



Universidade do Estado do Rio de Janeiro

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Notoungulata: Henricosborniidae da “Fenda 1968”, Paleógeno da Bacia de Itaboraí, Estado do Rio de Janeiro: estudo taxonômico dos elementos dentários.

Rio de Janeiro

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Dissertação apresentada como requisito principal para obtenção do título de Mestre, ao Programa de Pós-Graduação em Geociências da Universidade do Estado do Rio de Janeiro. Área de concentração: Geociências.

Orientador: Prof. Dr. Hermínio Ismael de Araújo Júnior

Coorientadores: Prof.^a Dra. Lílian Paglarelli Bergqvist

Prof. Dr. Daniel Alfredo García-López

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Assinatura

Data

Luis Otavio Rezende Castro

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DEDICATÓRIA

Dedico este trabalho à minha família e meus amigos.

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Aos meus orientadores e amigos Dr. Hermínio Ismael de Araújo Júnior (UERJ), Dra Lílian Paglarelli Bergqvist (UFRJ) e Dr. Daniel García-López (Universidad Nacional de Tucumán), por todo estímulo e ensinamentos que proporcionaram meu desenvolvimento intelectual e científico, e que resultou na elaboração desta dissertação.

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Não é o mais forte que sobrevive, nem o mais inteligente. Quem sobrevive é o mais disposto a mudanças.

Charles Darwin

RESUMO

CASTRO. Luis Otavio Rezende. *Notoungulata: Henricosborniidae da "Fenda de 1968", Paleógeno da Bacia de Itaboraí, Estado do Rio de Janeiro: estudo taxonômico dos elementos dentários*. 2020. 60 f. Dissertação (Mestrado em Geociências) – Faculdade de Geologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2020.

Um novo notoungulado basal é descrito neste trabalho. Este morfótipo é representado por fragmentos de maxilar, de dentário e por dentes isolados. O holótipo e o material referido foram coletados na "Fenda de 1968" da Bacia de Itaboraí, Estado do Rio de Janeiro, Brasil. Esta bacia é de idade Itaboraiense, que tem sido considerada como do Eoceno inicial em recentes contribuições. A dentição do morfótipo é braquiodonte, apresentando alguns caracteres (entolofido pouco desenvolvido, coluna de metacone bem desenvolvida, etc.) que indicam tratar-se de um Gen. et Sp. Nov. de Henricosborniidae, é diferente de todos os outros henricosborniídeos por uma combinação de caracteres, como presença de um longo crochê, desenvolvimento de duas pequenas cristas no ectolofio, grande cúspide acessória no trigonido, dentre outras. É também facilmente distinguível dos Typotheria pela ausência da crista 1 e de Toxodontia pela ausência da crista intermédia. A análise filogenética na qual foram incluídos todos os henricosborniídeos não nos permite chegar a conclusões sólidas da relação Gen. et sp. nov com os demais membros deste grupo. Ela também não revelou evidências conclusivas sobre a sinonímia entre *Itaboraitherium atavum* e *Othnielmarshia pristina* sugerida anteriormente, assim como seu posicionamento dentre os henricosborniídeos, devido ao complexo padrão dentário observado na face oclusal de ambas as espécies. Por fim, com base nas observações feitas no presente estudo, a cúspide acessória do trigonido, referida em algumas contribuições como paraconido, pode estar associada a algumas cúspides localizadas mesialmente ao metaconido e identificadas como pseudoparaconido em estudos anteriores.

Palavras-chave: Notoungulata. Henricosborniidae. Bacia de Itaboraí. "Fenda de 1968".

ABSTRACT

CASTRO. Luis Otavio Rezende. *Notoungulat: Henricosborniidae from “1968 Fissure”, Paleogene from the Itaboraí Basin, Rio de Janeiro State: taxonomic study of the teeth elements*. 2020. 60 f. Dissertação (Mestrado em Geociências) – Faculdade de Geologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2020.

A new basal notoungulate is described here. This is represented by maxillary and dental fragments, and by isolated teeth. The holotype and referred material were recovered from the “1968 Fissure” of the Itaboraí Basin, Rio de Janeiro State, Brazil. This basin, of Itaboraian age, has been regarded as early Eocene in recent contributions. The generalized appearance and brachydont dentition of the studied specimens, together with the presence of some typical traits (poorly developed entolophid, well-developed metacone column, etc.) indicate that it represents a Gen. et sp. nov. of Henricosborniidae. It is distinct from all other henricosborniids by a combination of characters, such as the presence of a long crochet, the development of two small cristae at the ectoloph, the large accessory trigonid cusp, among others. It is also easily distinguishable from typotherians by the absence of crista 1 and from toxodontians by the absence of crista intermedia. The phylogenetic analysis including all henricosbornid genera does not allow us to reach solid conclusions about the relationship of the new taxon with the other members of this group. It did not present conclusive evidence for the synonymy between *Itaboraitherium atavum* and *Othnielmarshia pristina*, previously suggested. Moreover, the reference of these forms as henricosborniids, based on the complex occlusal dental pattern observed in both cases, is questioned. Finally, based on the observations made in the present study, we consider that the accessory trigonid cuspid, referred in some contributions as a paraconid, may be associated with some cusps located mesially to the metaconid and identified as pseudoparaconids in past studies.

Keywords: Notoungulata. Henricosborniidae. Itaborai basin. “1968 Fissure”.

LISTA DE ABREVIATURAS E SIGLAS

MACN A	Museo de Ciencias Naturales “Bernardino Rivadavia”, Colección Ameghino, Buenos Aires, Argentina
MCTer	Museu de Ciências da Terra
MCT-M	Museu de Ciências da Terra – Coleção de Mamíferos Fósseis
CPRM	Serviço Geológico do Brasil, Rio de Janeiro, Brasil
MLP	Museo de La Plata, La Plata, Argentina
MN	Museu Nacional, Rio de Janeiro, Brasil

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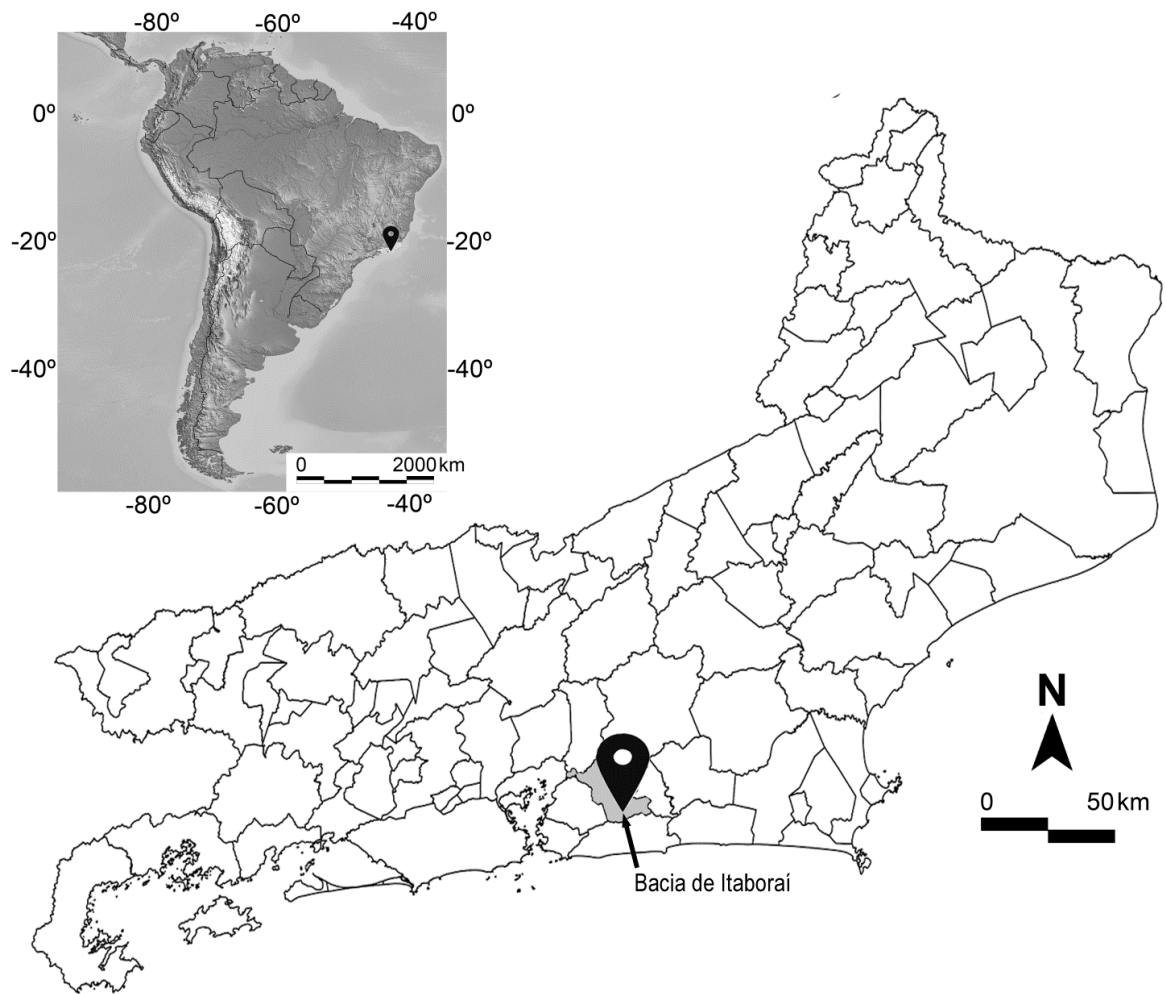
INTRODUÇÃO

A Bacia de Itaboraí está localizada no bairro São José, município de Itaboraí, Estado do Rio de Janeiro, (22°50'26.46"S; 42°52'43.89"O; Fig. 1). Descoberta no final da década de 1920, a exploração das rochas carbonáticas para fabricação de cimento se iniciou em 1933, encerrando suas atividades em 1984. Os primeiros fósseis encontrados na bacia se tratavam de fragmentos de gastrópodes que foram estudados por Maury (1929), antes mesmo do início da atividade exploratória, sendo estes ainda facilmente encontrados na bacia nos dias de hoje. Ao longo de mais de 50 anos, inúmeros fósseis de vertebrados, invertebrados, vegetais e palinórfos de idade paleogênica foram coletados (Bergqvist et al., 2005). Dentre os registros fossilíferos encontrados em Itaboraí, um pequeno depósito de idade pleistocênica, contendo ossos de animais da megafauna, foi encontrado sobreposto ao embasamento ao lado sul da Falha São José (Price & Campos, 1970).

Os grupos de vertebrados fósseis da Bacia de Itaboraí são representados por aves, répteis, anfíbios e mamíferos, sendo este último grupo o de maior número de espécies descritas até o presente momento. Ao todo, os mamíferos compreendem sete ordens conhecidas: Metatheria, Astrapotheria, "Condylarthra", Litopterna, Notoungulata, Xenarthra e Xenungulata, além da Proboscidea, que está restrita ao registro pleistocênico (Bergqvist et al., 2005). Segundo Bergqvist et al. (2005), os metatérios são os mais diversificados, superando em muito a representatividade em gênero de ungulados nativos descrito para este depósito.

A área da antiga Fazenda São José, local onde ocorria a extração das rochas carbonáticas para fabricação de cimento, foi desapropriada pela Prefeitura Municipal de Itaboraí por meio do Decreto 42 publicado em 25 de abril de 1990, tornando a área de utilidade pública. Passados cinco anos, por meio da Lei 1.346 de 30 de dezembro de 1995, a Prefeitura de Itaboraí criou o Parque Paleontológico de São José de Itaboraí, revogando todas as licenças exploratórias e estabelecendo neste mesmo ato jurídico algumas restrições de uso. Dada à carência de regulamentação para se enquadrar ao Sistema Nacional de Unidade de Conservação (SNUC), por meio do Decreto Municipal 102/2018, foi criado o Parque Natural Municipal Paleontológico de São José de Itaboraí. O parque foi criado devido à sua grande diversidade e quantidade de material fossilífero coletado, somado à sua importância no contexto geológico das rochas carbonáticas continentais e magmáticas, além de seus importantes achados arqueológicos.

Figura 1 - Mapa de localização da Bacia de Itaboraí, situada no Parque Natural Municipal Paleontológico de São José de Itaboraí, com polígono preenchido de amarelo.



Fonte: O autor, 2020, com base nos sites: <https://mapswire.com/south-america/physical-maps/>; e <https://www.gestaoeducacional.com.br/mapa-do-rio-de-janeiro-tipos-de-mapa-e-curiosidades>. (Mapa do Estado do Rio de Janeiro).

