* sp.

Discussion

Systematic affinities of *Streptorhynchus*

Streptorhynchus gen. nov. is a derorhynchid based on the following combination of features: the presence of moderate styler shelf, developed StB, StC, and StD; dilambdodont “V-shaped” centrocrista, moderate protocone, protocone with distal expansion (=protoconal bulge; sensu Muizon and Ladevèze 2020), transversally aligned metaconid and protoconid, large entoconid, procumbent lower canine, hypertrophied and semi-procumbent i2-3, elongated anterior part of the dentary, dentary with an increase in the height ventral to p3-m1, and convex/angled posterior border of the dentary.

Streptorhynchus is the sister taxon of *Coona* and *Pauladelphys* (i.e., Cooninae new) based on the presence of relatively more bunodont crowns, pyramidal or labiolingually compressed entoconid and m4 with a labial contact of the cristid obliqua with the distal border of the trigonid. However, *Streptorhynchus* differs from these two in the presence of relatively more developed hypoconulids on lower molars.

Streptorhynchus tropicalis and *Coona pattersoni* are morphologically very similar (e.g., m4 with a talonid slightly narrower than the trigonid, m4 with a cristid obliqua with a labial contact with the distal border of the trigonid). However, the more significant difference between these two taxa is related to the size of the hypoconulid. In *Streptorhynchus*, the hypoconulid is subequal to larger than the entoconid on m4 (MN 2347-V and MN 2354-V), whereas, in *Coona*, this cusp is much smaller than the entoconid (AMNH 28907, holotype of *Coona pattersoni*; see Simpson 1938). The presence of a reduced hypoconulid is also observed in *Pauladelphys*, which suggests that the reduction in the size of the hypoconulid is a synapomorphy this taxon and *Coona*. Moreover, *Pauladelphys* and *Coona* share relatively broader crowns compared to other derorhynchids.

Streptorhynchus and *Diogenesia* sp. are more similar in their molar morphometrics and morphofunctional indexes compared to other derorhynchids from Itaboraí, including *Diogenesia brevirostris*. However, several features prevent us from considering both as synonyms. *Diogenesia* sp. displays an StC more closely spaced to StB, whereas *Streptorhynchus* displays a StC more closely spaced to StD. The proximity between StB and StC is a symplesiomorphy of Sudameridelphia (i.e., the clade that includes all taxa more closely related to Marsupialia than to Peradectia, Alphadontia sensu Carneiro and Oliveira 2017b, and Archimetatheria sensu Carneiro and Oliveira 2017a; see Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023), as this condition is observed on several South American early taxa and clades, especially on M1-2 (e.g., *Bergqvistherium*, *Bobbschaefferia*, *Carolopaulacoutoia*, *Didelphopsis*, *Diogenesia*, *Gaylordia*, *Itaboraidelphys*, *Marmosopsis*, *Patene*, Peradectoidea gen. nov., Pucadelphyda gen. nov. etc., see Carneiro 2023 [unpublished data]). Moreover, a relatively more distally placed StC (i.e., more closely placed to StD) is also observed among derorhynchids in *Pauladelphys* (a coonine), whereas a StC more closely spaced to StB is observed on *Derorhynchus* sp. (see specimens UFRJ-DG 145-M and UFRJ-DG 155-M). In short, the distal shift

of StC is recovered as an apomorphic condition for Sudameridelphia (see the results of the phylogenetic analysis). *Derorhynchus* sp. and *Diogenesia* sp. also share the presence of a distally placed ectoflexus.

Based on these observations, it is possible to infer that the ancestral condition of derorhynchids is a distally placed and relatively shallow ectoflexus, a StC more closely spaced to StB on M1-3, slight contact of the cristid obliqua with the distal border of the trigonid on m3, conical entoconid, non-procumbent lower canine, and shallow and short (i.e., lacking diastemata) dentary. Therefore, *Streptorhynchus tropicalis* has a greater combination of derived features than *Diogenesia* sp. and *Derorhynchus* sp.