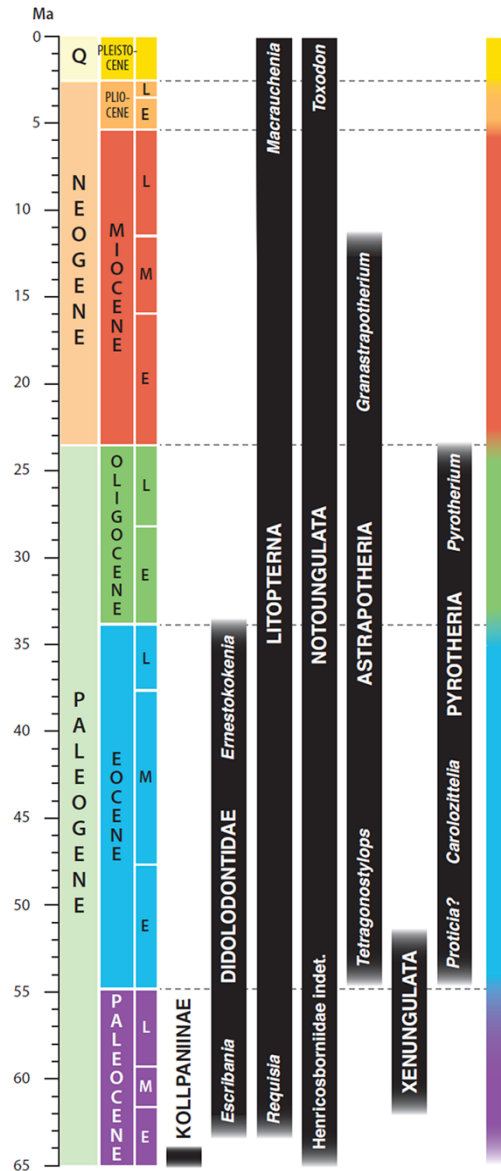
1 CONTEXTO HISTÓRICO

1.1 Ungulados Sul-americanos

Durante a maior parte da Era Cenozoica, a América do Sul ficou isolada dos demais continentes, o que proporcionou o surgimento de uma fauna endêmica no continente sul-americano (Simpson, 1980; Carrilo et al., 2018). Nesse endemismo, os mamíferos fósseis estão representados por cinco ordens (Litopterna, Notoungulata, Astrapotheria, Xenungulata e Pyrotheria) e tem sido agrupado como uma superordem placentária separada (Meridiungulata) (e.g. Croft et al., 2020). Essa diversidade de mamíferos presente no registro fóssil nas mais variadas latitudes da América do Sul, deu origem ao termo “*South American native ungulates* (SANUs)” que é seguido por diversos autores (e.g., Rodrigues et al., 2018; Bauzá et al., 2019; Croft et al., 2020). Por meio de análise filogenética com base em proteínas, os Litopterna e Notoungulata quaternários foram agrupados em um novo clado denominado Panperissodactyla (Welker et al., 2015), no entanto, essa classificação não tem sido seguida em publicações recentes (e.g. Schmidt et al. 2018; Wizz et al. 2018; Corona et al., 2019)

Aparecendo no início do Paleógeno, esses mamíferos evoluíram e se diversificaram, originando diversas linhagens, como atestam os abundantes registros de fósseis no continente sul-americano. Grande parte destas linhagens se extinguiu no final do Mioceno, embora algumas espécies de Litopterna e Notoungulata tenham persistido até o limite Pleistoceno-Holoceno (Rodrigues et al., 2018) (Fig. 2).

Figura 2 - Intervalo temporal dos Ungulados nativos da América do Sul (em inglês “*South American native ungulates, SANUs*”) durante o Cenozoico.



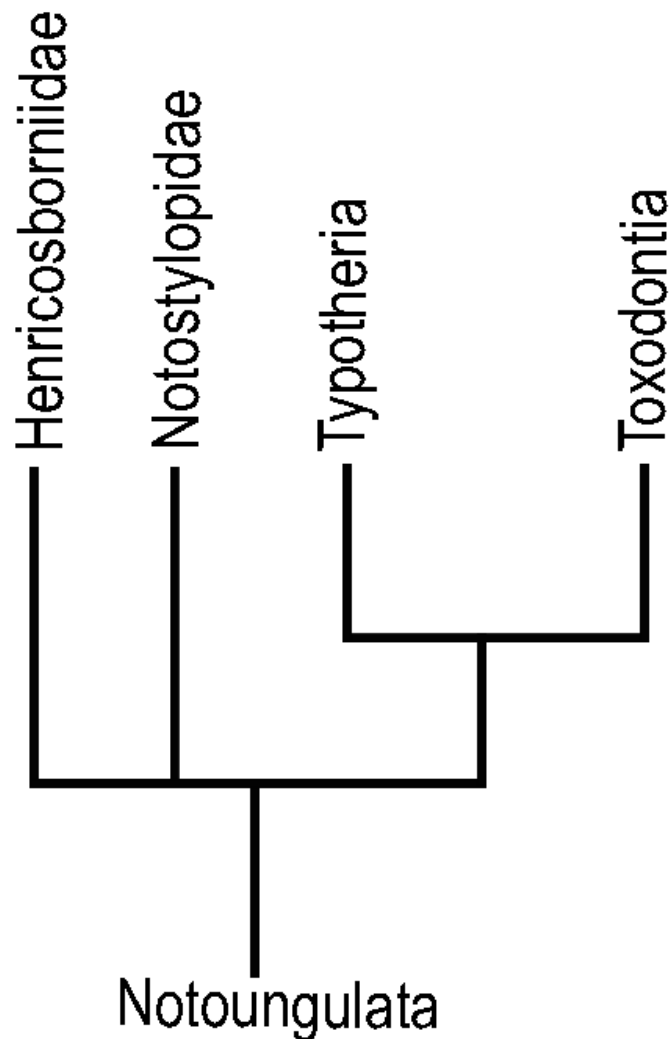
Fonte: Modificada de Croft et al., 2020.

1.2 Notoungulata

A ordem Notoungulata foi estabelecida por Roth (1903) e possui a maior variação morfológica dentre os ungulados sul-americanos, desde animais com tamanho muito pequeno, como *Punapithecus*, do Eoceno (López & Bond, 1995) a formas com mais de uma tonelada, como *Toxodon*, do Pleistoceno (Owen, 1837). Tamaña diversidade do grupo fez com que estes

ocupassem os mais diversos nichos ecológicos e, por consequência, serem os mais bem sucedidos da América do Sul (Babot et al., 2017). Essa ordem engloba as subordens Toxodontia e Typotheria, e as famílias basais Notostylopidae e Henricosborniidae (*sensu* Billet, 2011) (Fig. 3).

Figura 3 - Cladograma ilustrando a relação entre os principais grupos da Ordem Notoungulata com base do trabalho de Billet (2011).



Fonte: Billet, 2011.

Estudos taxonômicos dos notoungulados têm sido realizados com base no grande número de caracteres crânio-dentárias presentes neste grupo (e.g. Billet, 2010, 2011, Bauzá et al., 2020). Atualmente, a subordem Typotheria é dividida em seis famílias: “Oldfieldthomasiidae”, Mesotheriidae, Archaeopithecidae, Hegetotheriidae, Interatheriidae e “Archaeohyracidae”, já a subordem Toxodontia está dividida em cinco: Toxodontidae,

“Isotemnidae”, “Notohippidae”, Leontiniidae e Homalodotheriidae, sendo duas dessas famílias parafiléticas (e.g., García-López & Powell, 2009; Billet, 2011; Vera, 2014; Carrilo et al., 2018; Bauzá et al., 2020).

A família Henricosborniidae, a qual pertence o morfótipo descrito neste trabalho, possui, até o momento, cinco gêneros consolidados na literatura: *Henricosbornia* Ameghino, 1901; *Othnielmarshia* Ameghino, 1901; *Peripantostylops* Ameghino, 1901; *Simpsonotus* Pascual et al., 1978 e *Orome* Bauzá et al., 2019. Os Henricosborniidae possuem amplo registro geográfico no continente Sul-Americano, sendo encontrados no Brasil (Itaboraí), Argentina (Paso del Sapo/Las Flores/Cañadón Hondo/Las Violeta/Bajo de La Palangana/Tres Cruces) e Bolívia (Tiupampa). O range biocronológico dos henricosborniídeos vai do Daniano (61,6 a 66,0 milhões de anos, equivalente à idade SALMA (*South American Land Mammal Age*) Tiupampense até o Bartoniano (37,8 a 41,2, equivalente à SALMA Casamaiorense (Bauzá et al., 2020).

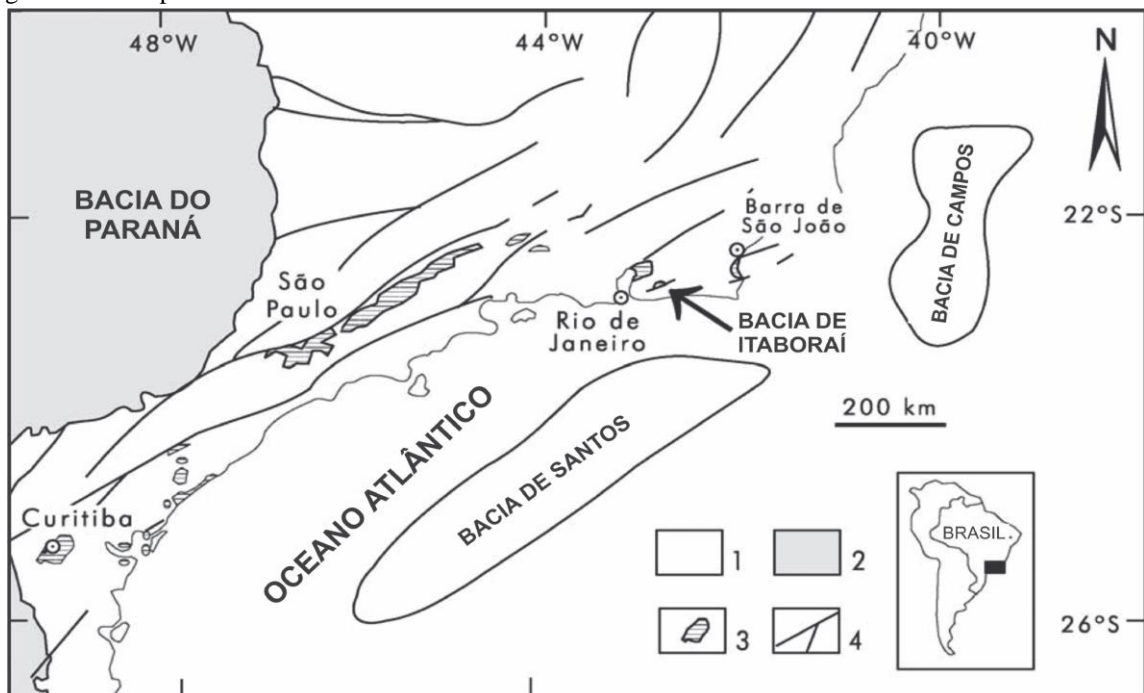
Atualmente os notoungulados da Bacia de Itaboraí são representados pelas espécies *Colbertia magellanica* (Price & Paula-Couto 1950) Paula-Couto, 1952, *Itaboratherium atavum* (Paula-Couto 1954) Paula-Couto, 1970 e *Othnielmarshia pristina* (Paula-Couto 1978) Paula-Couto, 1979, sendo as duas primeiras espécies pertencentes à subordem Typhotheria, e a última à família Henricosborniidae (Aquino, 2012). Dentre as três espécies descritas para Bacia de Itaboraí, *C. magellanica* é a que possui o maior número de exemplares fósseis, além de ter sido a mais citada (e.g., Paula-Couto, 1952; Paula-Couto, 1979; Bond, 1981; García-López, 2011; Babot et al., 2017; García-López et al., 2019).

2 GEOLOGIA

A Bacia de Itaboraí é uma das menores bacias sedimentares brasileiras, compondo o conjunto de bacias geradas pelo Rifte Continental do Sudeste Brasileiro (RCSB) (Sant'ana & Riccomini, 2001). Possui formato elíptico (1.400 m no sentido SW-NE e 500 m no sentido SE-NO) e profundidade em torno de 100 m (Rodrigues-Francisco & Souza-Cunha, 1978). Essa bacia é a única de preenchimento majoritariamente carbonático desse seguimento (Ferrari, 2001; Sant'Anna et al., 2004; Adler et al., 2017).

Segundo Sant'Anna et al., (2004), a Bacia de Itaboraí está situada no início de formação do RCSB, que é resultado do processo tardio de quebra do Gondwana durante a separação entre Brasil e África. De idade cenozoica, o RCSB possui uma extensão aproximada de 1000 km, indo de Curitiba-PR à Barra de São João-RJ (Fig. 4).

Figura 4 - Seta apontando a Bacia de Itaboraí no contexto do Rifte Continental do Sudeste Brasileiro



Legenda: (1) Embasamento Pré-Cambriano; (2) Rochas vulcânicas e sedimentares paleozoicas e mesozoicas da Bacia do Paraná; (3) Depósitos sedimentares cenozoicos do Rifte Continental do Sudeste do Brasil; (4) Zonas de cisalhamento Pré-Cambrianas parcialmente reativadas no Mesozoico e no Cenozoico.

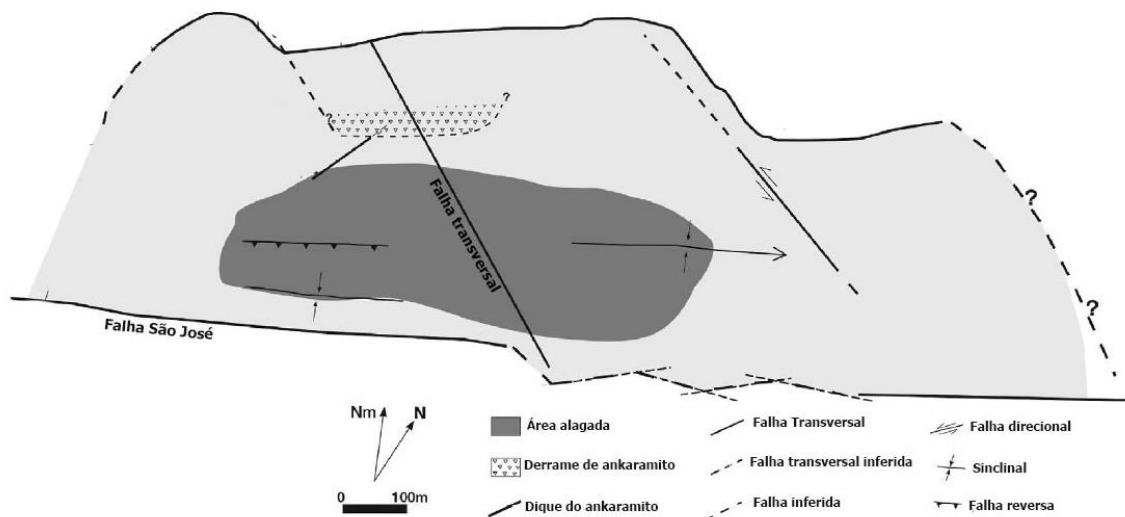
Fonte: Retirado de Adler et al., 2017.