In summary, despite some similarities between *Streptorhynchus tropicalis*, *Coona pattersoni*, and *Diogenesia* sp., these taxa can be securely considered as independent lineages within Derorhynchidae.

Dietary inferences for *Streptorhynchus*

Streptorhynchus displays a combination of dental and dentary features indicative of an omnivorous diet. The most significant morphofunctional indexes that support this conclusion (see Table 3) are m2ra (average: 0.90), and RGA (average: 0.79). Zimicz (2012) observed that greater RGA values (greater than 0.80) are associated with more omnivorous to frugivorous diets. Similarly, lower values of RPS (lower than 2.60), PS (premolar shape: Wp3/Lp3; lower than 0.58), and relatively short trigonid and more developed talonids (m2rh and m2ra; see Carneiro et al. 2024a, 2024d) indicate frugivorous and omnivorous diets. Van Valkenburgh (1991), Zimicz (2012), and Maga and Beck (2017) considered higher values of RPS and PS as indicative of inflated to bulbous (i.e., highly inflated) premolars, with the last regarded as indicative of a durophagous diet (see Zimicz 2012, Carneiro and Oliveira 2017a, 2023; Maga and Beck 2017; Churchill et al. 2023). Moreover, Zimicz (2012) considered RPS values higher than 2.60 indicative of durophagy for hypercarnivorous taxa, ruling out a durophagous diet for *S. tropicalis*.

A list of some morphological and morphometric indices of *Derorhynchus*, *Diogenesia*, and *Streptorhynchus* gen. nov. are presented below (Table 3):

Table 3 Morphological and morphometrical indexes (range and [average]) calculated for *Derorhynchus* spp., *Diogenesia* spp., and *Streptorhynchus* gen. nov. from the Itaboraí Basin. **A**, area; **DH**, dentary height; **dt**, diastema/diastemata length; **h**, height (measured from the base of the crown to the apex of the tallest cusp of the trigonid or talonid); **L**, length (in mm); **m**, molar; **p**, lower premolar; **ra**, talonid/trigonid areas ratio (Atal/Atri); **RDS**, relative dentary shape (DH/Lm1-4); **RGA**, relative grinding area ($^2\sqrt{\text{Atal/Lm4tri}}$); **rh**, talonid/trigonid heights

ratio (Htal/Htri); **RPM**, length of the anterior part of the dentary (Lp1-3 + dt) by the length of the lower molar series (Lm1-4); **RPS**, relative premolar shape ($Wp3/\sqrt{BM}$) **tal**, talonid; **tri**, trigonid; **W**, width

	RPS	m2rh	m2ra	RGA	RPM	RDS
<i>Streptorhynchus tropicalis</i>	~1.57	0.64-0.80 [0.73]	0.86-0.95 [0.90]	0.74-0.84 [0.79]	0.62-0.68 [0.65]	0.45-0.48 [0.47]
<i>Derorhynchus singularis</i>	1.65	0.71-0.77 [0.74]	0.83-0.84 [0.83]	0.71-0.75 [0.73]	1.21	0.58
<i>Derorhynchus</i> sp.	2.38	0.70-0.71 [0.70]	0.69-0.77 [0.73]	0.57	0.80	0.34-0.43 [0.40]
<i>Diogenesia brevirostris</i>	1.80	0.56	0.53	0.62	0.52	0.34
<i>Diogenesia</i> sp.	1.77-1.90 [1.83]	0.67	1.05	1.02	0.58-0.64 [0.61]	0.38-0.40 [0.39]

Considering *Streptorhynchus tropicalis*' dental and dentary morphologies (besides the above-mentioned features), *Streptorhynchus* has moderately developed StDs, protocones, hypoconids, and pyramidal entoconids. The presence of pyramidal entoconids is observed among derorhynchids within Cooninae subf. nov. (*Streptorhynchus*, *Pauladelphys*, and *Coona*; see Fig. 12a-c). The presence of a similar entoconid shape is also observed on *Procaroloameghinia pricei*, *Protodidelphis vanzolinii*, *Robertbutleria mastodontoidea*, and roughly on *Didelphopsis* sp. (Fig. 12d-g), which are considered as omnivorous-frugivorous or frugivorous taxa (see Goin et al. 1998; Oliveira and Goin 2011, 2012; Zimicz 2012; Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023). Consequently, this shared feature between *S. tropicalis* and some frugivorous metatherians from Itaboraí suggests a more important frugivorous component in the diet of *S. tropicalis*.

Following the results of the PCA2, *Streptorhynchus tropicalis* is morphofunctionally more similar to *Diogenesia* sp. than to any other derorhynchid from the Itaboraí Basin. However, these taxa differ mainly on the following features: *Streptorhynchus tropicalis* has a more robust dentary and a longer anterior part of the dentary. On the contrary, *Diogenesia* sp. has a proportionally larger talonid on m2 and m4 and a relatively lower talonid on m2.

Considering the results of the phylogenetic analysis, the morphological features (and consequently, the morphofunctional indexes) of *Diogenesia* sp. represent symplesiomorphies for derorhynchids: relatively taller trigonid than talonid (lower m2rh values), short anterior part of the dentary (lower values of RPM), and shallower dentary (low values of RDS). The higher value of RGA for this taxon is a consequence of the more plesiomorphic pattern of its m4, as earliest sudameridelphians have relatively longer talonids on m4 (see, e.g.,

Bergqvistherium primigenia, *Bobbschaefferia fluminensis*, *Carolopaulacoutoia* spp., *Didelphopsis* spp., the *Paradectoidea* gen. nov. spp., protodidelphids; see, e.g., Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023). In summary, except for its higher values for m2ra, the other morphofunctional indexes considered for *Diogenesia* sp. indicate that this taxon is the most generalized derorhynchid (i.e., it displays a greater combination of plesiomorphies) from the Itaboraí Basin. This combination of features supports the taxonomic distinction of *Diogenesia* and *Streptorhynchus* (see also the results of the phylogenetic analysis).

Evidence of different trophic niches between derorhynchids in the Itaboraí Basin

The results of the second PCA analysis focused on some morphofunctional indexes (Fig. 11b) recovered *Derorhynchus singularis*, *Diogenesia brevirostris* and *Derorhynchus* sp., and *Diogenesia* sp. and *Streptorhynchus* gen. nov. in “three” different morphospaces. This result indicates different morphofunctional patterns between them, suggesting that these taxa had probably explored different trophic niches.

Diogenesia sp. displays a combination of features indicative of an insectivorous diet. This taxon has mesiodistally compressed M3s, asymmetric styler shelves (i.e., the mesial and distal lobes of the styler shelf have different widths, in which the distal lobe is broader than the mesial one) on M1-3, closely spaced paracone and metacone on M3 (in lower molars, the hypoconid is mesiodistally compressed), very mesiodistally compressed protocone on M3 (m3 has a relatively reduced talonid), not inflated p3, and relatively short and shallow dentary. On the contrary, *Diogenesia* sp. displays the most developed talonid on m2 among Itaboraí’s derorhynchids. This condition can be linked with proportionally broad protocones on M2. Curiously, the m3 of this taxon has a mesiodistally compressed trigonid (see MCT.M.812), very likely a consequence of the robust size of the protocone on M2. In summary, *Diogenesia* sp. has several features indicative of an insectivorous diet; however, fruits cannot be ruled out as possible food for this species, as its M2 protocone/talonid is relatively well-developed (i.e., generalized insectivory; sensu Carneiro et al. 2024c).