De acordo com Ferrari, (2001), foram identificados dois campos distintos de paleotensões relacionado à tectônica da Bacia de Itaboraí. Uma extensão NW-SE que foi responsável pela formação da bacia, pela deposição dos sedimentos, pelo adernamento das

camadas contra a Falha São José, pela intrusão dos veios de calcário travertino e pela intrusão do dique de ankaramito. A segunda paleotensão, que atuou de modo compressivo na orientação NW-SE, foi responsável pela inversão da bacia, gerando falha reversa de direção ENE-WSW interna a ela, as fatias do embasamento sobre os sedimentos da bacia e os veios calcários travertino horizontais.

A extensão ortogonal a essa compressão, de direção NE-SW, pode ter gerado o adernamento das camadas da porção oriental da bacia para NE (Fig. 5). O embasamento da bacia é composto por gnaiss entrelaçado com lentes de mármore e rocha calco-silicato de origem Neoproterozoico (Pereira et al., 2017).

Figura 5 - Mapa estrutural da Bacia de Itaboraí.



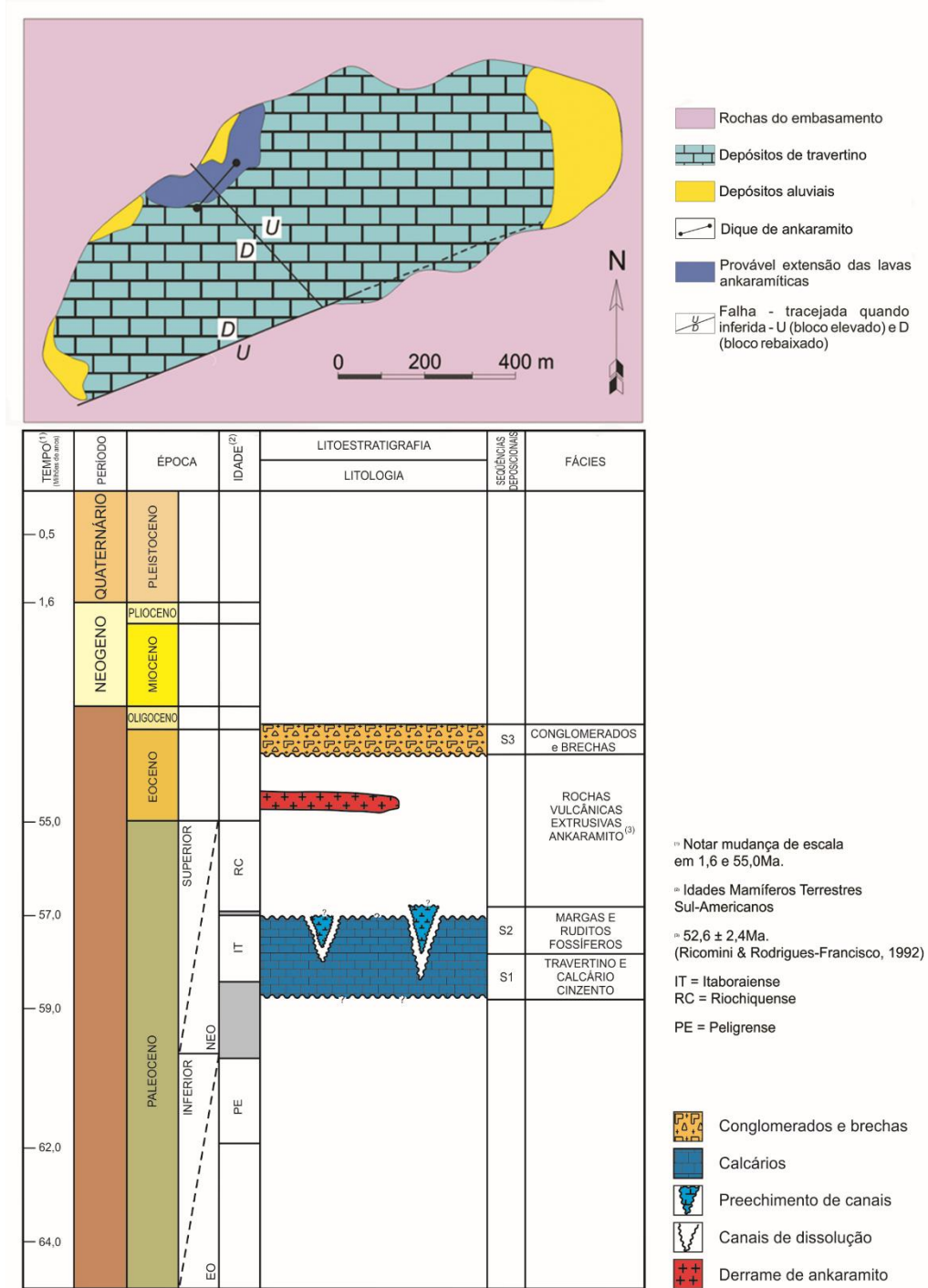
Fonte: Modificado de Ferrari, 2001.

Medeiros & Bergqvist, (1999) dividiram a Bacia de Itaboraí em três seqüências deposicionais (da base para o topo): S1, compreendendo uma intercalação de carbonatos de origem química e clásticos; S2, compreendendo os depósitos de margas e brechas de colapsos preenchendo canis de dissolução que cortavam verticalmente os calcários; e S3, depositada após o encerramento do ciclo carbonático (Fig. 6).

Segundo esses autores, a litologia da S1 está relacionada a fluxo hidrotermal rico em CaCO_3 que deu origem ao calcário travertino laminado descrito por (Leinz, 1938), intercalados com uma margas carbonática originada por fluxo hidrogravitacional com inúmeros fósseis de gastrópodes de coloração acinzentada. Após a deposição desta seqüência se iniciou o processo de carstificação do carbonato, dando origem a fendas que foram preenchidas pela S2, a qual consiste numa margas fracamente consolidada formada por fluxo hidrogravitacional rica em

conteúdo fossilífero. A S3 foi formada após cessar o ciclo tectônico da bacia e a fácies desta sequência é composta por sedimentos terrígenos que cobriram as rochas carbonáticas. Um derrame de ankaramito cortou os sedimentos calcários na porção norte da bacia, com espessura de 10 m e um dique com 150 m (Pereira et al., 2017). Uma nova datação, desta vez analisando a relação Ar/Ar (Mota et al., 2015) encontrou a idade de 54.89 ± 1.4 Ma para o derrame.

Figura 6 - (A) Mapa geológico e (B) carta cronoestratigráfica da Bacia de Itaboraí.



Fonte: Retirado de Bergqvist et al., 2005.

3 OBJETIVO

O objetivo geral desta dissertação é dar a conhecer a fauna de notoungulados presente na “Fenda de 1968” e ampliar o conhecimento da paleobiota da Bacia de Itaboraí.

Os objetivos específicos deste trabalho são:

- a) Identificar e classificar taxonomicamente os elementos dentários da ordem Notoungulata provenientes da “Fenda 1968”;
- b) Avaliar as singularidades taxonômicas observadas nessa fenda, a exemplo da ocorrência única de alguns táxons na mesma;
- c) Correlacionar os táxons identificados com formas argentinas a fim de refinar a classificação taxonômica dos táxons presentes nesta fenda.

4 MATERIAL E MÉTODOS

4.1 Material

Foram analisados cerca de 300 espécimes, incluindo dentes isolados, maxilas e mandíbulas pertencentes a notoungulados, depositados na Coleção de Mamíferos Fósseis do Museu de Ciências da Terra (MCTer) da Companhia de Pesquisa de Recursos Minerais (CPRM), procedentes da “Fenda de 1968”. Todos os fósseis provenientes desta fenda possuem coloração marrom escura ou marrom clara, o que não é visto nas demais fendas. Dentre estes, foram selecionados 11 (onze) exemplares representados por dentes molares e pré-molares isolados ou associado a fragmentos de dentário e fragmento de maxila, para descrição da nova espécie: MCT 4388M, M2D; MCT 4389M, M2E; MCT 4390M, M1D; MCT 4396M, P4E; MCT 4397M, P3E; MCT 4400M, P2D; MCT 4403M, m1 ou m2E; MCT 4420M, M2D; MCT 4419M, Fragmento de maxila esquerda com P3, P4, M1 e M2; MCT 4421M, M3E; MCT 4422M, Fragmento de dentário direito de um juvenil com dp2, dp3, dp4 e m1 (no alvéolo).

4.2 Métodos

A metodologia empregada consistiu no levantamento bibliográfico inerente à Bacia de Itaboraí, à “Fenda 1968”, aos notoungulados registrados nas tafocenoses das fendas de dissolução e em depósitos paleogênicos da América do Sul, especialmente os da Argentina.

Embora a bacia tenha sido muito estudada, pouco se conhece a respeito do material proveniente da “Fenda de 1968” e muitos desses fósseis ainda se encontram junto ao sedimento depositados no MCTer/CPRM, como foi o caso de um desses exemplares. Na preparação de um dos blocos de sedimentos da “Fenda 1968” foi utilizada a metodologia de “*screenwashing*” (*sensu* Cifelli, 1995).

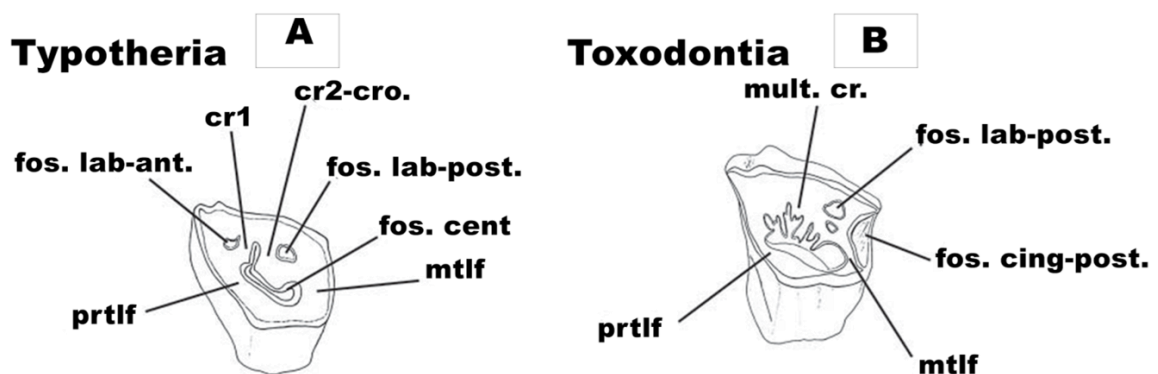
As imagens dos espécimes foram capturadas com o estéreomicroscópio Zeiss Stemi 2000-C com câmera AxionCam ERC 5S acoplada. Os espécimes foram posicionados com a coroa paralela ao plano de foco. Múltiplas fotos foram feitas, com foco em diferentes níveis do

dente, e posteriormente unidas e tratadas no Adobe Photoshop CS6 para melhor visualização das estruturas dentárias.

Com intuito de fazer uma correta classificação taxonômica foi adotado o critério de identificação a partir da observação das assinaturas taxonômicas da face oclusal (Fig. 7), e seguido os seguintes passos:

- a) Identificação do posicionamento do dente *in loco* para os dentes isolados;
- b) Descrição das estruturas dentárias e suas variações sob lupa binocular, acoplada ou não a um computador e câmera digital;
- c) Medição dos dentes (dimensões externas e internas) com paquímetro mecânico ou digital;

Figura 7 - Nomenclatura da morfologia na face oclusal e as respectivas diferenças entre as duas principais subordens (A) Typotheria e (B) Toxodontia da Ordem Notoungulata



Legenda: fos. lab-ant., fosseta labial anterior; cr1, crista 1; cr2-cro, crista 2 crochê; fos. cent., fossa central; fos. cing-post., fosseta cingular posterior; mtlf, metalofo; mult. cr., múltiplas cristas; fos. lab-post., fosseta labial posterior; prtlf, protolobo.

Fonte: Modificado de Billet, 2011.

A análise filogenética foi realizada com base em uma matriz de 145 caracteres e 74 táxons, modificada de García-López et al. (2017), que por sua vez foi modificada de Deraco & García-López (2016) e Billet & Muizon (2013). O grupo interno compreende alguns notoungulados basais e derivados, com representantes de Litopterna e outros mamíferos definidos *a priori* como grupos externos. A matriz foi analisada com o software TNT (Goloboff et al., 2008), conduzindo uma pesquisa tradicional com 1000 sequências aleatórias adicionais, salvando 10 árvores por rodada. A seleção dos caracteres ordenados segue o mesmo padrão utilizado por Billet (2011) e Billet & Muizon (2013). Foram realizadas duas análises principais, uma tratando todos os caracteres igualmente ponderados e outra com ponderação implícita.

A terminologia das estruturas dentárias foi adaptada a partir de contribuições clássicas e recentes relacionadas à dentição de mamíferos (Herskovitz, 1971) e dos notoungulados (Deraco & García-López, 2016; García-López et al., 2019; Bauzá et al., 2019), observando sempre o nível de desgaste dentário para identificar de forma correta as estruturas presente na face oclusal.

5 RESULTADO E DISCUSSÃO

Os dados referentes a metodologia utilizada, bem como o detalhamento deste trabalho, resultado e discussão que englobam a análise dos fósseis de notoungulados e a descrição de uma nova espécie que foram coletados na Bacia de Itaboraí no ano de 1968, denominado fenda de 1968, estão presentes no Apêndice A (p.29) em formato de artigo, intitulado “A new basal notoungulate from the Itaboraí Basin (paleogene) of Brazil”, submetido ao Periódico Ameghiniana, classificação B2 no Qualis CAPES.

CONCLUSÃO

O novo táxon aqui descrito representa um novo gênero e uma espécie de notoungulado, exclusivo da “Fenda 1968”, que apresenta uma posição basal no contexto desta ordem. Que tem como característica, dentição braquidonte, colunas do paracone e metacone bem desenvolvidas, crista 1 ausente e crista intermedia que indicam que esse novo táxon não pode ser incluído nem no Notostylopidae nem nas outros subordens de notoungulados conhecidas (Typotheria e Toxodontia). Nesse sentido, essa espécie mostra um padrão semelhante ao observado nas espécies tradicionalmente conhecidas como henricosborniídeos.

A presente análise filogenética falha em resolver as relações entre os henricosborniídeos e entre esses táxons e os demais da Notoungulata. Esforços futuros devem ser tomados para uma definição mais acurada para filogenia do grupo buscando testar seu monofiletismo, provavelmente utilizando caracteres não qualitativos e discretos.

Não encontramos evidências conclusivas sobre a sinonímia entre *Itaboratherium atavum* e *Othnielmarshia pristina* proposta por (López, 2008) e mencionada como duvidosa por (Bauzá 2020). Embasado em nossas análises, questionamos a referência dessas espécies como henricosborniídeos, com base no complexo padrão dentário oclusal observado em ambos os casos.

Com base nas observações feitas no contexto do presente estudo, consideramos que a cúspide acessória do trigonídeo, referida em algumas contribuições como paraconido, pode estar associada a algumas cúspides localizadas mesialmente ao metaconido e identificada como pseudoparaconido em estudos anteriores.

A singularidade taxonômica do novo táxon aqui descrito, somado ao fato que ele não coexistiu com as demais espécies de notoungulados da Bacia de Itaboraí, suporta a proposta de Bergqvist & Carneiro (2014) de um assincronismo da “Fenda 1968” com relação às outras prospectadas na bacia.

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APÊNDICE A – A New Basal Notoungulate From the Itaboraí Basin (Paleogene) Of Brazil
(Artigo Científico)

**A NEW BASAL NOTOUNGULATE FROM THE ITABORAÍ BASIN (PALEOGENE)
OF BRAZIL**

**UN NUEVO NOTOUNGULADO DE LA CUENCA DE ITABORAÍ (PALEÓGENO) DE
BRASIL**

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39 pag.; 4 figs.; 1 table

Running Header: CASTRO *ET AL.*: NEW BASAL NOTOUNGULATE FROM ITABORAÍ

Short Description: We describe a new basal notoungulate and discuss its significance in the
context of the SANUs of middle latitudes.

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Abstract. A new basal notoungulate, *Nanolophodon tutuca* gen. et sp. nov., is described. This is represented by maxillary and dental fragments and by isolated teeth. The holotype and referred material were found at the “1968 Fissure” of the Itaboraí Basin, Rio de Janeiro State, Brazil. This basin has been regarded as early Eocene in recent contributions. The generalized appearance and brachydonty of the studied specimens, together with the presence of certain typical traits (poorly developed entolophid, well-developed metacone column, etc.) indicate that *N. tutuca* can be considered among the group of genera traditionally known as henricosborniids, easily distinguishable from tyotherian by the absence of crista 1 and from Toxodontia by the absence of crista intermedia. It is also different from all other henricosborniids by a combination of characters, such as the presence of a long crochet, the development of two small cristae in the ectoloph, the large paraconid, among others. In the context of a phylogenetic analysis performed, we do not find conclusive evidence about the synonymy between *Itaboraitherium atavum* and *Othnielmarshia pristina*. Moreover, we question the reference of these forms as henricosborniids, based on the complex occlusal dental pattern observed in both cases. Finally, based on the observations made in the present study, we discuss the identification of the paraconid in notoungulates, which may be associated with some cusps located mesially to the metaconid and identified as pseudoparaconids in past studies.

Keywords. Lophodont, Henricosboniidae, phylogeny, “1968 Fissure”.

Resumen. UN NUEVO NOTOUNGULADO DE LA CUENCA DE ITABORAÍ (PALEÓGENO) DE BRASIL. Se describe un nuevo notoungulado basal, *Nanolophodon tutuca* gen. et sp. nov. El mismo está representado por fragmentos de maxilar y dentario y dientes aislados. El holotipo y material referido fueron encontrados en la “Fisura de 1968” de la cuenca de Itaboraí en el Estado de Río de Janeiro, Brasil. Esta cuenca ha sido referida al Eoceno temprano en contribuciones recientes. La apariencia generalizada y la braquidontia de los especímenes estudiados, junto con la presencia de ciertos rasgos típicos (entolofido poco desarrollado, columna del metacono bien desarrollada, etc.) indican que *N. tutuca* puede ser considerado entre el grupo de géneros tradicionalmente conocidos como henricosbornidos, y fácilmente distinguible de tipoterios por la ausencia de crista 1 y de toxodontes por la ausencia de crista intermedia. Es también diferente de todos los otros henricosbornidos por una combinación de caracteres, como la presencia de un largo crochet, el desarrollo de dos pequeñas cristas en el ectolofio y un gran paracónido, entre otros. No hallamos evidencia concluyente sobre la sinonimia entre *Itaboraitherium atavum* y *Othnielmarshia pristina*. Más aún, consideramos que la referencia de estas formas como henricosbornidos es cuestionable en base a la compleja morfología oclusal observada en ambos casos. Finalmente, en base a las observaciones realizadas en el presente estudio, discutimos la identificación del paracónido en notoungulados, el cual podría ser asociada con algunas cúspides localizadas mesialmente al metacónido e identificadas como pseudoparacónidos en estudios anteriores.

Palabras clave. Lofodonte, Henricosboniidae, filogenia, “Fisura de 1968”.

DESPITE ITS REDUCED SURFACE, THE SÃO JOSÉ DE ITABORAÍ BASIN (BEST KNOWN AS ITABORAÍ BASIN) stands as one of the most important Paleogene localities for the understanding of the early evolutionary phases in the history of South American mammals. Most of the limestone rocks that fills the basin were explored for economic purposes for approximately 50 years (1933-1984; Bergqvist *et al.*, 2005), and over this time span several fieldworks (1948, 1949, 1950, 1953, 1961, 1967, 1968, and 1976) were undertaken and a large number of fossil vertebrates were recovered from this basin, mainly composed by mammals (*e.g.*, Bergqvist *et al.*, 2005; Bergqvist *et al.*, 2018; Zanesco *et al.*, 2019). The extensive fossil record of this locality has been used as a base for the Itaboraian SALMA (Paula-Couto, 1952a). The chronological context of this SALMA has been extensively discussed and it has changed through the last decades (Bergqvist *et al.*, 2005). Here, we follow recent contributions, which consider the Itaboraian as early Eocene (Gelfo *et al.* 2009; Woodburne *et al.*, 2014a), and provisionally include the “1968 Fissure” within this scheme. Nevertheless, it should be noted that the precise chronological framework of this and other fissures need further study, and that this point of view is potentially subject to change in the future.

Four orders out of five of the so-called South American native ungulates (hereafter, SANUs) are present in the Itaboraí Basin, with the exception of Pyrotheria (*e.g.*, Bergqvist *et al.*, 2005). Traditionally, the SANUs include Litopterna, Notoungulata, Astrapotheria, Xenungulata, and Pyrotheria, which are sometimes grouped in the superorder Meridiungulata (McKenna, 1975); together, these major groups include some 50 families and well over 250 genera (Croft *et al.*, 2020). Recently, genomic and proteomic evidences suggest that Notoungulata and Litopterna are sister taxa of the extant Order Perissodactyla, integrating all together the clade Panperissodactyla (Welker *et al.*, 2015).

Within the SANUs, the Notoungulata represent the most diverse clade, with over 150 genera organized traditionally into 13 families, most of which are included within two suborders, Typotheria and Toxodontia, excluding the Henricosborniidae and the Notostylopidae (Billet, 2010; Croft *et al.*, 2020). In the Itaboraí Basin the Typotheria of the family Oldfieldthomasiidae are represented by *Colbertia magellanica* (Price & Paula-Couto, 1950) and the putative oldfieldthomasiid *Itaboraitherium atavum* (Paula-Couto, 1954). The former is perhaps one of the best studied taxa in the basin; the later, in turn is known for more fragmentary material and was described originally as a Notostylopidae (Paula-Couto, 1954). A third genera was also originally described as an oldfieldthomasiid (*Camargomendesia pristina* Paula-Couto, 1978) but almost immediately recombined as another species of the

henricosborniid genus *Othnielmarshia* (Paula-Couto, 1979). This new combination (*O. pristina*) was not fully accepted, as in some contributions (e.g., Bergqvist *et al.*, 2005; Billet and de Muizon, 2013), the name *Camargomendesia* Paula-Couto, 1978 was still used. Furthermore, recent studies pointed to the possible inclusion of *Itaboraitherium atavum* within Henricosborniidae (López & Bond, 2010; Bauzá *et al.*, 2020), although some workers followed the original position of the species in the Oldfieldthomasiidae (see Woodburne *et al.*, 2014b), and the junior synonymy of *Othnielmarshia pristina* (= *Camargomendesia pristina*) regarding the former taxon have been also claimed (Bauzá *et al.*, 2020 and references therein). However, these taxonomic proposals have not been phylogenetically tested.

Almost all fossil vertebrate specimens recovered from the Itaboraí Basin came from fissure fill deposits (Bergqvist *et al.*, 2005). The fissures were discovered with the advance of the economic exploration of the limestone. Specimens unearthed from fissures discovered in 1949 and 1968 are housed at Museu de Ciências da Terra/MCT, in Rio de Janeiro/RJ (Bergqvist *et al.*, 2018). Little is known about the location and the fossil mammals of the "1968 Fissure", from where the specimens here studied proceed (e.g., Cifelli, 1983; Bergqvist *et al.*, 2011; Carneiro, 2019; Zanesco *et al.*, 2019). The fossils of the "1968 Fissure" are peculiar and distinct from all other specimens recovered in Itaboraí Basin due to its brown color (see Bergqvist *et al.*, 2011). Despite the great abundance of teeth with notoungulate morphology, these have never been analyzed and their taxonomy have remained obscure.

In this paper we describe a new genus and species of an henricosborniid notoungulate from the Itaboraí Basin (Itaboraian SALMA) collected in the "1968 Fissure". This new taxon is based on fragmented upper and lower jaws and isolated upper and lower teeth of different wear stages. We also include this new taxon in a general phylogenetic test and discuss its significance in light of the rich fauna of SANUs of middle latitudes of South America.

Geographical and geological settings

The Itaboraí Basin is located about 9 km SSE of the Itaboraí city, Rio de Janeiro state, and about 30 km East from the city of Rio de Janeiro. It is the smaller sedimentary basin of Brazil (Fig. 1), it is part of the eastern portion of the Continental Rift of Southeastern Brazil (Riccomini *et al.*, 1996), and is mostly composed by limestones (Ferrari, 2001; Sant'Anna *et al.*, 2004; Bergqvist *et al.*, 2005; Adler *et al.*, 2017; Pereira *et al.*, 2017). The basin has an elliptical shape with major length of 1400 m in NE-SW direction, 500 m in N-S direction, and 100 m deep (Rodrigues-Francisco & Souza-Cunha, 1978).

The limestone rocks of the Itaboraí Basin consist of a travertine system and platy, massive, brecciated, and nodular calcretes (Leinz, 1938; Adler *et al.*, 2017). Medeiros and Bergqvist (1999) divided the basin into three depositional sequences – S1, S2, S3 – (from bottom to top): S1 comprises an intercalation of travertine and calcretes; S2, marl deposits and collapsing breccias filling hydric dissolution that cut S1 sequence vertically and clastic rocks of S3 deposited after the ending of the limestone cycle. Cutting S1 sequence (no confident relation can be made with S2), at the northwestern portion of the basin, a magmatic extrusion of ankaramite provided the sole radiometric date within the basin: 54.89 ± 1.4 My.

As mentioned before, little is known about the “1968 Fissure”, except that it was discovered twenty years after the first fissure, in a lower topographic (and probably stratigraphic) position in the basin (see Paula-Couto, 1950; Bergqvist *et al.*, 2018). The “1968 Fissure” also calls attention for the great abundance and exclusive record within the basin of the *Litopterna* species *Protolipterna ellipsodontoides* Cifelli, 1983 (Zanesco *et al.*, 2019).

Institutional abbreviations. **MACN A**, Museo de Ciencias Naturales “Bernardino Rivadavia”, Colección Ameghino, Buenos Aires, Argentina, **MCT-M**, Museu de Ciências da Terra, Companhia de Pesquisa de Recursos Minerais, Fossil Mammal Collection, Rio de Janeiro, Brazil, **MLP**, Colección Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina, **MN**, Museu Nacional, Rio de Janeiro, Brazil.

Anatomical abbreviations. **dp**, lower deciduous premolar; **M/m**, upper/lower molar; **P/p**, upper/lower premolar.

Other abbreviations. **SALMA**, South American land mammal age.

MATERIALS AND METHODS

With one exception, the specimens have been already removed from the sediments. They comprise one maxillary fragment, one incomplete dentary, eight isolated upper teeth, and one isolated lower tooth. They are all brown colored, being the teeth darker than the bones. Teeth image were captured under a stereomicroscope Zeiss Stemi 2000-C with a camera AxioCam ERC 5S attached. The pictures were treated with Adobe Photoshop CS6 for a better visualization of the structure. The measurements were taken at the level enamel base, with ImageJ software.

The phylogenetic analysis was performed on the basis of a matrix of 145 characters and 75 taxa. The matrix is a modified version of that published by García-López *et al.* (2017), which in turn was modified from Deraco and García-López (2016) and Billet and de Muizon (2013).

The ingroup comprises some primitive and derived notoungulates, with representatives of Litopterna and other mammals as *a priori* outgroups. The matrix was analyzed with the TNT software (Goloboff *et al.*, 2008), using the New Technology Search function. The selection of ordered characters follows Billet (2011) and Billet and de Muizon (2013). An initial analysis was conducted including a recently described basal notoungulate, *Archaeogaia macaachae* Zimicz *et al.*, 2020, reported for the Paleogene of Northwestern Argentina (Mealla Formation). Nevertheless, the high percentage of missing entrances of this taxon resulted in a highly unresolved consensus tree. Thus, we also conducted two additional analyses excluding *A. macaachae*, one treating all characters as equally weighted and one under implicit weighting. We focused the main discussion on these last two phylogenetic hypotheses; however, some comments about the Mealla taxon and the analysis performed including it were incorporated as well. The matrix and the character list are provided at Supplementary Online Information.