Among the two species from the Itaboraí Basin, *Diogenesia brevirostris* had a more specialized insectivorous diet in comparison with *Diogenesia* sp. based on its smaller size (about 17% smaller than the smallest *Diogenesia* sp.), relatively taller cusps and trigonid (m2rh: 0.56; i.e., tribosphenic crown; sensu Marshall 1987), smaller talonids (m2ra: 0.53; RGA: 0.62), p3 relatively longer than p2 (Lp2/Lp3: 0.67; Lp2/Lp3 *Diogenesia* sp.: 0.80-1.04), and shallower dentary (RDS: 0.34; RDS *Diogenesia* sp.: 0.39). The combination of features displayed by *D. brevirostris* indicates that this taxon was a specialized insectivore, preying mainly on soft exoskeleton invertebrates as food (see, e.g., Oliveira et al. 2021; Carneiro and Oliveira 2023). Moreover, *Diogenesia* spp.

specimens exhibit a weak enamel layer on their molars, which is also compatible with exploiting “soft” food.

Derorhynchus displays a combination of features indicative of a specialized insectivorous diet (strict insectivory of Zimicz 2012) of hard exoskeleton invertebrates. The type species of the genus (*Derorhynchus singularis*) have several features that agree with this conclusion (see, e.g., Thomason 1991; Carneiro and Oliveira 2017; Carneiro and Oliveira 2023): mesiodistally compressed and distolingually oriented hypoconid, labiolingually compressed premolars (RPS: 1.65; see specimens MN 1348-V [holotype] and MN 2896(c)-V), long diastemata between c-p1, p1-2, and variably present between p2-3 (i.e., has an elongated anterior part of the jaw [i.e., the part with lower incisors, canine, and premolars]; see specimens MN 1348-V [holotype], AMNH 49826, and MN 2896(c)-V), evident increase in the height of the dentary ventral to p3-m1 (i.e., uneven height of the dentary; see specimens MN 1348-V [holotype], AMNH 49826), and robust dentary (RDS: 0.58).

The presence of long diastemata between lower canine and premolars is commonly observed on specialized/strict insectivorous (sensu Zimicz 2012) metatherians (e.g., *Marmosopsis juradoi*, *Minusculodelphis modicum*; see Paula Couto 1962; Oliveira et al. 2016; Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023). Nevertheless, robust dentaries indicate the exploitation of resistant and hard food, like hard exoskeleton invertebrates. The robust dentaries of *Derorhynchus singularis* clearly depart this taxon from *Diogenesia*, which has shallower dentaries (indicative of the exploitation of soft exoskeleton invertebrates as food). Moreover, *Derorhynchus singularis* has relatively higher talonids than the trigonids (m2rh: 0.71-0.77 [0.74]), indicating the ingestion of hard exoskeleton invertebrates as food. Metatherians that are specialized to prey soft exoskeleton invertebrates (e.g., *Diogenesia brevirostris*, *Marmosopsis juradoi*, *Minusculodelphis* spp.; see Zimicz 2012; Oliveira et al. 2016, 2021) have relatively lower and smaller talonids (lower values of m2rh and m2ra, respectively) in comparison with insectivores that prey on hard exoskeleton invertebrates (like *D. singularis*). Moreover, *Derorhynchus singularis* also displays an evident increase in the height of the dentary at the level of p3-m1. This morphology could have increased jaw strength, allowing this taxon to prey on hard and resistant food (like hard exoskeleton invertebrates).

In summary, *Derorhynchus singularis*, *Diogenesia brevirostris*, and *Diogenesia* sp. probably had some trophic niche overlapping (insectivory). However, their co-existence can be partially explained by the exploitation of differential/preferential food (specialized “durophagous” insectivore, specialized/strict insectivore, and generalized insectivore [i.e., mainly preying on soft exoskeleton invertebrates, but fruits cannot be ruled out as explored food], respectively).

In line, Carneiro (2023 [unpublished data]) had identified a new species of *Derorhynchus* in the Itaboraí Basin. This taxon differs from *D. singularis* primarily by its dentary morphology: absence of diastemata between c and premolars (i.e., short anterior part of the dentary; RPM: 0.80), and presence of a relatively less robust and

shallower dentary (DHm3-4: 2.35-3.34, RDS: 0.34-0.43 [Average: 0.40]; DH *Derorhynchus singularis*: 4.24; RDS: 0.58; see Table 3), and less developed uneven in the height of the dentary ventral to p3-m1 (evidently more developed in *D. singularis*). In addition, *Derorhynchus* sp. also differs from *D. singularis* in the presence of p1 not reduced in comparison with p2 (considering alveoli length), presence of a mesial cuspule on p3 (absent in *D. singularis*), and p3 less labiolingually compressed (RPS: 2.38; RPS *Derorhynchus singularis*: 1.65; see Table 3). The m2 of *Derorhynchus* sp. has a relatively taller trigonid (m2rh: 0.70-0.71 [Average: 0.70]) and a less developed talonid (m2ra: 0.69-0.77 [Average: 0.73] and RGA: 0.58) in comparison with those of *Derorhynchus singularis* (m2rh: 0.71-0.77 [Average: 0.75], m2ra: 0.83-0.84 [Average: 0.83], and RGA: 0.71-0.75 [Average: 0.74]; see Table 3).

Derorhynchus sp. had an insectivorous diet, with soft and hard exoskeleton invertebrates as potentially explored food. Nevertheless, its morphofunctional indexes (RPS, m2rh, m2ra, RGA, RPM, and RDS) indicate a less “durophagous” diet than *Derorhynchus singularis*. Nevertheless, this taxon probably had a more critical “durophagous” invertebrate component in its diet than *Diogenesia*, especially *D. brevirostris*. The similar morphofunctional placement for *Derorhynchus* sp. and *D. brevirostris* supports this conclusion, as both taxa were placed in a more similar morphospace than other derorhynchids from the Itaboraí Basin.

Furthermore, *Diogenesia* and *Derorhynchus* were insectivores, with *Diogenesia* exploring mainly soft exoskeleton invertebrates. In contrast, *Derorhynchus* included relatively harder exoskeleton invertebrates (see also Zimicz 2012 for other data that support these conclusions). *Derorhynchus singularis* is the most specialized derorhynchid in preying on hard exoskeleton invertebrates. On the contrary, *Streptorhynchus* might have an omnivorous diet (insectivory-frugivory; sensu Zimicz 2012), with invertebrates and turgent fruits (sensu Zimicz 2012) as explored food. Despite the potential exploitation of fruits for *Diogenesia* sp. and *S. tropicalis*, the overall dental and dentary morphologies of the latter suggest a more important frugivorous component in its diet compared with *Diogenesia* sp.

The Paleocene-Eocene Thermal Maximum (PETM) + Early Eocene Climatic Optimum (EECO) and the derorhynchid trophic structure in the Itaboraí Basin

The PETM + EECO represented two paleoenvironmental events that occurred during the late Paleocene-early Eocene that culminated in the increase in global temperatures by about 5 °C to 8 °C (see Goin et al. 2012, 2016; Bowen et al. 2015), allowing the expansion of tropical biomes throughout South America (Goin et al. 2012, 2016; Zimicz 2012; Woodburne et al. 2014a, 2014b). Among South American SALMAs, the Itaboraense

comprehended faunas during the PETM + EECO. In contrast, the Riochican comprehended faunas from the late EECO (see Woodburne et al. 2014a). These biochrons are characterized by increased diversity of metatherians with bunodont crowns (e.g., caroloameghiniids, protodidelphids), with omnivorous and frugivorous diets (see Goin et al. 2012, 2016; Zimicz 2012).

In line, the fauna from the Itaboraí Basin preserved an omnivorous derorhynchid, *Streptorhynchus tropicalis* (Oliveira and Goin 2006, 2011; Carneiro 2023 [unpublished data]; Carneiro and Oliveira 2023). *Streptorhynchus tropicalis* is the oldest known coonine, occurring during the early Eocene (Itaboraiense SALMA) of Brazil and Argentina (Itaboraí and Las Flores). The occurrence of an omnivorous derorhynchid during this biochron can be linked with the paleoclimatic events resulting from the PETM + EECO, as previously concluded by Goin et al. (2012, 2016) and Zimicz (2012).