Terminology on dental features is adapted from classic and recent contributions dealing with mammal dentition in general (Herskovitz, 1971) and notoungulates (Deraco and García-López, 2016; García-López *et al.*, 2019; Bauzá *et al.*, 2019). General terms applied to molar morphology are illustrated in Figure 2. For practical reasons and except in Systematic Paleontology, the names of some families usually considered as paraphyletic (*e.g.*, Henricosborniidae, Oldfieldthomasiidae) will be written without quotation marks.

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Panperissodactyla Welker *et al.*, 2015

Notoungulata Roth, 1903

“Henricosborniidae” Ameghino, 1901

Nanolophodon gen. nov.

Type species. *Nanolophodon tutuca* new species. Itaboraí Basin, Río de Janeiro, Brazil, early Eocene.

Etymology. From the Latin word *nanos* (meaning dwarf or small) and *lophos* (meaning crest), and the latinization of the Greek term *odontos* (meaning tooth), in reference to the small size and lophodonty of the teeth.

Diagnosis. As for the type and only known species.

Nanolophodon tutuca sp. nov.

Figure 3

Etymology. Tutuca in honor to the scholar Dr. Maria Antonieta Rodrigues (Tutuca), for her contribution, commitment, and struggle to the implementation and preservation of the São José de Itaboraí Paleontological Park.

Type material. MCT 4419M, fragment of left maxilla with P3-M2 (moderate to advanced wear).

Referred material. MCT 4400M, isolated right P2; MCT 4397M, isolated left P3; MCT 4396M, isolated left P4; MCT 4390M, isolated right M1; MCT 4388M, isolated right M2; MCT 4389M, isolated right M2; MCT 4420M, isolated right M2; MCT 4421M, isolated left M3; MCT 4403M, isolated left lower molar; MCT 4422M, fragment of left jaw with dp2, dp3, dp4 and m1 (in alveolus).

Geographic occurrence. 22°50'23.58"S, 42°52'31.97"W. Itaboraí city, Rio de Janeiro State, Brazil.

Stratigraphic occurrence. Itaboraí Basin, Itaboraí Formation, "1968 Fissure" located at the bottom of the basin; Itaboraian SALMA (early Eocene *sensu* Woodburne *et al.*, 2014a).

Diagnosis. Small notoungulate bearing the basic tetralophodont pattern of the order. It is excluded from Typotheria by the absence of mesiolabial fossette limited distally by the crista 1 and from the Toxodontia by the absence of crista intermedia near the mesial end of the crochet. Among basal forms, it is excluded from Notostylopidae by the presence of a strong metacone column on the ectoloph, the absence of crenulations on the crochet (characteristic of some notostylopids), and the greater development of the paraconid. Regarding genera traditionally considered as henricosborniids, the new taxon shows the following combination of characters: upper molars with tetralophodont pattern more developed and marked than in all other henricosborniids, and particularly regarding *Henricosbornia* Ameghino, 1901, *Perispantostylops* Ameghino, 1901, and *Othnielmarshia*; crochet proportionally longer than in all other henricosborniids except *Orome* Bauzá *et al.*, 2019; paracone and metacone columns more developed than in *Henricosbornia*, *Perispantostylops*, *Othnielmarshia*, and *Orome*, but similar to *Simpsonotus* Pascual *et al.*, 1978; and mesial and distal cingulae not developed in the lingual wall of protocone and hypocone, differing from *Henricosbornia* and *Perispantostylops*. Upper premolars with strong parastyle, separated from the paracone column by a deeper flexus than in *Henricosbornia* and *Simpsonotus*, conspicuous crochet in P3-4 (differing from all the mentioned genera), and more triangular and less transverse outline than in *Simpsonotus*. Lower molars similar to *Henricosbornia* but with a larger paraconid than in *Othnielmarshia*, *Perispantostylops*, *Simpsonotus*, and *Archaeogaia* Zimicz *et al.*, 2020; trigonid proportionally

less developed than in *Othnielmarshia*; and protolophid more oblique and entolophid less developed than in *Archaeogaia*.

DESCRIPTION

Upper dentition

Premolars. All isolated premolars (Fig. 3.1–4) show three roots and are subtriangular, with an oblique ectoloph, a well-developed parastyle and paracone, angulated metastylar area, and a somewhat rounded lingual side. Measurements are given in Table 1.

The P2 is smaller and occlusally simpler than the following premolars. The parastyle is well developed and mesiolabially projected, with an occlusal outline rounded at the tip, being clearly differentiated and separated from the paracone by a wide labial flexus. This last cusp is dominant at the crown, both in occlusal surface and in relative height, presenting a prominent labial column. Distally, the paracone shows a vestigial flexus. Although the tooth lacks a conspicuous metacone labial column, the ectoloph is gently convex between the paracone and the metastylar area. The metastyle is visible as a small and rounded distal spur, considerably reduced in comparison to the parastyle. The protocone is smaller than the paracone and bears an oblique preprotocrista (=protoloph) which points to the mesial edge of the parastyle. Distally, the wall of the protocone shows a crescent-shaped wear facet on the postprotocrista, which widens labially and occupies the distal half of the occlusal surface of the crown. Both the mesial and distal cingula are present and vestigial, with the distal cingulum slightly more lingually extended than the mesial one and showing subtle crenulations. There is no trace of central fossa, and the central surface of the crown is a wide and smooth basin, showing only a prominence or “bump” corresponding to the lingual wall of the paracone.

The P3 is a little more molarized than the P2, but its molarization is still incipient, although some typical molar structures are present but vestigial (see below). The parastyle is conspicuously developed, although its occlusal surface is less mesially projected than P2. Other traits of this structure are very similar to the previous tooth, with a wide labial flexus separating the cusp from the paracone column. In teeth with little wear, like MCT 4397M, the mesiolabial tip of the parastyle is rounded; as wear advances, it turns wide and blunt. The large paracone shows a wide and smooth labial column, widened at its base, as in P2. There is some intraspecific variation regarding the development of the metacone area (ch. 38 of the matrix, scored as polymorphic for *Nanolophodon*). In the specimen MCT 4397M, there is a slightly convex area (although more developed than in P2) separated from the paracone column by a

faint flexus. In turn, the specimen MCT 4419M shows a completely flat area at this zone, with no traces of the metacone column. The metastyle is larger than in P2, although clearly smaller than the parastyle. With the advance of the tooth wear, the metastyle widens, although maintaining its angulated aspect. The protocone is smaller than the paracone, slightly compressed and mesiodistally elongated. In the specimen (MCT 4397M), that bears little wear, it is possible to see an exceedingly small cusp attached to the protocone. With the increase of the tooth wear, it disappears (as in MCT 4419M), but it may also represent an individual variation. This structure is only visible in occlusal view, as there is no entoflexus or other traits to differentiate this cusp lingually or labially. The nature of this small cusp remains unsolved; although its position is that of a hypocone, future discussion on the homologies of this and other structures should be addressed (see below). A sharp preprotocrista (= protoloph) runs from the mesial wall of the protocone to the mesial wall of the parastyle. Once again, there is intraspecific variation regarding this area, since the specimen MCT 4419M presents a clearly visible paraconule. This trait, although unusual in notoungulates, has been reported in some Paleogene forms (*e.g.*, *Pampahippus* Bond and López, 1993; Deraco and García-López, 2016). This paraconule is relatively large and conspicuous on the crown and, since it was not visible in the specimen with little wear, its presence is a wear-independent intraspecific variation. On the distal side, an apparently true metaloph runs from the cusp located distal to the protocone, showing a small wear facet and a roughly transverse arrangement in the specimen MCT 4397M. A vestigial crochet is connected to the metaloph and ends independently at the labial slope of the central fossa. Both the metaloph and the zone of the crochet widens with tooth wear, and the latter structure is visible as a convex wear facet rounded by enamel. The central fossa is well differentiated and narrow toward the lingual side but shows a gentle labial slope, which is interrupted by a small crista near the crochet. The mesial and distal cingula are more developed than in P2, particularly the distal one, which is also more lingually extended. There is also a faint labial cingulum, mostly visible at the base of the metacone area in both specimens.

Most features mentioned for the P3 are also applicable to the P4. The last premolar also shows a low molarization, although several structures are stronger and more robust in this case. The P4 is represented in the maxillary fragment MCT 4419M and by the isolated tooth MCT 4396M (which is slightly less worn). Both the paracone and parastyle shows a similar development and wear pattern than in the P3, being also separated by a wide and conspicuous flexus. This is also true for the metastyle, which widens in the older individual. The most striking difference regarding previous premolars is the presence of a small but conspicuous

metacone attached to the distal area of the paracone and separated from this cusp by a short and narrow ectoflexus. It should be noted that this cusp is absent in the specimen MCT 4419M; however, this may be due to a more advanced wear, as in the younger specimen the metacone is mostly conspicuous on its apical (occlusal) end. The protocone is sharp and in this case, there is no trace of the small cusp located distal to the protocone (absent in both specimens). The development of preprotocrista (=protoloph) and metaloph in the P4 is more symmetrical than in the previous premolars. A short crochet projects mesially from the metaloph and joins two small parallel cristae, both equivalent to the crista 2 (as they are located in close proximity). In the specimen with advanced wear, these structures are fused by wear, forming an angulated spur on the central fossa (which shows a similar morphology regarding the P3). The protoloph in this case does not points to the mesial wall of the parastyle, but instead it ends labially and mesially on the area between parastyle and paracone. Cingula are stronger on this tooth, particularly the distal one. Both mesial and distal cingulae merge on the lingual area of the base of the protocone in the specimen MCT 4396M. This cannot be corroborated on MCT 4419M since in that case the base of the protocone is broken. The labial cingulum is particularly developed on MCT 4396M, although it does not show a sharp edge and is present as a blunt and extended enamel fold, particularly visible on the base of the metacone.

Molars. The first two molars show the basic pattern of lophs present in Notoungulata (ectoloph, protoloph, metaloph, and crochet) and have a trapezoidal occlusal outline (Fig. 3.1,5–6). Regarding the M3 (Fig. 3.7), the hypocone and metaloph are strongly reduced, as usual for Paleogene notoungulates. Measurements are given in Table 1.

The M1 and M2 will be described together as they are very similar teeth, differing mostly in size (M1 smaller) and loph development (greater in M2). The mesiodistally elongated ectoloph in these molars (not oblique as in the case of the premolars) is marked by the conspicuous development of parastyle, paracone, metacone, and metastyle. The parastyle is moderately developed in both molars. This is spur-like in specimens with low wear and becomes a rounded prominence in older individuals. The parastyle is separated from the paracone by a labial flexus. A slight variation can be observed regarding the development of this structure (being somewhat marked in the specimen MCT 4419M); nevertheless, it is mostly shallow in all the molars of the sample. The paracone is small and shows a conspicuous labial column, which maintains an almost constant diameter trough the labial wall. The metacone area is slightly more extended mesiodistally, and the labial column of the metacone tends to widens toward the base of the crown, particularly in the M2. However, these differences in size are

very subtle, and the overall appearance of the labial columns of both cusps is mostly symmetrical in labial view. Unlike the condition observed in premolars, the metastyle here is larger than the parastyle. It is also a spur-like structure, but it maintains a more angulated appearance in advanced wear. Protocone and hypocone are also almost identical, but the protocone is slightly larger in occlusal view, and usually shows a more labial position, particularly in the case of the M1. The entoflexus, between the lingual wall of protocone and hypocone shows some variation, being shallow in some specimens (*e.g.*, MCT 4420M) and moderately deep in others (*e.g.*, MCT 4388M, MCT 4390M). There seems to be no pattern of differentiation of the entoflexus between the M1 and the M2. The protoloph is oblique, running from the protocone to the area of the ectoloph between paracone and parastyle. In specimens with low wear, the protoloph (=preprotocrista) is mostly straight (slightly bent distally near the protocone). In addition, the development of this protoloph seems to be greater in the unworn M2 than in the M1. As wear advances, the mesial edge of the protoloph becomes completely straight in the M1 but it is barely convex in the M2. The metaloph is shorter than the protoloph and mostly transverse, with the lingual end on the hypocone and the labial end on the area between metacone and metastyle (hence, the metaloph is slightly bent distally). A slender crochet extends mesially from the area between the lingual and middle third of the metaloph. This crochet is relatively longer compared to the condition observed in some other henricosborniids (*e.g.*, *Henricosbornia*). It is also straight and slightly oblique, pointing towards the parastyle and reaching the distolingual slopes of the paracone. This morphology is quite constant along the sample of both the M1 and M2 and is discernible even in advanced wear (*e.g.*, MCT 4419M). A somewhat variable pattern of cristae is present on the lingual wall of the ectoloph, pointing towards the central fossa. Although the pattern is difficult to assess indisputably, there seems to be very close cristae in the specimens identified as M1 (this cannot be corroborated in the M1 preserved in situ on the maxillary fragment MCT 4419M, given its advanced wear), with the mesial crista smaller than the distal one. Both can be interpreted as equivalent to the crista 2, as they join the crochet (it is worthy to note that the mesial end of the last loph remains independent). Hence a distolabial basin is isolated, that can be regarded as a shallow and wide distolabial fossette in the M1. As wear advances this fossette becomes bowl-shaped, but disappears almost completely in the first molar of older individuals, such as MCT 4419M. As for the M2, this bears apparently a single crista, barely stronger than in the case of the M1, which connects to the crochet and isolates a more conspicuous and somewhat deeper distolabial fossette. This fossette persists in the specimen MCT 4419M (where the M2 is less

worn than the M1) as a clear structure. As for the M1, the mesial end of the crochet in the M2 remains free. It should be noted that in advanced wear, this mesial end tends to strangle the mesiolabial zone of the central fossa, hence faintly separating a small enamel area. Judging by this morphology, even if an enamel basin is isolated, this cannot be interpreted as homologous to the mesiolabial fossette of tyotherian notoungulates. On these forms, this fossette is isolated by the crista 1, a structure rising from the ectoloph and connecting to the protoloph (Billet, 2011). In this case, there is no true crista 1, since the structure possibly isolating a mesiolabial basin is the mesial end of the crochet. Hence, such structures should not be considered homologous (and the mesial end of the crochet acts as a “pseudo-crista 1”). The central fossa shows a typical arrangement for Paleogene forms, it is straight and oblique, with a deeper and rounded distal area. The central fossa tends to be shallower on the M1, and in the case of MCT 4419M, this structure is almost completely erased. The only cingulae visible in the observed molars are the mesial cingulum and the distal cingulum. Both are well developed, being the distal one wider. There is a considerable separation between the metaloph and the distal cingulum, so that both structures only merge with considerable wear.