Conclusions

Streptorhynchus tropicalis gen. et sp. nov. was a small-sized, omnivorous, early Eocene (Itaboraiense SALMA) derorhynchid. *Streptorhynchus* is sister to *Pauladelphys* and *Coona*. These three genera are grouped within Cooninae new, a subclade of Derorhynchidae.

Itaboraí's derorhynchids explored differential insectivorous trophic niches: *Streptorhynchus tropicalis* was an omnivorous taxon (insectivory-frugivory), *Diogenesia* sp. was a generalized insectivore, *Diogenesia brevirostris* was a specialized insectivore, mainly preying on soft exoskeleton invertebrates; *Derorhynchus* sp. was an insectivore, preying on soft and hard exoskeleton invertebrates, and *Derorhynchus singularis* was a specialized insectivore, primarily preying on hard exoskeleton invertebrates.

The occurrence of an omnivorous derorhynchid in the Itaboraí fauna supports previous conclusions about the increase in diversity of metatherian clades with bunodont crowns and omnivorous to frugivorous diets during the Itaboraiense SALMA.

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FIGURE CAPTIONS

Fig. 1 The Itaboraí fauna: locality and biochron. **a**, Map showing the region and the coordinates of the Itaboraí Basin, municipality of Itaboraí, Rio de Janeiro, Brazil (22° 45' 9'' S; 42° 51' 53'' W). **b**, The stratigraphic relationships of the Itaboraiense SALMA with other Paleogene SALMAs. A plausible age range for the Itaboraí SALMA is highlighted in grey. The occurrence of the gen. et sp. nov. is suggested by a black arrow and a digital image of the MN 2894(a2)-V, a right M3. **PETM**, Paleocene-Eocene Thermal Maximum; **SALMA**, South American Land Mammal Age. The scale bar represents 1000 Km

Fig. 2 Diagnostic combination of features of *Streptorhynchus* gen. nov.: **a**, MN 2894(a2)-V, a right M3 in occlusal view; **b**, MN 2886-V, an incomplete right dentary with m2-3 and partially preserved p2 in occlusal view. Scale bars = 1 mm

Fig. 3 Comparative upper molar differences between *Streptorhynchus* gen. nov. and *Derorhynchus* Paula Couto, 1952. *Streptorhynchus tropicalis* gen. et sp. nov.: **a**, MN 2894(a2)-V, a right M3 in occlusal view; **d**, MN 2886-V, an incomplete right dentary with m2-3 and partially preserved p2; *Derorhynchus* sp.: **b**, UFRJ-DG 154-M, a left M3 in occlusal view; **e**, MCT.M.4425, a left m3 in occlusal view; *Derorhynchus singularis* Paula Couto, 1952: **c**, MCT.M.803, a left maxilla with M1-2, M4, and alveoli of M3 in occlusolingual view. Scale bars = 1 mm

Fig. 4 Comparative upper molar differences between *Streptorhynchus* gen. nov. and *Diogenesia* Oliveira, Carneiro and Goin, 2021. *Streptorhynchus tropicalis* gen. et sp. nov.: **a**, MN 2894(a2)-V, a right M3 in occlusal view; **b**, MN 2886-V, an incomplete right dentary with m2-3 in occlusal view; *Diogenesia* sp.: **c**, MCT.M.4434, a left M2 in occlusal view; *Diogenesia brevirostris* Oliveira, Carneiro and Goin, 2021: **d**, MCT.M.650, holotype, an incomplete right dentary with m2-4 in occlusolabial view. Scale bars = 1 mm

Fig. 5 Specimen MCT.M.4875 (holotype), incomplete left maxilla with M1-3, alveoli of M4, and partially preserved zygomatic arch, of *Streptorhynchus tropicalis* gen. et sp. nov. shown in **(a)** labial; **(b)** occlusal; **(c)** lingual views; **(d)** SEM image of this specimen in occlusolabial view. Scale bars = 1 mm

Fig. 6 Upper molars and maxillae of *Streptorhynchus tropicalis* gen. et sp. nov. from the Museu Nacional (MN), Rio de Janeiro, Brazil: **a**, MN 2506-V, an incomplete left maxilla with M1-3, alveoli of P2-3, and partially

preserved alveoli of M4 in occlusolingual view; **b-c**, MN 2352-V, a very fragmentary left maxilla with M1 in **(b)** occlusal; **(c)** occlusolabial views. Scale bars = 1 mm. Credits: The image of the specimen MN 2506-V (image **a**) is a property of L.P. Bergqvist (UFRJ)

Fig. 7 SEM images of some specimens of *Streptorhynchus tropicalis* gen. et sp. nov. of the Museu Nacional (MN): **a-b**, MN 2894(a2)-V, a right M3, shown in **(a)** occlusal; **(b)** occlusodistal views; **c-e**, MN 2886-V, an incomplete right dentary with m2-3 and partially preserved p2, shown in **(c)** lingual; **(d)** occlusal; **(e)** labial views. Scale bars = 1 mm

Fig. 8 Specimen MCN-PV 1795, incomplete left dentary with m2, and alveoli of i2-5, c, p1-3, m1, m3, and anterior alveolus of m4 of *Streptorhynchus tropicalis* gen. et sp. nov. shown in **(a)** occlusal; **(b)** lingual; **(c)** labial views. Scale bars = 1 mm

Fig. 9 Specimen MN 2354-V, an incomplete left dentary with m1-4 and damaged p3, of *Streptorhynchus tropicalis* gen. et sp. nov. shown in **(a)** labial; **(b)** lingual; **(c)** occlusal views. Scale bars = 2 mm

Fig. 10 Consensus tree of the single most parsimonious trees found in the phylogenetic analyses (Score: 1967; CI: 0.367; RI: 0.610). Numbers below and above the branches indicate Bremer support values. *Streptorhynchus* gen. nov. is highlighted in bold. Derorhynchidae is highlighted in grey

Fig. 11 Principal component analyses (PCA) of some morphometric and morphofunctional indexes based on lower molar measurements for *Streptorhynchus tropicalis* gen. et sp. nov., *Derorhynchus singularis* Paula Couto, 1952, *Derorhynchus* sp., *Diogenesia brevirostris* Oliveira et al., 2021; and *Diogenesia* sp. **a**, First PCA with lower molar's loci (m1, m2, m3, and m4) morphometric indexes (Lm, Ltri, Ltal, Wtri, and Wtal); **b**, second PCA with six morphofunctional indexes (m2ra, m2rh, RGA, RDS, RPM, and RPS). **A**, area; **BM**, body mass; **dt**, diastema/diastemata; **H**, height; **L**, length; **m1-4**, lower molar series length; **m**, lower molar with the numbers corresponding to its positioning (m1-4); **p**, lower premolars with the numbers corresponding to its positioning; **p1-3**, lower premolar series length (p1-3); **PC**, principal component; **R/r**, ratio; **RDS**, relative dentary shape (DH/Lm1-4); **RGA**, relative grinding area ($2\sqrt{\text{Atal/Lm4tri}}$); **RPM**, length of the anterior part of the dentary (Lp1-3 + dt) by the length of the lower molar series (Lm1-4); **RPS**, relative premolar shape ($\text{Wp3}^3/\sqrt{\text{BM}}$); **tri**, trigonid; **W**, width. Schematic drawings are not at scale. Credits: The artistic drawings of Itaboraí's metatherians were made by Felipe A. Elias from the PaleoZOOBR (www.paleozoobr.com)

TABLE TITLES

Table 1. Size categories considered for early Eocene Itaboraí's metatherians (sensu Carneiro et al. 2024a) based on their lower molar series length (in mm) and maximum and minimum limits of estimated body masses (BM) in grams (g) and kilograms (kg). BM, estimated body mass; Lm1-4, lower molar series length