A single specimen, MCT 4421M, corresponding to an almost unworn tooth, represents the M3 in the sample. Its occlusal outline can be regarded as subtriangular or almost elliptical. As usual, the M3 presents several structural differences regarding previous molars. In this case, the ectoloph is oblique (as in the condition present in premolars). Parastyle and metastyle are reduced; the former is spur-like and is separated from the paracone labial column by a shallow flexus. The metastyle is about the same size, and is separated from the metacone column by a similar flexus. Both the labial columns of paracone and metacone are nearly symmetrical in development; they maintain an almost constant diameter through the labial wall and are separated by a relatively wide and shallow ectoflexus. The protocone is a large cusp in occlusal view, which apex is located near the central area of the crown. It is connected to the parastyle-paracone area by a relatively short, roughly straight, and sharp protoloph (with low wear). The hypocone is vestigial and the metaloph is short and oblique. The lingual end of the latter is bent mesially and connects with the distal wall of the base of the protocone, forming a structure similar to a short entocrista. On the opposite side, the metaloph changes drastically in direction by its middle length and turns towards the metastyle. A small crochet projects mesially from the middle point of the metaloph, running to contact the protoloph. Four cristae are present rising from the lingual wall of the ectoloph. The most mesial crista is independent, the other three contact the crochet, isolating small enamel basins, including that corresponding to the

distolabial fossette. The central fossa is relatively deep and narrow, and its occlusal outline is lingually concave. The mesial cingulum is larger than the distal one. The former shows a sharp edge and reaches the mesiolingual area of the base of the protocone. The distal cingulum is very short and runs transversally from near the lingual end of the metaloph to the base of the metastyle. No other cingula are visible.

Lower dentition

The permanent lower dentition of *Nanolophodon tutuca* (Fig. 3.8–9) is represented only by a partially erupted and hence unworn m1, preserved in a left dentary which also preserves deciduous premolars (MCT 4422M) and an isolated left molar, with light wear, identified as a m1 or m2 (MCT 4403M). The molars will be described together, given their virtually identical morphology. Neither permanent premolars nor the m3 are represented in the sample. Measurements are given in Table 1.

Molars. The trigonid presents a very oblique protolophid. The protoconid presents a rounded angle on its distolabial wall. Mesially, this cusp is continuous with a short paracristid with a hook-like mesiolingual end. The paracristid is completely detached from the mesial cingulid (see below) in both molars. The metaconid is the highest and more developed cusp of the tooth. Its lingual wall represents a somewhat slender column and there is a well-developed paraconid attached to the mesiolabial zone of the metaconid. Both cusps are connected by a metacristid mesiodistally oriented (this gives a spur-like appearance to the paraconid, differing from the more bunoid condition in *Simpsonotus*). The paraconid is relatively larger and more mesiodistally oriented than in *Henricosbornia* (e.g., MACN A 10810), *Peripantostylops* (e.g., MLP 56-XII-18-49), and particularly *Othnielmarshia* (e.g., MACN A 10806). The trigonid basin is small and shallow, and is mesially closed by a small although well-developed cingulid, restricted to the mesial wall of the tooth, which surrounds the base of the mesial part of the paracristid.

Trigonid and talonid are separated labially by a deep ectoflexid (=hypoflexid). On the opposite side, the lingual aperture of the talonid basin is distally placed regarding the ectoflexid, a usual trait of Paleogene notoungulates, but it is particularly conspicuous in *N. tutuca*, given the oblique arrangement of the protolophid. Also, as usual in these forms, the hypolophid and cristid obliqua are integrated into a continuous mesiodistal structure containing the hypoconid and the hypoconulid, and connected to the trigonid at the median part of the protolophid, and in a point much lower than the occlusal level of that lophid in unworn molars. The position of

the hypoconid is marked by a subtle angle, as in other Paleogene genera such as *Henricosbornia*. The hypoconulid is relatively large and separated from the entoconid by a deep distolingual flexid. The entoconid is almost isolated in the talonid, being only slightly expanded transversely by a weak entocristid. The talonid basin is wide, with a triangular bottom, and shallow. Besides the mesial one, no other cingulids are visible on these teeth.

Deciduous dentition. As mentioned above, the dentary MCT 4422M preserves dp2 to dp4. These three teeth are light colored and proportionally longer than wider, in comparison to their successors, as typical of deciduous teeth. The occlusal structure of the dp2 is very simple, although the trigonid and talonid can be vaguely differentiated. The crown is marked by a sinuous and mesiodistally continuous cristid. It ends mesially in a “hook” which descends lingually forming a small mesiolingual cingulid. The higher point of the mesiodistal cristid corresponds to a single cusp, as metaconid and protoconid cannot be discriminated. The labial wall of this cristid is relatively wide and smooth, while the lingual wall is slenderer and forms a more conspicuous column. Distally, a lingual flexion of the mesiodistal cristid (forming a wide and shallow ectoflexid) marks the limit of a rudimentary talonid where a small cusp can be observed (probably the hypoconid). Neither the hypoconulid nor the entoconid are evident. There are weak cingulids developed on the labial wall of the trigonid and the lingual side of the talonid.

Molarization increases in the dp3, which shows a more clearly separated trigonid and talonid, being the occlusal surface of the former much larger than that of the latter. In this case, protoconid and metaconid are separated. The protoconid is the higher cusp and is continuous mesially with a long and lingually concave paracristid. Like in the dp2, the mesial end of this paracristid descends forming a faint mesiolingual cingulid. A columnar vertical crest marks the distolingual wall of the protoconid, and the occlusal surface of this cusp is located roughly at the center of the crown. The metaconid is located near the protoconid. Unlike the permanent molars, the metaconid is expanded distolingually into a large postmetacristid, which allows a better discrimination between trigonid and talonid in this case and penetrates the zone of the talonid basin. The ectoflexid, as in the dp2, is very wide and relatively shallow. The talonid, although simple, allows recognition of a small cristid obliqua, a hypoconid marked by an angle (as in permanent molars), and a short and transverse hypolophid. The hypoconulid and the entoconid are not evident. The talonid basin is small and shallow and the lingual and labial cingulids present in the dp2 are absent, although a faint enamel fold can be observed in the same areas.

As usual for placental mammals, the dp4 is fully molariform. Almost all observations made for the permanent molars (excluding the m3 not only for its absence in the sample but also for its usual differentiated structure) can be applied to the dp4. Main differences are related to lighter color of the enamel (related to the lesser thickness of the enamel layer) and lower crown. For other traits see the description of the permanent molars.

PHYLOGENY

The first analysis including *Archaeogaia macachae* was conducted under implied weights as the treatments of all characters as equally weighted resulted in almost completely unresolved trees. The analysis resulted in 2252 most parsimonious trees (MPT) which strict consensus is shown in Figure 4.1 (the results correspond to the analysis developed under $K = 7$, as most stable results were achieved under this value). This tree shows a large basal polytomy including all henricosborniids, notostylopids, and some tyotherians and toxodontians. Given the high percentage of missing entrances in *A. macachae*, it is a very unstable taxon in the analysis. Future phylogenies should emphasize lower dental characters in order to better test the position of this taxon and its relationships in the context of basal notoungulates. Nevertheless, as this exceeds the aim of our contribution, we choose to perform additional analysis excluding this species in order to gain resolution.

The first of the two additional analysis, developed under equally weighted characters, resulted in 1070 MPTs (402 steps). The resolution of the consensus tree in this case was also very low (Fig. 4.2), showing a large basal polytomy including all henricosborniids, part of Oldfieldthomasiidae, the Archaeopithecidae, the informal taxon “*Campanorco*” Bond *et al.*, 1984, and part of Interatheriidae. The remaining notoungulates are located following the traditional clusters, including the rest of Interatheriidae, the pool of Archaeohyracidae plus Mesotheriidae and Hegetotheriidae, and the monophyletic Toxodontia.

In order to seek for a better resolution, we performed a third analysis under implied weighting (results showed under $K = 3$, as most stable results were achieved under this value). In this case, relationships were much resolved (60 trees), including the monophyly of Tyotheria and Toxodontia (Fig. 4.3). Nevertheless, henricosborniids were still recovered in a basal polytomy and their inner relationships remained obscured. In turn, an interesting result was the recovery of a monophyletic group integrated by two of the Itaboraian species: *Itaboraitherium atavum* and *Othnielmarshia pristina* (= *Camargomendesia pristina*). However, only two homoplastic synapomorphies support this group: character 33, state 1 (distolabial

fossette disappears before the closure of the central fossa) and character 43, state 0 (absence of the lingual sulcus after the isolation of the central fossa on upper molars). These characters are hardly informative in the context of these basal forms and the support values are low (Fig. 4.3). Still, this result fits with previous statements about these species and will be discussed below.

DISCUSSION

The assessment of the identity and nature of the so-called Henricosborniidae is perhaps one of the most difficult issues among the basal Notoungulata. This is due to several factors; first, most of the members are only known by isolated teeth, precluding in some cases an unambiguous identification of the *loci* and the assessment of taxonomically relevant information. Moreover, as in other Paleogene representatives, the number of individuals known per taxon is very low in some cases (*e.g.*, *Simpsonotus*, *Orome*) leading to a poor evaluation of possible intraspecific variations and thus, to the possible overestimation of certain traits as potential taxonomic differences. An additional problem is the general lack of cranial characters, a fact that stands as a considerable barrier to establish solid phylogenetic hypothesis and hence, to improve the knowledge of the early radiation of Notoungulata (Bauzá *et al.*, 2020).

The case of *Nanolophodon tutuca* does not scape to this context. The generalized appearance and brachydonty of the studied specimens, together with the presence of a combination of certain typical traits (see below) indicate that *N. tutuca* can be included among the group of genera traditionally known as henricosborniids. Among them, the combination of characters indicates unequivocally the presence of a new taxon with more developed lophs, a long and straight crochet on its molars, and a conspicuous parastyle on its premolars, among other traits. Nevertheless, the phylogenetic analysis performed, in which all known henricosborniids were included, does not allow reaching solid conclusions on the relationships within these forms, although it concurs with previous results regarding their position as early-diverging members located on the stem leading to all other notoungulates (Cifelli, 1993; Billet, 2011; Billet & de Muizon, 2013).

Although efforts have been made lately in order to evaluate the phyletic nature of these mammals, with analyses including some new characters other than discrete qualitative morphological traits and even leading to a reconsideration of the monophyly of the family (Bauzá *et al.*, 2019, 2020), its characterization based on dental characters remains problematic. Bauzá *et al.* (2020) mention a series of traits that they consider useful for the identification of the group: well-developed paracone and metacone columns on the ectoloph of molars, crochet

present with variable development, triangular occlusal outline of the M3 (with vestigial hypocone), reduced trigonid, short paralophid, and entoconid mostly isolated. Although the combination of all these traits may be considered as taxonomically informative, once again we face the problem of isolated teeth and incomplete information. Moreover, some of these characters are widely distributed in other Paleogene forms. The triangular shape and reduction of the hypocone of the M3 is a condition widely present among early Cenozoic notoungulates (and another eutherians), even within well-differentiated clades, such as tyotherians (*e.g.*, *Colbertia* Paula-Couto, 1952b, *Notopithecus* Ameghino, 1897) and Eocene Toxodontia (*e.g.*, *Pampatemnus* Vucetich and Bond, 1982, *Pleurostylodon* Ameghino, 1897, *Plexotemnus* Ameghino, 1904, among others); and the same can be said about the presence of a crochet. In turn, other features may be considered in a more solid characterization, as the relative isolation of the entoconid: poorly expanded as an entolophid or only developing a small entocristid. At this point, it should be noted that *Archaeogaia macachaeae* shows a well-developed entolophid, differing from all other henricosborniids in our matrix. Nevertheless, the low resolution of the analysis including this taxon precludes any further discussion on its phylogenetic relationships (see above). In this context, the attempts to resolve the phylogeny recurring to the mentioned non-qualitative characters is particularly valuable and future contributions surely will introduce new points of discussion on this matter.

Despite the limitations of the present study and considering all evidences together, it may be stated that *Nanolophodon tutuca* and the tyotherian *Colbertia magellanica* are the Itaboraian taxa with a relatively stable taxonomic affiliation. *Nanolophodon* stands among the basal stock of Notoungulata and cannot be considered as a possible member of Notostylopidae (*e.g.*, differs in the more developed metacone column), Tyotheria (*e.g.*, differs by the absence of crista 1 and mesiolabial fossette), or Toxodontia (*e.g.*, differs by the absence of crista intermedia). Moreover, it can be easily differentiated from *Itaboraiterium atavum* and *Othnielmarshia pristina* (= *Camargomendesia pristina*). Regarding the first taxon, this shows well-developed entolophid on its lower molars and reduced paraconid. As for *O. pristina*, besides its larger size (see Table 1), the occlusal morphology of its upper teeth shows evidence of several large cristae (see below) that are absent in *N. tutuca*, and the metacone column in the new taxon is much more conspicuous, among other differences. The position of *I. atavum* and *O. pristina* should also be considered as more problematic. The occlusal morphology in these cases have proven to be more difficult to evaluate, and they have been considered as part of Notostylopidae, Oldfieldthomasiidae, and Henricosborniidae. In our third analysis (under

implied weights), both taxa are clustered into a monophyletic group. Although the support is low, and homoplastic features define the group (see above), this result is suggestive, as it may agree with the synonymy proposed by previous authors regarding these species (López, 2008; López & Bond, 2010; Bauzá *et al.*, 2020). Nevertheless, their position is more debatable. The most recent posture states that *Itaboraitherium* Paula-Couto, 1970 (including its possible synonym) should be considered as a henricosborniid (Bauzá *et al.*, 2020 and references therein). In this sense and to our understanding, the occlusal morphology (particularly that of the upper molars) does not seem to support this idea. For example, if we consider the specimen MCT 400M, the holotype of *O. pristina*, the occlusal pattern is somewhat more complex than that expected for a henricosborniid. As mentioned above, this pattern includes the presence of at least three cristae running lingually from the ectoloph toward the central fossa. These structures merge at their lingual ends (or with a possible long crochet) isolating three small fossettes on M2. Additionally, this pattern is suggested by the morphology present in some isolated teeth referred as *Itaboratitherium*, at least regarding deciduous dentition. Even if we consider the traits mentioned by Bauzá *et al.* (2020) as possibly useful for the morphologic identification of henricosborniids, the pattern present in *I. atavum* and *O. pristina* does not fit with these characters (*e.g.*, the metacone column is very weak in MCT 400M, the holotype of *O. pristina*, and the entolophid is well-developed in the lower molars, as in MN 1992V, holotype of *Itaboraitherium*). Although these species are grouped together in the present analysis, we do not find conclusive evidence about their proposed synonymy. In turn, the inclusion of these forms or its close relationship with the notoungulates traditionally referred as henricosborniids is, from our perspective, questionable. A future and extensive phylogeny should deal with this problem, including all available indicia.

The new taxon gives us a more complete idea of the taxonomic diversity of notoungulates in the Itaboraí Basin, and particularly the fauna present in the “1968 Fissure”. At this point, it should be considered that, although many remains have been found, this diversity is proportionally low compared to that of other Paleogene localities. The temporal span represented in the basin and its geographic location makes the reassessment of its multiple fossils and its contextualization a critical issue, especially considering the presence of some of its taxa (at least at generic level) in other Paleogene sites on the same latitudinal belt and outside it (*e.g.*, northwestern region and Patagonia, in Argentina).

A singular trait within Notoungulata was recently discussed by Bauzá *et al.* (2020) and deserve some final comments – the presence/absence of paraconid. The basic pattern of the

trigonid in notoungulates includes an usually short paracristid which descends lingually on the crown and disappears without being associated to a cusp, and a small cusp located near the mesial wall of the metaconid (that we indicate as the paraconid in the text), sometimes bunoid (e.g., *Simpsonotus*, *Dolichostylodon* García-López and Powell, 2009, *Pampatemnus*, *Pampahippus*) while crest-like in other taxa (e.g., *Henricosbornia*, *Nanolophodon*). Several authors have dealt with this cusp considering different identities for it. Initially, it was recognized as “evidently not a true paraconid” by Simpson (1967:146). This idea was followed in subsequent contributions and Cifelli (1993) mentioned the lack of paraconid as a typical notoungulate trait. In the same way, other studies have followed this criterion and referred to this as a “small cusp”, “accessory cusplule”, or simply “cusp/crest” (e.g., Bond, 1981; Billet, 2011; Deraco and García-López, 2016; García-López *et al.*, 2019). However, a somewhat opposite posture was considered in other contributions. Pascual *et al.* (1978) refer to this cusp (although with doubts) as a paraconid. Bond (1988) also mention this cusp and Soria (1989) establish that the paraconid is present in Paleocene and Eocene notoungulates, and a similar criterion is followed by recent contributions (García-López & Powell, 2009; Bauzá *et al.*, 2020).

Discussion of dental homologies is sometimes difficult in fossil specimens, as some criteria cannot be easily applied. In this case, the first criterion to apply should be topographic and hence, this cusp can be considered as a paraconid as we indicate in the preceding description and comparison. Moreover, there are no initial phylogenetic arguments to consider other nature for this structure, as current hypotheses do not show the absence of this cusp in ancestral forms of Notoungulata and the latter appearance of this trigonid cusp as a homoplastic structure. However, it should be noted that proper phylogenetic analyzes dealing with the ancestry of notoungulates do not show enough resolution to properly test the nature of this cusp. In other word, although we do not have enough phylogenetic support to challenge the usual identification of this structure as a paraconid, we can explore some preliminary alternatives based on previous contributions.

A similarly positioned cusp, the stylid f, was recognized by Hershkovitz (1971) as a pseudoparaconid, stating that it is present in some primates and that it is originated from the lingual part of the mesial cingulid and “in the metaconid field” (Hershkovitz, 1971:127). In this sense, the similar position of the notoungulate paraconid could lead to consider this as a potential homologue and hence be referred in the same way. A possible problem for this interpretation is the lack of connection between this cusp and the mesial cingulid widely present in Paleogene notoungulates. Nevertheless, it could be interpreted as a large outgrowth of the

lingual end of the cingulid, which becomes independent from it. Moreover, other cusps in a similar location were observed later by Hershkovitz (1984) and named as stylid t (and also referred as pseudoparaconid). This represents an alternative interpretation to the disconnection of the paraconid and its later distal migration to the metaconid zone, as considered in previous studies (Cifelli, 1983). At this point, it is important to clarify that this possible pseudoparaconid is not the same structure mentioned by Shockey *et al.* (2012) for some Toxodontia. In that contribution, the term “pseudoparaconid” refers to the lingual widening of the paralophid, present in several representatives in the usual position of the paraconid.

The assessment of the true nature of this cusp must be discussed in future studies, and opens the debate about the identification of some other notoungulate traits, as the origin of the hypocone in the upper molar, which was discussed for other mammalian groups (Hunter & Jernvall, 1995), and the true nature of the so-called transverse entolophid in the lower molars. This is urgently needed in order to establish more reliable homologies and more solid phylogenetic hypothesis.

CONCLUSIONS

Nanolophodon tutuca represents a new genus and species of notoungulate, exclusive from the “1968 Fissure” on the Itaboraí Basin, which shows a basal position in the context of the order. Its brachydonty, well-developed columns of paracone and metacone, and lack of crista 1 and crista intermedia indicates that this new taxon cannot be included neither in the Notostylopidae nor in the other known notoungulate suborders (Typotheria and Toxodontia). In this sense, this species shows a similar pattern to that observed in the species traditionally known as henricosborniids.

The present analysis fails to resolve the relationships among henricosborniids and between these taxa and the rest of Notoungulata. Future efforts should point to a more accurate and phylogeny-based definition of the group (is it recovered as monophyletic) probably using non-qualitative and discrete characters.

We do not find conclusive evidence about the proposed synonymy between *Itaboratherium atavum* and *Othnielmarshia pristina*. Regarding the reference of these forms as henricosborniids, we question this affiliation based on the complex occlusal dental pattern observed in both cases.

Based on the observations made in the context of the present study, we discuss the identification of the notoungulate paraconid, considering that it may be associated with some cusps located mesially to the metaconid and identified as pseudoparaconids in past studies.

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FIGURE CAPTIONS

Figure 1. Map showing the geographic location of the Itaboraí basin in the context of the State of Rio de Janeiro (Brazil) and South America. Image of South America from <https://mapswire.com/south-america/physical-maps/>; map of the State of Rio de Janeiro from <https://www.gestaoeducacional.com.br/mapa-do-rio-de-janeiro-tipos-de-mapa-e-curiosidades/>

Figure 2. Figure detailing the names of the main dental structures mentioned in the text for upper and lower molars. **1**, upper molar; **2**, lower molar.

Figure 3. *Nanolophodon tutuca* gen. et sp. nov. 1. **1**, MCT 4419M (holotype), fragment of left maxilla with P3-M2 in occlusal view; **2**, MCT 4400M, isolated right P2 in occlusal view; **3**, MCT 4397M, isolated left P3 in occlusal view; **4**, MCT 4396M, isolated left P4 in occlusal view; **5**, MCT 4390M, isolated right M1 in occlusal view; **6**, MCT 4388M, isolated right M2 in occlusal view; **7**, MCT 4421M, isolated left M3 in occlusal view; **8**, MCT 4403M, isolated left lower molar in occlusal view; **9**, MCT 4422M, fragment of left jaw with dp2, dp3, dp4 and m1 (in alveolus) in occlusal view. Scale bars equal 1 mm.

Figure 4. **1**, Consensus tree of the analysis performed under implied weights ($K = 7$) including all taxa of the matrix; **2**, Consensus tree of the analysis excluding *Archaeogaia macachaae* and performed with equally weighted characters; **3**, Consensus tree of the analysis excluding *Archaeogaia macachaae* and performed under implied weights ($K = 3$). Number in boxes indicate Jackknife support values.