Table 2 Dental measurements (in mm) of *Streptorhynchus tropicalis* gen. et sp. nov. The holotype is highlighted in bold. For lower molars, the measurements are expressed in the following order: trigonid length. (taloid dimensions – length or width), and – total length. **L**, length; **M/m**, molar; **P/p**, premolar; **W**, width; (), taloid dimensions; [], length of premolar alveoli; ~, incomplete tooth, alveoli or molar series; *, based on alveoli dimensions

Table 3 Morphological and morphometrical indexes (range and [average]) calculated for *Derorhynchus* spp., *Diogenesia* spp., and *Streptorhynchus tropicalis* gen. et sp. nov. from the Itaboraí Basin. **A**, area; **DH**, dentary height; **dt**, diastema/diastemata length; **h**, height (measured from the base of the crown to the apex of the tallest cusp of the trigonid or taloid); **L**, length (in mm); **m**, molar; **p**, lower premolar; **ra**, taloid/trigonid areas ratio (A_{tal}/A_{tri}); **RDS**, relative dentary shape ($DH/Lm1-4$); **RGA**, relative grinding area ($\sqrt{A_{tal}/Lm4tri}$); **rh**, taloid/trigonid heights ratio (H_{tal}/H_{tri}); **RPM**, length of the anterior part of the dentary ($Lp1-3 + dt$) by the length of the lower molar series ($Lm1-4$); **RPS**, relative premolar shape ($Wp3/\sqrt[3]{BM}$) **tal**, taloid; **tri**, trigonid; **W**, width

ONLINE RESOURCE

Online resource 1: Studied metatherian specimens from the Itaboraí Basin. AMNH, American Museum of Natural History, New York, NY, USA; **MCN-PV**, coleção de paleovertebrados do Museu de Ciências Naturais, Porto Alegre, RS, Brazil; **MCT**, Museu de Ciências da Terra, Rio de Janeiro, RJ, Brazil; **MN**, Museu Nacional, Rio de Janeiro, RJ, Brazil; **UFRJ-DG**, coleção de paleovertebrados da Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil.

Online resource 2: Body masses calculations for studied Itaboraí's metatherians. Equations based on Myers (2001). **BM**, body mass; **LM/m1-4**, upper or lower molar series length; log, natural logarithm; **MCN-PV**, coleção de paleovertebrados do Museu de Ciências Naturais, Porto Alegre, RS, Brazil; **MCT**, Museu de Ciências da Terra,

Rio de Janeiro, RJ, Brazil; **MN**, Museu Nacional, Rio de Janeiro, RJ, Brazil; **UFRJ-DG**, coleção de paleovertebrados da Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil. *, based on upper or lower molar's alveolar series length.

Online resource 3: Measurements of studied derorhynchids from the Itaboraí Basin.

Online resource 4: Characters and states of phylogenetic analysis. Characters and states used in the phylogenetic analysis. Characters are coded with respect to *Kielantherium gobiense* as outgroup. Some characters are treated as ordered.

Online resource 5: Characters and states by taxon. Characters and states used in the phylogenetic analysis for each taxon. Characters are coded with respect to *Kielantherium gobiense* as outgroup. Some characters are treated as ordered.

Online resource 6: List of autapomorphies and synapomorphies of the single most parsimonious tree found by the analysis. List of autapomorphies and synapomorphies recovered for included taxa.

Online resource 7: Data matrixes of PCA analyses. PCA1. L, length; m, lower molar; tal, talonid; tri, trigonid; W, width. **PCA2.** A, area; BM, body mass; DH, dentary height; H, height; L, length; M/m, upper/lower molar; m1-4, lower molar series length; p, premolar; PPA, preparacrista; PM, postmetacrista; RDS, relative dentary shape; RPS, relative premolar size; tal, talonid; tri, trigonid; W, width.

Online resource 8: R scripts of the PCA analyses.