Fig. 1

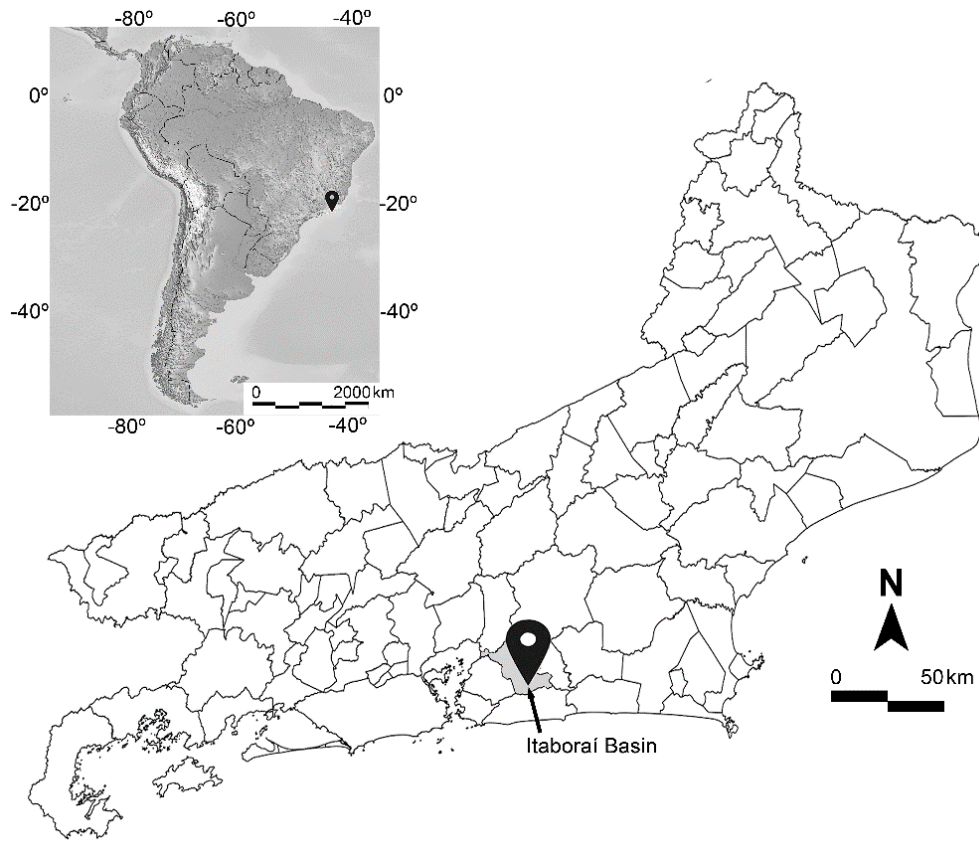


Fig. 2

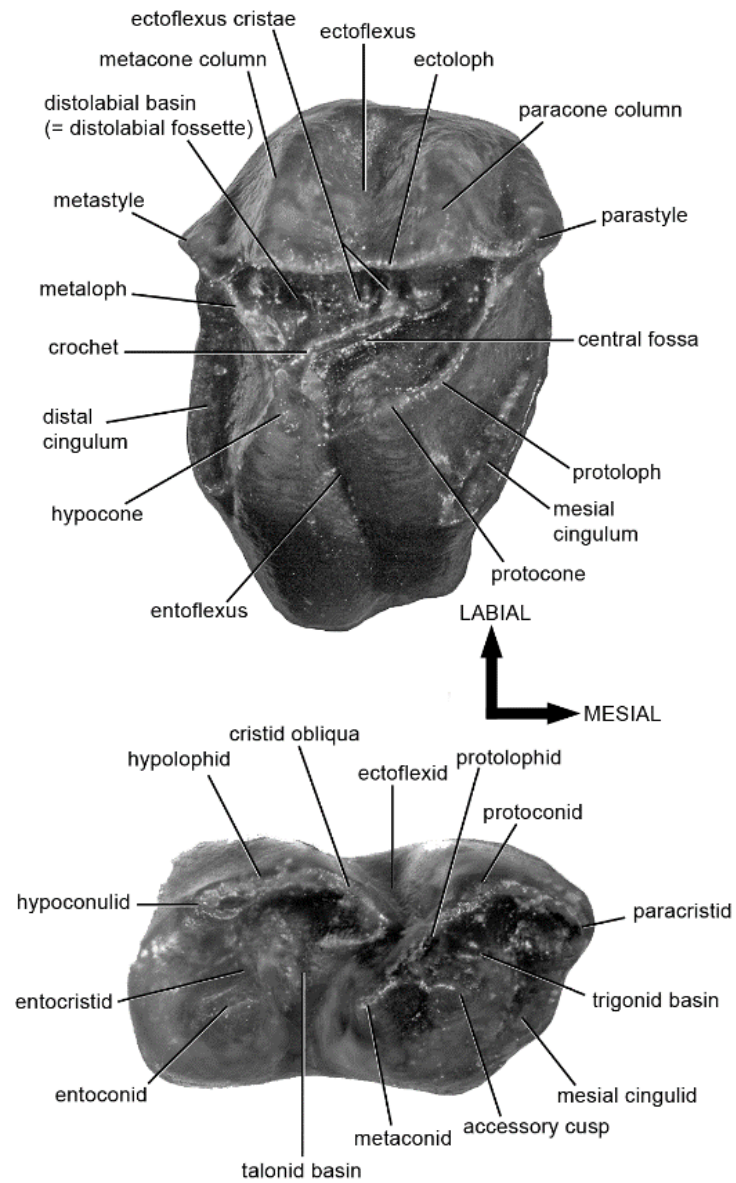


Fig. 3

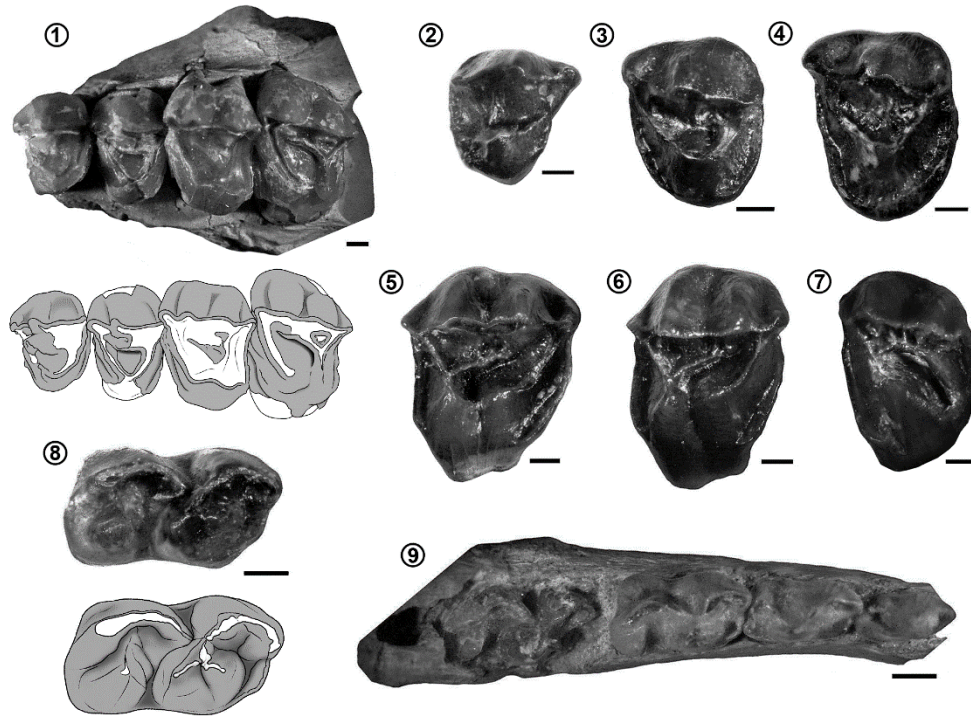


Fig. 4 (estrela representa Gen. et Sp. Nov.)

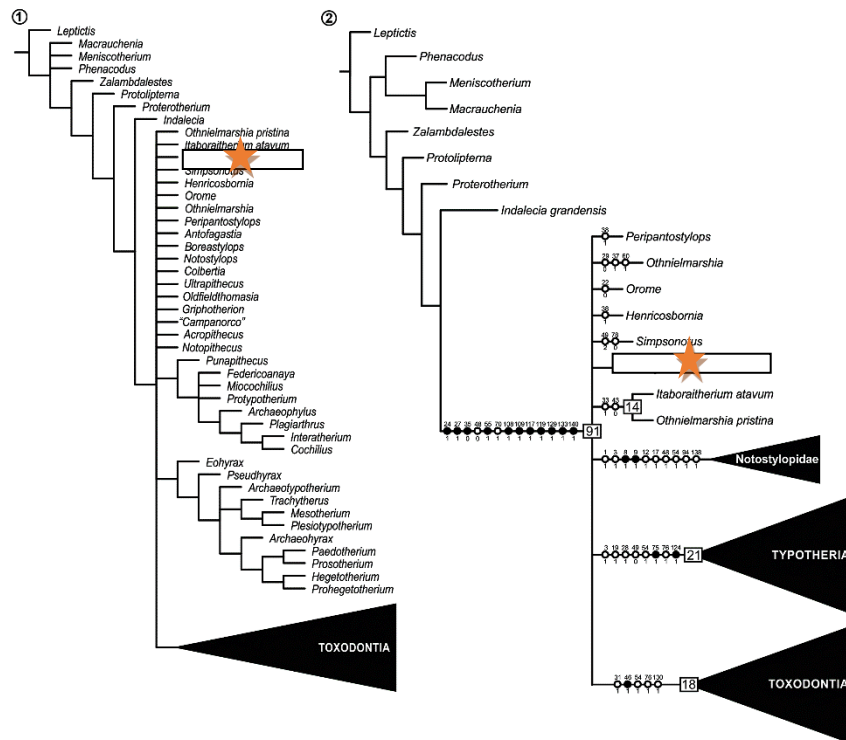
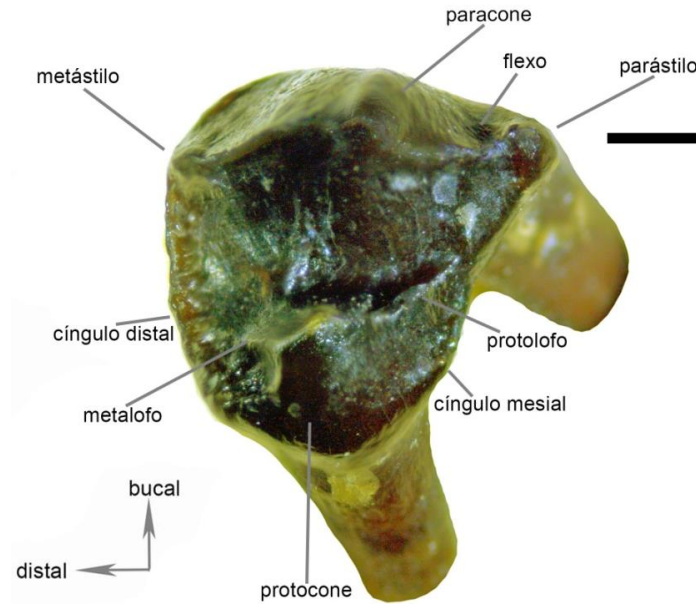


TABLE 1. Tooth measurements (in mm) of the *Gen. et Sp. Nov.*, *Othnielmarshia pristina*, and *Itaboraitherium atavum*.

<i>Specimen</i>	<i>P2</i>		<i>P3</i>		<i>P4</i>		<i>M1</i>		<i>M2</i>		<i>M3</i>		
	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	
Gen. et Sp. Nov.	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	
<i>MCT 4419M</i>	-	-	3.1	4.7	3.5	5.1	4.2	5.6	4.3	6.7	-	-	
<i>MCT 4420M</i>	-	-	-	-	-	-	-	-	5.6	7.3	-	-	
<i>MCT 4389M</i>	-	-	-	-	-	-	-	-	4.8	5.8	-	-	
<i>MCT 4421M</i>	-	-	-	-	-	-	-	-	-	-	4.3	6.6	
<i>MCT 4388M</i>	-	-	-	-	-	-	-	-	4.6	6.2	-	-	
<i>MCT 4400M</i>	2.7	3.3	-	-	-	-	-	-	-	-	-	-	
<i>MCT 4397M</i>	-	-	3.3	4.2	-	-	-	-	-	-	-	-	
<i>MCT 4396M</i>	-	-	-	-	3.6	4.8	-	-	-	-	-	-	
<i>MCT 4390M</i>	-	-	-	-	-	-	4.2	5.1	-	-	-	-	
<i>O. pristina</i>													
<i>MCT 400M</i>	3.5	5.2	4.7	7.2	4.6	9.3	6.3	9	6.5	9.3	5.1	8.8	
			<i>dp2</i>		<i>dp3</i>		<i>dp4</i>		<i>m1</i>		<i>m2</i>		<i>m3</i>
Gen. et Sp. Nov.	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	<i>L</i>	<i>W</i>	
<i>MCT 4422M</i>	2.5	1.3	3.1	1.5	3.5	1.9	3.9	2.1	-	-	-	-	
<i>MCT 4403M</i>	-	-	-	-	-	-	-	-	5.2	2.9	-	-	
<i>I. atavum</i>													
<i>MN 1992V</i>	-	-	-	-	-	-	4.4	4.6	4.5	2.7	6.7	3.1	

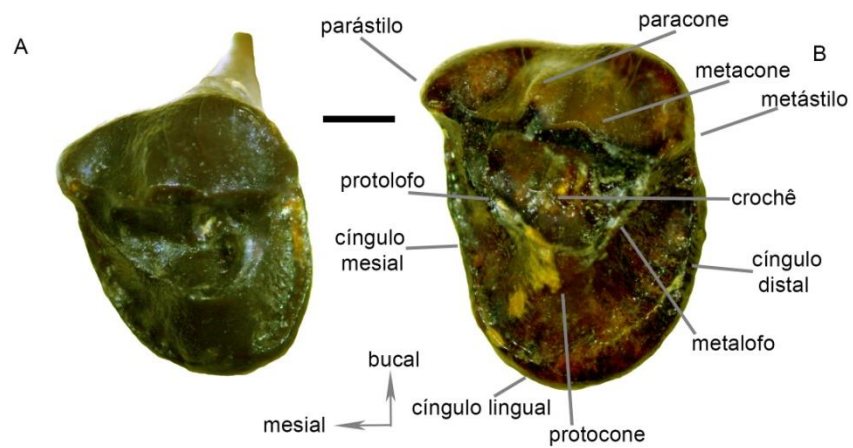
APÊNDICE B – Figuras complementares

Figura 1 - P2 MCT 4400M com as principais estruturas dentárias sinalizadas. (escala de 1mm)



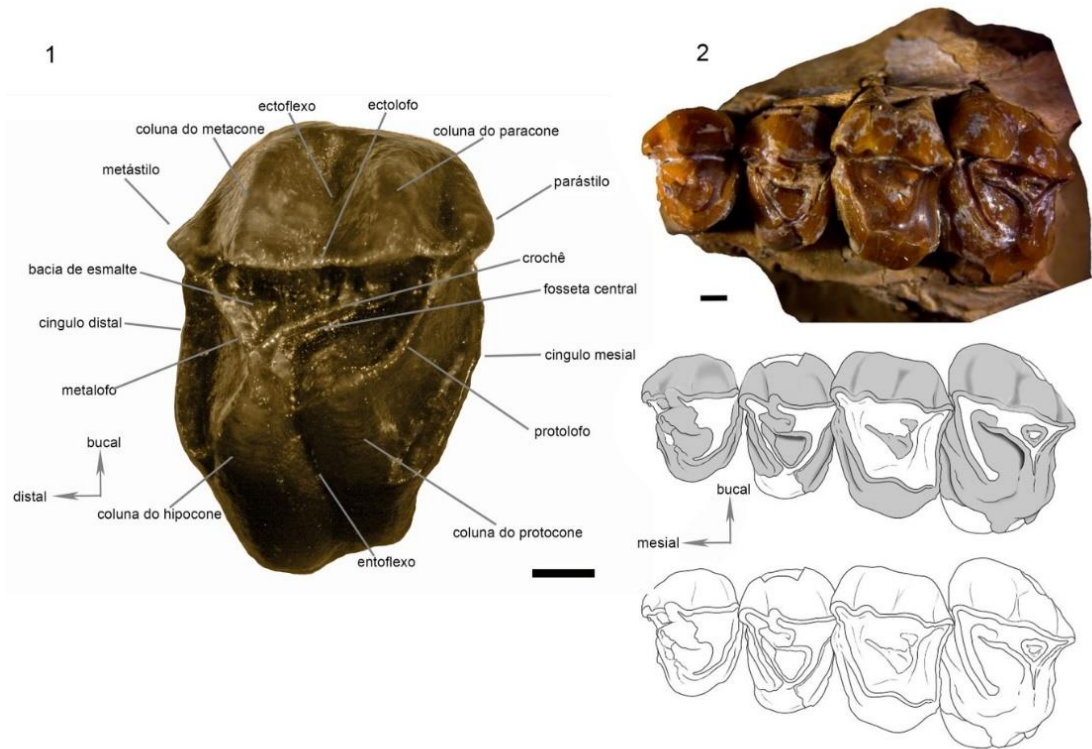
Fonte: O autor, 2020

Figura 2 - A= P3 esquerdo MCT 4397M e B= P4 esquerdo MCT 4396M, com estruturas dentárias sinalizadas (escala de 1 mm).



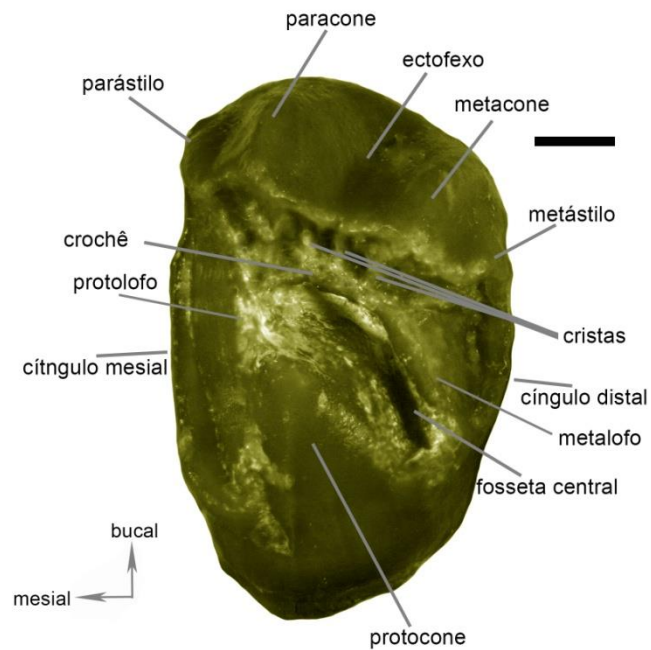
Fonte: O autor, 2020.

Figura 3 - 1= MCT 4388M, M2 direito com baixo desgaste e MCT 4419M, maxila esquerda com P3-M2 com ilustrações do espécime, ambos em vista oclusal. (escala 1 mm)



Fonte: O autor, 2020.

Figura 4 - MCT - 4421M, M3 direito em vista oclusal com morfologias dentária sinalizada e coloração editada para melhor visualização das estruturas.



Fonte: O autor, 2020

ANEXO A – E-mail de Aceite do Artigo ao Periódico Ameghiniana

[AMGH] Submission Acknowledgement

De: Editor-in-chief (editor.ameghiniana@apaleontologica.org.ar)

Para: tavinhobio@yahoo.com.br

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